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Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013

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We report on the data from an extensive monitoring programme for the occurrence of escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers for 25 years. This monitoring started as a 3-year research programme in 1989 and was followed by management authorities to cover the proportional occurrence of escaped farmed Atlantic salmon in rivers during summer and autumn before spawning. Farmed salmon were distinguished from wild salmon by growth patterns in the scales. More than 362 000 salmon were registered by this programme. Here we present the historical data on escaped farmed salmon in catches 1989–2013 and a methodology for calculating averages across summer and autumn capture in rivers, across years and in regions, using weighted and unweighted observations. Catches of escaped farmed salmon show large spatial and temporal variation, with the early 1990s and early 2000s being periods of large influxes of farmed fish. Western Norway and parts of middle and northern Norway have shown particularly high incidences of escaped farmed fish. Because escaped farmed Atlantic salmon are competing and interbreeding with wild Atlantic salmon, as well as increasing the spread of disease-causing agents, they have become a major force driving the abundance and evolution of Atlantic salmon.

Keywords: aquaculture, Atlantic salmon, escaped farmed salmon, fisheries management, *Salmo salar*.

Introduction

Increased production of farmed Atlantic salmon (*Salmo salar*) worldwide and declining wild salmonid populations have caused concerns that salmon aquaculture is a major driver of abundance and viability of wild salmonid populations (Maitland, 1986; Fleming *et al*., 2000; McGinnity *et al*., 2003; Ford and Myers, 2008; Taranger *et al*., 2015; Forseth *et al*., 2017). One concern relates to competitive interactions and interbreeding between escaped farmed and wild Atlantic salmon, another to increased transmission rates of fish disease agents (ICES, 2016). In this article, we analyse the results of a 25-year monitoring programme (1989–2013) documenting presence and proportion of escaped farmed salmon in catches from wild Atlantic salmon populations in Norway, currently the world's largest producer of farmed and wild Atlantic salmon. An article in this issue (Glover *et al.*, in 2019) describes the continuation of this monitoring programme after 2014.

Escaped farmed Atlantic salmon were observed in the wild from the mid-1980s and were registered in several Norwegian rivers on a large scale from 1987 to 1988 (Gausen and Moen, 1991). A 3-year research programme from 1989 organized reports of escaped farmed Atlantic salmon caught along the coast and in the rivers (Lund *et al.*, 1991). The research programme was followed by monitoring that prioritized registrations of escaped farmed salmon in rivers, financed by the Directorate for Nature Management and the Directorate of Fisheries. Escaped farmed salmon have over the years been found throughout Norway in proportions varying from 0 to more than 80% of the salmon caught (Gausen and Moen, 1991; Fiske *et al.*, 2001, 2006, 2014; Diserud *et al.*, 2010, 2013; Glover *et al.*, 2017; Svenning *et al.*, 2017). During the last 30 years, escaped farmed salmon have also been found all around the North Atlantic, as well as outside the native range of the species (references in ICES, 2016; Glover *et al.*, 2017).

Farmed salmon escape to the wild at all life stages, but particularly after structural failures of marine net pens (ocean cages) (Jensen *et al.*, 2010). Escapes also occur during the daily operation of fish farms, sea-lice treatment, and transport of fish to and from marine fish farms. A smaller number of juvenile escapes have been reported from land-based freshwater production facilities (Clifford *et al.*, 1998a). Escape events and the number of fish escaping are reported to the Norwegian Directorate of Fisheries (http://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk) but some go unnoticed. Estimating the real number of escapes has been attempted during three periods: 1989–1997 (Lund, 1998), 1998–2004 (Sægrov and Urdal, 2006), and 2005–2011 (Skilbrei *et al.*, 2015) and suggested that the true number of escapes are two to four times as high as the reported numbers. The reported number of farmed salmon escaping from fish farms has declined considerably during the study period, and if we take the growth of the industry into account and estimate the number of escaped farmed salmon per tonne of biomass in fish farms, the rate of decline is substantial. New official standards for technical equipment (Jensen *et al.*, 2010) and improved (reduced) handling of farmed salmon are likely causes of the reduced number of escapes (Skilbrei *et al.*, 2015).

Escaped farmed salmon can be distinguished from wild salmon by external morphology (Fiske *et al.*, 2005), growth patterns in scales (Lund and Hansen, 1991; ICES, 2011), carotenoid pigments (Lura and Sægrov, 1991), and fatty acid profiles (Thomas *et al.*, 2008). Most differences result from differences in rearing environment and are primarily useful for identifying farmed escapes after the smolt stage, as escapes would be hard to distinguish from intentional releases of salmon juveniles (Fiske *et al.*, 2005). Genetic markers have been useful following fish from large escapes where one or a few sources were possible (Crozier, 1993; Clifford *et al.*, 1998a, b; Glover, 2010), but a generic, genetic tool for distinguishing escaped farmed from wild salmon has not been available until recently (Karlsson *et al.*, 2011). These single-nucleotide polymorphism (SNP) markers have been used to estimate introgression in a large number of wild salmon populations in Norway (Glover *et al.*, 2013; Karlsson *et al.*, 2016; Diserud *et al.*, 2017), and to estimate proportional farmed ancestry in individual wild salmon for understanding the fitness effects of introgression (Bolstad *et al.*, 2017).

The goal of this study is to document the extensive time series of escaped farmed salmon in Norwegian river catches from 1989 to 2013. We present the results of the longest continuous monitoring programme for escaped farmed Atlantic salmon. We devise methods for analysing data from various monitoring activities, discuss some of the associated statistical challenges, and describe temporal and spatial patterns of escapes in Norwegian rivers during 1989–2013. We discuss our findings in light of the hypotheses of salmon migration emerging from experimental releases of farmed Atlantic salmon (Hansen, 2006).

An accompanying article by Glover *et al.* (2019) describes the second generation of riverine monitoring of escaped farmed salmon, made possible after 2014 by an enlarged grant from the Norwegian Directorate of Fisheries. This new programme builds on experiences during 25 years of monitoring described here but expands the number of rivers and sampling methods.

Material and methods

Samples

The Norwegian Institute for Nature Research (NINA) has monitored escaped farmed salmon in wild Norwegian Atlantic salmon populations from 1989 to 2013, together with partner institutions Rådgivende Biologer, the Norwegian Veterinary Institute, Uni Research Environment, and the Natural Resources Institute Finland (LUKE) for the two rivers shared between Norway and Finland (River Tana/Teno, and River Neiden/Näätämö in Norwegian/Finnish). These annual monitoring datasets have been presented only in reports and publications in Norwegian (Lund, 1998; Fiske *et al.*, 2001, 2014; Urdal, 2006; Diserud *et al.*, 2010, 2013), except in publications by Lund *et al.* (1991), Fiske *et al.* (2006) in Norway, and Erkinaro *et al.* (2010, 2018) for the Rivers Tana and Neiden. The salmon were either caught in the regular angling season during summer (June–August), or by various methods during organized autumn fishing after the regular fishing season (e.g. broodstock fishing).

