

**Demographic and genetic description of Greenland's only
indigenous Atlantic salmon (*Salmo salar*) population**

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Abstract

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

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

SIGNIFICANCE STATEMENT

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

INTRODUCTION

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

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

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

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

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

METHODS AND MATERIAL

Study area

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

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

Water temperature and chemistry

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

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

Collection of fish

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

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

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

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

Fish processing

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

Genetic processing

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

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

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

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

RESULTS

Water temperature and water chemistry

The water temperatures measured in Lake A and in River II (Fig. 1) were strongly correlated (Pearson's r , $r=0.99$, $p<0.0001$, Fig. 2). The daily temperature variation was greater in the river than in the lake during spring, summer and autumn (Fig. 2). Mean temperature during one year (September 2012 – September 2013) was 5.3°C (range 0.1 - 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.

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

Juvenile Atlantic salmon

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

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

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

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

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

Stomach samples

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

Genetic analyses

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

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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

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CONTRIBUTIONS

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 generation. J.V.A, J.G.D, S.J.L, I.R.B., L.R., A.D.S., G.K. and B.A.L contributed to data analyses. All authors contributed to manuscript preparation and funding.

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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
Chironomidae	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
Terrestrial 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
Chironomidae	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
Terrestrial 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



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).

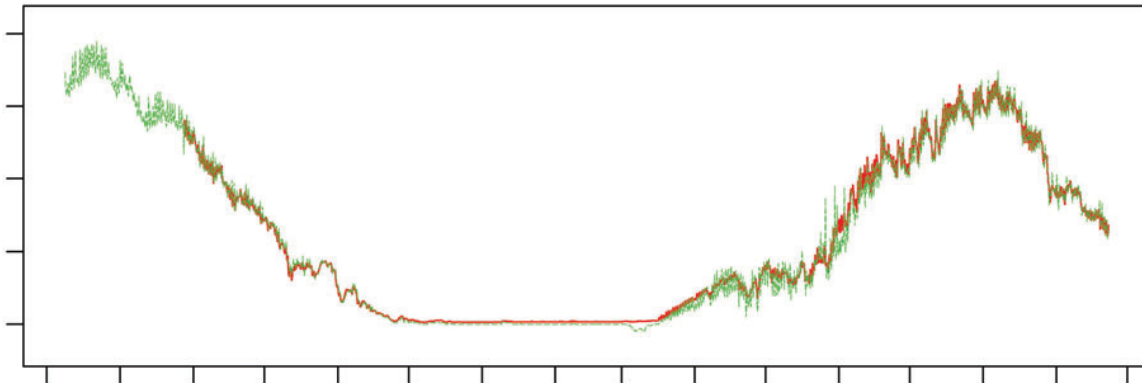


Figure 2. Average daily water temperature recorded during the period August 7, 2012 – September 21, 2013 at River II (TD1, green) and Lake A (TD2, red).

