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The future looks like the past: Introgression of domesticated Atlantic salmon escapees in a risk assessment framework

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Abstract

Escapes of domesticated fish from aquaculture, followed by interbreeding with wild conspecifics, represent a threat to the genetic integrity and evolutionary trajectory of natural populations. Approximately fifty years of Atlantic salmon production has left an unprecedented legacy of widespread introgression of domesticated escapees in wild Norwegian populations. A major question, however, is whether current aquaculture practice will lead to additional introgression in the near future. As part of the updated Norwegian risk assessment of fish farming, we conducted a risk assessment for *further introgression of domesticated escapees in wild populations* in Norway. Extensive data of reported numbers of escapees, observed proportions of escapees in rivers, removal of escapees pre-spawning, and the resilience of wild populations through demographic and genetic status informed the risk assessment. The analysis revealed that rivers in 10 of the 13 aquaculture production zones covering Norway display a moderate or high risk of further introgression of domesticated escapees. This comes in addition to widespread introgression that is already documented. We therefore conclude that so long as aquaculture production continues at its present level and form, there is a moderate-to-high risk of further introgression of domesticated salmon in many native populations throughout much of Norway.

KEYWORDS

admixture, aquaculture, environmental impact, environmental sustainability, genetic interactions, risk assessment

1 | INTRODUCTION

Aquaculture represents one of the most rapidly expanding food production sectors, and hundreds of fin-fish species are currently being cultured around the globe. Among these, Atlantic salmon (*Salmo salar*, Salmonidae) represents the most economically significant (Bostock et al., 2010), with a production that has continually increased in volume and value since the pioneering days of the industry in the early 1970s. Today, Atlantic salmon aquaculture, that is primarily based on juvenile production in freshwater and rearing to market size in sea cages, is practised in multiple countries in the

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Atlantic and Pacific oceans. Global production reached ~2.6 million tons in 2019, with Norway, Chile and Scotland representing the three main producing countries.

Aquaculture may alleviate overexploitation of biological resources by reducing the requirement for traditional harvest in the wild (Teletchea & Fontaine, 2014). This potential benefit is significant given that exploitation of living resources has become increasingly unsustainable (Hutchings, 2000; Myers & Worm, 2003). Nevertheless, aquaculture can itself elicit challenges for wild conspecifics (Ford & Myers, 2008), as well as the ecosystems and environments in which it is conducted (Buschmann et al., 2006). These challenges to environmentally sustainable aquaculture are diverse, and for salmon aquaculture they range from benthic and organic pollution (Kutti, Ervik, & Hoisaeter, 2008), parasites that infect local wild populations (Torrissen et al., 2013; Vollset et al., 2016), access to feed resources (Naylor et al., 2000; Torrissen et al., 2011), and domesticated escapees that display both ecological (Jonsson & Jonsson, 2006) and genetic interactions with domesticated conspecifics (Glover et al., 2017).

One of the factors for successful aquaculture, if not a prerequisite, is the partial or complete domestication of the species to increase its productivity in the human-controlled environment (Teletchea & Fontaine, 2014). Domestication of Atlantic salmon was initiated in Norway in the early 1970s (Gjedrem, 2010) and has now approached 15 generations or more for several strains. As a consequence, domesticated salmon now display a wide range of genetic differences to wild salmon (Glover et al., 2017). Domesticated salmon often escape into the wild, and as a result, escapees have been observed in rivers supporting native populations of salmon in multiple countries (Diserud, Fiske, et al., 2019; Gausen & Moen, 1991; Glover et al., 2019; Morris et al., 2008; Walker, Beveridge, Crozier, Ó Maoiléidigh, & Milner, 2006). Introgression has been documented in many populations (Glover et al., 2013; Karlsson, Diserud, Fiske, & Hindar, 2016; Sylvester et al., 2018), and differences in life-history traits between wild and feral or admixed salmon hatched in the wild have been observed (Bolstad et al., 2017). Results from modelling have also indicated that where introgression is high enough, life-history and demographic changes are expected in recipient wild populations (Castellani et al., 2018). In Norway, which is both the world's largest farmed salmon producer and simultaneously home to >400 rivers supporting wild populations, genetic interactions between domesticated escapees and wild conspecifics have been outlined as the most important contemporary challenge to wild salmon populations (Forseth et al., 2017). This is also regarded as an important challenge for other anadromous or marine fish that are being subject to aquaculture and domestication (Bekkevold, Hansen, & Nielsen, 2006; Waples, Hindar, Karlsson, & Hard, 2016).

Long-term and widespread escapes from aquaculture have already led to extensive introgression of domesticated salmon in wild populations in Norway (Glover et al., 2012, 2013; Karlsson et al., 2016). Therefore, further impact from escapees needs to be minimized and mitigation efforts on several levels are required. In order to help achieve this, a proper understanding of the key factors or events influencing genetic changes in wild populations is required. An annual risk assessment of diverse environmental problems arising from salmonid aquaculture has been conducted in Norway since 2011 (Taranger et al., 2015). This has been used by the Norwegian government to advise further development of the industry. Specifically for the challenge of escapees, the assessment of risk for genetic changes to wild populations has been based on the proportion of domesticated escapees observed on the spawning grounds as reported by the national monitoring programme for >200 rivers annually (Glover et al., 2019). In the Norwegian monitoring programme, a system was implemented whereby >10% escapees in a river were taken as a high risk of genetic changes in that population and <10% escapees were taken as a low-to-moderate risk. These values are a simplification of the system whereby 0–4, 4–10 and >10% escapees on the spawning grounds were suggested as representing low, moderate and high probability for genetic changes based upon all available knowledge (Taranger et al., 2012). In addition to the monitoring programme itself, data from the national monitoring programme have been used in a government-legislated aquaculture programme to organize targeted efforts to remove farmed escapees from rivers pre-spawning in order to mitigate potential genetic interactions.

In 2019, a new approach to the risk assessment of Norwegian aquaculture was established (Grefsrud et al., 2019). Specifically for the challenge of escapees and genetic interactions, it was designed to assess the risk of introgression of domesticated escapees in wild populations in the future. However, as many wild populations in Norway are already introgressed with domesticated escapees (Glover et al., 2013; Karlsson et al., 2016), the assessment of risk of introgression was defined as the assessment of risk of *further introgression* of domesticated escapees in wild populations. Here, we present and analyse the main factors influencing the risk of further introgression including the results of the risk assessment.

