

24 **Abstract**

25 In Greenland, Atlantic salmon are known to reproduce in only one river, the Kapisillit
26 River. Little is known about the population characteristics or the relationship to other
27 salmon populations across the species range, and consequently, a survey of the system was
28 conducted in 2005 and 2012. Juvenile salmon were captured in all stations surveyed within
29 the lower river with the highest densities lower in the river and decreasing densities with
30 increasing distance from the river mouth. Captured juveniles ranged from 0+ to 7+ years
31 old and the predominant smolt age was between 4-6 years. Median length of 0+ and 1+
32 juveniles in August-September was 38.8 and 70.4 mm, respectively. The proportion of
33 mature male parr increased from 4% for 1+ year old fish to 95% for fish greater than 2
34 years old. Genetic analysis using 96 single nucleotide polymorphisms (SNPs) revealed a
35 high degree of genetic similarity between collections, extremely low genetic diversity, and
36 low estimates of effective population size ($N_e=28.7$; 95% CI: 19.7-42.4). Genetic
37 comparison to range-wide salmon populations demonstrated that the Kapisillit River
38 salmon is an outgroup of the eastern Atlantic stock complex, which is consistent with the
39 hypothesized colonization from the east. River morphology and the absence of glacier
40 runoff are hypothesized to be the main reasons for the relatively high river temperatures
41 supporting this self-sustaining population of Atlantic salmon. Given its uniqueness and
42 persistence, this population represents an important part of range-wide biodiversity of
43 Atlantic salmon.

44

45 Key words: immigration history; juveniles; Kapisillit River; life history traits; population
46 genetics.

47 **SIGNIFICANCE STATEMENT**

48 Kapisillit River is the only known salmon river in Greenland. The present results show
49 that predominant smolt age was 4-6 years and the proportion of mature male parr 95% for
50 fish greater than 2 years old. A high degree of genetic similarity between collections,
51 extremely low genetic diversity, and low effective population size ($N_e=28.7$; 95% CI:
52 19.7-42.4) was found. It was concluded that the Kapisillit River salmon is an outgroup of
53 the eastern Atlantic stock complex.

54 **INTRODUCTION**

55 Atlantic salmon (*Salmo salar* L.) is native to many watersheds draining to the
56 subarctic regions of the North Atlantic Ocean from Ungava Bay, Canada, in the west to the
57 Barents and Kara Sea areas of Russia in the east (Thorstad *et al.*, 2011(Thorstad *et al.*,
58 2010). Due to global warming of the oceans and the accompanying northward migration
59 of many fish species (Nielsen *et al.*, 2013), it is important to characterize the Atlantic
60 salmon populations currently at the northernmost limit of their distribution range to predict
61 future changes in their life history traits (Todd *et al.*, 2011, Nielsen *et al.*, 2013). While life
62 history traits of the populations of Atlantic salmon in northeast Canada, northern Norway
63 and western Russia have been described (Power 1969, Kazakov 1994, Veselov *et al.* 1988,
64 Morin 1991, Zubchenko *et al.* 1999, Økland *et al.*, 2004, Finstad *et al.* 2004, Jensen *et al.*
65 2014), few data exist on native Atlantic salmon in Greenland. Despite the species’
66 widespread distribution in subarctic areas and that large numbers of North American and
67 European origin salmon congregate off the coast of Greenland each summer and autumn
68 to feed (ICES 2018), only one river, River Kapisillit, is known as a spawning site for
69 Atlantic salmon in Greenland (Nielsen, 1961, Fig 1).

70 The coastal waters off Greenland are an important feeding area for Atlantic salmon
71 from across the North Atlantic (MacCrimmon & Gots 1979, Rikardsen & Dempson 2011,
72 Redding *et al.* 2012, Miller *et al.* 2014). In Greenland, the distribution of this species varies
73 from year-to-year, with the northernmost boundary in the Disko Bay Region on the west
74 coast, and Ittoqqortoormiit on the east coast (Jensen & Christensen 2003, Fig. 1). Jonas
75 (1974) reported a total of 20 rivers containing Atlantic salmon in Greenland although most
76 reports consisted of only a single capture. Three of these rivers were electrofished and no

77 juveniles were captured except in the Kapisillit River (Kapisillit is the Greenlandic word
78 for “salmon”). In recent years, sporadic catches of adult Atlantic salmon have been reported
79 from several rivers in south-western Greenland (Lars Heilmann, Greenland Institute of
80 Natural Resources, personal communication 2012; Peter Borg, local sheep farmer, personal
81 communication, 2012). However, it is unknown if these are stray fish from distant
82 populations that use coastal waters off Greenland for feeding.

83 It seems likely that adult Atlantic salmon enter rivers in Greenland, but that they
84 are not able to establish self-sustaining populations probably due to cold temperatures in
85 these freshwater habitats that prevent juvenile development (Salonius 1973). Efforts to
86 stock salmon in six Greenlandic rivers in the same region as Kapisillit River were
87 conducted from 1956-1959 (Nielsen 1959; Nielsen 1961). Eyed eggs obtained from
88 hatcheries in Hammerfest, Northern Norway ($n = 40\ 000$) and from Miramichi, New
89 Brunswick, Canada ($n = 100\ 000$), were planted. In addition, 330 parr from the Kapisillit
90 River were transplanted to a nearby stream (Nielsen 1961). Periodic electrofishing
91 documented small numbers of juvenile Atlantic salmon up to six years later in four of the
92 six streams (Jonas, 1974). However, annual Arctic charr fisheries conducted at the mouth
93 of five of the six streams reported zero adult Atlantic salmon captured, and Jonas (1974)
94 concluded that the stocking experiments were unsuccessful. Additionally, results from
95 habitat surveys of 72 streams in south-west Greenland suggest that significant natural
96 production of any salmon species in southwest Greenland is not possible (Jonas, 1974). In
97 addition to cold waters, the stocking program may, however, also have been inhibited by
98 the general poor efficiency of Atlantic salmon stocking programs (Lever, 1996).

99 Given that there appears to be only one Greenlandic river capable of sustaining
100 Atlantic salmon and a lack of information about this population, there is a desire to learn
101 more about the Kapisillit River and its Atlantic salmon population. This information could
102 be used to conduct a more thorough evaluation of the suitability of other Greenlandic rivers
103 to sustain an Atlantic salmon population. In addition, further information is sought to
104 describe the Atlantic salmon population of the Kapisillit River to better understand its
105 genetic relationship with the rest of the species across its native range. The objective of
106 this paper is to describe the environmental conditions of the Kapisillit River and the
107 biological characteristics and genetic relationships of the Kapisillit River's Atlantic salmon
108 population to other populations within the species range.

109

110 **METHODS AND MATERIAL**

111 Study area

112 The Kapisillit drainage system is located at 64°26.2'N 50°12.8'W (mouth of the
113 river), situated at the bottom of one of the innermost arms of the Nuuk fjord about 25 km
114 from the edge of the inland ice and 90 km from the coast (Fig. 1). Surface geology of the
115 area consists of granodioritic gneisses of lower Precambrium age (Jonas, 1974). The
116 drainage area accessible to anadromous fish is approximately 19 km² and comprises a chain
117 of nine glacially eroded lakes situated in a relatively open U-shaped valley that is
118 approximately 29 km in length. The lower part of the basins consists of five lakes, which
119 lie within 6 km from the fjord and are below 100 m elevation whereas the uppermost lake
120 is situated at 240 m elevation. The area of the lakes varies between 0.02 and 7.40 km².
121 Boulder moraine is typical along the lake shores.

122 The lakes are connected by relatively high-gradient rivers, except for river III (Fig.
123 1), which has a slight gradient. The rivers are mainly shallow (<0.7 m depth), but some
124 deeper pools are found, especially in river III and IV (Fig. 1). The river beds consist mostly
125 of boulders and rocks with small areas of suitable Atlantic salmon spawning grounds
126 scattered among rubble. The spawning areas are more common around the outflow of lake
127 A and within rivers III and VI. The approximate lengths of the rivers (I – IX, Fig.1) are
128 310, 160, 650, 700, 250, 1900, 800, 400 and 1850 meters, respectively. River width varies,
129 but is generally 10-20 m. Typical summer discharges (July-October) in river III vary
130 between 3 and 7 m³ s⁻¹ (Jonas 1974). The drainage system has no contact with the inland
131 ice cap, and receives no melt water from the ice.

