

Genetic stock identification reveals greater use of an oceanic feeding ground around the Faroe Islands by multi-sea winter Atlantic salmon, with variation in use across reporting groups

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While it is known that the oceans around the Faroe Islands support an Atlantic salmon (*Salmo salar*) feeding ground, the relative use of this resource by different age classes and populations remains largely unexplored. Using genetic stock identification and run–reconstruction modelling, we observed a consistent pattern whereby the proportion of multi-sea winter salmon (MSW—fish that have spent multiple winters at sea) for a reporting group was substantially greater around the Faroes than the MSW proportion among that group's corresponding pre-fisheries abundance. Surprisingly, MSW fish from Ireland and the United Kingdom were as likely to occur around the Faroes as were MSW fish from more north-eastern regions. While 1SW salmon (single sea-winter fish) from Ireland and the United Kingdom as well as Southern Norway occurred in similar proportions around the Faroes, 1SW fish from the north-eastern regions were virtually absent. Our results indicate that the oceans around the Faroes host a predominantly MSW feeding ground and use of this resource varies across age classes and reporting groups. Furthermore, these results suggest that MSW fish from some reporting groups preferentially migrate to the Faroes. Variation in spatial resource use may help buffer salmon populations against localized negative changes in marine conditions via portfolio effects.

Keywords: age class structure, Faroe Islands, migration, phenotypic diversity, *Salmo salar*, spatial variation in resource use.

Introduction

Understanding patterns of resource use provides insight into the evolution and maintenance of the intraspecific phenotypic diversity observed within many aquatic taxa (Hawley *et al.*, 2016; Kang and Thibert-Plante, 2017; Kane *et al.*, 2022). Differential resource use can limit intraspecific competition across life stages as well as buffer against extinction risk by spatially segregating a population into different habitats (Schindler *et al.*, 2015; Østbye *et al.*, 2020). From an applied perspective, knowledge of which and when individuals in a population exploit a given resource can be used to determine the efficacy of marine protected areas (Harada *et al.*, 2015; Hernández *et al.*, 2019), regulate fisheries (Armstrong *et al.*, 2013), and generate anticipatory predictions to help inform policy (Eikeset *et al.*, 2013; Ayllón *et al.*, 2018, 2019). However, the ecology of resource use remains poorly understood for many taxa with oceanic life stages. One such taxon where many aspects of the marine ecology are poorly understood is Atlantic salmon, *Salmo salar*.

The marine ecology of Atlantic salmon was, until relatively recently, almost completely unknown. There has been a sustained effort at determining migration routes (Hansen

and Jacobsen, 2003; Sjøvold *et al.*, 2007; Strøm *et al.*, 2017, 2018; Bradbury *et al.*, 2021; Gilbey *et al.*, 2021; Rikardsen *et al.*, 2021), dietary composition (Jacobsen and Hansen, 2001; Rikardsen and Dempson, 2010; Utne *et al.*, 2021), disease transmission (Teffer *et al.*, 2020), oceanic predation (Strøm *et al.*, 2019), and the populations from which salmon caught at sea originate (Bradbury *et al.*, 2016, 2021; Gilbey *et al.*, 2017; Ó Maoiléidigh *et al.*, 2018). This increase in research effort has coincided with a realization that changes in the oceanic environment have precipitated declines in the marine survival rate and abundance of Atlantic salmon (ICES, 2021; Thorstad *et al.*, 2021). For example, a reduction in the growth of salmon at sea (Vollset *et al.*, 2022) and a deterioration in marine feeding conditions (Utne *et al.*, 2021) have both been observed. Czorlich *et al.*, (2022) demonstrated that anthropogenic exploitation of capelin, *Mallotus villosus*, in the Barents Sea has induced evolution towards earlier maturation in salmon from the Teno watercourse. Together, these studies suggest that the decrease in survival/abundance of Atlantic salmon is influenced by the availability of oceanic food resources and that human-induced changes are unequivocally responsible.

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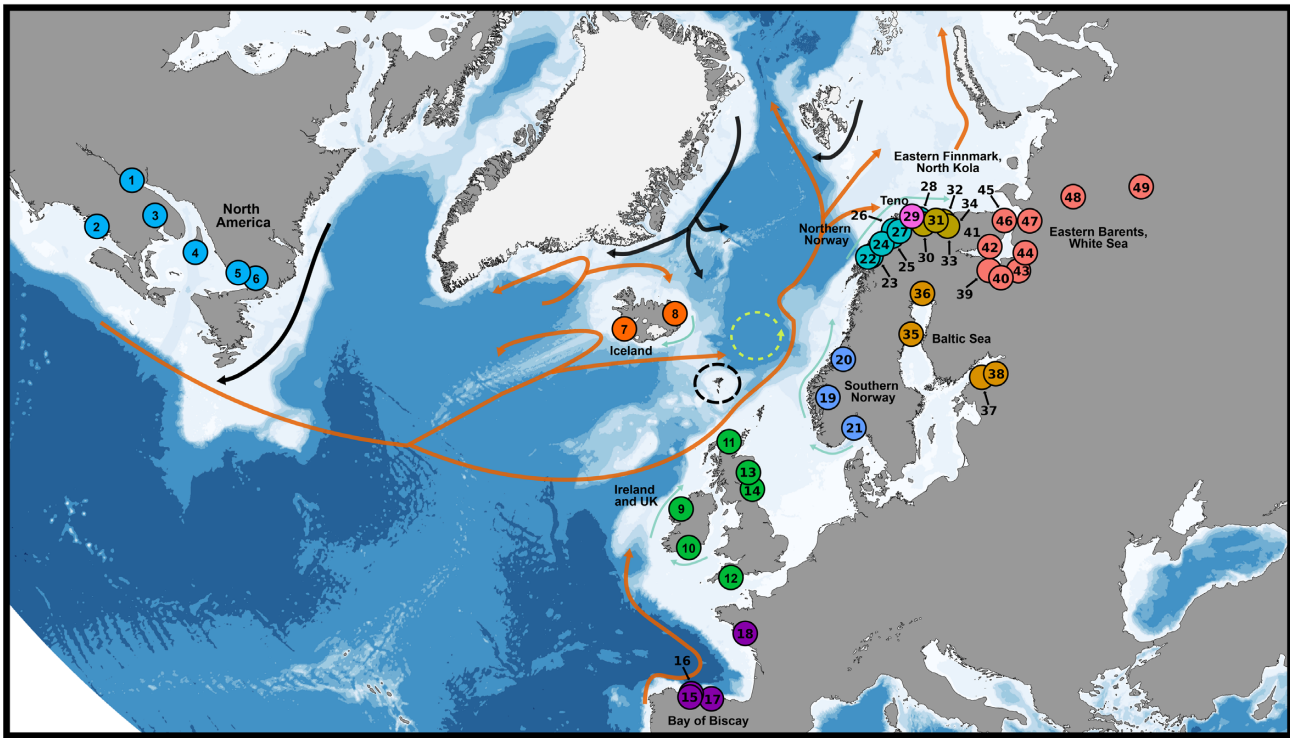


Figure 1. Agglomerative reporting groups of Atlantic salmon (bold, black text) and the populations in each reporting group used in the genetic baseline. Numbers correspond to population names in Supplementary Tables S1 and S3. Warm Atlantic currents are denoted using orange arrows, cold polar currents from the Arctic Ocean using black arrows, and coastal currents using turquoise arrows. The Vøring Gyre and its direction of flow are denoted using the lime arrow. Increasing ocean depth represented by a darkening blue scale. Map made using the ggOceanMaps R package (Vihtakari, 2022) with data from Natural Earth Data, Amante and Eakins (2009), Geonorge.no, the General Bathymetric chart of the Oceans, and Inkscape 1.1.