Scales from 362 616 salmon were analysed to determine their origin, based on growth patterns (Fiske *et al.*, 2005, and details below), 304 474 of these were from catches in the regular fishing season in summer, and 58 142 were from autumn catches. Of these, 26 079 were escaped farmed salmon, 13 595 caught in summer, and 12 484 in autumn. Some samples were excluded due to non-representative sampling, for example, in rivers where the wild salmon population was unnaturally small from infestations of the non-native parasite *Gyrodactylus salaris* (Johnsen and Jensen, 1991), or from other causes, and in rivers where only escaped farmed salmon or only wild brood stock were targeted and sampled. Samples with fewer than 20 fish for a given river and year were excluded from the analyses.

Scale reading

The scales of Atlantic salmon record age and growth rate of fish from juveniles start forming scales at ca. 40 mm length. Growth is typically slow in fresh water and faster in sea water, is faster in summer than in winter, and slows with age. The transition during smoltification and outmigration into brackish and full sea water is recorded as an abrupt increase in growth rate, and maturation may be associated with increased growth rate during the early stages of hormonal change. Spawning is recorded as reduced growth rate and erosion of the edge of the scales (ICES, 2011).

Farmed salmon show a high growth rate throughout life. Their scales do not show the seasonality of growth between summer and winter nor an abrupt increase in growth during smoltification (Fiske *et al.*, 2005) due to a more constant food supply. Farmed salmon scales may show arrests in growth rate because of treatments against parasites and pathogens. Scales may shed when farmed (and hatchery-reared) fish are handled, leading to a higher proportion of replacement scales than in wild salmon. Scales formed late in life have a large central plate with no record of earlier life. Escapes may stop growth at the time of escape from captivity, as they commonly do not start feeding immediately after the escape (Fiske *et al.*, 2005).

Scale readings, combined with assessments of external body morphology, gill-cover erosion, and fin damage, were used to determine if salmon were of farm origin, and thus estimate the proportion of farmed escapees in the samples (Fiske *et al.*, 2005). When the origin assigned by scale reading and morphological assessment differed, the origin of the fish was determined based on the scale reading alone, but when origin could not be determined conclusively from the scale reading, morphological assessment was used to assign the sample. Summer samples represented a proportion of the total catch in each river. Autumn scale samples were obtained mainly from fish close to spawning caught by designated anglers after the sport angling season, but samples were also obtained from fish caught by fish traps and nets. Most of the fish judged to be wild salmon by the field personnel in the autumn samples were released after the scale samples were taken or were stripped for gametes to produce fish for stocking.

We used the following scale features (Figure 1) to distinguish between wild salmon and escaped farmed salmon (Fiske *et al.*, 2005):

- Smolt size: Farmed fish larger than wild fish. Back calculations using the assumption of direct proportions between scales and fish length were performed when in doubt about origin
- Smolt age: Difficult to determine from farmed fish because of more even growth pattern
- Transition from freshwater to saltwater: More diffuse in farmed salmon
- Sea winter band: More clearly defined in wild salmon
- Summer checks (areas of narrow circuli within the summer growth period): More checks in scales from farmed fish
- Replacement scales: More replacement scales in farmed fish, however, this criterion has become less useful as less manual handling of farmed fish is taking place

An index for the proportion of escaped farmed salmon in the population

Samples of scales from tens of thousands of anglers in summer cover more rivers and include more fish than autumn samples. The analyses can underestimate the proportion of escapees in the wild population as escaped farmed salmon often ascend rivers later in the season than wild salmon (Hansen, 2006; Thorstad *et al.*, 2008; Erkinaro *et al.*, 2010). Ideally, autumn samples better represent the proportion of escaped farmed salmon in the wild spawning population, as they are collected after most of the salmon have arrived at the spawning grounds. However, autumn samples can often give uncertain estimates due to small sample sizes. Catchability can also differ between wild and escaped farmed salmon, with farmed escapees more likely to bite late in the season (Svenning *et al.*, 2015).

A method using information from both summer and autumn catches in one index was developed by Fiske *et al.* (2006) and termed "incidence" or "annual percentage" (by Diserud *et al.*, 2010; we use incidence hereafter). The "true" proportion likely lies between summer and autumn estimates—but varies among rivers and years, since the variation in the proportion of escapees in catches depends on river characteristics and the spatiotemporal distribution of escaped farmed fish in the sea. To normalize observations and stabilize the variance we arcsine-square root transform the proportion data, take the mean of the two transformed proportions, and perform the inverse transformation to obtain the incidence estimate. This approach standardized how we treated mixtures of summer and/or autumn observations and adjusted for seasonal variation. From a comparison of all rivers and years with both summer and autumn sample proportions ($n = 284$), Fiske *et al.* (2006) developed equations to estimate incidence from just one sample. This also made it possible to estimate incidence when only the summer or the autumn sample proportion was available. In this study, we recalibrated these equations by including all samples with both summer and autumn sample proportions collected 1989–2013 ($n = 535$), except samples considered non-representative or too small ($n < 20$ salmon).

National and regional averages of the proportion of escaped farmed salmon in wild salmon populations have been calculated by two alternative methods. In the first, an average of the total (national or regional) population proportion is calculated by proportions unweighted by river, and in the second, proportions are weighted by the total catch in a river (as a proxy for relative population size). Estimates of regional proportions can differ substantially between these weighting approaches, because larger populations tend to have smaller estimated proportions of escaped farmed salmon and because escape proportions vary among years and among rivers in a region. We followed the same

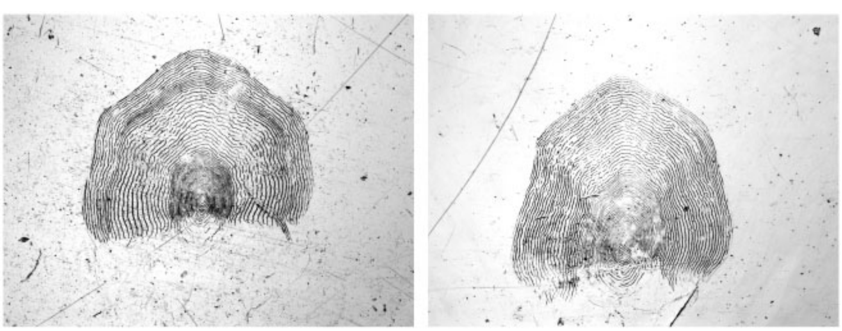

Figure 1. Scale from a one-sea winter wild salmon (left: ca. 1500 g and 540 mm) and from a farmed salmon that has spent its entire life in captivity (right: 968 g, 448 mm). Note the more even growth pattern in the scale from the farmed salmon.

regional partitioning of Norway as in Fiske *et al.* (2006). Records from the south-eastern counties, from Østfold to Vest-Agder, were pooled into one region, because of limited aquaculture activity. Each county from Rogaland to Finnmark was considered a separate region. We used county configurations as they were in 2013 and do not consider the regional reforms currently being implemented in Norway.

Uncertainties in estimation

Several factors led to uncertainties in the estimates, including small sample sizes, potentially biased observations, misclassifications, measurement imprecision, and natural population variability in space and time. Potential limitations and biases for the sampling and estimation methods are discussed in Glover *et al.* (2019). Quantification of uncertainties or correcting for errors requires an understanding of error model structure and parameters, knowledge that we rarely have. Nevertheless, management decisions must be made and, if required, mitigating actions taken. In Norway, the Directorate of Fisheries launched a system in which actions to reduce the number of escaped farmed salmon in a river should be planned when an incidence exceeds 10% and should be contemplated if the incidence is between 4% and 10% (https://www.fiskeridir.no/Akvakultur/Dokumenter/Hoeringer/Hoeyring-om-fellesansvar-for-utfisking-av-roemt-oppdrettsfisk).

