

A review of genetic influences from escaped farmed Atlantic salmon on wild Atlantic salmon populations

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<i>Summary:</i> <p>Denne rapporten gjennomfører en kritisk gjennomgang av dagens kunnskap om interaksjoner mellom oppdrettslaks og ville laksepopulasjoner med spesifikk relevans for Norge, samt diskuterer dagens kunnskap om effektiv forvaltning av ville bestander av denne arten. Rapporten beskriver i detalj informasjon om akvakulturproduksjon, livssyklus, utbredelse og populasjonsstruktur, genetiske interaksjoner og bevaring av atlantisk laks. Et eget kapittel drøfter hvilke forskningsområder som trenger spesiell oppmerksomhet i tiden fremover.</p> <p>This report entails a critical review of current knowledge concerning the interactions between farmed and wild Atlantic salmon populations with specific relevance to Norway, and also discusses current knowledge regarding the effective management of wild populations of this species. The report details information on the aquaculture production, life history, distribution and population structure, genetic interactions and conservation of Atlantic salmon. Furthermore, a separate chapter discusses future research areas which need attention.</p>		

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1 Summary and conclusions

1.1 Norsk sammendrag

Denne rapporten gjennomfører en kritisk gjennomgang av dagens kunnskap om interaksjoner mellom oppdrettslaks og ville laksepopulasjoner med spesifikk relevans for Norge, samt diskuterer dagens kunnskap om effektiv forvaltning av ville bestander av denne arten. Rapporten er delt inn i seks hovedkapitler som i detalj beskriver problemstillinger knyttet til akvakulturproduksjon, livssyklus, utbredelse og populasjonsstruktur, genetiske interaksjoner og bevaring av atlantisk laks. Videre drøfter et eget kapittel hvilke forskningsområder som trenger spesiell oppmerksomhet i tiden fremover.

Evaluering av oppdrett av atlantisk laks i Norge.

Norsk oppdrettslaks nedstammer fra ville stammer av atlantisk laks i Norge og har gjennomgått seleksjon for en rekke egenskaper av relevans for akvakultur, herunder vekst, senere kjønnsmodning, resistens mot enkelte sykdommer, filetfarge og fettinnhold. Etter opp til 9-10 generasjoner av styrt seleksjon, er både fenotypiske og genetiske avvik tydelig i oppdrettslaksen i forhold til deres ville artsfrender.

Livssyklus og struktur i populasjoner av vill atlantisk laks.

Livssyklus er av spesiell betydning for populasjonsstrukturen i atlantisk laks. De fleste laks er anadrome, men laks som gjennomfører hele livssyklus i ferskvann finnes også i hele utbredelsesområdet. Anadromitet, tilbakevandring og feilvandring er tre evolusjonære strategier som fremmer optimal vekst gjennom den marine fasen, lokal tilpasning på grunn tilbakevandring til samme elv, og et stort reservoar av genetisk variasjon på grunn av genflyt mellom populasjoner som følge av feilvandring. Bestander av laks er oppdelt i metapopulasjoner, dvs. sub-populasjoner som er sammenknyttet i varierende grad via genflyt (dvs. fra feilvandring). Metapopulasjoner krever at forvaltning baseres på graden av genflyt mellom sub-populasjonene, grad av lokal tilpasning som er unik for hver sub-populasjon og størrelsen på både sub-populasjoner og hele metapopulasjonen.

Lokal tilpasning og adaptiv variasjon

Mye av kunnskapen om lokal tilpasning hos atlantisk laks er basert på indirekte mål knyttet til respons på seleksjon og grad av overlevelse for fremmede stammer i nye miljøer. Grad av lokal tilpasning er viktig da naturlig seleksjon vil favorisere individer som er godt tilpasset levmiljøet. Adaptiv (genetisk) variasjon i en populasjon er også viktig da det sikrer den langsiktige levedyktigheten til populasjonen. Nyere studier har vist at lokal tilpasning i

atlantisk laks, og mengden av felles adaptiv variasjon henger sammen med graden av geografisk nærhet (og dermed genflyt) mellom populasjoner.

Genetiske interaksjoner mellom oppdrettslaks og vill atlantisk laks og bevaring av populasjoner

Årlig rømmer store mengder laks fra oppdrettsanlegg i Norge, og det er en økende bekymring for at interaksjoner med ville stammer vil føre til redusert produktivitet eller i verste fall utryddelse av villaksen. De fleste studier av genetiske effekter av rømt oppdrettslaks har vurdert variasjon i nøytrale allelfrekvenser over tid. Selv om variasjon i noen tilfeller er funnet, har en i andre tilfeller ikke observert noen endringer, selv i populasjoner med stort innslag av rømt oppdrettslaks. Oppdrettet atlantisk laks har vist seg å ha dårligere overlevelse og reprodutiv suksess i naturen, men har overlegen vekst i tidlige livsfaser og kan potensielt utkonkurrere vill lakseyngel på dette stadiet. Dette har blitt bekreftet i to empiriske studier som sammenlikner suksess av oppdrettet og vill laks. Imidlertid indikerte de samme studiene også at naturlig seleksjon virker klart i favør av vill laks, sett over hele livssyklusen. Ingen publiserte studier har til nå forsøkt å identifisere hvorvidt norsk villaks er utsatt for endret naturlig seleksjon (målt via markører for adaptiv genetisk variasjon) som følge av interaksjoner med oppdrettslaks. Oppdrettslaks er selektert for å fungere optimalt i et oppdrettsmiljø, mens i en vill bestand (av tilstrekkelig størrelse og med tilstrekkelig lokal tilpasning og adaptiv genetisk variasjon) vil naturlig seleksjon i all hovedsak dreie seg om å selektere de best tilpassede (ville) individene. Imidlertid kan dette ikke generaliseres til alle ville populasjoner, da deres demografi og egenskaper knyttet til livssyklus vil ha stor betydning for deres evne til å tilpasse seg trusler.

Hvis målet er å bevare de ville laksestammene i Norge, er det viktig at undersøkelser av populasjoner og metapopulasjoner er utført med tanke på å bestemme grad av utveksling av genetisk materiale mellom stammene, effektive bestandsstørrelser og mengden av adaptiv genetisk variasjon. Kun da vil en være i stand til å vurdere hvorvidt populasjonen er truet, både med hensyn på interaksjoner med rømt oppdrettslaks og andre miljøtrusler.

1.2 English summary

This report entails a critical review of current knowledge concerning the interactions between farmed and wild Atlantic salmon populations with specific relevance to Norway, and also discusses current knowledge regarding the effective management of wild populations of this species. To achieve this purpose, the report is sectioned into six main chapters detailing information on the aquaculture production, life history, distribution and population structure,

genetic interactions and conservation of Atlantic salmon. Furthermore, a separate chapter discusses future research areas which need attention.

Evaluation of aquaculture production of Atlantic salmon in Norway.

Norwegian aquaculture strains of Atlantic salmon are derived from natural populations of Atlantic salmon in Norway and have undergone selection for improved traits including growth rate, later sexual maturity, specific disease resistance, colour and fat content. After up to 9-10 generations of artificial selection, both phenotypic and genetic divergence is evident in aquaculture strains in comparison to their wild counterparts.

Life history and structuring of wild Atlantic salmon populations.

The life history of Atlantic salmon is of special significance in the structuring of populations. Most salmon are anadromous, although freshwater resident salmon also exist throughout its range. Anadromy, homing and straying are three evolutionary strategies that promote optimal growth through the marine phase, local adaptation due to homing, and a large reservoir of genetic variation due to gene flow from straying. Populations of salmon are structured into metapopulations; that is, sub-populations which are connected to various degrees via gene flow (i.e. from straying). Metapopulations require specialised management decisions based on the degree of connectivity among sub-populations, the amount of local adaptation unique to each subpopulation and the size of both the sub-populations and the metapopulation itself.

Local adaptation and adaptive variation

Much of the knowledge of local adaptation of Atlantic salmon has been based upon indirect evidence related to response to selection and the relative survival of translocated stocks. The degree of local adaptation is important as natural selection will act to select individuals with superior fitness to their environment. Adaptive variation in a population is also important as it ensures the long-term viability of a population. Recent studies have shown evidence for local adaptation in Atlantic salmon, and the amount of shared adaptive variation is correlated to the degree of geographic connectivity of populations.

Genetic interactions between farmed and wild Atlantic salmon and conservation of populations

Large numbers of Atlantic salmon escape from aquaculture facilities in Norway each year and there is a concern that interactions will lead to reduced productivity and even extinction of wild Atlantic salmon. Most studies of genetic effects of aquaculture escapes have assessed temporal variation in neutral allele frequencies. Although some temporal variation

has been found, in other populations known to have received large numbers of Atlantic salmon, no changes have been observed. Farmed Atlantic salmon have been shown to have poorer survival and reproductive success in a natural environment, yet have superior growth at early life stages and may outcompete their wild counterparts at this stage. This has been confirmed in two empirical studies of the comparative success of farmed and wild Atlantic salmon. However in these studies it was also apparent that natural selection acts in favour of wild Atlantic salmon. No published studies to-date have attempted to identify the response of Norwegian wild salmon to interactions with farmed salmon using markers for adaptive genetic variation. Farmed salmon are selected for improved fitness in the cultured environment, so it can be expected that in a wild population of sufficient size and with sufficient local adaptation and adaptive genetic variability, natural selection will act to select the fitter (wild) individuals. However, this benchmark cannot be applied to all wild populations, as their demographics and life history will play a significant role in their ability to adapt to threats.

