

Original Article

Origin of Atlantic salmon (*Salmo salar*) at sea in Icelandic waters

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The origin and life history of 186 Atlantic salmon caught at sea within Icelandic waters were investigated using microsatellites to assess the origin and scales and otoliths to assess freshwater and sea age. A total of 184 samples were aged using scales or otoliths or both. Most of the samples were from individuals in their first year at sea (72.8%). The freshwater age varied from 1 to 5 years with an average of 2.6 years. The most common freshwater age was 2 years (42%), with a further substantial proportion of 3-year-old fish (28%). Genetic assignment of individual fish to their most likely population of origin was performed using Bayesian genetic individual assignments with a baseline consisting of 284 Eastern Atlantic rivers and 466 sample sites genotyped at the 14 microsatellite. A total of 186 samples of salmon caught at sea were assigned to their origin. Eight samples, from post-smolts and caught close to land, were assigned as having come from Iceland. Of the remaining 178 samples, 121 individuals (68%) were from the Southern Group, i.e. from mainland Europe, the UK, and Ireland, 53 individuals (30%) were from the Northern Group, i.e. Scandinavia and Northern Russia, and 4 individuals were from Iceland (2%). Stock mixture proportions were estimated for four periods using ONCOR and cBAYES. Stock mixture analysis generally supported the individual assignments, but did not suggest a seasonal component to the distribution of salmon stocks. These results indicate that the sea south and east of Iceland are important as feeding areas for migrating Atlantic salmon, particularly for salmon originating in the UK, Ireland, and southern Europe. Furthermore, the lack of adult Icelandic fish so close to Iceland is remarkable and suggests that Atlantic salmon from Icelandic stocks are using different feeding grounds.

Keywords: age determination, Atlantic salmon, individual assignment, microsatellite.

Introduction

The Atlantic salmon (*Salmo salar*), a native of North Atlantic temperate waters, shows a complex and diverse biology and life history (Aas *et al.*, 2010). Individuals are generally anadromous: spawning in freshwater, followed by a freshwater juvenile phase (1–8 years; Klemetsen *et al.*, 2003) and subsequent (1–4 years) oceanic feeding migrations, culminating their return to natal rivers to spawn (Hutchings and Jones, 1998). Atlantic salmon are hierarchically structured into distinct populations on regional, river, and tributary levels (Shelton, 1985; McConnell *et al.*, 1995; Verspoor *et al.*, 1999; King *et al.*, 2001; Spidle *et al.*, 2001; Gudmundsson *et al.*, 2013).

Although the biological aspects of Atlantic salmon in freshwater have been extensively studied, there is still a lack of knowledge of their marine phase, particularly related to stock-specific ocean migration and feeding patterns (Verspoor *et al.*, 2007; Aas *et al.*, 2010). Information on their distribution at sea is largely based on studies of tags recaptured in marine fisheries in feeding areas of West Greenland, near the Faroe Islands, and in the northern Norwegian Sea (Shelton, 1985; Reddin and Friedland, 1999; Hansen and Jacobsen, 2003). Outside these well-known salmon feeding areas, both post-smolts (PS) and immature adults are believed to be widely, but unevenly, distributed, and salmon originating in several rivers may be caught in the same areas at

the same time (Hansen and Jacobsen, 2003). PS have been caught during pelagic trawl and driftnet surveys north of Scotland (Shelton *et al.*, 1997), in the Norwegian Sea (Holm *et al.*, 2000), and along Labrador (Reddin and Short, 1991). Migration routes in the Northeast Atlantic most likely depend on large-scale currents, especially the gyre systems (Dadswell *et al.*, 2010), together with active directional swimming (Mork *et al.*, 2012). Salmon originating in North America generally remain in the western North Atlantic (Ritter, 1989), although migration to Europe has occurred (Reddin and Friedland, 1999). Feeding areas north of the Faroe Islands are used by salmon from Norway, Scotland, Russia, and Ireland (Hansen and Jacobsen, 2003). Salmon from southern Europe, the UK, and Ireland are also abundant off West Greenland (Went, 1973; Swain, 1980; Sheehan *et al.*, 2010). There is still a lack of knowledge of the distribution of salmon at sea in areas not previously studied and in areas commercial without salmon fisheries.

