

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

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20 Abstract

21 Combining detailed temporal and spatial catch data, including catch per unit effort, with a high-
22 resolution microsatellite genetic baseline facilitated the development of stock-specific coastal
23 migration models for the four largest Atlantic salmon (*Salmo salar*) populations, Målselv, Alta, Tana
24 and Kola rivers, contributing to the Barents Sea mixed-stock fishery. Målselv salmon displayed a
25 restricted coastal movement with 85% of the fish captured within 20 km of their natal river. Kola
26 salmon also demonstrated limited coastal movements in Norwegian waters, with most salmon (>
27 90%) caught in proximity to the Varanger Fjord, eastern Finnmark. Compared with Målselv salmon,
28 the majority of MSW Alta salmon were caught west of Alta fjord across a broader stretch of coast
29 with 1SW fish showing some more extensive movement along the coast prior to river entry. Salmon
30 originating from the River Tana were detected over a broad expanse (600 km) of the North-
31 Norwegian coast, possibly because of the large diversity inherent within the River Tana stock
32 complex. For all populations there were distinct age-specific return peaks with multi-sea-winter
33 (MSW) salmon dominating catches earlier in the season (May – June) while one-sea-winter (1SW)
34 fish were more common from July to August. This study provides an example of how traditional catch
35 and effort information may be combined with genetic methods to obtain insights into spatial and
36 temporal changes in Atlantic salmon catch composition and their associated migration patterns in a
37 mixed-stock coastal fishery.

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

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43 **Introduction**

44 One of the greatest challenges for the management and conservation of fish species whose
45 populations coningle during ocean migration and feeding (e.g. Atlantic and Pacific salmon) involves
46 understanding the spatial and temporal use of marine coastal environments and the identification of
47 stocks that contribute to coastal mixed-stock fisheries (e.g. Hess et al., 2014; Satterthwaite et al.,
48 2015; Gilbey et al., 2017). This is particularly relevant for managing Atlantic salmon populations
49 originating from the rivers along the Kola Peninsula, White Sea and as far east as the Pechora River
50 that may be heavily exploited and contributes to the fisheries in northern Norway (Svenning and
51 Prusov, 2011). Furthermore, the Atlantic salmon sea-fishery in the northern Norway, and especially
52 in Finnmark County, has a long cultural tradition, and any reduction in the fishery must be balanced
53 against the need to preserve the rich tradition and local economic importance of the resource (e.g.
54 Crozier et al., 2004).

55

56 The feasibility of using genetic techniques to discriminate among different salmon stocks depends on
57 the degree of isolation among the populations or regions (Griffiths et al., 2010), the diversity and
58 numbers of markers used (Jeffery et al., 2018) and whether there is sufficient representation of the
59 spatial genetic diversity in the genetic baseline (Bradbury et al., 2015). Until recently it was only
60 possible to identify the region of origin of wild Atlantic salmon contributing to mixed-stock coastal
61 fisheries. Genetic stock identification methods have been used to define the home region of Atlantic
62 salmon contributing to past (e.g. Faroes - Gilbey et al., 2017) or current ocean fisheries (Labrador -
63 Bradbury et al., 2015; West Greenland - Bradbury et al., 2016a; Northwest Atlantic, St. Pierre and
64 Miquelon - Bradbury et al., 2016b), as means of identifying incidental captures of salmon in coastal
65 waters (Iceland - Olafsson et al., 2016), on small geographic scales, as an evaluative technique to
66 validate management decisions and more precisely exploit single stocks capable of maintaining a
67 harvestable surplus (Ensing et al. 2013). Elsewhere, GSI methods have been used to examine spatial
68 and temporal distributions, stock composition, abundance and migration pathways of various species

69 of Pacific salmon species (*Oncorhynchus* spp.) (e.g. Clemento et al., 2014; Beacham et al., 2014, 2016;
70 Satterthwaite et al., 2015; Urawa et al., 2016). Further refinements to genetic stock identification
71 methods now allowed identification of the natal river with a high degree of certainty (Ozerov et al.,
72 2017; Vähä et al., 2017; Bradbury et al., 2018). For North Norway and Russia, a comprehensive
73 genetic baseline for Atlantic salmon populations has been developed (Ozerov et al., 2017), making it
74 possible to identify the home region of salmon captured in the North-Norwegian coastal fisheries
75 and in most cases to determine the natal river of origin (Ozerov et al., 2017).