We briefly illustrate the magnitude of the "pure" random sampling uncertainty, either as a binomial sampling process, when population size is much larger than sample size, or as a hypergeometric process for smaller populations relative to sample size. Even with perfect representative sampling, certain classification of salmon as farm or wild origin and no bias in the estimation of incidence, the uncertainty in a proportion estimate will usually be substantial for small sample sizes that were used to limit the potential harm to wild salmon populations. This is the unavoidable lower threshold for uncertainty with a given sampling effort, an uncertainty that fisheries and nature management agencies and the aquaculture industry have to accept as long as we sample only a part of the population. Figure 2 shows the approximate 95% confidence intervals for the proportion estimates, as a function of the true proportion, and sample and population sizes. Our illustrations were set at the limits between the categories employed by Norwegian management authorities (proportion $p = 0.04$ or 0.10), for evaluating the influence of escaped farmed salmon on wild salmon populations. Note that even at sample sizes approaching 1000 fish, the 95% confidence interval for the binomial sample proportion is approximately ± 0.02 around the point estimate.

Results

Observations were made in 225 Norwegian rivers for various number of years over 25 years from 1989 to 2013, for a total of 2038 river years (Supplementary Table S1). Scales from 362 616 fish were analysed for origin based on growth patterns; of these 26 079 were categorized as escaped farmed salmon, giving a total proportion across rivers, years and catch methods of 0.072.

In summer catches, 13 595 of 304 474 (p=0.045) fish analysed were categorized as escaped farmed salmon. We obtained 1331 estimates from summer samples that included 20 or more fish from all rivers and years, with an unweighted mean proportion of 0.102 ($SD = 0.173$). In autumn catches, the overall proportion of escaped farmed salmon was 0.215 (12 484 of 58 142 fish). There were 901 estimates from autumn samples with an unweighted mean proportion of 0.206 ($SD = 0.229$).

The 11 *Gyrodactylus*-infected rivers, excluded from the analyses because of small wild salmon population sizes, gave an overall proportion of escaped farmed salmon across rivers, years, and catch methods of 0.115 (675 of 5856 fish). The unweighted mean proportion across samples was 0.140 ($SD = 0.169$). The proportion of escaped farmed salmon was smaller in summer samples from infected rivers (221 of 3555 fish, unweighted mean $p = 0.098$, $SD = 0.142$) than in autumn samples (454 of 2301 fish, unweighted mean $p = 0.225$, $SD = 0.266$).

Incidence calculations

The incidence index for summer- or autumn-catch samples was estimated from the whole time-series from 1989 to 2013 (Figure 3).

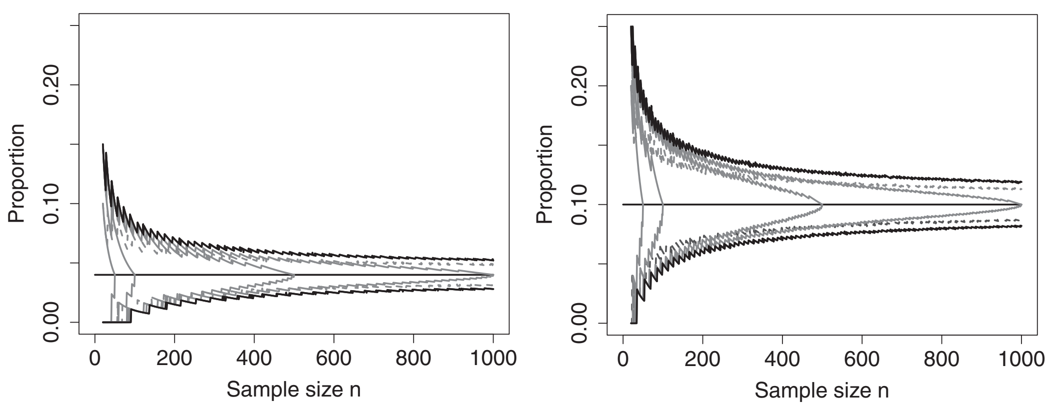

Figure 2. Approximate upper and lower bounds of the 95% confidence interval for the estimated sample proportions, shown as functions of the true proportion p (0.04 in the left panel and 0.10 in right panel) and sample size n from 20 to 1000. Black lines show the bounds for the binomial process, which assumes that the population size is much larger than the sample size; gray dashed lines show bounds for the hypergeometric process where sample size n is always half the population size N, and the gray, solid lines give the bounds for population sizes fixed at 50, 100, 500, or 1000 fish.

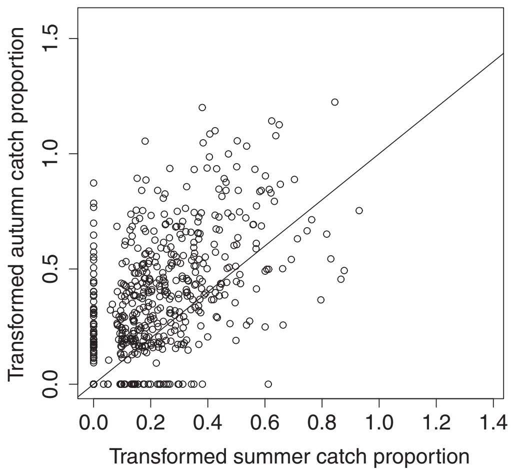

Figure 3. Proportions of escaped farmed salmon in summer and autumn samples from 535 paired observations in Norwegian rivers (1989–2013) (correlation = 0.53). Proportions are arcsin-square-root-transformed.

We fitted linear models to data of transformed proportions and incidences to estimate the incidence index in cases where only summer [Equation (1)] or autumn [Equation (2)] samples were available:

$$\arcsin\left(\sqrt{\text{Incidence}}\right) = 0.103 + 0.878 \times \arcsin\left(\sqrt{p_{\text{Sum}}}\right) \quad (1)$$

$$arcsin\left(\sqrt{\text{Incidence}}\right) = 0.046 + 0.685 \times \arcsin\left(\sqrt{p_{\text{Aut}}}\right) \quad (2)$$

where p_{Sum} and p_{Aut} are the proportions of escapes in the summer or autumn sample respectively. These recalibrated equations, based on a larger dataset ($n = 535$ data pairs of summer and autumn proportions in a river), were not significantly different from the previous version (Diserud *et al.*, 2010; all *p*-values >0.05 when testing difference of model coefficients), indicating no major temporal changes in these relationships. The original incidence equations (Fiske *et al.*, 2006) were forced through the origin, whereas the equations by Diserud *et al.* (2010) and Equations (1) and (2) allowed intercepts different from 0. The calculated incidence may, therefore, be larger than 0.0, even though summer or autumn proportions are 0.0. The results for both models were highly significant with $R^2 = 0.68$ for the summer model of incidence ($SE_{\text{gradient}} = 0.026$) and $R^2 = 0.84$ for the autumn model of incidence ($SE_{\text{gradient}} = 0.013$).

We obtained 1590 incidence estimates for all rivers and years, based on either summer or autumn catches, or both (Supplementary Table S1 and Figure S1) with a mean of 0.124 ($SD = 0.147$). Mean incidence from 1989 to 2013 was calculated for 173 rivers that had at least one acceptable incidence estimate (Supplementary Table S2).

