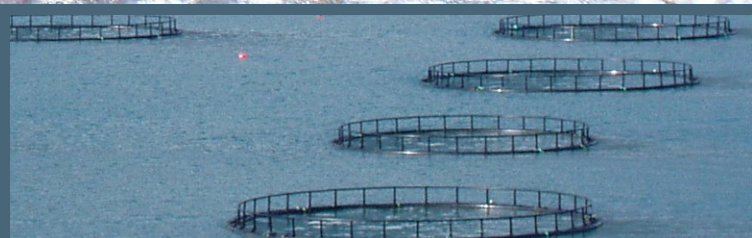
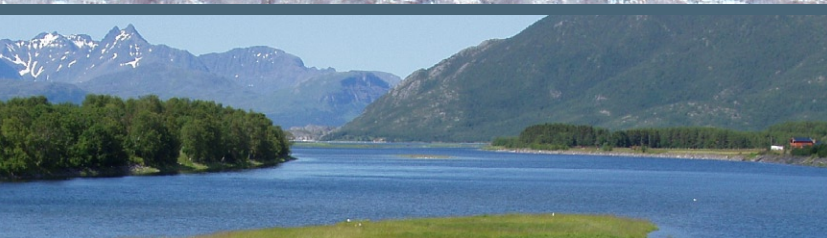


Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature

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Report from the Technical Working Group on
Escapes of the Salmon Aquaculture Dialogue

Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature

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-

This report was commissioned by the Salmon Aquaculture Dialogue. The Salmon Dialogue is a multi-stakeholder, multi-national group which was initiated by the World Wildlife Fund in 2004. Participants include salmon producers and other members of the market chain, NGOs, researchers, retailers, and government officials from major salmon producing and consuming countries.

The goal of the Salmon Aquaculture Dialogue is to develop and implement verifiable environmental and social performance levels that measurably reduce or eliminate key impacts of salmon farming and are acceptable to stakeholders. The group will also recommend standards that achieve these performance levels while permitting the salmon farming industry to remain economically viable.

The Salmon Aquaculture Dialogue focuses their research and standard development on seven key areas of impact of salmon production including: social; feed; disease/parasites; escapes; chemical inputs; benthic impacts and siting; and, nutrient loading and carrying capacity.

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More information on the Salmon Aquaculture Dialogue is available at <http://www.worldwildlife.org/what/globalmarkets/aquaculture/dialogues-salmon.html>

SHORT SUMMARY

Since the mid-1960s, Atlantic salmon *Salmo salar* farming has grown into a large industry within and beyond the native range of the species. Norway, Chile, Scotland and Canada are the largest producers (46, 31, 10 and 7% of total production in 2005). A number of environmental concerns have arisen from the phenomenal growth of the industry. This report from the Technical Working Group on Escapes of the Salmon Aquaculture Dialogue aims at examining and evaluating i) the incidence and impacts of escaped farmed salmon in nature, and ii) the technologies and efforts to prevent escapes and to reduce their impacts upon wild salmon and the environment. This document:

- reviews the status of current research and our understanding of the issues,
- identifies significant conclusions/issues resolved by past research, and
- documents specific knowledge gaps and research needs.

Detailed information on salmon production, reported escapes from fish farms and monitoring of escaped farmed salmon in nature is given for each of the salmon producing countries. Escapes from fish farms occur from marine net pens in all salmon producing countries, as both repeated “trickle” losses of relatively small numbers of fish, and through large-scale episodic events. Numbers of farmed salmon escaping to the wild are large relative to the abundance of their wild conspecifics. Nearly all salmon producing countries have established routines for reporting at least large-scale escapes from sea cage sites, but the magnitude of unreported escapes is unknown. Information on low-level leakage and escapes from freshwater hatcheries remains uniformly poor.

Negative effects by escaped farmed salmon on wild Atlantic salmon populations have been scientifically documented. Negative effects include both ecological interactions and genetic impacts of inter-breeding. A large number of studies point to negative effects, and outcomes for wild populations are either mostly negative and at best neutral. It has been shown that inter-breeding of farm with wild salmon can result in reduced lifetime success, lowered individual fitness, and decreases in production over at least two generations.

Nearly one third of the total world production of Atlantic salmon is in regions where the species is exotic. There is evidence of successful spawning of Atlantic salmon in three streams in British Columbia, Canada, but whether escaped Atlantic salmon have established breeding populations along the North American West Coast still remains uncertain. Spawning of escaped farmed Atlantic salmon has not been documented in Chile or Tasmania. The Atlantic salmon is a poor colonizer outside its native range. The probability that escaped Atlantic salmon will establish populations where the species is exotic seems low, but the possibility cannot be ruled out. It is difficult to predict if or how Atlantic salmon will adapt to the regions where they are exotic, partly because research to study potential impacts in many of these regions is limited.

The most important management issue at present is the need to reduce the numbers of escaped farmed salmon in nature. Among technologies and efforts to reduce impacts of escapes, sterilisation and farm exclusion zones look to be among the most promising, although significant research to fine-tune and study the effects of these approaches is needed. Given the compelling evidence pointing towards a high risk of negative impacts by escaped farmed salmon on wild salmon populations (or on native fish/other organisms in the case of escapes as alien species), and recognising the need to continually improve on our knowledge of the interactions between cultured and wild Atlantic salmon, the members of this working group would like to emphasise that the most pressing research priorities are linked to: 1) technologies and efforts for containment (escape prevention), and 2) approaches to reduce impacts of escapees.

EXTENDED SUMMARY

Since the mid-1960s, Atlantic salmon *Salmo salar* farming has grown into a large industry within the native range of the species (northern Europe and eastern North America), and beyond (western North America, Chile, Australia). Norway, Chile, Scotland and Canada are the largest producers (46, 31, 10 and 7% of total production in 2005). A number of environmental concerns have arisen from the phenomenal growth of the industry.

This report from the Technical Working Group on Escapes of the Salmon Aquaculture Dialogue aims at examining and evaluating i) the incidence and impacts of escaped farmed salmon in nature, and ii) the technologies and efforts to prevent escapes and to reduce their impacts upon wild salmon and the environment. This document:

- reviews the status of current research and our understanding of the issues,
- identifies significant conclusions/issues resolved by past research, and
- documents specific knowledge gaps and research needs.

Geographical and temporal trends in numbers and proportions of escaped farmed salmon in nature

This document presents detailed information on salmon production, reported escapes from fish farms and the monitoring of escaped farmed salmon in nature for each of the world's salmon producing countries. Escapes from fish farms occur from marine net pens in all salmon producing countries, as both repeated "trickle" losses of relatively small numbers of fish, and through large-scale episodic events such as storms. The reporting of escapes from fish farms to government authorities is required by law, regulation or as a condition of the operating permits in most salmon producing countries, and these escape statistics are available to the public in most of these countries. Most of the reported escapes from sea cages seem to be large episodic events, and despite requirements for mandatory reporting the magnitude of unreported escapes is unknown. Information on low-level leakage and escapes from freshwater hatcheries remains uniformly poor. The threat from such freshwater escapes is generally insufficiently recognized.

Escaped farmed Atlantic salmon can be distinguished from wild Atlantic salmon based on external morphology, scale characters, biochemical markers, marks left in the internal body cavity by vaccination and genetic differences. Farmed salmon that escape at an early life stage, and that have been in the wild for some time, are more difficult to identify than recently escaped salmon.

Distribution and survival of escaped farmed salmon in the wild depends on the life-stage and time of the year at release. Salmon released as smolts tend to home to the area of release and enter nearby rivers for spawning. However, survival and homing precision vary with the time of release (poorest survival for fish released in late summer and autumn, and poorest homing precision for fish released in winter). In contrast, salmon that escape as pre-adults seem to have a weak homing instinct and show a low propensity to return to the release area for spawning. Many appear to move with the current and enter rivers in the vicinity of where they are when they are ready to spawn. Escaped salmon are usually recorded within 500 km of the escape site, but have been recorded up to 2 000-4 500 km from the escape/release site.

Ecological and behavioural interactions between wild and farmed Atlantic salmon in nature

Farmed salmon differ morphologically and in physical condition from wild salmon, which likely affects their behaviour, competitive ability and spawning success relative to wild salmon. These characteristics are of both environmental and genetic origin.

Escaped farmed salmon occur on feeding grounds in the Atlantic Ocean and seem to consume similar food resources as wild salmon. It is unlikely that availability of food in the Atlantic Ocean limits Atlantic salmon production, and food competition from escaped farmed salmon is unlikely to be strong.

Escaped farmed salmon are present on spawning grounds during the spawning period, and even in high numbers in some rivers. The reproductive behaviour and success of farmed and wild Atlantic salmon have been extensively studied in experimental spawning arenas and in nature. Escaped farmed salmon can spawn successfully in rivers both within and outside their native range. The spawning success of farmed salmon, however, is lower than that of wild salmon, and that of escaped farmed males is lower than that of escaped farm females. Successful spawning by escaped farmed salmon in nature appears to most often result from breeding between farmed females and wild males.

Following successful breeding, or the escape of farm juveniles from freshwater facilities, behavioural and life-history characteristics of farm salmon and 'hybrid' (wild x farm) offspring will influence their performance and effects on native fish in the natural environment. At juvenile stages, farm salmon and hybrids can be expected to interact and compete directly with wild salmon for food, habitat and territories. Farm juveniles and hybrids are generally more aggressive and consume similar resources as their wild counterparts. In addition, they grow faster than wild fish, which may give them a competitive advantage during certain life stages. However, the outcome of aggressive interactions between wild and farm juveniles vary, and depends upon the environment and the genetic background of the competitors.

Invasions of escaped farmed salmon have the potential to impact negatively on the productivity of wild salmon populations through juvenile resource competition and competitive displacement. While the outcome of interactions between farm and wild salmon will be context-dependent, varying with a number of environmental and genetic factors, they will frequently be negative for wild salmon.

Genetic differences between farmed and wild Atlantic salmon and the effects of inter-breeding on wild populations

Natal homing for spawning, the discontinuous distribution of spawning and juvenile habitat, and a capacity for local adaptation promote genetic structuring within and among Atlantic salmon populations. Wild Atlantic salmon are structured into populations and meta-populations with little gene flow between them, but the mechanisms providing the boundaries within and among river systems, remain to be resolved in detail. Evidence for local adaptation of wild Atlantic salmon is compelling.

World farmed salmon production is largely based on a few breeding strains. Current farm strain selective breeding programmes are focused on multiple traits. Farmed strains differ genetically from wild populations, which is expected due to: 1) the effects of limited numbers in establishing farm strains and the non-random choice

and sourcing of wild founders, 2) domestication selection, 3) loss of variability by genetic drift (increased by using small numbers of brood fish), and 4) selective breeding for economic traits. Differences between wild and farmed salmon due to domestication and trait selection are likely to exist for growth rate, body size, survival, delayed maturity, stress tolerance, temperature tolerance, disease resistance, flesh quality and egg production, whereas unintentional correlated changes may occur for fitness-related traits including survival, deformity, spawning behaviour and success, spawning time, morphology, fecundity and egg viability, aggression, risk-taking behaviour, sea water adaptation and growth hormone production.

Hybridisation of farmed with wild salmon, and gene flow from farmed to wild salmon through backcrossing of these hybrids in subsequent generations, can cause 1) a change in the level of genetic variability, and 2) changes in the frequency and type of alleles present. Hence, hybridisation of farmed with wild salmon has the potential to genetically alter native populations, reduce local adaptation and negatively affect population viability and character. Several molecular marker studies have shown that escaped farmed salmon breeding in the wild have changed the genetic composition of wild populations.

Large-scale whole-river experiments undertaken in Ireland (Burrishoole) and Norway (Imsa), though conducted under different conditions, gave similar results. Both released farm strain, and/or wild x farm strain fish to rivers, and found highly reduced survival and lifetime success of farm and hybrid salmon compared to wild salmon.

Effects of escaped farmed salmon in regions where the Atlantic salmon is an exotic species

Atlantic salmon is farmed in the Pacific Ocean outside of its natural distribution range, mainly in Chile, along the West Coast of North America (Canada and US) and in Tasmania (Australia). In 2005, 36% of the total world production was in regions where the species is exotic. Escapes of Atlantic salmon in these regions potentially pose special problems. Questions relevant to the escape issue include whether escaped Atlantic salmon can establish self-reproducing populations in these regions, whether they are able to hybridize with native fishes, and what ecological effects might escaped salmon have on native species and ecosystems.

Historical attempts to introduce anadromous populations of Atlantic salmon around the world have failed generally, indicating that Atlantic salmon is a poor colonizer outside its native range. The probability that escaped Atlantic salmon will establish populations where the species is exotic seems low, but the possibility cannot be ruled out. Where native populations of salmonids are currently depressed or in decline, conditions for the establishment of Atlantic salmon may be more favourable now than in the past.

Mature escaped Atlantic salmon are recorded in freshwater streams in British Columbia, Canada, and there is evidence of successful spawning of Atlantic salmon in three streams. Whether escaped Atlantic salmon have actually established breeding populations along the North American West Coast streams still remains uncertain. Mature escaped Atlantic salmon are recorded in Chile. However, the spawning of escaped farmed Atlantic salmon in the wild has not been documented in either Chile or Tasmania.

The likelihood of successful hybridisation between Atlantic salmon and Pacific salmonid species seems small. However, if populations of Atlantic salmon establish,

juveniles could be competitors to juvenile Pacific salmonids. The outcome of the competition between juvenile Atlantic salmon and Pacific salmonids in nature is difficult to predict. It seems that Atlantic salmon is often competitively inferior to Pacific salmonids, but that this is context dependent, with body size and prior residency being important. Escapees seems to have greater difficulties in adapting to the marine environment in the Pacific Ocean and Tasmania than in the Atlantic Ocean, with large proportions of empty stomachs recorded in escapees captured at sea. However, escaped Atlantic salmon do feed and prey on native marine species in regions where it is an exotic.

Unlike the situation within its native range, there have been no clearly documented impacts of escaped farmed Atlantic salmon on native fauna in regions where it is an exotic. However, this may be because there is only limited research being conducted to study impacts. It is generally difficult to predict if or how Atlantic salmon will adapt to the regions where they are exotic.

Technologies and other efforts for escape prevention

A prerequisite for escape prevention is knowledge of why, when and from where salmon escape. Such information, which is frequently inadequate, is needed to identify critical factors related to culture technologies, techniques and sites. When this information is combined with knowledge of the survival and distribution of escaped salmon at different life stages, times of the year and locations to identify the most critical escape periods, risk analyses can be performed and the high priority areas for improvement and development identified.

There has been continuous research and development to improve cage technologies and operating methodologies. Novel or alternative technologies, however, have been slow to develop to date. Technical improvements to facilities and operations to prevent escapes are tremendously important for wild populations, and of potential direct economic benefit to fish farmers.

A Norwegian standard has been developed that specifies technical requirements for the dimensioning, design, installation and operation of floating fish farms. This standard is the first of its kind internationally, and Norway is currently working on internationalization of the standard through the ISO.

Technologies and efforts to reduce impacts of escapes

The use of sterile salmon is a measure that should be carefully appraised, considering the positive effects it could have on reducing direct genetic effects of farmed salmon on wild salmon populations. It may also reduce ecological effects. However, it is unlikely to greatly reduce threats from the transmission of diseases and parasites. The most effective method of sterilising Atlantic salmon is high pressure induction of triploidy in newly fertilised eggs. Triploids have a number of disadvantages in commercial aquaculture, but results from different studies vary with regards to triploid growth, survival and the occurrence of deformities. Triploidy is a procedure that can be applied to different stocks which, as diploids, are likely to exhibit different morphological, behavioural and performance characteristics. It is therefore unlikely that the characteristics of different triploid stocks will be the same. Use of triploid (i.e. sterile) salmon in commercial farming would require research and development to determine optimum rearing conditions and boost triploid disease resistance. Ecological interactions of farmed sterile fish with wild fish must be critically evaluated before large-scale use of sterile fish can be encouraged.

Domesticating cultured fish to the point where they are unable to breed successfully in nature, or even to survive in nature, could be an effective means of reducing or eliminating genetic and ecological threats to wild populations. However, this would potentially be a complicated and long-term process to select for a truly domesticated farmed salmon, while at the same time not affecting characteristics that may reduce the culture yield.

Protection zones where salmon farming is prohibited may be an effective way of protecting wild salmon populations. Such zones have been established in fjords in both Norway (pre-existing farms however were not always relocated) and in Iceland. Only a few zones seemed to provide the intended effect of reducing the proportion of escaped farmed salmon in nearby rivers, according to a preliminary evaluation in Norway. This may be a consequence of the small size of the zones, with the two largest appearing to be the most successful thus far. In addition, there are pre-existing farms in some of the zones which have been permitted to remain. New protection zones have recently been established. Research into design of protection zones to protect rivers from intrusion of escaped farmed salmon is needed. The numbers of escaped farmed salmon vary among rivers, and some large rivers seem to attract escaped farmed salmon even though they are situated far from any fish farms. Information on what characterises rivers that attract a high number of escaped farmed salmon is needed to evaluate the effectiveness of protection zones and influence their design.

Escaping post-smolts seem to move away from the release site within a few hours of escape, and even a huge effort over large areas may not effectively recapture salmon after large-scale escapes. Often only a small percentage (< 3%) of escaped salmon can be recaptured despite organised fishing efforts following large escape episodes. Models need to be developed that predict survival and migration pattern for escaped fish. Field data is required to parameterise these models. With such knowledge, measures to reduce impacts of escapes can be identified more easily.

MAIN CONCLUSIONS

Numbers of farmed salmon escaping to the wild are large relative to the abundance of their wild conspecifics. Escaped farmed salmon are clearly an international issue, with frequent observations of their crossing national borders.

Potential negative effects by escaped farmed salmon on wild salmon populations have been scientifically documented. Negative effects include both ecological interactions and genetic impacts of inter-breeding. A large number of studies point to negative effects, and outcomes for wild populations are either mostly negative and at best neutral. It has been shown that inter-breeding of farm with wild salmon can result in reduced lifetime success, lowered individual fitness and decreases in production over at least two generations.

Throughout their native distribution, Atlantic salmon populations are in decline. Several factors acting in concert have probably contributed to this decline, and the multiple stressors can mask the relative contribution of each factor and exacerbate the overall effects of any individual stressor. This has two important implications regarding escaped farmed salmon: 1) potential effects of escaped farmed salmon on population size and production are difficult to separate from other factors, and 2) wild salmon populations are likely to be more vulnerable to effects of escaped farmed salmon because of the synergistic effect of other negative pressures. The maintenance of strong wild salmon populations may reduce the likelihood and magnitude of negative impacts by escaped farmed salmon.

The most important management issue at present is finding measures to reduce the numbers of escaped farmed salmon in nature. Among the technologies and efforts proposed to reduce impacts of escapes, sterilisation and farm exclusion zones look to be among the most promising, although significant research needs to be done to fine-tune and confirm the benefits of these approaches. Given the compelling evidence pointing towards a high risk of negative impacts by escaped farmed salmon on wild salmon populations (or on native fish/other organisms in the case of escapes as alien species), and recognising the need to continually improve on our knowledge of the interactions between cultured and wild Atlantic salmon, the members of this working group would like to emphasise that the most pressing research priorities are linked to: 1) technologies and efforts for containment (escape prevention), and 2) approaches to reduce impacts of escapees.

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1 Introduction

Many fish species are cultivated for aquaculture purposes, and about 40% of all fish consumed by humans worldwide are now farmed (FAO 2006). Since the mid-1960s, Atlantic salmon *Salmo salar* farming has grown into a large industry within the native range of the species (northern Europe and eastern North America), and beyond (western North America, Chile, Australia) (**Figure 1.1**). Norway, Chile, Scotland and Canada are now the largest producers (46, 31, 10 and 7% of total production in 2005, respectively; ICES 2007). The worldwide production of farmed Atlantic salmon is approximately 600 times the reported catch of salmon in the North Atlantic (ICES 2006).

During the past 25 years, the production of farmed Atlantic salmon in the North Atlantic has increased from less than 5 000 t¹ in 1980 to 804 908 t in 2005, with farms in Norway accounting for 73% of the current production, Scotland 16%, Canada 5%, Faroe Islands 2%, Ireland 2%, and Iceland, USA, Northern Ireland and Russia less than 1% each (ICES 2007).

Beyond the native range of the Atlantic salmon, the production has increased from 53 t in 1987 to 456 827 t in 2005, with farms in Chile accounting for 84% of the current production, west coast of Canada 11%, Australia 4%, west coast of USA 1% and South Korea and China less than 1% (ICES 2007).

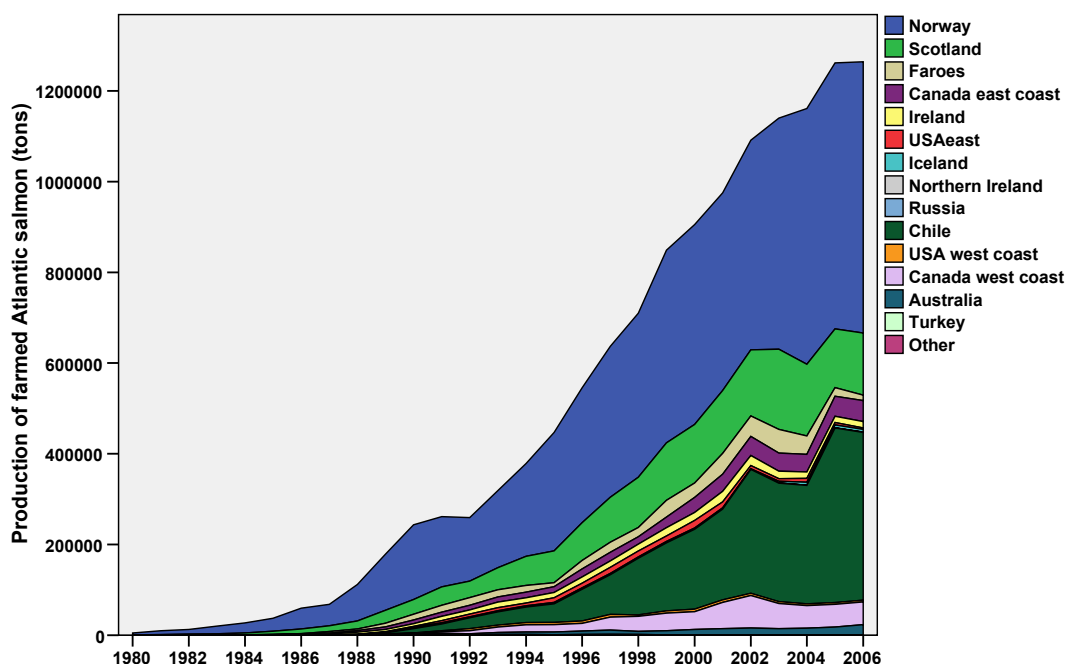


Figure 1.1. Total production of farmed Atlantic salmon during 1980-2006 (in metric tons round fresh weight). Note that data for 2006 are provisional. Source: ICES (2007).

¹ t is used as shortening for metric tonne, i.e. 1000 kg.

Net-pen culture in marine systems can result in loss of farmed salmon² into the wild, and up to two million salmon are thought to escape from farms around the North Atlantic each year (Schiermeier 2003). That is around 50% of the total number of wild salmon at sea in the area in 2000 (ICES 2006 terms this prefishery abundance), which was estimated at 4.2 million fish (Atlantic Salmon Federation 2004). Escaped salmon from aquaculture activities could thus have profound effects on marine and freshwater fauna (Naylor et al. 2005).

This report from the Technical Working Group on Escapes of the Salmon Aquaculture Dialogue aims at examining and evaluating i) the incidence and impacts of escaped farmed salmon in nature, and ii) the technologies and efforts to prevent escapes and to reduce their impacts, by

- reviewing the status of current research and our understanding of the issues,
- identifying significant conclusions/issues resolved by past research, and
- identifying specific knowledge gaps and research needs.

Box 1: Atlantic salmon life history

Most Atlantic salmon populations are anadromous*, which means they spawn and have their juvenile phases in freshwater and migrate to the ocean for feeding, although some populations are freshwater resident and complete their life cycle in fresh water (Klemetsen et al. 2003).

Anadromous Atlantic salmon spawn in rivers in autumn and winter, and the eggs hatch the following spring. The juveniles (parr) remain in freshwater for 1-8 years, before they transform physiologically and morphologically (i.e. smoltify) into the smolt stage and migrate to sea for feeding. At sea, Atlantic salmon are distributed over large areas in the North Atlantic Ocean. Adult salmon mature after 1-5 winters in the sea and return to freshwater for spawning. Some young males may, prior to migrating to sea, sexually mature as parr ('precocious parr'), capable of successful reproduction with adult females. Atlantic salmon return with a high precision to their home river for spawning, although a small percentage can stray to other rivers (average 4%, range 0-20% of the sexually mature salmon return to rivers other than the one they were hatched in [Stabell 1984]). Atlantic salmon may spawn up to seven times during their lifetime, but the mortality is high and most individuals spawn only once or twice.

**Diadromy* is a migration pattern characterised by migrations between freshwater and marine environments. *Diadromy* can be divided into *anadromy*, in which adult fish migrate from the sea to spawn in fresh water, *catadromy*, in which adult fish migrate from fresh water to spawn in the sea, and *amphidromy*, with a migration of larval fish to sea soon after hatching for early feeding and then return to freshwater as juveniles (i.e. migration occurs at other life stages than for the purpose of breeding) (McDowall 1997, 2007).

² The term "salmon" when used in the following refers to Atlantic salmon, unless otherwise stated.

Box 2: Farmed salmon *versus* hatchery-reared and sea ranched salmon

Farmed salmon are grown with the intended purpose of consumption. Wild salmon populations provide the genetic material for the development of farmed salmon strains, which have been selected over several generations for commercially important traits and adaptation to farm environments (see chapter 4 for details).

Hatchery-reared salmon are produced and released in many rivers to enhance wild populations, for example as compensation for lost spawning areas or to re-establish lost populations. Usually, hatchery-reared salmon are first generation offspring of wild parents, with an increasing focus on using the river's native population for stocking purposes. Hatchery-reared salmon might be released at the fry, parr or smolt stage. The artificial selection in a hatchery is different from natural selection in a river, and hatchery-reared salmon can differ genetically from the wild fish even after as little as one generation in a hatchery, but not to the same extent as salmon that has been farmed for multiple generations.

Sea ranched salmon are released as smolts or post-smolts in rivers or into the sea, with the aim to capturing all of the fish on their return to the release site as adults.

References used in this report

This report is based mainly on peer-reviewed scientific studies of farmed salmon, but with references to other sources (e.g. the “grey literature”) to cover local and regional aspects. Studies of hatchery-reared or sea ranched salmon are included only when they are considered relevant to the issue of the impacts of escaped farmed salmon. Such studies might be particularly relevant in terms of the escape of farmed salmon at early life stages (i.e. the smolt stage or younger), because they are deprived of early river experiences in a similar way as farmed salmon. However, hatchery-reared and sea ranched salmon often do not differ genetically from wild salmon to the same extent as farmed salmon, which have undergone directed selection. When studies of hatchery-reared and sea ranched salmon are referred to, this is specifically stated in the text or in a footnote.



2 Geographical and temporal trends in numbers and proportions of escaped farmed salmon in nature



Atlantic salmon net pens in a fjord in Northern Norway.

Photo: Eva B. Thorstad

2.1 Norway

Aquaculture production

The production of farmed salmon in Norway increased 136 fold, from 4 312 to 586 512 t between 1980 and 2005 (**figure 2.1**). Fish farms are distributed along most of the coast, with most of the production along the west coast from Rogaland to Finnmark counties. The counties with the highest production are Nordland and Hordaland (Statistics Norway, www.ssb.no).

Reported and unreported loss from fish farms

The annual reported loss from fish farms to the wild through escapes/leakages was on average 440 000 salmon (range 240 000-715 000) during 1993-2005 (**figure 2.2**)³. The reported loss did not change during this period (linear regression, $r^2 = 0.036$, $p = 0.53$), even though the total production increased 277% (**figure 2.1**). Preliminary numbers of reported escaped salmon for 2006 and 2007 (until 1 December 2007) are 920 000 and 319 999 salmon, respectively (Norwegian Directorate of Fisheries). Fish farmers are

³ This was 1.5 times the total reported catch of wild salmon in the commercial and recreational fisheries in the same time period (average 263 000) (ICES 2006).

required to report all escape incidents to the authorities. When a fish farmer suspects that an escape has occurred, the farmer is obliged to report this to the regional Fisheries Directorate, using a standardized form. The form requires details of estimated number of fish escaped, age, health condition and whether the fish had been recently medicated. The cause of the escape must also be reported. All information is available to the public. The Directorate of Fisheries has collected and presented statistics on the scale and causes of escapes since 1993.

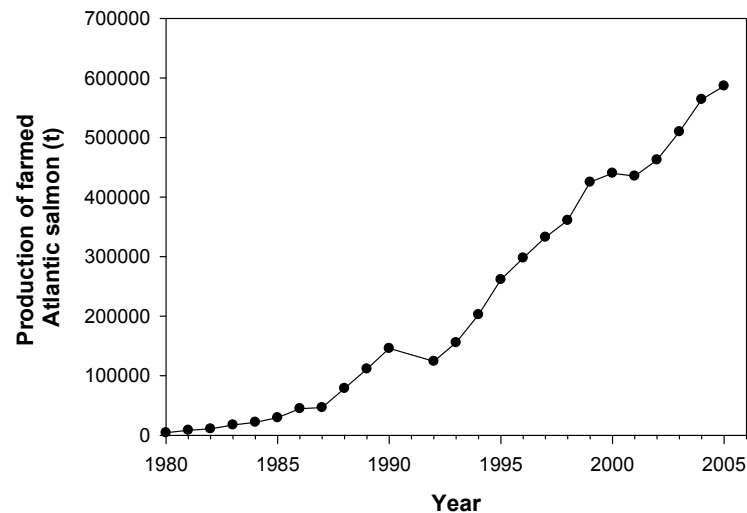


Figure 2.1. Production of farmed Atlantic salmon in Norway during 1980-2005. Source: Statistics Norway (www.ssb.no).

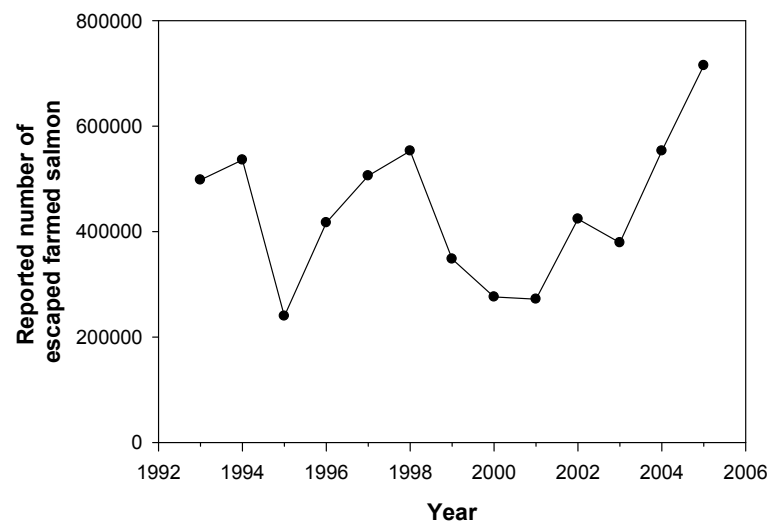


Figure 2.2. Reported loss of Atlantic salmon from fish farms in Norway through escapes/leakages during 1993-2005. Source: Statistics Norway (www.ssb.no).

Official data on the numbers of escaped farmed salmon are derived mainly from large-scale events reported by fish farmers, and little is known about the contribution of

unreported escapes to the total escapement (Baarøy et al. 2004). The official statistics seem to underestimate the numbers of escaped farmed salmon owing to non-reporting or under-reporting from some escape events (Fiske et al. 2006a, Sægrov & Urdal 2006). Sægrov & Urdal (2006) estimated (based on a number of assumptions) that only 12-29% of the actual number of escaped farmed salmon is reported. They estimated that the mean annual number of farmed salmon escaping were 2.4 million during 1998-2004. As a comparison, the reported number of escaped salmon varied between 250 000 and 550 000 annually during this period.

Escapees from small-scale unreported escape events seem to make up a large proportion of the escaped farmed fish, based on a four-year study in the sea in Hordaland County (Skilbrei & Wennevik 2006). Further, the size variability of the catches implied that the escapees originated from several different escape events. A similar conclusion was made by Fiske et al. (2005, 2006b, 2007), based on the fact that escaped farmed salmon sampled at one locality had escaped at a wide range of body lengths (based on scale analyses), indicating that they originated from many different escape events. Most salmon had escaped when they were between 50 and 80 cm long (52-66%), but a relatively large proportion had also escaped as smolts or post-smolts (19-42%) (Fiske et al. 2005b, 2006b, 2007). A study from the 1990s suggested that up to 50% of the escaped farmed salmon caught in bag nets on the coast of Norway had escaped as smolts or post-smolts (Lund 1998b).

Occurrence of escaped farmed salmon in sea and river catches

Reports of escaped farmed salmon in Norwegian salmon rivers first appeared in the 1980s (Gausen & Moen 1991, Lund et al. 1991, Heggberget et al. 1993b). The occurrence of fish farm escapes has been monitored in catches in several Norwegian sea localities annually since 1986, and in rivers annually from 1989 (Lund et al. 1991, Fiske et al. 2001, 2006a, Hansen et al. 2007, ICES 2007). The number of localities monitored every year has varied between 8-17 sea localities and 18-39 rivers (Fiske et al. 2001).

During 1989-2006, the mean annual proportion of escaped farmed salmon varied between 21-54% in coastal fisheries (average 38%), 10-43% in fjord areas closer to the river mouths (average 25%), 4-16% in angling catches in rivers in summer (average 7%), and 11-35% in samples from the spawning populations in rivers close to the spawning season (average 21%) (Fiske et al. 2001, Hansen et al. 2007, Peder Fiske, Norwegian Institute for Nature Research, unpublished data, **figures 2.3-2.4**).

Generally, the proportions of escaped farmed salmon in the catches are lowest during the angling season in the rivers, higher in the spawning populations in the rivers close to the spawning period, and even higher in the sea fisheries (higher on the coast than in the fjord areas closer to the river mouths, when comparing localities monitored every year during 1993-2005) (Fiske et al. 2001, Hansen et al. 2007). The higher proportion of farmed salmon in the river catches close to the spawning season (September-November) than during the angling season (June-August) indicates that most farmed salmon enter the rivers later than the wild salmon (Lund et al. 1991, Fiske et al. 2001).

The proportions of escaped farmed salmon have decreased in the sea fisheries in recent years, when considering those localities monitored annually during 1993-2006 (Hansen et al. 2007, **figure 2.3**). However, when all monitored localities are included, the proportion of escaped farmed salmon in fjord fisheries increased from 1997 (Hansen et

al. 2007, **figure 2.3**). This coincides with the inclusion of localities from the outer Hardangerfjord, an area with a large number of fish farms and weak wild salmon populations, in the surveys. Hence, a high proportion of escaped farmed salmon were observed in the catches (Hansen et al. 2007).