2 | METHODOLOGICAL APPROACH

2.1 | Design of the Norwegian risk assessment

We are currently developing a new approach to methodology for use in risk assessment of environmental impact of aquaculture (Andersen, unpublished). Here, we present an outline of the methodology and a first approach of its use through the Norwegian risk assessment of fish farming that was updated in 2019 and covered a set of environmental consequences and associated uncertainties hereunder *further introgression of domesticated escapees in wild populations* (Grefsrud et al., 2019). The main purpose was to create an understanding of risk among decision-makers in the public administration as a basis for governance in line with Norwegian and European sustainability objectives. Risk is defined in accordance with the Society of Risk Analysis Glossary (SRA, 2018) as *the consequences of an activity and associated uncertainties* where any deviation from a predefined *desired status* is considered a consequence. According to SRA, 2018, we let the triplet (C', U and K) describe risk, where C' denotes the specific consequences of commercial aquaculture included in the risk assessment, U denotes uncertainties related to C', and K is the knowledge that forms the basis for describing C' and U. The uncertainties U are related to the scope and severity of the consequences C' and how likely it is that they may happen. All available knowledge forms the basis for assessing C' and U, that is observations, measurements, modelling and scientific papers and reports. The strength of the background knowledge K is evaluated and communicated as an important part of the risk assessment. According to Aven (2014), strong knowledge about C' and U inspires confidence in the result of the risk assessment, while weak knowledge carry little weight, may conceal critical risk elements and give rise to surprises.

In the Norwegian risk assessment, Bayesian network structures (Jensen & Nielsen, 2009) were used as a tool for visualizing risk in order to support arguments about risk and strengthen risk understanding. The graphical structures consist of nodes and arrows illustrating cause–consequences, individual factors' degree of impact and strength of background knowledge. The nodes describe factors influencing the risk of *further introgression of domesticated escapees* on different levels. A reference level, *desired status*, is defined for each influencing factor (node). *Desired status* could be anchored in policy documents at an overall level in the hierarchical cause–consequence structures (Anon., 2018; Taranger et al., 2012). At a more detailed hierarchical level, *desired status* can emerge from unified scientific statements and/or the authors expertise. The degree of deviation from the *desired status* is categorized as low (green), moderate (yellow) and high (red) inside the nodes, while the strength of knowledge is expressed as high (green border), moderate (orange border) and low (red border) for each node.

Aquaculture is conducted throughout most of Norway's extensive coastline. Recently, the government divided the country into 13 production zones (PZ) spanning from the south-east to the north-east (Figure 1). These zones were determined to address sustainability and aquaculture production with respect to the challenge of salmon lice (*Lepeophtheirus salmonis*) infestations. They were geographically determined using dispersal models and oceanic current knowledge. In order to align with the implemented zoning system, the current risk assessment for further introgression of domesticated escapees was based on these 13 zones. Limitations in using these zones are addressed in the discussion.

There is a chain of key events and underlying factors starting at the fish farm that lead up to genetic changes in wild salmon populations (Figure 2). Based upon available knowledge, we have chosen five main categories: (a) the extent of domesticated salmon escaping from sea cages into the wild*, (b) to what degree domesticated escapees enter freshwater post-escape*, (c) whether domesticated escapees enter a specific river post-escape*, (d) to what degree domesticated escapees successfully spawn in native populations and their offspring complete their life cycle in the wild, and (e) the degree to which the population's evolutionary trajectory and long-term status is modified as a result of introgression of domesticated escapees. A further explanation of many of these key events and factors, and their connections to each other in the chain, is provided in File S1. Extensive background information on this topic, which also underpins the rationale for this, is available from an extensive review (Glover et al., 2017).

> *Salmon can and do escape from freshwater rearing facilities directly into rivers containing wild populations (Carr & Whoriskey, 2006; Clifford, McGinnity, & Ferguson, 1998; Gilbey et al., 2018), and thus interact directly with wild conspecifics without having to migrate back to freshwater. This specific form of escape has not been taken into consideration here because it represents a minor challenge in Norway due to the fact that juvenile and smolt production is rarely performed in systems linked to anadromous rivers as is the case in other regions of the world such as Scotland and Canada.

Not all of the underlying factors involved in the chain of events leading up to introgression of domesticated salmon in wild populations will play a major role (Figure 2). Furthermore, data do not exist for many of these factors, and some aggregate and/or are highly

FIGURE 1 Map showing the 13 aquaculture production zones covering Norway. Zones are numbered sequentially starting with 1 in the south-east to 13 in the north-east [Colour figure can be viewed at wileyonlinelibrary.com]

interlinked with each other. Therefore, in the present Norwegian risk assessment, a set of five key influencing factors were chosen (Figure 3). All of these factors are both regarded as having a major influence on the extent of genetic interactions between domesticated escapees and wild populations, and, at the same time, have extensive available data in Norway. It is also important to note that these five factors have not been directly extrapolated from the chain of events but are closely linked to them. For each production zone, the five main factors include reported numbers of escapees, observed proportions of escapees in rivers, targeted removal of escapees in rivers pre-spawning, demographic status of the wild population and documented historical introgression from domesticated escapees. Each of these factors is considered in the Bayesian network in the direction from bottom to top, cumulating in a final assessment of risk of further introgression of domesticated salmon in each of the PZs (Figure 3). Each of these influencing factors, their underlying data and how they link together are presented in detail below.

2.2 | Description of the five key factors chosen to assess the risk of further introgression of domesticated escapees

2.2.1 | Domesticated escapees on the spawning grounds

The extent of gene flow from domesticated salmon in wild populations is closely linked with the numbers and proportions of domesticated escapees in the spawning population (Glover et al., 2013; Heino, Svåsand, Wennevik, & Glover, 2015; Karlsson et al., 2016). Therefore, the numbers and proportions of domesticated salmon on the spawning grounds are possibly the most important factors in the risk assessment. The proportion of domesticated escapes on the spawning grounds is directly and indirectly a consequence of the state of three underlying factors (Figure 3). Of these underlying factors, the proportion of domesticated escapees observed in the river, as measured by the Norwegian monitoring programme each year (Diserud, Fiske, et al., 2019; Glover et al., 2019), and the numbers of escapees removed from the rivers prior to spawning, represent the primary drivers. Therefore, these are given greatest weight when determining deviation from *desired status* in each PZ. However, the numbers of fish escaping from fish farms in the region are also subjectively used as supplementary information. The strength of knowledge for this factor was determined for each PZ based on the combined strength of knowledge of the underlying factors.

