

On the origin of escaped farmed salmon

Øystein Skaala and Kevin A. Glover examine how old questions and new problems are addressed by genetics

Human impacts on wild salmonid populations have been the subject of a significant amount of attention in the course of the past few decades, and impact factors have been well documented. In 1983, an intergovernmental organization, the North Atlantic Salmon Conservation Organization (NASCO; www.nasco.int) was established with the objectives of conserving, restoring, enhancing, and rationally managing the Atlantic salmon through international cooperation. In the course of the subsequent thirty years, a series of international symposia have addressed and documented these effects (Anon, 1991; Hutchinson, 1997, 2006).

In Norway, which has management responsibility for a significant proportion of the remaining wild salmon populations, not to mention a multibillion-euro salmon farming industry, the Ministry of Fisheries and Coastal Affairs drew up a “Strategy for an Environmentally Sustainable Norwegian Aquaculture Industry” (Taranger *et al.*, 2011). This stressed the following five potential impacts of salmon farming: 1) genetic impact on wild fish, 2) organic discharge, 3) transmission of diseases and salmon lice to wild populations, 4) allocation of aquatic habitat to fish farming, and 5) the problem of obtaining adequate feed resources from an already heavily exploited marine ecosystem.

While escaped farmed salmon give management authorities a headache, the problem has presented an opportunity for scientists to develop advanced genetic and statistical methods that are now being employed to learn more about the Atlantic salmon and assess its genetic impact on wild populations: How does natural selection shape and adapt local populations? Are salmon populations adapted to their local environment? How and to what extent does gene flow from domesticated salmon affect survival and production in wild populations? And finally, can we identify the origins of the escapees?

There is little doubt that wild salmon have been an important resource for many communities for centuries, and that the species has been the source of many conflicts in the course of the years. Written

sources tell us that as early as the 14th century there were conflicts regarding how salmon should be managed, for example in Suldalslågen, where farmers, the monks of Halsnøy Monastery, and landowners with fishing rights in the lower reaches of the river broke into open warfare. As far back as 400 years ago the priest Peder Clausson Friis (1545–1614) observed that salmon populations from different rivers could have different characteristics, and that spawning salmon migrated to their home river to spawn.

“...and what is most to be wondered at, every salmon seeks the stream and the very place in which it was born, which is demonstrated thus. First, each river and stream has its own particular type and difference from the salmon of other rivers. Lyngdal, Undal, Mandal, Torridal, and Topdal salmon have each their own characteristics, by which we can to some extent recognize which stream they belong to (even) if they should mistake their way and are taken in another stream.”

The priest was right!

Almost 400 years later, salmon scientists carried out a DNA-based project to which Peder Clausson Friis would probably have given a nod of approval. The reasons for our anxiety regarding the genetic impact of escaped farmed salmon are to be found to some extent in a comprehensive literature that has largely confirmed the priest’s observations, and which, with the help of advanced molecular genetics and statistical analyses has quantified the genetic differences between wild salmon populations. We now know, for example, that the genetic distinctions between salmon stocks on the eastern and western seaboard of the Atlantic are approaching the level of species differences. We also know that within its European distribution range, there are major differences between the salmon of the Baltic and the Atlantic, and between salmon from Russia and northern Norway and more southerly stocks. In collaboration with other research centres, the Institute of Marine Research has charted the genetic relationships of 284 salmon stocks via the SALSEA project.



Ladies from Voss with their catch one fine day in 1912. Photo: The Voss hatchery foundation. The Vosso salmon has survived in the Norwegian Gene Bank for Atlantic salmon.

We can also identify robust differences within individual regional stocks, for example within a single county, and in some cases even within individual large rivers. The background for these differences lies in the life history of the salmon, in which fish that are ready to spawn have an extremely well-developed ability to find their way back to the native river in which they themselves had hatched, in order to reproduce. The consensus of a large number of tagging experiments has been that, of the wild salmon that survive the feeding migration to the open sea and return to a river, 95 per cent or more reach their natal river. Scientists have long asked themselves just why salmon have evolved such an orientation ability. According to the theory of evolution, such behaviour ought to have advantages for the individual, and in nature, the prize should be a larger number of surviving offspring. In theory, evolution via natural selection should lead to a stock becoming well adapted to its environment. There exists a great deal of scientific literature that suggests that this works in practice; for example, many stocks of Atlantic salmon and other salmonid species are well-adapted to local conditions.

