




Regional and temporal variation in escape history of Norwegian farmed Atlantic salmon

Nina Strand ¹, Kevin A. Glover¹, Sonnich Meier¹, Fernando Ayllon¹, Vidar Wennevik¹, Abdullah Madhun¹, Øystein Skaala¹, Kristin Hamre¹, Per Gunnar Fjellidal ², Tom Hansen², Eero Niemelä^{3,4,5}, Sofie Knutar¹, Per Tommy Fjeldheim¹, Monica F. Solberg ^{1,*}

¹Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway

²Institute of Marine Research, Matre Research Station, Matre 5, 5984 Matredal, Norway

³University of Turku, Biodiversity Unit, 20014 Turku, Finland,

⁴Tmi Olli van der Meer, Hiomonkatu 14, Haukipudas, Finland

⁵County Governor of Troms and Finnmark, Damsveien 1, 9800 Vadsø, Norway

*Corresponding author. Tel: +00 47 922 98 650; E-mail: monicafs@imr.no

Abstract

Each year thousands of farmed Atlantic salmon escape from seawater net pens, and introgression has been documented in a range of wild populations. Due to greater experience in the wild, escapees that have been on the run for a longer period, and successfully transitioned to a wild diet (classified: “early escapees”), could potentially have a higher spawning success and contribute more to introgression than those that have been on the run for a shorter period and/or have not transitioned to a wild diet (classified: “recent escapees”). This is the first study to examine how the escape history of farmed Atlantic salmon captured in multiple rivers and coastal fisheries, varies in time and space. During 2011–2021, adult farmed escaped salmon were captured in four rivers and at six coastal sites in Norway. The level of linoleic acid, a terrestrial fatty acid high in commercial salmon feeds but low in the natural diet of wild salmon, was used to classify the farmed salmon as early or recent escapees. We observed temporal declines in the relative proportions of escaped vs. wild salmon in the catches, and the relative proportion of early vs. recent escapees in the most southern river (driven by samples from 2011 to 2015). Overall, 14% of the escaped salmon caught in the period were classified as early escapees. The relative proportion of early escapees was lower in the two southernmost rivers (21.2% and 6.30%), as compared to the coastal fisheries (40.9%) and the northernmost river (77.6%). Both aquaculture–management regulations and production strategies have likely influenced these observations.

Keywords: salmon farming; aquaculture management; escaped farmed salmon; domestication; chemical markers; fatty acids; genetic introgression; *Salmo salar*; environmental impacts; lipids

Introduction

Farmed Atlantic salmon (*Salmo salar* L.) escapees pose several threats to wild populations, with interbreeding with wild salmon being of the most concern (Forseth et al. 2017, Glover et al. 2017). Farmed salmon represent a threat to the genetic integrity of wild salmon populations as they differ from their wild conspecifics in a broad range of traits (Glover et al. 2017). It is well-documented that escapees can spawn and produce viable offspring in the wild (Sægrov et al. 1997, Clifford et al. 1998, Crozier 2000, Glover et al. 2013, Karlsson et al. 2016), and that introgression can have multiple impacts on recipient wild populations, including the reduction of interpopulation genetic structure (Skaala et al. 2006, Glover et al. 2013) and changing life history traits (Bolstad et al. 2017, 2021, Besnier et al. 2022). The offspring of farmed salmon have also been shown to be more susceptible to predation (Solberg et al. 2020), which may contribute to why they have been found to have higher levels of mortality compared to the progeny of wild salmon in the natural environment (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019, Sylvester et al. 2019, Wacker et al. 2021). Ultimately, any selection against pure farm or genetically introgressed individuals in wild populations (Wringe et al. 2018, Sylvester et al. 2019, Wacker et al.

2021) could lead to reduced productivity (Castellani et al. 2018).

A correlation has been found between the relative abundance of escapees in rivers and the level of introgression (Heino et al. 2015, Karlsson et al. 2016, Keyser et al. 2018, Diserud et al. 2022). However, these analyses do not explain all of the variance in introgression rates among rivers. One of several factors, which has been suggested to contribute to the observed patterns in interpopulation introgression rates from farmed salmon is escapee acclimatization (Diserud et al. 2022). While a lower spawning success has been demonstrated in farmed as compared to wild salmon (Fleming et al. 1996, 2000) it is possible that escapees, which escaped as smolts or postsmolts and migrated to and from the oceanic feeding grounds before entering a river to spawn, are better competitors and have a higher spawning success than escapees that escaped from a farm more recently prior to entering a river. Variation in maturation status between escapees that have been on the run for an extended period of time and acclimatized to the wild diet vs. those that have not acclimatized, has also been documented (Madhun et al. 2023). Thus, a better understanding of the escape history of farmed escapees and how this varies in time and space, could potentially contribute toward elucidating the unexplained variation in introgression levels.

The total global farm production of Atlantic Salmon was 2.7 million tonnes in 2020 (FAO 2022), with Norway being the largest producer at 1.39 million tonnes (Norwegian Directorate of Fisheries 2023). The standard method of producing farmed salmon in Norway involves rearing them from smolt to market size in open net pens in the marine environment. These net pens are prone to unintentional release of fish, following small- or large-scale escape events, including unobserved drip effect of fish into the environment. Between 2011 and 2021, 1.73 million farmed salmon were reported to have escaped from salmon farms in Norway (Norwegian Directorate of Fisheries 2022). There has been an overall decline in the reported number of escapees in recent years, despite a simultaneous increase in production. This decline has been linked to the implementation of the Norwegian technical standard NS9415 for sea-based fish farms in 2004 (Jensen *et al.* 2010). However, the reported numbers of escapees are hard to quantify (Norwegian Directorate of Fisheries 2022) as escape events may be unreported or undetected by fish farmers (Skilbrei and Wennevik 2006, Glover 2010, Zhang *et al.* 2013). During the period 2005–2011, 2.89 million farmed salmon were reported to have escaped, while the actual number was estimated to be 2–4 times higher (Skilbrei *et al.* 2015a). Furthermore, the deviation between reported and estimated numbers were probably largest for salmon escaping shortly after marine transfer as smolts as opposed to fish escaping later in the production cycle (Skilbrei *et al.* 2015a). In particular, the loss of smolts and postsmolts escaping through cages with too large mesh sizes (Harboe and Skulstad 2013) are likely to go unreported, as they are difficult to detect.

Farmed salmon escapees can be distinguished from wild salmon through scale reading (Lund *et al.* 1991) and from other morphological traits such as spotting patterns (Jørgensen *et al.* 2018). Relatively recently, a fatty acid (FA)-based method was developed to characterize escapees in relation to those escaping early during the aquaculture production cycle and had converted to a natural marine diet (classified as “early escapees” by Skilbrei *et al.* 2015b) vs. those that had escaped later in the production cycle and/or had not transitioned to a marine diet (classified as “recent escapees” by Skilbrei *et al.* 2015b). The FA method is based upon detecting the presence of high levels of linoleic acid, a terrestrial FA, typically found in commercial aquaculture feeds. Levels of this terrestrial FA have increased in commercial feed in recent years (Aas *et al.* 2019, 2022). In the present study, we further validate the FA method in two controlled experiments, and thereafter, used it to investigate the escape history of > 900 adult farmed salmon captured in four rivers and six coastal fisheries in Norway during the period 2011–2021. Finally, regional variation in the relative proportion of early escapees was investigated up against regional variation in out-of-season smolt transfer (here defined as smolts transferred to sea between August and March), a production strategy, *i.e.* associated with reduced survival post escape, as compared to in-season smolt transfer (Skilbrei 2013).

Materials and methods

Sampling

During the period 2011–2021, a total of 947 adult farmed escapees and 1442 wild Atlantic salmon were sampled in four rivers (Vestre Jakobselv, Namsen, Etne, and Suldal) and from

six coastal fishing stations in Norway (Fig. 1). Tissue (adipose fin or muscle tissue) and scales were sampled from all fish, and weight and length were measured. All tissue samples were shipped frozen to the Institute of Marine Research in Bergen at the end of the fishing season and stored at -80°C until FA analysis could be carried out. Scales were read by a skilled laboratory technician in order to separate the salmon into farmed escapees and wild salmon as in Lund *et al.* (1991). The salmon were further divided into wild, early escapees, intermediate escapees, and recent escapees based on a combination of scale readings and FA profiling. These groups are hereafter referred to as salmon group(s).

