Genetic Impacts on Wild Atlantic Salmon (Salmo salar L.) Stocks from Escaped Farm Conspecifics: An Assessment of Risk

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Abstract

The potential exists for river stocks of wild Atlantic salmon (*Salmo salar* L.) to be genetically altered when escaped farm conspecifics enter rivers. Changes can occur indirectly, through ecological interactions, or directly, by interbreeding. Wild salmon stocks are composed of locally adapted populations whose gene pools are moulded by selection to increase survival and reproductive success i.e. fitness, and adaptive differences can be assume to exist between farmed and wild salmon. As a result, genetic changes have the potential to alter fiftness. The resulting fitness change is unlikely to be positive. Limitations in our knowledge, and in our ability to detect and monitor both changes and fitness, make it difficult to predict the extent of fitness depression which might occur. Variation in the genetic characteristics of farm and wild stocks, and the environmental circumstances associated with interactions, ensure each outcome will be more or less unique, and impacts could be short or long term. Where relative numbers of farm salmon or genetic differences with wild stocks are small, interbreeding is sporadic, and wild stocks are healthy, natural selection can be expected to reverse most adaptive genetic change. If relative numbers of farm salmon or genetic differences are large, interbreeding is persistent, and stocks are declining, stock viability can be expected to be further reduced. Long term, or even permanent, changes to stock character may result and contribute to the demise of wild stocks or their constituent populations. In the absence of a predictive capacity, current management must proceed using a precautionary approach. Where feasible, escapes of reproductively competent farm fish should be eliminated. Otherwise escapes shoud be reduced below natural straying rates and the sustainable abundance of wild stocks maximized. Research should focus on increasing empirical understanding by assessing specific interaction scenarios, and enhancing understanding of the nature and extent of local adaptation in the Atlantic salmon.

Résumé

Il est possible que des stocks sauvages de saumon de l'Atlantique (*Salmo salar* L.) de cours d'eau soient génétiquement modifiés lorsque des saumons d'élevage échappés se trouvent dans les mêmes eaux. De tels changements peuvent survenir indirectement, par interactions écologiques, ou directement, par croisements. Les stocks sauvages sont formés de populations adaptées aux conditions locales et dont les pools géniques se sont adaptés par sélection de façon à accroître la survie et le succès de la reproduction, c'est-à-dire la valeur adaptative, et l'on peut présumer l'existence d'écarts entre la valeur adaptative des stocks sauvages et d'élevage. Toute variation génétique pourrait donc modifier cette valeur de façon nuisible. Les limites de nos connaissances et de nos capacités à déceler et à contrôler tant les modifications que la valeur adaptative rendent difficile la prévision de l'ampleur d'une éventuelle baisse de la valeur adaptative. La variation des caractéristiques génétiques des stocks d'élevage et sauvages et les circonstances environnementales liées à ces interactions font que chaque résultat est plus ou moins unique et que les incidences apparaissent à court ou moyen terme. Lorsque le nombre relatif de saumons d'élevage ou de différences génétiques par rapport aux stocks sauvages est faible, les croisements sont sporadiques, les stocks sauvages sont en bonne condition et l'on peut s'attendre à ce que la sélection naturelle annule la plupart des modifications génétiques adaptatives. Mais si le nombre de saumons d'élevage ou de différences génétique est important, les croisements constants et les stocks sont en déclin de sorte que l'on peut s'attendre à une réduction encore plus poussée de la viabilité du stock. Des variations à long terme ou permanentes des caractéristiques des stocks peuvent donner lieu à la disparition des stocks sauvages ou de leurs populations constituantes et l'accentuer. En l'absence de moyens de prévision, les gestionnaires doivent appliquer l'approche préventive. Lorsque cela est possible, il faut procéder à l'élimination des poissons d'élevage capables de se reproduire qui se sont échappés. Sinon, le nombre de poissons échappés devrait être réduit en deçà des taux naturels et l'abondance des stocks sauvages devrait être maximisée et soutenue. Les recherches devraient être axées sur une meilleure connaissance empirique de par l'évaluation de scénarios d'interaction et sur l'étude de la nature et de l'ampleur de l'adaptation locale chez le saumon de l'Atlantique.

Introduction

Atlantic salmon (*Salmo salar* L.) have for thousands of years been an integral part of the natural biodiversity of river ecosystems in temperate and subarctic regions bordering the North Atlantic. Today, for man, the species is also an important recreational and aquacultural resource. Unfortunately, river stocks in many parts of the species' range are in a state of decline, and their viability and character are threatened. As a result, the restoration of self-sustaining stocks to their former abundance and the conservation of existing species biodiversity have become a primary management concern. Not only are abundant, self-sustaining stocks a clear indicator of ecosystem "health", they also give the greatest recreational return for the least management cost. "Healthy" stocks also constitute the best way to preserve heritable variation for growth, disease resistance, and other traits, which can be productively exploited by the farming industry, and on which the industry's future is likely to depend.

Current declines in Atlantic salmon have a number of potential natural and anthropogenic causes. Of these, one of the least poorly understood is the threat to wild stocks from farm salmon which escape fresh and salt water culture facilities. Escapes frequently find their way into rivers with wild stocks where they can cohabit and interbreed (Lund et al., 1991; Lura and Saegrov, 1991; Webb et al., 1991, 1993; Carr et al., 1997; Clifford et al., 1997; Youngson et al., 1997); they can also mix with wild stocks at sea (Hansen et al., 1993, 1997; Webb and Youngson, 1992; Youngson et al., 1997). The potential risk that biological interactions between the two poses to wild stocks needs to be understood, both to identify when negative impacts are likely and to formulate appropriate management responses.

