



Caught in the trap: over half of the farmed Atlantic salmon removed from a wild spawning population in the period 2014–2018 were mature

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ABSTRACT: Whilst aquaculture continues its global expansion, containment of fish in sea cages remains a persistent environmental challenge. Within Atlantic salmon *Salmo salar* farming, widespread escapes over several decades have left a legacy of ecological and genetic impacts on wild populations. Quantifying the characteristics of escapees, and how they vary in time and space, is important to understand how environmental impacts will vary and how mitigation strategies need to be tuned. Using a fish trap located in the River Etne on the west coast of Norway, we created an ecological and genetic profile for 616 escapees entering the river. The most important findings of the present study were (1) the annual number of escapees entering the trap declined in the period 2014–2018; (2) more than half of the escapees entering the river were mature; (3) the vast majority of escapees entering the river were categorised as recent escapees; (4) nearly all (96%) of the early escapees were mature upon entry to the river, while just over half (55%) of the recent escapees were mature; and (5) the escapees originated from multiple sources every year. We conclude that without the fish trap, this population would have been at risk of exposure to further spawning and introgression of domesticated salmon. Furthermore, the current findings of maturation status and escape history highlight the fact that mitigation efforts to reduce escape of smolts, post-smolts and larger fish all need continued attention from the management authorities and aquaculture industry.

KEY WORDS: *Salmo salar* · Escaped farmed salmon · Escape history · Maturation stage · Genetic profile · Time of river ascending · Fatty acid profiling

1. INTRODUCTION

Commercial Atlantic salmon *Salmo salar* aquaculture was initiated in the early 1970s, and production has steadily increased to a level where global annual production now exceeds 2 million metric tonnes (FAO 2022). Currently, this industry represents the economically most significant form of aquaculture in

the world (Bostock et al. 2010). Atlantic salmon aquaculture is primarily based upon rearing juveniles in land-based tanks followed by on-growing to market size in open sea cages. However, this and similar forms of production, which are used not only for Atlantic salmon but for a wide variety of aquaculture species, have not developed without causing environmental impacts. These impacts are diverse and

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comprise sustainability issues of salmon aquaculture linked to feed production (Torrissen et al. 2011), benthic impacts under sea cages (Wu 1995, Kutti et al. 2008), widespread antiparasitic drug use with possible influence on non-target organisms (Urbina et al. 2019), infestations of sea lice on both farmed and wild salmonids (Torrissen et al. 2013, Fjørtoft et al. 2017), potential disease interactions with wild populations (Glover et al. 2013b, Madhun et al. 2015, Madhun et al. 2017) and farmed escapees that display both ecological (Jonsson & Jonsson 2006, Bradbury et al. 2020) and genetic interactions with wild conspecifics (McGinnity et al. 1997, Fleming et al. 2000, Skaala et al. 2012, Glover et al. 2017). A risk assessment addressing the major challenges linked to salmon aquaculture in Norway identified sea lice and farmed escapees as the most critical issues (Taranger et al. 2015).

Each year, tens of thousands of farmed salmon escape into the wild. In Norway, where farmers are legally required to report escape events, the official statistics have shown a decline in reported numbers since 2006, when nearly one million escapees were reported (Norwegian Fishery Directorate, <https://www.fiskeridir.no/>). These numbers are to be treated with some caution due to likely underreporting, as evidenced by simulation studies (Skillbrei et al. 2015) and the fact that DNA methods to identify the farm of origin have been implemented in multiple cases where unreported escapes have occurred (Glover et al. 2008, Glover 2010). In addition, the number of salmon escaping during reported events may be hard to quantify (<https://www.fiskeridir.no/>). Nevertheless, the decline in the reported numbers of escapees since 2006 has to some degree been mirrored by a decline in the proportions of farmed escapees that are observed in salmon rivers in Norway (Diserud et al. 2019, Glover et al. 2019). As the production of Atlantic salmon has more than doubled since 2006, this decline is in part accredited to improved escape mitigation practises (Jensen et al. 2010, Føre & Thorvaldsen 2021).

Directional selection for economically important traits in addition to the general effects of domestication has led to farmed salmon displaying a variety of genetic differences in comparison with wild conspecifics (Glover et al. 2017). For example, studies conducted in the natural environment have demonstrated lower survival of farmed and hybrid offspring in comparison with the offspring of wild salmon (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019), and rivers displaying introgression from domesticated escapees have shown life-history and phenological changes (Bolstad et al. 2017, 2021,

Besnier et al. 2022) as well as selection against introgressed individuals (Sylvester et al. 2019, Wacker et al. 2021). Therefore, the documented widespread introgression of farmed salmon in wild populations in Norway (Glover et al. 2013a, Karlsson et al. 2016), Scotland (Gilbey et al. 2021) and North America (Wringe et al. 2018) gives cause for concern over the genetic integrity, productivity and evolutionary trajectory of recipient wild populations.

The main factor affecting introgression of farmed salmon in wild populations is the proportion of farmed salmon observed in wild populations over time (Glover et al. 2013a, Heino et al. 2015, Karlsson et al. 2016, Diserud et al. 2022). However, other factors, such as abundance density of the wild population (Glover et al. 2012, Heino et al. 2015, Sylvester et al. 2018, Mahlum et al. 2021), river discharge (Diserud et al. 2022) and migration barriers that hinder escapees from reaching spawning grounds in a river (Sylvester et al. 2018, Diserud et al. 2022), also shape inter-population patterns in introgression. In addition, the relative success of farmed escapees in the wild is conditioned by (1) the stage of maturity at the time of ascending the rivers; (2) the life stage at which they escaped, which may in turn affect their relative competitiveness on the spawning grounds (Fleming & Einum 1997, Fleming et al. 1997); (3) their sex, as female escapees are presumed to display greater spawning success than males (Fleming et al. 1996, 2000); and (4) whether they are infected with pathogens (Madhun et al. 2015, 2017). Thus, monitoring programmes aiming to assess the frequency of farmed escapees in the wild (such as the one that is conducted annually in approximately 200 Norwegian rivers; Glover et al. 2019) need to be complemented with studies designed to identify the most critical factors affecting the outcome of the interactions of escapees with wild conspecifics, such as behaviour and movements of escapees in rivers (Moe et al. 2016), background of the escapees including genetic origin, their escape history, maturity and disease status (Quintela et al. 2016, Madhun et al. 2017), and timing of entry to freshwater (Gausen & Moen 1991, Erkinaro et al. 2010, Svenning et al. 2017).