Validation of the time-since-escape methodology I: the feed experiment

FA profiles obtained from a feed experiment executed at Matre Research Station (IMR), Western Norway, were used as a quality control to account for potential changes in level of linoleic acid (18:2n-6) in feed since the start of this project in 2011. The experimental protocol (permit number 20211) was approved by the Norwegian Animal Research Authority and performed according to the Norwegian Animal Welfare Act. All personnel involved in the experiment had training approved by the Norwegian Food Safety Authority, as mandated by the Animal Welfare Act. Adult salmon were either given a standard commercial grow-out ($N = 18$) or broodstock feed ($N = 36$) during the marine rearing (as a measure of level of linoleic acid to be expected in recent escapees). The two feeds were included, as the brood stock feed is expected to be higher in marine FAs. Sampling took place throughout the course of the study from January 2020 to June 2021 (Supplementary Table S1); the fish were terminated prior to sampling at an average weight of 7.76 kg (range: 2.04–15.1 kg).

Validation of the time-since-escape methodology II: the hatchery-release experiment

Smolts used in this study was part of a large-scale release experiment (~20 000 individuals) and were from wild-origin broodfish collected in the river Etne, Western Norway. Smolts were produced following standard aquaculture protocols at the IMR research station in Matre (Solberg *et al.* 2013). Smolts were PIT-tagged prior to being released at the mouth of the river Etne in May 2018 and 2019. Returning adult salmon were captured by a fish trap in the river in 2020 [1 sea winter (SW), $N = 10$] and 2021 (2 SW, $N = 10$). Muscle tissue for FA analysis was collected from these released fish, both from 20 smolts prior to release (as a measure of level of linoleic acid in smolts prior to sea transfer) and from 20 adults upon return as detailed above (as a measure of level of linoleic acid to be expected in smolt escapees after one or two years on a natural diet, *i.e.* early escapees). The experiment was approved (permit number 14503) by the Norwegian Food Safety Authority, as mandated by the Animal Welfare Act.

FA analysis

Adipose fin or muscle tissue was used for FA profiling of the body fat store triacylglycerol (TAG) following the recommendations from Olsen *et al.* (2013). Lipids were extracted using the Hara method (Hara and Radin 1978) with the modifications of extraction and HPLC separation methods described in Madhun *et al.* (2017). The TAG fraction was methy-

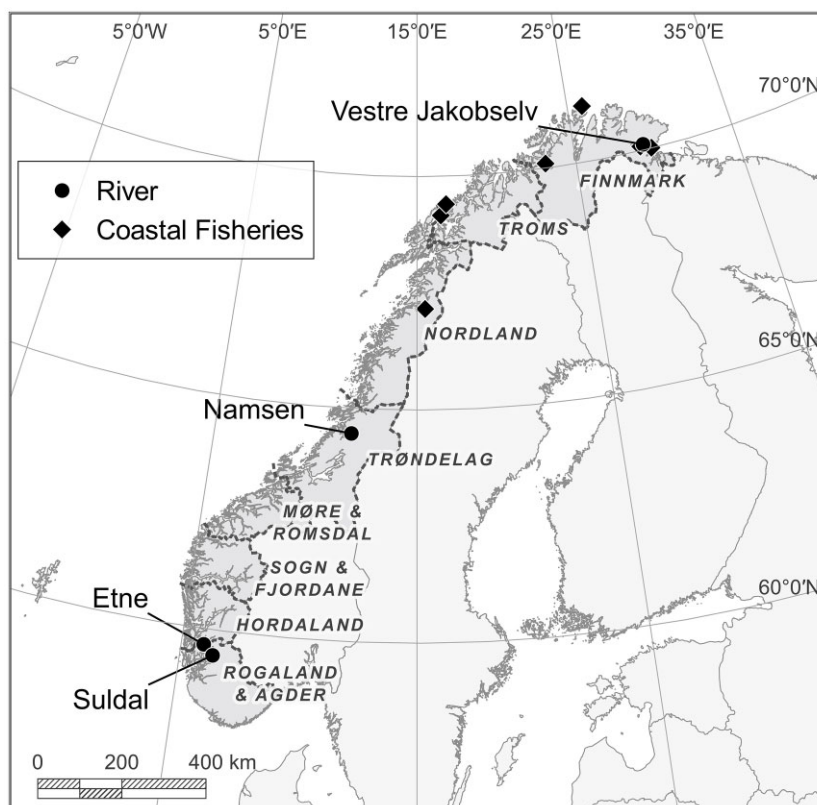


Figure 1. Map of Norway showing sampling locations. The sites of collection varied between years; Vestre Jakobselv (2012–2019), coastal fisheries (2012 and 2020), Namsen (2018–2021), Etne (2014–2021), and Suldal (2011–2015, 2018–2019, and 2021).

lated, the resulting FA methyl esters (FAME) were extracted with hexane before being analyzed on a HP-7890A gas chromatograph (Agilent, USA) with a flame-ionization detector (GC-FID) as previously described in Meier et al. (2006). The chromatograms were integrated using the software OpenLab EXChrom (Agilent Technologies, USA). The method can distinguish between 97 different FAs that are identified based on a comparison of retention time with standard mixtures of FAME, retention index card, and mass spectrum library (GC-MS; <http://www.chrombox.org>). Data are presented as FA profiles (% of total FAs). FAs were standardized across the different years and study sites, with only the FAs, which were common for all samples being kept. Subsequently, only the 51 FAs, which had a mean value above 0.2% within at least one of the salmon groups in one of the study sites were chosen. The adult farmed escapees, as confirmed by scale reading, were further divided into early, intermediate, and recent farmed escapees based on the percentage of the terrestrial FA 18:2n-6 as described in Skilbrei et al. (2015b): escapees with < 2.5% were classified as early escapees (fully transitioned to the marine diet), escapees with 2.5%–7% were classified as intermediate (transition to a marine diet initiated but not completed) and escapees with > 7% were classified as recent (FA profile still reflecting the commercial aquaculture diet).

Data on the commercial use of out-of-season smolt

To investigate the potential association between regional aquaculture practices and the relative proportion of early vs. late escapees observed in rivers, we collected data on the use of out-of-season-smolts vs. in-seasons smolts (see Skilbrei 2013).

These data were transformed into the proportion of smolt transferred per month per county annually. The season for smolt migration from rivers differs between the north and south but was here defined as April through July. Smolts transferred during the rest of the year were defined as out-of-season smolts. These data were downloaded from the Norwegian Directorate of Fisheries and included the number of smolt transferred to net pens per month per county from 2011 to 2019. Only the counties where rivers from the current study are located, as well as the national average, were included; i.e. Rogaland and Agder (Suldal), Hordaland (Etne), Trøndelag (Namsen), and Finnmark (Vestre Jakobselv).

Removal of outliers

Individuals with a condition factor smaller than 0.6 ($N = 20$) or larger than 1.8 ($N = 9$) were removed from the data set. A total of three wild individuals were grouped as recent ($N = 1$) or intermediate ($N = 2$) escapees due to high levels of 18:2n-6. These individuals were removed from the data set, as the discrepancies between scale reading and their FA profiles indicated a human error in data registration.

Statistical analysis

Statistical analyses were performed using R version 4.0.0. (R Core Team 2020). Graphics were produced with *ggplot2* (Wickham 2011) in combination with the following packages: *grid*, *gridExtra* (Auguie 2017), *ggpubr* (Kassambara 2020), and *factoextra* (Kassambara and Mundt, 2020). Generalized linear models (GLM) were plotted using *sjPlot* (Lüdtke 2021). Model fitting was done using the packages *lme4* (Bates

et al. 2014) and *lmerTest* (Kuznetsova et al. 2017). *MuMIn* was used for model selection (Bartoń 2022) and *emmeans* (Lenth 2021) was used for pairwise comparisons. Additionally, the packages *stringr* (Wickham 2019), and *tidyverse* (Wickham et al. 2019) were used for data manipulation.