> The desired status is few or no domesticated escapees on the spawning grounds of rivers in the PZ.

Escapees

Norwegian fish farms are legally obliged to report all escapees to the Norwegian Directorate of Fisheries who are both responsible for and have a periodically updated overview of escapees available online https://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk. However, the official statistics of escapees represent a minimum estimate as evidenced by results from simulated escape

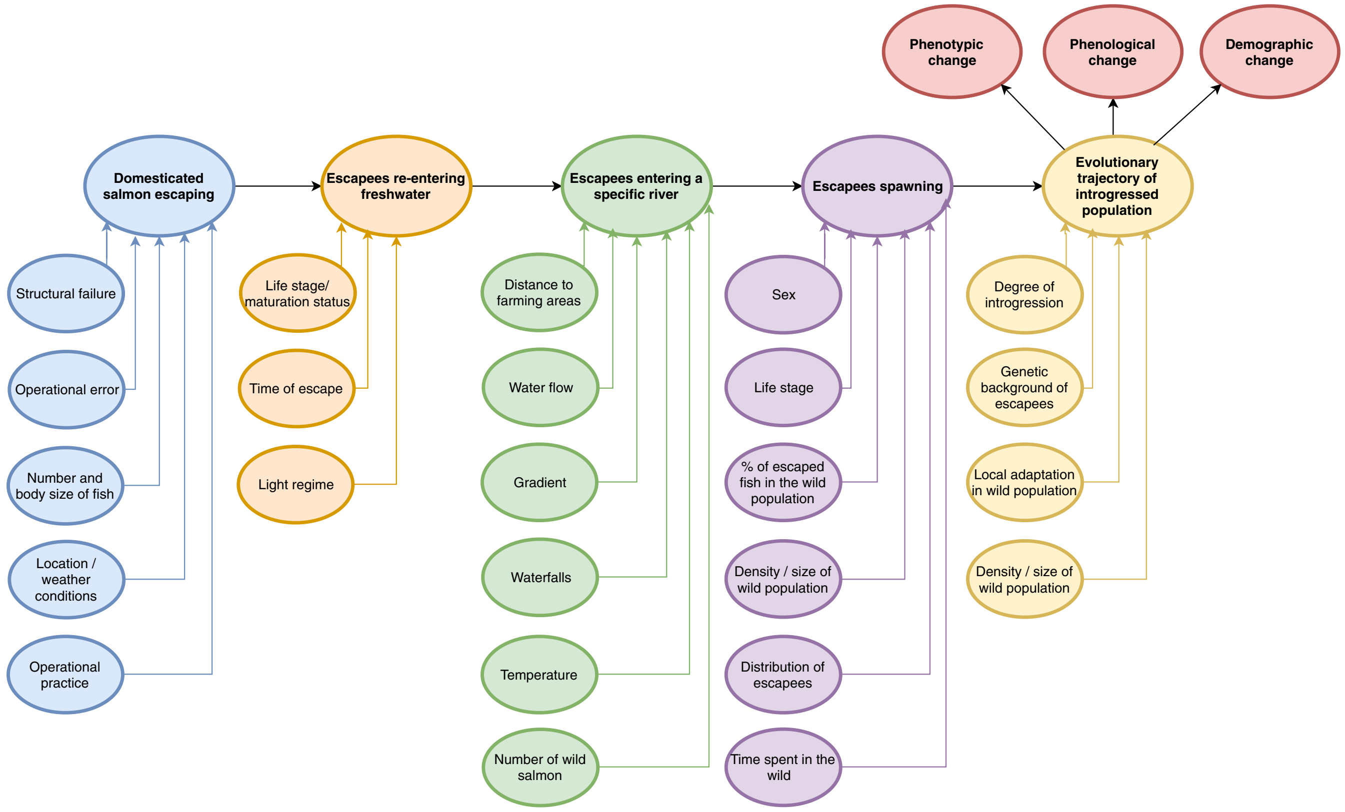
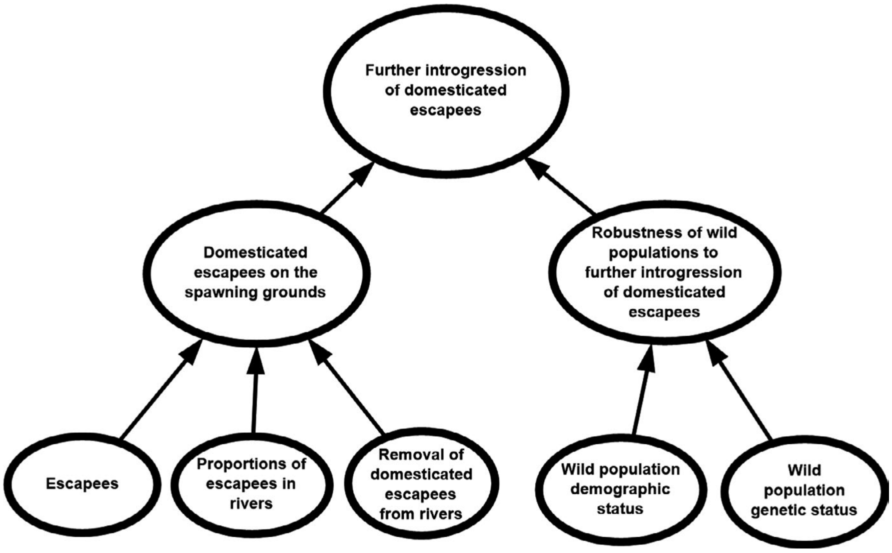


FIGURE 2 Key events and factors involved in the chain of events from escape of domesticated salmon into the wild, to the evolutionary trajectory of populations following introgression. Colours for illustrative purposes only. See File S1 for a description of the underlying factors and processes. [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Design of the Norwegian risk assessment for further introgression of domesticated escapees in Atlantic salmon populations. Arrows dictate what factors flow into and influence aggregating factors above. Each node contains extensive data that are evaluated according to threshold values or expert evaluation as detailed in the methods. Figure is translated from Norwegian (Grefsrud et al., 2019)



studies (Skilbrei, Heino, & Svåsand, 2015) and the fact that DNA methods to identify the farm of origin for unreported escapees have been implemented by the authorities in Norway for more than a decade (Glover, 2010; Glover, Skilbrei, & Skaala, 2008). Domesticated escapees can travel large distances (Hansen, 2006; Hansen & Jacobsen, 2003; Hansen, Reddin, & Lund, 1997). However, other factors being equal, there is a higher likelihood of escapees entering a river closer to the site of escape (Skilbrei, 2010a). Therefore, the official escape statistics were aggregated for the period 2014–2018 to identify the degree of deviation from the *desired status* in each PZ (Table S1). In that period, a total of 730 179 domesticated escapees were reported. PZs with an annual average of 0–999, 1,000–9,999 and >10,000 reported escapees were categorized as having low, moderate and high deviation from the *desired status*. This was based on a subjective determination of these thresholds, as a way of differentiating between the PZs. Strength of knowledge for this factor, for all PZs, was given moderate status as the correct number of escapees is not known due to underreporting.

