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Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the sea around the Faroe Islands based on analysis of historical tag recoveries

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A database of 2651 tags applied to Atlantic salmon (*Salmo salar*) smolts in 13 countries or jurisdictions and recovered in the Faroes longline salmon fishery from 1968 to 2000 was analysed for geographic distribution and origin of the salmon captured with respect to differences in sea age, season of the fishery, and hydrographic features in the Faroes area. The results indicated that salmon were not distributed randomly in the Faroes area by fishing season, sea age, or country of origin. The distribution of salmon in the Faroes zone partly depends on their geographic origin; salmon from countries in the northern European stock complex were distributed significantly farther northeast than those from countries in the southern European stock complex. Furthermore, the proportion of tag recoveries from southern European countries was higher in autumn, and the proportion recovered from northern European countries higher in winter. The apparent temporal and spatial segregation of stocks of different origin suggests that there may have been differential exploitation on these stocks, which provides information that could inform fishery management with regard to temporal and/or spatial fishery options for the Faroes commercial salmon fishery should it recommence in future.

Keywords: Atlantic salmon, distribution, GIS, GLM, Iceland–Faroe Front, migration, Northeast Atlantic, SST, tagging.

Introduction

The distribution of Atlantic salmon (*Salmo salar*) in the ocean is poorly understood, but available information indicates that it is related to environmental factors including sea surface temperature (SST; Reddin and Shearer, 1987; Jákupsstovu, 1988; Reddin, 1988), surface currents (Reddin and Friedland, 1993), and probably the availability of suitable prey (Jacobsen and Hansen, 2000, 2001). Marine migration routes in the Northeast Atlantic probably depend on large-scale current systems, especially the gyre systems (Dadswell *et al*., 2010). Salmon of North American origin appear to remain mainly in the Northwest Atlantic (Reddin *et al*., 2012), although some fish move into the Northeast Atlantic. It is also evident that a relatively large proportion of the southern European multi-sea-winter (MSW) salmon stock moves into the Northwest Atlantic to feed. Scarnecchia (1989) suggested that MSW salmon of Icelandic origin may move farther from home-waters than one-sea-winter (1SW) salmon. Hansen and Jacobsen (2003) suggested that salmon originating in most of the species' distributional area were present in Faroes waters, but at different times of the year and in different proportions. The duration of sea residence varies among salmon populations, and different sea age classes from the same population can be present at the same time in the same area (Hansen, 1993).

The Faroe Islands (62°N 07°W; Figure 1) are located in an area of large exchanges of water masses between the southern and northern basins of the North Atlantic (Hansen *et al*., 2008). This creates extensive frontal systems, especially north of the Faroes (Iceland–Faroe Ridge), that may play an important role in the temporal and spatial distribution of salmon (Jacobsen *et al*., 2001; Hansen and Jacobsen, 2003). In that area, warm and saline Atlantic water from the southwest meets cooler, less saline water from the northwest, creating the Iceland–Faroe Front (IFF), in a northwest–southeast direction north of the Faroes (Figure 1). It should be noted that the location of the IFF in the study area does not vary substantially either seasonally or annually because its position is determined mainly by topographic features (Hansen and Østerhus, 2000; Hansen *et al*., 2008). In late autumn, SSTs south of the IFF average ~8°C compared with ~4°C north of the IFF. During winter, the average SST decreases by ~1°C in both areas (Read and Pollard, 1992; Debes *et al*., 2009). These frontal systems appear to create favourable conditions for the production of zooplankton, e.g. copepods, euphausiids, and amphipods (Dalpadado *et al*., 1998), and mesopelagic fish that are prey for the large pelagic stocks in the Northeast Atlantic, e.g. herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and blue whiting (*Micromesistius poutassou*; Dalpadado, 2000; Prokopchuk and Sentyabov, 2006; Utne *et al*., 2012). There are important feeding areas for salmon on both sides of the IFF (Jacobsen and Hansen, 2001). The Faroes longline fishery targeted salmon aggregating around the IFF during late autumn and winter, suggesting that the spatial and temporal distribution of salmon is related to environmental conditions in the area. Historically, salmon tagged as smolts in European home-waters have been recovered in that fishery (Jákupsstovu, 1988; Hansen, 1993; Jacobsen *et al*., 2001). Some of the tag-recovery data have been published, but large amounts of information remain unreported, although some countries have presented information to ICES (ICES, 2007, 2008, 2009). The aim of this study is to describe differences in the temporal and spatial distribution of salmon captured in the Faroes longline fishery in the period 1968–2000, with respect to their sea age and origin and hydrographic features in the Faroes area, using information obtained from tags applied to smolts in various countries and recovered in the fishery. Although there is currently no salmon fishery in Faroes waters, the North Atlantic Salmon Conservation Organization (NASCO) is developing a risk framework for the management of the fishery should it recommence in future.

Material and methods

The salmon fishery at Faroes commenced in the late 1960s. Initially, the area fished was relatively close to and around the