Although these are simple and fundamental questions in both evolutionary biology and salmon management, testing them in ways that can give us hard data is both time and resource intensive. How rapidly does a local adaptation develop? What is the geographical distribution of a locally adapted stock? Some very recent studies carried out by a Danish-Canadian group (Fraser *et al.*, 2011) have dealt with these questions. Their results show that in more than half of the cases studied, the salmon stocks have adapted to their environment, and on average, the survival rate of the local population is 1.2 times as great as that of non-local populations. The geographical distribution ranges from a few kilometres to more than 1000 km. The local adaptation unit need not be a single river, but may be a larger or smaller area, although increasing geographical distance tends to lead to stronger adaptation.

Are wild and farmed salmon genetically different?

There currently exists an extensive scientific literature that documents genetic differences between wild and farmed salmon. This is scarcely surprising, given that farmed salmon have been selected for specific production characteristics such as rapid growth and delayed sexual maturation for eight to ten generations. In tank trials, farmed salmon grow at least twice as rapidly as wild salmon, and a number of other differences between these groups have been documented; these include aggressive behaviours and responses to predators. So what do we know about the impact of escaped salmon on

wild stocks? Over the course of the approximately 25 years during which we have identified escaped salmon in the spawning grounds of wild salmon, we have seen that their incidence is very variable, both from year to year, between different parts of the country, and between individual rivers. What we do not know so much about is the extent to which the offspring of escapees survive and modify the inherited characteristics of wild salmon populations.

Performance of wild and farmed salmon under natural conditions

Two earlier studies, one in Burrishoole in Ireland (McGinnity *et al.*, 2003) and one in Imsa in Norway (Fleming *et al.*, 2000), have concluded that the offspring of farmed salmon have a much lower survival rate in nature than those of wild salmon. Different crosses of wild and escaped salmon have different survival rates, ranging from poor to practically as good as wild salmon among offspring whose mother is wild. The Burrishoole study found that the offspring of farmed salmon had a very low survival rate through the marine stage compared with wild salmon, but such differences were not found in Imsa.

In order to obtain a more accurate understanding of the fate of the offspring of farmed salmon in nature, we carried out an experimental field trial at the Institute of Marine Research's field station in Guddalselva (Skaala *et al.*, 2012). Studies of this sort in a natural environment are demanding and time-consuming, which means that they are seldom carried out. At the same time, they are an important complement to model studies and laboratory experiments, precisely because the animals are observed in their natural element. A prerequisite for performing such studies is the existence of facilities (Figure 1) that offer good control conditions and representative collection of experimental animals, which means that there exist extremely few places where such field studies can be carried out. In our study, we compared genetic differences in survival, age, time, and size at smoltification and choice of diet in families of farmed and wild salmon and crosses of these two groups. Since escaped salmon tend to have poor spawning success compared to wild salmon, we started our study by setting out a known number of eyed eggs, so that differences in spawning success due to environmental differences would not create "noise" in the results. We set out a total of 205,266 eyed eggs from 69 individual salmon families above the smolt trap in the River Guddal, some of which were pure farmed salmon families, while others were pure wild families.



Figure 1
When salmon smolts pass the trap in River Guddal on their way to the Norwegian Sea, they have to “deliver” a little DNA sample for parentage testing and comparison of survival rates in farm and wild salmon families.

The survival rates of the eyed eggs to the yolk-sac stage were extremely good in all three of the year classes. What was most surprising was the wide variation in survival among the farmed salmon families, some of which had very high survival rates. Moreover, some of the crosses with farmed mothers had more or less the same survival rate as the wild salmon. Since the observed rates of survival differed so widely between families, we developed a statistical model to describe the variation on the basis of the available parameters. The model showed that egg size had a major influence on survival until the smolt stage. This was perhaps not particularly unexpected, but that we were able to specifically demonstrate this effect, and moreover at family level, was rather more than we had expected when we started. In this particular study, the parents of the farmed families were much larger (12–14 kg as compared to 4 kg) than those of the wild salmon. This environmental effect camouflaged the real genetic differences between the

groups, and at first glance, therefore, there appeared to be only minor differences between the offspring of wild salmon and escapees. In order to be certain that the model was not misleading us, we also compared half-sibling families; i.e. we divided the eggs from a number of farmed hen fish into two groups and fertilized one group with milt from a farmed male and the other with milt from a wild male. In 15 of the 17 comparisons that we performed, the half-sibling families that were offspring of wild fathers had higher survival rates than the half-siblings both of whose parents were farmed fish (Figure 2). Egg size is influenced by both genetic and environmental factors; large fish produce the largest eggs. At the same time, it has been shown that domestication reduces the size of the eggs they produce. Since egg size is highly variable in both cultivated and wild fish, this experiment shows that it would be extremely difficult to predict the outcome of an influx of escaped salmon in any given case in a river.