Though purely freshwater resident populations are known (Hutchings *et al.*, 2019), the majority of Atlantic salmon populations are anadromous. Anadromous salmon hatch in freshwater where they spend one to several years before undertaking an oceanic feeding migration. In most cases, this migration lasts between one and four years (Thorstad *et al.*, 2010), after which the fish returns to breed in its natal river (although straying and breeding in non-natal rivers occurs [Keefer and Caudill, 2014]). Salmon that spend a single winter at sea are referred to as “one-sea winter” fish, and those spending longer are known as “multi-sea winter”. Marine feeding opportunities are far greater and more nutritious than those found in freshwater (Gross *et al.*, 1988). As such, when anadromous salmon return to spawn, they are larger and, thus, more fecund than they would have been had they remained in freshwater (though the costs and benefits of anadromy differ between sexes, see Fleming, 1998). These potential fitness benefits are balanced against far greater mortality rates in the marine environment, due to greater predation, starvation, and exploitation at sea (Aas *et al.*, 2010). For evolved behaviours such as marine feeding migrations to remain adaptive, the anadromous portions of Atlantic salmon populations must be able to exploit suitable feeding habitat across multiple generations (i.e. inter-annual abundances in prey). Thus, disruption to the spatio-temporal availability of marine prey such that migrations no longer coincide with peaks in resource availability could negatively impact Atlantic salmon populations in much the way as has already been observed (ICES, 2021; Utne *et al.*, 2021; Vollset *et al.*, 2022). If resource use

varies spatially across age classes within populations, this likely exposes those populations to a larger suite of stressors than if resource use patterns were uniform across age (cf. Schindler *et al.*, 2015). As a corollary, variation in resource use between populations could make some more susceptible to the deleterious effects of anthropogenic change than others.

How oceanic resource use varies spatially across age classes of Atlantic salmon, both within and between populations remains largely unexplored (Rikardsen and Dempson, 2010). Quantifying this spatial variation has the potential to inform discussion as to which age classes and populations are most likely to be impacted by spatio-temporally dependent changes in marine conditions and resource availability. To investigate this topic, Atlantic salmon were sampled at one of their known feeding grounds around the Faroe Islands (Figure 1; Supplementary Figure S1). Sampled fish were assigned to their group of origin using a geographically broad genetic baseline of 50 populations ranging from the Pechora in the Russian Federation to the east coast of North America. This baseline allowed for the genetic assignment of individual salmon to one of six eastern Atlantic reporting groups and one western Atlantic group. Coupled with scale-read sea ages, we determined the proportion of multi-sea winter (MSW) salmon from each reporting group represented in the fishery. Run-reconstruction was then used to provide a quantitative comparison of the proportions of MSW salmon caught around the Faroes to the proportion of MSW salmon for each reporting group among high-seas pre-fisheries abundance (PFA).

Methods

Sample collection

Samples used were originally described in Jacobsen and Hansen (2001). Samples were collected as part of an experimental longline fishery over two seasons, referred to as the 1993 season and the 1994 season. Each season lasted from November of the preceding year until March of the following year, with no fishing in January due to poor sea conditions. To illustrate, in the 1993 season, samples were collected in November and December of 1992 and in February and March of 1993. Longlines baited with European sprat, *Sprattus sprattus*, were left to soak from around dawn to noon. The hook size of the experimental fishery was not recorded in the original study, but were recalled to most likely have been Mustad #3/0 hooks. (JAJ, pers. obs., Supplementary Figure S2). Size selectivity of the sampled fish might also have occurred if bait size favoured larger conspecifics (Ingólfsson *et al.*, 2017; see Discussion). The date and capture location of each sampled fish were recorded. Scales were sampled and the sea ages of individual fish determined by the number of winters spent at sea. In this study, individuals were designated as either one-sea winter or MSW. Atlantic salmon are traditionally considered to still be in the post-smolt life stage up to the 31st December of the year in which they went to sea (ICES, 2019), after which they are considered 1SW. We extend the definition of 1SW to include the final two months of the post-smolt stage (1st November–31st December). We believe this is justified given that winter around the Faroe Islands begins from October. This combination of date- and location-specific catch records, coupled with sea age phenotypes, allowed for the proportion of MSW salmon present in the fishery to be estimated. See Jacobsen and Hansen (2001) for further details of the fishery and sample processing. Summary statistics of fork length across sea age, sex, and fishing season are displayed in Supplementary Figure S3.

Genotyping and genetic stock identification

The genetic baseline used to assign fish to specific reporting groups was generated by combining SNP data from previously published Atlantic salmon studies (Supplementary Table S1) with unpublished data for the Alta and Teno rivers. Where DNA had been pooled ($n = 40$ populations), individual genotypes were generated from the allele frequency estimates, assuming both Hardy–Weinberg and linkage equilibrium ($n = 40$ per population). This was done using a bespoke software, as genetic stock identification (GSI) requires individual genotype data rather than allele frequency estimates (see details in Ozerov *et al.*, 2013). Given that individual populations in the baseline were geographically dispersed and we were interested in broad-scale macroecological patterns, we used agglomerative reporting groups instead of specific populations to define the origin of the salmon sampled around the Faroes. Reporting groups (Figure 1) were defined using a neighbour joining tree (Supplementary Figure S4), information from previous studies exploring population-level genetic variation in Atlantic salmon (e.g. Ozerov *et al.*, 2013, 2017; Gilbey *et al.*, 2017), as well as expert opinion from this study's authors. DNA from Faroese-sampled and Teno salmon was extracted from archived scales. For Alta fish, fin clips stored at -20°C were used in lieu of scales. Extraction was conducted using a QIAamp 96 DNA QIAcube HT Kit (Qiagen) following the manufacturer's protocol. Samples were further genotyped

by targeted sequencing at 167 SNP markers using a GTSeq approach (Campbell *et al.*, 2015) as outlined in Aykanat *et al.*, (2020).

The origin for each successfully genotyped individual was estimated using the conditional maximum likelihood GSI methodology (Millar, 1987) implemented in ONCOR (Kalinowski *et al.*, 2008). Since estimation of population origin using GSI methods can be affected by the population composition of the mixture sample (Pella and Masuda, 2001), we divided the total number of fish to be assigned into the individual fishing seasons (1993, 1994), seasons (autumn, winter), and location (north, south) in which they were caught. The inclusion of such spatio-temporal variation in reporting group distribution can improve GSI sensitivity (Vähä *et al.*, 2017). In total, 1674 samples were divided into six temporally and spatially distinct subsets for the GSI analysis. The assignment probability (p) threshold for reporting groups was set at ≥ 0.7 (Vähä *et al.*, 2011, 2014; Bradbury *et al.*, 2015).

The ability of our baseline to successfully assign fish to their reporting group of origin was evaluated with 100% simulation and leave-one-out cross-validation methods (Anderson *et al.*, 2008) implemented in ONCOR. For the 100% simulation evaluation, we set the mixture sample sizes to 200 and simulations were repeated 100 times for both the individual populations as well as for the defined reporting groups. The leave-one-out test was performed by removing fish from baseline populations (one at a time) and then estimating their origin to evaluate how well a fish could be assigned to their population or reporting group of origin. Fish with incomplete genotypes (i.e. no value at one or more loci) were not used for the leave-one-out cross-validation, however, they were retained in the baseline to estimate the origin of fish (Kalinowski *et al.*, 2008).