In many contexts, such as flood management, assessments of risk are empirical and prior incidence is used to project the likelihood in the future of having an impact of a given severity. Empirical approaches can be used where the impacts are easy to quantify and there is a historical record. Unfortunately, neither is true in relation to the genetic impacts of farm escapes on wild populations. The mechanistic pathways of interaction and their consequent effects are potentially complex (Youngson and Verspoor, 1998), and the viability and character of wild populations can be expected to vary due to other factors, both natural and anthropomorphic. Thus attributing changes in stock viability and character to a particular cause is generally difficult. Furthermore, farm-wild interactions are a recent phenomena, only arising in the last two decades. As a result, any assessment of the risk they pose for wild populations must be based on expectations derived from the framework of relevant theory on the genetics of populations, both qualitative and quantitative, and what is specifically known about the genetics of wild and farm stocks.

Theoretical Framework

Biological theory holds that the viability and observed character of a group of animals is determined by the interaction of their genetic character with their environment. Thus to understand how the viability and character of wild salmon stocks might be affected by farm escapes, it is necessary to appreciate the genetic processes underlying gene-environment interactions where two genetically different groups mix. The most relevant issues in this regard are:

- the mechanisms of genetic change

- the general nature of intraspecific variation and how stocks can differ genetically,

-how variation in genetic structure within and among stocks can be important to survival and reproductive success i.e. local adaptation

- the effects of population mixing on local adaptation

Before delving into these issues, it will be useful to clarify the meaning of the following terms used:

Stock - the collective group of salmon born in a given river system or, in relation to farmed

salmon, a group of salmon sharing a common genetic background; commonly used interchangeably with "population" but here used to define a distinct biological unit.

Populations - groups of individuals of a species and their relatives, within which interbreeding is more or less random but among which interbreeding is more or less constrained; the basic biological and genetic unit underpinning species survival in a given location.

Natural selection - the change in frequency of different genetic variants in a population due to their differential survival and reproductive success.

Fitness - the relative ability of different genetic types of individuals to survive and transmit their genes to the next generation.

Genetic variants - forms of a gene which differ in their DNA sequence and often in their affect on the character or behaviour of an individual.

Genetic drift - random fluctuations of gene frequencies in populations from one generation to the next due to chance differences in survival and breeding success of different variant types; tends to increase as numbers of breeders in a population decreases.

Gene-environment interaction - when the character of a fish with a given genetic type varies under different environmental conditions.

Inbreeding depression - decreased fitness due to the crossing of closely related individuals.

Outbreeding depression - decreased fitness due to the crossing of unrelated individuals.

Mechanisms of genetic change

The presence of non-native salmon can in principle give rise, either indirectly or directly, to genetic change in native river stocks of salmon (Figure 1; Youngson and Verspoor, 1998). Changes can occur indirectly as a result of ecological interactions and directly as a consequence of interbreeding.
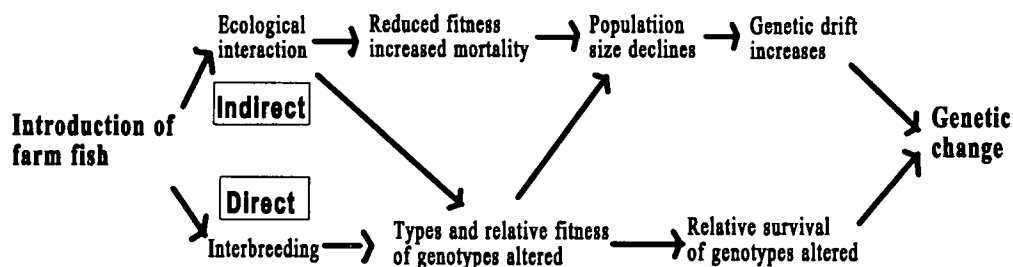

Figure 1   Pathways by which the introduction of farm fish can result in genetic changes to a wild population of Atlantic salmon.

Genetic change can occur indirectly through ecological interactions when the presence of juvenile or adult farm fish alters the level and type of natural selection. The interaction can occur during the marine or freshwater phases of the life cycle. They can result when the presence of farm fish modifies the nature and extent of intraspecfic competition (Einum and Flemming, 1997; McGinity et al., 1997), increases exposure to predators (Hvidsten and Lund, 1988), or introduces new pathogens or parasites (Johnsen and Jensen, 1991; Hastein and Linstad, 1991). Such interactions may increase mortality, reducing the recruitment of spawners and subsequent population size, thus promoting genetic drift and the loss of genetic variants (Hartl and Clarke, 1989). Where changes in mortality, or affects on reproductive success, are different for different genetic types of salmon, directional changes in the frequencies of genetic variants in the population will occur. These changes can be manifest as a loss of genetic variance for quantitative traits such as growth performance, age of maturity, egg size, etc, or the loss of heterozygosity and polymorphism for qualitative traits such as allozyme variants.

Interbreeding can occur where juveniles escape from hatcheries into rivers, or at the adult state when escaped juveniles return or anadromous adults escape from marine sites and ascend local rivers. A proportion of males can mature in freshwater and make a major contribution to the fertilization of eggs in the redds of anadromous females (e.g. Jordan and Youngson, 1992). Genetic changes can occur directly through interbreeding when resulting hybrids show lower mean fitness than wild fish. As with indirect effects, lower fitness may reduce the numbers of recruits and breeders, increasing genetic drift. However, additionally, where hybrids are viable, reproductively competent and possess different frequencies or types of variants, their contribution to genetic variation in subsequent generations will alter the frequencies of genetic variants in the population's gene pool. This will change the probabilities of particular genetic combinations. Where novel genetic variants are introduced (i.e. introgression - Verspoor and Hammar, 1991) novel genetic combinations (i.e. genotypes), not previously seen in the population will occur among offspring. As the genotypic composition among spawners changes, so will change the character of the population with regard to both quantitative and qualitative traits.