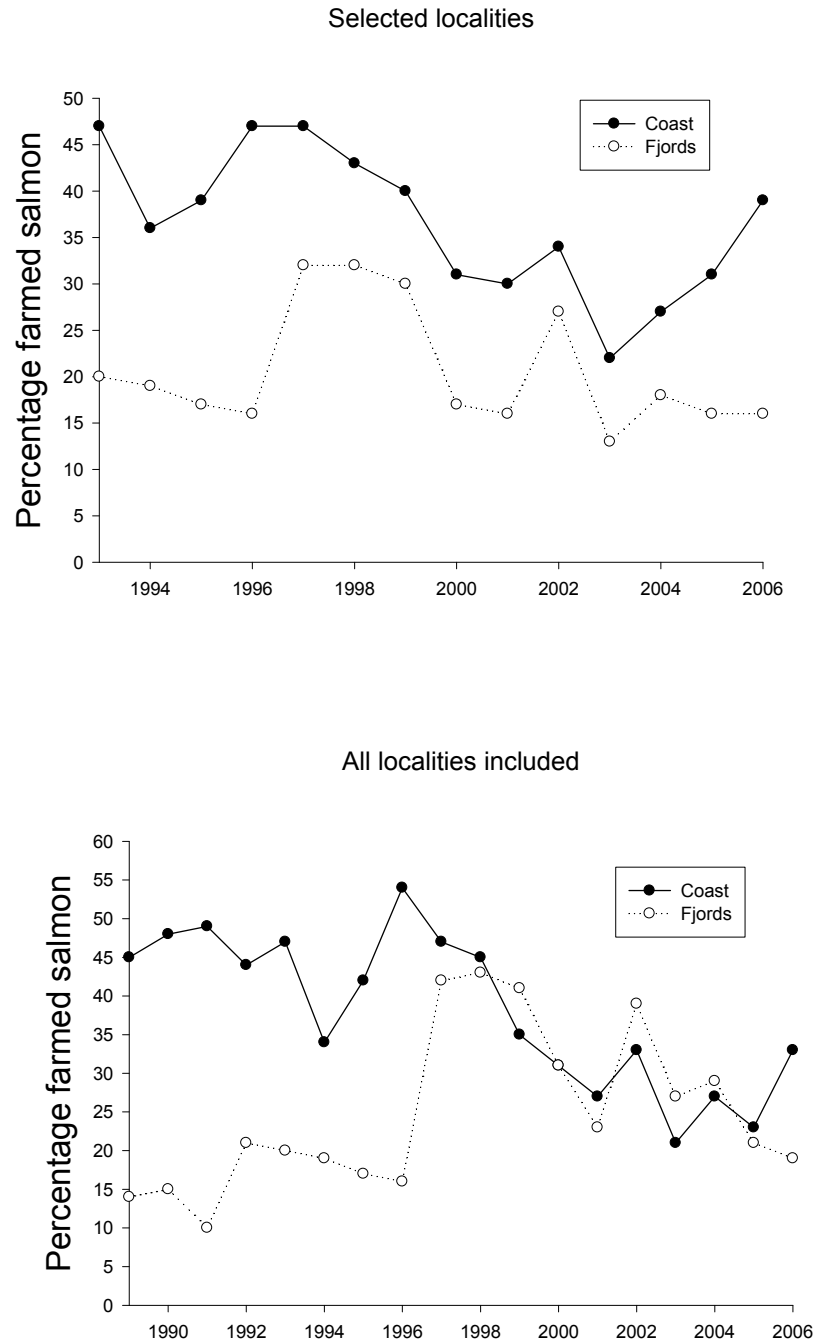


Figure 2.3. Average proportion of escaped farmed salmon in sea fisheries during 1989-2005, given for coastal areas and fjords closer to the river mouths separately (un-weighted average of localities). Upper figure shows data from only those localities monitored every year during 1992-2005 ("selected localities"), for standardisation (see text), whereas the lower figure shows data from all monitored localities. Source: Hansen et al. (2007), with labels translated to English (figures made by Peder Fiske, NINA).

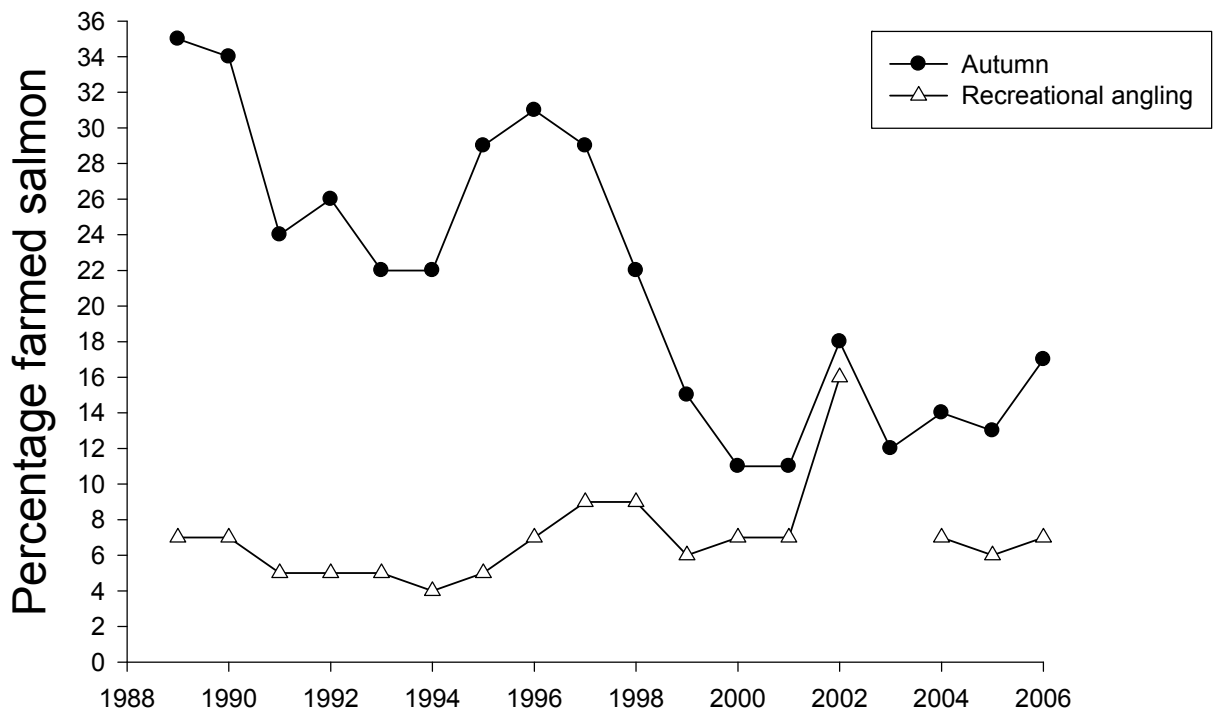


Figure 2.4. Average proportion of escaped farmed salmon in catches in sport fisheries in rivers (recreational angling 1 June - 18 August during 1989-1994 and 1 June - 31 August from 1995), and in catches in spawning populations in rivers in the autumn (September-November) during 1989-2005. The sport fisheries were not monitored in 2003. The proportions in spawning populations are obtained from broodstock fisheries or monitoring by angling or net fishing. The average is un-weighted average of localities. Source: Hansen et al. (2007), with labels translated to English (figure made by Peder Fiske, NINA).

The proportions of escaped farmed salmon in samples from the spawning populations have also declined in the last number of years (**figure 2.4**). However, this reduction is not reflected in the angling catches, which might be due to an extension of the angling season starting in 1995 (extended from 18 to 31 August), and thereby increasing the likelihood of catching late entering farmed salmon (Fiske et al. 2006a). There is a higher proportion of males than females among the escaped salmon sampled from the spawning populations (average 65% males during 1989-2000). In most years, the females have been larger than the males (average total length females 72 cm, males 68 cm) (Fiske et al. 2001). Most of the escaped farmed salmon sampled in the rivers during the spawning season are mature. The proportion mature fish was 87% among females and 92% among males during 1989-2000 (Fiske et al. 2001).

The proportion of escaped farmed salmon in catches is dependent on the size of the wild salmon populations. For instance, if the wild salmon populations are in decline, the proportion of escaped farmed salmon will increase even though the number escaping is constant. Therefore, to achieve information on time-trends in the number of fish escaping from fish farms, the number of farmed salmon captured in the salmon fisheries has been estimated (Hansen et al. 2006, **figure 2.5, 2.6**). These are not absolute numbers, but reflect a time-trend since the calculation is performed in a similar way

every year. The estimated numbers of escaped farmed salmon caught in the fisheries varied between 40 000 and 60 000 every year from the last half of the 1980s until 2002 (Hansen et al. 2006, **figure 2.5, 2.6**). However, during the last three years, the numbers have been below 40 000. Since the production of farmed salmon increased 12 times from 1987 to 2004, this indicates that the relative proportion of fish escaping from fish farms has decreased.

In conclusion, proportions of escaped farmed salmon in catches were high during the 1990s, but seem lower from about 2000 onwards, with a mean proportion of escaped farmed salmon in samples from the spawning populations of 13% (range 11-18%) during 2000-2005 (Hansen et al. 2006, Peder Fiske, Norwegian Institute for Nature Research, unpublished data). A consistent decline in the proportion of farmed salmon recorded in samples from the spawning populations during 1989-2004 probably reflects a reduction in the number of escaped farmed salmon in wild populations (Fiske et al. 2006a). However, changes in fishing seasons, resulting in more effort late in the season in both the sea and rivers, might also have increased catches of farmed salmon and contributed to a reduced number in the spawning populations. Hindar & Diserud (2007) have recommended in a recent report that average intrusion rates should not exceed 5% escaped farmed salmon in wild spawning populations.

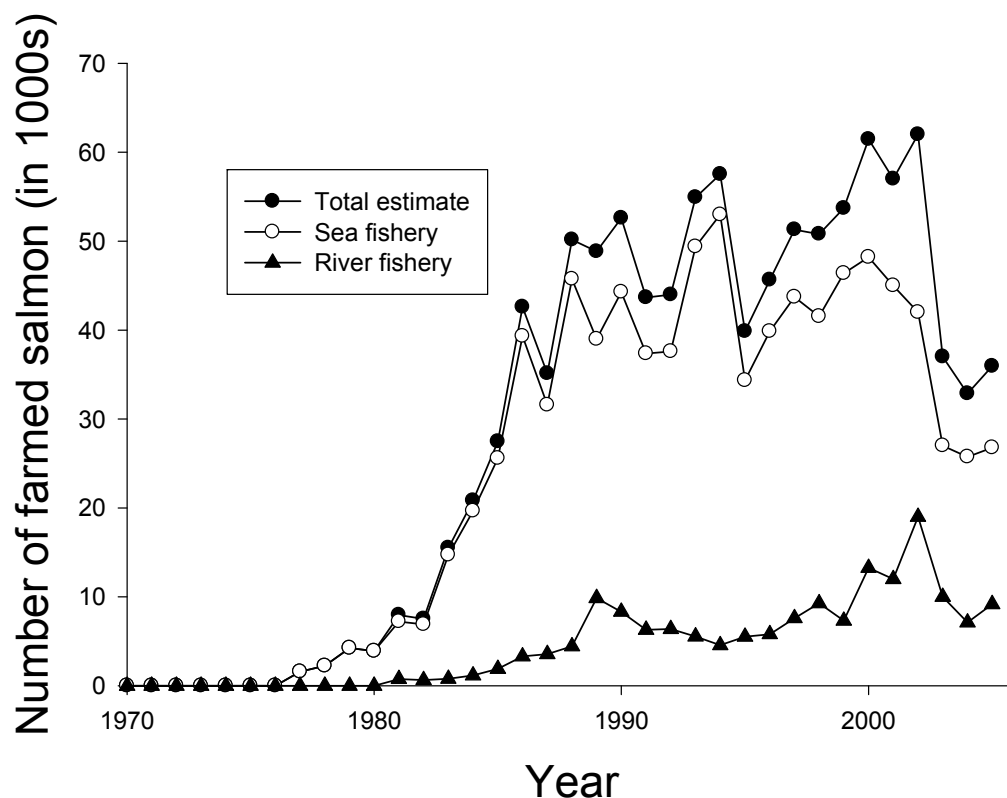


Figure 2.5. Estimated number of escaped farmed salmon in the nominal salmon catches during 1970-2005. Source: Hansen et al. (2006), with labels translated to English (figure made by Peder Fiske, NINA).

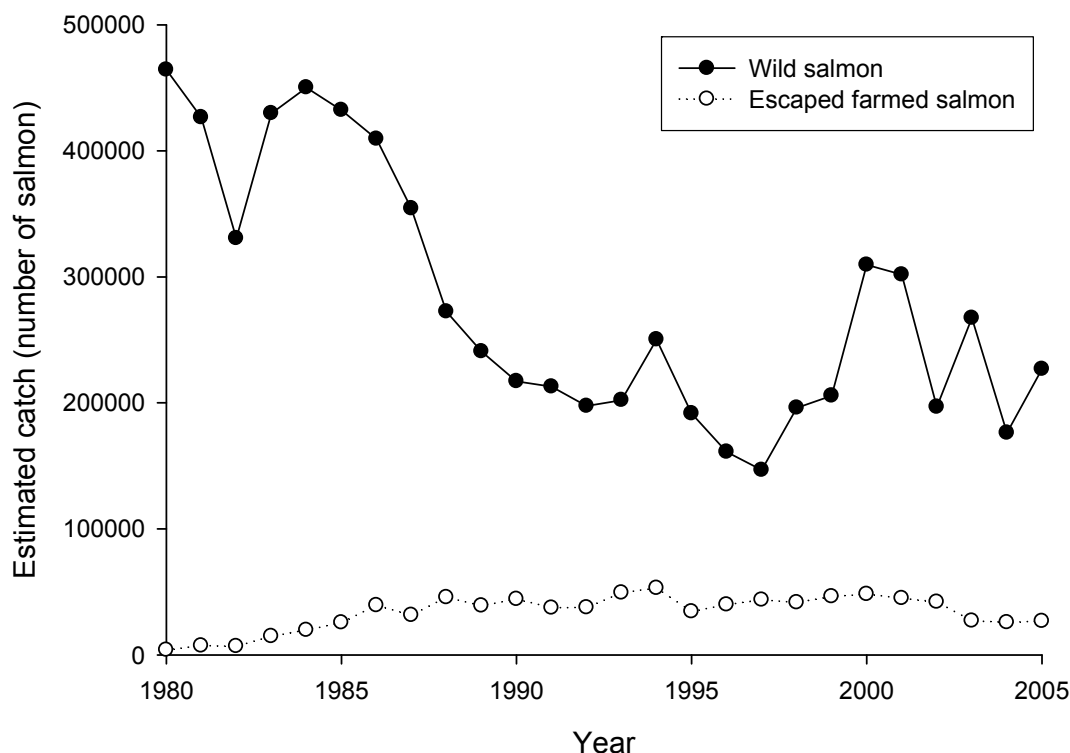


Figure 2.6. Estimated number of wild and escaped farmed salmon in the nominal salmon catches during 1980-2005. Source: Hansen et al. (2006), with labels translated to English (figure made by Peder Fiske, NINA).

Status of wild salmon populations

It was estimated that a total of 700 000 wild salmon returned from the ocean to the Norwegian coast in 2005, before exploitation in the fisheries (Hansen et al. 2006). Of these, 263 000 (38%) were caught (ICES 2006). In total, 450 rivers in Norway have, or had, self-reproducing Atlantic salmon stocks, of which 45 are categorised as lost (10%), 32 threatened (7%), 114 vulnerable or reduced (25%), 246 moderately or little affected (55%), and 13 status unknown (3%) (Hansen et al. 2007). Acidification and the parasite *Gyrodactylus salaris* are the most common reasons for the extinct or threatened status of populations. Hydropower regulation is suspected to be the main contributing factor to salmon population declines in the highest number of river systems (83), followed by other physical alterations, acidification, *Gyrodactylus salaris* and salmon lice.

The size of the wild salmon populations decreased during the 1980s and 1990s, although not to the same extent as seen in some regions of Scotland, Ireland and Canada (Hansen et al. 2006). The population sizes increased from the end of the 1990s up to the present, but not to the high levels recorded during the 1980s. In addition to local problems, a colder ocean climate has probably contributed to a reduction in Atlantic salmon populations throughout the species' range. To what extent the incidence of escaped farmed salmon in wild salmon spawning populations might have contributed negatively to the wild salmon production is not known, but is considered a contributing factor by both Hansen et al. (2006) and Jonsson et al. (2006).

2.2 North Atlantic Ocean

Wild Atlantic salmon are distributed over large areas in the North Atlantic Ocean (Hansen & Quinn 1998). In some areas, Atlantic salmon of exploitable size are sufficiently abundant that commercial high seas fisheries developed. Such areas are off west Greenland, where North American and European fish are harvested, and in the Norwegian Sea, north of the Faroe Islands, where mainly European fish are exploited. (Apart from some experimental fishing, these fisheries have since been closed under international agreement.) Escaped farmed salmon have been observed in several areas in the northeast Atlantic.

Long-term time series data from the long-line fisheries north of the Faroe Islands showed a low proportion of farmed salmon until 1989 (< 5%), then an increase to about 40% in 1989-1991, followed by a decrease to 20-25% in the mid 1990s (Hansen et al. 1993, Hansen & Jacobsen 1998, Hansen et al. 1999). Most of the farmed salmon in this area are probably escapes from Norwegian fish farms (Hansen & Jacobsen 1998). In contrast, at west Greenland in 1991 and 1992, the incidence of farmed salmon appeared to be very small (< 2%, Hansen et al. 1997).

2.3 Chile

Production and geographical distribution

Chilean salmon farming has experienced an exponential growth, currently accounting, for over 70% of global salmon aquaculture production together with Norway (FAO 2005). In 2004, salmon production in Chile reached 569 000 tons shared by the contributions of Atlantic salmon (61%), coho salmon *Oncorhynchus kisutch* (22%), rainbow trout *Oncorhynchus mykiss* (16%) and Chinook salmon *Oncorhynchus tshawytscha* (1 %), respectively. Atlantic salmon production has been the fastest growing within Chilean aquaculture (**figure 2.7**).

Currently, a large proportion of the production of smolts (all species) is carried out in lakes and rivers while a smaller, but growing percentage, are being produced inland in re-circulated water systems. It is estimated that around 50% of smolts are produced in the large lakes Llanquihue, Rupanco and Puyehue, with the highest proportion in the Llanquihue. Several small lakes on Chiloe Island such as Huillinco, Natri, Tarahuin and Tepuhueico (among others) produce between 30 and 40% of the smolts.

Until five years ago, more than 90% of the total salmonid production was concentrated in the X region, or so called Lakes Region. This is an area of coastal channels, islands and fjords approximately between 72° 20' W and 74° 30' W, and between 41°S and 43° 30' S (Leon 2006). The population of the area is below 1 million people. Today this region is responsible for 78% of the Chilean salmon production (all species combined), though production in the next region to the south (Aysen; south from 43°S) has been increasing the production and by 2005 was responsible for 21% of the production. In terms of Atlantic salmon production alone, 80% was farmed in the Lakes Region in 2005, but it is expected that production to the south will increase very quickly in the coming years.

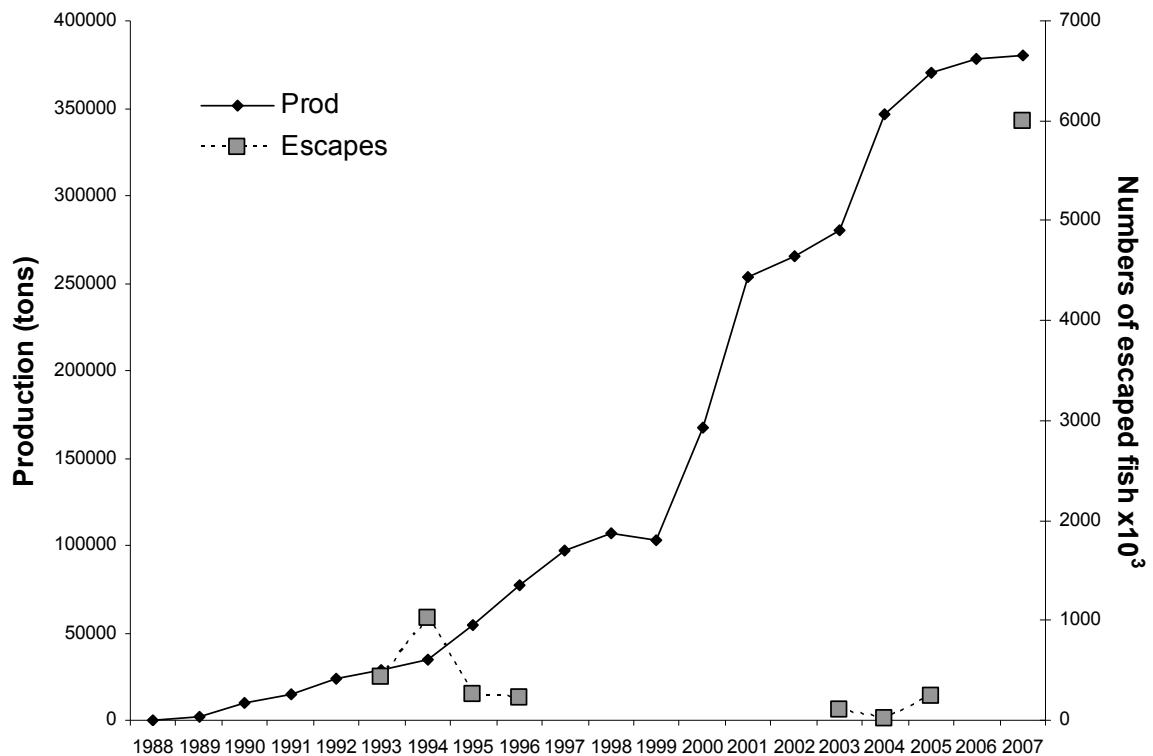


Figure 2.7. Atlantic salmon production in Chile and estimated number of escaped fish. Data for 1994-1996 from Soto et al. (2001). Data for 2003 and on provided by Subsecretaria de Pesca, Chile. Reported escapes after the earthquake in 2007 is an estimate from news reports, not official data. The 2007 value for production is also a preliminary estimate and not a confirmed value.

Escaped Atlantic salmon and other species

Salmon escapes in Chile have been mostly reported or estimated after large and or catastrophic events. During 1994 and 1995, there were massive escapes after major storms (Soto et al. 1996, 2001). Between 1993 and 1996, escaped Atlantic salmon amounted to about 1.5 million fish, and constituted 57% of total estimated salmonid escapes at the time. However, there appears to have been a decline since then, with fewer reported escapes despite increasing production of this species (**figure 2.7**). Some of the largest recently reported salmonid escapes (ca. 2 million fish), took place in the Aysen Región in 2004 (Leon 2006) and consisted mostly of coho salmon and rainbow trout. Reports to Subsecretaria de Pesca for 2004 and 2005 blamed bad weather conditions for damaging cage structures and being responsible for 87% of all escapes.

Niklitschek et al. (2006) suggested that about 1 to 2 % of farmed fish could escape. That is 2 to 3 fish for each ton produced. Much of this is thought to happen when changing nets, during transport and harvesting, etc. It is possible that these “silent”, slow escapes reached nearly 700 thousand Atlantic salmon in 2005, given a total production of 370 thousand tons. However, this estimate has not been evaluated directly and remains somewhat speculative. A very large salmon escape occurred in April 2007 when a violent earthquake shook the Aysén Fjord in Southern Chile’s Region XI,

creating a landslide and localized tsunami. The 14 salmon farms operating within the fjord at this time may have housed up to 14 million fish. The events caused serious damage to the farms, and while no official figures have been provided, as many as 5 million fish may have escaped⁴. If this figure is correct, then this would be the largest escape ever of farmed Atlantic salmon from a single event in any farming region. The circumstances which led to the escape are highly unusual and unpredictable, and could not have been countered by any existing technologies.

Presently, there are no monitoring programs in place to follow up on escapes of salmon. However, the current environmental legislation for aquaculture (RAMA) requires that mitigation measures be in place to control escapes and that escapes be reported to authorities. The Subsecretaria de Pesca has been compiling these reports since 2004, and they are publicly available upon request. The only available evaluation of the presence of escaped salmon in nature was that provided Soto et al. (2001) for the period 1994-1996.

2.4 United Kingdom

Salmon culture began in the coastal waters of Scotland in the late 1960s (Walker et al. 2006). Marine salmon farms are sited along the west coast of mainland Scotland, around the Western, Orkney and Shetland Isles, and on the north coast of Northern Ireland. There are no salmon farms operating in the coastal waters of England and Wales. There are wild salmon present in all these areas, except the Orkney and Shetland Isles. An overview of escapee monitoring programmes is given by Walker et al. (2006).

Scotland

The total production of farmed Atlantic salmon in Scotland increased from approximately 600 t in 1980 to a high of approximately 177 000 t in 2003, but decreased again to 130 000 t in 2005 (ICES 2007).

The Scottish Executive introduced legislation that requires the mandatory notification of all escapes of farmed fish in May 2002 (Anon. 2004b). Any suspected escape, or circumstance which gives rise to a significant risk of escape, should be reported to the Executive. Information on escapes used to be regarded as commercially confidential and was not available to the public, except as a yearly total. However, the Freedom of Information Scotland Act (FOISA) allowed people to request this information, and it has recently been released to the public, broken down by individual fish farm company.

In the period 2002-2006, an annual average of 215 903 salmon were reported escaped from sea water localities, and 94 539 from freshwater hatcheries in Scotland (dead fish excluded, statistics provided by Paul Haddon, Scottish Executive Environment and Rural Affairs Department, Scotland).

There is no centralised source of information about the incidence of escaped farmed salmon in Scottish rivers and coastal areas at this time, and the information that does exist is of limited value in assessing the current numbers (David Hay, Fishery Research Services, Scotland, personal communication). According to a summary by Walker et al.

⁴ <http://www.patagoniatimes.cl/content/view/91/26/>

(2006), escapees occur on average at low frequencies in coastal and freshwater fisheries: < 5% in the Northwest and < 1% in the Western Isles and Southwest Areas (see also Webb & Youngson 1992, Youngson et al. 1997). However, escapees occur at higher frequencies in the coastal fisheries in areas where farms are situated. Frequencies of escapees have in some years in the Northwest Area been up to 22% in coastal and 19% in freshwater fisheries. It should be noted that most identifications are based on external morphology alone, and relying on anglers and net fishers to examine their own catches. Such use of the fishery catch statistics is not regarded as ideal for identifying the incidence of escaped farmed salmon (Walker et al. 2006). In 1991, progeny of escaped farmed females were detected in 14 of 16 sampled rivers in western and northern Scotland, with an average frequency of occurrence among sampled parr of 5.1% in the rivers examined (Webb et al. 1993b).

In the River Ewe, western Scotland, farmed salmon occurred in the rod fishery in 13 of 15 years during 1987-2001, contributing to at least 5.8% of the total catch, with a maximum annual frequency of 27% (Butler et al. 2005). It was estimated that < 1% of fish escaping from the marine cages entered the river, but contributed at least 27% of potential anadromous spawners in 1997.

Northern Ireland

The total production of farmed Atlantic salmon in Northern Ireland is much smaller than Scotland, and varied between < 100 t and 338 t during 1990-2005. In Northern Ireland, it has always been a condition of the operating licence that marine salmon farms report escape incidents to the Fisheries Division of the Department of Agriculture and Rural Development (DARD) (Walker et al. 2006). However, these data are not available to the public because they may be commercially sensitive.

Escaped farmed salmon were monitored in a coastal salmon fishery in County Antrim, Northern Ireland, during 1992-1995, and at an adjacent freshwater location (the River Bush) during 1991-1995, based on morphological characteristics (Crozier 1998). In the sea fishery, 2.4% of the examined salmon were identified as escaped from sea cages (annual averages from 0.26-4.0%). In the river, 0.88% of fish entering an adult trap were identified as escaped salmon (annual averages from 0.13-2.6 %). According to a summary by Walker et al. (2006), escapees have occurred in coastal catches across years at an average level of 4.2% and at a maximum of 14%.

After a large escape of adult salmon from Glenarm Bay fish farm in Northern Ireland following storm damage in August 2001, escaped farmed salmon were found in rivers of Northwest England and North Wales (Milner & Evans 2003). The distances between Glenarm and the receiving rivers ranged from 181 to 276 km.

2.5 North American East Coast: Canada and US

Commercial sea farming of Atlantic salmon on the east coast of North America began in the late 1970's. Farm sites are concentrated around the Canada/US border in the southwestern Bay of Fundy/northwestern Gulf of Maine region, although a few farms are dispersed outside of this region to parts of Maine, New Brunswick (NB), and Newfoundland (NF). A major salmon farming expansion is planned in the immediate

future for southern Newfoundland. More than 90% of all the fish grown on the East Coast are farmed in NB and Maine. Canada produced 93% of the fish on the East Coast in 2005 (ICES 2006). However, the farmed salmon produced in this region in 2005 (42 649 t) was only about 3.4% of the 1 261 683 t estimated global production of this species in this year (ICES 2006, **figure 2.8**).

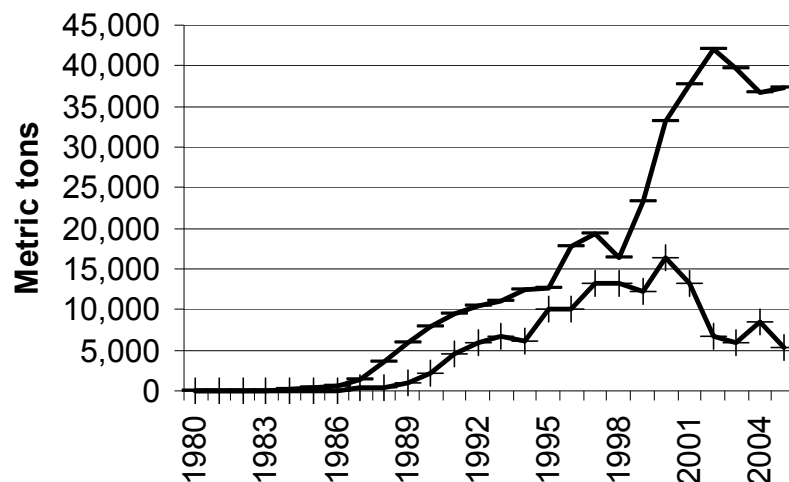


Figure 2.8. Production of farmed Atlantic salmon (t) on the East Coast of North America. The upper (-) and lower (+) lines are Canadian and US production, respectively. Data source: ICES (2006).

The first Canadian salmon crop from this region was marketed in 1980, with US farms coming on line in 1987. Production in both countries increased rapidly, peaking at about 50 808 t in 2001 (**figure 2.8**), and declining thereafter. A paucity of acceptable sites in the NB/Maine region, and a combination of regulatory requirements, losses to disease and a necessity to fallow some sites on a regular basis to control diseases, has resulted in a decline in production in recent years. Regulatory regimes differ between the US and Canada, although the same companies have traditionally operated on both sides of the border.

In the NB and Maine regions where salmon farming occurs, wild Atlantic salmon populations in 40 rivers are officially listed as endangered by national authorities in Canada and the USA (Amiro 2003, NRC 2004), and those in the other rivers in the area are severely depleted (Jones et al. 2004). The exact cause or causes for recent declines remain speculative; however, the depressed status of these wild salmon populations is believed to make them particularly vulnerable to impacts from escaped farm fish.

Farmers in NB are required to report escape events to Provincial authorities, but this information is treated as confidential and not released to the public. Thus a complete record of escapes is not available. In cases of catastrophic failures, newspapers will on occasion cover the story, providing records of the events and in some cases estimates of the number of fish escaping. Growers in Maine are also required to report escape events to the State government, and these reports have been made public in recent years. The few reports which have been submitted have been from relatively large losses due to catastrophic events (e.g. storms, boat collisions with cages; Whoriskey 2001).

Governments in this region do not maintain a specific program dedicated to the detection of escaped farm salmon in rivers or in the sea. However, in New Brunswick a non-governmental organization (the Atlantic Salmon Federation) has maintained a targeted research and monitoring program on interactions among wild and farmed salmon, funded by private sector contributions and with grants from the New Brunswick Wildlife Trust Fund and the NB Environmental Trust Fund. In addition, in both countries governments and NGOs have established counting facilities on a limited number of wild salmon rivers in the region, and fish entering these facilities are screened for escaped farmed salmon, which are identified and counted using standard techniques (e.g., DFO 1999, Baum 2000, ICES 2006).

In general, counts of escaped farmed salmon are highest in rivers near the centre of the farming region, and much lower in rivers farther away. NB's Magaguadavic River is very close to the core of the industry, and has been used as an indicator site for interactions among wild and farmed fish (Carr et al. 1997a). Sporadic counts were made of wild salmon returns to this river in the early 1980's, and systematically of wild and farmed salmon since 1992 (**figure 2.9**). Wild runs have declined precipitously since the 1980s when they were about 1 000 per year. Numbers of escaped farmed salmon peaked in 1994 when they outnumbered the wild fish by 10:1, and farmed escapees outnumbered the wild fish by about 3:1 until 2005. In 2006, the number of escaped fish entering the river declined to the lowest value in the time series, presumably due to improved equipment and operating procedures, and reduction in production. 2006 was the first year since 1994 that wild fish outnumbered farm fish in river returns. Work is presently underway to document the genetic changes which occurred in the wild fish population of this river due to the influx of farmed fish.

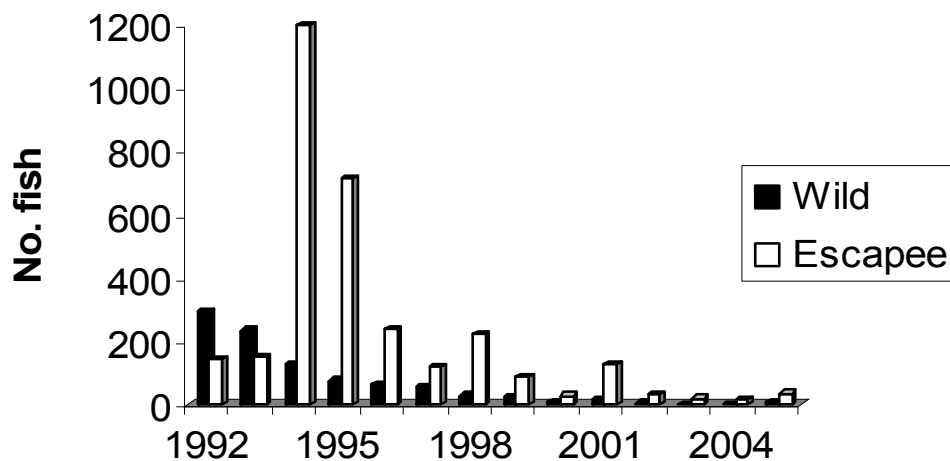


Figure 2.9. Returns of wild and escaped farmed salmon to the Magaguadavic River, New Brunswick, Canada.

Recent targeted studies on escapes in the region have shown that juvenile farmed salmon are chronically escaping to the wild from hatchery sites, although the numbers of fish escaping is unknown (Carr & Whoriskey 2006, Baum 2000). A sonic telemetry

study on experimentally escaped farm salmon from sea cage sites documented high levels of mortality soon after release, and none of the experimental fish were detected entering any salmon river in the region to spawn (Whoriskey et al. 2006).

