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New evidence for the establishment of coastal cod *Gadus morhua* in Svalbard fjords

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ABSTRACT: The Arctic is experiencing increasing water temperatures, leading to a northward shift of Atlantic species into Arctic waters. Arctic marine ecosystems are therefore subject to substantial changes in species distributions and occurrence due to anthropogenic climate change. Atlantic cod is one of the most important commercial fish species in the northern seas. The largest known stock is the migrating Northeast Arctic cod (NEAC) that is distributed along the Norwegian coast, the Barents Sea and off Svalbard. Atlantic cod in Svalbard waters are generally reported in the literature as belonging to the NEAC ecotype. The more stationary coastal cod (CC) spawn together with NEAC in the Lofoten region and several other areas along the Norwegian coast. The aim of this study was to investigate the population structure of Atlantic cod in Svalbard waters. We used single nucleotide polymorphic (SNP) markers, the pantophysin locus (*Pan* I) and otolith structure to categorize the 2 cod ecotypes collected in Svalbard fjords between 2017 and 2019. Our results show that both NEAC and CC appear in Svalbard fjords and revealed that 0-group and adult CC individuals caught in Svalbard fjords differ genetically from those along the Norwegian coast, indicating a separation into a local Svalbard CC population. The establishment of CC in Svalbard fjords may be another keystone of the ongoing borealization of the Arctic, with consequences for the local Arctic fjord ecosystem.

KEY WORDS: Arctic · Climate change · Kongsfjorden · Otolith shape analysis · Population genetics · Cabled coastal observatory

1. INTRODUCTION

The Arctic is facing substantial changes as a result of oceanic warming (Polyakov et al. 2005) and Arctic sea ice loss (Christiansen et al. 2014). Consequences of increasing water temperatures include northward shifts of boreal species into Arctic waters (Fossheim et al. 2015). The increased water temperatures and subsequent higher food availability in the northern Barents Sea and Svalbard have also been identified as driving forces for migration toward the Arctic (Misund et al. 2016). Both warm and cold water masses characterise the hydrography around Svalbard and adjacent fjords. Cold water from the Arctic Ocean moves southward, mainly along the east coast of Svalbard (Eriksen et al. 2020), and influences the hydrography of the region; for example, towards polar conditions in Hornsund. In contrast, warm, highly saline Atlantic water originating from the Norwegian Atlantic Current (NwAC) and the Gulf Stream is transported northward by the diverging West Spitsbergen Current (WSC) along the west coast of

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Svalbard (Cottier et al. 2005). Therefore, fjords on the west coast of Svalbard, such as Isfjorden and Kongsfjorden, are typical Atlantic-influenced warmer fjords (Beszczynska-Möller et al. 2012). The hydrography of the Kongsfjorden system has been observed for several years, with moorings in deep waters and cabled underwater observatories in shallow areas (Fischer et al. 2017, Hop et al. 2019a). There has been a significant increase in water temperature over the last few years (Hop et al. 2019a, Fischer et al. 2021). For example, the inflow of warm water into Kongsfjorden beginning in the winter of 2005–2006 prevented the fjord from being completely covered by ice (Cottier et al. 2007) for more than a decade until 2020, when an exceptionally cold winter resulted in ice covering the inner region of the fjord (L. Spotowitz pers. obs.).

Like salinity and food availability, water temperature is one of several environmental factors playing a key role in the recruitment, spawning, migration and distribution patterns of Atlantic cod *Gadus morhua* (Ottersen et al. 2006). Atlantic cod is a key species in the North Atlantic across Norway, Iceland, Greenland and the Barents Sea up to Canada (Jónsdóttir et al. 2002, Berg et al. 2016), widely distributed along the continental shelves from 40–80° N (Sundby 2000, Neat & Righton 2007). Its northernmost distribution extends to the west and north coast of Svalbard, but Svalbard fjords are rarely included in stock assessment surveys. Over recent decades, reports have shown that specimens in the Svalbard area belong to the Northeast Arctic cod (NEAC) stock (Brander 2005). This stock undergoes a seasonal migration between its main spawning grounds in the Lofoten region, extending southward to Møre and northward to Finnmark (Brander 2005, Sundby & Nakken 2008), and feeding grounds in northern waters following its main prey, capelin (Mehl et al. 1985). Eggs and larvae of NEAC are transported passively by the Norwegian Coastal Current from the Norwegian coast towards Svalbard and the Barents Sea. At the end of their pelagic transport phase, the cod larvae settle down and remain in the settlement area for the first 2 yr of their life, only performing small seasonal migrations. With increasing age, the migration extends towards the foraging grounds in the Barents Sea and the spawning grounds along the Norwegian coast (Brander 2005, Ottersen et al. 2014).

There is a second ecotype of Atlantic cod, the Norwegian coastal cod (CC), that inhabits the Norwegian coast and adjacent fjords and does not perform long-distance migrations (Michalsen et al. 2014, Johansen et al. 2018). Although NEAC and CC use some of the same spawning areas along the Norwegian coast, mingling and interbreeding appear to be limited (Nordeide 1998, Johansen et al. 2018, Jorde et al. 2021). The spawning areas of CC in most of the fjords and coastal areas consist of smaller side bays (Jakobsen 1987). Peak spawning of NEAC takes place from mid-March to mid-April (Pedersen 1984); spawning of CC can occur 3–4 wk later than NEAC (but may vary between latitudes) and lasts for a longer period. Vertical segregation is partly observed, with NEAC being more abundant in deeper water than CC (Nordeide 1998). NEAC and CC share some spawning sites and, in some areas, time of spawning, and like the eggs of the NEAC, CC eggs are transported with the Norwegian Coastal Current from the Norwegian coast towards Svalbard fjords. Over recent decades, the cold hydrographic regime in the local fjords has impeded potential settlement, but this situation may have changed in recent years. Increasing water temperatures along the Norwegian coast may decrease egg survival and result in a reduction of suitable spawning habitat (Dahlke et al. 2018). The question arises if warming may also provide more suitable spawning conditions for Atlantic cod on the Svalbard shelf and within fjords due to decreased sea ice cover. The potential settlement of CC in Svalbard fjords deserves attention, specifically regarding the extent to which more favourable hydrographic conditions can promote habitat suitability.

Atlantic cod has a general thermal niche between −1.5 and 19°C and requires lower temperatures of 1–8°C during spawning season (Righton et al. 2010). Past reports have shown that feeding grounds in the northern Barents Sea and Svalbard waters are as cold as −1°C (Ottersen et al. 1998). But certain fjords on the west coast of Svalbard experience different temperature regimes depending on the inflow of colder, less-saline Artic water masses or warmer, more saline Atlantic water masses. Changes in the Arctic hydrographic regime, such as an increased inflow of warm water masses towards Svalbard, have the potential to be involved in the changing distribution patterns of CC.

