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Original Article

Domesticated escapees on the run: the second-generation monitoring programme reports the numbers and proportions of farmed Atlantic salmon in >200 Norwegian rivers annually

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Norway is the world's largest producer of farmed Atlantic salmon and is home to ~400 rivers containing wild salmon populations. Farmed escapees, a reoccurring challenge of all cage-based marine aquaculture, pose a threat to the genetic integrity, productivity, and evolutionary trajectories of wild populations. Escapees have been monitored in Norwegian rivers since 1989, and, a second-generation programme was established in 2014. The new programme includes data from summer angling, autumn angling, broodstock sampling, and snorkelling surveys in >200 rivers, and >25 000 scale samples are analysed annually. In 2014–2017, escapees were observed in two-thirds of rivers surveyed each year, and between 15 and 30 of the rivers had >10% recorded escapees annually. In the period 1989–2017, a reduction in the proportion of escapees in rivers was observed, despite a >6-fold increase in aquaculture production. This reflected improved escape prevention, and possibly changes in production methods that influence post-escape behaviour. On average, populations estimated to experience the greatest genetic introgression from farmed salmon up to 2014 also had the largest proportions of escapees in 2014–2017. Thus, populations already most affected are those at greatest risk of further impacts. These data feed into the annual risk-assessment of Norwegian aquaculture and form the basis for directing mitigation efforts.

Keywords: angling, aquaculture, domestication, environment, farming, genetic impact, scale-reading

Introduction

Aquaculture represents one of the fastest growing food production sectors and plays a major role in the global blue revolution. Among finfish, the aquaculture of Atlantic salmon (*Salmo salar* L., hereon referred to as salmon) represents the most economically significant global aquaculture product (Bostock *et al.*, 2010). Salmon aquaculture started in Norway in the late 1960s and thereafter established as a significant industry in several countries. Half a century later, the increase in world-wide production showed no signs of slowing down, exceeding 2.3 million tons in 2014, of which Norway contributed 1.2 million.

The expansion of salmon aquaculture has not occurred without impact on the environment. Farmed escapees (fish that are domesticated but for simplicity are hereon referred to as farmed), which interact ecologically (Jonsson and Jonsson, 2006) and genetically (Glover *et al.*, 2017) with wild conspecifics, represent one of the most persistent issues. Norway is the world's largest farmed salmon producing country and is home to ~400 rivers that support some of the world's largest wild salmon populations. Escape of farmed salmon is regarded as one of the two most critical issues influencing the environmental sustainability of Atlantic salmon aquaculture, in addition to sea lice infections (Taranger *et al.*, 2015; Forseth *et al.*, 2017). For example, genetic introgression is widespread in Norwegian salmon populations (Glover *et al.*, 2013; Karlsson *et al.*, 2016; Diserud *et al.*, 2017), and differences in age and size at maturation between wild and admixed individuals have been reported in native populations (Bolstad *et al.*, 2017). Internationally, farmed escapees and genetic interactions with wild conspecifics continues to be a long-standing topic of concern (Hindar *et al.*, 1991; Ferguson *et al.*, 2007; Glover *et al.*, 2017).

Globally, hundreds of thousands or millions of farmed salmon escape from cages into the sea each year (Glover *et al.*, 2017). Most escapees are never seen again, falling foul to predation (Whoriskey *et al.*, 2006), starvation (Hislop and Webb, 1992), parasitism (Vollset *et al.*, 2016), or other undocumented causes. However, some escapees survive and thereafter enter rivers, occasionally after migration to and from the Atlantic Ocean (Hansen and Jacobsen, 2003; Jensen *et al.*, 2013). Salmon may also escape from freshwater rearing installations directly into rivers where juvenile and smolt production is permitted in association with natural watercourses (Clifford *et al.*, 1998; Carr and Whoriskey, 2006; Gilbey *et al.*, 2018). Not all escapees are reported, despite legislation in many countries where aquaculture is practised. This is evidenced by legal cases in Norway that used DNA methods to trace escapees to their farms of origin (Glover *et al.*, 2008; Glover, 2010). The true number of fish escaping from Norwegian farms has been estimated to be 2–4 times higher than the official statistics in the period 2005–2011 (Skilbrei, Heino, *et al.*, 2015). Farmed escaped salmon have been reported in rivers in a variety of salmon producing countries, on the high seas, and in rivers outside farming regions (reviewed by Thorstad *et al.*, 2008; Glover *et al.*, 2017).

Escapees from sea cages display diverse behaviours (Hansen, 2006; Skilbrei, 2010a, b; Skilbrei, Heino, *et al.*, 2015). Nevertheless, a relationship between the intensity of local aquaculture production and the incidence/proportion of farmed escapes has been reported in Norwegian (Fiske *et al.*, 2006; Diserud *et al.*, this issue) and Canadian rivers (Keyser *et al.*, 2018). In Scotland, lower numbers of farmed escapees occur in rivers on the east coast, where there are no marine salmon farms, than on the west coast where farming occurs (Youngson *et al.*, 1997; Green *et al.*, 2012). However, in many regions where aquaculture is practised, a lack of systematic monitoring hinders the ability to investigate escapes in time and space.

In Norway, the proportion of farmed escaped salmon has been registered annually in a selection of rivers since 1989 (Fiske *et al.*, 2006; Diserud *et al.*, this issue). In 2014, additional public resources were allocated to establish a second-generation national monitoring programme with quantitative and qualitative improvements. Since 2014, five research institutes, together with an extensive collaborative network, have implemented the new monitoring programme that has reported the proportion of farmed escapees in ~200 rivers annually. This has resulted in annual reports to the management ministries, and these data have been used in the annual risk assessment of Norwegian aquaculture (Taranger *et al.*, 2015). Significantly, these data serve as the basis to choose rivers where active removal of farmed escapees is financed through a fish-farming fund to reduce the potential for genetic impacts on native populations (http://utfisking.no/).