Intraspecific variation

Genetic variation among individual fish can take a number of different forms and involve the mitochondrial as well as the nuclear genome. The former, of which a single copy of which is located in each cellular mitochondria, represents <1% of cellular DNA, is maternally inherited and does not recombine with other mitochondrial DNA (mtDNA) due its asexual inheritance. In contrast, the remaining 99% of DNA resides in the nuclear genome (i.e. nDNA), located in the cell nucleus. It is packaged into the discrete molecular units commonly referred to as chromosomes, each of which is represented by two copies, one inherited from each parent. Most mtDNA variation arises from differences among individuals in the specific DNA base sequence in the genes each possesses. Sequence variation within genes is also widespread in nuclear DNA both between individuals as well as between the different copies of DNA within an individual. However, nDNA also varies in how functional DNA units (i.e. genes) are organized between and within chromosomes. This organizational variation may be expressed with regard to chromosome number, gene distribution among chromosomes, or gene order within chromosomes.

These modes of variation can involve in the order of 50,000 to 100,00 different genes, each of which is made up of unique sequences of hundreds or even thousands of DNA bases. Without even considering variation in chromosome structure or number, the number of different genetic types which can be generated by base sequence variation within genes is astronomical. Consider only 100 genes, each having only two different variants and giving rise to three different genetic types for each locus. For these 100 genes $> 5 \times 10^{47}$ (3^{10}) different overall genetic types of salmon could be created. Even if < 1% of these combinations are able to produce viable salmon, over 50 million different types are still possible. The actual amount of variation will be much larger given that this has probably taken into account a small fraction of all variable genes, most genes will have more than two variant types, and variation at the level of the chromosome has not been considered. Thus, while individuals will to varying degrees share

genetic variants in common, their collective genetic types will in most cases be unique.

The variation occurring among individuals may not be uniformly distributed in space and time. It can be expected to vary among populations. The structuring of the species into populations will occur where there is a spatial, physical or temporal barrier to reproductive mixing. Isolation allows populations to differentiate through the processes of gene mutation, random genetic drift, migration and natural selection. This differentiation can be manifest with regard to the types or frequencies of genetic variants in the population, and will be affected by how recently populations share a common ancestry, historical patterns of genetic exchange, and the similarity of their selective regimes. In general the relatedness of populations will decrease with geographical separation, given that migration and environmental differences among habitats tend to be positively correlated with geographic distance. In the absence of complete physical barriers to population mixing, structuring and differentiation will be genetically reinforced by natural selection if there is variation among individuals in their tendency to home to natal areas to spawn, and if such homing leads to increased reproductive fitness i.e. confers an adaptive advantage.

Population differentiation is often quantified in terms of variant frequencies at gene loci. In such cases, often only differences in the frequencies and not the types of variants are quantified, leading to the impression that the populations are genetically more or less the same. However, looking only at gene frequencies can be misleading. Even small differences in variant frequencies will produce big differences in the expected genotype composition of a population. Consider Figure 2. This shows four hypothetical populations of 100 fish sharing two common variants at each of four genes, but differing in their variant frequencies as indicated. It can be seen that genotypic differentiation increases with allelic differentiation. It also increases as the number of genes involved increases. Indeed, differences in frequencies of variants of only 0.2 at 20 loci would be enough to ensure that two populations of 100 fish would be unlikely to share any genotypes in common. While in theory all genotypes are possible in each population, real populations are of a finite size and only the most probable genotype combinations, and a chance selection of less probable genetic types, will occur. This differentiation will be sharpened by selective mortality where different genotypes are adaptively favoured in different populations. When this is the case, the frequencies of the adaptive genotypes in each population can be expected to be increased among juveniles, and among breeders.

Local adaptation

Natural selection increases the likelihood of adaptive genotypes occurring in a population in the next generation. The specific selective genetic adjustment of a population's gene pool increases fitness and constitutes local adaptation at the genetic level. Selection for the fittest genotypes increases the frequencies in the gene pool of the variants associated with those genotypes. This makes the occurrence of those advantageous genotypes selected in the previous generation more likely when variants assort during gametogenesis and zygote formation to produce recruits for subsequent generations; assortment can be expected to be to a large extent random with genes at this stage being subject to recombination and many independently located on different chromosomes. Thus, it is not successful gene combinations that are passed on from one generation to the next, but an increased probability of their occurrence.

Fixation of populations for a single adaptive variant at each gene is unlikely as many genotypes can be expected to have a similar average fitness across the life-cycle of an individual. Performance of different genotypes at different stages of the life cycle is likely to differ, as is performance due to spatial and intergenerational variation in the environment a population experiences. As a result one genotype may
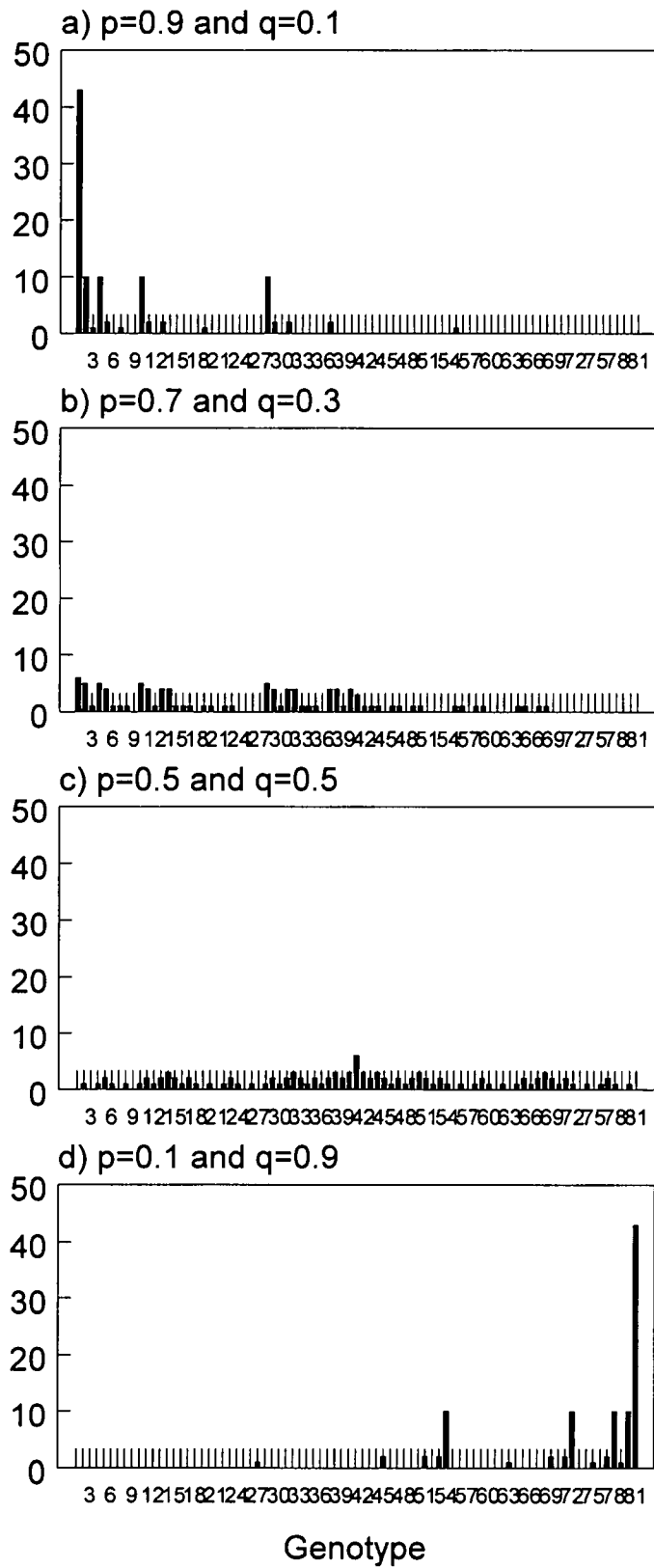
Figure 2 The distribution of genotypes for four hypothetical populations of 100 individuals with four genes with two variants of frequencies of p and q.