If the goal is to preserve Norway's wild stocks of Atlantic salmon, it is imperative that surveys of population and metapopulation dynamics are conducted to determine levels of gene flow, effective population sizes and the amount of adaptive variation. Only then will we be able to obtain accurate assessments of environmental risks to the populations, including those associated with escaped farmed salmon.

2 Introduction – project design and tender

2.1 Background

The objective of breeding programs is to create fish strains that are more productive in farming than can be achieved by catching wild broodstock year after year. Breeding programs for Atlantic salmon in Norway have contributed to enhanced and more profitable production through selection based on breeding values over several generations for traits such as increased growth, delayed sexual maturity, fillet fat and colour and disease resistance. Such artificial selection results in a shift in allele frequencies over generations, both in functional and non-functional genes, a shift that has resulted in genetic divergence from wild stocks of Atlantic salmon (e.g. KARLSSON *et al.* 2010; MJØLNERØD *et al.* 1997; RENGMARK *et al.* 2006; SKAALA *et al.* 2004).

Escapes of cultured Atlantic salmon may result in interactions with wild stocks, and associated threats to wild populations include the spreading of disease and parasites, competition for food and habitat, and genetic interactions. Each of these threats can potentially alter the genetic diversity of wild stocks, and may potentially result in extinction of local genetic stocks. It is important to preserve the genetic diversity of wild salmon stocks as this diversity represents a large genetic reservoir, an essential requirement in enabling each population to adapt to changing environmental conditions and habitat disturbances. High genetic diversity can also be used to restore variation into cultured strains via backcrossing, as has been necessary in farming of other livestock, and which has been recognised as critical for sustainable farming practices in the FAO (2007) report entitled: “The state of the world’s animal genetic resources for food and agriculture”.

In order to quantify threats to the natural genetic diversity of Atlantic salmon, and to protect unique genetic variation, it is necessary to first assess the degree of structuring among populations. Atlantic salmon typically have an anadromous life cycle, a life history trait which is recognised as promoting gene flow via migration and dispersal through straying to non-natal rivers for spawning. However homing, where fish return to their natal rivers to spawn, counteracts the dispersal benefit of anadromy to some extent and thus results in populations that are locally structured to varying extents. Yet at the same time ‘straying’, where a salmon migrates to a non-natal river for spawning, is believed to be an evolutionary trait that counteracts the potential problems associated with homing (i.e. inbreeding and loss of genetic variability) and promotes diversity among populations (MCDOWALL 2001). As a direct

result of these life history traits, there is both genetic structuring *among* Atlantic salmon populations; yet a large degree of genetic diversity exists *within* Atlantic salmon stocks.

Anthropogenic influences such as aquaculture, river acidification and hydropower plants can affect the natural environment of the Atlantic salmon and potentially threaten its genetic diversity. Indeed, Hansen, *et al.* (2008) reported that of 452 salmon rivers in Norway, salmon is now extinct in 45, endangered in 32 and vulnerable in 51. It is however not realistic that many of these anthropogenic activities, such as aquaculture, cease in order to prevent consequences to Atlantic salmon stocks. Therefore, management strategies are needed so that activities essential to Norwegian society can co-occur with the continued and sustainable existence of wild Atlantic salmon stocks.

2.2 Goals

There are conflicting studies concerning the effect of interactions of escaped cultured salmon with wild stocks, particularly in relation to the relative fitness of cultured and wild stock in the natural environment. This study proposes to critically review available scientific literature to address several key questions related to interactions of cultured and wild salmon and effective tools for management of genetic diversity. In particular, this report will consider the following key questions:

Are there robust data that quantify detrimental genetic influences of escaped farmed salmon?

1. Is the hypothesis that hybrids will be selected back to the indigenous tribe in the course of a few of generations robust?
2. Are published models of the potential impact built on reasonable assumptions?
3. Must it be assumed that gene flow from farmed fish to wild fish is entirely negative?
4. Can a strategy to preserve the genetic diversity of wild salmon stocks be based on investing in less than 100% of the populations?
5. Can a management strategy based on metapopulations may be more effective than a river management strategy? Could this also be a strategy for the waterways which alone can be considered as a metapopulation?
6. We will also refer to other questions and issues that are embedded in the text above.

In addition, we will highlight areas where knowledge is lacking and areas that require further research to effectively answer the questions listed above.

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3 An overview of aquaculture production of Atlantic salmon in Norway

3.1 Selective breeding in Aquaculture programs

In order to assess impacts of aquaculture on wild populations of a species, it is essential to understand the level of differentiation between them, and the cause of this differentiation. Selective breeding programs in aquaculture rely upon additive genetic variation between individuals for particular desirable traits. A proportion of the observed phenotypic differences among individuals for a given trait or character is typically complex and polygenic (i.e. caused by the combined small effects of many genes rather than large effects of single genes), although there are exceptions to this (e.g. MOEN *et al.* 2009). The magnitude of this proportion (the heritability of the trait) varies among traits and is typically in the order of 20-30% for production traits like growth, specific disease resistance and carcass quality traits, but typically lower for fitness traits like survival and reproductive traits (FALCONER and MACKAY 1996). However, the heritability of trait is a property of the population and the environment. This general view may be different for traits of a population of animals brought from one environment (farmed) to another (wild) or vice versa, and the time (e.g. generations). Therefore, temporal as well as systematic environmental differences also play a major role in an individual's phenotype.

3.2 Norwegian aquaculture of Atlantic salmon

Selective breeding programs in Norwegian Atlantic salmon aquaculture began in the early 1970's with broodstock collected from 41 Norwegian rivers over a four year period, resulting in four breeding populations (GJEDREM *et al.* 1991). Initially, mating was conducted to create full- and half-sib families on a within-strain basis (as this took place at the location of each river strain), and in subsequent generations between the best performing individuals irrespective of strain. Selection was achieved initially based on growth rate (measured as body weight at slaughter), and selection against early sexual maturity was added as a breeding goal for the 1980-year class during the third round of selection. Several more quantitative traits have since been added to the breeding goal including specific disease resistance traits, fillet colour and fat (GJØEN and BENTSEN 1997). After three generations, the four populations were analysed for strain composition and it was found that one to three strains dominated each population with the Namsen River strain being most prominent (GJEDREM *et al.* 1991). This Atlantic salmon material was the basis of the breeding program of AquaGen AS.

In Norway there are also three other selective breeding programs for Atlantic salmon with a somewhat different base population and selection history. The Mowi strain was established in the late 1960s with a major contribution from the River Bolstad in the Vosso watercourse, and the River Aaroy with additional contributions from wild salmon captured in the sea near the Osterfjord and Sotra in western Norway (GLOVER *et al.* 2009). Both of these populations are characterised by large multi-sea winter fish. Individual (phenotypic) selection for increased growth was employed from the beginning until 1999 by crossing five year old males and four year old females. After 1999, a family selection program was initiated based on 250 females and 80 males characterised by DNA fingerprints with a generation time of 4 years (Reidar Våge, Marine Harvest pers. comm. as referred to in (GLOVER *et al.* 2009)).

The SalmoBreed strain was established in 2000 with Atlantic salmon of the Bolaks and Jakta strains that had been used in farming since the early 1980s and that had been selected for several generations for growth and late sexual maturation. Both Bolaks and Jakta originate mainly from the rivers Vosso in the county Hordaland, and Årøy in the county Sogn og Fjordane (Håvard Bakke, pers. comm.). Since the establishment of the family-based program in 2000, the breeding goal has included growth, specific disease resistance traits and carcass quality traits like fillet fat and colour.

The Rauma-strain was established with farmed fish from several commercial salmon farmers. In the first generations, individual selection for increased growth was applied with systematic crossing of different year-classes to keep the rate of inbreeding at an acceptable level. In 1999 a family-based program was established using DNA fingerprinting for parental assignment and with selection for growth, fillet colour and survival (www.raumagruppen.no).

Currently, the farmed fish reared in the sea today are the offspring of parents that have been through up to nine-ten generations of selection.

3.2.1 Variation within and among Norwegian aquaculture strains of Atlantic salmon

Genetic marker studies of individuals from different strains as well as measures of growth and other traits of different strains reared under the same farmed environmental conditions may indicate that the variation among individuals within strain make up a very large proportion (50-80 %) of the total genetic variation for quantitative traits among all individuals (BENTSEN 1994), thus representing a large buffer within strains against different threats.