While our GSI baseline contained samples from at least one population in each of the major Atlantic salmon phylogenetic groups (Bourret *et al.*, 2013), downstream analyses focused on six eastern Atlantic reporting groups (Ireland and the United Kingdom, Southern Norway, Northern Norway, Eastern Finnmark/North Kola, Teno, and Eastern Barents Sea/White Sea), as well as the North American reporting group. This was due to no fish being assigned to Icelandic, Baltic, or Bay of Biscay reporting groups (Supplementary Table S1).

Estimation of MSW proportion among Faroese-sampled fish and among the high-seas PFA Faroese fish

We estimated the proportion, and associated uncertainty, of MSW fish sampled around the Faroes from each of the reporting groups using a generalized linear model with a logit link and a binomial response variable (success = MSW, failure = 1SW), reporting group as a fixed factor, a categorical link function, and a flat prior on the probability scale. For the fixed effects, we used the prior $N(0, I \times (1 + \pi^2/3))$, where 0 is a vector of zeros and I is the identity matrix, both with dimensions equal to the number of reporting groups (six in this case). We fixed the residual variance at one. The model was run using MCMCglmm (Hadfield, 2010), which allowed for the uncertainty around each proportion estimate to itself be estimated (since parameter values estimated using MCMCglmm are probabilistic due to the software package implementing a Bayesian paradigm). The median of the generated

Table 1. The numbers (nMSW) and proportion of MSW Atlantic salmon assigning to each of the six eastern Atlantic reporting groups sampled in an experimental fishery (Faroe Islands), and the proportion of MSW fish among the high-seas PFA estimated for each reporting group.

Reporting group	Location	n1SW, nMSW	MSW proportion	2.5% credible interval	97.5% credible interval
Ireland and the United Kingdom	Faroe Islands	130,324	0.749	0.702	0.793
	PFA		0.154	0.129	0.183
Southern Norway	Faroe Islands	32,785	0.974	0.963	0.982
	PFA		0.197	0.175	0.220
Northern Norway	Faroe Islands	0,115	0.995	0.978	0.999
	PFA		0.285	0.249	0.324
Teno	Faroe Islands	0,24	0.980	0.899	0.998
	PFA		0.294	0.245	0.349
Eastern Finnmark/North Kola	Faroe Islands	0,10	0.959	0.740	0.997
	PFA		0.277	0.247	0.310
Eastern Barents/White Sea	Faroe Islands	3,107	0.979	0.947	0.993
	PFA		0.270	0.247	0.293

The number of one-sea winter fish used to calculate the Faroese MSW proportion are denoted by “n1SW”.

posterior distribution and the 95% credible intervals (95% CI) were used to express the MSW proportion and its associated uncertainty, respectively. Chains were run for 2000000 iterations with the first 500000 iterations discarded as burn-in. Realizations of the Markov chain were sampled every 150 iterations.

Pre-fisheries abundance

The natural abundance of salmon in the North Atlantic Ocean prior to Faroese and coastal fisheries is termed the pre-fishery abundance (PFA). We reconstructed PFA using the run–reconstruction model (Potter *et al.*, 2004) described in the stock annex of the ICES Working Group on North Atlantic Salmon (WGNAS; ICES, 2021). Briefly, this was done by first correcting abundance in the oceans upwards, using the reported catch of 1SW and MSW salmon of each reporting group, to estimate the number of salmon returning to the coastal “home waters” of these groups by taking into account the non-reported catch and an exploitation rate (specified as uniform distributions). These numbers were further corrected (increased) by accounting for natural mortality (assumed to be 2–4% per month, uniformly distributed) across the average number of months until the return of both age classes in the different reporting groups. This number is now an estimation of the PFA as of 1st January in a given year. The model uses Monte Carlo simulation (9999 iterations) to quantify PFA with uncertainty. We used the data collated by the WGNAS (ICES, 2021) to quantify 1SW and MSW PFA for the years 1993 and 1994. We did this separately for Ireland and the United Kingdom (ICES WGNAS regions: England and Wales, Scotland east and west, Northern Ireland Foyle Fisheries Area and DAERA area, and Ireland), Southern Norway (Norway south-east, south-west, and middle), Northern Norway (Norway north), Teno (Finland), Eastern Finnmark/North Kola (Russia Kola Peninsula, Barents Sea Basin), and Eastern Barents/White Sea (Russia Kola Peninsula, White Sea Basin, Archangelsk and Karelia, and Pechora River). Note we estimate PFA on January 1st of the year so as to maintain consistency with the methodology used by WGNAS for run–reconstruction. Furthermore, we are interested in the abundance of salmon when sampling is taking place, hence, the middle of the sampling period provides an ideal date at which to construct abundance estimates. The reconstructed abundance data were then used to estimate the proportion of MSW

fish in the high seas. We used the median and 95% CI to describe the MSW proportion and its uncertainty for each of the reporting groups.

To further explore the observed differences in MSW proportions (see Results), we estimated the relative likelihood of occurrence of a given sea age class for each reporting group sampled around the Faroes by normalizing the number of salmon assigned to each reporting group/age class to the PFA of each reporting group. This was done as follows:

$$\text{Relative likelihood of occurrence } 1SW_j = N_{FOi} \times (1 - P_{MSWi}) / PFA_{ij}; \quad (1)$$

$$\text{Relative likelihood of occurrence } MSW_j = N_{FOi} \times P_{MSWi} / PFA_{ij} \quad (2)$$

where subscripts j and i denote the reporting group and sea age group of fish, respectively, N_{FO} is number of fish assigned to each reporting group, P_{MSW} is the posterior distribution of proportion of MSW fish, and PFA is the Monte Carlo sampling distribution of the PFA. Note, relative likelihood of occurrence is an arbitrary measure that provides a convenient means to compare between sea ages and reporting groups the likelihood of a salmon migrating to the Faroes, relative to their abundance at sea.

Consistency of pattern across MSW age classes

Is increasing sea age associated with increasing likelihood of presence around the Faroes, or does the pattern exist solely as a dichotomy between 1SW and MSW fish? To further explore this, we decomposed the MSW component of the Northern and Southern Norway reporting groups into their constituent 2SW and 3SW components. We used the same run–reconstruction model as above but with an additional age class (3SW). This model used the MSW exploitation rate and unreported catch reported to ICES for both 2SW and 3SW fish. Note that in order to estimate PFA as accurately as possible, the run–reconstruction model took into account reported catch statistics from all possible years in which the three age classes could have returned to the coasts of Northern and Southern Norway. Therefore, the model in-