132

133 Water temperature and chemistry

134 From August 2012 through September 2013 water temperature at 1 m depth was
135 recorded in Lake A (TD1; Fig. 1) using a HOBO TidbiT v2 data logger
136 (www.onsetcomp.com) and in River II (TD2) using a Star-Oddi DST model centi-T
137 (www.star-oddi.com). Water samples from Lake A and Lake C (Fig. 1) were obtained
138 from 0.5 m depth at August 26-27 2012 and were stored in PVC bottles for analysis back
139 in the laboratory. Water samples were analyzed for the following parameters: turbidity,
140 water color, total nitrogen, total phosphorus and total organic carbon, according to
141 international standards. Measurements of pH, specific conductance (K₂₅) and water
142 temperature were taken with a WTW pH/Dissolved Oxygen/Conductivity Measuring
143 Instrument (<http://www.wtw.de>) in Lakes A and E and in Rivers I, II and IV from August
144 26-28, 2012. Calcium concentrations were also determined in situ by a titrimetric test using

145 an Aquamercl111110 analyzing kit in Lake A and River I. Lake color and water
146 transparency via a Secchi disc was also recorded in Lake A and C.

147

148 Collection of fish

149 Atlantic salmon juveniles were sampled in 2005 (September 14-17, $n = 109$) and
150 2012 (August 25-28, $n = 311$). Sampling consisted of electrofishing stream sections and
151 gillnetting lake sites at the lower part of the watershed including lakes A-C and rivers I –
152 IV (Fig. 1). The uppermost part (Lakes E to I and Rivers VI – IX, Fig. 1) were not surveyed.
153 Electrofishing was conducted at five cross sections (station 1-5, Fig. 1) both years, using a
154 Terrik Technology AS backpack electroshocker (type FA4, certificate IEC 335-2-86EN
155 50082-1:1992, www.terik.no) powered by 12V DC (10-13.5 VDC), output 170-1500 V,
156 max 12 A, frequency 35 -70 Hz. An area of 100 – 236 m² at each station was sampled,
157 using three successive removals according to Bohlin *et al.* (1989) and Zippin (1958), except
158 on station 5 in 2012, where only one removal was made because of low density of fish.
159 Captured specimens were identified to species; total length (L_t , mm) was recorded and all
160 specimens were kept in small plastic tanks on shore until release post-survey. Subsamples
161 of the electrofished salmon were frozen (2005, $n = 109$) or preserved in 96% ethanol (2012,
162 $n = 126$) for further examination of age, total length (L_N , mm), sex, maturity stage and to
163 sample tissue for genetic analysis back in the laboratory. Stomachs from all lethally
164 sampled fish were removed and preserved individually in 96% ethanol.

165 In 2005, four 1.5 x 25 m gillnets (mesh size 10 mm, 12.5 mm, 15.5 mm and 21 mm,
166 each net with one mesh size) were set in the littoral zone (depth < 10 m) of Lakes A and B
167 for approximately 12 hours per night in two nights. In 2012, four Nordic multi-mesh

168 bottom gillnets made up of 12 panels of different mesh sizes (5-55 mm, (Appelberg *et al.*,
169 1995) were set in the littoral zone (depth < 10 m) of Lakes A and B for approximately 12
170 hours in one night. All juvenile salmon caught in gillnets ($n = 14$) were sacrificed and
171 examined for total length (Lt, mm), sex, maturity stage and stomach fullness in the field.
172 Sagittal otoliths were extracted and stored in envelopes and stomachs were extracted and
173 frozen (2005) or preserved in 96% ethanol (2012) for examination back in the laboratory.
174 A pectoral fin sample from all captured fish was preserved in 96% ethanol (2005) or
175 RNAlater™ (ThermoFisher Scientific) stabilization solution (2012), for subsequent
176 genetic analysis.

177 All sampling activities were authorized by the Government of Greenland and were
178 covered under Survey License G12-008.

179 Fish processing

180 As storage of fish in ethanol or by freezing generally results in shrinkage of length,
181 the length data were adjusted by 2% and 3%, respectively (Thorstad *et al.*, (2007). Age of
182 the lethally sampled juveniles was estimated from the sagittal otoliths and stomach content
183 analysis (SCA) was used to describe the diets of sampled individuals. In the laboratory the
184 total fullness of each stomach was visually determined on a scale from empty (0%) to full
185 (100%). Individual prey items were identified to family or higher level. The number of
186 prey items of each category (Table 1) was counted and were summarized by % volume, %
187 number, % frequency. An Index of Relative Importance (IRI) and % IRI was also
188 calculated to quantify the importance of various prey groups in the diet as IRI integrates
189 mass, occurrence and abundance into a single measure (Cortes, 1997). Standardizing IRI
190 values as a percent facilitates meaningful and direct comparison among taxa.

191

192 Genetic processing

193 DNA was extracted using the Qiagen DNeasy 96 Blood and Tissue extraction kit
194 (Qiagen) following the guidelines of the manufacturer and quantified using QuantIT
195 PicoGreen (Life Technologies). All samples were screened using a 96 locus SNP panel
196 allowing comparison to range wide populations (Jeffery *et al.* 2018). A total of 285 range-
197 wide populations were genotyped by Jeffery *et al.* (2018) with an additional 16 populations
198 (including Kapisillit) recently genotyped using the same SNP panel (ICES, 2018) equating
199 to a total of 302 populations for comparison across the Atlantic salmon range. SNP
200 genotyping of recent samples was performed using SNPtype assays (Fluidigm) per the
201 manufacturer's protocols, without the STA step, using 96.96 genotyping IFCs (Fluidigm),
202 read on an EP1 (Fluidigm) and analysed using SNP Genotyping Analysis software
203 (Fluidigm). Each 96 well plate setup included 10 redundant samples that were repeated on
204 the plate to detect processing errors (row or plate reversal) and ensure consistent clustering
205 interpretation, positive controls (see above for details) and the required negative controls.
206 Any samples with > 9 failed loci were removed from the final data set.

207 Using data from the 96 SNPs, genetic diversity estimates, including observed
208 heterozygosity and inbreeding coefficient, were examined using *diveRsity* (Keenan *et al.*
209 2013). Confidence interval (CI) for inbreeding coefficient (F_{IS}) was calculated from 1000
210 bootstrap replicates across loci. *NeEstimator v2* (Do *et al.* 2014) was used to estimate
211 effective population size (N_e) with a parametric 95% CI using minor allele frequency
212 (MAF) cutoffs ranging between 0 and 0.05. Genetic relationships among the Kapisillit
213 population and 301 populations from the western and eastern Atlantic (Jeffery *et al.* 2018)

214 were examined using a neighbour-joining (NJ) tree based on Cavalli-Sforza and Edwards
215 (1967) chord distances with 1000 bootstrap replicates using the program POPULATIONS
216 v.1.2.33 (Langella 2012). Relationships from the NJ tree were visualized using FigTree
217 v1.4 (Rambaut 2012). Genetic structure was further examined using individual genotypes
218 for principal component analysis (PCA) in the R package *adegenet* (Jombart 2008).
219 Pairwise genetic divergence (F_{ST}) values were calculated using ARLEQUIN v.3.5
220 (Excoffier and Lischer 2010) and a heatmap of F_{ST} values was generated using *gplots*
221 (Warnes *et al.* 2016).

222 Comparisons were also performed between the two sampling years (2005 and 2012)
223 within the Kapisillit population to examine temporal stability. Genetic divergence (F_{ST})
224 was estimated between sampling years and estimates of genetic diversity and effective
225 population size were also compared between years. Each collection year was also analyzed
226 for the presence of full sibling families using the program COLONY v2.0 (Wang and
227 Santure 2009). Assumptions used were male and female polygamy, genotyping error
228 information calculated using *genepopedit* (Stanley *et al.* 2017), no inbreeding, long run
229 length with the full likelihood analysis method, high likelihood precision, no allele
230 frequency updates, and no sibship prior. Samples were analyzed as offspring without
231 assignment of individuals as candidate males or females, as these data were not available
232 for the samples.