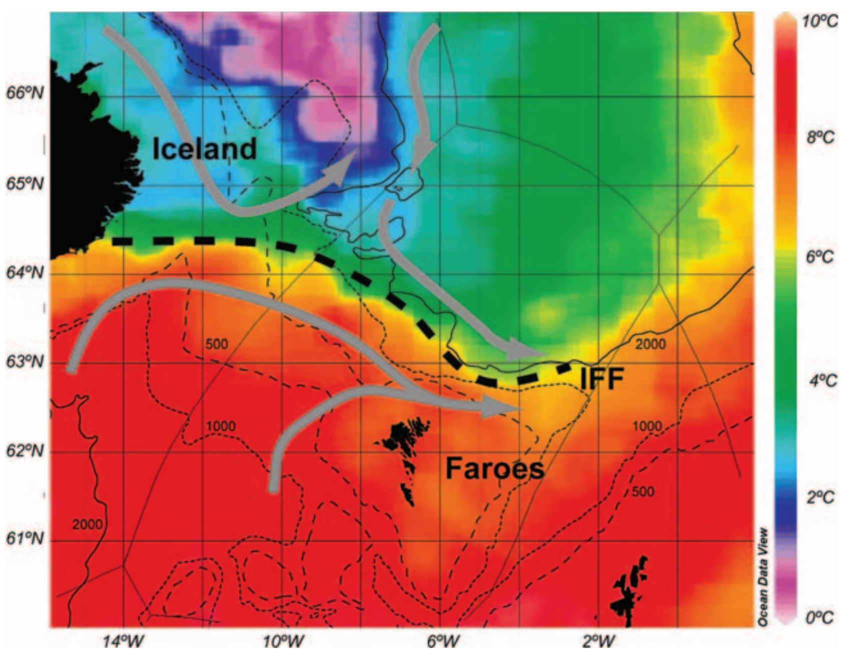

Figure 1. Average sea temperature (October–May since 1950) 100 m deep (after Nilsen *et al*., 2008), illustrating the fronts in the southern part of the Nordic Seas. The typical location of the IFF is represented by the thick dashed line (Hansen and Østerhus, 2000; Hansen *et al*., 2008). The main flow patterns on both sides of the IFF are shown as grey arrows. The 500-m (dashed line), 1000-m (broken line), and 2000-m (whole line) depth contours and national EEZs (solid thin lines) are also shown.

islands, with annual catches of <50 t of mainly (60–90%) 1SW salmon. However, in 1979, 2 years after the establishment of the 200 nautical mile exclusive economic zone (EEZ) around the Faroes, the fishery extended northwards and increased substantially, with practically no fishery south of the islands. Catches peaked in 1981 (at 1025 t) and with significantly greater proportions (80%) of two-sea-winter (2SW) salmon in the catches (Jákupsstovu, 1988). Since NASCO's establishment in 1984, the fishery has been subject to internationally agreed regulatory measures and decisions; as a result, catches in the fishery declined from 630 t in 1984 to around 300 t in 1990. Since summer 1991, there has been no commercial fishing at the Faroes, but a research fishery was conducted in some years during the 1990s (Jacobsen, 2000). The fishing season was from November to the following April, and was divided by a Christmas break into autumn (November–December) and winter (January–April) seasons.

During the period 1968–2000, 2651 tags were recovered from the salmon fishery (2268 individually numbered Carlin tags (Carlin, 1955) and 383 batch-numbered coded wire tags; Table 1). These tags had been applied to salmon in 13 countries or jurisdictions (hereinafter countries): Canada, Denmark, Iceland, Ireland, Faroes, France, Norway, Spain, Sweden, the United States, and the UK (England and Wales, Northern Ireland and Scotland). Tagged groups were not initially intended to be representative of national stocks, and different proportions of the tagged salmon in each country were hatchery-reared. The tagged salmon released in the Faroes were originally introduced from Norway (Sundalsøra, northwestern Norway) for salmon farming, but were used in ocean ranching in the 1980s and early 1990s. These ranched salmon were only included in the analyses by country and not by region.

The recovery data obtained from the fishery included tag number, recovery position, origin (country), date of tag recovery, and size of tagged salmon. A database containing this information is held by the Faroe Marine Research Institute. The precise tag-recovery location was known for 2508 salmon. The recovery data were allocated by season, i.e. whether the tag was recovered during the autumn or the winter fishery. To use all available recovery data, a small number of salmon (<25) recovered in May were allocated to the winter period. Because of missing values for one or more of the variables, some countries (United States, Canada, Denmark, France, and Spain) were excluded from the analyses, resulting in a total of 1678 valid records (Table 1). Tags recovered from Iceland (18 tags) were excluded from the analyses among countries and by season because of insufficient data (3 tags) in winter (Table 1). No tag-recovery data were available for Russia. The tags recovered from the UK (Northern Ireland) and Ireland were merged into one group (Ireland) for the analysis because of the small number (7) of recoveries from the UK (Northern Ireland; Table 1).

Sea age of the salmon was calculated from the release date to the date of tag recovery. Salmon in their first winter at sea were termed 1SW salmon, irrespective of whether they were recovered during autumn or the following winter, and those in their second, third, etc., winters at sea were collectively termed MSW salmon. For MSW salmon, recovery information from 2 and 3SW salmon was available for inclusion in the analyses (Table 1). The implications of the sea-winter definition are that the sea age was considered to change in summer and not at the beginning of the year. Hence, salmon were assumed to have the same sea age throughout autumn and following winter fishing seasons, i.e. from November in the year i to July in the year $i + 1$.

A dividing line along the IFF was established with endpoints of 64°50′N 9°25′W to 61°34′N 2°55′W (Figure 2). Rather than using two geographic coordinates (latitude and longitude) that would complicate the statistical analyses, the locations of tag recoveries in the area were assigned a single value distance vector measured perpendicular to this dividing line. A perpendicular vector (DIST) was created from the dividing line to the tag-recovery position (Figure 2), and the measured-distance vector was used as the response variable in the statistical analyses (see below). The distance from the dividing line to a tag-recovery position was assigned a positive value if the recovery location was northeast of the line and a negative value if it was southwest of the line (Figure 2). Clearly, this approach must be applied with care because the difference between DIST vectors for tag recoveries is

Table 1. Country of origin of the 2651 tags recovered from the Faroes salmon fishery in the period 1968–2000.

