

Genetic diversity among Atlantic salmon (*Salmo salar* L.) populations

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The effect of deliberate or inadvertent transfers of cultured Atlantic salmon (*Salmo salar* L.) on wild conspecifics depends on the nature and extent of biologically important genetic diversity among wild and transferred fish. Tagging and genetic studies show that salmon are divided into local, reproductively discrete populations associated with individual river systems or tributaries within systems. These are likely to be linked by historical patterns of gene flow into larger aggregations, which can be conceptualized as metapopulations, within which an evolutionary dynamic of local population formation, genetic exchange and extinction probably occurs. Diversity among populations has been documented within and between rivers, between North American and European population groups, and between Baltic and Atlantic subgroups within Europe. Diversity is in most cases associated with differences in biological performance relevant to survival and recruitment. As such, transfers have the potential to genetically alter native populations, reduce local adaptation, and negatively affect population viability and character.

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Introduction

The deliberate or inadvertent transfer of cultured Atlantic salmon (*Salmo salar* L.) into watersheds with existing native populations has a long history (McCrimmon and Gots, 1979) and is currently widespread (e.g. Mills, 1991; Webb and Youngson, 1992; Webb *et al.*, 1993; Hansen *et al.*, 1997). Transfers include escapes, both from hatcheries into fresh water (e.g. Clifford *et al.*, 1997) and from farm cages into the sea (e.g. Webb *et al.*, 1991), as well as fish planted out into rivers in attempts to re-establish extinct stocks or to enhance existing ones (e.g. Mills, 1991). Understanding of the consequences of transfers for native populations of salmon is limited (Hindar *et al.*, 1991), but of central importance will be the nature and extent of biologically important genetic diversity between native and transferred fish.

Genetic diversity is biologically important when it affects Darwinian fitness, either in the short or long term, i.e. on whether it is of adaptive relevance. The greater the adaptive differentiation between wild and transferred fish, the larger the expected decrease in survival and recruitment among hybrid offspring. This decrease can be viewed as outbreeding depression

(Emlen, 1991) and results in reduced frequencies, in the population, of genotypes suited to local conditions. The greater the reduction, the lower overall survival and recruitment will be and the bigger the impact on population viability and character.

Views on the nature, extent and biological significance of genetic diversity in *S. salar* have fluctuated considerably since the species was formally described by Linnaeus in 1758. Taxonomic subdivisions based on phenotypic traits, most of which are developmentally labile (Clayton *et al.*, 1991), have been controversial and, since the refutation by Wilder (1947) of the classification of anadromous and non-anadromous populations as distinct subspecies, there has been a tendency to view the species as monotypic. Yet field observations have led many salmon biologists over the years (e.g. Nordqvist, 1924; also see references in Taylor, 1991) to contend that each salmon river contains its own heritably distinct stock.

Genetic diversity can be distributed within individuals, among individuals within populations, and among populations (Weir, 1996); populations, in the genetic sense, being groups of individuals within which interbreeding is more or less random but among which interbreeding is constrained. It is the nature and extent

of genetic diversity, between native populations and sources of transferred fish, which determines the extent of any resulting outbreeding depression. Given that the genetic character of cultured fish is strongly influenced by their wild origins, understanding the true nature of population structuring in wild salmon, and its adaptive significance, is central to appreciating the implications of transfers of conspecifics. Our current understanding of the nature, extent, and biological importance of genetic diversity within *S. salar* is reviewed here.