At present, there is no requirement that farmed salmon grown on Canada's east coast be marked to distinguish them from wild salmon. In Maine, to operate growers must possess a Maine Pollutant Discharge Elimination System General Permit for Atlantic Salmon Aquaculture. This permit is issued pursuant to requirements of Federal and State law, and to protect wild salmon has required a phase-in of marking of farmed fish since 2004. Section I4h of the permit states: "By July 31, 2007, all fish placed in net pens must be identifiable through external means as commercially reared and identifiable as to the individual facility into which they were placed." The regulatory authorities may, however, modify the terms of this requirement if circumstances warrant. At present, farmed fish scale patterns are considered a commercial mark, and other marks are genetic or possibly a right ventral fin clip (M. Young, personal communication).

2.6 North American West Coast: Canada and US

Atlantic salmon are farmed on the West Coast, where the species is exotic. Farming in this region occurs in a limited (< 6000 t per year) operation in Washington State in the US, with most production in British Columbia, Canada (**figure 2.10**). The first reported crop from the industry in both the US and Canada was in 1989, and combined production peaked at a value of about 76 600 t in 2002, declining thereafter. No plans for expansion in the USA have been reported. In British Columbia, the industry would like to expand, but has run into opposition and has had difficulty in getting new farm sites approved. In 2005, US and Canadian West Coast Atlantic salmon farmers grew 54 000 t, about 4.3% of global production (ICES 2006).

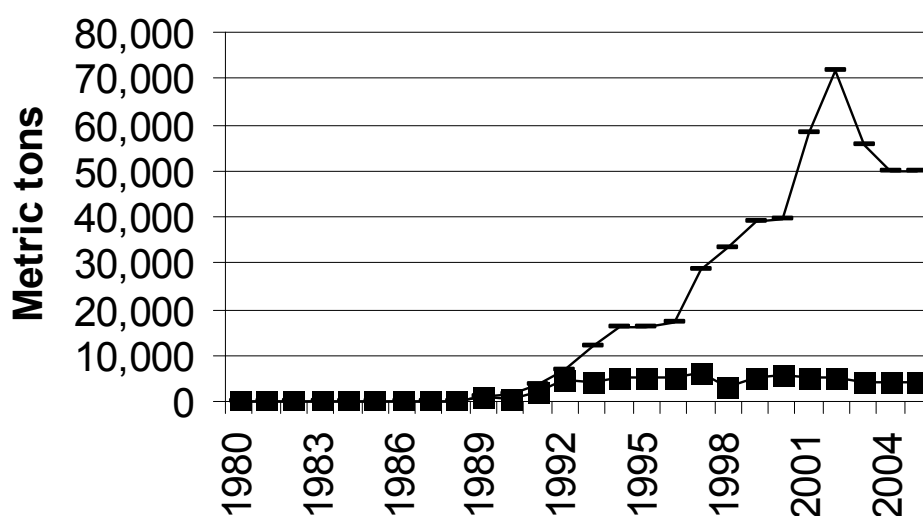


Figure 2.10. Production of farmed Atlantic salmon (t) on the West Coast of North America. The upper (-) and lower (■) lines are Canadian and US production, respectively. Data source: ICES (2006).

The Canadian Department of Fisheries and Oceans and the British Columbia's Ministry of Agriculture, Food, and Fisheries have maintained a formal "Atlantic Salmon Watch Program" *"to study the abundance, distribution and biology of Atlantic salmon in British Columbia and its adjacent waters. The ASWP monitors commercial and sport catches and observations of Atlantic salmon throughout British Columbia, Alaska and Washington in co-operation with the Alaska Department of Fish and Game and the Washington Department of Fish and Wildlife."*⁵. Washington State also receives and publicizes reports of escaped fish⁶. Postings of escape numbers up until 2003 are available on the web sites for both British Columbia, and Washington State. While escapes have been reported from both freshwater hatcheries and marine cage sites, no clear trend in increases or decreases in the number of fish released is evident and captures of farm-origin salmon occur regularly in wild fisheries despite the absence of reports of escapes. This may reflect a tendency to report large scale catastrophic losses, rather than "trickle" losses (e.g., Weir & Fleming 2006).

Independent research on the ecology, behaviour and potential impacts of escaped Atlantic salmon on the West Coast is being carried out (reviewed in Weir & Fleming 2006). Escaped farmed salmon have been found in more than 80 rivers in British Columbia, with feral juvenile Atlantic salmon having been discovered at three locations (Volpe et al. 2000). Escaped farmed Atlantic salmon have dispersed widely in the North Pacific Ocean (McKinnell et al. 1997).

The use of the exotic Atlantic salmon, a potential competitor for Pacific salmonids, in cage culture on the west coast of North America is controversial (reviewed in Nash 2001, Waknitz et al. 2002, Whoriskey 2003). However, persistent attempts to deliberately introduce the species to the area historically failed. This has led some to suggest that Atlantic salmon may be the best possible species to use here, to minimize the impacts of an industrial farming industry upon wild salmonids. Others argue that a steady release of escaped Atlantic salmon will ultimately result in a release of fish to the wild at time highly favourable to the species' widespread colonization, with major impacts on wild salmonids. The debate continues.

At present, there is no requirement that farmed salmon grown on Canada's west coast be marked to identify them. In Washington State, all cultured fish are tagged with an otolith thermal mark in order to distinguish escapees originating from the State from those originating in nearby British Columbia, Canada (John Kerwin, Washington State Department of Fish and Wildlife, personal communication).

2.7 Faroe Islands

The total production of farmed Atlantic salmon increased from 1 370 t in 1986 to 52 526 t in 2003, but decreased again to 18 962 t in 2005 (ICES 2007). All farmed salmon are produced in seawater cages, on 23 sites (www.industry.no). There is a fish farm in almost every suitable bay and fjord in the Faroe Islands, and the production in the sea has reached its natural limit given current farming technology (www.industry.no). Freshwater sites raise smolts, and most of the smolts are reared in

⁵ www.pac.dfo-mpo.gc.ca/sci/aqua/ASWP_e.htm

⁶ www.wdfw.wa.gov/fish/atlantic/comcatch.htm

tanks in land-based farms using recirculating systems. The recirculating systems have solved the problem of fresh water scarcity in the Faroe Islands (www.industry.no).

An annual average of 253 t of farmed salmon was reported escaped from sea cages in the period 1998-2003, with escapes occurring at one or two localities every year (Marita Rasmussen, Faroe Fish Farming Association, personal communication). In 2004-2005, there were no reports of escapes. The escape numbers are regarded as uncertain. At present there is no monitoring of escapes other than what the farmers note themselves. Escapes are reported to the environmental authorities, but this is not enforced by law (Marita Rasmussen, Faroe Fish Farming Association, personal communication). Fish farmers, however, are now required to report escapes to the veterinary authorities, but this has not been followed up by the veterinarians as yet (Jan Arge Jacobsen, Faroese Fisheries Laboratory, personal communication). However, a new electronic reporting system will be available in 2007.

Currently, there is no monitoring of escaped farmed salmon in nature in the Faroes. In the early to mid 1990s, however, proportions of escaped farmed salmon in the ocean north of the Faroes were monitored in the fisheries (see section on North Atlantic Ocean above).

2.8 Australia

There was a gradual increase in the production of farmed salmon in Australia (i.e. Tasmania) from 20 t in 1986 to a high of 16 800 t in 2005 (ICES 2007). Tasmania is the main state in Australia where environmental conditions are suitable for Atlantic salmon farming, though South Australia has some minor commercial operations. The salmon farming is located in four distinct geographic areas around Tasmania (DPIW 2006). Escapes of salmon into the marine environment have occurred since the industry began in the mid-1980s, with escapes occurring in all geographical areas. Escapes occur both through low level leakage and major escapes. The low level leakage over the course of the growing cycle equates to around 2-3 % of fish stocked, however included in these figures are also losses due to predation by birds, sharks and seals. It is a licence condition to report major large-scale escapes (i.e. escapes in excess of 1000 individuals at any one time) to the Department of Primary Industries and Water. During 2000-2006, a total of 208 000 salmon were reported escaped in Tasmania during 11 escape episodes. The reasons for the escapes included storms in two cases, net tears in two cases, a net hole in one case, loss during fish transfer in one case and unknown causes in five cases (DPIW 2006).

Atlantic salmon is an exotic species in Australia. It is unlikely that escaped salmon will form viable populations in Tasmania (DPIW 2006), but little is known about the fate and impacts of the escaped salmon.

2.9 Ireland

There was a gradual increase in the production of farmed salmon in Ireland from a level of approximately 6 323 t in 1990 to a high of approximately 23 000 t in 2001.

Production has subsequently fallen for five consecutive years since 2001 to 11 174 t in 2006 (Browne et al. 2007). This is the lowest annual production volume since 1996. Salmon farms are principally located along Ireland's west coast. As a result of licensing restrictions there has been little change in the distribution of farms since their establishment.

Fish farm operators in the Republic of Ireland have been required by law (S.I. 253 1996) to report on losses of salmon from their sites as a condition of their license. Information is provided to the Department of Communications, Marine and Natural Resources (DCMNR) about the site location; the number, age, time at sea, and average weight of escaped fish; the reason for the escape; and measures taken to reduce the impact of the escape (Anon. 2004a). Official statistics from this source indicate that approximately 415 000 salmon were reported to have escaped from salmon farms in coastal waters of the Republic of Ireland in the period 1996-2004, with an annual range of 0-160 000. There were no reports from the industry of escape incidents in 2004, 2005 or 2006

Salmon catches have been examined for farm salmon on a routine basis in Ireland since 1991, including fish from commercial landings and from the premises of fish dealers (ICES 2006). The catch examined comprises principally drift net catches from the major salmon fishing areas of Donegal, Mayo, Galway and Limerick and the South West (Cork and Kerry). Generally between 20% and 50% of the declared catch is examined specifically for escapees. In some areas the scanning rate is much higher, e.g. Donegal, Mayo and Galway areas where the aquaculture industry is mainly situated. The identification of all escapees is based on a combination of external characteristics, particularly abnormalities of the snout and opercula, and of the dorsal, caudal and paired ventral fins. Irish escaped fish are not subject to secondary examination such as scale reading.

The average percentage of escapee salmon occurring in coastal commercial fisheries from 1991 to 2004 ranges from less than 0.1% in Donegal to 0.6% in Mayo. However, the commercial fisheries are operated for a short period of eight weeks in the summer, whereas most large scale escapes are likely to occur in the winter as a result of storm damage to cages. There is no systematic reporting of fish farm escapees in river catches in Ireland. However, a genetic study (Clifford et al. 1998b) of two rivers in the Donegal region in 1993, 1994 and 1995 following an escape of 29 000 adult farm salmon in the area in the spring of 1992 showed that the proportion of juveniles of maternal farm parentage in two rivers ranged from 18% in 1993 to 2% in 1995, with an average of 7% in both rivers and a maximum frequency of 70% in an individual sample.

The annual pre-fisheries abundance of returning wild salmon to Irish rivers between 1996 and 2004 has been estimated to range from 494 257 to 1 180 181 fish. The spawning escapement of wild salmon, after both commercial and recreational fisheries, for the same period is estimated at between 178 949 and 395 581 fish per annum (ICES 2006). The total reported number of farm fish escaping in the period 1996 to 2004 from Irish farms was 415 000.

2.10 Iceland

The total production of farmed Atlantic salmon varied between 1 053 t in 1988 and 6 300 t in 2005 (ICES 2007). The Icelandic coastline is mostly open and rugged with high tidal exchange and limited shelter to conduct cage rearing of fish in the sea. Experimental cage farming conducted in the late 1980s more or less confirmed this and no sea cages were operating in Iceland after 1990 (NASCO 2006).

In 2000, there was a renewed interest in sea-cage farming of salmon, mostly in deep sheltered fjords in eastern Iceland, and farming was started in three fjords in 2001 (NASCO 2006). Recent incidents involving stinging jellyfish *Cyanea capillata* have reduced this interest (Árni Ísaksson, Agricultural Authority of Iceland, personal communication). As an almost yearly occurrence on the east coast of Iceland in September, large swarms of *Cyanea capillata* get squeezed into the cages and burn both the skin and eyes of the salmon, with large mortality. The fish farm in one of the fjords has already closed, and after 2007, only one sea-cage facility with a current production of 500 t is expected to remain (NASCO 2006).

During the first period of sea cage farming in the 1980s, escaped farmed salmon were recorded in some salmon rivers. The proportions of escaped farmed fish varied between 5 and 63 % in four monitored rivers in 1987-1989 (Gudjonsson 1991). Escaped farmed fish entered the rivers later in the season than wild fish. The proportions of escaped farmed fish were larger in S.W. Iceland, where much of the salmon-culture occurred, than in North Iceland.

Farms are now required to tag approximately 10% of the salmon reared in sea cages with coded wire tags (CWT). The Agriculture Authority of Iceland pays for the tags and operates a tagging database (ICES 2006). Since this tagging was introduced in 2001, more than 600 000 smolts have been tagged and released into cages. Out of these, only one tagged adult has been recovered in an east coast river (NASCO 2006), despite the salmon rivers being fairly well monitored for coded wire tags (Árni Ísaksson, Agricultural Authority of Iceland, personal communication).

Systematic screening for tagged fish relies on voluntary notification by anglers. There is no systematic screening of fish farm escapees by the authorities. There is also no systematic monitoring along the Icelandic coastline, because there are no sea-fisheries for salmon.

The low recapture rates of CWT-tagged farmed salmon are likely due to salmon farms being located far from the salmon rivers and major escapes are probably infrequent (NASCO 2006). Accidental farm escapes should be reported to the authorities (ICES 2006). No significant accidental releases have been observed or reported, but in 2003 an accidental release of 3 000 farmed salmon from a holding cage at a slaughtering facility occurred due to a minor collision with a boat (NASCO 2006). Subsequently, nine escaped farmed salmon were reported from angling in three nearby rivers.

Since 2004, salmonid farming in sea cages has been prohibited in fjords and bays close to major salmon rivers (NASCO 2004). Escapes from sea cages are currently not regarded as a problem for wild Atlantic salmon populations in Iceland (NASCO 2006).

Salmon has been farmed in land-based units since the 1980s (Gudjonsson 2006). There are currently no land-based farms producing Atlantic salmon in any quantity for slaughtering (Árni Ísaksson, Agricultural Authority of Iceland, personal communication). The land-based farms are mostly used for on-growing of smolts, sometimes to the post-smolt stage, but also to a greater extent for production of other marine species. None of the land-based farms are located in sensitive areas. Most of these facilities have outflows which run directly into the sea. Smolt farms, producing smolts for commercial rearing, are required to have rotating screens in their outflows. There are no indications of escapes from these facilities (Árni Ísaksson, Agricultural Authority of Iceland, personal communication).

2.11 Other geographical areas

Relatively few farm escapees are probably found in the Baltic Sea (Fiske et al. 2006), but some escaped farmed salmon have been recorded in Danish rivers even though there is no Atlantic salmon farming (Jepsen et al. 2003a,b), with up to 20% in some river samples (Jepsen et al. 2003a,b). Escaped farmed salmon have not been recorded in Estonia and Germany. Rare records of escaped farmed salmon have been reported in Lithuania, Latvia, Poland and Sweden (Fiske 2006).

In Finland, there is no Atlantic salmon farming (NASCO 2005a), but the proportion of escaped farmed salmon has been monitored in the Teno River fisheries since the mid-1980s (ICES 2006). This river holds one of the largest Atlantic salmon populations of the world and is shared with Norway (lower part). The proportion of escaped farmed fish has been low during the fishing season (maximum 0.7%), but with higher incidences later in the autumn, with up to 40-50% in some samples. However, the sample sizes in the autumn have been small (ICES 2006).

There is only one commercial marine cage rearing facility for Atlantic salmon in Russia, on the Kola Peninsula (NASCO 2005a). Only one small scale leakage of salmon juveniles has been reported from cages at an on-growing site at Trifonojarvi Lake in 2004 (NASCO 2005a). Escaped farmed salmon from Norway might potentially spread to Russian rivers on the Kola Peninsula, as one recapture was made in the River Tuloma after an intentional release of farmed salmon in Southern Norway (Hansen 2006a).

2.12 Escapes of juveniles from freshwater hatcheries

Farmed salmon can escape from containment both during juvenile freshwater stages in hatcheries and from sea cages. Escapes from sea cages have attracted most attention, whereas little is known about the extent of parr escapes into rivers and sea from juvenile rearing units. The threat from such freshwater escapes is generally insufficiently recognized (Ferguson et al. 2007).

The occurrence of farm genotypes and the independent occurrence of mtDNA and minisatellite markers in several parr samples taken from a river in Northwest Ireland has shown conclusively that juvenile farm salmon that escape from a hatchery can complete their life cycle, breed and/or interbreed with native fish, upon their return to the river as adults (Clifford et al. 1998a). In this study escaped fish were also found to

home accurately, as adults, to the site of escape, i.e. the area adjacent to the hatchery outflow in the upstream part of the river. Furthermore the return of adults of farm origin to the river to breed was indicated in adults netted in the estuary of the river on which the hatchery was located.

In the Magaguadavic River on the east coast of Canada, 36%, 59% and 43% of the juveniles sampled in 1996, 1997 and 1998, respectively, were identified as escapes from commercial hatcheries (Stokesbury et al. 2001). In 1996, between 51% and 67% of the smolts migrating from this river were juvenile escapes from commercial hatcheries (Stokesbury & Lacroix 1997). Some of these escaped juveniles were later found to return to the river as adults, although survival at sea was considerably less than that of the wild salmon (Lacroix and Stokesbury 2004). A long-term monitoring program in the Magaguadavic River (1996-2005) revealed that juvenile escapees outnumbered wild salmon parr in most years (Carr & Whoriskey 2006). Escaped juvenile salmon were also recorded in 75% of the streams located close to freshwater hatcheries in New Brunswick (east coast Canada) (Carr & Whoriskey 2006).

In those countries where juvenile rearing units discharge to wild salmon rivers, the extent of juvenile escapes to these rivers may be substantial, although to date this has not been adequately studied (Ferguson et al. 2007). In New Brunswick, Canada, 18 commercial freshwater hatcheries were rearing juveniles in 2004. Of these, four were closed recirculating systems in which containment of fish should be 100%, five were situated next to seawater, and nine had some form of discharge into freshwater drainages (Carr & Whoriskey 2006). In Scotland, there are no regulations that state that commercial freshwater hatcheries should have outlets into the sea (Annie Hetherington, Aquaculture Policy and Development, Scotland). In Iceland, freshwater farms producing salmon smolts for commercial rearing are required to have rotating screens in their outflows, and are not located in sensitive areas. In Norway, discharge from freshwater hatcheries is required to be into the sea. The survival and behaviour of juvenile salmon if they escape from such freshwater hatcheries into the sea is not known.

In Chile, most of salmon smolts (probably more than 70%) are still produced in cages in lakes and rivers (see chapter 2.3). Escapes have occurred in all lakes with rearing sites as evidenced by the presence of all four species of farmed salmonids (Atlantic salmon, coho salmon, rainbow salmon and Chinook salmon) in experimental and recreational fisheries. The salmonid biomass is often much greater than that of native species (Soto et al. 2006). Atlantic salmon is present, and at times abundant in all the studied lakes with salmon farming (Soto et al. 2006). These fish may come from escapes, as well as intentional releases. For example in Lake Todos Los Santos where there are no salmon farms and natural access for fish is nearly impossible due to water falls. The highest reported abundance of Atlantic salmon was in Lake Rupanco, where it accounted for 35% the catch during experimental fishing (Soto et al. 2002). In general, however, the fish had a low condition index, suggesting that feeding conditions were poor. There are no reports in these basins and rivers of reproductive returns of this species. The most abundant fish are rainbow trout and brown trout *Salmo trutta*, which were introduced species prior to aquaculture and are believed to inhibit the establishment of other salmonids (Soto et al. 2006, Basulto 2003).

2.13 Methods to identify and monitor escaped farmed salmon

Outside the native range of Atlantic salmon, escaped farmed salmon are easier to identify when encountered in nature. Within the native range, escaped farmed salmon might be more difficult to distinguish from their wild counterparts. Several methods can be used to distinguish escaped farmed salmon from wild salmon, which are based on external morphology, scale characters, biochemical markers, effects of vaccination and genetics (reviewed by Fiske et al. 2005a).

Morphology and scale characters

Farmed salmon can differ morphologically from wild salmon in several ways: shortened gill covers such that the gills are visible when the covers are normally closed; snout/jaw deformations; bud fins (when dorsal or pectoral fins are worn down to a cartilage-like hump where the rays are no longer visible); wavy rays on dorsal or pectoral fins; rounded tail lobes; higher numbers of dark spots below the lateral line (Lund et al. 1989, Fleming et al. 1994, Fiske et al. 2005a). Newly escaped farmed salmon may be identified with near 100% precision using morphological criteria. However, in some instances fin damage might recover after some time in nature (Fleming et al. 1994), and in one study only 35% of samples of hatchery-reared smolts could be classified correctly as being of hatchery origin by these criteria (Lund et al. 1989). Farming practises have changed since Lund et al.'s (1989) study, and the occurrence of fin deformities has decreased as a consequence of more refined rearing techniques, making morphological characteristics less suitable for identifying escaped farmed salmon at present (Fiske et al. 2005a). Shortened gill covers, snout/jaw deformations and bud fins normally result in downgrading of fish quality at harvest with consequent severe reductions in market price, consequently the industry is making a concerted effort to reduce the incidence of such deformities (James Ryan, personal communication).



Escaped farmed salmon with shortened gill-cover and wavy rays on pectoral fin.

Photo: Eva B. Thorstad

At least six traits that influence scale characteristics differ between wild and farmed salmon, including smolt size, smolt age, transition from fresh water to salt water, sea age, summer growth and scale loss and replacement (Lund et al. 1989, Lund & Hansen 1991, Fiske et al. 2005a). The combined use of these characteristics in a score system

correctly classified 97% of farmed salmon and 55% of recaptured hatchery-reared smolts. Only 2% of wild salmon were incorrectly classified. By using an image processing system, the classification efficiency to separate farmed, recaptured hatchery-reared smolts and wild salmon was 74% (Friedland et al. 1994).

Image processing of scales provides an objective way of classifying fish to farmed or wild origin (Friedland et al. 1994), but is more resource demanding than manual scale reading and is not immediately available in the field. Therefore, it is not used in surveillance programmes (Fiske et al. 2005a). Otoliths can be used much in the same way as scales to identify escaped farmed salmon (Hindar & L'Abée-Lund 1992), but require more work.

One limitation of using both morphological and scale characters to identify escaped farmed salmon is that it is biased towards recently escaped fish, which have spent less time in nature. This implies that proportions of escaped farmed salmon in nature will be underestimated. In the Norwegian monitoring programme, morphological and scale characters are used in combination to enhance correct identification (Fiske et al. 2005a). A score classification has also been used in Chile using morphological characteristics and scale analysis, which can differentiate a fish that has been more than six months in the wild with up to 70% certainty (Soto et al. 1996).

Biochemical methods based on carotenoid content or stable isotopes

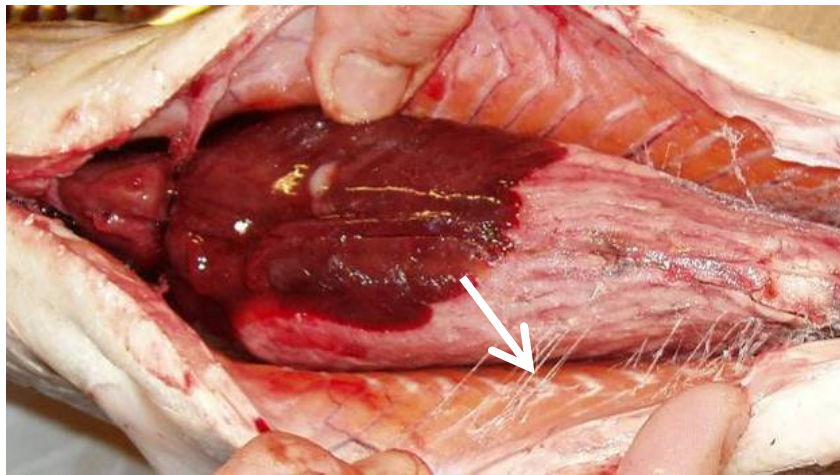
The natural carotenoid pigment in wild Atlantic salmon is astaxanthin. Earlier, synthetic canthaxanthin was used in the diet as the main source of pigmentation in the farming industry. By analysing for canthaxanthin content, farmed fish fed on a diet with canthaxanthin, and the eggs and newly hatched fry from farmed females could be identified (Craik & Harvey 1987, Poole et al. 2000). This method was used to identify farmed salmon in the spawning populations and the offspring from farmed females in Scottish rivers (Webb et al. 1993a,b, Youngson et al. 1993). Synthetic canthaxanthin is not commonly used in farmed fish diets at present.

In later years, synthetic astaxanthin has become the most commonly used source of pigment enhancement (Lura & Sægrov 1991a). The proportions of isomers of astaxanthin differ between the diets fed farmed salmon and that in the natural diet of wild salmon. Like canthaxanthin, this can be used to identify farmed fish, and the eggs and alevins of escaped females (Lura & Sægrov 1991a). However, the contribution of farmed fish to wild populations will be underestimated, because escaped fish may start feeding on natural prey items and accumulate natural pigment after escape (Lura & Økland 1994). Overall, it was predicted that 46% of females and 61% of males of escaped farmed salmon in Norwegian rivers could be correctly classified using this method.

Stable isotopes of carbon and nitrogen reflect diet characteristics and can be used to identify escaped farmed salmon from wild salmon, at least during the first few months following escape (Dempson & Power 2004). However, it is not known how long escaped fish retain their characteristic isotope signature once they have begun feeding on organisms similar to those utilised by wild salmon.

Visual markers after intra-abdominal vaccination

Intra-abdominal vaccination of salmon to prevent disease is extensively used in commercial farming, which may cause an apparently permanent, internal mark suitable for identification of escaped farmed fish (Lund et al. 1995, Fiske et al. 2005a). Nearly all salmon parr in commercial aquaculture are intraperitoneally vaccinated. An abdominal mark results from the adherence of connective tissue between the abdominal wall and the abdominal organs, which is observable in 81-100% of vaccinated fish (Lund et al. 1995). However, improved vaccines have resulted in less severe adhesions, and now more than one third of the vaccinated fish have almost no adhesions and are therefore difficult to detect (Fiske et al. 2005a).



Adherences of connective tissue between the abdominal wall and organs caused by intra-abdominal vaccination.

Photo: Peder Fiske

Genetic methods

Several studies have demonstrated that there are genetic differences between strains of aquaculture salmon and wild salmon populations (Mjølnerød et al. 1997, Norris et al. 1999, Skaala et al. 2004, 2005, Rengmark et al. 2006). Skaala et al. (2004) investigated the variation at 12 microsatellite loci in five aquaculture strains and four wild populations from Norway. They found significant differences both between wild and farmed salmon, and also between the different aquaculture strains. The pair wise genetic distances between the different aquaculture strains were 2-8 times higher than among the wild populations. Employing assignment tests, they found that < 4% of farmed-origin individuals were misclassified as wild salmon.

However, the results of this study do not guarantee that escaped salmon of aquaculture origin can be identified by genetic methods under all circumstances. The high precision in assignment tests was achieved due to the significant differences in allele frequencies at a large number of microsatellite loci, not to the existence of any specific allele at a locus that can unambiguously distinguish aquaculture salmon from wild salmon. The alleles present at neutral loci in aquaculture salmon are probably all present in wild populations. The genetic variation at such loci in the aquaculture strains is lower than in

the wild populations, but they represent a subset of the variation found in wild populations.

Genetic methods can be used to identify salmon of non-local origin (whether escaped aquaculture salmon or strays) in a river by comparing the individuals' multilocus genotype to a genetic baseline for the local population. If the genetic baselines of the aquaculture strains are known, it can also be compared to these and its origin may be determined. However, the existence of multiple strains in the net pens in the area may complicate the matter. Although the main aquaculture strains may be clearly differentiated and distinguishable, the aquaculture salmon present in the net pens may differ from these strains due to cross breeding of different strains at the local breeding stations where the smolts are produced. This implies that the number of different genetic baselines needed to identify aquaculture salmon is much higher than the number of strains at the main breeding centres.

A further complication is that if aquaculture produced salmon continue to escape at the present rates and interbreed with wild salmon, the genetic differences between wild and aquaculture salmon may steadily diminish, making it more difficult to identify the escaped fish and hybrids of escaped and wild fish (Hindar et al. 2006).

At present, there is no marker available that definitely distinguishes aquaculture salmon from wild fish. However, the ongoing breeding program and selection on traits suitable for farming has probably resulted in genetic differences in coding DNA that may provide a useful source of diagnostic markers in the future. Indications that such differences exist were found by Roberge et al. (2006) in a study comparing the transcription profiles of a large number of genes in progeny of wild and farmed salmon. They found clear differences between the farmed and the wild fish, and also evidence of parallel changes in two different farmed strains.

2.14 Migration, dispersal and survival of escaped farmed salmon

Dispersal and survival

Hatchery-reared smolts released at marine sites tend to return to the release area as adults, entering nearby rivers later in the season for spawning (Carlin 1969⁷, Sutterlin et al. 1982⁶, Gunnerød et al. 1988⁶, Eriksson & Eriksson 1991⁶, Hansen & Jonsson 1991⁶, Heggberget et al. 1991⁶, reviewed by Jonsson 1997). Homing precision and survival seem to depend on time of release. Hatchery-reared post-smolts held in saltwater and released sequentially for one year, showed poor survival when released during late summer and autumn, and poor homing precision when released during winter (Hansen & Jonsson 1989⁸, 1991⁷). Dispersal may also depend on proximity to the coast and coastal currents. In sea ranching experiments conducted in Norway in the 1990s, fish released at one locality in western Norway, and in two localities in northern Norway, showed differing dispersal patterns. The fish released at the locality in western Norway, which was situated on the open coast close to the strong coastal current, showed greater

⁷Studies based on marine releases of first generation hatchery-reared smolts from wild parents.

⁸Studies based on marine releases of first generation hatchery-reared smolts from wild parents, kept in seawater from the smoltification stage until release between one week and 14 months later.

dispersal than the fish released in northern Norway in areas without strong coastal currents (Skilbrei et al. 1998).

Pre-adult salmon that escape both in early summer, autumn and winter tend to disperse more widely than smolts (Hansen et al. 1987⁹, Hansen 2006a). The pre-adults in these Norwegian studies seemed to move north with the current, and when they were ready to spawn, many entered rivers in the nearby area. Post-smolt farmed salmon released during summer have also been recaptured north of the Faroe Islands (Hansen et al. 1987⁸). Further, farmed salmon caught in the Faroese longline fishery that have been tagged and released, have been recaptured in Norway (Hansen & Jacobsen 1993, 2003).

Salmon experimentally released from Norwegian fish farms in autumn one year before attaining sexual maturity appeared to survive poorly to sexual maturation, whereas salmon escaping later in winter showed greater survival (Hansen 2006a). This suggests that the closer to maturity the adult salmon are when they escape, the higher the probability of survival to maturity. The released salmon appeared to move north with the current and appeared to have a very weak homing instinct, if any. Most recaptures in rivers occurred within 500 km from the release site, but there were also recaptures in rivers up to 2000 km from the release site (**figure 2.11**). (Escaped farmed salmon have also been encountered in Alaska, up to 4500 km from the nearest sea pens in British Columbia and Washington, McKinnell et al. (1997).)

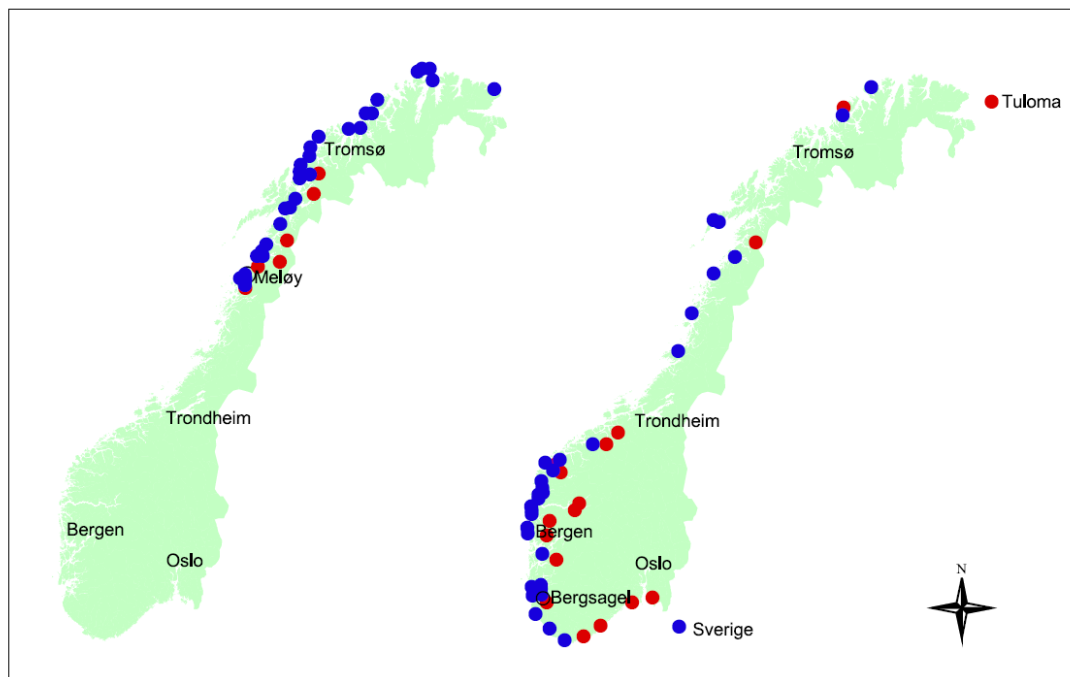


Figure 2.11. Geographical distribution of recaptures of farmed salmon tagged and released at Meløy in Northern Norway (figure to the left) and Bergsagel in Southern Norway (figure to the right) in 1993-1995. Blue dots indicate recaptures in the sea and red dots indicate recaptures in rivers. Figure from Hansen 2006b.

⁹ Study based on marine release of first generation hatchery-reared fish from wild parents, kept in a seawater pond in the hatchery for one year after smoltification, and then transferred to a sea farm for one year before release.

Similar results were obtained in a study where adult salmon fitted with acoustic transmitters were released from a fish farm in Cobscook Bay, Maine, USA (Whoriskey et al. 2006). The fish dispersed > 1 km from the cage site within a few hours after release. Mortality was high within Cobscook Bay and the surrounding region, and was higher during spring (84%) than winter (56%) releases. Mortality was probably mainly due to seal predation, and the higher mortality in spring was consistent with a higher abundance of seals. Most surviving fish exited the coastal zone and entered the Bay of Fundy along the routes of the dominant tidal currents, passing through Canadian waters. No tagged fish entered rivers in the Cobscook Bay or Bay of Fundy area during the spawning season.

If post-smolt salmon close to maturity escape from a fish farm, a relatively large proportion and number of these fish may survive and enter nearby rivers. Fifty per cent of maturing (determined by the development of secondary sexual characters) salmon released from a fish farm 2 km from the mouth of the Norwegian River Alta in early August entered the River Alta, after spending only average 106 hours in the sea (Heggberget et al. 1993a). Large rivers seem to attract a larger proportion of the escaped farmed salmon than smaller rivers (Heggberget et al. 1993a, Thorstad et al. 1998).