In Icelandic waters, the fishing of salmon at sea has been banned since 1932, and as a result little opportunity has existed for learning about distribution and origin of salmon in these waters from domestic fisheries (Mathisen and Gudjonsson, 1978; Guðbergsson, 2013). Ísaksson (1980) suggested that the Irminger and the Iceland Sea eddies probably serve as major feeding grounds for grilse from the southern and northern Iceland, respectively, and that multi-sea-winter (MSW) salmon migrate into the Norwegian Sea from northern populations. Little is known about the distribution of salmon in the Irminger Sea. In June 1966, four salmon were caught by the research vessel Dana at 62°N and at 26,50°W and 37,20°W in the Irminger Sea (Jensen, 1967). During summer 1966 and 1973–1975, 80 salmon (mostly grilse) were caught in the Irminger Sea by a research vessel, and scale analysis suggested a European origin for most of them (Jensen and Lear, 1980). MacKenzie *et al.* (2011) and Trueman *et al.* (2012) suggested from their studies of isotopes of two salmon populations in the British Isles that one used the area south of Iceland for feeding whereas the other was more likely using areas in the Norwegian Sea. The ocean around Iceland is therefore likely to be important for salmon, both from Iceland and also from other countries. More studies are therefore needed on salmon in these feeding areas.

Salmon catches from Iceland rivers have been correlated with variations in sea surface temperature and salinity (Scarnecchia, 1984; Scarnecchia *et al.*, 1989, 1991). Oceanic conditions around Iceland vary from year-to-year, but generally fluctuate more in the north and east of Iceland than in the south and west. This variation, in turn, affects primary production and abundance of zooplankton in those areas (Astthorsson *et al.*, 1983; Valdimarsson *et al.*, 2012). A small branch of the Irminger current flows north along the western shelf of Iceland and northeastwards to the shelf area north of Iceland (Malmberg and Valdimarsson, 2003) where it meets the colder East Greenland current and the Icelandic currents, northwest and north of Iceland. In years where this current does not flow north of Iceland, the result is low water temperature, low salinity, little turbulent mixing, and low primary production (Gudjonsson *et al.*, 1995). This oceanographic variability has a marked influence on the living conditions for various biota (Astthorsson *et al.*, 2007), and consequently, on the interannual growth and survival of salmon (Scarnecchia, 1984).

Available information on the oceanic distribution of Icelandic stocks of Atlantic salmon has come mainly from tagging of smolts, which began in the early 1960s at the Kollafjörður Experimental

Fish Farm near Reykjavik. From 1982 until 1995, ~1 million salmon were tagged with coded wire tags and released into Icelandic rivers (Ísaksson *et al.*, 2002). Analysis of tag recoveries of these releases from 1967 and 1995 identified 55 tags from two sea-winter (2SW) Icelandic salmon collected in the salmon fisheries in West Greenland and north of the Faroes. Most of the recoveries in West Greenland had been tagged in the southern and western Iceland, whereas most of the recoveries north of the Faroes had been tagged in northern and eastern Iceland (Ísaksson *et al.*, 2002). This pattern suggested that 2SW salmon from the south and west coast of Iceland tend to migrate west towards Greenland, whereas 2SW salmon from the north and east coasts migrated to a large extent into the Denmark Strait and the Norwegian Sea. The abundance of salmon returning to western and southern rivers is not closely correlated with abundance in northern and eastern rivers, which had previously suggested that salmon from these areas were using different feeding areas (Scarnecchia 1984; Gudjonsson *et al.*, 1995). Salmon populations in southern and western rivers in aggregate are twice as abundant as those in aggregate from the northern rivers, when measured as the 10-year average of the number of returning in-river salmon (1SW and MSW; ICES, 2013).

In 2005, Icelandic commercial fishers (i.e. targeting other species) were formally queried with a questionnaire in an effort to determine the number of salmon incidentally caught at sea around Iceland. Results of the questionnaire indicated that, on average, just over 5000 salmon (5110, 3165–7055 95% CL) were caught by Icelandic fishers annually (Guðbergsson, 2009). A 3-year effort begun in 2007 requesting fishers to return samples for genetic analysis from all salmon caught at sea. However, this programme yielded only 26 samples. More recently, the Directorate of Fisheries in Iceland started a salmon bycatch monitoring project in 2010 in the Icelandic pelagic mackerel (*Scomber scombrus*) fishery. The bycatch of the fleet was estimated as 5.5 salmon for every 1000 ton of mackerel caught in the years 2010 and 2011 (Ísaksson and Óskarsson, 2012). Some additional samples were also obtained during research fisheries by the Marine Research Institute.