Population structuring

The tendency of salmon to home back to their natal streams to spawn was noted by many early salmon biologists (e.g. Nordqvist, 1924) and has been strongly supported by more recent studies (Stabell, 1984). This tendency, combined with the spatial isolation of river systems and a sometimes patchy, discontinuous distribution of spawning and rearing habitat within river systems, provides the opportunity for salmon to segregate into distinct reproductive groups and provides the basis for the species to subdivide into local populations. That this potential has been realized, at least to the extent that salmon in different river systems belong to different populations, is supported by a considerable body of circumstantial evidence and generally accepted (Saunders, 1981; Thorpe and Mitchell, 1981; Stabell, 1984; Ståhl, 1987). Less well appreciated is the extent to which salmon in river systems are a composite of local populations. That this might be the case was indicated by Møller's (1970) early work, which found spatial heterogeneity in the Miramichi River, New Brunswick, for variation at the *Tf* gene which codes for the blood protein transferrin. This view has been further supported by multi-locus allozyme studies of the Miramichi system (Ståhl, 1987) as well as of other rivers, such as the Blackwater in south-west Ireland (McElligot and Cross, 1991), the Alta in northern Norway (Heggberget *et al.*, 1986), the Kyles of Sutherland river system in north-east Scotland (Verspoor *et al.*, 1991), and the Teno in northern Scandinavia (Elo *et al.*, 1994). The subdivision of anadromous and non-anadromous salmon within river systems into reproductively distinct populations has been documented in Newfoundland (Verspoor and Cole, 1989) and Norway (Vuorinen and Berg, 1989).

The existence of multiple populations within larger river systems is supported by recent tagging studies. Youngson *et al.* (1994) observed minimum rates of homing to the Girnock Burn, a tributary of the River Dee in north-east Scotland, of 45%. Various considerations point to this being a substantial underestimate of homing accuracy. Most importantly, the Girnock trap, from which the estimates derive, probably spans rather

than borders the population unit to which the estimates relate. This view is consistent with no tagged Girnock salmon yet being detected in the Baddoch Burn ~30 km upstream, or *vice versa*, since 1988, when the trap was put in the Baddoch (Hay, 1995) and tagging of smolts in both tributaries has been routine. Reproductive isolation of the two tributary stocks is further supported by levels of genetic differentiation shown for allozyme, mtDNA, and minisatellite variation (Verspoor, 1995).

Defining the spatial boundaries of local populations, particularly within river systems and for anadromous populations at sea, remains problematic because the movements of juveniles and adults often result in the spatial mixing of salmon from different tributaries and river systems. For example, resident and anadromous populations of salmon coexist in Little Gull Lake, Newfoundland, even though the latter spawns in inlet and outlet streams (Verspoor and Cole, 1989). Anadromous populations from tributaries within rivers are likely to mix both during the smolt run (e.g. the Miramichi River – Møller, 1970) and at sea. Mixing of anadromous populations from different rivers occurs at sea although the extent to which this occurs is unclear as population distributions at sea are poorly understood owing to the difficulties of studying salmon in the marine environment.

Defining population boundaries on a temporal scale is also problematic. Some gene flow among local populations, particularly within river systems, could occur, though it might be sporadic and depend on geographic separation. Furthermore, current population structuring can be viewed as part of a dynamic, evolving scenario ongoing since the species colonized its current range following the last glaciation. Within this scenario local populations, depending on distributional discontinuities and patterns of movement, are likely to be associated into larger genetically related groupings. Within these groupings, a dynamic of local population establishment, genetic exchange and, as a consequence of factors such as fluctuations in climatic conditions (Roy *et al.*, 1996) or stochastic reductions in abundance, extinction is likely to operate. Such evolutionary groupings, connected by descent and gene flow, can be viewed as metapopulations within the context of the currently developing metapopulation paradigm (Hanski and Gilpin, 1997).

The existence of historical gene flow among populations is supported by analyses of levels of genetic differentiation among and within river systems (Ståhl, 1987; Verspoor *et al.*, 1991; Jordan *et al.*, 1997). However, from these analyses it is not clear whether this gene flow occurred in the past or is currently ongoing. Certainly, the tagging studies (Youngson *et al.*, 1994; Hay, 1995) suggest that current levels of gene flow are very low. However, as tagging studies are based on relatively limited time periods, the sporadic occurrence of

substantial amounts of gene flow among current populations, perhaps dictated by unusual environmental and demographic circumstances, cannot be ruled out. Certainly, recent recolonizations of river systems and tributaries in which salmon were extinct, such as the River Clyde in Scotland (Gardiner and McLaren, 1991), suggest that gene flow from one location to another can still occur.