This study had four primary objectives: (i) to present the design of the new Norwegian monitoring programme established in 2014, (ii) to present the spatial and temporal observations of farmed escapees in ~200 Norwegian rivers in the period 2014–2017, (iii) to investigate trends in the proportions of farmed escapees in Norwegian rivers in the period 1989–2017 using data from the current programme and the 1989–2013 monitoring programme (Fiske *et al.* 2006; Diserud *et al.*, this issue), (iv) to compare observations of escapees in Norwegian rivers in the period 2014–2017 with cumulative estimates of genetic introgression of farmed escapees that exist for 175 Norwegian rivers (Glover *et al.*, 2013; Karlsson *et al.*, 2016; Diserud *et al.*, 2017).

Design of the monitoring programme

Criteria for choice of rivers to monitor

The Norwegian coastline is ~2500 km long, extending from the Skagerrak coastline in the southeast to the Barents Sea in the northeast. The country has about 400 rivers with salmon populations (Forseth *et al.*, 2017). Salmon aquaculture is practised throughout most of the coastline to various degrees (https://kart.fiskeridir.no/). Criteria for selecting rivers to include in the monitoring programme included: (i) geographic coverage, (ii) existing time series—to ensure that as many rivers as possible, surveyed in the period 1989–2013, are included, (iii) existing infrastructure—to ensure that local contacts established in preceding years are included, which secures coordinated and efficient use of national resources, (iv) river status—to ensure that the majority of the National Salmon Rivers (rivers designated extra protection) is included, (v) river characteristics—to ensure that a range of river types are included in the programme.

Identification of escapees and sampling methods

Methods used to distinguish wild from farmed salmon have been discussed previously (Fiske *et al.*, 2005; Thorstad *et al.*, 2008). Here, we only present the methods used in the current programme: scale reading and visual identification.

Scale reading to estimate age and growth patterns of salmon was developed in the early 1900s (Dahl, 1910), and has been standardized internationally (ICES, 2012). Due to differences in feeding opportunities and seasonality, at least six characters may differ between the scale patterns of farmed and wild salmon: smolt size, smolt age, the transition from fresh to salt water, sea winter bands, summer checks, and number of replacement scales (Lund and Hansen, 1991; Fiske *et al.*, 2005). Salmon raised for supportive breeding and stocked into the wild will typically bear a "farmed signature" from the freshwater phase of their life (Lund and Hansen, 1991; Fiske *et al.*, 2005). This makes it potentially difficult to differentiate salmon deliberately released for stocking, and farmed salmon escaped as smolts. However, over the past years, farmed salmon have become on average larger when released into the sea cages, which reduces the potential challenge of misidentification. In addition, stocked salmon are often fin clipped before released, making them easier to be recognized.

Due to rearing in tanks and cages, farmed salmon display morphological differences from wild salmon (Fleming *et al.*, 1994), including fin erosion (Noble *et al.*, 2007) and increased numbers of spots (Jørgensen *et al.*, 2018). In addition, some farmed salmon display adhesions in the abdomen caused by vaccination side-effects (Lund *et al.*, 1997). The degree to which these morphological characteristics differentiate farmed and wild salmon depends on several factors, but especially on whether a fish escapes as a juvenile or an adult. Farmed salmon that have escaped early in their life-cycle and that have spent one or more years at sea are more difficult to visually identify than fish that have escaped later in their life cycle. Fatty acid profiles show that most escapees entering Norwegian rivers have escaped from farms in the same year that they entered freshwater (Skilbrei, Normann, *et al.*, 2015; Quintela *et al.*, 2016; Madhun *et al.*, 2017). Hence, based on morphological examination, some escapees may not be readily detectable to the untrained eye, or at all, for early escapees.

Estimates of proportions of farmed escapees in Norwegian rivers are primarily obtained from the following four sampling methods: summer angling surveys (verification by scale reading), autumn pre-spawning angling surveys (verification by scale reading), autumn pre-spawning broodstock collection for local supportive breeding programmes (verification by scale reading), and autumn pre-spawning snorkelling surveys (visual identification with some removal and subsequent verification by scale reading). In addition, data from the fish trap located in the River Etne, where farmed salmon are removed, are included (verification by scale reading).

In many rivers, anglers are requested to take scale samples of both wild and farmed salmon captured during the fishing season. Hundreds of rivers are sampled by anglers throughout the entire river for three summer months, therefore, this represents a cost-effective way to collect samples. Obtaining a random sample of the population from rod catches can be a challenge, however. For example, catch and release without sampling scales is becoming increasingly commonplace, potentially leading to sampling bias and overestimation of escapees. Suspected farmed escapees are not released back into the river and are thus sampled, whereas those believed to be wild salmon are released without sampling. Furthermore, farmed escaped salmon may enter rivers later than wild salmon (Gausen and Moen, 1991; Gudjonsson, 1991; Carr *et al.*, 1997; Erkinaro *et al.*, 2010), although exceptions are known (Svenning *et al.*, 2017). Therefore, this method may underestimate the proportion of escapees in situations where the escapees arrive later than the wild fish to the river.

Dedicated autumn pre-spawning angling surveys by fishing clubs are used to fish representatively in certain rivers after the official angling season has ended, up to ∼2 weeks prior to the initiation of spawning. All captured fish are sampled for scales, and fish suspected to be farmed escapees are removed. Wild fish are returned to the river once sampled. In some rivers, local hatcheries that practice supportive breeding often collect broodfish by angling in the early autumn. Where possible, broodfish collection programmes have been expanded to fish representatively to provide both broodfish for the local hatchery, and data for proportion of farmed escapees for the monitoring programme. Scale samples are taken from all broodfish to verify their origin (i.e. farm or wild) and genetic background (i.e. pure wild or domestication-admixed). Autumn fishing surveys, including broodfish sampling, have an advantage over summer angling surveys as they include farmed escapees that have potentially entered rivers late in the season. One of the disadvantages is that these autumn surveys require a larger effort to manage than summer angling surveys, and hence sample sizes are limited. Another disadvantage is that farmed escapees may display a higher catchability than wild salmon in this period of the year (Svenning *et al.*, 2015). Greater catchability may be due to their typically later entry to freshwater than wild salmon, and differences in maturation timing, both of which may influence catchability. This is indirectly supported by the fact that the likelihood of a wild salmon being captured by angling declines significantly just weeks after entering freshwater (Harvey *et al.*, 2017).