have an advantage at one time and another at other times, with their overall fitness the same. Fixation for a single genotype is also unlikely as some genotypes will include genes where heterozygous individuals (i.e. those with different maternal and paternal gene copies) are favoured (i.e. heterozygote advantage), perhaps because of higher fitness over a broader range of experienced environmental conditions.

Selection for genotypes, which are locally at an adaptive advantage, can lead to the structuring of a species into multiple local adapted populations. Such population development can be expected where breeding areas are disjunct, environmental conditions vary among breeding areas more than among different generations, and there is heritable variation among individuals for homing to natal habitat to breed. Under these conditions, genotypes which are more fit locally and have a greater tendency to home will produce more recruits. As a result the frequencies of variants associated with these adaptive genotypes and the probability of such genotypes occurring will increase in subsequent generations. This will in turn reduce the amount of straying further and in time split a river stock into a series of locally adapted populations among which gene flow is more or less absent. As adaptive genetic change involves changes to phenotypic traits, this process will also give rise to genetic heterogeneity in stock character. While this character heterogeneity will often be confounded with environmentally determined character variation, it will still increase the mean fitness of individuals at the local level and increase overall stock abundance (or biomass) over that which would occur in the absence of population subdivision.

Local adaptation does not necessarily have one genetic solution. For a given river system, there may be more than one solution. Just as this is true at the interspecific level where many river systems contain more than one salmonid species, the same is possible at the intraspecific level. For a given stock of fish in a given environment, there may be more than one life-history or morphological solution to achieving viability. In so far as these solutions are the product of different sets of related genotypes, selection could drive allele frequencies or population structuring toward different adaptive genetic optima; which one evolves will be determined by the specific historical, genetical and environmental circumstances which have prevailed. In general, the complexity of the process of local adaptation, the importance of historical conditions, and the confusion of environmental and genetic forces in shaping population character, make the identification of situations with multiple adaptive genetic optima difficult. However, it can be assumed that the genetic character of a wild population or stock will be selectively optimized toward one optimum.

Effects of population mixing

Where a population is locally adapted, most hybrid individuals produced by interbreeding between native and migrant individuals (i.e. outbreeding) can be expected to have a lower mean fitness in the local environment than local native fish; this assumes the local population is not suffering from inbreeding depression by having its numbers severely reduced. This outbreeding depression is expected because there is a higher probability of producing genotypes with a lower than average fitness. It can occur in the first generation but is likely to be more important when first generation hybrids breed and backcross with natives (Emlen, 1991). While outbreeding tends to be associated with increased heterozygosity (Tave, 1993), this in itself is not advantageous as it can be in culture when highly inbred lines (i.e. hybrid vigour). When such lines are crossed, fitness is reduced due to a loss of heterozygosity which masks rare lethal or semi-lethal recessive variants shared in common among the relatives. Thus with inbred lines, outbreeding the increase in heterozygosity will increase fitness. Most wild populations are unlikely to be highly inbred such that this effect is unlikely to arise in the crossing of different populations in the wild.