233

234 **RESULTS**

235 Water temperature and water chemistry

236 The water temperatures measured in Lake A and in River II (Fig. 1) were strongly
237 correlated (Pearson's r , $r=0.99$, $p<0.0001$, Fig. 2). The daily temperature variation was
238 greater in the river than in the lake during spring, summer and autumn (Fig. 2). Mean
239 temperature during one year (September 2012 – September 2013) was 5.3°C (range 0.1-
240 16.7°C , $\text{SD}=5.1$) in the river and 4.8°C (range 0.0- 17.4°C , $\text{SD}= 5.1$) in the lake.

241 The water quality was characterized by relatively low values of calcium, total
242 organic carbon, total nitrogen and total phosphorus (Table 2). Also, low values of turbidity,
243 water color and a 7 m Secchi-depth in Lake C reflects its oligotrophic conditions. Specific
244 conductance ranged from $34\ \mu\text{Scm}^{-1}$ in Lake A to $54\ \mu\text{Scm}^{-1}$ in River IV, while pH ranged
245 from 7.58 to 7.93 (Table 2). Consequently, the Kapisillit River is a clear-water river.

246

247 Juvenile Atlantic salmon

248 A total of 420 juvenile Atlantic salmon were captured (2005: $n = 109$, 2012: $n =$
249 311). In both years, the highest densities of salmon were observed in the lowermost part of
250 the surveyed river system (st.1). The majority of salmon were captured in the river (106 in
251 2005 and 296 in 2012) with smaller numbers were caught in lakes (3 in 2005 and 15 in
252 2012). Densities of Atlantic salmon parr ($>0+$) at station 1-5 (Fig. 1) varied between 1.4
253 and 17.9 individuals per $100\ \text{m}^2$ in 2005 and between 2.9 and 84.5 individuals per $100\ \text{m}^2$
254 in 2012 (Fig. 3). Overall densities (both years) of young of the year ($0+$) varied between
255 0.7 and 24.1 individuals per $100\ \text{m}^2$. Atlantic salmon juveniles were recorded at all five
256 stations in both years. However, at the uppermost station (st. 5, Fig. 1) only 9 (2005) and
257 5 (2012) parr $>0+$ were captured. River stretches further upstream were not sampled and
258 the uppermost distribution of Atlantic salmon in the river system remains undetermined.

259 Although a full survey of the river was not conducted, no migratory obstacles were
260 observed downstream of Lake E (Fig. 1).

261 Overall, median length of age 0+ was 38.8 ± 4.0 mm. Median length of age 0+ was
262 40.8 ± 4.5 mm in 2005 ($n = 50$) and $37.8 \text{ mm} \pm 2.3$ mm in 2012 ($n = 37$, Fig. 4). Median
263 length of age 1+ was 70.4 ± 9.0 mm overall, 69.1 ± 5.9 mm in September 2005 ($n = 9$), and
264 70.9 ± 9.2 mm in August 2012 ($n = 62$). Age 2+ fish were poorly represented in both 2005
265 ($n = 1$) and in 2012 ($n = 6$), but their overall median length was 94.9 ± 22.5 mm. Overall,
266 median length of age 3+ was 141.4 ± 21.9 mm. Median length for age 3+ was $135.2 \text{ mm} \pm$
267 9.8 in 2005 ($n = 30$) and $146.9 \text{ mm} \pm 24.3$ in 2012 ($n = 34$). The considerable drop in
268 number of age 4+ and 5+ parr in both years (Fig. 4) suggests that 4-5 years is the most
269 common smolt age for Kapisillit River salmon. The oldest parr observed was 7 years (161
270 mm) and the largest parr was 220 mm (age 4).

271 In total, 95 % of male parr $\geq 2+$ were sexually mature. The proportion of mature
272 male parr increased from 4 % for age 1+ to 88-100 % in age group 2+ to 7+ (Table 2). In
273 total, mature male parr were dominating among older ($\geq 2+$) males both in 2005 (89.5%)
274 and 2012 (98%). The smallest of the mature parr was 86 mm (age 2+) in 2005 and 93 mm
275 (age 1+) in 2012. Mature males were on average larger (146.9 mm) than immature
276 juveniles (139.6 mm) within age class 3+, but the difference was not statistically significant
277 (Student t-test, $p = 0.12$, $n = 59$). We found no mature female in the material (Table 3).

278 In addition to Atlantic salmon, Arctic charr (*Salvelinus alpinus* L.) and threespined
279 stickleback (*Gasterosteus aculeatus* L.) were captured at all five stations.

280

281 Stomach samples

282 In 2005 we found eight food categories in stomach samples ($n = 73$) and in 2012
283 nine food categories were detected ($n = 160$). Simuliidae had the highest % IRI in both
284 samples: 92.1% and 71.8% in 2005 and 2012, respectively, followed by Trichoptera which
285 had a significant importance (7.4% and 5.1 % IRI, Table 1). In 2012 Chironomidae (13.9
286 % IRI) and Lymnaeida/Planorbidae (8.8 % IRI) had a significant importance. Other food
287 categories like Tipulidae, Oligochaeta and fish had very low relative importance in both
288 years, representing <0.01– 0.02 % IRI.

289

290 Genetic analyses

291 Using the 96 SNP panel, genetic analyses revealed low genetic diversity within the
292 Kapisillit population ($n = 110$), as Kapisillit had the lowest mean observed heterozygosity
293 (7.9%) across all 302 populations from the western and eastern Atlantic. Additionally,
294 more than half (56%) of the SNPs were monomorphic within the Kapisillit population;
295 whereas the mean percentage of monomorphic SNPs across all populations was only 19.5%
296 (range 0-63.5%). Despite low diversity, inbreeding coefficient (F_{IS}) for Kapisillit was
297 0.012 with bootstrap confidence interval (CI) of -0.019-0.037 suggesting a randomly
298 mating population. Estimated effective population size (N_e) was quantified for a range of
299 minor allele frequency (MAF) cutoffs (Table 4). A MAF cutoff of 0.02 is considered
300 appropriate to balance bias and precision of N_e estimates (Do *et al.* 2014) suggesting N_e for
301 Kapisillit is 28.7 (95% CI: 19.7-42.4) individuals.

302 A neighbour-joining tree revealed a clear split between populations from the eastern
303 and western Atlantic with the Kapisillit population clustering with the eastern Atlantic
304 genetic group (Figure 5A). Similarly, an individual-based PCA revealed two distinct

305 clusters separating eastern and western Atlantic individuals based on the first two principal
306 component axes, which explained 26.3% and 4.4% of the genetic variation, respectively
307 (Figure 5B). All individuals from Kapisillit clustered with the eastern Atlantic genetic
308 group (Figure 5B). Further analysis (PCA) within the eastern Atlantic group revealed that
309 Kapisillit salmon was genetically distinct from other eastern Atlantic salmon populations
310 (Figure 6A). Pairwise F_{ST} values were calculated between all populations within the eastern
311 Atlantic cluster, and Kapisillit was highly and significantly divergent from all eastern
312 Atlantic sites (mean pairwise $F_{ST} = 0.57$; range 0.44-0.68; all p-values < 0.001) (Figure
313 6B). The North Esk River in Scotland had the lowest F_{ST} (0.44) with Kapisillit but this was
314 still highly divergent. Pairwise F_{ST} values of population comparisons with Kapisillit were
315 much higher relative to population comparisons between eastern Atlantic populations
316 (without Kapisillit) where mean pairwise F_{ST} was 0.08 (range -0.009-0.38) among all
317 eastern Atlantic populations (Figure 6B).

318 No genetic differentiation was found between Kapisillit salmon collected in 2005
319 and 2012 ($F_{ST} = -0.00132$; $p = 0.53$). There was no significant difference in observed
320 heterozygosity between the years (t-test: $t = -0.13$, $df = 189.35$, $p = 0.89$). Estimates of
321 effective population size did not differ significantly between years, where N_e estimates
322 (allele frequency cutoff of 0.02) were 23.5 (95% CI: 14.7-40.8) individuals in 2005 and
323 31.3 (95% CI: 18.1-62.5) individuals in 2012. No significant differences were found
324 between years when other allele frequency cutoffs were implemented.