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4 Life history characteristics of wild Atlantic salmon, with special relevance to population structure and adaptation

4.1 The evolutionary relationship of anadromy, homing and straying

Anadromy, where juvenile fish migrate out to sea to feed and grow and then migrate back to freshwater to reproduce, is believed to be a life history strategy that promotes growth through access to richer food resources and genetic diversity through population mixing (GROSS *et al.* 1988). However, a negative attribute of anadromy is that adaptation to local environmental conditions is offset by population mixing. Natal-river homing occurs in some anadromous species, including Atlantic salmon; and it has been suggested that homing is an adaptive evolutionary strategy to overcome the negative attributes of anadromy. In particular, homing facilitates local adaptation, as salmon return to environments that possess favourable spawning conditions. Nevertheless, homing also has negative consequences, as spawning is thereby restricted to the natal environment and will consequently increase inbreeding and decrease the genetic diversity of the population. Straying is believed to be an evolutionary adaptation to overcome this problem; where some individuals within a population return to a river other than their natal river to reproduce, thus ensuring some gene flow between populations and increasing the within-population genetic diversity (MCDOWALL 2001a; MCDOWALL 2001b). In addition, straying will make it possible for the species to spread to new locations whenever feasible, thus enabling re-establishment of previously extinct populations (PERRIER *et al.* 2010).

4.2 Variation in life history

Although Atlantic salmon is typically an anadromous species, there are also populations which exist entirely in freshwater environments. This is known as “loss” of diadromy and is a phenomenon common in most, if not all diadromous (anadromous, catadromous and amphidromous) fish species. Loss of the anadromous life history may occur as a result of landlocking (where geographic barriers prevent sea migration); yet there is also evidence that populations can exist in a freshwater-restricted life history even with access to the sea (MCDOWALL 2001a). It is unknown to what degree the variation in life history in salmonids is a result of plasticity or genetic adaptations. However it has been suggested that plasticity is at least partially responsible, as individuals have been reported to switch from an anadromous to a freshwater life history within a single generation and then revert back to anadromy in subsequent generations (JONSSON and JONSSON 1993; MCDOWALL 2001a). This loss of diadromy has been hypothesised to be due to non-obligate smolting; where smolting occurs as a result of a failure to meet necessary conditions for successful

maturation in freshwater (THORPE 1994). Within anadromous populations there is also a large degree of variability and plasticity of life history traits, with the time spent at sea varying between populations from the typical one sea winter (1SW) to 5SW fish (JENSEN 2004; JONSSON and JONSSON 2001; KLEMETSEN *et al.* 2003). Even within particular SW types there is variation in spawning characteristics; for instance some populations tend to migrate large distances while at sea, whereas others remain in confined bays or inlets (KLEMETSEN *et al.* 2003). Furthermore, there is evidence of non-anadromy and residence of some individuals within an otherwise anadromous spawning population (QUINN *et al.* 2001). In Norway, anadromous Atlantic salmon consist of 1SW, 2SW and multiple (MSW), with 1SW typically for populations in rivers situated along the coast and 2SW and MSW for populations in rivers found deep into fjords (JENSEN 2004).

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5 Population structuring of Atlantic salmon

In addition to knowledge regarding differences between farmed and wild populations of a species, one must also consider differentiation among the wild populations before investigating the potential effects of farmed salmon on wild salmon strains. In chapter 4 the diversity of Atlantic salmon populations in regards to their observed life history traits and their habitat requirements was discussed. To what extent these differences also portray genetic adaptation of similar magnitude is not well documented. In this chapter we will discuss aspects of population genetics which are relevant for both the determination of structure among Atlantic salmon populations; and also in assessing how they may respond to different threats, in particular those due to interactions with escaped farmed Atlantic salmon.

5.1 Evidence of population structuring in Atlantic salmon

5.1.1 Broad scale (phylogeographic) structure

Genetic studies suggest that on a broad distributional scale, wild populations of Atlantic salmon are heterogeneous (JOYCE 1998; KING *et al.* 2001; NILSSON *et al.* 2001; TONTERI *et al.* 2005; VERSPOOR *et al.* 1999). Populations of Atlantic salmon on either side of the Atlantic Ocean are so divergent they differ in karyotype (chromosome changes including chromosomal number) and separation is believed to have occurred some 600 000 years ago based on mitochondrial DNA (KING *et al.* 2007). There is also structuring on a broad scale evident among Atlantic salmon on each side of the Atlantic Ocean (KING *et al.* 2001), and in Europe several main groups of Atlantic salmon have been identified as having divergent ancestry (refer to Figure 5-1). Population heterogeneity has also been suggested on a shallower scale among European, North American and Norwegian Atlantic salmon populations (BERG 1985; KING *et al.* 2007; STÅHL 1987; SÄISÄ *et al.* 2005; VERSPOOR *et al.* 2005).

The pattern observed in Norwegian Atlantic salmon is believed to reflect historic geographic isolation in glacial refugia, with northern Norwegian and Russian populations exhibiting polymorphisms for gene variants that are otherwise monomorphic for alternate alleles in North American and other European populations; indicating a zone of current, or recent gene flow between these two continents (Figure 5.1, KING *et al.* 2007; STÅHL 1987; VERSPOOR *et al.* 2005).

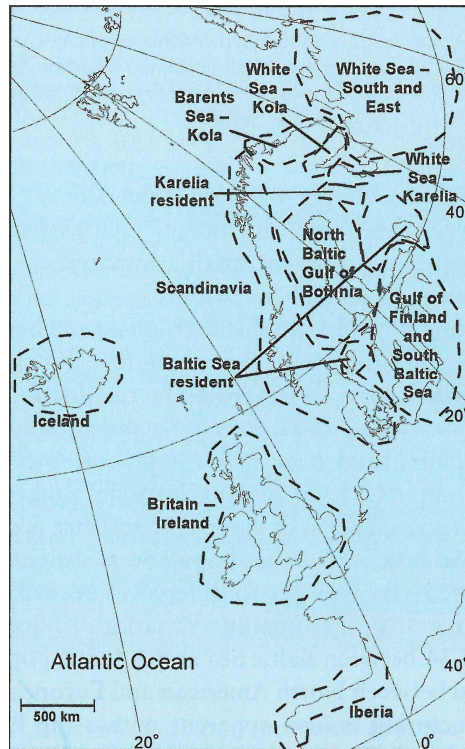


Figure 5-1: Population variation of Atlantic salmon in European regions (KING *et al.* 2007)

Studies which have assessed genetic population and phylogenetic variation in Atlantic salmon have typically used neutral or nearly-neutral markers. Neutral markers are traditionally preferred to non-neutral (coding) markers for such evolutionary questions, as any patterns of significant structuring at multiple neutral loci can be safely presumed to represent the neutral evolutionary history of the populations, rather than patterns of selection in different environments which may change from generation to generation. Independent separation of lineages may however be difficult to detect using neutral markers if isolation has occurred recently. Furthermore, no assessment of adaptive variation can be assessed using neutral markers. The use of adaptive markers for population genetic studies will be further discussed in sections 5.2, 6.4 and chapter 7 in this report.

5.1.2 Fine scale structure

Population structuring in Atlantic salmon was first suggested through studies of natal homing (STABELL 1984), but was debated vigorously at the time. The advancement of genetic studies of populations provided insight into structuring of wild populations. Wild Atlantic salmon are throughout their range typically structured into populations and/or sub-populations both within and between regions. This has been demonstrated with both protein (reviewed in VERSPOOR *et al.* 2005) and DNA studies (KING *et al.* 2001). Spatial patterns of genetic differentiation are typically stable over time, indicative of true division of populations; however exceptions have

been noted where anthropogenic disturbances such as interactions with cultured populations, and environmental degradation occur (DILLANE *et al.* 2008; GARANT *et al.* 2000; KINNISON *et al.* 2011; VERSPOOR *et al.* 2005 and references therein).

Most studies of fine-scale structure in Atlantic salmon have assessed variation between rivers or catchments and few have looked at variation within rivers or tributaries within a major river system. Given the propensity for homing in Atlantic salmon and possibilities of adaptation to local conditions, assessment of within river structure may be relevant for management directives. The few studies which have addressed this issue have found evidence of within river structuring, both in genetic and ecological traits (DIONNE *et al.* 2009; VÄHÄ *et al.* 2007).

5.2 Genetic variation and local adaptation

Natural selection works by promoting success of individuals that possess better characteristics for conditions. How successful an individual is throughout its life-history is largely dependent on its genetic composition. *Individuals* with gene variants which are better suited to particular conditions (local adaptation) will be more successful throughout life than maladapted individuals. As such, natural selection via local adaptation is a major driver of evolution. However, the environment is constantly changing and adaptation to local conditions at a particular point in time may not necessarily enable a population to persist over longer timescales. Therefore, a population which consists of individuals with many different gene variants will have a large 'catalogue' of genetic variation making that population better equipped for successful adaptation to changing environmental conditions. This works by ensuring that at least some individuals in the population will have gene variants that are favourable under the new conditions; these individuals will then pass on the favourable variants to their offspring. This 'catalogue' of genetic variation in a population can be directly measured and is referred to as genetic diversity.