Models

The effect of area and year on the proportion of (i) escaped relative to wild salmon and (ii) early relative to recent escapees in the sample sets, was investigated using binomial GLMs with an area-by-year interaction term. Intermediate escapees were excluded from analysis ii since few individuals fell into this category. Due to the low sample size escapees collected in the river Namsen were excluded from analysis (ii). Principal component analysis (PCA) was performed, including all individuals with FA data, using the function *PCA* from *FactoMineR* (Lê et al. 2008) and visualized as a biplot using the package *factoextra* (Kassambara and Mundt, 2020). The spatial and temporal use of out-of-season smolt in commercial production was investigated using a linear model (*lm*) with county and year as the predictors, and also including a county-by-year interaction term.

Model selection and validation

The models were assessed using the second-order Akaike Information Criterion (AICc). Model selection was done using backward selection through the package *MuMIn* (Bartoń 2022). The best model was defined to be the model with the lowest AICc score. Due to the principle of parsimony, the simplest model was chosen if the AICc scores were < 2 apart. The linear model was validated by checking for patterns in the residuals, in respect of the predicted values. The significance of the predictor variables and interactions in the GLMs were investigated using ANOVA with a chi-square test. Pairwise comparisons within the groups were performed using a Tukey's *post hoc* HSD test in *emmeans* (Lenth 2021).

Results

Overall proportion of escapees in rivers and coastal fisheries

The overall proportion of escapees observed in the rivers and coastal fisheries studied here declined in the period 2011–2021 (GLM: year, $P < .0001$; Fig. 2). Differences in the proportion of escapees were detected among sampling areas (GLM: area, $P < .0001$; Fig. 2), and although most areas included in this study have experienced a decline in the proportion of escapees, there were individual differences between them in the degree of the decline (GLM; area-by-year, $P < .0001$). A stronger decline was detected in the samples from Suldal than in the other areas (all pairwise comparisons $P < .05$), except for Namsen where there is a small increase in the more limited dataset (2018–2021, a total of five escapees, pairwise comparison $P > .1$).

Validation of the time-of-escape methodology

A PCA in respect of all salmon groups, including farmed fish on grow-out feed and broodstock feed (from the feed experiment) and released smolt and recaptured adult salmon (from the hatchery-smolt release experiment), was fitted to identify

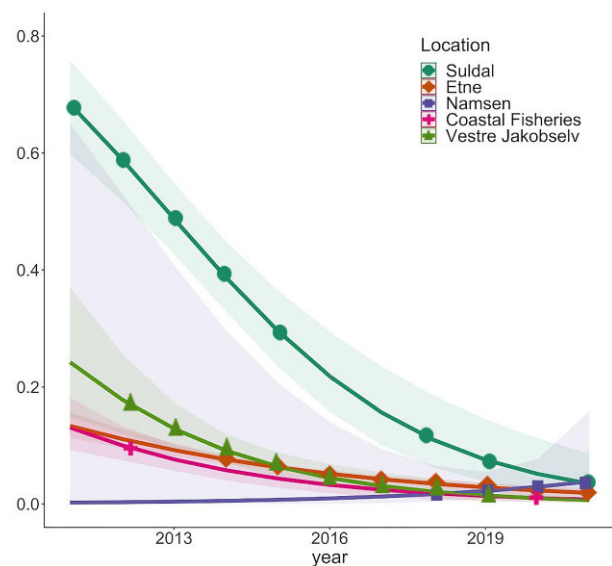


Figure 2. The proportion of escaped salmon from 2011 to 2021 in the studied rivers. The model shows the expected value (solid line) as well as the 95% confidence interval (shaded area) and which years the different locations were sampled (dots).

the main differences in the FA profile of salmon with aquaculture and wild diets (Fig. 3). PC1 explained 49.8% of the variation among the individuals and identified the terrestrial FAs 18:2n-6, 18:1n-9, and 20:2n-6, as well as 20:0 and 18:1n-5 as contributing the most to the overall observed differences in FA between escaped and wild salmon in PC1. Whereas PC2 explained 10.8% of the variation, there was no separation between the different salmon groups but contained large individual variability. Overall, the PCA shows that the recently escaped salmon had similar FA profiles to the individuals on grow-out and broodstock feeds (from the feed experiment), and all had negative PC1 scores, i.e. were dominated by terrestrial FAs (18:2n-6, 18:3n-3, and 18:1n-9) as well as their elongation products (20:2n-6 and 20:3n-3). In contrast, the early escapees, the recaptured salmon (from the hatchery release experiment), and wild salmon, had positive PC1 scores and were dominated by FAs typical of those acquired in the marine environment. Intermediate escapees were in-between the two with a mixture of negative and positive scores. The experimental smolt release group, prior to its release, clustered with the intermediate escapees, but had similar to recent escapees, only negative scores i.e. more terrestrial FAs.

Adult farmed salmon on grow-out feed had an average 18:2n-6 level of 14.59% (range 14.08–15.20), while the corresponding levels of farmed salmon on broodstock feed were 12.20% (range 10.63–13.82). Smolts prior to sea water transfer had an average 18:2n-6 level of 7.69% (range 6.57%–8.75%), while returning adults from the smolt releases had an average 18:2n-6 level of 1.35% (range 1.35%–1.65%).

The relative proportion of early vs. recent escapees captured in rivers and coastal fisheries

In total, 131 early, 36 intermediate, and 766 recent escapees were caught during the study period in the four rivers and six coastal fisheries. Except for in 2011, recent escapees outnumbered early escapees in the data set. The ratio of early vs. recent

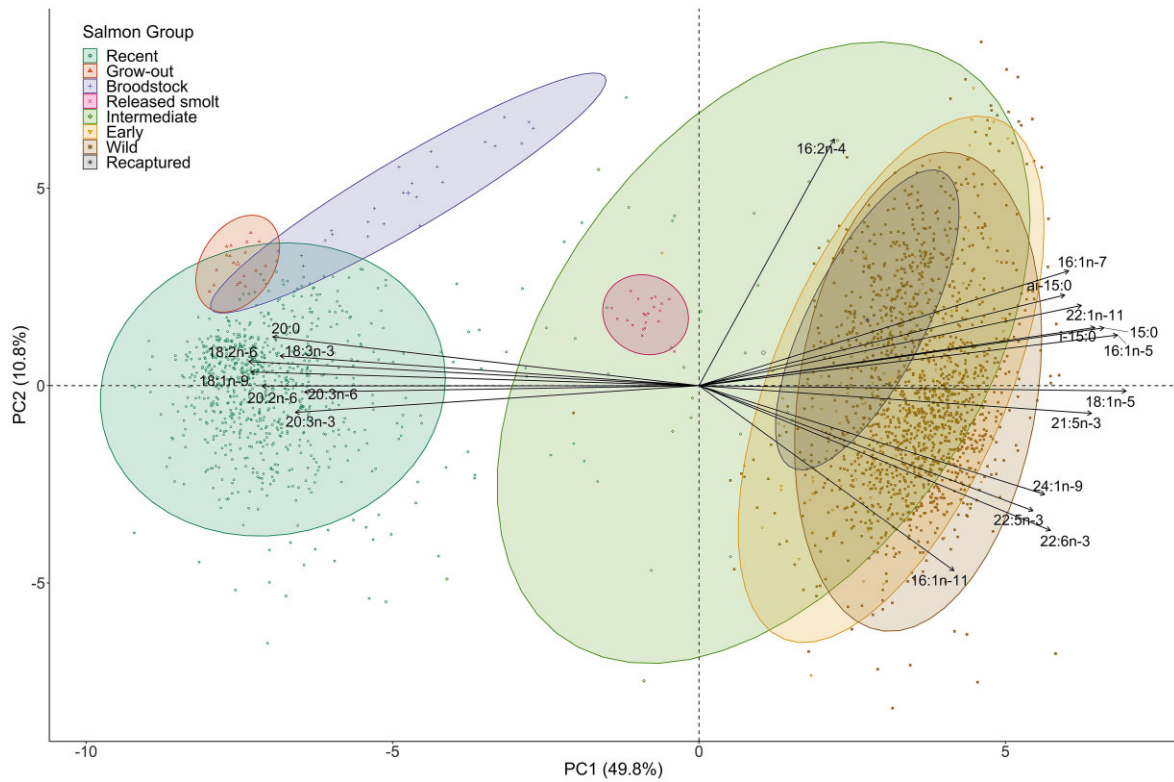


Figure 3. Biplot of the PCA of FA composition (% of total TAG) for recent escapees, intermediate escapees, early escapees, farmed fish on grow-out feed, farmed fish on broodstock feed, released smolts, recaptured released smolts, wild, and farmed salmon. Each point represents a single sample, the 95% confidence ellipses are of preassigned groupings (based on 18:2n-6 values and origin). The vectors depict the loadings to show the contribution and direction of the top 20 contributing FA.