76

77 Atlantic salmon (*Salmo salar*) have a complex life cycle, spending their first years as juveniles in
78 freshwater, and then migrating to the open sea to feed and grow for one to five years before
79 returning to their natal river to spawn (Mills, 1989). Rivers in northernmost Norway, Finland and
80 Russia, i.e. in the Barents Sea basin, support some of the world's largest wild Atlantic salmon stocks,
81 and salmon in these areas have high socio-economic value associated with commercial, subsistence
82 and recreational fisheries (Svenning and Prusov, 2011). The total catch from coastal and riverine
83 fisheries in this area during the last 10-15 years (2005-2018) constitutes more than 50 % of the total
84 harvest of wild Atlantic salmon in the world (ICES, 2018). Although a few of these salmon stocks have
85 suffered from reduced numbers of spawners in recent decades, most of them are unique insofar as
86 the majority have not declined, and currently retain a high level of production, especially when
87 compared to southern populations (Zubcheno et al., 1994; Svenning and Prusov, 2011; Zubchenko
88 and Prusov, 2011; Ozerov et al., 2017; ICES, 2018; Anon, 2018). The conservation and sound
89 management of these stocks is important given their size, contribution to fisheries, and diversity of
90 life-history forms (Erkinaro et al., 2019). For example, the average annual landings of the north
91 Norwegian multi-stock Atlantic salmon coastal fishery over the last 20 years (1998-2017) have varied
92 between 110 and 345 tonnes and are on par with the total in-river landings from the hundreds of
93 North-Norwegian and Kola Peninsula salmon rivers in the Barents Sea (www.ssb.no; Table 08991).

94

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

106

107 The aim of this study was to develop a temporal and spatial stock-specific migration model for four of
108 the largest Barents Sea Atlantic salmon populations, i.e. the Målselv, Alta and Tana (Norway) and
109 Kola (Russia) salmon based on a mass sampling of wild Atlantic salmon caught in the sea fisheries
110 along the North Norwegian coast in 2011 and 2012. The approach is analogous to those that have
111 used genetic stock identification and relative abundance from catch-per-unit effort (CPUE) data to
112 determine distributions and seasonal migrations of various chinook (*Oncorhynchus tshawytscha*) and
113 sockeye salmon (*Oncorhynchus nerka*) stocks along the west coast of North America (Beacham et al.,
114 2014; Satterthwaite et al., 2014; Bellinger et al., 2015). In addition to providing a more
115 comprehensive understanding of the direction and timing of the coastal movements of returning
116 Atlantic salmon, results from this study will also assist in providing a more precise, and informed
117 regulatory regime for the management of Barents Sea Atlantic salmon stocks.

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121 **Materials and Methods**

122 **Sampling of adult Atlantic salmon**

123 A total of 17383 adult wild Atlantic salmon were sampled in 2011 and 2012 (Table 1) along
124 approximately 950 km of the North-Norwegian coast from 12.5 to 30.5 °E and 67.5 to 69.5 °N (Figure
125 1). Samples were obtained from 58 Norwegian Environment Agency licensed professional fishers
126 who employed commercial fishing gears (bend nets and/or bag nets) and were allowed to fish
127 beyond the official fishing season, i.e. from early May until early September in these two years
128 (Svenning et al., 2014).

129

130 Numbers of Atlantic salmon caught, location, capture method, and date were recorded. Fork length
131 (FL, cm) and body mass (g) were measured and a scale sample was taken for: 1) age and growth
132 determination, 2) genetic analysis, and 3) establishing the frequency of escaped farmed fish in the
133 catch. Based on scale pattern analysis fish were categorized as wild or escaped farmed fish, with only
134 wild fish being subsequently used for genetic analysis.

135

136 ***Genetic analyses***

137 Total genomic DNA was extracted from the scales of 16096 (92.6%) wild fish (Table 1) using protocols
138 described in Ozerov et al. (2017) and surveyed for genetic variation at 31 microsatellite DNA loci
139 identified and applied in previous studies (Ellis et al., 2011; Vähä et al., 2017). Genotype data were
140 generated at University of Turku, Finland, and the Institute of Marine Research, Norway, and cross-
141 calibrated and compared (Ozerov et al., 2017). The amplification procedure was only slightly
142 modified from Vähä et al. (2008), where the genotyping error rate for the described procedure was
143 estimated to be low (<0.4 %). To minimize genotyping errors, electropherograms and allele scores
144 were reviewed by two persons independently. Further, all genotype calls were subjected to manual
145 checking by two persons independently. The genotyping quality threshold was initially set to having
146 29 of 31 loci producing unambiguous data with failure resulting in re-analysis from either the DNA

