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The effects of climate change and climate variability on the distribution of Atlantic cod (*Gadus morhua*) in the Arctic

by

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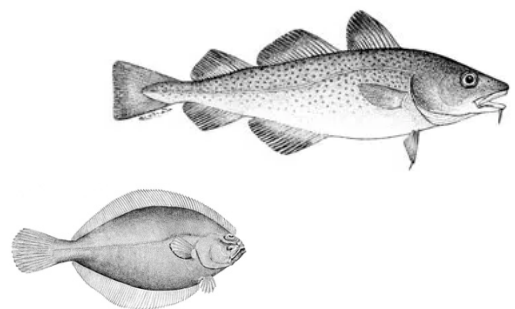
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Brewer's Dictionary of Phrase and Fable



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Abbreviations

AW - Atlantic Water

AWI - Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research

AWIPEV - French-German Arctic Research Base in Ny-Ålesund, Svalbard

BEAI - Bear Island

BIFJ - Billefjorden

CAO - Central Arctic Ocean

CC - Coastal Cod

COSYNA - Coastal Observing System for Northern and Arctic Seas

HAFE - Hammerfest

KOFJ - Kongsfjorden

LOE - Lofoten East

LOW - Lofoten West

MOFF - Moffen

NAO - North Atlantic Oscillation

NCC - Norwegian coastal Cod

NEAC - Northeast Arctic Cod

NRT - Near real-time

Pan I - Pantophysin locus

PCoA - Principal of coordinate analysis

RAFJ - Raudfjorden

RemOS - Remote Optical System

RV - Research vessel

SCC - Svalbard Coastal Cod

SL - Standard Length

SNP - Single-Nucleotide Polymorphism

SST - Sea-Surface Temperature

SvalSat - Svalbard Satellite Station

WSC - West Spitsbergen Current

Summary

The Arctic is experiencing warming to a much higher degree compared to other regions on Earth. The annual mean surface temperature between 1971 and 2019 was three times higher than the global average (AMAP 2021). A detailed, continuous, and reliable observation of the Arctic marine ecosystem can thereby deliver knowledge and insights into ongoing processes of climate change. While previous warm episodes like the Early Arctic warming occurring from the 1920s to 1960s are known to be driven by natural processes like changes in the North Atlantic Oscillation (NAO), recent studies provide evidence that the ongoing Arctic warming process differs from the earlier phases and that it is caused by anthropogenically induced large-scale global warming. The characteristics are large-scale fluctuations in the Atmosphere-Ocean interaction, which result in an increased influx of warm water from the Atlantic Ocean into Arctic fjords. Interestingly, records over the last decade show a fast-changing hydrographic regime, with extremes going in both directions. Observations show warm and cold short-time events, whereas an overlaying general trend towards a warming Arctic is observed. These short-term variations can occur on a daily, but also a seasonal or annual basis. The resulting decrease in sea ice coverage and the acceleration of glacier melt lead to a change in salinity and an overall increase in coastal water temperature.

Consequences for the local marine ecosystem can be, among other things, a shift in species abundance and distribution from a polar towards a more boreal community. In this context, fish species like the Atlantic cod (*Gadus morhua*) are reported to have risen in abundance in the Arctic region over the last decades. This may result in significant interspecies competition with local Arctic species, such as the Polar cod (*Boreogadus saida*). A detailed and continuous observation of Arctic marine ecosystems is required to provide knowledge and insights for a better functional understanding of the climatic effects on this particular ecosystem.

This dissertation focuses on the effects of climate change and climate variability on the population structure and spatial distribution of juvenile and adult Atlantic cod in the fjords of Svalbard. A combination of different methods was used and included fishing campaigns in several locations on the coast of Svalbard, genetic studies on the ecotype composition of the catches, otolith studies on subpopulation structure, and year-round *in situ* camera observations on the occurrence of juvenile cod in the shallow waters of the Kongsfjorden ecosystem. Fishing campaigns were conducted from 2012 to 2014 and from 2017 to 2020 with a focus on

Kongsfjorden whereby other fjords like Raudfjorden, Billefjorden, and Rijpfjorden were included in the sampling as well. During the sampling campaigns of 2019 and 2020, special emphasis was laid on sampling the 0-group of Atlantic cod. The fishing was performed by fyke nets, beach seine, plankton nets, and also rod fishing. The overall objective was to obtain a holistic overview of all age groups of Atlantic cod by sampling the shallow as well as the deep parts of Svalbard fjords, but especially Kongsfjorden. Specimens caught during the different sampling campaigns were measured and weighed to obtain basic growth parameters. Furthermore, otolith, stomach content samples and fin clips were taken.

A genetic approach was used to differentiate species, relatedness, and different ecotypes of Atlantic cod by analysing the pantophysin locus *Pan I* and single nucleotide polymorphisms (SNPs). It could be shown that Atlantic cod is the dominant Gadoid species among the 0-group specimens in the shallow water zone of inner Kongsfjorden. Furthermore, different ecotypes of Atlantic cod could be clearly distinguished. Those are the locally well-known Northeast Arctic cod (NEAC), and additionally two coastal cod ecotypes related to the Norwegian coastal cod (NCC). One of these coastal cod ecotypes, the Svalbard coastal cod (SCC) has not been described in the past and is therefore considered a new local ecotype. The latter finding is of overall importance for the study, as coastal cod ecotypes have never been reported or described in Svalbard waters before. In this context, it is noteworthy that coastal cod ecotypes form local, non-migratory cod stocks at the Norwegian coast.

Otolith microstructure analyses of the inner and outer otolith shape and specific forming of the growth zones were likewise used to determine stock affiliation. Hereby, the ecotypes Northeast Arctic cod, Norwegian coastal cod, and the established otolith shape of a Svalbard cod, which is based on the NEAC otolith type, could be classified.

Overall, it is important to note that the classification by otolith analysis did not always correspond with the results of the genetic analysis. Individuals assigned by otolith type to, e.g., NEAC did not always correspond to this type genetically. Interestingly, the otolith shape “Svalbard cod” correspond often to the fish that are genetically related to Norwegian coastal cod and not to NEAC.

Both approaches have their advantages. Otolith analyses are easy to do on site and cost-efficient. Growth properties are based on effects of environmental factors (Hüssy 2008) and can thereby show local adaptations of ecotypes. The genetic approach gives a better insight in the overall occurrence of different ecotypes in Svalbard waters, which is not fully resolvable by otolith shape.

The otolith structure analysis was also used for the age class determination of the individuals. It showed that in the shallow water of Kongsfjorden 0-group, 1+ and 2+ groups are most abundant. The Svalbard coastal cod was found as adult and as 0-group individuals in Kongsfjorden and other fjords on Svalbard. Besides Atlantic cod, also other species, such as Polar cod, were found in the shallow water areas. This indicates that both species co-occur temporarily in the same shallow waters of Svalbard, and interactions between the two species are likely.

In the framework of this thesis, it was assumed that the increasing water temperatures within the Arctic might have led to improved conditions for the spawning of Atlantic cod in Kongsfjorden. Therefore, the occurrence of fish eggs in Kongsfjorden was assessed by using zooplankton nets. However, eggs of Atlantic cod could not be found in the surveys. Interestingly, eggs of long rough dab were found instead. This is of interest as the Arcto-boreal long rough dab has a similar life cycle as Atlantic cod, and eggs of this species have not been sampled or found before in fjords like Kongsfjorden. It is important to note that during the ichthyoplankton sampling in spring and early summer 2020, the hydrographic conditions of Kongsfjorden were much colder than in previous years. This might have led to better spawning and survival conditions for Arctic species. The ichthyoplankton sampling results might therefore not be representative of previous years in which an overall warmer hydrographic regime was registered.

Literature indicates that non-anthropogenic events like the Early Arctic warming periods in the early 20th century promoted higher numbers of Atlantic cod in Arctic waters. It is therefore likely that today's global warming-influenced hydrographic regime also promotes a similar species distribution and results in the borealization of Svalbard fjords. Recent measurements in the shallow water zone of Kongsfjorden show an average temperature increase of approx. 0.2 °C over the last few years (Hop et al. 2019a, Fischer et al. 2021a). Furthermore, a noticeable high number of Atlantic cod was observed at the same time in these areas. This suggests a close link between warmer waters and potential settlement processes. Fluctuations and extreme events may affect the Arctic ecosystem not only in the long term over decades, but also on shorter time scales seasonal or annually. It adds another layer of complexity in understanding the species shift in Arctic ecosystems as they are overlaying the gradual long-term shifts in hydrography. Especially as the precise effects of e.g., a short-term elevated inflow of warm- or cold-water masses over several days or within a season into a fjord system are not precisely known. The ongoing analysis of the distribution pattern of Atlantic cod might help to better

understand how these extreme events might affect the abundance of boreal species in Kongsfjorden.

In summary, this study shows a high abundance of Atlantic cod in Kongsfjorden and several other fjords on Svalbard. The distribution and occurrence of Atlantic cod in Svalbard waters seem to be affected by environmental factors such as water temperature. Based on the combined use of observation, otolith shape, and genetic tools, a local ecotype, the “Svalbard coastal cod (SCC)” could be identified as a potential permanent resident in Svalbard fjords. Eggs or larvae of Atlantic cod could not be identified in the catches, nevertheless, eggs of long rough dab have been found during the ichthyoplanktonic surveys indicating spawning in the area. In the past, spawning grounds of the long rough dab have been reported in the Barents Sea and increasing water temperature might have a direct impact on a potential shift of spawning grounds towards the Svalbard shelf. Both, Atlantic cod, and the long rough dab share a similar lifestyle and demonstrate the recent invasion of boreal species into the Arctic marine ecosystem.

This PhD study also provides strong evidence that the water temperature regime plays an important role in the overall Atlantic cod distribution and occurrence in West Svalbard waters. The new insights into the population structure of Atlantic cod in Svalbard waters provide strong evidence that progressively warming waters in the area have a significant effect on the Svalbard coastal ecosystem. The findings contribute to the discussion of ongoing changes in the Arctic ecosystem and potential effects on the local marine food web. While seasonal and interannual changes have been observed for several decades, a further increase in boreal species together with a decrease in local Arctic species over the coming years and decades can be expected. In this context, it is important to mention that extreme temperature events have been observed in the past to expand to both, warm and cold events. These extreme events make it difficult to differentiate short- and long-term changes caused by anthropogenic global warming. Past observations have shown strong fluctuations in e.g., the abundance of Atlantic cod in Northern waters. The discovered local ecotype of Svalbard coastal cod might be an indicator for a permanent presence of Atlantic cod in the Arctic. It seems likely that the ecosystem will change towards a more boreal-influenced system. The response of other Arctic species such as Polar cod and *Calanus* sp. will also play a key role in the future development of Atlantic cod in the Arctic.

Introduction

About cod, the climate, and the Arctic community

Climate change is not only challenging humankind but also threatens whole ecosystems and marine life. Especially the Arctic, which is warming more rapidly compared to any other part of the world (AMAP 2021), is confronted with unique changes unlike in any previous observation. In the marine ecosystem, seasonal and interannual fluctuations of the hydrography have been shown to occur on a regular basis, but the amplitude of alterations nowadays is more elevated and indicates a long-term trend of a warming Arctic (Polyakov et al. 2005, Cottier et al. 2007). As a part of this, increasing water temperatures, sea ice loss, glacier melt, habitat loss of Arctic species, and a northward shift of boreal species are only some of the widespread observations made over the last decades in Arctic marine waters (Christiansen et al. 2014, Fossheim et al. 2015, Descamps et al. 2017). Some fish species have shown to be resilient and adaptable to short-term changes in water temperature and salinity, originating from water mass changes and atmosphere-ocean-interactions (Righton et al. 2010). One of these key species in the ongoing Atlantification and borealization processes is the Atlantic cod (*Gadus morhua*), gaining importance in the Arctic and especially in the fjords of Svalbard. We are only at the beginning to understand the long-term distribution changes in the local Arctic community.

Arctic amplification

Arctic air temperature has been recorded continuously since approx. 1880 and clearly shows that warming in the Arctic region is higher than anywhere else on the planet (AMAP 2021). Nowadays, the Arctic is considered a hotspot for climate change (Hoegh-Guldberg & Bruno 2010) and the warming is about twice as fast compared to the global average (Cohen et al. 2014). The main reason for Arctic warming is the melting of sea ice and snow which reveals darker surfaces where the amount of absorbed solar energy increases and results in associated warming also known as the albedo effect (AMAP 2021, IPCC 2013). Overall, sea ice has diminished by 49 % compared to the average extent from 1979 to 2000, with a minimum record in 2012 (Polar Portal 2020).

The causes of sea ice loss are complex and involve changes in atmospheric and ocean heat, internal feedbacks of the Arctic atmosphere-ice-ocean system and others (Carmack et al. 2015). In the past, ocean advection was the main driver for warming trends south of the winter ice edge along Atlantic water pathways through the Barents Sea (Åsbjørnsen et al. 2020). The loss

in sea-ice cover, primarily in late summer, reduces reflection and the total albedo of the remaining Arctic sea-ice zone (Riihelä et al. 2013). Snow-covered sea ice reflects up to 85 % of the incident solar energy, whereas the dark ocean only reflects 7 % (Perovich et al. 2009). In addition, the solar heat absorbed in the ocean facilitates further melting and a decrease in ice albedo (Perovich et al. 2009). The resulting decrease in sea ice will likewise result in more absorption of solar energy and thus more warming of the seawater (Polar Portal 2020). Warmer seawater also influences the thickness of sea ice, as the increasing sea-surface temperature will delay sea ice formation (Polar Portal 2020). In addition, a larger open sea area leads to an increased transfer of oceanic heat to the atmosphere, which contributes to atmospheric warming (Onarheim et al. 2014). The retreating ice cover changes the overall surface conditions and reduces reflection, in addition to positive surface albedo feedback in summer and positive cloud feedback in winter (Jenkins & Dai 2021). This shows that Arctic sea ice cover is a crucial driver of the Northern Hemisphere ice-albedo feedback which contributes to the polar amplification of climate (Perovich et al. 2009).

Consequences can be observed on many levels: Ocean warming (Polyakov et al. 2005) and Arctic Sea ice loss (Christiansen et al. 2014), glacier melt runoffs (Descamps et al. 2017), thawing permafrost (Biskaborn et al. 2019) and Arctic Ocean acidification (AMAP 2018). Especially when permafrost thaws, it releases carbon dioxide, methane, and water vapor into the atmosphere, contributing to the greenhouse gas-based warming of the whole planet (Knoblauch et al. 2018). The specific interactions between the ocean and the atmosphere, however, are highly complex and not yet fully understood.

The North Atlantic Oscillation (NAO) is known to play a key role in the North Atlantic climate system. It affects the hydrophysical and hydrometeorological properties of the Arctic Ocean and participates in the regulation of the Atlantic water inflow into the Nordic Seas (Mikhailova et al. 2021). The NAO has an interannual variability and the ocean climate around Svalbard is closely connected to this large-scale circulation (Hanssen-Bauer et al. 2019). These hydrographic fluctuations are important for a better understanding of the regional climate in Svalbard fjords.