In evaluating the stock or continent of origin of individual Atlantic salmon taken in mixed-stock fisheries at sea, genetic methods have proved especially useful (Manel *et al.*, 2005; Hauser *et al.*, 2006). Salmon stocks in Icelandic waters have been divided genetically by origin into three primary geographic groups: Iceland; Northern (Scandinavia and Northern Russia); and Southern (Mainland Europe, Britain, and Ireland). The accuracy of the assignment of individuals to stock or region depends crucially on the level of differentiation between baseline populations. Although low levels of genetic differentiations are observed in several migratory marine fish species (Hauser and Carvalho, 2008), the high level of genetic differentiation between salmon stocks makes the use of microsatellite for assignment an effective approach (Wennevik *et al.*, 2004; King *et al.*, 2005; Griffiths *et al.*, 2010; Olafsson *et al.*, 2014). Microsatellite loci have, for example, proved useful to trace recaptured farmed escaped salmon back to their farm of origin (Glover *et al.*, 2008) and have demonstrated their usefulness in managing populations of Pacific salmon (Beacham *et al.*, 2006).

The objective of this study was to sample salmon around Iceland, in areas that have not been studied before, but are likely as important feeding areas for salmon. For the salmon that were sampled, their age was determined from scales and otoliths and a newly developed genetic baseline (Gilbey *et al.*, 2015) was used to assign the fish to their population of origin.

Material and methods

Sampling of fish

A total of 186 samples of marine-caught salmon, including PS and adult fish, were collected for this study over the period 2007–2010 (Supplementary Table S1). One hundred and sixty (86%) of the 186 salmon originated from the pelagic fisheries in Icelandic waters in 2010, when the Directorate of Fisheries in Iceland monitored the occurrence of salmon in the bycatch of the Icelandic pelagic mackerel fleet (Ísaksson and Óskarsson, 2012). Most of those samples were caught from June until September (Figure 1) off the east coast. The other 26 salmon were acquired over the period 2007–2009 either as bycatch from several vessels in the Icelandic fishing fleet, or, for a few specimens and most of the PS, with a salmon trawl (Holst and McDonald, 2000) in research cruises by the Marine Research Institute, Reykjavik.

For each sample, data collected typically included catch date, geographical location, fishing gear, total length (T_L , cm), ungutted weight (g), sex, age structures (scales and otoliths), and maturation state. Information obtained for each fish also included tissue samples for genetic analysis (fin clips), estimates of stomach fullness, visual inspection for cataracts, presence or absence of external parasites and tags (Carlin tags, fin clips, and coded wire tags), and presence or absence of deteriorated fins (a sign of probable hatchery rearing).

Five individuals in our sample had been previously tagged with either a coded wire tag or a Carlin tag. Four individuals had been tagged in Norway (Imsa river, Drammen, Dale Elvatn, and Vosso River), and one had been tagged in the Delphi fisheries in Ireland. The fish from the Vosso River had been tagged, then released at sea.

Age and growth analyses

In all, 184 samples were aged using either or both scales and otoliths. Scales were, in nearly all cases, removed from the area above and close to the lateral line midway between the dorsal fin and the adipose fin (ICES, 1984) and stored dry. Scales were mounted on cellulose acetate slides and plastic impressions made of both PS and adult scales. Otoliths were extracted in the laboratory, cleaned, and stored dry in envelopes. After soaking in ethanol, the otoliths were viewed under direct light against a black background with a stereo/dissecting binocular microscope using reflective light. Both scale impressions and otoliths were then photographed with a JVC KY55 digital camera (Heidarsson *et al.*, 2006) mounted on a

dissecting microscope (Olympus Corp., Tokyo, Japan; Model SZX9). Each photograph of both scales and otoliths was analysed and annuli counted using the Fishalysis software (www.fishalysis.com).

