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This report presents the results of marine and freshwater scientific work carried out by Marine Scotland Science.

Examination of levels of farm/wild hybridisation in southwest Scotland and Northwest England following a large-scale farm salmon escape event in 2020

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Executive summary

A genetic survey was undertaken in 2020 and 2021 of salmon obtained from rivers in areas of Scotland and England local to an escape event that occurred from the Carradale North fish farm during Storm Ellen in August 2020. Taking into consideration all results, there is no indication that this escape event resulted in significant interbreeding of escaped farm fish with wild stocks in the 2020 spawning season in the months immediately after the escape.

On August 20th 2020, Mowi's Carradale North fish farm shifted position after its seabed anchors became dislodged during Storm Ellen. This damage resulted in a reported 48,834 farmed Atlantic salmon escaping into the wild. There were reports that large numbers of farmed origin salmon were present in the areas surrounding the escape location in the weeks immediately after the escape event, with a minimum estimate of 3,000 fish entering rivers. This was of concern to local fisheries managers, as escaped farm fish have the potential to breed with wild individuals, resulting in hybrids that are less fit than their wild counterparts, potentially leading to a significant detrimental impact on wild populations.

Genetic material was obtained from wild salmon fry captured during surveys undertaken in 2020 and 2021 to examine if any hybridisation between the escaped fish and wild stocks had occurred. Using similar genetic methods to those previously employed to estimate levels of hybridisation (introgression) in wild Scottish salmon populations, the samples were examined to identify the presence of signatures of first generation (F1) hybrid fish (from crosses of wild and farm individuals). In Scotland, the prevalence of any existing F1 fish was determined in the 2020 cohort (2,358 samples), which could not have been influenced by the escape event. These levels were then compared to those in the 2021 cohort (2,586 samples), which could potentially be impacted by hybridisation from escapees from

the event. For samples collected from rivers in Cumbria in the North of England during 2021, prevalence's of F1 fish in fry (279 fish) were determined and compared to parr (58 fish), as no fry samples were available from 2020. The proportions of F1 fish were then compared between these age classes, with parr acting as a background estimate with which to compare the 2021 fry cohort.

In the samples obtained from Scotland, a single F1 fish was observed in the 2020 cohort and none in the 2021 cohort. In the samples from England, a single F1 fish was identified in the 2021 fry. Considering the complete lack of fish identified as F1 in the Scottish 2021 fry, and only a single individual in the English 2021 fry, there was, overall, no evidence of substantial hybridisation occurring in the 2021 spawning season in both countries due to the escape event. This is likely a result of the farmed fish being immature and therefore unable to breed with wild individuals in the year of the escape.

It should be noted that the lack of immediate impact on levels of hybridisation in the wild stocks under investigation does not mean that such a large escape event resulted in no negative impacts on wild fish stocks. Even if no immediate introgressive impact was seen in the local area, there may still be hybridisation occurring in either the area of the escape, or further afield, as it is known that immature fish escaping may migrate long distances and return to either the area of escape and/or rivers far from their escape location at a later time. Thus, the impacts of any escape event may not be immediate and/or local but may spread across both time and space. Relating such impacts to a single escape incident would be extremely difficult.

The results of this investigation indicate that immediately following the Carradale escape, hybridisation with wild salmon was very limited in this specific case. However, in other such large-scale escapes, immediate impacts have been seen. Thus, it is evident that each such event should be considered based on the particular situation pertaining at the time in regards to factors such as numbers, timing, wild stocks, and, of particular importance, the maturation status of the escapees. As such, there is a continuing requirement to strengthen both practical (on site) and regulatory regimes to prevent escapes occurring.

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Background

On August 20th 2020, Mowi's Carradale North fish farm shifted position after its seabed anchors became dislodged during Storm Ellen. The farm comprised ten circular net pens containing a total of 550,700 Atlantic salmon (*Salmo salar*), with an average weight of approximately 4.2 kg each. Four pens were damaged, two of which experienced torn netting. Mowi reported that this damage resulted in 48,834 salmon escaping into the wild (Anon, 2020). In the weeks immediately after the escape event, there were reports that large numbers of farmed origin salmon were observed in rivers in the areas near to the escape location. It was estimated that a minimum of 3,000 farmed fish entered Scottish rivers (Burns *et al.*, 2021).

The potential presence of such large numbers of farmed fish entering Scottish rivers raised concerns for the health of the wild populations they could interact with. Interbreeding between escaped farmed salmon and wild conspecifics, and the resulting introgression of genetic material from farm stocks into the wild, brings risks to the diversity, genetic integrity, fitness, and viability of wild salmon populations (Naylor *et al.*, 2005; Glover *et al.*, 2020). In Scotland, significant introgression has previously been found in areas of both marine and freshwater farm production with a focus along parts of the Scottish west coast and western Isles (Gilbey *et al.*, 2021). To examine whether the 2020 Carradale escape event resulted in detectable levels of introgression, a genetic survey was undertaken.

Materials and Methods

A genetic survey was undertaken in 2020 and 2021. In both years, fin clip tissue samples of fry (0+ fish) were collected around the Scottish west coast in the vicinity of the escape event. In 2021, at the request of the Environment Agency, samples of both fry and parr were collected from English northwest coast rivers. These samples were used to:

- Estimate the prevalence of introgression in juvenile salmon populations in the vicinity of the North Carradale fish farm prior to any potential influence of the 2020 escape event.
- Estimate the prevalence of introgression following the 2020 escape event.
- Compare the prevalence of introgression within the rivers between years.

Survey design

To ensure that the samples collected were representative of salmon populations in the Scottish survey area, and were not affected by sampling biases, a formal statistical survey design was employed. This survey design followed the methodology of the National Electrofishing Programme for Scotland (NEPS) (Malcolm *et al.*, 2020) and used a Generalised Random Tessellation Stratified (GRTS) (Stevens and Olsen, 2004; Kincaid and Olsen, 2017) design which provided a spatially balanced survey across the area of interest.

The survey design employed was an equal probability stratified survey with over-samples. The sample frame (i.e. the rivers that could potentially be sampled) included all rivers greater than Strahler River Order 2 that were below impassable barriers for salmon. The design included sample sites split across four strata; Carradale/Arran (East coast of Kintyre peninsula and West coast of Arran), Argyll, Clyde (including Lomond) and Ayrshire (Figure 1). The sites were surveyed in the autumn/winter of 2020 and early spring of 2021 prior to any effects of the 2020 farm escape, and again in the autumn/winter of 2021 after escaped fish would have had the opportunity to spawn.

Together with the GRTS sites, additional sites were added to the survey (termed here: ad-hoc sites). These were: 1) additional sites within the GRTS strata, but not part of the formal survey design, that were of particular interest to the local fisheries managers in these areas; 2) sites requested by NatureScot on the river Bladnoch, which is designated a Special Area of Conservation (SAC) with regard to Atlantic salmon; and 3) sites requested by the Environment Agency on SAC rivers along the northwest coast of England, which may also have been impacted by the escape event. In the case of the English rivers, sampling was undertaken in 2021 only.