Arctic fjords and coastal systems are highly sensitive to climate change and alterations in short- and long-term hydrographic properties which affect the fjord ecosystem in Svalbard and its inhabitants directly (Węśławski et al. 2011). Fjords on Svalbard are influenced by short-term seasonal and interannual variability of glacial water runoffs (AMAP 2018), the sea ice

coverage, and the inflow of Atlantic and Arctic water masses. Studies show that today the west coast of Svalbard is increasingly affected by an inflow of warm, saline Atlantic water from the West Spitsbergen Current (WSC) (Cottier et al. 2005). Their antagonists are cold polar water masses from the Arctic Ocean, which move southwards along the east coast of Svalbard (Eriksen et al. 2018). Kongsfjorden lies on the west coast of Svalbard and is one of the best-studied fjords in the Arctic. It can be characterized as a sub-Arctic fjord with glacial inflow. Salinity and sediment load in the fjord are affected by large marine-terminating and some smaller land-terminating glaciers (Hop et al. 2002). Observations from moorings in the deep parts of the fjord and observatories in the shallow water zones recorded a significant increase in water temperature of more than 0.15 °C over the last decade (Hop et al. 2019a, Fischer et al. 2021a). This increase in water temperature could be observed as a long-term trend over multiple years, and in the form of extreme short-term multiple-day events within a season. Cottier et al. (2007) described that in 2005/2006 warm Atlantic water masses prevented a full ice coverage of Kongsfjorden. This became a regular phenomenon in the following years. Larger ice coverage was only present in the winter of 2019/20 when a cold phase has been observed with sub-zero degrees in water temperatures up to the summer months (pers. observation, Fischer et al. 2021b; c). Nowadays, it is difficult to characterize a typical year for e.g., Arctic sea ice extent, as hydrographic fluctuations appear to happen on short-term scales and with higher amplitude in both directions, and due to their interactions, effects from either climate variability or anthropogenic climate change are difficult to separate (Kay et al. 2011, Ding et al. 2017, Fischer et al., in prep.).

It is known that phases of warm water inflow in the Svalbard fjord system have been recorded in the past, known as the Early Arctic warming (Yamanouchi 2011). Two of them are major events, the first in the 1920s to 1930s and the second one in the 1950s and 1960s. According to literature, the 1920s warming is considered to have had a major influence on the regime shift of Atlantic cod (Drinkwater 2006). A third warming period starting in the 1990s is still evolving into the present time (Drinkwater 2009). In general, Atlantic cod fisheries in the Arctic date back to the 1870s (Misund et al. 2016), but fisheries in the Northern Seas were always strongly affected by sea ice and hydrographic conditions. Strong fluctuations allowed extensive fishery in one year, whereas in other years fisheries almost collapsed (Iversen 1934), potentially due to fast changes in the hydrographic conditions. In previous decades, sea ice coverage was observed as far south as Bear Island in the Barents Sea (Iversen 1934), limiting the exploration of Svalbard fjords during spawning season. During warm periods as the observed Early Arctic warming (1920s to 1960s; Drinkwater 2006), Atlantic cod moved northwards, into Svalbard

fjords and even spawning could be recorded during these years at the entrance of Isfjorden (Iversen 1934), a fjord that is known to be influenced by Atlantic water masses similar to Kongsfjorden.

Ecotypes of Atlantic cod

Atlantic cod observed in Svalbard waters belongs mostly to the Northeast Arctic cod (NEAC) stock, the biggest and commercially most important Atlantic cod stock in the North Atlantic (Brander 2005). NEAC performs an extensive migration movement between the feeding grounds in the Barents Sea and along the coast of Svalbard and its spawning grounds along the Norwegian coast (Mehl et al. 1985). Spawning is concentrated at the Lofoten and along the northern Norwegian coast extending from Møre in the South towards Finnmark in the North (Brander 2005, Sundby & Nakken 2008). NEAC is sharing spawning grounds with the local, non-migrating Norwegian coastal cod (NCC) (Michalsen et al. 2014, Johansen et al. 2018), whereas mingling and interbreeding are observed, but seem to be limited (Nordeide 1998, Johansen et al. 2018, Jorde et al. 2021). This might partly be explained by the observation that during peak spawning, which takes place from mid-March to mid-April (Pedersen 1984) NEAC is to be found more abundant in deeper waters, while NCC is rather present in the fjords (Nordeide 1998). The Norwegian Coastal Current can transport pelagic eggs and larvae passively into the Barents Sea and to the west coast of Svalbard where larvae settle down after their pelagic phase and remain in the settlement area for the first 2 years (Ottersen et al. 2014). The Northeast Arctic cod stock was assumed to be the only Atlantic cod ecotype present in Svalbard waters (Brander 2005). This was based on the known migration pattern and the fact that regional hydrographic conditions in the past would inhibit settlement and spawning in Svalbard fjords. Atlantic cod is a generalist, supporting a wide temperature range from -1.5 °C up to 19 °C, but requires a narrower range from 1 to 8 °C for spawning (Righton et al. 2010). Interestingly, Atlantic cod eggs and larvae are remarkably resistant when it comes to exposure to sub-zero temperatures even though they cannot produce antifreeze glycoproteins (Valerio et al. 1992). Freeze-resistance in early life stages is particularly important as ice contact could affect survival and reduce spawning success in Northern Seas (Valerio et al. 1992).

Tools as key to the Atlantic cod population structure

Polar night, cold temperatures, harsh weather conditions and sea ice are factors that affect the year-round observation of fish and other benthic organisms in Arctic waters and require specially adapted observation systems. In Kongsfjorden, long-term monitoring takes place

since 2002 when moorings were installed at different positions within the fjord (Hop et al. 2019a). Physical, chemical, and biological data are recorded, providing important information about the seasonal variability and the general hydrographic regime. Unfortunately, moorings can only cover the water column from the bottom up to 10 - 15 m below the surface and acquired data can only be accessed after recovery. For the observation of fish eggs and larvae, the surface layers of the water column are essential, and observation systems are needed to cover the shallow-water region. In 2012, a cable-connected, online underwater observatory was installed in the framework of the COSYNA network project (Baschek et al. 2017). It is positioned close to the Old Pier in the research settlement of Ny-Ålesund. The system is operated year-round and can provide near real-time data (NRT-data) of the shallow-water zone between 12 m water depth and the surface. The underwater observatory comprises a land-based FerryBox system and an underwater profiling sensor unit. This unit is recording similar data as the deep-water moorings but is in addition equipped with a remote optical system (RemOs 1), designed for the stereoscopic observation of fish (Fischer et al. 2017). This system provides access to the water column even when fishing or diving activities are not possible due to harsh polar weather and climate conditions. One of the objectives of the installation was the assessment of the shallow water fish community. Between 2012 and 2014, Brand & Fischer (2016) performed several fishing campaigns to analyse the spatial distribution of the fish community. The results showed a high percentage of Gadidae, especially Atlantic cod. The study focused mainly on juvenile and adult individuals, as fyke nets were used for the sampling. However, images from the RemOs 1 system clearly showed 0-group Gadidae as a numerically dominating specimen in the shallow water zone (Figure 1; Fischer et al. 2017).

Unfortunately, it is problematic to identify individuals by optical methods reliably to either Atlantic cod, Polar cod, or another Gadoid species. The markers such as colour and shape can be used for initial species discrimination but proved to be insufficient for reliable identification. Therefore, numerical data of fish abundance identified to species level has to be seen critically and with care. The observational approach made it possible to deepen the knowledge about the shallow water fish community, but a combination of different tools, including fishing, is necessary to clearly distinguish species and their potential ecotypes.



Figure 1 Observation of juvenile Gadidae in the water column close to the Old Pier, Kongsfjorden

A very reliable approach to differentiate between ecotypes of Atlantic cod is the use of otoliths. The inner structure not only provides insight into the age structure of individuals based on annual growth zones (Campana & Thorrold 2001), but the inner otolith shape analysis can also be used to assign individuals to either NEAC, NCC, or a Svalbard type (Rollefsen 1933, Jakobsen 1987, Mjanger et al. 2000). Particularly, the inner otolith shape from NEAC and NCC can be clearly distinguished (see figure 2). In recent years, the outer otolith shape is likewise used for stock identification (Stransky et al. 2008). This method has the advantage that otoliths do not have to be broken for the analysis, but it only gives very limited information about the age of the specimen. Another method that indicates stock affiliation is the use of otolith microchemistry and stable isotopes (Campana & Gagné 1995, Kerr & Campana 2014, Andrade et al. 2020). The use of the microchemical composition has the advantage that not only the stock itself can be assigned, but that migration and settlement areas can be tracked.

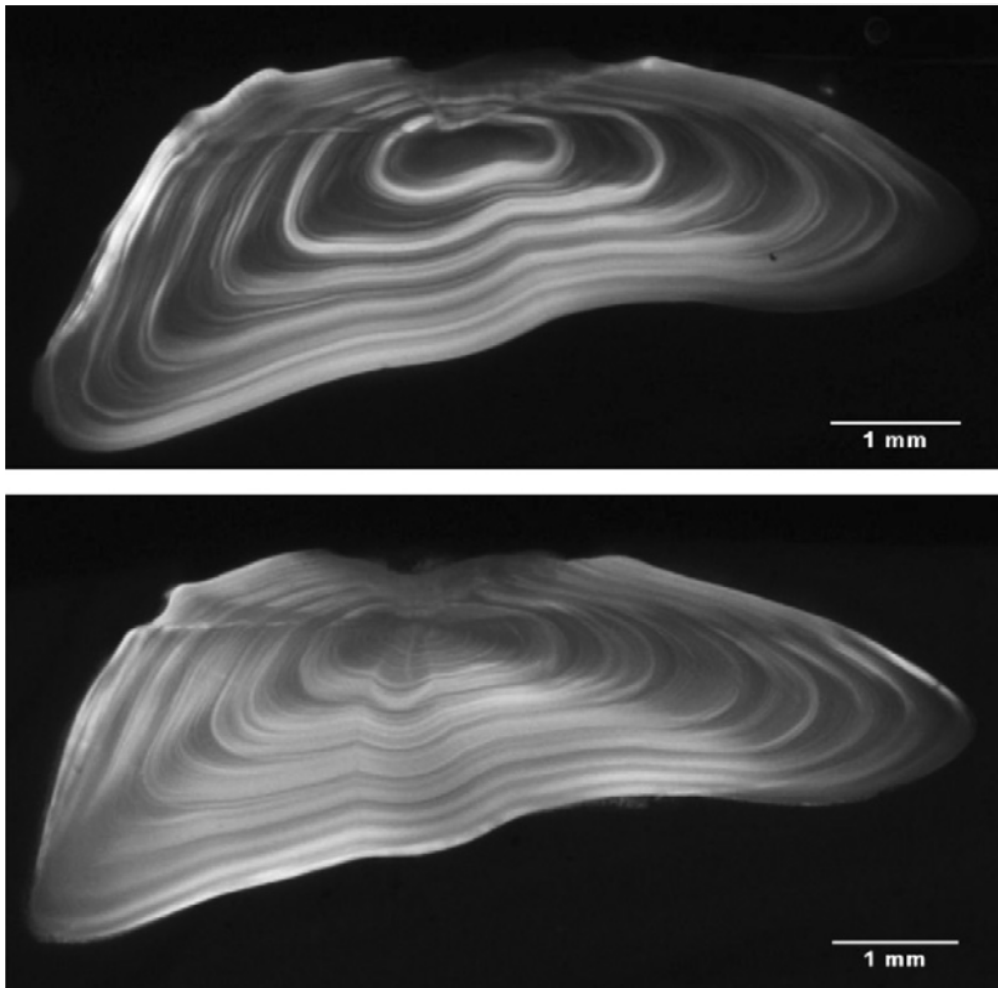


Figure 2 Otolith types typical for Norwegian coastal cod (upper picture) and Northeast Arctic cod (lower picture) (Stransky et al. 2008)

In light of climate change, using only otoliths for stock identification has another big disadvantage. Migration movements, spawning as well as settlement are highly affected by climate change processes. Even though otoliths may assign specimens to a certain stock or can give an indication for migration, the formation underlies phenotypic plasticity (Chevin et al. 2010). Changes in behaviour or morphology can affect the clear identification of an individual, especially when external factors such as temperature change the known life cycles. Independent methods are therefore needed to identify ecotypes. Genetic markers such as single nucleotide polymorphisms (SNPs) are highly valuable and adequate for stock separation (Skarstein et al. 2007, Wennevik et al. 2008, Johansen et al. 2018). In addition, the pantophysin locus *Pan I* has been used for several decades to differentiate between NEAC and NCC (Fevolden & Pogson 1997). The combination of genetic tools, known otolith shape patterns, and the observation of biotic and abiotic factors have the potential to give a clearer picture of the distribution of Atlantic cod in the Arctic and ongoing processes of Atlantification.

Atlantification of the Kongsfjorden marine ecosystem and its consequences

The local marine ecosystem is responding to changes in the hydrographic regime. Especially, the increase in water temperature is affecting Arctic marine life (Ingvaldsen et al. 2021). Local species like Polar cod (*Boreogadus saida*) are affected by changes in the biotic and abiotic environment which influence suitable habitats and distribution areas (Eriksen et al. 2020, Geoffrey et al. (submitted)). Nowadays, boreal species are observed on a more regular basis in Arctic waters, indicating an ongoing northward shift towards the Arctic region (Fossheim et al. 2015). Higher food availability due to higher water temperatures is also considered to be a factor for migration into Arctic waters (Misund et al. 2016).

Zooplankton species are likewise affected by the hydrographic properties (Willis et al. 2006) and show similar dependency on different water masses as observed in some fish species (Hop et al. 2019b). Zooplankton species such as the copepod *Calanus finmarchicus* are an important food source and primary prey for the early development stages of Atlantic cod (Sundby 2000). If warming continues, these early larvae stages of Atlantic cod will be extremely vulnerable as a decrease in egg survival and a potential loss of the spawning grounds can be expected (Dahlke et al. 2018).

Polar cod plays an important role within the Arctic marine food web but despite being the dominant fish species in Arctic waters, the spawning distribution of Polar cod in the Svalbard area is still not fully understood (Eriksen et al. 2020, Aune et al. 2021). It is known that spawning generally occurs during wintertime (Benoit et al. 2010). Reports from the Canadian high Arctic describe in autumn large schools of juvenile Polar cod which can be observed in shallow water (<10 m) (Hop et al. 1997). In Svalbard waters, spawning seems to be local as young-of-the-year Polar cod are widely distributed in the fjords (Nahrgang et al. 2014). This suggests that local changes in temperature, predation and prey availability will likewise affect local species like Polar cod (Nahrgang et al. 2014). Co-occurrence of juvenile Atlantic and Polar cod has been observed in Svalbard waters, where interspecific food competition appears to be low due to limited dietary overlap (Renaud et al. 2012). In contrast, adult Atlantic cod has been observed to prey on Polar cod when performing upward migration for feeding (F. Mark; pers. comment, Geoffrey et al. 2016).