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

155

156 **Genetic stock identification**

157 River of origin for each successfully genotyped adult individual was estimated using the Bayesian GSI
158 methodology described in Pella and Masuda (2001) and implemented in cBayes 5.0.1 (Neaves et al.,
159 2005). Genetic information on 185 Atlantic salmon populations spanning from the R. Pechora
160 (Russia) in the East to the R. Beiarelva (Norway) in the West was used as baseline population data,
161 described in detail in Ozerov et al. (2017). The advantages of the Bayesian method when compared
162 to the conditional maximum likelihood approach (e.g. in ONCOR, Kalinowski et al., 2008) for GSI have
163 been illustrated in earlier studies (e.g., Beacham et al., 2005; Koljonen et al., 2005; Vähä et al., 2017;
164 Ozerov et al., 2017). Of particular note is the fact that the Bayesian approach provides more accurate
165 estimates in the power analysis of the applied baseline genetic data (see Ozerov et al., 2017).

166

167 Stock estimates were expected to be affected by the population composition of the mixture sample
168 since GSI methods utilize this information (Pella and Masuda, 2001). Thus, dividing large mixture
169 samples into subsets based on location, time or life-history characteristics of individuals may be
170 beneficial to improve the sensitivity of stock estimates (Vähä et al., 2017). As the number of fishery
171 catch samples of adult wild Atlantic salmon from each of the 58 localities per month of each year
172 were small, they were grouped into 24 analysis regions and two time periods within each sampling

173 year: period 1 (May-June) and period 2 (July-August). Collectively, the 16 096 samples were divided
174 into 88 temporally and spatially distinct subsets for analysis, including four subsets, which were
175 combined within each year (Table 2, Fig. 1). Genetic stock identification analyses were performed
176 using five independent chains of 100K iterations starting from three random stocks in cBAYES. These
177 specifications appeared sufficient as sample-wise Raftery-Lewis diagnostics (Lewis and Raftery, 1997)
178 of the preliminary test runs suggested that 40K-80K iterations were adequate to reach a MCMC
179 convergence. The last 10K iterations of each chain were combined and used to estimate individual
180 assignment to the population (river) of origin to remove the influence of initial starting values, with
181 data for n = 5448 individuals from the Målselv, Alta, Kola and Tana rivers retained for further analysis
182 (Table 2).

183

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

187

188 **Catch Data and Statistical Analyses**

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

196

197 Catch data for each of the four river systems were used to model the inshore migration pattern of
198 wild Atlantic salmon. Initial analyses and visual inspection of the data suggested that the migration

199 patterns in 2011 and 2012 were similar (Svenning et al., 2014). Therefore, to investigate the general
200 pattern of migration, irrespective of year, we combined data from both years in the analyses. Initial
201 analyses also suggested differences in the timing of migration for different sea age classes.
202 Consequently, we modeled one sea-winter (1SW) and multi-sea winter (MSW) separately.
203 We used Generalized Additive Models (GAM) from the “mgcv” library (Wood 2006) in R v.2.13.0
204 (R_Development_Core_Team 2011) to model how the CPUE of Atlantic salmon from different rivers
205 and age classes changed geographically over time. Weekly CPUE of 1SW and MSW (CpueS)
206 originating from the four study rivers were modeled as dependent variables using a negative
207 binomial distribution and a log-link function. Fishing location and time in the fishing season were
208 used as independent variables. Fishing location was defined by a two-dimensional coordinate system
209 where Axis 1 (CoastY) is the distance (in km) along the outer Norwegian coastline (Figure 1) from the
210 southwestern limit of the study area to the fishing location, and Axis 2 (CoastX) is the inshore-
211 offshore gradient defined by the perpendicular distance (in km) from the fishing location to the outer
212 coastline. The time in the fishing season (Time) was defined by the week number since May 1st. The
213 CpueS was modeled with a three-dimensional smoothing function dependent on CoastX, CoastY and
214 Time using thin plate regression splines (Wood 2006). Based on the fitted models, we used the
215 “predict” function in the “mgcv” library to predict the average spatial distribution for a given week on
216 a 2x2 km² grid covering the area inshore of the outer coastline from Nordland county (ca 12.5 °E,
217 30.5 °E, 67.5 °N) in the southwest to the Norwegian border to Russia in the northeast (69.5 °N). The
218 area covered all fishing locations as shown in Figure 1.

