

# Natural and anthropogenic drivers of escaped farmed salmon occurrence and introgression into wild Norwegian Atlantic salmon populations

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Marine aquaculture of Atlantic salmon (*Salmo salar*) is a relatively new industry where breeding programs have led to rapid genetic change in the captive populations that were built up alongside conspecific wild individuals. Throughout its 50-years history, marine aquaculture of Atlantic salmon has been associated with escapes, and studies have shown that escapees may enter rivers, spawn successfully, and this may lead to farmed-to-wild genetic introgression and maladaptation in wild populations. Yet, an open question is what factors can best explain the variability in the proportion of farmed escapees in wild populations, and when present, which additional factors lead to introgression. Here, we combine two large-scale data sets from monitoring escaped farmed salmon and introgression in Norwegian rivers between 2006 and 2018 to model how anthropogenic, environmental, and population factors influence proportion of escapees and level of introgression. We found that increasing farming intensity and river discharge increase the expected proportions of escaped farmed salmon in rivers, whereas a larger wild salmon population size reduces the expected proportion of escapees despite increasing the expected absolute numbers of escaped farmed salmon. On a large scale, introgression is primarily a function of proportions of escaped farmed salmon, and only to a minor extent a function of local environmental factors or salmon population characteristics. This suggests that as long as salmon aquaculture is based on technologies where non-sterile fish can escape, all anadromous wild Atlantic salmon populations are at risk. Large marine protected areas without salmon aquaculture may slow down the rate of intrusion and introgression by increasing the distance between intensive aquaculture and wild populations.

**Keywords:** admixture, aquaculture, Atlantic salmon, escaped farmed salmon, gene flow, *Salmo salar*.

## Introduction

The rapid domestication of fish species for aquaculture means that we are in position to follow the genetic process of domestication as it happens. We are also able to follow the side-effects of domestication on wild populations as large-scale aquaculture, in some years, has produced as many escapees as there are wild conspecifics (Hindar *et al.*, 1991).

Successful domestication depends on controlling the life cycle from fertilization until market size. Artificial reproduction of salmonids was mastered on a large scale from the 1850s onwards, when unfed salmonid fry (alevins) were produced in large numbers for release into the wild (Berg, 1986). The technology to raise Atlantic salmon (*Salmo salar*), hereon referred to as salmon, to market size in marine net pens was developed in the 1960s and led to the growth of a salmon aquaculture industry both within and outside its natural distribution range

(Heen *et al.*, 1993). The production of salmon in fish farms has increased from half of nominal catch of wild salmon in 1980 to outnumbering it 2000 times in 2019 (ICES, 2020).

In 1986, the first concerns about escaped farmed salmon entering rivers were published (Maitland, 1986). High proportions of farmed salmon were found in many rivers in Norway during the autumn of 1987 and 1988 (Gausen and Moen, 1991). In 1989, a nationwide monitoring system for escaped farmed salmon was implemented in Norway (Lund and Hansen, 1991; Diserud *et al.*, 2019), and is now into its second and more comprehensive generation with annual sampling of more than 200 rivers (Glover *et al.*, 2019). The accumulated number of individuals being classified as wild or farmed escapees, based on growth patterns in the scales (Lund and Hansen, 1991), amounts to more than 470 000 since 1989.

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Around 1990, methods were developed to show that escaped farmed salmon could produce offspring in the wild. The first methods were based on demonstrating that feed additives (synthetic astaxanthin and canthaxanthin) were found in salmon eggs deposited in the riverbed in Scotland and Norway (Lura and Sægrov, 1991a, b; Webb *et al.*, 1991). Moreover, *ad hoc* genetic methods based on skewed allele frequencies in allozyme markers were used to show that wild salmon juveniles in Ireland had farmed parents (Crozier, 1993; Clifford *et al.*, 1998a, b). Later, microsatellite markers were used to document temporal genetic changes in wild populations, including a reduction in wild population differentiation, that were likely a result of escaped farmed salmon interbreeding (Skaala *et al.*, 2006; Glover *et al.*, 2012).

In 2011, a SNP panel to distinguish farmed and wild salmon was developed in Norway based on screening 4514 SNP markers in 12 breeding lines of Norwegian aquaculture salmon and 13 wild Atlantic populations throughout Norway, sampled before the growth of the aquaculture industry (Karlsson *et al.*, 2011). Using this method, scale samples with a confirmed wild growth pattern (Fiske *et al.*, 2005) can be used as a source of DNA, lending themselves to genetic screening for determining the degree of farm wild admixture. More than 50 000 individuals with a wild life cycle from 239 Norwegian rivers have been analyzed to estimate their probability of belonging to a wild salmon population (Karlsson *et al.*, 2016; Diserud *et al.*, 2020) by using the methodology developed by Karlsson *et al.* (2014).

In this study, we analyze the predictors that can be associated with the occurrence of escaped farmed salmon and their introgression into wild salmon in Norway, improving preliminary models presented in reports for Norwegian authorities (Fiske *et al.*, 2013; Hindar *et al.*, 2018). Heino *et al.* (2015) found that the observed proportion of escaped farmed salmon in catches and the average annual angling catch weights for rivers could provide a predictor for cumulative introgression in 20 populations, where catch served as a proxy for current population size. Sylvester *et al.* (2018) showed that within-river distribution of hybrid parr was associated with the migration effort required to reach spawning sites; the hybrid proportion decreased with increasing elevation, geographic distance, and the presence of obstructions. Keyser *et al.* (2018) predicted the distribution of escaped farmed salmon and degree of introgression in wild populations in the Northwest Atlantic from aquaculture facility locations, production estimates, reported escape events, and in-river detections of escaped farmed salmon. Mahlum *et al.* (2021) found that aquaculture intensity, wild salmon abundance, mean yearly discharge, and the interaction between the distance from river mouth to open ocean and wild salmon abundance were important predictors of escapee abundance in western Norwegian rivers. Proximity to fish farms or other indices of farm production intensity had also been found by Gausen and Moen (1991) and Fiske *et al.* (2006) to correlate with high proportions of escapees.

In autumn 1989, Norwegian authorities established a system of 52 temporary protection zones (with 125 salmon rivers) for wild salmon populations in fjords that were attractive for further development of aquaculture. These were later formalized by the Norwegian parliament (Anon, 2006) as a system of 29 National Salmon Fjords and 52 National Salmon Rivers along the Norwegian coast intended as a general protection of the wild salmon resource. The purpose of

this protection system is to give the most important salmon populations in Norway a special protection against harmful anthropogenic activities in the rivers, and in adjacent fjord and coastal areas.

Here, we combine data sets on escaped farmed salmon and introgression from c. 200 rivers along the Norwegian coast, from 58°N to 71°N, to answer the questions: (1) what determines the occurrence of escaped farmed salmon into Norwegian rivers, (2) what determines the level of introgression in Norwegian salmon populations, and (3) does the establishment of protection zones for wild salmon reduce introgression from escaped farmed salmon?