Sample collection

Fish were sampled by the staff from the representative bodies in each area (Argyll Fisheries Trust, Ayrshire Rivers Trust, Clyde River Foundation, and Loch Lomond Fisheries Trust, NatureScot, Environment Agency). In Scotland, caudal fin clip samples were collected from fry (juvenile salmon spawned in the year of collection) in both 2020 and 2021. This approach allowed direct comparison between years using the same age class. The samples collected in 2020 provided a ‘background’ point estimate of prevalence of introgression and numbers of first generation (F1) farm/wild hybrid fish at the sites. The samples collected in 2021 included fry whose genetic composition could potentially have been impacted by any escapees breeding with wild individuals, with the production of F1 hybrids in this cohort. Numbers of F1 hybrid fish were compared across the two sample years to identify any impacts. In order to provide direct comparisons with previous studies of introgression in Scotland (Gilbey *et al.*, 2021), the same sampling protocols were followed. Target samples of up to 30 fry were to be obtained from each site. Where no fry were captured within 10 minutes of arrival at a site, surveyors proceeded to use over-samples (spare sites that maintain the integrity of the overall design) to maintain the targeted site numbers.

There was no opportunity to sample in 2020 in England as the English SAC rivers were not included in the survey until requested by the Environment Agency in 2021 and, so, both parr and fry were collected in 2021. Here, levels of introgression and numbers of F1 hybrid fish were compared between age classes, taking into account the potential influence of differential mortality between age classes of farm/hybrid/wild individuals, which is known to occur (e.g. Skaala *et al.*, 2012; Solberg *et al.*, 2015; Glover *et al.*, 2017).

Genetic analysis

Genotyping of wild samples

All fish were genotyped using a set of 74 Single Nucleotide Polymorphic (SNP) genetic markers, developed to maximise the power to detect and quantify levels of introgression between farmed fish of Norwegian origin (which the escapees in this case were) and wild Scottish fish (Gilbey *et al.*, 2021). DNA was extracted from fin tissue using a Chelex extraction protocol (Walsh *et al.*, 1991). Genotyping was carried out on a Fluidigm EP1 platform (Fluidigm, San Francisco, CA, USA) following the manufacturer's protocols. Samples with < 95% successful genotype calls were removed from the analysis.

Family structure

The family structure of the samples was examined at each site. This step was undertaken as samples containing many full-sibs (sharing both parents) may influence interpretation of results. This is of particular importance, as in most cases the samples consisted of fry alone and, as such, dispersal from the redd may have been limited compared to older fish (Eisenhauer *et al.*, 2020 and references therein). For each site, the presence of full-sibs was examined using maximum likelihood estimations as implemented in the COLONY 2.0.6.6 software package (Jones and Wang, 2010). Numbers of full-sibs in each year were compared using paired-t tests carried out in R (R Core Team, 2015).

Reference samples

Hybrid fish were identified by comparing individual genotypes of the wild sampled fish to two sets of reference samples using the approaches outlined in Gilbey *et al.* (2021) following the procedures described below.

This analysis was performed using the same wild reference panel as used in Gilbey *et al.* (2021) based on wild fish captured from around Scotland as these have previously been shown to be representative of Scottish wild fish. However, within this study, a new set of farm reference samples were used. These new farm reference samples were obtained from Mowi and comprised tissue samples from 100 fish of the same breeding line as the escaped fish (Mowi pers. comm.). Using these reference fish allowed maximum power for the analytical quantification of genetic interbreeding from the specific escape event. The farm fish were genotyped for the 74 SNP markers as described above, and reference centroids produced consisting of 100 *in silico* generated reference fish produced in HYBRIDLAB 1.0 (Nielsen *et al.*, 2006), as described in Gilbey *et al.* (2021).

Simulating farm x wild crosses

To identify first generation (F1) crosses, a set of simulated F1 crosses were produced. Their hybrid status was then determined, as described below for wild fish. Genotypes of 500 simulated F1 hybrid fish were produced in HYBRIDLAB by random mating between Mowi farmed fish of the same breeding line as the escapees and wild fish captured in 2020 only. Such crossings provided the most accurate match to any F1 fish that may have been captured in 2021 and which might be a result of mating between the actual escapees and wild fish in 2020. The distribution in individual levels of introgression measured in the simulated F1 fish provided confidence bounds with which to classify any 2021 F1 hybrid fish captured in the wild (mean ± 2 x standard deviation).

Estimating levels of introgression and identifying first generation hybrids

The proportion of the genome of an individual fish that is of farm strain origin was estimated by comparing the genetic signature of that fish against the reference samples. The probability of belonging to the wild reference sample, *P(wild)*, was then determined using a systematic Bayesian clustering approach applying Markov Chain Monte Carlo (MCMC) estimation, as implemented in the STRUCTURE 2.3.4 software package (Pritchard *et al.*, 2000). This was performed using 50,000 repetitions as burn-in, followed by a further 100,000 repetitions with no *a priori* information of sampling locality/origin, and assumed two populations (wild and farm). Each fish was analysed separately, together with the farm and wild reference populations, to prevent biases that may be introduced if all samples were included in a single analysis (Kalinowski, 2011; Karlsson *et al.*, 2014). For each fish, the probability of belonging to the wild centre point *P*(wild) was individually calculated and recorded. Expected *P(wild)* probability distributions range from around 1 for pure wild fish to around 0 for pure farmed fish, with F1 hybrids (first generation) having *P(wild)* values distributed around 0.5 (Gilbey *et al.*, 2021). To compare levels of introgression to that observed previously (Gilbey *et al.*, 2021), the same hybrid identification cut-off *P*(wild) of 0.747 was used (i.e. the value below which the fish is classified as a hybrid). However, some care must be taken in interpreting these observations, as the cut-off used in the previous analysis was developed based on different reference samples than those used here. However, it is utilised here to allow the observations in the current analysis to be put into a qualitative comparative context with the previously published work.

Results

Samples and genotyping

In total, 118 sites were fished as part of the survey, with 2,390 and 2,932 samples collected in 2020 and 2021 respectively (Figure 1, Table 1, Appendix 1). An overall genotyping success rate of 99.2% resulted in 5,281 samples available for analysis.