escapees varied between the sampling locations (GLM: area, $P < .0001$; Fig. 4). The river Vestre Jakobselv in the north was dominated by early escapees (78%) whereas the river Etne in the south had very few early escapees (6%). The other rivers and the coastal fisheries had between 21% and 41% early escapees.

An overall temporal decline in the proportion of early relative to recent escapees was found (GLM: year, $P < .05$; Fig. 4), however, when examined across areas, the change in recent vs. early escapees varied (GLM: area-by-year: $P < .001$). In the rivers Etne and Suldal, negative slopes were detected (Fig. 4; GLM: Etne, $est. = -2.60$, $SE = 0.158$; GLM: Suldal, $est. = -3.73$, $SE = 0.758$). In contrast, positive slopes were detected in the coastal fisheries (2012 vs. 2020) and in Vestre Jakobselv (Fig. 4; GLM: Coastal fisheries, $est. = 0.209$, $SE = 0.572$; GLM: Vestre Jakobselv, $est. = 2.338$, $SE = 0.821$). However, only the river Suldal had a significant decline in the ratio of early to recent escapees (driven by samples from 2011 to 2015; $z = -3.47$, $P < .001$). The other locations showed no significant changes in the ratio of early to recent escapees over time ($P > .05$).

Geographical and temporal changes in the use of out-of-season smolt

Overall, the proportion of out-of-season smolts increased slightly over time in the counties included in the analysis as well as the national average (Fig. 5; LM: 2011–2019, $F = 22.0$, $P < .0001$). However, clear differences in the use of out-of-season smolts were also observed between counties (LM: county, $F = 64.3$, $P < .0001$). Out-of-season smolts were used

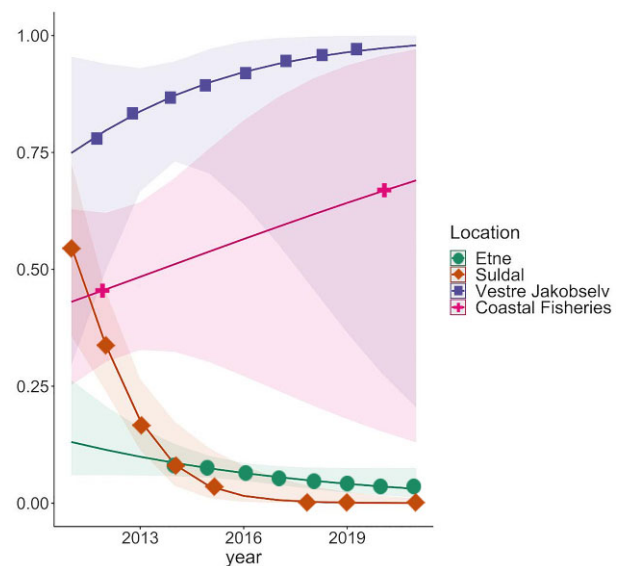


Figure 4. Variation in early escapees relative to recent escapees from 2011 to 2021 for each location. The model shows the expected value (solid line) as well as the 95% confidence interval (shaded area) and which years the different locations were sampled (dots). (Note large confidence intervals in VJ and CF; see Supplementary Table S2 for sample sizes)

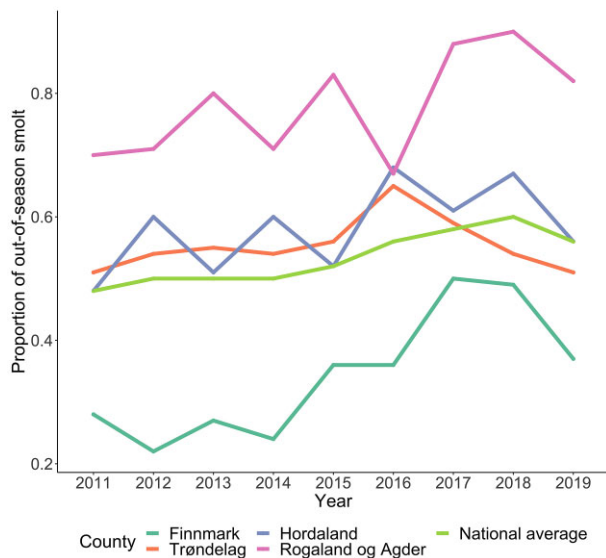


Figure 5. Overview over the use of out-of-season smolts (transferred to see August–March) in the commercial production of salmon in Norway by county from 2011 to 2019. (Data from: fiskeridir.no/Akvakultur/Tall-og-analyse.)

least in the north/Finnmark (all pairwise comparisons to other counties $P < .0001$), and greatest in the south/Rogaland and Agder (all pairwise comparisons to other counties $P < .0001$). The counties of Hordaland and Trøndelag, which are located between Rogaland and Finnmark displayed similar proportions to the national average (pairwise comparisons to national average $P > .05$).

Discussion

To our knowledge, this is the first study to examine how the escape history of farmed Atlantic salmon captured in multiple rivers and coastal fisheries, varies in time and space. Throughout the 10-year study period, the majority of escapees caught in rivers and coastal fisheries were classified as recent escapees and had not converted to a marine diet in the wild. However, this unique data set also revealed regional differences in the relative proportions of early vs. recent escapees, with higher proportions of early escapees in the northernmost locations as well as indications of regional variation in temporal declines. For example, the most precipitous temporal decline in the proportion of early escapees, relative to recent escapees, was found in Suldal, which is the southernmost river, over the period 2011–2021. Overall, these observations could reflect geographical and temporal differences in aquaculture practices as well as management actions that are discussed below.

Temporal decline in the overall proportion of escaped salmon

Across all sampling locations, including coastal stations and rivers, the overall proportion of escapees declined from 2011 to 2021. This is in accordance with the more comprehensive national monitoring program in Norway, which estimates the proportion of escapees in ~200 rivers annually (Diserud et al. 2019, Glover et al. 2019, Wennevik et al. 2021). The observed proportions of escapees in rivers are influenced by the number of wild salmon, and hence do not directly translate to number

of escapees. However, this data strongly suggest that there are now fewer farmed escapees in rivers that can interbreed and thus cause genetic interactions with wild conspecifics (Glover et al. 2017), and/or, partake in other ecological interactions (Bradbury et al. 2020). This nation-wide reduction in numbers of farmed escaped fish and the proportions of farmed escaped fish in rivers is important because there is a positive correlation between the proportion of escapees in rivers and the resulting level of introgression, implying that more escapees leads to greater levels of introgression (Heino et al. 2015, Keyser et al. 2018, Diserud et al. 2022), which in turn leads to greater changes in affected populations (Castellani et al. 2018).

In the current study, the rate of decline in the proportion of escapees observed in rivers and coastal fisheries was dependent on the location. The river Suldal displayed the largest decline in the proportion of escapees, most likely due to an overestimation in the proportion prior to 2015 and an underestimation post-2015, caused by the change in the fishing location from below to above a waterfall at the mouth of the river, i.e. difficult for farmed escaped salmon to pass (Urdal 2014). This change additionally contributed to the large decline in the proportion of escapees in the overall dataset. Escapees are known to accumulate below migration barriers such as waterfalls, most likely because many of them, especially the recent escapees with body conditions not acclimatized to the wild, are not able to pass the obstacle as easily as wild salmon. For the remaining rivers investigated in this study, the fishing (sampling) location remained unchanged across the study period, and thus reflects the overall decline in proportion of escapees as documented by the national monitoring program (Diserud et al. 2019, Glover et al. 2019, Wennevik et al. 2021).