Microsatellite analysis

Fish were genotyped with 15 microsatellite loci: SsaF43, Ssa14, Ssa289, Ssa171, Ssa197, Ssa202, SSsp1605, SSsp2201, SSsp2210, SSsp2216, SsspG7, SsaD144, SsaD157, SsaD486, and SSsp3016; and PCR condition as well as genotyping procedures followed Olafsson *et al.* (2010).

Assignment of individual fish to origin

The genetic baseline used, as well as the molecular methodologies used to generate it, is described in Gilbey *et al.* (2015). This database (SALSEA-Merge project) consists of 26 813 fish from 13 European countries, 284 rivers, and 466 sample sites genotyped at the 14 of 15 microsatellite loci used in this study, and represents ~85% of the non-Baltic European salmon production. The baseline has been divided using a hierarchical approach to identify useful assignment units and at level 1 the baseline is split into three primary units: Southern Group, i.e. from mainland Europe, the UK, and Ireland; Northern Group, i.e. Scandinavia and Northern Russia; and Iceland. The assignment strength of the baseline has previously been estimated using blind samples from rivers spanning the whole scope of the baseline. An assignment score cutoff of 70% using the level 1 baseline correctly assigns salmon to these top level regions 95% of the time (Gilbey *et al.*, 2015).

The assignment of individual fish to their most likely population of origin was performed using the Bayesian assignment method implemented in GENECLASS2 (Rannala and Mountain, 1997; Piry *et al.*, 2004) using an assignment threshold of 0.05 followed by the Monte-Carlo resampling algorithm (Paetkau *et al.*, 2004) for probability computation. Furthermore, the analysis of stock mixture proportions was performed using cBAYES (Neaves *et al.*, 2005) and ONCOR (Kalinowski *et al.*, 2008). To evaluate whether there was any seasonal variation in the distributions of stocks, the sample base for the mixture analysis was divided into four periods: January–May, June, July, and August–December.

Results

Most individuals (134 of 186 fish; 73%) were in their first year at sea (1SW); MSW salmon comprised 40 fish (23%) and PS 7 fish (4%; Table 1). T_L of PS ranged from 19.5 to 35 cm, of 1SW fish from 40 to 73 cm, and of MSW fish from 68 to 108 cm (Figure 2). Freshwater age ranged from 1 to 5 years (Table 1), with a mean of

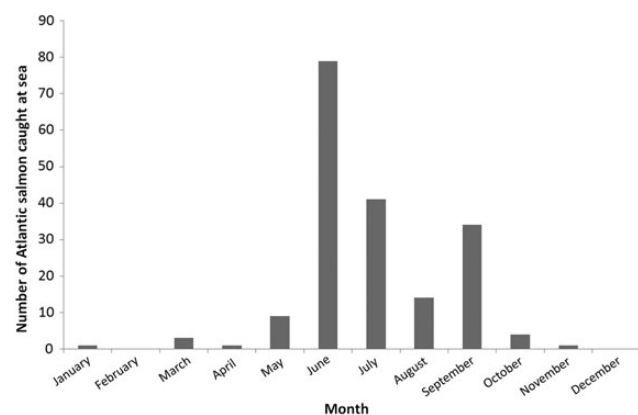


Figure 1. Number of Atlantic salmon caught at sea in Icelandic waters by months.

Table 1. Freshwater and sea age composition of salmon caught at sea in Icelandic waters 2007–2010.

Freshwater age	Sea age					Total	Percentage
	PS	1SW	2SW	3SW	4SW		
1	0	18	3	0	0	21	11.4
2	3	59	15	1	0	78	42.4
3	3	37	12	0	0	52	28.3
4	1	15	7	0	1	24	13.0
5	0	5	3	0	1	9	4.9
Total	7	134	40	1	2	184	
Sea age (%)	3.8	72.8	21.7	0.5	1.1		

PS, post-smolts; SW, number of winters spent at sea.