Autumn snorkelling surveys are conducted by trained personnel who snorkel parts of, or in most cases, the entire length of a river and count the number of wild and farmed salmon. Identifications of escapees are visual and are made according to Norwegian standards (NS 9456:2015). These surveys are also used to estimate population abundances in many rivers. One of this method's positive attributes is that it typically covers the entire river. This is of importance as farmed escapees may congregate in different areas of the river than wild fish (Moe *et al.*, 2016). Snorkelling also facilitates the removal of farmed escapees from the pre-spawning populations. After the survey has been conducted, the team may re-enter the river to remove farmed escapees by harpoon or nets. Snorkelling surveys require clear and low-water conditions to be able to make accurate counts and to distinguish between farmed escapees and wild fish however. Also, snorkelling surveys have unquantified error in the identification of farmed escapees (Svenning *et al.*, 2015; Anon., 2017). Scale-sample verification of the farmed salmon selectively removed from the river is routinely conducted, although farmed escapees that are potentially mis-classified as wild fish in the river remain unverified. The four sampling methods are hereon referred to as "Summer", "Autumn", "Snorkelling", and "Other".

Quality checking data and estimates of proportions

Data from each sampling method implemented in each river are assessed by the responsible institute according to the following criteria. Summer angling surveys: fraction of the angling catch that is sampled (higher is better), length of fishing season (longer is better), N-samples analysed (higher is better), frequency of catch and release (lower is better), other fishing regulations influencing representability of the sampled angling catch (less is better), and other local-specific conditions that are known to influence likelihood of representative sampling (expert subjective evaluation). Autumn angling surveys: N-samples analysed in relation to total summer angling catch in the river (higher is better), registered fishing effort (higher is better), N-samples analysed (higher is better), division of the fishing efforts in relation to river length (more dispersed fishing is better). Autumn broodfish sampling (same as for autumn angling surveys, but with two extra criteria): frequency or number of farmed salmon that were removed from the population and not sampled for one reason or the other (lower is better), and frequency of released of wild fish not used as broodfish and not sampled for one reason or the other (lower is better). Snorkelling surveys: visibility and observation conditions (greater is better), challenges linked to reliable identification of farmed escapees, such as deep dark pools, turbulent river sections, and high water discharge (less challenges is better), coverage across the entire river profile (full coverage of the cross-section is better), the relative length of the river, or relative proportion of the population that is surveyed (greater is better), and timing (closer to spawning is better).

The overall quality score for the data is summarized on a 1–4 scale, that is based on the partially subjective but expert opinions of the involved institutes (1 = very good, 2 = good, 3 = moderate, 4 = poor). Only sampling method and river combinations that achieve a quality score of 1–3 are used in the overall assessment of the proportion of farmed escaped salmon in that river. Data that are classified as poor (i.e. quality 4) are not used in the final evaluation of the proportion of farmed escapees in the river, but, are nevertheless used to produce statistics over the total number of escapees, and how many rivers in which escapees have been observed.

In most rivers surveyed, and for several reasons (e.g. some of these data are used for multiple purposes), more than one sampling method is used to estimate the proportion of farmed escapees in the river. However, averaging the estimates across the different methods would not be statistically justified and has not been done. This is because the methods have their prerequisites, strengths and weaknesses, and can therefore give different estimates. Nevertheless, these estimates can still be equally valuable as they measure the proportion of escapees at different times during the season.

Results are presented in three forms. First, the results for Summer, Autumn, and Snorkelling surveys in a river are presented; second, the estimate for the river is made using the incidence computation *sensu* Fiske *et al.* (2006), based on the Summer and Autumn surveys; third, a simplified system, based on all available data, is used to classify rivers with proportions clearly above and below 10%.

The incidence calculation was devised to compensate for the potential biases of the proportion estimates arising from summer angling surveys and autumn fishing surveys (Fiske *et al.*, 2006; Diserud *et al.*, 2010). It increases the proportion estimated from the summer angling surveys and decreases the proportion estimated from the autumn angling surveys. It also creates an average of these two estimates after respective direction adjustments for rivers where both methods are implemented (Diserud *et al.*, this issue).

The simplified 10% criteria method was designed to take into consideration all sources of data and to provide the regulatory authorities with a simplified estimate of farmed escapees to prioritize rivers for mitigation. To achieve this, the expert group considers all data for each river, together with any other relevant information, and makes a collective interpretation whether the incidence is low to moderate (<10%), moderate (not possible to conclude whether its > or <10%), or high (>10%). The results of the monitoring programme are presented in annual reports (https://www.hi.no/en/hi/publikasjoner).

Additional data and analyses

The primary focus of this study was to describe the monitoring programme and present the results for the period 2014–2017. However, we included other data to enable additional analyses. The first additional analysis compared the long-term trends in proportions of escapees in Norwegian rivers for 1989–2013 (Diserud *et al.*, this issue). Second, we investigated how domesticated salmon genetic introgression estimates (up to 2014) correlated with observed frequencies of escapees in the same rivers in the period 2014–2017. This was not to investigate cause and effect, but to investigate whether rivers displaying the greatest introgression of farmed escapees historically are still those exposed to greatest risk of further introgression. For this comparison we used genetic introgression data from Diserud *et al.* (2017).

Statistical analyses

All statistics were computed in R. Trend analyses were conducted with generalized linear mixed models using proportions of escaped salmon as a binomial response variable, year as a regression variable, and river as a random effect. Comparisons between the regions were analysed with similar models but treating year and region as fixed factors. The significance of the main effects was tested with likelihood ratio tests.

Results

Numbers of rivers surveyed and escapees recorded in 2014–2017

The number of rivers surveyed increased from 168 in 2014 to 241 in 2017 (Figure 1, Supplementary File S1). The total number of farmed escapees observed across sampling methods and rivers ranged from 1094 in year 2017 to 2000 in year 2014 (Figure 1), although it is important to note that this does not reflect the total number of escapees in these rivers. This typically gave a mean number of escapees observed per river of 4–12 (Figure 1), except for the sampling method “Other”, which included the upstream fish trap in the river Etneelva where >100 escaped salmon were captured in several years (Supplementary File S1) (Quintela *et al.*, 2016; Madhun *et al.*, 2017). Escapees were observed in approximately two-thirds of the surveyed rivers each year.