Few fishing activities have been conducted in Svalbard waters because of the harsh winter conditions and the continuous seasonal ice coverage that has historically extended south as far as Bear Island (Iversen 1934). For approximately 140 yr, Norwegian fishermen have used the Svalbard shelf fishing grounds, reporting high fluctuations in the number of Atlantic cod caught (Iversen 1923, Misund et al. 2016). Early Arctic warming scenarios observed from

the 1920s–1930s and 1950s–1960s complement these fluctuations and display the dependency of Atlantic cod on specific water temperatures (Drinkwater 2006, 2009).

Stock identification plays a key role when considering environmental adaptation, but also in the assessment of the productivity of a fish population. Tools for stock separation have only become available over the last few decades, so until that time, it was assumed that all Atlantic cod in Svalbard waters belonged to NEAC. No studies have evaluated whether CC was also present in northern waters and able to survive and settle in the fjords due to the warmer water.

Over the years, several methods for cod stock identification have been established. An older approach to differentiate between cod stocks is based on the number of vertebrae. NEAC and CC can be discriminated in this way, as a fixed number of vertebrae are formed during the embryonic phase. However, according to Løken et al. (1994), vertebral counts can only serve as an indicator because the final number is affected by environmental factors such as temperature.

Otoliths have been used for decades to estimate the age of fish based on the inner structure of annual growth zones (Campana & Thorrold 2001). Rollefsen (1933) observed differences between NEAC and CC in the shape and size of the 2 innermost zones. The classification of 5 different otolith types as described by Jakobsen (1987) and Mjanger et al. (2000) is currently accepted. Type 1 describes a typical CC, and Type 2 describes an uncertain CC. Otoliths from the Bear Island and Svalbard areas were defined as Type 3. Type 4 is an uncertain NEAC, and Type 5 is a typical NEAC. In addition to the inner otolith shape (Berg et al. 2005), Stransky et al. (2008) used outer otolith shape analysis based on Fourier descriptors, a widely applied morphological approach to stock identification (Stransky 2014), to investigate the differences between CC and NEAC. Other otolith-based stock identification methods use the microchemical composition of the otoliths or stable isotope relationships (Campana & Gagné 1995, Kerr & Campana 2014). In this framework, Andrade et al. (2020) laid the foundation for the hypothesis of a potential settlement of CC on Svalbard based on otolith chemistry.

Genetic markers, such as microsatellites and single nucleotide polymorphic markers (SNPs), have become more valuable for stock separation in recent years (Skarstein et al. 2007, Wennevik et al. 2008, Johansen et al. 2018, 2020). The pantophysin locus (*Pan* I) is a membrane protein known to be attributed to temperature and depth, both of which are relevant for migratory behaviour (Pampoulie et al. 2008, Fevolden et al. 2012). *Pan* I is also frequently used to differentiate between NEAC and CC (Fevolden & Pogson 1995, Sarvas & Fevolden 2005) and in real-time monitoring of the 2 ecotypes (Dahle et al. 2018, Johansen et al. 2018). Allele frequency differs among ecotypes, with high frequencies of the *Pan* I^{AA} genotype characteristic of CC and *Pan* I^{BB} predominating in NEAC (Fevolden & Pogson 1995, Stransky et al. 2008, Wennevik et al. 2008, Dahle et al. 2018). A set of multiple SNPs can be used for genotyping source populations and identifying genetically distinct groups (Therkildsen et al. 2013). A panel of 40 SNPs were developed and can complement the *Pan* I analysis in identifying the 2 ecotypes (Johansen et al. 2018). This panel of SNP loci are located across 11 of the 23 chromosomes in cod and can assign the individual to CC or NEAC with high certainty (Johansen et al. 2018, Jorde et al. 2021). SNPs provide insight into the genetic structure of Atlantic cod independent of environmental factors and are particularly useful in differentiating the cod ecotypes (Hemmer-Hansen et al. 2011, Berg et al. 2016, Johansen et al. 2020, Jorde et al. 2021).

In the present study, we analysed the genetic composition of Atlantic cod collected over 2 yr from different fjords on Svalbard and compared these individuals to reference samples from the Norwegian coast and Bear Island (Barents Sea). In addition, we analysed the shape of the inner and outer otolith to complement the genetic analysis. Our goal was to evaluate the genetic population structure of Atlantic cod and to provide a substantial survey of the different Atlantic cod ecotypes in Svalbard fjords.

2. MATERIALS AND METHODS

2.1. Sampling campaigns

Atlantic cod were collected during several research cruises to Svalbard between 2017 and 2019 (see Table 1), with sampling conducted between August and October each year. In addition, individuals from a location close to Hammerfest (HAFE) were collected in July 2017 as a reference sample for the Norwegian CC. Furthermore, reference samples of both CC and NEAC, caught in the Lofoten area during spawning in 2003 (LOE: Lofoten East; LOW: Lofoten West), were added to the SNP analysis (Fig. 1). Fin clips and muscle tissue were collected