The historical interconnection of salmon from different tributaries within a river, or different rivers, does not rule out the development of genetically distinct local populations on shorter evolutionary time scales. Recent studies of the blackcap (*Sylvia atricapilla*) (Berthold, 1995), a passerine bird, indicate that as few as 50 generations may be required for new reproductively distinct populations to evolve. Given its greater fecundity, there is even greater scope in Atlantic salmon for natural selection to act on geographically separated groups of individuals to evolve locally adapted populations. Thus local salmon populations are still likely to be important biological units in the short to medium term even though they may be more transient entities on larger evolutionary time scales.

Genetic diversity

The scope for genetic diversity to evolve among Atlantic salmon populations is substantial. Genetic variation can arise in both the nuclear and mitochondrial genomes and is likely to involve in the order of 100 000 genes. At the nuclear level, variation may occur in how genes are organized into chromosomes as well as with regard to the DNA base sequence of each gene. In the mitochondrial genome, diversity is limited largely to DNA sequence variation. Even if polymorphisms were restricted to nDNA sequence variation and only 20 genes were polymorphic for just two allelic variants each, this variation could generate over 3 billion genetically different individuals.

Understanding of the actual amount of genetic diversity among populations can be obtained in a number of ways. It can be derived indirectly from studies of the inheritance of morphological or performance variation within and between families from different populations that have been reared in a common environment (Tave, 1993). More directly, diversity can be quantified by the electrophoretic analysis of specific proteins (e.g. Hillis *et al.*, 1996), such as metabolic enzymes, where a direct relationship can be established with a specific gene. Variation in nuclear gene organization can be assessed directly by the microscopic analysis of chromosomes with regard to chromosome number (2N), chromosome arm number (NF), and the position and number of fluorescently staining regions of heterochromatin (Hartley, 1987; Phillips and Hartley, 1988); the latter are

regions with high concentrations of DNA with repeated DNA base sequences. Most recently, however, analysis has focused on molecular methods that allow the direct analysis of DNA base sequence variation, both in the nuclear and mitochondrial genomes (e.g. Hillis *et al.*, 1996). In Atlantic salmon, nuclear analyses have focused on minisatellite and microsatellite genes, regions of DNA composed of tandemly repeated sequences of 6–20 base pairs and 2–5 base pairs, respectively.

More than 20 specific genes are already known to be variable (McConnell *et al.*, 1995; Taggart *et al.*, 1995; Wilson *et al.*, 1995), some with 38 or more alleles. In addition, variation has been observed in mtDNA base sequences (Bermingham *et al.*, 1991; Knox and Verspoor, 1991; McVeigh *et al.*, 1991) and in the organization of the nuclear genome (Phillips and Hartley, 1988). Evidence that even larger numbers of genes are variable comes from inheritance studies of variation in quantitative traits (Tave, 1993). Thus the amount of genetic diversity available for the evolution of divergence among populations is likely to be high.