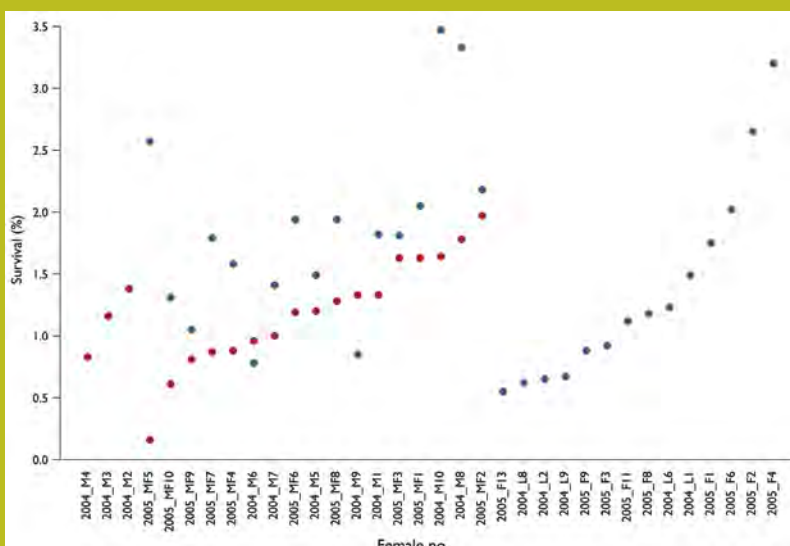


Figure 2
Pairwise comparison of survival from eyed egg to smolt stage in salmon half-sib families in a natural river habitat. All mothers are farmed females. Red: sired by farmed male; blue: sired by wild male.

Competition for resources reduces the production of wild salmon

In rivers, the availability of food is limited, and survival depends on fish density. In the River Guddal study, we were also interested in looking at whether the density of young fish in the river had an influence on the relative competitiveness of cultivated, hybrid, and wild salmon. We did this by increasing the quantity of eyed eggs in each year class. In practice, this meant that the density of the fry increased for each year class, while at the same time, each new year class also had a year class of elder salmon fry to deal with, as well as the river's stock of trout. Small salmon fry are on the menu of both large salmon fry and trout, so popping their heads out of the gravel when the yolk sac has been consumed is a risky business for the former. We found that compared to that of half-siblings with a wild father, the survival rate of cultivated salmon fell as fish density increased, from 0.86 in the 2004 year class to 0.62 in the 2005 year class. This is an indication both of a difference in competitiveness, and that the higher the density of wild salmon in a river, the lower the survival rate of the offspring of escaped salmon.

Wide variations in size between the families at the same age were also observed in the study, and in the material as a whole the smolt with farmed parents were around one gramme heavier than the hybrids, which in turn were about one gramme heavier than the wild smolt. We also observed that the offspring of farmed salmon were in a hurry to leave the river in spring. In any given year, the offspring of farmed salmon arrived at the smolt trap on average several days before the hybrids and the wild fish. The most usual prey of salmon fry in rivers are mayflies, caddisflies and stoneflies, in addition to chironomids and gnats. There was nothing to suggest that farmed and wild salmon have different dietary preferences, and their choice of diet overlapped completely. In most rivers the availability of food is limited, which means that the offspring of cultivated salmon are competing with wild fish for the same food, which leads to a reduction in the production of wild salmon smolts.

Populations differ in their resilience

Since it is difficult to predict the extent of interbreeding on the basis of observations of the proportion of escaped salmon in a river, we also compared the stability over time of the DNA profiles of wild populations with a large proportion of escaped salmon (Skaala *et al.*, 2006; Glover *et al.*, 2012). These studies also gave us new and to some extent

unexpected insight. It is not surprising that we found that the DNA profile of some stocks with a relatively large proportion of escapees in their spawning grounds had changed. In the samples taken following the return migration of escaped salmon, we found genetic variations that were not present in older samples taken before there were significant numbers of escaped salmon in the rivers. We also observed that the genetic difference between populations had shrunk in the course of time; i.e. stocks have become more similar, as scientists predicted they would some twenty years ago, before we had DNA-based tools capable of quantifying the changes. Although stocks are influenced by a number of natural and anthropogenic factors, escaped farmed fish are the most likely explanation of these genetic changes. Our study identified clear changes in six out of 21 populations (29%) along the coast of Norway (Glover *et al.*, 2012). Perhaps the biggest surprise was that we did not find any changes in several populations that had contained a large proportion of escapees for many years. One example of this phenomenon is the River Etne in the Hardangerfjord, which has held a large number of escaped farmed salmon for at least 20 years. This suggests that we still have a number of wild salmon stocks that have been little affected or completely unaffected by escaped farmed salmon.