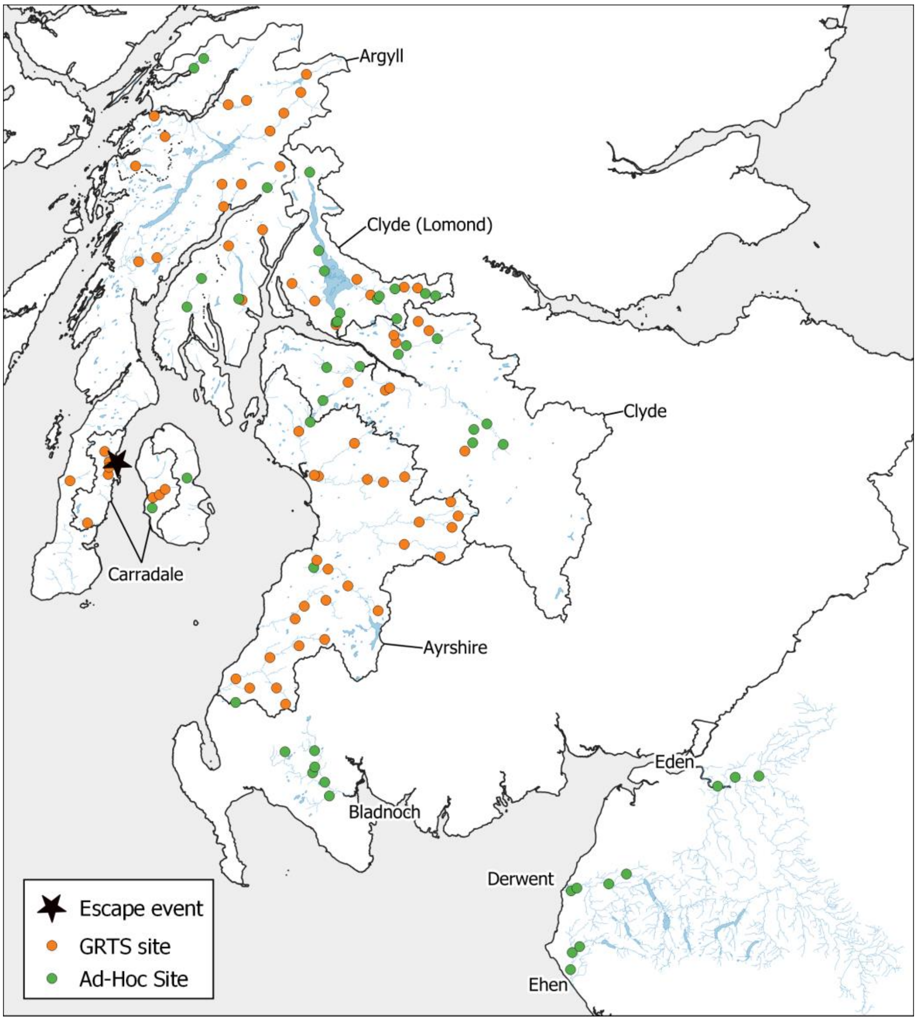

Figure 1 Map showing location of the escape event and the sampled sites in Scotland and England. Generalised Random Tessellation Stratified (GRTS) regions are identified (Argyll, Ayrshire, Carradale, Clyde) together with GRTS and ad-hoc sites within these regions. Additional ad-hoc sites on the Scottish river Bladnoch, and English rivers Eden, Derwent and Ehen also shown.

Table 1

Summary of sites surveyed, samples genotyped and genotyping success. Full breakdown in Appendix 1.

Origin	Sites	Samples genotyped	Samples after QC	Genotyping success (%)
Scotland				
2020	90	2390	2358	98.7
2021	98	2594	2586	99.7
England				
2021	10	338	337	99.7
Totals	198	5322	5281	99.2

Family structure

The majority of families in both years (88.8% and 86.8% in 2020 and 2021, respectively) consisted of single fish (i.e. there were no full siblings) or family groups of two full sib members (8.6% and 9.2% in 2020 and 2021, respectively) (Table 2, Figure 2). In 4% of cases, in both years, full-sib family sizes ranged from 4 up to a maximum of 24 individuals. Overall, in most cases, family groups were small, suggesting the sampling had captured the diversity present at a site. As such all data were retained for analysis.

Table 2

Full-sib family size across the two years of screening. Values represent the proportion (%) of families of a particular size observed across the two years.

Family size	Year	
	2020	2021
1	88.8	86.8
2	8.6	9.2
3	1.4	1.5
4	0.3	0.8
5	0.3	0.3
6	0.1	0.3
7	0.3	0.3
8	0.1	0.1
9	0.0	0.3
10	0.0	0.2
11	0.1	0.1
12	0.1	0.1
13	0.1	0.1
24	0.0	0.1

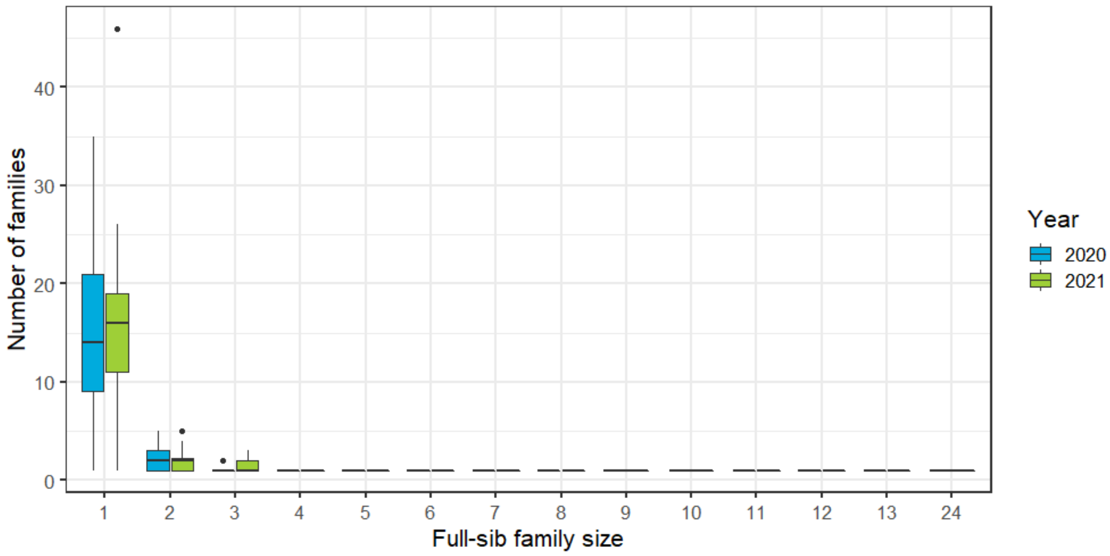

Figure 2 Full-sib family sizes per site in 2022 and 2021.

There was no significant difference in family composition between the two years of sample collection (Paired t-test df = 13, p-value = 0.215).

Levels of introgression as measured in simulated first generation (F1) hybrids

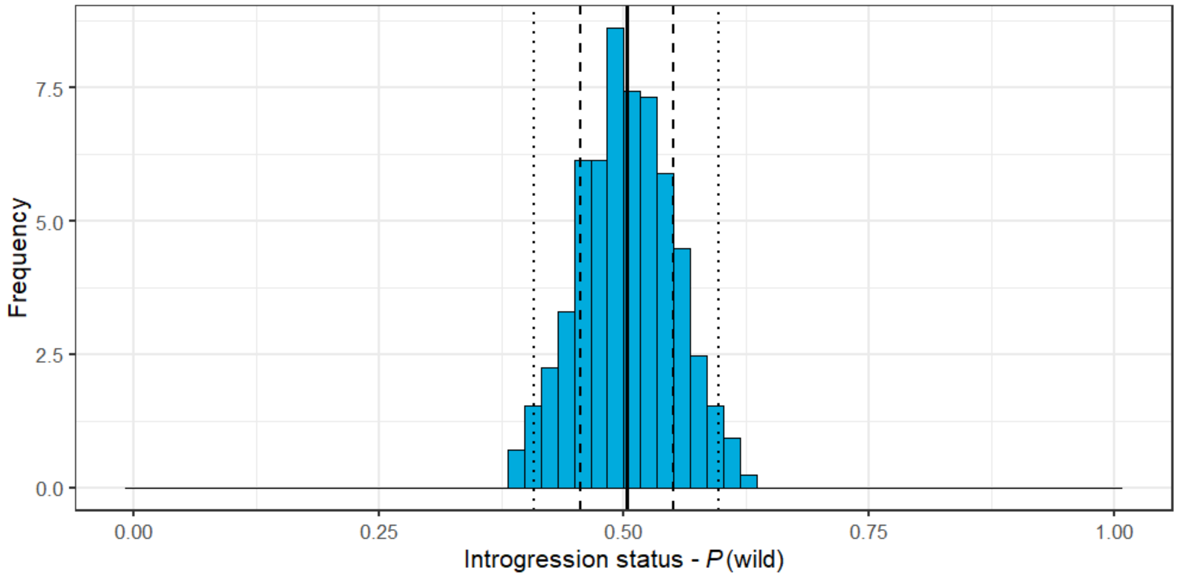

Figure 3 Introgression status, as measured by *P*(wild), for 500 *in silico* generated F1 hybrid fish. Vertical lines represent mean (solid), plus/minus one standard deviation (dashed), and plus/minus two standard deviations (dotted).