Other fish species are likewise considerably affected by increasing water temperatures in Arctic waters. An understudied species is the long rough dab (*Hippoglossoides platessoides*), which only has very limited commercial value but can be found in high abundance in the Northern Seas (Welch et al. 1993). The long rough dab is considered an Arcto-boreal species due to its large distribution from the northern Norwegian coast up to the north coast of Svalbard. The preferred temperature range and distribution of the long rough dab is in some regards similar to the one of Atlantic cod. A general east-west migration in the Barents Sea has been suggested (Walsh & Mokeeva 1993) with spawning grounds in the warmer western and central Barents Sea (Walsh 1996). Interestingly, a part of the long rough dab population is known to be found north of Svalbard, but it is unclear if this part of the population participates to the same extent in the migration movement (Walsh & Mokeeva 1993). In the past, reports of larvae or 0-group long rough dab along the west coast or within the fjords of Svalbard are very rare (Walsh 1996). Fluctuations in water temperature are affecting likewise the distribution of Atlantic cod and long rough dab in the Barents Sea / Svalbard area and show similar changes in density with increasing temperatures (Walsh 1996). Therefore, mechanisms of population distribution may be similar.

Research objective & Overview

Recent studies show that climate change and climate variability are key factors for the increase of Arctic water temperatures (AMAP 2021, Hoegh-Guldberg & Bruno 2010), which might lead to borealization processes and an Atlantification of the Arctic (Ingvaldsen et al. 2021). In light of climate change and the recently observed temperature increase in the Arctic, this dissertation is evaluating if new or re-established spawning and settlement areas of Atlantic cod in Svalbard fjords exist. A key factor, therefore, is a more profound understanding of the changes in the hydrographic regime of Svalbard fjords, and its effects on the fish community. A special focus is hereby on the potential adaptations of Atlantic cod and other fish species such as the long rough dab.

In this study, several approaches were combined to gather data about Atlantic cod in Svalbard fjords, to identify potential settlement areas and to strengthen the hypothesis of a successful establishment of a local ecotype of Atlantic cod in Svalbard waters. The data assessment was mainly conducted in the shallow water zone in Ny-Ålesund, Kongsfjorden, and complemented with research cruises of the RV Heincke and RV Helmar Hanssen. Hereby juveniles and adult Atlantic cod, fish larvae, and eggs were sampled and processed.

Detailed analysis of the inner and outer otolith shapes was complemented with baseline data of length, weight, and growth. These results have been compared and improved with genetic data based on SNPs and *Pan I*.

Three research questions are the basis for this dissertation:

Research question 1: Is the Atlantic cod stock on the west coast of Svalbard genetically / morphologically distinguishable from that of the Norwegian coast, where the migratory origin of the NEAC stock (*Gadus morhua*) is assumed?

Research question 2: Is there a local stock of *Gadus morhua* in Kongsfjorden with a successful spawning population?

Research question 3: Is there a significant correlation between the overall abundance and distribution patterns of Atlantic cod stocks at the coast of Svalbard with longer-term temperature patterns? Is the increase in the overall abundance of *Gadus morhua* related to the periods of warmer Atlantic water surrounding Svalbard?

Chapter 1 lays the basis for the following chapters and provides fundamental data on Atlantic cod in the shallow-water zone of Kongsfjorden, Svalbard. Otolith-based classification was used to identify age classes and to determine growth rates in the local environment. These results are complemented with data from stomach content analysis to determine if the shallow-water zone provides prey and might thereby be a potential nursery ground for Atlantic cod.

In **chapter 2**, genetic tools such as *Pan* I and SNPs were used for the identification of different Atlantic cod ecotypes. The results are supplemented with data from otolith shape analysis. Both methods provide a first insight into the recent population structure of Atlantic cod in Svalbard fjords and provide answers to all research questions.

Chapter 3 was initially intended to focus on the observation of Atlantic cod eggs and larvae in Kongsfjorden. The presence of eggs and larvae could not be confirmed, but instead, the ichthyoplanktonic sampling campaign resulted in the finding of long rough dab (*Hippoglossoides platessoides*) eggs. Even though the long rough dab is widely distributed over the Barents Sea and Svalbard, eggs have never been observed in Kongsfjorden. Adaptation to warmer water temperatures similar to those observed for Atlantic cod might be linked to this observation.

The correlation between distribution, settlement and the warming trend is an extensive part of the general discussion. Hydrographic events are linked to the temporal dynamic of the shallow-water benthic fish community in Kongsfjorden, Svalbard. In this framework, the year-round operated underwater observatory was used to provide stereoscopic images, temperature, salinity, and other hydrographic data relevant to understand the distribution patterns of Gadidae.

Chapter 1

Age class composition and growth of Atlantic cod (*Gadus morhua*) in the shallow water zone of Kongsfjorden, Svalbard

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Contributions: MB performed the whole sampling campaign described in the proposed manuscript. The initial explorative age reading of otoliths were conducted by LS with support from MB. ELL performed a complete age reading of all otoliths. JMW performed the analysis of stomach content samples. The analysis of the dataset was performed by MB. All listed authors participated equally in the writing process, whereas PF is the PI of the project and JB as well as FM supported the discussion fundamentally so that without them it would not be possible to submit the proposed manuscript.

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Age class composition and growth of Atlantic cod (*Gadus morhua*) in the shallow water zone of Kongsfjorden, Svalbard

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Abstract

Although Atlantic cod has been observed in Svalbard waters since the 1880s, knowledge about the presence in the Arctic shallow water zone is limited. The regular catch of juvenile Atlantic cod in Kongsfjorden since 2008 is in line with an overall northward shift of boreal fish species toward the Arctic. This is the first study showing the age class composition, growth rates, and stomach content of Atlantic cod in the shallow water zone of Kongsfjorden, Svalbard. From 2012 to 2014 a total of 721 specimens were sampled in 3 to 12 m water depth. The primary age classes were identified as 0+, 1+, and 2+ using otolith age analysis. The different cohorts of these specimens show stable growth rates during the polar day and night. By stomach content analysis, we show that these specimens primarily feed on benthic food sources. These observations support the assumption that the shallow water zone of Kongsfjorden is likely to be a nursery ground for Atlantic cod.

Keywords *Gadus morhua* · Northeast Arctic cod · Fish growth · Svalbard · Kongsfjorden · Climate change

Introduction

Atlantic cod (*Gadus morhua*) is generally distributed along the continental shelves of the North Atlantic between 40° N and 80° N (Sundby 2000; Neat and Righton 2007). Ottersen et al. (2014) describes the Northeast Arctic cod (NEAC) in the Barents Sea as the currently largest stock. One of the

most northern components can be found around Svalbard and its fjords, like Kongsfjorden. Here, Atlantic cod has been observed and to some degree commercially caught in periods since the 1880s, with juveniles regularly caught and documented since 2008 (Berge et al. 2015b). The presence of Atlantic cod in Kongsfjorden is likely connected to a northward shift of marine fish species in the Northern hemisphere (Christiansen et al. 2014; Fossum et al. 2015; Misund et al. 2016). Kongsfjorden at the west coast of Svalbard at 79°N, 12°E is characterized as a sub-Arctic glacial fjord (Fig. 1). The sub-Arctic character is based on its hydrography, with a strong influx of Atlantic water masses that have increased over the last two decades (Beszczynska-Möller et al. 2012; Payne and Roesler 2019; Hop et al. 2019). The increased temperatures in Kongsfjorden are within the thermal niche of Atlantic cod, which is reported to range from -1.5 to 19 °C, with a narrower range of 1 to 8 °C during the spawning season (Righton et al. 2010).

Characteristic for NEAC is an annual long-distance migration between spawning and foraging areas. One foraging area is in the eastern Barents Sea at Novaya Zemlya and the other is on the western continental shelf of the Svalbard archipelago (Brander 2005). The main spawning area of NEAC is located on the west coast of Norway from Møre in the south to Finnmark in the north, with the main

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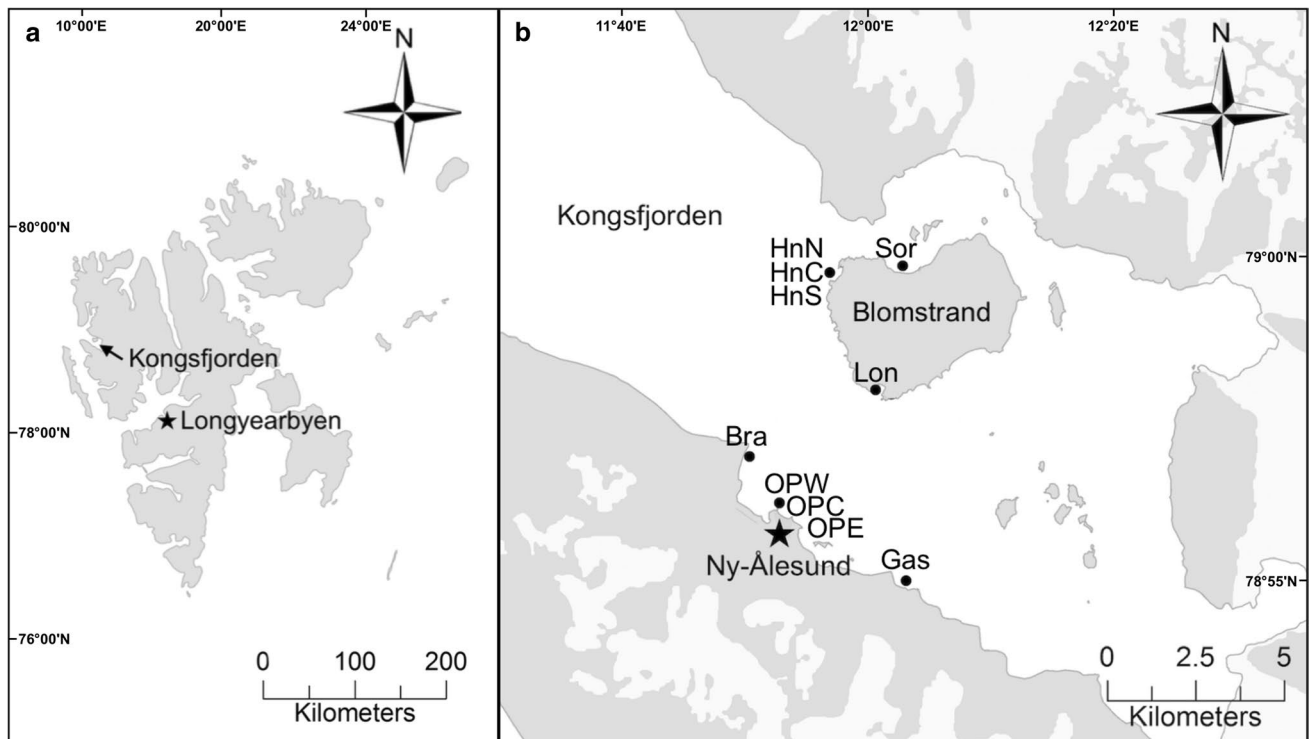


Fig. 1 Map of Kongsfjorden at 79°N, 12°E. **a** The Svalbard archipelago with its primary settlement Longyearbyen and the study site Kongsfjorden. **b** Kongsfjorden with the settlement Ny-Ålesund and its island Blomstrandhalvøya. Light areas on land represent glacier surfaces. The sampling sites are marked as follows: Sor—Sørvågen, HnN—Hansneset North, HnC—Hansneset Central, HnS—Hansneset

South, Lon—London, Bra—Brandal, OPE—Old Pier East, OPC—Old Pier Central, OPW—Old Pier West, and Gas—Gåsebu. At the locations Hansneset and Old Pier, three sampling sites were spaced 100 m apart in a perpendicular orientation to the coastline. The map data were provided by the Norwegian Polar Institute (from Brand and Fischer 2016)

spawning grounds at the Lofoten (Godø 1984a, b; Brander 2005; Sundby and Nakken 2008). NEAC spawning occurs from February to May, with the main spawning period in March and April (Brander 2005). Suthers and Sundby (1993) observed post-larval cod with a standard length (SL) of 25.2 mm in the spawning areas and up to 68 km offshore in July. About 10–40% of the total larval abundance is transported to the west coast of Svalbard with the WSC, while the majority (60–90%) drifts with the North Atlantic Current and is transported to the Barents Sea (Ottersen et al. 1998). The settlement of juveniles is known to occur from September to October (Ottersen et al. 2014). After settlement, the juveniles can be referred to as age class 0+.

All Atlantic cod at the Svalbard archipelago and its associated fjord systems are described in the literature as NEAC (Brander 2005), but a recent study could show that Atlantic cod in Kongsfjorden and other Svalbard fjords not only belong to the NEAC ecotype but also to the Norwegian Coastal cod (NCC) which normally can only be found along the Norwegian coast (Spotowitz et al. 2022).

Atlantic cod find a highly structured shallow water zone in Kongsfjorden, including hard bottom areas that are covered with kelp forests. By their characteristics, these areas

are potential nursery areas for Atlantic cod (Seitz et al. 2014). From 2012 to 2014, a combined study of the shallow water zone of Kongsfjorden was conducted. Data were gathered by a permanently deployed underwater observatory (Baschek et al. (2017), Fischer et al. 2017) and an extensive baseline fishing campaign from 2012 to 2014. The first results of the fishing campaigns of 2012 and 2013 showed a high abundance of Atlantic cod with a standard length (SL) ranging from 5 to 20 cm (Brand and Fischer 2016). By literature, it is known that age classes 0+ to 2+ remain in the settlement area and might only perform limited seasonal migrations (Woodhead 1959; Ottersen et al. 1998). Individuals in age class 3+ typically start migrations toward their later spawning habitats on the west coast of Norway (Ottersen et al. 1998).

With this study, we present a first-time report about the life history of Atlantic cod in the shallow water zone (0–12 m water depth) of Kongsfjorden for the years 2012–2014. We used otolith-based age determination to identify age classes and age–length relationships. We show the temporal distribution of different age classes, as well as growth rates in different years and seasons. Furthermore, stomach content analysis identifies the food sources of the specimens. The

Arctic is expected to be one of the focal areas facing climate change-induced temperature increases in the coming decades (IPCC 2014). These data may provide a valuable snapshot for comparison with past and future studies of the Arctic coastal ecosystem. Dramatic changes in species distribution in the central Arctic can already be seen today (Snoeijs-Leijonmalm et al. 2022), and it is expected that rising seawater temperatures further foster the establishment of non-Arctic species (Fossheim et al. 2015).

Materials and methods

Sampling

Sampling was conducted in 2012, 2013, and 2014. Two sampling episodes per year were done in the months of June and September. The sampling started in June 2012 at two locations: one at the southern shoreline (Fig. 1, OPC - Old Pier Central) and the other on the shoreline of Blomstrandhalvøya (HnS - Hansneset South). Paired sampling was performed using one fyke net (diameter 40 cm, length 90 cm, bar mesh size 12 mm, deployed in 3m water depth) and a trammel net (inner/outer mesh size 1/15 cm, length 20 m, height 2 m, deployed in a depth of 5–12 m). The net was deployed perpendicular to the shoreline, with recovery and redeployment every 24 h. The 24-h interval was extended to 48 h if bad weather conditions did not allow recovery.