Removal of escaped farmed salmon from spawning areas

The Institute of Marine Research has documented that escapees are in the process of altering the genetic make-up and structure of wild salmon populations (Skaala *et al.*, 2006; Glover *et al.*, 2012). It is difficult to imagine that even large-scale efforts by the aquaculture industry to prevent escapes would have a realistic prospect of significantly reducing the extent of escapes as long as current production technology remains in use. In the short term, it will therefore be necessary to implement measures that make it easier to identify escaped salmon in nature, so that it is possible to differentiate between escaped and wild salmon and remove the escapees from spawning stocks. One simple and cost-effective method that has been suggested, and that would not harm farmed salmon, would be to remove the adipose fin (Figure 3). This would mean that escapees could be identified at the river's edge without time-consuming and expensive studies of patterns of growth or morphology or DNA testing. At the same time, it is essential to possess technology that would prevent escaped fish from migrating into the spawning grounds of wild salmon. It must be possible to sort out escapees while leaving wild fish with access to their spawning grounds in the river.

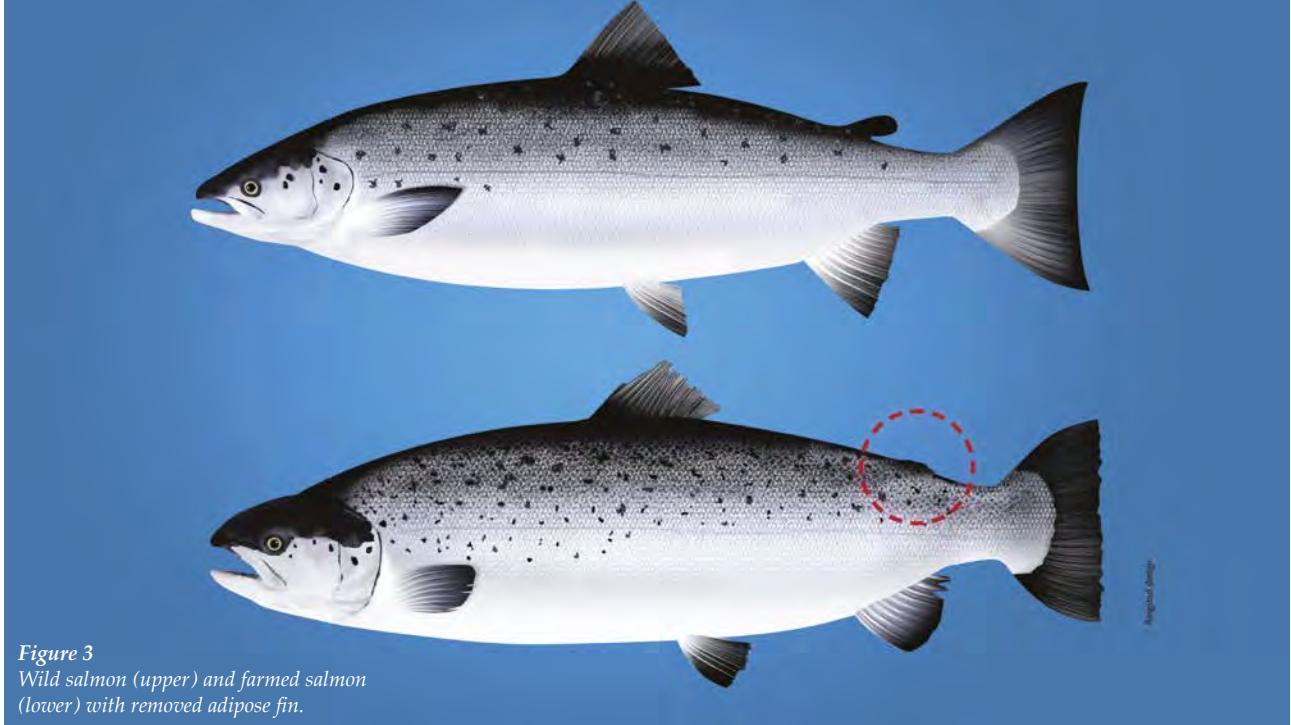


Figure 3
Wild salmon (upper) and farmed salmon (lower) with removed adipose fin.