Individual *P*(wild) values for the 500 *in silico* generated F1 hybrid fish can be seen to have a distribution with a mean of 0.503 and standard deviation (SD) of 0.047 (Figure 3). Identification of F1 fish in the Scottish wild collected samples was thus undertaken using the mean ± two SD of the simulated F1 fish, which resulted in confidence bounds which spanned from 0.409 to 0.597.

Levels of introgression of wild fish

Introgression in Scotland

Examination of the *P*(wild) values across both years in Scotland (Figure 4) identified a single F1 fish. This was a fish from 2020 from the river Clyde that had a *P*(wild) value of 0.5. No F1 fish were detected in 2021.

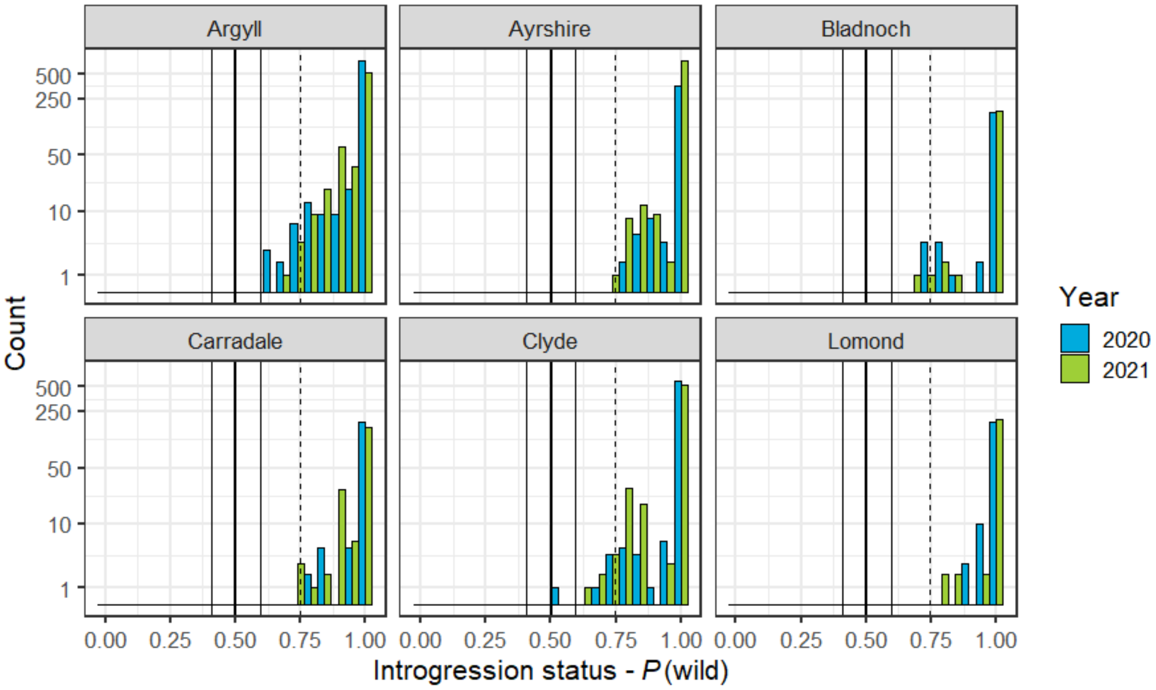

Figure 4 Introgression status, as measured by *P*(wild), for wild caught fish in Scotland in 2020 and 2021. Vertical solid lines represent mean (thick) and ± 2 x SD (thin) of simulated F1 fish. Vertical dashed line represents the hybrid cut-off used in Gilbey *et al.* (2021) to identify farm/wild hybrid fish.

Twelve and fifteen fish in 2020 and 2021, respectively, had *P*(wild) values below the cut-off used by Gilbey *et al.* (2021) to identify farm/wild hybrid fish (Table 3). These proportions of hybrid fish are similar to those previously found in the areas under investigation here (Gilbey *et al.*, 2021).

Table 3

All wild caught fish in Scotland with *P*(wild) values below the cut-off used by Gilbey *et al.* (2021) for the identification of hybrid fish.

Area	River	Site	Latitude	Longitude	*P*(wild)
2020					
Argyll	Glen Rosa Water	CarGenArgyllAdhoc_001	55.59401	-5.18084	0.692
Argyll	Lusragan Burn	CarGen_Argyll_059	56.43569	-5.39851	0.609
Argyll	River Creran	CarGenArgyllAdhoc_007	56.56396	-5.23203	0.690
Argyll	River Creran	CarGenArgyllAdhoc_007	56.56396	-5.23203	0.726
Argyll	River Creran	CarGenArgyllAdhoc_006	56.58804	-5.19216	0.744
Argyll	River Fyne	CarGenArgyllAdhoc_005	56.28921	-4.89669	0.616
Argyll	River Shira	CarGen_Argyll_076	56.29638	-5.00610	0.638
Clyde	River Kelvin	CarGen_Adhoc_Clyde_008	55.90655	-4.31539	0.526
Clyde	River Kelvin	CarGen_Clyde_172	55.93929	-4.33814	0.676

Area	River	Site	Latitude	Longitude	*P*(wild)
Clyde	River Kelvin	CarGen_Clyde_170	55.98858	-4.24113	0.745
Clyde	River Leven	CarGen_Clyde_161	56.02686	-4.67677	0.721
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_001	54.8554	-4.53795	0.714
2021					
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_005	54.92281	-4.60209	0.719
Argyll	River Eachaig	CarGen_Argyll_047	56.14867	-5.05116	0.715
Argyll	River Eachaig	CarGen_Argyll_047	56.14867	-5.05116	0.744
Argyll	River Fyne	CarGenArgyllAdhoc_005	56.28921	-4.89669	0.679
Argyll	River Ruel	CarGenArgyllAdhoc_009	55.99864	-5.21408	0.724
Ayrshire	Water Of Girvan	CarGen_Ayrshire_111	55.31707	-4.57661	0.736
Carradale	Machrie Water	CarGen_Carradale_028	55.56547	-5.26877	0.747
Clyde	River Clyde	CarGen_Clyde_165	55.67757	-4.02746	0.621
Clyde	River Clyde	CarGen_Clyde_165	55.67757	-4.02746	0.707
Clyde	River Clyde	CarGen_Clyde_196	55.95109	-4.33743	0.713
Clyde	River Clyde	CarGen_Clyde_165	55.67757	-4.02746	0.723
Clyde	River Clyde	CarGen_Adhoc_Clyde_010	55.73413	-3.98817	0.731
Clyde	River Kelvin	CarGen_Clyde_191	55.96901	-4.19301	0.682
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_005	54.92281	-4.60209	0.708
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_004	54.95613	-4.72664	0.744

Introgression in England

The same F1 identification confidence bounds were used for the fish from English rivers as were used for the Scottish sample. However, it must be remembered that all wild reference samples used here were based on individuals collected from Scotland. These represented the most relevant available reference fish and had been chosen such that the influence of any wild phylogeographic structure across the whole country was minimised. Thus, even though there were no wild English fish in the reference samples, there is no reason to expect that the results would be influenced to a significant degree.