The September 2012 sampling period showed problematic interactions between young seals and the trammel nets. To avoid harming the wildlife, we stopped using trammel nets and relied exclusively on paired sampling using fyke nets. The new configuration comprised two fyke nets (diameter 40 cm, length 90 cm, bar mesh size 12 mm, deployment in 3 and 12m water depth) and one double-fyke net (diameter 60 cm, length 110 cm, bar mesh 12 mm, deployment in 5–8-m water depth). The double-fyke net was connected by an 80 cm high steering net (18 mm bar mesh). All three nets were deployed perpendicular to the shoreline and fish tissue was used as bait. This new standard configuration was used for all further sampling. Species-level identification of Atlantic cod specimens was performed based on morphological traits using the methods proposed by Hayward and Ryland (2009) and Klekowski and Węśławski (1990). The primary features of distinction were the structure of the lateral line, the coloration of the ventral side, and the protruding upper or lower jaw. In the laboratory, the SL and wet weight (WW) of all the sampled fish were measured. A total of 720 Atlantic cod were caught in all sampling periods. For a listing of all other species caught in the sampling periods of 2012 and 2013, see Brand and Fischer (2016). The sagittal otoliths were extracted, cleaned in distilled water, and stored

for later analysis. Stomach content samples were weighed and stored in formalin.

After evaluation of the sampling episodes in 2012, sampling in 2013 and 2014 was extended to five sites on Blomstrandhalvøya and five sites on the southern shore (Fig. 1). The exposure time of the nets was by standard 24 h. Owing to logistical and weather constraints, the exposure was extended to a maximum of 96 h. This extended exposure time was deemed reasonable due to the generally low saturation of the fyke nets. As a metric for fish abundance, catch per unit effort (CPUE) was used to standardize fish catch for differences in exposure times. CPUE represents the number of fish per net per 24-h exposure time. Previous analysis by Brand and Fischer (2016) showed no effect of different exposure times on CPUE. Due to the differences in sampling setup, no CPUE of 2012 is compared to 2013 or 2014. All quantitative analyses in this study use exclusively CPUE of 2013 and 2014, where identical sampling strategies and gears were used (Table 1). For comparison of CPUE of the years, 2013 and 2014, a Kruskal-Wallis rank sum test (Kruskal and Wallis 1952) was performed. The results were further analyzed by a post hoc Tukey (Tukey 1949; Driscoll 1996). Data from 2012 are included for qualitative comparison as, e.g., standard length composition. We compared the standard length (SL) distribution of the sampling years 2012, 2013, and 2014 by Kruskal-Wallis rank sum test (Kruskal and Wallis 1952) and Dunn's test for multiple comparisons using rank sums for post hoc analysis (Dunn 1964). This analysis was later repeated for the age class composition of those years. The analysis was performed in R (R Core Team 2021) using the package PMCMRplus (Pohlert 2021).

Otolith analysis and age-length keys

We performed otolith structure analysis (Stevenson and Campana 1992) on sagittal otoliths to reliably assign age classes based on the SL. From a total of 720 specimens, we sampled the sagittal otoliths of 551 specimens. Of those we successfully processed samples of 533 specimens (see Table 2). Otolith analysis was performed with a Leica M60 binocular zoom microscope with an ACHRO 0.8X lens, zoom level set to 2.0, and binoculars with 10× magnification. A part of the otoliths was embedded in resin and prepared on slides. Those were read in 'bright field' setting. The other otoliths, which were untreated, were broken in two in the transversal plane, and the piece with the core was mounted on a modeling compound, with the fracture side up. The otolith was illuminated from the side so that the light is scattered up through the fracture.

Length classes were binned by centimeters. An age frequency per length class table was created and used to compute an age-length key (ALK), see also Ailloud and Hoenig (2019). ALK were calculated separately for June and

Table 1 Overview of Catch per Unit effort (CPUE) per sampling site and season

Year	Season	Sampling site		Blomstrandhalvøya (North)									
		South shore											
		Brandal	Old Pier West	Old Pier Central	Old Pier East	Gasebu	London	Hansneset South	Hansneset Central	Hansneset North	Sorvagen		
2013	June	0.0325	0.0739	0.1154	0.0106	0.0146	0.0303	0.1775	0.1254	0.094	0.0464		
	September	0.0724	0.2381	0.2552	0.2636	0.2841	0.2033	0.3012	0.2936	0.2507	0.1885		
2014	June	0.0484	0.4355	0.1690	0.4194	0.3069	0.0969	0.0969	0.0339	0	0.1777		
	September	0.5217	0.3745	0.1250	0.0971	0.4444	0.3785	0.0648	0.0195	0.0542	0.2381		

A CPUE value of 1 represents one fish in 24-h exposure time in one-fyke net

September of 2012, 2013, and 2014. The age–length key was used to assign age class information to specimens for which no otolith sample was available (Fig. 3). The full method is presented in Ogle (2016).

Growth rates

Cohorts of fish were tracked over multiple sampling periods to calculate intra- (June to September) and inter-annual (September of actual to June of the following year) growth rates. Per year and season, the average SL per age class and sampling period were calculated. Age information was gathered by otolith analysis. The number of days between the middle of successive sampling periods was calculated (Table 3), and the changes in average SL per age class were standardized to growth per day. Additionally, the standard length and wet weight were plotted against each other to visualize the length-to-weight relationship as a growth parameter (s. SI Fig. 1).

Food sources

The stomach contents were removed and its weight was determined. We calculated a fill index (FI) by the formula $FI = W_i * 10,000 / W$ (W = bodyweight of fish, W_i = weight of stomach content). The stomach content was stored in formalin (4%). A subset of 47 stomach content samples from the 2013 sampling campaign were analyzed for the presence of different food items. Food items were identified to the lowest possible taxonomic level by an expert taxonomist. We recorded the presence of food categories by sampling season and age class. The food items were categorized as *benthic*, *demersal*, *pelagic*, or *fish tissue*. In Table 4 the two most common items per group are shown, while the remaining items per category are presented cumulatively. We compared the FI of the sampling years 2012, 2013, and 2014 by Kruskal-Wallis rank sum test (Kruskal and Wallis 1952) and Dunn's test for multiple comparisons using rank sums for post hoc analysis (Dunn 1964).

Water temperature

The water temperature was recorded at 12 m water depth by the AWIPEV underwater observatory at the Old Pier in Ny-Ålesund (Fischer et al. 2017). The data are published in Fischer et al. (2018a, b, c). We calculated the average water temperature from June 17 to October 17 of each year, as this time frame corresponds with the fishery assessments. A corresponding box plot was created in R (R Core Team 2021).

Table 2 Overview of samples and corresponding age class composition

Year	Season	Total number of specimen	Specimen with sampled otoliths	Successfully analyzed otoliths	Number of specimen by age-class - Based on otolith analysis (and if not available by age length key)								
					0+	1+	2+	3	4	5	6	7	8
2012	June	52	52	50	–	47 (2)	2 (0)	1 (0)	–	–	–	–	–
	September	71	71	67	7 (0)	57 (4)	–	2 (0)	–	1 (0)	–	–	–
2013	June	84	64	61	–	29 (13)	30 (10)	–	2 (0)	–	–	–	–
	September	274	147	143	65 (0)	49 (52)	21 (78)	1(1)	4 (0)	2 (0)	–	–	1 (0)
2014	June	111	92	87	–	78 (20)	6 (4)	3 (0)	–	–	–	–	–
	September	129	125	125	7 (0)	105 (4)	6 (0)	7 (0)	–	–	–	–	–

Age class was determined by otolith analysis or alternatively calculated by age length keys (in brackets)

Table 3 Growth rate of specimen per season and age class in millimeter standard length per day based on otolith analysis

Time interval			Growth rate in mm SL/d		
Start	End	Duration (d)	Age class 0+	Age class 1+	Age class 2+
June 2012	Sept. 2012	75	NA	0.33	NA
Sept. 2012	June 2013	286	0.14	0.08	NA
June 2013	Sept. 2013	75	NA	0.48	0.62
Sept. 2013	June 2014	288	0.16	0.13	NA
June 2014	Sept. 2014	81	NA	0.51	0.70

Results

In six sampling campaigns from 2012 to 2014, a total of 721 Atlantic cod were sampled, measured, and weighted (see SI Fig. S1). We removed sagittal otoliths from 552 specimens for age class determination.

Comparison of spatial and temporal differences in species abundance

A significant difference in the overall Catch per Unit Effort (CPUE) was observed between the four sampling campaigns of 2013 and 2014 (Kruskal-Wallis test: $H_3 = 10.931$, $p = 0.015$). Post hoc analysis shows only the sampling campaign of June 2013 (0.073 ± 0.055 , $n = 10$) and September 2013 (0.235 ± 0.067 , $n = 10$) are significantly different (Tukey test: $p < 0.03$). No significant difference in CPUE could be found between the different sampling sites (Kruskal-Wallis test: $H_9 = 5.5327$, $p = 0.7856$).

Length frequency distribution and age class determination

The standard length (SL) frequency distribution in Fig. 2 shows characteristic differences between the six sampling seasons. It is recognizable that in the June campaigns of all years the number of specimens below 10 cm SL was very low. Additionally, it is recognizable that the September

season of 2013 had a higher number of specimens above 21 cm SL than the other campaigns. Statistically significant differences regarding SL distribution could be observed between the sampling years 2012, 2013, and 2014 (Kruskal-Wallis test: $H_2 = 10.76$, $p < 0.01$). The post hoc test revealed significant differences between 2012 and 2013 (Dunn's test: $p = 0.019$) and 2013 and 2014 ($p = 0.014$). Additionally, significant differences in age class composition could be detected between the sampling years (Kruskal-Wallis test: $H_2 = 25.367$, $p < 0.01$). Here the post hoc test also revealed significant differences between 2012 and 2013 (Dunn's test: $p < 0.01$) and 2013 and 2014 ($p < 0.01$).

Comparison of length frequency and age class distribution

Regarding length class distribution, a slight overlap between age class 1+ and 2+ is given. Additionally, in September 2013 an overlap between 0+ and 1+ specimens was detected (see Fig. 3). Overall age class 1+ was the dominant fraction of all specimens in all sampling episodes with a total share of 63.8%. Age class 2+ represents overall 22.05% of all specimens. Age class 0+ was only detected in September and represented 10.96% of all specimens. Age classes greater than 2+ accounted for 3.19% of all samples. The details given in Fig. 4 also show that the age class composition in 2013 deviates from 2012 to 2014. For June 2013 the share of age class 2+ specimens was clearly higher in 2013 (46.43%) than in 2012 (23.08%) and 2014 (13.51%).

Table 4 Results of stomach content analysis per age class and season

Season	Atlantic cod		Benthic (%)		Demersal (%)		Pelagic (%)		Fish tissue e (%)		
	Age class	No. of specimen	<i>Caprella septentrionalis</i>	<i>Harpacticoida</i> n. det.	Other	<i>Ischyrocerus</i> spp.	<i>Anonyx sarsi</i>	<i>Amphipoda</i> spp.		<i>Calanus</i> spp. remains	<i>Thysanoessa inermis</i>
June	0+	–	–	–	–	–	–	–	–	–	–
	1+	10	10.0	0.0	20.0	70.0	0	60.0	10.0	20.0	0.0
	2+	10	10.0	20.0	60.0	40.0	0	60.0	10.0	10.0	0
September	0+	12	33.3	25.0	16.7	16.7	0.0	50.0	16.7	0.0	0.0
	1+	7	28.6	42.9	42.9	14.3	14.3	85.7	0.0	14.3	0.0
	2+	8	12.5	0	12.5	12.5	25.0	50.0	0.0	12.5	12.5
	All	47	19.1	17.0	29.8	31.9	6.4	59.6	10.6	14.9	4.3
			66.0			97.9			29.8		8.5

Percentage of stomach that contain at least one item of a certain food category are given

Also, in September 2013 the share of 0+ and 2+ specimens was elevated. Age class 0+ specimens represent 23.40%, which was more than double that observed in 2012 (9.72%) and 2014 (7.26%). Age class 2+ specimens represented 35.82%, a distinctively higher amount than in 2012 (0%) and 2014 (14.52%). In between the sampling campaigns of 2012–2014, we saw per age class no difference in average SL beyond the standard deviation (see Fig. 5).

Growth rate over the years

We detected an overall growth rate of 0.176 mm SL/day for the 2011 cohort, 0.217 mm SL/day for the 2012 cohort, and 0.216 mm SL/day for the 2013 cohort (see SI Fig. S2). Growth in the summer months was higher 0.49 ± 0.10 mm SL/day ($n=5$) than in winter months 0.14 ± 0.04 mm SL/day ($n=4$) (see Table 3).

Stomach content analysis

Stomach content analysis of 47 samples revealed 35 different food items. These food items were categorized into benthic organisms ($n=14$), demersal organisms ($n=14$), pelagic organisms ($n=4$), and the category fish tissue. Amphipods were present in 97.9% of all samples, with *Ischyrocerus* spp. and *Anonyx sarsi* being the most abundant. Further, benthic items were present in 66% of all the samples, and *Caprella septentrionalis* and Harpacticoida were the most frequent. Prey in the pelagic category was present in 29.8% of all samples with *Calanus* spp. and *Thysanoessa inermis* being the most frequent groups in this category. Fish tissue was found in 8.5% of all the samples (Table 4). A more detailed analysis showed that fish tissue was only found in September and only in age classes 1+ (14.3%) and 2+ (37.5%). Items in the benthic and demersal categories were found in all age classes from all sampling episodes.

The fullness indices (FI) in June were significantly lower than in September (Kruskal-Wallis test: $H_1=4.7985$, $p=0.028$), see Fig. 6. We also detected differences in the FI between the different sampling years (Kruskal-Wallis test: $H_2=9.2056$, $p=0.01$). The highest average FI was for 2012, followed by 2014 and 2013. The post hoc analysis showed significant differences between 2012–2013 (Dunn's test: $p<0.01$) and 2012–2014 ($p<0.02$).

Water temperature

At the sampling site Old Pier in Ny-Ålesund we detected the following water average water temperatures for June–September. In 2012 (4.30 ± 0.93 , $n=1750$), 2013 (4.70 ± 0.94 , $n=1907$), and 2014 (5.43 ± 1.05 , $n=2107$), see SI Fig. S3.