The actual extent to which genetic diversity has evolved among as opposed to within populations is still a matter of much debate. Early studies found major heritable differences between North American and European salmon and on the basis of differences in allele frequencies at the transferrin locus, *Tf*, Payne *et al.* (1971) proposed the designation of European and North American salmon as distinct subspecies, *Salmo salar europaeus* and *S. s. americanus*. The proposed nomenclature was disputed (Gruchy, 1971) and, while the proposition was supported by some (Nyman and Pippy, 1972), others (Behnke, 1972) felt single locus frequency differences were an insufficient basis for delineating subspecies. However, additional evidence accumulated over the past two decades confirms the phylogenetic distinctiveness of the two continental population groups. Differences have now been observed with regard to chromosome arm number (Europe NF=74; North America NF=72 – reviewed in Hartley, 1987), chromosome number (Europe 2N=56–58; North America 2N=54–56; Roberts, 1970; Phillips and Hartley, 1988; García-Vázquez *et al.*, 1992; Morán *et al.*, 1993) and the occurrence of regions of fluorescently staining heterochromatin (Phillips and Hartley, 1988). Variation at the protein loci *AAT-3**, *MDH-1**, *MDH-3,4**, *MEP-2**, *IDDH-2**(=Sdh-2), *PGM-1R**(=Pgm-2r), and *ME** (Ståhl, 1987; Verspoor, 1988a; Verspoor and Jordan, 1989; Verspoor and McCarthy, 1997) loci show patterns of continental differentiation similar to *Tf*. An extensive study by Taggart *et al.* (1995) of the minisatellite locus *Ssa-A45/I* shows almost complete fixation of North American and European salmon for alternative alleles and McConnell *et al.* (1995) found substantive allelic divergence at three microsatellite loci – *Ssa4*, *Ssa14*, and *Ssa289*. Fixed differences in mtDNA haplotypes have

also been reported (Bermingham *et al.*, 1991), though McVeigh *et al.* (1991) found two of three cytochrome b haplotypes unique to North America while a third, constituting the only European type, was found on both continents, though only at low frequencies in North America. The observations by McVeigh *et al.* are supported by more extensive surveys of variation in the ND1/16sRNA region of the mtDNA (Verspoor, unpublished data). Thus there is a strong case to be made for the division of the species into North American and European phylogenetic groups and for historical introgression between the two continental types in some parts of North America.

Further regional subdivision of North American populations has been suggested based on transferrin variation (Møller, 1970). However, this is not supported by more extensive analyses of allozyme (Payne, 1974; Verspoor, 1986, 1988a, 1994) and mtDNA variation (Verspoor, unpublished), and allozyme data (Verspoor, 1994) support the polyphyletic origin of non-anadromous populations (Behnke, 1972; Berg, 1985). In contrast, geographic subdivision of European salmon into Atlantic and Baltic population groups as proposed by Cross (1983) and Ståhl (1987) is supported by allozyme (Verspoor, 1988a; Bourke *et al.*, 1997) and mtDNA studies (Bermingham *et al.*, 1991; Verspoor, unpublished data), though no fixed genetic differences are detectable. This separation is consistent with tagging studies which show no movement of salmon between Baltic and Atlantic drainages (Stabell, 1984). Subdivision of salmon in the British Isles into Celtic and Boreal races has also been proposed (Payne *et al.*, 1971; Child *et al.*, 1976), based on small but consistent differences in *Tf* frequencies, but is not supported by the distribution of allozyme (Ståhl, 1987; Bourke *et al.*, 1997) or mtDNA variation (Verspoor, unpublished data). As in North America, comparisons of anadromous and non-anadromous European populations (Ståhl, 1987) point to the latter population type being polyphyletic in origin.

Within different geographic regions significant genetic differentiation is widespread among salmon populations within river systems (Møller, 1970; Heggberget *et al.*, 1986; Ståhl, 1987; Verspoor and Cole, 1989; McElligot and Cross, 1991; Verspoor *et al.*, 1991; Elo *et al.*, 1994) as well as among river systems (Ståhl, 1987; Verspoor, 1988a, 1994; McElligot and Cross, 1991; Jordan *et al.*, 1992) and appear to be temporally stable (Jordan *et al.*, 1992). When considered together with data on regional differentiation a pattern of increasing genetic differentiation with increasing geographic distance (Ståhl, 1987; Verspoor, 1994; Jordan *et al.*, 1997) emerges.