Mean incidence for 107 rivers with 4 or more years with incidence estimates was 0.124 ($SD = 0.121$), and the distribution was skewed with median 0.092 (Figure 4).

Spatial variation in incidences of escaped farmed salmon

The largest mean incidence estimates of escaped farmed salmon in Norwegian rivers were in western Norway (Figure 5). In the County of Hordaland (HO), most of the rivers studied showed long-term average incidences above 0.2, including rivers that received special protection as national salmon rivers (Anon., 1999), such as the Etne and Vosso rivers (ID-nos 041.Z and 062.Z in Supplementary Table S2). In southeastern Norway (SE) and the County of Finnmark (FI) in north-eastern Norway most of the rivers showed low incidences of escaped farmed salmon—both regions with low productions of farmed salmon during 1989–2013. However, some rivers, such as the Glomma and Nidelva rivers (ID-nos 002.Z and 019.Z in Supplementary Table S2) showed incidences >0.2. The border river between Norway and Finland, the Tana/Teno, which is likely to hold the world's largest production of wild Atlantic salmon, had a low incidence of escaped farmed salmon at 0.019 (ID-no. 234.Z, Supplementary Table S2).

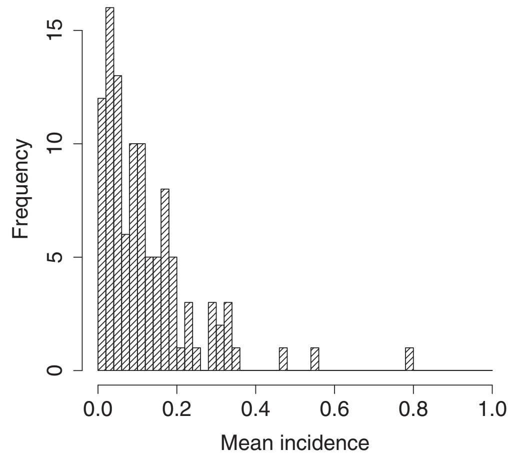

Figure 4. Mean incidences of escaped farmed salmon over the years from 1989 to 2013, for 107 Norwegian rivers with four or more years of representative samples. Bin width = 0.02.

Contrasting high and low incidences were found in some neighbouring rivers, and in all regions in Norway (Figure 5). A notable example is the large River Namsen in North Trøndelag (NT) that showed a high incidence at 0.113 (ID-no. 139.Z), whereas three small rivers in the same fjord showed incidences below 0.02 (ID-nos. 138.5Z, 138.6Z, and 138.Z in Supplementary Table S2).

The HO was the region with the largest mean incidence of escaped farmed salmon (Table 1), measured both when all rivers were given equal weight ($\bar{I}_{\text{eq}} = 0.291$) and weighted by catch ($\bar{I}_{cat} = 0.298$). These values are substantially larger than for the region with the smallest mean incidence of escaped farmed salmon in the FI with $\bar{I}_{\text{eq}} = 0.062$ and $\bar{I}_{\text{cat}} = 0.026$.

National and regional temporal trends in incidences of escaped farmed salmon

National trends in mean summer and autumn proportions of escaped farmed salmon demonstrated considerable temporal variation in catches over 1989–2013 (Figure 6). Here, the river proportions were either unweighted (Figure 6, left panel) or by catch size (Figure 6, right panel). The trend in the mean annual incidence index is shown in red, for both weighted average alternatives.

Unweighted mean proportions of escaped farmed salmon in Norwegian rivers (Figure 6, left panel) were larger than summer

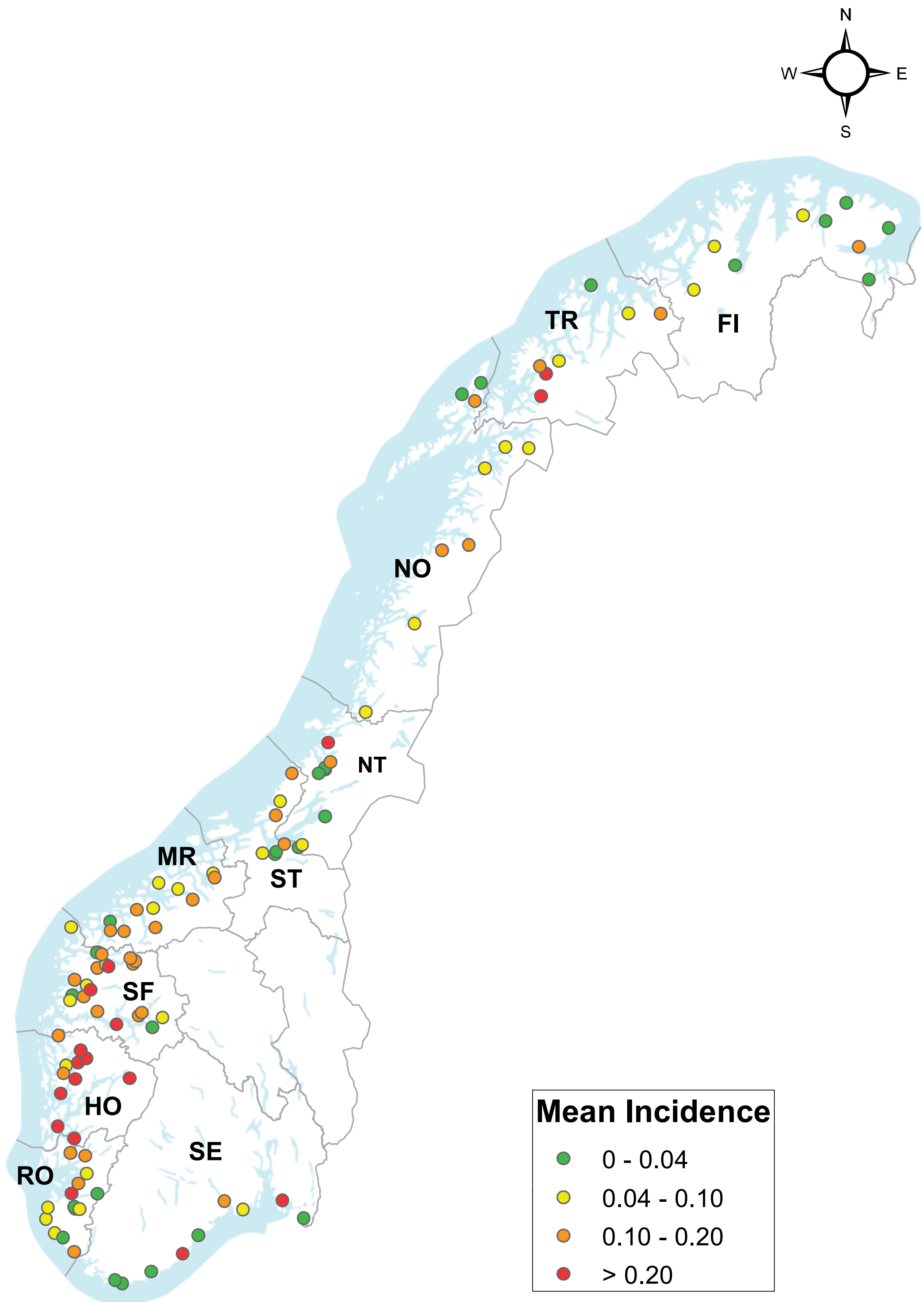

Figure 5. Mean incidence of escaped farmed salmon in 107 Norwegian rivers 1989–2013. Means are only shown for rivers having incidence data from four or more years during this period. SE, South East Norway; RO, Rogaland County; HO, Hordaland County; SF, Sogn og Fjordane County; MR, Møre og Romsdal County; ST, South Trøndelag; NT, North Trøndelag; NO, Nordland County; TR, Troms County; FI, Finnmark County.

