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High gene flow in polar cod (*Boreogadus saida*) from West-Svalbard and the Eurasian Basin

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Abstract

The current and projected environmental change of the Arctic Ocean contrasts sharply with the limited knowledge of its genetic biodiversity. Polar cod *Boreogadus saida* (Lepechin, 1774) is an abundant circumpolar marine fish and ecological key species. The central role of polar cod in the Arctic marine food web warrants a better understanding of its population structure and connectivity. In this study, the genetic population structure of 171 juveniles, collected from several fjords off West-Svalbard (Billefjorden, Hornsund and Kongsfjorden), the northern Sophia Basin and the Eurasian Basin of the Arctic Ocean, was analysed using nine DNA microsatellite loci. Genetic analyses indicated moderate to high genetic diversity, but absence of spatial population structure and isolation-by-distance, suggesting ongoing gene flow between the studied sampling regions. High levels of connectivity may be key for polar cod to maintain populations across wide spatial scales. The adaptive capacity of the species will be increasingly important to face challenges such as habitat fragmentation, ocean warming and changes in prey composition. In view of a limited understanding of the population dynamics and evolution of polar cod, a valuable next step to predict future developments should be an integrated biological evaluation, including population genomics, a life-history approach, and habitat and biophysical dispersal modelling.

KEYWORDS
central Arctic Ocean, connectivity, DNA microsatellites, population differentiation, population structure

1 | INTRODUCTION

Polar cod *Boreogadus saida* (Lepechin, 1744; Gadidae; also referred to as "Arctic cod") is an abundant circumpolar marine fish in the Arctic Ocean. It inhabits a rapidly changing ecosystem characterized by rising temperatures, sea ice loss and an extended melt season (Benoit *et al*., 2008; David *et al*., 2016; Steiner *et al*., 2019; Stroeve *et al*., 2014). Polar cod are adapted to life at sub-zero temperatures in close association with sea ice through the production of antifreeze glycoproteins (Osuga & Feeney, 1978). Sea ice loss likely poses a serious threat to polar cod, as it usually spawns under ice and the floating eggs develop close to the surface under ice cover (Christiansen, 2017; Dahlke *et al*., 2018; Geoffroy *et al*., 2011; Graham & Hop, 1995). Furthermore, the sea ice provides protection from predators such as seabirds and marine mammals (Crawford & Jorgenson, 1993; Geoffroy *et al*., 2011; Welch *et al*., 1993) and serves as feeding habitat for polar cod juveniles (Gradinger & Bluhm, 2004; Kohlbach *et al*., 2017). Polar cod is a key species in the high-Arctic food web, because it channels almost 75% of zooplankton production to predatory marine mammals and seabirds (Benoit *et al*., 2014; Hop & Gjøsæter, 2013; Welch *et al*., 1992). Changes in its distribution, abundance and trophic ecology might have consequences for the energy flow and community

dynamics throughout the entire ecosystem (Christiansen *et al*., 2012; Hop & Gjøsæter, 2013; Kohlbach *et al*., 2017; Welch *et al*., 1992). Moreover, northward expansion of boreal species into Arctic regions could affect polar cod through competition, resulting in modified energy fluxes within the Arctic ecosystem (Fossheim *et al*., 2015).

Despite its ecological importance, knowledge on horizontal polar cod movement throughout the Arctic region remains scarce. In particular, their distribution and abundance in the central Arctic Ocean (CAO) are practically unknown (Snoeijs *et al*., 2020). Polar cod has been observed in two types of distributional patterns: low densities of non-schooling individuals (Crawford & Jorgenson, 1990; Crawford & Jorgenson, 1993) and large aggregations (Bradstreet, 1986; Melnikov & Chernova, 2013; Ponomarenko, 1967). The latter, most often observed nearshore inside bays as well as near ice edges, seem to be a life cycle peculiarity despite the high predation pressure (Bradstreet, 1986; Melnikov & Chernova, 2013; Ponomarenko, 1967). The ubiquitous presence of polar cod under sea ice in the CAO could be related to ice formation areas, from which juvenile polar cod passively drift with the sea ice (David *et al*., 2016). Advection by sea ice drift has been hypothesized to be important for the genetic connectivity of circum-Arctic populations (David *et al*., 2016). In addition, Kessel *et al*. (2017) documented long-distance movements (>100 km) of polar cod. In general, environmental heterogeneity and oceanographic factors have a large influence on distribution and population connectivity, which affects genetic diversity and evolutionary potential. While climate effects are commonly studied at the species level, environmental changes impact populations differently (Heath *et al*., 2012; Pauls *et al*., 2013). Therefore, decomposing single species into genetic units provides a better understanding of biogeographical patterns and improves predictions of the impacts of climate change on distribution range, abundance, competition with boreal species and the role in the food web (Durant & Hjermann, 2017; Fossheim *et al*., 2015; Marcer *et al*., 2016; McNicholl *et al*., 2018).