Validation of the method to distinguish between recent escapees, early escapees, and wild salmon using FAs

The method for distinguishing time-since-escape is based on the FA profile farmed salmon acquire from consuming aquaculture feed (Skilbrei et al. 2015b). This feed may differ between producers and the types of feed (hatchery feed, grow-out feed, broodstock feed, and so on), and thus vary among fish farms (Olsen et al. 2013, Skilbrei et al. 2015b). Additionally, due to sustainability concerns and lower costs (Bell et al. 2004), commercial salmon feed has gone from 90% marine ingredients in 1990 to 71% plant-based ingredients in 2016 (Ytrestøyl et al. 2015, Aas et al. 2019). In the Norwegian salmon industry, rapeseed oil has primarily replaced the use of fish oils (Aas et al. 2019) markedly affecting the FA profile of salmon feed with levels of the terrestrial FAs oleic acid (18:1n-9), linoleic acid, (18:2n-6), and α -linolenic acid, (18:3n-3), which are several fold higher than in fish oils (Bell et al. 2003, Sprague et al. 2016). This has subsequently altered the FA profile of farmed salmon with a pronounced increase in the terrestrial FAs (Sprague et al. 2016). Consequently, the method used in this study, first established by Skilbrei et al. (2015b), was validated using salmon on commercial feeds of newer date as well as the release and recapture of hatchery reared smolts with known FA profiles. This analysis revealed that 18:2n-6 levels in adult farmed salmon caught in the wild, still accurately distinguish early escapees from recent escapees (Fig. 3). Furthermore, these analyses have validated that salmon escaping from broodstock facilities (broodstock

facilities represent $\ll 1\%$ of all commercial aquaculture production), that are fed a diet with a higher content of marine FAs, will also be identified as recent escapees shortly after escape. For smolts escaping from fish farms, the majority would also be identified as recent escapees if sampled shortly after escape, although the level of $18:2n-6$ are lower in smolts as compared to older individuals reared for a longer period of time under marine commercial rearing conditions. However, smolts are unlikely to seek entry into freshwater directly after escape (Skilbrei 2010a, b).

Experimental studies indicate that after approximately a year on a marine diet the escapee will be classified as an early escapee (Skilbrei et al. 2015b). The release and recapture of hatchery reared smolts presented here demonstrates that smolt escapees returning to freshwater one year after escaping will indeed be classified as early escapees. How long the elevated levels $18:2n-6$ at the time of escape is maintained in the wild, given assumed access to an entirely marine diet, is unknown. Also, if adult escapees were to remain close to the farm from which they escaped and consume surplus feed spilling out of the cage, their experience in the wild is likely to be similar to that of recent escapees. However, the time of escape significantly affects the survival, migration, and recapture of escapees and experimental releases of farmed salmon indicates that adults rarely survive for a year or longer postescape (Skilbrei et al. 2015a).

Time-since-escape: early vs. recent

Most escapees collected throughout the 10-year study were classified as recent (82%), while 14% were classified as early escapees. Only 4% of the escapees were classified as intermediate escapees, indicating that few escapes survive until maturation, if not escaping early (likely as smolts or postsmolts during the summer) or as adults close to maturation (Skilbrei et al. 2015a). Furthermore, we observed large regional differences in the relative proportion of early vs. recent escapees. For example, in the river Vestre Jakobselv, the northernmost river included in this study, 78% of the escapees were identified as early and this number was stable throughout the 8-year period this river got sampled (2012–2019). This stands in stark contrast to e.g. the river Etne in southern Norway where only 6% of the escapees were classified as early. Some 41% of the farmed samples collected from the six coastal fisheries in northern Norway, were composed of early escapees (the three southernmost locations had 20%–26% early escapees, while the three northern most locations had 60%–100% early escapees ($N = 3$ –19 per coastal location)). For the farmed individuals caught in Namsen in Mid Norway, 40% were early escapees ($N = 5$). This is consistent with the findings of Aronsen et al. (2020), who used scale reading to estimate the time-of-escape for escapees captured in the same fjord system as Namsen. In addition to geographical differences in the relative proportion of early vs. recent escapees, there was an area-specific temporal decline in this ratio. The southernmost river Suldal, experienced temporal declines in the relative proportion of early escapees, evident at the start of the study period (2011–2015).

Introgression of farmed escapees has been examined by genetic methods in all rivers included in this study (Glover et al. 2013, Karlsson et al. 2016, Diserud et al. 2020, Besnier et al. 2022). The river Etne has the highest documented introgression of farmed salmon of the rivers included in the present

study with a level of $\sim 20\%$ – 25% (Glover et al. 2013, Karlsson et al. 2016, Diserud et al. 2020, Besnier et al. 2022). In the rivers Namsen and Vestre Jakobselv, moderate levels of introgression at $\sim 5.5\%$ have been documented, whereas no introgression has been documented in the river Suldal (Diserud et al. 2020). The proportion of escapees in rivers, and thus the level of introgression has been shown previously to increase with farming intensity (Heino et al. 2015, Diserud et al. 2022), and the rivers included in this study are located in regions (production zones) with different farming intensities. The three southernmost rivers are located in production zones where farming intensity is more than tenfold higher than the production zone in which the most northern river, Vestre Jakobselv, is located (Norwegian Directorate of Fisheries 2022). Lower production intensity is related to lower incidences of farmed escapees (Diserud et al. 2022) and since salmon escaping as adults tend to remain locally while smolts disperse further (Skilbrei et al. 2015a) it is possible that this had an impact on the ratio of early vs. recent escapees, and that the early escapees detected in Vestre Jakobselv had not escaped from a local fish farm but from a farm further away in an area with higher production. This may inflate the ratio of early escapees, as new escape events in the vicinity of the river are less likely to occur just by chance when production intensity is low. In addition to farming intensity, the proportion of escapees and resulting levels of introgression have been demonstrated to increase with river discharge and decline with population sizes (Diserud et al. 2022).

Migration hinders close to the outlet of the river, such as difficult to pass waterfalls, lower the susceptibility of a wild population to introgression from farmed escapees (Diserud et al. 2022). This likely explains why escaped salmon have not introgressed in the wild population inhabiting the river Suldal, despite being located in a high intensity salmon farming area. In the river Suldal, only one farmed escapee was caught above the waterfall located in the lower reaches of the river. However, this individual was an early escapee, thus providing anecdotal evidence that early escapees have greater access to the upper reaches of the river i.e. the spawning grounds, and therefore suggests greater opportunity to spawn. A recent study has also shown that while only about half (55%) of the recent escapees were mature when they entered the fish trap in river Etne, almost all (96%) of the early escapees were mature (Madhun et al. 2023). Combined with the knowledge that early life experience, albeit in fresh water, has been shown to influence adult reproductive success in the wild (Fleming et al. 1997), variation in the proportion of early escapees between regions, and rivers, could potentially contribute to some of the unexplained variation in models investigating the drivers of introgression (Heino et al. 2015, Keyser et al. 2018, Diserud et al. 2022).

Impact of management and aquaculture practices

We suggest that both management and aquaculture production strategies have contributed to the decline in the proportion of escapees and to the observed regional differences in the proportion of early vs. recent escapees. These practices include efforts nationally to standardize mesh size relative to the fish (smolt) size, and the gradual shift from in-season smolt to also using out-of-season smolt transfers into sea cages. In 2009, the Norwegian regulations on the operation of aquaculture facilities were amended to state that the mesh size of the

net should be appropriate to fish size (Norwegian Ministry of Trade Industry of Fisheries 2009). What is appropriate is not specified, but recommendations for what mesh size to use has been available at the Directorate of Fisheries webpages since around 2006, and which has been further updated in 2013 and 2022 to incorporate new findings (Norwegian Directorate of Fisheries 2023). When this is properly implemented it is expected to reduce trickle escapes of smolts and postsmolts (Harboe and Skulstad 2013, Sistiaga *et al.* 2020). Thus, we suggest it is likely that the observed decrease in the relative frequency of early escapees in some of the sampling areas is at least in part linked to the recommendations for mesh size. This suggestion is difficult to validate as little is known about drip escape during this period of the production cycle as it is hard to detect and is therefore often likely to go unreported. Moreover, it is possible that the use of “supersmolts” (i.e. very large smolts) has worked in conjunction with reducing mesh size, since larger fish require larger holes to escape.