219

220 **Results**

221 Genetic stock identification

222 In total, 11 320 of the 16 096 genotyped individuals could be assigned to specific rivers (cut-off $p \geq$
223 0.7). The cut-off at $p \geq 0.7$ was supported by analyzing a limited set of 27 Carlin-tagged Alta salmon

224 presented in Vähä et al. (2014) which allowed reaching the accuracy of > 90% while keeping 88% of
225 the samples (Table 3). Thus, of the 11 320 salmon that could be identified to river of origin, 4 527
226 were assigned to the four large rivers included in this study (see Table 4), while the remaining 6 793
227 fish were assigned to another 134 rivers spread from southern Nordland, Norway, to Pechora area,
228 Russia (see Figure 1 in Ozerov et al. 2017).

229

230 Total catches

231 The total catches of wild salmon (n=17 383, Table 1) were dominated by 1SW (41.6 %) and 2SW (41.0
232 %) fish, while 3-5SW salmon constituted 17.4 % of the catch. Catches in May and June were dominated
233 by MSW (2-5 SW; 82 %) salmon, while 1SW salmon were more commonly captured in July-September
234 (61 %). Catches of both 1SW and MSW salmon decreased during August.

235 The catch per unit of effort (weekly CPUE) varied from 0 to 23.5, while the average CPUE of wild salmon
236 (May-August) in 2011 (3.91) and 2012 (4.33) was similar (t-test, p=0.43; Table 1). Highest CPUE
237 occurred in July and was lowest in May for both years. September was excluded from CPUE-analysis
238 since very few fishers continued fishing in September, and thus few Atlantic salmon were caught (Table
239 1). CPUE varied among localities, with the highest values in mid-Troms (vest of Malangen/Målselv fjord
240 system) and in Finnmark (Figure 1).

241

242 GAM-models (Målselv, Alta, Tana and Kola salmon)

243 The GAM-models of the weekly CPUE as a function of fishing location and the time in the fishing season
244 for the four rivers Målselv, Alta, Tana and Kola, explained from 51 to 91 % of the variation in the CPUE
245 data. The three-dimensional smoothing term (CoastX, CoastY, Time) was highly significant in all of the
246 river-specific age group models (Table 5). Predicted values showed strong patterns with a clear peak

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

259

260 Catches of Målselv salmon

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

270

271 Catches of Alta salmon

272 MSW Alta salmon dominated in catches during May-June (93.3 %), while 1SW and MSW-salmon
273 contributed equally to the catches from June to September (52.6 and 47.4 %, respectively; Table 4).
274 The CPUE of MSW Alta salmon increased in western Finnmark during the last week of May, increased
275 towards southwest in mid-June (e.g. Senja and southwards to Lofoten; Figure 1), and overall remained
276 high throughout July and most of August (Figure 2). CPUE of 1SW salmon was moderately high both in
277 western Finnmark and Troms counties from July until mid-August, with many 1SW Alta-salmon being
278 captured in the southwestern, western, and north-western coastal areas adjacent to the Alta Fjord.
279 The majority of Alta salmon were caught west of the Alta fjord and generally across a broader stretch
280 of the coast by comparison with Målselva salmon. In total, 45 % of Alta salmon were captured along a
281 60 km section of the coast proximate to the Alta River, while 15 % were captured more than 200 km
282 from the Alta fjord.

283

284 Catches of Tana salmon

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

296

297 Catches of Kola salmon

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

302 MSW salmon were present in the catches in the Varangerfjord from the beginning of May and
303 increased in late May to a mid-July peak before tapering off to the point where they were absent from
304 catches in August. The coastal exploitation pattern of MSW salmon followed a similar geographical
305 pattern as that of the 1SW salmon, with higher CPUE being observed mostly in the Varangerfjord. Some
306 catches of Kola salmon, especially MSW fish, were also recorded in the May-June period in Nordland
307 and western Finnmark (Figure 2). In total, 92 % of Kola salmon were captured within the Varangerfjord,
308 i.e. within a radius of 20 km from the mid-Varangerfjord.