> The desired status is few or no escapes of domesticated fish in the PZ.

Proportions of escapees in rivers

Each year, the proportions of domesticated escapees is reported for >200 Norwegian rivers in the national monitoring programme (Glover et al., 2019). The programme utilizes several survey methods, which measure slightly different things (i.e. observations during autumn diving surveys versus proportion catch during summer angling versus autumn organized fishing) and thus give slightly different proportions. Therefore, an expert evaluation of all available data has been performed in the monitoring programme itself, and resulted in a simplified system whereby all available data from the period 2014–2017 (Glover et al., 2019) are used to categorize each river in each year as having low, moderate or high proportions of escapees in them for each year they are surveyed (Table S2).

In the present risk assessment, PZs were categorized as having low, moderate or high deviation from the *desired status* in the following manner. First, results from the simplified system to categorize each river by the monitoring programme for escapees (Glover et al., 2019) were aggregated for each PZ over the four years. For example, if ten rivers were surveyed annually within a PZ, this would result in 40 rivers by year estimates. Then, we implemented the following set of guidelines to categorize each PZ. Low deviation from the desired status: At least 90% of the river by year estimates within the PZ must have a low proportion of escapees as defined by the monitoring programme, and none of the river by year estimates within the PZ display a high proportion of escapees. High deviation from the desired status: Over 10% of the proportion of river by year estimates within the PZ display a high proportion of escapees as defined by the monitoring programme, or less than 50% of the river by year estimates in the PZ display a low proportion of escapees as defined by the monitoring programme. Moderate deviation from the desired status is defined as any combination not falling into the two categories defined above.

The above rules were used as a guideline, and in borderline cases, an expert evaluation was used to modify the classification based on all available knowledge. The strength of knowledge for this factor was qualitatively based on the proportion of rivers within the PZ that are included in the monitoring programme.

> The desired status is few or no domesticated escapees being observed in rivers in the PZ.

Removal of domesticated escapees from rivers

Domesticated escapees are removed from Norwegian rivers through several processes including capture during the angling season, when captured/observed in the national monitoring programme itself, and under direct instructions from the Norwegian Directorate of Fisheries. In addition, a dedicated programme (OURO http://utfisking.no/) was recently established to finance and coordinate removal of domesticated escapees from rivers prior to spawning. This comes in addition to and separate to the monitoring programme itself. Results from the national monitoring programme for escapees are used to guide allocation of resources to rivers where large numbers of escapees have been observed in previous years. In 2016–2018, OURO-financed removal of escapees was performed in approximately 50–60 of the 448 rivers in Norway (Table S3). The method of removal varies between snorkelling and harpooning, to angling, netting and trapping. While removal is important, and in some rivers also effective in significantly reducing the numbers of escapees and thus the likelihood of further introgression, this mitigation strategy has several limitations. The first is that there are insufficient resources to cover all rivers, and thus, rivers are prioritized based on them having data from the monitoring programme for escapees and have displayed a moderate or high proportion of escapees in the previous year(s) monitoring. Therefore, in practice, unmonitored rivers may harbour escapees in them, and rivers that have displayed low proportions of escapees previously may have a moderate or high proportion of escapees in them in a given year without being targeted for removal. Furthermore, the effect of removal, which is visual-based in most rivers, depends on weather and water conditions, and as such, small clear rivers are more easily targeted than large turbid rivers with lakes and deep dark pools. Finally, it is not possible to remove all escapees from a river, and it is not possible to exclude the possibility that escapees enter the river after removal has occurred. These factors limit the extent to which removal of escapees from rivers can eliminate the possibility for introgression, despite the fact that in some rivers in some years, the method may be highly effective. Due to the factors above, and that none of the PZs have all of their rivers covered by the national monitoring programme for escapees, the *desired status* is not given the category low deviation in any of the PZs. In PZs with a good coverage from the monitoring programme, together with good coverage of rivers in need of mitigation, OURO removal was categorized as a moderate deviation from the *desired status*. In PZs with a low coverage from the monitoring programme and/or limited removal, the removal was categorized as having a high deviation from the *desired status*. Strength of knowledge for this factor was set to good for all PZs as the numbers of fish removed are well documented through the programme itself (http://utfisking.no/ and Table S3).

> The desired status is that each year, effective removal of escapees is conducted in all rivers in the PZ where there are escapees.

2.2.2 | Robustness of wild populations for further introgression of domesticated escapees

As spawning is highly competitive and domesticated escapees generally display poor spawning success (Fleming et al., 2000; Fleming, Jonsson, Gross, & Lamberg, 1996), their relative success will be very dependent on the number of wild competitors present (Heino et al., 2015). In Norway, most rivers are also managed by an adult spawning target, which is defined as the number of deposited eggs required to fully utilize the river's potential juvenile production (Forseth et al., 2013). This is based on computations using the number of females estimated to be in the river after the angling season, their average sizes and thus fecundities, and finally, the size of the river. Rivers achieving this spawning target will experience higher competition on the spawning grounds than rivers not achieving this target. Competition will be even stronger if there are more competitors on the spawning grounds than required for the spawning target. Such rivers are classified as having a high harvest potential (Anon, 2018).

As rivers have a limited smolt production capacity defined by the territorial behaviour of salmon, juvenile competition is greater in rivers with a high deposition of fertilized eggs, that is those fulfilling or exceeding their spawning targets. Although mature male part of domesticated origin may display high reproductive success in comparison with wild counterparts (Garant, Fleming, Einum, & Bernatchez, 2003), their offspring are in general poor competitors in freshwater (McGinnity et al., 2003; Skaala et al., 2019; Skaala et al., 2012). There are also indications that as juvenile density and competition increase, the relative survival of domesticated offspring declines (Skaala et al., 2012). Consequently, it is assumed that rivers achieving their spawning targets are more robust to further introgression than rivers that do not achieve their spawning targets in the risk assessment.