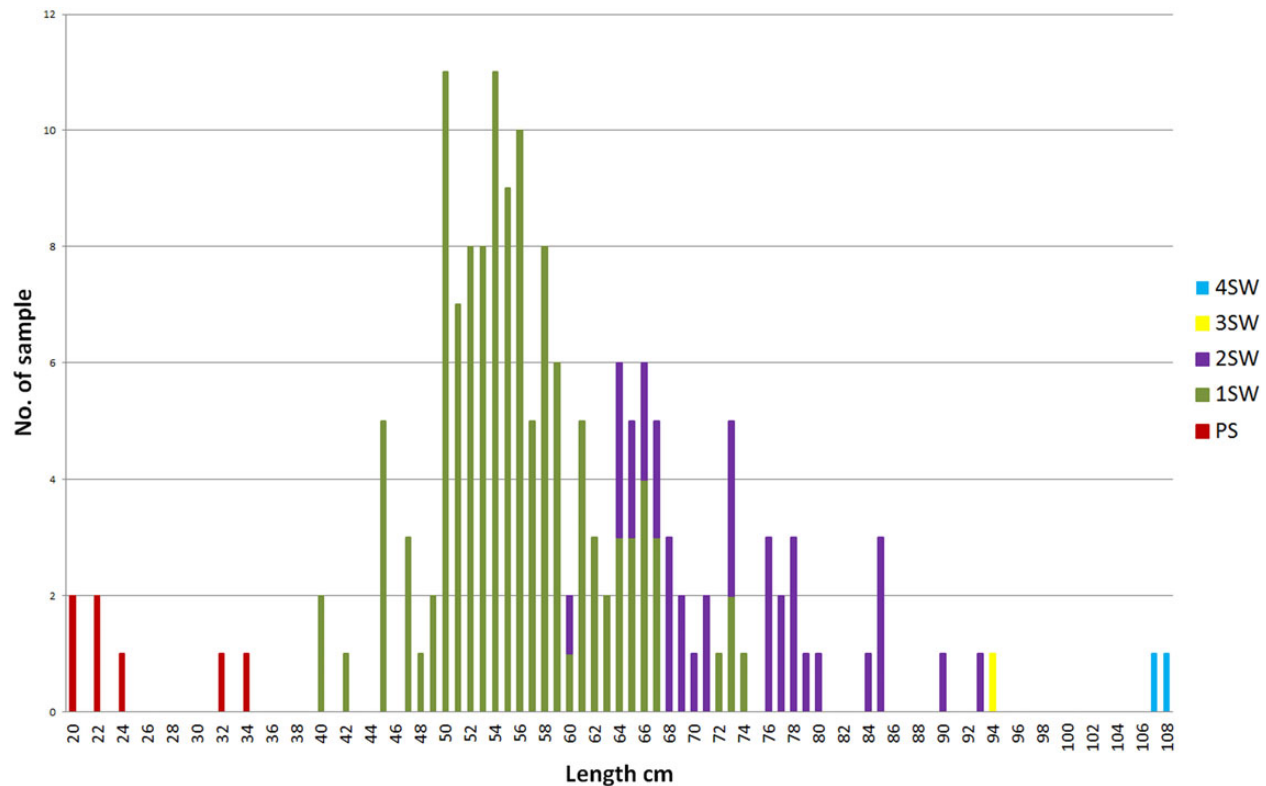


Figure 2. Distribution of T_L by sea age. PS, post-smolts; SW, number of winters spent at sea.

2.6 years. Salmon spending 2 years in freshwater were most common (42%), but those spending 3 years in freshwater were also well represented (28%). Salmon spending 4–5 years in freshwater constituted 18% of the total sample, whereas salmon staying only 1 year in freshwater constituted 11%.

Genotype success was 92% for the samples with an average of 16.8 alleles per locus ranging from 2 at locus SsaD486 to 31 at locus SsaD144. SsaD486 was nearly monomorphic showing only two alleles [178 and 182] with frequencies of 0.984 and 0.016, respectively. Of the 186 salmon assigned to the level 1 baseline, eight PS caught close to the Icelandic coast were assigned to Iceland. Of the remaining 178 samples, 121 were assigned to the Southern group (68%), 53 to the Northern group (30%), and only 4 to Iceland (2%; Figure 3). A total of 29 samples had an assignment score under 70% and are marked with a black fill in Figure 3. Estimated stock mixture proportions were similar to the individual assignments for all periods, except January–May (see Figure 4 and Supplementary Table S2 for full details). Only 13 samples were in the January–May group; therefore, the results for this period have a large standard deviation.