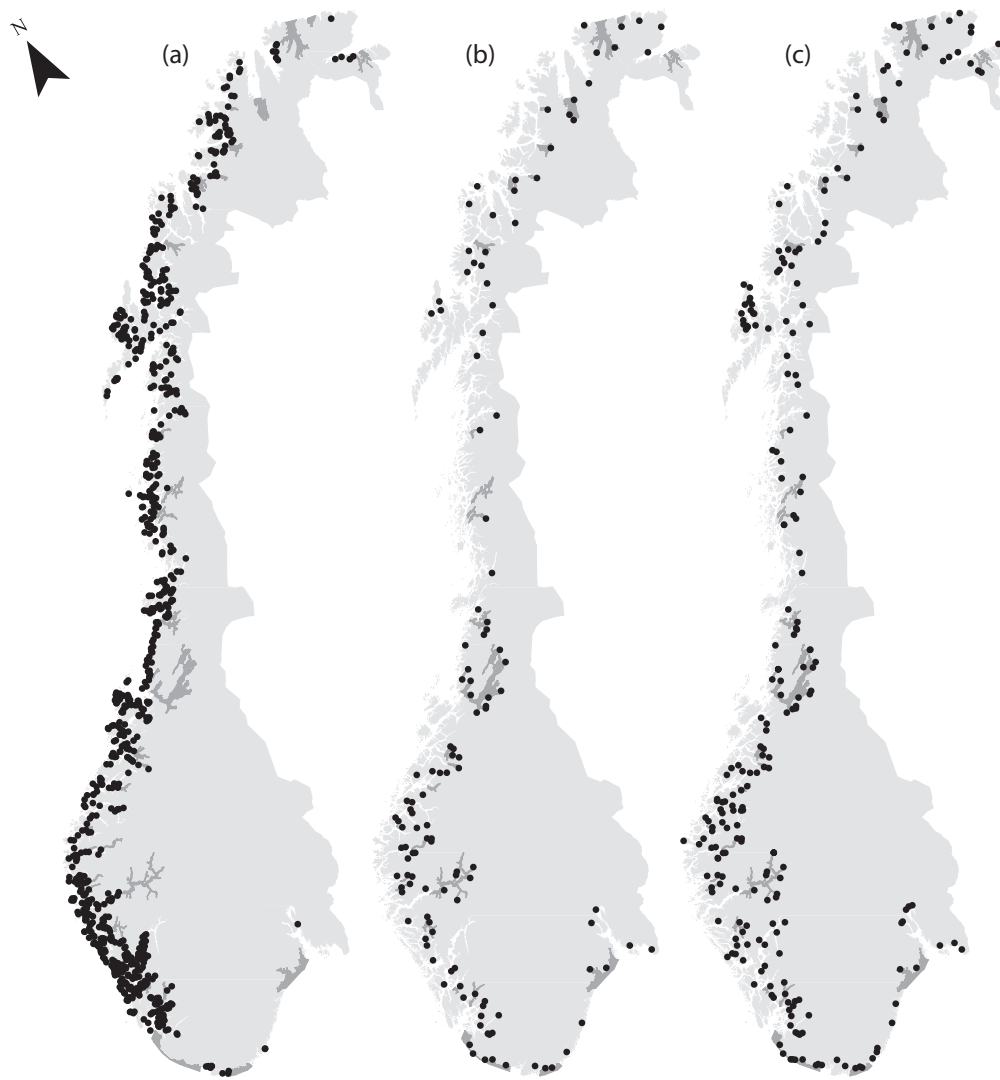
## Material and methods

### Materials

Data on the proportions of escaped farmed salmon in Norway come from two papers that reported the distribution of escapees in rivers from 1989 to 2013 (Diserud *et al.*, 2019) and on a more comprehensive scale from 2014 (Glover *et al.*, 2019). Scales from more than 470 000 individuals, caught during summer recreational angling, autumn pre-spawning angling surveys, and broodstock fishing, have been analysed to determine their origin (escaped farmed or wild) according to fish scale growth pattern (Fiske *et al.*, 2005; see also Diserud *et al.*, 2019). Proportions estimated from summer catches may underestimate the proportion of escapees in the wild spawning populations as escaped farmed salmon often ascend rivers later in the season than wild salmon (Lund *et al.*, 1991; Crozier, 1998; Erkinaro *et al.*, 2010), while autumn samples may give uncertain proportion estimates due to small sample sizes and biased estimates due to potentially differing catchabilities or spatial distribution close to the spawning period (Moe *et al.*, 2016; Svenning *et al.*, 2017). An *Incidence index* that combined the information from summer and autumn catch samples was, therefore, developed for management purposes to give the best possible annual estimate of the proportion of escaped farmed salmon in wild salmon populations (Fiske *et al.*, 2006; Diserud *et al.*, 2010).

The estimated proportions of escaped farmed salmon in the wild salmon populations were averaged over the years from 2006, when the estimates for wild population status were improved (Forseth *et al.*, 2013), to 2018. Each annual estimate were given the same weight when calculating the average. This period covers the last two to three wild salmon generations. We analysed the *Incidence index* averaged over this prolonged period rather than including the temporal variation in escape proportions. This was done because genetic introgression is accumulated over time, the frequency and quality of catch reports may vary considerably, and associations can be both time-lagged and smoothed out over several years, making “correct” temporal assignments difficult. Models were fitted to 129 wild salmon populations with a minimum of 4 years of *Incidence index* estimates (Figure 1b). With a lower limit at 4 years of data, we focus on the more permanent characteristics of a population and its environment that may influence the proportion of escaped farmed salmon.

Data on introgression from escaped farmed to wild salmon in Norway was obtained from Karlsson *et al.* (2016) and the report by Diserud *et al.* (2020), which present information on introgression in 239 wild salmon populations and more than 50 000 genetically analyzed individuals with a wild



**Figure 1.** Maps of Norway showing: (a) locations with sea water net pens in 2015–2016, (b) rivers with incidence indices estimates ( $n = 129$ ), and (c) rivers with genetic introgression estimates ( $n = 239$ ). Grey areas along the coast indicate the National Salmon Fjord protection zones.

growth-scale pattern confirming that individuals were hatched in the wild (Figure 1c). Historical samples collected before significant farmed salmon introgression (c. 1990) have been analyzed for 59 of the 239 wild salmon populations, to serve as wild origin references.

The underlying estimate of introgression (or lack thereof) is the probability an individual belongs to a reference of wild salmon ( $P(\text{Wild})$ ), using the SNP panel developed by Karlsson *et al.* (2011) and a statistical method developed by Karlsson *et al.* (2014).  $P(\text{Wild})$  is, thus the unscaled proportion of wild origin and not the estimate of introgression. Introgression is a population property accumulated over time, expected to vary among cohorts depending on escape episodes and stochastic environmental variation. We have, therefore, used the population mean  $P(\text{Wild})$  as the model response variable, estimated from a contemporary sample pooled over the last salmon generation with sufficient total sample size (Diserud *et al.*, 2020). During model fitting, we only include populations with a genetic sample size of 20 fish or more. Most populations are represented by recent samples; 75% of the

populations are from 2014 or later, while the oldest are from 2005.

