

Review Article

Coastal migration patterns of the four largest Barents Sea Atlantic salmon stocks inferred using genetic stock identification methods

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Combining detailed temporal and spatial catch data, including catch per unit effort, with a high-resolution microsatellite genetic baseline facilitated the development of stock-specific coastal migration models for the four largest Atlantic salmon (*Salmo salar*) populations, Målselv, Alta, Tana and Kola rivers, contributing to the Barents Sea mixed-stock fishery. Målselv salmon displayed a restricted coastal movement with 85% of the fish captured within 20 km of their natal river. Kola salmon also demonstrated limited coastal movements in Norwegian waters, with most (> 90%) caught in eastern Finnmark. Multi-sea-winter (MSW) Alta salmon were caught west of Alta fjord across a broader stretch of coast while one-sea-winter (1SW) fish migrated more extensively along the coast prior to river entry. Tana salmon, however, were detected over a broad expanse (600 km) of the North-Norwegian coast. For all populations MSW salmon dominating catches earlier in the season (May–June) while 1SW fish were more common from July to August. This study provides an example of how traditional catch and effort information may be combined with genetic methods to obtain insights into spatial and temporal changes in Atlantic salmon catch composition and their associated migration patterns in a mixed-stock coastal fishery.

Keywords: Atlantic salmon, Barents Sea, coastal fishery, genetics, migration models, salmon stock origin

Introduction

One of the greatest challenges for the management and conservation of fish species whose populations comingle during ocean migration and feeding (e.g. Atlantic and Pacific salmon) involves understanding the spatial and temporal use of marine coastal environments and the identification of stocks that contribute to

coastal mixed-stock fisheries (Hess *et al.*, 2014; Satterthwaite *et al.*, 2014; Gilbey *et al.*, 2017). This is particularly relevant for managing Atlantic salmon populations originating from the rivers along the Kola Peninsula, White Sea, and as far east as the Pechora River that may be heavily exploited and contributes to the fisheries in northern Norway (Svenning and Prusov, 2011).

Furthermore, the Atlantic salmon sea-fishery in northern Norway, and especially in Finnmark County, has a long cultural tradition, and any reduction in the fishery must be balanced against the need to preserve the rich tradition and local economic importance of the resource (Crozier *et al.*, 2004).

The feasibility of using genetic techniques to discriminate among different salmon stocks depends on the degree of isolation among the populations or regions (Griffiths *et al.*, 2010), the diversity and numbers of markers used (Jeffery *et al.*, 2018), and whether there is sufficient representation of the spatial genetic diversity in the genetic baseline (Bradbury *et al.*, 2015). Until recently it was only possible to identify the region of origin of wild Atlantic salmon contributing to mixed-stock coastal fisheries. Genetic stock identification (GSI) methods have been used to define the home region of Atlantic salmon contributing to past (e.g. Faroes—Gilbey *et al.*, 2017) or current ocean fisheries (Labrador—Bradbury *et al.*, 2015; West Greenland—Bradbury, Hamilton, Sheehan, *et al.*, 2016; Northwest Atlantic, St. Pierre and Miquelon—Bradbury, Hamilton, Chaput, *et al.*, 2016), as means of identifying incidental captures of salmon in coastal waters (Iceland—Olafsson *et al.*, 2016), on small geographic scales, as an evaluative technique to validate management decisions and more precisely exploit single stocks capable of maintaining a harvestable surplus (Ensing *et al.*, 2013). Elsewhere, GSI methods have been used to examine spatial and temporal distributions, stock composition, abundance, and migration pathways of various species of Pacific salmon species (*Oncorhynchus* spp.) (Beacham *et al.*, 2014; Clemento *et al.*, 2014; Satterthwaite *et al.*, 2014). Further refinements to GSI methods now allowed identification of the natal river with a high degree of certainty (Ozerov *et al.*, 2017; Vähä *et al.*, 2017; Bradbury *et al.*, 2018). For North Norway and Russia, a comprehensive genetic baseline for Atlantic salmon populations has been developed (Ozerov *et al.*, 2017), making it possible to identify the home region of salmon captured in the North-Norwegian coastal fisheries and in most cases to determine the natal river of origin (Ozerov *et al.*, 2017).

Atlantic salmon (*Salmo salar*) have a complex life cycle, spending their first years as juveniles in freshwater, and then migrating to the open sea to feed and grow for 1–5 years before returning to their natal river to spawn (Mills, 1989). Rivers in northernmost Norway, Finland, and Russia, i.e. in the Barents Sea basin, support some of the world's largest wild Atlantic salmon stocks, and salmon in these areas have high socio-economic value associated with commercial, subsistence, and recreational fisheries (Svenning and Prusov, 2011). The total catch from coastal and riverine fisheries in this area during the last 10–15 years (2005–2018) constitutes >50% of the total harvest of wild Atlantic salmon in the world (ICES, 2018). Although a few of these salmon stocks have suffered from reduced numbers of spawners in recent decades, most of them are unique insofar as the majority have not declined, and currently retain a high level of production, especially when compared to southern populations (Zubchenko *et al.*, 1994; Svenning and Prusov, 2011; Zubchenko and Prusov, 2011; Ozerov *et al.*, 2017; Anon., 2018; ICES, 2018). The conservation and sound management of these stocks is important given their size, contribution to fisheries, and diversity of life-history forms (Erkinaro *et al.*, 2019). For example, the average annual landings of the North-Norwegian multi-stock Atlantic salmon coastal fishery over the last 20 years (1998–2017) have varied between 110 and 345 tonnes and are on par with the total in-river

landings from the hundreds of North-Norwegian and Kola Peninsula salmon rivers in the Barents Sea (www.ssb.no; Table 08991).