Perceptions of genetic differentiation are often based on observed differences in the frequencies of variants for individual genes. These show allelic diversity among salmon populations to be largely quantitative rather

than qualitative, i.e. they involve differences in variant frequencies rather than in variant types. However, variant frequencies do not give a good reflection of the overall genetic differentiation among individuals in two populations. To clarify this point, consider two populations that share the same alleles at three diallelic loci and, at each locus, the respective frequencies of the two alleles in each population are 0.9 and 0.1, and 0.1 and 0.9. The expected frequencies of the 27 possible genotypes in the two populations are radically different (Fig. 1). Indeed, the most common genotype expected for individuals in each population (which is the least common genotype in the other population) is over 500 000 times more likely than the least common genotype and, in each population >88% of individuals are expected to have genotypes possessed by <0.006% of individuals in the other population. Given a finite population size of ca. 5000, then the probability that the common genotypes in the one population are absent in the other population is greater than 75%. Where natural selection favours common genotypes (i.e. local adaptation) this difference will be even more extreme. When this same argument is extended to the 20 or so known polymorphic genes, let alone the hundreds of variable genes likely to exist, it becomes clear that most local populations are highly genetically divergent.

Population adaptation

Understanding of the extent to which genotypic diversity among local populations is adaptive and maintained by natural selection is still very limited. What can be gleaned from studies of salmonid populations generally indicates that diversity is important to survival and recruitment under local environmental conditions (Taylor, 1991; Carvalho, 1993). From what is known, the Atlantic salmon does not appear to be an exception. The basic requirements for the evolution of local adaptation in Atlantic salmon exist. The species shows heritable variation for a wide range of performance-related traits, such as growth and maturity (Tave, 1993), and there is heterogeneity among the habitat patches in relation to environmental factors which can affect such performance traits. Furthermore, in those cases where studies designed to test for adaptation have been carried out, the evidence supports local population adaptation being a general phenomenon.

At least some aspects of body morphology appear to be adaptive. Heritable differences in body morphology have been demonstrated between salmon from the Sabbies River and Rocky Brook tributaries of the Miramichi River, New Brunswick, which are associated with differences in tributary flow characteristics (Riddell and Leggett, 1981; Riddell *et al.*, 1981). Rocky Brook