Variables that were assumed *a priori* to be potential predictors for occurrence of escaped farmed salmon or extent of introgression, or both, are listed in Table 1. The predictors can be divided into three categories: population, environmental, and anthropogenic. Population predictors include variables like the phylogenetic group of the wild salmon, number and density of spawners, adult body size, and juvenile growth rate in fresh water. Environmental predictors include variables such as river size (discharge), migration obstacles, and the river's location along the coast. Anthropogenic predictors include factors affecting the number of escapees along the coast and in-river human activities such as hydropower regulation, release of hatchery fish, or liming. Farming intensity was estimated based on January and June biomass (or numbers) in seawater net pens for c. 1000 locations along the Norwegian coast 2006–2016 (Data courtesy of the Norwegian Directorate of Fisheries) and on measurement of the distances between river mouths to all farming locations (Figure

**Table 1.** List of population, environmental, and anthropogenic predictor variables that may be associated with occurrence of escaped farmed salmon in wild salmon rivers (*Incidence index*) and/or genetic introgression of farmed salmon in wild populations. The table presents a short name for each variable, variable type, data quantity (number of rivers or populations and the variable range), and *a priori* assumed effect on escapee proportion or genetic introgression. The number of populations or rivers listed in the data column refers to the 224 populations we have either escape proportions or genetic data from, or both. All predictors that vary temporally are averaged over the period from 2006 to 2018. Variables indicated with an asterisk (\*) in the *Short name* column are included in one or more of the final models.

Predictor variable	Short name	Type and unit	Data	Potential effect on ...		References
				Incidence index	Genetic introgression	
Phylogenetic group	<i>Pbyl</i> *	Factor [North-East Atlantic—NEA, Barents Sea—BS, and Transition zone—TZ]	Population variables 224 populations ( $n_{NEA} = 181$ , $n_{BS} = 27$ , and $n_{TZ} = 16$ )		Farmed salmon originates from NEA group so represent an endemic farmed fish in South Norway and an exotic one in Barents Sea rivers in North Norway; Introgression has larger ecological consequences where farmed salmon are exotic	Bourret <i>et al.</i> (2013), Karlsson <i>et al.</i> (2014), Bolstad <i>et al.</i> (2017), Wacker <i>et al.</i> (2021)
Population size—estimated both as pre-fishery abundance and spawner abundance.	<i>PopSize.PFA</i> * <i>PopSize.SA</i> *	Count	146 populations, (range PFA 119–38 822; range SA 71–16 962)	Escapees follow wild salmon back to rivers; more farmed escapees but lower proportion with larger wild salmon population size	salmon are exotic Spawner density affects spawning success of escapees negatively through competition; juvenile density affects relative survival of farmed offspring negatively	Mahlum <i>et al.</i> (2021), Lura (1995), Fleming <i>et al.</i> (1997), Skaala <i>et al.</i> (2019), Anon (2021)
Spawning target—spawning stock conservation limit that ensure an acceptable smolt production and population viability	<i>SpawnTarget.no</i> * <i>SpawnTarget.att</i>	Number of female spawners (no.), or ratio between realized spawner abundance and spawning target (attainment)	214 populations, (range 9–11 483 females)		Wild spawner abundance lower than target may indicate vacant spawning territory and increased success of escapees; potential for establishing feral populations	Fleming <i>et al.</i> (1996, 2000), Youngson <i>et al.</i> (1998), Naylor <i>et al.</i> (2005), Hindar <i>et al.</i> (2007), Forseth <i>et al.</i> (2013), Pulg <i>et al.</i> (2021)

Table 1. Continued

Predictor variable	Short name	Type and unit	Data	Potential effect on ...	Genetic introgression	References
Spawning target relative to sum of all spawning targets in proximity of river (< 60 km by water)	<i>RelTarget*</i>	Proportion	153 rivers, (range 0.0025–1)	Incidence index A population may “compete” with neighbouring populations for escapees as relatively large populations are more attractive? Spawning targets used instead of actual spawner abundances since we lack abundance estimates for many populations.	Neighbouring populations may serve as a source of introgressed strayers.	Hindar (1992), Jonsson and Jonsson (2017)
Growth rate in fresh water—proxy mean smolt age	<i>SmoltAge</i>	Continuous [years]	176 populations, (range 2.0–5.1 years)		Younger age at smoltification indicates good juvenile growth opportunities; farmed offspring may outgrow and displace wild offspring in favorable growing conditions	Symons (1979), McGinnity <i>et al.</i> (2003), Fleming <i>et al.</i> (2000)
Adult body size—mean catch weight	<i>BodySize</i>	Continuous, [kg]	131 populations, (range 1.2–6.0 kg)		Large body size is associated with high fecundity (females) and dominant access to females (males); less strong relationship in farmed escapees than in wild salmon	Fleming <i>et al.</i> (1996, 1997)
Water discharge—mean annual water discharge	<i>WaterDis*</i>	Continuous, [m <sup>3</sup> s <sup>-1</sup> ]	<b>Environmental variables</b> 223 rivers, (range 0.4–705 m <sup>3</sup> s <sup>-1</sup> )		High waterflow is attractive to salmon	Hindar (1992), Diserud <i>et al.</i> (2019), Mahlum <i>et al.</i> (2021), <a href="https://atlas.nve.no/Html5Viewer/index.html?viewer=nveatlas#">NVE Atlas (https://atlas.nve.no/Html5Viewer/index.html?viewer=nveatlas#)</a>

Table 1. Continued

Predictor variable	Short name	Type and unit	Data	Potential effect on ...		References
				Incidence index	Genetic introgression	
Length of anadromous stretch	<i>AnadrStr</i>	Continuous, [km]	169 rivers, (range 1–1 100 km)		Longer rivers may be harder to ascend to reach spawning grounds	Schaffer and Elson (1975)
Migration obstacles—proportion of section above first migration obstacle (rapid or fish ladder) encountered.	<i>Obstacle*</i>	Proportion	167 rivers, (range 0–1)	Distribution of escaped farmed spawners limited because of poor swimming abilities through rapids/waterfalls/fish ladder that are passable only by wild salmon	Obstacles may limit access of escapees to spawning grounds and degree of interbreeding.	Svenning <i>et al.</i> (2021), Sylvestre <i>et al.</i> (2018)
Distance to outer coast	<i>CoastDist</i>	Continuous [km]	213 rivers, (range 0.6–213 km)	Straying escaped farmed salmon may choose the first river encountered when approaching coast from the ocean		Hansen <i>et al.</i> (1993)
River discharge relative to all rivers in proximity (< 60 km by water)	<i>RelDis</i>	Proportion	175 rivers, (range 0.006–1)	Large neighbouring rivers can “compete” for escapees as relatively high discharge is more attractive		Hindar (1992), Jonsson <i>et al.</i> (2003), Kuparinen <i>et al.</i> (2010)
Lakes present or not in anadromous stretch of river.	<i>Lake</i>	Factor [No = 0, Yes = 1]	196 rivers, (n <sub>No</sub> = 87, n <sub>Yes</sub> = 109)	Can affect success of up-river migration and overwintering of escapes	Higher vulnerability of farmed offspring to predation from lake-dwelling species	Huitfeldt-Kaas (1923), Solberg <i>et al.</i> (2020)
Distance from river mouth to closest fish farm	<i>FarmDist</i>	Continuous [km]	Anthropogenic variables 212 rivers, (range 0.6–191 km)	Higher proportion of escaped farmed spawners in rivers < 20 km from fish farm; Increased distance means reduced propagule pressure		Norwegian Directorate of Fisheries data, Gausen and Moen (1991), Fiske <i>et al.</i> (2006), Bradbury <i>et al.</i> (2020), Mahlum <i>et al.</i> (2021)