Outbreeding depression is readily observed and usually severe for populations differentiated at the species level and beyond (Verspoor and Hammar, 1991). In contrast, the relationship of the degree of fitness depression to levels of population differentiation at the intraspecific level is poorly understood. It is not known whether the expected relationship between the fitness of hybrid progeny and the relatedness of
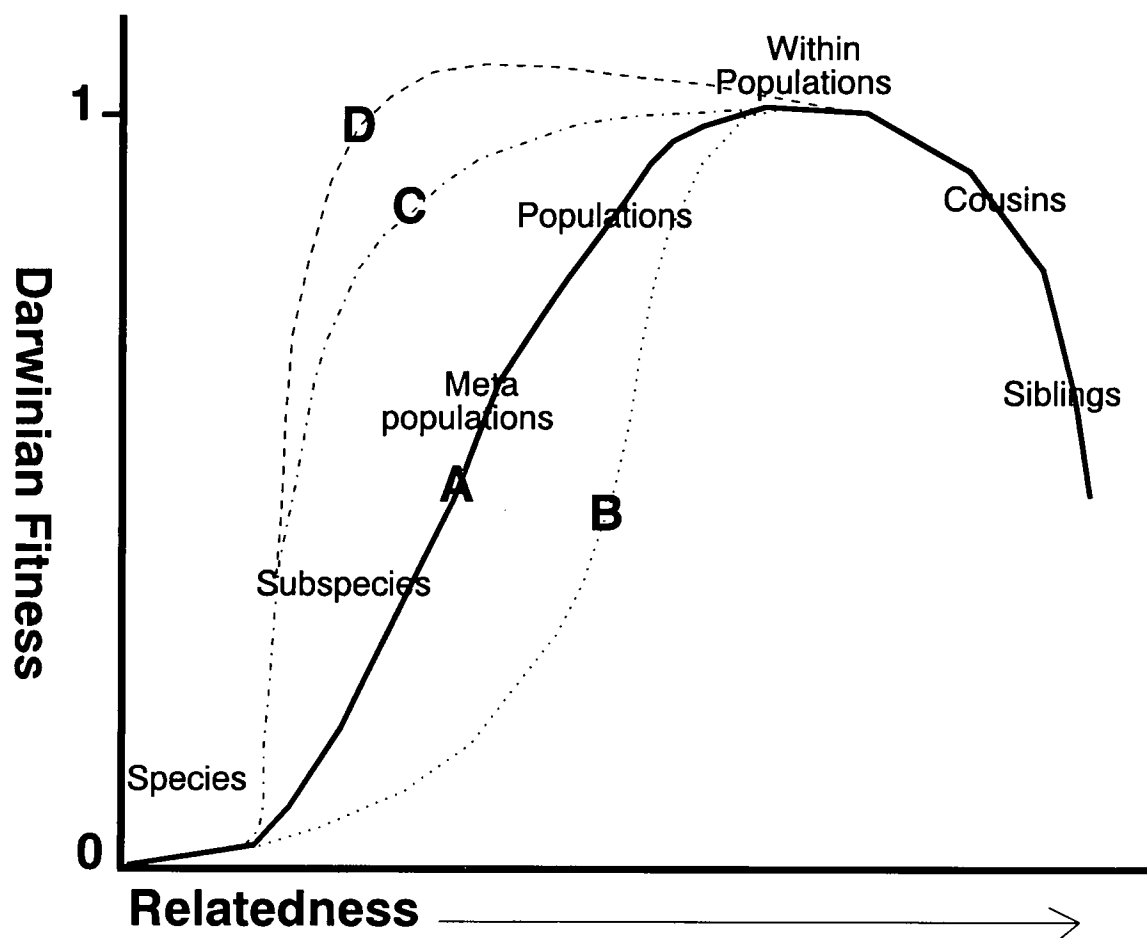
Figure 3   The potential relationships between the fitness of hybrid offspring and the degree of genetic relatedness of their parents. Metapopulations are historically related assemblage of populations within which an evolutionary dynamic of genetic exchange, population establishment and extinction occurs.

the two interbreeding populations is more like curve A, B, or C in Figure 3. Curve D seems unlikely, except in exceptional circumstances where a population had first been subjected to high levels of inbreeding. This would arise in a population which had continual and severe population bottlenecks.

The genetic effect of population mixing can be to change either the frequency or the types of variants in the generations following hybridization. Minor gene frequency changes associated with a reduction in mean fitness can generally be expected to be reversed by selection, provided hybridization has not caused selectively important variation to be lost by genetic drift, or has not caused population extinction. However, given multiple adaptive genetic optima exist, it is conceivable that major frequency changes could shift a population to an alternative adaptive optima. Furthermore, where introgression of selectively advantageous novel genetic variants occurs, a new adaptive optima will be created. Until further genetic perturbations occur or genetic drift restores variant frequencies or types to their previous state, the resulting changes will become fixed and permanent changes to population character can be expected. Where a new optima is established, mean population fitness will increase and the selective loss of some

existing genetic variants, which are no longer advantageous, may occur. The actual outcome in each case of mixing can be expected to be unique, depending on the specific nature of genetic variation within and among the populations involved, and the specific environmental circumstances prevailing during and after it occurs.

Specific Knowledge

The genetic nature of wild Atlantic salmon stocks

Atlantic salmon, along with other salmonids, represent some of the best studied fish species from the perspective of the genetics of populations. Despite this, the understanding provided by the available information still extremely limited. Genetic and behavioural research does show that river stocks of anadromous Atlantic salmon constitute at least one and, in the case of larger river systems, probably multiple genetically distinct populations (Verspoor, 1997). This appears to be true across the species range. The occurrence of structuring in rivers in eastern Canada is evidenced from studies of genetic differentiation in relation to electrophoretically detected protein variation (Møller, 1970; Verspoor, 1988; Verspoor and Jordan, 1989; Verspoor, 1994; Verspoor, unpublished), microsatellite loci (McConnell et al., 1995; Fontaine et al., 1997) and quantitative traits (Saunders, 1981). Evidence also exists for within river population structuring in the Miramichi (Møller 1970; Ståhl et al., 1983; Riddell et al., 1981). Studies of genetic structuring within the smaller rivers, such as those draining into the Bay of Fundy in eastern Canada, are lacking. However, structuring has been detected in some of the smaller Scottish rivers which are of a similar size (e.g. the Kyles of Sutherland - Verspoor et al., 1991; the Aberdeenshire Dee - Verspoor, 1995; the North Esk - Gilbey et al., submitted). In the Polla, a small Scottish river with only 7 km accessible to anadromous salmon, no substructuring was detectable (Verspoor, unpublished). However, proving structuring doesn't exist is more difficult than proving that it does.