Over the past 15–20 years, the use of out-of-season, i.e. autumn, smolt production has increased in Norwegian salmon aquaculture (Norwegian Directorate of Fisheries 2022, Skilbrei 2013) (Fig. 5). Out-of-season smolts have been shown to have ~40 times lower survival rate than in-season smolts when escaping (based on the experimental recapture rates as adults reported by Skilbrei (2013) at which were 0.004% and 0.17%, respectively). Thus, a temporal increase in the use of out-of-season smolts may have contributed to the observations here that the frequency of early escapees has declined, in at least one area, in the period 2011–2021. The out-of-season smolt production strategy has been much less prevalent in Northern Norway than in Southern Norway (Norwegian Directorate of Fisheries 2023) (Fig. 5), which may be why the ratio of early relative to recent escapees was higher in the Northern populations than the Southern populations. Vestre Jakobselv had 78% early escapees and is located in a region where mostly in-season sea pen smolt introductions are used. When Finnmark is split into its two production zones, the dominance of the in-season smolt strategy close to Vestre Jakobselv become even more apparent as 100% of smolts transferred to sea cages in this region were in-season from 2018 to 2020. Whereas among other counties the transfer to sea is spread throughout the year, perhaps leading to the more median rates of early escapees. Interestingly, in 1989–1991, prior to the widespread use of out-of-season smolts, 48% of escapees in Etne had spent over a year in the wild, based upon estimates based on the detection of the synthetic food additive astaxanthin (Lura and Økland 1994). In 2011, 24% of escapees in four southwestern Norwegian rivers, including Etne, were classified as early escapees using FA profiling (Skilbrei *et al.* 2015b), which is in stark contrast to the 6% early escapees in the current study (Etne: 2014–2021). It has been estimated that the majority of trickle escapes due to small size will happen within the first 5 days post-transfer to net pens (Harboe and Skulstad 2013). Assuming the rates of these escapes are equal in the different regions, using in-season rather than out-of-season smolts would lead to higher survival rates for escaped smolts, and thus, more early escapees coming back to the river to spawn.

Studies on the diet of wild postsmolts migrating through fjords in different regions in Norway has shown that postsmolts in northern fjords have a higher proportion of high quality prey such as fish larvae in their diet, and also a higher feeding ratio (FR: an estimate of the wet weight of the

stomach content relative to the fish weight) than postsmolts in more southern fjords (Rikardsen *et al.* 2004, Hellenbrecht *et al.* 2023). It is, therefore, possible that smolts escaping in the north have a better chance of survival due to better food availability. While in contrast, elevated smolt mortality in the South, especially Hardangerfjorden, due to the high presence of salmon lice is also possible (Johnsen *et al.* 2021), and is another potential reason for the observed difference in the ratio of early escapees in the South than in the North where salmon lice is less of an issue (Grefsrud *et al.* 2022).

Conclusions

The majority of the farmed escapees caught in the time period 2011–2021 were classified as recent escapees and had not converted to a marine diet in the wild. This study shows that in conjunction with the overall temporal decline in the proportion of escapees caught throughout the study period, there was an indication of a spatio-temporal decline in the proportion of early escapees, relative to recent escapees. This was driven by the southernmost river and could be linked to standardization of mesh size relative to fish size. The northernmost locations had in general a much larger proportion of early escapees that had transitioned to a wild diet, than the southernmost rivers. This can, amongst many other factors, potentially be connected to differences in the ratio of in-season vs. out-of-season smolts used in their respective production zones and the aquaculture intensity. Thus, our findings suggest that both management strategies and various aquaculture practices have likely had an impact on the reduction and/or variation of early escapees in the sampling locations of this study. Regional variation in the relative proportion of early vs. recent escapees could potentially elucidate some of the unexplained variation in models investigating the drivers of introgression, whereas a better understanding of the effect of escape history upon their reproductive performance is still needed.

Acknowledgements

We would like to acknowledge the pivotal work of the late Ove T. Skilbrei in initiating this long-term study. We furthermore thank Elisabeth Stöger for construction of the map, as well as Arve Fossen and Therese Aase for FA laboratory analysis.

Supplementary data

Supplementary data is available at *ICESJM Journal* online.

Conflict of interest: None declared.

Data availability

The data underlying this article are subject to an embargo of 24 months. Once the embargo expires the data will be available at the Norwegian Marine Data Centre (<https://nmdc.no>).

Author contributions

N.S., K.A.G., S.M., and M.F.S. conceived the ideas and designed methodology; V.W., Ø.S., A.M., K.H., P.G.F., T.H., E.N., S.K., and P.T.F., and collected the samples; N.S., S.M., F.A., S.F., P.T.F., and M.F.S. processed the raw data; N.S., S.M.,

and M.F.S. analyzed the data; N.S., K.A.G., and M.F.S. interpreted the data, N.S. led the writing of the manuscript, M.F.S. led the study. All authors contributed critically to the drafts and gave final approval for publication.