5.2.1 Inter- and intra-population genetic variation in Atlantic salmon

Genetic diversity can be distributed within individuals, among individuals within a population and among populations (WEIR and COCKERHAM 1984). Typically, a large amount of genetic variation has been reported within Atlantic salmon samples (STÅHL 1987). However, the amount of within-sample variation varies widely, and will not surprisingly depend on the sample size, number of and type of gene loci tested, whether temporal samples were obtained, and also how a 'sample' is defined (e.g. as a sampling locality, an entire river, a catchment, a time point etc.). In Atlantic salmon, the amount of genetic diversity found within samples is likely to vary according to the spatial scale of the study due to the genetic

consequences of homing and propensity of salmon to stray to a nearby river (see section 4.1). Furthermore, the temporal scale of the study is important as a result of overlapping generation times. These factors underline the benefit of accurate *a priori* definitions of population boundaries before defining population-specific genetic variation; this will be discussed further in section 5.4.

5.2.2 Patterns of genetic diversity related to life history variation

There is a relatively large degree of genetic diversity found both among and within anadromous Atlantic salmon populations, concordant with genetic studies of other diadromous species. In contrast, levels of genetic diversity are typically lower within freshwater-restricted populations, and these populations tend to show a pattern of greater genetic differentiation across drainage divides (KING *et al.* 2001; STÅHL 1987; VUORINEN and BERG 1989). This is consistent with other studies comparing genetic diversity levels between freshwater-restricted and diadromous populations of the same species (GYLLENSTEN 1985; MCDOWALL 2001; WARD *et al.* 1994). These life-history related patterns of genetic diversity are likely to be due to restricted opportunities of gene flow between freshwater-restricted populations, in contrast with the greater gene flow opportunities among anadromous populations facilitated by straying behaviour. Furthermore, genetic differences between anadromous and freshwater-restricted populations of Atlantic salmon from the same river system are usually larger than the genetic differences observed between regions (VERSPoor *et al.* 2005). This also is typical of freshwater-restricted populations of normally diadromous species (MCDOWALL 2001; WATERS and WALLIS 2001).

Phenotypic differences also occur between freshwater-restricted and anadromous Atlantic salmon (KING *et al.* 2007), and although some of these may be attributed to selection and thus adaptation to different environmental variables, anadromy provides fish with opportunities for more rapid growth (hence larger size), and thus higher fecundity, through the exploitation of rich food resources (MCDOWALL 2001). These patterns of variation further reinforce the importance of knowledge regarding not only population boundaries, but also life history and phenotypic characteristics for the effective management of Atlantic salmon genetic resources.

5.2.3 Local adaptation in wild Atlantic salmon populations

While sections 5.1.1 and 5.1.2 discussed evidence of population structuring in Atlantic salmon on both broad and large scales, most of these studies assessed structuring using putatively neutral loci. As a consequence, no assessment of local adaptation can be made using such markers. It is important to determine the extent to which local adaptation exists in populations, as this can be used to make assessments on how natural selection works in

particular populations, a crucial question when assessing how a population will respond to threats (GARCIA DE LEANIZ *et al.* 2007; PRIMMER 2009). Local adaptation may include heritable variation in phenotypes, molecular variation in genes that are affected by selection, and variation in the interactions of genotypes and the environment to produce phenotypes of varying plasticity (GARCIA DE LEANIZ *et al.* 2007). Recently, advances in genomic technology have made it cheaper and quicker to identify gene loci or chromosome regions which show evidence of selection. In addition to allowing an assessment of the effect of natural selection in pristine environments, this also enables one to identify selection occurring in response to certain environmental or anthropogenic threats. The existence of local adaptation in salmonid populations as a result of homing has been debated in the literature (PRIMMER 2011). Other indirect evidence of local adaptation in salmonids has been suggested due to the comparative performance of translocated stocks (KINNISON *et al.* 2011; MCGINNITY *et al.* 2003; SAURA *et al.* 2006), and variation in phenotypic traits in aquaculture strains. Recently, genomic tools have confirmed that local adaptation does in fact exist in wild Atlantic salmon populations (BOURRET *et al.* 2011; MEIER *et al.* 2011). FRASER *et al.* (2011), in a meta-study review, found a significant relationship for local stock to out-compete and have greater survival than foreign stock, and from this estimated that local populations have approximately a 20% greater average fitness advantage over foreign stock. Furthermore, they found that local adaptation can occur rapidly (6-30 generations) and is evident on both fine and broad spatial scales, not surprisingly being stronger with increasing distance. The pattern of stronger adaptation in comparisons with populations of greater geographic separation is also confirmed by MEIER *et al.* (2011) for brown trout (*Salmo trutta*). Evidence of local adaptation in wild Norwegian populations of Atlantic salmon is largely indirect.

5.3 Genetic diversity, genetic drift and population size

Genetic diversity is a cornerstone of population and conservation genetics as it enables an assessment of the 'robustness' of a population and is directly related to the effective size of a population. Effective population size (N_e) is a term that was coined by Sewell Wright (1931) and refers to an ideal (imaginary) population that is affected by genetic drift at the same rate of the population under study. This enables one to quantify genetic drift, the other major contributor to evolution. This is a fundamental principle in conservation genetics as small populations are more vulnerable to loss of genetic variation due to genetic drift than due to selection (FRANKHAM *et al.* 2003). Different gene variants only arise in a population via mutations or via gene flow; therefore small, isolated populations are expected to have limited capabilities for adaptive responses to environmental disturbances as mutational recovery of lost variation is a slow process, even for polygenic traits (LANDE and SHANNON 1996; LYNCH and LANDE 1998; WILLI *et al.* 2006).

5.3.1 Effective population size and gene flow in metapopulations

Most salmon populations are not completely isolated from each other, as straying facilitates some gene flow among populations. Straying has been shown to occur more commonly among adjacent rivers (JONSSON and JONSSON 2001); thus it is expected that salmon populations are structured into metapopulations (SCHTICKZELLE and QUINN 2007); where nearby populations share more migrants among each other than they do with distant populations. The definition of a metapopulation is a network of populations which are somewhat connected by gene flow but that they also have a somewhat independent demography with frequent extinction and recolonisation. Migration (e.g. due to straying) is one cause of gene flow between sub-populations within a metapopulation, and for this reason these terms are often used inter-changeably. However it is important to note that migration does not always result in gene flow. Species which are structured into metapopulations rather than closed populations make estimations of N_e difficult, and thus special consideration of both temporal and spatial scales is necessary (HARE *et al.* 2011; HARRISON and HASTINGS 1996).

In completely isolated populations, N_e will be much smaller than the N_e in a metapopulation and each isolated population will contain a small fraction of the total genetic diversity (HARE *et al.* 2011). Whereas in a metapopulation system, little gene flow is needed to ensure that populations share most of the genetic diversity within the metapopulation (e.g. Wright's island model of metapopulation structure states that only one migrant per generation is needed for this to occur). Demographic information (e.g. number of contributing parents and mating systems) and genetic data can be used to infer N_e , but it is especially worth noting that N_e can never be 'known' and at best can only be estimated. In Atlantic salmon, demographic information makes estimates of N_e difficult due to overlapping generation times and variability in spawning times; therefore genetic estimates are commonly used.

There are many ways in which N_e can be estimated using genetic data, and these methods vary according to temporal and spatial scales. Common methods include long-term coalescent estimations, contemporary single time point estimations and contemporary temporal methods (reviewed in HARE *et al.* 2011). Although flexibility in the choice of method is advantageous, the challenge with flexible methods for N_e estimation is that appropriate sampling strategies must also be considered. Contemporary N_e methods allow estimations of N_e strictly over the timescale that the samples were collected; whereas coalescent modelling methods allow one to estimate N_e among populations over many *prior* generations until the most recent common ancestor. Estimations at temporary time scales represent a harmonic mean of N_e over time, and thus may not show detailed fluctuations of N_e . Furthermore, long

term estimates of N_e in particular can be misleading if they fail to account for metapopulation structure, as localized sampling methods assume complete or near complete population isolation and estimates will thereby underestimate the long-term global N_e of the metapopulation. In short, any estimation of N_e should be interpreted in the context of the spatial and temporal boundaries in which the genetic information was obtained (refer to HARE *et al.* 2011 for a review on this topic). Given the complex life history components of Atlantic salmon (refer to sections 4.1 and 5.2.2), it is particularly necessary to pay special attention to sampling methods and choice of appropriate N_e estimation method.

5.3.2 The effect of migration on estimates of effective population size

Many methods for estimating N_e are based on models which make the assumption of no migration. For most populations, especially aquatic species (and Atlantic salmon in particular), this assumption is incorrect and can substantially bias estimates of N_e . For example, it has been shown that when compared to a population which is only influenced by genetic drift, a population which is affected by both migration and genetic drift results in allele frequency changes that are greater in the short term and smaller in the long term, leading to under- and overestimations of N_e , respectively if migration is ignored (WANG and WHITLOCK 2003). For this reason, methods have been developed by which the joint estimation of N_e and migration rate can be made over both spatial and temporal scales (e.g: BEERLI and FELSENSTEIN 1999; BEERLI and FELSENSTEIN 2001; WANG and WHITLOCK 2003). Furthermore, the direction of migration in a metapopulation system is also critical in estimating metapopulation and subpopulation N_e (TUFTO and HINDAR 2003).