Table 1. Continued

Predictor variable	Short name	Type and unit	Data	Potential effect on ...		References
				Incidence index	Genetic introgression	
Farming intensity (numbers or biomass), distance weighted by a gaussian distribution.	<i>FarmIntens</i> .no = Numbers* .bm = biomass	Continuous	212 rivers and 1 377 potential farming locations	Farm production in region better predictor for proportion of escapes in river than reported escapes in region		Derived from semiannual data on standing biomass on each location (Norwegian Directorate of Fisheries data), Ford and Myers (2008), Hindar et al. (2018), Keyser et al. (2018), Mahlum et al. (2021) Karlsson et al. (2014)
Populations that were main sources to farmed strains.	<i>FarmSource*</i>	Factor [No = 0, Yes = 1]	8 populations		Source populations of farmed salmon different P(Wild) levels from other wild populations? Risk that escaped farmed salmon are taken as broodstock; high cultivated proportion may also be a proxy for wild population vulnerability	Hagen et al. (2019)
Proportion cultivated smolt of total smolt migration	<i>CultSmolt</i>	Proportion	165 populations, (range 0 –0.85)	May lead to errors in estimation of proportion of escaped farmed salmon, as cultivated released smolt are similar to farmed salmon escaping as smolt		
Hydropower regulation of river	<i>RivReg</i>	Factor [0 = no to 3 = heavy impact]	165 rivers, (n <sub>0</sub> = 110, n <sub>1</sub> = 17, n <sub>2</sub> = 22, and n <sub>3</sub> = 16)	Changed water flow regime may affect attractiveness of river to farmed escapees—some hydropower regulations reduce waterflow, others increase it	Hydropower regulation may reduce wetted area and wild population size, leaving easier access for escaped farmed salmon	Forseth et al. (2013, 2017)
Liming of acidified river	<i>Liming</i>	Factor [No = 0, Yes = 1]	224 rivers, 19 of them limed		Younger history of introgression in recently limed rivers; proxy for population vulnerability? The protection status may entail actions that make populations more robust	Hesthagen et al. (2011)
National salmon fjords and National salmon rivers with special protection status	<i>NSF and NSR</i>	Factor [No = 0, Yes = 1]	224 rivers, n <sub>NSF</sub> = 33, n <sub>NSR</sub> = 52	NSF are areas without net pens and increase distance between rivers and fish farms		Anon (2006), Hindar et al. (2018)

1a). The contribution from the standing stock in each fish farm was weighted by a decreasing Gaussian function with a *SD* of 60 km. This resembles the calculation of “propagule pressure” for each river by Keyser *et al.* (2018). It was inspired by early reports of escaped farmed salmon in rivers in relation to regional fish farms (Gausen and Moen, 1991; Fiske *et al.*, 2006) and the dispersion of smolt and later stages of farmed salmon from known release localities (Jonsson *et al.*, 2003; Hansen, 2006; Skilbrei *et al.*, 2015). We also tested other alternatives for quantifying the accumulated influence from surrounding farms on wild salmon populations but found none that explained incidence of escaped farmed salmon better (see Hindar *et al.*, 2018). Table 1 presents a short name for each variable, variable type, data quantity (number of rivers; variable range), and an *a priori* assumed effect on escapee proportion or introgression. It is acknowledged that there are other variables that could be included in this analysis, but those in Table 1 are the ones that we identified as biologically relevant and that we have been able to quantify with sufficient precision.

All variables were averaged over the same period as the escape proportions, i.e. from 2006 to 2018, giving each annual observation the same weight. Some variables are constant, some are already given as temporal averages (e.g. mean annual discharge), some may have large uncertainty due to small annual sample sizes, and some may reflect properties accumulated or lagged over longer periods, which makes it difficult to allocate them to appropriate years or cohorts.

## Methods

Here, we logit-transformed the responses, i.e. proportions of escaped farmed salmon in wild salmon populations and introgression as proportional wild ancestry, to stabilize the variance, arguing that the resulting error distributions becomes approximately normal so that traditional multiple linear regression models can be used for the transformed responses. We could not fit generalized linear models (GLMs) with binomial error distributions because neither of the responses are direct results of binomial experiments (i.e. they cannot be expressed as ratios of two integers). To validate our assumptions when applying the logit-transform, residuals are checked for constancy of variance and normality of errors.

The wild salmon population's mean  $P(\text{Wild})$  is partly a result of natural genetic variation, i.e. the estimated mean levels from historical samples will vary among populations (Diserud *et al.*, 2020) and between phylogenetic groups [North-East Atlantic (NEA), Barents Sea (BS), and a transition zone (TZ) between them; Bourret *et al.*, 2013; Wennevik *et al.*, 2019]. A model predicting the variation in historical  $P(\text{Wild})$  population means from phylogenetic group and other predictors is presented in the Supplementary material (S1). These associations among pre-introgression  $P(\text{Wild})$  levels and predictors need to be accounted for before studying factors that affect introgression from escaped farmed salmon.

Some predictors may affect both the presence of escapees in salmon rivers and subsequent introgression (Table 1). To separate these two effects, we first modelled the proportion of escaped farmed salmon to identify predictors associated with presence of escapees. Finally, we modelled contemporary mean population  $P(\text{Wild})$  and aimed to sort contributions from natural variation, presence of escapees in rivers, and potential predictors that may modify introgression, given

that escaped farmed salmon were present in the spawning population.

Our variable selection procedure was initially based on residual deviance and  $\Delta\text{AIC}$ , but as most predictors have missing observations for some populations, two models' AIC values may not be directly comparable. Data collection for some factors were initiated by a specific event (anthropogenic intervention), so samples may be far from random. In addition, as we wanted to predict an outcome based on multiple predictors where some may covary, the variable selection procedure had to consider this correlation structure. Therefore, model selection, and interpretation of individual predictor contributions, had to be made with caution, and should, where possible, be guided by supportive information to augment confidence in the results. Some predictors could also be considered as proxies for factors hard to quantify directly.

A sizeable proportion of the variation in predictor variables may be caused by measurement and sampling uncertainty. The slope of the regression is expected to be underestimated even with unbiased measurement and sampling uncertainty, and this underestimation increases as uncertainty increases (Carroll *et al.*, 2006). Therefore, we strived for functional simplicity and chose, among correlated variables, those with best accuracy.

Predictions based on models are often used by managers to guide mitigation of anthropogenic pressures. It is, therefore, important to validate models and evaluate their predictive performance. Model selection can be viewed as a trade-off between minimizing bias and variance for predicted values. Predictions will be biased when explanatory variables with true non-zero regression coefficient are not included in the model. To minimize prediction bias, the best strategy will be to include as many variables as possible. But as we include more variables, the prediction variance will increase. The optimal model complexity is, therefore, a model with a moderate number of parameters so that the sum of the bias and the variance (mean square prediction error) is minimized. Minimizing the AIC is in accordance with this line of thought; it strives to improve model fit (log-likelihood) and reduce model complexity (number of parameters). A model with large prediction variance can be termed “overfitted” and will be poor at predicting observations outside the calibration data set. Here, we evaluated the prediction variance by a leave-one-out cross-validation procedure, i.e. we fitted the model to all observations except one and then used this model to predict the left-out observation. By comparing the coefficient of determination  $R^2_{\text{Cal}}$  for the model calibrated to the complete data set to  $R^2_{\text{Val}}$  calculated from the observed response and the corresponding leave-one-out predictions, we could evaluate the prediction variance. For an overfitted complex model, the  $R^2_{\text{Val}}$  will be much lower than the  $R^2_{\text{Cal}}$ . An illustration of this validation approach can be found in the Supplementary material (S2).

Interaction terms were evaluated, but none were found to improve model performance. All calculations and modelling were performed using the statistical software R, version 4.0.3 (R Core Team, 2020).