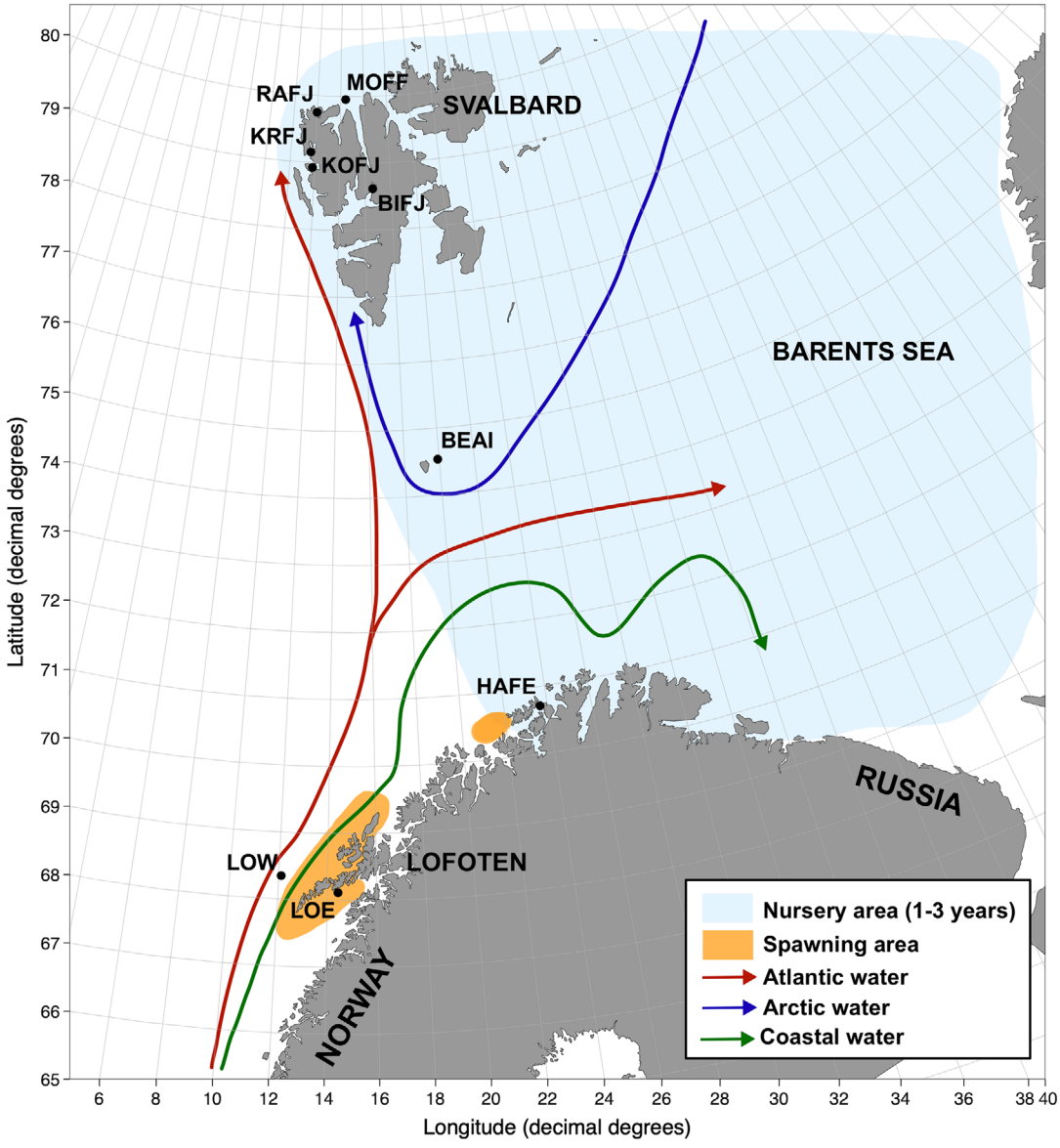

Fig. 1. Sampling sites for Atlantic cod around Svalbard, Bear Island and the coast of northern Norway. MOFF: Moffen; RAFJ: Raudfjorden; KRFJ: Krossfjorden; KOFJ: Kongsfjorden; BIFJ: Billefjorden; BEAI: Bear Island; HAFE: Hammerfest; LOW: Lofoten West; LOE: Lofoten East

and stored in 96% ethanol at −20°C. In addition, sagittal otoliths were removed and stored dry. Length and weight parameters were measured for all individuals used in this study, except for the HAFE samples, for which no weight was determined. Different fishing gears were used in this study, depending on the available platform/infrastructure and different targeted fish sizes.

Sample collection was conducted during 4 separate expeditions. (1) In July 2017, individuals were obtained in HAFE by recreational fishing with a fishing rod. A total of 29 individuals were caught; 16 were used for genetic and otolith shape analysis. (2) In August 2017, cod were collected within the framework of a University of Svalbard (UNIS) research cruise with the RV 'Helmer Hanssen' to investigate the benthic community in several fjords on Svalbard. A total of 156 individuals were caught with benthic and pelagic trawls in Kongsfjorden. (3) Between September and October 2018, 348 specimens were caught during the research cruise HE519 of the RV 'Heincke'. Fish were collected from Bear Island, Hornsund, Billefjorden, Kongsfjorden, Krossfjorden, Raudfjorden and Moffen. Cod were caught with a

bottom trawl net, a pelagic net and a fish lift (Holst & McDonald 2000) for juvenile fish. A total of 176 fish were used for genetic analysis and 170 for otolith shape analysis. (4) In September 2019, a local fishing campaign was performed in Kongsfjorden, Svalbard, specifically for juvenile Atlantic cod. A total of 62 individuals, most of them 0-group individuals, were caught with beach seine in the harbour of Ny-Ålesund.

2.2. DNA extraction

DNA was extracted from frozen muscle tissue and ethanol-preserved fin clips using the Qiagen QIAamp DNA Mini and Blood Mini protocol. For extraction, we used the Qiagen QIAamp DNA Mini Kit. The concentration and quality of the extracted DNA were assessed using a Thermo Fisher Scientific NanoDrop ND-1000 UV-Vis spectrophotometer. Based on the results, a dilution with a concentration of 20 ng μl^{-1} was prepared for the *Pan* I and SNP analyses.

2.3. Genetic analysis

Fish stock population structure can be analysed using a genotyping approach with SNPs. These SNPs are measure of genetic variation and are independent of environmental variables even though correlation can be observed (Berg et al. 2015). Cod were genotyped by *Pan* I and 40 SNP markers (see Table 1) to assign them to either the NEAC or CC ecotype, as described by Johansen et al. (2018). The markers are a combination of SNPs across 11 chromosomes, with chromosomes 1, 2, and 7 showing the highest differentiation between the 2 ecotypes (Johansen et al. 2018); the combination of all SNP markers also shows genetic variation within CC (Jorde et al. 2021). *Pan* I was genotyped using an allele-specific TaqMan assay adapted to a Roche Lightcycler 480 II real-time PCR instrument (Roche Diagnostics), and the SNPs were genotyped using matrix-assisted laser desorption/ionization time-of-flight mass spectroscopy (MALDI-TOF MS) assays (Agena Bioscience). Genotyping was performed using the IPLEX® protocol, following the manufacturer's instructions (Agena Bioscience). MassARRAY Typer software was used for automated genotype calling (Agena Bioscience). SNPs with more than 20% missing data per sample were discarded, resulting in 38 SNPs remaining for subsequent statistical analyses. Missing values among the total sample (including reference samples) averaged 8.3% SNP^{-1}.

2.4. Statistical analysis of SNP

Departure from Hardy-Weinberg Equilibrium (HWE) was tested in each sample separately, locus by locus, using the 'genepop' v.1.1.4 package (Rousset 2008) in R (R Core Team 2021). Corrections for multiple testing (i.e. false discovery rate) were performed according to the Benjamini-Hochberg procedure, with a Q-value of 0.05 as a threshold for significance (Benjamini & Hochberg 1995). Observed and expected heterozygosity (H_o and H_e) within each sample and at each locus and the fixation index (F_{ST}), measuring genetic variance, were calculated using genepop. The weighted average of F_{ST} values (10 000 permutations) between all pairwise samples was all calculated in genepop and corrected for multiple testing. The independent allele frequency and no admixture model in STRUCTURE v.2.3.4 (Pritchard et al. 2000) was used to assign the individual cod to its corresponding ecotype. To identify clusters in the data set, 7 independent runs and 10 repetitions for each value of K (=assumed populations or groups) were performed, with a burn-in period of 300 000 followed by 1 000 000 Markov chain Monte Carlo iterations. Delta K and the best K-value for the data set were identified via the online web page STRUCTURE HARVESTER (Earl & von Holdt 2012), using the Evanno method (Evanno et al. 2005). CLUMPP v.1.1.2 (Jakobsson & Rosenberg 2007) was used to generate a permuted outfile. A STRUCTURE bar plot, based on the outfile created with CLUMPP, was generated in R with the package 'ggplot2' v.3.3.5 (Wickham 2016).