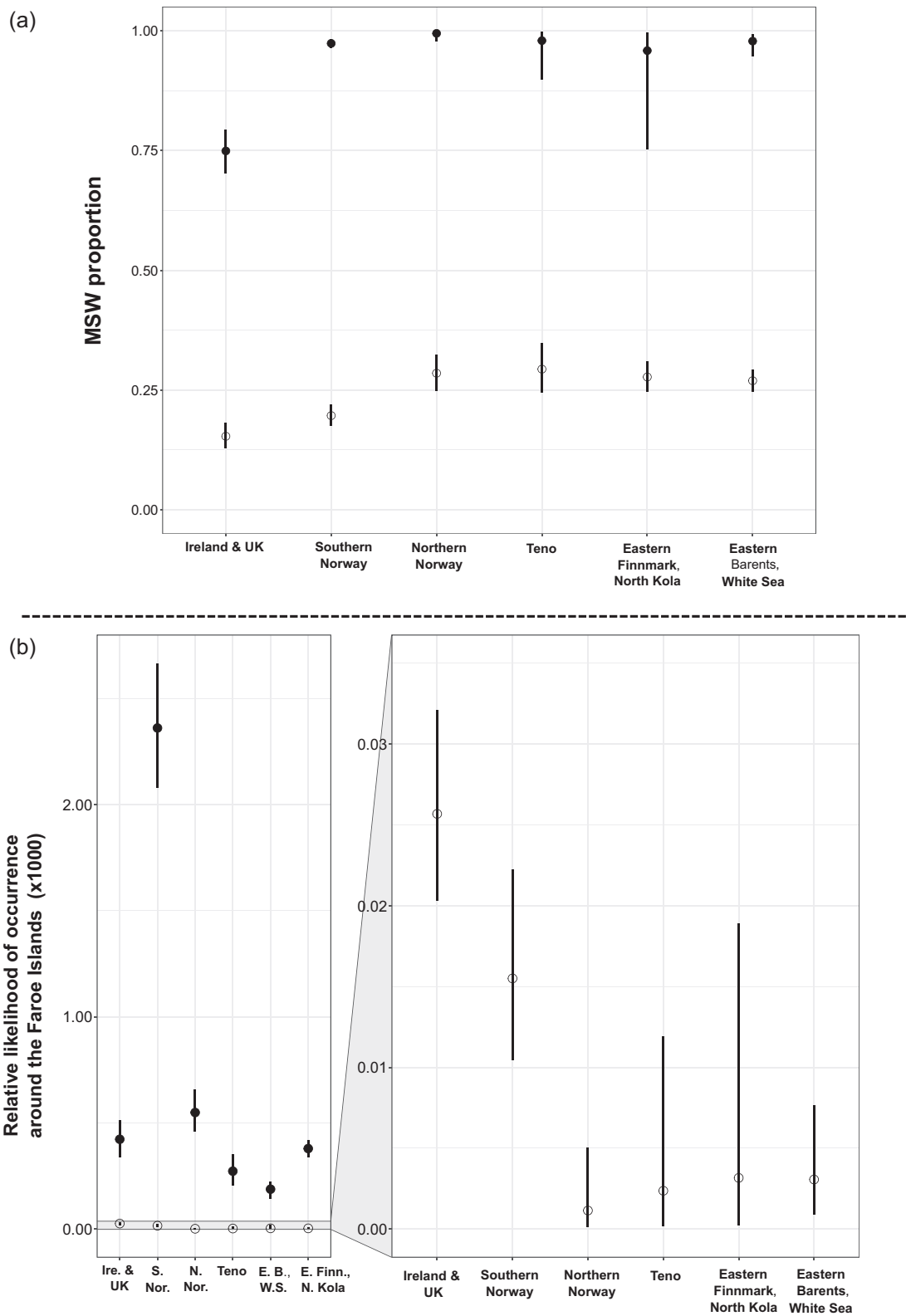


Figure 2. (a) Differences in the proportion of MSW Atlantic salmon sampled from around the Faroe Islands (filled circles) during the 1993 and 1994 fishing seasons and the proportion of MSW fish among the estimated PFA, totaled across the years 1993–1994 (open circles); (b) Differences in the relative likelihood of occurrence of MSW (filled circles) and one-sea winter 1SW (open circles) Atlantic salmon with respect to their age-specific, high-sea PFA. For both (a) and (b), point estimates and uncertainty represented with medians and 95% credible intervals, respectively. Abbreviations of reporting groups on the x axis of the left panel of (b) correspond to the following: “Ire. & UK” = Ireland and the United Kingdom, “S. Nor.” = Southern Norway, “N. Nor.” = Northern Norway, “E.B., W.S.” = Eastern Barents, White Sea, “E. Finn., N. Kola” = Eastern Finnmark, North Kola.

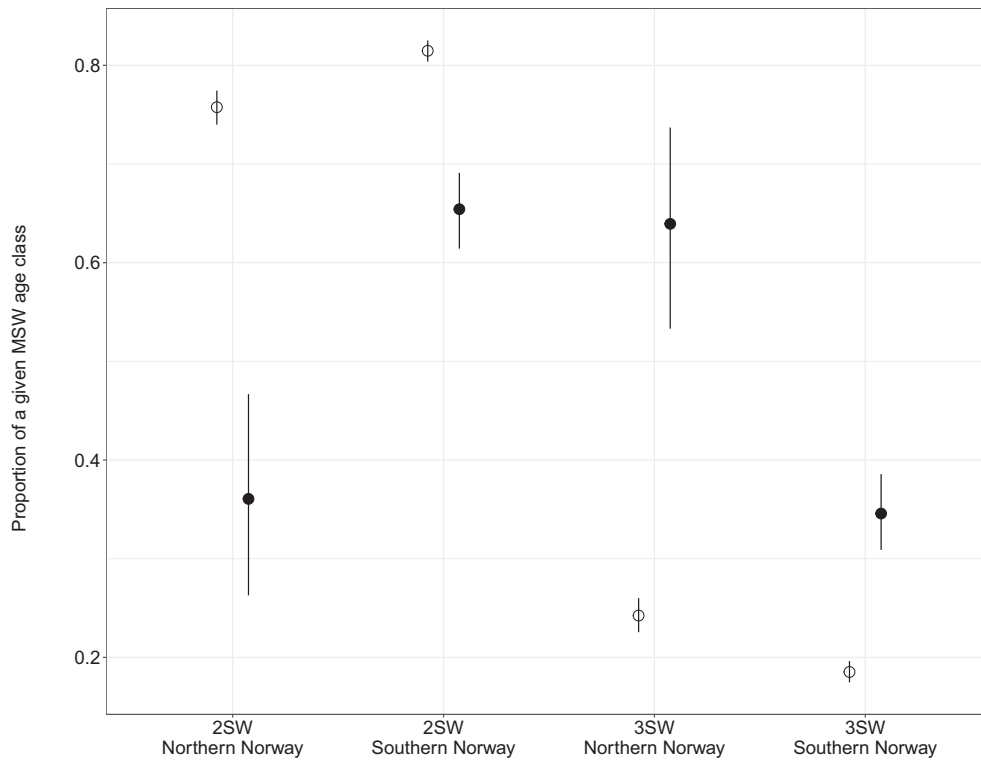


Figure 3. Proportion of 2SW and 3SW Atlantic salmon within the MSW age class sampled around the Faroe Islands (filled circles) and estimated for the high-seas PFA (open circles) for the Southern Norway and Northern Norway reporting groups. Point estimates and uncertainty represented with medians and 95% credible intervals, respectively.

cluded catch data from the years 1993–1996 (Supplementary Table S4).

We then calculated the proportion of 3SW fish to 2SW fish around the Faroes separately for both Southern and Northern Norway. We then repeated this calculation, but instead we used the PFA for each age class. Finally, we divided the 3SW to 2SW proportion for the Faroes by the 3SW to 2SW proportion for the PFA. This figure provides an estimate of the proportional increase of 3SW salmon relative to 2SW salmon around the Faroes, normalized to the PFA of each age class.

Analyses and plots can be recreated using the code and data stored at <https://github.com/Helsinki-Ronan/MSW-Faroes-migration-paper>. All analyses were conducted in R 4.1.2 (R Core Team, 2021). Visual inspection of Markov chains suggested that models mixed well and that model parameter estimates had converged upon stable distributions.