In 2013, an upstream fish migration trap was installed in the River Etne, located on the west coast of Norway (Fig. 1), one of the most intensive salmon-farming regions in Norway. The river supports a wild population of Atlantic salmon with an annual adult run of typically 1000–2000 fish (Harvey et al. 2017, 2022) and displayed an average of approximately 24% introgression from farmed escapees during the period 2013–2016 (Glover et al. 2013a, Karlsson et al.

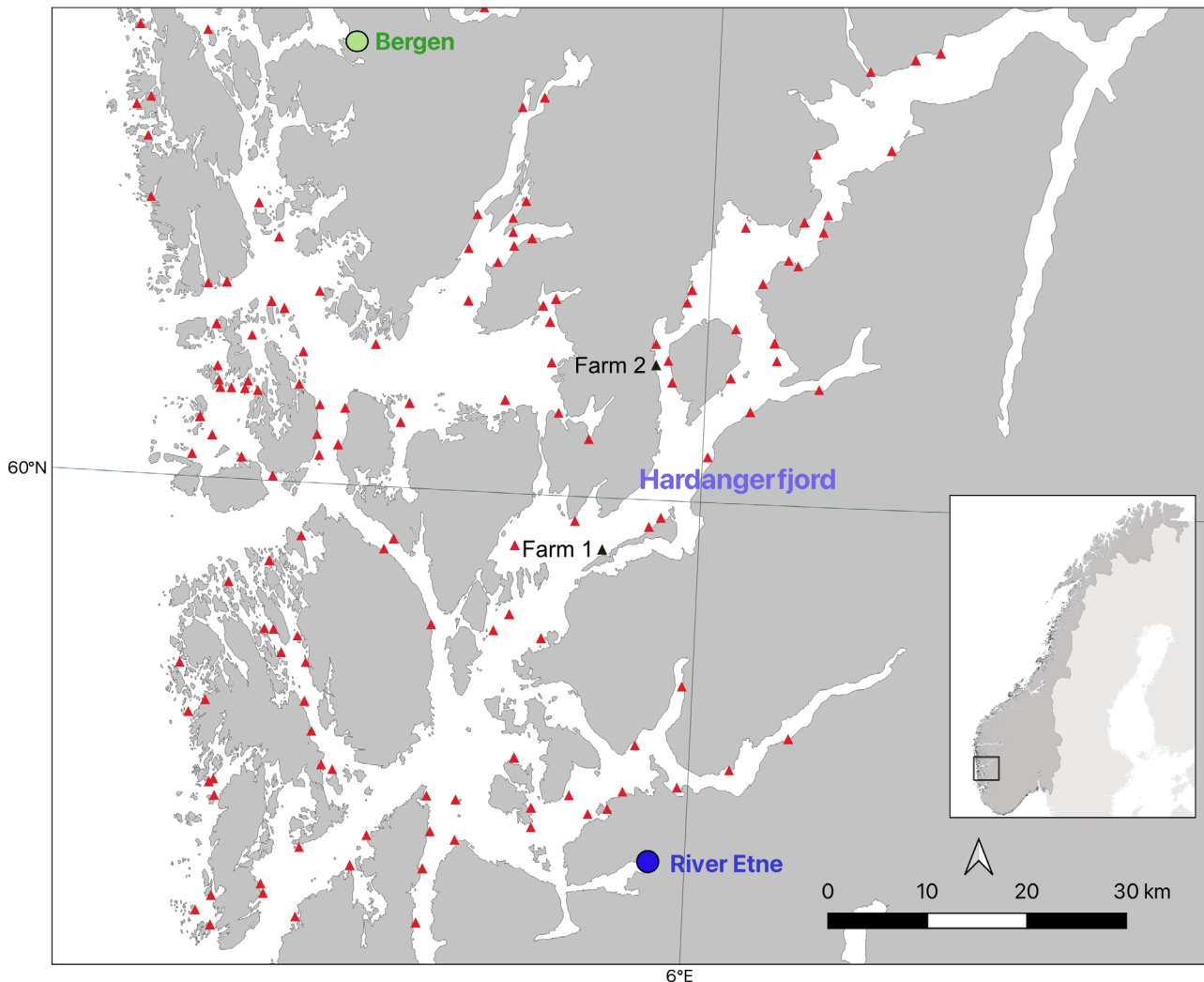


Fig. 1. Location of the River Etne (blue circle) and salmon farms (red triangles) in western Norway. The potential farms of origin are shown as black triangles (see Section 4 for details)

2016, Besnier et al. 2022). The trap is monitored daily in the period April to November and provides novel opportunities to capture and study nearly all of the escapees entering the river (Quintela et al. 2016, Madhun et al. 2017). In the present study, we characterised the escapees entering the river in a 5 yr period between 2014 and 2018 using a multidisciplinary approach, thus providing the most comprehensive overview of escapees in a single river system to date.

2. MATERIALS AND METHODS

2.1. Sampling farmed escapees in the River Etne

The River Etne is located in the outer reaches of the Hardangerfjord, western Norway (Fig. 1). In this

region, aquaculture production is very high, and many of the wild populations are not only below their spawning targets (Thorstad et al. 2021), but have also undergone genetic changes as a result of introgression of farmed escapees (Skaala et al. 2006, Glover et al. 2012, 2013a, Karlsson et al. 2016). The trap, based on a resistance board system (Stewart 2003), captures most of the farmed and wild salmon entering the river during the period April to November.

In the period 2014–2018, all fish entering the trap were assessed for external morphological characteristics to differentiate between farmed escapees and wild salmon, and the classification was later verified by reading scales (Lund & Hansen 1991, Fleming et al. 1994, Noble et al. 2007, Jørgensen et al. 2018). After sampling (scale, tissue, biometric data), phenotypically wild salmon were released back into the

river to continue their spawning migration, while farmed escapees were euthanised and thereafter intensively sampled. The sampling procedure and the data relating to the wild salmon are described in detail elsewhere (Harvey et al. 2022). The numbers and types of samples taken from the farmed escapees varied between years. It is therefore important to keep this in mind while examining the results, as different numbers of fish were used for the different analyses (Table 1). In addition to recording weight, sex and stage of maturation, a tissue sample was taken for DNA analysis. Finally, the adipose fin was removed and stored at -80°C for fatty acid profiling. Of the escapees that were captured in the trap during the period 2014–2018 (total $N = 644$, Ø. Skaala et al. unpubl. data), results from analyses of 616 fish were available and therefore used in the present study (Table 1).