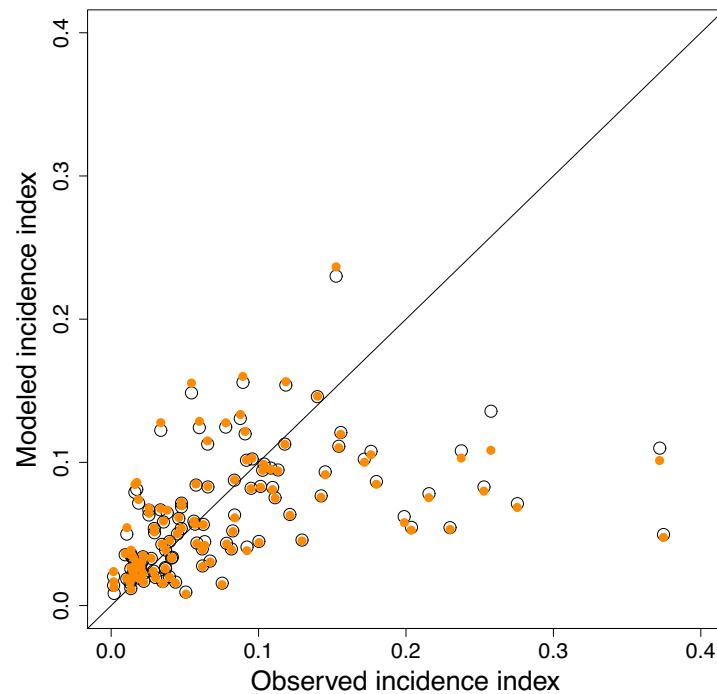
## Results

We started by investigating associations between the *Incidence index*, i.e. the estimated mean annual proportion of escapees



**Table 2.** Results from the regression model used to identify predictors associated with  $\text{logit}(\text{Incidence Index})$ . Predictors were farming intensity (numbers weighted with distance), estimated wild population spawner abundance, mean annual water discharge ( $\text{m}^3 \text{s}^{-1}$ ), and population spawning target relative to sum of all spawning targets in near proximity (< 60 km by water). Note that the  $\text{log}()$  function refers to the natural logarithm. \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

	Estimate	Std. Err	t-value
Intercept	-3.87	0.874	-4.43***
$\text{log}(\text{FarmIntens.no})$	0.21	0.043	4.88***
$\text{log}(\text{PopSize.SA})$	-0.67	0.092	-7.25***
$\text{log}(\text{WaterDis})$	0.59	0.085	6.95***
RelTarget	0.69	0.261	2.63**



**Figure 2.** Model predictions from the calibration model presented in Table 2 (black open circles) and predictions from the corresponding leave-one-out validation models (orange filled circles) for the same observations.

in rivers, and relevant predictors (Table 1). The model for *Incidence index* was primarily applied as an intermediate step in the process of separating escapee attraction and introgression sensitivity, but this model could also be used as a prediction model for the proportion of escaped farmed salmon in a wild salmon population lacking data of sufficient quality. Next, we wanted to understand drivers of introgression observed in contemporary samples. A key question was if we could detect predictor variables explaining variation in the population sample mean probability of belonging to a wild salmon population  $P(\text{Wild})$  in addition to those associated with historical variation and escapee proportions, indicating populations sensitive or robust to introgression.

### Modelling the proportion of escaped farmed salmon in wild salmon spawner populations

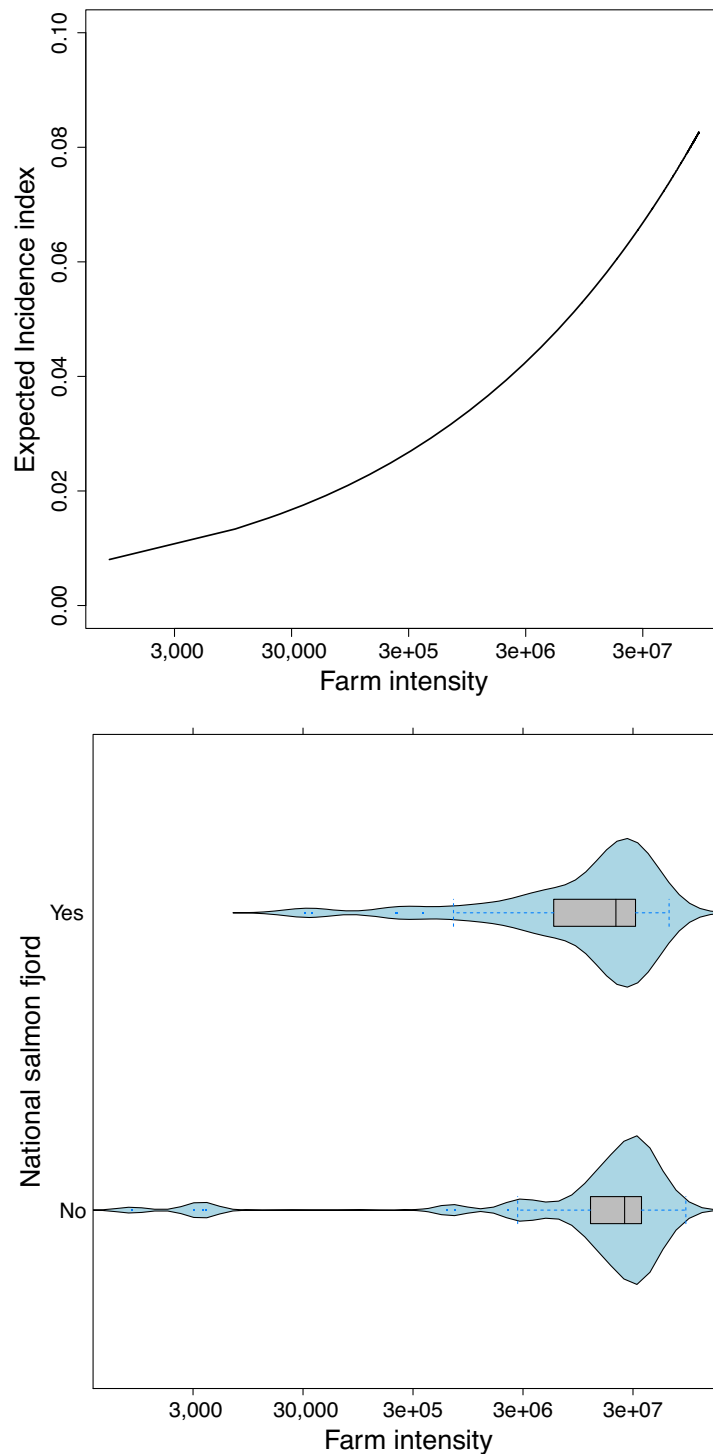
An increase in expected *Incidence index* was associated with higher farming intensity *FarmInten.no*, smaller population size *PopSize.SA*, a larger water discharge *WaterDis*, and the population having a relatively large spawning target compared to the other rivers in the vicinity *RelTarget* (Table 2).

The full model with all potential predictors included (ref. Table 1) was strongly overfitted (28 out of 129 populations excluded due to missing observations:  $R^2_{\text{Cal}} = 0.51$  and

$R^2_{\text{Val}} = 0.24$ ). After variable reduction from the full model, we got the more parsimonious model for logit-transformed *Incidence index* presented in Table 2 (17 populations missing,  $R^2_{\text{Cal}} = 0.43$  and  $R^2_{\text{Val}} = 0.37$ ). Figure 2 illustrates the model fit and validation. Note that the model underestimate all the incidence indices larger than c. 0.2.