2.5. Otolith analysis

For age determination and identification of ecotypes, sagittal otoliths were used. The otoliths were removed immediately after individuals were caught and were stored dry. Visual inspection of the shape of the inner otolith (see Section 2.6) was used to assess the ecotype of each fish. In addition, based on the genetic results, an outer otolith shape analysis was performed to reveal possible significant traits which could help identify the different ecotypes only via outer shape analysis (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m696p119_supp.pdf).

For analysis of outer otolith shape, otoliths from individuals with a size range of 40–80 cm were used to minimise the effects of morphometric variation. At some sampling sites, only juvenile individuals (smaller than 40 cm) were caught and these were therefore excluded from the analysis due to varia-

tions in growth patterns. Otoliths were cleaned with water and a brush, and the outlines were digitised using a Leica M80 stereo microscope with a Leica DFC420 camera and Leica KL200 LED light source. Pictures were colour-corrected using the imaging software Leica Application Suite (LAS Core), and colour was inverted for further processing in RStudio v.1.3.1093 (RStudio Team 2021). To assess the stock-dependent differences in outer otolith shape, the R package 'ShapeR' v.0.1-5 (Libungan & Pálsson 2015) was used. The package uses Fourier and wavelet transforms to extract the outlines and visualise the shape of the otoliths. The results of the ShapeR analysis (Fig. S2) were used to further analyse significant variation among groups based on ANOVA testing, which was also implemented in RStudio.

2.6. Otolith classification

A total of 175 cod specimens were separated into CC and NEAC based on the structure of growth zones in the otoliths, as described by Rollefsen (1933, 1934). This method has been used in Norway for more than 50 yr to distinguish between the 2 cod ecotypes. After breaking them into 2 pieces, the otoliths were typed and checked under reflected light using a stereo microscope (Williams & Bedford 1974). Otoliths from CC have a smaller and more circular first translucent zone than those from NEAC and the distance between the first and second translucent zone (winter zone) is larger. The shape of the first translucent zone in NEAC is similar to the outer edge of the broken otolith and to other established translucent zones. This pattern is established at the age of 2 yr, and the error in differentiating between the 2 major types does not increase with age because the established growth zones do not change with age (Rollefsen 1934).

Typing was performed on a random selection of 175 cod otoliths by experienced cod age readers. The only information given to the readers was the catch date. The otoliths were classified into one of the following 5 types: (1) CC, (2) uncertain CC, (3) Svalbard cod, (4) uncertain NEAC and (5) NEAC. 'Uncertain' meant that the reader could only conduct a qualitative classification owing to difficulties in reading the otoliths. The Svalbard otolith type (Type 3) characterises NEAC settled in shallow areas in the Bear Island–Svalbard region, and its otoliths exhibit only minor differences from NEAC (for example, clear winter zones) (see also Mjanger et al. 2000). For statistical testing, the otolith classifications were subsequently combined into only 2 groups: Types 1 and 2 were defined as CC and Types 3, 4 and 5 as NEAC. Currently, age readers mainly use Types 1, 2, 4 and 5; therefore, assignment to Type 3 is assumed based on the knowledge of an experienced age reader.

3. RESULTS

3.1. Sampling campaigns

In the sampling campaigns conducted between 2017 and 2019, a total of 548 Atlantic cod were caught and used in the analysis (Table 1). The *Pan* I and SNP analyses were performed with 238 individuals from these expeditions and 73 reference cod from Lofoten. A total of 175 otoliths were used for the analysis of the inner otolith shape. In all sampling campaigns, including the HAFE individuals, the total length of the smallest fish was 3.6 cm and the largest was 105 cm. Individuals within a 5–10 cm size range were the most abundant during the sampling campaigns (Fig. S2), whereas fish smaller than 15 cm represented the age-0 group.

3.2. Genetic assignment

Of the 40 SNPs analysed, 2 loci were deleted because of low scoring. There were 4 departures from HWE from a total of 342 tests (Table S1). Heterozygote deficit across all loci, suggesting population mixture, was found for all sampled fjords except Billefjorden, which showed a slight excess of heterozygotes (Table 2). For statistical analysis of the SNP markers, a hierarchy procedure was applied. Based on only the 38 SNP markers (excluding *Pan* I), the first STRUCTURE analysis divided the cod into 2 ecotypes: CC (including the CC reference sample from HAFE) and NEAC (Fig. 2a). All CC were assigned to the cluster as certain CC (*Q*-values ranging from 0.7 to 1.0) except 5 fish which were assigned as uncertain CC (*Q*-values between 0.5 and 0.69) (Fig. 2a).

After sorting cod into the NEAC and CC ecotypes, the *Pan* I assignment for most NEAC showed the typical genotype of *Pan* I^{BB} (n = 99); 5 cod showed an assignment to *Pan* I^{AB} (Table 3). The *Pan* I results among the CC clusters from the Svalbard fjords showed high frequencies of all 3 genotypes (*Pan* I^{BB}, *Pan* I^{AB} and *Pan* I^{AA}). Genotype *Pan* I^{AA} is character-

Table 1. Sampling campaigns for Atlantic cod in Svalbard waters. If fishing took place over more than 1 d, the GPS position of the start of the first trawl was used. Samples from Lofoten East and West (LOE and LOW) were used as reference material representing Norwegian coastal cod and Northeast Arctic cod, respectively. n: number of cod caught at each sampling site; the following columns indicate how many of these individuals were used for each of the individual analyses. *Pan* I: pantophysin locus; SNP: single nucleotide polymorphic marker

Location	Abbr.	Year	Date	Position	Sampling gear	n	Juveniles	Adults	*Pan* I	SNP	Otolith shape
Kongsfjorden	KOFJ	2017	8–9 Aug	79° 2′ 16″ N, 11° 21′ 10″ E	Benthic/pelagic trawl	156	1	155	2	2	0
	KOFJ	2018	3–4 Oct	78° 54′ 11″ N, 12° 14′ 8″ E	Benthic/pelagic trawl, fish lift	88	22	66	54	54	48
	KOFJ	2019	2–17 Sep	78° 55′ 39″ N, 11° 55′ 59″ E	Beach seine	44	44	0	44	44	0
Moffen	MOFF	2018	30 Sep	80° 14′ 30″ N, 13° 16′ 46″ E	Fishing rod	22	0	22	22	22	22
Raudfjorden	RAFJ	2018	1 Oct	79° 47′ 00″ N, 12° 5′ 43″ E	Benthic/pelagic trawl, fish lift	95	73	22	21	21	19
Billefjorden	BIFJ	2018	5–6 Oct	78° 32′ 58″ N, 16° 23′ 52″ E	Benthic/pelagic trawl, fish lift	40	3	37	31	31	28
Krossfjorden	KRFJ	2018	2 Oct	79° 11′ 38″ N, 11° 48′ 51″ E	Benthic/pelagic trawl, fish lift	9	0	9	7	7	8
Bear Island	BEAI	2018	28 Sep	74° 26′ 23″ N, 19° 34′ 50″ E	Benthic/pelagic	65	2	63	41	41	45
Hammerfest	HAFE	2017	10–20 Jul	70° 39′ 18″ N, 23° 29′ 27″ E	Fishing rod	29	0	29	16	16	16
Lofoten East	LOE	2003	29 Apr	68° 7′ 12″ N, 14° 26′ 24″ E	Bottom/pelagic trawl	41	0	41	41	41	0
Lofoten West	LOW	2003	2 Apr	68° 21′ 7″ N, 12° 8′ 13″ E	Bottom/pelagic trawl	32	0	32	32	32	0