Results

Genetic stock identification

A total of 1616 fish were confidently assigned back to their reporting group and used in further analyses. A total of 454 fish (28.1%) assigned back to Ireland and the United Kingdom, 817 (50.6%) to Southern Norway, 115 (7.1%) to Northern Norway, 24 (1.5%) to Teno, 10 (0.6%) to Eastern Finnmark/North Kola, 110 (6.8%) to the Eastern Barents/White Sea (Table 1), and 86 (5.3%) to North America. See Supplementary Tables S2 and S3 for assignment confidence at the population and reporting group levels, respectively.

Estimation of MSW proportions

The MSW proportion for each reporting group found around the Faroes was consistently larger than the proportion of MSW individuals among PFA for each of the six aforementioned European reporting groups (Figure 2a; Table 1). For individual reporting groups, the proportion of MSW Atlantic salmon sampled from around the Faroes ranged from 0.749 (95% CI: 0.702, 0.793) for Ireland and the United Kingdom to 0.995 for Northern Norway (95% CI: 0.978, 0.999). The proportion of MSW for Ireland and the United Kingdom was strikingly lower than in all other reporting groups (with pairwise non-overlapping 95% credible intervals) except when compared to the Eastern Finnmark, North Kola group, which had a high observed proportion but this was likely due to high uncertainty of the estimate as a result of small sample size (Figure 2a; Table 1).

The relative likelihood of occurrence for 1SW salmon around the Faroes relative to 1SW PFA was greater for Ireland and the United Kingdom (0.026, 95% CI: 0.020, 0.032) as well as for Southern Norway (0.016, 95% CI: 0.010, 0.022) compared to the other four reporting groups where the relative likelihood of occurrence was virtually zero (Figure 2b). The relative likelihood of occurrence for MSW salmon around the Faroes relative to their PFA was greatest for Southern Norway (2.36, 95% CI: 2.08, 2.67), with Northern Norway displaying the second largest rate of occurrence (0.55, 95% CI: 0.46, 0.66). Strikingly, MSW salmon from Ireland and the United Kingdom were as likely to be found around the Faroes as MSW fish from more north-eastern reporting groups (Teno and Eastern Barents/White Sea), despite Ireland and the United Kingdom being far closer geographically to the Faroes than these latter groups (Figure 1).

Consistency of pattern

For Southern Norway, 3SW Atlantic salmon were 8.31 (95% CI: 6.90, 9.98) times more likely to be present around the Faroes than 2SW fish, with respect to the PFA of each sea age. For Northern Norway, this figure was 1.76 (95% CI: 1.11, 2.77; Figure 3).

Discussion

Faroese feeding ground versus PFA MSW proportions

By genotyping spatially and temporally explicit Atlantic salmon individuals of known sea age sampled around the Faroe Islands, we were able to demonstrate that MSW fish from six European reporting groups use this oceanic feeding ground in greater proportions than 1SW salmon from the same groups (Figure 2a). In particular, MSW fish, especially those from more northern areas, appear to make greater use of multiple, large-scale ecosystems (Barents Sea, Norwegian Sea) over the course of their marine migration than do 1SW fish from those same reporting groups, at least during the sampled study period. Such phenotype-specific exploitation of spatially dislocated areas suggests that Atlantic salmon might preferentially migrate to specific feeding grounds and that fish spending more than one winter at sea might move between feeding areas. The greater-than-expected number of 3SW fish around the Faroes provides further evidence that older fish preferentially migrate there (Figure 3).

Intriguingly, MSW salmon from the Ireland and the United Kingdom reporting group were only as likely to be found around the Faroes as MSW fish from much more geographically distant north-eastern reporting groups (Figure 2b). In turn, 1SW fish from Ireland and the United Kingdom were generally more likely to be present at the Faroes than 1SW fish from the other reporting groups, with Southern Norway being an exception to this general pattern. These two groups displayed similar rates of migration to the Faroes for 1SW fish (Figure 2b), whereas MSW fish from Southern Norway were more likely to migrate to the Faroes than MSW fish from the rest of the reporting groups. These results suggest that, despite their proximity to the Faroes, many MSW salmon from Ireland and the United Kingdom do not migrate there. The main feeding ground of these MSW salmon remains unknown. One potential candidate is the Labrador Sea to the west of Greenland (Figure 1). Bradbury *et al.*, (2016) found that 22% of salmon sampled from the Labrador Sea displayed European heritage. Subsequent fine-scale GSI has assigned many salmon sampled in the Labrador Sea back to Ireland and the United Kingdom (Bradbury *et al.*, 2021). Furthermore, a large number of tagged salmon from Scotland, England, and Wales have been recovered in the Labrador Sea, providing further support for an Ireland and UK-Labrador Sea migration route (Swain, 1980).

How this general pattern of spatial resource use emerges appears to be related to the flow of currents around the North Atlantic. Based on a combination of tagging data, isotope analysis, and fishery patterns, Dadswell *et al.*, (2010) suggested Atlantic salmon oceanic migrations are determined by the North Atlantic subpolar gyre. This gyre flows counter-clockwise between North America and north-western Europe, with various regional currents and eddies within it (Figure 1). Many salmon post-smolts from Ireland and the United King-

dom likely take advantage of these regional oceanographic features and migrate directly to the Faroes, with the eddy system between the islands and the Vøring Plateau likely helping them to stay in this general area (Figure 1). This supposition is supported by an annual concentration of southern origin post-smolts at the Vøring Plateau (Gilbey *et al.*, 2021). The lower-than-expected proportion of MSW salmon from Ireland and the United Kingdom around the Faroes, along with the results of Bradbury *et al.*, (2016, 2021) and Swain (1980), suggests that a portion of the Ireland and the United Kingdom post-smolts in this concentration of fish might undergo a further migration to the Labrador Sea. In addition to the aforementioned oceanographic and geographic explanations, there might also be a genetic component to the oceanic migration patterns of salmon from specific reporting groups. If this is the case, then how much of the variation in migration routes between reporting groups is due to genetic versus environmental (i.e. oceanographic, geographic) effects remains to be explored.

The feeding grounds of Atlantic salmon from the north-eastern reporting groups are not as well-known as the feeding grounds of more southern groups (Rikardsen and Dempson, 2011; Strøm *et al.*, 2018; Rikardsen *et al.*, 2021). However, most of our knowledge of these feeding grounds comes from tagged adult salmon who had previously spawned at least once and whose oceanic migration behaviour may be different from that of maiden fish (see also Rikardsen *et al.*, 2021). It is probable that fish from these north-eastern reporting groups are less likely to undergo long oceanic migrations, such as to the Faroes, and remain on feeding grounds closer to their source populations within the Barents and White Seas (Jensen *et al.*, 1999; Rikardsen *et al.*, 2008). Gilbey *et al.*, (2021) found no post-smolts from the north-eastern reporting groups in the Faroes, which they suggested was likely due to such fish being carried in the opposite direction by eastward currents (Figure 1). Despite this potential initial displacement, we assigned a substantial number of MSW fish back to the north-eastern reporting groups ($n = 257$; Table 1). The relative likelihood of occurrence of MSW salmon around the Faroes from these groups was sometimes as high as that of Ireland and the United Kingdom (Figure 2b), suggesting this is a significant feeding ground for northeastern MSW fish.