Hybrids and back-crossed individuals between domesticated and wild salmon generally display intermediate phenotypes in traits such as survival (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2019; Skaala et al., 2012), growth (Bolstad et al., 2017; Glover et al., 2009; Skaala et al., 2019), predation susceptibility (Monica F. Solberg, Robertsen, Sundt-Hansen, Hindar, & Glover, 2020), stress tolerance (M.F. Solberg, Glover, Nilsen, & Skaala, 2013), age at maturation (Bolstad et al., 2017; McGinnity et al., 2003; Skaala et al., 2019) and phenology (Skaala et al., 2019). Therefore, it is assumed that domesticated escapees are likely to have a relatively greater spawning success in competition with domestication-admixed as opposed to pure wild salmon. In addition, offspring of domesticated salmon probably have a higher relative freshwater survival rate when competing with domesticated-admixed as opposed to completely wild salmon. Consequently, it is assumed that populations already displaying introgression of domesticated salmon (Diserud, Hindar, Karlsson, Glover, & Skaala, 2019) will be compromised in their future robustness for further introgression of domesticated escapees.

In the risk assessment, we have combined the two underlying factors, wild population demographic status and wild population genetic status, in order to determine the general population robustness to further introgression. It is assumed that the demographic status of the wild population, as measured by spawning target achievement, has a greater influence on the relative success of domesticated escapees in a given river than the degree of introgression in the population (although there may be time/space exceptions to this). Therefore, the demographic status is given greater weight for scoring this factor than the genetic status. Robust populations (low deviation from *desired status*) are those achieving or exceeding their spawning targets with little to no detected introgression of escapees from earlier. Moderately robust populations (moderate deviation from *desired status*) are those that are close to achieving their spawning targets with little or only modest introgression of domesticated escapees from earlier, or populations that achieve or exceed their spawning targets but display intermediate degrees of introgression from earlier. Populations displaying low robustness to introgression (high deviation from *desired status*) are those that are far from achieving their spawning target, independent of whether introgression has already occurred or not, and populations that are close to but do not achieve their spawning targets, and are heavily introgressed from before.

The strength of knowledge relating to the factor robustness of wild populations to further introgression of domesticated escapees is set at moderate for all PZs as there is limited knowledge of the combined influence of these two underlying factors, despite the fact that we have good knowledge of their influence individually.

> The desired status is a numerically strong population with little or no previous introgression of domesticated salmon.

Wild population demographic status

Data on the annual achievement of the spawning target and harvest potential for each river are available from the Norwegian Scientific Advisory Committee for Atlantic Salmon (Anon, 2018). These data have been used in the Norwegian quality norm (Forseth et al., 2017) to categorize the status of salmon populations in all rivers in Norway for the period 2014–2017. Using these data, the mean achievement of the spawning target and harvest potential was estimated for rivers within each PZ (Table S4). This was computed using both the unweighted and weighted mean according to the spawning target (i.e. size) of each river in the PZ. The weighted estimate increases the relative influence of the large rivers in PZs, while in the unweighted estimate, all rivers contributed equally. Rivers with the category “good” and “very good” in the quality norm for both achievement of spawning target and harvest potential were given the status low deviation from *desired status* in the risk assessment here, while quality norm category “moderate” was given the risk assessment category moderate deviation from *desired status*, and finally, the quality norm categories “poor” and “very poor” were given the category high deviation from the *desired status* in the risk assessment.

> The desired status is a population that achieves its spawning target and has a normal or high harvest potential.

Wild population genetic status

Estimates of introgression of domesticated salmon in wild salmon populations, as revealed from genetic analysis of >40,000 salmon hatched in the wild, currently exist for 225 populations in Norway (Diserud, Hindar, et al., 2019), using molecular genetic methods (Karlsson, Diserud, Moen, & Hindar, 2014; Karlsson, Moen, Lien, Glover, & Hindar, 2011). These data have also been put into an introgression classification system whereby the genetic status of populations is categorized as "very good or good," "moderate," "poor" and "very poor," reflecting the degree of introgression (Diserud, Hindar, et al., 2019). In the present risk assessment, the genetic status of each population was summarized per PZ using the unweighted and weighted means, where contributions from individual rivers counted equally, or in relation to the spawning target (Table S5). PZs with the average status of "very good or good" were categorized as having a low deviation from the *desired status*, PZs with the average status of "moderate" were given moderate deviation from the *desired status* in the risk assessment, and finally, PZs with average status "poor" or "very poor" were categorized as having a high deviation from the *desired status*. Strength of knowledge was primarily connected to the proportion of the total wild salmon resources within each production zone that was classified.

> The desired status is that the wild population has little or no detectable introgression of domesticated salmon.