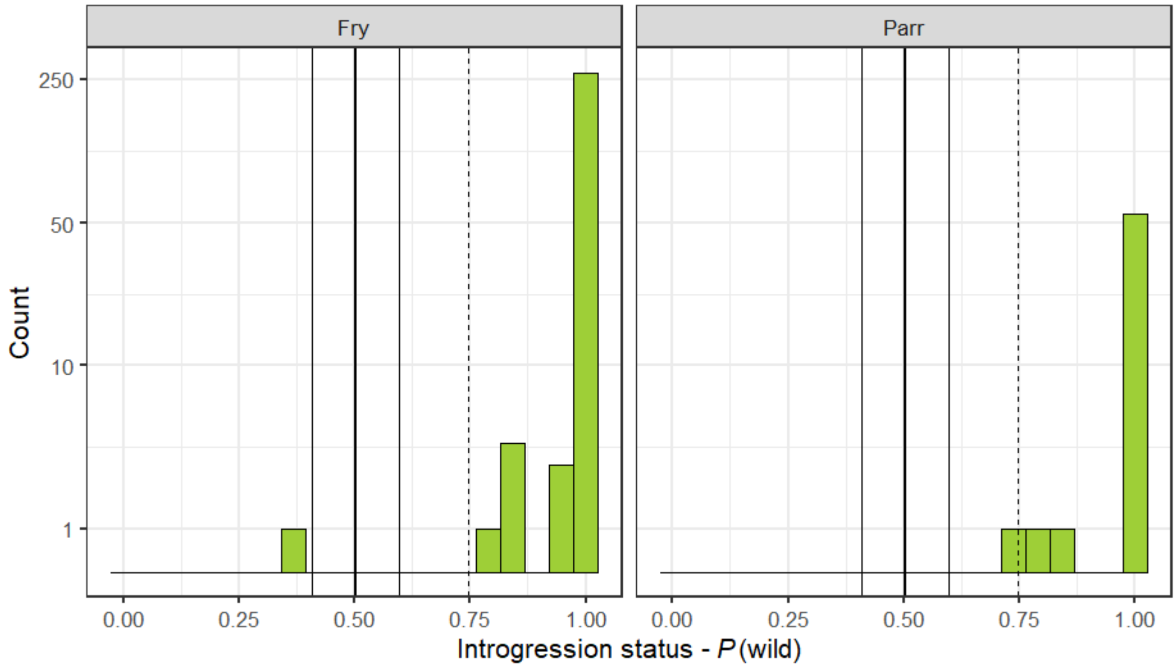

Figure 5 Introgression status, as measured by *P*(wild), for wild fry and parr caught in England in 2021. Vertical solid lines represent mean (thick) and ± 2 x SD (thin) of simulated F1 fish. Vertical dashed line represents the hybrid cut-off used in Gilbey *et al.* (2021) to identify farm/wild hybrid fish.

There was a single fish whose *P*(Wild) fell just below the lower bound used to identify F1 fish. The fish was from the Aglionby Crosby site on the river Eden (Lat. 54.923169, Long. -2.8732639) and had a *P*(wild) value of 0.369. This was also the only fish with a *P*(wild) value below the cut-off used by Gilbey *et al.* (2021) to identify farm/wild hybrid fish.

Discussion

A total of 5,281 wild-caught salmon were examined for the presence of F1 hybrids, which may have arisen from the escape event that occurred from the Carradale North fish farm during Storm Ellen in August 2020. Taking into consideration all results, there is no evidence that the fish that escaped during this event bred with wild fish in the areas sampled in the months immediately after the escape, during the 2020 spawning season.

A single F1 fish was observed in Scotland in 2020. This fish could not have been a result of any hybridisation resulting from the Carradale farm escape as it is from a cohort of fish produced from spawning from the year before the escape. No F1 fish were identified in 2021, the year any impacts would have initially been expected to be observed. The numbers of farm/wild hybrid fish identified in both years are similar to those previously observed in these Scottish areas (see Figure 19 in Gilbey *et al.*, 2021). This indicates that while there is an overall presence of farm introgression in these areas in both years, there was no immediate increase as a result of the Carradale escape event.

A single fry from the English samples was identified as a possible hybrid F1 fish, and no other hybrids were identified. Analysis of the English samples was based on comparing levels of introgression between age classes. Parr, which could not have been influenced by the escape, were compared to fry, which had the potential to be impacted. Care must be taken when interpreting such a comparison, as it is well known that there are behavioural, physiological and mortality differences between hybrid fish and wild conspecifics between juvenile age classes (e.g. Skaala *et al.*, 2012; Solberg *et al.*, 2015; Glover *et al.*, 2017) and so, a fry vs. parr comparison is not a like-for-like one. It is difficult, then, to come to firm conclusions based on a single individual and the comparisons available. The picture may become clearer with a more detailed survey of both parr and fry to determine true levels of 'background' introgression in these English areas.

Immediately following the escape event, large numbers of escaped farm fish, purportedly escapees from the event, were observed in rivers relatively near to the farm (Fisheries Management Scotland, pers. comm.; Burns *et al.*, 2021). However, this did not translate into an increase in the detection of F1 hybrids in these areas, despite it being known that escaped farm fish can enter rivers and breed with wild individuals wherever such interactions occur (e.g. Glover *et al.*, 2017; Gilbey *et al.*, 2018; Wringe *et al.*, 2018; Diserud *et al.*, 2020; Glover *et al.*, 2020; Gilbey *et al.*, 2021).

Successful spawning relies on the simultaneous fecundity of both parental fish. Salmon in aquaculture have, and continue to be, selected for delayed sexual maturation (Iversen *et al.*, 2016; Rivera *et al.*, 2021). The escape event occurred in August 2020, with natural spawning in the areas of investigation following just a few weeks later, in the early autumn. Gametogenesis takes significant resource investment and takes a number of weeks to complete (Thorpe, 1994; Fleming, 1996; Mobley *et al.*, 2021). The lack of an impact of the escaped fish may thus be a result of them not becoming sexually mature after escaping so close to this spawning period.

There is evidence that adult farm escapees may not necessarily use the same stretches of river for spawning as wild fish (Økland *et al.*, 1995; Thorstad *et al.*, 1998; Moe *et al.*, 2016). In addition, there may also be differences in the timing of spawning compared to wild fish (Webb *et al.*, 1991; Saegrov *et al.*, 1997; Fleming *et* *al.*, 2000; Moe *et al.*, 2016). Thus, a likely lack of maturation, together with a mismatch in “time and space” (Glover *et al.*, 2017) may all have contributed to a mismatch of spawning relative to the wild salmon, thereby reducing the potential for introgression and resulting in the low numbers of F1 hybrids detected.