325 Analyses of family structure in COLONY suggested that both collections were
326 dominated by a relatively small number of families. In total, COLONY assigned
327 individuals to a total of 32 families (with 1-3 full siblings per family; inclusion probabilities

328 > 0.48) in 2005 and 37 families (with 1-5 full siblings per family; inclusion probabilities >
329 0.35) in 2012. Using a posterior probability threshold >0.30, a total of 18 full sibling and
330 156 half sibling dyads could be identified in 2005 and 35 full sibling and 270 half sibling
331 dyads were observed in 2012.

332

333 **DISCUSSION**

334 An understanding of small, marginal populations is central to the characterization
335 and conservation of intraspecific biodiversity. This study documents the presence and
336 biological and genetic composition of the only self-sustaining population of Atlantic
337 salmon in Greenland, which is located in the Kapisillit River. Sampled juvenile salmon
338 displayed normal species values for juvenile length at age and age distribution, but had a
339 high proportion of mature male parr. Genetic analyses demonstrated that the salmon in
340 Kapisillit River are highly distinct from populations across the Atlantic salmon range and
341 that the population was likely founded by a small number of individuals from the eastern
342 Atlantic. The population appears to be temporally stable with very low genetic diversity.
343 Collections were dominated by a small number of families with overall low effective
344 population size. The existence of this population is probably due to the uniqueness of the
345 river morphology and the absence of glacier runoff resulting in relatively high river
346 temperatures relative to other Greenland rivers (Jonas 1974) and hence the ability to
347 support juvenile production.

348 Genetic evidence strongly supports the hypothesis that the Kapisillit River
349 population is a small bottlenecked population originating from the eastern Atlantic.
350 Genetic diversity was low overall for the Kapisillit River. In fact, Kapisillit had the lowest
351 mean heterozygosity observed for any of 302 range-wide populations included in the
352 baseline. Somewhat surprisingly, over half (56%) of loci were monomorphic and this was
353 almost triple (2.9 times) the average observed across the range. Low genetic diversity was
354 further evident by the low estimate of effective population size ($N_e = 28.7$; 95% CI: 19.7-
355 42.4). With the existing genetic data it is difficult to estimate colonization time for

356 Kapisillit River accurately; however, genetic data indicate that the Kapisillit population is
357 highly divergent from all other sampled populations. The presence of a salmon population
358 in Kapisillit was first reported by Fabricius (1780) and it may have existed since the ice
359 retreated from the area and possibly caused an elevation in the water temperature. Despite
360 the fact that the river is close in proximity to large numbers of North American and
361 European origin salmon which migrate to the waters of West Greenland to feed, the genetic
362 divergence detected between Kapisillit River and other rivers in the east or west Atlantic
363 make it highly unlikely that strays from other populations occur in this river.

364 Overall densities of parr, on average 9.3 individuals per 100 m² in 2005 and 32.3 in
365 2012, were low compared to findings in other northern rivers (e.g. L'Abée-Lund &
366 Heggberget 1995, Ugedal *et al.* 2008). However, the catchability and density estimates of
367 juvenile Atlantic salmon based on electrofishing are strongly dependent on environmental
368 conditions like water conductivity, water temperature and water discharge (Jensen &
369 Johnsen 1988, Bohlin *et al.* 1989). Low catchability of age 0+ individuals gave uncertain
370 quantitative estimates compared to older parr. Given the low densities and small rearing
371 area in the lower Kapisillit River the relatively low density of juveniles is supportive of a
372 low abundance of Atlantic salmon in this system, which is supported by the estimated low
373 effective population sizes. Unfortunately, estimating census population size (N_c) from
374 effective population size (N_e) is difficult. The conversion for effective population size to
375 census population size can vary widely by population of Atlantic salmon (Palstra and
376 Fraser 2012). However, Palstra and Fraser (2012) found an average N_e/N_c ratio of 0.31
377 (range 0.01-0.95) across Atlantic salmon studies and populations. Regardless, we know
378 that the census population size is greater than the effective population size which was

379 estimated to be between 20 to 42 (95% CI) individuals. The electrofishing data provide
380 information regarding the distribution of the population. Our survey efforts were restricted
381 to the lower river. Within this river part most juveniles were detected in the lowermost
382 river section with low occupancy in the lake habitats. However, due to our limited lake
383 sampling, we cannot exclude that the juvenile production in the lake habitats were more
384 common than observed here.

385 The Kapisillit River consists mainly of hard rock minerals, unaffected by glacier
386 activity, limited bog areas and no forest. The relatively low levels of nutrients, turbidity
387 and color were therefore expected. The river bottom consisted mainly of boulders and
388 stones, probably providing good shelter for juveniles (Finstad *et al.* 2007). However, gravel
389 beds suitable for spawning were rare, but age class 0+ were observed at all five stations.
390 The areas suitable for salmon production in the lowermost river stretches (River I – IV) are
391 in the order of 15000 – 20000 m². Both the relatively low production area and the small
392 and scattered suitable spawning areas are likely restricting salmon production in the system
393 (Einum and Nislow 2011).

394 We found an average length of 0+ fish in August-September being 37-40 mm and
395 1+ juveniles being 68-72 mm. This lies within a normal range for length-at-age data of
396 many northern salmon populations (Jensen *et al.* 2012, Ugedal *et al.* 2008, Forseth *et al.*
397 2011). Unfortunately, we do not have temperature data for the whole 2012 growing season
398 to analyze effects of abiotic factors on growth. Atlantic salmon exhibit great variation in
399 freshwater growth, and the combined effects of temperature, density, physical habitat and
400 discharge levels on growth are documented (Teichert *et al.* 2010). The lake system in the
401 watershed likely mediates both the water temperature and discharge, thereby providing a

402 relatively stable and suitable environment year-round for Atlantic salmon. This system
403 coupled with the lack of direct glacial melt is hypothesized to be the main reason why this
404 river system contains Greenland's only known spawning salmon population. The age
405 distribution of juveniles indicates that most of the Atlantic salmon at Kapisillit smoltified
406 at an age of 3-6 years, with smoltification at 4 and 5 years probably being dominant. This
407 is a smolt age normally found in the northernmost regions of Norway (Jensen *et al.* 2012,
408 Ugedal *et al.* 2008). Across the species range, smolt age increases with latitude, from
409 mainly 1- 2 year olds in the south to 4 + year old smolts in the north (Metcalf & Thorpe
410 1990, Chaput *et al.* 2006, ICES 2018).

411 Analyses of stomach content showed that Simuliidae was the dominant prey type
412 found in the juvenile Atlantic salmon during both years. However, in 2012 terrestrial
413 insects also constituted a large portion of the diets. The composition of benthic and
414 terrestrial insects observed during our sampling correlated well with the prey items found
415 in the stomach samples. Diet data provided information about feeding preferences during
416 the few days prior to sampling. However, notable differences in prey composition among
417 seasons have been identified in other subarctic regions. In general, the seasonal transition
418 in diet in juvenile Atlantic salmon moves from Ephemeroptera, Diptera and Plecoptera in
419 spring, to Ephemeroptera, Diptera (including Simuliidae) and terrestrial insects in summer.
420 By autumn, Trichoptera larvae become dominant, while in winter the diet shifts to a
421 combination of Plecoptera, Ephemeroptera and Trichoptera (Johansen *et al.*, 2011). The
422 sampling of juvenile individuals from River Kapisillit in both years occurred in the late
423 Arctic summer. Our findings correspond well to the overall feeding preferences of juvenile
424 Atlantic salmon found elsewhere (Johansen *et al.* 2011).

425 In River Kapisillit, the majority (95%) of male parr $\geq 2+$ are sexually mature.
426 Approximately 60-100 % mature male parr in a population is high, but lies within the range
427 of variation in surveyed Atlantic salmon populations (Myers *et al.* 1986, Heinimaa and
428 Erkinaro 2004, Aubin-Horth and Dodson 2004). For instance, in the River Bævra, central
429 Norway, the majority (>75 %) of male parr older than 1+ were sexually mature (L'Abée-
430 Lund 1989). Early maturity may have both a heritable basis (Garant *et al.* 2003, Duston *et*
431 *al.* 2005) and an environmental component (Metcalfé 1998, Aubin-Horth *et al.* 2005a) and
432 Pichè *et al.* (2008) showed that thresholds for early maturation differs among populations.
433 Early maturation does result in increased survival to maturation and may increase the
434 likelihood of repeat spawning either as a sneaker spawner or as an anadromous male
435 following seaward migration (Fleming & Einum 2011). Moreover, this tactic has been
436 suggested as the default developmental pathway based on evidence by Aubin-Horth *et al.*
437 (2005b), who found that brain gene expression profiles of sneaker males were more similar
438 to those of immature females than immature males.