istic of CC, but *Pan* I^{BB} is not frequently observed in CC. To investigate the CC cluster further, the individuals that clustered into the CC group (including both certain and uncertain CC) were included in a second run of STRUCTURE (Fig. 2b), which gave $K = 2$ and identified 87 'CC-A' (pink bars in Fig. 2b) and 30 'CC-B' (green bars in Fig. 2b) cod in each group. Within those 2 CC clusters, *Pan* I^{AA}, which is common for CC in Norwegian waters, was present in both

Table 2. Mean total observed heterozygosity (H_o), expected heterozygosity (H_e), and F_{IS}-value per sampling location (see Table 1 for full names) of Atlantic cod from Norway, Bear Island and Svalbard across all single nucleotide polymorphic loci. A negative F_{IS} value indicates heterozygote excess; positive indicates heterozygote deficit

Location	n	H_o	H_e	F_{IS}
LOW	32	0.1703	0.1740	0.0215
LOE	41	0.3524	0.3649	0.0341
HAFE	13	0.3533	0.3619	0.0238
BEAI	40	0.1880	0.2018	0.0681
BIFJ	31	0.1919	0.1915	−0.0019
KOFJ	93	0.2387	0.2423	0.0148
KRFJ	6	0.2377	0.2395	0.0075
RAFJ	21	0.2236	0.2341	0.0447
MOFF	18	0.1973	0.2018	0.0223

Table 3. *Pan* I genotypes (see Section 3.2. for details) of Atlantic cod analysed from the study area. See Table 1 for location names in full; ecotypes are CC: coastal cod; NEAC: Northeast Arctic cod

Location_ecotype	n	*Pan* I^{AA}	*Pan* I^{AB}	*Pan* I^{BB}
LOW	32	2		30
LOE	41	28	11	2
HAFE_CC	13	10	3	
KOFJ_CC-A	10	5	5	
BEAI_CC-B	16		14	2
BIFJ_CC-B	10		10	
KOFJ_CC-B	43	6	33	4
RAFJ_CC-B	9		7	2
MOFF_CC-B	6		6	
BEAI_NEAC	22		2	20
BIFJ_NEAC	20			20
KOFJ_NEAC	40		3	37
RAFJ_NEAC	10		1	9
MOFF_NEAC	11			11

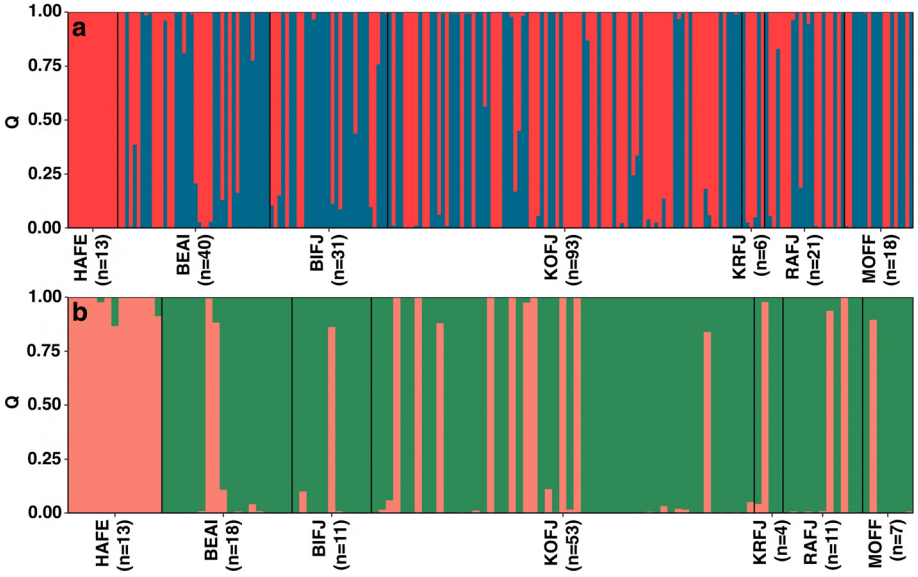

Fig. 2. Atlantic cod from Norway, Bear Island and Svalbard divided into different groups (*K*) by the software STRUCTURE v.2.3.4 (Pritchard et al. 2000) based on allele frequency in the sampling site. Each vertical line represents an individual. *Q*-values describe each individual score to the different groups. Plots include (a) 7 sampling sites (*K* = 2 and n = 222) from the present study; red: coastal cod (CC); blue: Northeast Arctic cod (NEAC) and (b) CC from (a) divided into 2 groups (*K* = 2 and n = 117): pink: CC-A; green: CC-B

CC-A and CC-B (*Pan* I^{AA}: n = 6 and n = 7, respectively); however, the number of heterozygotes was more frequent in CC-B (*Pan* I^{AB} = 72) compared to CC-A (*Pan* I^{AB} = 10), which indicates a clear deviation from HWE in CC-B. A high number of heterozygotes in the CC-B cluster suggest this cluster may be a hybrid. During further analysis of the share of adults and 0-groups within the NEAC, CC-A and CC-B types in Kongsfjorden, we found that all 3 groups contained 0-group and adults. The share of 0-group and adults of CC for both CC-A (0-group: n = 5; adult, n = 5) and CC-B (0-group: n = 22; adult: n = 21) were almost equally distributed, whereas NEAC individuals showed a higher fraction of adults than juveniles (0-group: n = 13; adult: n = 27).

In the pairwise genetic comparison (F_{ST}), the CC reference samples from Norway (HAFE and LOE) were significantly different from all Svalbard fjord CC samples (Table 4). The Svalbard CC-B was significantly different from both CC-A (93.3% of the samples) and NEAC (80% of the samples), including the reference samples from LOW and LOE (Table 4). This pattern was also present in the principal coordinate analysis (PCoA), where the CC-A was grouped with LOE and HAFE whereas the CC-B type cod grouped separately (Fig. 3). The first axis drives the differentiation between typical CC and all NEAC samples from LOW, Bear Island, and Svalbard fjords; CC-B is grouped between the 2 clusters.