A key element in the life history of Atlantic salmon is natal homing, which serves to maintain reproductively isolated stocks and local adaptation through natural selection (García de Leániz *et al.*, 2007; King *et al.*, 2007). Divergent selection on heritable traits enhancing the survival and reproductive success of individuals under differing physical and biotic determinants has led to significant variation in many morphological and life-history traits, as well as in behavioural characteristics within and among populations (reviewed in García de Leániz *et al.*, 2007). As a result, Atlantic salmon inhabiting different rivers have accumulated significant inter-population genetic variation with high levels of differentiation at sub-basin levels, for instance between tributary populations of Atlantic salmon in the River Tana (Vähä *et al.*, 2007, 2017). This genetic divergence provides the basis for the use of genetic techniques to identify the population origin of individuals.

The aim of this study was to develop a temporal and spatial stock-specific migration model for four of the largest Barents Sea Atlantic salmon populations, i.e. the Målselv, Alta, and Tana (Norway) and Kola (Russia) salmon based on a mass sampling of wild Atlantic salmon caught in the sea fisheries along the North-Norwegian coast in 2011 and 2012. The approach is analogous to those that have used GSI and relative abundance from catch-per-unit effort (CPUE) data to determine distributions and seasonal migrations of various Chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*Oncorhynchus nerka*) stocks along the west coast of North America (Beacham *et al.*, 2014; Satterthwaite *et al.*, 2014; Bellinger *et al.*, 2015). In addition to providing a more comprehensive understanding of the direction and timing of the coastal movements of returning Atlantic salmon, results from this study will also assist in providing a more precise, and informed regulatory regime for the management of Barents Sea Atlantic salmon stocks.

Material and methods

Sampling of adult Atlantic salmon

A total of 17 383 adult wild Atlantic salmon were sampled in 2011 and 2012 (Table 1) along ~950 km of the North-Norwegian coast from 12.5 to 30.5°E and 67.5 to 69.5°N (Figure 1). Samples were obtained from 58 Norwegian Environment Agency licenced professional fishers who employed commercial fishing gears (bend nets and/or bag nets) and were allowed to fish beyond the official fishing season, i.e. from early May until early September in these 2 years (Svenning *et al.*, 2014).

Numbers of Atlantic salmon caught, location, capture method, and date were recorded. Fork length (FL, cm) and body mass (g) were measured and a scale sample was taken for: (i) age and growth determination, (ii) genetic analysis, and (iii) establishing the frequency of escaped farmed fish in the catch. Based on scale pattern analysis fish were categorized as wild or escaped farmed fish, with only wild fish being subsequently used for genetic analysis.

Genetic analyses

Total genomic DNA was extracted from the scales of 16 096 (92.6%) wild fish (Table 1) using protocols described in Ozerov *et al.* (2017) and surveyed for genetic variation at 31

microsatellite DNA loci identified and applied in previous studies (Ellis *et al.*, 2011; Vähä *et al.*, 2017). Genotype data were generated at University of Turku, Finland, and the Institute of Marine Research, Norway, and cross-calibrated and compared (Ozerov *et al.*, 2017). The amplification procedure was only slightly modified from Vähä *et al.* (2008), where the genotyping error rate for the described procedure was estimated to be low (<0.4%). To minimize genotyping errors, electropherograms and allele scores were reviewed by two persons independently. Furthermore, all genotype calls were subjected to manual checking by two persons independently. The genotyping quality threshold was initially set to having 29 of 31 loci producing unambiguous data with failure resulting in re-analysis from either the DNA extraction or PCR

amplification step. Samples showing evidence of contamination were re-extracted using single scale and re-genotyped. If contamination persisted, the sample was discarded. Furthermore, samples were screened for cross-contamination using the percentage of alleles that matched between pairs of multilocus genotypes in the Microsatellite Toolkit for Excel (Park, 2001). If two individuals shared >95% of alleles in 27–31 loci, they were considered as cross-contaminated. If both samples of the pair were provided by the same fisher the sample with less complete information or later reported sampling time was discarded. In all other cases, both samples were discarded.

Genetic stock identification

River of origin for each successfully genotyped adult individual was estimated using the Bayesian GSI methodology described in Pella and Masuda (2001) and implemented in cBayes 5.0.1 (Neaves *et al.*, 2005). Genetic information on 185 Atlantic salmon populations spanning from the R. Pechora (Russia) in the East to the R. Beiarelv (Norway) in the West was used as baseline population data, described in Ozerov *et al.* (2017). The advantages of the Bayesian method when compared to the conditional maximum likelihood approach (e.g. in ONCOR, Kalinowski *et al.*, 2008) for GSI have been illustrated in earlier studies (Beacham *et al.*, 2005; Koljonen *et al.*, 2005; Ozerov *et al.*, 2017; Vähä *et al.*, 2017). Of particular note is the fact that the Bayesian approach provides more accurate estimates in the power analysis of the applied baseline genetic data (see Ozerov *et al.*, 2017).

Stock estimates were expected to be affected by the population composition of the mixture sample since GSI methods utilize

Table 1. Number and CPUE of wild Atlantic salmon captured monthly in the extended coastal fishery in Northern Norway in 2011 and 2012, and the numbers of Atlantic salmon genotyped.

Year	Wild adult salmon	May	June	July	Aug	Sep	Total
2011	# Salmon captured	783	2 539	3 435	511	9	7 277
	CPUE	1.55	4.68	7.88	2.22		3.91
	# Salmon genotyped	757	2 391	2 958	479	4	6 589
	CPUE	0.85	6.68	7.46	2.51		4.33
2012	# Salmon captured	381	3 989	4 335	1 353	48	10 106
	CPUE	0.85	6.68	7.46	2.51		4.33
	# Salmon genotyped	368	3 750	4 094	1 254	41	9 507
	CPUE	1.16	5.82	7.64	2.40		4.15
Total	# Salmon captured	1 164	6 528	7 770	1 864	57	17 383
	CPUE	1.16	5.82	7.64	2.40		4.15
	# Salmon genotyped	1 125	6 141	7 052	1 733	45	16 096

CPUE in September was not calculated, since only five localities were fished in this month, and only for a few days.