5.3.3 Gene flow among Atlantic salmon populations

Given the key evolutionary roles that homing and straying play in the biodiversity of Atlantic salmon populations, it seems plausible that there is an optimum rate of migration that maintains sufficient genetic diversity within a population without causing a detrimental loss in local adaptation. It is therefore not surprising that straying of salmon to rivers near their natal river occurs more often than straying to rivers further away, due to stronger 'imprinting' of the natal environment than the subsequent environment the salmon inhabits by the use of olfactory senses (DITTMAN and QUINN 1996). In support of this theory, it has been shown that salmon which return to freshwater after one year at sea show less straying rates than salmon which spend two years at sea (JONSSON and JONSSON 2001). Furthermore, changes to the natal environment while the salmon are at sea have been suggested to result in increased straying, due to the fish's imprint of its natal environment no longer matching the signatures of its natal environment (e.g. LEIDER 1989; WHITMAN *et al.* 1982). Many studies, such as these mentioned above, estimate straying rates using mark-recapture studies; however it is important to consider not the occurrence of straying, but the reproductive success of the

migrant individuals, as this is the only measure of the genetic contribution of straying behaviour.

Estimation of the effective number of migrants ($N_e m$) into a population is therefore a way in which one can attempt to quantify the amount of gene flow into a population. This is especially relevant in metapopulation studies, where one is interested in further understanding the dynamics of migration between connected subpopulations. Estimates of $N_e m$ are also fraught with difficulties, for many of the same reasons given above regarding N_e estimation. Due to the difficulty in obtaining estimates of gene flow, indirect methods are often used which rely upon allele frequency data (e.g: SLATKIN 1985; SLATKIN 1987). The most common of these methods to estimate the $N_e m$ includes an interpretation of Wright's island model of population differentiation; where a simple relationship is suggested between a population's differentiation from neighbouring populations (F_{ST}) and the number of migrants it receives (N_m). However using this model for estimates of $N_e m$ in metapopulation systems violates many assumptions of the model, including (most relevantly) the assumptions of no migration, no selection and equal population sizes. As such, indirect measures of N_m are imprecise and may provide significantly biased estimates of gene flow in population systems where gene flow is not negligible (see WHITLOCK and MCCAULEY 1999 for a review of applications of indirect measures of gene flow).

In metapopulation studies of Atlantic salmon, it is often assumed that gene flow via migration follows a source-sink model of connectivity. That is, that gene flow occurs mainly from larger rivers (the source) to smaller tributaries (the sinks). However metapopulations are not limited to source-sink models of structure and alternatives to the source-sink model are often overlooked in population genetic studies of Atlantic salmon. It is important in studies of this species that aspects of the life history are incorporated into population models, as the direction of gene flow will also be influenced by the degree of selection acting in the subpopulations, (e.g. by local adaptation due to homing behaviour.) Furthermore, the effect of selection will vary according to the spatial scale and the size of the population. Indeed, a study by (PALSTRA *et al.* 2007) rejected the hypothesis of a source-sink model of population structure in Canadian Atlantic salmon and concluded that the direction of migration is dependent on the temporal scale in which gene flow is assessed. Furthermore, they found that the direction of the magnitude of gene flow differed between different regions and was compatible with demographic and life history characteristics of the different populations.

The rate of straying between populations of Atlantic salmon has been estimated at approximately 4% (STABELL 1984). The effective number of migrants between populations

each generation was inferred to be between two and 12 (HINDAR *et al.* 2004). However this estimate is flawed in that firstly, it is based on an indirect calculation using F_{ST} estimates from STÅHL (1987) and BOURKE *et al.* (1997) (refer to section 5.3.1). And secondly, this estimate was not given in terms of the spatial and temporal scales of the studies (which were variable).

5.4 Landscape genetics – incorporating ecological, geographic and genetic data for a holistic approach to population genetics

Knowledge of the role that habitat and life history plays in shaping genetic connectivity and divergence among Atlantic salmon populations is essential for understanding their patterns of diversity, migration and population size (PALSTRA *et al.* 2007; VÄHÄ *et al.* 2007). Previous sections in this chapter have highlighted the need for appropriate sampling strategies for Atlantic salmon genetic studies. In particular, information regarding life history and habitat use is useful for effectively defining populations for sampling. Despite this, very few studies on this species have incorporated such information, instead relying upon clustering populations by either sampling locality or by the use of model-based genetic clustering methods (e.g: PRITCHARD *et al.* 2000). Defining genetic populations based on sampling locality may not be effective where no physical barriers to migration occur, and such methods may over or underestimate levels of genetic diversity and hence estimates of population size and gene flow among populations. Model-based genetic clustering has been shown to correctly delineate populations even where low levels of genetic differentiation exists (eg Latch *et al.* 2006), however these models may be very case-dependent (WAPLES and GAGGIOTTI 2006) and should be treated with caution in real-world populations.

Landscape genetics refers to the combined use of geographic and ecological data with genetic surveys to enhance studies of population demography (STORFER *et al.* 2010). These methods use life history and habitat-use models to estimate population boundaries and aid sampling strategies, and this information can be compared with genetic data to confirm population boundaries. To-date there have been no published studies using landscape genetics in Atlantic salmon in Norway, however such studies have been conducted elsewhere (e.g: DILLANE *et al.* 2008; DIONNE *et al.* 2008; VÄHÄ *et al.* 2007).

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6 Interactions between aquaculture and wild populations of Atlantic salmon

6.1 Escape events

Atlantic salmon are known to escape from aquaculture cages into the natural environment, largely due to technical and operational errors of aquaculture farming. From 2001 – March 2011, approximately 4.41 million salmon escaped from aquaculture facilities in Norway (Figure 6-1, Norwegian Directorate of Fisheries). It is important to know the number of escapes because this will affect the impact they have on wild populations. This relies on accurate reporting of escape events as this is more efficient than estimates based on catch statistics. However, in an experiment with simulated escapees from three farms it was found that salmon that were released in the autumn had a lower catch percentage than those released in the spring (HANSEN 2006). For non-tagged escapees, catch information is difficult to obtain because of the need to adequately distinguish farmed from wild strains. This is often done using scale morphology, snout and fin condition and measurements of synthetic astaxanthin have also been used (SÆGROV *et al.* 1997). Otolith microchemistry can also be utilised to differentiate fish in the wild that have origins in aquaculture areas (GAO and BEAN 2008).

There are several problems in using these measures of farmed strain identification in the natural environment. Firstly, all of these methods rely upon catch data. However, catch data may be biased in that fish of certain phenotype and/or behaviour may be more likely to be caught than others. Secondly, morphological identification has been argued as an imprecise method of identification (FERGUSON *et al.* 2007). Otolith identification requires the culling of the catch and with the numbers required to estimate catch percentage this may be a costly method, both in terms of time, money and cost to the sustainability of the local population. Thirdly, and perhaps most importantly, none of these methods provide any measure of the reproductive success of escaped farmed salmon in the natural environment. Considering that local adaptation is likely to give an advantage of the local population over maladapted migrants, it is important that a measure of the number of offspring from farmed salmon and their crosses and descendants can be obtained.

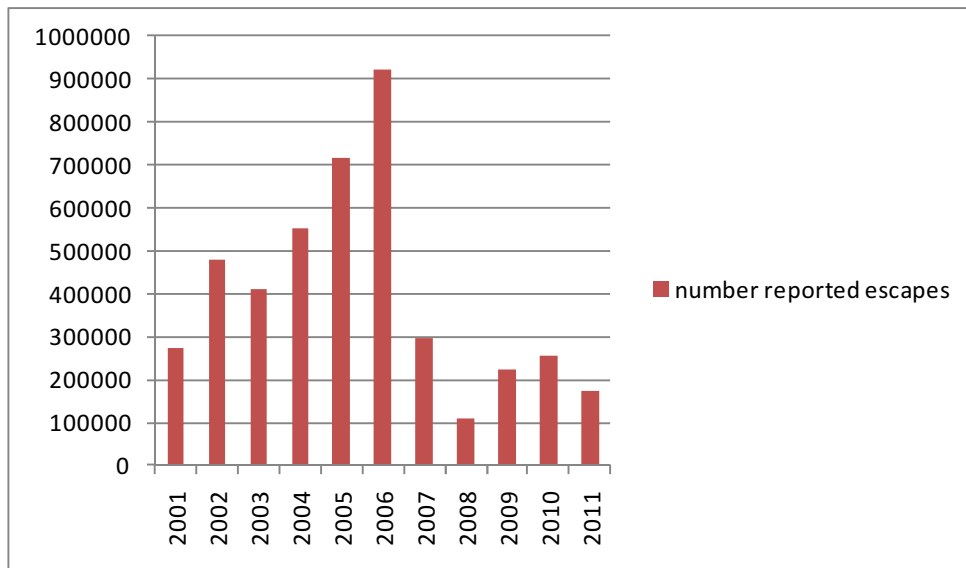


Figure 6-1: Number of reported escapes of Atlantic salmon from aquaculture facilities in Norway from 2001-March 1 2011.