Proportions of escapees 2014–2017

The unweighted mean proportion of farmed escapees varied greatly among sampling methods, years and rivers (Figure 2, Table 1). Overall, proportions were highest for the autumn angling surveys, lowest for the autumn snorkelling surveys, and low to intermediate for the summer angling surveys. The largest three estimates were observed for the autumn angling surveys in the River Oselva in 2014 (86%), the River Salvassdraget in 2016 (75%), and the River Salangsvassdraget in 2014 (62%).

In general, the numbers (Figure 1) and proportions (Figure 2) of escapees declined in 2014–2017. This is qualitatively consistent with the official statistics from the Norwegian Directorate of

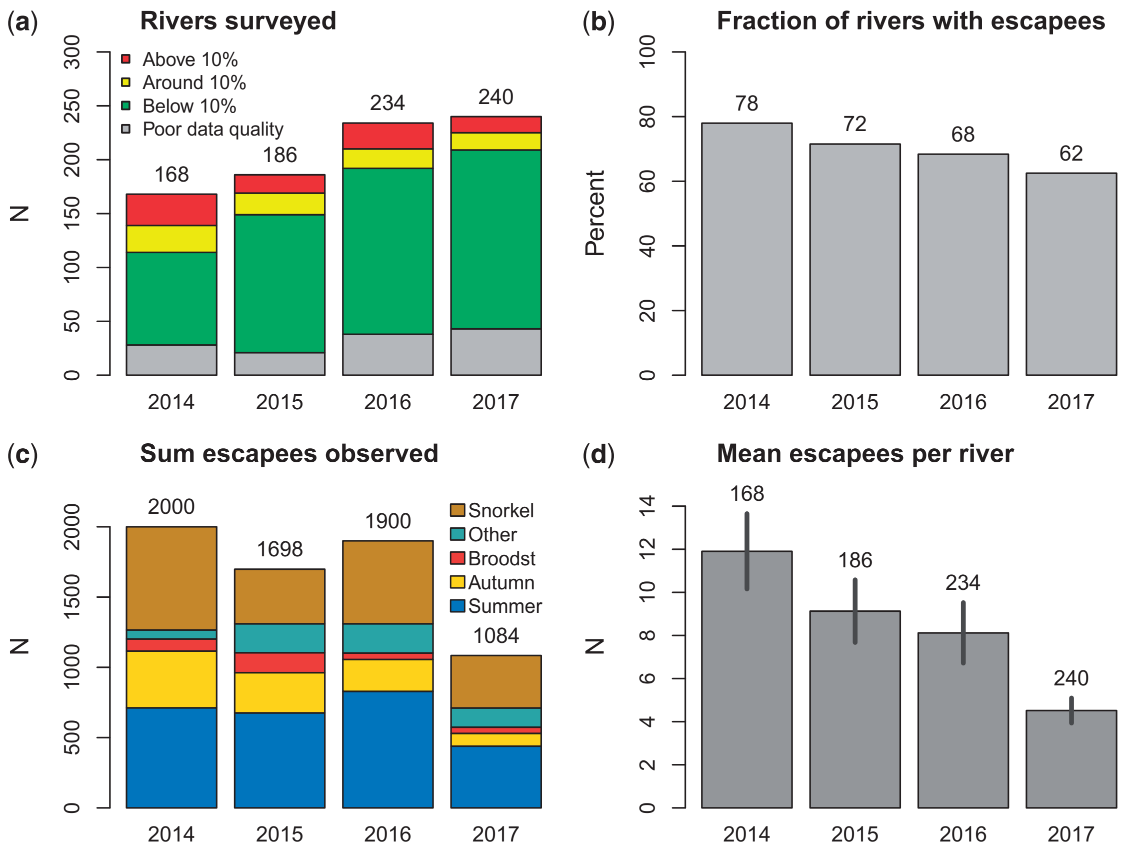

Figure 1. (a) Numbers of rivers surveyed (grey = not achieving high enough quality, therefore not used to estimate proportions of escapees, green = <10% escapees, yellow = >< 10% escapees, red = >10% escapees—these estimates are based on combining all data as described in methods), (b) fraction of rivers displaying ≥1 escapee (using data from all rivers), (c) total number of escapees observed by sampling method (see legend for category), (d) mean number of escapees observed per river (number of rivers surveyed given at top). It is important to note that numbers of escapees observed does not equate to numbers of escapees in the rivers.

Fisheries (www.fiskeridir.no), who reported 287 000, 170 000, 132 000, and 15 000 farmed escapees for the respective years. The number of rivers displaying >10% of farmed escapees varied annually in the combined data from all sampling methods: 30 of 140 (21%) surveyed rivers in 2014, 17 of 165 (10%) surveyed rivers in 2015, 24 of 196 (12%) surveyed rivers in 2016, and 15 of 198 (8%) surveyed rivers in 2017 (Figure 3).

Regional differences in proportions of escapees differed in all region by method combinations (Table 1, $p < 0.003$). We used the generally little-impacted county of Finnmark as a spatial reference and found significantly higher ($p < 0.05$) proportions of escapees in the summer surveys than in two other northern regions, Troms and Nordland, and in two western regions, Sogn og Fjordane and Hordaland. In the autumn surveys, only Troms had a significantly larger proportion of escapees compared to Finnmark, whereas SE Norway had a marginally significantly smaller proportion. In the snorkelling surveys, Hordaland and Troms had elevated proportions of escapees, whereas Rogaland had significantly smaller proportions. In all cases, differences between the years were highly significant ($p \ll 0.001$).