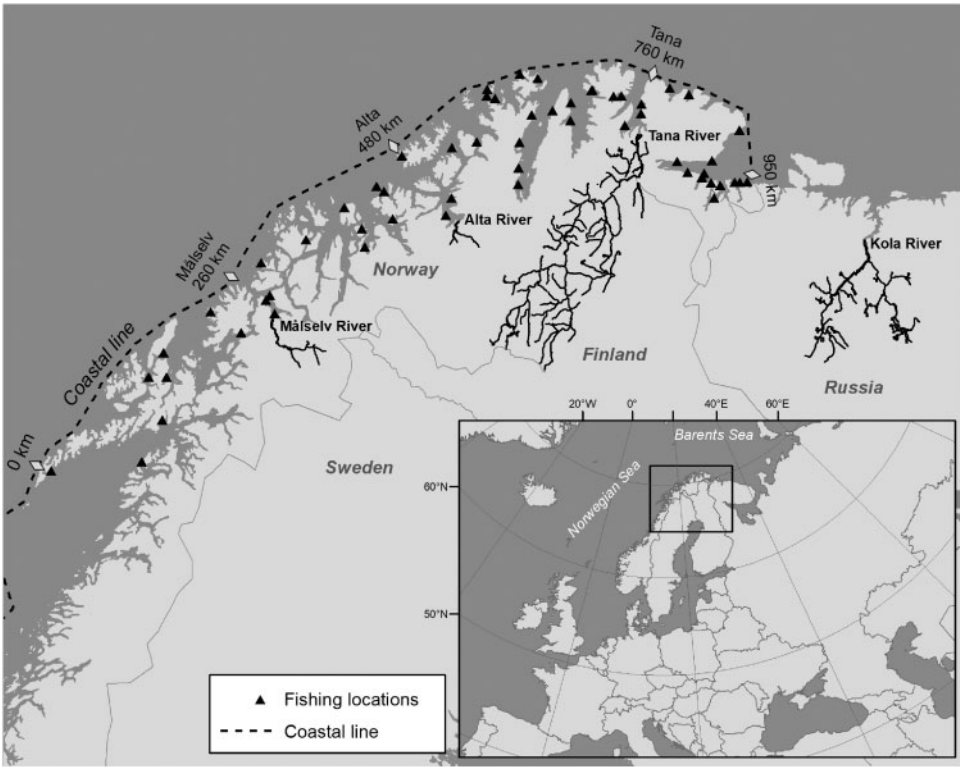


Figure 1. Map showing the outer Norwegian coast line (stippled line), the 58 fishing locations (triangle dots), and the four rivers (Målselv, Alta, Tana, and Kola) featured in this study.

Table 2. Coastal fishery samples arranged in 88 subsets for GSI analyses based on their spatial and temporal distribution (1: May–June; 2: July–August).

Region name	Year Period	2011		2012		Total
		1	2	1	2	
1—Sør-Varanger—East		295	96	407	117	915
2—Sør-Varanger—West		657	567	548	651	2 423
3—Nesseby—Fjord		151	146	159	234	690
4—Vadsø		130	247	180	274	831
5—Vardø		50	91	47	81	269
6—Båtsfjord—Berlevåg		90	51	105	86	332
7—Tana		80	6*	78	179	343
8—Gamvik		131	253	6*	12	402
9—Lebesby		168	229	129	539	1 065
10—Nordkapp—Outer		100	85	116	425	726
11—Nordkapp—Inner		15	8*	233	192	448
12—Porsanger				26	327	353
13—Måsøy		9*	46	147	122	324
14—Kvalsund—Hammerfest		81	73	38	59	251
15—Hasvik		108	45	123	30	306
16—Loppa		83	126	139	232	580
17—Alta		44	254	123	202	623
18—N.-Troms—Inner		187	287	236	420	1 130
19—N.-Troms—Outer				86	144	230
20—S.-Troms—North out		281	166	162	155	764
21—S.-Troms—Middle out		313	481	480	624	1 898
22—S.-Troms—Middle in		79	86	158	113	436
23—Nordland—North		59	63	108	44	274
24—Nordland—South		37	35	284	127	483
Total		3 148	3 441	4 118	5 389	16 096

Samples with low number of individuals (*) were combined within a year and region.

this information (Pella and Masuda, 2001). Thus, dividing large mixture samples into subsets based on location, time or life-history characteristics of individuals may be beneficial to improve the sensitivity of stock estimates (Vähä *et al.*, 2017). As the number of fishery catch samples of adult wild Atlantic salmon from each of the 58 localities per month of each year were small, they were grouped into 24 analysis regions and two time periods within each sampling year: period 1 (May–June) and period 2 (July–August). Collectively, the 16 096 samples were divided into 88 temporally and spatially distinct subsets for analysis, including four subsets, which were combined within each year (Table 2, Figure 1). GSI analyses were performed using five independent chains of 100 K iterations starting from three random stocks in cBayes 5.0.1 (Neaves *et al.*, 2005). These specifications appeared sufficient as sample-wise Raftery–Lewis diagnostics (Lewis and Raftery, 1997) of the preliminary test runs suggested that 40–80 K iterations were adequate to reach an Markov chain Monte Carlo (MCMC) convergence. The last 10 K iterations of each chain were combined and used to estimate individual assignment to the population (river) of origin to remove the influence of initial starting values, with data for $n = 5448$ individuals from the Målselv, Alta, Kola, and Tana rivers retained for further analysis (Table 2).

Following Vähä *et al.* (2011, 2014) and Bradbury *et al.* (2015) the probability (p) threshold for assignment of an individual to a population was ≥ 0.7 and was applied to all four stocks (Alta, Målselv, Kola, and Tana).