3.3. Inner otolith shape

A total of 175 cod were aged and assigned to either CC or NEAC by otoliths (Table S2). Most of the cod were in the age groups of 3–7 yr, and none were older than 10 yr. The age distribution is somewhat different from the known age distribution of the NEAC stock during the same period (ICES 2020). In 2017–2019, there were still some old fish from the numerous 2004- and 2005-year classes left in the stock. Nine cod originating from HAFE were classified as CC (Type 1 and 2), whereas the rest were classified as NEAC. However, the experienced age reader noted that 94 of all otoliths classified as NEAC could be a Svalbard type of cod (Type 3).

3.4. Genetic vs. otolith assignment to ecotype

A comparison of the cod ecotypes classified according to otolith inner shape and genetic assignment was performed to evaluate the possible consistency between analyses. Otolith classification was performed on all cod, excluding the 0-group. For the CC and NEAC ecotypes, we used results from the genetic assignment (Fig. 2). For convenience, the otolith assignment 'Svalbard type' corresponds to Type 3 otoliths. A total of 175 otoliths were compared with the associated genetic assignments

Table 4. Pairwise genetic distances of samples of Atlantic cod in Norway, Bear Island and Svalbard. F_{ST} values are below the diagonal; p-values are above. Significant values ($p < 0.05$) are given in **bold**; p-values are corrected for false discovery rate. Cod were divided into Northeast Arctic cod (NEAC) (Fig. 2a) and coastal cod clusters (CC, CC-A and CC-B) (Fig. 2b) by the software STRUCTURE v.2.3.4 (Pritchard et al. 2000). Reference samples from Lofoten (LOE: Lofoten East [CC]; LOW: Lofoten West [NEAC]) are included. See Table 1 for further location abbreviations

Location_ ecotype	n	LOW	LOE	HAFE_ CC	KOFJ_ CC-A	BEAI_ CC-B	BIFJ_ CC-B	KOFJ_ CC-B	RAFJ_ CC-B	MOFF_ CC-B	BEAI_ NEAC	BIFJ_ NEAC	KOFJ_ NEAC	RAFJ_ NEAC	MOFF_ NEAC
LOW	32		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**	**0.002**	**0.033**	0.799	0.254	0.342	1.000	1.000
LOE	41	0.1942		0.844	**0.028**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
HAFE_CC	13	0.2831	0.0063		**0.028**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
KOFJ_CC-A	10	0.1982	0.0315	0.0447		**<0.001**	**<0.001**	**<0.001**	**0.013**	0.134	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
BEAI_CC-B	16	0.0496	0.1127	0.1623	0.0967		1.000	1.000	1.000	1.000	**<0.001**	**<0.001**	**<0.001**	0.084	**0.008**
BIFJ_CC-B	10	0.0577	0.1165	0.1800	0.1168	0.0129		0.648	1.000	1.000	**<0.001**	**<0.001**	**<0.001**	0.427	0.060
KOFJ_CC-B	43	0.0627	0.1201	0.1721	0.0950	−0.0004	0.0160		1.000	1.000	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**
RAFJ_CC-B	9	0.0539	0.1015	0.1472	0.0781	−0.0185	0.0111	−0.0048		1.000	**<0.001**	**<0.001**	**<0.001**	0.177	**0.013**
MOFF_CC-B	6	0.0701	0.1109	0.1424	0.0727	−0.0202	−0.0022	−0.0101	−0.0136		**0.005**	**0.004**	**<0.001**	0.540	0.246
BEAI_NEAC	22	0.0093	0.2131	0.3017	0.2134	0.0593	0.0673	0.0661	0.0675	0.0596		1.000	1.000	1.000	1.000
BIFJ_NEAC	20	0.0219	0.2133	0.2977	0.2038	0.0737	0.0746	0.0755	0.0767	0.0623	−0.0139		1.000	1.000	1.000
KOFJ_NEAC	40	0.0039	0.2287	0.3173	0.2161	0.0682	0.0746	0.0685	0.0706	0.0732	−0.0016	−0.0018		1.000	1.000
RAFJ_NEAC	10	0.0006	0.1758	0.2447	0.1500	0.0396	0.0718	0.0542	0.0472	0.0345	−0.0205	−0.0188	−0.0079		1.000
MOFF_NEAC	11	0.0029	0.1990	0.2707	0.1825	0.0597	0.0537	0.0597	0.0627	0.0461	−0.0151	−0.0133	−0.0100	−0.0161	

(Fig. 4). Half of the cod genetically assigned to CC from Svalbard fjords showed the NEAC otolith pattern (Fig. 4). A total of 46 individuals were assigned to NEAC by both genetic analysis and otolith inner shape, and 41 individuals showed genetic properties of NEAC but the otoliths resembled Svalbard Type 3. In contrast, 36 individuals assigned genetically to the CC-B type could be assigned to otolith characteristics for NEAC. We found 27 fish which were genetically identified as CC-B type and showed otoliths according to the known Svalbard type. Nine individuals were assigned to the HAFE-CC cluster by both methods. Three HAFE-CC individuals showed otolith properties from the NEAC type, and one individual was assigned genetically to HAFE-CC but showed the Svalbard otolith type. A small number of individuals from the CC-A cluster were assigned to either the NEAC otoliths (n = 7) or the Svalbard otolith type (n = 5). None of the individuals which were assigned to CC based on otolith assignment genetically corresponded to CC-A, NEAC or the Svalbard type.

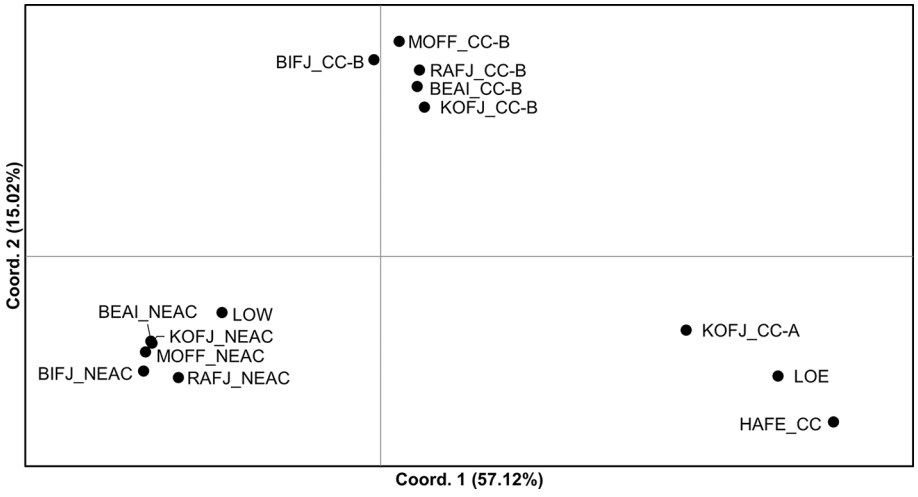

Fig. 3. Atlantic cod from Norway, Bear Island and Svalbard divided into Northeast Arctic cod (NEAC) (Fig. 2a) and the coastal cod (CC) types CC-A and CC-B (Fig. 2b) based on the software STRUCTURE v.2.3.4 (Pritchard et al. 2000). The threshold for *Q*-values (i.e. for assigning individuals to each groups) was set at 0.7. Reference samples from Lofoten East (LOE; CC) and Lofoten West (LOW; NEAC) were included. Sampling sites with less than 5 individuals were excluded. Axis 1 explains 57.12% of the variance; axis 2 explains 15.02%. The groups of cod separated into 3 clear clusters which differed from each other