Trends in the proportions of escapees 1989–2017

The proportions of escapees in rivers showed an overall decline in both summer and autumn surveys (Figure 4), when calculated as raw means (yellow circles) and as binomially distributed predicted mean proportions of escapees in an "average" river (bold black curves). The decline is, however, much more marked for the autumn surveys, which showed very high proportions at the start of the time series. In summer surveys, an overall decline in the means is partly overshadowed by relatively large proportions observed in the middle of the time series, from mid-1990s to around 2010. The analyses showed that the declining trends were highly significant ($p < 0.001$) in all cases.

Historical genetic introgression vs. proportion of escapees 2014–2017

An important question is whether specific rivers consistently attract more farmed escapees than others. In general, modest to high correlations between the relative proportions of escapees observed within rivers in one year, and the following year, were observed in the period 2014–2017 (Figure 5). Introgression of farmed escapees in wild populations has been estimated for 175 Norwegian rivers up to 2014 (Glover *et al.*, 2013; Karlsson *et al.*, 2016; Diserud *et al.*, 2017). All but three rivers overlapped with the rivers surveyed in the present monitoring programme. There was a correlation between the point estimates of farmed salmon introgression up to 2014, and the observed mean proportions of escapees in the rivers in the following period 2014–2017 (Figure 5).

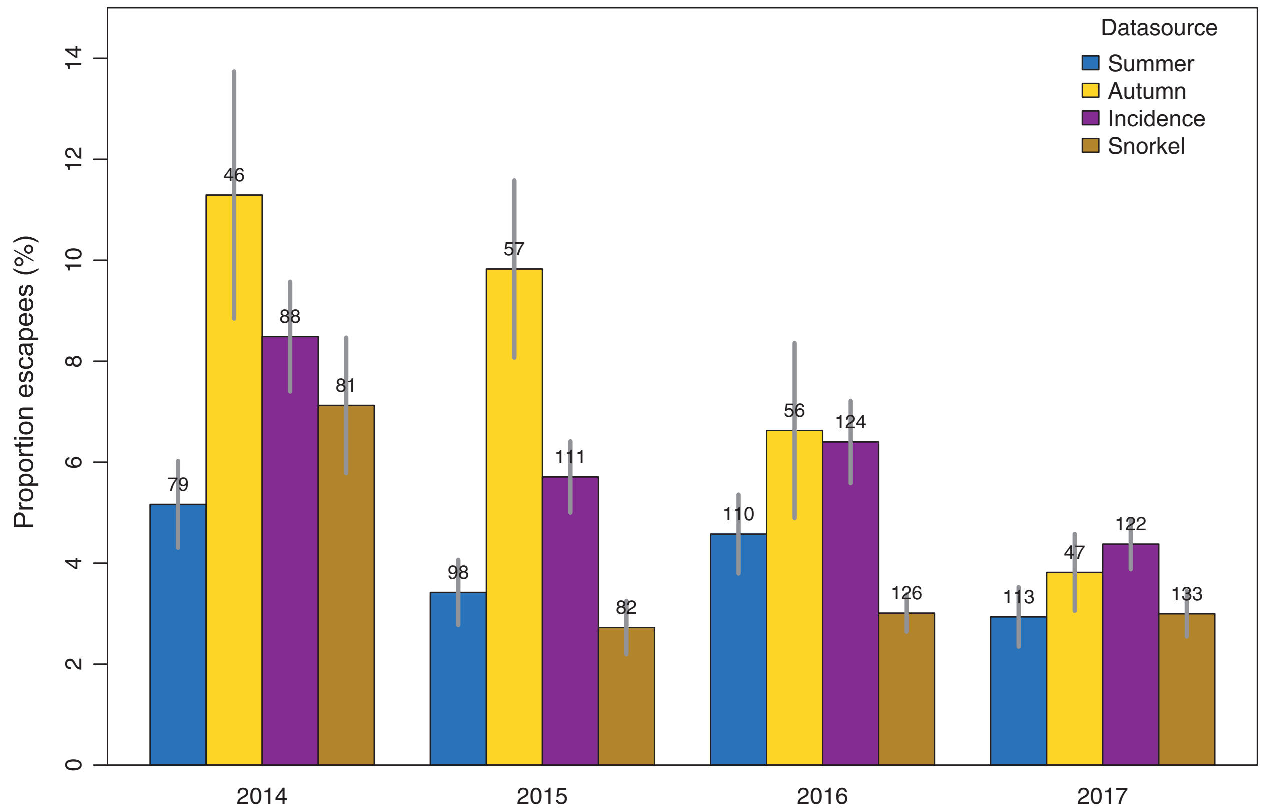

Figure 2. Mean proportions (%) of farmed escaped salmon observed across rivers by sampling method and year. Numbers above bars refer to number of rivers surveyed by each method. Note that some rivers are surveyed by more than one method.

Discussion

This monitoring programme, which started in 1989 (Diserud *et al.* this issue), and entered its second generation in 2014, provides estimates of farmed escaped Atlantic salmon in >200 rivers annually, and likely represents the most extensive programme to monitor the proportion of any domesticated or farmed animal in wild populations. Genetic interactions between farmed escapees and wild conspecifics represents a threat to the genetic integrity, productivity, and evolutionary trajectories of wild populations (Glover *et al.*, 2017), making this work of vital importance. The monitoring programme provides data to estimate the risk of further genetic introgression in Norwegian salmon populations (Taranger *et al.*, 2015), and information to assess management practices and to assess efforts by the farming industry and wild salmon management to reduce the numbers and proportions of farmed escapees over time. Finally, the programme provides authorities with the ability to channel resources into the most affected small- and medium-sized rivers for coordinated removal of escapees. We believe this programme could serve as a model to monitor farmed escaped salmon in other countries and to monitor farmed escapees of other commercially cultured fishes.

Spatial and temporal trends

In 1989–2017, the Norwegian salmon aquaculture production expanded from ~200 000 to >1 200 000 tonnes per year (>6-fold increase). While the reported annual numbers of escapees have varied (Figure 5), our analyses demonstrated a reduction in the proportion of farmed escaped salmon in Norwegian rivers with time. The proportion of farmed escaped salmon in a river is also influenced by the number of wild salmon returning from the sea (see below discussion). Furthermore, the increase in data volume in this second-generation programme means that interpretations of long-term trends in proportions should be made cautiously. Nevertheless, our analyses suggest an improvement in escape prevention and/or a reduction in the likelihood of farmed escapees entering rivers after they have escaped from commercial farms.