It can be concluded from the studies referred to above that if many salmon escape as smolts or early in the post-smolt stage, the incidence of escapees in rivers close to fish farms may be higher than if the farmed fish escape at later life stages, except when nearing maturity. A positive correlation was found between the incidence of escaped farmed salmon in the rivers and the intensity of salmon farming on a county level in Norway (Fiske et al. 2006a). This appears contrary to the results of Hansen (2006a) that adult farmed salmon move with the current and do not home to the release site. However, the results by Fiske et al. (2006a) might imply that a large proportion of the fish escaping from fish farms do so close to the smolt stage (also found by Lund 1998b) and home to their release area. Whoriskey & Carr (2001) captured farm escapees entering New Brunswick's Magaguadavic River during the spawning season, tagged them, and transported them up to 50 km away to see if they would home back. In one of three years, they found evidence of homing to this river, perhaps reflecting the imprinting of these fish as smolts to one of the commercial hatcheries in the river system. These hatcheries generated up to about 30% of the region's smolt production.

In Chile, the very few reports on escaped salmon suggest that most of the salmon remain near the farming areas where they are captured rather quickly by artisanal fishing (Soto et al. 1996, 2001). However, farmed salmon were experimentally tagged and released from a farm site to evaluate different recapture methodologies, but this was not successful (Melo 2004), probably because the recapture methodologies were not effective. Escaped salmon have also been captured in rivers nearby farms, where fishing is often intense. There is, however, no monitoring of rivers, except that provided ad hoc by sport fishermen.

Within-river migration and distribution

Despite being seemingly physically inferior (see chapter 3), escaped farmed salmon entering the rivers migrate upstream as fast as wild salmon, and a higher proportion of farmed than wild salmon distribute themselves in the upper parts of the rivers (Thorstad et al. 1998, Heggberget et al. 1993a, 1996, Butler et al. 2005). This physical ability was confirmed by a laboratory study, where endurance in forced swim trials did not differ

between adult farmed and sea-ranched Atlantic salmon (Thorstad et al. 1997). However, there are indications that escaped farmed salmon are less capable of passing large and difficult waterfalls than wild salmon (Johnsen et al. 1998).

No erratic movement pattern was found in farmed compared to wild salmon during the upstream migration phase (Heggberget et al. 1996), but farmed salmon showed more and longer up- and downstream movements during the spawning period (Thorstad et al. 1998, Økland et al. 1995). Even though farmed salmon were distributed higher up in the river, wild and farmed salmon were not geographically separated during spawning, and farmed salmon stayed in parts of the river with important wild salmon spawning areas (Økland et al. 1995, Heggberget et al. 1996, Thorstad et al. 1998, Butler et al. 2005). The erratic movement patterns in the river during spawning might have several explanations (see chapter 3.3).

The distribution of escaped farmed salmon high up in the rivers might be explained by their lack of previous river experience and imprinting, and thereby lack of a 'stop signal' in a particular home area of the river (Thorstad et al. 1998, Heggberget et al. 1996). In contrast, previous studies reported farmed salmon to be more confined to the lower reaches than wild salmon (Webb et al. 1991, 1993a,b). However, the farmed salmon in these studies originated from a hatchery using river water from lower reaches before being transported to sea pens, and they were therefore probably imprinted to the lower reaches. Non-maturing escaped farmed salmon have been shown to enter a Canadian river (Lacroix et al. 1997), but failed to migrate to known spawning areas, likely due to their failure to mature sexually (Carr et al. 1997b).

2.15 Conclusive statements

- Escapes from fish farms occur both through repeated low-number incidents and through large-scale episodic events such as storms.
- Reporting escapes from fish farms to government authorities are required by law, regulation or as a condition of the operating permits in most salmon producing countries. Also, the number of reported escapes is available to the public in most salmon producing countries. The exceptions are New Brunswick, Canada, and Northern Ireland, UK, where the escape statistics are treated as confidential and not available to the public. In the Faroe Islands, there have been no requirements to report escapes until now, but escape events were still reported in the past, and information on number of escapes was provided by the industry for this report.
- Most of the reported escapes seem to be large scale events, when a large number of salmon have escaped due to bad weather, accidents, technological failures etc. The magnitude of unreported escapes is not known.
- Actual numbers of escaped farmed salmon occurring in different localities in nature is not known for any geographical area. The existence and quality of monitoring programmes of escaped salmon in nature differ among geographical areas. The most extensive and longest lasting monitoring programme exists in Norway, where a number of coastal localities and rivers are monitored annually.

- There are requirements to tag farmed salmon in Iceland (10% of all farmed salmon are tagged with coded wire tags) and Washington State, US (all cultured salmon are given an otolith thermal mark to distinguish escapes from those originating in nearby British Columbia, Canada).
- Little is known about the extent of escapes into rivers and sea from juvenile rearing units. The threat from such freshwater escapes is generally insufficiently recognized, especially where juvenile rearing units discharge to wild salmon rivers, or in rivers where juvenile Atlantic salmon can establish populations outside the native range of the species. Juvenile farm salmon that escape from a hatchery can complete their life cycle, breed and/or interbreed with native salmon, upon their return to the river as adults.
- Studies in Norway indicate that escaped farmed salmon found in different localities in nature originate from many different escape events and not only from certain reported large-scale events. A relatively large proportion of the escaped farmed salmon captured in the rivers and on the coast seems to have escaped as smolts or post-smolts (up to 50%).
- Most of the escaped farmed salmon in Norwegian rivers during spawning are mature (87% of females and 92% of males). There is a higher proportion of males (65%) than females among the escaped salmon in the spawning populations. In contrast, high numbers of immature escaped farmed salmon have been reported to enter rivers in North America.
- Escaped farmed Atlantic salmon are easier to identify when encountered in nature outside their native range than inside.
- Escaped farmed Atlantic salmon can be distinguished from wild Atlantic salmon based on external morphology, scale characters, biochemical markers, effects of vaccination and genetic differences. Farmed salmon that escape at an early life stage, and that have been in the wild for some time, are more difficult to identify than recently escaped salmon.
- Genetic methods can be used to, for instance, identify salmon of non-local origin in a river. At present, however, no genetic markers are available that can distinguish farmed from wild salmon without error.
- Distribution and survival of escaped farmed salmon in the wild depends on the life-stage and time of the year at release.
- Salmon released as smolts tend to home to the area of release and enter nearby rivers for spawning. However, survival and homing precision vary with the time of release (poorest survival for fish released in late summer and autumn, and poorest homing precision for fish released in winter).
- Salmon that escape as pre-adults seem to have a weak homing instinct and show a low propensity to return to the release area for spawning. Many appear to move with the current and enter rivers in the nearby area when they are ready to spawn. Escaped salmon are usually recorded within 500 km of the escape site, but have been recorded up to 2 000-4 500 km from the escape/release site.
- Escaped farmed salmon enter the inner fjord areas and rivers later in the season than wild salmon. When escaped farmed salmon enter the rivers, they migrate fast upstream.

- Mature escaped farmed salmon entering rivers generally distribute themselves high up in the rivers when there are no large migration barriers. They stay in parts of the rivers with important wild salmon spawning areas together with the wild salmon.

2.16 Knowledge gaps and research needs

- The actual numbers of salmon escaping from farms is not known for any geographical area. More information on why, which (e.g. life stage) and how many fish are escaping is needed.
- Information on the survival and dispersal of escaped farmed salmon at different life stages, different sites and different times of the year is still missing. Much of the previous information is based on studies of releases of first generation hatchery-reared fish. More studies with domestically selected commercial farm reared salmon are needed, including simulated releases. This is critical for determining optimal strategies for the location of farms to reduce the potential impacts of escapees. With an increasing move to site fish farms in off-shore localities, and the potential to massively expand salmon production there, there is a need for knowledge on how off-shore escapees will behave, distribute themselves and survive.

3 Ecological and behavioural interactions between wild and farmed Atlantic salmon in nature

3.1 Morphological characteristics and physical condition of farmed salmon

Morphological characteristics

The characteristics of farmed salmon may singly, or together, affect their behaviour, competitive ability and spawning success relative to wild salmon. Farmed salmon can differ morphologically from wild salmon, including shortened gill covers such that the gills are visible when the covers are closed, snout/jaw deformations, bud fins, wavy rays on dorsal or pectoral fins and rounded tail lobes (see chapter 2, Fiske et al. 2005a). These deformities are mainly attributed to the fish farming environment (Soderberg & Meade 1987, Latremouille 2003, Fleming et al. 1994, Fiske et al. 2005a). Farming practise has changed markedly recent years, and the occurrence of fin deformities may have decreased as a consequence of improved rearing techniques (Fiske et al. 2005a). The occurrence of such deformities on escaped fish is dependent on the life stage when the fish escaped and the time since escape (see chapter 2).

Farmed salmon also show morphological differences from wild salmon such as decreased rayed-fin sizes and reduced body streamlining, which are probably both genetically and environmentally induced (Fleming et al. 1994, Fleming & Einum 1997, reviewed by Jonsson & Jonsson 2006). Fleming & Einum (1997) have reviewed the genetic changes in salmon associated with farming. Reduced body streamlining and increased body depth may reflect a relaxation of natural selection for sustained swimming performance. Additionally, the fish have been subjected to directed artificial selection for rapid growth based on body weight, which may have generated a correlated positive response in body depth. The reduced fin sizes might be attributed to mechanical abrasion as well as relaxed selection for swimming performance combined with artificial selection generated by high levels of fin nipping and erosion.

Fat content and physical condition

Farmed salmon have a higher fat content in the white muscle than wild salmon (Aksnes et al. 1986, Thorstad et al. 1997¹⁰). It is likely that the fat content is highest in recently escaped salmon, and declines with time in nature. Outside the native range of the Atlantic salmon, escaped salmon may feed poorly and the condition factor become low (Soto et al. 1996, see also chapter 5).

Reduced potential for swimming in net pens compared to in the wild may reduce the physical condition of the fish. However, farmed salmon may now be reared in water with a higher current speed than was used in earlier stages of the industry's development (James Ryan, personal communication). Heart mass relative to somatic mass, which may reflect physical condition, was smaller for farmed than for wild females, but did not differ between farmed and wild males (Fleming et al. 1996). Further, the hearts of farmed salmon are rounder, and the angle between the ventricular axis and the axis of the bulbus arteriosus is more acute in wild than in farmed salmon

¹⁰ Comparison of farmed and sea ranched salmon (first generation offspring of wild parents)

(Poppe et al. 2003). This could be linked to increased mortality, reduced physical capabilities and reduced abilities to handle stressful situations in farmed salmon.

Morphological deformities, reduced body streamlining, shorter fins, higher fat content and reduced physical condition of the fish would likely lead to a reduced swimming performance of farmed compared to wild salmon. However, the short-term (up to 200 min) endurance in a swim speed chamber did not differ between farmed and sea ranched¹¹ salmon (Thorstad et al. 1997). The long distance migrations reported for some escaped farmed salmon in tagging studies also demonstrates considerable swimming capabilities for some farmed salmon.

Common garden experiments, testing for genetic differences between farm and wild salmon, indicate that swimming and cardiac performance (heart rate and stroke volume) did not differ between adult wild and farmed salmon (Dunmall & Schreer 2003). However, farm juveniles had 12-29% higher total swimming costs than wild juveniles in respirometry experiments, which was attributed to their deeper bodies and smaller fins (Enders et al. 2004).

3.2 Food competition in coastal areas and in the ocean

Escaped farmed salmon in the Atlantic Ocean seem to consume similar food resources as wild salmon. Wild and escaped farmed salmon caught on the marine feeding grounds north of the Faeroe Islands had similar condition factors, suggesting that the escapees that had survived and migrated to this region had been able to adapt effectively to the wild environment (Jacobsen & Hansen 2001). They showed no differences in frequency, number or weight proportions of prey compared with wild salmon, and there were no differences in diet. Moreover, a higher proportion of farmed fish contained food items in their stomach than wild fish. Farmed salmon caught in Scottish coastal waters also appear to adapt to feeding on natural prey (Hislop & Webb 1992).

Few studies have investigated feeding competition between wild and farmed salmon in coastal areas and in the ocean. However, ocean mortality of salmon appears to be density-independent, indicating that the marine abundance is beneath the carrying capacity for the species (Jonsson & Jonsson 2004). A generally reduced marine growth rate observed in wild salmon is probably best explained by cooler marine water temperatures (Jonsson & Jonsson 2004). Hence, it is not likely that availability of food in the ocean is a limitation for Atlantic salmon production, and that feeding competition with escaped farmed salmon limits food availability for wild salmon. However, Jonsson & Jonsson (2006) note that little is known about the effects of large numbers of escaped farmed salmon on food resources in coastal areas and suggest that competitive interactions may occur in areas with high densities of cultured fish.

¹¹ Hatchery-reared salmon of wild parents, released as smolts and captured for experiments when returning from the sea as adults.

3.3 Interactions during spawning, spawning success and production

Escaped farmed salmon are present on spawning grounds during the spawning period, and even in high numbers in some rivers (see chapter 2). Successful spawning by escaped farmed female salmon has been documented frequently (e.g. Lura & Sægrov 1991b, Crozier 1993, Lura & Sægrov 1993, Lura et al. 1993, Webb et al. 1991, 1993a,b, Sægrov et al. 1997, Clifford et al. 1998a,b, Crozier 2000, Volpe et al. 2000). However, different phenotypic and genetic characteristics might affect spawning behaviour and success of escaped farmed salmon compared to wild salmon (reviewed by Weir & Fleming 2006).

Studies of spawning behaviour and success in experimental spawning arenas

The reproductive behaviour and success of farmed and wild Atlantic salmon have been thoroughly studied in experimental spawning arenas (Fleming et al. 1996, 2000, Garant et al. 2003, Weir et al. 2004, 2005). The farmed and wild females had similar levels of competitive behaviour but differed in reproductive behaviour and success (Fleming et al. 1996). Farmed females displayed less breeding behaviour, constructed fewer nests, retained a greater weight of eggs unspawned, were less efficient at nest covering, incurred more nest destruction, and suffered greater egg mortality than wild females. As a result, farmed females had 20-40% of the reproductive success of wild females. The farmed males were even less successful than the farmed females in competition with the wild fish. They were less aggressive, courted less, partook in fewer spawnings, and achieved only an estimated 1-3% of the reproductive success of the wild males. Hence, the farmed males exhibited inappropriate mating behaviour that led to poor fertilization success, even in the absence of competition with wild males. Moreover, farmed males incurred more wounding and had a higher mortality during the breeding season. Body size was a key determinant of spawning success in wild, but not in farmed salmon. It was concluded that hybridisation¹² between farmed females and wild males in nature is likely to occur (Fleming et al. 1996). Similar results were obtained in a later study in the same experimental spawning arenas, but notably with a higher breeding success for farmed males (24% of the breeding success of wild males: Fleming et al. 2000). The differences in spawning behaviour and success between wild and farmed salmon were probably both genetically and environmentally induced (Fleming et al. 1996, 2000).

The spawning success of farmed males was further explored by Weir et al. (2004) in the same spawning arenas. Farmed males did not establish dominance hierarchies as effectively as wild males. However, they courted and spawned with females in larger numbers, but frequently failed to release sperm when females released eggs. This study emphasises that the degree of reproductive inferiority displayed by farmed relative to wild males can vary, and that the spawning success of farmed males will depend upon the rearing history and genetic background of the farmed and wild populations. This indicates that it is important to adopt a case-dependent approach when assessing the effects that a given farmed population may have on the persistence of a particular wild population is underscored (Weir et al. 2004).

¹² The term 'hybridisation' is used both for reproduction between individuals of different species and for reproduction between individuals of wild and farmed salmon in this report.

The variation in farm male reproductive success was further emphasized in a study of males that mature precociously in freshwater (i.e. males reaching maturity as parr, while still in freshwater, and sometimes as early as their first year of life) (Garant et al. 2003). The male parr of farmed parents had a higher breeding and fertilization success than wild and hybrid (farm x wild) individuals. Specifically, hybrid parr had 57% and wild parr 25% of the reproductive success of farm parr. Escaped early maturing males could thus promote introgression of domesticated and/or non-native traits into wild populations. The differences observed in this study were likely genetic in origin, as the groups were reared under nearly identical environmental conditions (Garant et al. 2003). The results were later supported by the work of Weir et al. (2005).

The studies described above, except those examining spawning success of male mature parr (Garant et al. 2003, Weir et al. 2005), are believed to be representative of the spawning behaviour and success of newly escaped farmed salmon, as the farmed salmon used in the experiments were taken directly from a fish farm (Fleming et al. 1996, 2000). What about farmed salmon that have escaped at an earlier life stage and spent a longer time in nature - do they have a higher spawning success than newly escaped farmed salmon?

Studies of the spawning behaviour and success of farmed salmon escaping at an early life stage have not been performed, but results from sea ranched salmon indicate that even first generation salmon of wild offspring that have been released as smolts have a reduced spawning success compared to wild salmon, although not to the same extent as the farmed salmon (Fleming et al. 1997). The aggression levels of sea ranched and wild males were similar, but sea ranched males were involved in more prolonged aggressive encounters and incurred greater wounding and mortality than wild males. Furthermore, they were less able to monopolise spawnings, and as a result, obtained 51% the reproductive success of wild males. No difference was found in breeding performance between sea ranched and wild females, but sea ranched females produced smaller eggs, apparently in response to their higher juvenile growth rate (Fleming et al. 1997). This study demonstrates that previous experience, even in early life, has implications for the subsequent reproductive performance. Compared to the sea ranched salmon, farmed salmon escaping at an early life stage would not only be affected by differences in early experience, but also by genetic divergence from the wild fish. Thus, the spawning success of farmed salmon escaping at an early life stage is probably somewhere between that of the salmon taken directly from the fish farms (Fleming et al. 1996, 2000), and that of the sea ranched salmon (Fleming et al. 1997).

Large-scale experiment in the small Norwegian River Imsa: lifetime success and interactions of farmed salmon invading a native population

Work in the experimental arenas was followed up by a large-scale experiment to quantify the lifetime success and interactions of farmed salmon invading a small Norwegian river (1 km long) (Fleming et al. 2000). The lifetime success of the farm salmon (adult to adult) was 16% of that of the native wild salmon. Breeding was the major bottleneck impeding the invasion. The farm salmon were competitively and reproductively inferior, and the farmed adults had only 19% of the reproductive success of the native adults up to the 0+ stage (i.e. breeding and early survival). Similar to the arena results, this inferiority was sex biased, being more pronounced among farmed males than females. Few, if any of the farm x native offspring captured from the river were fathered by farmed males. Thus, gene flow occurred mainly through native males

breeding with farmed females. A lower early survival of the farm genotypes also appeared to constrain the invasion, though to a lesser extent than observed differences in breeding success. Interestingly, evidence for resource competition and competitive displacement was found, as the invasion of the farmed salmon reduced the river's smolt production by 28% compared to what was expected from the number of eggs produced. For wild females, this reduction was more than 30%. Thus, invasions of escaped farmed salmon have the potential for impacting negatively on population productivity (Fleming et al. 2000). The depression in smolt production may reflect fluctuating selection on offspring type, with competition from the farm and hybrid offspring depressing the wild offspring survival during one or more life-history episodes - and maladaptation depressing the farm and hybrid offspring at other times (Fleming et al. 2000, see also McGinnity et al. 1997).

Observations of farmed salmon spawning success in the wild

The first study of farmed female spawning success in the wild reported that the proportion of spawning redds from farmed females matched their proportion in the spawning population in two rivers, indicating a high spawning success (Lura & Sægrov 1991b). In a third river, spawning redds of farmed females were not fertilized (Lura & Sægrov 1991b), which might reflect inappropriate reproductive behaviour of farmed males (Fleming et al. 1996).

High spawning success of farmed females was reported from the River Vosso, Norway (Sægrov et al. 1997). The frequency of spawning redds made by farmed females was in accordance with their estimated representation (81%) in the spawning population, and the egg survival was high and similar to previous estimates for wild salmon. For unknown reasons, the wild population in this river declined and has been low since the early 1990s (Sægrov et al. 1997). A lack of competition with wild fish during spawning due to the reduced wild population might have facilitated this high spawning success of the escaped farmed salmon. In the same river, excavation of stranded redds revealed differences in spawning behaviour between farmed and wild salmon (Lura et al. 1993). The redd of a farmed salmon contained more egg pockets and fewer eggs per pocket. No other pocket measures differed.

Genetic changes to native populations were studied in two rivers in Ireland following an escape of 29 000 salmon from sea cages adjacent to the estuaries of the rivers in March 1992 (Clifford et al. 1998b). The proportion of juveniles of maternal farm parentage ranged from 18% in 1993 to 2% in 1995, with an average of 7% in both rivers and a maximum frequency of 70% in an individual sample. Thus, only a small proportion of the farmed salmon that escaped in spring 1992 appeared to have bred successfully in these two rivers. Another study from Ireland has documented that juveniles escaping from a commercial freshwater rearing unit into a river were able to complete their life cycle, breed and interbreed with native fish, upon their return to the river (Clifford et al. 1998a).

The behaviour of radio tagged farm escapees and wild salmon during the spawning period was studied in two large rivers, with results indicating that the farmed salmon had a lower spawning success than the wild salmon (Økland et al. 1995, Thorstad et al. 1998). The farmed salmon had a more erratic movement pattern, with more and longer movements up and down in the river during the spawning period than the wild salmon. This movement pattern may have several explanations. The lack of previous river

experience and a possible competitive disadvantage stemming from these fish arriving late on the spawning grounds, which robs them of a prior residence effect, may have lead to difficulties in selecting and defending spawning sites. Farmed salmon may roam from spawning area to spawning area because they have poor success in mating and/or because dominant wild fish chased them off. A lower proportion of escaped farmed (25%) than wild (82%) males was recorded in a spawning area, but there was no such difference between females (Økland et al. 1995).

Timing of spawning

Escaped farmed salmon may spawn before, during or after the peak spawning period in a river, depending on the spawning time of the wild fish in that river and of the farmed salmon (e.g. Webb et al. 1991). Studies of the spawning time of escaped farmed salmon in Norwegian rivers all report a peak spawning period some time in November, which in some rivers was before and in some rivers after the normal wild salmon spawning period (L'Abée-Lund 1988, Lura & Sægrov 1993, Thorstad et al. 1996, Sægrov et al. 1997, Fleming et al. 2000). This indicates that there is a genetic component determining timing of breeding in both wild and farmed salmon.

The spawning time of wild populations in Norway varies among rivers, even within relatively small geographic areas, and ranges from October to January (Heggberget 1988). For a given river, the spawning time is relatively consistent among years. The timing of spawning is suggested to be an adaptation to local temperature conditions in the river (Heggberget 1988). The eggs hatch in the spring as development is completed. This development in turn is temperature-dependent and correlates tightly with incubation temperatures (measured as accumulated number of degree-days), and with the spawning time (Crisp 1981, Heggberget & Wallace 1984, Wallace & Heggberget 1988). The variation in spawning time might thus be a local adaptation to ensure hatching and initial feeding at an optimal time in the spring in rivers with different temperature regimes (Heggberget 1988).

The early or late spawning of escaped farmed salmon could result in offspring hatching and initially feeding during a sub-optimal period in the spring, and thereby a higher juvenile mortality (Lura & Sægrov 1993). However, an increasing water temperature in the spring might be more important for triggering hatching than the accumulated degree days during incubation (Heggberget & Wallace 1984, Wallace & Heggberget 1988), such that eggs spawned at different times in the autumn might still hatch at the same time in the spring. Thus, the effects of earlier or later spawning on the survival of the juveniles might be river specific and therefore difficult to predict.

Differences in the timing of spawning between escaped farmed and wild salmon might reduce the level of hybridisation and the spawning success of the farmed fish. Based on the poor spawning success of farmed males in the experimental studies described above, farmed females might be dependent on wild males for successful spawning. However, wild males are usually active on the spawning grounds for a longer time period than the wild females (Webb & Hawkins 1989), such that wild males can be available even though the spawning time of farmed females differs slightly from that of wild females. With a larger difference in spawning time, one might speculate that the reproductive success of farmed fish would be reduced due to a lack of males.

With farmed fish spawning later than wild fish, there is a danger of destruction of redds of wild fish (Lura & Sægrov 1993). Nest destruction through nest superimposition may be an important cause of female egg mortality (Lura & Sægrov 1991b), but the extent to which happens is not known.

3.4 Performance of farmed salmon offspring and effects on wild populations

Following successful breeding, or escape from freshwater facilities, behavioural and life-history characteristics of farmed salmon offspring (and farmed x wild hybrids) will influence their performance and effects on native fish in the natural environment (reviewed by Weir & Fleming 2006).

Diet, foraging and habitat selection

No differences in diet were found among farm, hybrid (wild x farmed) and wild 0+ offspring for fish released into a stream for two months (Einum & Fleming 1997). Furthermore, there was no difference among the groups in current or depth preferences, but the farm juveniles tended to stay in slower flowing parts of the stream than hybrids and native juveniles. Similarly, a large diet overlap was found among farm, hybrid and native wild 0+ offspring produced in a small river (Fleming et al. 2000).

The overlap in habitat use and diet suggests that farm, wild and hybrid juveniles compete for territories and food, and that the presence of farm and hybrid juveniles in the river environment limits food and habitat resources for wild fish. It has been demonstrated that faster growing farm and hybrid juveniles can competitively displace smaller native juveniles downstream (McGinnity et al. 1997, 2003). Also Fleming et al. (2000) found that the distribution of smaller native juveniles differed from that of farm and hybrid juveniles and related this to competitive displacement. In contrast to McGinnity et al.'s results (1997, 2003), the native juveniles were distributed further upstream than the farm and hybrid juveniles.

The studies referred to above considered farmed salmon offspring born into the wild, being the offspring of successful farmed spawners. Farmed fish escaping as juveniles from freshwater rearing facilities (Carr & Whoriskey 2006) may in many ways be more equivalent to hatchery-reared fish deliberately released, although hatchery-reared fish are often first generation offspring of wild parents and do not differ genetically from wild fish to the same extent as farm fish.

Growth

Having been subjected to intentional selection for increased growth, it is not surprising that both farm salmon and hybrids (farm x wild) show a higher growth rate than wild fish, and that farm and hybrid offspring of a given age are larger than their wild counterparts (Einum & Fleming 1997, Fleming & Einum 1997, McGinnity et al. 1997, 2003, Fleming et al. 2000, 2002, Handeland et al. 2003). The discrepancies in growth between farm and wild offspring are even more evident in salt water than in fresh water (Fleming et al. 2002).

Increased growth rate in farmed versus wild salmon is a result of both greater feed consumption and more efficient feed utilization (Thodesen et al. 1999, Handeland et al.

2003). Faster growth of farm relative to wild juveniles has been shown to be associated with increased growth hormone levels in farm fish, but this difference was age and stage dependent (Fleming et al. 2002). Growth hormone might for instance stimulate dominance, foraging rate and growth (Martin-Smith et al. 2004).

Higher growth rates in farm juveniles might result in their smolting at a younger age. Age at smoltification was younger (Fleming et al. 2000) or similar (McGinnity et al. 2003) to wild fish in the natural environment. Also, weight and length at smoltification tended to be higher among farm and hybrid fish in both hatchery and river environments (Fleming & Einum 1997, Thodesen et al. 1999, Fleming et al. 2003, Handeland et al. 2003).

Aggression and dominance

In the hatchery, farm and hybrid (farm x wild) juveniles were more aggressive than wild salmon juveniles and tended to dominate them in pair-wise contests (Einum & Fleming 1997, Fleming & Einum 1997). However, it has been suggested that the expression of aggression and dominance may be context-dependent; farm juveniles were more aggressive and tended to dominate in a tank environment typical of culture facilities, whereas wild juveniles dominated in the stream-like environment (Fleming & Einum 1997). Aggression also seems to be dependent on the origin of the wild and farm fish (Einum & Fleming 1997). Prior residency might also lead to dominance, as shown by Metcalfe et al. (2003). Farmed fish were dominant over wild fish in pair-wise contests in a tank environment if both were raised in a hatchery environment. However, fish of wild origin could dominate farm fish when they had a prior residency time of two days. Wild fish that spent some time in a natural environment could also dominate both wild and farm fish raised in a farm environment (Metcalfe et al. 2003).

It was concluded by Weir & Fleming 2006 that the outcome of aggressive interactions between wild and farm juveniles depends upon the environment and the genetic background of the competitors. Wild fish might out-compete farmed fish in simulated natural environments, particularly if they have a prior residency advantage because they hatch earlier than farm juveniles or because farmed fish enter the river environment following escape from freshwater aquaculture facilities. However, in the latter case, larger body size of farmed juveniles may enable them to displace wild fish from their territories.

Predator avoidance

Farm juveniles are less risk averse, leaving cover sooner after a simulated predator attack than wild juveniles (Einum & Fleming 1997, Fleming & Einum 1997). Similar results were obtained by Johnsson et al. (2001), who found a more pronounced flight and heart rate response in wild than farm age 0+ juveniles, but not in older juveniles.

3.5 Conclusive statements

- Farmed salmon differ morphologically (e.g., morphological deformities, reduced body streamlining, shorter fins) and in physical condition (higher fat content, reduced swimming performance, differently shaped hearts) from wild salmon, which likely affects their behaviour, competitive ability and spawning success

relative to wild salmon. These characteristics are of both environmental and genetic origin.

- Escaped farmed salmon in the Atlantic Ocean seem to consume similar food resources as wild salmon.
- It is unlikely that availability of food in the Atlantic Ocean limits Atlantic salmon production, and food competition from escaped farmed salmon is unlikely to be strong.
- Escaped farmed salmon are able to spawn successfully in rivers both within and outside their native range.
- The spawning success of farmed salmon, however, is lower than that of wild salmon. Moreover, the spawning success of anadromous farmed salmon is sex biased, with that of males being lower than that of females. Thus, successful spawning by escaped farmed salmon in nature will most often result from breeding between farmed females and wild males.
- Anadromous farmed salmon that have escaped at an earlier life stage and spent a longer time in nature are likely to have a higher spawning success than recently escaped farmed salmon.
- Escaped farm female spawning success in rivers might be higher when the size of the spawning population and number of wild females, and thereby the competition level, are low.
- Escaped farmed salmon spawn before, during or after the peak wild fish spawning period in a river. There is a genetic component to breeding time in salmon.
- When farmed salmon spawn later than wild salmon, there is the danger of the destruction of the redds of wild fish.
- At juvenile stages, farm salmon and hybrids (farm x wild) can be expected to interact and compete directly with wild fish for food, habitat and territories.
- Farm juveniles and hybrids (farm x wild) are generally more aggressive and consume similar resources as wild fish. In addition, they grow faster than wild fish, which may give them a competitive advantage during certain life stages.
- The outcome of aggressive interactions between wild and farm juveniles vary, and depends upon the environment and the genetic background of the competitors.
- Prior residency can affect the outcome of competition for territories, but a larger body size of farmed juveniles may enable them to overcome any such effect.
- Farm juveniles are less risk averse than wild juveniles in the presence of a predatory threat.
- Invasions of escaped farmed salmon have the potential to impact the productivity of wild salmon populations negatively through juvenile resource competition and competitive displacement.
- While the outcome of interactions between farm and wild salmon will be context-dependent, varying with a number of environmental and genetic factors, they will frequently be negative for wild salmon.

3.6 Knowledge gaps and research needs

- Spawning success of farmed salmon likely varies at different competition levels (densities of spawners), but this has not been quantified.
- It is not known how a continuous influx of escaped farmed salmon influences wild salmon production over many years/generations in different rivers. Only studies of the ecological impacts over a single generation have been performed.

4 Genetic differences between farmed and wild Atlantic salmon and the effects of inter-breeding on wild populations

Recent reviews and summaries of genetic differences between farmed and wild salmon and the effects of inter-breeding on wild populations are given by Naylor et al. (2005), Ferguson et al. (2007) and Verspoor et al. (2006, 2007). Some sections of this chapter (parts of sections 4.1 and 4.2) are based on the Salmon leaflet produced by Verspoor et al. (2006) as part of the GENIMPACT project (www.genimpact.imr.no/), and used with the kind permission from Eric Verspoor. The Genimpact project is funded under the EU Framework Programme 6 to provide scientific advice in support of policy. We also refer to Ferguson et al. (2007), which should be consulted for a more extensive review than is provided here.

Escaped farmed salmon not only inter-breed with wild salmon, but also with wild brown trout (*Salmo trutta*), an issue, which is also highlighted in this chapter

4.1 Population structure and local adaptations in wild Atlantic salmon

Population structure

Natal homing for spawning, the discontinuous distribution of spawning and juvenile habitat, and a capacity for local adaptation promote genetic structuring among Atlantic salmon populations. The existence of structuring and a highly restricted contemporary gene flow, even among tributaries within many rivers, is indicated by observed temporally stable molecular genetic differentiation (reviewed by Verspoor 1997, Verspoor et al. 2005, 2007). Limited but sporadic gene flow among populations may locally link populations within or among rivers into evolutionarily connected meta-population groups, but this is poorly understood.

Genetic isolation has been sufficient for phylogenetic and evolutionary divergence to develop at all spatial scales (Verspoor et al. 2005). Atlantic salmon can be divided into three major phylogenetic groupings; Western and Eastern Atlantic salmon, and Baltic salmon (Ståhl 1987). A number of studies have demonstrated further structuring within these major units on different spatial scales (King et al. 2001, Verspoor 2005, Verspoor et al. 2005, 2007), including within large river systems (Primmer et al. 2006).

Local adaptation

Local adaptation is defined as a process whereby natural selection increases the frequency of traits within a population that enhance the survival or reproductive success of individuals expressing them (Taylor 1991). The conditions needed for local adaptation in Atlantic salmon exist and the evidence for it is compelling, though largely inferential (reviewed by Taylor 1991, Verspoor 1997, Verspoor et al. 2005, 2007, Garcia de Leaniz et al. 2007; see also McGinnity et al. 2004).

High heritabilities exist for variation in fitness-related traits such as growth and body composition, disease resistance, survival and maturation schedules. Further, genotype-environment interactions and genetic correlates occur for many traits, translocations of salmon generally fail, performance of domesticated stocks in the wild is poor (see chapter 3 and this chapter below), performance differences occur among wild stocks in common-garden experiments, and there are non-random patterns of inherited resistance to some parasites in the wild. Local adaptation is also indicated in other salmonids (Taylor 1991, Pakkasmaa & Piironen 2001, Quinn 2005).

A major component of local adaptation is likely to involve a genetic response to water temperature, water quality (e.g. pH), photoperiod and related variables, and disease vectors, as these factors are of particular biological importance and can vary spatially in a predictable way, likely to promote adaptive evolutionary change (Verspoor et al. 2006). However, local adaptation most likely varies spatially and can be expected to be lower within meta-populations.

4.2 Genetic differences between wild and farmed salmon

Breeding programs

The European industry is now largely based on a few selectively bred strains of mostly Norwegian origin (Cross & Challanain 1991, Skaala et al. 2005, GjØen & Berntsen et al. 1997). Much of the present-day farmed salmon production is based on five Norwegian strains dating from the 1960s to 1970s (Skaala et al. 2005). Four of the strains, which constitute the Akvaforsk breeding programme, represent four distinct cohorts of fish collected from 40 rivers in the central coastal area of Norway in successive years between 1971 and 1974 (Gjedrem et al. 1987, 1991, GjØen & Bentsen 1997, Bentsen & Thodesen 2005). These four strains are kept separately, and bred every fourth year using a family based selection programme which has been conducted since the beginning of the programme (Skaala et al. 2005). Aqua Gen is currently in the process of amalgamating these separate breeding lines in order to widen the genetic base of the farm population (www.aquagen.no). A fifth strain (established by Mowi A/S in the 1960s), mainly based on wild populations sourced from the River Bolstad in the Vosso watercourse and the River Årøy, Norway, is based on mass selection. Body weight at slaughter, age of sexual maturation, survival in challenge tests with furunculosis and infectious salmon anaemia (ISA), flesh colour, total fat content, and amount of fat tissues are traits included in the breeding goal (GjØen & Bentsen 1997).