In general, marine fish experience high levels of gene flow through dispersal via planktonic eggs and larvae that may drift over large spatio-temporal scales (Hellberg *et al*., 2002; Hilbish, 1996; Waples, 1998). Adults may also disperse over large distances (Frisk *et al*., 2014). In combination with large effective population sizes and weak migration barriers, dispersal leads to low levels of genetic drift and consequently faint or absent genetic differentiation in marine fish populations (Nielsen *et al*., 2009; O'Reilly *et al*., 2004; Palumbi, 2003; Poulsen *et al*., 2006). Nevertheless, in the past decades a growing number of studies documented weak, but significant population structuring at evolutionary neutral loci in marine fishes (O'Reilly *et al*., 2004; Vinas *et al*., 2010). Environmental and oceanographic features such as water temperature, salinity, bathymetry and advection are considered important for gene flow and connectivity. The interaction between these abiotic factors with biological traits, such as egg buoyancy, larval behaviour and dispersal capacity, determine the population differentiation in the ocean (André *et al*., 2016; Doherty *et al*., 1995; Pepin & Carr, 1993; Selkoe & Toonen, 2011). Altered environmental conditions could strongly impact this interaction and consequently, the distribution and genetic signature of marine fishes as seen in Atlantic herring (Barrio *et al*., 2016). Therefore, identifying spatial, temporal and life cycle structuring in marine fishes is imperative for species conservation and sustainable fisheries management (André *et al*., 2016; Laikre *et al*., 2005), especially in species threatened by overfishing and altered environmental conditions under climate change.

Although the circumpolar genetic population structure of polar cod has recently been investigated (Nelson *et al*., 2020), knowledge gaps remain especially in the CAO and the European Arctic. Previous research found little to no geographic structuring in the northern Atlantic Ocean (Fevolden *et al*., 1999; Pálsson *et al*., 2009) and Beaufort, Bering and Chukchi Seas (Wilson *et al*., 2017; Wilson *et al*., 2019). Yet, Madsen *et al*. (2016) described genetic differentiation between fjord and oceanic populations of polar cod in the Greenland Sea. Moreover, significant temporal variability, but low estimates of spatial genetic differentiation, was found in polar cod of the Russian Arctic seas (Gordeeva & Mishin, 2019). Nelson *et al*. (2020) identified four genetic groups (Canada East, Canada West, Europe and the USA) on a circumpolar scale with little to no genetic differentiation within these groups. Nonetheless, no samples from the European shelf (Svalbard, Barents Sea and Kara Sea) were included, and none from the CAO. In this study, the authors focus on the relationships between fish advected from Siberia across the CAO and potentially different sink populations near Svalbard, based on a more detailed analysis of the genetic variability of polar cod in the fjords of West-Svalbard (Kongsfjorden, Billefjorden and Hornsund), the northern Sophia Basin and the Eurasian Basin of the Arctic Ocean. The authors used microsatellite loci optimized for polar cod (Nelson *et al*., 2013) to investigate genetic diversity, population differentiation and isolation-by-distance (IBD). The authors test the hypothesis that the genetic population structure of polar cod is uniform, showing little differentiation between the fjords of Svalbard and potential nursery grounds in the CAO on the Siberian shelf.

2 | MATERIALS AND METHODS

2.1 | Fish sampling

In total, 171 juvenile polar cod were collected during four expeditions between 2012 and 2015 (Boetius, 2013; Mark, 2013; Peeken, 2016; Figure 1, Table 1). All specimens from the Eurasian sector of the Arctic Ocean and Sophia Basin were collected in ice-covered waters, whereas fish from Billefjorden, Hornsund and Kongsfjorden were collected in open water. All specimens were juveniles between 56 and 175 mm total length (Table 1), therefore, likely belonging to age class 1 and 2. Fish were identified morphologically by experts on board and frozen at −20°C. Morphological identification was checked again by different examiners in the laboratory to exclude any potential misidentification. Larvae of *B. saida* can be confused with *Arctogadus glacialis*, but in this case all specimens were of sufficient size for confident identification. In addition, genetic data (see below) did not indicate any strongly diverging individual, as would be expected from misidentified samples.