6.2 What do we mean by genetic interactions?

It is not just interbreeding that can result in changes to a population's genetic make-up as a result of genetic interactions with escaped aquaculture individuals. Competition for resources without interbreeding can also result in genetic changes. Also diseases and parasites that the farmed fish introduce may affect the wild population by selecting individuals which have better fitness or resistance to the pathogen (COUGHLAN *et al.* 2006). But of course interbreeding also needs to be considered, what effect interbreeding may have is largely reliant on how different the two stocks are and other aspects of their genetics. In particular, life history traits relevant for successful reproduction, survival and growth of offspring will play a major role in the lifetime success of an immigrant. Such life history traits have been suggested to have a genetic component in salmonids, as homing promotes the successful reproduction of individuals with locally adapted gene variants (see section 4.1).

Hybridisation of two divergent taxa may have a variety of effects on the fitness of the offspring. Heterosis or hybrid vigour refers to the improved performance of hybrid offspring in relation to their pure strain parents. However, the hybrid vigour in fitness will decrease (by 50%) if hybrid animals are interbred. Outbreeding depression however refers to the reduced performance of hybrid progeny in comparison with their pure-strain parents (within the same environment). There are two main causes of outbreeding depression: loss of local adaptation (environmental component) (refer to section 5.2), and breakdown of co-adapted gene complexes (or epistasis breakdown) (physiological component) (TEMPLETON *et al.* 1986).

6.3 How different are Norwegian farmed salmon and Norwegian wild salmon populations?

A requisite for assessing impacts on wild populations from farmed populations is knowledge of to what degree the respective populations differ. On the one hand, a high level of genetic divergence between farmed and wild stock can be expected to eventually result in reproductive isolation due to selective fitness in differing environments (e.g. offspring of farmed salmon may eventually have no survival in a natural environment). However, many generations of selection for different environments is required for such reproductive differences to accumulate; and in Norwegian Atlantic salmon, separation has only existed for a maximum of nine generations.

6.3.1 Phenotypic differences as a result of artificial selection

Published documentation on genetic changes for traits selected for in Atlantic salmon breeding programs are few. Offspring of salmon selected for increased growth in five generations grew better in the freshwater phase and were significantly heavier at slaughter than offspring of wild salmon from the river Namsen, corresponding to an average realized genetic gain of 15 % per generation (GJERDE *et al.* 1999) and similar to the expected genetic gain of 13 % per generations calculated based on realized selection differentials (GJERDE and KORSVOLL 1999). In a comparison of two year-classes of farmed salmon selected for seven-eight generations of selection (mainly for increased growth and delayed sexual maturity), and wild salmon and their crosses under farming conditions, it was found that the farmed fish at slaughter were twice the size of wild salmon, whilst the hybrids were intermediate. While for the quality traits, studied differences were observed between the three experimental groups (GLOVER *et al.* 2009). For the trait early sexual maturity (grilse), the latter mentioned study documented a 3.1 %-unit expected reduction per generation in the proportion of early sexual maturing fish over four generations of selection. For feed efficiency, an accumulated genetic gain of 25 % over five generations of selection has been documented, most likely as a correlated response of the selection performed for increased growth over the same period of time (THODESEN *et al.* 1999). For specific disease resistance, a substantial response to one generation of selection for increased survival to IPNV in challenge test has been documented (STORSET *et al.* 2007). For carcass quality traits like fillet fat content and fillet colour, no published documentation of realized responses is available.

6.3.2 Genetic differences as a result of artificial selection

Given that Norwegian Atlantic salmon aquaculture is based on genetic stock from Norwegian rivers, it can be expected that Norwegian farmed Atlantic salmon have no alleles that are

unique to the farmed stock when compared with wild (Norwegian) populations. Rather, the allele *frequencies* are different as a result of artificial selection for quantitative traits over nine generations. In support of this, it has been shown that genetic differences, on a genomic scale, between Norwegian farmed and wild populations are the result of small allele frequency changes at a large number of loci, rather than large allele changes at few loci (KARLSSON *et al.* 2011). This corresponds with the expectation that most quantitative traits involved in selective breeding are polygenic (see section 3.1) and thus that a large response to artificial selection for a particular trait will involve many minor changes at multiple loci across the genome, and will thus not result in a loss of genetic variability or fixation of alleles (BENTSEN 1994) However, initiation of captive breeding programs instigates a genetic bottleneck in the breeding population and alleles may therefore be lost from the captive population more quickly than they would in the wild populations due to the greater effect of genetic drift in small populations (see chapter 5 in this review). In this scenario farmed populations are likely to have lost some alleles which are rare in the wild populations as a result of sampling effects.

6.4 How to measure the genetic impact of interactions

The genetic impact of escapees is expected to be highly variable depending on the adaptive genomic divergence of farmed and local fish, the level of interbreeding between them and the fitness of their offspring. For this reason it is not possible for a generic definition of impact to be reported for all populations based on data from only a few populations; rather impact must be addressed separately for each separate population or metapopulation system (refer to section 5.4).

The Norwegian wild salmon commission (Villaksutvalget) wrote in a report¹ that the increased and sustained immigration from a common donor to many recipients is expected to make the recipients more and more like the donor, and will reduce the differences that existed between the recipients before the new immigration regime. This generalised statement neglects important criteria for such an affect to occur. The lifetime success of an immigrant donor requires that donor to have selective fitness to survive in the new (recipient) environment. Furthermore, the recipient population must also have poorer fitness and poor adaptive variation for the effects of the donor to increase and to be sustained over many generations. In Norway, farmed Atlantic salmon have undergone artificial selection for up to nine generations for fitness traits in the farmed environment. Therefore as a donor, escaped

¹ Villaksutvalget 1999 pg. 81 and 243

<http://www.regjeringen.no/Rpub/NOU/19991999/009/PDFA/NOU19991999009000DDDPDFA.pdf>

farmed salmon are likely to have poorer fitness for the natural (recipient's) environment, and subsequent offspring would become more and more like the recipient as a result of local adaptation to local conditions rather than the converse. However, if the recipient population does have poorer fitness than the donor immigrants, and does not have sufficient adaptive variation to allow the population to respond to the threat of farmed salmon, sustained immigration may result in changes to the recipient population.

When assessing potential gene flow from escaped aquaculture species to their wild conspecifics, phenotypic and/or genetic differences between them must exist. Attempts have been made to estimate gene flow in wild populations that have been known to receive farmed immigrants based on reported escape events. However a limiting factor in this method is that a presumption of a particular fish being an aquaculture escapee is made based on morphology and the timing of fish ascending the river where the escape event occurred (e.g: CLIFFORD *et al.* 1998; CROZIER 1993). Sampling errors are likely unless genetic markers for differentiation can be confirmed in the aquaculture and wild environments and then subsequently used to assign individuals caught in the river to population of origin (i.e. local wild population or aquaculture escapee).

Other studies assessing changes in wild Atlantic salmon populations as a result of interactions with aquaculture escapees have assessed temporal changes in allele frequencies in the wild populations that are known to have received escaped Atlantic salmon. This method however does not enable an assessment of how natural selection responds to the interactions (e.g. local adaptation is likely to select against maladapted migrants). Temporal change in allele frequencies can be due to selection occurring in a population, however neutral alleles may shift also as a result of genetic drift which is more pronounced in smaller populations (refer to section 5.3).

Although neutral markers are very useful for describing population structure, they are of little use for studying important phenotypic traits and local adaptation. Most polymorphisms are neutral or nearly neutral, (due to a faster rate of mutation in non-coding genes) and until recently a limited number of available markers in Atlantic salmon have been found and acknowledged as non-neutral. In recent years, with the application of genomic technology, it is now possible to distinguish neutral loci from those which show signatures of selection and several studies have identified molecular markers which display evidence of being subject to directional selection in Atlantic salmon (BOURRET *et al.* 2011; KARLSSON *et al.* 2011). These findings suggest that there is potential for identifying genetic markers that can not only be applied to a neutral evolutionary framework, but can also be used for describing local adaptation and potential phenotypic changes due to natural and artificial selection.

6.4.1 Review of empirical studies of genetic interactions between farmed and wild Atlantic salmon

SKAALA *et al.* (2006) – In this study the authors assessed the temporal variation of seven Atlantic salmon rivers in Norway (totalling 17 temporal samples) at eight microsatellite loci (totalling 106 alleles). Assuming non-linkage of the microsatellite loci, this sampling strategy is considered adequate to assess the temporal stability of the populations (at these loci). The authors detected temporal allele frequency changes in three populations (Opo, Vosso and Eio Rivers) known to have received large numbers of escaped farmed salmon. However, in other similarly affected rivers no temporal changes were detected. This study also detected linkage disequilibria in one of the three populations (the Opo R.). Temporal changes in allele frequency and linkage disequilibrium may be due to genetic drift, selection, the mixed sampling of multiple non-interbreeding populations or interbreeding between divergent populations. A sharp decline in census size of the three populations where temporal changes were detected was expected to correspond in low levels of genetic diversity. Yet the converse was found to be true, with stable levels of diversity and heterozygosity. The authors conclude that given the observed temporal shift in allele frequencies, linkage disequilibria, and maintenance of genetic diversity levels, these three populations have probably experienced interbreeding with escaped farmed salmon.