			Autumn				Winter			
Country[a]	**All data**	**Accepted data**	**1SW**	**2SW**	**3SW**	**Total**	**1SW**	**2SW**	**3SW**	**Total**
United States	1	–	–	–	–	–	–	–	–	–
Canada	6	–	–	–	–	–	–	–	–	–
Denmark	10	–	–	–	–	–	–	–	–	–
France	1	–	–	–	–	–	–	–	–	–
Spain	1	–	–	–	–	–	–	–	–	–
Ireland[b]	166	128	73	18	1	92	27	9		36
England and Wales	69	47	9	18	2	29	2	14	2	18
Scotland	135	51	3	13	6	22	6	20	3	29
Iceland[c]	27	18	1	12	2	15	1	2		3
Norway	1 760	1 183	33	323	15	371	114	591	107	812
Sweden	376	182	8	55		63	14	90	15	119
Faroes	99	69		40	2	42	1	25	1	27
Total	2 651	1 678	127	479	28	634	165	751	128	1 044

The "Accepted data" column shows the number of tags recovered with geographic location information and with the season of recovery by sea age. The final dataset used in the analyses excluded tags recovered from Canada, Denmark, France, Spain, and the United States because of lack of data.
[a]No tag recovery data were available for Russia.
[b]Ireland and the UK (Northern Ireland) merged into one group (designated Ireland).
[c]Iceland removed from the data used for analyses among countries split on seasons.

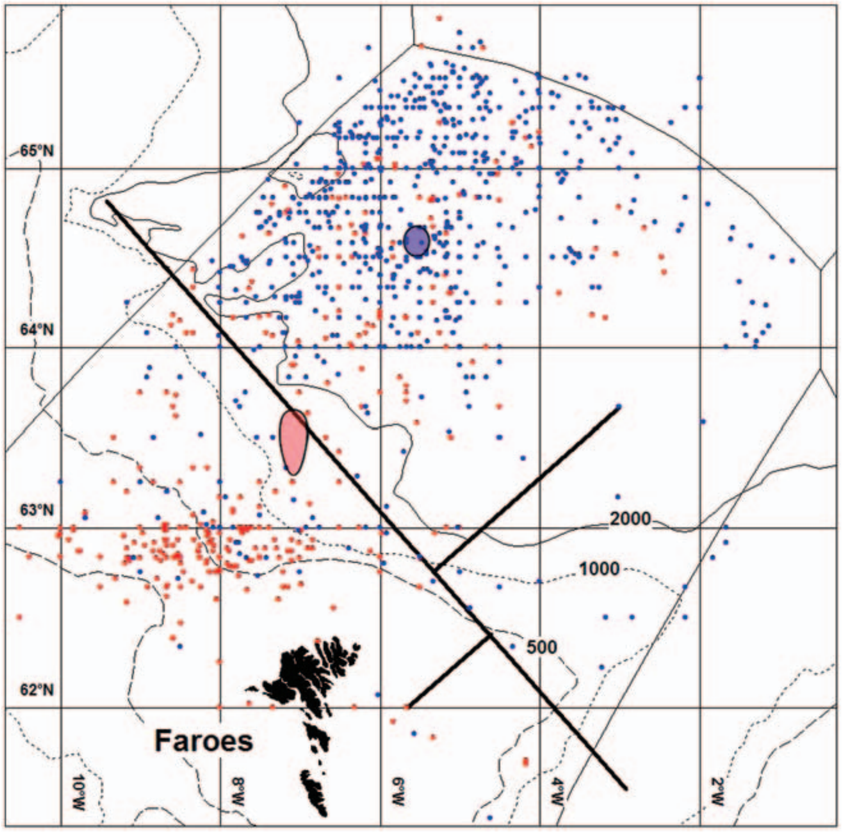

Figure 2. Recapture locations of tagged salmon during autumn (red dots, November–December) and winter (blue dots, January–April) north of the Faroes. The dividing line in a northwest–southeast direction was drawn by hand for use in the analysis and has endpoints at 64°50′N 9°25′W and 61°34′N 2°55′W. Two examples of the perpendicular distance vectors from the dividing line to a recapture location are shown, one positive (northeast of the line) and one negative (southwest of the line). The average geographic location of the tag recoveries is shown as 95% confidence areas (ellipses) for autumn (red) and winter (blue), respectively. The 500-m (dashed line), 1000-m (broken line), and 2000-m (solid line) depth contours and national EEZs (solid thin lines) are also shown.

used as a simple way to show separation across the front between salmon, and will not necessarily reflect the actual distance between them that will also be affected by their orientation relative to each other.

Statistical analyses were conducted using generalized linear models (GLMs; Venables and Ripley, 2002; Crawley, 2007). The locations of tag recoveries (represented by the distance vector DIST) were used as continuous response variables, and season (Se), sea age (SW), and country of origin (Country) were the categorical (factor-type) predictor variables. Further, the origin of the salmon, grouped by region (either the northern or southern European stock complex as defined for assessment purposes by ICES), was used as a predictor variable in some analyses. The northern European stock complex consists of salmon from Finland, Norway, Russia, the west coast of Sweden, and northeast Iceland, and the southern European stock complex salmon from France, Ireland, the UK (England and Wales), the UK (Northern Ireland), the UK (Scotland), and southwest Iceland (ICES, 2011).

Sequential *F*-ratio tests of nested GLMs, i.e. models with different numbers of variables, with all variables in the smallest model included in the larger model(s), were used to evaluate the ability of specific predictor variables to explain variation in the response in addition to, and independent of, other variables (Venables and Ripley, 2002). *Post hoc* comparison between levels of factor-type predictors were made by re-running the full models several times using treatment contrasts (e.g. Crawley, 2007), each time with a different (combination of) factor level(s) as level 1 for each factor. This allowed direct testing of deviations from zero of coefficients for combinations of factor levels. Before the separate tests, the models were checked for statistical interactions (non-additive relationships) between predictor variables. Errors were assumed to be normal. All tests were run with the R package version x (R Development Core Team, 2011). An overview of the GLMs tested is provided in Table 2. Model 1 included season as the predictor variable and was tested against a basic model, with all the variation in the data included in the model. Model 2 included sea age as the factor variable, and the variation attributable to season as covariable; this model was tested against a reduced model excluding sea age. In addition to season and sea age, Model 3 included region (stock complex), and Model 4 included country of origin. Models 3 and 4 were both tested against a simpler model without sea age (Table 2). Models 5–7 were run with the sea-age factor fixed, either for 1SW or for 2SW salmon. Model 5 included season, region, and sea age at recapture for 2SW salmon, Model 6 included season, country of origin, and sea age at recapture for 2SW salmon, and Model 7 included season, country of origin, and sea age at recapture for 1SW salmon (Table 2). Models 5–7 were tested against reduced

Table 2. Overview of the results of the analysis of factors associated with the location (DIST) of tags recovered relative to the season of fishing (Se), sea age of fish at recapture (SW), region (either northern or southern European stock complex) of origin (Region), and country of origin (Country).