proportions during the whole period, except for 2 years in the early 2000s. In 2002 and 2003, fewer rivers were sampled and the selection was biased toward the most affected regions Hordaland and Sogn og Fjordane. Some of the smaller populations in western Norway had especially large proportions of escapes in the 2002 summer catches, as indicated in Figure 6 where the unweighted annual mean has a large peak in 2002 while the catch-weighted annual mean shows a much more moderate peak. The weighted-by-catch mean proportions (right panel) showed larger autumn proportions over the entire period. The weighted means also showed a clear downward trend in autumn proportions whereas the summer proportions remained less variable over time. Both unweighted and weighted mean proportions—and the incidence calculations for both methods of indicating means—demonstrated that the late 1980s and early 1990s had particularly large proportions of escaped farmed salmon in Norwegian rivers.

Trend differences between the two weighted average alternatives (Figure 6) indicated that we have a relationship between the proportion or incidence of escapes and catch size in the rivers, as shown in Supplementary Figure S2. However, large rivers may still show large proportions of escaped farmed salmon (see e.g. River Namsen in Supplementary Table S2 with annual details in Supplementary Table S1), although the largest salmon river in Norway showed low proportions (River Tana/Teno, Supplementary Table S2).

Temporal trends by region (Supplementary Table S3 and Figure S3) varied substantially among regions, partly because the number of rivers sampled in a region was small for some years and estimates of year-to-year variation depend on which rivers were included.

We divided the 25-year period 1989–2013 into four sections, each about one Atlantic salmon generation long (1989–1995, 1996–2001, 2002–2007, 2008–2013), to reduce some of the variation caused by small samples and to better illustrate any difference in regional trends (Figure 7). The western regions (Rogaland RO, Hordaland HO, Sogn og Fjordane SF, and Møre og Romsdal MR) all started with high incidence levels, with Hordaland (HO) having by far the largest incidence. In the next two periods, contrasting trends indicated that Rogaland (RO) showed a strong reduction and Troms (TR) the largest increase in the incidences of escaped farmed salmon. Troms remained the region with the second largest incidence, whereas Rogaland remained among the smallest incidence.

All regions, except South Trøndelag (ST) and South East (SE), showed a reduction in incidence during the last 6-year period of this time series, 2007–2013 (Figure 7).

Table 1. Regional and national averages of incidence of escaped farmed salmon in Norway (1989–2013).

Region ID	Region name	$\bar{I}_{eq}$	$\bar{I}_{cat}$
SE	South East	0.095	0.061
RO	Rogaland	0.094	0.064
HO	Hordaland	0.291	0.298
SF	Sogn og Fjordane	0.156	0.120
MR	Møre og Romsdal	0.127	0.129
ST	South Trøndelag	0.075	0.055
NT	North Trøndelag	0.085	0.080
NO	Nordland	0.102	0.083
TR	Troms	0.178	0.109
FI	Finnmark	0.062	0.026
	Norway	**0.126**	**0.103**

$\bar{I}_{eq}$ = equal weight for incidence estimates for all populations. $\bar{I}_{cat}$ = weighted incidence averages by catch as a proxy for population size.

Discussion

Farming of Atlantic salmon was made possible through inventions in the late 1960s and soon after emerged as a way of using the coastline for large-scale production of animal protein (Glover *et al.*, 2017 and references therein). After a strong build-up of production during the 1970s and 1980s and a demonstration that it was possible to produce farmed salmon at an acceptable market cost, fish farming was viewed as a relief to wild salmon populations, especially in oceanic, coastal and riverine areas with large fisheries. In 1986, the first warning emerged that farmed salmon, and in particular escaped farmed salmon, might constitute a threat to wild salmon diversity and viability (Maitland, 1986). This concern followed from genetic studies showing that natural genetic diversity differed among populations of salmonid species and that indiscriminate releases of cultured fish could represent a threat to this diversity (Billingsley, 1981; Ryman, 1981).

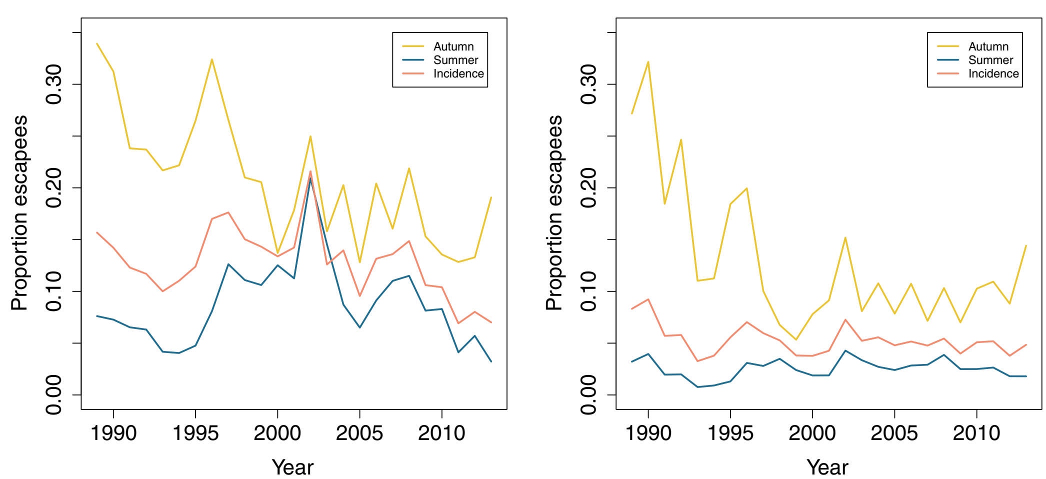

Figure 6. National trends for summer proportion, autumn proportion and incidence of escaped farmed salmon in Norwegian rivers (1989–2013). Left panel shows unweighted means, right panel means weighted by river catch.