In the Northeast Atlantic region, similar family based breeding programmes exist in Iceland, Ireland, Faeroe Islands and Scotland (Verspoor et al. 2006). Little genetic exchange occurs between programmes, but fish are widely exported within and outside Europe. In British Columbia, Canada, farmed salmon are primarily descendants of early imports from Norwegian and Scottish strains, but strains of North American origin have also been used (Withler et al. 2005). In Eastern Canada, the principal aquaculture strain is based on salmon from the St. John River (Ferguson et al. 2007), and were in part developed with a family-based selection program (Friars et al. 1997). In the Eastern USA, principally Maine, the farmed salmon were initially derived from crosses between European fish and St. John River fish (Ferguson et al. 2007). These fish have subsequently been crossed with Penobscot River (Maine, USA) fish. Baum (1998) estimated that there was a European genetic influence in 30-50% of the production of

farmed salmon in Maine. It is now mandated legally that farm salmon stocks used in Maine should not have significant European ancestry (Ferguson et al. 2007). In Australia, Atlantic salmon were imported from the River Philip in Canada in 1964/65, which all farmed salmon are based on, and there have been no imports of Atlantic salmon since (Rob Gott, Department of Primary Industries and Water, personal communication). Atlantic salmon for the most recent aquaculture burst in Chile were brought from Scotland and Norway.

Genetic differentiation between farmed and wild stocks

Differentiation of farmed strains from wild populations is expected due to: 1) the effects of limited numbers, and a non-random choice and sourcing of wild founders (i.e. founder effects), 2) domestication selection, 3) loss of variability by genetic drift (increased by using small numbers of brood fish), and 4) selective breeding for economic traits (reviewed by Ferguson et al. 2007). Differences have been seen with regard to variation at protein genes, at mitochondrial and nuclear DNA loci and for phenotype variation (Youngson et al. 1989, 1991, Cross & Challanain 1991, Danielsdottir et al. 1997, Mjølnerød et al. 1997, Einum & Fleming 1997, Fleming & Einum 1997, McGinnity et al. 1997, Clifford et al. 1998a,b, Norris et al. 1999, Thodesen et al. 1999, Johnsson et al. 2001, Fleming et al. 2002, Singer et al. 2002, Garant et al. 2003, Handeland et al. 2003, McGinnity et al. 2003, Metcalfe et al. 2003, Enders et al. 2004, Skaala et al. 2004, 2005, Weir et al. 2005, Roberge et al. 2006, reviewed by Ferguson et al. 2007, Roberge et al. 2008). Molecular studies using neutral markers show reductions in allelic variation and mean heterozygosity of farmed strains compared to wild populations of up to 50% (Mjølnerød et al. 1997, Clifford et al. 1998a,b, Norris et al. 1999, Skaala et al. 2004, 2005, Whitler et al. 2005) and the differentiation between strains and wild founder populations are 2-6 times higher than among wild populations generally (Skaala et al. 2004). The differences in coding sequences are expected to be somewhat higher than those observed at neutral loci (Merilä & Crnokrak 2001).

Differences between farmed strains and wild populations due to domestication and trait selection exist for growth rate, body size, survival, delayed maturity, stress tolerance, temperature tolerance, disease resistance, flesh quality and egg production, whereas unintentional correlated changes occur for fitness-related traits including survival, deformity, spawning time, morphology, aggression, risk-taking behaviour, sea water adaptation, and growth hormone production (Einum & Fleming 1997, Fleming & Einum 1997, McGinnity et al. 1997, Clifford et al. 1998a,b, Thodesen et al. 1999, Johnsson et al. 2001, Fleming et al. 2002, Singer et al. 2002, Garant et al. 2003, Handeland et al. 2003, McGinnity et al. 2003, Metcalfe et al. 2003, Enders et al. 2004, Weir et al. 2005, reviewed by Ferguson et al. 2007). Genetic gains of > 100% and 20% have been recorded for growth and feed conversion efficiency, respectively, after 5-6 generations in one Norwegian farm strain (Thodesen et al. 1999) hence, farm salmon outgrow wild salmon both in culture and the wild (Ferguson et al. 2007).

4.3 Genetic impact of inter-breeding on wild salmon

There are two main types of genetic change that can occur due to hybridisation of farmed with wild salmon, and from gene flow from farmed to wild salmon through backcrossing of these hybrids (introgression) in subsequent generations (Ferguson et al.

2007). The first is a change in the level of genetic variability, and the second is a change in the frequency and type of alleles present. Such genetic changes will only be important if the extent and nature of genetic variability is important for survival and recruitment (i.e. fitness) of wild populations. It does not, however, require that there are adaptive differences among wild populations, but only that hybrids between wild and farmed salmon have lower fitness than wild salmon as a result of genetic changes in farmed fish during domestication (Ferguson et al. 2007). However, the extent of fitness reduction will be increased due to local adaptive differentiation. Genetic changes due to hybridisation and introgression may also change the characteristics of a population even if there are no obvious changes in fitness (Ferguson et al. 2007). Characteristics such as age and timing of adult return are important for angling exploitation and alteration of such characteristics may have economic consequences irrespective of whether it impacts on the survival and recruitment of that population.

Genetic effects of spawning of farmed salmon recorded in wild populations

Several studies have documented genetic effects of inter-breeding of escaped farmed and wild salmon in nature. Genetic changes in the wild salmon population in the Glenarm River, Northern Ireland, resulting from the spawning of escaped farmed salmon were described by Crozier (1993). A follow up sample was taken from the river seven years later (Crozier 2000). Overall genetic variation across eight polymorphic allozyme loci indicated that the wild population remained significantly different from the pre-escape population and from the immediate post-escape population. The presence of an allele not having been previously detected in this population suggested that further incursion(s) of farmed salmon may have taken place. Genetic changes to native populations, as revealed by molecular genetic markers, were also shown in three rivers in Ireland (Clifford et al. 1998a,b).

Changes in genetic profiles have also been demonstrated for three Norwegian rivers (Rivers Opo, Vosso and Eio) when historical and contemporary scale samples were genotyped at eight microsatellite loci and compared (Skaala et al. 2006a). No changes in the genetic profiles were found in four other rivers (Rivers Namsen, Etne, Granvin and Hå). Escaped farmed salmon have been recorded in large proportions in all the studied populations except the Hå River. It was concluded that the most likely explanation for the observed changes in the Opo, Vosso and Eio Rivers is gene flow from escaped farmed salmon. The populations in the Opo, Vosso, Eio and Granvin Rivers are relatively small (the Vosso and Eio being historically large, but experiencing severe population declines since about 1990), whereas the Namsen River holds one of the largest populations in Norway, and with relatively large populations also in the Etne and Hå Rivers. Thus, large and healthy salmon populations may be less vulnerable to genetic impacts of escaped farmed salmon than small populations. Small reductions in F_{ST} values and genetic distances among populations were observed in the contemporary samples compared with the historical samples, indicating a reduction in population differentiation over time, most likely due to immigration of escaped farmed salmon.

Large scale common garden experiments in Ireland and Norway

Two major experiments have been performed to determine the impact on natural populations of escaped farmed salmon entering and spawning in the wild (McGinnity et al. 1997, 2003, Fleming et al. 2000). Both experiments demonstrated a reduced lifetime success of farmed salmon and hybrids compared to wild fish. The study of Fleming et

al. (2000) in the Norwegian River Imsa is described in chapter 3.2. The experiment conducted in the Burrishoole River is described below.

To determine the likelihood and impact of genetic change in a wild population from breeding of escaped farmed salmon, an experiment was undertaken in a natural spawning tributary of the Burrishoole system in western Ireland (McGinnity et al. 1997). The aim was to compare the performance of wild, farmed and hybrid salmon progeny. The experiment was conducted as a “common garden” experiment in the wild, and wild, hybrid and farm were planted as eyed eggs in the experimental river. Thus, both this and a later study (McGinnity et al. 2003, see below) were designed to eliminate behavioural differences between spawning adults and to examine the effect of genetic differences on survival and performance. Survival of the progeny of farmed salmon to the smolt stage was significantly lower than that of wild salmon, with increased mortality being greatest in the period from the eyed egg to first summer. However, progeny of farmed salmon grew fastest and competitively displaced the smaller native fish downstream. The offspring of farmed salmon showed a reduced incidence of male parr maturity compared with native fish. The latter also showed a greater tendency to migrate as autumn pre-smolts. Growth and performance of hybrids were generally either intermediate or not significantly different from the wild fish. The overall farmed smolt output was only 56% relative to the wild.

This first study from the Burrishoole system (McGinnity et al. 1997) was later extended by examining the freshwater performance of second-generation F_2 hybrids and BC_1 back crosses to wild and farm salmon, as well as adult return from the sea for all cohorts (McGinnity et al. 2003). The results from all cohorts were combined to allow estimation of two-generation lifetime success. Offspring of farm and ‘hybrids’ (i.e. all F_1 , F_2 and BC_1 groups) showed reduced survival compared with wild salmon, but grew faster as juveniles and displaced wild parr, which as a group were significantly smaller. The farm salmon consistently showed the lowest freshwater and marine survival in all cohorts. The relative estimated lifetime success ranged from 2% (farm) to 89% (BC_1 wild) of that of wild salmon, indicating additive genetic variation for survival. There was no evidence for hybrid vigour, with F_1 and BC_1 hybrids being intermediate between wild and farm salmon in survival, growth and parr maturity. There was clear evidence of outbreeding depression in the F_2 hybrids. Wild salmon primarily returned to fresh water after one sea winter (1 SW), but farm and ‘hybrids’ produced proportionally more 2 SW salmon. However, due to an overall reduced survival, this would result in reduced recruitment despite increased 2SW fecundity.

Significantly the outcome of both the Norwegian and Irish studies, though conducted under different conditions, are similar in that they show highly reduced survival and lifetime success of farm and hybrid salmon compared to wild salmon. There were some differences in that Fleming et al. (2000) found no differences in wild, farm and hybrid offspring types in body size and sea age at maturity, but the mean age at maturity of hybrids were lower than the wild fish due to differences in age at smolting. Further, Fleming et al. (2000) found no differences in marine survival between the wild, farm and hybrid groups. Differences between the Norwegian and Irish experiments are likely due to different strains of farmed salmon being used, and different environmental conditions experienced by the fish during the experiments (McGinnity et al. 2003).

Modelling genetic and ecological effects from experimental results

Predictions of impact, based on modelling, vary depending on the assumptions made in constructing the model (e.g. Hutchings 1991, Mork 1991, Tufto & Hindar 2003, Hindar et al. 2006). The future of wild salmon populations experiencing invasions of escaped farmed salmon based on data from the Burrishoole and Imsa experiments (McGinnity et al. 1997, Fleming et al. 2000, McGinnity et al. 2003) were modelled by Hindar et al. (2006). Simulations with a fixed intrusion rate of 20% escaped farmed salmon at spawning suggest that substantial changes take place in wild salmon populations within ten salmon generations (≈ 40 years). Low-invasion scenarios suggest that farmed offspring are unlikely to become established in the population, whereas high-invasion scenarios suggest that populations are eventually mixtures of hybrid and farmed descendants. Recovery of the wild population is not likely under all circumstances, even after many decades without further intrusion.

Effects of density-dependence and population regulation were excluded from the model of Hindar et al. (2006). However a model incorporating density-dependent effects of escaped farmed fish on wild populations was previously developed by Tufto (2001). He used a quantitative genetic model that included immigration of maladapted individuals into wild populations, where the outcome was determined by density-dependent regulation and local stabilizing selection. One result was a reduction in total equilibrium size (carrying capacity), when immigrants deviated more than 2.8 genetic standard deviations from the local optimum and immigration was high, relative to the strength of stabilizing selection.

4.4 Indirect genetic effects of farm escapes

Escaped farmed salmon can also have an indirect impact on the genetic composition of wild populations, which may occur due to behavioural, ecological and disease interactions with the wild population (reviewed by Ferguson et al. 2007). These interactions may reduce the success of wild fish, thereby reducing the effective population size of the wild population and increasing genetic drift. Interaction of farm salmon with wild fish may also result in changes in selection pressures in natural populations through differential impacts on particular size, life history, geographical, or temporal components of the wild stock (Ferguson et al. 2007). Further, diseases originating from aquaculture could indirectly be an important mechanism of evolutionary change in wild salmon populations and could have negative consequences for the long-term persistence of the species in the wild (de Eyto et al. 2007) (see also chapter 4.5).

4.5 Direct and indirect genetic effects of Atlantic salmon aquaculture on brown trout

Hybridisation between escaped farmed salmon and brown trout

Brown trout coexist with Atlantic salmon in many watersheds throughout their distribution range. Evidence from rivers in Norway and Scotland suggest that escaped farmed salmon hybridize with brown trout more frequently than their wild conspecifics (Youngson et al. 1993, Hindar & Balstad 1994). The incidence of first generation (F1) hybrids in Norwegian rivers close to salmon farms increased three-fold over the past

decade (from average 0.24 to 0.87%), and with higher hybridisation rates in rivers with a high proportion of escaped farmed salmon on the spawning grounds (up to 8% in one locality, Hindar & Balstad 1994). Direct evidence that farm salmon may increase rates of interspecific hybridisation of Atlantic salmon and brown trout comes from the Imsa experiment (see chapter 3.3), where 3.2% of the offspring were hybrids, and the salmon parent was significantly more often of farm than native origin (Hindar & Fleming 2005). In Ireland, the impact of escaped farmed fish on levels of hybridisation was found to be minimal compared to Norway and Scotland (Matthews et al. 2000). This was attributed to the small scale of Ireland's salmon farming industry.

The likelihood of hybridisation may depend on the timing of spawning of the wild salmon, farmed salmon and brown trout in the river, presumably with a higher likelihood if the spawning time of the farmed salmon coincides with the brown trout spawning period instead of the wild salmon spawning period (see chapter 3 and Timing of spawning).

Hybrids survive well but rarely reproduce and, thus, may lower the productivity of local populations, and in very rare cases lead to introgression of genetic material from one species into the other.

Indirect genetic effects of aquaculture activities

A study in an Irish river indicated that salmon aquaculture activities can also indirectly (without inter-breeding) affect the genetics of cohabiting sea trout (i.e. anadromous brown trout) by reducing variability at major histocompatibility class I genes, most likely mediated by disease or parasites introduced or increased in incidence by salmon aquaculture activities (Coughlan et al. 2006). The major histocompatibility class (MHC) genes play a critical role in controlling immune responses.

4.6 Conclusive statements

- Wild Atlantic salmon are structured into populations and meta-populations with little gene flow between them, but the mechanisms promoting spatial boundaries, within and among river systems, remain to be resolved in detail.
- Evidence for local adaptation in wild Atlantic salmon is compelling,
- World farmed salmon production is largely based on a few breeding strains established from wild Norwegian populations and developed using family based selection programmes with large effective population sizes, but showing genetic drift due to founder effects. Some farm strains originating from North American wild populations are used in North American farm salmon production.
- Current farm strain selective breeding programmes are focused on multiple traits, including body weight at slaughter, age of sexual maturation, survival in challenge tests with furunculosis and infectious salmon anaemia (ISA), flesh colour, total fat content, and amount of fat tissues.
- Differentiation of farmed strains from wild populations is expected due to: 1) the effects of limited numbers in establishing farm strains and the non-random choice and sourcing of wild founders, 2) domestication selection, 3) loss of variability by

genetic drift (increased by using small numbers of brood fish), and 4) selective breeding for economic traits.

- Norwegian farmed salmon are significantly genetically different from the wild populations from which they were founded. Farmed salmon are genetically different from wild fish with respect to a range of molecular and phenotypic traits, and display reduced genetic variation.
- Differences between wild and farmed salmon due to domestication and trait selection are likely to exist for growth rate, body size, survival, delayed maturity, stress tolerance, temperature tolerance, disease resistance, flesh quality and egg production, whereas unintentional correlated changes may occur for fitness-related traits including survival, deformity, spawning behaviour and success, spawning time, morphology, fecundity and egg viability, aggression, risk-taking behaviour, sea water adaptation and growth hormone production.
- Two main types of genetic change can occur due to hybridisation of farmed with wild salmon and gene flow from farmed to wild salmon through backcrossing of these hybrids in subsequent generations; 1) a change in the level of genetic variability, and 2) changes in the frequency and type of alleles present. Hence, hybridisation of farmed with wild salmon has the potential to genetically alter native populations, reduce local adaptation and negatively affect population viability and character.
- Several molecular marker studies have shown that escaped farmed salmon breeding in the wild have changed the genetic composition of wild populations.
- As only a few farm strains are used throughout the industry, gene flow from escaped farmed salmon will reduce the natural inter-population heterogeneity found in Atlantic salmon. The small reduction in population differentiation over time observed in some Norwegian rivers is most likely due to increased immigration of escaped farmed salmon.
- Large-scale experiments undertaken in Ireland (Burrishoole) and Norway (Imsa), though conducted under different conditions, gave similar results, both showing highly reduced survival and lifetime success of farm and hybrid salmon compared to wild salmon.
- The relative estimated lifetime success observed in the field experiments ranged from lowest for the farm progeny to highest for the local wild progeny with intermediate performance for the hybrids, indicating additive genetic variation for survival.
- A reduction in juvenile recruitment of 15-30% in the first generation (recorded in the Burrishoole experiment) may be within the range of natural variability for strong wild populations, but such reductions would have a significant impact on severely depressed wild populations. Since farm escapes are repetitive, often with ongoing repeated intrusions in some rivers, such reductions in fitness and productivity are cumulative and could potentially lead to an extinction vortex.
- Escaped farmed salmon can also have an indirect impact on the genetic composition of wild populations, which may occur due to behavioural, ecological and disease interactions with the wild population.

- Escaped farmed salmon increase rates of hybridisation between Atlantic salmon and brown trout. Salmon-trout hybrids survive well but rarely reproduce and, thus, may lower the productivity of local populations, and in very rare cases lead to introgression of genetic material from one species into the other.

4.7 Knowledge gaps and research needs

- It has been shown that inter-breeding of farm with wild salmon can result in reduced lifetime reproductive success, lowered fitness and decreased population productivity over at least two generations, however, there are no data on the long-term effects beyond the second generation. It is not known whether these effects will lead affected populations into extinction vortices, or whether a balance between changes caused by inter-breeding with escaped farmed salmon and the natural selection counteracting these changes might be reached. There will likely be different outcomes in different wild populations, dependent on factors such as the type and numbers of escaped farmed salmon entering rivers, whether escape events will be ongoing, the genetic composition of the wild salmon, the size and status of the recipient wild population, and the importance of local adaptations. Given the length and cost of field experiments, which limits them to a small number of sites, the most realistic way forward is to continue the development of computer-based predictive models, which allow for risk assessment across the range of escape scenarios. Research into indirect genetic ecological impacts associated with issues such as introduction of disease and effects of density-dependent population dynamics will be necessary components of these future models.
- Realistic models can be used to both assess risks of direct genetic interactions, and to identify further research priorities.
- Are large, complex rivers likely to be less impacted by hybridisation of wild and escaped farmed salmon than small, simple ones? Systematic monitoring of possible genetic changes in wild populations with continuous incursions of escaped farmed salmon can give insights into which are the most vulnerable wild populations and the reason for their vulnerability.
- Meta analyses are needed to look for broad scale indications of declines in population productivity. The coupling of information on intrusion rates (or even genetic change) with long-term population dynamics could provide invaluable insight. While research has shown case specific indications of declines (e.g. Burrishoole and Imsa experiments), little is known with regards to broad scale patterns over multiple generations. Long term data sets should be able to provide such insight, especially if examined across broad geographical regions.

5 Effects of escaped farmed salmon in regions where the Atlantic salmon is an exotic species

Atlantic salmon is farmed in the Pacific Ocean outside of its natural distribution range, mainly in Chile, along the West Coast of North America (Canada and US) and in Tasmania (Australia). In 2005, 36% of the total world production was in regions where the species is exotic (ICES 2007). Escapes of Atlantic salmon in these regions potentially pose special problems. Questions relevant to the escape issue include whether escaped Atlantic salmon can establish self-reproducing populations in these regions, whether they are able to hybridize with native fishes, and what ecological effects might escaped salmon have on native species and ecosystems.

5.1 Are escaped farmed salmon able to establish self-reproducing populations?

Prior to the development of the sea cage industry, attempts were made to introduce the Atlantic salmon to the Pacific region for sport fishing reasons. Over 8.6 million Atlantic salmon (Miramichi River origin) were introduced to more than 60 lakes and streams in British Columbia, Canada, and none are known to have resulted in the establishment of a self-sustaining population (Ginetz 2002). Waknitz et al. (2002) reported that more than 130 attempts have been made to introduce Atlantic salmon across 32 states in the US and all failed.

Because of the West Coast colonization failures, and the poor colonization success of the Atlantic salmon compared to other salmonids when the species has been introduced outside of its natural range, some have concluded that the escapes of Atlantic salmon from sea cage sites will not pose a long-term threat to Pacific salmon on the North American West Coast (Nash 2001, Ginetz 2002, Waknitz et al. 2002). Worldwide, no self-sustaining populations of anadromous Atlantic salmon have been established outside the natural range of this species, except in the Faroe Islands, although landlocked populations appear to have become established in the Southern Hemisphere in Argentina, and in the mountains of New Zealand (MacCrimmon & Gots 1979, Lever 1996). However, under the right conditions, Atlantic salmon can be a successful invader. A number of range extension attempts within the species' indigenous geographic area have been successful (Whoriskey 2000, Mullins et al. 2003).

Since the time period in which deliberate introductions of Atlantic salmon failed, there has been a major downturn in the population status of Pacific salmonids on the North American West Coast, especially the rainbow trout (*Oncorhynchus mykiss*) (see references in Gross 1998, Whoriskey 2003). Hence, conditions may be more favourable for colonization now than in the past (Gross 1998, Whoriskey 2003).

Results from an experimental stream study suggested that Atlantic salmon escaping from aquaculture facilities are likely to experience low spawning success in coastal British Columbia, Canada, but that they are capable of successfully excavating redds and spawning viable eggs (Volpe et al. 2001b). A large proportion of the salmon

obtained from a local commercial marine net-pen operation matured (17 of 19 males and 24 of 30 females), and up to 9 females successfully deposited eggs. Eggs from five of six redds yielded valuable progeny when the eggs were collected and incubated in trays.

Mature escaped salmon have been recorded in freshwater streams in British Columbia (McKinnell et al. 1997). Evidence of successful natural spawning of Atlantic salmon in British Columbia exists, with the first documentation from the Tsitika River on Vancouver Island, where repeated successful spawning (minimum of two years, 1997 and 1998) was recorded (Volpe et al. 2000). Three Pacific salmon-bearing systems in British Columbia have been found to support wild-spawned juvenile Atlantic salmon (Amor de Cosmos Creek, Adam and Eve River and Tsitika River, Volpe 1999, 2000, Volpe et al. 2000). Whether escaped Atlantic salmon have actually established breeding populations in British Columbia streams still remains uncertain (Bisson 2006). Only a small proportion of the streams possessing potential Atlantic salmon habitat have been surveyed for this species on the West Coast of North America (British Columbia, Alaska and Washington) (Bisson 2006).

There have been no documented reports of escaped Atlantic salmon spawning in the wild in either Chile or Tasmania (Soto et al. 2001, 2006, DPIW 2006). Surveys have failed to turn up feral juveniles from escapees in Chile (Soto et al. 2001, 2006). Thus despite large numbers of escaped individuals in Chile, and despite the fact that some mature individuals have been recorded, there is no evidence of self-sustaining populations having established as yet (Soto et al. 2001). Other farmed Pacific salmon species such as coho and Chinook have been able to successfully reproduce, and in the latter case there are reports of several self sustained populations (Soto et al. 2007). Coho salmon seems to be reproducing in the Aysen region, where mature individuals are found returning to local rivers (Niklistcheck & Aedo 2002). On the other hand, Chinook salmon, the species with the lowest production and fewer escapees, is establishing reproductive populations in many basins of southern Chile and Argentina (Soto et al. 2007, Ciancio et al. 2005). Both species, coho and Chinook, have also been part of ranching programs in the past, which eventually may also play a role in their establishment, especially in the case of Chinook salmon. Therefore, not all is to blame on present aquaculture activities.

5.2 Are escaped farmed salmon likely to hybridize with native salmonids?

There are no reported cases of hybridisation in nature between Atlantic and Pacific salmonid species in North or South America, New Zealand or Europe (Waknitz et al. 2002). Furthermore, laboratory studies carried out in controlled conditions have failed to produce viable progeny when crossing Atlantic salmon with the Pacific pink *Oncorhynchus gorbuscha*, chum *Oncorhynchus keta*, coho or sockeye *Oncorhynchus nerka* salmon (Chevassus 1979, Loginova & Krasnoperova 1982, Gray et al. 1993, Nash 2001, Waknitz et al. 2002), except in one study where 0.02% of crosses with pink salmon survived to the hatching stage (Waknitz et al. 2002). Laboratory studies have also failed to produce viable progeny when crossing Atlantic salmon and rainbow trout (Refstie & Gjerdem 1975, Sutterlin et al. 1977, Blanc & Chevassus 1979, 1982), except in one recent study where 6.1% of the crosses between Atlantic salmon and steelhead

Oncorhynchus mykiss survived to the hatching stage (Nash 2001, Waknitz et al. 2002). However, due to different spawning times, interbreeding between Atlantic salmon and steelhead is unlikely to occur in the wild on the West Coast of North America (Nash 2001, Waknitz et al. 2002). Thus, the probability of successful hybridisation between Atlantic salmon and Pacific salmonid species seems remote.

5.3 Ecological effects on native species and ecosystems

Effects of unsuccessful hybridisation

Hatchery-reared adult Atlantic salmon were released into a Lake Ontario tributary to examine spawning interactions with fall-spawning exotic salmonids found in the same stream (Scott et al. 2005b). Chinook and coho salmon were observed interacting with spawning Atlantic salmon in nearly one-quarter of the observation bouts, with Chinook salmon interacting most frequently (Scott et al. 2005b). It should be noted that this study was designed to monitor effects by Pacific salmonids on Atlantic salmon spawning, and not the other way around. However, it demonstrates, the attraction of Pacific salmonids and the Atlantic salmon to similar spawning areas at similar times, and the possibility for behavioural interactions during spawning.

The indirect genetic impact of Atlantic salmon males attempting to hybridize with females in populations of native salmonids that are locally endangered is of concern (Gross 1998). Each Pacific salmonid female that has her eggs fertilized by an Atlantic salmon parr or other male has her eggs removed from the gene pool. A population with only a few native females may therefore lose a significant proportion of its reproductive output with even minor hybridisation events. Spawning experiments with farmed Atlantic salmon and Pacific salmonids have not been performed, and the likelihood of hybridisation attempts to happening is therefore not known.

Agonistic behaviour, feeding, growth and competition among juveniles

Juvenile Atlantic salmon of farmed origin may occur in rivers either as escapees from freshwater hatcheries, or as progeny spawned in the wild by escaped farmed salmon spawning in the wild. The extent to which juvenile Atlantic salmon influence, or are influenced by, Pacific salmonid species are therefore important questions.

The presence of Chinook salmon and brown trout affected Atlantic salmon juveniles in an artificial stream study by increasing their agonistic behaviour, and thereby likely their energetic costs, but without reducing their foraging success (Scott et al. 2005a). In sum, this could presumably affect the long-term growth of the Atlantic salmon (Scott et al. 2005a). Thus, the results showed that attempts to re-introduce Atlantic salmon to Lake Ontario streams (where they were once native) may be difficult if brown trout or Chinook salmon are present in those streams (Scott et al. 2005a). It should be noted that this study was designed to monitor effects by Pacific salmonids on Atlantic salmon juveniles, and not the opposite.

The habitat preferences of juvenile Atlantic salmon and juvenile steelhead overlap considerably (Hearn & Kynard 1986). A major concern has therefore been that Atlantic salmon juveniles could negatively affect already depressed steelhead populations (Bisson 2006). Investigations generally indicate that Atlantic salmon juveniles are competitively inferior to size-matched or larger steelhead and coho salmon (e.g. Beall et

al. 1989, Jones & Stanfield 1993), although Gibson (1981) obtained contradictory results in experimental stream experiments. Previous studies typically involved wild or hatchery populations, which may differ from farm salmonids that are subjected to artificial selection over multiple generations.

Recently, agonistic behaviour and growth of juvenile steelhead placed with farm-origin juvenile Atlantic salmon at low, medium and high densities were monitored in experimental stream channels in British Columbia (Volpe et al. 2001a). Juvenile steelhead were more aggressive than Atlantic salmon, but steelhead were more than two times more likely to direct aggression at conspecifics than toward Atlantic salmon. Atlantic salmon, although less aggressive overall, were twice as likely to attack juvenile steelhead as other Atlantic salmon. Atlantic salmon juveniles fared poorly when released into habitats already populated by steelhead, but when Atlantic salmon were released into the experimental channels first and had an opportunity to establish foraging territories prior to the introduction of steelhead, the salmon generally out-competed steelhead. Therefore, prior residency is a key factor in predicting the relative performances of Atlantic salmon and steelhead in competition (Volpe et al. 2001a). Atlantic salmon spawn two or more months before most steelhead, and their progeny would be likely to have established feeding territories in streams before steelhead fry emerge from the spawning gravel, which could give the Atlantic salmon juveniles a competitive advantage (Volpe et al. 2001a).

A series of experiments were undertaken to investigate the relative competitive ability of farmed Atlantic salmon juveniles and Pacific salmonids (Blann & Healey 2006). In equal contests between farm Atlantic salmon and similar sized fish from two wild coho populations or a coastal cutthroat trout (*Oncorhynchus clarki clarki*) population, Atlantic salmon were subordinate in all cases. When Atlantic salmon were given a residence advantage, however, they were competitively equal to fish from both wild coho populations, but remained subordinate to the cutthroat trout. When Atlantic salmon were 10-30% larger, they were competitively equal to fish from one wild coho salmon population, but remained subordinate to the other. In semi-natural stream channels, both coho and farm Atlantic salmon grew significantly more in the presence of the other species than when reared with conspecifics alone. The coho salmon apparently obtained additional food by out competing Atlantic salmon, whereas Atlantic salmon were stimulated to feed more in the presence of heterospecific competitors. These results suggest that wild coho salmon and cutthroat trout should out-compete farm Atlantic salmon of a similar size in nature. As the relative competitive ability of Atlantic salmon improved through size or residence advantages, they may compete on a more equal basis.

From the few existing studies, it can be concluded that should Atlantic salmon establish populations in areas naturally occupied by Pacific salmonids, their juveniles could compete with juveniles of the native species. However, given the fluctuating competitive asymmetries documented above and the complicated nature of the timing and avenues of potential colonization events, a priori it is difficult to predict the outcome of the competition between juvenile Atlantic salmon and Pacific salmonids.

Feeding of adults

Gut analyses of marine-captured Atlantic salmon in the Northeast Pacific Ocean found that only 6-21% of the escaped fish contained food items (McKinnell & Thomson 1997,

McKinnell et al. 1997), which suggests that the escapees had greater difficulties in adapting to the marine environment in the Pacific Ocean than in the Atlantic Ocean (see chapter 3). In samples collected at sea inside Vancouver Island, Canada, 0-24% of the salmon contained food items (Morton & Volpe 2002). An unusual observation was made in the Salmon River, where more than 53% of the escaped Atlantic salmon had been feeding in fresh water despite advanced gonadal development; this is unusual because maturing Atlantic salmon usually do not feed during the freshwater stage (McKinnell & Thomson 1997).

In Chile, escaped Atlantic salmon seem to adapt poorly to feeding in the wild and have the highest frequency of empty stomachs (42%) of all the farmed and escaped salmonid species in this region (Soto et al. 2001). Other escaped species, such as rainbow trout and coho salmon, have a wide diet spectrum, with coho salmon being more piscivorous.

Little is known about the fate and impacts of the escaped salmon in Tasmania, Australia. A study in Macquarie harbour indicated that escaped salmon were losing condition and did not appear to successfully forage outside the nets. However, some of the examined fish did have prey in their stomachs, indicating that they were feeding on native species (DPIW 2006).

Ecosystem effects

Studies or analyses of ecosystem effects resulting from escaped farmed salmon competing and interacting with native species in areas where the Atlantic salmon is exotic do not exist. For example, direct competition by escaped salmonids with native fish species and indirect effects through feeding on benthic invertebrates are expected in the Chilean inner ocean and fjords (Soto et al. 2001). Yet, it is difficult to predict the outcome in a situation like Chile, where there are significant knowledge gaps about the biology, ecology, genetics and evolution of native fish species and aquatic communities, especially in the fjords, channels and marine environment in general (Fernandez et al. 2000, CBSG 2003, Soto et al. 2007). In lakes and rivers, most escaped farmed salmonids are often piscivorous, feeding on small native galaxid fish (Soto et al. 2002).

Unlike the situation within its native range, impacts of escaped farmed Atlantic salmon on native fauna in regions where it is an exotic species are not as well documented. Yet, in Chile this species has been suggested to have a lesser effect than the other escapees (coho salmon and rainbow trout). However, it is difficult to make a general global statement on this respect, because there is only limited research being conducted to study impacts (Gross 1998).

5.4 Conclusive statements

- Historical attempts to introduce anadromous populations of Atlantic salmon around the world have failed, indicating that Atlantic salmon is a poor colonizer outside its native range. The probability that escaped Atlantic salmon will establish populations where the species is exotic seems low, but the possibility can not be ruled out. Especially where native populations of salmonids are in decline (e.g. the Pacific coast of North America), conditions for the establishment of Atlantic salmon may be more favourable now than in the past.

- Mature escaped Atlantic salmon are recorded in freshwater streams in British Columbia, Canada, and there is evidence of successful spawning of Atlantic salmon in three streams. Whether escaped Atlantic salmon have actually established breeding populations along the North American West Coast streams still remains uncertain.
- The spawning of escaped farmed Atlantic salmon in the wild has not been documented in either Chile or Tasmania.
- The likelihood of successful hybridisation between Atlantic salmon and Pacific salmonid species seems small.
- If populations of Atlantic salmon establish, juveniles could be competitors to juvenile Pacific salmonids. The outcome of the competition between juvenile Atlantic salmon and Pacific salmonids in nature is difficult to predict. It seems that Atlantic salmon is often competitively inferior to Pacific salmonids, but that this is context dependent, with body size and prior residency being important.
- Gut analyses of marine-captured Atlantic salmon suggests that the escapees have greater difficulties in adapting to the marine environment in the Pacific Ocean and Tasmania than in the Atlantic Ocean. However, escaped Atlantic salmon do feed and prey on native marine species in regions where it is an exotic.
- Studies or analyses of ecosystem effects by escaped farmed salmon competing and interacting with native species in areas where Atlantic salmon is exotic do not exist.
- Unlike the situation within its native range, there have been no clearly documented impacts of escaped farmed Atlantic salmon on native fauna in regions where it is an exotic. However, this may be because there is only limited research being conducted to study impacts
- It is generally difficult to predict if or how Atlantic salmon will adapt to the regions where they are exotic.