439 The Kapisillit Atlantic salmon population is small, and contains a high proportion
440 of mature male parr. Given the age distribution of the sampled population and the lack of
441 mature female salmon detected in the parr samples, it is clear that female spawners enter
442 the river to spawn annually. However, we do not have an estimate of the number of adult
443 salmon entering this river and we have no information about the fjord migration and
444 feeding areas of adult salmon from the Kapisillit population. Of the 986 individual samples
445 collected and genetically screened from the 2017 Atlantic salmon fishery off the coast of
446 West Greenland, no individuals from Kapisillit River were detected (ICES 2018).

447 In conclusion, a small population of juvenile Atlantic salmon was found in the
448 lowermost part of the watercourse. Life history traits such as length at age, smolt age, smolt
449 length and proportion of mature male parr were within the normal range described in
450 Atlantic salmon, but a high proportion of mature male parr (95%) was observed. The river
451 morphology of several shallow lakes and short river stretches combined with no melting
452 ice water provides for a relatively high summer water temperature. This is hypothesized to
453 be the main reason why Atlantic salmon have been able to maintain a self-sustaining
454 population in the Kapisillit River.

455 We found a minimum of 7 years of reproducing Atlantic salmon in Kapisillit. High
456 genetic stability between samples from 2005 and 2012 are indicative of temporal stability.
457 The collections were dominated by a small number of families with low genetic diversity.
458 The Kapisillit population is highly genetically distinct from both the Western Atlantic and
459 Eastern Atlantic populations but seems to have been colonized from the east. Because this
460 population is small, has high genetic stability, is highly genetically distinct from the
461 European and North American populations, and has not been supported through random
462 strays from the mixed-population offshore, the Atlantic salmon found in the Kapisillit river
463 system represent a very unique population and warrants consideration for special
464 protection.

465

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472

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474 J.V.A, J.G.D, T.S. L.R., A.D.S., G.K. and K.J.N contributed to the ideas and data
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477

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Table 1. Summary of diet data collected from Atlantic salmon (*Salmo salar*) juveniles samples from the Kapisillit River in 2005 (n=73) and 2012 (n=139). Diet data are presented according to percent volume (%V), percent number (%N), percent occurrence (%O), the Index of Relative Importance (IRI), and the percent IRI.

| Food type | % V | % N | % O | IRI | % IRI |
|------------------------|------------|------------|------------|------------|--------------|
| 2005 | | | | | |
| Trichoptera | 16.0 | 15.6 | 34.3 | 1083.9 | 7.5 |
| Lymnaeidae | 1.6 | 0.4 | 2.7 | 5.4 | 0.04 |
| Oligochaeta | 0.1 | 0.1 | 1.4 | 0.3 | <0.01 |
| Chronomidae | 2.1 | 2.4 | 12.3 | 55.4 | 0.4 |
| Simuliidae | 70.3 | 81.5 | 87.7 | 13312.9 | 92.1 |
| Tipulidae | 0.1 | 0.02 | 2.7 | 0.3 | <0.01 |
| Terresrial insects | 0.2 | | 1.4 | | |
| Other | 9.7 | | 27.4 | | |
| 2012 | | | | | |
| Trichoptera | 18.7 | 6.1 | 18.7 | 463.8 | 5.1 |
| Lymnaeidae/Planorbidae | 9.9 | 14.2 | 33.2 | 800.1 | 8.8 |
| Oligochaeta | 0.1 | 0.9 | 0.7 | 0.7 | <0.01 |
| Chronomidae | 7.4 | 18.8 | 48.2 | 1262.8 | 13.9 |
| Simuliidae | 35.6 | 58.7 | 69.1 | 6516.1 | 71.8 |
| Tipulidae | 0.1 | 0.5 | 3.6 | 2.2 | 0.02 |
| Terresrial insects | 27.4 | | 1.4 | | |
| Fish | 7.9 | 0.3 | 10.1 | 23.9 | 0.3 |
| Other | 8.2 | | 16.4 | | |

Table 2. Water chemistry parameters of the Kapisillit River measured from August 26-27, 2012. Entries indicated by a ‘-‘ identify that no sample was collected.

| Locality | Water temp. (°C) | pH | Specific cond. (K ₂₅) | Ca (mg l ⁻¹) | Turbidity (NTU) | Color (410 nm) | Tot. N (µg l ⁻¹) | Tot. P (µg l ⁻¹) | Tot. org. C (mg l ⁻¹) | Secchi depth (m) |
|----------|------------------|------|-----------------------------------|--------------------------|-----------------|----------------|------------------------------|------------------------------|-----------------------------------|------------------|
| Lake A | 14.3 | 7.93 | 34 | <2 | 0.33 | 7 | 130 | 2.3 | 2.5 | > 4.5 m |
| Lake C | - | - | - | - | 0.46 | 7 | 230 | 5.2 | 2.9 | 7 |
| Lake E | 14.8 | 7.58 | 38 | - | - | - | - | - | - | - |
| River I | 14.2 | 7.66 | 37 | <2 | - | - | - | - | - | - |
| River II | 15.0 | 7.84 | 52 | - | - | - | - | - | - | - |
| River IV | 13.9 | 7.69 | 54 | - | - | - | - | - | - | - |

Table 3. Number, length and sex ratio of immature and mature Atlantic salmon (*Salmo salar*) parr by age collected from the Kapisillit River. The 2005 and 2012 data were pooled for presentation (n=165). na = measurement

| Age | 1+ | | 2+ | | 3+ | | 4+ | | 5+ | | 6+ | | 7+ | |
|-----------------------------|-----------|-----------|------------|------------|------------|------------|------------|------------|------------|------|------------|----|------|----|
| | M | F | M | F | M | F | M | F | M | F | M | F | M | F |
| Numbers immature | 22 | 38 | 0 | 5 | 1 | 35 | 1 | 5 | 1 | 1 | 0 | 0 | 0 | 0 |
| Mean length cm (±SD) | 7.2 (0.8) | 7.4 (1.0) | na | 10.7 (2.6) | 11.6 | 14.0 (1.0) | 15.6 | 15.4 (2.2) | 14.7 | 13.6 | na | na | na | na |
| Numbers mature | 1 | 0 | 2 | 0 | 24 | 0 | 18 | 0 | 7 | 0 | 3 | 0 | 1 | 0 |
| Mean length cm (±SD) | 9.5 | na | 10.2 (1.3) | na | 14.7 (2.8) | na | 17.2 (2.9) | na | 16.3 (2.6) | na | 15.1 (0.6) | na | 16.6 | na |
| Percent mature | 4 | 0 | 100 | 0 | 96 | 0 | 95 | 0 | 88 | 0 | 100 | 0 | 100 | 0 |
| Male:Female ratio | 23 | 38 | 2 | 5 | 25 | 35 | 19 | 5 | 8 | 1 | 3 | 0 | 1 | 0 |

Table 4. Estimates of effective population size (N_e) with 95% confidence intervals (parametric) for Atlantic salmon (*Salmo salar*; n = 110) from the River Kapisillit using a panel of 96 single nucleotide polymorphisms (SNPs) and a range of minor allele frequency (MAF) cutoffs.

| MAF cutoff | Estimated N_e | Parametric 95% CI |
|-------------------|-----------------------------------|--------------------------|
| 0 | 12.8 | 10.7-15.2 |
| 0.01 | 22.7 | 16.9-30.5 |
| 0.02 | 28.7 | 19.7-42.4 |
| 0.05 | 82.2 | 39.2-301.8 |