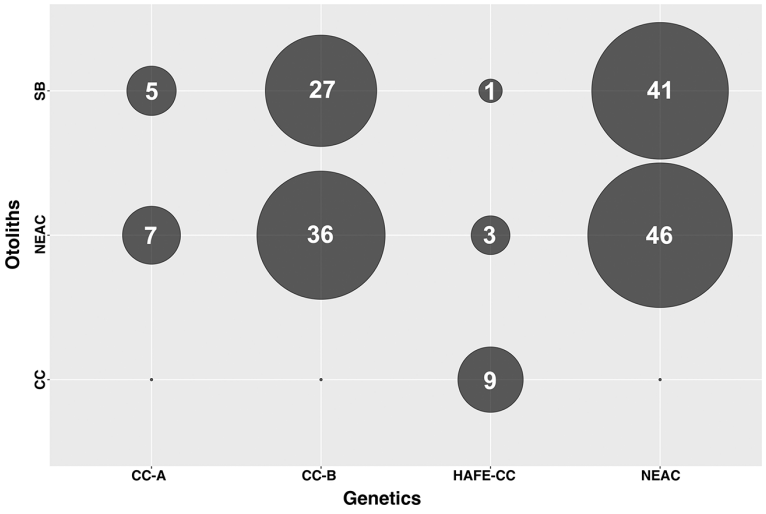

Fig. 4. Classification results for inner otolith shape versus genetic assignment for Northeast Arctic Cod (NEAC) and coastal cod (CC). For otolith typing, CC = Types 1–2, Svalbard type (SB) = Type 3, NEAC = Types 4+5

4. DISCUSSION

Svalbard and the Barents Sea are known for their extensive stocks of Atlantic cod, but the Svalbard fjords are poorly investigated. It was historically assumed that the NEAC stock with its migratory ecotype inhabited the west coast of Svalbard. Our study has shown that NEAC are indeed present in all studied Svalbard fjords, but that local CC can also be found. Based on the analysis of *Pan* I and SNP markers, we found 2 types of CC: the typical CC and an assumed hybrid type, which were both genetically significantly different from CC in Norwegian waters. The number of CC observed gave no information of how long this ecotype has already inhabited Svalbard waters, but this study provides the first genetic foundation for the presence of both CC and NEAC in Svalbard fjords. This is of particular interest, as commercial fisheries on the Svalbard shelf date back to the 1870s (Misund et al. 2016) but lack essential information about population structure and spawning behaviour. However, spawning was observed at the mouth of Isfjorden, Svalbard, in the 1930s during an Arctic warming event (Iversen 1934). The Norwegian Institute for Marine Research (IMR) performs 2 annual surveys on the Svalbard shelf in winter and autumn, outside spawning season, but the fjords are not covered during these surveys. Potential settlement processes of Atlantic cod in these areas, therefore, have not been studied but are fundamental to understand future ecological interactions with the Arctic marine ecosystem in the light of climate change.

Both CC and NEAC spawn along the Norwegian coast. NEAC then migrate to the Barents Sea and the Svalbard area following its main prey, capelin (Mehl et al. 1985). CC remain within the Norwegian coast and fjords. The transport of eggs and larvae towards settling grounds is mainly driven by local hydrographic conditions (Vikebø et al. 2007). The NwAC is the main driver for this passive transport (Cottier et al. 2005), providing a gateway for both NEAC and CC eggs to be transported into Svalbard waters. Based on the assumption that warming provides more suitable settlement conditions in Svalbard fjords, CC could have found spawning grounds in the investigated fjords.

4.1. Svalbard CC

Both CC types from Svalbard were observed in all sampled fjords (Fig. 3), although CC-B was found in higher numbers. In Kongsfjorden, the results are more notable as we found both adult and juvenile CC in high numbers. We assume that CC-A represents the more typical CC, as they are more similar to the Norwegian CC component, whereas CC-B is a hybrid component containing a high number of heterozygotes. The otolith structure can be used as an environmental marker as type 3 is typical for the Svalbard region. In addition, these individuals also have the genetic properties of a stationary ecotype which supports the idea of settlement. (see Fig. 4). Fewer cod were assigned to the CC-A type; however, as they were significantly different from the CC in the HAFE area, they might be an old component which has been present in the fjord for several decades and not observed earlier due to a lack of surveys and scientific investigations. Independent of the component of CC found in Svalbard fjords, we can assume that hydrographic temperature fluctuations play a key role in the potential settlement scenarios. As we found both juvenile and adult individuals of Svalbard CC, it is likely that the temperature regime, especially in Kongsfjorden, may be suitable for successful reproduction. Historically, several early Arctic warming scenarios may have led to better survival conditions in fjords like Kongsfjorden, which is strongly influenced by warm Atlantic water masses. The most prominent warm periods occurred during the 1920s–1960s, and later in the 1990s, with noticeable changes in the distribution

of Atlantic cod (Drinkwater 2009). These Arctic warming events have been associated with variations in temperature and sea ice coverage, followed by an expansion of the Atlantic cod stock northwards (Drinkwater 2006). Iversen (1934) mentioned fluctuations in the Atlantic cod stock and that some spawning seems to occur in the Svalbard area but is strongly affected by ice and the temperature of the water. Events like these might have led to potential settlement. Unfortunately, this study cannot provide any timeframe for the proposed establishment of CC in Svalbard fjords in conjunction with previous and ongoing warming scenarios. The Svalbard CC may have been derived from the CC along the Norwegian coast, whose eggs and larvae passively drifted towards Svalbard, finding suitable conditions for survival and the establishment of a local population. Published studies have not yet provided conclusive evidence of how long this process has been ongoing, but Andrade et al. (2020) recently investigated the chemical composition of otoliths taken from cod samples originating from Kongsfjorden. These individuals seem to have spawned within the fjord or nearby. The chemical component of otolith analysis complements our hypothesis of a local signal of Atlantic cod inhabiting Kongsfjorden and potentially other fjords on Svalbard. Recent borealization processes in the light of climate warming (Fossheim et al. 2015, Bergstad et al. 2018) could reinforce this settlement process and increase the number of Atlantic cod in Arctic fjords.