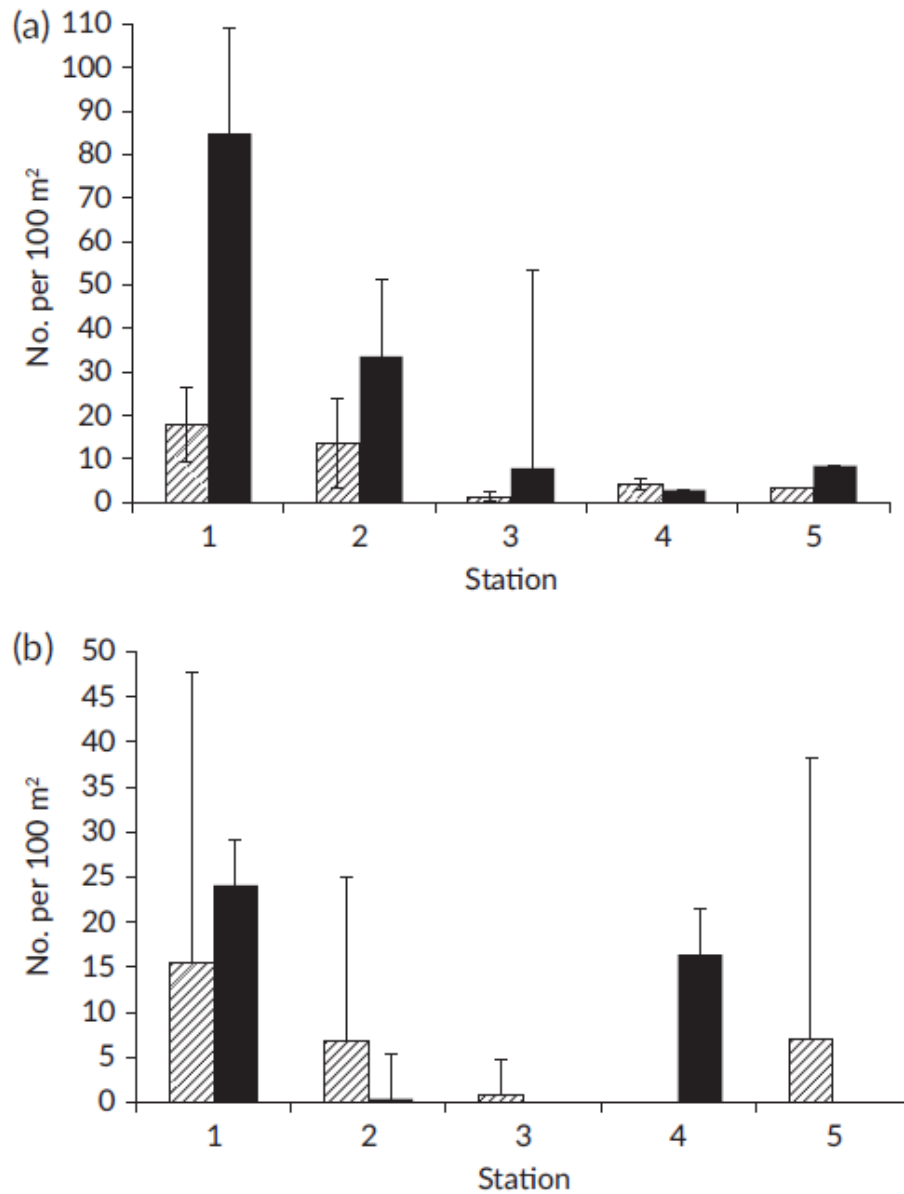


Figure 3. Estimated densities ($n/100\text{m}^{-1} \pm 95\%$ CI) of Atlantic salmon (*Salmo salar*) parr (>0+, upper panel) and young of the year (0+, lower panel) at stations 1-5 in the Kapisillit River in 2005 and 2012. The estimates of the densities were based on depletion estimators generated by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