Fig. 1

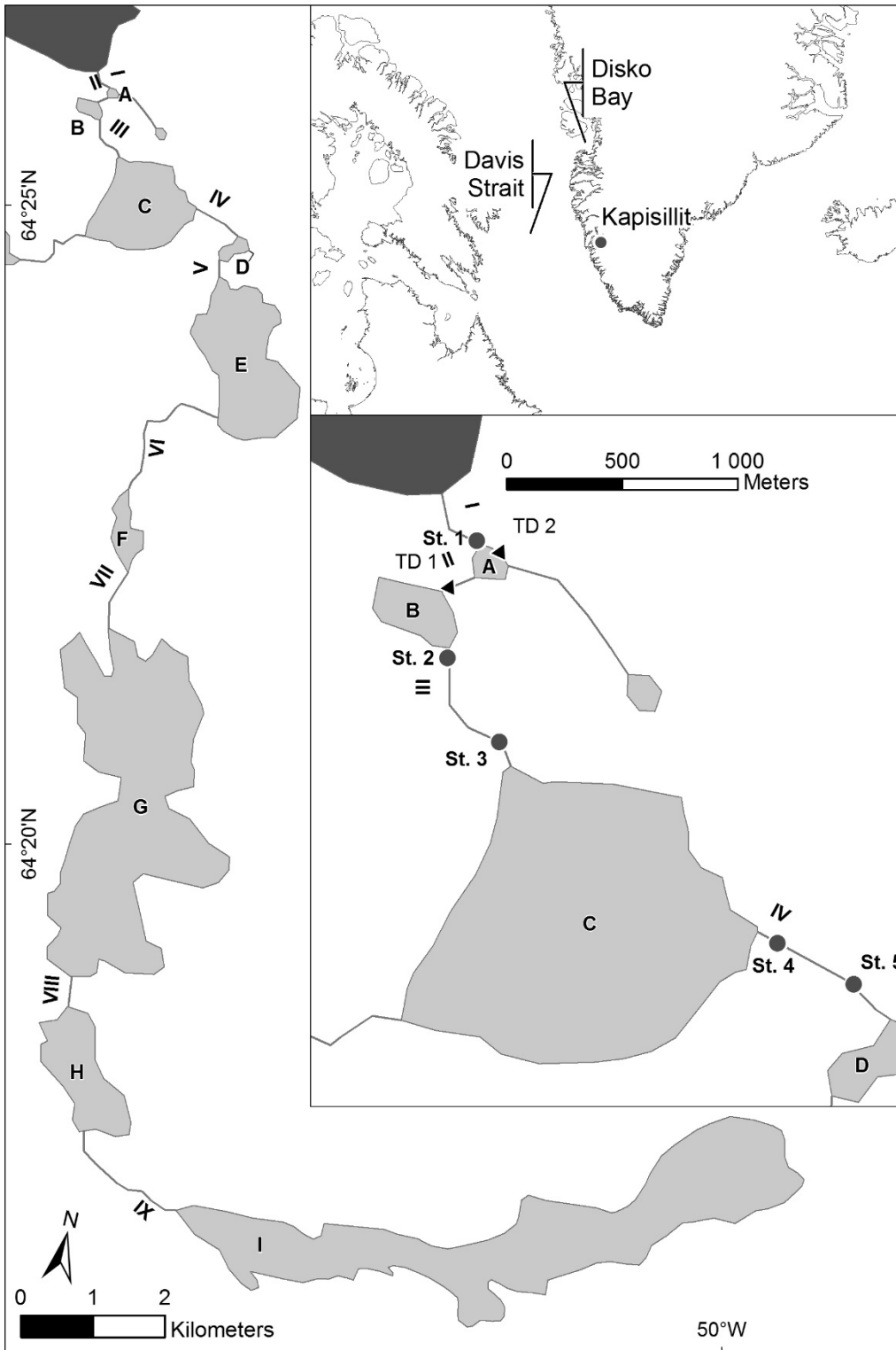


Fig. 2.