The average freshwater age for samples assigned to the northern area was 2.94 [± 0.16 standard error of mean (SEM)] and 2.33 (± 0.09 SEM) for samples assigned to the southern area.

The posterior probabilities of a specific origin using the level 1 baseline ranged from 37 to >99%, with an average probability of 87%. Posterior probabilities and assignment results for the baselines are detailed in Supplementary material. Four of the five tagged salmon were correctly assigned to their primary region. The incorrectly assigned individual, despite having a large assignment

score (98%), originated from the Vosso River, but was assigned to the Southern group.

Discussion

The Icelandic economic zone is vast, spanning over 758 000 km². It has many characteristics of idle feeding grounds for migrating salmon, but there has been little research on salmon migration in this region. This is mainly because landings of salmon caught at sea have been more or less banned since 1932, so information from domestic fisheries has not been available (Mathisen and Gudjonsson, 1978; Guðbergsson, 2013). Therefore, large knowledge gaps remain whether the salmon population use Iceland's Exclusive Economic Zone during their feeding migration, and, if so, what is their origin and age distribution.

In the surveys of Jensen and Lear (1980) in the Irminger Sea, tagged fish were recovered both from North America and Europe, which suggested the possibility of salmon originating in North America in Icelandic waters. The locus SsaD486 is not included in the genetic baseline as it is almost monomorphic in eastern populations of Atlantic salmon (King et al., 2005). However, this locus is polymorphic in North American populations and as such can indicate whether individuals are from North American populations of salmon. In our results, this locus was monomorphic, as is characteristic of the eastern stocks of salmon. It is therefore unlikely that salmon originating in North America were in our sample.

Four of the tagged fish caught in the study were assigned correctly. One salmon tagged in the Vosso River and released at sea was not correctly assigned. The Vosso River experienced an almost total collapse towards the end of the 1980s (Sægvog, 1997). The narrow fjords