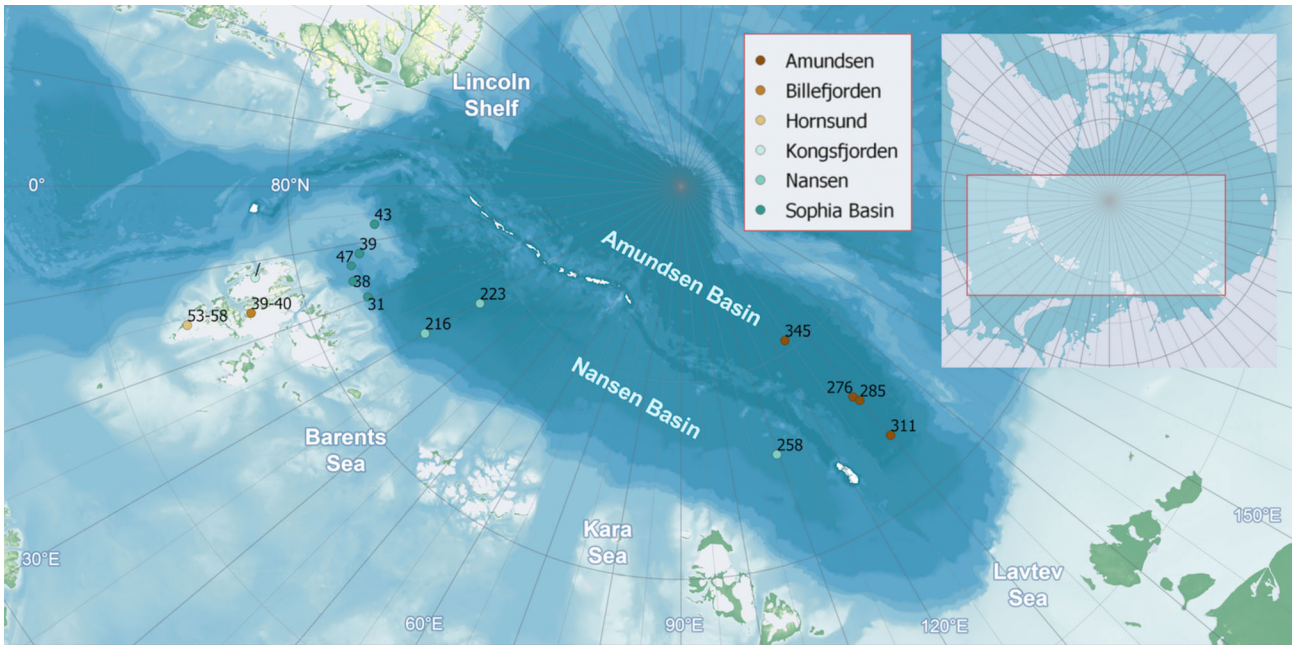

FIGURE 1 Map of study region where polar cod (*Boreogadus saida*) was collected in the Eurasian Basin and Svalbard (detail map). Station names are shown for sampling locations in the Sophia Basin (31, 38, 39, 43 and 47), Nansen Basin (216, 223 and 258), Amundsen Basin (276, 285, 321 and 345), Hornsund (53–58), Billefjorden (39–40) and Kongsfjorden (no station number, indicated by /)

TABLE 1 Sampling details of polar cod, *Boreogadus saida*, collected for population genetic analysis.

Study site	Station ID	Lat.	Long.	Sampling month	Cruise	Gear	Sample size	Mean L_T in mm (min–max)
Nansen Basin	223	84.07	30.47	Aug 2012	PS80	SUIT	3	111 (102–118)
Nansen Basin	216	82.48	30.02	Aug 2012	PS80	SUIT	7	98 (76–137)
Nansen Basin	258	82.74	109.62	Aug 2012	PS80	SUIT	8	76 (56–105)
Amundsen Basin	276	83.07	129.12	Aug 2012	PS80	SUIT	7	72 (65–90)
Amundsen Basin	285	82.89	129.77	Aug 2012	PS80	SUIT	5	86 (69–100)
Amundsen Basin	321	81.71	130.03	Sep 2012	PS80	SUIT	3	86 (67–111)
Amundsen Basin	345	85.25	123.84	Sep 2012	PS80	SUIT	6	67 (59–78)
Sophia Basin	31	81.55	19.58	June 2015	PS92	SUIT	5	121 (93–147)
Sophia Basin	38	81.32	16.31	June 2015	PS92	SUIT	1	118
Sophia Basin	39	81.65	11.82	June 2015	PS92	SUIT	2	96 (87–105)
Sophia Basin	43	82.15	7.07	June 2015	PS92	SUIT	1	63
Sophia Basin	47	81.38	13.65	June 2015	PS92	SUIT	3	109 (75–127)
Billefjorden°	39–40	78.62	16.55	Aug 2013	HE408	JFT	49	103 (80–130)
Kongsfjorden*	/	78.97	12.40	Jan 2013	HH	BT	60	145 (112–177)
Hornsund°	53–58	76.99	15.77	Sep 2013	HE408	JFT	11	113 (105–120)

Note. Latitude (Lat.) and longitude (Long.) are reported in decimal degrees. Sampling was conducted using a SUIT, bottom trawl (BT) or juvenile fish trawl (JFT) with the RVs *Helmer Hansen* (HH), *Heincke* (HE) and *Polarstern* (PS). Polar cod mean total length (mean L_T) with minimum and maximum range for each station is reported in millimetre. Fjords indicated with an asterisks (*) are predominantly influenced by Atlantic water masses, whereas fjords indicated with a degree symbol (°) are more influenced by Arctic water.

2.2 | Ethical statement

Polar cod were sampled and processed according to and within laws, guidelines and policies of the German Animal Welfare Organization and no specific permissions were required. The fish collected are neither endangered nor protected in the central Arctic waters and coastal waters of the Svalbard Archipelago. Polar cod were killed immediately after sampling.

2.3 | Study regions

Offshore regions and fjords of Svalbard are influenced by both warm Atlantic water, originating from the Gulf Stream, and cold Arctic water from the Polar Basin, in addition to local conditions (Walkusz *et al*., 2003). Billefjorden and Hornsund are predominantly influenced by Arctic water masses, whereas Kongsfjorden is largely dominated by warm water masses directly from the West-Spitsbergen Current (Cisek *et al*., 2017; Cottier *et al*., 2005; Table 1), hereafter referred to as Atlantic and Arctic fjords analogous to Nahrgang *et al*. (2014). These fjords differ significantly in salinity, water temperature, freshwater content, bloom dynamics, nutrient supply and species composition (Promińska *et al*., 2017; Walkusz *et al*., 2009). In the Eurasian Basin, two environmental regimes have been identified, coherent with the Amundsen and Nansen Basin (David *et al*., 2015; Flores *et al*., 2019). In 2012, sea ice in the Eurasian Basin originated from the Laptev Sea coast and drifted into the Amundsen Basin, whereas sea ice formed in the Kara Sea drifted into the Nansen Basin (David *et al*., 2016). In addition, surface salinity and nutrient concentrations were higher in the Nansen Basin than in the Amundsen Basin because of larger influence of Atlantic water (David *et al*., 2015).