Several methods of removing escaped farmed salmon from the spawning areas of wild populations have been tested through a series of small projects, ranging from angling, gillnetting and harpooning in the rivers, to fykenets in the estuaries, and trawling in the fjord. In a series of studies that involved setting out farmed salmon, Skilbrei (2010) and Skilbrei *et al.* (2010) showed that as soon as farmed salmon escape they spread out over a large area, and after as little as a week may migrate as much as 40 km from the farm from which they had escaped. A significant proportion of these escapees also dive to depths that make it difficult to catch them with traditional fishing gear.

Portable trap facilities (Figure 4), such as resistance board weirs (RBWs), which have been in use in North

America for about two decades (Tobin, 1994), would appear to be rather useful in removing farmed salmon escapees from rivers. At the same time, such systems would provide good opportunities to improve the monitoring of wild anadromous populations by introducing a consistent sampling method, reducing sampling bias in datasets and allowing for development of time-series, all of which are extremely valuable management tools. RBWs are a relatively new modification to very old technology, and are typically operated in close proximity to known spawning areas. This American fish-capture technology is currently being tested in Europe for the first time on Atlantic salmon in the Norwegian salmon river Etneelva, with the aim of preventing escaped salmon from migrating into the spawning ground of wild salmon.



Figure 4
The North American resistance board weir portable salmon trap system now tested in River Etneelva, Norway, to eliminate farmed salmon from the spawning grounds of wild salmon.

Tracing the origin of escapees through their DNA

We do not know just how many farmed salmon escape. Some regions have more escapes than others; in many rivers there are very few escapees, while in others, in some years there may be as many escaped salmon as there are wild fish. Small numbers of escapees are difficult to detect, and probably mostly go unreported. The tracing studies carried out by the Institute for Marine Research for the national fisheries management authorities also show that some escapes are not reported, although fish farmers are obliged to report escapes when they realize that they have occurred.

There are two reasons why we wish to identify escaped farmed salmon, and these make different demands on the methodology used to identify escaped fish. As far as recapturing escaped farmed salmon is concerned, it is sufficient to decide whether a fish is wild or an escapee. In such cases, the aim is to remove the escapee before it spawns, possibly affecting the genetic make-up of the wild population. However, if we wish to identify the origin of the escaped fish (i.e. the farm of origin), a more stringent methodology is required. The point of identifying the origin of an escapee is that it also allows us to identify the cause of the escape, implement measures to prevent its recurrence in order to reduce the extent of escapes, and learn from what has happened. At the same time, the authorities can decide whether there are circumstances associated with an escape that need to be further investigated, in case a fish farmer should be made responsible for an escape and its potential environmental and economic consequences.

DNA has been used in forensic medicine since the 1980s, when Professor Peter Gill and his colleagues of the Forensic Science Service in the UK realized that DNA could be used to identify criminals. All of us have our unique DNA “fingerprint”, and when developments in molecular genetics made it possible to identify differences in DNA, we gained a new and very powerful tool that led to a revolution in forensic medicine. DNA is found in every cell of the body, and the quantity in a hair root or even on a fork or a cigarette stub can be sufficient to identify a person. For our purposes, a piece of a fish-scale may be sufficient. DNA exists in virtually all biological material, is extremely stable, is not affected by what you eat or drink or by your physical environment, and it does not change in the course of the life of the individual. The DNA that we inherit from our mother and father stays with us all our life, and for long after. The use of DNA in forensic medicine is based on extremely strict procedures with very high standards of quality assurance.

When Norwegian politicians suggested tagging all farmed fish (White Paper no. 12 (2001–2002): “Clean and rich seas”, and Parliamentary Proposition no.134 (2002–2003): “On designating national salmon rivers and salmon fjords”), the aim was to develop a method of identifying the sources of unreported escapes. A national Tagging Commission was appointed that included representatives of the authorities, research and the aquaculture industry. The Commission surveyed all known methods of tagging, including external tags, electronic, physical and chemical tags, and DNA, and identified six criteria that a tag would have to fulfil:

1. Tags must not affect the health or welfare of the fish.
2. Tags must not affect either the market for fish, or public health.
3. Physical tags must be so small that fish can be tagged before they are transferred to enclosures in the sea.
4. The results of analyses must be easily available.
5. Tags must be suitable for use on large numbers of fish.
6. The total cost per tagged fish must be low.