Catch data and statistical analyses

Along with the location of capture, fishers provided daily information on when the fishing gear was set and hauled. To calculate CPUE, we combined the catch data (data on individual fish) with the data on fishing effort (reported from individual fishers). Because effort was regulated by a maximum allowed number of fishing days per week, week was used as the basic unit in the calculations. Thus, weekly CPUE was calculated as the number of fish caught during a week divided by the number of fishing days in the same week. Weekly CPUE data were averaged over months to provide monthly maps of CPUE by region of origin.

Catch data for each of the four river systems were used to model the inshore migration pattern of wild Atlantic salmon. Initial analyses and visual inspection of the data suggested that the migration patterns in 2011 and 2012 were similar (Svenning *et al.*, 2014). Therefore, to investigate the general pattern of migration, irrespective of year, we combined data from both years in the analyses. Initial analyses also suggested differences in the timing of migration for different sea age classes. Consequently, we modelled one sea-winter (1SW) and multi-sea-winter (MSW) separately.

We used Generalized Additive Models (GAMs) from the “mgcv” library (Wood, 2006) in R v.2.13.0 (R Development Core Team, 2011) to model how the CPUE of Atlantic salmon from different rivers and age classes changed geographically over time. Weekly CPUE of 1SW and MSW (CpueS) originating from the four study rivers were modelled as dependent variables using a negative binomial distribution and a log-link function. Fishing location and time in the fishing season were used as independent variables. Fishing location was defined by a two-dimensional coordinate system where Axis 1 (CoastY) is the distance (in km) along the outer Norwegian coastline (Figure 1) from the southwestern limit of the study area to the fishing location, and Axis 2 (CoastX) is the inshore–offshore gradient defined by the perpendicular distance (in km) from the fishing location to the outer coastline. The time in the fishing season (Time) was defined by the week number beginning 1st May. The CpueS was modelled with a three-dimensional smoothing function dependent on CoastX, CoastY, and Time using thin plate regression splines (Wood, 2006). Based on the fitted models, we used the “predict” function in the “mgcv” library to predict the average spatial distribution for a given week on a 2×2 km² grid covering the area inshore of the outer coastline from Nordland county (ca. 12.5°E, 30.5°E, 67.5°N) in the southwest to the Norwegian border to Russia in the northeast (69.5°N). The area covered all fishing locations as shown in Figure 1.

Results

Genetic stock identification

In total, 11 320 of the 16 096 genotyped individuals could be assigned to specific rivers (cut-off $p \geq 0.7$). The cut-off at $p \geq 0.7$ was supported by analysing a limited set of 27 Carlin-tagged Alta salmon presented in Vähä *et al.* (2014) which allowed reaching the accuracy of >90% while keeping 88% of the samples (Table 3). Thus, of the 11 320 salmon that could be identified to river of origin, 4527 were assigned to the four large rivers included in this study (see Table 4), while the remaining 6793 fish were assigned to another 134 rivers spread from southern Nordland, Norway, to Pechora area, Russia (see Figure 1, Ozerov *et al.*, 2017).

Table 3. GSI of tagged adult salmon, originating from the River Alta and caught in North-Norwegian coastal fisheries in 2011.

ID	Assigned to	<i>p</i>	Catch region	Date of catch	Tag ID
Kola201104208	R. Alta	1.000	18—N.-Troms—Inner	6 July 2011	NL-051256
Kola201104803	R. Alta	0.593	18—N.-Troms—Inner	19 July 2011	NK-046305
Kola201105386	R. Alta	0.999	10—Nordkapp—Outer	19 July 2011	NL-021595
Kola201106148	R. Alta	0.999	22—S.-Troms—Middle in	4 July 2011	NL-032207
Kola201106286	R. Mandalselva	0.928	22—S.-Troms—Middle in	12 July 2011	NL-23355
Kola201106290	R. Alta	0.996	22—S.-Troms—Middle in	13 July 2011	NL-001633
Kola201106304	R. Alta	0.996	22—S.-Troms—Middle in	19 July 2011	NK-099517
Kola201106435	R. Alta	0.933	14—Kvalsund—Hammerfest	26 July 2011	NL-031834
Kola201106497	R. Klokkelv	0.371	15—Hasvik	27 July 2011	NK-053352
Kola201106790	R. Alta	1.000	22—S.-Troms—Middle in	26 July 2011	NL-022404
Kola201106833	R. Alta	0.998	22—S.-Troms—Middle in	27 July 2011	NK-099170
Kola201107005	R. Skøelv	0.422	21—S.-Troms—Middle out	28 July 2011	NL-24089
Kola201107075	R. Alta	1.000	18—N.-Troms—Inner	2 August 2011	NL-029309
Kola201107671	R. Alta	1.000	17—Alta	15 July 2011	NL-030938
Kola201107688	R. Alta	0.998	17—Alta	19 July 2011	NL-097074
Kola201107693	R. Alta	1.000	17—Alta	20 July 2011	NL-030889
Kola201107808	R. Alta	0.999	17—Alta	3 August 2011	NK-042475
Kola201107841	R. Alta	1.000	17—Alta	29 July 2011	NK-044284
Kola201108212	R. Alta	0.999	17—Alta	6 July 2011	NL-029568
Kola201108280	R. Alta	1.000	17—Alta	8 August 2011	NL-030511
Kola201108281	R. Alta	1.000	17—Alta	8 August 2011	NL-000872
Kola201108286	R. Alta	1.000	17—Alta	9 August 2011	NK-097353
Kola201105064	R. Alta	1.000	16—Loppa	6 July 2011	NL-027274
Kola201107788	R. Alta	0.996	17—Alta	26 July 2011	NL-028834
Kola201107061	R. Salangsvassdraget	0.954	18—N.-Troms—Inner	28 July 2011	NL-027515
Kola201107859	R. Alta	1.000	17—Alta	12 July 2011	NL-027909
Kola201106724	R. Alta	0.970	22—S.-Troms—Middle in	13 July 2011	NL-028865

Table 4. Number of wild Atlantic salmon captured in coastal areas of Northern Norway in 2011 and 2012 assigned to the Målselv, Alta, Tana, and Kola Rivers with an assignment probability threshold $p \geq 0.7$.