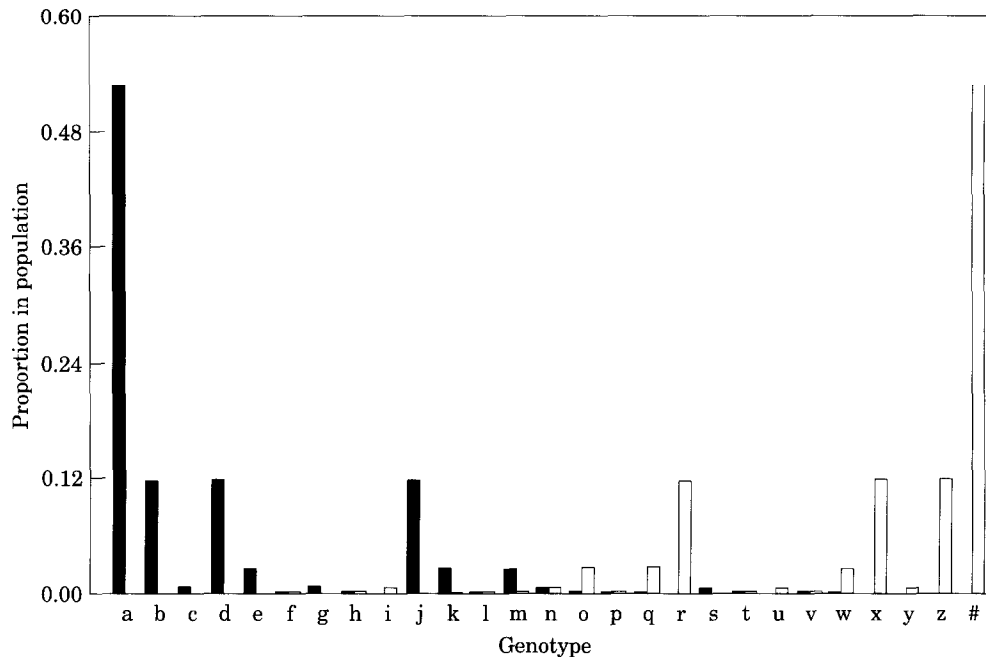


Figure 1. The expected proportions of individuals for each of 27 shared genotype combinations in two hypothetical populations with the same two alleles, 1 and 2, at three loci A, B, and C. Allele frequencies at the loci differ with the first population having frequencies of $A1=0.9$, $A2=0.1$, $B1=0.9$, $B2=0.1$, $C1=0.9$, $C2=0.1$ and the second population having frequencies of $A1=0.1$, $A2=0.9$, $B1=0.1$, $B2=0.9$, $C1=0.1$, $C2=0.9$. Population 1 (■); population 2 (□).

fish have more fusiform bodies and larger fins, more suited to holding position in the Brook's faster flow. Adaptations to water quality also appear to exist. Two tributary stocks of the Kyles of Sutherland River system in north-east Scotland show heritable differences in egg mortality associated with adaptation to low pH (Donaghy and Verspoor, 1997). Mortalities were eight-fold higher for the non-native stock in the tributary where the low pH conditions occurred. Genetic differences were also found between the same two stocks in the timing of hatching in the wild, with the stock inhabiting the less extreme environment hatching consistently earlier. However, the adaptive significance of the differences in hatch timing is not clear. It may reflect a balance between the competitive advantages of early hatching and a need to hatch when food availability is optimal. The latter is likely to be locally variable and could be earlier under less extreme environmental conditions.

Apparent adaptive differences have also been identified between river stocks in relation to the time of return of adults to rivers and in smolt age. Hansen and Jonsson (1991) found the stock from the River Figga returned earlier than those from the River Imsa when both were hatchery reared and released as smolts in the Imsa. This difference was consistent with the River Figga having suitable flow conditions for spring and summer entry, whereas water levels in the Imsa are generally too low

for entry except during the autumn. Timing differences were also observed in relation to synchronously spawned eggs from two Scottish rivers, the Nith and the Shin, planted out as fertilized eggs in a river in north-east Scotland. The latter had an earlier age of smolting (Fig. 2) which is probably caused by differences in growth patterns of fish arising from adaptation to their native river environments.

Differences in growth and digestion rates have been documented between Shin salmon and salmon from the River Narcea, in northern Spain, under hatchery conditions (Nicieza *et al.*, 1994a, b). The former grew faster in the first summer but not during the following winter period, ending up marginally smaller at the time of smolting. Superior growth of Shin fish during the first summer has also been observed in a comparison with native stock in the River Ulla based on planted out eyed ova (C. García de Leániz, Dirección General De Montes y Conservación De La Naturaleza, Santander, Spain, pers. comm.). Furthermore, in the Ulla, Shin juveniles suffered significantly higher mortality and smolt production was up to nine times higher for the native stock. The higher juvenile mortality of the non-native salmon may in part account for the poor return rates of stocked Scottish salmon to the angling fisheries of two other Spanish rivers, the Áson and the Nansa (García de Leániz *et al.*, 1989; Verspoor and García de Leániz, 1997).