Model number	Predictor	Covariable(s)	Deviance	Deviance explained	CE	d.f.	F	$p(F)$
1	f(Se)	–	2.44e + 13	6.94e + 12	0.284	1 676	666.3	**<0.001**
2	f(SW)	f(Se)	1.75e + 13	1.06e + 11	0.006	1 674	5.1	**0.006**
3	f(SW)	f(Se) + f(Region)	1.60e + 13	4.48e + 10	0.003	1 604	2.2	0.106
4	f(SW)	f(Se) + f(Country)	1.72e + 13	1.60e + 10	0.001	1 668	0.8	0.460
5	f(Region)	f(Se), SW = 2	1.07e + 13	1.18e + 11	0.011	1 148	12.9	**<0.001**
6	f(Country)	f(Se), SW = 2	1.18e + 13	1.15e + 11	0.010	1 209	2.4	**0.037**
7	f(Country)	f(Se), SW = 1	3.96e + 12	9.05e + 10	0.023	265	3.1	**0.047**

CE is the fraction of total deviance explained by the model.
F and p refer to marginal F-tests of the model.
Significant p-values at the $\alpha = 0.05$ level are shown emboldened.

models including season only for the respective sea ages. The generally unbalanced nature of the recovery data may have affected some of the analyses, so p-values were interpreted conservatively when they were close to 0.05.

Results

The locations of the tag recoveries for each season suggest that the geographic distribution of salmon differed between the autumn and the winter fishing seasons (Figure 2). Tag recoveries were distributed significantly farther northeast during winter than during autumn (Model 1, $p < 0.001$, Table 2). The average location of the tags recovered during winter was 125 km northeast of the dividing line, but it was 7 km southwest of the dividing line during autumn (Figure 2). Model 1 explained 28.4% of the total deviance, i.e. the variation in tag-recovery location between seasons explained less than one-third of the variation in the data. This leaves a large proportion of the deviance unexplained, so weakens the inferences from the analyses. As a significant proportion of the variation in the data was explained by season of tag recovery (Model 1, Table 2), season was included as a covariate in all subsequent models to examine the effects of other predictors (sea age, country of origin, or region) on DIST that are additional to, and independent of, the effect of season.

An overview of the tag-recovery data for each country, season, and sea age in terms of the DIST parameter is shown as a boxplot in Figure 3. The median distance from the dividing line in the overall data was positive for the UK (Scotland), Norway, Sweden, and Faroes, and negative for Ireland, the UK (England and Wales), and Iceland. For Norway and Sweden, the data within the inter-quartile range (IQR, between the 25 and 75th percentiles) were all greater than zero, i.e. located exclusively northeast of the dividing line. The median distance was also positive for all sea ages. For 3SW salmon and salmon recovered during winter, the location was almost exclusively northeast of the dividing line (Figure 3).

Overall, there was a significant difference in the average geographical location of tag recoveries by sea age, after variation attributable to season had been accounted for (Model 2, $p = 0.006$, Table 2). However, the additional deviance explained was just 0.6%, indicating that sea age is not an important predictor of recovery location. *Post hoc* tests showed that there were no differences in the location of salmon among sea ages during autumn. However, significant differences in location were found between sea ages 1 and 2 ($p < 0.001$), and between sea ages 1 and 3 ($p = 0.020$) during winter, but not between sea ages 2 and 3 (Table 3). Therefore, the observed differences in location among sea ages in Model 2 were caused by differences during winter (Figure 4a).

To test if the distribution of tagged salmon caught at the Faroe Islands is independent of geographic origin of the stocks

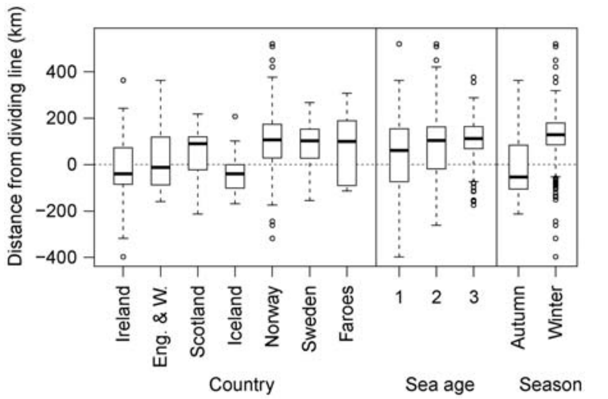

Figure 3. Boxplots of the distance vector (DIST, km) by country of origin, sea age (1, 2, and 3SW), and season (autumn and winter). DIST is zero at the artificial dividing line, positive in a northeasterly direction, and negative in a southwesterly direction. The median values of the data are indicated within each box, with the lower and upper edges indicating the IQR, i.e. the first quartile (the 25th percentile) and the third quartile (the 75th percentile), respectively. The whiskers extend from the minimum to the maximum value. Open circles indicate outlier values >1.5 times the IQR from the IQR limits.

Table 3. Estimates of the average distance at recapture (DIST, km), grouped by sea age (1SW, 2SW, 3SW) within the autumn (November – December) and winter (January – April) seasons, with p-values of *post hoc* tests for the effects of sea age within season on DIST.