		Målselv			Alta			Tana			Kola			Total		
		1SW	MSW	Total	1SW	MSW	Total	1SW	MSW	Total	1SW	MSW	Total	1SW	MSW	Total
2 011	May–June	18	223	241	14	69	83	43	275	318	37	109	146	112	676	788
	July–September	176	82	258	337	212	549	147	52	199	144	15	159	804	361	1 165
	Total	194	305	499	351	281	632	190	327	517	181	124	305	916	1 037	1 953
2 012	May–June	54	264	318	6	188	194	136	313	449	35	84	119	231	849	1 080
	July–September	314	159	473	240	312	552	223	100	323	125	21	146	902	592	1 494
	Total	368	423	791	246	500	746	359	413	772	160	105	265	1 133	1 441	2 574
Total	May–June	72	487	559	20	257	277	179	588	767	72	193	265	343	1 525	1 868
	July–September	490	241	731	577	524	1 101	370	152	522	269	36	305	1 706	953	2 659
	Total	562	728	1 290	597	781	1 378	549	740	1 289	341	229	570	2 049	2 478	4 527

Total catches

The total catches of wild salmon ($n = 17\,383$, Table 1) were dominated by 1SW (41.6%) and 2SW (41.0%) fish, while 3–5 SW salmon constituted 17.4% of the catch. Catches in May and June were dominated by MSW (2–5 SW; 82%) salmon, while 1SW salmon were more commonly captured in July–September (61%). Catches of both 1SW and MSW salmon decreased during August.

The catch per unit of effort (weekly CPUE) varied from 0 to 23.5, while the average CPUE of wild salmon (May–August) in 2011 (3.91) and 2012 (4.33) was similar (t -test, $p = 0.43$; Table 1). Highest CPUE occurred in July and was lowest in May for both years. September was excluded from CPUE-analysis since very few fishers continued fishing in September, and thus

few Atlantic salmon were caught (Table 1). CPUE varied among localities, with the highest values in mid-Troms (vest of Malangen/Målselv fjord system) and in Finnmark (Figure 1).

GAMs (Målselv, Alta, Tana, and Kola salmon)

The GAMs of the weekly CPUE as a function of fishing location and the time in the fishing season for the four rivers Målselv, Alta, Tana, and Kola, explained 51 to 91% of the variation in the CPUE data. The three-dimensional smoothing term (CoastX, CoastY, Time) was highly significant in all of the river-specific age group models (Table 5). Predicted values showed strong patterns with a clear peak in catch close to the respective river mouths (Målselv, Alta, and Tana) and increased catches of salmon originating from Kola in the northeast (Figure 2). For all

Table 5. Summary of GAM results modelling the weekly CPUE of wild Atlantic salmon as a function of the fishing location (CoastX, CoastY) and the time in the fishing season (Time).

River origin	Age-group	Estimated degrees of freedom	Estimated residual degrees of freedom	Chi-square	<i>p</i>	Deviance explained (%)
Målselv	1SW	15.7	16.6	277.2	<0.0001	87.2
	MSW	28.7	33.4	348.6	<0.0001	91.6
Alta	1SW	28.0	33.7	336.3	<0.0001	75.6
	MSW	39.8	47.7	589.7	<0.0001	76.3
Tana	1SW	29.3	35.6	250.3	<0.0001	55.8
	MSW	38.9	47.1	368.9	<0.0001	51.7
Kola	1SW	9.0	9.0	150.1	<0.0001	82.5
	MSW	28.3	34.2	240.4	<0.0001	69.7

Separate models are shown for each river system and two sea-age-groups. Fishing location and time were modelled with a three-dimensional smooth function [s(CoastX, CoastY, Time)]. CPUE was modelled with a negative binomial distribution with a log-link function. Sample size was 1 176 observations (Atlantic salmon) for each model.

river systems, the GAMs indicated a slightly earlier arrival of MSW salmon compared to 1SW fish. In general, the models indicated that all salmon from the Målselv River arrived directly from the sea and relatively close to the Målselv River mouth, with little evidence of any extensive movement along the coast. This was also partly true for MSW Alta salmon, while 1SW Alta salmon were found to be more spatially spread-out with small local peaks west and east of the Alta River (Figure 2). In contrast, River Tana salmon migrate more extensively along the coast to both the east and west of the Tana Fjord, although the CUPE values were highest in areas closest to the Tana Fjord. Kola salmon showed limited coastal movements in North-Norwegian waters, with most salmon (>90%) caught proximate to the Varanger Fjord, eastern Finnmark, although some MSW fish were noted from Nordland and western Finnmark very early (mid- to late May) in the season.

Catches of Målselv salmon

MSW fish dominated Målselv salmon catches during May–June (523; 87.3%), while 1SW fish were more common from July to September ($n = 528$; 66.7%). Only MSW-salmon were captured in May, while CPUE increased during late May and remained high until the first week of August and then decreased strongly during mid- to late August (Figure 2). Most 1SW salmon were caught in a limited area located around outer coastal islands west of the Malangen Fjord and in coastal areas proximate to the Målselv River (Figures 1 and 2). Similar catch patterns were observed for MSW-salmon. In total, >85% of Målselv salmon were captured at sea <20 km from the river mouth, and >91% were caught along a rather restricted 60 km stretch of the nearly 950 km long coastal line extending from southwestern Nordland to northeastern Finnmark (see Figures 1 and 2).

Catches of Alta salmon

MSW Alta salmon dominated in catches during May–June (93.3%), while 1SW and MSW-salmon contributed equally to the catches from June to September (52.6 and 47.4%, respectively; Table 4). The CPUE of MSW Alta salmon increased in western Finnmark during the last week of May, increased towards southwest in mid-June (e.g. Senja and southwards to Lofoten; Figure 1), and overall remained high throughout July and most of August (Figure 2). CPUE of 1SW salmon was moderately high in both western Finnmark and Troms counties from July until

mid-August, with many 1SW Alta-salmon being captured in the southwestern, western, and north-western coastal areas adjacent to the Alta Fjord. The majority of Alta salmon were caught west of the Alta fjord and generally across a broader stretch of the coast by comparison to Målselva salmon. In total, 45% of Alta salmon were captured along a 60 km section of the coast proximate to the Alta River, while 15% were captured >200 km from the Alta fjord.