309

310

311 **Discussion**

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

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

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

344 There were also distinct age-specific return peaks for each population with MSW salmon dominating
345 catches earlier in the season (May – June) while 1SW fish were more common from July to
346 September. This is in accordance with several previous studies from Scotland (Shearer, 1992),
347 Norway (Svenning et al., 2017), and the Baltic Sea (Siira et al., 2009), showing a general tendency for
348 earlier coastal return of MSW versus 1SW salmon. While the recent study of Ulvan et al. (2018) found
349 a temporal difference in returns to River Alta, with MSW fish returning earlier than 1SW fish, they
350 found no significant differences in the spatial distribution of age-related recaptures. Ulvan et al.
351 (2018) relied recaptures obtained during the regulated fishing season, i.e. lasting two weeks in
352 Nordland, four to six weeks in Troms and up to eight weeks in Finnmark county (see Figure 1). As a
353 result, the spatial fraction of MSW and 1SW salmon in coastal areas estimated by Ulvan et al. (2018)
354 may be less representative by comparison with our study where all fishers were given a special
355 licence to fishing from the first week of May until early September, i.e. for more than 17 weeks along
356 the whole North-Norwegian coast. Further, Ulvan et al. (2018) had no information on how many days
357 per week the different fishers actually fished, while each fisherman had to report daily-CPUE in our
358 study.

359

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

370

371 The requirement to better understand and resolve stock-specific migration patterns, however, is not
372 unique to ocean fisheries for Atlantic salmon. GSI methods are becoming integrated into fisheries
373 management for other species, particularly Pacific salmon, where GSI results have been shown to be
374 consistent with those of conventional methods (e.g. coded-wire tags) for understanding run-timing
375 and estimating abundance (Hess et al., 2014; Beacham et al., 2014; Bellinger et al., 2015). Similarly,
376 use of GSI to examine Baltic Sea brown trout (*Salmo trutta*) dispersal and migration routes and rates
377 has been deemed essential for understanding of migration patterns and estimating exploitation rates
378 for fisheries management purposes (Östergren et al., 2016).

379

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

391

392 Recaptures of adult salmon tagged as out-migrating hatchery-reared smolts from the several
393 Norwegian rivers have indicated that Atlantic salmon approach the coast from both north and south
394 of their natal rivers (Hansen et al., 1993; Ulvan et al., 2018). Despite the wide geographical dispersion
395 of tag recaptures, the majority of fish in the Ulvan et al. (2018) study were caught in areas proximate

396 to the Alta Fjord, particularly the larger MSW fish. Their findings parallel results from the current
397 study that noted the return migration of 1SW Alta Atlantic salmon extended over hundreds of
398 kilometres of coastline while MSW Alta Atlantic salmon approached the coast over a more restricted
399 area. Directed, non-random patterns of movement have been noted in other migratory species,
400 including chum salmon, *Onchorhynchus keta*, (Friedland et al., 2001) and striped bass, *Morone*
401 *saxatilis* (Callihan et al., 2015). Although older evidence for Atlantic salmon suggests fish may first
402 encounter the coast as much as a 1000 km from their river of origin, location of their natal river by
403 trial and error has been ruled out on the basis of migration speeds and abilities to keep an apparent
404 constant compass course close to the surface (see Hansen et al., 1993). The directed nature of
405 returning migrations is similarly highlighted by our CPUE data, with the highest CPUE values of more
406 than 1500 salmon genetically identified as originating from the Alta River also occurring in areas
407 close to their natal river.

408

409 Salmon identified as originating from the River Tana returned over a broad expanse of the North-
410 Norwegian coast although the CUPE values were highest in areas closest to the Tana Fjord. The
411 greater dispersion of returning Tana salmon may, in part, be due to the large diversity inherent
412 within the River Tana stock complex (Vähä et al., 2017; Erkinaro et al., 2019). Several studies have
413 concluded that both genetics and environment influenced migration timing (see Jonsson et al., 2007
414 and references therein), and in the Baltic, Siira et al. (2009) noted large variations in migration
415 patterns and run timing between sea age groups, stock components and among and within regions.
416 Thus, distinct main stem and tributary populations within the Tana system may reflect variations in
417 life-history attributes, including homeward migration patterns. This would be consistent with other
418 studies that have noted salmon of differing sea-ages can use variable oceanic areas that result in fish
419 returning at different times and from different directions (Spares et al., 2007; Dadswell et al., 2010;
420 Ulvan et al., 2018). Variable stock-specific migrations may, therefore, contribute to differences in