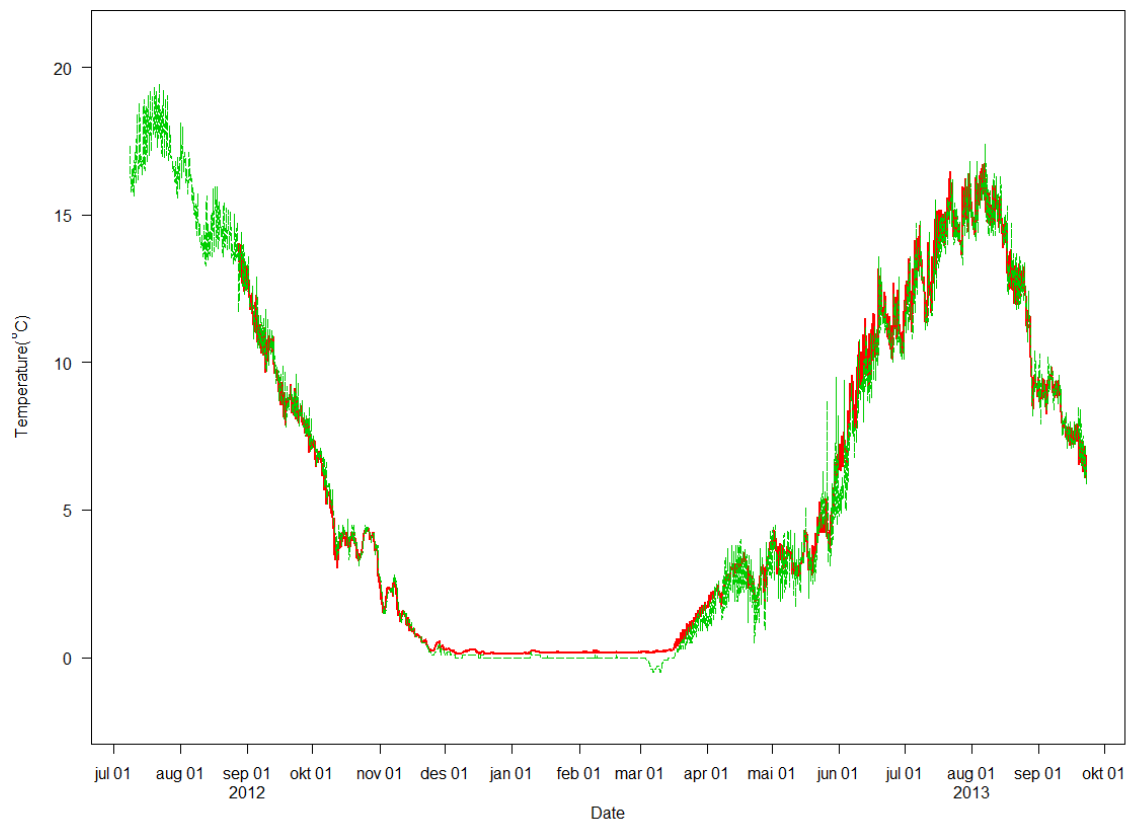


Fig. 3

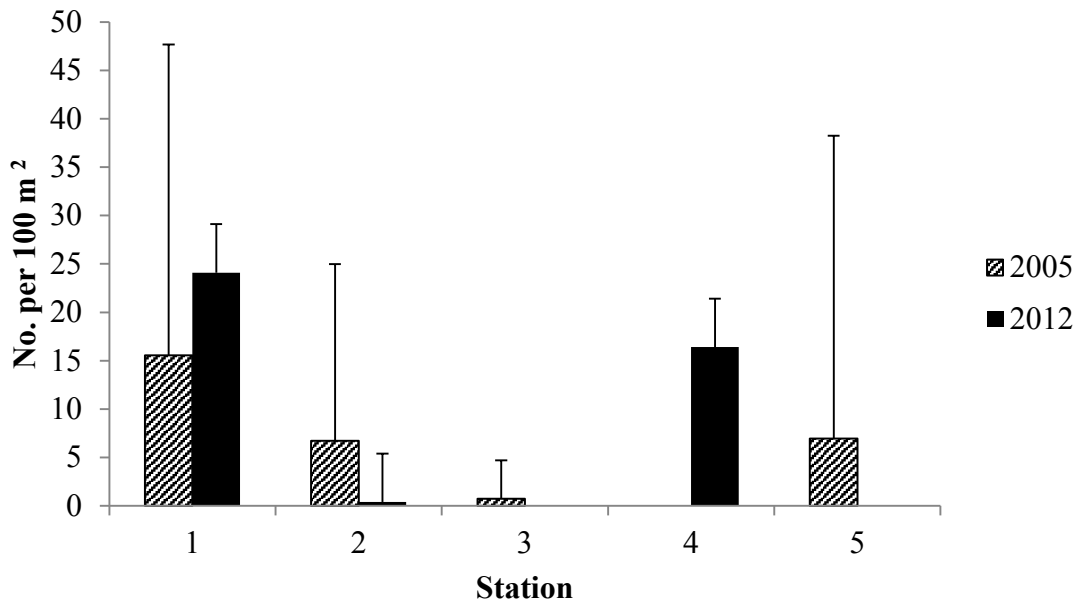
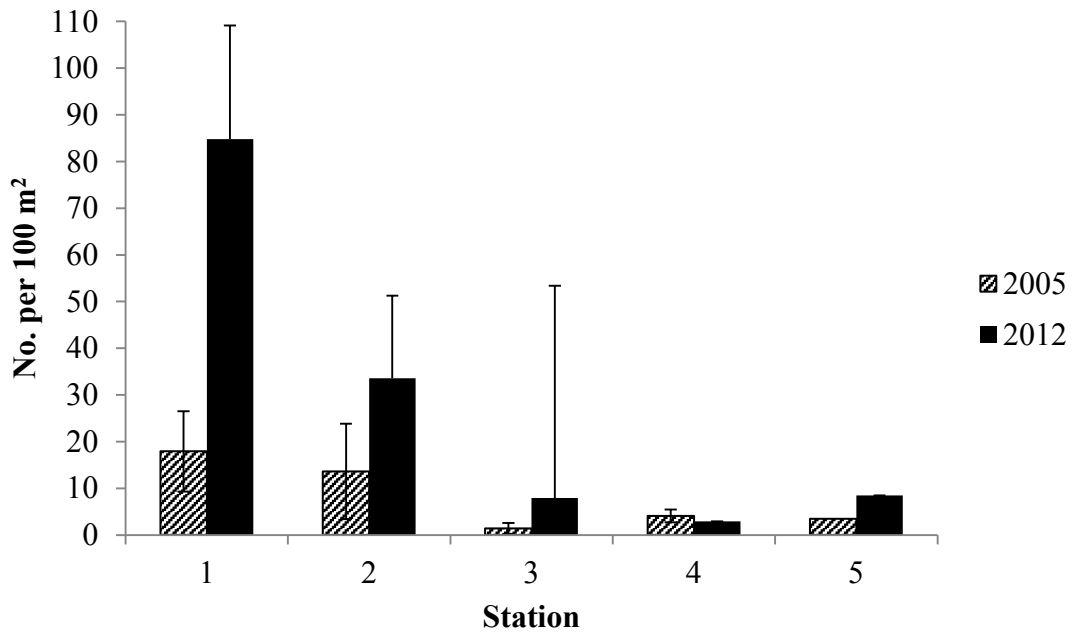


Fig. 4

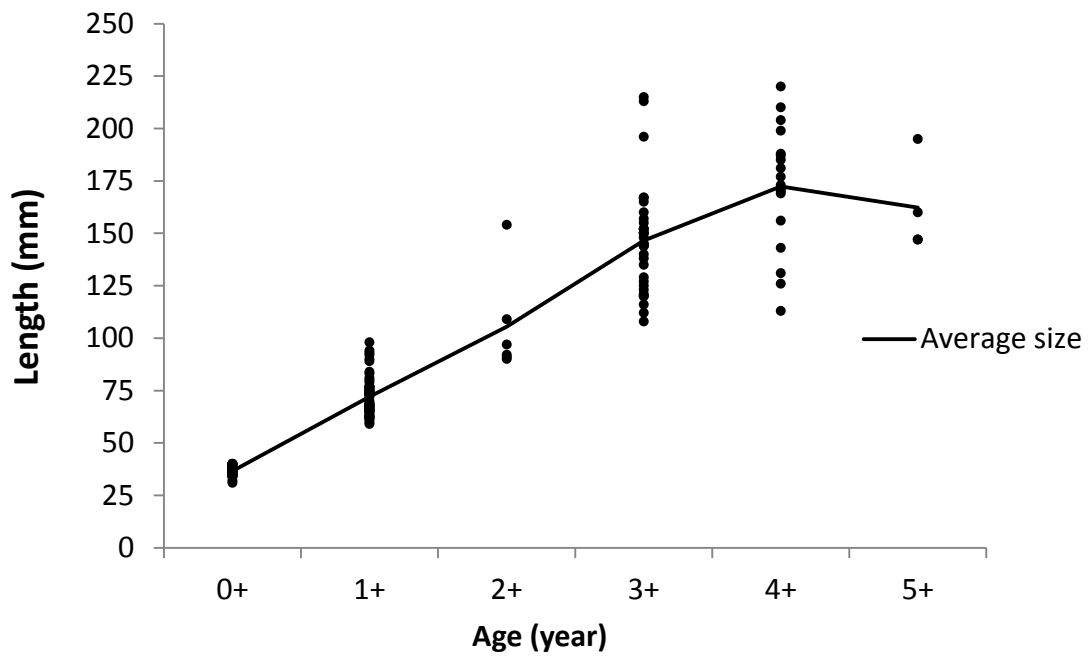
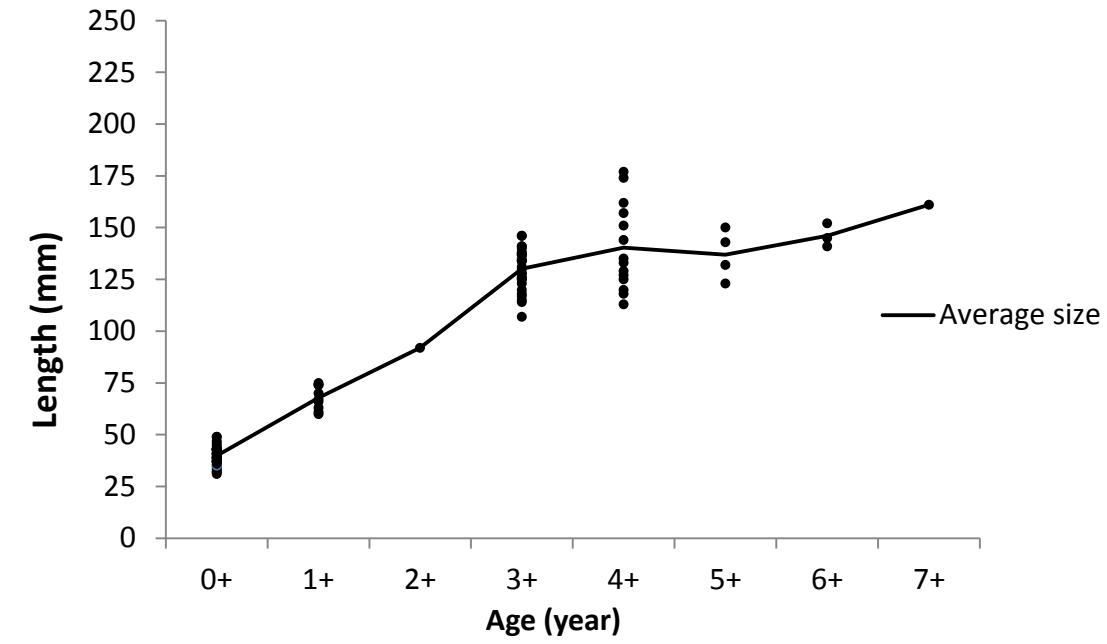


Fig. 5.