River stocks are associated, on a larger scale, into genetic assemblages broadly associated with different geographical regions (Verspoor, 1997; unpublished). The data show a primary split of river stocks into North American and European assemblages, each characterized by near fixation for different variant types at a number of allozyme, minisatellite and microsatellite DNA loci as well as with regard to mtDNA haplotypes. The two stock groupings also appear to have different chromosome numbers, though this is based on the analysis of relatively few populations. The European stock grouping also shows a major division between river stocks, with one subgroup associated with the Baltic Sea and the other with those in rivers draining directly into the Atlantic. Genetic differentiation between them, as revealed by protein electrophoresis and mtDNA, is only with regard to the frequencies of variant types. However, some fixed genetic differences may exist, for example, for genes associated with genetically based differences in resistance to the skin parasite *Gyrodactylus salaris* (Bakke and Mackenzie, 1993). Within North America, molecular analyses have as yet revealed no consistent evidence of further subgrouping of populations (Verspoor, 1994, 1997; Fontaine et al., 1997). Furthermore, there is no evidence that anadromous and non-anadromous populations constitute distinct phylogenetic lineages (Ståhl, 1987; Verspoor, 1994).

A general hierarchical organization of river stocks into regional stock groupings in relation to genetic relatedness might be expected, based on geographical discontinuities in patterns of genetic exchange among groups of populations and regional environmental differences. However, supporting evidence is lacking. What has been observed for anadromous populations, within each of the continental stock groupings, is a broad association of genetic differentiation with geographic distance (Jordan et al., 1997; Ståhl, 1987; Fontaine et al., 1997). This association may in part be explained by a negative correlation between dispersal and geographic distance, or it may be due to historical colonization patterns related to the existence of multiple differentiated refugial stocks at the end of the last glaciation. However, positive association of geographic distance with genetic differentiation may also reflect local adaptation to environmental variables, such as temperature, which are correlated with distance variables such as latitude. There is strong evidence that this is the explanation for observed population differentiation at the

MEP-2* enzyme locus (Verspoor and Jordan, 1989; Jordan et al., 1997; Verspoor, 1997).

Compelling circumstantial evidence exists for the adaptation of Atlantic salmon populations to their local environments, both within as well as among river stocks (Verspoor, 1997) and the phenomena would appear to be widespread in salmonids (Taylor, 1991; Carvalho ,1993) . Perhaps the best example of local adaptation is the genetic differentiation between the Baltic and Atlantic population assemblages with regard to resistance to *G. salaris*. Studies indicate that resistant salmon populations occur only within the endemic range of *G. salaris* in the Baltic. There is also evidence that local adaptation occurs among populations within river stocks. For example, strong circumstantial cases exist for adaptive differentiation of genetically determined morphological traits among tributary populations of the Mirimichi (Riddell et al., 1981) and for resistance to egg mortality induced by acid water in the Kyles of Sutherland river system in Scotland adaptive differences in (Donaghy and Verspoor, 1997). Studies of the MEP-2* polymorphism suggest that local adaptation occurs at all geographic scales from within rivers to between continents (Verspoor and Jordan, 1989). This conclusion is born out by transplantation experiments (C. Garcia de Leaniz, unpublished; Verspoor, unpublished). In these experiments, ova from two Scottish rivers were transplanted to a neighbouring river system, where they showed high survival rates compared to rates in a stream in Spain; in Spain survival to smolting of the non-native fish was an order of magnitude lower, both when compared to survival in Scotland and to survival rates for native Spanish ova. This work clearly shows that there are different genetic optima for different environmental circumstances.

Support for the position that there can be multiple genetic solutions to local adaptation comes from the sympatric co-existence within some river systems of genetically distinct non-anadromous and anadromous populations of Atlantic salmon (e.g. Verspoor and Cole, 1989). The occurrence of the two life-history types of populations is widespread in Newfoundland and occurs in some river systems in the Maritimes (e.g. the Magaguadavic , or the St. Croix river systems) as well as in Scandinavia (e.g. Ståhl, 1987) and Russia (e.g. Lake Onega). It is not known whether the genetic basis of the life history difference is always the same but it is conceivable that the two strategies can be achieved by a number of different genetic routes; this might even involve the same set of variant types but at different frequencies. The resulting differences in the genotypic arrays produced may be associated with variation in life history traits such as size and age at maturity, run-timing and sea-age, etc. In any case, despite the evolutionary basis of life history variation not being well understood, (Ståhl, 1987; Verspoor, 1994), the co-existence of anadromous and non-anadromous populations demonstrates the clear potential for the same river system to be capable of sustaining different, heritably and adaptively distinct salmon populations.

Genetic nature of farm salmon

Stocks of farm salmon are, with few exceptions, recently derived from wild (usually anadromous) salmon populations. As a result they can be expected to share with their founding wild populations the same genetic variants. The number of generations in culture is unlikely to have been sufficient for new advantageous mutations to have spread within any of the different stocks. However, a given farm stock may have genetic variants which are not present in other wild populations, by virtue of an existing difference between that population and the river population(s) from which the farm stock was established. For example, farm salmon of North American origin have many variant types not present in wild Scottish stocks and Scottish origin farm salmon will have variants absent among native stocks in the Bay of Fundy region (Verspoor, unpublished). Farm stocks established from the same continental stock groups as the wild populations with which they are compared generally share the same genetic variants (Youngson et al., 1991; Cross and Challanain, 1991; Cross et al. 1993; Verspoor et al. in prep).

Farm lines will differ from the wild populations from which they derive due to genetic drift and deliberate, as well as inadvertent, selection. Genetic drift may change frequencies and cause the loss of particular genetic variants. It can operate in the form of founder effects where the number of breeders, used to establish the farm line, are small and by chance unrepresentative of the source population, something

documented to occur (Verspoor, 1988). It can also occur once a farm line has been established where small numbers of breeders are used to perpetuate a farm stock (Cross and King, 1983) and probably explains the increased variance of allele frequencies observed for farm lines compared to wild populations (Youngson et al., 1991). However, the level of change can be minimized by the use of large number of breeders and this may explain the lack of significant differentiation detected at allozyme loci between St. John farm and wild stocks (Cross et al., 1993); changes in allele frequency at the *MEP-2** locus in one line of St. John farm stock and in Scottish farm salmon may be due to inadvertent selection (Youngson et al., 1991; Cross et al., 1993). Heritable changes in performance characteristics such as growth rate among farm and wild stocks are general and a case of a deliberate selective change (Gjøen and Bentsen, 1997). Domesticating selection, largely for behavioural traits, is also likely to be widespread (Tave, 1993). Thus differences in traits such as growth, an important component of fitness, can be assumed to exist between all farm and wild stocks. Studies, where controlled comparisons have been made between farm and wild stocks, indicate that many genetic differences with fitness implications are likely to be found which will affect the outcome of any interaction (McGinity et al., 1997; Flemming and Einum, 1997).