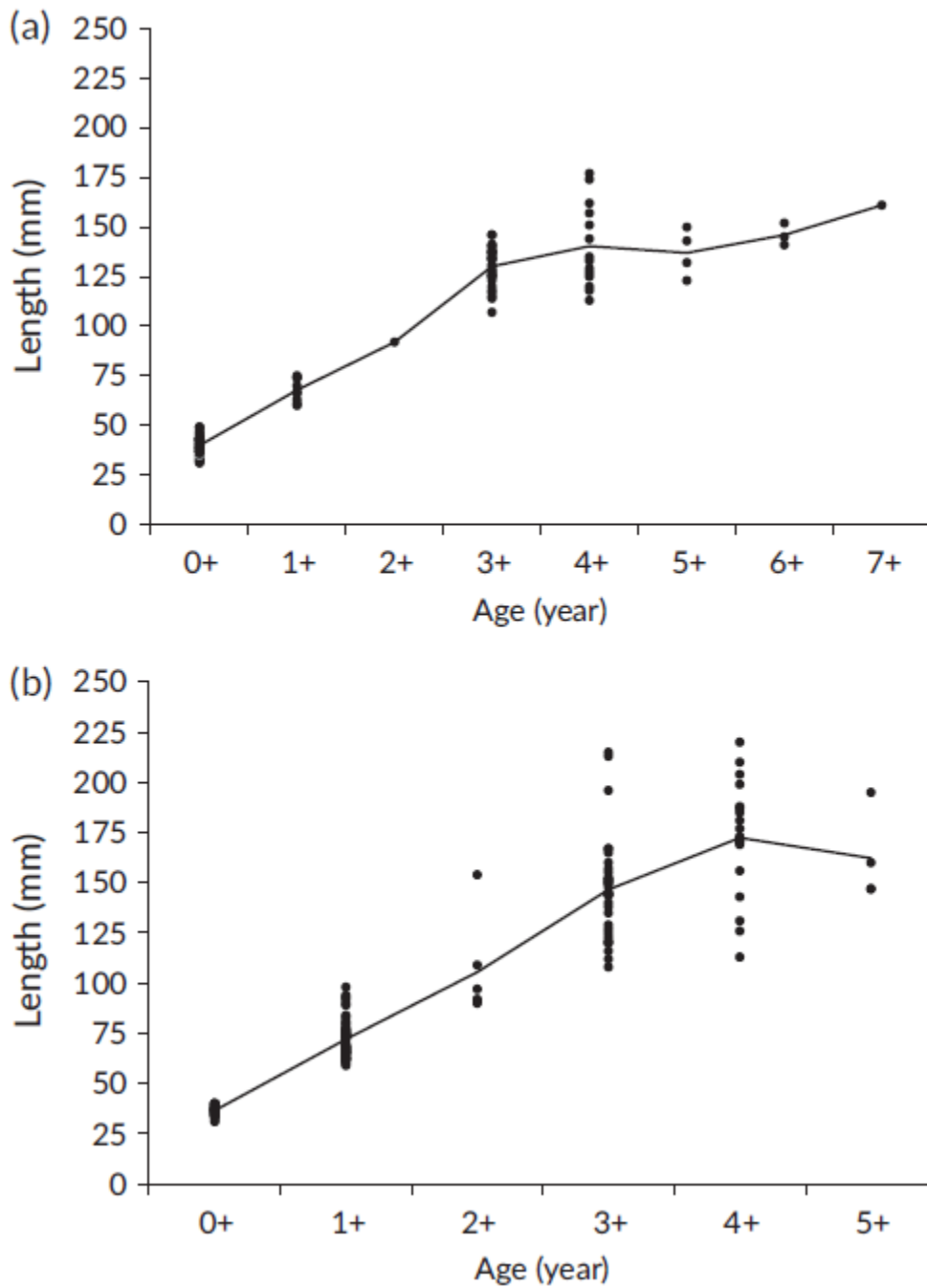


Figure 4. Total length and age of Atlantic salmon (*Salmo salar*) caught in the Kapisillit River in 2005 (upper figure, n=103) and 2012 (lower figure, n=162). Line shows the median body length for the different age-classes.