In October and November each year, immediately prior to the spawning timepoint in the river, escaped farmed fish were also captured by angling in the ~500 m section of river between the estuary and the trap itself. This activity was specifically targeted to remove any farmed fish that entered the river but remained in the short section below the trap itself. In most years, only sporadic data were collected from these escapees, with the exception of 22 and 26 individuals captured in 2017 and 2018, respectively. The numbers and the available data on sex, maturation and escape history for escapees captured below the fish trap in 2017 and 2018 are shown in Table S1 in Supplement 1 at www.int-res.com/articles/suppl/q015p271_suppl1.pdf. These additional data were used for some below/above trap comparisons in those years.

2.2. Maturation stage determination

The fish were classified to immature and mature as described by Dahl (1917) and Glover et al. (2016a). Briefly, maturation stage of the fish was determined based on the morphology and the length of gonads. Generally, fish with the length of expanded gonads (filled with gametes) more than 50% of the length of the abdominal cavity (gonadal stages 3–5) were considered to be mature (fish that will spawn in the coming autumn).

Table 1. Number (percentage in brackets) of escaped fish per year, the median day of ascending (MDA) to the river (range) and average weight (kg) \pm SD divided into maturity status, sex and time of escape ('Early' category includes escapees with intermediate terrestrial fatty acid levels; see Section 2)

Year	Total	Maturity status			Sex		Time of escape	
		Immature	Mature	Female	Male	Early	Recent	
2014	Number	155	58 (41)	59 (39)	94 (61)	10 (7)	142 (93)	
	MDA	284 (118–323)	251 (169–315)	287 (169–323)	251 (118–315)	271 (233–295)	285 (118–323)	
	Weight	3.29 \pm 1.84	3.52 \pm 2.12	3.22 \pm 1.70	3.39 \pm 1.91	4.07 \pm 1.97	3.21 \pm 1.83	
2015	Number	182	138 (82)	74 (41)	105 (59)	19 (11)	150 (89)	
	MDA	218 (179–306)	217 (179–306)	214 (186–304)	223 (179–306)	247 (190–271)	214 (179–273)	
	Weight	4.78 \pm 2.06	5.15 \pm 1.89	4.87 \pm 1.70	4.75 \pm 2.24	4.78 \pm 2.09	4.82 \pm 1.98	
2016	Number	126	47 (40)	68 (55)	56 (45)	5 (4)	119 (96)	
	MDA	181 (150–306)	194 (152–305)	178 (150–306)	189 (165–305)	247 (213–276)	180 (151–306)	
	Weight	3.86 \pm 1.46	4.24 \pm 1.48	3.98 \pm 1.50	3.71 \pm 1.42	6.39 \pm 1.98	3.75 \pm 1.35	
2017	Number	75	47 (66)	34 (45)	41 (55)	22 (30)	52 (70)	
	MDA	226 (164–316)	220 (164–315)	230 (167–316)	217 (164–315)	230 (212–315)	220 (164–316)	
	Weight	4.26 \pm 1.96	4.75 \pm 1.72	4.53 \pm 2.16	4.02 \pm 1.78	5.78 \pm 1.98	3.67 \pm 1.53	
2018	Number	78	50 (66)	37 (47)	41 (53)	2 (3)	74 (97)	
	MDA	241 (137–311)	241 (150–310)	238 (137–310)	242 (150–311)	258 (257–258)	239 (137–311)	
	Weight	4.16 \pm 1.96	4.52 \pm 1.71	4.41 \pm 1.68	3.92 \pm 2.16	6.91 \pm 0.53	4.09 \pm 1.94	
Total	Number	616	340 (59)	272 (45)	337 (55)	58 (10)	537 (90)	
	MDA (Range)	229 (118–323)	228 (150–315)	228 (137–323)	231 (118–315)	245 (190–315)	227 (118–323)	
	Weight (\pm SD)	4.07 \pm 1.95	4.60 \pm 1.92	4.18 \pm 1.81	4.01 \pm 2.03	5.25 \pm 2.09	3.96 \pm 1.87	

2.3. Fatty acid (FA) profiling

A FA-based method has been developed to classify escapees as individuals that have escaped early in the production cycle and converted to a marine diet by the time they are captured as adults in the wild, or as individuals that have escaped later in the production cycle and been captured soon after escape before having transitioned to a marine diet (Olsen et al. 2013, Skilbrei et al. 2015). The methodology is based on the principle that farmed salmon are reared on a commercial diet containing high levels of FAs of terrestrial origin (Ytrestøyl et al. 2015, Aas et al. 2019), which separates adult farmed salmon with different escape histories based upon their percentage of the terrestrial FA linoleic acid (18:2n-6). This FA is low in the marine environment, and thus low in wild salmon as well as in farmed escapees that have escaped early in the life cycle and grown on a primarily marine diet before entering the river. Thus, following the methodology of Skilbrei et al. (2015); individuals with >7% of linoleic acid out of total FAs measured were classified as 'recent', individuals with 2.5–7% were classified as 'intermediate' and individuals with <2.5% were classified as 'early' escapees and thus fully transitioned to the marine diet. Full details of the FA analytical conditions have been provided elsewhere (Olsen et al. 2013, Skilbrei et al. 2015).

In the present study, the few fish (2.5%) with intermediate levels of terrestrial FA (linoleic acid) were included in the early escapees category for simplicity and consistency with previous studies from the same river system (Quintela et al. 2016, Madhun et al. 2017).

2.4. Genetic analysis

Escapees were genotyped and thereafter organised into genetic clusters (groups) within each year of ascending the river. This was performed to serve as a proxy for estimating whether they originated from one or multiple sources (Quintela et al. 2016, Madhun et al. 2017). This approach is based upon the principle that cages on farms most often hold fish from one source and therefore form a single genetic cluster (Glover et al. 2008, 2009, Glover 2010). Therefore, if multiple genetic clusters are identified within the escapees entering the river in a single year, it strongly suggests that the escapees originated from multiple sources, which could be different cages in a single farm and/or cages in different farms. However, it is important to note that this analysis cannot

give the number of cages or farms of origin, but rather, structures the data in a way that permits identification of patterns in the phenotypic data that are not immediately evident when all escapees are treated as a single homogeneous source.