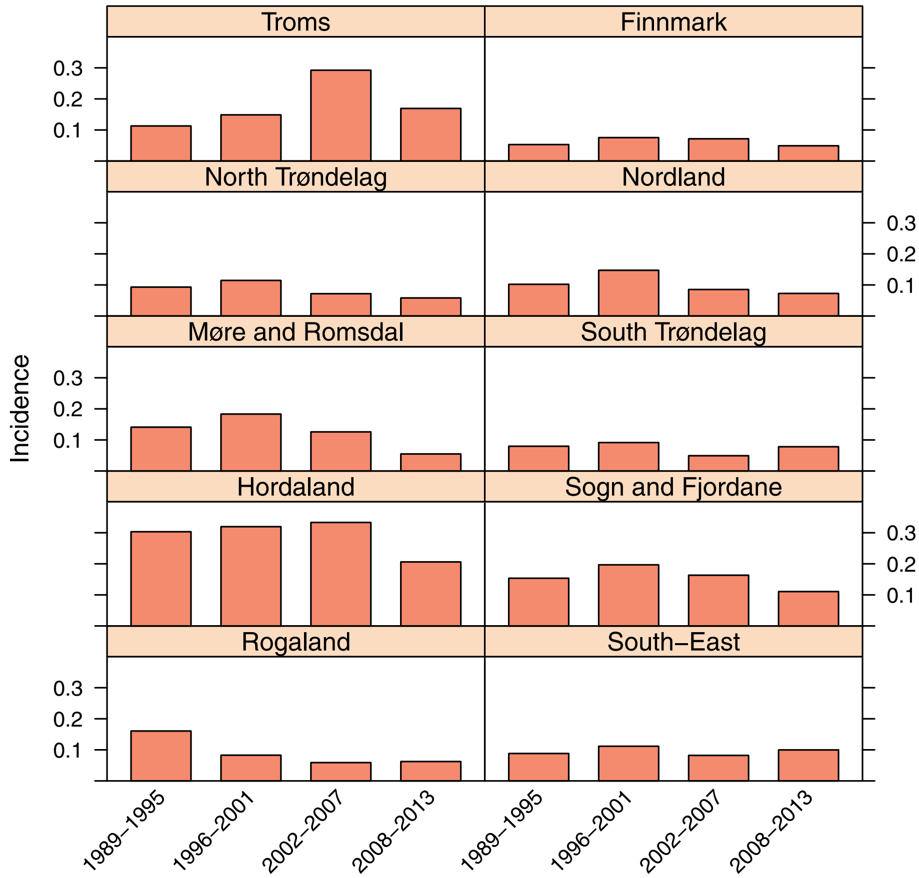

Figure 7. Mean incidence of escaped farmed salmon shown for all rivers, with equal weights, for time periods of 6 years which reflects approximately one generation of wild Atlantic salmon.

In Norway, large number of escaped farmed salmon were found in some rivers in the autumn of 1987–1988 during sampling of wild salmon populations for the cryopreservation of sperm (Gausen and Moen, 1991). A 3-year research programme for sampling wild and escaped farmed salmon along the coast and in rivers was established in 1989, and monitoring was later financed by environmental and fisheries management authorities. Detailed reporting of the number of salmon escaping began in 1993. During these first years of monitoring, two severe storms during the New Year periods of 1988–1989 and 1991–1992 led to extraordinarily large-scale escapes of farmed salmon. An intergovernmental group estimated that about 1.6 million salmon escaped each year during the 4-year period (1989–1992) in Norway (Lund, 1998). Such large escapes have not occurred since 1993, even though farmed salmon production increased 10-fold over the last 25 years. Official statistics show that farm production in Norway has increased substantially, wild population sizes have been reduced while the incidence has decreased, so the proportion of farmed salmon produced that escape is now 100-fold less than it was in the period leading up to 1993.

Spatial variation and national and regional temporal trends

Escaped farmed salmon have, with few exceptions, been found in all rivers at least once during the monitoring programme (Supplementary Table S1). This supports the conclusion that farmed salmon that escape from marine sites throughout the year and at different life stages spread over vast areas. This has been shown experimentally by controlled releases of farmed salmon (Hansen, 2006; Hansen and Youngson, 2010; Skilbrei *et al.*, 2015) and by observations of escaped farmed salmon at sea, far away from fish farming areas (Hansen *et al.*, 1999; Jensen *et al.*, 2013).

The largest proportion of escapes in Norway was recorded early in the sampling period 1989–2013 and was likely associated with large-scale escapes from net pens that were unable to withstand harsh weather conditions. Since then, both the handling of fish and farming equipment have improved (Jensen *et al.*, 2010) to reduce the number of farmed salmon escaping despite an increase in production.

Even though escaped farmed salmon can spread over vast areas, the largest incidences of escaped farmed salmon occur in intensive fish-farming areas (Fiske *et al.*, 2006; Ford and Myers, 2008), such as in the County of Hordaland (Table 1, Figure 5) in other regions of western Norway and in the County of Troms in the north. Contrasts between incidences of escaped farmed salmon among neighbouring streams must have other causes, such as the size of the salmon population or the size of the river. This will be treated in more detail in a later publication on factors explaining variation in proportion of escaped farmed salmon and genetic introgression in wild salmon populations.

In southernmost Norway, the last decades have seen a recovery of wild salmon populations in formerly acidified rivers (Hesthagen *et al.*, 2011) and a concomitant reduction of escaped farmed salmon in our samples. This is most evident in the low-incidence rivers in the southern part of the County of Rogaland (RO) and the southernmost rivers in the SE region.

A monitoring programme ideally includes large representative samples to be able to understand trends and verify the effects of management actions meant to alleviate negative trends identified by the programme. However, several practical constraints influence sampling design. Compared with wild salmon, escaped farmed salmon enter rivers later (Lund *et al.*, 1991), their spatial distribution within a river differs (Moe *et al.*, 2016), and they may have different catchabilities (Svenning *et al.*, 2015). Inevitably, there also remains uncertainties from sampling randomness. We know that escaped farmed salmon can successfully reproduce in the rivers (Lura and Sægrov, 1991) and may in extreme cases dominate spawning (Sægrov *et al.*, 1997). Genetic introgression of escaped farmed salmon into wild salmon populations has been demonstrated (Glover *et al.*, 2013; Karlsson *et al.*, 2016), and statistically significant introgression was detected in half of 175 populations studied in Norway (Diserud *et al.*, 2017). These 175 rivers represent more than 80% of Norway's wild salmon resource (measured as a percentage of the total spawning target for Atlantic salmon). Moreover, changes in sea age at maturity and body size and condition factor at which spawners return for introgressed offspring occur on a large scale (Bolstad *et al.*, 2017). The concerns expressed by Maitland (1986), Skaala *et al.* (1990), Hutchings (1991), and Waples (1991) have come true (Glover *et al.*, 2017), although not necessarily as predicted. For example, there is considerable unexplained variation in the relationship between the estimated incidence of escaped farmed salmon in a given river over the last 25 years and the estimate of genetic introgression of farmed into wild salmon in that river (Karlsson *et al.*, 2016). It is clear, however, that considerable introgression occurs even in some rivers with estimated long-term proportions of escaped farmed salmon in the range 4%–10% (Fig. 4 in Karlsson *et al.*, 2016). This could be due to variable reproduction success of escaped farmed salmon in the river in question, but also to offspring of escaped farmed salmon straying from a neighbouring stream with higher influxes of farmed salmon (Jonsson and Jonsson, 2017).

Averages and incidence

The goal of the monitoring programme established in 1989 was to estimate the proportion of escaped farmed salmon in catches where data were easily available. About 100 000 anglers fish in Norwegian rivers during June, July, and August—angling before 1 June and after 31 August is allowed in only a few rivers. The occurrence of escaped farmed salmon vary considerably temporally and spatially even in the same river (Moe *et al.*, 2016) so that seasonal variation must be accounted for in the collection of fish scales from anglers along a river segment.

It was thought that sampling from the angler catch or wild-salmon broodstock collection after August but before spawning in October–December would give more accurate estimates of the proportion of escaped farmed salmon than sampling during the summer angling season, because escaped farmed salmon ascend rivers later in the season than wild salmon in most rivers and years (Lund *et al.*, 1991). Experience, however, shows this may not be the case. Sample sizes are smaller later in the season, the number of locations where salmon are captured is more limited, escaped farmed salmon take artificial bait more readily than wild salmon (Svenning *et al.*, 2015), and immature farmed escapes may occasionally make up a large proportion of autumn samples (Lund *et al.*, 1992). We excluded the samples from calculations in the cases where the aim of the fishery was to target only wild salmon or only escaped farmed salmon.