Catches of Tana salmon

MSW Tana-salmon were captured along the majority of coastal Troms and Finnmark counties in the beginning of May, with CPUE increasing throughout May and remaining high in the outer coastal areas of Troms and Finnmark throughout June until mid-July (Figure 2). CPUE decreased during the last half of July, and in August only a few MSW salmon were caught in the North-Norwegian coastal area. The CPUE of 1SW salmon increased from the second half of June across a broad region stretching from Lofoten, Nordland, in the southwest to Varanger in the east. The highest catches were recorded along the outer coast of Troms and Finnmark in mid-July, before tapering off in early August. Although many Tana salmon were caught close to the River Tana, with many captured in the Tana Fjord itself, a relatively high fraction were caught both east and west of the Tana Fjord, and even in the same weeks. In total 25% of Tana salmon were captured >250 km east of Tana Fjord, and 40% were captured >300 km west of Tana fjord.

Catches of Kola salmon

MSW fish dominated the Kola catches in the May–June period (71.3%) whereas 1SW fish dominated in July–September (88.9%). The relative abundance of Kola River salmon, as inferred from CPUE, was close to zero throughout May and early June (Figure 2). From mid-June onwards, CPUE increased in the Varangerfjord (Eastern Finnmark) in the first half of July, before decreasing in late July and August.

MSW salmon were present in the catches in the Varangerfjord from the beginning of May and increased in late May to a mid-July peak before tapering off to the point where they were absent from catches in August. The coastal exploitation of MSW salmon followed a similar geographical pattern as that of the 1SW salmon, with higher CPUE being observed mostly in the Varangerfjord. Some catches of Kola salmon, especially MSW

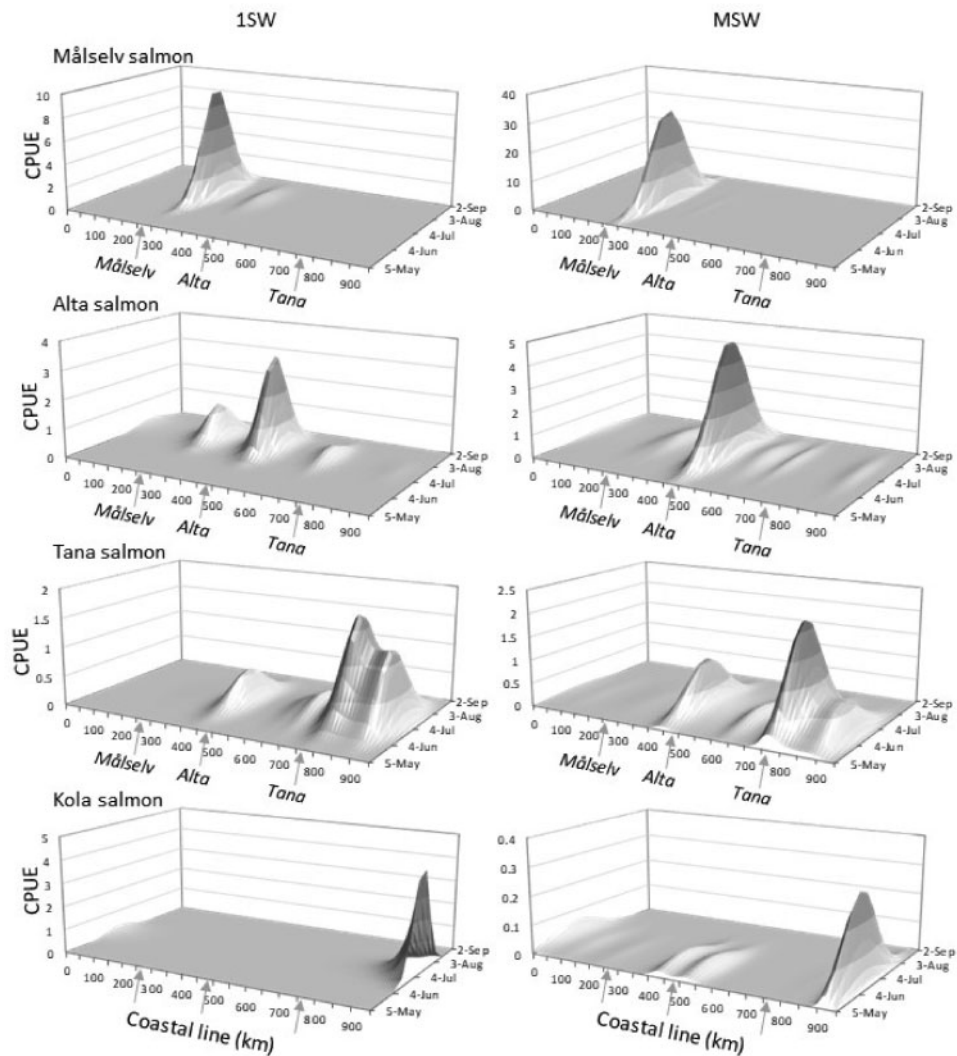


Figure 2. Predicted CPUE by week (z-axis) of 1SW and MSW wild Atlantic salmon from Målselv, Alta, Tana, and Kola Rivers along 950 km of the North-Norwegian coast (x-axis) from South-western Nordland to Eastern Finnmark (see Figure 1) from early May to late August (y-axis). The coastal study area corresponds to the dashed line shown on the map in Figure 1. The location of the river mouths along the coast (x-axis) is Målselv, 260 km; Alta, 480 km; Tana, 760 km. The Russian (Kola and White Sea) rivers are found outside the range of the x-axis (i.e. outside the range of the coastal fishing locations).

fish, were also recorded in the May–June period in Nordland and western Finnmark (Figure 2). In total, 92% of Kola salmon were captured within the Varangerfjord, i.e. within a radius of 20 km from the mid-Varangerfjord.