References

- Aas TS, Åsgård T, Ytrestøyl T. Utilization of feed resources in the production of Atlantic salmon (*Salmo salar*) in Norway: an update for 2020. *Aquacult Rep* 2022;26:101316. <https://doi.org/10.1016/j.aqrep.2022.101316>.
- Aas TS, Ytrestøyl T, Åsgård T. Utilization of feed resources in the production of Atlantic salmon (*Salmo salar*) in Norway: an update for 2016. *Aquacult Rep* 2019;15:100216. <https://doi.org/10.1016/j.aqrep.2019.100216>.
- Aronsen T, Ulvan EM, Naesje TF *et al.* Escape history and proportion of farmed Atlantic salmon *Salmo salar* on the coast and in an adjacent salmon fjord in Norway. *Aquacult Env Interact* 2020;12:371–83. <https://doi.org/10.3354/aei00370>.
- Auguie B. gridExtra: miscellaneous functions for “grid” graphics. Version 2.3. R package. CRAN, 2017. <https://CRAN.R-project.org/package=gridExtra> (18 May 2020, date last accessed).
- Bartón K. MuMIn: multi-model inference. Version 1.46.0. R package. CRAN, 2022. <https://cran.r-project.org/web/packages/MuMIn/> (25 February 2022, date last accessed).
- Bates D, Mächler M, Bolker B *et al.* Fitting linear mixed-effects models using lme4. *J Stat Softw* 2014;67. <https://doi.org/10.18637/jss.v067.i01>.
- Bell JG, Henderson RJ, Tocher DR *et al.* Replacement of dietary fish oil with increasing levels of linseed oil: modification of flesh fatty acid compositions in Atlantic salmon (*Salmo salar*) using a fish oil finishing diet. *Lipids* 2004;39:223–32. <https://doi.org/10.1007/s11745-004-1223-5>.
- Bell JG, McGhee F, Campbell PJ *et al.* Rapeseed oil as an alternative to marine fish oil in diets of post-smolt Atlantic salmon (*Salmo salar*): changes in flesh fatty acid composition and effectiveness of subsequent fish oil “wash out”. *Aquaculture* 2003;218:515–28. [https://doi.org/10.1016/S0044-8486\(02\)00462-3](https://doi.org/10.1016/S0044-8486(02)00462-3).
- Besnier F, Ayllon F, Skaala Ø *et al.* Introgression of domesticated salmon changes life history and phenology of a wild salmon population. *Evol Appl* 2022;15:853–64. <https://doi.org/10.1111/eva.13375>.
- Bolstad GH, Hindar K, Robertsen G *et al.* Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. *Nat Ecol Evol* 2017;1:124. <https://doi.org/10.1038/s41559-017-0124>.
- Bolstad GH, Karlsson S, Hagen IJ *et al.* Introgression from farmed escapees affects the full life cycle of wild Atlantic salmon. *Sci Adv* 2021;7:eabj3397. <https://doi.org/10.1126/sciadv.abj3397>.
- Bradbury IR, Burgetz I, Coulson MW *et al.* Beyond hybridization: the genetic impacts of nonreproductive ecological interactions of salmon aquaculture on wild populations. *Aquacult Env Interact* 2020;12:429–45. <https://doi.org/10.3354/aei00376>.
- Castellani M, Heino M, Gilbey J *et al.* Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. *Evol Appl* 2018;11:1010–25. <https://doi.org/10.1111/eva.12615>.
- Clifford SL, McGinnity P, Ferguson A. Genetic changes in Atlantic salmon (*Salmo salar*) populations of Northwest Irish rivers resulting from escapes of adult farm salmon. *Can J Fish Aquat Sci* 1998;55:358–63. <https://doi.org/10.1139/f97-229>.
- Crozier WW. Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: genetic status of the wild population 7 years on. *Fish Manag Ecol* 2000;7:437–46. <https://doi.org/10.1046/j.1365-2400.2000.00219.x>.
- Diserud O, Fiske P, Karlsson S *et al.* Natural and anthropogenic drivers of escaped farmed salmon occurrence and introgression into wild Norwegian Atlantic salmon populations. *ICES J Mar Sci* 2022;79:1363–79. <https://doi.org/10.1093/icesjms/fsac060>.
- Diserud OH, Fiske P, Saegrov H *et al.* Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013. *ICES J Mar Sci* 2019;76:1140–50. <https://doi.org/10.1093/icesjms/fsy202>.
- Diserud OH, Hindar K, Karlsson S *et al.* Genetisk påvirkning av rømt oppdrettslaks på ville laksebestander—oppdatert status 2020. NINA Rapport 1926. Trondheim: Norsk Institutt for Naturforskning, 2020. <https://hdl.handle.net/11250/2720874> (3 October 2023, date last accessed).
- FAO. *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation*. Rome: FAO, 2022. <https://doi.org/10.4060/cc0461en> (3 October 2023, date last accessed).
- Fleming IA, Hindar K, Mjølnerod IB *et al.* Lifetime success and interactions of farm salmon invading a native population. *Proc R Soc Lond B Biol Sci* 2000;267:1517–23. <https://doi.org/10.1098/rspb.2000.1173>.
- Fleming IA, Jonsson B, Gross MR *et al.* An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *J Appl Ecol* 1996;33:893–905. <https://doi.org/10.2307/2404960>.
- Fleming IA, Lamberg A, Jonsson B. Effects of early experience on the reproductive performance of Atlantic salmon. *Behav Ecol* 1997;8:470–80. <https://doi.org/10.1093/beheco/8.5.470>.
- Forseth T, Barlaup BT, Finstad B *et al.* The major threats to Atlantic salmon in Norway. *ICES J Mar Sci* 2017;74:1496–513. <https://doi.org/10.1093/icesjms/fsx020>.
- Glover KA, Pertoldi C, Besnier F *et al.* Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. *BMC Genet* 2013;14:74. <https://doi.org/10.1186/1471-2156-14-74>.
- Glover KA, Solberg MF, McGinnity P *et al.* Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. *Fish Fish* 2017;18:890–927. <https://doi.org/10.1111/faf.12214>.
- Glover KA, Urdal K, Naesje T *et al.* Domesticated escapees on the run: the second-generation monitoring programme reports the numbers and proportions of farmed Atlantic salmon in >200 Norwegian rivers annually. *ICES J Mar Sci* 2019;76:1151–61.
- Glover KA. Forensic identification of fish farm escapees: the Norwegian experience. *Aquacult Env Interact* 2010;1:1–10. <https://doi.org/10.3354/aei00002>.
- Grefsrud ES, Andersen LB, Bjørn PA *et al.* Risikorapport norsk fiskeoppdrett 2022. Bergen: Havforskningsinstituttet, 2022. <https://hdl.handle.net/11250/3012254> (3 October 2023, date last accessed).
- Hara A, Radin NS. Lipid extraction of tissues with a low-toxicity solvent. *Anal Biochem* 1978;90:420–6. [https://doi.org/10.1016/0003-2697\(78\)90046-5](https://doi.org/10.1016/0003-2697(78)90046-5).
- Harboe T, Skulstad OF. Undersøkelse av maskeåpning og smoltstørrelse. Bergen: Havforskningsinstituttet, 2013. <http://hdl.handle.net/11250/116802> (12 April 2022, date last accessed).
- Heino M, Svasand T, Wennevik V *et al.* Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. *Aquacult Env Interact* 2015;6:185–90. <https://doi.org/10.3354/aei00126>.
- Hellenbrecht LM, Utne KR, Karlsen O *et al.* Diet analysis of Atlantic salmon (*Salmo salar*) post-smolts after the ecological regime shift in the Northeast Atlantic. *Fish Res* 2023;262:106672. <https://doi.org/10.1016/j.fishres.2023.106672>.
- Jensen O, Dempster T, Thorstad EB *et al.* Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention. *Aquacult Env Interact* 2010;1:71–83. <https://doi.org/10.3354/aei00008>.
- Johnsen IA, Harvey A, Sævik PN *et al.* Salmon lice-induced mortality of Atlantic salmon during post-smolt migration in Norway. *ICES J Mar Sci* 2021;78:142–54. <https://doi.org/10.1093/icesjms/fsaa202>.
- Jørgensen KM, Solberg MF, Besnier F *et al.* Judging a salmon by its spots: environmental variation is the primary determinant of spot patterns in *Salmo salar*. *BMC Ecol* 2018;18:1–13. <https://doi.org/10.1186/s12898-018-0170-3>.