2.4 | DNA extraction and DNA microsatellite amplification

DNA was extracted from fin clips with the spin-column protocol for purification of total DNA from animal tissues using the DNeasy Kit (Qiagen N.V.) according to manufacturer's instructions. Nine previously used DNA microsatellite loci (Nelson *et al*., 2013) were amplified in three multiplexed PCR reactions (Supporting Information Table S1). Each reaction consisted of 5 μl QIAGEN Multiplex Master Mix, 0.4 μl forward and reverse primer (multiplex 1, 2 and 3) and 10 ng template DNA. The forward primer was labelled with fluorescent green dye HEX or blue dye 6-FAM. PCR consisted of initial denaturation at 95°C for 15 min, followed by 30 cycles of 94°C for 30 s, 57°C for 1 min and 30 and 72°C for 1 min followed by a final elongation step at 60°C for 30 min. PCR products of multiplex 1 were diluted by 1:15, whereas products of multiplex 2 and 3 were diluted by 1:20. GeneScan™ 500 ROX™ size standard was added to the PCR products. Labelled fragments were separated on an automated capillary sequencer (ABI prism 310). DNA fragment sizes were determined using the Microsatellite Plugin v1.3 in the *Geneious* software v6.1.8 (Biomatters Ltd.; Kearse *et al*., 2012). The 250 bp peak of the GeneScan™ 500 ROX™ size standard was excluded from all analyses to fit the ladders. Automated scoring of microsatellite loci was manually checked for each sample. Microsatellite scoring was performed independently by three different persons to exclude subjective biases. Samples were screened for errors and abnormalities with the *MICRO-CHECKER* v2.2.3 software (Van Oosterhout *et al*., 2004).

2.5 | Statistical analyses

2.5.1 | Measures of genetic diversity

Each locus was analysed independently to avoid bias introduced by a single locus prior population level analyses. The number of alleles (A), expected (H_e) and observed (H_o) heterozygosity, Weir and Cockerham (1984) fixation index F_{ST} with 95% confidence intervals and inbreeding coefficient F_{IS} with 95% confidence intervals at each locus and per putative population were determined using the *diveRsity* package v1.9.90 (Keenan *et al*., 2013) in R (R Core Team, 2017). Nei's G_{ST}, Jost's D and Hedrick's G''_{ST} for each locus with 95% confidence intervals were also calculated with the *diveRsity* package after bootstrapping (10,000 permutations), as the different estimators are known to behave differently (Jost, 2008; Meirmans & Hedrick, 2011). The number of private alleles was estimated per putative population with the *poppr* package v2.8.1 (Kamvar *et al*., 2014). Allelic richness (AR) and private allelic richness (PAR) were calculated accounting for differences in sample size following rarefaction using the *HP-Rare* software v1.1 (Kalinowski, 2005). For each putative population and locus, departures from Hardy–Weinberg proportions (HWPs) were assessed after 10,000 permutations with R package *pegas* v0.10 (Paradis, 2010). Linkage disequilibrium tests were performed with *GENEPOP* v4.6 (Raymond, 1995; Rousset, 2008).

2.5.2 | Measures of population differentiation

Population differentiation was measured using pairwise F_{ST} comparisons according to Weir & Cockerham (1984) with R package *diveRsity* v1.9.90% and 95% confidence intervals were estimated after bootstrapping (10,000 permutations; Keenan *et al*., 2013). A discriminant analysis of principal components (DAPCs) was performed to assess genetic differentiation and clustering patterns. The analysis was conducted in R using *adegenet* package v2.0.0 (Jombart & Ahmed, 2011) based on 15 principal components and two discriminant functions. In this multivariate approach, variance in each individual is partitioned into a within-group and between-group component to maximize the discrimination (Jombart *et al*., 2010).

2.5.3 | Measures of population structure

Clustering analysis with *STRUCTURE* v2.3.4, which uses a Bayesian clustering approach to assign individuals to populations assuming markers are not linked and populations are panmictic, was performed with 10,000 burn-ins, 10,000 MCMC repeats, an admixture model and 10 iterations for each *K* from 1 to 10 (Hubisz *et al*., 2009; Pritchard *et al*., 2000). *STRUCTURE HARVESTER* Web v0.6.94 was used to visualize the output and to assess the most likely number of clusters (Earl, 2012). IBD was determined with R package *adegenet*. A Mantel test was performed to assess the correlation between

TABLE 2 Standard genetic diversity measurements of polar cod from six study regions based on nine microsatellite loci

Study site	N	A	PA	AR	PAR	H_o	H_e	PHWP	F_{IS}
Nansen Basin	18	38	0	3.28	0.10	0.58	0.52	0.69	−0.12 (−0.25, −0.07)
Amundsen Basin	21	42	1	3.51	0.19	0.52	0.55	1.00	0.03 (−0.08, 0.10)
Hornsund	11	35	0	3.45	0.19	0.46	0.53	0.73	0.12 (−0.11, 0.26)
Kongsfjorden	60	49	7	3.39	0.18	0.54	0.56	0.12	0.01 (−0.05, 0.07)
Billefjorden	49	48	7	3.37	0.22	0.48	0.54	**0.03**	0.10 (0.02, 0.17)
Sophia Basin	12	33	1	3.12	0.26	0.42	0.49	0.70	0.11 (−0.08, 0.19)