	Autumn			Winter		
Sea age	**DIST (km)**	**1SW**	**2SW**	**DIST (km)**	**1SW**	**2SW**
DIST (km)	–	−18	−5	–	+103	+129
2SW	−5	0.297	–	+130	**<0.001**	–
3SW	+6	0.345	0.633	+128	**0.020**	0.804

Significant p-values at the $\alpha = 0.05$ level are shown emboldened.

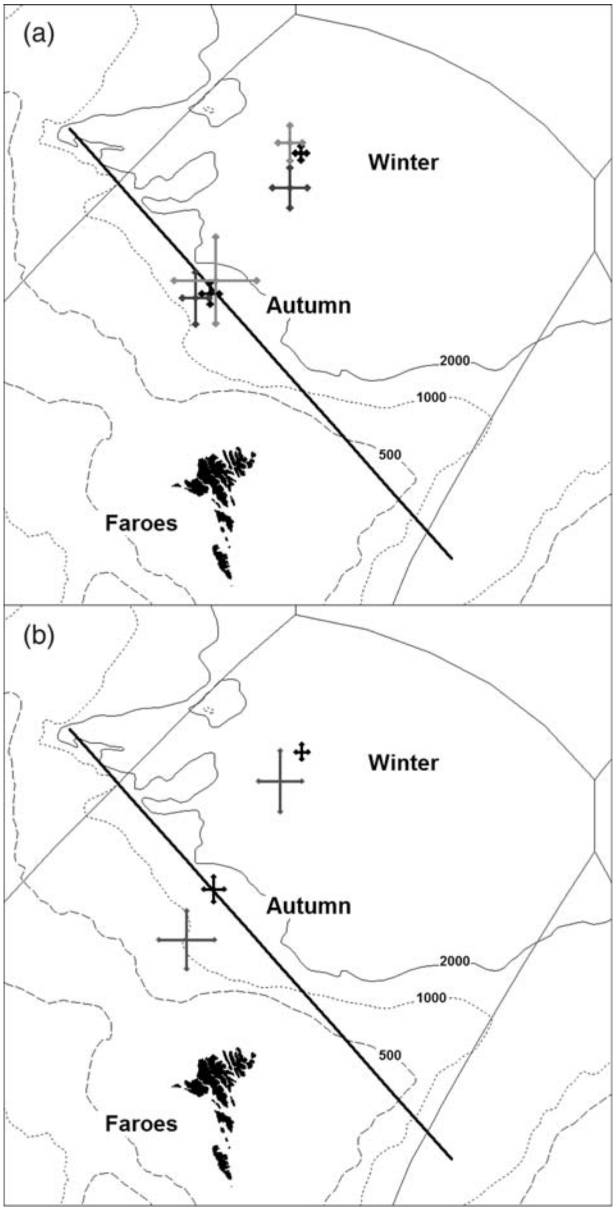

Figure 4. Average geographic locations of recapture of salmon indicated by crosses representing 95% confidence intervals for latitude and longitude directions by (a) sea age (1SW dark grey, 2SW black, and 3SW grey crosses) during autumn (November–December) and winter (January–April), and (b) from the southern (grey crosses) and northern (black crosses) European stock complexes during autumn and winter for 2SW salmon. The 500-m (dashed line), 1000-m (broken line), and 2000-m (solid line) depth contours and national EEZs (solid thin lines) and the dividing line are also shown.

(i.e. northern vs. southern European stock complexes or country of origin), fishing season and sea age would ideally have been used as covariables. However, the number of observations within each sea-age class was very small, especially for sea ages 1 and 3 (Table 1), when assigned by fishing season, country of origin, or region (stock complex). A model with sea age as a predictor, with both season and region or country of origin as covariables, was not, therefore, expected to explain a significant portion of the variation in recapture location (DIST). This expectation was substantiated by both Model 3 ($p = 0.106$, Table 2) and Model 4 ($p = 0.460$, Table 2). However, for some combinations of country and sea age, the number of tag recoveries was sufficient for sea age to be used as a factor to analyse geographic location in relation to country of origin. Two examples were for recaptures of 2SW salmon from the Faroes, Norway, Sweden, Ireland, the UK (Scotland), and the UK (England and Wales), and for 1SW salmon from Norway, Sweden, and Ireland (Table 1). Therefore, sea-age-specific analysis was used in three models (5–7) of the origin of the tag recoveries. These were age-specific analyses for 2SW salmon by region (Figure 4b) and by country of origin (Table 4), and for 1SW salmon by country of origin (Table 5).

The distribution of salmon at sea appears to depend on the geographic origin of the stocks. Tags recovered from 2SW salmon originating in countries in the southern European stock complex were located significantly farther southwest than those recovered from 2SW salmon from the northern European stock complex, even after variation attributable to season was accounted for (Model 5, $p < 0.001$, Table 2). The additional deviance explained by region was 1.1%. Additionally, *post hoc* tests showed that during both autumn ($t = -2.5$, d.f. $= 425$, $p = 0.012$) and winter ($t = -2.3$, d.f. $= 723$, $p = 0.021$), tags recovered from salmon from the southern European stock complex were located significantly farther southwest than those from the northern European stock complex. The estimated average locations (DIST) from the dividing line were -45 and -1 km during autumn and $+101$ and $+131$ km during winter for 2SW salmon from the southern and northern European stock complexes, respectively (Figure 4b).

Model 6, with country of origin as the predictor variable and fishing season as the covariable, indicated that the distribution of tag recoveries varies depending on country of origin. Significant differences in the average distance vector from the dividing line were found among tags recovered from 2SW salmon from different countries, after variation attributable to season was accounted for (Model 6, $p = 0.037$, Table 2). The additional deviance explained by country of origin was 1.0%. *Post hoc* tests were run to test for pairwise, among-country differences in the location of tags recovered from 2SW salmon for each season (Table 4). During the autumn season, tags recovered from the UK (England and Wales) were located significantly farther southwest than those from Faroes, Norway, and Sweden, but no significant differences in location were found between tags from the UK (England and Wales) and tags from either Ireland or the UK (Scotland; Table 4). The remaining tests in autumn revealed no significant differences among countries. During the winter season, 2SW salmon from Ireland were located significantly farther southwest than salmon originating in all other countries (Table 4).