5.5 Knowledge gaps and research needs

- There is generally little knowledge on the performance of escaped farmed Atlantic salmon in regions where the Atlantic salmon is an exotic species. There is also little knowledge on the interactions of the escaped Atlantic salmon with native species, especially non-salmonids, and ecosystems on which to base predictions of impacts should feral Atlantic salmon populations become established.

6 Disease and parasite transfer

For a comprehensive discussion of disease and parasite issues and interactions among farmed and wild salmonids, we refer readers to the report of the disease group of the Salmon Aquaculture Dialogue. From the descriptions that we have provided in Chapter 2 of this report, it is clear that escaped farmed salmon can disperse widely and over large distances from the release site, which makes them potential vectors for disease and parasite transfer.

One important question is whether wild or escaped salmon are attracted to fish farms and, thereby, increasing the probability of disease and parasite transfer. Wild salmon might, for instance, be attracted to fish farms in fjords and coastal areas during the outwards smolt migration or during the return spawning migration. There are no studies, that we are aware of, that indicate that this might occur, but at the same time, no studies have specifically looked into the question. Escaped farmed salmon have been observed to stray to other farms in the area, and stay at a farm for several hours (Furevik et al. 1990). Sonic telemetry work in Canada found that tagged hatchery-reared Atlantic salmon smolts moved quickly through areas of sea cage culture with no delays in the migration due to an attraction to farm infrastructure (Lacroix et al. 2004). By contrast, Bridger et al. (2001) reported that experimentally released, sonically-tagged farmed steelhead released from cage sites in Newfoundland resided for up to two months in the vicinity of the release point. Whoriskey et al. (2006) documented one experimentally-released farmed Atlantic salmon moved extensively among the cross-border East Coast salmon farming region over a period of a number of months.



Salmon slaughter. Fortune Bay, Newfoundland.

Photo: Ian A. Fleming

7 Technologies and other efforts for escape prevention

7.1 Why, when and from where do salmon escape?

A prerequisite for escape prevention is knowledge on why, when and from where salmon escape. Such information is needed to identify relationships between particular culture technologies, techniques and site locations and escapes. When this information is combined with knowledge of survival and distribution of escaped salmon at different life stages, times of the year and locations to identify the most critical escape periods (i.e. periods resulting in the largest proportion of salmon entering rivers to spawn), risk analyses can be performed and the high priority areas for rapid improvement in containment can be identified.

In Norway, the Directorate of Fisheries has collected statistics on the scale and causes of reported escapes from fish farms since 1993. The causes for escape are divided into the following categories: technical deficiencies, towing, handling, running over by boat, boat propellers, predators, floating objects and technical deficiencies in smolt production (Valland 2005). The main cause of reported escapes vary from year to year (**figure 7.1**). Causes of reported escapes summarized for salmon and rainbow trout during 2001-2006 showed that 52% resulted from technical failure, 13% from running over by boat, 5% from predators, 5% from boat propellers, 5% from floating objects, 5% from technical failure in smolt production, 3% from handling and 12% from other causes (NASCO 2005). The categorizing may be inaccurate, as causes are not investigated in detail (Valland 2005).

An analysis was conducted based on in-depth interviews with Norwegian fish farmers to analyse causes of reported escapes in 2001-2002 (Rist et al. 2004). It was concluded that the majority of escape episodes resulted from inadequate operation procedures and lack of appropriate training (80%), with equipment problems (lack of equipment or poorly maintained equipment) being responsible for an additional 15% of the escape episodes, and extreme weather and other factors outside human control being responsible for only 4% of the episodes. However, episodes due to extreme weather and other factors outside human control often resulted in a large number of salmon escaping during each episode. An analysis of eight escape episodes during winter storms in Norway in 2006 concluded that the episodes resulted from a combination of circumstances, but that number of escape episodes and number of escapees during each episode would have been reduced if the “best known practice” for operation procedures had been followed (Jensen 2006). Still, there are uncertainties regarding the general question of why, when and from where salmon escape, because the contribution of non-reported escapes is unknown (see chapter 2.1).

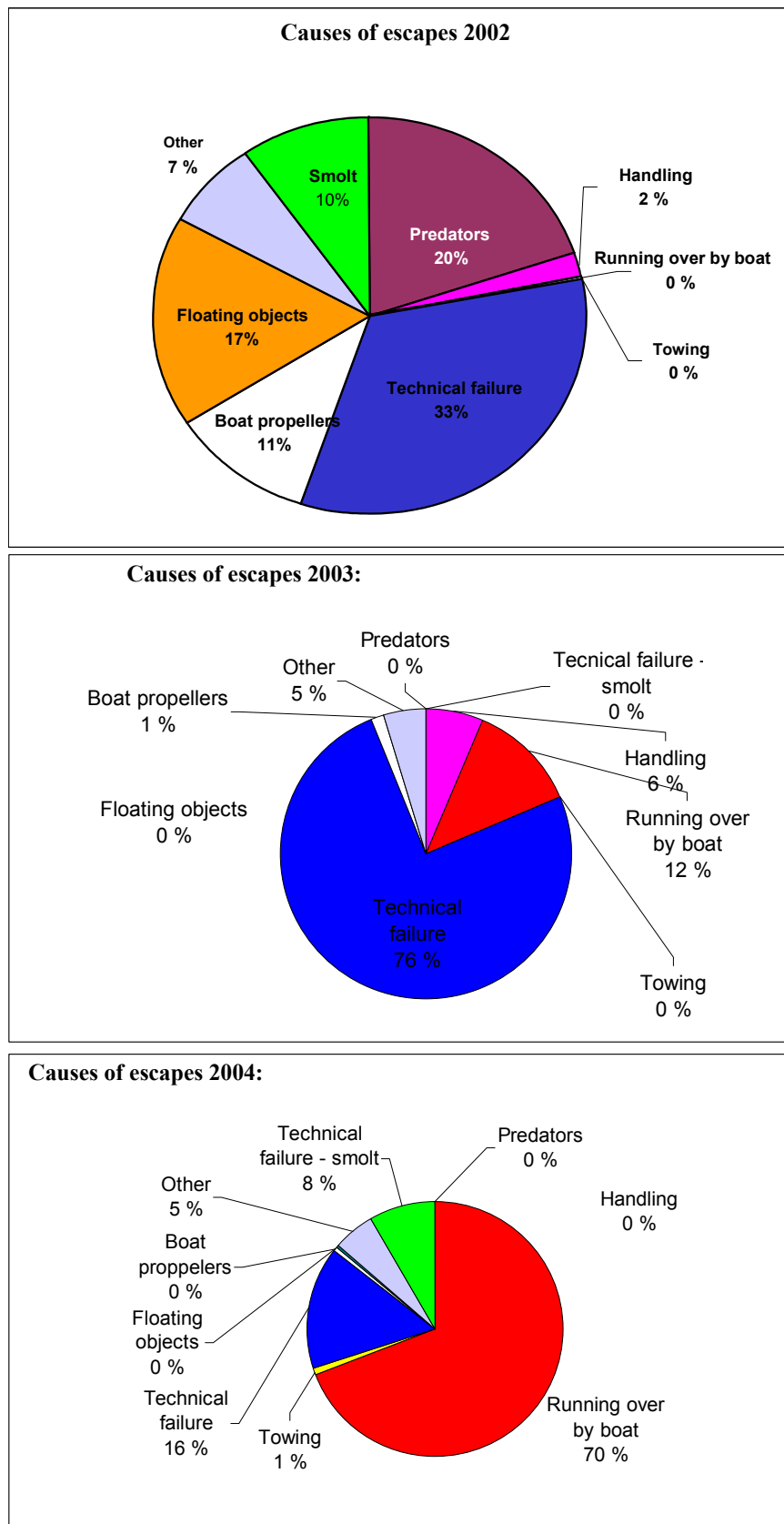


Figure 7.1. Causes of reported escapes from Norwegian salmon farms in 2002, 2003 and 2004. Data source: Directorate of Fisheries. Figures from Valland (2005).

The Ministry of Agriculture and Lands in British Columbia has maintained a database of all reported escape events since 1987. The factors contributing to escapes can be roughly divided into six general categories, which include system failure, boat operations, net failure related to predators, net failure related to maintenance and handling. In the period 1996-2000, on average there were 5.2 reported escape events per year. Of these 26 events, 42% resulted from net failures (including six due to predator attacks), 4% from system failures (none from mooring problems), 39% from handling, and 15 % from boat events (Whoriskey 2001).

Causes of reported escapes in Scotland during May 2002 - December 2006 has been summarized (NASCO 2007). Of 86 escape incidents (excluding 14 incidents during the 2005 January storms), 27% resulted from predation, 23% from equipment failure, 16% from weather, 16% from human error, 14% from hole in the net, 2% from vandalism/foul play and 1% from other causes.

It can be generally concluded that information on why, when and from where salmon escape is lacking for all farm salmon producing countries, even though statistics exist on reported large-scale escapes from several countries. There are large uncertainties regarding the contribution of non-reported escapes, both from freshwater hatcheries and sea cages (see chapter 2).



Salmon cage sites in Fortune Bay, Newfoundland, Canada.

Photo: Ian A. Fleming

The Norwegian Ministry of Fisheries and Coastal Affairs took the initiative to establish a national committee to elucidate the best possible methods to identify the sea cage of origin of escaped salmon (Baarøy 2004), to determine the relative proportion of reported and non-reported escapes, and from which sea cages they originated. The committee concluded that two different methods should be investigated further (Baarøy 2004): coded wire tagging (cwt, which is used for tagging 10% of farmed salmon in Iceland, see chapter 2.10) and “red alert”, which is a case-based approach using a combination of genetic markers, fatty acid and trace element analyses to identify farm of origin of escaped farmed salmon. The latter approach has the advantage that there is no need for large-scale investments in tagging of fish that may never escape, but only infers costs when an escape event has taken place. A project (TRACES) is now being developed to test the precision of the “red alert” approach (Skaala et al. 2006b).

7.2 Management measures - some examples

Standard for design, dimensions, performance, installation and operation of fish farms

Government authorities and the industry in Norway have worked together on determining what technical specifications should be required at floating fish farming installations to prevent escape and how this should be regulated since the mid-1980s (Norwegian Ministry of Fisheries and Coastal Affairs 2005). The result of this work was the development of a Norwegian Standard (NS) that specifies the dimensions, design, installation and operating procedures at floating fish farming installations - NS 9415:2003. This standard, which is the first of its kind internationally, was developed by Standards Norway in cooperation with representatives from the industry, research institutions and authorities. Norway is currently working on internationalization of the standard through the ISO (Norwegian Ministry of Fisheries and Coastal Affairs 2005).

The regulations stipulate that fish farmers can only use new installations and structural components that are certified in accordance with NS 9415, and that such certification shall be performed by an accredited certification body (Norwegian Ministry of Fisheries and Coastal Affairs 2005). Existing installations were required to have a capability certificate stating that the installations meet the operational requirements in NS 9415 by 1 January 2006 in accordance with the regulations. The standard contains requirements for the physical design of the installation and the associated documentation. This includes calculation and design rules, as well as installation, operation and maintenance requirements. There are, for example, requirements for the physical design of all the main components in an installation, and how the installation shall be operated to prevent escape. The standard stipulates what parameters shall be used to determine the natural conditions at a given locality and the procedure for classification of localities (Norwegian Ministry of Fisheries and Coastal Affairs 2005).

Other management measures

A national plan to prevent escapes, ‘Vision zero escape’, has been prepared by the Norwegian Directorate of Fisheries. The plan identifies measures to be implemented over a two year period (2006 and 2007), and focuses on five main areas: 1) improved regulations, 2) improved management tools, 3) increased containment efforts stressing control and preparedness, 4) improved communication and interaction with other

government services and 5) improved communication and interaction with the industry. Several specific measures are defined within each of these five areas.

In Maine, in collaboration with non-governmental agencies concerned with conservation of wild salmonids, salmon farmers developed and implemented a Hazard Assessment Critical Control Point (HACCP) approach for containment of farmed fish in both sea cages and freshwater facilities. The process involved a site-specific evaluation of the most probable points for escapes to occur during the production process, and the identification of preventative measures to be implemented to pre-empt escapes from occurring in the first place. A log is kept documenting actions taken at each Maine farm to prevent escapes, and of the occurrence of containment failures. The latter information will be used to design better equipment and operating procedures to reduce future escapes. An independent audit is required of the implementation of the HACCP plan at each farm annually (Goode & Whoriskey 2003).

In Chile, according to the aquaculture environmental regulation (RAMA¹³) since 2004 every farm must have prevention systems to avoid escapes, and must also have clear contingency plans to deal with accidental escapes. This shall include the implementation of a recapture strategy, capture or fencing system to be put in place up to 400 m from the broken or sinister cage for five days. Escapes shall be immediately reported to the nearby Port Captain, and a written report should be submitted to the “Servicio Nacional de Pesca” within seven days of the event. This report must include detailed information on the species, number of individuals, weight, sanitary status, potential medication etc. Therefore, fisheries authorities already have information on the most common causes of escapes, and these seem to be related more often to extreme weather events often together with structural failures.

7.3 Farming technologies

Salmon farming sites are generally located in sheltered or semi-sheltered inshore waters, and the cages usually consist of either a steel or plastic floating collars with net enclosures hanging beneath (Ryan 2004). These can be described as ‘gravity cages’, because they depend on weights hanging from the nets to keep their open form and have no underwater structural framework. Gravity cages have been the staple of fish farming for the past 30 years. Rigid steel collar cages have also been used, which comprise a solid framework of steel or other suitable material to which the fish containing net is attached. Individual cages can contain between 50 and 1 000 tonnes of fish, and typical seawater farming sites for salmon have annual production levels ranging from 1 000 to 4 000 tonnes (Ryan 2004). Continuous research is underway to improve cage technology and operating methodologies. Farming and cage technologies is beyond the expertise of this working group, and a further outline is, therefore, not given here. However, technical improvements to facilities and operations to prevent escapes are tremendously important, and should be the focus of future working groups.

¹³ Reglamento Ambiental para la Acuicultura (D.S. N° 320-01).
http://www.sernapesca.cl/index.php?option=com_content&task=view&id=71&Itemid=175

7.4 Conclusive statements

- A prerequisite for escape prevention is knowledge on why, when and from where salmon escape. Such information is needed to identify critical factors related to culture technologies, techniques and sites. When this information is combined with knowledge of the survival and distribution of escaped salmon at different life stages, times of the year and locations to identify the most critical escape periods, risk analyses can be performed and the high priority areas for improvement and development identified.
- There has been continuous research and development underway for improved cage technologies and operating methodologies. Novel or alternative technologies, however, have been slow to develop to date.
- Technical improvements to facilities and operations to prevent escapes are tremendously important.
- A Norwegian standard has been developed that places technical requirements on the dimensioning, design, installation and operation of floating fish farming installations. This standard is the first of its kind internationally, and Norway is currently working on internationalization of the standard through the ISO.

7.5 Knowledge gaps and research needs

- Information on why, when and from where salmon escape is commonly lacking for all farm salmon producing countries, even though statistics exist on reported large-scale escapes from several countries. There seem to be large uncertainties regarding the contribution of non-reported escapes, both from freshwater hatcheries and sea cages. Such information is needed to identify critical factors related to culture technologies, techniques and sites (see chapter 7.5 above).
- Technological and operational research to prevent escapes (refinement of existing technologies and operation procedures, and the development of novel and alternative technologies), and evaluation of standards and management measures to reduce number of escapees.

8 Technologies and efforts to reduce impacts of escapes

8.1 Sterilization

The use of sterile fish in farming would be an effective way of reducing the direct genetic effects resulting from the interbreeding of escaped farmed with wild salmon. This would also likely reduce, but not eliminate ecological effects (e.g. linked to competition etc.). However, it may have little, if any effect on reducing the transmission of diseases and parasites.

The most effective method of sterilising Atlantic salmon is high pressure induction of triploidy in newly fertilised eggs (a detailed description is given in Ferguson et al. 2007). The process results in complete sterility of females, but not males, and a two generation process using sperm from hormonally masculinized genotypic females is therefore involved to produce all-female salmon. In diploid fish, the cell nucleus contains two sets of chromosomes, whereas in triploid fish a third set of chromosomes is retained in the cell nucleus resulting in functionally sterile fish. Although there are many similarities between triploid and diploid fish, there are also basic differences, which are addressed in a review by Benfey (1999).

Triploids have a number of disadvantages in commercial aquaculture. There has been concern due to reduced growth rate and survival compared to diploids, and increased frequency of deformities such as the development of a characteristic lower-jaw deformity that affects growth and marketability, suppression of the immune system leading to increased susceptibility to diseases, and the absence of primary gill filaments (Benfey 2001, Sadler et al. 2001). There have also been worries that marketability is hindered by consumer perception that triploids are genetically modified organisms or GMOs (which they are not in the sense of transgenic fish) (Ferguson et al. 2007). Triploids are not commercially raised today (Naylor et al. 2005), except in Tasmania, Australia. In Tasmania, approximately 10% of the farmed salmon is triploid, and the reason for using triploid stock is to close the harvest gap, so that salmon are available for the market year round (Rob Gott, Department of Primary Industries and Water, personal communication) instead of being confined to a few months between when adequate body size for market is achieved and maturation occurs.

The use of sterile salmon is a measure that should be carefully appraised, given its potential to reduce direct genetic effects of escapees on wild salmon populations. On the down side, experiments on the commercial culture of triploid Atlantic salmon were abandoned in the Fundy region of Canada when the triploids proved highly susceptible to the infectious salmon anaemia virus. A study by Cotter et al. (2002) showed more promising results than previous studies, with the performance of triploid salmon considered commercially acceptable in the freshwater phase. In the sea cages, however, the yield of triploids was less than that of diploids, largely as a consequence of the higher mortality sustained by triploids during atypically severe conditions associated with an infestation with a protozoan gill parasite *Amoeba* spp. The incidence of deformities was generally low. A higher proportion of the diploids had hump-back

deformities, whereas a higher proportion of the triploids had severe eye cataracts (Cotter et al. 2002). In ranching experiments, the return to the coast and to freshwater was lower for triploid than for diploid salmon (Cotter et al. 2000, Wilkins et al. 2001). However, it is not known whether the triploids remained in the ocean and failed to migrate towards the coast and rivers because as sterile fish they had no reason to return, or whether their mortality was higher. Triploids entered freshwater later than diploids, and did not show increased straying frequency compared to diploids (Wilkins et al. 2001). Thus, triploidy may, in addition to eliminating direct genetic effects, also reduce ecological effects of escaped farmed salmon in near coastal areas and rivers. It must be emphasized that ecological interactions of farmed sterile fish with wild fish must be critically evaluated before large-scale releases of sterile fish can be encouraged.

Use of triploid salmon in commercial farming would require research and development to determine optimum rearing conditions. Specifically, research is needed on determining environmental tolerances and optima (temperature, oxygen, salinity etc), nutritional requirements (energy, micronutrients etc.), disease resistance and behaviour (aggression, competition with diploids etc.) (Benfey 2001). The specific problem of deformities must also be addressed. For an overview of the pros and cons of using sterile salmon in farming, see also Johnstone (2005), Wilkins (2005), Webster (2005) and Benfey (2005).

One important general observation on triploidy is that when the procedure is applied to genetically divergent strains of Atlantic salmon, the resultant fish may exhibit different morphological, behavioural and performance characteristics. Because of this, it is technically incorrect to refer to triploid salmon as a single entity (Webster 2005, see also Friars et al. 2001 for family differences).

At present, induced triploidy is the only effective method for mass production of sterile salmon for aquaculture. Other methods of producing sterility are becoming available through gene manipulation (Ferguson et al. 2007). However, at present little research is being done on such methods due to worries about potential customer resistance, and there are different legislative approaches to regulating gene-modified salmon in different countries.

8.2 Domestication

Domesticating cultured fish to the point where they are unable to breed successfully in nature, or even to survive in nature, could be an effective means of reducing or eliminating genetic and ecological threats to wild populations (Fleming 1995, Balon 2004). Even though farmed salmon already differ genetically from wild salmon, it might be a long, expensive and complicated process to select for a truly domesticated farmed salmon, while at the same time not affecting those characteristics that make it worth farming in the first place. There is no aquaculture species that has been truly domesticated, except the common carp (*Cyprinus carpio*), and there have been no successful efforts to breed a fish that is unable to reproduce and survive in the wild (Fleming 1995, Balon 2004, Naylor et al. 2005).

8.3 Site selection

Escaped farmed salmon are likely to have different survivals, straying rates and straying behaviour, depending on the specific site they escape from (e.g. from exposed areas compared to shallow near-shore areas; see chapter 2.14 and 8.6). Thus, the proportion of escaped fish entering rivers may differ among sites, and the success of organised recapture attempts may differ. Increased knowledge of the survival rates and movement patterns of fish escaping from different locations could be used in site selection, to either avoid using sites assessed as being high risk, or to deploy technologies specially adapted for such sites.

8.4 Areas without Atlantic salmon farming - protection zones

Experiences from Norway: establishment of temporal protection zones and national salmon fjords

In 1989, 52 protection zones in fjords distributed along the Norwegian coast were designated, within which the further establishment of salmon farming units beyond those already in existence were not allowed. The intention was to provide special protection for wild salmonid populations against diseases and genetic interaction from farm sites and escaped farmed fish. In total, the salmonid populations of 125 important river systems draining into these protection zones are believed to benefit.

When the protection zones were evaluated (Lund et al. 1994), a positive correlation was found between the proportion of escaped farmed salmon in coastal fisheries and spawning populations and a) the densities of salmon farm units, and b) the number of smolts released into cages, on a regional basis. However, there was no difference in proportions of escaped farmed salmon in spawning populations between rivers inside and outside of the zones.

The lack of a difference in proportions of farmed salmon in spawning populations was most probably a consequence of the small size the zones (49% of the zones were < 50 km² and 75% < 200 km²) combined with the presence of pre-existing salmon farming units within the zones when they were established (Lund et al. 1994). Only a few zones seemed to have the intended effect of reducing the proportion of escaped farmed salmon in nearby rivers. The most successful zones were the largest, which coincidentally had a limited pre-existing fish farming activity within their boundaries compared to the size of the zone (Trondheimsfjord 1500 km², Sognefjord 515 km²).

In 2003, 21 national salmon fjords and 37 national salmon rivers distributed along the entire coastline were designated to protect the wild Atlantic salmon (Sivertsen 2006). The national salmon fjords replaced the previous protection zones. No new licences for salmonid farming will be given in the Norway's national salmon fjords (Sivertsen 2006). Thirteen of the fjords/areas should be completely free of farming, which means that existing farms must be moved before 1 March 2011. Most of these areas are already without farming activity, but some farms in the Altafjord and Trondheimsfjord must be moved. In those designated national salmon fjords where pre-existing farming will be allowed to continue, stricter farm operation regulations (fish health and escapes) will apply.

A proposal was put forward to the Norwegian Parliament to establish an additional 8 national salmon fjords and 15 national salmon rivers (Anon. 2006). This proposal was approved in the spring 2007. Hence, there is now a total of 29 national salmon fjords and 52 national salmon rivers, protecting almost 50 of the most important wild salmon populations in Norway containing three quarters of the total wild salmon resource (Anon. 2006).

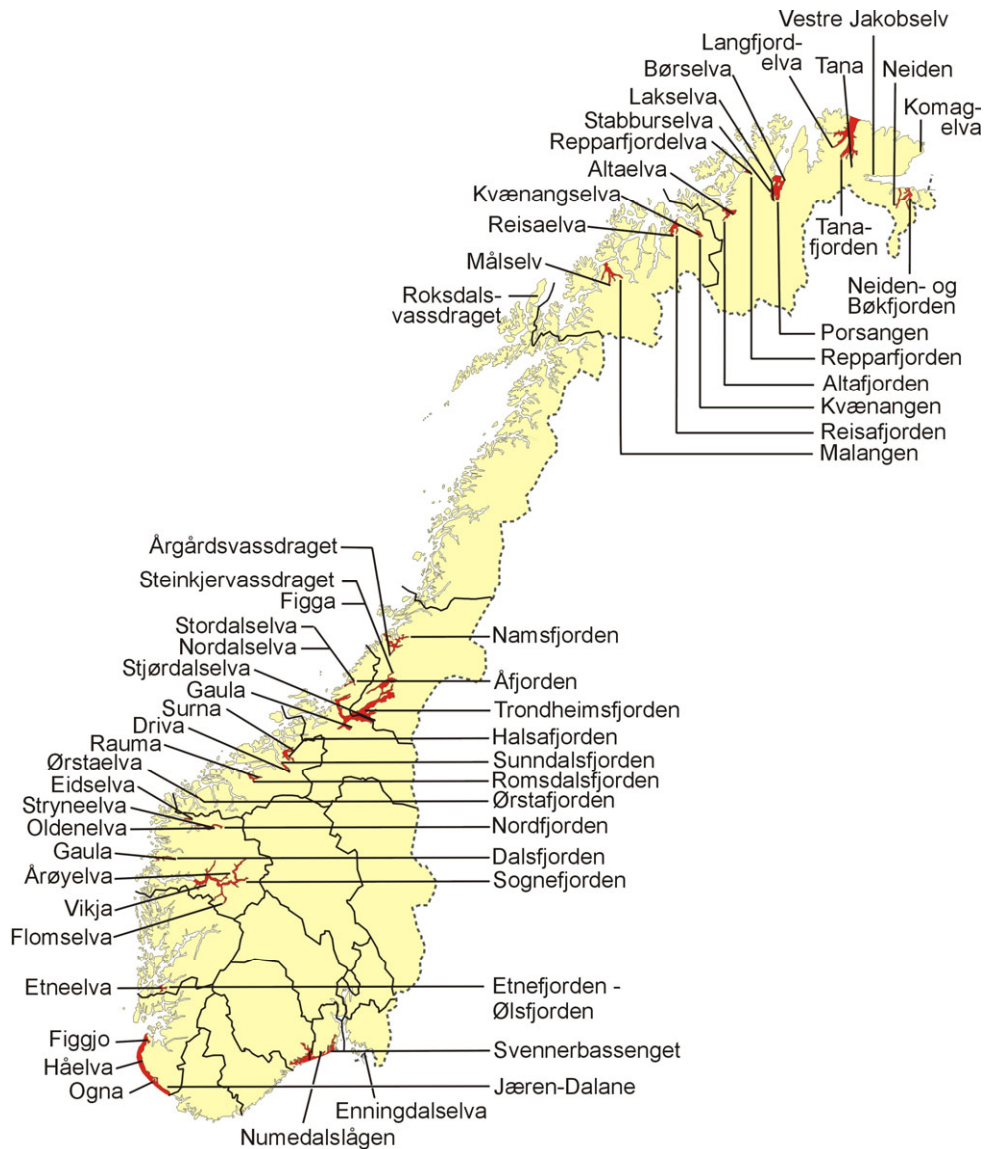


Figure 2.3. National salmon fjords and rivers in Norway. Source: Sivertsen (2006), Norwegian Directorate for Nature Management.

The effects of the salmon fjords have yet to be evaluated, but this is to be accomplished within ten years of their nomination. The relation between densities of fish farms and

occurrence of escaped farmed salmon on a regional basis found by Lund et al. (1994) and Fiske et al. (2006a) indicate that the largest protected areas maybe having the desired effect. However, the benefits of the smallest protection areas remain questionable.

It has been suggested that large rivers can attract escaped farmed salmon even though they are situated far from any fish farms (Lund et al. 1994). If such rivers drain into narrow fjords with an outward current flowing past areas with fish farming activity, they can potentially attract escaped farmed salmon, especially when rivers are discharging high volumes of freshwater into the sea in the autumn (Lund et al. 1994). Information on the characteristics of rivers that attract a high number of escaped farmed salmon is therefore needed to be able to support the design of protection zones.

Protection areas in Iceland

Since 2004, salmonid farming in sea cages has been prohibited in fjords and bays close to major salmon rivers in Iceland (NASCO 2004). This ban was introduced on the basis of the precautionary approach, and replaced a previous regulation established in 2001 that prohibited rearing of fertile salmon in the same areas.

Chile

In Chile, there are specifically allocated areas for aquaculture. However, some NGOs and social organizations are challenging these, specifically proposing some large marine protected areas without salmon farming (Leon 2006).

8.5 Gene banks

Salmon from more than 30 rivers are, or have been, kept in living gene bank centres in Norway (Directorate for Nature Management 2001). In addition, sperm has been taken from more than 170 salmon populations, deep frozen and kept in a milt bank. This national gene bank programme for salmon was established in 1986, to secure genetic material from individual wild salmon stocks at a time of declining wild salmon stocks. Living gene banks have been targeted specifically at the preservation of seriously threatened salmon populations, for instance those infected with the parasite *Gyrodactylus salaris*, which were to be subjected to rotenone treatment, and then re-established with native genetic material secured from the live gene bank. The milt bank programme aims eventually to collect and store sperm from at least 50 individuals from each of 170 identified stocks, with collection taking place over at least two years. The living gene bank aims to maintain a minimum effective population size of 50 for each generation. Conservation programmes using the gene bank programme are time-limited, and the threat necessitating use of the gene bank must be removed (Skår 2005). Gene banks have also been established in other countries, such as Canada and the United States, for similar purposes.

Gene bank programmes can only be expected to preserve a small fraction of the genetic characteristics of the wild salmon populations and to achieve this for only short periods of time. Hence, it is unrealistic to believe that gene bank material can be used as a long term and effective conservation strategy for re-establishing wild populations following large scale introgressions with hatchery fish.

8.6 Efforts to recapture escaped farmed salmon

Efforts have been made to recapture escaped farmed salmon to reduce their impacts, either immediately after large-scale reported escape episodes, or as a general measure to reduce the amounts of escaped farmed salmon in nature.

Recaptures immediately after large-scale escapes

What do we know about the success of efforts to recapture escaped salmon after large escape episodes? In the Bay of Fundy, no farmed salmon were caught in the two attempts made to recapture them after they escaped from Canadian cage sites, including from a large release of > 100 000 fish in 2005 (Whoriskey, unpublished data). On the west coast of Norway (Tustna), almost 500 000 salmon escaped during one episode in August 2005. A fishery was opened both for commercial and recreational fishers, and the farming company paid 10 NOK per kg salmon to stimulate recaptures. A total of 12 500 escaped salmon were recaptured (2.5% of the escapes) (Anfinssen 2005, referred to in Skilbrei 2006). In Northern Norway (Alta Fjord), approximately 95 000 salmon escaped in June 2005. A fishery was organised, starting two weeks after the release, lasting almost one month. In this organised fishery, 2.9 % of the escaped salmon were recaptured (Skilbrei 2006). A larger proportion was probably captured by commercial bag and hook net fishers during the first days after the escape. It can be concluded from these episodes that a huge effort is needed to effectively recapture salmon after such large-scale escapes (Skilbrei 2006), and it may even be unrealistic to recapture a significant percentage of the escapes with such efforts.

The success of recapture strategies implemented immediately after large-scale escapes is dependent on the fish behaviour and catchability after release. Farmed salmon have been shown to stray far from the release site within a few hours of release (Furevik et al. 1990, Whoriskey et al. 2006). The time it took before fish to depart the site of release varied throughout the year, from immediate departure to an approximate six hour delay (Furevik et al. 1990). Similar results were obtained by Whoriskey et al. (2006), with the salmon dispersing more than 1 km from the release site within an average of 2.4 hours in the winter and 5.8 hours in the spring.

An ongoing study on the behaviour of farmed salmon after simulated escape was initiated in southwestern Norway in 2005 using acoustic transmitters (Skilbrei 2006). Preliminary results show that three days after release the fish were spread over an area covering tens of square kilometres, such that a fishery 1-2 km from the release site would have had a limited effect. Immediately after release, the salmon dove to 10-80 m depth, where they remained during the first hours. During the next six days, the salmon were gradually recorded in shallower water, and thereafter, typically found at depths of less than 5 m (Skilbrei 2006). This diving activity after release further decreases the likelihood of recapture using traditional fishing gears. Skilbrei (2006) hypothesized that the migration rates and directions after release may be dependent on site and time of the year, and that there may be differences between localities in sheltered fjords and more exposed coastal areas (see also Skilbrei 1998). Increased knowledge on the detailed behaviour after escape is needed to be able to develop effective methods for recapture, if it is to be even considered an option.

Recaptures as a general measure to reduce the amounts of escaped farmed salmon

In Norway, there has been an attempt to extend the marine fishing season in the autumn and winter to increase the exploitation of escaped farmed salmon (Fiske 2004, Syvertsen & Vatne 2000). During 1998-2002, an annual average of 9 200 salmon, or 32 t, was captured in this extended fishery (Fiske 2004). The estimated proportion of escaped farmed salmon in examined catches was 33-94% in checked samples. In the extended marine fishery in Hordaland County, annual catches of escaped farmed salmon varied between 5 and 15 t, with only small catches of wild salmon (Skilbrei & Wennevik 2006). An extended fishing season, however, may affect local sea trout populations negatively (Fiske 2004). In conclusion, the catches of escaped farmed salmon in the extended marine fishery are small compared to the number of salmon escaping, and the effects on the number of escaped farmed salmon entering the rivers is not known.

In Canada, fishing seasons have been prolonged in some farming areas where escaped farmed fish occurred (e.g., Bras d'Or Lakes on Cape Breton for escaped steelhead), however, no records were garnered to determine how many of the escapees were captured and the number of escapees was not known.

Attempts have also been made to recapture escaped farmed salmon with drift nets and bag nets after they have entered river mouths (Lund 1998a). These methods, however, proved not to be successful in large rivers with high water discharges. Angling, or sorting out escaped farmed salmon when passing fish ways, may be the most effective ways to recapture salmon after they have entered the rivers, especially those with high water discharges. However, both are labour intensive, and it is difficult to identify farmed salmon that escaped early in life and have little or no morphological signs of having been farmed. Angling will also require catch and release of wild salmon, as both wild and escaped farmed salmon will be captured.

In Chile, it has been proposed to at least examine the potential of artisanal fishing as a way of recovering escaped salmon (Soto et al. 2001), and the use of angling and recreational fishery to control escaped salmonids in lakes and rivers (Soto et al. 2006, 2007). Strong political commitment and willingness is needed in order to make this a reality. Additionally, it is necessary to give greater relevance to the social and economic implications of escaped farmed salmon, which may differ greatly among countries and regions, an issue which has not been discussed here.

8.7 Conclusive statements

- The use of sterile salmon is a measure that should be carefully appraised, considering the positive effects it could have on reducing direct genetic effects of farmed salmon on wild salmon populations. It may also reduce ecological effects. However, it is unlikely to greatly reduce threats from the transmission of diseases and parasites.
- The most effective method of sterilising Atlantic salmon is high pressure induction of triploidy in newly fertilised eggs. Triploids have a number of disadvantages in commercial aquaculture, but results from different studies vary with regards to triploid growth, survival and the occurrence of deformities. Triploidy is a

procedure that can be applied to different stocks which, as diploids, are likely to exhibit different morphological, behavioural and performance characteristics. It is therefore unlikely that the characteristics of different triploid stocks will be the same.