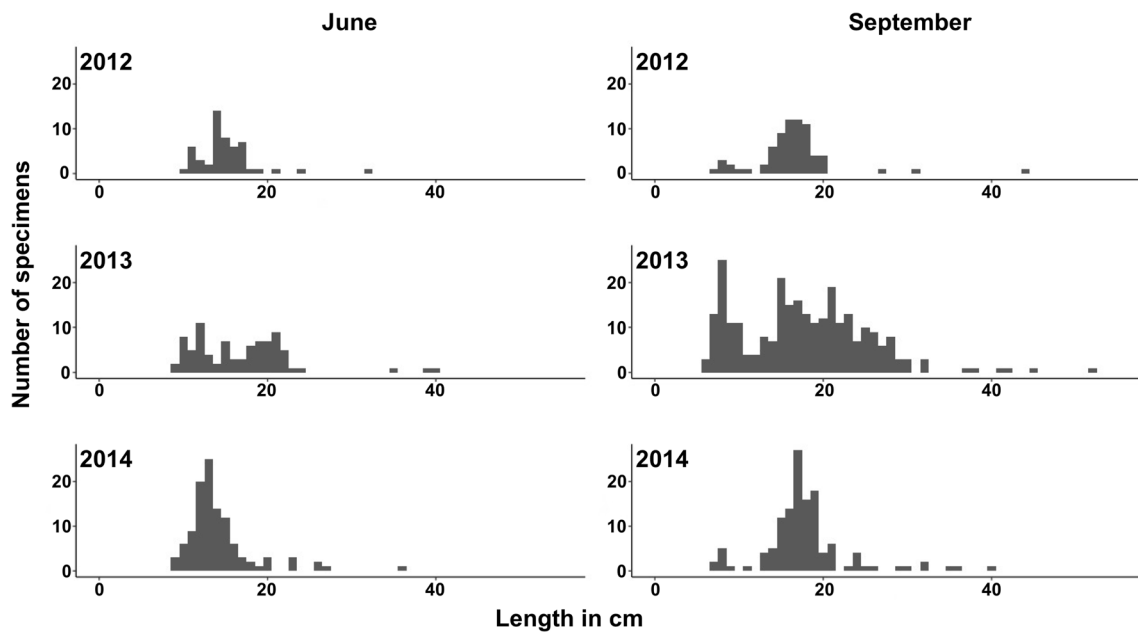


Fig. 2 Standard length frequency distribution of all specimens, shown per sampling year and campaign (nN = 720)

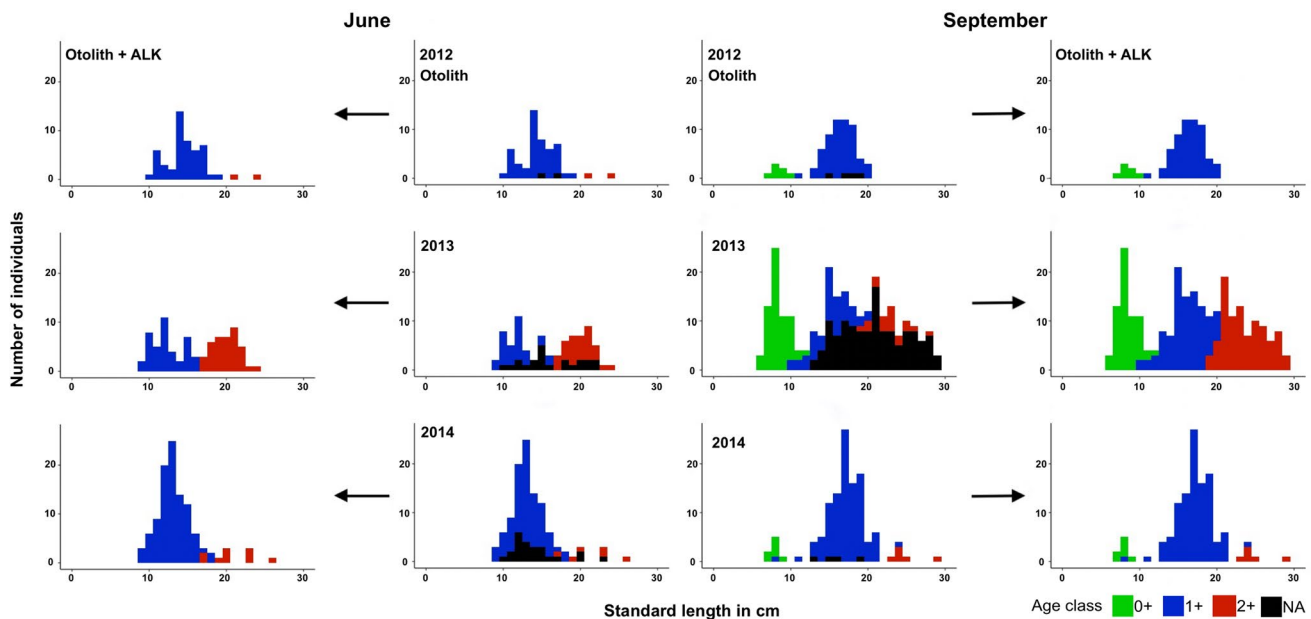


Fig. 3 Detailed age and length distribution of the age classes 0+ to 2+. The results based on the otolith analysis are shown in center left and right. Specimens without age class (black, NA) had no oto-

lith sample or the sample was unreadable. Specimens with NA were given an age class based on the developed age length key. The results are shown to the very left and right

Discussion

Atlantic cod in Kongsfjorden

This study offers the first quantitative and detailed report about the age class composition of Atlantic cod in the

shallow water zone (0–12 m water depth) of Kongsfjorden, Svalbard. The specimens with a standard length of 5–20 cm as described in Brand and Fischer 2016 could be identified as belonging to the age class 0+ and 1+. For 2012 and 2014 these age classes account for more than 88% of all specimens. For 2013 we could detect a high share of age class 2+

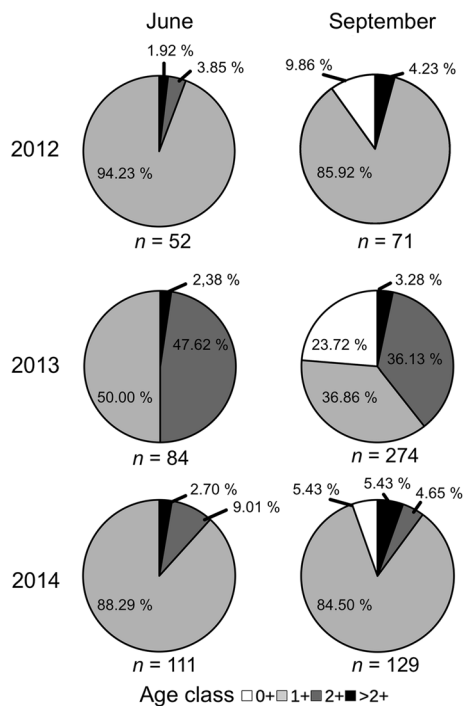


Fig. 4 Age class composition per sampling campaign in percent. The results are based on the otolith analysis. Specimens without otolith sample were given an age class based on the developed age length key

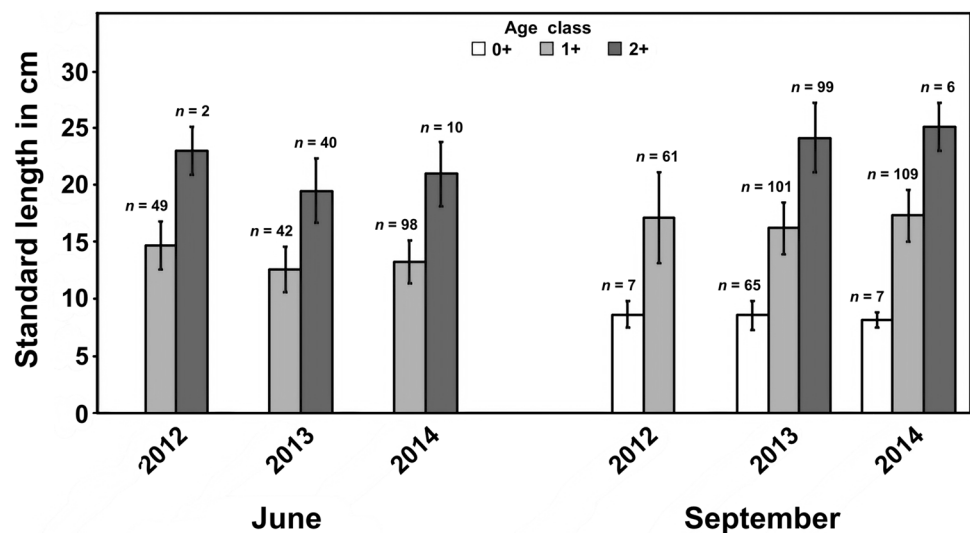
in June (47%) and September (36%). According to Ottersen et al. (1998) Atlantic cod will not undertake large seasonal movements in their first 2 years, after settlement which coincides well with the permanent presence of age class 0+ and 1+. The absence of age class 0+ in June 2012, 2013, and 2014 could be explained by the reported spawning period of Northeast Arctic Cod (NEAC) from February to early May at the Lofoten (Brander 2005) and the subsequent transport

by the West Spitsbergen Current (WSC). As the settlement is reported at an age of 5–6 months (Ottersen et al. 2014), it seems reasonable that specimens arrive in Kongsfjorden in August. This assumption is also supported by Mark (2013a, b), who reported that Atlantic cod with a SL ranging from 5.5 to 9.5 cm were observed in Forlandsundet and the mouth of Kongsfjorden in August 2013. The specimens with the lowest SL sampled in this study were 6.5 cm and had a body height of 10 mm. Age class 0+ specimens below 12 mm body height might be underrepresented in this study because the sampling gear had a bar mesh size of 12 mm. Consequently, the average SL shown for age class 0+ specimens could be overestimated, as the smallest specimens might not have been sampled. By year-round observation data from the Kongsfjorden underwater observatory, it is most likely that no age class 0+ specimens were present before August (Fischer et al. 2017). Therefore, the absence of age class 0+ specimens from any June sampling episodes in this study is unlikely to be an artifact of gear selectivity.

Shallow water kelp forests as a foraging ground

The presence of age class 0+ and 1+ in the shallow water zone and its kelp forests opens the question of what the ecological function of this zone is. The analysis of stomach content shows that these age classes feed primarily on benthic and demersal food items. Only a small number of specimens show pelagic food sources, primarily *Calanus* spp. and *Thysanoessa inermis*. Both are usually not available in the shallow water zone. Importantly, these zooplankton species are known to conduct diel vertical migration throughout the year, which could explain how shallow water cod are able to prey on these species (Berge et al. 2009). Gotceitas et al. (1995) highlighted that juvenile Atlantic cod use kelp forests as structural protection to avoid active predators. Fish size

Fig. 5 Average standard length per sampling season for the dominant age classes 0+, 1+, and 2+. The values are based on otolith analysis and for samples without otolith age an age class was assigned based on the developed ALK



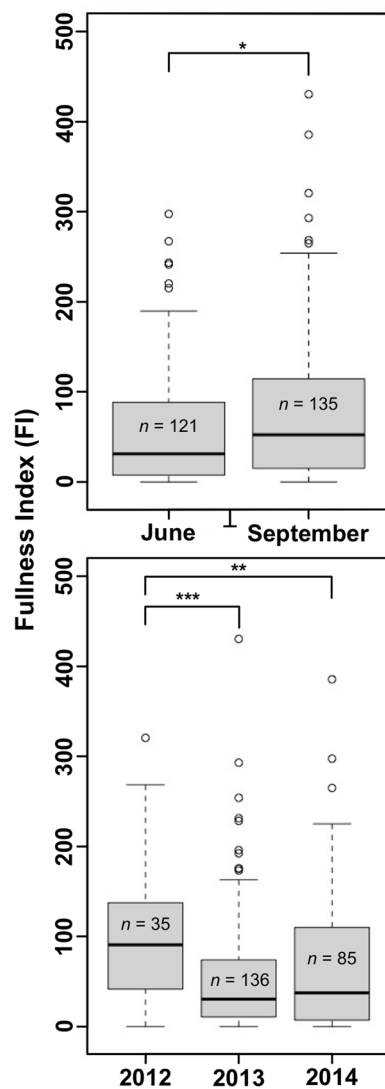


Fig. 6 Fullness Index (FI) per Year and Season. The upper panel show the FI of all specimens separately for the June and September campaigns. The lower panel shows the FI of all specimens separately per sampling year

in relation to the density of the kelp forests seems to be an important factor, as fish that exceed a certain size cannot swim easily through the kelp forest. Depending on the structure and density of the kelp forest, this might facilitate age class separation. The kelp forests between 2.5 m and 15 m depth (Bartsch et al. 2016) might fulfill a dual function by providing structural protection against predators and being a feeding ground. Norderhaug et al. (2005) showed that Atlantic cod is feeding on a large range of kelp-associated invertebrates, as also shown in this study. These kelp-associated species might find food year-round in the kelp forests. Renaud et al. (2015) showed that most benthic taxa feed on a broad mixture of particulate organic matter and macroalgal detritus. During the polar night, the infauna of the decaying

kelp beds of Kongsfjorden might be an important energy and food resource for Atlantic cod. This concurs with Berge et al. (2015b), who observed the feeding activity of Atlantic cod during the polar night and a high abundance of fauna associated with *Saccharina latissima*. This suggests that the polar night is not a time of biological quiescence (Berge et al. 2015a). Also, in this study, we observe a growth of Atlantic cod between September and June. The average growth rate is lower than during the summer months (June–September). This might be connected to lower water temperatures and an overall lower amount of available food. Fittingly we detected that the fullness index (FI) for specimens was highest in September at the end of the summer season. The combination of these facts suggests that Atlantic cod uses kelp forests and subtidal soft bottoms of Kongsfjorden as nursery areas, as also reviewed by Seitz et al. (2014).

Differences in age class separation

Our results showed that age classes 0+ to 1+ are the dominant age classes in the shallow water zone. Specimens of age classes 2+ or greater were very low in abundance, indicating that these might have shifted their habitat as part of their life history. This concurs with Ottersen et al. (1998), who showed that after settlement, fish do not undertake large seasonal movements in their first 2 years. After this period, Atlantic cod in the Barents Sea have been reported to show horizontal migrations, which are connected to predation avoidance and prey availability. Brander (2005) and also this study show a more fish-based diet starting in age class 2+. On the vertical migrations in the Barents Sea *Mallotus villosus* is one of the main prey items that is followed.

In this study, it was notable that specimens of age class 2+ and above were sampled only in 2013 in larger quantities in the shallow water zone between 0 and 12 m. The reason therefore could be differences in this year's class strengths, sampling effects, or differences in the hydrographic regime. While the sampling technique and effort remained comparable, differences in year class strength cannot be entirely excluded, as Kongsfjorden is an open system. Movement of Atlantic cod into and out of the fjord, as well as migration to different water layers is possible. As shown in Ingvaldsen (2017) adult Atlantic cod can be expected generally in between 150- and 600-m water depth on Svalbard. It is reported for 2013 that the subsurface (Payne and Roesler, 2019) and bottom waters (Fransson et al. 2016) of Kongsfjorden were colder in 2013 (~ 2–4 °C) than in 2014 (~ 3.5–6 °C). The temperature in the shallow water zone remained rather constant (4.3–5.4 °C). It is known that adult Atlantic cod prefers higher temperatures (Nakken and Raknes 1987) than juveniles. The cold temperatures in the deeper water layers could have led to a partial avoidance by adults. This might have resulted in the special mix of

different age classes in the shallow water zone that could only be observed in 2013 (see Fig. 2, 3).