All escapees were genotyped at 31 polymorphic microsatellite loci for which amplification and screening conditions are extensively detailed by Harvey et al. (2017). Escapees were classified into different genetic groups by clustering analyses conducted in STRUCTURE v.2.3.4 (Pritchard et al. 2000) under a model assuming admixture and correlated allele frequencies without using population information. STRUCTURE analyses were independently conducted for each set of individuals collected during the same ascending year. Ten runs with a burn-in period consisting of 100 000 replications and a run length of 1 000 000 Markov chain Monte Carlo iterations were performed for $K = 1$ to 5 clusters. The number of genetic groups was determined by using a combination of visual inspection of the barplots at different K s together with the *a posteriori* analyses of STRUCTURE outcome; i.e. the test of Evanno et al. (2005) and the 4 statistics of Puechmaille (2016). Individuals were assigned to a genetic group using a threshold for the q -value of $q > 0.75$, whereas individuals that failed to reach such a threshold were considered as 'non-assigned'. It is important to note that each cluster represents a genetic group of fish identified in that specific year, and therefore possibly (but not necessarily) originating from the same source. For example, the genetic make-up of individuals belonging to e.g. Cluster 1 from 2 different years does not coincide. Likewise, individuals belonging to the 'non-assigned' group are not necessarily linked to each other nor do they originate from the same source.

2.5. Statistical analysis

All statistics were conducted in R (version 4.2.2) (R Core Team 2016). Two-sample chi-squared tests performed in R were used to investigate differences in the proportions of escapees of different sexes within maturation stages and time of escape events, and maturation stage within time of escape events.

Variations in weight between and within maturation stage, sex, time of escape and genetic clusters within each year were investigated using a generalised linear model (GLM). The response variable was weight in grams, modelled using a Gaussian distribution with a log-link function with the 'glmmTMB' package. The explanatory variables were maturation stage

(MS, 2 levels: mature and immature), sex (S, 2 levels: female and male) and time of escape (ToE, 2 levels: early and recent), all modelled as categorical variables with 2 levels. Genetic clusters (C) for each year were included as a categorical explanatory variable with 25 levels. The 2-way interactions between sex and time of escape, sex and maturation stage, and time of escape and maturation stage were included. Year was included in the dispersion model to account for heteroscedasticity. The model was as follows:

$$\begin{aligned} \text{Weight} \sim & S + MS + \text{ToE} + C + S \times \text{ToE} \\ & + S \times MS + MS \times \text{ToE} \end{aligned} \quad (1)$$

Model fit was assessed by examining scaled residuals using the 'DHARMA' package (Hartig 2022). The 'Anova' function from the 'car' package (Fox & Weisberg 2019) was used to assess the significance of the explanatory variables. For significant 2-way interactions, pairwise comparisons between each level of the variable were carried out using the 'pairs' function from the 'emmeans' (estimated marginal means) package (Lenth 2016) with the default Tukey adjustment for multiple comparisons.

A series of Mood's median tests from the 'RVAide-Memoire' package were used to assess whether there were differences in the median day of ascending (MDA, day of year [DOY] on which 50% of the fish had entered the fish trap) between escaped farmed fish of different maturation stage, sex, time of escape and genetic cluster (5 levels) within each year. Where there was a significant difference in the MDA between genetic clusters, a pairwise comparison was carried out using 'pairwiseMedianTest' from the 'rcompanion' package (Mangiafico 2020) to determine differences between each cluster within a year. It was decided not to group years, as between-year differences in time of arrival to river are essentially random and not linked over time.

3. RESULTS

Of the 644 fish removed from the upstream fish trap that were phenotypically classified as escapees, 9 fish were subsequently classified as wild based on detailed scale reading, leaving 635 fish categorised as farmed escapees. In contrast, 39 salmon initially classified as phenotypically wild were subsequently classified as farmed escapees based on scale reading. As mentioned above, the number of escaped farmed fish in the original dataset with data on weight, sex, genotype, maturation status and FA profile differed, and so a total of 616 escaped farmed

salmon captured in the upstream fish trap of the River Etne in the period 2014–2018 were included in the present study. Numbers varied by year, with fewer escapees entering the river in later years (Table 1). Escapees had a mean weight of 4.07 kg (range: 0.38–11.07 kg) and mean length of 72 cm (range: 35–105 cm). Although more than half (59%) of all fish were mature, the annual proportion of mature escapees entering the river varied from 40 to 82%. Of the 609 fish for which sex was determined, 45% were females, and the proportion of females varied between years, ranging from 39 to 55%. Fish identified as recent escapees dominated the fish ascending the river over the whole time period (90%, 2014–2018), with the percentage of early escapees varying from 3 to 30% among years.

The distribution of individuals into genetic clusters was conducted by using a combination of *a posteriori* analyses of the STRUCTURE results and visual inspection of the histograms at different *K*s, and *K* = 4 was selected as the best number of genetic clusters on the year basis (Fig. S1). The threshold of $q \geq 0.75$ defined 4 groups of uneven sizes per year with a proportion of individuals per cluster ranging between 6.4 and 45.2%. In every sampling year, the individuals belonging to the 'non-assigned' group ranged in proportion between 9% (2018) and 14% (2016), being ~11% in the remaining years. Results from genetic analyses indicate that fish entering the river originated from multiple sources each year (Table 2).

In addition to the escapees captured in the trap, some data were available on escapees captured below the trap in 2017 and 2018. Significantly, all of the escapees captured below the trap were identified as recent escapees according to the FA profiling analysis, and most (86%) of them were immature (Table S1). The mean weight of these fish was 3.0 kg (range: 1.2–9.0 kg) and 3.57 kg (range: 1.2–7.1 kg) in 2017 and 2018, respectively. The weight of escapees captured below the trap was significantly lower than fish captured in the trap in 2017 but not in 2018.