- Domesticating cultured fish to the point where they are unable to breed successfully in nature, or even to survive in nature, could be an effective means of reducing or eliminating genetic and ecological threats to wild populations. However, this would potentially be a complicated and long-term process to select for a truly domesticated farmed salmon, while at the same time not affecting characteristics that may reduce the culture yield.
- Protection zones where salmon farming is prohibited may be an effective way of protecting wild salmon populations. Such zones have been established in fjords in both Norway (pre-existing farms however were not always relocated) and Iceland. Only a few zones seemed to gain the intended effect of reducing the proportion of escaped farmed salmon in nearby rivers, according to a preliminary evaluation in Norway. This may be a consequence of the small size the zones, with the two largest zones appearing to be the most successful thus far, and the presence of pre-existing farms in some of the zones. New protection zones have recently been established in Norway, and an evaluation will be done within the next ten years.
- Gene bank programmes can only be expected to preserve a small fraction of the genetic characteristics of the wild salmon populations and to achieve this for only short periods of time. Hence, it is unrealistic to believe that gene bank material can be used as a long term and effective conservation strategy for re-establishing wild populations following large scale genetic introgressions with hatchery fish.
- Escaping post-smolts seem to move away from the release site within a few hours of escape, and even a huge effort over large areas may not effectively recapture salmon after large-scale escapes. Only a small percentage (< 3%) of escaped salmon has been recaptured through organised fishing after large escape episodes.
- In Norway, there has been an attempt to extend the fishing season in the sea in the autumn and winter to increase the exploitation of escaped farmed salmon. An extended fishing season in the sea seems to have a limited impact on wild populations. However, the catches of escaped farmed salmon are small compared to the number of salmon escaping, and the effects on the number of escaped farmed salmon entering the rivers is not known.
- Angling, or separation of escaped farmed from wild salmon when passing fish ways may be the most effective ways to recapture escapees after they have entered the rivers, especially in rivers with a high water discharge. However, both are labour intensive methods, and it is difficult to identify farmed salmon that have escaped at an early stage and have little or no morphological signs of have been farmed. Angling requires catch and release of wild salmon, as both wild and escaped farmed salmon will be captured.

8.8 Knowledge gaps and research needs

- Use of triploid (i.e. sterile) salmon in commercial farming would require research and development to determine optimum rearing conditions and boost triploid disease resistance. Ecological interactions of farmed sterile fish with wild fish must be critically evaluated before large-scale releases of sterile fish can be encouraged.
- Research into design of protection zones without fish farming to protect rivers from escaped farmed salmon in rivers is needed. The numbers of escaped farmed salmon vary among rivers, and some large rivers seem to attract escaped farmed salmon even though they are situated far from any fish farms. Information on what characterises rivers that attract a high number of escaped farmed salmon is needed to evaluate the effectiveness of different existing protection zones and to design new ones.
- Models need to be developed that predict survival and migration pattern for escaped fish. Field data is required to parameterise these models. With such knowledge, measures to reduce impacts of escapes can more easily be identified.

9 General conclusions

For detailed conclusive statements, knowledge gaps and research needs regarding the issues raised in the different chapters of the report, we refer the reader to the respective chapters. Here, we highlight our main conclusions and identified research needs.

9.1 Main conclusions

- Farm salmon are escaping into the wild in large numbers relative to the numbers of their wild conspecifics.
- Escaped farmed salmon are clearly an international issue, with frequent observations of their crossing national borders. Escapes from fish farms occur in all salmon producing countries. Information on the extent and causes of escapes is poor for all salmon producing countries, but is worse for some countries than others. Nearly all salmon producing countries have established routines for reporting at least large-scale escapes. Information on low-level leakage and escapes from freshwater hatcheries remains uniformly poor.
- Potential negative effects by escaped farmed salmon on wild salmon populations are well documented and many verified through research. Negative effects are linked to both ecological interactions and genetic impacts of inter-breeding. A large number of studies point to negative effects, and outcomes for wild populations are either mostly negative or neutral. It has been shown that inter-breeding of farm with wild salmon can result in reduced lifetime success, lowered fitness and production over at least two generations.
- Throughout their native distribution, Atlantic salmon populations are in decline, despite the reduction in marine fisheries (Parrish et al. 1998, Klemetsen et al. 2003, ICES 2004). Several factors have contributed to this decline, and human impacts, such as overexploitation, acid deposition, transfer of parasites and diseases, aquaculture, freshwater habitat degradation, hydropower development and other river regulations seem to be important contributors (Johnsen & Jensen 1991, Parrish et al. 1998, Anon. 1999, NRC 2004, ICES 2004). In the future, wild salmon populations are expected to be under further pressure from the effects of climate change. Most factors affecting salmon numbers do not act singly, but rather in concert, which masks the relative contribution of each factor and may exacerbate the overall effects of the individual stressors. This has two important implications regarding escaped farmed salmon: 1) potential effects of escaped farmed salmon on population size and production are difficult to separate from other factors, and 2) wild salmon populations are likely to be more vulnerable to effects of escaped farmed salmon because of the synergistic effect of other negative pressures. The maintenance of strong wild salmon populations may reduce the likelihood and magnitude of negative impacts by escaped farmed salmon.
- In 2004, 28% of the total world production of Atlantic salmon was in regions where the species is exotic. The questions in these regions are whether escaped Atlantic

salmon are able to establish self reproducing populations, whether they are able to hybridize with native fishes, and what ecological effects escaped salmon may have on native species and ecosystems. Historical attempts to introduce anadromous populations of Atlantic salmon around the world have mostly failed, confirming that Atlantic salmon is a poor colonizer outside its native range. The probability that escaped Atlantic salmon will establish populations where the species is exotic seems low, but the possibility cannot be ruled out. It is difficult to predict if or how Atlantic salmon will adapt to the regions where they are exotic. This is partly because only limited research is being conducted to study potential impacts in many of these regions. The probability for hybridisation between Atlantic salmon and Pacific salmonid species seems small.

- The most important issue at present is to implement measures reducing the numbers of escaped salmon in nature.
- Among technologies and efforts to reduce impacts of escapes, sterilisation and farm exclusion zones look to be among the most promising. The use of sterile salmon is a measure that should be carefully appraised, considering the positive effects it could have on reducing direct genetic effects of farmed salmon on wild salmon populations. It may also reduce ecological effects. However, it is unlikely to greatly reduce threats from the transmission of diseases and parasites. The most effective method of sterilising Atlantic salmon is high pressure induction of triploidy in newly fertilised eggs. Triploids have a number of disadvantages in commercial aquaculture, but studies show different results regarding growth, survival and occurrence of deformities. Use of triploid salmon in commercial farming would require research and development to determine optimum rearing conditions and to boost disease resistance. Regarding protection zones without salmon farming, preliminary results from Norway show that only a few zones seemed to gain the intended effect of reducing the proportion of escaped farmed salmon in nearby rivers, which may be a consequence of the small size of many of the zones. New protection zones have recently been established in Norway, however, their benefits remain to be evaluated. An important focus at present for preventing escapes involves technology development and improvement of operating regimes. However, this alone is unlikely to be sufficient, at least in the short to medium term.

9.2 Key research needs

- As long as significant numbers of escapees continue to occur, there will be significant research needs regarding the ecological and genetic impacts of escaped farmed salmon on wild populations (see chapters 3 and 4). However, given the compelling evidence pointing towards a high risk of negative impacts by escaped farmed salmon on wild salmon populations (or on native fish/other organisms in the case of escapes as alien species), and recognising the need to continually improve on our knowledge of the interactions between cultured and wild Atlantic salmon, the members of this working group would like to emphasise that the most pressing research priorities are linked to: 1) technologies and efforts for containment (escape prevention), and 2) approaches to reduce impacts of escapees (with main focus on sterilisation and protection zones, see chapter 9.1 above).

- There is generally little knowledge on the performance of escaped farmed salmon in regions where the Atlantic salmon is an exotic species. There is also little knowledge about the interactions of Atlantic salmon with native species in these regions, especially non-salmonids. This hinders our ability to predict the impacts, e.g. whether or not feral Atlantic salmon populations can become established. However, a focus in these regions on escape prevention would reduce the likelihood of potential impacts.
- A prerequisite for escape prevention is knowledge on why, when and from where salmon escape. Such information is needed to identify critical factors related to culture technologies, techniques and sites. When this information is combined with knowledge of survival and distribution of escaped salmon at different life stages, times of the year and locations to identify the most critical escape periods, risk analyses can be performed and the high priority areas of improvement and development can be identified
- More knowledge is required about the genetic population structure of wild populations, particularly the importance of local adaptation in determining their long-term productivity and resilience in natural environments. Also contemporary baseline genetic information, both molecular and quantitative, should be collected for all populations throughout the species distribution. This with the genetic analyses of archival material such as scale collections should be utilised to determine the impact of farm escapes in the past and as a basis to assess the genetic effect of future escapes.



Salmon farm in Middle Norway.

Photo: Eva B. Thorstad

Box 3: Relevant reviews previously published

- Ferguson, A., Fleming, I., Hindar, K., Skaala, Ø., McGinnity, P., Cross, T.F. & Prodöhl, P. 2007. Farm escapes. In: The Atlantic salmon: Genetics, Conservation and Management (Verspoor, E., Stradmeyer, L. & Nielsen, J.L., eds.). Blackwell Publishing Ltd, pp. 357-398.
- Gross, M.R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences 55 (Supplement 1): 131-144.
- Hansen, L.P. & Windsor, M. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: Science and management, challenges and solutions. Conveners' report of the symposium held in Bergen, Norway, 18-21 October 2005. Norwegian Institute for Nature Research, NINA Special Report 34: 1-74.
- Heggberget, T.G., Johnsen, B.O., Hindar, K., Jonsson, B., Hansen, L.P., Hvidsten, N.A. & Jensen, A.J. 1993b. Interactions between wild and cultured Atlantic salmon: a review of the Norwegian experience. Fisheries Research 18: 123-146.
- Hindar, K., Ryman, N. & Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48: 945-957.
- Huntingford, F.A. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. Journal of Fish Biology 65 (Supplement A): 122-142.
- Jonsson, B. 1997. A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. ICES Journal of Marine Science 54: 1031-1039.
- Jonsson, B. & Jonsson, N. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. ICES Journal of Marine Science 63: 1162-1181.
- Jonsson, B. (ed.), Boxaspen, K., Fiske, P., Gjerde, B., Poppe, T. & Wennevik, V. 2006. Interaksjoner mellom lakseoppdrett og villaks: Oppdatering av kunnskapen etter NOU 1999:9. Kunnskapssenter for laks og vannmiljø 2: 1-80. (In Norwegian)
- NASCO 2005b. Wild and farmed salmon - working together. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group, Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, 86 pp.
- Naylor, R., Hindar, K., Fleming, I.A., Goldburg, R., Williams, S., Volpe, J., Whoriskey, F., Eagle, J., Kelso, D. & Mangel, M. 2005. Fugitive salmon: assessing the risks of escaped fish from net-pen aquaculture. BioScience 55: 427-437.
- Thorpe, J.E. 2004. Life history response of fishes to culture. Journal of Fish Biology 65 (Supplement A): 263-285.
- Weir, L.K. & Fleming, I.A. 2006. Behavioural interactions between farm and wild salmon: potential for effects on wild populations. In: A Scientific Review of the Potential Environmental Effects of Aquaculture in Aquatic Ecosystems, Volume V. Canadian Technical Report of Fisheries and Aquatic Sciences 2450: 1-29.
- Whoriskey, F. 2003. Exotic species in aquaculture. Bulletin of the Aquaculture Association of Canada 103 (2): 1-7.
- Youngson, A.F. & Verspoor, E. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55 (Supplement 1): 153-160.

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References

- Aksnes, A., Gjerde, B. & Roald, S.O. 1986. Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. *Aquaculture* 53: 7-20.
- Amiro, P.G. 2003. Population status of inner Bay of Fundy Atlantic salmon (*Salmo salar*), to 1999. Canadian Technical Report of Fisheries and Aquatic Sciences 2488: 1-39.
- Anon 1999. Til laks åt alle kan ingen gjera? Om årsaker til nedgangen i de norske villaksbestandene og forslag til strategier og tiltak for å bedre situasjonen. NOU 1999:9, 297 pp. (In Norwegian with English abstract)
- Anon. 2004a. Status of Irish Aquaculture, 2003. Marine Institute, Bord Iascaigh Mhara and Taighde Mara Teo., Rinville, Oranmore, Co. Galway, Ireland, 51 pp.
- Anon. 2004b. What to do in the event of an escape of fish from a fish farm. Guidance on the registration of fish farming and shellfish farming business (Amendment) (Scotland) order 2002. The Scottish Executive Environment and Rural Affairs Department May 2002, 6 pp.
- Anon. 2006. Om vern av villaksen og ferdigstilling av nasjonale laksevassdrag og laksefjorder. Stortingsproposisjon nr 32 (2006-2007), Det kongelige miljøverndepartement, 143 pp. (In Norwegian)
- Atlantic Salmon Federation 2004. Atlantic salmon aquaculture - a primer. Available at <http://www.asf.ca/Aquaculture/ASFaquaculture2004.pdf>
- Baarøy, V., Gjerde, B., Heggberget, T.G., Jensen, P.E., Maroni, K., Sandvik, S., Skaala, Ø., Taranger, G.T., Veie-Rossvoll, B. & Haldorsen, M. 2004. Identifisering av rømt oppdrettslaks. Utredning fra utvalg nedsatt av Fiskeridirektøren (Identification of escaped farmed salmon. Report from Committee to the Director of Fisheries), 55 pp. (In Norwegian)
- Balon, E.K. 2004. About the oldest domesticates among fishes. *Journal of Fish Biology* 65 (Supplement A): 1-27.
- Basulto, S. 2003. El largo viaje de los salmones: una crónica olvidada, Propagación y cultivo de especies acuáticas en Chile. Maval Limitada Editores, Santiago, Chile, 102 pp. (In Spanish)
- Baum, E.T. 1998. Maine Atlantic salmon - a national treasure. Atlantic Salmon Unlimited, Hermon, ME.
- Baum, E. 2000. Documented aquaculture escapees in Maine Rivers. ICES Working Group for North Atlantic salmon, Working paper 2000/26.
- Beall, E., Heland, M. & Marty, C. 1989. Interspecific relationships between emerging Atlantic salmon, *Salmo salar*, and coho salmon, *Oncorhynchus kisutch* juveniles. *Journal of Fish Biology* 35(A): 285-293.
- Benfey, T.J. 1999. The physiology and behaviour of triploid fishes. *Reviews in Fisheries Science* 7: 39-67.
- Benfey, T.J. 2001. The use of sterile triploid Atlantic salmon (*Salmo salar* L.) for aquaculture in New Brunswick, Canada. *ICES Journal of Marine Science* 58: 525-529.
- Benfey, T.J. 2005. Improving the performance of sterile salmon for use in farming. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group, Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, pp 48-51.

- Bentsen, H.B. & Thodesen, J. 2005. Genetic interactions between farmed and wild fish, with examples from the Atlantic salmon case in Norway. In: Selections and Breeding Programmes in Aquaculture (Gjedrem, T., ed.). Springer, the Netherlands.
- Bisson, P.A. 2006. Assessment of the risk of invasion of national forest streams in the Pacific Northwest by farmed Atlantic salmon. General Technical Report PNW-GTR-697. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 28 pp.
- Blanc, J.M. & Chevassus, B. 1979. Interspecific hybridization of salmonid fish: I Hatching and survival up to the 15th day after hatching in F1 generation hybrids. *Aquaculture* 18: 21-34.
- Blanc, J.M. & Chevassus, B. 1982. Interspecific hybridization of salmonid fish: II Survival and growth up to the 4th month after hatching in F1 generation hybrids. *Aquaculture* 29: 383-387.
- Blann, C.A. & Healey, M.C. 2006. Effects of species, culture history, size and residency on relative competitive ability of salmonids. *Journal of Fish Biology* 69: 535-552.
- Bridger, C.J., Booth, R.K., McKinley, R.S. & Scruton, D.A. 2001. Site fidelity and dispersal patterns of domestic triploid steelhead trout (*Oncorhynchus mykiss* Walbaum) released to the wild. *ICES Journal of Marine Science* 58: 510-516.
- Browne, R., Deegan, B., O'Carroll, T., Norman, M., Ó Cinnéide, M. 2007. Status of Irish Aquaculture. A compilation report of information on Irish Aquaculture (with a review of key programmes during the years 2000 to 2006). Marine Institute, Bord iascaigh Mhara and Taighde Mara Teo, pp 113.
- Butler, J.R.A., Cunningham, P.D. & Starr, K. 2005. The prevalence of escaped farmed salmon, *Salmo salar* L., in the River Ewe, western Scotland, with notes on their ages, weights and spawning distribution. *Fisheries Management and Ecology* 12: 149-159.
- Carlin, B. 1969. Migration of salmon. Lectures Series. Atlantic Salmon Association Special Publication, Montreal, pp 14-22.
- Carr, J.W. & Whoriskey, F.G. 2006. The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. *ICES Journal of Marine Science* 63: 1263-1268.
- Carr, J.W., Anderson, J.M., Whoriskey, F.G. & Dilworth, T. 1997a. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *ICES Journal of Marine Science* 54: 1064-1073.
- Carr, J.W., Lacroix, G.L., Anderson, J.M. & Dilworth, T. 1997b. Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *ICES Journal of Marine Science* 54: 1082-1085.
- CBSG (Conservation Breeding Specialist Group) 2003. Exploitation and management of exotic and naturalized aquatic genetic resources in relation to native biodiversity: FINAL REPORT. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA, 55 pp.
- Chevassus, B. 1979. Hybridization in salmonids: Results and perspectives. *Aquaculture* 17: 113-128.
- Ciancio J.E., Pascual, M.A., Lancelotti, J., Rossi, C. & Botto, F. 2005. Natural colonization and establishment of a Chinook salmon *Oncorhynchus tshawytscha*, population in the Santa Cruz River, an Atlantic basin of Patagonia. *Environmental Biology of Fishes* 74: 219-227.

- Clifford, S.L., McGinnity, P. & Ferguson, A. 1998a. Genetic changes in an Atlantic salmon population resulting from escaped juvenile farm salmon. *Journal of Fish Biology* 52: 118-127.
- Clifford, S.L., McGinnity, P. & Ferguson, A. 1998b. Genetic changes in Atlantic salmon (*Salmo salar*) populations of Northwest Irish rivers resulting from escapes of adult farm salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 358-363.
- Cotter, D., O'Donovan, V., Drumm, A., Roche, N., Ling, E.N. & Wilkins, N.P. 2002. Comparison of freshwater and marine performances of all-female diploid and triploid Atlantic salmon (*Salmo salar* L.). *Aquaculture Research* 33: 43-53.
- Cotter, D., O'Donovan, V., O'Maoiléidigh, N., Rogan, G., Roche, N. & Wilkins, N.P. 2000. An evaluation of the use of triploid Atlantic salmon (*Salmo salar* L.) in minimising the impact of escaped farmed salmon on wild populations. *Aquaculture* 186: 61-75.
- Coughlan, J., McGinnity, P., O'Farrell, B., Dillane, E., Diserud, O., de Eyto, E., Farrell, K., Whelan, K., Stet, R.J.M. & Cross, T.F. 2006. Temporal variation in an immune response gene (MHC I) in anadromous *Salmo trutta* in an Irish river before and during aquaculture activities. *ICES Journal of Marine Science* 63: 1248-1255.
- Craik, J.C.A. & Harvey, S.M. 1987. A biochemical method for distinguishing between wild and farmed salmonid fishes by their carotenoid pigmentation. *Journal of Forensic Science Society* 27: 47-55.
- Crisp, D.T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. *Freshwater Biology* 11: 361-368.
- Cross, T.F. & Challanain, D.N. 1991. Genetic characterisation of Atlantic salmon (*Salmo salar*) lines farmed in Ireland. *Aquaculture* 98: 209-216.
- Crozier, W.W. 1993. Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L.). *Aquaculture* 113: 19-29.
- Crozier, W.W. 1998. Incidence of escaped farmed salmon, *Salmo salar* L., in commercial salmon catches and fresh water in Northern Ireland. *Fisheries Management and Ecology* 5: 23-29.
- Crozier, W.W. 2000. Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: genetic status of the wild population 7 years on. *Fisheries Management and Ecology* 7: 437-446.
- Danielsdottir, A.K., Marteinsdottir, G., Arnason, F. & Gudjonsson, S. 1997. Genetic structure of wild and reared Atlantic salmon (*Salmo salar* L.) populations in Iceland. *ICES Journal of Marine Science* 54: 986-997.
- Dempson, J.B. & Power, M. 2004. Use of stable isotopes to distinguish farmed from wild Atlantic salmon, *Salmo salar*. *Ecology of Freshwater Fish* 13: 176-184.
- DFO (Department of Fisheries and Oceans, Canada) 1999. Interaction between wild and farmed Atlantic salmon in the Maritime Provinces. DFO Maritimes Regional Habitat Status Report 99/1E.
- Directorate for Nature Management 2001. The Norwegian Gene Bank Programme for Atlantic Salmon. Brochure, Directorate for Nature Management, Norway. Available at: <http://www.dirnat.no/content.ap?thisId=500003655&language=0>.
- DPIW (Department of Primary Industries and Water) 2006. An overview of escaped salmonids and their potential impacts in Tasmania. Unpublished note, 8 pp.

- Dunmall, K.M. & Schreer, J.F. 2003. A comparison of the swimming and cardiac performance of farmed and wild Atlantic salmon, *Salmo salar*, before and after gamete stripping. *Aquaculture* 220: 869-882.
- Enders, E.C., Boisclair, D. & Roy, A.G. 2004. The costs of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 61: 2302-2313.
- Einum, S. & Fleming, S. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *Journal of Fish Biology* 50: 634-651.
- Eriksson, T. & Eriksson, L.O. 1991. Spawning migratory behaviour of coastal-released Baltic salmon (*Salmo salar*). Effects on straying frequency and time of river ascent. *Aquaculture* 98: 79-87.
- de Eyto, E., McGinnity, P., Consuegra, S., Coughlan, J., Tufto, J., Farrell, K., Megens, H.-J., Jordan, W., Cross, T. & Stet, R.J.M. 2007. Natural selection acts on Atlantic salmon major histocompatibility (MH) variability in the wild. *Proceedings of the Royal Society of London series B* 274: 861-869.
- FAO (Food and Agriculture Organization of the United Nations) 2005. FishStat - Fishery Information, Data and Statistics Unit, FAO, ROME.
- FAO (Food and Agriculture Organization of the United Nations) 2006. State of world aquaculture: 2006. FAO Fisheries Technical Paper No. 500. FAO, Rome, 134 pp.
- Ferguson, A., Fleming, I., Hindar, K., Skaala, Ø., McGinnity, P., Cross, T.F. & Prodöhl, P. 2007. Farm escapes. In: *The Atlantic salmon: Genetics, Conservation and Management* (Verspoor, E., Stradmeyer, L. & Nielsen, J.L., eds.). Blackwell Publishing Ltd, pp. 357-398.
- Fernandez, M., Jaramillo, E., Marquet, P.A., Moreno, C.A., Navarrete, S.A., Ojeda, F.P., Valdovinos, C.R. & Vasquez, J.A. 2000. Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. *Revista Chilena de Historia Natural* 73: 797-830.
- Fiske, P. 2004. "Utvidet fiskesesong" for fiske etter rømt oppdrettslaks i sjøen høst og vinter. Sammenstilling av data fra undersøkelser om fiske etter rømt oppdrettslaks. DNs ref. nr 03040045, 11 pp. (In Norwegian)
- Fiske, P. 2006. NOBANIS - invasive alien species fact sheet - *Salmo salar*. Online Database of the North European and Baltic Network on Invasive Alien Species - NOBANIS, available at www.nobanis.org.
- Fiske, P., Lund, R.A. & Hansen, L.P. 2001. Rømt oppdrettslaks i sjø- og elvefiskeriet i årene 1989-2000. NINA Oppdragsmelding 704: 1-26. (In Norwegian)
- Fiske, P., Lund, R.A. & Hansen, L.P. 2005a. Identifying fish farm escapees. In: *Stock identification methods* (Cadrin, S.X., Friedland, K.D. & Waldman, J.D., eds.), pp 659-680. Elsevier Academic Press, Amsterdam.
- Fiske, P., Lund, R.A. & Hansen, L.P. 2006a. Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L., in wild salmon populations and fish farming activity in Norway, 1989-2004. *ICES Journal of Marine Science* 63: 1182-1189.
- Fiske, P., Lund, R.A., Østborg, G. & Heggberget, T.G. 2007. Karakterisering av rømt oppdrettslaks fanget ved utfisking med kilenot i Salvatnet i 2006. Report, Norwegian Institute for Nature Research, 6 pp. (In Norwegian)
- Fiske, P., Lund, R.A., Østborg, G., Heggberget, T.G. & Thorstad, E.B. 2005b. Rømt oppdrettslaks i Salvassdraget i 2004 - kommer fiskene fra en eller flere rømmingsepisoder? NINA Minirapport 103: 1-9. (In Norwegian)

- Fiske, P., Lund, R.A., Thorstad, E.B., Heggberget, T.G. & Østborg, G. 2006b. Rømt oppdrettslaks i Salvassdraget i 2004 og 2005. NINA Rapport 172: 1-13. (In Norwegian)
- Fleming, I.A. 1995. Reproductive success and the genetic threat of cultured fish to wild populations. In: Protection of aquatic biodiversity (Philipp, D.P., Epifanio, J.M., Marsden, J.E. & Claussen, J.E., eds.), pp 117-135. Proceedings of the World Fisheries Congress, Theme 3. Oxford and IBH Publishing, New Delhi, India.
- Fleming, I.A. & Einum, S. 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES Journal of Marine Science* 54: 1051-1063.
- Fleming, I.A., Jonsson, B. & Gross, M.R. 1994. Phenotypic divergence of sea-ranched, farmed and wild salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2808-2824.
- Fleming, I.A., Lamberg, A. & Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. *Behavioural Ecology* 8: 470-480.
- Fleming, I.A., Jonsson, B., Gross, M.R. & Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild salmon (*Salmo salar*). *Journal of Applied Ecology* 33: 893-905.
- Fleming, I.A., Augustsson, T., Finstad, B., Johnsson, J.I. & Björnsson, B.T. 2002. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1323-1330.
- Fleming, I.A., Hindar, K., Mjølnerød, I.B., Jonsson, B., Balstad, T. & Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society of London series B* 267: 1517-1523.
- Friars, G.W., Bailey, J.K. & O'Flynn, F.M. 1997. A review of gains from selection in Atlantic salmon (*Salmo salar*) in the Salmon Genetics Research Program. *World Aquaculture* 28: 68-71.
- Friars, G.W., McMillan, I., Quinton, V.M., O'Flynn, F.M., McGeachy, S.A. & Benfey, T.J. 2001. Family differences in relative growth of diploid and triploid Atlantic salmon (*Salmo salar* L.). *Aquaculture* 192: 23-29.
- Friedland, K.D., Esteves, C., Hansen, L.P. & Lund, R.A. 1994. Discrimination of Norwegian farmed, ranched and wild-origin Atlantic salmon, *Salmo salar* L., by image processing. *Fisheries Management and Ecology* 1: 117-128.
- Furevik, D., Rabben, H., Mikkelsen, K.O. & Fosseidengen, J.E. 1990. Migratory patterns of escaped farmed Atlantic salmon. *ICES C.M.* 1990/F:55, 19 pp.
- Garant, D., Fleming, I.A., Einum, S. & Bernatchez, L. 2003. Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecology Letters* 6: 541-549.
- Garcia de Leaniz, C., Fleming, I.A., Einum, S., Verspoor, E., Jordan, W.C., Consuegra, S., Aubin-Horth, N., Lajus, D., Letcher, B.H., Youngson, A.F., Webb, J., Vøllestad, L.A., Villanueva, B., Ferguson, A. & Quinn, T.P. 2007. A critical review of inherited adaptive variation in Atlantic salmon. *Biological Reviews* 82: 173-211.
- Gausen, D. & Moen, V. 1991. Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 426-428.
- Gibson, R.J. 1981. Behavioural interactions between coho salmon, Atlantic salmon, brook trout and steelhead trout at the juvenile fluvial stages. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1029.

- Ginetz, R.M.J. 2002. On the risk of colonization by Atlantic salmon in BC waters. BC Salmon Farmers Association. Campbell River, B.C.
- Gjedrem, T., Gjerde, B. & Refstie, T. 1987. A review of quantitative genetic research in salmonids at AKVAFORSK. Second International Conference on Quantitative Genetics. Raleigh, North Carolina, 9 pp.
- Gjedrem, T., GjØen, H.M. & Gjerde, B. 1991. Genetic origin of Norwegian farmed salmon. *Aquaculture* 98: 41-50.
- GjØen, H.M. & Berntsen, H.B. 1997. Past, present, and future of genetic improvement in salmon aquaculture. *ICES Journal of Marine Science* 54: 1009-1014.
- Goode, A. & Whoriskey, F. 2003. Finding resolution to farmed salmon issues in North America. In: *Salmon at the edge* (Mills, D., ed.), pp 144-158. Blackwell Science Ltd, Oxford, UK.
- Gray, A.K., Evans, M.A. & Thorgaard, G.H. 1993. Viability and development of diploid and triploid salmon hybrids. *Aquaculture* 122: 125-142.
- Gross, M.R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. *Canadian Journal of Fisheries and Aquatic Sciences* 55 (Supplement 1): 131-144.
- Gudjonsson, S. 1991. Occurrence of reared salmon in natural salmon rivers in Iceland. *Aquaculture* 98: 133-142.
- Gudjonsson, S. 2006. Towards sustainable salmon aquaculture - zoning of the Icelandic coastline. NINA Special Report 34: 40.
- Gunnerød, T.B., Hvidsten, N.A. & Heggberget, T.G. 1988. Open sea releases of Atlantic salmon smolts, *Salmo salar*, in Central Norway, 1973-83. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1340-1345.
- Handeland, S.O., Bjørnsson, B.Th., Arnesen, A.M. & Stefansson, S.O. 2003. Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. *Aquaculture* 220: 367-384.
- Hansen, L.P. 2006a. Migration and survival of farmed Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. *ICES Journal of Marine Science* 63: 1211-1217.
- Hansen, L.P. 2006b. Vandring og spredning av rømt oppdrettslaks. NINA Rapport 162: 1-21. (In Norwegian)
- Hansen, L.P. & Jacobsen, J.A. 1998. Salmon research at Faroe Islands. NINA Oppdragsmelding 524: 1-37. (In Norwegian with English abstract)
- Hansen, L.P. & Jacobsen, J.A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. *ICES Journal of Marine Science* 60: 110-119.
- Hansen, L.P. & Jonsson, B. 1989. Salmon ranching experiments in the River Imsa: effect of timing of Atlantic salmon (*Salmo salar*) smolt migration on survival to adults. *Aquaculture* 82: 367-373.
- Hansen, L.P. & Jonsson, B. 1991. The effect of timing of Atlantic salmon smolt and post-smolt release on the distribution of adult returns. *Aquaculture* 98: 61-67.
- Hansen, L.P. & Quinn, T.P. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 55 (Supplement 1): 104-118.
- Hansen, L.P. & Windsor, M. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: Science and management, challenges and solutions. Conveners' report of the symposium held in Bergen, Norway, 18-21 October 2005. Norwegian Institute for Nature Research, NINA Special Report 34: 1-74.

- Hansen, L.P., Døving, K.B. & Jonsson, B. 1987. Migration of farmed Atlantic salmon with and without olfactory sense, released on the Norwegian coast. *Journal of Fish Biology* 30: 713-721.
- Hansen, L.P., Jacobsen, J.A. & Lund, R.A. 1993. High numbers of farmed Atlantic salmon, *Salmo salar* L., observed on oceanic waters north of the Faroe Islands. *Aquaculture and Fisheries Management* 24: 777-781.
- Hansen, L.P., Jacobsen, J.A. & Lund, R.A. 1999. The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon. *ICES Journal of Marine Science* 56: 200-206.
- Hansen, L.P., Reddin, D.J. & Lund, R.A. 1997. The incidence of reared Atlantic salmon in the commercial fishery at West-Greenland. *ICES Journal of Marine Science* 54: 152-155.
- Hansen, L.P., Fiske, P., Holm, M., Jensen, A.J. & Sægrov, H. 2006. Bestandsstatus for laks. Rapport fra arbeidsgruppe. Utredning for DN 2006-3: 1-48. Directorate for Nature Management, Trondheim, Norway. (In Norwegian)
- Hansen, L.P., Fiske, P., Holm, M., Jensen, A.J. & Sægrov, H. 2006. Bestandsstatus for laks 2007. Rapport fra arbeidsgruppe. Utredning for DN 2007-2: 1-88. Directorate for Nature Management, Trondheim, Norway. (In Norwegian)
- Hearn, W.E. & Kynard, B.E. 1986. Habitat utilization and behavioural interaction of juvenile Atlantic salmon (*Salmo salar*) and rainbow trout (*S. gairdneri*) in tributaries of White River of Vermont. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1988-1998.
- Heggberget, T.G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 45: 845-849.
- Heggberget, T.G. & Wallace, J.C. 1984. Incubation of eggs of Atlantic salmon, *Salmo salar*, at low temperatures. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 389-391.
- Heggberget, T.G., Økland, F. & Ugedal, O. 1993a. Distribution and migratory behaviour of adult wild and farmed Atlantic salmon (*Salmo salar*) during return migration. *Aquaculture* 118: 73-83.
- Heggberget, T.G., Økland, F. & Ugedal, O. 1996. Prespawning migratory behaviour of wild and farmed Atlantic salmon, *Salmo salar* L., in a north Norwegian river. *Aquaculture Research* 27: 313-322.
- Heggberget, T.G., Hvidsten, N.A., Gunnerød, T.B. & Møkkelgjerd, P.I. 1991. Distribution of adult recaptures from hatchery-reared Atlantic salmon (*Salmo salar*) smolts released in and off-shore of the River Surna, western Norway. *Aquaculture* 98: 89-96.
- Heggberget, T.G., Johnsen, B.O., Hindar, K., Jonsson, B., Hansen, L.P., Hvidsten, N.A. & Jensen, A.J. 1993b. Interactions between wild and cultured Atlantic salmon: a review of the Norwegian experience. *Fisheries Research* 18: 123-146.
- Hindar, K. & Balstad, T. 1994. Salmonid culture and interspecific hybridization. *Conservation Biology* 8: 881-882.
- Hindar, K. & Diserud, O. 2007. Vulnerability analysis of wild salmon populations towards escaped farmed salmon. NINA Report 244: 1-45. (In Norwegian with English abstract)
- Hindar, K. & L'Abée-Lund, J.H. 1992. Identification of hatchery-reared and naturally produced Atlantic salmon, *Salmo salar* L., juveniles based on examination of otoliths. *Aquaculture and Fisheries Management* 23: 235-241.