While this is indeed possible, it is important to note that neutral loci do not allow one to distinguish the effects of genetic drift from those of selection or interbreeding as is essential for detecting farmed and wild genetic interactions. Furthermore, the stable levels of genetic diversity found at neutral loci in this study may be due to the fact that insufficient generations have passed for the effect of genetic drift to be evident. It is also important to consider the varying patterns of temporal changes observed in the populations in this study; although six of the seven populations were known to have received large numbers of farmed escapees, potential genetic effects were only identified in three populations. This outlines the fact that the effect of interactions of farmed and wild salmon is dependent on the demographics of the recipient population.

FLEMING *et al.* (2000) – The Imsa experiment. This study is the only experimental study in Norway to-date which has looked at the comparative lifetime success of farmed Atlantic salmon invading the natural environment. The study noted that reproductive success of the farmed salmon was limited, especially in males, with farmed fish achieving less than one third of the breeding success of the wild fish. Selection was apparent against farmed genotypes at early life stages and resource competition was evident with farmed fish more competitive than wild fish. Ultimate lifetime success of the farmed Atlantic salmon (adult-adult) was measured to be 16%. The reduced success is mainly due to a much lower

spawning success of farmed salmon than wild salmon (FLEMING *et al.* 2000). Assuming 17% of farmed salmon on the spawning grounds (FISKE *et al.* 2001), this would give a total amount of gene flow from farmed salmon to wild salmon through F1-hybrids of 2.7%.

MCGINNITY *et al.* (2003) – The Burrishoole experiment. This study involved a two-generation experiment to examine the life-time success of farmed fish relative to wild fish and of hybrids between the two (including F1, F2 and backcrosses). The study was undertaken in the Burrishoole system in Ireland which is inhabited by 1SW wild salmon. For farmed salmon, 2SW individuals from the Norwegian Mowi strain were used. Similar to the Imsa study, farmed salmon had faster rates of growth at the juvenile stage than wild salmon. The relative gene flow of hybrid salmon was found to be higher than for pure farmed salmon, 35% for F1 hybrids, 31% of the crossings between the F1 hybrids and farmed salmon and 89% for the crossings between the F1 hybrids and wild salmon. These results indicate significant selection for the wild salmon.

Norwegian data on relative survival at the sea period for F1 hybrids of farmed and wild Atlantic salmon are largely unknown due to insufficient data. By combining the Norwegian data for the spawning stock and spawning success (FLEMING *et al.* 2000) and Irish data for survival in fresh water and sea (MCGINNITY *et al.* 2003), the gene flow per generation from farmed salmon to wild salmon through F1 - hybrids $0.17 \times 0.40 \times 0.35 = 2.4\%$.

6.4.2 Review of theoretical studies to predict the effect of genetic interactions between farmed and wild Atlantic salmon

- TUFTO (2001): Effect of releasing maladapted individuals: A demographic-evolutionary model.

In this paper Tufto models a wild population under stabilizing selection, assuming that there is genetic variation in the population. Variation is a fitness cost, as it leads to production of new suboptimally adapted individuals every generation (even in a wild population). Varying numbers of maladapted (e.g. farmed) individuals are also migrating into this population, causing reduced average fitness. Natural selection is, however, counteracting the unfavourable effect of immigration. Provided that the differentiation among the local and immigration populations is sufficiently large (more than 2.83 genetic standard deviations), it is found that the population size will stabilize at a lower level compared with the initial population, but the population is not going extinct (as natural selection eventually will balance effect of immigration). If there are smaller differences between the populations, the population size may actually increase as a result of immigration.

The assumptions of this study seems relatively sound, however some simplifications are made. Tufto assumes that immigration affects the population mean. However, the study does not take into account that this effect is very unevenly distributed in the population (as immigrant animals will only affect their own offspring). In other words, the "poor fitness genes" will (at least initially) be accumulated in a smaller fraction of the population (offspring of immigrants) rather than being evenly distributed. Hence, the genetic variation among animals in a mixed population may be much larger than the standard additive genetic variance in a pure population (as a result of mixing population of genetic different means). For this reason we believe that natural selection during the first generations after immigration will be more efficient than assumed in this study.

- TUFTO (2000): Quantitative genetic models for the balance between migration and stabilizing selection.

In this paper Tufto compares a more realistic model with a more simplified one (e.g. the model discussed above). In the more realistic assumptions, genetic variance increases as a result of migration and the genotypic values will no longer be normally distributed in a mixed population. However, it is concluded that for weak selection or large genetic variance, the simplified model closely matches the exact results, while for strong selection, these approximations gradually break down.

Evidence suggests that selection in salmon juveniles is indeed strong, especially when comparing survival of farmed relative to survival of wild salmon. Hence, as discussed above, natural selection may be even more effective than assumed by TUFTO (2001).

- HINDAR *et al.* (2006): Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results.

This is a widely cited publication (42 citations according to Google scholar in February 2011) presenting a model to predict the effects of escaped farmed salmon interbreeding with wild salmon stocks. Very few of the citations are critically reviewing the assumptions of the model.

The model is aiming at predicting genetic effects in a wild stock caused by repeated interbreeding with escaped farmed salmon over a series of generations. The main output of the model is given as the proportion of hybrids and of feral farmed fish in the wild stock in each generation. Results from the model have been used to provide predictions and

guidelines for the salmon management authorities. However, there are several problems with the basic assumptions of the model that should be taken into account when considering the results that are presented.

1) The model seems to assume that salmon populations are genetically distinct from each other, while the individuals within each population are genetically more uniform. This is the opposite of what has been empirically shown for wild as well as farmed stocks. Populations are genetically overlapping, and most of the genetic variation (often more than 90%) occurs as genetic differences between individuals within the populations (BENTSEN 1994; several marker studies). Furthermore, the inheritance in hybrids seems to be considered as fixed, stable and uniform proportions of the pure-bred ancestors' gene pools. This does of course not make sense, given that the general knowledge about random segregation and recombination of genes during inheritance applies to this case. Applying the assumptions of the model to Norwegian farmed salmon populations would lead to the conclusion that all farmed salmon are wild stock hybrids, since all their ancestors came from wild stocks less than 10 generations ago. The problem with the model is that it does not account adequately for the effects of natural selection.

2) The model does not really account properly for more than two generations of interbreeding. Second generation hybrids (F2 hybrids and backcrosses) are removed from the computations before generating the next generation and are replaced with F1 hybrids or purebreds at a rate corresponding to the genetic origin of their grandparents. This seems to be based on the false assumption that all second generation hybrids inherit equal proportions of their grandparents' genes. However, the genetic contributions from the grandparents are variable because of the random segregation and recombination during gamete formation in the parent generation. Because of the intense natural selection, successful second (and later) generation hybrids are expected to be those that have inherited low proportions of their genes from farmed ancestors. Consequently, the model is biased and will overestimate the impact of interbreeding.

3) The model assumes that the inheritance from farmed escapees is stable over generations and distinct from the wild local stock. However, it is well documented that the farmed stocks are derived entirely from Norwegian wild stocks less than 10 generations ago (GJEDREM *et al.* 1991), and consequently that their allele repertoires are entirely overlapping (with the exception that some rare alleles may be lost in some farmed populations). It is also shown that farmed and wild stocks differ by small changes in allele frequencies across a large number of genes (KARLSSON *et al.* 2011), as expected after divergent selection for a range of

polygenic traits. Progeny of farmed escapees will be subjected to intense reverse selection by the natural mortality in the wild stock environment. After some generations of natural selection, it makes no sense to classify the inheritance from farmed ancestors together with that of first generation hybrids, as done in the model. On the contrary, such individuals are expected to be increasingly similar to wild stock individuals (both regarding their allelic and fitness constitution) as generations pass.

To conclude, the model does not predict genetic effects of interbreeding beyond second generation hybrids. In later generations, the output of the model is a simplified and biased prediction of ancestry proportions and their effect if they had occurred in first or second generation hybrids (i.e. in the absence of natural selection).

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7 Conservation genetics and management of populations

Atlantic salmon are species of great importance to fisheries. They occupy complexes of connected habitats between or through which passage is needed at two or more life history phases. They therefore pose special problems for conservation which relate to: a. diversity of habitats; b. huge areas occupied; c. the spatial separation of the various habitats used; d. need for fish passage; e. often heavy exploitation.