Significant differences in the average distance vector from the dividing line were also found among 1SW tag recoveries from different countries, after variation attributable to season was accounted for (Model 7, $p = 0.047$, Table 2). The additional deviance explained by country of origin was 2.3%. *Post hoc* tests revealed a significant difference only between Norway and Ireland during winter, with 1SW salmon from Ireland located significantly farther southwest than Norwegian salmon (Table 5). No differences were found during autumn. It should be noted that only tag recoveries from Norway, Sweden, and Ireland were included in this analysis because there were insufficient data for 1SW salmon from other countries (Table 5).

Table 4. Estimates of the average distance (DIST, km) for 2SW salmon by country and within season (autumn and winter) with corresponding *p*-values of *post hoc* tests for the effects of country of origin on DIST.

Country	DIST (km)	Faroes	Norway	Sweden	Ireland	Scotland	England and Wales
Autumn							
DIST (km)	–	+12	−2	+10	−40	−29	−63
Faroes	+12	–	–	–	–	–	–
Norway	−2	0.478	–	–	–	–	–
Sweden	+10	0.932	0.488	–	–	–	–
Ireland	−40	0.124	0.189	0.123	–	–	–
Scotland	−29	0.284	0.431	0.293	0.189	–	–
England and Wales	−63	**0.027**	**0.035**	**0.025**	0.564	0.429	
Winter							
DIST (km)	–	+138	+133	+117	+47	+122	+105
Faroes	+138	–	–	–	–	–	–
Norway	+133	0.754	–	–	–	–	–
Sweden	+117	0.275	0.106	–	–	–	–
Ireland	+47	**0.005**	**0.002**	**0.016**	–	–	–
Scotland	+122	0.531	0.586	0.811	**0.024**	–	–
England and Wales	+105	0.664	0.439	0.173	**0.004**	0.339	–

Significant *p*-values at the $\alpha = 0.05$ level are shown emboldened.
Iceland was excluded from the analysis because of insufficient data.

Table 5. Estimates of the average distance (DIST, km) for 1SW salmon by country and within season (autumn and winter) with corresponding *p*-values of *post hoc* tests for the effects of country of origin on DIST.

Country	DIST (km)	Norway	Sweden	Ireland
Autumn				
DIST (km)		+6	−23	−28
Norway	+6	–	–	–
Sweden	−23	0.506	–	–
Ireland	−28	0.146	0.905	–
Winter				
DIST (km)		+117	+113	+58
Norway	117	–	–	–
Sweden	+113	0.912	–	–
Ireland	+58	**0.033**	0.195	–

Significant *p*-values at the $\alpha = 0.05$ level are shown emboldened.
The Faroes, Iceland, the UK (Scotland), and the UK (England and Wales) were excluded from the analysis because of insufficient data.

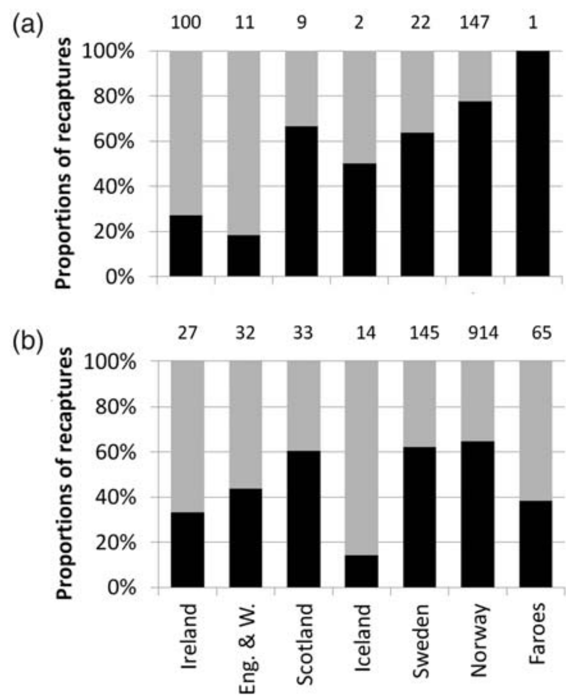

Figure 5. Proportions of tags recovered from (a) 1SW and (b) 2SW salmon during autumn (grey, November–December) and winter (black, January–April) by country of origin. The total number of tags recovered by country for each sea age is stated above each bar.

Models 2, 5, 6, and 7 (Table 2) show that the recaptured tagged salmon were not distributed randomly with respect to season, sea age (1 and 2), or country of origin. Among countries belonging to the northern European stock complex, the proportion of the total number of tags recovered during winter for both 1SW and 2SW salmon was >60% for Norway and Sweden, but <20% for 2SW salmon from northeast Iceland (Figure 5). Only two tags were recovered from 1SW salmon from Iceland in autumn, and these were not used in the analyses. For 1SW salmon from countries in the southern European stock complex, only Ireland had sufficient numbers of tag recoveries, and about one-quarter were recovered during winter (Figure 5a). Among countries belonging to the southern European stock complex, the proportion of tags recovered from 2SW salmon during winter decreased from ~60% for the UK (Scotland) in the north to 40% for the UK (England and Wales), to 33% for Ireland to the south (Figure 5b). For the Faroes (although not part of the northern European stock complex used by ICES), the proportion of tagged 2SW salmon recovered in winter was 40% (Figure 5b), whereas no 1SW salmon were recovered during autumn, and only one 1SW salmon was recovered in winter (Figure 5a). The proportion of tag recoveries by sea age (1, 2, and 3SW) for individual countries indicates that tags recovered from 2SW salmon dominated (60–80%) for all countries except Ireland (~20%; Table 1).