3.1. Phenotypic and genetic characteristics of the escapees

On average, the GLM used to analyse weight revealed that females were slightly heavier than males, mature salmon were heavier than immature salmon, and early escapees were heavier than recent escapees (Table 1, Fig. 2a). Furthermore, the average size of the escapees differed significantly depending on their sex within each maturation stage and their

Table 2. Number (N) of escaped fish within each genetic cluster per year and within maturation stage and time of escape, the median day of ascending (MDA) to the river (range in brackets) and average weight (kg) \pm SD for each genetic cluster. Note that numbers within maturation stage or within time of escape may differ to the total numbers per cluster due to the numbers of fish analysed for each parameter

Year		Genetic cluster				
		1	2	3	4	None
2014	Total N	46	45	24	19	18
	Immature N	42	17	9	5	11
	Mature N		25	15	13	5
	Early N		3		5	2
	Recent N	46	42	24	14	16
	MDA	287 (284–298)	250 (175–297)	235 (226–320)	271 (118–315)	283.5 (169–323)
	Weight	3.15 \pm 1.27	4.12 \pm 1.57	0.95 \pm 0.21	4.67 \pm 2.00	3.12 \pm 1.67
2015	Total N	70	30	30	23	16
	Immature N	7	14	5	1	4
	Mature N	60	16	26	22	14
	Early N	3	7	5		4
	Recent N	67	23	25	23	12
	MDA	204.5 (187–299)	246 (179–295)	237 (187–305)	193 (185–306)	223 (186–298)
	Weight	5.63 \pm 1.55	3.50 \pm 2.41	3.28 \pm 1.90	5.84 \pm 0.74	4.79 \pm 2.08
2016	Total N	56	17	16	13	17
	Immature N	38	8	6	6	12
	Mature N	15	9	11	6	6
	Early N			2	3	
	Recent N	56	17	16	13	17
	MDA	175 (150–228)	178 (152–280)	210 (179–285)	253 (156–306)	182 (170–292)
	Weight	3.85 \pm 0.90	3.43 \pm 1.05	4.85 \pm 2.39	3.73 \pm 2.16	3.40 \pm 0.80
2017	Total N	29	14	13	10	8
	Immature N	11	2	7	2	2
	Mature N	18	10	5	8	6
	Early N	4	3	1	9	5
	Recent N	25	11	12	1	3
	MDA	217 (167–294)	274 (185–316)	213 (164–293)	232 (214–315)	238.5 (212–301)
	Weight	4.18 \pm 1.60	3.59 \pm 1.43	3.73 \pm 1.50	5.95 \pm 2.88	4.19 \pm 2.13
2018	Total N	27	22	15	5	7
	Immature N	10	9	6		1
	Mature N	17	13	9	5	6
	Early N			1		1
	Recent N	27	22	14	5	6
	MDA	240.5 (160–282)	224 (137–309)	254 (217–311)	254 (239–261)	254 (224–268)
	Weight	3.88 \pm 1.32	5.19 \pm 2.29	2.75 \pm 1.84	5.19 \pm 0.77	4.43 \pm 1.74

time of escape (Table 1; Table S2). Immature females were significantly heavier than immature males (t -ratio = 5.13, df = 513, p < 0.0001), and mature females were also significantly heavier than mature males (t -ratio = 4.03, df = 513, p = 0.0001) (Fig. 2b). While early escaped females were significantly heavier than early escaped males (t -ratio = 5.82, df = 513, p < 0.0001), there was no difference in weight detected between the sexes in the recent escapees (t -ratio = 0.84, df = 513, p = 0.402) (Fig. 2c).

Mean weight varied among escapees belonging to the different genetic clusters within the same year (Table 2; Table S3). To illustrate; in 2014, individuals originating from Cluster 3 displayed

significantly lower weight than individuals from all other genetic clusters in the same year. In 2015, individuals in Clusters 2 and 3 were lighter compared to the other clusters, and in 2018, individuals in Cluster 3 were significantly lighter than those from Cluster 2 (Table 2).

When examining the differences in proportion of escapees based on maturation stage and escape history (Fig. 3a), overall, 96% of the early escapees were mature, while only 55% of the recent escapees were mature (χ^2 = 33.77, df = 1, p < 0.0001). For maturation stage within sex (Fig. 3b), there were significantly more mature males (75%) than females (40%) (χ^2 = 67.87, df = 1, p < 0.0001).