Note. A: number of alleles; AR: allelic richness after rarefaction; F_{IS}: inbreeding coefficient with 95% confidence interval; H_e: expected heterozygosity; H_o: observed heterozygosity; *N*: number of polar cod per study region; PA: number of private alleles; PAR: private allelic richness after rarefaction; PHWP: *P*-values for the likelihood of deviating from Hardy–Weinberg proportions ($P < 0.05$ marked in bold).

geographic and pairwise genetic distance using R package *ade4* (Dray & Dufour, 2007). Statistical power of the microsatellite data to detect genetic differentiation was estimated using *POWSIM* v4.1 (Ryman & Palm, 2006). This is achieved by varying the number of generations of drift while keeping effective population size constant. The following POWSIM settings were used: 1000 dememorizations, 1000 iterations per batch and 100 batches. The statistical power for two different effective population sizes (N_e = 1000, N_e = 10,000) was simulated. The power of these tests can be interpreted as the percentage of significant outcomes for predefined F_{ST}-values (F_{ST} = 0.001, 0.01 and 0.05) following Wright (Wright, 1984).

2.5.4 | Data availability

The microsatellite trace files, Genepop file, metadata and R markdown that support the findings of this study are publicly available on Zenodo (https://doi.org/ 10.5281/zenodo.4557603). The occurrence metadata is cross-linked on the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/96epc7).

3 | RESULTS

3.1 | Genetic diversity of polar cod

A total of 171 polar cod juveniles from six study regions were successfully genotyped. Population genetic parameters such as observed number of alleles (A), expected and observed heterozygosity (H_e, H_o), probabilities of HWPs (PHWPs), inbreeding coefficient F_{IS} and fixation index F_{ST} with 95% confidence intervals are summarized for each locus in Supporting Information Table S1. The number of alleles across all 171 individuals ranged from four (*gmo8*) to nine (*bsa6* and *bsa60*). Heterozygosity among loci ranged from 0.09 (*gmo8*) to 0.75 (*bsa101*). Locus *gmo34* showed a significant fixation index (F_{ST} = 0.001). Three other indices for genetic differentiation, including Nei and Chesser's G_{ST}, Hedrick's corrected standardized fixation index G'_{ST} and Jost's D with 95% confidence intervals, are summarized for each locus in Supporting Information Table S2. No loci were significant for these three genetic differentiation indices, which is in accordance with Weir and Cockerham's F_{ST} (except for locus *gmo34*).

Rarefied AR was highly similar among study regions, with the lowest AR in the Sophia Basin (AR = 3.12) and the highest in the Amundsen Basin (AR = 3.51; Table 2). The highest average of private alleles per sample was found in the Sophia Basin (PAR = 0.26). The lowest average of private alleles per sample was found in the Nansen Basin samples (PAR = 0.10). Observed and expected heterozygosity values were similar among the study regions, with observed heterozygosity ranging from 0.42 to 0.58 from the Sophia Basin to the Nansen Basin, respectively. Five of the 54 tests for conformity to HWPs per locus per study site were significant following Bonferroni correction (Supporting Information Table S3). These included three tests in the Billefjorden samples and one test in the Sophia Basin and Kongsfjorden samples, respectively. The inbreeding coefficient in the populations ranged from −0.12 to 0.12, with the highest values in Hornsund and the Sophia Basin (F_{IS} = 0.12 and F_{IS} = 0.11, respectively) (Supporting Information Table S3). Tave (1993) suggested an inbreeding coefficient of 0.05 as a conservative estimate and 0.10 as a tolerable measurement. Yet, there is no unified theory to explain inbreeding levels (Slate *et al*., 2004; Tian *et al*., 2017). Linkage disequilibrium tests revealed possible linkage in two of the 216 pairwise comparisons: loci *bsa7-bsa60* ($P < 0.001$) for Kongsfjorden samples and loci *gmo34-bsa6* ($P = 0.03$) for Billefjorden samples.

3.2 | Population differentiation and structure

Pairwise F_{ST} values among all six locations indicated a lack of genetic differentiation with all confidence intervals overlapping zero for both F_{ST} (Table 3) and Jost's D (Supporting Information Table S4). The DAPCs considered individuals from the same study regions as *a priori* defined groups based on 15 PCs. DAPC showed no obvious genetic divergence between these groups (Figure 2). Accordingly, STRUCTURE did not resolve any population clustering for K = 2–4 (Supporting Information Figure S1). All study regions shared the same colours, referring to genotypes, proportionally, indicating no clear population structure. The Mantel test between

TABLE 3 Pairwise F_{ST} (after Weir and Cockerham) values of polar cod for each study site pair (lower diagonal) with 95% confidence intervals after 10,000 bootstraps (upper diagonal) based on nine microsatellite loci