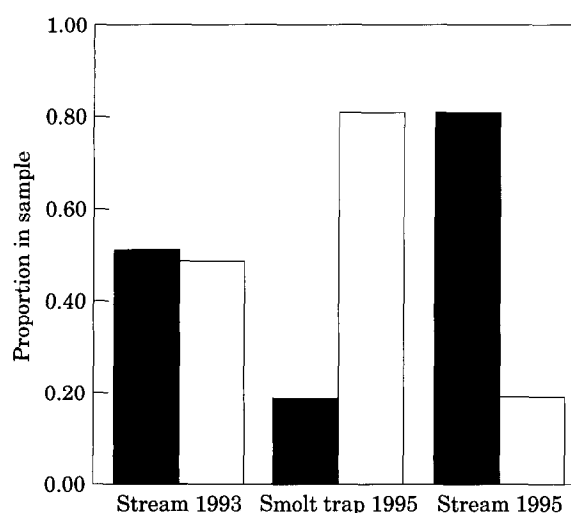


Figure 2. The relative proportion of River Nith and River Shin salmon in the River Loth in 1993 as 0+ juveniles compared to the proportions recorded at the age of 2+ in the smolt trap below the stocking site in 1995 and in the stream above the trap after the smolt run. No smolts were recorded in 1994 (Source: Verspoor, unpublished data). Nith stock (■); Shin stock (□).

Adaptive population differences have also been observed for parasite resistance and are associated with differences in the presence or absence of pathogens in their native environments. Salmon stocks in the Baltic, where the monogenean ectoparasite *Gyrodactylus salaris* is endemic, are relatively resistant to infestation, whereas populations outside the Baltic, where the parasite has recently been introduced, are susceptible and suffer almost 100% mortality (Bakke *et al.*, 1990; Bakke and MacKenzie, 1991; Rintamakikinnunen and Valtonen, 1996). Thus it would appear that adaptive genetic differentiation occurs at the level of regional population assemblages.

Studies of *MEP-2**, a gene which codes for malic enzyme, indicate that adaptive differentiation among salmon populations generally increases with the geographic separation. Variation at the gene is clinically associated with latitude, and more particularly temperature, in both Europe and North America as well as with temperature within river systems (Verspoor and Jordan, 1989; Verspoor *et al.*, 1991). This argues strongly for the genetic changes among populations being an adaptive response mediated by natural selection. The basis for the response may lie in the observed connection between variation at *MEP-2**, or a closely linked gene, and growth (Jordan and Youngson, 1991; Jordan *et al.*, 1990), a performance trait strongly influenced by temperature.

Implications for fish transfers

It is clear that Atlantic salmon are highly subdivided into local populations associated with individual river

systems, or tributaries and lakes within river systems. Furthermore, it is clear that each local population has evolved to become genetically distinct. Where salmon are taken into culture, further genetic changes relative to the source population are likely (e.g. Verspoor, 1988b; Youngson *et al.*, 1991). Thus it can reasonably be assumed that transferred fish, many of which have been kept in culture, will differ genetically from native populations. As a consequence, where transferred fish mix reproductively with native fish, changes will occur to the genetic composition of the native populations.

Whether genetic changes caused by transfers will have a negative effect on population survival, recruitment, or character depends on whether the transferred and native populations are adaptively differentiated. The specific evidence that is available on adaptive differentiation of Atlantic salmon populations is largely circumstantial but strongly suggestive. When considered together with evidence from other salmonids, and placed in the context of current biological theory, the conclusion must be that adaptively important genetic differences will exist between most, if not all, transferred and native populations.

The greater the geographic distance separating native and transferred populations, the greater the potential for adaptively important genetic change. This potential is likely to be greatest where transferred fish are from a different regional population group than the native population, i.e. North America as opposed to Europe, or the Baltic as opposed to the Atlantic regions within Europe. Adaptive differences are also likely to be increased by genetic changes incurred by transferred fish while in culture. Whether the potential for genetic change is realized will depend on the relative numbers of transferred fish which survive to breed in the native population. This may in fact decrease as adaptive divergence from native salmon increases.

If adaptive differences exist between transferred and native salmon, and transferred fish survive to breed, then interbreeding will lead to an overall reduction in survival and recruitment in the native population. This reduction may or may not pose a threat to the viability and character of the native population. Where adaptively important genetic changes are small and quantitative, natural selection may be able to restore the genetic composition of the population to its previous adaptive state. However, where changes are large or qualitative, due either to the loss of local genetic variants or to the introduction of new variation, genetic changes may not be reversible by natural selection. In such cases the induced changes could threaten the long-term viability of the population or permanently alter population character.

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