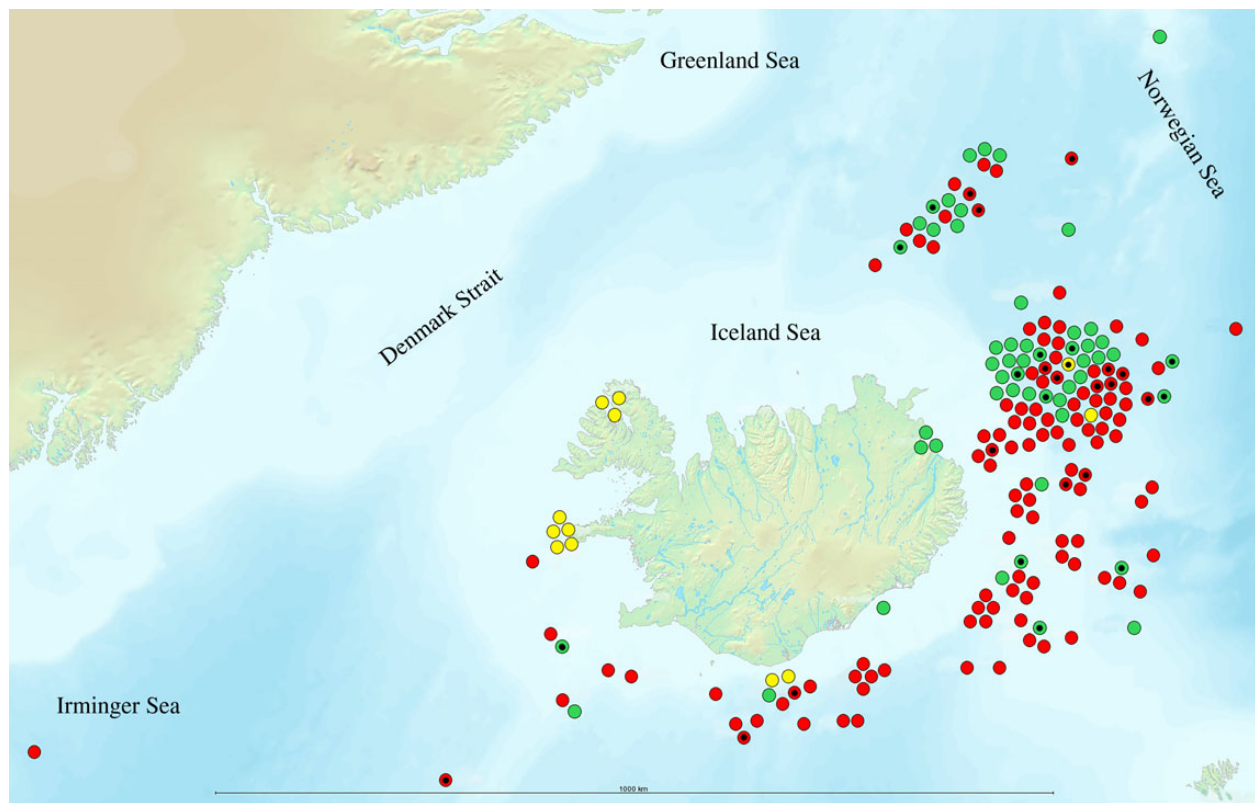


Figure 3. A schematic representation of the individual assignment to origin, where red indicates a Southern Group origin (mainland Europe, UK, and Ireland), green a Northern Group origin (Scandinavia and Northern Russia), and yellow an Icelandic origin. Samples with an assignment score lower than 70% have a black fill.

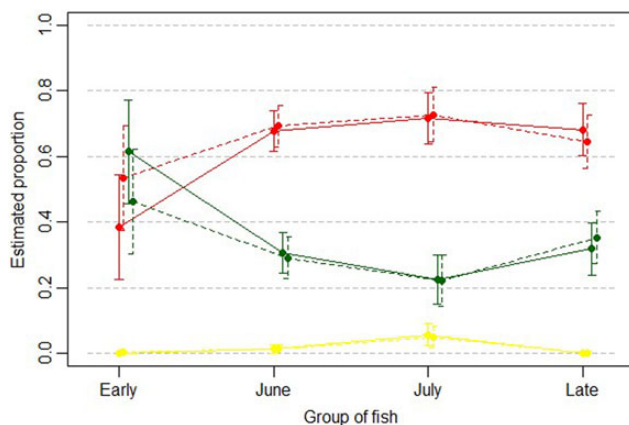


Figure 4. Estimated mixture proportions from ONCOR (solid line) and cBAYES (dotted line). Points represent the mean estimate with the standard error (SE) in bars. The same colour scheme is applied as in Figure 3, where red indicates a Southern Group, green a Northern Group, and yellow an Icelandic origin.

that separate the Vosso River and the outer coastline contain many fish farms and from 1993 to 1995 more than half of the spawning females in the river were of farmed origin (Sægrov, 1997). Furthermore, the river has been heavily restocked in recent years, so perhaps this “mis-assignment” is caused by a farmed salmon of southern origin inhabiting the river to some extent, rather than

an assignment or genotyping error. Genotyping error is, furthermore, an unlikely explanation, as this has been assessed for the Matis Ltd Laboratory (Reykjavík, Iceland) for these specific genetic markers, and is 0.004 ± 0.002 (mean across 14 loci; Ellis *et al.*, 2011).

The wide ranges of both freshwater and sea ages of the 186 salmon sampled at sea are consistent with what is known about Atlantic salmon life history. Atlantic salmon display considerable phenotypic plasticity and variability in life history characters, and smolt age can range between 1 and 8 years (Klemetsen *et al.*, 2003). A general trend of increasing smolt age has been identified with increasing latitude, but deviations from this trend can occur on a local scale for various reasons, including habitat productivity and density (Jensen and Johnsen, 1986). Smolt age in Icelandic rivers generally ranges between 2 and 5 years (Gudjónsson, 1978). The most common smolt age is 3 years in southern and western Iceland, but 4 years in the north and eastern part. The general trend of higher freshwater age with increasing latitude (Jensen and Johnsen, 1986) supports the genetic assignment results, as the most samples have a freshwater age of 1 and 2 years, indicating a southern origin rather than a northern one. Previous results for salmon caught in the Irminger Sea and East Greenland (Jensen and Lear, 1980) showed that the freshwater age of the salmon was low for most of the fish, indicating that these were salmon from the southern part of the distribution area. The mixture analysis does not suggest seasonal variation in the distributions of stocks. However, estimated proportions in the mixture analysis are similar to the individual assignments.