421 growth, survival and hence productivity among stocks as noted for populations of sockeye salmon
422 (*Oncorhynchus nerka*) (Beacham et al., 2014).
423
424 Understanding temporal patterns of return migrations of differing sea-age classes could assist in
425 managing fisheries to protect the important MSW component. For those populations where MSW
426 are caught earlier in the season, delaying the opening dates of coastal fisheries has the potential to
427 reduce the interception of the larger fish, allowing greater opportunities for them to return to their
428 natal streams. As studies have shown, large dominant MSW salmon have higher reproductive success
429 than smaller conspecifics (Grant et al., 2003) and are consequently more important for the
430 determination of overall population abundance. The strategy was implemented in Newfoundland to
431 reduce the interception of MSW salmon in commercial fisheries with desired effect (O'Connell et al.,
432 1992). Similarly, in the River Foyle, Ireland, understanding derived from GSI has been used to validate
433 fisheries management action plans designed to transform mixed-stock to single-stock fisheries
434 (Ensing et al., 2013), suggesting accurate and precise management rules can be implemented at local
435 scales provided the sort of stock-specific route and timing information derivable from GSI studies is
436 available.
437
438 The ability to use genetic stock identification (GSI) procedures to accurately identify river-specific
439 contributions in mixed-stock fisheries is dependent upon an adequate genetic baseline and sufficient
440 divergence among populations of interest. In this study, the Kola, Tana, Alta and Målselv populations
441 could reliably be distinguished owing to their high GSI accuracy (Ozerov et al., 2017). Because of the
442 high GSI accuracy, unsampled (ghost) populations (Bradbury et al., 2015) that were not included
443 within the existing baseline are unlikely to have influenced our results. Therefore, based on the
444 spatial distribution of CPUE of Alta and Målselv salmon, it is doubtful that these stocks are entering
445 Russian waters east of the Varangerfjord, while it is more likely that salmon originating from the
446 River Tana will be found in this area. Salmon fisheries in Russian waters of the Barents Sea are

447 prohibited and the lack of corresponding coastal fishery samples from Russian waters precluded
448 confirmation of Tana (or other) salmon in this area.
449
450 The understanding of the timing and movements of these four Barents Sea salmon stocks was
451 derived from two years of data, but as noted by Satterthwaite et al. (2014) for Chinook salmon, more
452 complex patterns may exist had studies continued over a longer period of years, particularly if
453 oceanic climate conditions differed substantially among years. Nevertheless, this study provides an
454 example of how traditional catch and effort information may be complemented by genetic methods
455 to construct a detailed understanding of spatial and temporal changes in catch composition and
456 hence migration patterns in a mixed-stock coastal Atlantic salmon fishery. Improved spatial and
457 temporal resolution in understanding the pattern of arrival timing provides more precise information
458 that could aid in the design of more informed regulatory regimes for the management and
459 conservation of Atlantic salmon populations in the Barents Sea. Further refinement of genetic
460 approaches, such as use of single nucleotide polymorphisms (SNPs; Bourett et al., 2013; Ozerov et
461 al., 2013), or the application of large sequenced microsatellite panels (Bradbury et al., 2018) and the
462 inclusion of additional contributory populations in the genetic baseline would add to the usefulness
463 of the approach applied here to the conservation and management of these important northern
464 Atlantic salmon populations.

465

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472

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- 669

670 **Table 1** Number and catch per unit effort (CPUE) of wild Atlantic salmon captured monthly in the
 671 extended coastal fishery in Northern Norway in 2011 and 2012, and the numbers of Atlantic salmon
 672 genotyped. CPUE in September was not calculated, since only five localities were fished in this
 673 month, and only for a few days.

674

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
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
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

675

676

677

678 **Table 2** Coastal fishery samples arranged in 88 subsets for GSI analyses based on their spatial and
 679 temporal distribution (1: May-June; 2: July-August). Samples with low number of individuals (*) were
 680 combined within a year and region.