The number of tags recovered each year was closely associated with the catches of salmon in the fishery between 1981 and 1991.

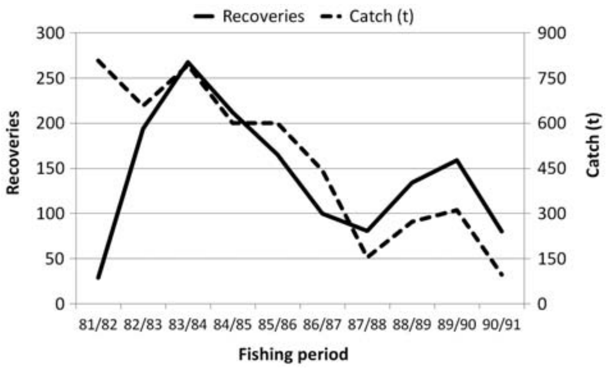

Figure 6. Catches of salmon in the Faroes area (dashed line) and the number of tagged salmon (solid line) recovered in the fishery during the period 1981–1991 (autumn and subsequent winter seasons have been combined for each fishing period in the graph). Catch data are from ICES (1994).

During that period, some 85% of the tags used in the study were recovered (Figure 6).

Discussion

This analysis of tags recovered from the fishery indicates that salmon are not distributed randomly in the sea around the Faroes during autumn and winter with respect to either sea age or country of origin. During autumn, more tags were recovered southwest and closer to the Faroes than during winter. However, it is not known if this is because salmon occupy the warmer waters south of the IFF during autumn and the cooler waters north of the IFF during winter or because of the migratory routes taken by the fish. Salmon from southern European countries were predominantly south of the IFF, whereas those from northern European countries were mainly north of it.

Our findings assume that the distribution of tag recoveries represents the distribution of salmon in the area. However, the distribution of tag recoveries depends on the distribution of fishing effort, both temporally and spatially. Therefore, the data might reflect the distribution of fishing effort rather than the true distribution of salmon. Although fishing effort data are available for the Faroes salmon fishery, they are not in a form suitable for analysis (i.e. disaggregated in time and space). However, aggregated catch-and-effort data show that the number of tags recovered was proportional to the catches of salmon by fishing period. Moreover, there was no trend in the catch per unit effort (cpue; number of salmon caught per 1000 hooks set) in the fishery (Hansen *et al*., 1999). Therefore, the results should not be biased by the varying numbers of salmon caught during the period analysed. The salmon fishery during autumn traditionally targeted warmer waters southwest of the IFF, whereas the winter fishery targeted the cooler waters north of the IFF (Jacobsen, 2000). These two areas were only fished simultaneously to a limited extent, especially during autumn, and it is possible, therefore, that fish from a specific country were distributed equally on both sides of the front even if tags were only recovered from one area. Conversely, the absence of tags from an area does not confirm that salmon were not present, because there may have been little fishing effort. However, we believe that the fishing fleet targeted areas with high cpue at any given time, similar to observations in the Pacific (Healey *et al*., 1990), so there is likely to be some general correspondence between the distribution of fish and fishing effort, and consequently, changes in the fishery are likely to be the result of changes in the abundance of salmon during the fishing seasons.

An analysis of cpue by month in the Faroes salmon fishery from 1981 to 1994 indicated good catch rates in early autumn (November), with catch rates decreasing in December and January, but increasing again towards the end of winter (ICES, 1994). If salmon abundance decreased south of the IFF in December, fishers would have been expected to seek new areas with higher densities of salmon or areas with larger and, therefore, more valuable salmon (assuming that the benefits outweigh the additional costs), and this could explain the northward shift of the fishery later in the season. It should be noted that 10–30 vessels fished simultaneously in the area during the fishing seasons in the 1980s. One of the scientific observers on board the vessels at that time reported that at the beginning of each season and whenever the fishery diminished in one area, it was normal practice for the vessels to disperse to seek more profitable areas with high cpue or with large salmon (R. Mouritsen, pers. comm.).

The apparent separation of salmon by season in relation to the IFF could be the result of differences in the abundance of the salmon's prey. Suitable food might be limited in late autumn in the oceanic area north of the Faroes. The spring bloom appears to commence earlier close to and northeast of the IFF than in the area south of the IFF (Debes *et al*., 2009). Jacobsen and Hansen (2001) noted that during autumn, just half (53%) the salmon examined contained food in their stomachs, significantly less than during late winter (79%). This suggests greater food availability north of the IFF in late winter than south of the IFF during autumn. Jacobsen and Hansen (2001) also reported an increase in stomach contents in winter because of the greater proportions of fish being consumed then.

Our findings indicate that the distribution of salmon at sea depends partly on their sea age. There were no differences in the distribution of tag recoveries by sea age during autumn, whereas during winter, the smaller 1SW salmon were distributed slightly farther southwest than 2 and 3SW salmon. It should be noted that the unbalanced data by sea age, especially sea ages 1 and 3 by country, mean that the significance of these findings is questionable. However, during winter, all sea ages of salmon were found north of the IFF, suggesting that 1SW and MSW salmon prefer cooler water (average SST 2–3°C; Read and Pollard, 1992). Previous reports from the Northwest Atlantic (Reddin and Shearer, 1987) and the Faroes area (Jákupsstovu, 1988) indicate that small salmon appear to prefer to feed in water warmer than 4°C. Jacobsen (2000) reported that the largest salmon caught during a tagging experiment north of the Faroes in the early 1990s were north of the IFF, where SSTs were as low as 2°C.