Like many studies using data from opportunely collected samples of wild individuals, inferences of our results must be made with knowledge of the data's shortcomings. For example, we cannot rule out that the hook size used in the experimental fishery was not selective against smaller 1SW fish, which are likely more abundant earlier in the fishing season (i.e. the November–December period). As a result, this would underestimate the 1SW proportion (JAJ, pers. obs.). However, we do not believe this bias to be detrimental to the overall conclusions of this study since the substantial difference in absolute numbers of 1SW and MSW fish is unlikely to be explained due to hook size selectivity alone. Furthermore, the pattern by which older fish exploit the Faroes feeding ground more than younger fish was also supported by the observed rate of occurrence between 3SW fish and 2SW fish (Figure 3). Similarly, group specific differences in 1SW occurrence in the Faroes is also robust to any size selectivity bias, as evidenced by the greater likelihood of occurrence around the Faroes of 1SW salmon from Ireland and the United Kingdom compared to southern Norway. This is despite the Norwegian 1SW fish being significantly larger than the Ireland and the United King-

dom 1SW fish when they were caught (see also Supplementary Text 1 and Supplementary Table S5).

The size of bait used on the hooks could potentially introduce bias by preferentially targeting larger fish (Ingólfsson *et al.*, 2017). However, we do not believe bias arising from bait size qualitatively impacts our results given that post-smolt/one-sea winter salmon during our sampling period were large enough (mean fork length \pm one standard deviation = 48.79 ± 4.33 cm) so as not to be gape-limited with respect to sprat (average size sprat = 10.1 cm - FishBase 2022).

As the fish in this study were all sampled in late autumn and early winter, and the fishery was almost exclusively located to the north and west of the Faroes, the data are both temporally and spatially unbalanced. However, Ó'Maoiléidigh *et al.*, (2018) demonstrated that salmon caught around the Faroes during May–June were also predominantly MSW fish. This suggests that the large proportion of MSW salmon sampled by the experimental fishery is observed at other times of the year and, thus, supports the idea that the seas around the Faroes predominantly support MSW fish. The effect of spatial unbalance on how representative our results are is more difficult to determine due to a lack of data to bring to bear on the question.

North American, Icelandic, and Bay of Biscay salmon

Eighty-six individuals were assigned to salmon populations in North America (5.3% of assigned fish). The total PFA for North America during the study period (1993–1994) was 1103500 fish (ICES, 2021) compared to 9213265 fish from the six European reporting groups in this study to which salmon were successfully assigned. All else being equal, this means that Atlantic salmon from North America were 2.2 times less likely to be found around the Faroes relative to fish from Europe. Overlap of Atlantic salmon from North America and from Europe in the ocean is a known phenomenon (Hansen and Jacobsen, 2003; Dadswell *et al.*, 2010; Bradbury *et al.*, 2016, 2021). Spares *et al.*, (2007) used isotope analysis to infer that 14.2% of 141 Canadian salmon had fed east of the Faroes. Additionally, fish tagged in the Faroes have been found in North American populations (Dadswell *et al.*, 2010). Similar to Bradbury *et al.*, (2016, 2021) and Gilbey *et al.*, (2017), this work corroborates these previous studies by providing direct genetic evidence for such movements by salmon. The large percentage 89.5% ($n = 77$ of 86) of MSW individuals among North American-assigned fish in this study tentatively suggests that the feeding grounds around the Faroes are indeed sought out by MSW salmon from North American populations.

In this study, no fish were assigned to Iceland, despite its proximity to the Faroes. Gilbey *et al.*, (2021) found a lower-than-expected number of Icelandic post-smolts in the same geographic area as this study. Similarly, only one salmon of 87 recaptures from an ocean tagging programme conducted around the Faroes was recovered in Iceland (Hansen and Jacobsen, 2003). Using estimated marine distributions, Guðjónsson *et al.*, (2015) suggest that Icelandic fish are more likely to migrate west of Iceland towards the Irminger Sea. Similarly, two post-spawned Atlantic salmon tagged in Iceland migrated directly to this area (Rikardsen *et al.*, 2021). Why the majority of Icelandic fish go westward instead of migrating east to the Faroes remains yet to be explored.

Similarly, none of the 1616 Atlantic salmon were assigned back to the Bay of Biscay reporting group. This was also surprising given Biscay salmon potentially share a northward migration route with fish from Ireland and the United Kingdom (Otero *et al.*, 2014). There are only two tag recoveries of Biscay salmon in the Faroese tag database (Ó'Maoiléidigh *et al.*, 2018). Our results suggest that Biscay fish, regardless of sea age, do not feed in the ocean around the islands during the November–March period of the year. While it is expected that fish from this reporting group would be present in low numbers around the Faroes (based on post-smolt distribution–Gilbey *et al.*, 2021), this raises the question of where do these post-smolts subsequently migrate to (though one of 14 tagged post-spawned adult salmon from the Lézé river in Spain is known to have migrated to the west Irminger Sea–Rikardsen *et al.*, 2021). Their absence from data sets might also reflect the generally poor status of Biscay salmon populations, with many already extirpated or declining (Parrish *et al.*, 1998).

Evolutionary and ecological implications in a changing ocean

Changes in the spatial availability of prey resources during the marine stage of Atlantic salmon might be changing the costs and benefits of undergoing migrations, such as that to the Faroes. Vollset *et al.*, (2022) documented lower abundances of key prey items taken by salmon during the early marine stage in the Norwegian Sea from 2005 onwards. This decrease in resources (e.g. a reduction in zooplankton) coincided with a decrease in both the abundance and body condition of 1SW salmon (Utne *et al.*, 2021), which could be the result of evolution towards an older age structure as a response to many fish not reaching their maturity threshold in their first year at sea. Interestingly, Czorlich *et al.*, (2022) demonstrated how a reduction in capelin availability was driving evolution of age structure towards early maturation among Teno salmon. While exhibiting opposite responses to reduced prey availability, the previous two studies share a common theme of changes in age structure resulting from altered availability of marine food resources. If our hypothesis is correct and different age classes and different reporting groups display variation in their utilization of the oceans around the Faroes, then any deleterious changes in the marine conditions around the Faroes will have age- and group-specific responses. As discussed, Vollset *et al.*, (2022) document a contemporary regime shift and its negative impact on the abundance of Atlantic salmon prey. Other such regime shifts are predicted to occur in the future (Beaugrand *et al.*, 2008), each of which carries the potential of adverse effects on the Faroese marine food web as well as other oceanic ecosystems. Future research should aim to quantitatively assess the likelihood of such regime shifts affecting food webs and, thus, the vulnerability of different age classes across individual reporting groups.

Conclusion

Using a combination of GSI and run–reconstruction models, we demonstrated that the proportion of MSW Atlantic salmon sampled on their feeding grounds around the Faroe Islands was consistently larger than the estimated MSW proportion among high-seas PFA. This pattern was observed across six eastern Atlantic reporting groups. Our results suggest that the seas around the Faroes are a preferred feeding ground for MSW salmon. Preferentially migrating to this area to ex-

exploit its resources is a behaviour likely mediated, in part, by an evolved feeding strategy. If the MSW proportion of a given reporting group is more likely to exploit a specific spatial resource (such as the Faroese feeding ground) than 1SW fish from the same reporting group, then changes in the spatial and temporal availability of such resources are likely to differentially affect intra-group age classes. Similarly, if MSW individuals from different reporting groups utilize the ocean around the Faroes to greater or lesser extents, then changes in feeding conditions at the Faroes will also induce reporting group-specific changes to the MSW component of reporting groups. Understanding the temporal and spatial dynamics of oceanic resource use both within (i.e. age classes) and between reporting groups is crucial in predicting how different Atlantic salmon populations might be affected by changes to marine food webs.