Discussion

Understanding ocean migrations of highly migratory species such as the Atlantic salmon is challenging as inferences are usually determined from the capture of fish in pelagic research surveys (Reddin and Shearer, 1987; Holm *et al.*, 2000), from the distribution of tag recoveries from surveys or capture fisheries (Jacobsen *et al.*, 2012; Reddin *et al.*, 2012; Downie *et al.*, 2018), or more recently, from biotelemetry methods (Crossin *et al.*, 2014). The latter methods, however, are usually dependent on the spatial and temporal distribution of fishing effort (Jacobsen *et al.*, 2012), with conclusions often based on a limited number of tag recaptures, frequently from only one or a few populations (Ulván

et al., 2018). In this study, stock identification and relative abundance from CPUE data were used to examine stock-specific coastal migration patterns of four of the largest Atlantic salmon populations contributing to the Barents Sea mixed-stock fishery, with coastal movements inferred from over 4500 individual assignments. Furthermore, sample fishing was designed to cover most of the areas along the North-Norwegian coast, and obtain detailed CPUE information from each fisher included in the study with a more prolonged fishing period as compared to the ordinary fishing season. Approaches used here parallel studies that have examined the ocean distribution and relative abundance of Chinook and sockeye salmon stocks along the west coast of North America (Beacham *et al.*, 2014; Bellinger *et al.*, 2015; Satterthwaite *et al.*, 2014), where in some situations the fishing season was also extended to cover a greater period of time stocks could potentially migrate through the region (Satterthwaite *et al.*, 2014).

Combining detailed temporal and spatial catch data, including detailed CPUE information, with a newly developed high-resolution microsatellite genetic baseline for North-Norwegian and Russian origin Atlantic salmon (Ozerov *et al.*, 2017) facilitated the development of stock-specific migration models for the Målselv, Alta, and Tana (Norway) and Kola River (Russia) Atlantic salmon populations. The use of GSI methods combined with stock-specific CPUE data have been shown to provide enhanced information over GSI alone in elucidating migratory patterns in situations where stock origin and relative abundance data are available (Bellinger *et al.*, 2015). Here, the combined use of techniques has provided more detailed understanding of both spatial and temporal migration patterns than either GIS or stock-specific CPUE data could alone. Results showed limited movement along the North-Norwegian coast by returning salmon for the Målselv population prior to river entry, with more extensive movement for fish originating from the River Alta and particularly from the River Tana. Most of Kola salmon (>90%) were captured within the Varangerfjord, ~250 km from the river mouth by coast, whereas some MSW fish were also recorded in Nordland and western Finnmark.

There were also distinct age-specific return peaks for each population with MSW salmon dominating catches earlier in the season (May–June) while 1SW fish were more common from July to September. This is in accordance with several previous studies from Scotland (Shearer, 1992), Norway (Svenning *et al.*, 2017), and the Baltic Sea (Siira *et al.*, 2009), showing a general tendency for earlier coastal return of MSW vs. 1SW salmon. While the recent study of Ulvan *et al.* (2018) found a temporal difference in returns to River Alta, with MSW fish returning earlier than 1SW fish, they found no significant differences in the spatial distribution of age-related recaptures. Ulvan *et al.* (2018) relied recaptures obtained during the regulated fishing season, i.e. lasting 2 weeks in Nordland, 4–6 weeks in Troms, and up to 8 weeks in Finnmark county (see Figure 1). As a result, the spatial fraction of MSW and 1SW salmon in coastal areas estimated by Ulvan *et al.* (2018) may be less representative by comparison to our study where all fishers were given a special licence to fish from the first week of May until early September, i.e. for >17 weeks along the entire North-Norwegian coast. Furthermore, Ulvan *et al.* (2018) had no information on how many days per week the different fishers actually fished, while each fisher had to report daily-CPUE in our study.

Atlantic salmon continue to be harvested at sea as a mixed-stock fishery along coastal regions of the Troms and Finnmark counties in north Norway. Mixed-stock migrations expose fish to common exploitation risks irrespective of existing population-specific viabilities or risks of population collapse such that the exploitation has the potential to differentially weaken populations (Griffiths *et al.*, 2010) because of among-stock differences in characteristics such as run timing (Hess *et al.*, 2014). Thus, it is important to understand the sequential movements of salmon as they migrate back to their natal rivers, especially in areas with well-developed interception fisheries. With improved information mixed-stock fisheries can avoid overharvesting smaller stocks, or those with existing conservation issues (Bradbury *et al.*, 2015; Bradbury, Hamilton, Chaput, *et al.*, 2016) and aid the development of essentially single-stock fisheries as has been documented for the River Foyle, Ireland (Ensing *et al.*, 2013).

The requirement to better understand and resolve stock-specific migration patterns, however, is not unique to ocean

fisheries for Atlantic salmon. GSI methods are becoming integrated into fisheries management for other species, particularly Pacific salmon, where GSI results have been shown to be consistent with those of conventional methods (e.g. coded-wire tags) for understanding run-timing and estimating abundance (Beacham *et al.*, 2014; Hess *et al.*, 2014; Bellinger *et al.*, 2015). Similarly, use of GSI to examine Baltic Sea brown trout (*Salmo trutta*) dispersal and migration routes and rates has been deemed essential for understanding of migration patterns and estimating exploitation rates for fisheries management purposes (Östergren *et al.*, 2016).