Management, industry, and the public often want to know what proportion of escaped farmed salmon in the wild are permissible. To answer this question with precision, the monitoring and sampling programme design must address several issues: (1) uncertainty in river arrival times for wild and escaped farmed salmon, (2) uncertainty in location in a river, (3) representative sampling, and (4) the efficiency of the methods used to discriminate between farmed and wild salmon. In the Material and Methods section, we showed that even if we consider only sampling uncertainty (binomial or hypergeometrical) to estimate the proportion of escaped farmed salmon in natural wild salmon populations, we are still left with considerable uncertainty about the true proportion. A precautionary approach would be to use the upper confidence limit as out limit for action, because of these uncertainties. An approach that strives not to limit farmed salmon production might be designed differently. We have chosen to focus on point estimates in our recommendations to the management and suggest limiting the proportion of escaped farmed salmon to the average proportion of returning adult salmon straying to other streams (4% in Stabell, 1984; 10% in Keefer and Caudill, 2014). This is in line with studies recommending low limits to straying of hatchery-produced Pacific salmon (Grant, 1997). Modelling studies show that 20% escaped farmed salmon would lead to rapid reductions in wild ancestry (Hindar *et al.*, 2006). In Norway, the suggestion that 4% and 10% incidence of escaped farmed salmon could be useful management action points was adopted by Taranger *et al.* (2015) who proposed that $<4\%$ incidence of escaped farmed salmon indicated a low risk of genetic change, 4%–10% incidence indicated moderate risk of genetic change, and $>10\%$ indicated high risk of genetic change to wild populations.

Early observations of the distributions of escaped farmed salmon showed that large proportions of escaped farmed salmon were found near intensive fish-farming areas (Gausen and Moen, 1991; see also Ford and Myers, 2008). The proportion of escapes in catches have decreased through the period, despite a large increase in farmed salmon production. There are large regional differences in proportion of escapes, though, where Hordaland stands out with the highest proportions during the whole period. Hansen (2006) suggested that high proportions in intensive fish-farming areas was a likely consequence of farmed salmon escaping at the smolt or early post-smolt stages tend to home to the coastal areas from which they escaped. Farmed salmon escaping at later life stages show no indication of homing behaviour and thus may disperse more widely (Hansen, 2006). In this article, we show that a quite large variation in proportion of escaped farmed salmon may exist among neighbouring rivers (Figure 5). This suggests that characteristics of rivers and their wild salmon populations modify local variation in proportion of escapes.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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References

Anon. 1999. Til laks åt alle kan ingen gjera? Om årsaker til nedgangen i de norske villaksbestandene og forslag til strategier for å bedre situasjonen. Norges offentlige utredninger, 1999–9: 1–297 (in Norwegian).

Billingsley, L. W. (Ed). 1981. Proceedings of the stock concept international symposium. Canadian Journal of Fisheries and Aquatic Sciences, 38: 1457–1921.

Bolstad, G. H., Hindar, K., Robertsen, G., Jonsson, B., Sægrov, H., Diserud, O. H., Fiske, P. *et al.* 2017. Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. Nature Ecology and Evolution, 1: 0124.

Clifford, S. L., McGinnity, P., and Ferguson, A. 1998a. Genetic changes in an Atlantic salmon (*Salmo salar* L.) population resulting from escaped juvenile farm fish. Journal of Fish Biology, 52: 118–127.

Clifford, S. L., McGinnity, P., and Ferguson, A. 1998b. Genetic changes in Atlantic salmon (*Salmo salar* L.) populations of northwest Irish rivers resulting from escapes of adult farm salmon. Canadian Journal of Fisheries and Aquatic Sciences, 55: 358–363.

Crozier, W. W. 1993. Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L.) in a Northern Irish river. Aquaculture, 113: 19–29.

Diserud, O., Fiske, P., and Hindar, K. 2010. Regional impact of escaped farm salmon on wild salmon populations in Norway. NINA Rapport, 622: 1–40 (in Norwegian, English summary).

Diserud, O., Fiske, P., and Hindar, K. 2013. Forslag til kategorisering av laksebestander som er påvirket av rømt oppdrettslaks – Oppdatering for perioden 1989–2012. NINA Rapport, 976: 1–24 (in Norwegian).

Diserud, O. H., Hindar, K., Karlsson, S., Glover, K., and Skaala, Ø. 2017. Genetisk påvirkning av rømt oppdrettslaks på ville laksebestander – status 2017. NINA Rapport, 1337: 1–55 (in Norwegian).

Erkinaro, J., Niemelä, E., Vähä, J.-P., Primmer, C. R., Brørs, S., and Hassinen, E. 2010. Distribution and biological characteristics of escaped farmed salmon in a major subarctic wild salmon river: implications for monitoring. Canadian Journal of Fisheries and Aquatic Sciences, 67: 130–142.

Erkinaro, J., Orell, P., Kylmäaho, M., Falkegård, M., Kuusela, J., Johansen, N., Haantie, J., and Länsman, M. 2018. Status of salmon stocks in the rivers Teno/Tana and Näätämöjoki/Neidenelva. ICES Working group on North Atlantic salmon, Working Document no 5. 15 pp.

Fiske, P., Aronsen, T., and Hindar, K. 2014. Overvåking av rømt oppdrettslaks i elver om høsten 2013. NINA Rapport, 1063: 1–44 (in Norwegian).

Fiske, P., Lund, R. A., and Hansen, L. P. 2005. Identifying fish farm escapees. *In* Stock Identification Methods; Applications in Fishery Science, pp. 659–680. Ed. by S. X. Cadrin, K. D. Friedland, and J. R. Waldman. Elsevier Academic Press, Amsterdam.

Fiske, P., Lund, R. A., and Hansen, L. P. 2006. 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. M., and Fløystad, L. 2001. Escapees of reared salmon in coastal and riverine fisheries in the period 1989–2000. NINA Oppdragsmelding, 704: 1–26 (in Norwegian, English Summary).

Fleming, I. A., Hindar, K., Mjølnerød, I. B., Jonsson, B., Balstad, T., and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London B: Biological Sciences, 267: 1517–1524.

Ford, J. S., and Myers, R. A. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. PLoS Biology, 6: e33.

Forseth, T., Barlaup, B., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A. *et al.* 2017. The major threats to Atlantic salmon in Norway. ICES Journal of Marine Science, 74: 1496–1513.

Gausen, D., and 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.

Glover, K. A. 2010. Forensic identification of fish farm escapees: the Norwegian experience. Aquaculture Environment Interactions, 1: 1–10.

Glover, K. A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., and Skaala, Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genetics, 14: 74.

Glover, K. A., Solberg, M. F., McGinnity, P., Hindar, K., Verspoor, E., Coulson, M. W., Hansen, M. M. *et al.* 2017. Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. Fish and Fisheries, 18: 890–927.