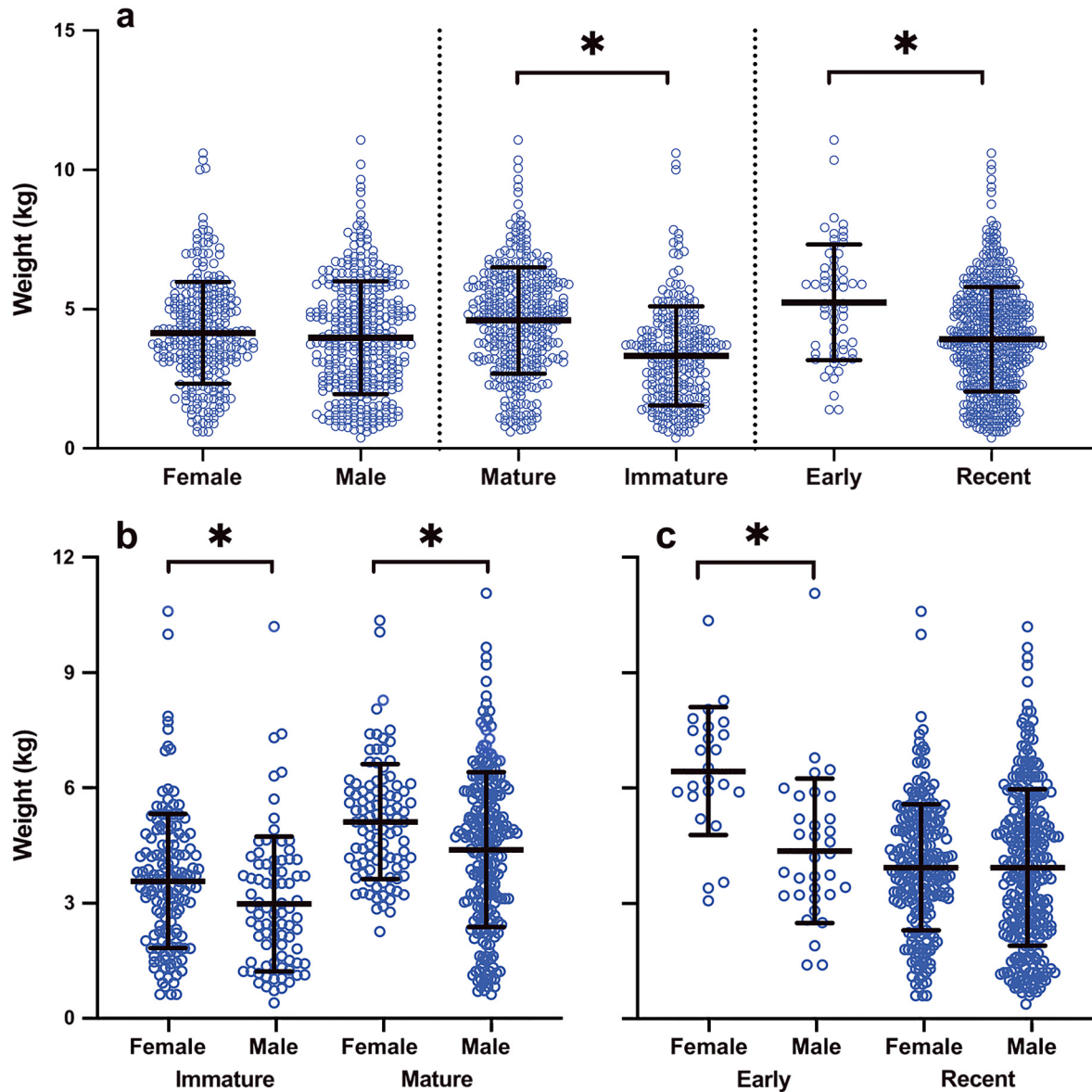


Fig. 2. Size of Atlantic salmon in relation to (a) sex, maturation and escape history; (b) sex within maturation; and (c) sex within escape history of escapees over all study years. The circles represent individual fish, the thick horizontal line within each plot is the mean weight (kg), and the solid vertical lines represent SD. *Significantly different at $p < 0.001$

3.2. Relationship between date of ascending, phenotypic traits and genetic clusters

Large differences in the MDA were observed among years (range: DOY 181–284). The MDA varied by more than 100 d between the most extreme years, 2014 and 2016 (Table 1). The MDAs of escaped farmed salmon were also compared to the wild salmon population in this river and showed that escaped farmed salmon entered the trap later than the wild salmon population (Ø. Skaala et al. unpubl. data). Briefly, escaped farmed salmon entered the trap later than the wild salmon population in this river.

In 2014, the immature escaped salmon had an MDA that was 36 d later than that of mature escapees, while in 2016 the immature escapees arrived 16 d earlier (Table 1). In other years, no differences were observed, and thus, there was no clear directional pattern in the difference in MDA between escapees of different maturity status. We detected a significant difference in the MDA between the sexes in 2014 and 2016, with females entering 36 d later in 2014 ($\chi^2 = 25.47$, $df = 1$, $p < 0.0001$) and 11 d earlier than males in 2016 ($\chi^2 = 8.24$, $df = 1$, $p = 0.004$). No discernible pattern in MDA was detected between the sexes of the escapees in the other years (Table 1;

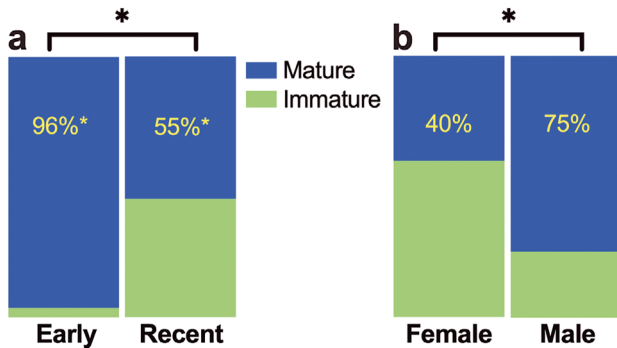


Fig. 3. Proportion of Atlantic salmon escapees (a) within maturation stage in relation to escape history and (b) within sex in relation to maturation stage over all study years. * Significantly different at $p < 0.0001$

Table S4). It should be noted that the MDA differences observed between mature and immature fish and between sexes in 2014 and 2016 are congruent, as the majority of immature fish in 2014 and in 2016 were female.

While recent escapees entered the river during the whole season in which the trap was operated, all early escaped farmed fish (except one) arrived to the river after DOY 200 and their range in day of ascending was smaller compared to recent escapees (Table 1). Except in 2014, the MDA was generally later in early escapees compared to recent escapees but was only significantly different in 2015.

In 2014–2017, the MDA was significantly different between escapees originating from the different genetic clusters (Table 2), while in 2018, no significant difference was detected. While most of the identified genetic clusters arrived in the river during the whole season, some specific clusters arrived in large numbers during a short period of time (Fig. 4; Table S5). Furthermore, data from FA analysis showed that these specific clusters contained only recent escapees, which also displayed relatively homogeneous size distributions (Table 2). This is very evident, for example, in fish from Clusters 1 and 3 in 2014 or alternatively in escapees from Cluster 1 in 2016. The Cluster 1 in 2014 (46 fish of total 155) arrived in the river late in the season, leading to skew/delay the MDA of escapees to DOY 284 compared to other years. In contrast, Cluster 1 in 2016 (57 fish of total 126) arrived in the river early in the season, leading to an MDA of DOY 181, the lowest in the present study.

4. DISCUSSION

To our knowledge, this study represents the most comprehensive investigation of the biological char-

acteristics of escaped farmed salmon ascending a river to date. Using a multidisciplinary approach, a total of 616 escapees captured in the upstream trap over a 5 yr period were profiled for a range of traits that may have implications for their potential impact on the native salmon population. The most important of these results are (1) the annual number of escapees entering the trap declined in the period 2014–2018; (2) more than half of the escapees entering the river were mature; (3) the vast majority of escapees entering the river were categorised as recent escapees; (4) nearly all (96%) of the early escapees were mature upon entry to the river, while just over half (55%) of the recent escapees were mature; and (5) the escapees originated from multiple sources every year.

4.1. Temporal decline in the number of escapees ascending the river in 2014–2018

The number of escapees entering the river declined during the 5 yr study period (Table 1). Although this timeline limits the ability to conclude whether this observation represents a trend or not, the decline is consistent with the observed decline in the proportions of farmed escapees seen in approximately 200 Norwegian rivers over a longer period of time (Diserud et al. 2019, Glover et al. 2019), and the official statistics for self-reporting escapees from the Norwegian Fishery Directorate (<https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Roemningsstatistikk>). Thus, it appears likely that a reduction in escapes from fish farms plays a role in the lower numbers of escapees observed in 2018 compared to 2014 in the River Etne.