Improvements in the technical standards of aquaculture installations have contributed to the observed reduction in proportions of farmed escapees in Norwegian rivers (Jensen *et al.*, 2010). However, biological conditions may have also contributed to the decrease in proportions of escapees. The first condition is the increased use of autumn smolt production with time, rather than the use of traditional summer smolt production methods. As revealed by behavioural studies, post-smolts escaping from Norwegian fish farms outside the summer wild smolt migration window are less likely to display appropriate migratory patterns and therefore are less likely to survive to adulthood and enter a river (Skilbrei, 2010b). The second condition is linked to the increased use of controlled lighting in sea cages to delay maturation (Taranger *et al.*, 2010), which in turn is likely to reduce

Table 1. Regional and temporal differences in proportions of escaped farmed salmon by method.

Area	Type	2014	2015	2016	2017	All
Finnmark	Summer	2.7	1.6	2.3	1.6	2.1
	Autumn	7.7	2.5	2.9	3.8	4.3
	Snorkelling	(0.3)	2.5	4.1	2.3	3.0
Troms	Summer	9.5	3.8	11.5	2.4	7.1
	Autumn	27.7	17.5	16.9	10.3	18.2
	Snorkelling	6.1	7.0	5.8	4.1	5.2
Nordland	Summer	11.2	9.0	7.1	7.8	8.7
	Autumn	(0)	5.3	2.0	5.4	3.9
	Snorkelling	2.8	2.2	2.5	2.7	2.6
Trøndelag	Summer	2.1	3.2	3.5	1.5	2.6
	Autumn	12.6	10.2	20.2	4.5	12.5
	Snorkelling	0.5	0.7	0.6	1.0	0.7
Møre og Romsdal	Summer	2.3	0.6	2.1	2.5	1.9
	Autumn	4.5	22.1	5.3	1.3	9.3
	Snorkelling	0.0		0.6	3.5	1.7
Sogn og Fjordane	Summer	7.9	5.2	5.5	3.1	5.3
	Autumn	12.4	14.7	6.6	2.7	9.5
	Snorkelling	4.6	1.6	2.5	1.0	2.4
Hordaland	Summer	8.1	4.5	8.4	6.9	6.9
	Autumn	19.0	15.9	7.3	6.8	11.7
	Snorkelling	18.1	4.1	4.3	5.1	7.8
Rogaland	Summer	2.6	2.3	1.4	1.1	1.8
	Autumn	5.4	2.0	1.5	1.9	2.5
	Snorkelling	1.4	0.4	0.8	0.8	0.9
SE Norway	Summer	3.0	4.4	1.4	1.6	2.5
	Autumn	8.7	3.6	0.6	0.6	2.6
	Snorkelling					
All	Summer	5.2	3.4	4.6	2.8	3.9
	Autumn	11.5	9.8	6.6	3.8	7.9
	Snorkelling	7.1	2.7	3.0	3.0	3.7

The displayed value is simple arithmetic mean proportion of escaped salmon across rivers. Estimates based on just one river are in parentheses.

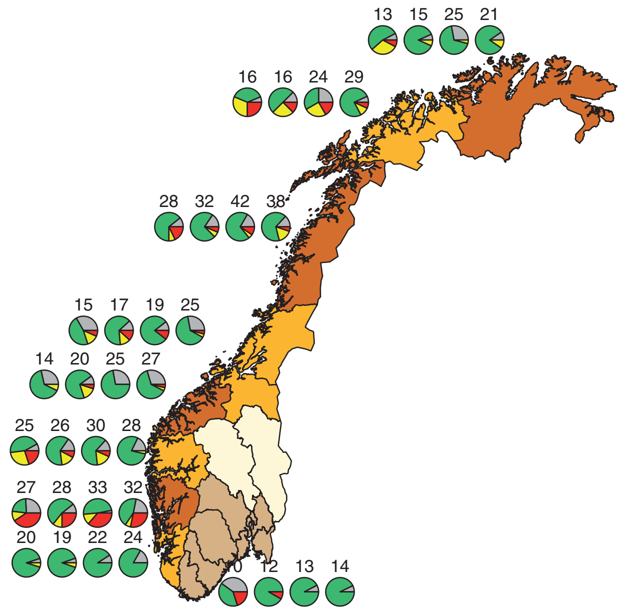

Figure 3. Pie-charts showing frequency of rivers displaying <10% (green), ±10% (yellow), and >10% (red) proportion of escapees from 2014 (left) to 2017 (right) for the different areas of Norway. Grey slices represent the rivers without sufficient data quality. Numbers above pie-charts represent the number of rivers contributing to the data. Background map colours are only for delineation of regions.

motivation of escapees to enter freshwater (or delay it). The third condition is linked to a possible decrease in the motivation of escapees to migrate to freshwater over time. Farmed Atlantic salmon have been subjected to domestication and directional selection ≥12 generations and display a wide range of genetic differences from wild salmon (Glover *et al.*, 2017). Although untested, domesticated may have altered farmed salmon's motivation or ability to migrate into rivers.

Significant differences in the proportions of farmed escapees in rivers were observed among regions of Norway (Figure 3, Table 1). Regional differences in the proportion of escapees in rivers have now been observed in several salmon-producing countries such as Norway (Fiske *et al.*, 2006; Diserud *et al.*, this issue), Scotland (Youngson *et al.*, 1997; Green *et al.*, 2012), and Canada (Keyser *et al.*, 2018). These patterns have been linked to differences in the intensity or volume of regional aquaculture production. In this study, we did not explicitly test the potential relationship between the level of regional aquaculture production and proportions of escapees in rivers, which was beyond the scope of the study. However, a region with very low aquaculture activity along the Jæren (south-Rogaland) coastline south and eastwards towards the border to Sweden had the lowest river-specific proportions of farmed escapees have been observed [Figure 3, Table 1 - areas Rogaland (part) and SE Norway].