The observation might only be true for central Kongsfjorden and its hydrography. Mark (2013a, b) reports for Forlandsundet, at the mouth of Kongsfjorden, vertical separation between different age classes with adult Atlantic cod at the bottom (170–220 m) and smaller specimens in the shallower waters (0–50 m). Such vertical separation is also reported for Atlantic cod along the Norwegian coastline, known as the Norwegian Coastal Cod (NCC). Juvenile specimens of this stock, which have a non-migratory lifestyle, are known to settle in shallow waters of coastal areas and fjords (Løken et al. 1994). After 2 years, these specimens start a vertical separation, and adult specimens can be found in deeper waters of up to 500 m (Bakketeig and Bakketeig 2018). In NCC a connection between increasing genetic differentiation and geographic distance has been shown by Dahle et al. (2018).

Origin of specimens

In Kongsfjorden, hydrographic conditions and sea ice show an inter-annual variability. Advection of seawater from the WSC leads to generally increasing water temperatures and is influencing food availability (Cottier et al. 2007; Hop et al. 2002, 2019; Hegseth et al. 2019). This might open an ecological window of opportunity for the Atlantic cod to establish a permanent non-migratory population. Iversen (1934) reported Atlantic cod in the spawning stage at Isfjorden bank and around Bear Island during the last Arctic warm period from 1920 to 1940. He also reported age class 0+ specimens at Grønfjorden on Svalbard and mentioned that sporadic spawning seemed to occur close to Isfjorden and in the Bear Island area. However, he stressed that the largest number of Atlantic cod in Svalbard waters was likely associated with the spawning grounds off the coast of Norway. Andrade et al. (2020) suggest that a NEAC population has established itself in Isfjorden and Kongsfjorden and that specimens in Isfjorden show limited local movement which is typical for NCC. NCC and NEAC both spawn at some adjacent locations along the Norwegian coast, and eggs and larvae can be subject to the same processes of transport and dispersal (Brander 2005). Therefore, eggs and larvae in Kongsfjorden could be transported via the Norway Coastal Current and WSC toward Svalbard and Kongsfjorden. Recent studies by Spotowitz et al. (2022) show that specimens of NEAC and NCC can be found in fjords on Svalbard. These NCC specimens were found in age class 0+ and adult form and showed genetic differences to NCC on the Norwegian coast. This indicates a separation into a Svalbard CC population.

Outlook

It is likely that the shallow water zone of Kongsfjorden can provide a nursery and foraging habitat for Atlantic cod, enabling growth rates comparable to conspecifics in the Barents Sea, as described in Brander (2005). The origin of Atlantic cod in Kongsfjorden is less clear than in the past because a mix of NEAC, NCC, and potential local forms need to be considered. For a better understanding of the current state and further development of the Atlantic cod population in Kongsfjorden, regular monitoring seems worthwhile. To differentiate between populations of Atlantic cod a mix of genetic and otolith analyses as applied in Spotowitz et al. (2022) seems to be reasonable. Automated underwater observatories with hydrographic sensors and camera systems can additionally provide valuable contributions. They allow year-round monitoring of local fish populations and may allow assessing the influence of the hydrographic regime on abundances. The sampling in shallow water and deep-water zones should be coordinated for a holistic assessment of the local fish communities, as it must be understood that the data of this study are strictly limited to 0–12 m water depth. Recent research has shown that the northward expansion of Atlantic cod might also affect the Greenland shelf (Strand et al. 2017). A reasonable effort in monitoring should be conducted to clarify the origins of these specimens as it might provide valuable insights into the change in Arctic fish communities.

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Author contributions MB performed the whole sampling campaign described in the proposed manuscript. The initial explorative age reading of otoliths were conducted by LS with support from MB. ELL performed a complete age reading of all otoliths. JMW performed the analysis of stomach content samples. The analysis of the dataset was performed by MB. All listed authors participated equally in the writing process, whereas PF is the PI of the project and JB as well as FM supported the discussion fundamentally so that without them it would not be possible to submit the proposed manuscript.

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Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that the submitted work was carried out in the absence of any personal, professional, or financial relationships that could potentially be construed as a conflict of interest.

Ethical approval The local regulations related to fauna harvest on Svalbard exclude saltwater fish, except for salmonids. Additionally, an application for the research project submitted to the local governor (Sysseimesteren) was approved by his authority in accordance with local legislation. All work was performed in accordance with the act on animal welfare and by accepted research methods. We were also in contact with NARA (Norwegian Animal Research Authority), and they confirmed that for our sampling no additional approval had to be applied for.

Consent to participate Not applicable.

Consent for publication Not applicable.

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Chapter 2

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

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Contributions: The idea, design, and execution of this study were performed by LS with advice from TJ and PF. LS performed the sampling campaigns and the DNA extraction for further processing. LS prepared otoliths for the outer shape analysis and TJ, AH performed the genetic analysis. The manuscript was written by LS, TJ, AH, and EB. CS and PF added advice for the writing of the manuscript.

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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 Arctic 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). Rollefson (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

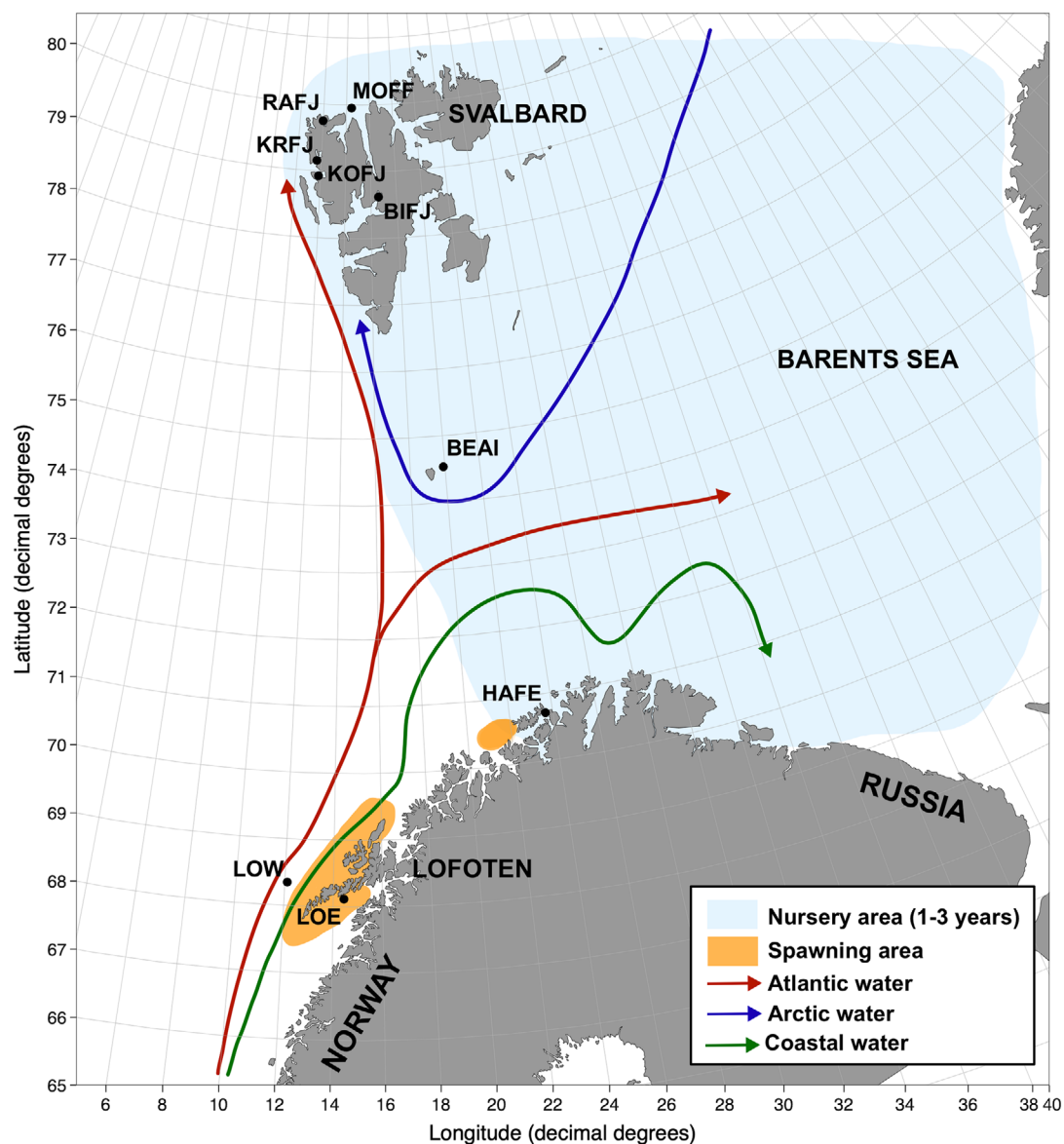


Fig. 1. Sampling sites for Atlantic cod around Svalbard, Bear Island and the coast of northern Norway. MOFF: Moffen; RAFJ: Raudfjorden; KRFJ: Krossfjorden; KOFJ: Kongsfjorden; BIFJ: Billefjorden; BEAI: Bear Island; HAFE: Hammerfest; LOW: Lofoten West; LOE: Lofoten East

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 Rollefson (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 (Rollefson 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	<i>Pan I</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	<i>Pan I</i> ^{AA}	<i>Pan I</i> ^{AB}	<i>Pan I</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

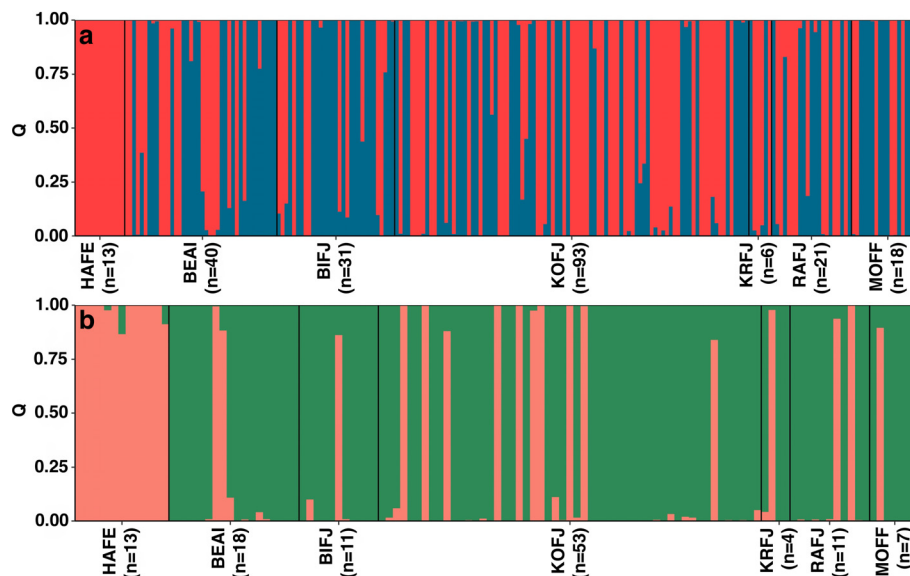


Fig. 2. Atlantic cod from Norway, Bear Island and Svalbard divided into different groups (K) by the software STRUCTURE v.2.3.4 (Pritchard et al. 2000) based on allele frequency in the sampling site. Each vertical line represents an individual. Q -values describe each individual score to the different 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	BEAL_ CC-B	BIFJ_ CC-B	KOFJ_ CC-B	RAFJ_ CC-B	MOFF_ CC-B	BEAL_ 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
BEAL_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
BEAL_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.

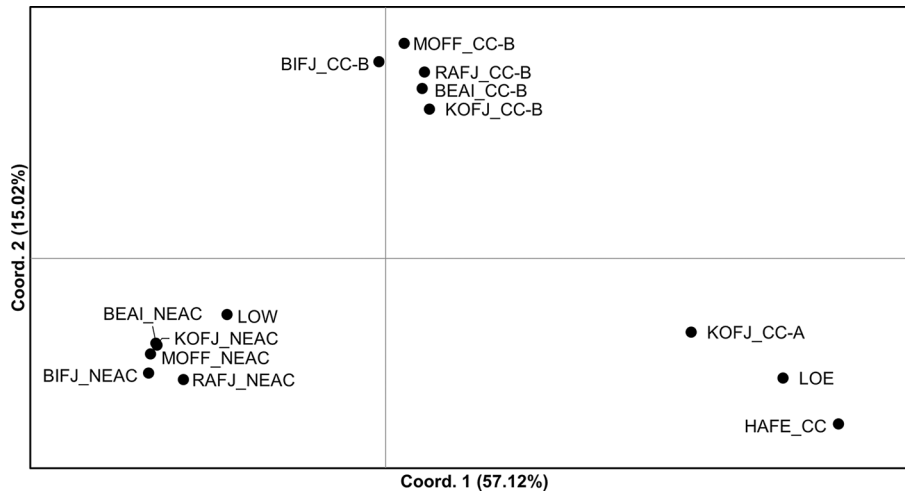


Fig. 3. Atlantic cod from Norway, Bear Island and Svalbard divided into Northeast Arctic cod (NEAC) (Fig. 2a) and the coastal cod (CC) types CC-A and CC-B (Fig. 2b) based on the software STRUCTURE v.2.3.4 (Pritchard et al. 2000). The threshold for Q-values (i.e. for assigning individuals to each groups) 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

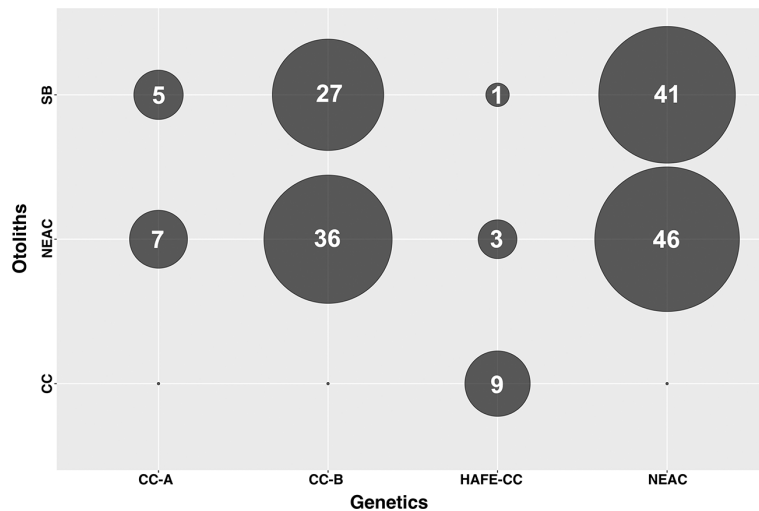


Fig. 4. Classification results for inner otolith shape versus genetic assignment for Northeast Arctic Cod (NEAC) and coastal cod (CC). For otolith typing, CC = Types 1–2, Svalbard type (SB) = Type 3, NEAC = Types 4+5

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. His-

torically, 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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Chapter 3

Observation of long rough dab (*Hippoglossoides platessoides*) eggs in Kongsfjorden, Svalbard

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Research Article

Observation of Long Rough Dab (*Hippoglossoides platessoides*) Eggs in Kongsfjorden, Svalbard

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The long rough dab (*Hippoglossoides platessoides*) is one of the most common bottom dwelling fish species in the Barents Sea with a limited commercial value, even though it is regularly caught as bycatch. Adult *H. platessoides* can be found in large numbers along the west coast of Svalbard, but nothing is known about the spawning area of this species or the distribution of their eggs and larvae within Svalbard fjords. Recent findings of *H. platessoides* eggs in Kongsfjorden indicate that a spawning population exists either within the fjord or on the west Spitsbergen shelf.