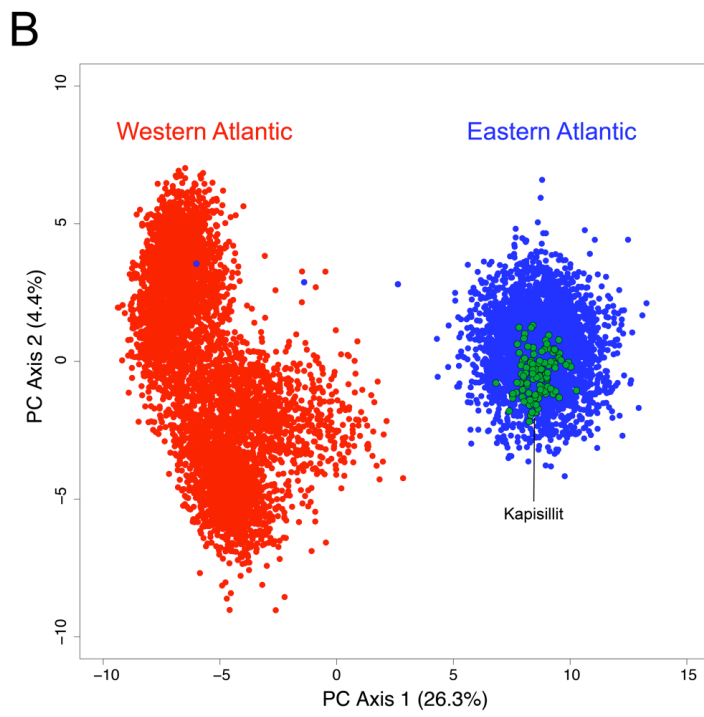
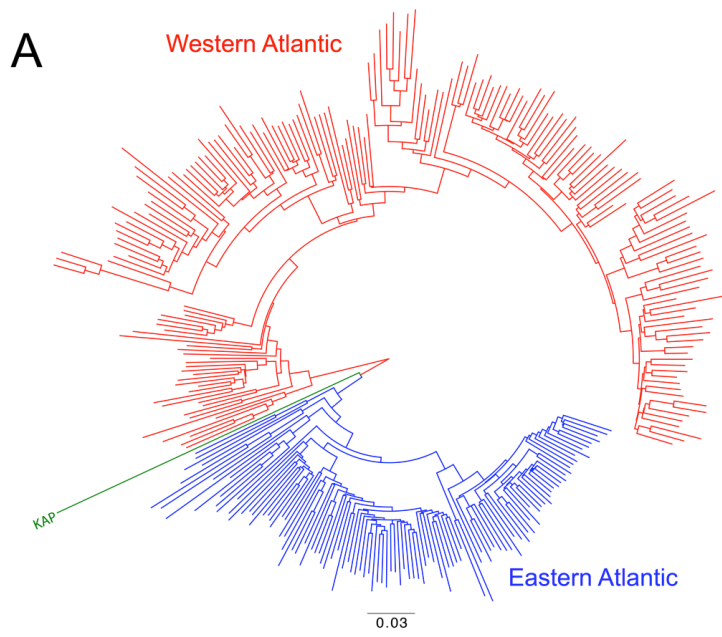


Figure 6.

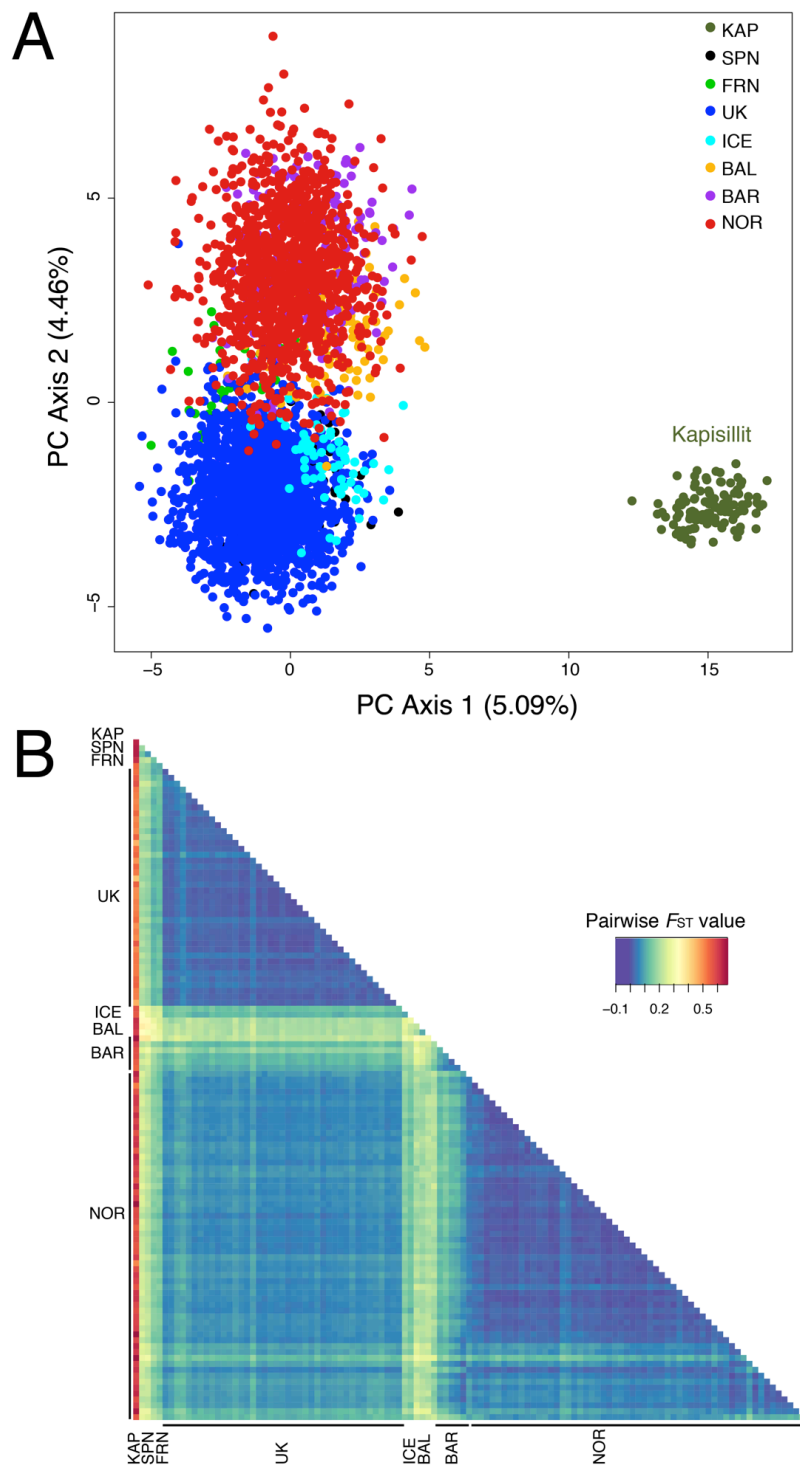


Figure 1. Map showing the Kapisillit drainage system. The lakes are indicated by A-I and the River stretches I-IX. The uppermost inserted map locates the Kapisillit River in Greenland while the second insert displays the lowermost part of the Kapisillit River, the sampling stations 1-5 (electrofishing, solid circles) and positions for logging water temperature (TD 1, TD 2, solid triangles).

Figure 2. Average daily water temperature recorded during the period August 7, 2012 – September 21, 2013 at River II (TD1, green) and Lake A (TD2, red).

Figure 3. Estimated densities ($n/100m^{-1} \pm 95\% CI$) of Atlantic salmon (*Salmo salar*) parr (>0+, upper panel) and young of the year (0+, lower panel) at stations 1-5 in the Kapisillit River in 2005 and 2012. The estimates of the densities were based on depletion estimators generated by three passes of an electrofisher over measured study areas, except for station 5 in 2012 (single pass electrofishing).

Figure 4. Total length and age of Atlantic salmon (*Salmo salar*) caught in the Kapisillit River in 2005 (upper figure, $n=103$) and 2012 (lower figure, $n=162$). Line shows the median body length for the different age-classes.

Figure 5. (A) Neighbour-joining tree based on Cavalli-Sforza and Edwards (1967) chord distance with 1000 bootstrap replicates for Atlantic salmon (*Salmo salar*) collections representing 302 populations across the species' range. (B) Individual-based principal component analysis (PCA) using the same populations. In both panels, eastern and western Atlantic populations are colored in blue and red, respectively, with the Kapisillit population colored in green.

Figure 6. (A) Principal component analysis of Atlantic salmon (*Salmo salar*) individuals from the eastern Atlantic (colored by regional group) and Kapisillit River (green). **(B)** Heatmap of pairwise genetic divergence (F_{ST}) between all populations in the eastern Atlantic and Kapisillit (KAP). Eastern Atlantic populations are arranged by geographic region, which includes Spain (SPN), France (FRN), United Kingdom (UK), Iceland (ICE), Baltic (BAL), Barents (BAR), and Norway (NOR).