4.2. Hybridization of CC

In this study, 2 types of CC were observed on Svalbard, albeit in low numbers, and they were both significantly different from CC at Lofoten and around HAFE on the coast of Norway (Table 4). The CC-B type has an excess of *Pan* I heterozygotes, indicating a possible hybrid population between CC and NEAC or other CC components with an opposite homozygous genotype or a heterozygote advantage (heterosis effect) (Zouros & Pogson 1994). This excess of heterozygotes was also observed from the SNP markers (data not shown). As mentioned in Section 1, *Pan* I^{AA} is the most common genotype in CC. *Pan* I is part of the inversion present in chromosome 1 (Kirubakaran et al. 2016, Johansen et al. 2020) and, together with chromosomes 2 and 7, is what drives the separation of CC and NEAC along the coast of Norway. The presence of *Pan* I^{BB} and *Pan* I^{AB} in CC in such high numbers, as seen in this study, is new and uncommon (Fevolden et al. 2012). Even though we expected to find NEAC individuals with Svalbard-type otoliths, it was unexpected to find this otolith type in the CC clusters. We also found other individuals in which genetic assignment and otolith structures differed. None of the Svalbard CC showed the typical CC otolith as observed in Norway, which could support the otolith type CC to be an environmental marker. In particular, the combination of genetically assigned NEAC with otoliths assigned to Svalbard Type 3, and the CC-B cluster with otoliths of the NEAC Type 5 is interesting, as knowledge regarding hybrid clusters with shared characteristics is still very limited.

4.3. Today's hydrographic regime in Svalbard fjords

When establishing new spawning and settlement grounds, requirements for survival must include an appropriate temperature regime and reliable food availability. Warming processes, either based on climate variability like the observed early Arctic warming and more recent anthropogenic influences, may lay the foundation for providing adequate conditions for survival.

Understanding the migration and drift patterns of Atlantic cod is the basis for understanding possible spawning behaviour in Svalbard waters. Increasing water temperatures in the Arctic environment, particularly around Svalbard, seem to be key to providing favourable conditions for establishing CC in Svalbard waters. Rising water temperatures have been measured over the last few years, both in deeper waters (Hop et al. 2019a) and the shallow water region (Fischer et al. 2021) of Kongsfjorden. In recent years, immature fish of several gadoid species (including *Gadus morhua* and *Boreogadus saida*) have been observed in the shallow waters of Kongsfjorden (Brand & Fischer 2016, Fischer et al. 2017). The size of these individuals ranged from approximately 4–10 cm in August, and 0-group individuals sampled in shallow water in September had an average length of 8.6 cm (M. Brand et al. unpubl. data); however, different fishing gear was used with a mesh size that did not allow for catching smaller individuals. Among the specimens of Atlantic cod sampled in September 2019 in Kongsfjorden, juveniles had an average length of 6 cm and consisted of both CC and NEAC. Recent studies from Svalbard fjords found 0-group specimens in deeper waters at Forlandsundet with a minimum size of 5.5 cm in August (Mark 2013), indicating that these individuals could have originated from a potential Atlantic cod spawning ground on the Svalbard shelf.

The atmospheric and hydrographic regime in Svalbard fjords seems to have changed over recent decades. Kongsfjorden, one of the best-studied fjords, has shown fundamental changes in sea ice coverage and overall temperature. For several years, warm Atlantic water has prevented the fjord from building a sea ice cover (Cottier et al. 2007). These water masses originate from the WSC, and interannual data has shown water temperatures have been increasing for more than 20 yr (Hop et al. 2019a, Fischer et al. 2021)

Adult specimens of the local Svalbard CC cluster were found over a wide geographical range, from Bear Island in the Barents Sea to Raudfjorden and Moffen on the north coast of Svalbard. Some individuals were also caught in Billefjorden, a neighbouring fjord of Isfjorden. Billefjorden has Arctic fjord properties of very low temperatures compared to the more Atlantic-influenced Isfjorden. A sill restricts the inflow of warmer water into Billefjorden, although the associated high number of prey items such as Polar cod *B. saida* could be a reason for the Atlantic cod being present in this fjord. Using side scan and trawling at different depths, we observed that Atlantic cod were present in shallower and warmer water layers above the thermocline (Mark 2018), indicating possible predation on the Polar cod that perform upward migration for feeding (Benoit et al. 2010, Geoffroy et al. 2016). Renaud et al. (2012) investigated the dietary overlap of co-occurring gadoid species such as Polar cod, Atlantic cod and haddock *Melanogrammus aeglefinus*. Intraspecific competition seems low; however, the increased abundance of Atlantic cod is likely to become a potential predatory threat to the Polar cod. Borealization and Atlantification of the Arctic occurs not only with fish species but also zooplankton (Vihtakari et al. 2018). Species such as *Calanus finmarchicus* and *C. glacialis* show similar behaviour depending on the water temperature (Hop et al. 2019b). In particular, *C. finmarchicus*, an important food source for Atlantic cod at its early development stages (Sundby 2000), will be affected by increasing water temperatures, providing a higher food availability in Arctic fjords.

4.4. Implications for monitoring activities and fishery management

Recent methodological developments allow for more detailed genetic differentiation among ecotypes, which is gaining importance as the Arctic ecosystem faces substantial changes due to climate change. Historically, the genetic markers *Pan* I and SNPs and otolith morphology have been adequate to separate fish stocks to effectively manage mixed-stock fisheries (Jakobsen 1987, Johansen et al. 2018). Fishery management is strongly dependent on reliable stock information, which is based on surveys in the particular fishing area. Monitoring and assessment efforts must be expanded to the Svalbard fjord system as rapid changes occur on a local scale and are dependent on each fjord's hydrographic characteristics.

The northern Atlantic cod fishery is strongly affected by temperature fluctuations and the recent warming of waters around Svalbard. These fluctuations make stock management difficult; only in recent years, based on more elaborated analysis methods, have we gained more insight into the population structure of Atlantic cod in Svalbard waters. With this study, we improve our knowledge about a potential coastal ecotype of Svalbard Atlantic cod which may have ecological implications for the whole Arctic marine ecosystem (Renaud et al. 2012).

5. CONCLUSIONS

This study has shown the first genetic proof of the presence of CC in Svalbard fjords. The genetic analysis is supported by the presence of the Svalbard Type 3 otoliths. Both methods have shown that specimens of Atlantic cod in Svalbard fjords belong to both the migratory NEAC ecotype and the stationary CC ecotype. The investigation furthermore revealed that CC on Svalbard can be genetically separated into 2 clusters. These local CC clusters have a significantly different genetic structure than Norwegian CC and are therefore of special interest. Future investigations are needed to clarify to what extent CC in Svalbard fjords have already formed a local spawning population, as indicated by the present study and that both 0-group and adult CC were detected. Future studies should focus on the detection of fertile spawning individuals and their eggs and larvae in Svalbard fjords. A local spawning component may influence the local ecosystem, especially in the light of overall ongoing borealization processes which are affecting the Arctic marine ecosystem.

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