1. Introduction

The long rough dab (*Hippoglossoides platessoides*) is boreo-arctic species and one of the most abundant pleuronectiform fishes in the Barents Sea [1]. It is a common bycatch species in bottom trawl surveys [2, 3] but has low commercial value for fisheries [4]. The overall distribution ranges from the southeast Barents Sea to the continental slope of the Norwegian Sea and from Norwegian and Russian coastal areas to the north of Svalbard [1, 4]. The average preferred depth ranges between 50 and 550 m, with most of them occurring between 100 and 300 m [2, 4, 5]. *Hippoglossoides platessoides* can tolerate water temperatures from -1.8°C to 7°C but is most abundant from -0.5°C to 4.0°C [1, 4, 6]. Three major currents affect the distribution and spawning behaviour of *H. platessoides* in the Barents Sea: the North Atlantic Current (NAC) with its warm and highly saline waters ($S > 35$), the Norwegian Coastal Current (NCC), which has lower salinity ($S < 34.7$), and the cold East Spitsbergen Current (ESC) [7]. Along the west coast of Svalbard, the NAC splits into the West Spitsbergen Current (WSC) and meets the ESC (Figure 1). The polar front where the cold Arctic ESC and warm Atlantic NAC waters meet appears

to be an area of high concentration of this species due to high primary production [2]. Overall spawning mainly occurs in the western and central Barents Sea [7]. A general east-west migration of *H. platessoides* between the polar front and spawning grounds in the Barents Sea has been suggested [2] but has never been validated. Furthermore, it is unknown whether *H. platessoides* around Svalbard and Bear Island display similar migration patterns [2]. Dolgova and Albert [4] did not report extensive migration movement for this species.

Spawning in the Svalbard area is thought to occur from March to July [8] and is related to increasing water temperature and day length. The average spawning temperature in the Svalbard area and Barents Sea is 2°C although higher mean spawning temperatures were measured on the continental shelf around Iceland (4.5°C) and in the North Sea ($< 7^{\circ}\text{C}$) [8]. Long rough dab eggs float in the upper water layers until hatching [8]. The egg shape is very characteristic and unique among fish eggs with a wide perivitelline space around the yolk and no oil globule (Figure 2; [9, 10]). The egg size in the Barents Sea ranges from 1.4 to 2.6 mm, and the hatch size of the larvae varies from 4 to 6 mm at a bottom spawning temperature of $1\text{--}3^{\circ}\text{C}$. Hatching occurs after 11–14 days at 4°C [11].

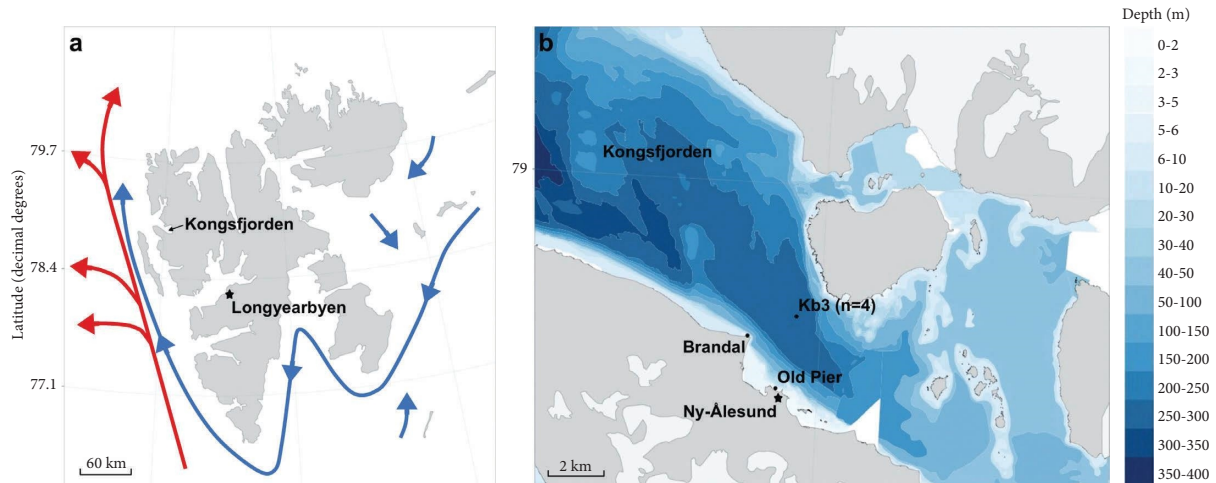


FIGURE 1: (a) Map of Svalbard with the major currents, the warm West Spitsbergen Current (red) and the cold East Spitsbergen Currents (blue). (b) Overview of sampling sites in Kongsfjorden, Svalbard. The number in parenthesis indicates the number of long rough dab eggs caught.

Small catches of 0-group individuals on the west coast of Svalbard are rare, but known [7]. There are no documented egg findings along the west coast or within the fjords of Svalbard. Therefore, the region is currently not considered a spawning area for *H. platessoides*.

An overall trend of increasing water temperatures in Arctic waters has been observed with the warmest temperatures in the Barents Sea recorded so far, affecting the local ecosystem and introducing boreal fish species [12]. Warm water periods might have affected the extension of spawning grounds of *H. platessoides* along the west coast of Svalbard and within fjords. In Atlantic-influenced fjords such as Kongsfjorden, observed increasing water temperatures could favour appearance and survival of eggs [13, 14].

In this study, we describe the occurrence of *H. platessoides* eggs captured during ichthyoplankton sampling aimed at gadoid fish eggs and larvae in Kongsfjorden, indicating either undescribed or expanded nearby spawning grounds.

2. Materials and Methods

2.1. Study Area. Kongsfjorden is located on the west coast of Svalbard at 79° N. It is oriented from NW to SE and shares its mouth with Krossfjorden. Neither of the fjords have a sill, allowing free water mass exchange with the adjoining ocean. The West Spitsbergen Current (WSC) runs along the continental slope of Svalbard, bringing warm saline ($S > 35$) water masses into the fjord. Cold Arctic water is transported from the north towards the west Spitsbergen shelf and flows into Kongsfjorden. Here, these water masses mix with fresh water from melting glaciers and riverine outflows.

Three different sampling sites were chosen in Kongsfjorden to assess the ichthyoplankton community (see Figure 1): one sampling site in the middle of the fjord (Kb3; 78°57.24' N, 11°57.38' E, sampling depth 0–50 m, and bottom depth approximately 300 m), a second sampling site in the shallow water (<10 m deep) with a known rocky bottom



FIGURE 2: Section of the *H. platessoides* egg, the head and front part with yolk sac.

and an associated algae cover (Old Pier), and a third sampling site with a sandy bottom (<10 m deep; Brandal).

Plankton sampling was conducted between 1 May and 16 July 2020. The station Kb3, which is used regularly for plankton monitoring, was chosen for the primary sampling over the entire period (see Figure 1). Until 26 June 2020, sampling was performed twice a week and then four times a week thereafter. From 1 July 2020, a shallow water (less than 10 m deep) transect approximately 300 m long was sampled twice per week close to the settlement Ny-Ålesund between Old Pier and the Ny-Ålesund harbour (78°55.715' N, 11°55.518' E). This sampling site was added to potentially catch fish larvae on their way to shallow water settlement areas. Brandal, a third sampling site west of Ny-Ålesund (78°56.789' N, 11°52.192' E), was sampled once on 6 July 2020. During the whole sampling campaign, the shallow water temperature was continuously recorded with the underwater observatory located at the Old Pier in approximately 11 m depth [15].

2.2. Sampling of Fish Eggs. Sampling at Kb3 was conducted using a standard CalCOFI plankton net with a diameter of 113 cm and mesh size of 500 μm . A smaller plankton net with a diameter of 67 cm was used at the other two sampling sites as sampling was conducted from a smaller boat that did not allow for deployment of the large CalCOFI net.

At the sampling site Kb3, each sampling comprised one vertical and one horizontal plankton net haul. Vertical net hauls were performed from 50 to 0 m with an average speed of $1\text{ m}\cdot\text{s}^{-1}$. The horizontal hauls were towed for 5 min at a speed of 1.5–2 km at approximately 1 m depth. Sampling at Brandal and along the transect between the Old Pier and the Ny-Ålesund harbour comprised of four horizontal net hauls, towed for 5 min at a depth of approximately 1 m. All plankton samples were visually checked for fish eggs and larvae. Before examining the samples under a dissecting microscope, fish larvae were removed and transferred to a Petri dish that was placed on a bed of crushed ice to keep it cool. Fish eggs were removed from the sample and stored in 96% ethanol at -20°C . If possible, representative images of all fish eggs per sample were taken, and if more than 20 eggs were caught, a random subsample of images was taken.

2.3. Fish Egg Identification. Fish eggs were identified to the species using morphological characteristics [9, 10]. Eggs of uncertain origin were photographed for further analysis.

3. Results

3.1. Pelagic Eggs. A total of 182 eggs of different fish species were caught over the entire sampling period entirely at the sampling site Kb3. The first fish eggs were found on 15th May, and the last eggs were found in late June. Four eggs were visually identified as *H. platessoides*. Although detailed information about egg stages was not obtained in this study, the analysis of the egg images suggests that only later stage eggs (stages 3 and 4) of the long rough dab were found (following egg staging criteria of [16]).

These eggs were only found in vertical and horizontal tows at the sampling site Kb3, but not in the shallow water zone. Two eggs were found on 19th May, another on 28th May, and the last one on 5 June 2020. After that date, no eggs of *H. platessoides* and from mid-June onwards none of any other fish species were caught, either at the pelagic or at the shallow water sampling site.

3.2. Water Temperatures. During the sampling period, the water temperature in the shallow water zone (<10 m) increased continuously from -0.8°C (01 May 2020, 11 m depth) to 5.6°C (16 July 2020, 11 m depth). In mid-May, the water temperature increased above 0°C .

The change from negative to positive degree Celsius values in 2020 was later compared to previous years, when it was often observed from March to early April. The maximum temperatures in 2020 increased to 8°C in early August which were the highest measured shallow water temperatures in that area since 2013 [15].

4. Discussion

Little is known about the occurrence and distribution of the long rough dab in the fjords of Svalbard. The eggs found in Kongsfjorden in this study did not confirm whether spawning occurred within the fjord or on the west Spitsbergen shelf. According to Walsh [7, 8], the distribution of eggs and larvae is mainly affected by local currents and physical oceanographic processes of the water masses. These currents and the local wind systems are also the main driver for advective processes between Kongsfjorden and the neighbouring shelf [17]. Therefore, the currents flowing into the mouth of Kongsfjorden may have transported the eggs into the fjord. The local hydrographic regime in combination with weather conditions such as wind directions from the west Spitsbergen shelf into the fjord could explain why the initial observation of eggs was exclusively in the centre of Kongsfjorden (the sampling station Kb3) rather than at the sampling sites close to the shore and in shallow waters.

Therefore, we assume that eggs were introduced into the fjord due to the hydrographic regime and local wind systems.

Alternatively, the long rough dab might have spawned within the inner parts of the fjord itself finding suitable spawning and settlement conditions in Kongsfjorden. Based on ecological indicators, the authors in [18] divided Kongsfjorden into four zones, two outer and two inner fjord zones, of which the two inner ones are least affected by advection processes [17]. Considering the development time of long rough dab eggs (11–14 days at 4°C [11]), the sampled eggs have an approximate age of at most 10 days, which could indicate spawning in the inner part of the fjord rather than being advected from the west Spitsbergen shelf.

The 0-group long rough dab could not be found in the deeper parts of Kongsfjorden so far, but small numbers of the 0 group were recorded off the west coast during surveys from 1985 to 1991 [7]. According to Walsh [7], small populations inhabit the fjords on the west coast of Svalbard, but the literature reporting catches within Svalbard fjords is sparse. Hop et al. [18], however, described the long rough dab as common for the deep-water regions of Kongsfjorden, particularly for their “transitional zone” between the inner and outer fjord close to which the outer boundary station Kb3 is situated. In general, the west coast of Svalbard and its adjacent fjords are generally not often surveyed for ichthyoplankton because of their isolated location. Available information about the egg and larval distribution is, thus, very limited.

Milinsky [5] inferred from seasonal catch distributions that in the Barents Sea, the long rough dab undertakes periodic spawning migrations once the adult stage is reached. More recent publications, however, indicate that this may not be the case [4]. Adult individuals are distributed north of the Svalbard bank and in coastal waters off western Svalbard, and there appears to be a distributional overlap between juveniles and adults [2]. Walsh [8] also mentioned that migration can be a response to temperature changes. In Kongsfjorden, advective processes within the hydrographic regime like the warm water inflow vary among years [19] and show very particular temperature characteristics in 2020

(own observation), with long-lasting low temperatures at the beginning of the year and high temperatures during summer compared to previous years.

Over recent years (2012–2019), a mean annual increase of 0.17°C in the shallow water masses (<12 m) has been observed [13]. In the shallow layers (up to 12 m), temperatures below 0°C were observed until May. In contrast, 2020 also had one of the highest maximum temperatures (8°C) observed in the last 8 years [13]. The long rough dab can tolerate a temperature range between –1.3°C and 5°C in the Barents Sea [1], and larvae were observed within near-surface temperature ranges of 3°C–5°C in May and 5°C–7°C in June/July [7]. These temperatures are in accordance with the temperatures recorded from May to July 2020 in the shallow water zone of Kongsfjorden. Ongoing changes of Kongsfjorden's temperature regime could make this fjord, like other Atlantic-influenced fjords of Svalbard more suitable for early life stages of boreo-arctic species like the long rough dab. A changing hydrographic regime towards warmer waters could affect the distribution and dispersion of eggs, and temperature could influence survival and vertical migration patterns. The observation of long rough dab eggs could be a result of a fluctuating temperature regime which affects the spawning success within Svalbard fjords. In 2020, it seems most likely that eggs have been advected into the fjord where larvae find an environment suitable for survival. It cannot be postulated with certainty that eggs were absent in the fjord before, but our observation do confirm their presence nowadays. Whether this observation indicates an existing local spawning population or results from adapted changes in spawning behaviour or is just a unique occurrence due to short-term changes in the temperature regime remains unclear.