Temporal regulations aimed at reducing fishing pressure on wild salmon have utilized knowledge of differential return time in an attempt to optimize management (Siira *et al.*, 2009). Yet, relatively little effort has been directed towards understanding the ocean migrations of Atlantic salmon originating from north Norway and Russia, particularly with respect to the timing and nature of their coastal movements as they return from the broad areas of the north Atlantic known to be used by Norwegian origin Atlantic salmon, e.g. East and West Greenland (Reddin *et al.*, 2012), Icelandic waters (Olafsson *et al.*, 2016), the Norwegian Sea (Holm *et al.*, 2000; Jacobsen *et al.*, 2001, 2012), and high latitude areas in the Eastern Barents Sea and north to Svalbard (Svenning and Ozerov, 2018). An exception is the recent study of Strøm *et al.* (2018) that followed the entire ocean migration of six post-spawned adult Atlantic salmon from the River Alta based on high-resolution light-based geolocation archival tags.

Recaptures of adult salmon tagged as out-migrating hatchery-reared smolts from the several Norwegian rivers have indicated that Atlantic salmon approach the coast from both north and south of their natal rivers (Hansen *et al.*, 1993; Ulvan *et al.*, 2018). Despite the wide geographical dispersion of tag recaptures, the majority of fish in the Ulvan *et al.* (2018) study were caught in areas proximate to the Alta Fjord, particularly the larger MSW fish. Their findings parallel results from this study that noted the return migration of 1SW Alta Atlantic salmon extended over hundreds of kilometres of coastline while MSW Alta Atlantic salmon approached the coast over a more restricted area. Directed, non-random patterns of movement have been noted in other migratory species, including chum salmon, *Oncorhynchus keta*, (Friedland *et al.*, 2001) and striped bass, *Morone saxatilis* (Callihan *et al.*, 2015). Although older evidence for Atlantic salmon suggests fish may first encounter the coast as much as a 1000 km from their river of origin, location of their natal river by trial and error has been ruled out on the basis of migration speeds and abilities to keep an apparent constant compass course close to the surface (see Hansen *et al.*, 1993). The directed nature of returning migrations is similarly highlighted by our CPUE data, with the highest CPUE values of >1500 salmon genetically identified as originating from the Alta River also occurring in areas close to their natal river.

Salmon identified as originating from the River Tana returned over a broad expanse of the North-Norwegian coast although the CUPE values were highest in areas closest to the Tana Fjord. The greater dispersion of returning Tana salmon may, in part, be due to the large diversity inherent within the River Tana stock complex (Vähä *et al.*, 2017; Erkinaro *et al.*, 2019). Several studies have concluded that both genetics and environment influenced migration timing (see Jonsson *et al.*, 2007 and references therein), and in the Baltic, Siira *et al.* (2009) noted large variations in migration patterns and run timing between sea age groups, stock

components and among and within regions. Thus, distinct main stem and tributary populations within the Tana system may reflect variations in life-history attributes, including homeward migration patterns. This is consistent with other studies that have noted salmon of differing sea-ages can use variable oceanic areas that result in fish returning at different times and from different directions (Spares *et al.*, 2007; Dadswell *et al.*, 2010; Ulvan *et al.*, 2018). Variable stock-specific migrations may, therefore, contribute to differences in growth, survival and hence productivity among stocks as noted for populations of sockeye salmon (*O. nerka*) (Beacham *et al.*, 2014).

Understanding temporal patterns of return migrations of differing sea-age classes could assist in managing fisheries to protect the important MSW component. For those populations where MSW are caught earlier in the season, delaying the opening dates of coastal fisheries has the potential to reduce the interception of the larger fish, allowing greater opportunities for them to return to their natal streams. As studies have shown, large dominant MSW salmon have higher reproductive success than smaller conspecifics (Grant *et al.*, 2003) and are consequently more important for the determination of overall population abundance. The strategy was implemented in Newfoundland to reduce the interception of MSW salmon in commercial fisheries with desired effect (O'Connell *et al.*, 1992). Similarly, in the River Foyle, Ireland, understanding derived from GSI has been used to validate fisheries management action plans designed to transform mixed-stock to single-stock fisheries (Ensing *et al.*, 2013), suggesting accurate and precise management rules can be implemented at local scales provided the sort of stock-specific route and timing information derivable from GSI studies is available.

The ability to use GSI procedures to accurately identify river-specific contributions in mixed-stock fisheries is dependent on an adequate genetic baseline and sufficient divergence among populations of interest. In this study, the Kola, Tana, Alta, and Målselv populations could reliably be distinguished owing to their high GSI accuracy (Ozerov *et al.*, 2017). Because of the high GSI accuracy, unsampled (ghost) populations (Bradbury *et al.*, 2015) that were not included within the existing baseline are unlikely to have influenced our results. Therefore, based on the spatial distribution of CPUE of Alta and Målselv salmon, it is doubtful that these stocks are entering Russian waters east of the Varangerfjord, while it is more likely that salmon originating from the River Tana will be found in this area. Salmon fisheries in Russian waters of the Barents Sea are prohibited and the lack of corresponding coastal fishery samples from Russian waters precluded confirmation of Tana (or other) salmon in this area.

The understanding of the timing and movements of these four Barents Sea salmon stocks was derived from 2 years of data, but as noted by Satterthwaite *et al.* (2014) for Chinook salmon, more complex patterns may exist had studies continued over a longer period of years, particularly if oceanic climate conditions differed substantially among years. Nevertheless, this study provides an example of how traditional catch and effort information may be complemented by genetic methods to construct a detailed understanding of spatial and temporal changes in catch composition and hence migration patterns in a mixed-stock coastal Atlantic salmon fishery. Improved spatial and temporal resolution in understanding the pattern of arrival timing provides more precise information that could aid in the design of more informed regulatory regimes for the management and conservation of Atlantic salmon populations in the Barents Sea. Further refinement of

genetic approaches, such as use of single nucleotide polymorphisms (Bourret *et al.*, 2013; Ozerov *et al.*, 2013), or the application of large sequenced microsatellite panels (Bradbury *et al.*, 2018) and the inclusion of additional contributory populations in the genetic baseline would add to the usefulness of the approach applied here to the conservation and management of these important northern Atlantic salmon populations.

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