As an illustration of the back-transformed association between farming intensity and the *Incidence index*, we calculated the model predictions when varying the farming intensity from observed minimum to maximum, while keeping the other predictors fixed at their averages (Figure 3a). The expected proportion of escaped farmed salmon for an “average” population and river increased from below 0.01 to 0.08 over the range of farming intensities. Figure 3(b) shows the distributions of *Farm Intensity* for rivers within (upper violin plot) and outside (lower) the National salmon fjord protection zones.

We also modelled the number of escaped farmed salmon in wild salmon populations because numbers, rather than proportions, may be more directly related to mechanisms for the spread of escaped farmed salmon from fish farms into rivers. Moreover, the number of immigrants into wild populations is interesting for analyses of the balance between immigration and genetic drift (Ryman *et al.*, 1995). Note that the numbers



**Figure 3.** (a) An illustration of the association between farming intensity and expected *Incidence Index* with the other predictors fixed at their averages. (b) The distributions of *Farm Intensity* (natural logarithmic scale) for rivers within vs. outside National salmon fjords shown by violin-plots.

of escapees in wild populations were calculated as the products of the two estimates *Incidence index* and population size, so the accumulated estimation uncertainty and potential bias may be large. The model for the *number* of escapees (Supplementary Table S3-1; Supplement 3) included the same predictors as the model for the *proportion* of escapees, although the sign of the estimated coefficient for population size changed. The expected number of escapees increases with the population's spawning target, while a dilution effect ensures that the

proportion of escapees decreases with increasing population size.

### Modelling population mean $P(Wild)$ for contemporary samples

We started by fitting a model for population mean  $P(Wild)$  based on *predicted* historical baseline levels (Supplementary Table S1-1) and *predicted* incidence indices (Table 2). Thereby,

**Table 3.** Linear regression model for  $\text{logit}(P(\text{Wild}))$ , where the populations' variance in predicted pre-introgression  $P(\text{Wild})$  level and *Incidence Index* are accounted for. \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

	Estimate	Std. Err	t-value
Intercept	-0.068	0.291	-0.23
Predicted $\text{logit}(\text{Incidence Index})$	-0.341	0.061	-5.58***
Predicted historical $\text{logit}(P(\text{Wild}))$	0.573	0.096	5.98***

**Table 4.** Model used to identify predictors associated with the residuals from the  $\text{logit}(P(\text{Wild}))$  model (Table 3). Predictors were upriver migration obstacles (proportion of anadromous section above first migration obstacle) and phylogenetic group. \*  $p < 0.05$ , \*\*\*  $p < 0.001$ .

	Estimate	Std. Err	t-value
Intercept	0.012	0.044	0.28
$\text{logit}(\text{Obstacle})$	0.025	0.012	2.05*
Phyl-BS	0.254	0.117	2.18*
Phyl-TZ	-0.598	0.174	-3.44***

we were not dependent on, or limited to, the actual historical samples or escapee observations as long as the relevant predictors were observed. Table 3 presents the linear model for  $\text{logit}(P(\text{Wild}))$  where pre-introgression level and expected *Incidence index* are accounted for (133 populations used to fit the model, 91 missing;  $R^2_{\text{Cal}} = 0.45$ ,  $R^2_{\text{Val}} = 0.41$ ).

Next, the residuals from this model, i.e. the variation in  $P(\text{Wild})$  not explained by historical levels or presence of escaped farmed salmon, were modelled by the predictor variables assumed to be relevant for introgression (Table 1). We found that phylogenetic group *Phyl* and upriver migration obstacles *Obstacle* could be associated with susceptibility for introgression, after the expected *Incidence index* had been accounted for (Table 4; 123 populations used to fit the model, 101 missing;  $R^2_{\text{Cal}} = 0.16$ ,  $R^2_{\text{Val}} = 0.08$ ). However, the proportion of variance explained was minor. The positive association between *Obstacle* and  $P(\text{Wild})$ -residuals indicated that a large proportion of the anadromous section above first migration obstacle reduces the expected introgression. Populations from the BS phylogenetic group were expected to have positive residuals and more robust against introgression compared to the NEA group, while populations from the TZ had lower  $P(\text{Wild})$  levels, i.e. more susceptible to introgression.

The fact that a river has status as a protected National salmon river or is discharging in a National salmon fjord (Marine Protected Area) did not influence the expected  $P(\text{Wild})$  level of a wild salmon population beyond what could be attributed to protection-relevant predictors from the *Incidence index* model, primarily farming intensity and population size.

## Discussion

This study demonstrates that genetic introgression is primarily determined by the proportions of escaped farmed salmon in rivers, and those proportions are primarily determined by farming intensity and wild population size. The main implication of these results is clear. There are currently no other sustainable mitigations than preventing farmed salmon from escaping or using sterile fish to stop further negative genetic impact on wild Atlantic salmon populations, given the present magnitude of farmed salmon production and high straying rate of escapees.

We analyzed several potential predictors (Table 1) that could modify the number and distribution of escaped farmed salmon and the introgression from escaped farmed to wild

salmon. The effect of many predictors on the proportions of escapees and resulting introgression can only be identified by large data sets including many rivers and populations, and over a long period of time. Strengths of the present study are the large amount of data on proportion of escaped farmed salmon and the level of introgression in wild salmon populations as well as the large number of potential predictors that may be associated with introgression. These aspects allowed us to explore generic factors across a large geographical scale and over an extended period, which is essential to be able to establish robust guidelines to prevent further introgression of genetic material from escaped farmed salmon into wild populations.

## Scale of analysis

A large spatial scale is necessary because of the wide distribution of fish farms and the far-reaching dispersal of farmed salmon after escapes. Escapees are found in major feeding areas near the Faroe Islands (Hansen *et al.*, 1999) and in the Arctic Ocean at Spitsbergen, more than 1000 km from the nearest fish farm (Jensen *et al.*, 2013). Recaptures of tagged farmed salmon released on the coast of Norway have been documented in rivers as far away as the Swedish west coast and the northern Kola Peninsula spanning a coastal distance of 3000 km (Hansen, 2006). Most escapees, however, end up in rivers in the same area as they escaped from, particularly if escaping as smolts or close to spawning time (Hansen, 2006; Skilbrei *et al.*, 2015; Jonsson and Jonsson, 2017).

Data sets covering a large temporal scale are necessary because introgression is a population property that represents a cumulative impact over time and is expected to vary among cohorts depending on escape episodes and stochastic environmental variation. The currently observed introgression is the result of more than three decades of spawning of escaped farmed salmon in rivers (Gausen and Moen, 1991). Thus, what we study here is the effect of introgression from escapees and their first- and later-generation offspring on a wide range of wild salmon populations. Salmon hatched in the wild are physically more fit and have a higher reproductive success than hatchery-produced salmon and farmed escapees (Jonsson *et al.*, 1990; Fleming *et al.*, 1996, 1997); hence, wild-born offspring of farmed escapees may disperse introgression beyond physical obstacles for farmed escapees, such as difficult-to-pass waterfalls. Furthermore, first-generation off-

spring of farmed salmon showed higher straying rates than native salmon when released as smolts in the river (Jonsson and Jonsson, 2017), and may, thus spread introgression to rivers where the proportion of direct farm escapees is very low.