Each of the methods has its advantages and disadvantages, and these are often related to level of accuracy, animal welfare, logistics, market or economics. Among the aquaculture representatives on the commission, for example, there was some anxiety that methods that involved the addition of chemicals or physical tags could have a negative influence on the market. The Institute of Marine Research has subsequently developed the DNA Stand-by method (Figure 5), which utilizes the DNA of the fish to identify the sources of escaped salmon. The method has now been thoroughly tested in 15 concrete cases, and has been documented and quality assured via publications in international scientific journals (Glover *et al.*, 2008; Glover, 2010). We therefore know the accuracy, limitations, and cost of this method, while other methods are still at an early stage of development (Table 1). The method is not based on parent-offspring relationships, but on comparing the DNA profile of individual escaped salmon with that of fish from farms within a certain distance of the appearance of escapees. The method was developed with the aim of identifying the source of concentrated unreported escapes, and is not suitable for small, diffuse losses of fish. The procedures for the Stand-by method are based on a rapid response on the part of the authorities. When members of the public register abnormal catches of escapees and contact the fisheries

management authorities, these must immediately find out whether losses of fish from nearby farms have been reported. If no-one has reported such losses, samples must be taken both of escaped fish and of fish from farms in the vicinity that contain fish of similar size.

In practice, it turns out that when the fisheries management authorities react quickly enough with the collection and processing of samples, and when we examine biological characteristics such as the size of the escapees, there are not so many farms that lie in the area within which the escape is likely to have occurred. One example of this is a tracking in the County of Troms, where there were nine potential sources of an unreported escape episode. Tests showed that 37 of the 48 recaptured escapees matched the profile of one particular farm (Figure 6), while the other eight farms were found “not guilty”

since the DNA profiles of the escapees did not match those of these farms. For the first farm, on the other hand, only 12 of the 48 escapees did not match up.

The DNA Stand-by method requires neither tagging of the fish nor the development, operation, and maintenance of a database of either farmed or wild salmon, as the other methods would have done. The method only begins to cost something when the authorities register a case that they wish to follow up. For a typical case, such as that in Troms, involving analyses of fewer than 1000 fish, the costs will be made up of the scientist’s and technician’s salaries, laboratory expenses, and the cost of collecting samples of escaped fish and reference samples from fish farms in the vicinity; a total of less than NOK 300,000. The DNA Stand-by method is thus both simple and cost-effective.