3 | RESULTS

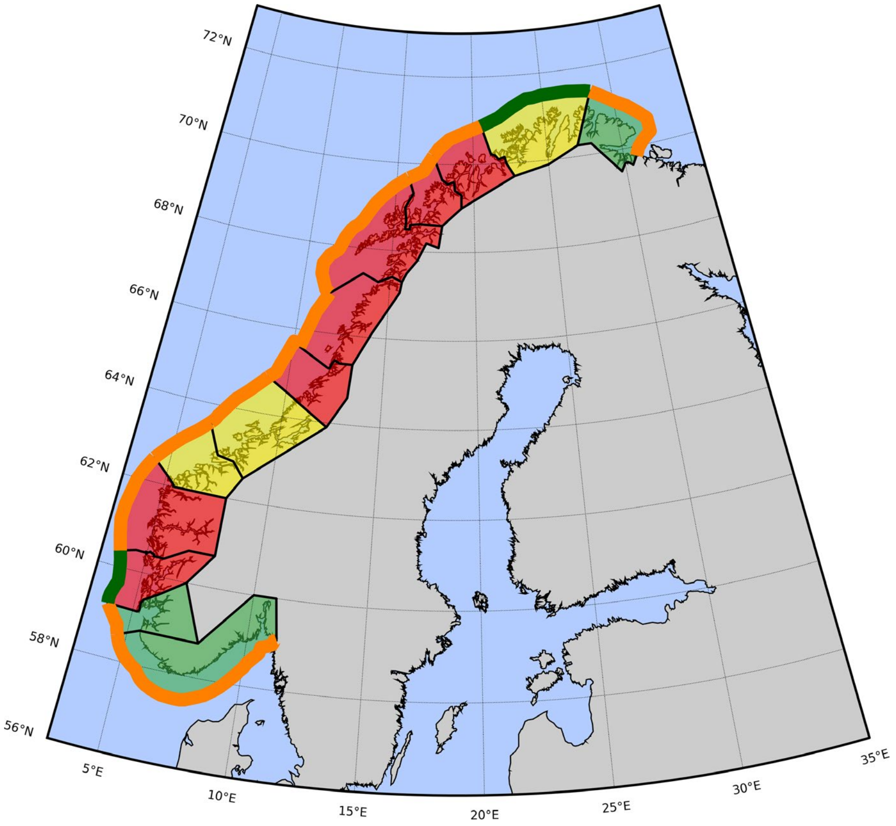
3.1 | Introduction of results

Results of the risk assessment from two contrasting PZs of Norway, PZ1 and PZ7, are presented here (Figure 4a, b), as is a graphical summary of the results from all PZs (Figure 5). A detailed description of results from all of the other PZs, translated from the Norwegian risk assessment (Grefsrud et al., 2019), is also attached (Supplementary results). Finally, all underlying data to determine the deviation from the desired status for each factor for each PZ are presented (Tables S1–S5). These data support all numerical statements below.

When interpreting the results below, and in the supplementary files, it is important to remember that both expert evaluation, based upon all available knowledge, and numerical thresholds have been

FIGURE 4 Risk assessment for further introgression of domesticated escapees in Atlantic salmon populations in Norwegian aquaculture production zones 1 (4a) and 7 (4b). Colours inside the nodes represent low (green), moderate (yellow) and high (red) deviation from the desired status. Colour of the nodes's border reflects high (green), moderate (orange) and low (red) status of knowledge for that specific factor. Striped border and white inside indicates not applicable. Figure is translated from Norwegian (Grefsrud et al., 2019) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Map showing the 13 aquaculture production zones covering Norway, and a summary of the results of the risk assessment for further introgression of domesticated escapees in wild salmon populations. Zones are numbered sequentially starting with 1 in the south-east to 13 in the north-east. Green-yellow-red colouring of the coastline illustrates low, moderate and high risk for further introgression of domesticated salmon in rivers within each zone. Green-orange-red lines on the outside of the coloured coastline represent high, moderate and low status of knowledge for these estimates (see methods) [Colour figure can be viewed at wileyonlinelibrary.com]



used to score (colour) the different risk factors and their interactions for each PZ, as described in the methods. Evaluations of deviation from the desired status for each of the five underlying factors cumulate in an integrated evaluation of risk of further introgression of domesticated salmon in rivers in the PZ.

3.2 | Results for PZ1

PZ1 is an extensive area from the south-east of Norway to the coastline of Jæren on the south-west of Norway (Figures 1 and 4a). This stretch of coastline is characterized by little aquaculture production (average ~6 million salmon in sea cages in 2018) with no reported escapes of domesticated salmon from farms in the period 2014–2018. Therefore, the factor *escapees* displays a low deviation from the desired status (green node). Strength of knowledge for this factor is considered moderate (node border orange) as we know unreported escapes may occur. With few exceptions, most of the rivers in this area that have been monitored have few domesticated escapees reported in them (95% of monitored rivers had a low proportion of escapees in the period 2014–2017), and thus, the factor *proportions of escapees in rivers* displays a low deviation from the desired status (green node). Strength of knowledge for this factor is regarded as moderate, however, due to the fact that only an average of 37% of the rivers in this PZ was monitored yearly in the 2014–2017.

Because of the low frequencies of domesticated escapees observed in rivers in this PZ, targeted escapee-removal activities have not been prioritized in this region by OURO http://utfisking.no/. Consequently, the factor *removal of domesticated escapees from rivers* was not considered in this PZ (white node with black striped border). Based upon the three described factors, there is a low probability of observing domesticated escapees on the spawning grounds for most of the rivers in this region. Therefore, their aggregating factor, *domesticated escapees on the spawning grounds*, displays a low deviation from the desired status (green node). However, due to the accumulated uncertainties from the three underlying factors, the strength of knowledge for this factor is set to moderate (node border orange).

Rivers in PZ1 do not always fulfil their spawning targets (determined as moderate attainment of spawning target), and there is therefore moderate deviation from the desired status for the factor *wild population demographic status* (yellow node). We have very good knowledge of this factor, and thus, the strength of knowledge is set to high (node border green). Based upon the analysis of molecular genetic markers, the genetic status of rivers in this region has been classified as 45% good to very good, 25% moderate, 13% poor and 8% very poor according to the system of Diserud, Fiske, et al. (2019) and Diserud, Hindar, et al. (2019). Therefore, the factor *wild population genetic status* has been given a moderate deviation from the desired status (yellow node). Knowledge of this factor has been set as high (node border green) as 24 of the 40 (95% of the spawning target) salmon rivers in this PZ have been studied with genetic methods. Because of its two underlying factors, the aggregating factor *robustness of wild populations for further introgression of domesticated escapees* has been classified as having a moderate deviation from the desired status (yellow node). The strength of knowledge for this factor was set as moderate (node border orange). This is because we have limited knowledge of the combined influence of the two underlying factors, despite the fact that we have good knowledge of their influence individually.

Based upon the deviation from the desired status for the two aggregating factors on the second level of the Bayesian network (Figure 4a), we have set the overall risk of further introgression of domesticated escapees in rivers in this production zone as low, that is a low deviation from the desired status (green node). The overriding factor is that all evidence strongly suggests that there are very few domesticated escapees on the spawning grounds of populations in PZ1. Strength of knowledge for this is set to moderate (node border orange) due to the accumulated uncertainties from all levels below.

3.3 | Results for PZ7

PZ7 is an area in mid-Norway that encompasses north Trøndelag (Figures 1 and 4a). The aquaculture production in this region is very large (average ~31 million salmon in sea cages in 2018), and the average numbers of reported escapees are ~24,000 per year for 2014–2018. Therefore, the factor *escapees* displays a high deviation from the desired status (red node). Strength of knowledge for this factor is considered moderate (node border orange) as we know unreported escapes may occur. Many of the rivers in this region display moderate or high proportions of escapees (12% and 19% of monitored rivers were classified as having moderate or high proportions of escapees in the period 2014–2017) (Glover et al., 2019), and thus, the factor *proportions of escapees in rivers* displays a high deviation from the desired status (red node). Strength of knowledge for this factor is regarded as moderate, however, due to the fact that only an average of 29% of the rivers in this PZ was monitored yearly in the 2014–2017.