The preferred unit for management purposes has traditionally been at the level of local populations. However, populations of Atlantic salmon are numerous and many are too small to maintain genetic diversity and avoid rapid increase of inbreeding if they are managed as separate units. The combination of populations into management units that comprise interchangeable, nested groupings of populations (i.e. metapopulations) that are important in terms of their life history, ecology and genetics is therefore a way in which management of salmonids can be better achieved. Maintenance of robust populations of wild fish is paramount for minimising effects of interactions with escaped aquaculture strains. However this is not limited to threats from genetic interactions with wild species and applies also to other environmental and anthropogenic effects including climate change, disease, damming and river acidification. By this, we mean that maintenance of the adaptive potential of populations should be prioritised, as populations with a large catalogue of genetic variation will ensure that the population can persist via adaptation even with the effects of natural selection (refer to section 5.2) (YOUNGSON *et al.* 2003).

7.1 Supportive breeding

In some populations which are too small to be viable, supportive breeding is considered an approach to increase the genetic variation within the population. For a population to remain viable over long time scales, it is important to maintain the capacity of the population's ability to evolve, rather than to preserve their current or their previous genetic condition. Therefore, where a population is threatened and where supplementation of the population is being considered, it is important to supplement by restoring variation in such a way that the population will continue to evolve, rather than to simply provide a greater census size (YOUNGSON *et al.* 2003). Local adaptation and co-adapted gene complexes play a pivotal role in a population's future viability. The extent of shared local adaptation between river stocks will depend on the evolutionary time frame since population fragmentation and the selective pressures at play. The choice of broodstock for supplementation programs will

therefore depend on the connectivity between the populations and the extent of adaptation between the source and recipient populations.

Hatchery stocking of salmonids has been used to supplement and re-establish natural populations throughout their range with mixed success. In some cases, supportive breeding has resulted in increased viability of the stocked population, evidently through supplementing beneficial adaptive variation. However other cases have reported no long-term benefit, sometimes despite an increase in the stock's neutral genetic diversity. In successful cases (e.g: SAURA *et al.* 2006; SPIDLE *et al.* 2004), the use of broodstock originating from nearby rivers has likely provided adaptive variation relevant for survival in the recipient river, as adaptive variation shared between populations has been shown to be correlated with geographic separation (FRASER *et al.* 2011; MEIER *et al.* 2011), and this appears to have promoted the adaptive viability of the restored population. Whereas in unsuccessful scenarios, (e.g: CIBOROWSKI *et al.* 2007), the use of broodstock from distant divergent populations, although promoting short-term increases in neutral genetic variation, has not increased the long-term viability of the restored population, likely due to the fact that adaptive variants in the source stock are less relevant for the new environment.

7.1.1 Can gene flow from farmed populations to wild populations be beneficial in supplementing genetic diversity?

Although the total genetic variation between farmed and wild stocks currently represents small allele frequency differences at a large number of loci, rather than many fixed differences (KARLSSON *et al.* 2011), this does not equate to panmixia and stock separation is evident both on genetic and phenotypic levels. Due to the mixed strain origin of Norwegian Atlantic salmon, the input of farmed variation into the natural gene pool may promote interbreeding between adjacent wild populations, and may consequently act to break down locally adapted genetic variation (refer to section 6.2), (BOURRET *et al.* 2011). In this regard, if supplementation is desired, it is considered to be more beneficial to supplement wild populations with genes from local or neighbouring wild populations through hatchery cultivation. Knowledge of metapopulation structuring can be used to identify suitable populations or sub-populations that can contribute to the enhancement of genetic variation of depleted stocks (YOUNGSON *et al.* 2003).

7.2 References from chapter 7

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8 Gaps in knowledge of interactions between Norwegian wild and farmed Atlantic salmon

Although much is known about the basic biology and broad distribution of Atlantic salmon, little is known about the extent of population division on finer geographic scales. In particular, extensive population surveys are needed for Norwegian Atlantic salmon to determine population boundaries and the degree of connectivity among and within metapopulations. Such surveys should also estimate the effective size of populations and metapopulations as this will enable improved knowledge-based decisions related to management and conservation of wild populations.

Aspects of the life history, ecology and habitat use vary among populations of Atlantic salmon in Norway, yet such information has not been included in genetic surveys of populations to-date. This information may be crucial in understanding the dynamics of wild salmon populations in Norway and needs to be addressed.

Knowledge of the extent to which Norwegian populations are locally adapted is largely circumstantial. Local adaptation and adaptive variation are key issues for long-term viability of populations, and specifically relate to the way in which populations will adapt to threats such as farmed salmon and environmental changes. Genetic surveys of population demographics therefore need to also address the degree of local adaptation in populations.

9 Appendix

Responses and references to specific questions regarding farmed and wild interactions put forward by Jan Arve Gjøvik (pers. comm.)

1 *Is the gene flow so great that wild salmon, over time, will be dominated by gene variants originating in farmed salmon?*

Gene variants in Norwegian farmed Atlantic salmon have originated from Norwegian wild populations, therefore they are not different. Insufficient generations have passed for new genetic mutations to arise in the farmed populations in any great frequency (if at all) (refer to sections 3.2 and 6.3). Differences in gene variants therefore relates to frequencies of these rather than the variants themselves. This question cannot be answered in general for all populations of wild salmon, each population or metapopulation will respond differently to threats depending on its demographics - particularly its effective population size and degree of local adaptation (refer to sections 5.2 and 5.3). Farmed Atlantic salmon have selective fitness for the farmed environment, not the wild environment; therefore it is likely that natural selection will favour the local wild population. However where gene flow is great (relative to the size of the wild population) and the recipient wild population has poor local adaptation and poor adaptive genetic variation, it is possible that changes in the genetic makeup of the population will occur due to genetic interactions with the escaped salmon (refer to chapter 6).

2 *If the progeny of escaped farmed salmon have much poorer survival through all stages in the life cycle, will natural selection not ensure that hybrids are selected back to the indigenous stock relatively quickly?*

In general the recipient wild population has better fitness (local adaptation) at all stages of the life history compared with offspring of farmed Atlantic salmon (both pure and crossbred) (refer to sections 5.2 and 6.2). Hence, natural selection is expected to gradually adapt the offspring of escapees (given that some of these survive) back to the natural environment. However, even though the farmed escapees over time may be increasingly adapted to the natural environment, genetic and phenotypic differences may still be detectable compared with the original indigenous stock.

3 *Is it certain that one-way gene flow from farmed salmon to wild salmon is exclusively negative? Could it be that it helps to increase the genetic diversity, and even provide hybrid-vigour at the population level?*

It is expected that Norwegian farmed Atlantic salmon have lost some genetic variation as a result of artificial selection for up to nine generations and genetic drift, which are more pronounced in small populations (refer to section 6.3). Furthermore, there is evidence that survival of farmed Atlantic salmon is diminished in the wild, as a result of selection in the farmed environment (refer to sections 6.3 and 6.4.1). Although on short timescales this may provide an increase in genetic diversity, it is not likely to result in an improved long-term viability of the population. If a wild population is threatened and has low genetic diversity, it would be more beneficial to supplement this population with salmon which have similar adaptive variation (i.e. connected sub-populations) as this will ensure the long-term adaptability of the population (refer to section 7.1).

4 *Farmed salmon are primarily selected for faster growth, later sexual maturation and better resistance to disease. Is it harmful that such characteristics may be transferred to wild salmon, if carriers of such genes are shown to have approximately the same or slightly lower survival / fitness than wild salmon?*

5 *It is probably true that bred salmon have less genetic variation but how large is the chance that this characteristic should prove to be viable in the natural environment? Is it not precisely this phenomenon that is weeded out by natural selection through the poorer survival in various stages of the salmon life cycle?*

In answer to both questions 4 and 5 above: It is true that captive populations as a rule lose some genetic variation due to artificial selection and genetic drift. Farmed Atlantic salmon may out-compete wild fish due to their faster growth and disease resistance; however this will only have a short term benefit to the productivity of the river. Natural selection does not act to select for increased *genetic variation* but selects for fitness irrespective of the genetic variation of the other individuals. A decrease in genetic variation (specifically adaptive variation) will affect the population's *long-term* viability to adapt to changing selection pressures (refer to section 5.2).

6 *Have there been measurements of the genetic variance in a metapopulation with a view to finding out whether small rivers within a metapopulation have a genetic stock that differs from the dominating river, or whether the allele frequencies are significantly different? Is it true that the dominant river has a gene content with such large variance that it also includes the variance in all the small rivers in the metapopulation?*

In short, the amount and type of variation in different subpopulations within a metapopulation will depend upon the local adaptation and the life history and ecology of the sub populations. Refer to section 5.3 for further details.

7 Can we imagine a model in which we group the waterways as genetically important and less important and concentrate efforts on preserving the most important river stocks?

Yes, it is rarely economically or physically viable to protect each river stock independently; in addition many river stocks are small and have insufficient genetic variation to be considered for long-term separate management. A way in which to concentrate efforts to counter these problems is to group metapopulations based on their connectivity and adaptive potential. Refer to chapter 7, also refer to the following relevant reviews: ARAKI and SCHMID (2010), WAPLES and GAGGIOTTI (2006), WEIR and GRANT (2005).

8 In relevance to the questions put forward regarding prioritising management of the Norwegian national salmon rivers, more information is needed on the stocks in these rivers, their demographics, life history and adaptive potential before prioritising rivers for conservation.

9.1 References from Appendix

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