	Nansen Basin	Amundsen Basin	Hornsund	Kongsfjorden	Billefjorden	Sophia Basin
Nansen Basin		[−0.0359, 0.0224]	[−0,0563, 0.0395]	[−0.0239, 0.0168]	[−0.0279, 0.0166]	[−0.0520, 0.0433]
Amundsen Basin	−0.0121		[−0.0451, 0,0403]	[−0.0205, 0.0172]	[−0.0236, 0.0164]	[−0.0435, 0.0334]
Hornsund	−0.0190	−0.0109		[−0.0390, 0.0280]	[−0.0434, 0.0253]	[−0.0670, 0.0575]
Kongsfjorden	−0.0074	−0.0059	−0.0127		[−0.0105, 0.0116]	[−0.0267, 0.0336]
Billefjorden	−0.0093	−0.0076	−0.0165	−0.0014		[−0.0340, 0.0314]
Sophia Basin	−0.0141	−0.0136	−0.0185	−0.0042	−0.0094	

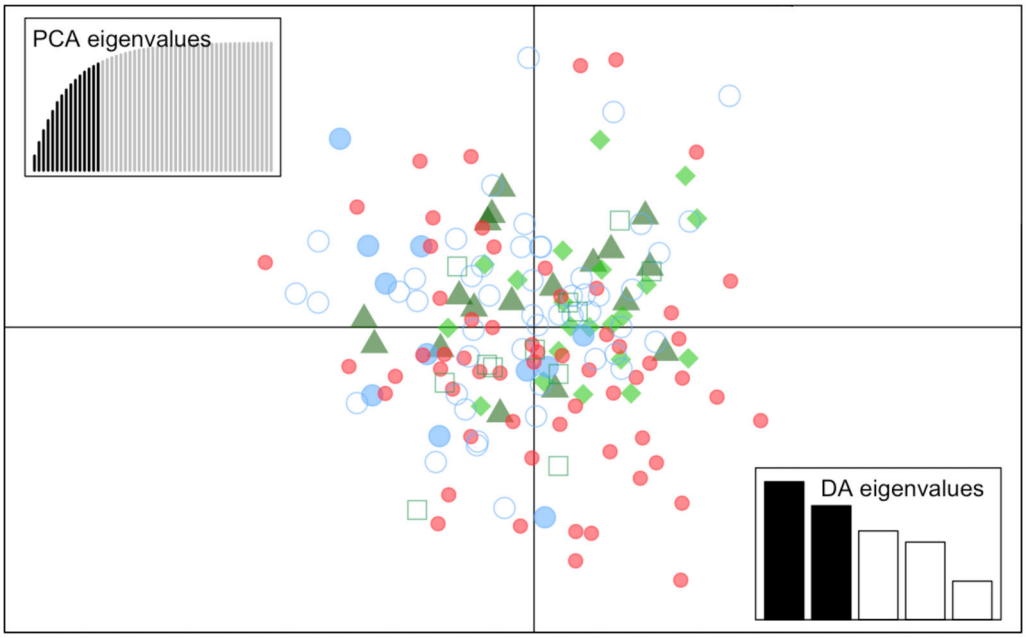

FIGURE 2 Population clustering of polar cod (*Boreogadus saida*) described by discriminant analysis of principal components (DAPCs) using 15 principal components and two discriminant functions based on nine microsatellites. Each symbol corresponds to individuals sampled in one study region. Eigenvalues of the discriminant functions and principal components are shown in the insets (▲) Nansen Basin, (◆) Amundsen Basin, (●) Hornsund, (●) Kongsfjorden, (○) Billefjorden, (□) Sophia Basin

TABLE 4 Power analysis of simulated data with POWSIM v4.1

	F_{ST}		
Effective population size (N_e)	**0.005**	**0.01**	**0.05**
1000	0.636	0.974	1.000
10,000	0.658	0.961	1.000

Note. Three levels of population differentiation (F_{ST} = 0.005, 0.01, 0.05) were pre-defined with effective population sizes N_e = 1000 and N_e = 10,000. The simulation was replicated 1000 times.

geographic and pairwise genetic distance based on exact coordinates and not *a priori* defined groups did not reveal a pattern of isolation by distance. There was no correlation between pairwise locality and genetic distance, indicating that geographic distance between groups does not explain genetic variability in the sampled areas (r = −0.27, P = 0.97). An analysis of statistical power to detect genetic differentiation between populations using POWSIM showed that the amount of microsatellite loci and samples sizes used in this study were sufficient for detecting low levels of genetic differentiation corresponding to F_{ST} = 0.005–0.05 (Table 4).

4 | DISCUSSION

The authors found no significant genetic population structure among polar cod populations at local to regional spatial scales. All microsatellite markers showed overall high rates of amplification success (96.2%) and suitable levels of polymorphism for population genetic analysis. Genetic diversity was generally moderate to high with little differences in AR and observed heterozygosity among study regions. No correlation between genetic and physical distance was apparent.

The highest number of alleles was observed in Kongsfjorden and Billefjorden, localities from where most individuals were available, which likely explains the higher allelic diversity. Indeed, when accounting for sample size, AR ranged from 3.12 (Sophia Basin) to 3.51 (Amundsen Basin), indicating that no strong clines in genetic diversity were present. The lower number of individuals from some localities did not affect the sensitivity of the results of this study, as the power analysis of microsatellite data of the authors showed a high probability of detecting population differentiation if present. Furthermore, the pairwise F_{ST} comparisons using various estimators revealed a striking absence of genetic differentiation among all samples. Accordingly, individual-based clustering failed to detect structure between locations. Therefore, this study very likely pointed to regular gene flow that erased signals of genetic divergence.