Another temporal component to consider is the genetic change that takes place in the farmed salmon across generations. Farmed salmon are changing genetically over time because of selective breeding for economically important traits (Gjedrem and Baranski, 2009), because of the general process of domestication, i.e. adaptation to the captive environment, and genetic drift. One might argue that selective breeding and adaptation to the captive environment will eventually lead to farmed salmon being unable to complete a life cycle in the natural environment. Theoretical models suggest that the highest impact of escaped farmed individuals on the viability of wild salmon populations is at intermediate levels of genetic difference between them (Baskett and Waples, 2012; Huisman and Tufto, 2012). Despite the reduced fitness of farmed individuals in the wild, the most recent data suggest that escaped farmed salmon are still able to enter salmon rivers and successfully reproduce (Diserud et al., 2020; Pulg et al., 2021; Karlsson et al., 2021).

We identified *a priori* a list of variables (Table 1) that might be important for determining the occurrence of escaped farmed salmon and level of introgression. For several reasons, not all of these variables were included in our final models. First, some were applicable to only a single or few rivers or populations and were, therefore, not suitable for modelling generic factors at the national scale but might be interesting to study in detail for a better understanding of underlying mechanisms. One example is seasonal environmental variation in rivers, such as long winters, that may affect juveniles of varying pedigree differentially as they grow older (Wacker et al., 2021). Second, other variables were excluded due to limited data quality. One example is predation pressure on juvenile salmon, as predation is one mechanism by which offspring of escaped farmed salmon may show higher mortality than offspring of wild salmon (Solberg et al., 2020), but which we cannot so far sufficiently quantify. Third, some variables are highly intercorrelated and could, thus be interchanged in the models without much change in the explanatory power of the models.

### Predictors for proportions of escaped farmed salmon

We found that the *Incidence index* of escaped farmed salmon in rivers was associated with farming intensity as well as river and population specific features, with population size, water discharge, and the relative spawning target being the most important predictors (Table 2). This model explained 43% of the variance in the *Incidence index*. Farming intensity is associated with escapees during post-smolt to adult stage from ocean farms (Thorstad et al., 2008). Norway's statistics on escapes from aquaculture, based on mandatory reporting of escape events and numbers by fish farmers (<http://www.fiskeridirektoratet.no/Akvakultur/Tall-og-analyse/Roemningsstatistikk>), was not used as input in the models for escaped farmed salmon in rivers. There are at least two reasons for this. First, it was shown that for the years 1989–2004 the regional (county) number of farmed fish in net pens was a better predictor for escaped farmed salmon in rivers than the reported escapes in the same regions (Fiske

et al., 2006), a result later supported by Mahlum et al. (2021). Second, studies have shown that the reported number of escapees may be an underestimation of the actual number of escapees; Skilbrey et al. (2015) found the actual number of escapees to be two to four times larger than reported during the period 2005–2011. Underestimation of the reported numbers is supported by the fact that high numbers of farmed escapees can be found where no escape event has been reported (Quintela et al., 2016), and furthermore, that DNA methods to trace the source of unreported escapees have been used by the Norwegian authorities on multiple occasions (Glover et al., 2008; Glover, 2010). The Norwegian Directorate of Fisheries states on their home page that the escape statistics must be viewed as estimates and that numbers are uncertain even when based on counting fish left in the net after escape (<http://www.fiskeridirektoratet.no/Akvakultur/Tall-og-analyse/Roemningsstatistikk>).

Estimates from the years 2010–2018 suggested that escapes from land-based facilities made up 7% and net pens 92% of the number of escapes in Norway (Føre and Thorvaldsen, 2021). Escapes from freshwater facilities may be more common in Scotland and Ireland, where more juveniles are reared to the smolt stage in net pens in lakes and where they have been shown to contribute to introgression (Clifford et al., 1998a; Gilbey et al., 2021), if not to the escape statistics.

The *Incidence index* of escaped farmed salmon increases with increasing average river discharge. This result was also found in an analysis of escaped farmed salmon in western Norway based on counts of escaped and farmed salmon in rivers (Mahlum et al., 2021), and in reports with preliminary modelling of the all-of-Norway analyses presented here (Fiske et al., 2013; Hindar et al., 2018). Also, Johnsen and Jensen (1994) found when studying the spread of furunculosis from an outbreak in fish farms that the disease spread faster with escaped farmed salmon to large rivers than to nearby small rivers.

The main reason for the positive association with river discharge is likely that higher discharge is an increasingly stronger signal for escaped farmed salmon, which are essentially homeless when escaping from net pens in the sea (Hansen, 2006), although most end up in rivers in the same region they escaped from. Discharge is also positively correlated with wild salmon body size (Jonsson et al., 1991) and late-escaping farmed females can be c. 40% bigger than co-occurring wild females (Hindar et al., 2006). On the other hand, offspring of escaped farmed salmon have also been found in smaller rivers than those analyzed in the present study, including those primarily dominated by sea trout *Salmo trutta* (Pulg et al., 2021).

Population size had a positive effect on the number of escapees ascending rivers (Supplement S3) and a negative effect on the proportion of escapees in the river (Table 2). Because population size may vary among years, the general effect on variation among rivers will only become apparent over many years. In western Norway, Mahlum et al. (2021) showed that wild salmon spawner abundance was an important predictor of escapee abundance and suggested that escaped farmed salmon, without a native river (Hansen, 2006), might follow wild migrants from the coast to the river. While this is possible, it cannot be the only explanation because some escaped farmed salmon may often enter rivers after the wild salmon run. More importantly, our model showed that population size has a “thinning effect” on the *Incidence index* of escaped

farmed salmon, i.e. the proportion decreases with increasing population size, and this should not be the case if escaped farmed salmon followed maturing wild salmon at random. Also, Hesthagen *et al.* (2011) showed that in formerly acidified rivers, salmon populations recovered more rapidly after liming in rivers with releases of juvenile salmon than in rivers with only natural colonization. The smell of salmon may, therefore, be an attractant (Jonsson *et al.*, 2003).

The relative spawning target enters as a factor in our model by increasing the expected *Incidence index* in rivers that have a high spawning target relative to neighbouring populations that may compete for the same pool of escapees in a fjord or a coastal region. Whereas escaped farmed salmon may be attracted to large rivers with abundant salmon populations, they may also seek a smaller population when there are no larger populations around, i.e. the relatively largest population in the region.

### Predictors for level of introgression

We found that the level of introgression was strongly related to proportion of escaped farmed salmon in the rivers and that a model for contemporary  $\text{logit}(P(\text{Wild}))$ , where pre-introgression level and expected *Incidence index* were accounted for, explained 45% of the variance in introgression (Table 3). This means that long term introgression can be modelled from the small number of predictors.

Still, a considerable amount of the variation in introgression remains unexplained. We modelled the residuals from the  $\text{logit}(P(\text{Wild}))$  model (Table 3) to see which predictors that could potentially shed light on the unexplained variation and found that phylogenetic group and upriver migration obstacles could be associated with susceptibility for introgression (Table 4). They were both significant but only accounted for 16% of the residual variance. Although potentially important for some rivers, these predictors may have a low influence on a large-scale model if they vary little for most of the populations.