The absence of an immediate observed impact on levels of hybrid F1 fish being produced does not equate to the absence of negative impacts on wild fish stocks from such large-scale escape events. Even if no immediate introgressive impact is seen in the local area, there may still, in the future, be hybridisation in either the area of the escape, or further afield. The migratory tendency of farm escapees is disrupted relative to wild fish (Hansen, 2006; Madhun *et al.*, 2017 and references within these). While the incidence of escaped farmed salmon in rivers is strongly correlated with the density of production in an area (Fiske *et al.*, 2006; Green *et al.*, 2012; Mahlum *et al.*, 2021), it is also the case that immature escapees may migrate long distances and then return to either the area of release or rivers far from their escape location (e.g. Hansen and Youngson, 2010; Glover *et al.*, 2017; Mahlum *et al.*, 2021). Thus, the introgressive impacts of an escape event may not be immediate and/or local but may spread across both time and space. However, it would be extremely difficult to disentangle these potential impacts from other reported escape events and/or unreported losses in areas where these issues could be a factor.

Together with genetic effects, escaped farm fish may also negatively impact wild populations through non-reproductive ecological interactions (Bradbury *et al.*, 2020 and references therein). Mechanisms such as pathogen transfer, competitive interactions, and ecological disturbance can all result in loss of productivity in wild populations and cause indirect genetic changes through the disruption of localised selective landscapes. Again, such outcomes from a specific escape event would be very difficult to disentangle from the ongoing farm/wild interactions occurring in the areas under investigation here.

The escape event on August 20th, 2020, at Mowi’s Carradale North fish farm resulted in an escape of tens of thousands of fish with thousands of them estimated to have entered rivers in the surrounding area. There was no immediate significant genetic impact in the spawning season immediately following the escape, probably due to the lack of maturity in these fish. This does not mean that there may not be ongoing impacts distributed over space and time following the event; however these would be extremely difficult to quantify and disentangle from other sources of introgression over the area in question.

The results indicate that immediately following the Carradale escape, hybridisation with wild salmon was very limited in this specific case. In other such large-scale escapes, immediate impacts have been seen (e.g. Wringe *et al.*, 2018). Thus, it is evident that each such event should be considered based on the particular situation pertaining at the time in regards to factors such as numbers, timing, wild stocks, and, of particular importance, the maturation status of the escapees.

Acknowledgments

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Appendix 1

Summary at site level of all fish included in the analysis.

Area	River	Sample Site	Latitude	Longitude	Year	Collected	Analysed
Scotland							
Argyll	Barr Water	CarGen_Argyll_051	55.5745	-5.6647	2020	30	29
Argyll	Barr Water	CarGen_Argyll_051	55.5745	-5.6647	2021	30	30
Argyll	Blackwater (Arran)	CarGenArgyllAdhoc_002	55.51925	-5.32022	2020	30	30
Argyll	Blackwater (Arran)	CarGenArgyllAdhoc_002	55.51925	-5.32022	2021	30	29
Argyll	Glen Rosa Water	CarGenArgyllAdhoc_001	55.59401	-5.18084	2020	23	23
Argyll	Glenfinart Burn	CarGenArgyllAdhoc_003	55.06807	-4.93814	2020	30	29
Argyll	Glenfinart Burn	CarGenArgyllAdhoc_003	55.06807	-4.93814	2021	30	30
Argyll	Lusragan Burn	CarGen_Argyll_059	56.43569	-5.39851	2020	30	30
Argyll	Lusragan Burn	CarGen_Argyll_059	56.43569	-5.39851	2021	6	6
Argyll	River Add	CarGen_Argyll_058	56.11482	-5.34392	2020	30	30
Argyll	River Add	CarGen_Argyll_058	56.11482	-5.34392	2021	30	30
Argyll	River Add	CarGen_Argyll_072	56.10404	-5.41893	2020	30	30
Argyll	River Add	CarGen_Argyll_072	56.10404	-5.41893	2021	30	30
Argyll	River Aray	CarGen_Argyll_056	56.24222	-5.07934	2020	30	30
Argyll	River Aray	CarGen_Argyll_056	56.24222	-5.07934	2021	27	27
Argyll	River Aray	CarGen_Argyll_070	56.29285	-5.08505	2020	30	29
Argyll	River Aray	CarGen_Argyll_070	56.29285	-5.08505	2021	21	21
Argyll	River Awe	CarGen_Argyll_042	56.42441	-4.89285	2020	30	30
Argyll	River Awe	CarGen_Argyll_042	56.42441	-4.89285	2021	30	30
Argyll	River Awe	CarGen_Argyll_053	56.51848	-4.77014	2020	30	30
Argyll	River Awe	CarGen_Argyll_053	56.51848	-4.77014	2021	30	30
Argyll	River Awe	CarGen_Argyll_079	56.45676	-4.82152	2020	30	30
Argyll	River Awe	CarGen_Argyll_079	56.45676	-4.82152	2021	8	8
Argyll	River Awe	CarGen_Argyll_090	56.56109	-4.74607	2020	10	10
Argyll	River Creran	CarGenArgyllAdhoc_006	56.58804	-5.19216	2020	30	30
Argyll	River Creran	CarGenArgyllAdhoc_006	56.58804	-5.19216	2021	30	30
Argyll	River Creran	CarGenArgyllAdhoc_007	56.56396	-5.23203	2020	30	30
Argyll	River Creran	CarGenArgyllAdhoc_007	56.56396	-5.23203	2021	30	30
Argyll	River Eachaig	CarGen_Argyll_047	56.14867	-5.05116	2020	30	30
Argyll	River Eachaig	CarGen_Argyll_047	56.14867	-5.05116	2021	30	30
Argyll	River Eachaig	CarGen_Argyll_067	56.02118	-4.98204	2020	30	30
Argyll	River Eachaig	CarGen_Argyll_067	56.02118	-4.98204	2021	30	30
Argyll	River Eachaig	CarGenArgyllAdhoc_004	56.02305	-4.99682	2020	30	30
Argyll	River Eachaig	CarGenArgyllAdhoc_004	56.02305	-4.99682	2021	24	24
Argyll	River Euchar	CarGen_Argyll_045	56.3264	-5.46047	2020	30	30
Argyll	River Euchar	CarGen_Argyll_045	56.3264	-5.46047	2021	30	30
Argyll	River Fyne	CarGen_Argyll_087	56.34161	-4.84473	2020	15	15
Argyll	River Fyne	CarGenArgyllAdhoc_005	56.28921	-4.89669	2020	30	30
Argyll	River Fyne	CarGenArgyllAdhoc_005	56.28921	-4.89669	2021	21	21
Argyll	River Goil	CarGen_Argyll_049	56.1909	-4.90774	2020	30	29
Argyll	River Goil	CarGen_Argyll_049	56.1909	-4.90774	2021	30	30
Argyll	River Kinglass	CarGen_Argyll_064	56.4816	-5.07741	2020	30	30
Argyll	River Kinglass	CarGen_Argyll_064	56.4816	-5.07741	2021	30	30
Argyll	River Kinglass	CarGen_Argyll_091	56.49351	-5.00109	2020	30	30
Argyll	River Kinglass	CarGen_Argyll_091	56.49351	-5.00109	2021	30	30
Argyll	River Nell	CarGen_Argyll_084	56.39831	-5.34045	2020	30	29
Argyll	River Nell	CarGen_Argyll_084	56.39831	-5.34045	2021	30	30