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Supplementary Data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

Author contributions

RJOS, TA, KH, and JG conceptualized the paper. KH organized sample retrieval from scale archives at NINA. MO conducted the GSI and wrote the relevant methods. RJOS conducted the statistical analyses. GHB conducted the run-reconstruction and wrote the relevant methods. JAJ coordinated the Faroese fieldwork. JE and AHR coordinated fieldwork and contributed data for the rivers Teno and Alta, respectively. TA genotyped the Faroese samples and wrote the relevant methods. RJOS and TA wrote the initial draft, with all co-authors contributing to subsequent drafts.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Data availability

The data underlying this article are available in a Github repository at <https://github.com/Helsinki-Ronan/MSW-Faroes-migration-paper>.

References

- Aas, Ø., Policansky, D., Einum, S., and Skurdal, J. 2010. Salmon ecological research and conservation. In *Atlantic Salmon Ecology*, pp. 445–456. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal Wiley-Blackwell.
- Amante, C., and Eakins, B. W. 2009. ETOPO1 1 arc-minute global relief model: procedures, data sources and analysis. NOAA technical memorandum NESDIS NGDC-24. National geophysical data center, NOAA. Distributed under the U.S. Government Work license.
- Anderson, E. C., Waples, R. S., and Kalinowski, S. T. 2008. An improved method for predicting the accuracy of genetic stock identification. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 1475–1486.
- Armstrong, M. P., Dean, M. J., Hoffman, W. S., Zemeckis, D. R., Nies, T. A., Pierce, D. E., Diodati, P. J. *et al.* 2013. The application of small scale fishery closures to protect Atlantic cod spawning aggregations in the inshore gulf of maine. *Fisheries Research*, 141: 62–69.
- Aykanat, T., Rasmussen, M., Ozerov, M., Niemelä, E., Paulin, L., Vähä, J., Hindar, K. *et al.* 2020. Life-history genomic regions explain differences in Atlantic salmon marine diet specialization. *Journal of Animal Ecology*, 89: 2677–2691.
- Ayllón, D., Nicola, G. G., Elvira, B., and Almodóvar, A. 2019. Optimal harvest regulations under conflicting tradeoffs between conservation and recreational fishery objectives. *Fisheries Research*, 216: 47–58.
- Ayllón, D., Railsback, S. F., Almodóvar, A., Nicola, G. G., Vincenzi, S., Elvira, B., and Grimm, V. 2018. Eco-evolutionary responses to recreational fishing under different harvest regulations. *Ecology and Evolution*, 8: 9600–9613.
- Baugrand, G., Edwards, M., Brander, K., Luczak, C., and Ibanez, F. 2008. Causes and projections of abrupt climate-driven ecosystem shifts. *Ecology Letters*, 11: 1157–1168.
- Bourret, V., Kent, M. P., Primmer, C. R., Vasemägi, A., Karlsson, S., Hindar, K., P. *et al.* 2013. SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). *Molecular Ecology*, 22: 532–551.
- Bradbury, I. R., Hamilton, L. C., Rafferty, S., Meerburg, D., Poole, R., Dempson, J. B., Robertson, M. J. *et al.* 2015. Genetic evidence of local exploitation of Atlantic salmon in a coastal subsistence fishery in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 83–95.
- Bradbury, I. R., Hamilton, L. C., Sheehan, T. F., Chaput, G., Robertson, M. J., Dempson, J. B., Reddin, D. *et al.* 2016. Genetic mixed-stock analysis disentangles spatial and temporal variation in composition of the West Greenland Atlantic Salmon fishery. *ICES Journal of Marine Science*, 73: 2311–2321.
- Bradbury, I. R., Lehnert, S. J., Messmer, A., Duffy, S. J., Verspoor, E., Kess, T. J. *et al.* 2021. Range-wide genetic assignment confirms long-distance oceanic migration in Atlantic salmon over half a century. *ICES Journal of Marine Science*, 78: 1434–1443.
- Campbell, N. R., Harmon, S. A., and Narum, S. R. 2015. Genotyping-in-Thousands by sequencing (GT-seq): a cost effective SNP genotyping method based on custom amplicon sequencing. *Molecular Ecology Resources*, 15: 855–867.
- Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., and Primmer, C. R. 2022. Rapid evolution in salmon life history induced by direct and indirect effects of fishing. *Science*, 376: 420–423.
- Dadswell, M. J., Spares, A. D., Reader, J. M., and Stokesbury, M. J. W. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the “Merry-Go-Round” hypothesis. *Journal of Fish Biology*, 77: 435–467.
- Eikeset, A. M., Richter, A., Dunlop, E. S., Dieckmann, U., and Stenseth, N. C. 2013. Economic repercussions of fisheries-induced evolution. *Proceedings of the National Academy of Sciences*, 110: 12259–12264.
- FishBase. 2022. *Sprattus sprattus* summary page. Available at <https://www.fishbase.org/summary/Sprattus-sprattus.html> (last accessed 1 July 2022).

- Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 59–76.
- Gilbey, J., Utne, K. R., Wennevik, V., Beck, A. C., Kausrud, K., Hindar, K., Garcia de Leaniz, C. *et al.* 2021. The early marine distribution of Atlantic salmon in the North-east Atlantic: a genetically informed stock-specific synthesis. *Fish and Fisheries*, 22: 1274–1306.
- Gilbey, J., Wennevik, V., Bradbury, I. R., Fiske, P., Hansen, L. P., Jacobsen, J. A., Potter, T. *et al.* 2017. Genetic stock identification of Atlantic salmon caught in the Faroese fishery. *Fisheries Research*, 187: 110–119.
- Gross, M. R., Coleman, R. M., and McDowall, R. M. 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science*, 239: 1291–1293.
- Guðjónsson, S., Einarsson, S. M., Jónsson, I. R., and Guðbrandsson, J. 2015. Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 1087–1098.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33: 1–22.
- Hansen, L. P., and Jacobsen, J. A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas North of the Faroe Islands. *ICES Journal of Marine Science*, 60: 110–119.
- Harada, A. E., Lindgren, E. A., Hermsmeier, M. C., Rogowski, P. A., Terrill, E., and Burton, R. S. 2015. Monitoring spawning activity in a southern California marine protected area using molecular identification of fish eggs. *Plos One*, 10: e0134647.
- Hawley, K. L., Rosten, C. M., Christensen, G., and Lucas, M. C. 2016. Fine-scale behavioural differences distinguish resource use by ecomorphs in a closed ecosystem. *Scientific Reports*, 6: 24369.
- Hernández, C. M., Witting, J., Willis, C., Thorrold, S. R., Llopiz, J. K., and Rotjan, R. D. 2019. Evidence and patterns of tuna spawning inside a large no-take Marine Protected Area. *Scientific Reports*, 9: 10772.
- Hutchings, J. A., Ardren, W. R., Barlaup, B. T., Bergman, E., Clarke, K. D., Greenberg, L. A., Lake, C. *et al.* 2019. Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences*, 76: 1697–1708.
- ICES 2019. Working Group on North Atlantic Salmon.
- ICES. 2021. Working Group on North Atlantic Salmon.
- Ingólfsson, Ó. A., Einarsson, H. A., and Løkkeborg, S. 2017. The effects of hook and bait sizes on size selectivity and capture efficiency in Icelandic longline fisheries. *Fisheries Research*, 191: 10–16.
- Jacobsen, J., and Hansen, L. P. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science*, 58: 916–933.
- Jensen, A. 1999. Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. *ICES Journal of Marine Science*, 56: 84–95.
- Kalinowski, S. T., Manlove, K. R., and Taper, M. L. 2008. ONCOR: a computer program for genetic stock identification (Version 2).
- Kane, A., Ayllón, D., O'Sullivan, R. J., McGinnity, P., and Reed, T. E. 2022. Escalating the conflict? Intersex genetic correlations influence adaptation to environmental change in facultatively migratory populations. *Evolutionary Applications*, 15: 773–789.
- Kang, J. koo., and Thibert-Plante, X. 2017. Eco-evolution in size-structured ecosystems: simulation case study of rapid morphological changes in alewife. *BMC Evolutionary Biology*, 17: 58.
- Keefer, M. L., and Caudill, C. C. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. *Reviews in Fish Biology and Fisheries*, 24: 333–368.
- Millar, R. B. 1987. Maximum likelihood estimation of mixed stock fishery composition. *Canadian Journal of Fisheries and Aquatic Sciences*, 44: 583–590.
- Ó Maoiléidigh, N., White, J., Hansen, L. P., Jacobsen, J. A., Potter, T., Russell, I., and Reddin, D. 2018. Fifty years of marine tag recoveries from Atlantic salmon. *ICES Research Report*, 343:121.
- Østbye, K., Hagen Hassve, M., Peris Tamayo, A., Hagenlund, M., Vogler, T., and Præbel, K. 2020. And if you gaze long into an abyss, the abyss gazes also into thee”: four morphs of Arctic charr adapting to a depth gradient in Lake Tinnsjøen. *Evolutionary Applications*, 13: 1240–1261.
- Otero, J., L'Abée-Lund, J. H., Castro-Santos, T., Leonardsson, K., Størvik, G. O., Jonsson, B., Dempson, B. *et al.* 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology*, 20: 61–75.
- Ozerov, M., Vähä, J.-P., Wennevik, V., Niemelä, E., Svenning, M.-A., Prusov, S., Diaz Fernandez, R. *et al.* 2017. Comprehensive microsatellite baseline for genetic stock identification of Atlantic salmon (*Salmo salar* L.) in northernmost Europe. *ICES Journal of Marine Science*, 74: 2159–2169.
- Ozerov, M., Vasemägi, A., Wennevik, V., Diaz-Fernandez, R., Kent, M., Gilbey, J., Prusov, S. *et al.* 2013. Finding markers that make a difference: DNA pooling and SNP-arrays identify population informative markers for genetic stock identification. *PloS One*, 8: e82434.
- Parrish, D. L., Behnke, R. J., Gephart, S. R., McCormick, S. D., and Reeves, G. H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 281–287.
- Pella, J., and Masuda, M. 2001. Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin*, 99: 151–167.
- Potter, E. C. E., Crozier, W. W., Schön, P.-J., Nicholson, M. D., Maxwell, D. L., Prévost, E., Erkinaro, J. *et al.* 2004. Estimating and forecasting pre-fishery abundance of Atlantic salmon (*Salmo salar* L.) in the northeast Atlantic for the management of mixed-stock fisheries. *ICES Journal of Marine Science*, 61: 1359–1369.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rikardsen, A. H., and Dempson, J. B. 2010. Dietary life-support: the food and feeding of Atlantic salmon at sea. In *Atlantic Salmon Ecology*, pp. 115–143. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal Wiley-Blackwell.
- Rikardsen, A. H., Hansen, L. P., Jensen, A. J., Vollen, T., and Finstad, B. 2008. Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70 to 78° N. *Journal of Fish Biology*, 72: 1792–1798.
- Rikardsen, A. H., Righton, D., Strøm, J. F., Thorstad, E. B., Gargan, P., Sheehan, T., Økland, F. *et al.* 2021. Redefining the oceanic distribution of Atlantic salmon. *Scientific Reports*, 11: 12266.
- Schindler, D. E., Armstrong, J. B., and Reed, T. E. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, 13: 257–263.
- Spares, A. D., Reader, J. M., Stokesbury, M. J. W., McDermott, T., Zikovskiy, L., Avery, T. S., and Dadswell, M. J. 2007. Inferring marine distribution of Canadian and Irish Atlantic salmon (*Salmo salar* L.) in the North Atlantic from tissue concentrations of bio-accumulated caesium 137. *ICES Journal of Marine Science*, 64: 394–404.
- Strøm, J. F., Rikardsen, A. H., Campana, S. E., Righton, D., Carr, J., Aarestrup, K., Stokesbury, M. J. W. *et al.* 2019. Ocean predation and mortality of adult Atlantic salmon. *Scientific Reports*, 9: 7890.
- Strøm, J. F., Thorstad, E. B., Chafe, G., Sørbye, S. H., Righton, D., Rikardsen, A. H., and Carr, J. 2017. Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada. *ICES Journal of Marine Science*, 74: 1356–1370.
- Strøm, J. F., Thorstad, E. B., Hedger, R. D., and Rikardsen, A. H. 2018. Revealing the full ocean migration of individual Atlantic salmon. *Animal Biotelemetry*, 6: 2.
- Swain, A. 1980. Tagging of salmon smolts in European rivers with special reference to recaptures off West Greenland in 1972 and earlier years rapports et procès-verbaux des réunions, conseil permanent international pour l'Exploration de la mer. *Rapports et Procès-Verbaux des Réunions, Conseil Permanent International pour l'Exploration de la Mer*, 176: 93–113.

- Teffer, A. K., Carr, J., Tabata, A., Schulze, A., Bradbury, I., Deschamps, D., Gillis, C.-A. *et al.* 2020. A molecular assessment of infectious agents carried by Atlantic salmon at sea and in three eastern Canadian rivers, including aquaculture escapees and North American and European origin wild stocks. *FACETS*, 5: 234–263.
- Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., Horsburgh, G. *et al.* 2021. Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31: 2654–2665.
- Thorstad, E. B., Whoriskey, F., Rikardsen, A. H., and Aarestrup, K. 2010. Aquatic nomads: the life and migrations of the Atlantic salmon. In *Atlantic Salmon Ecology*, pp. 1–32. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell.
- Utne, K. R., Pauli, B. D., Haugland, M., Jacobsen, J. A., Maoileidigh, N., Melle, W., Broms, C. T. *et al.* 2021. Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean. *ICES Journal of Marine Science*, 78: 2844–2857.
- Vähä, J.-P., Erkinaro, J., Falkegård, M., Orell, P., and Niemelä, E. 2017. Genetic stock identification of Atlantic salmon and its evaluation in a large population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 327–338.
- Vähä, J.-P., Erkinaro, J., Niemelä, E., Primmer, C. R., Saloniemi, I., Johansen, M., Svenning, M. *et al.* 2011. Temporally stable population-specific differences in run timing of one-sea-winter Atlantic salmon returning to a large river system: run timing of Atlantic salmon within a river system. *Evolutionary Applications*, 4: 39–53.
- Vähä, J.-P., Wennevik, V., Ozerov, M., Diaz Fernandez, R., Unneland, L., Haapanen, K., Niemelä, E. *et al.* 2014. Genetic structure of Atlantic salmon in the Barents region and genetic stock identification of coastal fishery catches from Norway and Russia. Kolarctic ENPI CBC—Kolarctic Salmon Project (KO197) Report.
- Vihtakari, M. 2022. ggOceanMaps: plot data on oceanographic maps using 'ggplot2' (R package 1.2.6).
- Vollset, K. W., Urdal, K., Utne, K., Thorstad, E. B., Sægvog, H., Raunsgard, A., Skagseth, Ø. *et al.* 2022. Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Science Advances*, 8: eabk2542.

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