The association between *Obstacle* and  $P(\text{Wild})$ -residuals was positive, suggesting that wild salmon populations having to pass obstacles close to the river mouth are less susceptible to introgression. The behaviour of escaped farmed salmon within rivers differs from wild salmon both in spatial distribution and within-river migration (Moe *et al.*, 2016). Farmed escapees are known to accumulate below migration obstacles, likely because they lack a “stop signal” in the river that native salmon may recognize as a home area (Thorstad *et al.*, 1998). Obstacles in the rivers, such as waterfalls and fish ladders, appear to prevent escaped farmed salmon from entering the upper parts (Anon, 2020). Although obstacles in the present study are pragmatically defined as proportion of anadromous section above first migration obstacle encountered, an obstacle for an escaped farmed salmon is likely to be very different between farmed salmon that escaped early and have spent a long time at sea and newly escaped one. In the River Målselva, northern Norway, fewer escaped farmed salmon have been observed above compared to below a fish ladder, but this has not translated into a lower level of introgression in adult salmon in the upper part of the river (Svenning *et al.*, 2021). This result is somewhat different from Sylvester *et al.* (2018), who found that migratory challenges may restrict the introgression of escaped farmed salmon in upstream spawning sites and from Bradbury *et al.* (2020) who found that, in a

model-based approach, waterfalls far down in the river could play a major role in observed introgression and numbers of escapees. The most likely explanation for this difference is that, even though the functional role of obstacles for the *Incidence index* of escaped farmed salmon seems similar in Norwegian and Newfoundland rivers, the longer history of introgression by farmed escapees in Norway results in accumulated introgression, which spreads into the whole population and to all spawning areas in the river.

The TZ between NEA and BS salmon in Norway is very sharp (Wennevik *et al.*, 2019; Diserud *et al.*, 2020). Wennevik *et al.* (2019) suggested that local environmental conditions in the TZ, with no obvious barriers to gene flow, are strong enough to maintain the genetic differentiation between them. If so, farmed salmon that originate from the NEA group (Karlsson *et al.*, 2016) should also be less successful in the BS group, which they are (Table 4). In contrast, phylogenetically admixed populations from the TZ seem more susceptible to introgression, after escapee incidence has been accounted for. Populations from the BS group have been demonstrated to migrate further east in the ocean than populations from the NEA group (Rikardsen *et al.*, 2021), and the two phylogenetic lineages could, thereby, differ in ecology (Kjærner-Semb *et al.*, 2016). This is supported by the finding that the marine life history changes more, or differently, with introgression in BS salmon than it does in NEA salmon (Bolstad *et al.*, 2017).

The higher susceptibility to introgression in the TZ is harder to explain. However, the small number of population samples in the TZ means that this result should be interpreted with caution.

### Limits to analysis of predictors

The limited number of factors determining introgression at the broad national scale, modelled in this study, means that we might have missed factors that are important in limiting introgression in some specific rivers and populations. This possibility is supported by the fact that our models show poor predictive ability for the lower  $P(\text{wild})$  levels and the higher escapee proportion observations (Figure 2).

Some of the unexplained variation might be found in haphazard combinations of river and population specific predictors, and the magnitude, timing, and type of escapees (Hamoutene *et al.*, 2018). A considerable, and variable, fraction of the escapees may be immature, affecting river migration behaviour, catchability, and reproduction. Factors like escapee acclimatization (time since escape), timing of spawning of wild salmon (Lura and Sægrov, 1991b), and spatial distribution of spawning grounds relative to migration obstacles may have to coincide to determine escaped farmed salmon spawning success. Aronsen *et al.* (2020) found that catches of escaped farmed salmon on the coast and in fjords came from several escape events over many years, and about half had one or more winter zones after escape. Madhun *et al.* (2017) showed, using fatty acid profiling and genetics, that escapees from multiple sources and ages entered a river in a single year. Some of the introgression may come from strayers from other rivers; Jonsson and Jonsson (2017) found that hybrids between wild and farmed salmon had a higher straying rate than pure wild salmon. In contrast, Skaala *et al.* (2019) found no difference in straying rate among offspring types. In addition to the rivers defined as salmon rivers, there are many small streams where spawning of salmon occasionally occur

and in some of these, escaped farmed salmon can be very successful and produce many offspring (Pulg *et al.*, 2021) that may stray to larger rivers.

The regression coefficients are expected to be underestimated due to measurement and sampling uncertainty (Carroll *et al.*, 2006), so better accuracy for presumed important variables is expected to improve model predictions. Some potential predictors were excluded from Table 1 due to limited data quality and will require more and improved collection efforts to become applicable, while other variables may be regarded as proxies for unmeasurable factors, and therefore, only partly describe the functional relationships. Populations that are excluded from the model calibration due to missing observations are on average much smaller than those included, so models may also be biased towards the situation in larger populations.

### Marine protected areas

The protection of wild salmon populations in Norway was suggested in the Norwegian Official Report (NOU, 1999) to consist of general measures to protect the most important wild salmon populations combined with actions in all aspects of society that affected wild salmon negatively. The general measures were the establishment of 52 National Salmon Rivers (out of Norway's c. 450 salmon rivers) and 29 National Salmon Fjords by the Norwegian parliament in 2006 (Anon., 2006).

Karlsson *et al.* (2016) found that when all populations were given equal weight, average introgression levels were the same in populations within National Salmon Fjords as in rivers outside these protection areas. When averages were weighted with population size, the introgression level was almost doubled outside the protection areas. The effect of National Salmon Fjords on introgression, therefore, works through the major predictor variables listed in Table 1. The conclusion of a Norwegian report that evaluated National Salmon Rivers and National Salmon Fjords after 10 years (Hindar *et al.*, 2018) was that the protective measures taken by the Norwegian parliament could delay the negative effects of escaped farmed salmon on wild populations but not prevent them.

In the present model, farming intensity was an important predictor for proportion of escaped farmed salmon in the rivers. We found only minor differences in the distribution of farming intensity between salmon rivers inside and outside National Salmon Fjords (Figure 3b). This is not surprising as the 29 National Salmon Fjords vary in area from 16 to 1526 km<sup>2</sup> (Serra-Llinares *et al.*, 2014). In conclusion, we believe that in order to further delay introgression into wild salmon populations, many protected areas should be increased in size, such that they could sufficiently reduce the number of escaped farmed salmon in rivers in these areas.

### Supplementary data

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

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### Data availability statement

No new data were collected in the course of this study. The data underlying this article can be accessed from sources in the public domain. The proportions of escaped farmed salmon in wild salmon populations (*Incidence index*) are described in Diserud *et al.* (2019), Glover *et al.* (2019), and in annual reports from the Institute of Marine Research on escaped farmed salmon in rivers (Reports | Institute of Marine Research (<https://www.hi.no/en/hi/nettrapporster>)). Data on genetic introgression are described in Karlsson *et al.* (2016) and Diserud *et al.* (2020). Data on salmon aquaculture locations and production are courtesy of the Norwegian Directorate of Fisheries. Additional data references can be found in Table 1. The data may be shared on reasonable request to the corresponding author, with permission of the Norwegian Directorate of Fisheries.

### Authors' contributions

OHD, KH, PF, SK, and KAG conceived the ideas and designed the methodology and analyses. All co-authors participated to the data collection. OHD, PF, SK, and KH analyzed the data. OHD, KH, PF, and SK drafted the manuscript. OHD, KH, PF, SK, KAG, and TFN revised the manuscript with additional contributions from the remaining authors. This manuscript is submitted with the approval of all the authors.

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