- Karlsson S, Diserud OH, Fiske P *et al.* Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES J Mar Sci* 2016;73:2488–98. <https://doi.org/10.1093/icesjms/fsw121>.
- Kassambara A, Mundt F. factextra: extract and visualize the results of multivariate data analyses. Version 1.0.7. R package. CRAN, 2020. <https://cran.r-project.org/web/packages/factextra/> (17 July 2020, date last accessed).
- Kassambara A. ggpubr: 'ggplot2' based publication ready plots. Version 0.3.0. R package. CRAN, 2020. <https://cran.r-project.org/web/packages/ggpubr/> (8 May 2020, date last accessed).
- Keyser F, Wringe BF, Jeffery NW *et al.* Predicting the impacts of escaped farmed Atlantic salmon on wild salmon populations. *Can J Fish Aquat Sci* 2018;75:506–12. <https://doi.org/10.1139/cjfas-2017-0386>.
- Kunzetsova A, Brockhoff P, Christensen R. lmerTest package: tests in linear mixed effect models. *J Stat Softw* 2017;82:1–26.
- Lê S., Josse, J., Husson, F. 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, 25:1–18.
- Lenth RV. emmeans: estimated marginal means, aka least-squares means. Version 1.6.1. R package. CRAN, 2021. <https://cran.r-project.org/web/packages/emmeans/> (1 June 2021, date last accessed).
- Lüdtke D. sjPlot: data visualization for statistics in social science. Version 2.8.8. R package. CRAN, 2021. <https://cran.r-project.org/web/packages/sjPlot/> (1 June 2021, date last accessed).
- Lund RA, Okland F, Hansen LP. Farmed atlantic salmon (*Salmo Salar*) in fisheries and rivers in Norway. *Aquaculture* 1991;98:143–50. [https://doi.org/10.1016/0044-8486\(91\)90379-L](https://doi.org/10.1016/0044-8486(91)90379-L).
- Lura H, Økland F. Content of synthetic astaxanthin in escaped farmed Atlantic salmon, *Salmo salar* L., ascending Norwegian rivers. *Fish Manag Ecol* 1994;1:205–16. <https://doi.org/10.1111/j.1365-2400.1994.tb00162.x>.
- Madhun AS, Harvey A, Skaala Ø *et al.* Saved by the trap: over half of the farmed Atlantic salmon removed from a wild spawning population by an upstream migration trap in the period 2014–2018 were mature. *Aquacult Env Interact* 2023;15:271–85. <https://doi.org/10.3354/aei00465>.
- Madhun AS, Wennevik V, Skilbrei OT *et al.* The ecological profile of Atlantic salmon escapees entering a river throughout an entire season: diverse in escape history and genetic background, but frequently virus-infected. *ICES J Mar Sci* 2017;74:1371–81. <https://doi.org/10.1093/icesjms/fsw243>.
- McGinnity P, Prodöhl P, Ferguson A *et al.* Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proc R Soc Lond B Biol Sci* 2003;270:2443–50. <https://doi.org/10.1098/rspb.2003.2520>.
- Meier, S., Mjøs, S. A., Joensen, H., Grahl-Nielsen, O. *et al.* 2006. Validation of a one-step extraction/methylation method for determination of fatty acids and cholesterol in marine tissues. *Journal of Chromatography A*, 1104: 291–298. <https://doi.org/10.1016/j.chroma.2005.11.045>.
- Norwegian Directorate of Fisheries. Smoltvekt og notmasker: Revidert tilråding (in Norwegian). 2023. <https://www.fiskeridir.no/Akvakultur/erfaringsbase-romming/fagstoff1/smoltvekt-og-notmasker-revidert-tilrading> (1 October 2023, date last accessed).
- Norwegian Directorate of Fisheries. Tall og analyse: Akvakultur (in Norwegian). 2022. <https://www.fiskeridir.no/Akvakultur/Tall-og-g-analyse> (14 September 2022, date last accessed).
- Norwegian Ministry of Trade Industry of Fisheries. *The Aquaculture Regulation. Forskrift om drift av akvakulturanlegg (akvakulturdriftsforskriften, in Norwegian)*. 2009. <https://lovdata.no/dokument/LTIU/forskrift/2009-12-18-1705> (10 October 2023, date last accessed).
- Olsen RE, Taranger GL, Svasand T *et al.* Improved method for triacylglycerol-derived fatty acid profiling by various non-lethal and lethal sampling techniques in Atlantic salmon. *Aquacult Env Interact* 2013;4:251–61. <https://doi.org/10.3354/aei00087>.
- R Core Team R: *A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, 2020. <https://www.r-project.org> (19 May 2020, date last accessed).
- Rikardsen AH, Haugland M, Bjorn PA *et al.* Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *J Fish Biol* 2004;64:1655–79. <https://doi.org/10.1111/j.0022-1112.2004.00425.x>.
- Sægvog H, Hindar K, Kålås S *et al.* Escaped farmed Atlantic salmon replace the original salmon stock in the River Vosso, western Norway. *ICES J Mar Sci* 1997;54:1166–72. [https://doi.org/10.1016/S1054-3139\(97\)80023-9](https://doi.org/10.1016/S1054-3139(97)80023-9).
- Sistiaga M, Herrmann B, Forås E *et al.* Prediction of size-dependent risk of salmon smolt (*Salmo salar*) escape through fish farm nets. *Aquacult Eng* 2020;89:102061. <https://doi.org/10.1016/j.aquaeng.2020.102061>.
- Skaala Ø, Besnier F, Borgstrøm R *et al.* An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. *Evol Appl* 2019;12:1001–16. <https://doi.org/10.1111/eva.12777>.
- Skaala Ø, Wennevik V, Glover KA. Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. *ICES J Mar Sci* 2006;63:1224–33. <https://doi.org/10.1016/j.icesjms.2006.04.005>.
- Skilbrei OT, Heino M, Svasand T. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. *ICES J Mar Sci* 2015a;72:670–85. <https://doi.org/10.1093/icesjms/fsu133>.
- Skilbrei OT, Normann E, Meier S *et al.* Use of fatty acid profiles to monitor the escape history of farmed Atlantic salmon. *Aquacult Env Interact* 2015b;7:1–13. <https://doi.org/10.3354/aei00132>.
- Skilbrei OT, Wennevik V. The use of catch statistics to monitor the abundance of escaped farmed Atlantic salmon and rainbow trout in the sea. *ICES J Mar Sci* 2006;63:1190–200. <https://doi.org/10.1016/j.icesjms.2006.05.005>.
- Skilbrei OT. Reduced migratory performance of farmed Atlantic salmon post-smolts from a simulated escape during autumn. *Aquacult Env Interact* 2010a;1:117–25. <https://doi.org/10.3354/aei00013>.
- Skilbrei OT. Adult recaptures of farmed Atlantic salmon post-smolts allowed to escape during summer. *Aquacult Env Interact* 2010b;1:147–53. <https://doi.org/10.3354/aei00017>.
- Skilbrei OT. Migratory behaviour and ocean survival of escaped out-of-season smolts of farmed Atlantic salmon *Salmo salar*. *Aquacult Env Interact* 2013;3:213–21. <https://doi.org/10.3354/aei00062>.
- Solberg MF, Robertsen G, Sundt-Hansen LE *et al.* Domestication leads to increased predation susceptibility. *Sci Rep* 2020;10:1–11. <https://doi.org/10.1038/s41598-020-58661-9>.
- Solberg MF, Zhang ZW, Nilsen F *et al.* Growth reaction norms of domesticated, wild and hybrid Atlantic salmon families in response to differing social and physical environments. *BMC Evol Biol* 2013;13:234. <https://doi.org/10.1186/1471-2148-13-234>.
- Sprague M, Dick JR, Tocher DR. Impact of sustainable feeds on omega-3 long-chain fatty acid levels in farmed Atlantic salmon, 2006–2015. *Sci Rep* 2016;6:1–9. <https://doi.org/10.1038/srep21892>.
- Sylvester EV, Wringe BF, Duffy SJ *et al.* Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. *Evol Appl* 2019;12:705–17. <https://doi.org/10.1111/eva.12746>.
- Urdal K. Analysar av skjelpøverar frå Rogaland i. 2013. Rådgivende Biologer AS, rapport 1894. Bergen: Rådgivende Biologer, 2014. <https://www.radgivende-biologer.no/rapporter/ar-2014/analy-sar-av-skjelpøverar-fra-rogaland-i-2013/> (2 October 2023, date last accessed).
- Wacker S, Aronsen T, Karlsson S *et al.* Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon. *Evol Appl* 2021;14:1450–60. <https://doi.org/10.1111/eva.13213>.
- Wennevik V, Ambjørndalen V, Aronsen T *et al.* Escaped aquaculture salmon in Norwegian rivers in 2020–report from the national monitoring program. Bergen: Havforskningsinstitutt

- tet, 2021. <https://www.hi.no/en/hi/nettrapper/rapport-fra-havfor-skingen-2021-27> (2 October 2023, date last accessed).
- Wickham H, Averick M, Bryan J *et al.* Welcome to the Tidyverse. *J Open Source Softw* 2019;4:1686. <https://doi.org/10.21105/joss.01686>.
- Wickham H. stringr: simple, consistent wrappers for Common String operations. version 1.4.0. R package. CRAN, 2019. <https://cran.r-project.org/web/packages/stringr/> (12 May 2020, date last accessed).
- Wickham H. *Wiley Interdisciplinary Reviews: Computational Statistics*. Vol. 3. ggplot2. New York: John Wiley & Sons, Inc., 2011, 180–5.
- Wringe BF, Jeffery NW, Stanley RRE *et al.* Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. *Commun Biol* 2018;1:9. <https://doi.org/10.1038/s42003-018-0112-9>.
- Ytrestøyl T, Aas TS, Åsgård T. Utilisation of feed resources in production of Atlantic salmon (*Salmo salar*) in Norway. *Aquaculture* 2015;448:365–74. <https://doi.org/10.1016/j.aquaculture.2015.06.023>.
- Zhang Z, Glover KA, Wennevik V *et al.* Genetic analysis of Atlantic salmon captured in a netting station reveals multiple escapement events from commercial fish farms. *Fish Manag Ecol* 2013;20:42–51.

Handling Editor: Stewart W. Grant