The lack of geographic genetic differentiation is in agreement with several previous studies on polar cod populations in both the North Pacific Ocean and the North Atlantic Ocean, and based on various molecular markers (Fevolden *et al*., 1999; Pálsson *et al*., 2009; Wilson *et al*., 2017). Nonetheless, a comparable analysis focusing on samples from Greenland and Svalbard found low but significant genetic differentiation between some fjords and open ocean samples (Madsen *et al*., 2016). As this is the only study indicating genetic differentiation over local (*c*. 200 km) to regional distances (*c*. 1000–1500 km), it remains to be confirmed how common such a pattern is. The results of this study suggest no differentiation over local to regional distances (*c*. 200–2000 km). Accordingly, isolation by distance is not present in polar cod populations on a regional scale (Fevolden *et al*., 1999; Madsen *et al*., 2016; Wilson *et al*., 2017), although a correlation between F_{ST} and physical distance was found over the entire species range (Nelson *et al*., 2020). Nonetheless, this pattern does not explain the homogeneity within regional groups such as the Canadian Arctic (Nelson *et al*., 2020) and the Eurasian Basin (this study). The results of this study provide further evidence that at least regionally, the population genetic dynamics of polar cod is not a function of physical distance but of more complex dynamics. In this study, the authors discuss several, not mutually exclusive scenarios potentially explaining the lack of genetic differentiation of polar cod in fjords of West-Svalbard and the Eurasian Basin: (a) high levels of genetic diversity are maintained by large census population size; (b) high gene flow maintains a single well-connected metapopulation in the Eurasian Arctic Ocean and (c) the apparent homogeneity revealed by neutral microsatellite loci might be underlain by adaptive heterogeneity elsewhere in the genome. These are described in detail below.

The lack of genetic structure and moderate to high diversity may be explained by a large population size. Large populations are expected to be more genetically diverse and to limit genetic drift. Conversely, small population sizes generally result in low genetic diversity and the loss of alleles (Frankham, 1996). Polar cod is one of the most widespread and abundant species in the Arctic Ocean (Craig *et al*., 1982; David *et al*., 2016; Falk-Petersen *et al*., 2011). The exact population sizes during sampling events are not known for all locations, but the literature provides some estimates. Like other gadoids, fecundity is high and ranges from 9000 to 67,000 eggs per female (Gjosaeter *et al*., 2020; Hop *et al*., 1995). Nahrgang *et al*. (2014) reported estimates of expected lifetime fecundity of each female, assuming iteroparity (multiple reproductive cycles), to be twice as high in Arctic-influenced fjords compared to Atlantic-influenced fjords (up to 75,000 and 39,000 eggs per female, respectively). Although the mortality rate for polar cod eggs is not known, Marsh *et al*. (2020) estimated a 10% survival chance of age 0 polar to age 1 on average in the Barents Sea. Moreover, spawning areas around Svalbard are becoming more important in terms of abundance in comparison to the declining southeastern Barents Sea polar cod stock (from 1.8 million tonnes in 2005 to 0.1 million tonnes in 2014) (Eriksen *et al*., 2020). At the time of sampling in the Nansen and Amundsen Basins in 2012, polar cod in the Eurasian Basin was ubiquitous with a median abundance of at least 5000 ind. km^{-2} (David *et al*., 2016). Yet, most of polar cod's under-ice habitat remains undersampled, especially in the High Arctic; so abundance estimates are associated with large uncertainty.

There are several ecological traits of polar cod that support the view of a typical marine high gene flow species. Polar cod perform large-scale migrations to spawning and feeding grounds in the vicinity of the ice edge (Fevolden *et al*., 1999; Welch *et al*., 1993). Buoyant polar cod eggs and planktonic young of the year (0-group) are primarily caught in surface waters (Hunter, 1979; Sekerak, 1982), where they disperse and are transported over considerable distances from their spawning areas (Sekerak, 1982). Young polar cod could migrate with sea ice as formulated in the "sea ice drift hypothesis" (David *et al*., 2016). Consequently, juvenile polar cod from the Siberian shelf might recruit to populations in the Greenland Sea, Svalbard and Barents Sea by advection with the Transpolar Drift (David *et al*., 2016). In conjunction with adult migration, this scenario of extensive dispersal at the egg, larva and juvenile stage would explain high levels of connectivity throughout the North-Atlantic and Eurasian distribution range of polar cod, resulting in no distinct genetic differentiation between populations as found in this study and Nelson *et al*. (2020). Following the sea ice back-tracking data of David *et al*. (2016), conducted at the same study sites in the Eurasian Basin as this study, it is highly likely that the juveniles from the Nansen and Amundsen basins originate from the Kara and Laptev Seas, respectively. The absence of genetic differentiation between these samples indicates a higher connectivity between the Siberian spawning grounds than anticipated. Possibly, juveniles mix effectively in the offshore Arctic Ocean before migrating to different spawning grounds to complete their life cycle. The latter would imply that a significant part of the population does not display natal homing behaviour. Observations of both mature individuals and juveniles broadly distributed in and around waters west and south of Svalbard indicate local spawning, apart from the assumption that polar cod conduct spawning migrations (Bergstad *et al*., 1987; Gjøsæter, 1973; Hognestad, 1966; Nahrgang *et al*., 2014). Accordingly, polar cod in the Barents Sea likely belong to local populations also inhabiting the White and Kara Seas (Bergstad *et al*., 1987; Ponomarenko, 1967). It is hypothesized that polar cod from the Kara Sea actively migrate to the Barents Sea for propagation (Antonov *et al*., 2017), with major spawning grounds

along the Novaya Zemlya archipelago (Ponomarenko, 2000). Yet, polar cod also seem to spawn locally in the Kara Sea (Moskalenko, 1964). All these observations point to a continuous connectivity of the Eurasian polar cod stocks, both along the shelves and across the CAO.