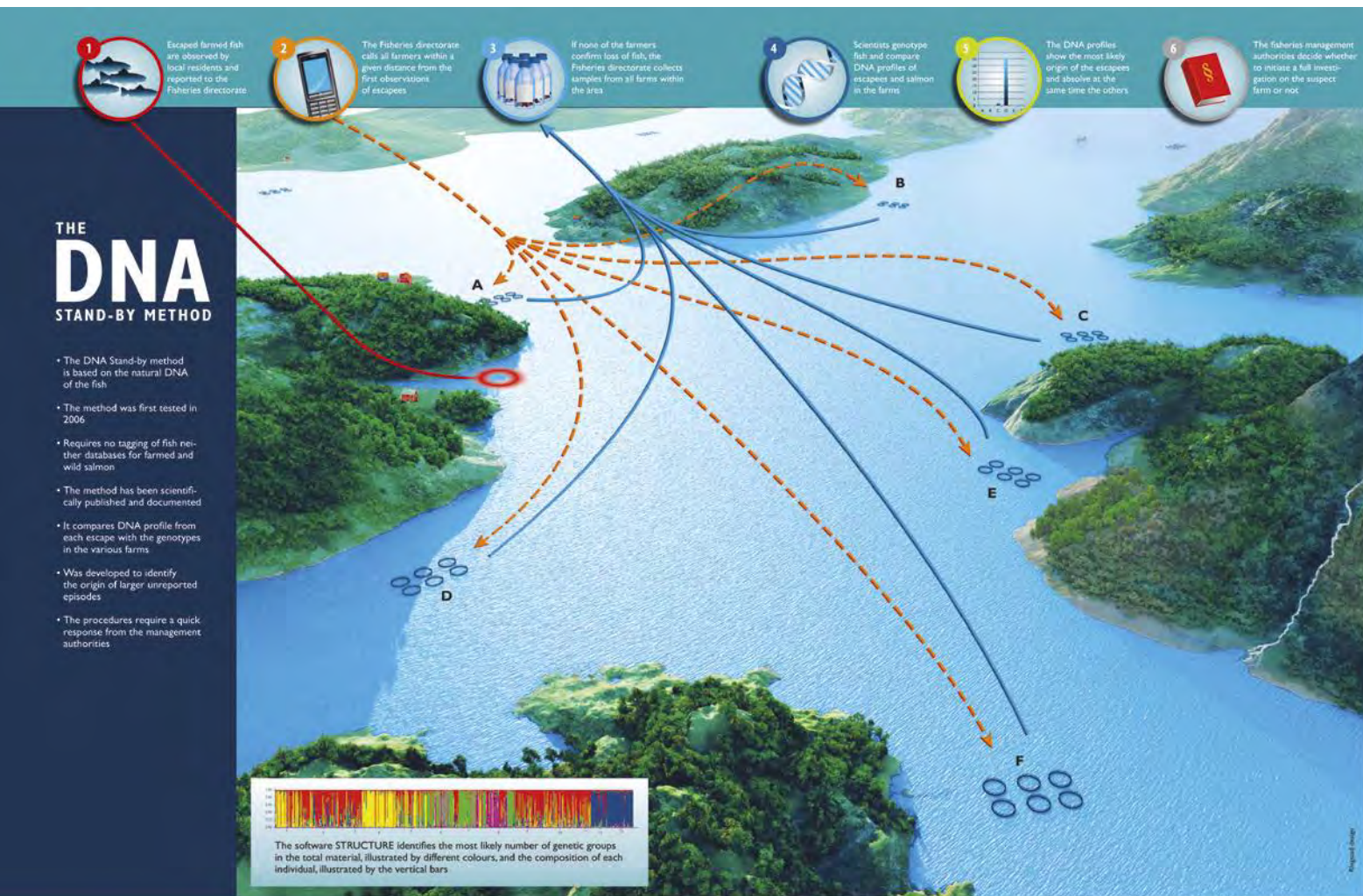


Figure 5
The DNA Stand-by method implemented by Norwegian fisheries management authorities to identify salmon farm of origin and escapees.

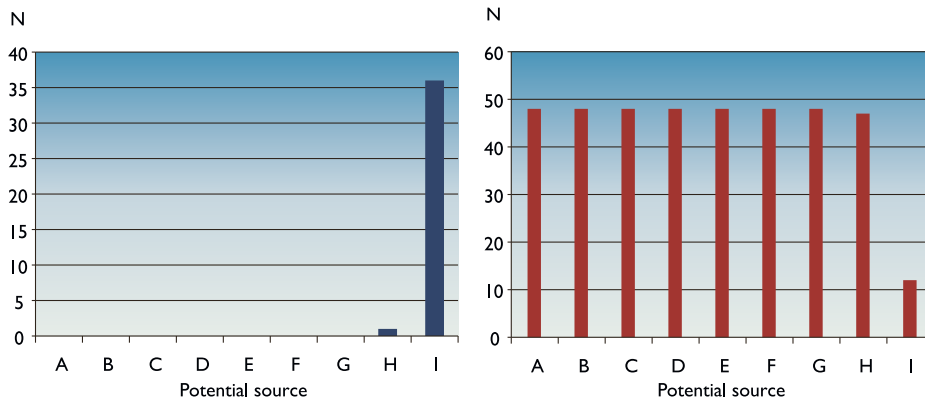


Figure 6
 In this case there were nine potential sources, A-I, for the captured escapees. The diagram on the left shows how many of the 48 captured escapees fit the DNA profiles of the various potential sources, and identifies the most likely source. The diagram on the right shows how many of the escapees that did not fit the DNA profiles of the potential sources.

Towards a scientifically based monitoring programme for escapees?

There is no doubt that salmon farming has become an economically significant industry that depends on the availability of coastal areas and large amounts of marine resources. At the same time, however, the negative consequences of salmon farming on wild anadromous stocks include a massive release of salmon lice and large numbers of escaped farmed fish. This in turn affects recreational values and other nature-based industries that depend on adventures, many of which are also dependent on marine and anadromous fish stocks. To gain an overview of whether salmon farming is sustainable or comes into conflict with the Norwegian government's Strategy for an Environmentally Sustainable Aquaculture Industry, the authorities need accurate information about the extent of individual impact factors, in addition to science-based management advice. While nation-wide professional monitoring of salmon lice in wild fish, which is another important impact factor of salmon farming, has been established, the registration of escaped farmed fish is still fragmented into a number of small, uncoordinated activities that lack a secure financial basis. One consequence of this is that information tends to be registered from a number of different sources, collected via different methods at different times and with