Glover, K. A., Urdal, K., Næsje, T. F., Skoglund, H., Florø-Larsen, B., Otterå, H., Fiske, P., Heino, M., Aronsen, T., Sægrov, H., Diserud, O., Barlaup, B., Hindar, K., Bakke, G., Solberg, I., Lo, H., Solberg, M. F., Karlsson, S., Skaala, Ø., Lamberg, A., Kanstad-Hanssen, Ø., Muladal, R. and Wennevik, V. 2019. Domesticated escapees on the run: The "second generation" monitoring program reports the numbers and proportion of farmed Atlantic salmon in >200 Norwegian rivers annually. ICES Journal of Marine Science, doi: 10.1093/icesjms/fsy207.

Grant W. S. (Ed.). 1997. Genetic effects of straying of non-native hatchery fish into natural populations: proceedings of the workshop. U.S. Department of Commerce, National Oceanic and Atmospheric Administration. Technical Memorandum, NMFS-NWFSC-30. 130 pp.

Hansen, L. P. 2006. Migration and survival of Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. ICES Journal of Marine Science, 63: 1211–1217.

Hansen, L. P., and Youngson, A. F. 2010. Dispersal of large farmed Atlantic salmon, *Salmo salar*, from simulated escapes at fish farms in Norway and Scotland. Fisheries Management and Ecology, 17: 28–32.

Hansen, L. P., Jacobsen, J. A., and 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.

Hesthagen, T., Larsen, B. M., and Fiske, P. 2011. Liming restores Atlantic salmon (*Salmo salar*) populations in acidified Norwegian rivers. Canadian Journal of Fisheries and Aquatic Sciences, 68: 224–231.

Hindar, K., Fleming, I. A., McGinnity, P., and Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon:

modelling from experimental results. ICES Journal of Marine Science, 63: 1234–1247.

Hutchings, J. A. 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. Aquaculture, 98: 119–132.

ICES. 2011. Report of the Workshop on Age Determination of Salmon (WKADS), 18–20 January 2011, Galway, Ireland. ICES CM 2011/ACOM: 44: 67 pp.

ICES. 2016. Report of the Workshop to Address the NASCO Request for Advice on Possible Effects of Salmonid Aquaculture on Wild Atlantic Salmon Populations in the North Atlantic (WKCULEF), 1–3 March 2016, Charlottenlund, Denmark. ICES CM 2016/ACOM: 42: 44 pp.

Jensen, Ø., Dempster, T., Thorstad, E. B., Uglem, I., and Fredheim, A. 2010. Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention. Aquaculture Environment Interactions, 1: 71–83.

Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L. P., Hindar, K., and Østborg, G. M. 2013. Escaped farmed Atlantic salmon grow, migrate and disperse throughout the Arctic Ocean like wild salmon. Aquaculture Environment Interactions, 3: 223–229.

Johnsen, B. O., and Jensen, A. J. 1991. The *Gyrodactylus* story in Norway. Aquaculture, 98: 289–302.

Jonsson, B., and Jonsson, N. 2017. Maternal inheritance influences homing precision and growth of hybrid offspring between wild and farmed Atlantic salmon. Aquaculture Environment Interactions, 9: 231–238.

Karlsson, S., Diserud, O. H., Fiske, P., and Hindar, K. 2016. Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. ICES Journal of Marine Science, 73: 2488–2498.

Karlsson, S., Moen, T., Lien, S., Glover, K. A., and Hindar, K. 2011. Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Molecular Ecology Resources, 11(Suppl. 1): 247–253.

Keefer, M. L., and Caudill, C. C. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries, 24: 333–368.

Lund, R. A. 1998. Escapes of reared salmon in marine homewater and in riverine fisheries in the period 1989–97. NINA Oppdragsmelding, 556: 1–25 (in Norwegian, English summary).

Lund, R. A., and 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., Økland, F., and Hansen, L. P. 1991. Farmed Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. Aquaculture, 98: 143–150.

Lund, R. A., Økland, F., and Hansen, L. P. 1992. Escapes of reared salmon in marine homewater and in riverine fisheries in 1991. NINA Oppdragsmelding, 143: 1–16 (in Norwegian, English summary).

Lura, H., and Sægrov, H. 1991. Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. Aquaculture, 98: 151–159.

Maitland, P. S. 1986. The potential impact of fish culture on wild stocks of Atlantic salmon in Scotland. *In* The Status of the Atlantic Salmon in Scotland. ITE Symposium No. 15, Huntingdon, U.K., pp. 73–78. Edited by D. Jenkins, and W. M. Shearer.

McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R. Ó., Maoiléidigh, N., Baker, N., Cotter, D. *et al.* 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 B: Biological Sciences, 270: 2443–2450.

Moe, K., Næsje, T. F., Haugen, T. O., Ulvan, E. M., Aronsen, T., Sandnes, T., and Thorstad, E. B. 2016. Area use and movement patterns of wild and escaped farmed Atlantic salmon before and during spawning in a large Norwegian river. Aquaculture Environment Interactions, 8: 77–88.

Ryman, N. (Ed.) 1981. Fish gene pools. Preservation of genetic resources in relation to wild fish stocks. Ecological Bulletins, 34: 1–111.

Sægrov, H., and Urdal, K. 2006. Rømt oppdrettslaks i sjø og elv; mengd og opphav. Rådgivende Biologer as, Rapport 947. 21 pp. (in Norwegian).

Sægrov, H., Hindar, K., Kålås, S., and 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.

Skaala, O., Dahle, G., Jorstad, K. E., and Naevdal, G. 1990. Interactions between natural and farmed fish populations: information from genetic markers. Journal of Fish Biology, 36: 449–460.

Skilbrei, O. T., Heino, M., and Svåsand, T. 2015. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. ICES Journal of Marine Science, 72: 670–685.

Stabell, O. B. 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. Biological Reviews, 59: 333–388.

Svenning, M.-A., Kanstad-Hanssen, Ø., Lamberg, A., Strand, R., Dempson, J. B., and Fauchald, P. 2015. Incidence and timing of escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers; inferred from video surveillance, fish trap monitoring and snorkelling. NINA Rapport, 1104: 1–53 (in Norwegian, English summary).

Svenning, M.-A., Lamberg, A., Dempson, B., Strand, R., Kanstad Hanssen, Ø., and Fauchald, P. 2017. Incidence and timing of wild and escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers inferred from video surveillance monitoring. Ecology of Freshwater Fish, 26: 360–370.

Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., Kvamme, B. O. *et al.* 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science, 72: 997–1021.

Thomas, F., Jamin, E., Wietzerbin, K., Guérin, R., Lees, M., Morvan, E., Billault, I. *et al.* 2008. Determination of origin of Atlantic salmon (*Salmo salar*): the use of multiprobe and multielement isotopic analyses in combination with fatty acid composition to assess wild or farmed origin. Journal of Agricultural and Food Chemistry, 56: 989–997.

Thorstad, E. B., Fleming, I. A., McGinnity, P., Soto, D., Wennevik, V., and Whoriskey, F. 2008. Incidence and impacts of escaped farmed Atlantic salmon Salmo salar in nature. Report from the Technical Working Group on Escapes of the Salmon Aquaculture Dialogue. NINA Special Report, 36, pp. 1–110.

Urdal, K. 2006. Analysar av skjellprøvar frå sportsfiske- og kilnenotfangstar i Sogn og Fjordane i 2005. Rådgivende Biologer as, Rapport 919. 50 pp. (in Norwegian).

Waples, R. S. 1991. Genetic interactions between hatchery and wild Salmonids - lessons from the Pacific-Northwest. Canadian Journal of Fisheries and Aquatic Sciences, 48: 124–133.

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