Differences in quantitative and behavioural traits between farm and wild stocks sharing origin from the same regional stock groups are generally only associated with differences in variant frequencies of in the order of 0.2 (Youngson et al., 1991). As previously discussed (see also Figure 1), even these small differences in frequencies can give rise to major differences in the proportions of genotypes present in each group. If Figure 2a represents the 100 broodstock in a small river stock and Figure 2c a random sample of 100 fish from a farm stock, then 44% of the salmon in the farm stock would have genotypes not expected to be present among the wild salmon. Given differentiation increases with the number of loci, and many more than four genes will be involved in the quantitative characters in which most farm and wild populations will differ, few genotypes would be expected to be shared in common between any two groups of farm and wild salmon.

Risk Assessment

A clear potential for effects on the viability and character of wild salmon stocks from interactions with farm escapes is indicated by quantitative and qualitative theory on the genetics of populations. Furthermore, the predications of theory are supported by what little is known about the specific genetic character of wild populations and farm stocks of Atlantic salmon. There can be no doubt that biological mechanisms exist whereby the presence of escapes may cause genetic changes. Changes will occur if farm fish differ in a way which makes them differently adapted to the local environment from the wild stock, either because of their genetic make-up or due to their culture environment (Youngson and Verspoor, 1998). While a long term impact on recruitment and stock character is not an inevitable consequence, the chance that farm escapes will have a positive impact on stock recruitment and character can be expected to be remote.

The relative importance of the indirect and direct routes for impacts is difficult to predict. Both are likely to be operative to some degree unless interbreeding does not occur. By either route, the expected end result for most river stocks will be to reduce one or both components of local adaptation. It will change either the frequencies of selectively important variants within populations, which determine both qualitative and quantitative traits, or it will change the nature and extent of the subdivision of the stock into distinct genetic populations. With current levels of understanding of genetic processes, and of the specific nature of farm and wild stocks, which of these will be affected and to what extent there will be an effect cannot be predicted. What can be said is that the severity and permanence of any genetic impact will dependent on both the quantity and quality of the farm fish involved in the interaction relative to the wild stock affected.

Quantitative considerations

The magnitude of both indirect and direct impacts on a wild stock will be directly related to the relative

proportion of farm fish mixing with it. The more escapes which interact, the more density dependent mortality which could occur due to intraspecific competition and the more likely recruitment of wild fish will be depressed. This loss is unlikely to be compensated for by the additional returns of both pure and hybrid farm fish. Even among wild fish, most individuals fail to survive to breed and pure farm fish are likely to have a lower fitness with the fitness of hybrids intermediate. In the case of indirect interactions, such as when farm fish harbour exotic pathogens, the likelihood that these will be introduced and become established will also increase as more farm escapes enter a river.

One farm fish poses a potential risk, particularly if it carries exotic pathogens. However, one or a few fish are unlikely to do so where wild populations are "healthy". This is because in small numbers, farm fish may be eliminated by chance mortality events. Also, a component of population mortality among the wild fish, at least during the juvenile phase, will be density dependent and should to some degree be able to buffer any increased juvenile mortality which might occur. However, as the proportion of farm fish increases, chance will become less important and any buffering capacity will be used up. Where populations are already in decline, and their viability threatened by other factors such as changes in marine survival, environmental degradation, or excessive angler exploitation, any buffer capacity will already be limited or even absent. In such cases, even small reductions in mean individual fitness may cause recruitment to decline below the level required to maintain existing population numbers.

Natural selection may be able to bring the population back to its pre-impact adaptive state, even within a single generation. This can be expected if the presence of farm salmon is not a reccurring event and any resulting genetic changes, reductions in recruitment, and shifts in population character are small. The longer the time scale of the interaction and the greater the ratio of escapes to wild fish, it will become less likely that the previously existing genetic state of the population can be restored and the risk of a long-term, or even permanent, negative impact will increase. In the extreme, if enough farm fish are involved, indirect effects may lead to population extinction. Where there is interbreeding, it may lead to the wild population being replaced by a farm stock (Saegrov et al. 1997) and depend on escapes to maintain wild spawning. As before, the risk of a major impact will be greater for populations where recruitment is already marginal for maintaining stock abundance and stock abundance is already depressed.

Qualitative considerations

The effects on the outcome of any interaction of increasing differentiation between farm and wild fish are difficult to predict. Where interbreeding does occur, the survival and reproductive success of any hybrid offspring produced can be expected to be increasingly reduced as the degree of adaptive differentiation between farm and wild fish increases. The direct impact of escapes from a first generation farm line on a wild population from which it was derived would be expected to be negligible, except perhaps where there had been extreme genetic drift in the farm stock, as genetic differences between farm and wild fish would be expected to be small. However, the expectation and severity of any impact would increase with the number of generations in culture as this would be expected to give rise to an increasing adaptive differentiation. The latter will also be the case as the farm stock is established from a wild stock which is an increasing geographical distance from the wild river stock being impacted. As previously mentioned this will be greatest where farm salmon and wild salmon derive from different continental stock groups e.g. farm salmon of North American origin in Scotland, or farm salmon of Scottish origin in the Bay of Fundy region. The impact could potentially be greatest for farm salmon which have been modified transgenically.