From monitoring to mitigation of genetic impacts

Introgression of farmed escaped salmon into native populations has been documented in rivers in several countries (Glover *et al.*, 2017). Differences in life-history traits in genetically admixed individuals hatched in the wild have also been observed in Norwegian rivers (Bolstad *et al.*, 2017), as has a reduction in among-population genetic diversity (Skaala *et al.*, 2006; Glover *et al.*, 2012). In light of the magnitude of aquaculture and documentation of genetic interactions in Norway, the monitoring programme described here can serve as an important model for other countries and farmed species where escapees and interactions with wild conspecifics is emerging as an issue (Bekkevold *et al.*, 2006).

A statistically significant positive relationship between the proportions of escapees observed in native populations, and degree of farmed salmon introgression has been reported in Norway (Glover *et al.*, 2013; Heino *et al.*, 2015; Karlsson *et al.*, 2016) and Canada (Keyser *et al.*, 2018). Thus, the proportions of farmed escapees within rivers remain as the single best predictor of introgression even though other factors play a role. For example, the degree of sexual maturation in fish from various escape events, the numerical size of the native population (Heino *et al.*, 2015; Keyser *et al.*, 2018), migratory barriers hindering farmed escapes from reaching spawning grounds and thus interbreeding (Sylvester *et al.*, 2018), the strength of natural selection and possibly straying patterns among wild populations (Castellani *et al.*, 2018) all contribute to shaping the inter-population variation in introgression.

Our results showed that from 2014 to 2017, rivers experiencing relatively high proportions of escapees in 1 year tended to have

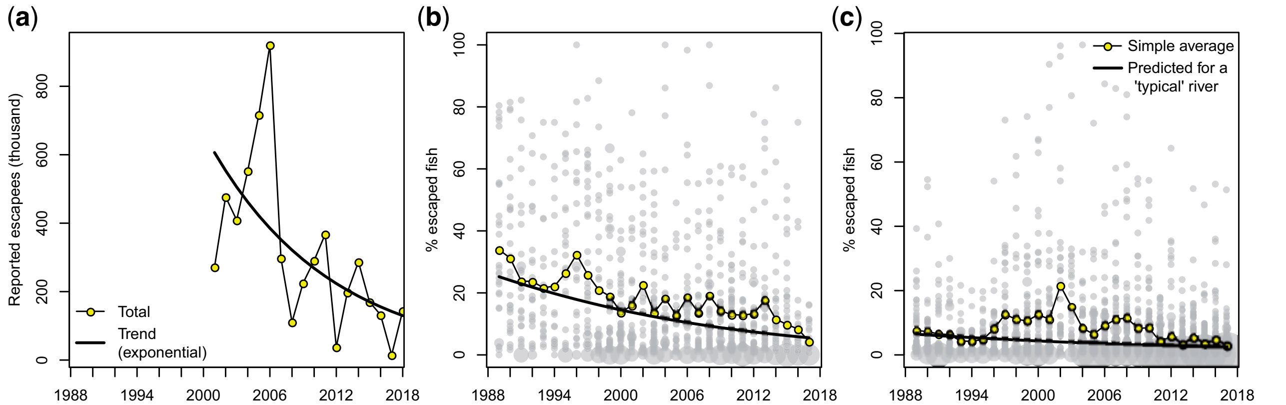

Figure 4. (a) The reported numbers of fish escaping from Norwegian farms in 2001–2018, (b) the proportion of farmed escaped salmon recorded in Norwegian rivers in the autumn surveys in 1989–2017, (c) the proportion of farmed escaped salmon recorded in Norwegian rivers in the summer surveys in 1989–2017. Escapee numbers are from the official statistics and represent the minimum estimates; data for 2017–2018 are preliminary (source: https://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk). Data from surveys are only included when at least 20 fish were recorded per year. Yellow symbols in b–c give arithmetic mean. Trend curves are based on Poisson (a) and logistic (b–c) regressions. The underlying data are shown by the grey circles (area proportional to number of rivers).

relatively high proportions in following years, and *vice versa* (Figure 5). This relationship suggests that the potential for introgression of farmed salmon in these populations was relatively consistent in this period. Our analyses also revealed a relationship between historical estimates of introgression of farmed escapees in these populations based on the analysis of molecular genetic markers (Glover *et al.*, 2013; Karlsson *et al.*, 2016; Diserud *et al.*, 2017), and the proportions of escapees in 2014–2017 (Figure 5). These observations collectively demonstrate that wild populations already subject to the greatest degree of introgression from farmed salmon in the past (and recent past), are those that are still at highest risk of further introgression. In addition to the location of the river in relation to intensity of regional or local aquaculture production, there may be characteristics of certain rivers which influence their "attractiveness" to farmed escapees which lack imprinting to a specific river and therefore use other criteria to choose a river to enter. Elucidating these factors may provide new insights into the post-escape migratory behaviours of farmed escapees. Finally, it is important to point out that the above discussed patterns do not mean that previously unaffected or relatively unaffected wild populations may not be subject to large numbers of escapees and introgression of escapees in the future. Escape events are local, and even large escapes can occur in areas where previously there have been few escapes.

Several factors can reduce the likelihood of further introgression of domesticated salmon in native populations, including reductions in the number of fish escaping from farms, reductions in the number of escapees in rivers through selective removal and the production of sterile fish to reduce mating with wild fish. Although especially challenging in large rivers (Næsje *et al.*, 2013), removal of farmed escapees prior to spawning has been conducted using a variety of methods by networks of local fishing organizations, private companies, and river owner associations in close connection with local regulatory authorities. In 2016, the Norwegian government established an aquaculture-financed fund to remove farmed salmon escapees from wild populations to reduce the probability of genetic impacts; OURO (http://utfisking.no/). OURO uses data from the programme presented here to identify the rivers most in need of mitigation. This is based on the principle that all other factors being equal, a high proportion of escapees is associated with a high probability of genetic introgression (Glover *et al.*, 2013; Heino *et al.*, 2015; Karlsson *et al.*, 2016; Keyser *et al.*, 2018).