- Hindar, K. & Fleming, I.A. 2005. Behavioural and genetic interactions between escaped farm and wild Atlantic salmon. In: Ecological and Genetic Implications of Aquaculture Activities (Bert, T.M., ed.). Kluwer Academic Publishers.
- Hindar, K., Ryman, N. & Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 945-957.
- Hindar, K., Fleming, I.A., McGinnity, P. & Dieserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. *ICES Journal of Marine Science* 63: 1234-1247.
- Hislop, J.R.G. & Webb, J.H. 1992. Escaped farmed Atlantic salmon (*Salmo salar*) feeding in Scottish coastal waters. *Aquaculture and Fisheries Management* 23: 721-723.
- Huntingford, F.A. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology* 65 (Supplement A): 122-142.
- Hutchings, J.A. 1991. The threat of extinction to native populations experiencing spawning intrusion by cultured Atlantic salmon. *Aquaculture* 98: 119-132.
- ICES (International Council for the Exploration of the Sea) 2004. Report of the ICES advisory committee on fishery management and advisory committee on ecosystems, 2004. ICES Advice, volume 1, number 2, 1544 pp.
- ICES (International Council for the Exploration of the Sea) 2006. Report of the working group on North Atlantic salmon. ICES CM 2006/ACFM:23, 254 pp.
- ICES (International Council for the Exploration of the Sea) 2006. Report of the working group on North Atlantic salmon (WGNAS). ICES CM 2007/ACFM:13, 253 pp.
- Jacobsen, J.A. & Hansen, L.P. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science* 58: 916-933.
- Jensen, Ø. 2006. Gjennomgang av tekniske krav til oppdrettsanlegg - basert på rømmingstilfeller i januar 2006. SFH80 A066056: 1-20, SINTEF Fiskeri og havbruk AS. (In Norwegian)
- Jepsen, N., Deacon, M. & Ejby-Ernst, M. 2003a. Laksens gydevandring i Varde Å systemet. DFU-rapport 125-03: 1-72. (In Danish with English abstract)
- Jepsen, N., Nielsen, E.E. & Deacon, M. 2003b. Linking individual migratory behaviour of Atlantic salmon to their genetic origin. In: Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy, 9-13 June 2003 (Spedicato, M.T., Lembo, G & Marmulla, G., eds.), pp. 45-51. FAO/COISPA, Rome.
- Johnsen, B.O. & Jensen, A.J. 1991. The *Gyrodactylus* story in Norway. *Aquaculture* 98: 289-302.
- Johnsen, B.O., Jensen, A.J., Økland, F., Lamberg, A. & Thorstad, E.B. 1998. The use of radiotelemetry for identifying migratory behaviour in wild and farmed Atlantic salmon ascending the Suldalslågen River in Southern Norway. In: Fish migration and fish bypasses (Jungwirth, M., Schmutz, S. & Weiss, S., eds.), pp. 55-68. Fishing News Books, Oxford.
- Johnsson, J.I., Höjesjö, J. & Fleming, I.A. 2001. Behavioural and heart rate response to predation risk in wild and domesticated Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 788-794.
- Johnstone, R. 2005. An overview of methods of control of maturation in salmonids. Wild and farmed salmon - working together. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group,

- Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, pp. 32-36.
- Jones, M.L. & Stanfield, L.W. 1993. The effects of exotic juvenile Salmonines on the growth and survival of juvenile Atlantic salmon (*Salmo salar*) in a Lake Ontario tributary. In: Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters (Gibson, R.J. & Cutting, R.E., eds.). Canadian Special Publication of Fisheries and Aquatic Sciences 118: 71-79.
- Jones, R.A., Anderson, L. & Goff, T. 2004. Assessments of Atlantic salmon stocks in southwest New Brunswick, an update to 2003. Department of Fisheries and Oceans (Canada), Canadian Science Advisory Secretariat Research Document 2004/19.
- Jonsson, B. 1997. A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. ICES Journal of Marine Science 54: 1031-1039.
- Jonsson, B. & Jonsson, N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 61: 2369-2383.
- Jonsson, B. & Jonsson, N. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. ICES Journal of Marine Science 63: 1162-1181.
- Jonsson, B. (ed.), Boxaspen, K., Fiske, P., Gjerde, B., Poppe, T. & Wennevik, V. 2006. Interaksjoner mellom lakseoppdrett og villaks: Oppdatering av kunnskapen etter NOU 1999:9. Kunnskapssenter for laks og vannmiljø 2: 1-80. (In Norwegian)
- King, T.L., Kalinowski, S.T., Schill, W.B., Spidle, A.P. & Lubinski, B.A. 2001. Population structure of Atlantic salmon (*Salmo salar* L.) a range-wide perspective from microsatellite DNA variation. Molecular Ecology 10: 807-821.
- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12: 1-59.
- L'Abée-Lund, J.H. 1988. Rømt oppdrettslaks gyter i norske lakseelver. Fauna 41: 49-50. (In Norwegian)
- Lacroix, G.L. & Stokesbury, M.J.W. 2004. Adult return of farmed Atlantic salmon escaped as juveniles into freshwater. Transactions of the American Fisheries Society 133: 484-490.
- Lacroix, G.L., McCurdy, P. & Knox, D. 2004. Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. Transactions of the American Fisheries Society 133: 1455-1471.
- Lacroix, G.L., Galloway, B.J., Knox, D. & MacLatchy, D. 1997. Absence of seasonal changes in reproductive function of cultured Atlantic salmon migrating into a Canadian river. ICES Journal of Marine Science 54: 1086-1091.
- Latremouille, D.N. 2003. Fin erosion in aquaculture and natural environments. Reviews in Fisheries Science 11: 315-335.
- Leon J. 2006. Synopsis of salmon farming impacts and environmental management in Chile. Technical Report World Wild Life Fund Chile, 46 pp.
- Lever, C. 1996. Naturalized fishes of the world. Academic Press, New York, 408 pp.
- Loginova, G.A. & Krasnoperova, S.V. 1982. An attempt at crossbreeding Atlantic salmon and pink salmon (preliminary report). Aquaculture 27: 329-337.
- Lund, R.A. 1998a. Rømt oppdrettslaks i Namsen og nære sjøområder. Fiske etter rømt oppdrettsfisk i elveutløpet. NINA Oppdragsmelding 564: 1-14. (In Norwegian)
- Lund, R.A. 1998b. Rømt oppdrettslaks i sjø- og elvefisket i årene 1989-97. NINA Oppdragsmelding 556: 1-25. (In Norwegian)

- Lund, R.A. & Hansen, L.P. 1991. Identification of wild and reared Atlantic salmon, *Salmo salar* L., using scale characters. *Aquaculture and Fisheries Management* 22: 499-508.
- Lund, R.A., Hansen, L.P. & Järvi, T. 1989. Identification of reared and wild salmon by external morphology, size of fins and scale characteristics. NINA Forskningsrapport 1: 1-54. (In Norwegian with English abstract)
- Lund, R.A., Hansen, L.P. & Økland, F. 1994. Escaped farmed salmon and geographical zones established for wild fish protection. NINA Oppdragsmelding 303: 1-15. (In Norwegian with English abstract)
- Lund, R.A., Midtlyng, P.I. & Hansen, L.P. 1995. Identification of Atlantic salmon escaped from fish farms by effects of disease preventive vaccination. NINA Fagrapport 12: 1-14. (In Norwegian with English abstract)
- Lund, R.A., Økland, F. & Hansen, L.P. 1991. Farmed Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. *Aquaculture* 98: 143-150.
- Lura, H. & Økland, F. 1994. Content of synthetic astaxantin in escaped farmed Atlantic salmon, *Salmo salar* L., ascending Norwegian rivers. *Fisheries Management and Ecology* 1: 205-216.
- Lura, H. & Sægrov, H. 1991a. A method of separating offspring from farmed and wild Atlantic salmon (*Salmo salar*) based on different ratios of optical isomers of astaxanthin. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 429-433.
- Lura, H. & Sægrov, H. 1991b. Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. *Aquaculture* 98: 151-159.
- Lura, H. & Sægrov, H. 1993. Timing of spawning in cultured and wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the River Vosso, Norway. *Ecology of Freshwater Fish* 2: 167-172.
- Lura, H., Barlaup, B.T. & Sægrov, H. 1993. Spawning behaviour of a farmed escaped female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* 42: 311-313.
- MacCrimmon, H.R. & Gots, B.L. 1979. World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada* 36: 422-457.
- Martin-Smith, K.M., Armstrong, J.D., Johnsson, J.I. & Björnsson, B.Th. 2004. Growth hormone increases growth and dominance of wild juvenile Atlantic salmon without affecting space use. *Journal of Fish Biology* 65 (Supplement A): 156-172.
- Matthews, M.A., Poole, W.R., Thompson, C.E., McKillen, J., Ferguson, A., Hindar, K. & Wheelan, K.F. 2000. Incidence of hybridization between Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in Ireland. *Fisheries Management and Ecology* 7: 337-347.
- McDowall, R.M. 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries* 7: 443-462.
- McDowall, R.M. 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and Fisheries* 8: 1-13.
- McGinnity, P., Prodöhl, P., Ó Maoiléidigh, N., Hynes, R., Cotter, D., Baker, N., O’Hea, B. & Ferguson, A. 2004. Differential lifetime success and performance of native and non-native Atlantic salmon examined under communal natural conditions. *Journal of Fish Biology* 65 (Supplement A): 173-187.
- McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., Cross, T. & Ferguson, A. 1997. Genetic impact of escaped farmed salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science* 54: 998-1008.

- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Ó Maoiléidigh, N., Baker, N., Cotter, D., O’Hea, B., Cooke, D., Rogan, G., Taggart, J. & Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London series B 270: 2443-2450.
- McKinnell, S. & Thomson, A.J. 1997. Recent events concerning Atlantic salmon escapees in the Pacific. ICES Journal of Marine Science 54: 1221-1225.
- McKinnell, S., Thomson, A.J., Black, E.A., Wing, B.L., Guthrie, C.M., Koerner, J.F. & Helle, J.H. 1997. Atlantic salmon in the North Pacific. Aquaculture Research 28: 145-157.
- Melo, T. 2005. Evaluación de la posición trófica y la eficiencia de los métodos de recaptura en salmónidos escapados de centros de cultivo. Informe final proyecto FIP¹: 2004-24, Fondo de Investigación Pesquera, Subsecretaría de Pesca, Chile, 199 pp. (In Spanish)
- Merilä, J. & Crnokrak, P. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. Journal of Evolutionary Biology 14: 892-903.
- Metcalf, N., Valdimarsson, S.K. & Morgan, I.J. 2003. The relative roles of domestication, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. Journal of Applied Ecology 40: 535-544.
- Milner, N.J. & Evans, R. 2003. The incidence of escaped Irish farmed salmon in England and Welsh rivers. Fisheries and Management and Ecology 10: 403-406.
- Mjølnerød, I.B., Refseth, U.H., Karlsen, E., Balstad, T., Jakobsen, K.S. & Hindar, K. 1997. Genetic differences between two wild and one farmed population of Atlantic salmon (*Salmo salar*) revealed by three classes of genetic markers. Hereditas 127: 239-248.
- Mork, J. 1991. One-generation effects of farmed fish immigration on the genetic differentiation of wild Atlantic salmon. Aquaculture 98: 267-276.
- Morton, A. & Volpe, J. 2002. A description of escaped farmed Atlantic salmon *Salmo salar* captures and their characteristics in one Pacific salmon fishery area in British Columbia, Canada, in 2000. Alaska Fishery Research Bulletin 9: 102-110.
- Mullins, C.C., Bourgeois, C.E. & Porter, T.R. 2003. Opening up new habitat: Atlantic salmon (*Salmo salar* L.) enhancement in Newfoundland. In: Salmon at the Edge (D. Mills, ed.), pp 200-221. Blackwell Sciences, Ltd. Oxford.
- NASCO (North Atlantic Salmon Conservation Organisation) 2004. A new regulation for the protection of wild Atlantic salmon. A paper presented by Iceland. Council document CNL(04)32. North Atlantic Salmon Conservation Organisation (NASCO), Scotland, UK, 2 pp.
- NASCO (North Atlantic Salmon Conservation Organisation) 2005a. Report of the meeting of the Liason Group with the North Atlantic salmon farming industry. Council document CNL(05)21. North Atlantic Salmon Conservation Organisation, Scotland, 49 pp.
- NASCO (North Atlantic Salmon Conservation Organisation) 2005b. Wild and farmed salmon - working together. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group, Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, 86 pp.
- NASCO (North Atlantic Salmon Conservation Organisation) 2006. Implementation plan for Iceland. Council document CNL(06)26. North Atlantic Salmon Conservation Organisation, Scotland, UK, 18 pp.

- NASCO (North Atlantic Salmon Conservation Organisation) 2007. Report of the meeting of the Liason Group with the North Atlantic salmon farming industry. Council document CNL(07)18. North Atlantic Salmon Conservation Organisation, Scotland, UK, 58 pp.
- Nash, C.E. (editor) 2001. The net-pen salmon farming industry in the Pacific Northwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-49, 125 pp.
- Naylor, R., Hindar, K., Fleming, I.A., Goldburg, R., Williams, S., Volpe, J., Whoriskey, F., Eagle, J., Kelso, D. & Mangel, M. 2005. Fugitive salmon: assessing the risks of escaped fish from net-pen aquaculture. *BioScience* 55: 427-437.
- Niklitschek, E. & Aedo, E. 2002. Estudio del ciclo reproductivo de las principales especies objetivo de la pesca deportiva en la XI región. 2002. Proyecto FIP (Fondo de Investigación Pesquera¹) 2000-25, Subsecretaria de Pesca, Valparaíso, Chile, 67 pp. (In Spanish)
- Niklitschek, E., Soto, D. & Lafon, A. 2006. The Salmon Sector. In: "Trade Liberalization, Rural Poverty and the Environment: A case study of Forest and Salmon sectors in Chile". World Bank & WWF, Report CT 05-02.
- Norris, A.T., Bradley, D.G. & Cunningham, E.P. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. *Aquaculture* 180: 247-264.
- Norwegian Ministry of Fisheries and Coastal Affairs 2005. Technical requirements for fish farming installations. Publication number L-0524 E, 17 pp.
- NRC (National Research Council) 2004. Atlantic Salmon in Maine. The National Academies Press, Washington, DC, 275 pp.
- Økland F., Heggberget T.G. & Jonsson B. 1995. Migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. *Journal of Fish Biology* 46: 1-7.
- Pakkasmaa, S. & Piironen, J. 2001. Morphological differentiation among local trout (*Salmo trutta*) populations. *Biological Journal of the Linnean Society* 72: 231-239.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* 55 (Supplement 1): 281-287.
- Poole, W.R., Webb, J.H., Matthews, M.A. & Youngson, A.F. 2000. Occurrence of canthaxanthin in Atlantic salmon, *Salmo salar* L. fry in Irish rivers as an indicator of escaped farmed salmon. *Fisheries Management and Ecology* 7: 377-385.
- Poppe, T.T., Johansen, R., Gunnes, G. & Torud, B. 2003. Heart morphology in wild and farmed Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss*. *Diseases of Aquatic Organisms* 57: 103-108.
- Primmer, C.R., Veselov, A.J., Zubchenko, A., Poututkin, A., Bakhmet, I. & Koskinen, M.T. 2006. Isolation by distance within a river system: genetic population structuring of Atlantic salmon, *Salmo salar*, in tributaries of the Varzuga River in northwest Russia. *Molecular Ecology* 15: 653-666.
- Quinn, T.P. 2005. The behaviour and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland.
- Refstie, T. & Gjerdem, T. 1975. Hybrids between salmonidae species. Hatchability and growth rate in the freshwater period. *Aquaculture* 6: 333-342.
- Rengmark, A.H., Slettan, A., Skaala, Ø., Lie, Ø. & Lingaas, F. 2006. Genetic variability in wild and farmed Atlantic salmon (*Salmo salar*) strains estimated by SNP and microsatellites. *Aquaculture* 253: 229-237.

- Rist, T., Skjeggedal, K., Haga, B., Monsen, B.-R.H., Rysjedal, J., Vad, J. & Åsvang, H. 2004. Fisken rømmer. En risikoanalyse av driftsrelaterte årsaker. Aqua Management AS, 35 pp. (In Norwegian)
- Roberge, C., Einum, S., Guderly, H. & Bernatchez, L. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. *Molecular Ecology* 15: 9-20.
- Roberge, C., Normandeau, É., Einum, S., Guderley, H. & Bernatchez, L. 2008. Genetic consequences of interbreeding between farmed and wild Atlantic salmon: insights from the transcriptome. *Molecular Ecology* 17: 314-324.
- Ryan, J. 2004. Farming the deep blue. Irish Sea Fisheries Board, Marine Institute, 69 pp.
- Sadler, J., Pankhurst, P.M. & King, H.R. 2001. High prevalence of skeletal deformity and reduced gill surface area in triploid Atlantic salmon (*Salmo salar* L.). *Aquaculture* 198: 369-386.
- Schiermeier, Q. 2003. Fish farms' threat to salmon exposed. *Nature* 425: 753.
- Scott, R.J., Poos, M.S., Noakes, D.L.G. & Beamish, F.W.H. 2005a. Effects of exotic salmonids on juvenile Atlantic salmon behaviour. *Ecology of Freshwater Fish* 14: 283-288.
- Scott, R.J., Judge, K.A., Ramster, K., Noakes, D.L.G. & Beamish, F.W.H. 2005b. Interactions between naturalised exotic salmonids and reintroduced Atlantic salmon in a Lake Ontario tributary. *Ecology of Freshwater Fish* 14: 402-405.
- Singer, T.D., Clements, K.M., Semple, J.W., Schute, P.M., Bystriansky, J.S., Finstad, B., Fleming, I.A. & McKinley, R.S. 2002. Seawater tolerance and gene expression in two strains of Atlantic salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 125-135.
- Sivertsen, A. 2006. Nasjonale laksefjorder. Fisken og havet, særnummer 2 - 2006: 55-57. Institute of Marine Research, Norway. (In Norwegian with English abstract)
- Skaala, Ø., Taggart, J.B. & Gunnes, K. 2005. Genetic differences between five major domesticated strains of Atlantic salmon and wild salmon. *Journal of Fish Biology* 67 (Supplement A): 118-128.
- Skaala, Ø., Wennevik, V. & Glover, K.A. 2006a. Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. *ICES Journal of Marine Science* 63: 1224-1233.
- Skaala, Ø., Wennevik, V. & Glover, K.A. 2006b. Sporing av rømt oppdrettslaks - kva no? Fisken og havet, særnummer 2 - 2006: 58-59. Institute of Marine Research, Norway. (In Norwegian with English abstract)
- Skaala, Ø., Høyheim, B., Glover, K. & Dahle, G. 2004. Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): allelic diversity and identification of individuals. *Aquaculture* 240: 131-143.
- Skår, K. 2005. Practical aspects of conserving and restoring wild Atlantic salmon. Wild and farmed salmon - working together. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group, Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, pp. 54-57.
- Skilbrei, O. 2006. Oppsummering av kunnskapsstatus innen rømming av oppdrettslaks - tiltak for gjenfangst etter rømming. Institute of Marine Research, Norway, 20 pp. (In Norwegian)
- Skilbrei, O. & Wennevik, V. 2006. The use of catch statistics to monitor the abundance of escaped farmed Atlantic salmon and rainbow trout in the sea. *ICES Journal of Marine Science* 63: 1190-1200.

- Skilbrei, O.T., Johnsen, B.O., Heggberget, T.G., Krokan, P.S., Aarset, B., Sagen, T. & Holm, M. 1998. Havbeite med laks - artsrapport. Norges Forskningsråd, 72 pp. (In Norwegian)
- Soderberg, R.W. & Meade, J.W. 1987. Effects of rearing density on growth, survival and fin condition of Atlantic salmon. *The Progressive Fish-Culturist* 49: 280-283.
- Soto, D., Jara, F. & Moreno, C. 2001. Escaped salmon in the inner seas, southern Chile: facing ecological and social conflicts. *Ecological Applications* 11: 1750-1762.
- Soto, D., Arismendi, I., Di Prinzio, C. & Jara, F. 2007. Establishment of Chinook salmon (*Oncorhynchus tshawytscha*) in Pacific basins of southern South America and its potential ecosystem implications. *Revista Chilena de Historia Natural* 80: 81-98.
- Soto, D., Arismendi, I., Leal, C. & Sanzana, J. 2002. Proyecto FNDR (Fondo Nacional para el Desarrollo Regional) X Región. 1999-2001. Investigación para la Evaluación, Ordenamiento y manejo del Potencial Biológico para la pesca deportiva de la Décima Región de Los Lagos. Gobierno Regional de los Lagos, 123 pp. (In Spanish)
- Soto, D., Jara, F., Moreno, C., Molinet, C., Guerrero, A. & Godoy, C. 1996. Evaluación de salmonidos de vida libre existentes en las aguas interiores de las regiones X y XI. Proyecto FIP (Fondo de Investigación Pesquera¹⁴) 95-31, Subsecretaría de Pesca, Valparaíso, Chile, 159 pp. (In Spanish)
- Soto, D., Arismendi, I., González, J., Sanzana, J., Jara, F., Jara, C., Guzman, E. & Lara, A. 2006. Southern Chile, trout and salmon country: invasion patterns and threats for native species. *Revista Chilena de Historia Natural* 79: 97-117.
- Stabell, O.B. 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. *Biological Reviews* 59:333-388
- Ståhl, G. 1987. Genetic population structure of Atlantic salmon. In: *Population Genetics & Fishery Management* (Ryman, N. & Utter, F.), pp 121-140. University of Washington Press, Seattle.
- Stokesbury, M.J. & Lacroix, G.L. 1997. High incidence of hatchery origin Atlantic salmon in the smolt output of a Canadian river. *ICES Journal of Marine Science* 54: 1074-1081.
- Stokesbury, M.J.W., Lacroix, G.L., Price, E.L., Knox, D. & Dadswell, M.J. 2001. Identification by scale analysis of farmed Atlantic salmon juveniles in southwestern New Brunswick rivers. *Transactions of the American Fisheries Society* 130: 815-822.
- Sutterlin, A.M., MacFarlane, L.R. & Harmon, P. 1977. Growth and salinity tolerance in hybrids within *Salmo* sp. and *Salvelinus* sp. *Aquaculture* 12: 41-52.
- Sutterlin, A.M., Saunders, R.L., Henderson, E.B. & Harmon, P.R. 1982. The homing of Atlantic salmon (*Salmo salar*) to a marine site. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1058: 1-6.
- Syvrtsen, H.A. & Vatne, T. 2000. Forsøksfiske etter rømt oppdrettslaks i Nordland. Fylkesmannen i Nordland Miljøvern avdelingen, 17 pp. (In Norwegian)
- Sægrov, H. & Urdal, K. 2006. Rømt oppdrettslaks i sjø og elv; mengd og opphav. Rådgivende Biologer AS, rapport nr. 947: 1-26. (In Norwegian)
- Sægrov, H., Hindar, K., Kålås, S. & Lura, H. 1997. Escaped farmed Atlantic salmon replace the original salmon stock in the River Vosso, western Norway. *ICES Journal of Marine Science* 54: 1166-1172.

¹⁴ All FIP project reports are available in full at www.fip.cl under "Proyectos Realizados"

- Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98: 185-207.
- Thodesen, J., Grisdale-Halland, B., Helland, S.J. & Gjerde, B. 1999. Feed intake, growth, and feed utilization of offspring from wild and selected Atlantic salmon (*Salmo salar*). *Aquaculture* 180: 237-246.
- Thorpe, J.E. 2004. Life history response of fishes to culture. *Journal of Fish Biology* 65 (Supplement A): 263-285.
- Thorstad, E.B., Heggberget, T.G. & Økland, F. 1996. Spawning migration and spawning behaviour of wild and escaped farmed Atlantic salmon (*Salmo salar*) in the River Namsen and the River Alta. NINA Fagrapport 17: 1-35. (In Norwegian with English abstract)
- Thorstad, E.B., Heggberget, T.G. & Økland, F. 1998. Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river. *Aquaculture Research* 29: 419-428.
- Thorstad, E.B., Finstad, B., McKinley, R.S., Økland, F. & Booth, R.K. 1997. Endurance of farmed and sea-ranched Atlantic salmon (*Salmo salar* L.) at spawning. *Aquaculture Research* 28: 635-640.
- Tufto, J. 2001. Effects of releasing maladapted individuals: a demographic-evolutionary model. *The American Naturalist* 158: 331-340.
- Tufto, J. & Hindar, K. 2003. Effective size in management and conservation of subdivided populations. *Journal of Theoretical Biology* 222: 273-281.
- Valland, A. 2005. The causes and scale of escapes from salmon farming. In: Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. ICES/NASCO Bergen 18-21 October 2005, pp. 15.
- Verspoor, E. 1997. Genetic diversity among Atlantic salmon (*Salmo salar* L.) populations. *ICES Journal of Marine Science* 54: 965-973.
- Verspoor, E. 2005. Regional differentiation of North American Atlantic salmon at allozyme loci. *Journal of Fish Biology* 67: 80-103.
- Verspoor, E., Stradmeyer, L. & Nielsen, J.L. 2007. The Atlantic salmon: Genetics, Conservation and Management. Blackwell Publishing Ltd, 500 pp.
- Verspoor, E., Beardmore, J.A., Consuegra, S., García de Leániz, C., Hindar, K., Jordan, W.C., Koljonen, M.-L., Mahkrov, A., Paaver, T., Sánchez, J.A., Skaala, Ø., Titov, S. & Cross, T.F. 2005. Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. *Journal of Fish Biology* 67 (Supplement A): 3-54.
- Volpe, J.P. 1999. The occurrence of Atlantic salmon in coastal streams of southern British Columbia during 1998. British Columbia Ministry of Environment Lands and Park Regional File Report. Nanaimo, British Columbia.
- Volpe, J.P. 2000. The occurrence of Atlantic salmon in coastal streams of southern British Columbia during 1999. British Columbia Ministry of Environment Lands and Parks Regional File Report. Nanaimo, British Columbia.
- Volpe, J.P., Taylor, E.B., Rimmer, D.W. & Glickman, B.W. 2000. Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia river. *Conservation Biology* 14: 899-903.
- Volpe, J.P., Anholt, B.R. & Glickman, B.W. 2001a. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 197-207.

- Volpe, J.P., Glickman, B.W. & Anholt, B.R. 2001b. Reproduction of aquaculture Atlantic salmon in a controlled stream channel on Vancouver Island, British Columbia. *Transactions of the American Fisheries Society* 130: 489-494.
- Waknitz, F.W., Tynan, T.J., Nash, C.E., Iwamoto, R.N. & Rutter, L.G. 2002. Review of potential impacts of Atlantic salmon culture on Puget Sound chinook salmon and Hood Canal summer-run chum salmon evolutionarily significant units. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-53, 83 pp.
- Walker, A.M., Beveridge, M.C.M., Crozier, W., O'Maoiléidigh, N. & Milner, N. 2006. Monitoring the incidence of escaped farmed salmon, *Salmo salar* L., in rivers and fisheries of the United Kingdom and Ireland: current progress and recommendations for future programmes. *ICES Journal of Marine Science* 63: 1201-1210.
- Wallace, J.C. & Heggberget, T.G. 1988. Incubation of the eggs of Atlantic salmon (*Salmo salar*) from different Norwegian streams at temperatures below 1°C. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 193-196.
- Webb, J. & Hawkins, A.D. 1989. The movements and spawning behaviour of adult Atlantic salmon in the Girnock Burn, a tributary of the Aberdeenshire Dee, 1986. *Scottish Fisheries Research Report* 40: 1-42.
- Webb, J.H. & Youngson, A.F. 1992. Reared Atlantic salmon, *Salmo salar* L., in the catches of a salmon fishery on the western coast of Scotland. *Aquaculture and Fisheries Management* 23: 393-397.
- Webb, J.H., Hay, D.W., Cunningham, P.D. & Youngson, A.F. 1991. The spawning behaviour of escaped farmed and wild Atlantic salmon (*Salmo salar* L.) in a northern Scottish river. *Aquaculture* 98: 97-110.
- Webb, J.H., McLaren, I.S., Donaghy, M.J. & Youngson, A.F. 1993a. Spawning of farmed Atlantic salmon, *Salmo salar* L., in the second year after their escape. *Aquaculture and Fisheries Management* 24: 557-561.
- Webb, J.H., Youngson, A.F., Thompson, C.E., Hay, D.W., Donaghy, M.J. & McLaren, I.S. 1993b. Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers: egg deposition by females. *Aquaculture and Fisheries Management* 24: 663-670.
- Webster, J. 2005. An industry perspective on the pros and cons of using sterile salmon in farming. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group, Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, pp. 44-47.
- Weir, L.K. & Fleming, I.A. 2006. Behavioural interactions between farm and wild salmon: potential for effects on wild populations. In: *A Scientific Review of the Potential Environmental Effects of Aquaculture in Aquatic Ecosystems, Volume V*. Canadian Technical Report of Fisheries and Aquatic Sciences 2450: 1-29.
- Weir, L.K., Hutchings, J.A., Fleming, I.A. & Einum, S. 2004. Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. *Journal of Animal Ecology* 73: 1069-1079.
- Weir, L.K., Hutchings, J.A., Fleming, I.A. & Einum, S. 2005. Spawning behaviour and success of mature male Atlantic salmon (*Salmo salar*) parr of farmed and wild origin. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1153-1160.
- Whoriskey, F.G. 2000. Atlantic salmon and exotic species. In: *Managing Wild Atlantic Salmon: New Challenges - New Techniques* (Whoriskey, F.G. & Whelan, K., eds.), pp 152-163. Atlantic Salmon Federation, St. Andrews, NB.

- Whoriskey, F.G. 2001. Causes of the escape of farmed Atlantic salmon from sea cages in British Columbia and East Coast North America. ICES Working Group for North Atlantic Salmon Working paper 01/09.
- Whoriskey, F. 2003. Exotic species in aquaculture. Bulletin of the Aquaculture Association of Canada 103 (2): 1-7.
- Whoriskey, F.G. & Carr, J.W. 2001. Returns of transplanted adult, escaped, cultured Atlantic salmon to the Magaguadavic River, New Brunswick. ICES Journal of Marine Science 58: 504-509.
- Whoriskey, F.G., Brooking, P., Doucette, G., Tinker, S. & Carr, J.W. 2006. Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. ICES Journal of Marine Science 63: 1218-1223.
- Withler, R.E., Supernault, K.J. & Miller, K.M. 2005. Genetic variation within and among domesticated Atlantic salmon broodstocks in British Columbia, Canada. Animal Genetics 36: 43-50.
- Wilkins, N.P. 2005. Minimising the impact of farmed salmon on wild stocks. Report of a one-day workshop organised by the NASCO/North Atlantic salmon farming industry Liaison Group, Trondheim, Norway, 9 August 2005. North Atlantic Salmon Conservation Organisation, Scotland, pp 37-43.
- Wilkins, N.P., Cotter, D. & Ó Maoiléidigh, N. 2001. Ocean migration and recaptures of tagged, triploid, mixed-sex and all-female Atlantic salmon (*Salmo salar* L.) released from rivers in Ireland. Genetica 111: 197-212.
- Youngson, A.F. & Verspoor, E. 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55 (Supplement 1): 153-160.
- Youngson, A.F., Martin, S.A.M., Jordan, W.C. & Verspoor, E. 1989. Genetic protein variation in farmed Atlantic salmon in Scotland: Comparison of farmed strains with their wild source populations. Scottish Fisheries Research Report 42: 1-12.
- Youngson, A.F., Martin, S.A.M., Jordan, W.C. & Verspoor, E. 1991. Genetic protein variation in Atlantic salmon in Scotland: comparison of wild and farmed fish. Aquaculture 98: 231-242.
- Youngson, A.F., Webb, J.H., MacLean, J.C. & Whyte, B.M. 1997. Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. ICES Journal of Marine Science 54: 1216-1220.
- Youngson, A.F., Webb, J.H., Thompson, C.E. & Knox, D. 1993. Spawning of escaped farmed Atlantic salmon (*Salmo salar*): hybridization of females with brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 50: 1986-1990.

Appendix: Origin of information referred to in the report

This report on incidence and impacts of escaped farmed Atlantic salmon was mainly based on peer-reviewed scientific publications, but with references to other sources to cover local and regional aspects. A total of 274 papers and reports have been cited (see reference list). An overview of the country origin of these references is given in the figure below. The country origin was determined mainly according to the location of the work and fish studied (hence, a few studies were designated to two different countries of origin). Review papers and reports with a general content (such as ICES and NASCO reports) were categorized as “general” information, and not sorted according to country.

This overview shows that Norway, with the largest production of farmed Atlantic salmon, also had a high number of publications relevant for this review of escaped farmed salmon. Countries such as Canada, Ireland and USA had a high number of publications relevant for this issue, seen in relation to their lower production of Atlantic salmon. Chile, on the contrary, had a very low number of publications relevant for this issue compared to the large production of Atlantic salmon.

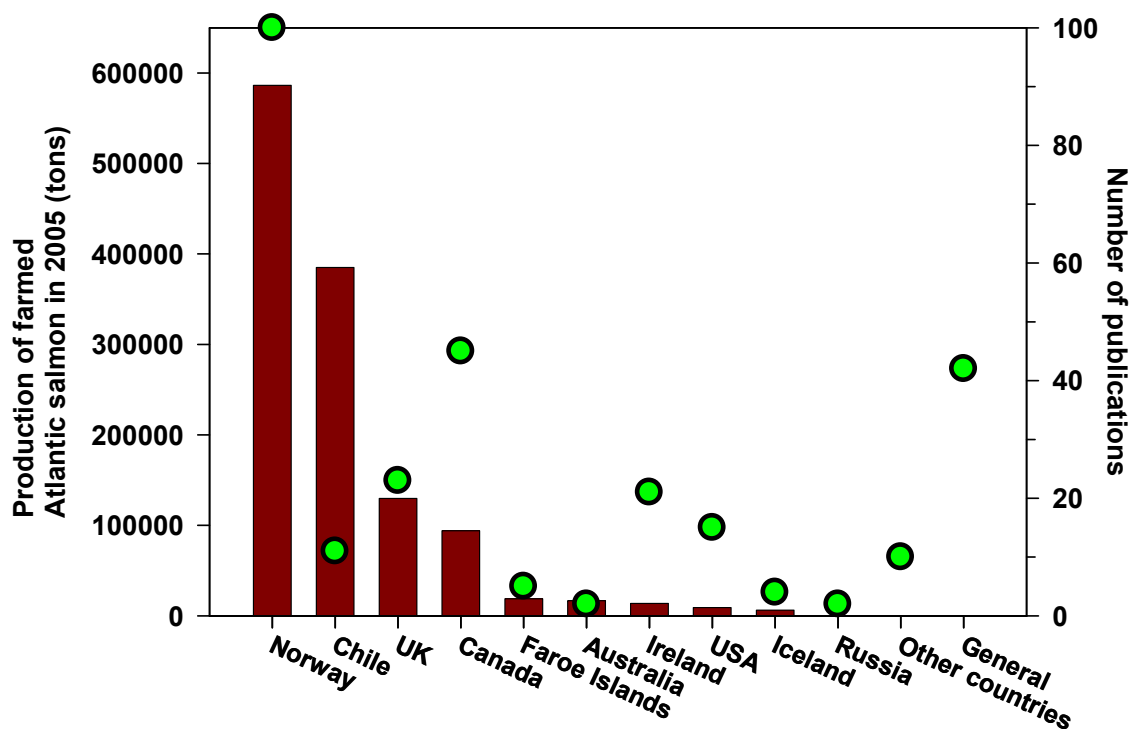


Figure 1. Production of farmed Atlantic salmon (vertical bars, data from ICES 2007) and number of publications used in this report originating from each country (green dots). 'Other countries' refers to countries not producing farmed Atlantic salmon. 'General' refers to general publications (review articles and general reports).



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