681

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	2423
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	1065
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	1130
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	1898
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		3148	3441	4118	5389	16096

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

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ID	Assigned to	p	Catch region	Date of catch	Tag ID
Kola201104208	R. Alta	1.000	18 - N.-Troms – Inner	6.7.2011	NL-051256
Kola201104803	R. Alta	0.593	18 - N.-Troms – Inner	19.7.2011	NK-046305
Kola201105386	R. Alta	0.999	10 - Nordkapp – Outer	19.7.2011	NL-021595
Kola201106148	R. Alta	0.999	22 - S.-Troms – Middle in	4.7.2011	NL-032207
Kola201106286	R. Manndalselva	0.928	22 - S.-Troms – Middle in	12.7.2011	NL-23355
Kola201106290	R. Alta	0.996	22 - S.-Troms – Middle in	13.7.2011	NL-001633
Kola201106304	R. Alta	0.996	22 - S.-Troms – Middle in	19.7.2011	NK-099517
Kola201106435	R. Alta	0.933	14 - Kvalsund-Hammerfest	26.7.2011	NL-031834
Kola201106497	R. Klokkarelv	0.371	15 - Hasvik	27.7.2011	NK-053352
Kola201106790	R. Alta	1.000	22 - S.-Troms – Middle in	26.7.2011	NL-022404
Kola201106833	R. Alta	0.998	22 - S.-Troms – Middle in	27.7.2011	NK-099170
Kola201107005	R. Skøelva	0.422	21 - S.-Troms – Middle out	28.7.2011	NL-24089
Kola201107075	R. Alta	1.000	18 - N.-Troms – Inner	2.8.2011	NL-029309
Kola201107671	R. Alta	1.000	17 - Alta	15.7.2011	NL-030938
Kola201107688	R. Alta	0.998	17 - Alta	19.7.2011	NL-097074
Kola201107693	R. Alta	1.000	17 - Alta	20.7.2011	NL-030889
Kola201107808	R. Alta	0.999	17 - Alta	3.8.2011	NK-042475
Kola201107841	R. Alta	1.000	17 - Alta	29.7.2011	NK-044284
Kola201108212	R. Alta	0.999	17 - Alta	6.7.2011	NL-029568
Kola201108280	R. Alta	1.000	17 - Alta	8.8.2011	NL-030511
Kola201108281	R. Alta	1.000	17 - Alta	8.8.2011	NL-000872
Kola201108286	R. Alta	1.000	17 - Alta	9.8.2011	NK-097353
Kola201105064	R. Alta	1.000	16 - Loppa	6.7.2011	NL-027274
Kola201107788	R. Alta	0.996	17 - Alta	26.7.2011	NL-028834
Kola201107061	R. Salangsvassdraget	0.954	18 - N.-Troms – Inner	28.7.2011	NL-027515
Kola201107859	R. Alta	1.000	17 - Alta	12.7.2011	NL-027909
Kola201106724	R. Alta	0.970	22 - S.-Troms – Middle in	13.7.2011	NL-028865

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688 **Table 4** Number of wild Atlantic salmon captured in coastal areas in Northern Norway in 2011 and
 689 2012 assigned to the Målselv, Alta, Tana and Kola rivers with an assignment probability threshold $p \geq$
 690 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-Jun	18	223	241	14	69	83	43	275	318	37	109	146	112	676	788
	Jul-Sep	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-Jun	54	264	318	6	188	194	136	313	449	35	84	119	231	849	1 080
	Jul-Sep	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-Jun	72	487	559	20	257	277	179	588	767	72	193	265	343	1 525	1 868
	Jul-Sep	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

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694 **Table 5.** Summary of GAM results modeling the weekly CPUE of wild Atlantic salmon as a function of
 695 the fishing location (CoastX, CoastY) and the time in the fishing season (Time). Separate models are
 696 shown for each river system and two sea-age-groups. Fishing location and time were modeled with a
 697 three-dimensional smooth function ($s(\text{CoastX}, \text{CoastY}, \text{Time})$). CPUE was modeled with a negative
 698 binomial distribution with a log-link function. Sample size was 1176 observations (Atlantic salmon)
 699 for each model.