Area	River	Sample Site	Latitude	Longitude	Year	Collected	Analysed
Argyll	River Ruel	CarGenArgyllAdhoc_008	56.06741	-5.15831	2020	30	29
Argyll	River Ruel	CarGenArgyllAdhoc_008	56.06741	-5.15831	2021	30	30
Argyll	River Ruel	CarGenArgyllAdhoc_009	55.99864	-5.21408	2020	30	29
Argyll	River Ruel	CarGenArgyllAdhoc_009	55.99864	-5.21408	2021	30	30
Argyll	River Shira	CarGen_Argyll_076	56.29638	-5.0061	2020	30	29
Argyll	River Shira	CarGen_Argyll_076	56.29638	-5.0061	2021	7	7
Ayrshire	River Ayr	CarGen_Ayrshire_095	55.50827	-4.19786	2020	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_095	55.50827	-4.19786	2021	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_106	55.49761	-4.06413	2020	21	21
Ayrshire	River Ayr	CarGen_Ayrshire_106	55.49761	-4.06413	2021	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_116	55.56214	-4.07443	2020	17	17
Ayrshire	River Ayr	CarGen_Ayrshire_116	55.56214	-4.07443	2021	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_119	55.42895	-4.11045	2020	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_119	55.42895	-4.11045	2021	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_132	55.45947	-4.24863	2021	30	30
Ayrshire	River Ayr	CarGen_Ayrshire_140	55.52877	-4.04281	2021	30	30
Ayrshire	River Doon	CarGen_Adhoc_Ayrshire_001	55.39454	-4.63713	2020	22	22
Ayrshire	River Doon	CarGen_Ayrshire_093	55.2976	-4.36347	2020	30	29
Ayrshire	River Doon	CarGen_Ayrshire_093	55.2976	-4.36347	2021	30	30
Ayrshire	River Doon	CarGen_Ayrshire_101	55.35376	-4.48829	2020	30	30
Ayrshire	River Doon	CarGen_Ayrshire_101	55.35376	-4.48829	2021	30	30
Ayrshire	River Doon	CarGen_Ayrshire_103	55.40775	-4.63422	2021	21	21
Ayrshire	River Doon	CarGen_Ayrshire_127	55.39179	-4.57552	2021	30	30
Ayrshire	River Garnock	CarGen_Adhoc_Ayrshire_002	55.7387	-4.67505	2020	30	29
Ayrshire	River Garnock	CarGen_Adhoc_Ayrshire_002	55.7387	-4.67505	2021	30	29
Ayrshire	River Garnock	CarGen_Ayrshire_139	55.72423	-4.74557	2021	30	30
Ayrshire	River Irvine	CarGen_Ayrshire_099	55.61763	-4.27183	2020	1	1
Ayrshire	River Irvine	CarGen_Ayrshire_099	55.61763	-4.27183	2021	5	5
Ayrshire	River Irvine	CarGen_Ayrshire_100	55.69719	-4.47585	2020	11	11
Ayrshire	River Irvine	CarGen_Ayrshire_100	55.69719	-4.47585	2021	30	30
Ayrshire	River Irvine	CarGen_Ayrshire_104	55.61166	-4.62872	2021	30	30
Ayrshire	River Irvine	CarGen_Ayrshire_108	55.60653	-4.4215	2021	30	30
Ayrshire	River Irvine	CarGen_Ayrshire_118	55.61166	-4.62872	2021	5	5
Ayrshire	River Irvine	CarGen_Ayrshire_142	55.60401	-4.35647	2021	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_097	55.2257	-4.57818	2020	30	29
Ayrshire	River Stinchar	CarGen_Ayrshire_097	55.2257	-4.57818	2021	30	29
Ayrshire	River Stinchar	CarGen_Ayrshire_098	55.20612	-4.68325	2020	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_098	55.20612	-4.68325	2021	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_102	55.12637	-4.94458	2020	13	13
Ayrshire	River Stinchar	CarGen_Ayrshire_102	55.12637	-4.94458	2021	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_109	55.17916	-4.80161	2020	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_109	55.17916	-4.80161	2021	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_112	55.06707	-4.74136	2021	30	29
Ayrshire	River Stinchar	CarGen_Ayrshire_126	55.10543	-4.77073	2021	30	30
Ayrshire	River Stinchar	CarGen_Ayrshire_137	55.10408	-4.88003	2021	30	30
Ayrshire	Water of Girvan	CarGen_Ayrshire_105	55.27114	-4.70513	2020	30	30
Ayrshire	Water of Girvan	CarGen_Ayrshire_105	55.27114	-4.70513	2021	24	24
Ayrshire	Water of Girvan	CarGen_Ayrshire_111	55.31707	-4.57661	2020	30	30
Ayrshire	Water of Girvan	CarGen_Ayrshire_111	55.31707	-4.57661	2021	30	30
Ayrshire	Water of Girvan	CarGen_Ayrshire_131	55.30382	-4.66727	2021	30	29
Carradale	Carradale Water	CarGen_Carradale_003	55.5951	-5.51126	2020	6	6
Carradale	Carradale Water	CarGen_Carradale_003	55.5951	-5.51126	2021	30	30
Carradale	Carradale Water	CarGen_Carradale_022	55.62443	-5.50914	2020	30	10