The location of 1SW salmon in the cooler waters north of the IFF in winter close to the MSW salmon was, therefore, unexpected. It is not known why the 1SW salmon occupy cooler waters in winter rather than moving to the warmer waters south of the IFF. As suggested above, this could be attributable to the improved feeding conditions north of the IFF during winter and early spring. Indirect support for this hypothesis is provided by the historical fishery data which indicate a decreasing trend in cpue south of the front in late autumn and early winter (ICES, 1994). It can be speculated that salmon from countries in the southern European stock complex commence their homeward migration and leave the area in late winter, resulting in a decline in cpue, but a lack of data prevents proper testing of this hypothesis.

The distribution of salmon at sea is related to the geographic origin of the stocks. 2SW salmon from countries in the southern European stock complex were distributed significantly farther southwest in the Faroes zone than 2SW salmon originating in countries in the northern European stock complex during autumn. Moreover, the proportions of tags recovered from southern European countries were significantly higher than expected owing to their random distribution during autumn. These findings may be relevant to the management of the salmon fishery at Faroes should it recommence in future.

The distribution of 1 and 2SW salmon at the Faroes differed significantly by country of origin. Salmon from the UK (Scotland) and Ireland were significantly farther southwest than those from the Faroes, Norway, and Sweden.

Most of the salmon recaptured around the Faroes originated in Norway, Sweden, Ireland, and the UK (Scotland). However, the number of tags recovered from each country depends on the number of smolts tagged, so this information does not necessarily represent the actual proportions of salmon present in the Faroes area from each country. Similarly, the tagged fish were not necessarily representative of all stocks from the respective countries. Tagging of wild adult salmon north of the Faroes during the years 1992–1995 indicated that ~40% of the fish were of Norwegian origin, and that 19 and 18% of the fish originated in the UK (Scotland) and Russia, respectively (Hansen and Jacobsen, 2003). Salmon from Ireland, Denmark, Canada, Sweden, and the UK (England and Wales) all accounted for low proportions of the total salmon population present in the Faroes area (Hansen and Jacobsen, 2003).

Results from previous tagging programmes in the Northeast Atlantic support the view that stocks from countries in the southern European stock complex are mostly caught during the autumn fishing season. Jákupsstovu (1988) noted that the large proportion (85%) of 1SW salmon available for tagging around the Faroes was the result of the relatively southern area (i.e. south of the IFF) sampled and that 2SW fish were more abundant to the north. Further, salmon from southern European countries dominated the returns from this early tagging experiment (Jákupsstovu, 1988), as opposed to the observation by Jacobsen *et al.* (2001) that ~90% of the recoveries during winter originated from northern European countries. In the early 1990s, salmon from both south and north of the IFF were tagged. Fish tagged in autumn were recovered in countries located closest to the Faroes [i.e. the UK (Scotland), Ireland, Sweden, and southern Norway], whereas those tagged during winter were recovered both in countries close to and farther away from (e.g. northern Norway, Russia, and Canada) the Faroes (Hansen and Jacobsen, 2003).

It has been estimated that between 80 and 90% of the salmon present in the area north of the Faroes become sexually mature during the same year and spawn in autumn, irrespective of age (Youngson and McLay, 1985; Hansen and Jacobsen, 2003). The observed reduction in the number of tags recovered from 1SW salmon from southern European countries in this area between autumn and winter might be due to these fish leaving the Faroes area to return home to spawn earlier than MSW fish. For example, salmon from the UK (England and Wales) and Ireland were distributed southwest of the IFF, significantly farther southwest than those from other countries, but it is not known if these fish leave their overwintering area relatively early. However, Hawkins (1987) found that MSW salmon return to, and ascend, the River Dee (Scotland) earlier than 1SW salmon, and Jonsson *et al.* (1990) found that MSW salmon returning to rivers in Norway approach coastal areas earlier than 1SW salmon. Similarly, Browne *et al.* (1994) found that 1SW salmon arrive in Irish coastal waters during early summer somewhat later than 2SW "spring" salmon that arrive from February to May.

Based on tags recovered at the Faroes from 1992 to 1995 and on smolt and sea-age distributions, Jacobsen *et al.* (2001) suggested that a change in the stock complexes entering and departing from the Faroes area may take place, with the southern 1SW salmon departing on their homeward migration in winter, resulting in an apparent change in stock structure, with fewer southern European fish present during late winter. Smolts from different areas enter the ocean at different times of the year. For example, salmon smolts from southern Europe may migrate to sea as early as April (Baglinière, 1976), whereas smolts from northern Norway enter the sea in late June (Hvidsten *et al.*, 1995). These spatial and temporal differences are likely to result in different distributions of post-smolts from different stock complexes in the sea. If this segregation continues through the first summer at sea, then there are likely to be differences in the timing and location of when and where salmon enter the Faroes area in autumn. It could be hypothesized that this spatial segregation continues throughout both fishing seasons and is related to the hydrographic conditions and especially food availability in the area. Hence, the apparent change in stock structure from autumn to late winter could be attributed to differences in the arrival time of various stocks from around the North Atlantic rather than differences in their departure time.

For the purposes of providing management advice, salmon from the southern and northern European stock complexes are assessed separately (see details in ICES, 2011). For example, salmon from northeast Iceland are currently included in the northern European stock complex and those from southwest Iceland in the southern European stock complex (ICES, 2011). However, in the present analyses, the small number of tags recovered from Iceland (17 from the northeast and 1 from southwest Iceland) were mainly reported in autumn far to the southwest of the IFF and at a similar location to salmon from the southern European stock complex. Furthermore, the proportion of tag recoveries by season indicated that Iceland had the largest proportions of tags recovered during autumn (15 of 18 tags). Based on the limited number of tags recovered, salmon originating in northeast Iceland appear to have a similar distribution to salmon from the southern European stock complex. This raises the question as to whether these salmon should continue to be included in the northern European stock complex for assessment purposes.

The apparent temporal and spatial separation of salmon by country of origin raises the possibility that temporal and/or spatial closure could be used as a conservation measure in the management of the Faroes salmon fishery if it recommences in future.

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