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

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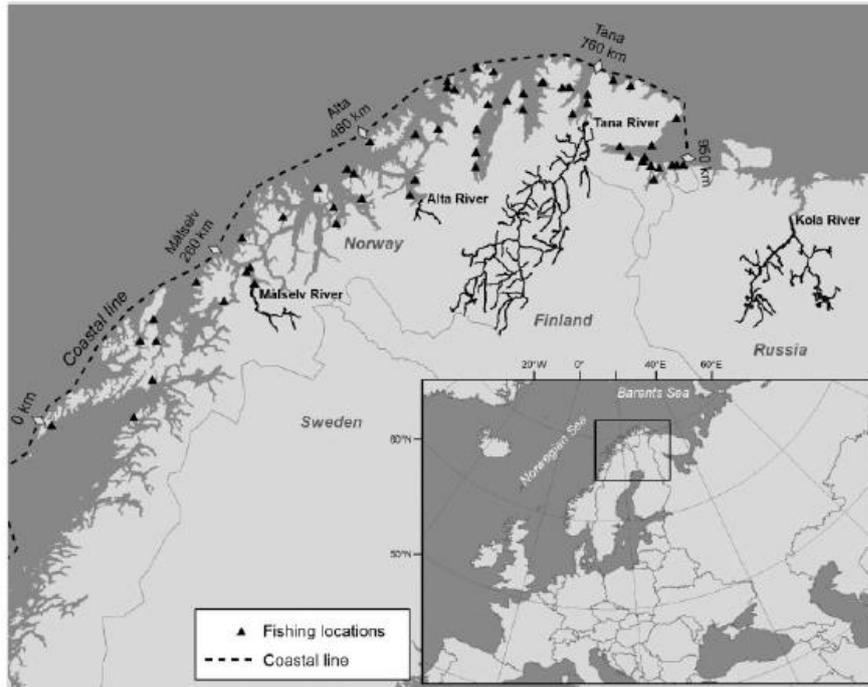


Figure 1. Map showing the outer Norwegian coast line (stipple line), the 58 fishing locations (triangle dots), and the four rivers (Målselv, Alta, Tana, and Kola) featured in this study.

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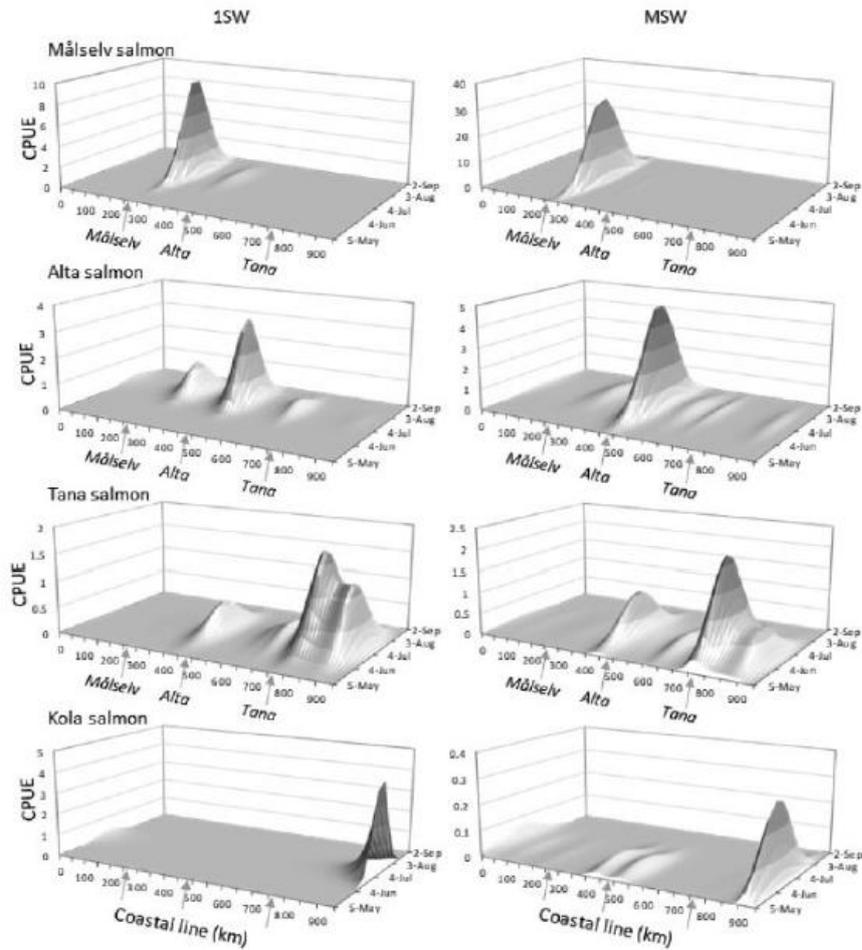


Figure 2. Predicted CPUE by week (z-axis) of 1SW and MSW wild Atlantic salmon from Målselv, Alta, Tana, and Kola Rivers along 950 km of the North-Norwegian coast (x-axis) from South-western Nordland to Eastern Finnmark (see Figure 1) from early May to late August (y-axis). The coastal study area corresponds 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).

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