Area	River	Sample Site	Latitude	Longitude	Year	Collected	Analysed
Carradale	Carradale Water	CarGen_Carradale_022	55.62443	-5.50914	2021	30	30
Carradale	Carradale Water	CarGen_Carradale_026	55.61361	-5.50817	2020	30	30
Carradale	Carradale Water	CarGen_Carradale_026	55.61361	-5.50817	2021	30	30
Carradale	Carradale Water	CarGen_Carradale_034	55.64873	-5.53024	2020	30	30
Carradale	Glenlussa Water	CarGen_Carradale_023	55.4814	-5.59252	2020	30	30
Carradale	Glenlussa Water	CarGen_Carradale_023	55.4814	-5.59252	2021	30	30
Carradale	Machrie Water	CarGen_Carradale_009	55.54526	-5.31073	2020	27	27
Carradale	Machrie Water	CarGen_Carradale_009	55.54526	-5.31073	2021	20	20
Carradale	Machrie Water	CarGen_Carradale_021	55.55336	-5.28956	2020	30	30
Carradale	Machrie Water	CarGen_Carradale_021	55.55336	-5.28956	2021	30	29
Carradale	Machrie Water	CarGen_Carradale_028	55.56547	-5.26877	2020	30	30
Carradale	Machrie Water	CarGen_Carradale_028	55.56547	-5.26877	2021	30	30
Clyde	Black Cart Water	CarGen_Adhoc_Clyde_001	55.79095	-4.6253	2020	30	30
Clyde	Black Cart Water	CarGen_Adhoc_Clyde_001	55.79095	-4.6253	2021	31	31
Clyde	Black Cart Water	CarGen_Clyde_171	55.83537	-4.52363	2020	30	30
Clyde	Black Cart Water	CarGen_Clyde_171	55.83537	-4.52363	2021	30	30
Clyde	Dargavel Burn	CarGen_Adhoc_Clyde_003	55.87478	-4.47514	2020	30	30
Clyde	Dargavel Burn	CarGen_Adhoc_Clyde_003	55.87478	-4.47514	2021	29	29
Clyde	River Clyde	CarGen_Adhoc_Clyde_004	55.70064	-3.86333	2020	60	60
Clyde	River Clyde	CarGen_Adhoc_Clyde_005	55.70252	-3.99129	2020	53	53
Clyde	River Clyde	CarGen_Adhoc_Clyde_009	55.74828	-3.93413	2020	30	30
Clyde	River Clyde	CarGen_Adhoc_Clyde_009	55.74828	-3.93413	2021	30	30
Clyde	River Clyde	CarGen_Adhoc_Clyde_010	55.73413	-3.98817	2020	30	30
Clyde	River Clyde	CarGen_Adhoc_Clyde_010	55.73413	-3.98817	2021	30	30
Clyde	River Clyde	CarGen_Clyde_165	55.67757	-4.02746	2021	30	30
Clyde	River Clyde	CarGen_Clyde_196	55.95109	-4.33743	2021	30	30
Clyde	River Gryfe	CarGen_Adhoc_Clyde_002	55.86915	-4.61475	2020	30	30
Clyde	River Gryfe	CarGen_Adhoc_Clyde_002	55.86915	-4.61475	2021	30	30
Clyde	River Kelvin	CarGen_Adhoc_Clyde_006	55.94646	-4.15333	2020	30	30
Clyde	River Kelvin	CarGen_Adhoc_Clyde_006	55.94646	-4.15333	2021	30	30
Clyde	River Kelvin	CarGen_Adhoc_Clyde_007	55.9277	-4.28274	2020	30	30
Clyde	River Kelvin	CarGen_Adhoc_Clyde_007	55.9277	-4.28274	2021	30	30
Clyde	River Kelvin	CarGen_Adhoc_Clyde_008	55.90655	-4.31539	2020	30	30
Clyde	River Kelvin	CarGen_Adhoc_Clyde_008	55.90655	-4.31539	2021	30	30
Clyde	River Kelvin	CarGen_Clyde_170	55.98858	-4.24113	2020	30	30
Clyde	River Kelvin	CarGen_Clyde_170	55.98858	-4.24113	2021	30	30
Clyde	River Kelvin	CarGen_Clyde_172	55.93929	-4.33814	2020	30	30
Clyde	River Kelvin	CarGen_Clyde_172	55.93929	-4.33814	2021	30	30
Clyde	River Kelvin	CarGen_Clyde_191	55.96901	-4.19301	2020	30	30
Clyde	River Kelvin	CarGen_Clyde_191	55.96901	-4.19301	2021	30	30
Clyde	River Leven	CarGen_Clyde_150	55.97397	-4.57213	2020	30	30
Clyde	River Leven	CarGen_Clyde_150	55.97397	-4.57213	2021	30	30
Clyde	River Leven	CarGen_Clyde_152	56.05925	-4.2358	2020	30	30
Clyde	River Leven	CarGen_Clyde_154	56.0403	-4.45291	2021	3	3
Clyde	River Leven	CarGen_Clyde_158	56.08109	-4.50139	2020	1	1
Clyde	River Leven	CarGen_Clyde_161	56.02686	-4.67677	2020	30	30
Clyde	River Leven	CarGen_Clyde_161	56.02686	-4.67677	2021	30	29
Clyde	River Leven	CarGen_Clyde_168	56.0643	-4.29961	2020	30	30
Clyde	River Leven	CarGen_Clyde_168	56.0643	-4.29961	2021	30	30
Clyde	River Leven	CarGen_Clyde_187	56.07331	-4.77593	2021	28	28
Clyde	White Cart Water	CarGen_Clyde_153	55.81023	-4.37596	2020	15	14
Clyde	White Cart Water	CarGen_Clyde_153	55.81023	-4.37596	2021	27	27
Clyde	White Cart Water	CarGen_Clyde_177	55.81023	-4.37596	2020	10	10

Area	River	Sample Site	Latitude	Longitude	Year	Collected	Analysed
Clyde	White Cart Water	CarGen_Clyde_177	55.81023	-4.37596	2021	15	15
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_001	54.8554	-4.53795	2020	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_001	54.8554	-4.53795	2021	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_002	54.88759	-4.55884	2020	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_002	54.88759	-4.55884	2021	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_003	54.90863	-4.60998	2020	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_003	54.90863	-4.60998	2021	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_004	54.95613	-4.72664	2020	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_004	54.95613	-4.72664	2021	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_005	54.92281	-4.60209	2020	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_005	54.92281	-4.60209	2021	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_006	54.9612	-4.60526	2020	30	30
Galloway	River Bladnoch	CarGen_Adhoc_Galloway_006	54.9612	-4.60526	2021	30	30
Lomond	River Leven	CarGen_Adhoc_Lomond_001	55.99946	-4.56749	2020	10	10
Lomond	River Leven	CarGen_Adhoc_Lomond_002	55.97735	-4.58221	2020	28	28
Lomond	River Leven	CarGen_Adhoc_Lomond_002	55.97735	-4.58221	2021	28	28
Lomond	River Leven	CarGen_Adhoc_Lomond_004	56.14494	-4.66752	2021	7	7
Lomond	River Leven	CarGen_Adhoc_Lomond_005	56.09731	-4.63994	2020	24	24
Lomond	River Leven	CarGen_Adhoc_Lomond_005	56.09731	-4.63994	2021	1	1
Lomond	River Leven	CarGen_Adhoc_Lomond_006	56.03505	-4.41238	2020	25	25
Lomond	River Leven	CarGen_Adhoc_Lomond_006	56.03505	-4.41238	2021	7	7
Lomond	River Leven	CarGen_Adhoc_Lomond_007	56.06105	-4.33863	2020	21	21
Lomond	River Leven	CarGen_Adhoc_Lomond_007	56.06105	-4.33863	2021	28	28
Lomond	River Leven	CarGen_Adhoc_Lomond_008	56.05226	-4.20959	2020	22	22
Lomond	River Leven	CarGen_Adhoc_Lomond_008	56.05226	-4.20959	2021	30	29
Lomond	River Leven	CarGen_Adhoc_Lomond_009	56.04802	-4.16623	2020	30	30
Lomond	River Leven	CarGen_Adhoc_Lomond_009	56.04802	-4.16623	2021	30	30
Lomond	River Leven	CarGen_Adhoc_Lomond_010	55.97918	-4.57688	2020	15	15
Lomond	River Leven	CarGen_Adhoc_Lomond_010	55.97918	-4.57688	2021	30	30
Lomond	River Leven	CarGen_Adhoc_Lomond_011	56.04241	-4.4034	2020	8	8
Lomond	River Leven	CarGen_Adhoc_Lomond_011	56.04241	-4.4034	2021	30	30
Lomond	River Leven	CarGen_Adhoc_Lomond_012	56.3296	-4.71869	2020	8	8
Lomond	River Leven	CarGen_Adhoc_Lomond_012	56.3296	-4.71869	2021	4	4
Lomond	River Leven	CarGen_Adhoc_Lomond_014	55.99051	-4.32679	2020	4	4
Lomond	River Leven	CarGen_Adhoc_Lomond_014	55.99051	-4.32679	2021	7	7

England							
England	Derwent	Curwen Park	54.64747	-3.53734	2021	10	10
England	Derwent	Isel Hall	54.68988	-3.31292	2021	36	36
England	Derwent	Ribton Hall	54.65424	-3.51421	2021	31	31
England	Derwent	The Cradles	54.66572	-3.38444	2021	32	32
England	Eden	Aglionby/Crosby on Eden	54.92317	-2.87326	2021	32	31
England	Eden	Gelt House	54.92647	-2.77556	2021	36	36
England	Eden	Sheepmount Athletic Stadium	54.90151	-2.94486	2021	30	30
England	Ehen	Kersey Bridge	54.46076	-3.53288	2021	32	32
England	Ehen	Longlands (US)	54.50136	-3.52739	2021	39	39
England	Ehen	Wath Brow Bridge	54.5157	-3.49806	2021	60	60

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