The apparent genetic homogeneity of polar cod in this study could not exclude significant heterogeneity in adaptive variation elsewhere in the genome. An increasing number of studies have found genetic evidence of local adaptation in various marine fishes (Andersen *et al*., 2008; Hemmer-Hansen *et al*., 2007; Lamichhaney *et al*., 2017; Tine *et al*., 2014). Moreover, previous studies support the view that genetic diversity and associated evolutionary potential are retained in the long-term mainly via standing genetic variation, despite selection driving evolution of divergent adaptations (Bernatchez, 2016). So far, most research suggests that polar cod form genetic sub-populations at the basin scale at most (Fevolden *et al*., 1999; Pálsson *et al*., 2009; Wilson *et al*., 2017). Yet, some local retention and/or varying selection regimes between fjord and (different) oceanic habitats as indicated in Madsen *et al*. (2016) is possible. Differences in gonadal development may exist between populations inhabiting fjords of Svalbard under the influence of different water masses (Nahrgang *et al*., 2014). Furthermore, a wide range of age composition, size and growth rates between polar cod in the Barents and Kara Seas might indicate their origin from distinct populations (Antonov *et al*., 2017). In addition, various morphotypes of polar cod regarding body morphometry and coloration have been described in the Kara, Laptev and Pechora Seas (Chernova, 2018; Moskalenko, 1964). One type associated with the open sea and the other type associated with coastal waters might imply that polar cod occur in genetically distinct stocks (Fevolden *et al*., 1999). A combination of high inflow of polar cod larvae from open-ocean spawning grounds despite advection of local polar cod eggs and larvae might explain the absence of a geographical pattern and lack of isolation by distance. Similar larval gene flow scenarios have been observed in Atlantic cod (Knutsen *et al*., 2004; Knutsen *et al*., 2007). Overall, despite potential spatially divergent selection regimes and local recruitment, genetic homogeneity may occur when connectivity and dispersal rates are sufficiently high (Adkison, 1995).

Given the documented phenotypic and environmental variations among polar cod populations, using a high number of genetic markers, such as SNPs, could provide a powerful tool for tracing local selection pressure (Benestan *et al*., 2015; Nielsen *et al*., 2009; Storz, 2005). Barth *et al*. (2019) found relatively widespread local directional selection associated with environmental factors on several geographical scales in Atlantic cod populations. This might as well be the case for polar cod populations. In addition, epigenetic mechanisms induced by particular environmental variables might contribute to the observed phenotypic differentiation (Johnson & Kelly, 2020). Significant genetic differentiation between populations over short spatial scales would imply low levels of dispersal (Palumbi, 2003), which seems an unlikely scenario for the polar cod populations studied here. Mechanisms such as local retention of planktonic eggs and larvae and/or homing behaviour of adults to their natal spawning grounds could contribute to polar cod's genetic structuring but might be masked by high levels of dispersal, and well-connected populations are not detectable by the microsatellite loci used.

Climate-induced pressures may cause genetically based adaptive evolution in population-specific traits such as thermal responses, dispersal, body size and reproductive timing (Franks & Hoffmann, 2012; Muñoz *et al*., 2015). In addition, fishing pressure has led to measurable changes in life-history traits such as post-maturation growth rate and reproductive investment (Heino *et al*., 2015). Even though polar cod is presently not commercially harvested, fisheries will increasingly take place in ice-free zones (Christiansen *et al*., 2014). Because fishing pressure is often concentrated in specific areas (Engelhard *et al*., 2014), the risk for extinction of local populations and irreversible changes to the gene pool is high (Árnason *et al*., 2009). Genetic connectivity along sea ice pathways as indicated here is important to avoid future fragmentation of polar cod populations. Otherwise spatially variable effects of climate change, harvesting and/or competition with boreal species such as Atlantic cod could lead to loss of local genetic variability or populations. The migratory behaviour, the spatial and temporal specificities of spawning, and the nursery and feeding grounds of polar cod remain poorly documented. An increased understanding of basic life-history properties is vital to enable predictions of the species' fate in the near future (Steiner *et al*., 2019). In view of the existing phenotypic variance and plasticity between distinct geographical populations, high resolution documentation of the genomic variation and structure of polar cod is needed to resolve the genetic structure and adaptive potential across large spatial and temporal scales.

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AUTHOR CONTRIBUTIONS

S.M.M., H.F. and H.C. conceptualized the study. H.F., F.C.M. and M.L. collected the samples. S.M.M., F.C.M. and M.L. created the data. S.M.M. and H.C. analysed the data and interpreted the findings. S.M.M. wrote the first draft of the manuscript. All the authors contributed to the interpretation of the findings and detailed manuscript revision.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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