Challenges and lessons learned

Representative sampling is vital to investigate spatial and temporal patterns in ecosystems and populations. The methods used in the monitoring programme for farmed escapees in Norway all gave different results (Figure 2). This was due to how representatively they sampled farmed and wild fish, and to the temporal and spatial differences in sampling. Hence, results from these methods are not directly comparable. Beyond the importance and challenge of representative sampling, the true proportion of escapees in a river is controlled by two factors: the number of escapees and the number of wild salmon.

The proportion of escapees provides the most relevant statistic to estimate the potential for introgression of farmed salmon in a wild population (Glover *et al.*, 2013; Heino *et al.*, 2015; Karlsson *et al.*, 2016). Thus, the estimated proportion of farmed salmon in a population is important to both assess the risk of further genetic introgression (Taranger *et al.*, 2015; Forseth *et al.*, 2017), and to direct mitigation efforts. However, the number of wild salmon returning to rivers varies over time (Chaput, 2012). Therefore, the number of escapees observed in rivers, in addition to the proportions, is required by the regulatory authorities to evaluate trends in the numbers of fish escaping from farms and their survival. Nevertheless, reporting the observed number of escapees in Norwegian rivers also includes potential sources of error, including differences between sampling methods and variation in sampling efforts in time and space. Given the extent of the monitoring programme, it is likely that these challenges will have to be accepted as sources of "noise" in the data. However, whole-river fish traps, for example the system installed in the River Etneelva, provide the ability to count and sample all wild and farmed salmon entering the system to provide accurate estimates (Quintela *et al.*, 2016; Madhun *et al.*, 2017).

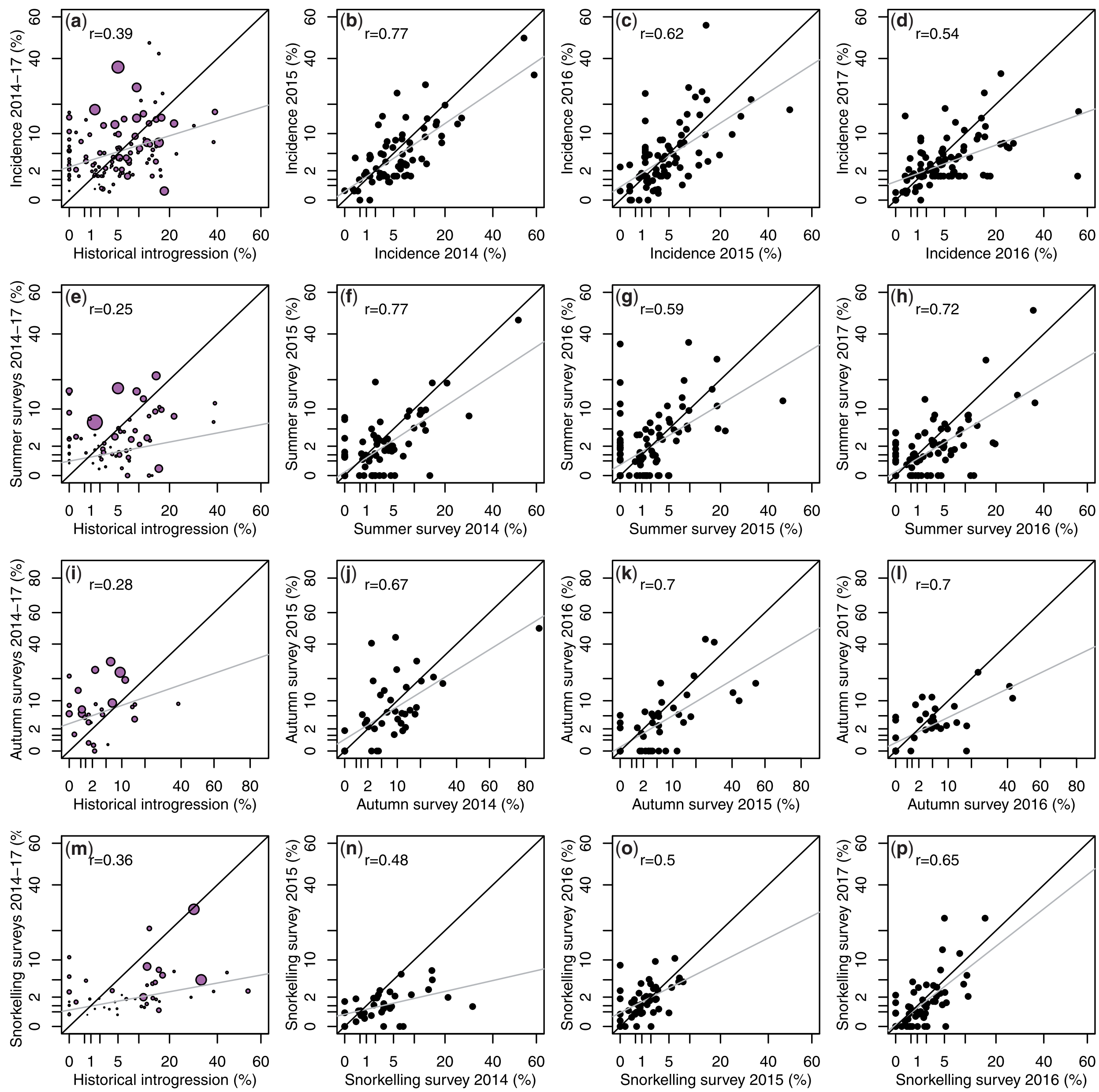

Figure 5. Consistency over time for proportions and three different data sources (rows). The left column compares historical genetic introgression (Glover *et al.*, 2013; Karlsson *et al.*, 2016; Diserud *et al.*, 2017) with mean proportion of escaped salmon over the period 2014–2017 (mean calculated for angular-transformed values). The size (area) of the plotting symbol is proportional to the value in the last year (2017). There is a generally positive relationship between historical introgression and proportion of escaped salmon in 2014–2017. The other panels show consistency across years within each type of data. Thus, rivers with high estimates in one year tend to have high estimates also the next year, but with an overall tendency towards somewhat lower values.

Supplementary data

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

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