Extensive data from the Norwegian monitoring programme of escaped farmed salmon have also suggested that the observed nationwide decline in proportions of escapees in rivers over time is mainly driven by improved containment within the industry itself (Glover et al. 2019). During the period 2005–2011, it was estimated that 2–4 times more salmon escaped than was reported by the fish-farmers themselves, and that the discrepancy was likely higher for smolts escaping shortly after sea transfer (Skilbrei et al. 2015). Drip leakage of small fish may be hard to detect, thus increased focus on correct mesh size relative to fish size, combined with the usage of larger smolts and out-of-season smolts (that display lower post-escape survival than in-season smolts; Skilbrei 2010), may also have contributed to the decline in escapees being observed in Norwegian rivers.

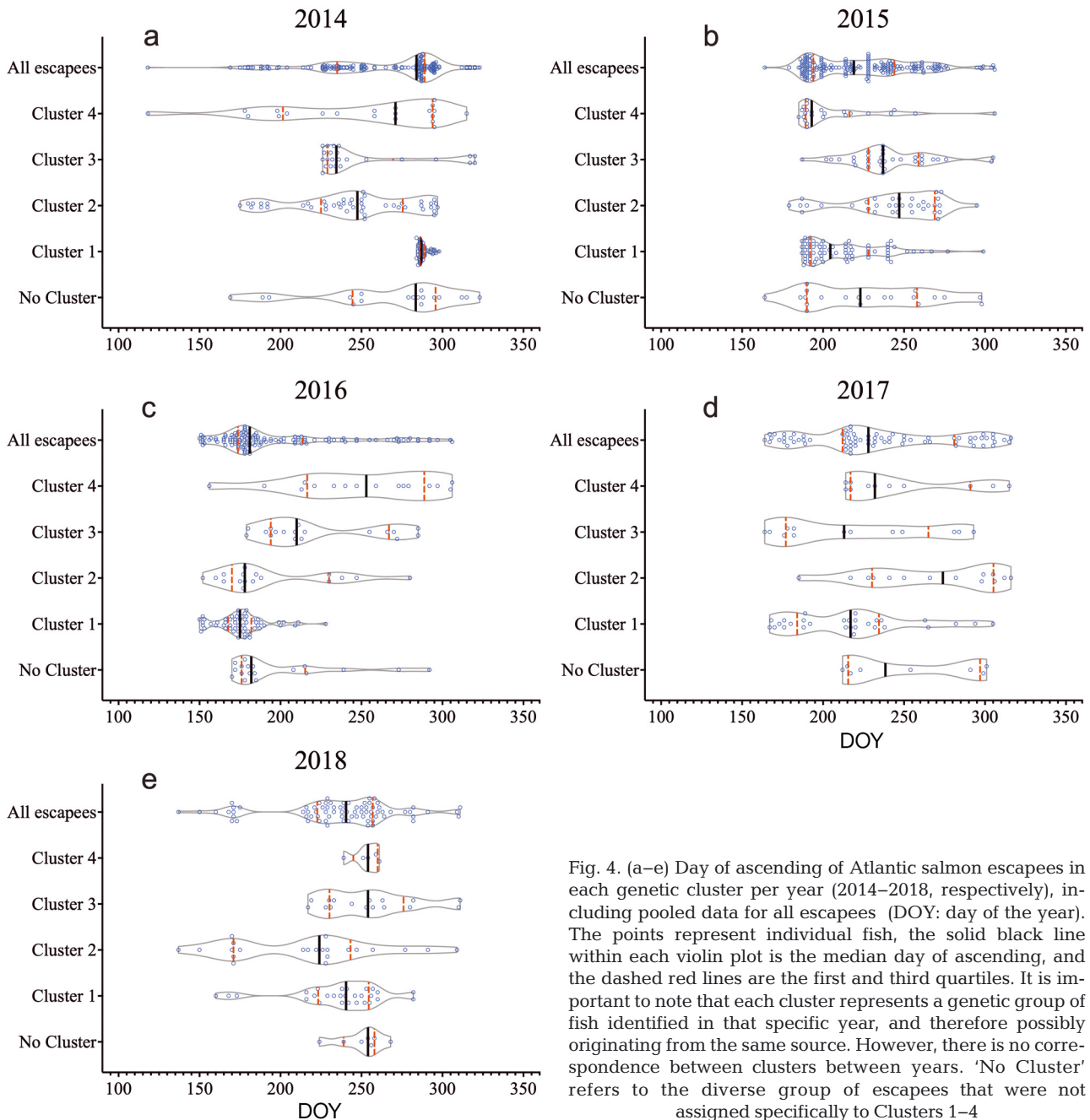


Fig. 4. (a–e) Day of ascending of Atlantic salmon escapees in each genetic cluster per year (2014–2018, respectively), including pooled data for all escapees (DOY: day of the year). The points represent individual fish, the solid black line within each violin plot is the median day of ascending, and the dashed red lines are the first and third quartiles. It is important to note that each cluster represents a genetic group of fish identified in that specific year, and therefore possibly originating from the same source. However, there is no correspondence between clusters between years. 'No Cluster' refers to the diverse group of escapees that were not assigned specifically to Clusters 1–4

4.2. More than half of the escapees entering the river were mature

Although maturation varied with sex and time of escape, overall, more than half (59%) of the escapees entering the trap were mature (Table 1). Previous studies have shown that most of the escapees entering other rivers in Norway were mature or maturing (Fiske et al. 2001, Moe et al. 2016). In contrast to the River Etne, all of 29 small (~0.4 kg) es-

capees captured in the River Steinsdalselva in western Norway in 2012, immediately after an escape event in a nearby farm, were immature (Madhun et al. 2015). Observations of large numbers of immature escapees have also been reported in rivers in Canada (Carr et al. 1997, Lacroix et al. 1997). However, maturation status may differ between escapees captured in the lower reaches of rivers and river mouths, and further up in the system where spawning grounds are typically located. Consistent with this suggestion, our

data showed that the escapees captured below the trap in the late autumn were recent escapees and most were immature (Table S1). Other reports have shown that triploid, and thus sterile, escapees display both reduced migration back to freshwater compared to their diploid counterparts, and are also captured low in the watercourse (Glover et al. 2016b), presumably due to lack of migration motivation that is linked with maturation.