The higher frequency of Northern Group salmon in the north-east and north, along with the higher frequency of the Southern Group in the south and southwest, shows a pattern similar to the results of past tagging studies. It has been suggested earlier that European salmon from rivers north of 62°N migrate to feeding grounds off the Faroe Islands and in the Norwegian and Barents Seas, whereas fish originating in European rivers south of 62°N are thought to feed farther west with some MSW-returning fish feeding in the Labrador Sea west of Greenland (Went, 1973; Crozier *et al.*, 2004; Friedland *et al.*, 2009; MacKenzie *et al.*, 2011). In our study, we found that the freshwater age was considerably lower for samples assigned to the southern region than those assigned to the northern region. MacKenzie *et al.* (2011) suggested from studies of isotopes that one English salmon population used the area south of Iceland for feeding, while another were more likely used areas in the Norwegian Sea. Our results support the findings that the area south of Iceland is important for south European salmon.

When compared with other salmon populations in the other two main areas of the genetic baseline, salmon production in Iceland is small, contributing only 4.7% of salmon in the northeastern Atlantic Ocean. In contrast, populations in Scandinavia and Northern Russia contribute 40.7%, and those in Europe, Britain, and Ireland contribute 54.6% (ICES, 2013). This, of course, reflects the probability of catching a salmon from Iceland at sea. Although few Icelandic salmon were encountered in this study, available results from the few Icelandic fish captured largely, but not completely, corroborate previous tagging results. Recoveries from previous tagging programmes over the period 1967–1995 yielded a total of 55 marine-caught salmon tagged in Iceland (Ísaksson *et al.*, 2002). The locations of returns suggested that 2SW Icelandic salmon from the south and west coasts tend to migrate west towards Greenland, whereas the 2SW salmon from the north and east coasts of Iceland seem to migrate more into the Iceland Sea and were caught to some degree in the Faroese fishery. Some 2SW salmon from that area have, however, shown up in West Greenland, and some west coast salmon in the Faroese fishery suggest that the migration is by no means unidirectional (Ísaksson *et al.*, 2002). One can speculate that the southern and western Icelandic populations primarily migrate westward towards Greenland, whereas grilse migrate a shorter distance into the Irminger Sea. The Irminger Sea gyre is a productive area with abundant food for salmon (Greene *et al.*, 2003), and salmon have previously been caught there (Jensen, 1967; Jensen and Lear, 1980). It has also been suggested as the feeding area for Icelandic salmon from South and West Iceland (Ísaksson, 1980). With respect to the northern and eastern Icelandic salmon stocks, they may migrate into the Denmark Strait to a greater extent than previous results suggested, rather than into the Iceland and Greenland Sea. Grilse from these areas migrate less extensively into the same general area. The EU research project, SALSEA-Merge, sampled in areas ranging from the west coast of Ireland through the Norwegian Sea towards Svalbard. Although the sampling scheme is temporal and covers the areas where we would expect the 2SW Icelandic salmon to be according to Ísaksson *et al.* (2002), there is an almost total absence of Icelandic salmon. Our results revealed fewer Icelandic fish than expected (SALSEA-Merge, 2012), although regional productivity and the general assumption that fish are distributed spatially and temporally at random.

Sampling salmon at sea using dedicated cruises is expensive. The use of the fishing fleet through the surveillance agency was a novel

approach which yielded good sampling coverage regarding both the number of samples and area covered. The amount of salmon bycatch during pelagic fisheries appears small (Ísaksson and Óskarsson, 2012), but some precautions should be applied when interpreting these results. Identifying a small PS within a large pelagic catch is difficult to achieve. Furthermore, this method of estimating bycatch does not account for fishing gear-induced mortality, which is not seen in the catch.

Our results indicate that the seas south and east of Iceland are far more important for Atlantic salmon than previously thought, especially in summer for salmon originating in the UK and Ireland. In recent years, marked changes have been observed in the distribution of many fish species in Icelandic waters most likely due to 1–2°C warming of the waters south and west of Iceland (Valdimarsson *et al.*, 2012). Salmon in these areas may be more in recent years due to these changes. The southern origin of the most salmon populations is further supported with the information that the observed freshwater age is predominantly what is expected in the southern distribution range.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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