Increasing adaptive differentiation is a double edged sword. On one hand it increases the likelihood of farm fish dying and reduces numbers likely to interact ecologically and likely to still exist to interbreed. This is true both for pure farm fish and for hybrid fish produced by interbreeding. Thus once farm and wild salmon do interbreed, increasing genetic differentiation causes an increasing impact on the next generation. This will decrease population size and increase genetic drift. However, as more hybrid

offspring die, the degree of genetic change in subsequent generations may, ironically, be lower than if adaptive differentiation is lower and more hybrids survive. However, what actually happens will be very much dependent on the specific genetic nature of the hybrids which survive to contribute genetically to the next generation. Specific genetic differences unrelated to general levels of differentiation may be of overriding importance in the outcome of actual interactions. For example, the introduction of a novel gene which increases disease resistance to an introduced pathogen could be expected in the short-term to increase survival among farm and hybrid fish relative to farm fish, and selectively favour hybrid fish in the long-term. Thus making generalizations about the qualitative effect of genetic differentiation on the extent of indirect impacts is difficult based on existing theory and empirical knowledge.

Risk Management

It is clear that current empirical understanding of the risk associated with farm-wild interactions is insufficient to specify the proportion of escapes or degree of genetic difference which can be absorbed by a population before longer term changes result. As such, if the conservation of wild rivers stocks is the objective, management needs to be guided by the precautionary principle and any programme to manage the risk from farm escapes should be based on three objectives:

> - elimination of the risk of farm escapes. Where elimination is not possible, the number and frequency of escapes should be reduced to the minimum feasible level. In addition to reducing escapes, selective trapping or angling of escaped fish entering rivers should be implemented.

> - minimization of the introduction of novel genetic variants by farm fish. This can be achieved by establishing farm stocks only from local or regional river stocks e.g. farmed salmon in the Bay of Fundy of European or Newfoundland origin, or those in Scotland should not be of Baltic, Spanish, or North American origin. Further genetic improvement should be confined to selective breeding of these local farm stocks. Promote technologies which render farm fish reproductively incompetent e.g. triploidization, which can avoid the risk of direct, but not indirect, genetic impacts.

> - maximization of the sustainable abundance of wild spawning stocks through habitat restoration or limitations on exploitation to increase the natural "buffering" capacity of wild populations. Depleted or declining populations will be particularly susceptible to negative impacts.

Research Needs

A more precise understanding is still needed of the genetic risk to wild populations posed by farm escapes. More precision will help to refine management policy to ensure the needs of both recreational and aquacultural sectors are properly balanced and ensure the greatest likelihood of a long term future with self-sustainable wild Atlantic salmon populations. Understanding the degree of risk posed by different levels of escapes and different degrees of genetic differentiation can be improved by a combination of empirical research, into specific river interaction scenarios, and broadly based generic research on the genetical processes involved in local adaptation. Both types of work will depend on integrating recently developed molecular methodologies, which allow the genetic characterization of individual Atlantic salmon as well as populations, with more traditional ecological and behavioural analyses.

Advancing empirical and theoretical understanding has, until recently, been constrained by an inability to track individuals and their offspring across generations, and to genetically characterize individuals and populations sufficiently to identify adaptively relevant differences. Fortunately, recent developments in DNA based molecular genetics have removed the first obstacle (McGinity et al. 1997) and make the second problem more tractable. However, the application of methods for the direct study of DNA variation

is still limited by the lack of specific development work on Atlantic salmon and by costs. However, the required development work is now under way. Of particular note in this regard is the automated screening of hypervariable microsatellite genes (O'Reilly et al. 1996) and the identification of markers for performance traits (Jackson et al., 1998). Additionally, technical refinements as well as the more widespread use of methodologies in a range of fields of study and automation, are all bringing down the costs of molecular analysis.

Using molecular markers, there is the potential for substantially increasing empirical understanding of the genetics of farm-wild interactions. This potential can be exploited in field studies to assess the actual effects of interactions on recruitment and reproductive success for known proportions of farm escapes and known levels of genetic differentiation. Molecular markers can also be used to advance understanding of the mechanisms, causes and hindrances to interbreeding, and to undertake generic studies into adaptive processes to provide the basis for the interpretation and generalization of empirical results. By doing so it will be possible to improve the capacity to predict impacts in situations where detailed studies are not possible, on the basis of more cursory assessments of numbers of escapes and the relative genetic characters of farm and wild fish. Such studies will also provide a better knowledge base for determination of appropriate actions for remedial work where river stocks have already suffered genetic changes which have reduced population viability or unacceptably altered stock character.

Conclusions

The potential exists for negative impacts on the genetic structure of wild Atlantic salmon populations where they interact with escaped farm conspecifics. Reductions in recruitment rates affecting population viability, as well as associated changes in population character, are expected.

The likelihood that the outcome of any interaction will be positive, with regard to population viability at least, is small. Wild salmon populations are genetically adapted to local environmental conditions and most genetic changes will reduce mean survival and reproductive success.

Increasing proportions of farm salmon and increasing adaptive differentiation from the wild population will increase the likelihood of a negative impact on the viability, and character of a wild stock. Natural selection can only be expected to prevent negative genetic changes in subsequent generations where proportions of farm salmon are relatively small. For populations already in decline this proportion will be smaller than for healthy populations.

Safe levels of farm escapes cannot be specified and the precautionary principle must be used to guide management. Where escapes cannot be eliminated, interactions should be minimized by reducing numbers of escapes and their genetic differences with wild stocks, and if feasible making farm salmon reproductively incompetent.

The capacity to accurately identify and quantify risk, and to remedy impacts, can be increased from its current state. Developments in molecular biology, which allow the specific genetic characterization of individual salmon and salmon populations, need to be exploited in empirical studies of ecological and reproductive interactions between farm and wild salmon. These developments should be used to monitor both the inputs and outcomes of existing interactions, and to develop a deeper understanding of the nature and extent of local adaptation in Atlantic salmon populations with regard to both qualitative and quantitative traits.

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