Although the number of early escapees in the present study was significantly lower than the number of recent escapees, almost all of them were mature. This observation is important in 2 respects. Firstly, more of them can therefore spawn, but secondly, these mature early escapees are more likely to successfully spawn in comparison with the mature recent escapees. This is because although farmed escapees display lower spawning success than wild salmon (Fleming et al. 1996, 2000), early experience (i.e. time spent in the wild) is potentially associated with higher relative spawning success (Fleming et al. 1997).

4.3. The majority of salmon had recently escaped before they entered the river (recent escapees)

The time of escape during the salmon production cycle influences post-escape behaviour and ultimately survival of the escapees (Skilbrei & Jørgensen 2010, Skilbrei 2013). Classification of farmed salmon into 'early' and 'recent' escapees is important in revealing the history of escapees entering rivers, which in turn has potential implications for interactions and interbreeding with wild salmon. In the present study, 90% of the fish were recent escapees, and hence had entered the river shortly after escaping without having transitioned to a marine diet. In contrast, the percentage of early escapees was low (10%) but varied from 3 to 30% among years.

Farmed salmon that escape shortly after sea transfer as smolt or post-smolt (early escapees), at the time when wild smolts migrate to the oceanic feeding ground, may also migrate out to sea (Skilbrei 2010). After 1–3 yr, a small percentage of these will return to the coast and enter rivers as mature adults (Skilbrei et al. 2015). Fish that escape later in the production cycle at an older age (recent escapees) are likely to have a different migratory behaviour. These individuals may stay near the area they escaped from for a prolonged period of time, hence increasing their recapture rate, while some of them may enter rivers near or far away from the farm of origin (Olsen &

Skilbrei 2010, Skilbrei & Jørgensen 2010, Madhun et al. 2015, Quintela et al. 2016). The motivation behind the diverse behaviour of recent escapees is not known and needs further study. The fact that the recent escapees were numerically most abundant (90%) and that 55% of them were mature highlights the need for more knowledge about spawning success of both early and recent escapees when entering rivers. As discussed above, despite being low in numbers, almost all early escapees were mature and they are considered, but not demonstrated, to have a greater spawning success compared to their relative numbers, potentially due to their life experience in the wild (Fleming et al. 1997).

4.4. Escaped farmed salmon originated from multiple sources

A pertinent question for the management authorities is whether the escapees entering a river during a given year primarily originate from a single or multiple sources. The genetic analyses conducted here are not able (nor were intended) to determine the precise number of sources (i.e. cages and/or farms) from which escapees originated each year. Nevertheless, extensive experience with genetic analyses of salmon on Norwegian fish farms (Glover et al. 2008, 2009) has demonstrated that a single cage typically contains fish from one source, although a farm may contain cages with fish from one or more sources (Glover et al. 2008, 2009, Glover 2010). Therefore, as multiple genetic clusters were identified within the escapees entering the River Etne every year, we conclude that these fish originated from multiple sources. This suggestion is strongly supported when the identified genetic clusters were overlaid with data on the timing of arrival in the trap, the mean sizes of fish for each cluster and not least whether the clusters comprised fish from recent or early escapes.

4.5. Some of the genetic clusters in specific years likely originated from recent and distinct escape events in the nearby area

Some of the genetic clusters identified within years contained fish that were heterogeneous in size, escape history (i.e. contained both early and recent escapees) and arrived in the river throughout the whole season. It is likely that fish belonging to these clusters escaped from multiple sources, and that they only overlap genetically as they originate from the

same breeding line and therefore resemble each other (Glover et al. 2009, Glover 2010). In contrast, some of the genetic clusters that were identified in some years contained only recent escapees, displayed a narrow size range and arrived in the river in numbers in a short time window (Table 2, Fig. 4). These 'homogeneous groups' of fish are likely to have originated from a recent single escape event, possibly from the nearby area (discussed further below). This suggestion is supported by the fact that earlier reports have shown that fish escaping from a farm may be captured in nearby rivers just a few days to weeks after escape (Madhun et al. 2015, Quintela et al. 2016). Clusters 1 and 3 in 2014 and Cluster 1 in 2016 are likely to reflect such escape events (Table 2, Fig. 4).

The publicly available data (<https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Roemningsstatistikk>) about reported escape events in the studied period have provided interesting insight into the potential origin of these specific genetic clusters. The reported data include fish farm, date of escape and estimated number and size of fish. Data for the reported escapes in 2014 showed that more than 48 000 (average weight ~1 kg) salmon had escaped from a farm 32 km from the River Etne (Farm 1, Fig. 1), indicating that escapees in Cluster 3 from the same year could have originated from this farm. In contrast, although Cluster 1 from the same year had the characteristics of a recent escape event, there was no matching record of an escape event in the area in the escapes database, and therefore it is possible that fish in this group originated from an unreported escape event. In 2016, a reported escape event of 36 700 (average weight ~4 kg) salmon from a farm located 50 km from the river is possibly the potential source of Cluster 1 from the same year (Farm 2, Fig. 1). The reporting dates of both escape events were 4–5 d before the arrival of the escapees to the river.

Cluster 1 in 2014 arrived in the river late in the season, with an MDA of DOY 284, whilst Cluster 1 in 2016 arrived in the river early, with an MDA of DOY 181 (Fig. 4). Therefore, the timing of such recent escape events and the number of escapees from such events may impact not only the total number of escapees ascending a river in a particular year but also the MDA of escapees in that particular river.

4.6. Management implications

This study provides extensive knowledge about the diversity of characteristics of escaped farmed

salmon entering a river located in an area with intensive aquaculture. This knowledge is invaluable for the authorities responsible for management of salmon farming. Based on our findings, we conclude that in the absence of mitigation, such as removal by the fish trap, the observed numbers and maturity status of the escapees demonstrates that the wild population in the River Etne would have been exposed to significant risk of further introgression from domesticated escapees. This conclusion is consistent with a recent risk analysis that concluded that without a change in current production volume or regimes, or substantial expansion of mitigation efforts, further introgression from domesticated escapees is expected to be observed in many wild salmon populations through much of Norway (Glover et al. 2020). Finally, the results presented here suggest that despite the fact that the recent escapees were numerically most abundant, a combination of lower maturation rates for them, and the fact that early escapees may be better spawning competitors than recent escapees (Fleming et al. 1997), means that escapes of smolts, post-smolts and larger fish all need continued attention from the management authorities and aquaculture industry.

Data availability. All genetic, biological and fatty acid data are archived together with this work in Supplement 2 at www.int-res.com/articles/suppl/q015p271_supp2.xlsx.

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