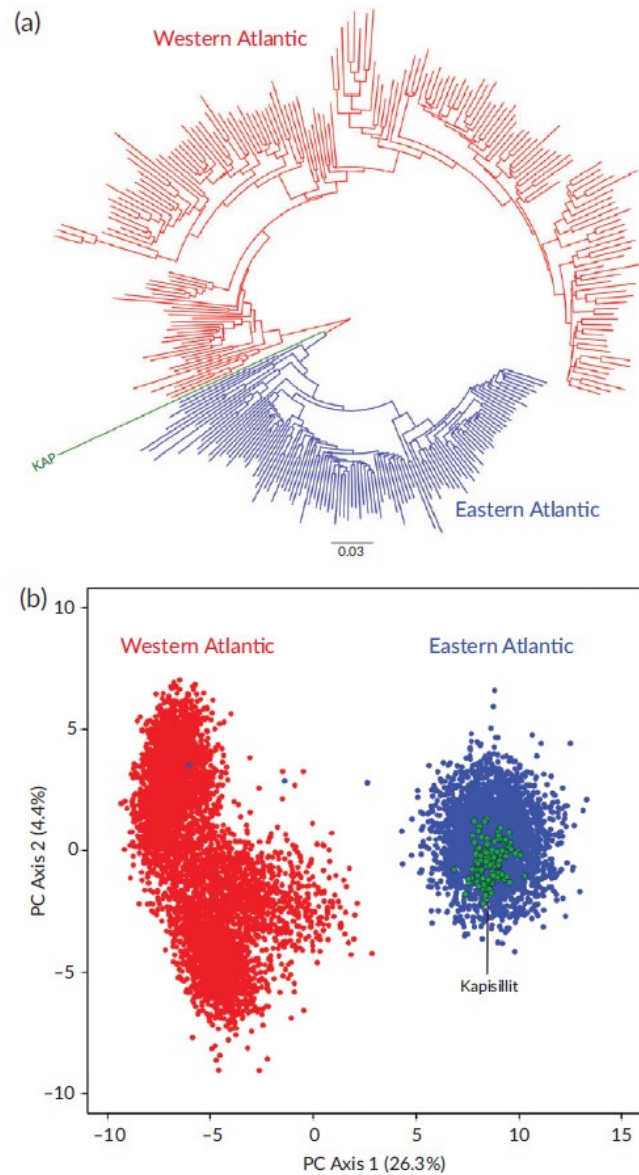


Figure 5. (A) Neighbour-joining tree based on Cavalli-Sforza and Edwards (1967) chord distance with 1000 bootstrap replicates for Atlantic salmon (*Salmo salar*) collections representing 302 populations across the species' range. (B) Individual-based principal component analysis (PCA) using the same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

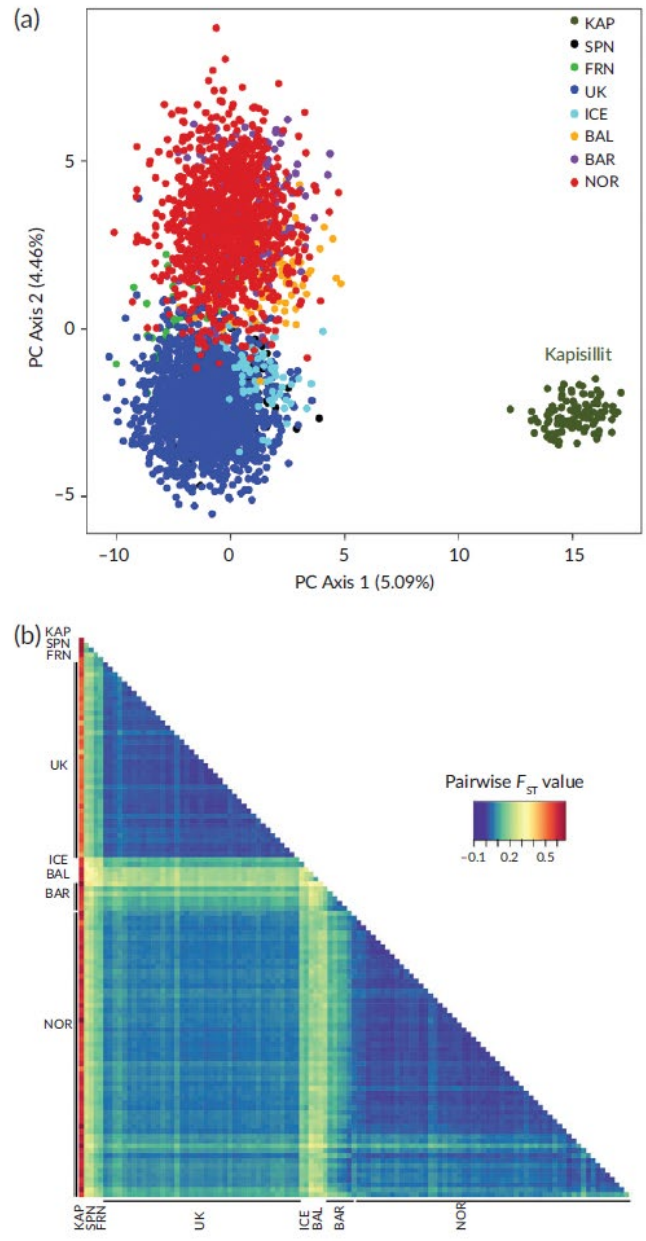


Figure 6. (A) Principal component analysis of Atlantic salmon (*Salmo salar*) individuals from the eastern Atlantic (colored by regional group) and Kapisillit River (green). (B) Heatmap of pairwise genetic divergence (F_{ST}) between all populations in the eastern Atlantic and Kapisillit (KAP). Eastern 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).