different standards of quality assurance. As a result, conclusions regarding numbers of escaped fish in Norwegian rivers tend to be widely divergent. We thus lack a national, coordinated, science-based, quality-assured programme under public-sector control that monitors escapes of farmed fish and removes escapees from the spawning grounds of wild salmon. This obviously makes it difficult for the authorities to monitor environmental effects of escapees and to manage wild salmon populations. Our experience of monitoring salmon lice demonstrates the value of official national coordination and quality-assurance of the impact factors of fish farming, with a predictable and necessary system of financing. Given the current scope of fish farming, it is unlikely that with existing production technology we will be able to completely prevent escapes, despite the serious efforts that are being made by the aquaculture industry. If escapes continue to occur at the same level as we have experienced until now, a growing number of wild salmon stocks will be affected and will become more similar to farmed salmon. This will bring about undesirable and irreversible loss of genetic resources. To avoid this, fish farms will have to be enclosed to a greater extent. It is also worth pointing out that sterile salmon, which are currently being trialled on a commercial scale, could significantly reduce the problem of negative genetic effects on wild stocks.

Tagging system	Advantages	Disadvantages
A: Physical tagging of all fish	<p>Accurate identification is possible.</p> <p>Also identifies “drip” escapes.</p> <p>Continues to identify fish long after they have escaped (even after slaughter).</p> <p>Allows farmed salmon to be identified in nature and to be removed from wild stocks.</p>	<p>Fish welfare, handling, stress, injuries.</p> <p>Major investments in logistics and equipment.</p> <p>Questions regarding relative times of tagging and escape.</p> <p>Tag has to be removed before fish can be consumed. Requires major documentation and management efforts on the part of the authorities.</p> <p>Potential loss of tags.</p> <p>Large annual operating costs.</p> <p>Major investment of resources on fish that do not escape.</p>
B: Removal of adipose fin	<p>Easy identification of escaped fish in rivers.</p>	<p>Useless for tracing escaped fish back to farm. Potential welfare problem when large-scale tagging involved.</p>
C: Chemical tagging via feed or vaccine	<p>Fish farmers pay for tagging process.</p>	<p>Tagging via feed requires widespread control of the production and sale of many individually tagged types of feed.</p> <p>Tagging via vaccines requires similar widespread control of the production and sale of many individually tagged types of vaccine.</p> <p>Potential consumer reactions to adding chemicals to fish.</p>
D: DNA with databases	<p>No physical or chemical tagging involved.</p> <p>Fish are not handled.</p> <p>Can be traced back to hatchery or on-growing farm.</p> <p>Costs can be claimed back from polluter rather than industry as a whole.</p>	<p>Requires establishment and operation of major databases.</p> <p>Requires reorganization of aquaculture industry logistics.</p> <p>Major investments in logistics and equipment.</p> <p>Requires major documentation and management efforts on the part of the authorities.</p> <p>Major annual costs.</p>
E: DNA Stand-by method	<p>No investments in equipment required.</p> <p>No fish handling or adaptation of aquaculture industry logistics required.</p> <p>No need to set up and operate databases of farmed fish.</p> <p>Costs begin to run only in event of an escape event.</p> <p>Extremely cost-effective.</p> <p>Costs can be claimed back from polluter rather than industry as a whole.</p>	<p>Not suitable for small “drip” escapes.</p> <p>Requires rapid response following escape.</p> <p>Requires the authorities to maintain a contingency team.</p> <p>Not every case will result in diagnostic identification of the individual farm involved.</p>

Table 1:
Advantages and disadvantages of the best-known tagging systems for identifying escaped farmed salmon.

Facts about escaped and wild salmon

Escapes of farmed salmon have led to genetic changes in at least six of 21 (29%) Norwegian salmon populations studied. These changes have taken place in the course of a relatively short time (15–30 years), i.e. within about three to six generations.

The genetic changes accumulate over time, and continued escapes will therefore lead to greater changes in wild salmon in the course of time.

Since the spawning success of farmed salmon is gender-specific and will also vary in time and space, at the same time as there are wide variations in survival rates of the offspring of farmed salmon in nature, it is unlikely that there is an absolute limit to the proportion of farmed salmon a wild salmon population can absorb.

There is no scientific evidence that crossing escaped farmed salmon with wild salmon populations has any positive effects on the latter.

An important aim of further efforts will be to develop good indicators of the effects of escaped farmed salmon on wild populations.

The fact that a large number of genetic combinations can produce salmon with identical phenotypes means that although we can select our way back to a salmon that resembles the “old” phenotype, we cannot re-create the genetic material of a population such as it was before the farmed salmon bred into the wild stock. Evolution is not reversible.

A number of measures have the potential to reduce the effects of farmed salmon on wild stocks; these include enclosed farms, introducing sterile farmed salmon, removing the adipose fin of farmed salmon, traps in rivers, gene banks, and planting out eggs of wild salmon.

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