Despite the fact that moderate and high proportions of domesticated escapees have been reported by the monitoring programme in some rivers in this region, only modestly effective activities from OURO http://utfisking.no/ have been implemented to remove escapees prior to spawning. Consequently, the factor *removal of domesticated escapees from rivers* has a high deviation from the desired status (red node). Strength of knowledge for this factor is set as high (node border green) as we have a good overview of where removal efforts have occurred. Based upon these three described factors, there is a high probability of domesticated escapees being observed on the spawning grounds for some of the rivers in this region, and thus, the aggregating factor, *domesticated escapees on the spawning grounds*, displays a high deviation from the desired status (red node). However, due to the accumulated uncertainties from the three underlying factors, the strength of knowledge for this factor is set to moderate (node border orange).

Rivers in PZ7 do not always fulfil their spawning targets (determined as moderate attainment of spawning target), and there is therefore moderate deviation from the desired status for the factor *wild population demographic status* (yellow node). We have moderate knowledge of this factor (node border orange). Based upon the analysis of molecular genetic markers, the genetic status of rivers in this region has been classified as 50% good to very good, 33% moderate, 0% poor and 17% very poor according to the system of Diserud, Fiske, et al. (2019) and Diserud, Hindar, et al. (2019). Therefore, the factor *wild population genetic status* has been given a high deviation from the desired status (red node). Knowledge of this factor has been set as moderate (node border orange) as 6 of the 24 (92% of the spawning target) salmon rivers in this PZ have been studied with genetic methods. As a consequence of its two underlying factors, the aggregating factor *robustness of wild populations for further introgression of domesticated escapees* has been classified as having a moderate deviation from the desired status (yellow node). The strength of knowledge for this factor was set as moderate (node border orange). This is because we have limited knowledge of the combined influence of the two underlying factors, despite the fact that we have good knowledge of their influence individually.

Based upon the deviation from the desired status for the two aggregating factors on the second level of the Bayesian network (Figure 4b), we have set the overall risk of further introgression of domesticated escapees in rivers in this production zone as high (red node). The overriding factor is that moderate-to-high proportions of domesticated escapees are observed on the spawning grounds of some of the rivers in this PZ, and some populations in this region are only regarded as moderately robust to further introgression of domesticated escapees. Strength of knowledge for this is set to moderate (node border orange) due to the accumulated uncertainties from all levels below.

3.4 | Combined results for all PZs

Based on the risk assessment, the following results were obtained: three PZs displayed low (PZ1, 2 and 13), three PZs displayed moderate (PZ5, 6 and 12), and seven PZs displayed high (PZ3, 4 and 7–11) risk of further introgression of domesticated salmon (Figure 5, Supplementary results). Salmon aquaculture production is extensive in all of these areas with the exception of PZ1 and PZ13, both of which are scored as having low risk for further introgression.

4 | DISCUSSION

To our knowledge, this work represents the most up-to-date and extensive risk assessment of genetic impact of domesticated escapees on wild populations for any species of fish. Based on an evaluation of extensive data on the reported numbers of escapees, population demographic and genetic status, and observations of escapees in >200 rivers annually, it is concluded that rivers within ten of the thirteen aquaculture production zones in Norway display moderate-to-high risk of further introgression of domesticated escapees (Figure 5). This comes in addition to already documented widespread introgression of domesticated escapees in Norwegian rivers. We therefore conclude that so long as the Norwegian aquaculture industry continues at its present level and form, there are moderate-to-high risks of further introgression of domesticated salmon in native populations in much of Norway.

4.1 | Past, present and future impacts

Wild salmon populations in Norway display highly significant population genetic structure among them (Glover et al., 2012; Wennevik et al., 2019), some of which may reflect adaptive variation (Fernando Ayllon et al., 2015; Barson et al., 2015; Kjaerner-Semb et al., 2016). Long-term and repeated escapes of domesticated salmon in Norway have already led to widespread introgression (Glover et al., 2013; Karlsson et al., 2016) and a decrease in among-population genetic structure (Glover et al., 2012; Skaala, Wennevik, & Glover, 2006). Changes in life-history traits have also been reported for admixed individuals in introgressed populations (Bolstad et al., 2017), although some of the phenotypic effects of introgression may be cryptic (Glover, Solberg, Besnier, & Skaala, 2018). The work conducted here, which indicates a moderate-to-high risk of further introgression in rivers in much of Norway, comes in addition to the extensive existing impacts of escapees over the past decades. Already introgressed populations are likely to become more admixed, and currently unaffected or only modestly affected populations may become more introgressed.

Until the numbers of escapees entering rivers and the level of gene flow are significantly reduced, it is unlikely that many of the introgressed populations will become less impacted in the near future despite the fact that there is a strong selection against domesticated and admixed offspring in the wild (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2019). Empirical analyses (Bolstad et al., 2017) and models (Baskett, Burgess, & Waples, 2013; Castellani et al., 2015, 2018; Yang, Waples, & Baskett, 2019) illustrate that life-history and demographic changes in wild populations following spawning intrusion of domesticated escapees are likely to be dependent on the level of gene flow. Therefore, there is a need to increase mitigation strategies in order to minimize future potential impacts.

4.2 | Limitations of the risk assessment

The objective of the risk assessment was to investigate potential for further introgression of domesticated escapees in rivers within each of the 13 aquaculture production zones that span Norway. These zones were produced to address sustainability and management issues for sea lice (Kristoffersen et al., 2018; Vollset et al., 2018), and were geographically determined by simulations from dispersion models and oceanic currents. Thus, these production zones do not necessarily reflect an optimal division of the Norwegian coastline for management of escapees. Some of the challenges associated with this are discussed below. Within all PZs, rivers display highly diverse physical, life-history and genetic characteristics. Therefore, a compromise in the risk assessment is that it ignores the fact that there are large differences between rivers within PZs, as evidenced by differences in, for example, the presence of escapees (Diserud, Fiske, et al., 2019; Glover et al., 2019) and level of historical introgression (Glover et al., 2013; Karlsson et al., 2016). Thus, there will be rivers within PZs that for one reason or the other are not attractive to escapees, and/or are more robust and thus may provide stronger competition to domesticated and admixed offspring. As a consequence, these populations may not become introgressed in the future despite being in a PZ defined as having high risk. Likewise, there will be more vulnerable rivers in PZs defined as having low risk that may become introgressed in the future. However, it is important to note that the risk assessment performed has not been used as a replacement for river-specific monitoring or management regimes where all the individual characteristics of rivers and populations are used. Its primary role is to advise on a management-area level where efforts to coordinate mitigation efforts could be coordinated and implemented.

Domesticated salmon escapees can travel large distances and enter rivers far from the escape site (Hansen, 2006; Hansen et al., 1997; Quintela et al., 2016). Thus, fish escaping from farms in one production zone will be able to freely migrate between production zones. Consequently, unlike for salmon lice for which the current management zones were developed, the challenge of further introgression of domesticated escapees will not necessarily be optimally addressed through the current size and location of the production zones. The current zoning system therefore represents a compromise if it is to be used to manage the challenge of escapees and genetic interactions, and as such, any regional-based mitigation strategies (see below) would need critical evaluation in the light of this knowledge. Despite this limitation however, data from extensive simulated release experiments indicate that it is more likely for an escapee to enter a river closer to the site of escape, all other factors being equal (Skilbrei et al., 2015). This is further supported by the higher proportions of escapees observed in rivers in aquaculture dense regions (Fiske, Lund, & Hansen, 2006; Keyser et al., 2018).

Another limitation of the risk assessment is that the level of introgression and degree of potential biological changes have not been quantified against pre-determined "environmental impact thresholds". In other words, we have not set specific limits for numbers of escapees nor levels of introgression upon which risk is measured. Consequently, the category *high risk of further introgression* was not connected to any specific level of introgression nor potential for biological change. Neither have we attempted to quantify how many rivers within a high-risk PZ are likely to be affected. Full life cycle eco-genetic models permit estimating the expected demographic, genetic and phenotypic changes to wild populations under different introgression scenarios (Castellani et al., 2015, 2018; Sylvester et al., 2019). It is therefore possible to set introgression thresholds in native populations with given levels of expected impact. However, this is beyond the scope of the current risk assessment. There is already overwhelming evidence of introgression in Norwegian salmon populations (Diserud, Hindar, et al., 2019), and as such, any thresholds for future impact would have to take historical impacts into consideration on a river by river basis. Another aspect linking to this is the fact that the risk assessment has been conducted with a projection into the future. However, in 2017 and 2018, some of the lowest recorded proportions of domesticated escapees were observed in Norwegian rivers since monitoring started in 1989 (Diserud, Fiske, et al., 2019; Glover et al., 2019). This is also reflected in the decline in the numbers of salmon escaping from fish farms escapees in the period 2006–2018 https://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk. Whether or not this represents a positive trend caused through increased retention of salmon in aquaculture cages remains to be seen, as the reported number of salmon escapees increased once again in 2019 to more than 270 000.

4.3 | The 3Rs of mitigation: Reduction, Removal and Reproductive barrier

This work has identified three key factors to mitigate the risk of further introgression from domesticated escapees. These strategies are largely transferrable to other species and aquaculture systems. The first mitigation strategy is to reduce the numbers of fish that escape from farms and thereafter migrate into rivers. This can be achieved by a reduction in the numbers of fish that escape per production unit, through, for example, further improved technical standards and husbandry. It may also be possible to reduce escapees entering rivers by increased use of production technologies that may reduce the ability for fish to survive and thereafter enter freshwater post-escape. Possible examples of these are the use of out-of-season smolt production (Skilbrei, 2010b), and/or application of continuous light and genetic selection to reduce early maturation in the domesticated strains (F. Ayllon et al., 2019). A long-term decline in the observed proportion of domesticated escapees in Norwegian rivers has been observed (Diserud, Fiske, et al., 2019; Glover et al., 2019). Thus, it appears that the industry has collectively made efforts to reduce escapes, although continued efforts to reduce them further are required.

The standing stock of salmon in Norwegian fish farms is approximately 400 million, while the annual number of wild adult salmon returning to the Norwegian coastline is approximately 0.5 million (Forseth et al., 2017). Consequently, one major incident has the potential to release more domesticated salmon into the wild than the collective wild Norwegian population returning to spawn. So long as salmon are farmed using current technology, that is grow out in sea cages, the risk of escapes, and potentially large numbers of escapees following catastrophic events, will always be present. Therefore, methods to reduce the numbers of escapees entering rivers are needed in order to decrease the numbers of fish that can potentially contribute to spawning once escapes have occurred. This can be performed by targeted removal of escapees from rivers as is currently practised in approximately 60 of Norway's 448 rivers in the government-legislated and aquaculture industry-financed OURO removal programme. This is viewed as a necessary strategy until the industry has implemented robust solutions to eliminate escapes. However, an increase in the number of rivers selected for targeted removal of escapees, as well as greater efforts per river, is needed if targeted removal is to have a greater effect than at present.

The final mitigation strategy may be described as a more permanent solution to genetic interactions. Farming sterile fish would eliminate further introgression of domesticated escapees in wild populations (Benfey, 2016). Finding robust approaches to produce sterile salmon with good welfare and production characteristics is of importance.

4.4 | Transfer of knowledge to other aquaculture risk assessments

Risk assessments of the environmental impacts of aquaculture have been conducted using various approaches in several countries, and for several potential types of impact (Grefsrud et al., 2019; Hallerman & Kapuscinski, 1995; Taranger et al., 2015). However, they are relatively few, still developing, and the Norwegian example presented here most likely represents the most advanced and detailed assessment of risk for genetic interactions between fish farm escapees and wild populations for any region or aquaculture system globally.

Norway has some of the most extensive monitoring programmes that exist for salmon. These cover all of the main factors underpinning the current risk assessment, including reported escapees from aquaculture, proportions of domesticated escapees in rivers, abundance and genetic status of wild populations, as well as mitigation strategies to remove escapees prior to spawning. In many other countries, and for most other aquaculture species of fish, the level of data availability and knowledge of interactions fall short of those presented here. Therefore, the primary challenge to conduct risk assessments for introgression of domesticated escapees in other countries and for other aquaculture systems is to find data upon which it is possible to identify and quantify the various risk factors. However, such an exercise in itself, which will identify some of the major knowledge bottlenecks and data gaps, can be useful as a first of many steps to address the situation.

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CONFLICTS OF INTEREST

None.

DATA AVAILABILITY STATEMENT

All raw/aggregated data associated with this work are provided in the supplementary files.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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