Future ichthyoplanktonic surveys in the Kongsfjorden system could help broaden the knowledge about the distribution of the long rough dab in a warming Arctic. A comparative analysis between the deeper areas of the fjord and the shallow water zone should be conducted to understand the role of the different habitats for this species.

In addition, the presented observation of long rough dab eggs might help to improve the knowledge about the egg distribution in Svalbard fjords and create a baseline in the future understanding of the distribution pattern due to increasing water temperatures.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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General Discussion

The Arctic marine ecosystem is facing rapid shifts in spatial species distribution and abundance (Fossheim et al. 2015, Wassmann et al. 2011), while the knowledge about the changes within Arctic fish communities is still limited. Thereby, precise knowledge about past, current, and future shifts in species distribution is essential for conservation efforts and effective stock management.

The present thesis contributes to a more profound understanding of the Arctic fish community and evaluates the effects of climate change and climate variability on the population structure of Atlantic cod. This commercially important species can be seen as an indicator of the ongoing borealization and Atlantification processes (Fossheim et al. 2015, Ingvaldsen et al. 2021) in Svalbard fjords like Kongsfjorden. This thesis aims to improve knowledge about the distribution dynamics of Atlantic cod in Svalbard waters and the appearance of a Svalbard ecotype in the Arctic environment. Furthermore, the potential establishment of Atlantic cod in the Arctic is evaluated.

This thesis investigated three research objectives: (1) The overall increase of Atlantic cod in Svalbard waters is evaluated and different Atlantic cod ecotypes are analysed. (2) In this context, the potential establishment of local spawning ecotype is discussed. (3) The spatial distribution patterns and settlement is correlated to climate fluctuations and the overall warming of the Arctic. Special emphasis is drawn to the assessment of Atlantic cod in the shallow water zone of Kongsfjorden with respect to the increase in water temperature measured by continuous water temperature recordings from 2012 to 2020. For these objectives, an approach was used that combined data assessments with the underwater observatory and fisheries in the shallow water zone in Kongsfjorden. Further, fishing campaigns by ship have been performed in several fjords along the western and northern coastline of the Svalbard archipelago.

In chapter 1, for three consecutive sampling years (2012 to 2014) juvenile Atlantic cod of the age class 0+ to 2+ could be identified in the shallow water zone of Kongsfjorden. Age and growth rates were determined via otolith analysis. Increased fish growth was observed during the warmer summer months, and it is likely that growth is altered by temperature and food

availability. Stomach content analysis indicates the use of kelp belts as a feeding ground. Thus, the shallow water zone seems to be an important nursery ground for Atlantic cod. This chapter provides basic information which is necessary to consider for a successful settlement in an Arctic fjord.

Chapter 2 shows the findings of a profound genetic and morphometric analysis of Atlantic cod from several fjords on Svalbard and compares these with reference samples from the Norwegian coast. The analysis of adult and juvenile individuals gives a clear indication to research questions 1 and 2, suggesting the presence of a local, non-migrating coastal cod ecotype. The results highlight the importance of combined analysis for the stock assessment of Atlantic cod, as only the combination of both methods shows a complete picture of the ecotype distribution within Svalbard fjords. The results are also discussed in the framework of research question 3.

Chapter 3 shows results based on research question 2. A single ichthyoplankton sampling was performed in Kongsfjorden in 2020. Hereby, no eggs of Atlantic cod were found. However, eggs of the long rough dab could be sampled and contribute to a more complex picture of the ichthyoplanktonic community in a sub-Arctic fjord. The environmental conditions during that sampling season were colder in comparison to previous years and suggest that the absence of Atlantic cod eggs might be related to these low temperatures. It is important to note that the absence of Atlantic cod eggs in a single sampling campaign does not exclude the presence in Kongsfjorden profoundly.

The dynamic hydrographic regime might result in major differences in the water body from year to year. It is known that the temperature of the surrounding water masses directly affects the recruitment of Atlantic cod and is linked to larval and juvenile growth (Ottersen & Sundby 1995, Vikebø et al. 2005). Atlantic cod on Svalbard lives at the lower limit of their temperature range (Righton et al. 2010). Therefore, warmer years could have a positive effect on potential local recruitment in Kongsfjorden, while in colder years, non-tolerable temperatures might be avoided by vertical or horizontal movement or result in an absence or skipped spawning.

Results from this thesis show that in Svalbard fjords, extreme cold and warm phases might significantly influence the vertical and horizontal distribution of boreal fish species. It is to mention that the sampling campaigns only show observations of one very temporally limited snapshot. Changes of the hydrographic regime in between the campaigns can lead to fluctuations in the fish communities. This shows the importance of solutions for a continuous monitoring of biotic and abiotic parameters.

Arctic warming and extreme events

The average Arctic sea surface temperature is rising nearly four times faster than the global average, causing rapid sea-ice loss (Rantanen et al. 2022). This process is known as Arctic amplification. In the 1970s began the increase of Arctic surface air temperatures which was faster than the global average and included likewise a rise in storm activities in the Atlantic region (Delworth et al. 2016, Chylek et al. 2022). Sea ice-wind interactions show a pull-push feature which is affecting how much sea ice is covering the area. Normally, sea ice reaches its maximum extent in March/April and a minimum in September (Åsbjørnsen et al. 2020).

In addition to the observed recently occurring global warming, the NAO is generally responsible for a multidecadal variability in the North Atlantic climate system (Delworth et al. 2016). Ocean-atmosphere interactions are affected by the NAO, which, in a positive phase reduces the amount of warm Atlantic water inflow into the Norwegian Seas as well as the heat transfer to the atmosphere (Mikhailova et al. 2021). Interestingly, Mikhailova et al. (2021) further report that cyclonic activities over the marginal seas of the Eurasian shelf are displaced northward and contribute to the advection of warm air to the Nordic Seas and the Barents Sea region, whereby the frequency of southerly winds increases. Furthermore, water temperature increases and results in a decrease in ice extent in the Barents Sea. Currently, the NAO is in a positive phase (NOAA 2023) and the lowest sea ice coverage since the recordings began in 1967 was observed in February 2023 as a result of changing southerly winds which are pushing the drift ice north and northeast away from Svalbard (Norwegian Meteorological Institute 2023). Overall sea ice cover in the Svalbard area has been strongly fluctuating over the last ten years (see Fig. 3). In contrast to the present observation, the overall strong sea ice coverage on Svalbard in 2020 can be correlated to a larger than normal ice coverage and low temperatures as observed, e.g., in Kongsfjorden.

The hydrographic regime during the sampling campaigns from 2012 to 2014 showed low sea ice extent in 2012 and 2014, whereas in 2013 comparably more sea ice was recorded around Svalbard (see Fig. 3). These interannual fluctuations could be correlated to the age class distribution of Atlantic cod in the shallow water zone of Kongsfjorden described in chapter 1 (Brand et al. 2022). The number of 2+ specimens in June 2013 was higher compared to 2012 and 2014. In addition, age class 0+ specimens more than doubled in the September campaign of 2013. Even though the surface temperature of the shallow water zone remained rather constant (4.3 - 5.4 °C), the subsurface and bottom water temperature was colder, indicating an inflow of cold water into the fjord (Brand et al. 2022). The cooling of the water column might

have resulted in the avoidance of 2+ specimens and therefore an increase in abundance in the warmer, shallow water.

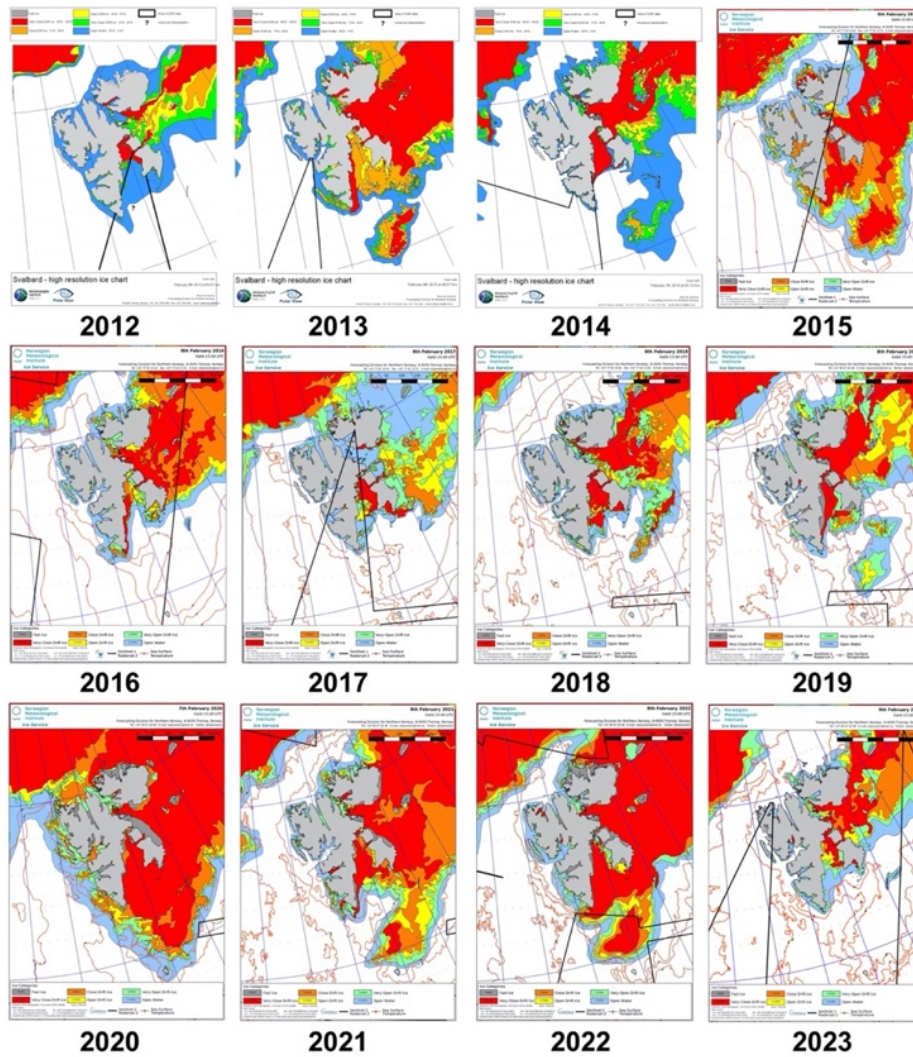


Figure 3 Ice charts from the Svalbard area between 2012 and 2023 (Norwegian Meteorological Institute (2023); adapted after the Norwegian Ice Service) with extended ice cover in 2020 and very low ice cover in 2023. All charts date from approx. 8th February in consecutive years. Red: Very Close Drift ice, Blue: Open Water

In this context, it is important to differentiate between changes in hydrography which occur within the water masses in the deep and changes in the surface waters. Atmospheric cooling, such as seasonal winter cooling, mixing and the inflow of freshwater might affect the shallow water zone and the surface layers but does not automatically affect or change the temperature in the deep. Storms, e.g., can promote the mixing of the water column and surface waters, whereas the loss of sea ice facilitates greater mixing (Cottier & Porter 2020). In contrast, the effect of the West Spitsbergen Current (WSC) and the resulting inflow of warm Atlantic water (AW) occur mainly in the deep as AW advects into Kongsfjorden along the bottom (Tverberg

et al. 2019). Continuous and reliable seasonal monitoring of the water column and changes in hydrography is strongly dependent on mooring systems and permanent sensor installations. Marine observatories are a powerful resource for determining the drivers and impacts of environmental change (Hop et al. 2019a). In Kongsfjorden the longest time series of a mooring gives temperature profiles since 2002 (Hop et al. 2019a). Time series like these are crucial for the understanding of long-term changes, but they allow likewise to identify potential extreme events and put them in a broader context. In this context, warm phases such as e.g., the wintertime warming in 2005/2006 (Cottier et al. 2007) and in 2014, respectively 2017 (see Fig. 4, Fischer et al., unpublished data) have been identified. The warming from 2005 to 2007 was also observed on a larger scale in the Atlantic water masses passing as the West Spitsbergen Current through the Fram Strait (Beszczynska-Möller et al. 2012). In Kongsfjorden, warming was observed over the last decades based on temperature data from the deep, as well as the shallow water zone and clearly show a significant increase in overall water temperature (Noufal et al. 2017, Hop et al. 2019a, Fischer et al. 2021b).

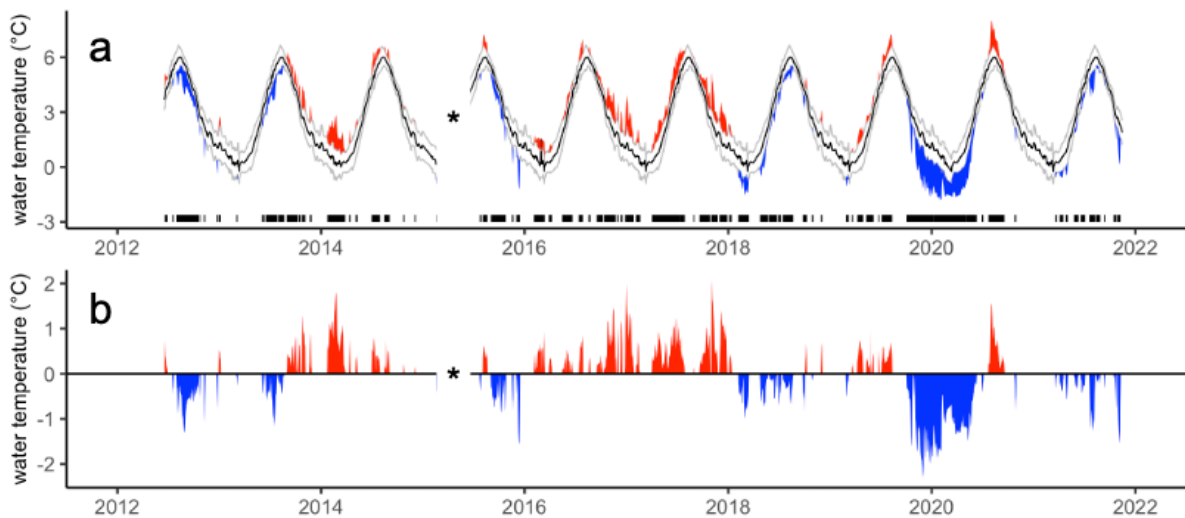


Figure 4 Water temperature from 2012 to 2020. The extreme phases are calculated after Hobday et al. (2016).

* = no data available due to iceberg collision. The black inlay above the x-axis indicates the temporal occurrence of extreme phases at all. The red areas identify the heat waves during this time and the blue areas the cold waves. For a better illustration of the extremes, the panel b shows only the magnitude and duration of the extreme temperature values (measured value - upper resp. lower 90% percentile)

Changes in the atmosphere-ice-ocean system such as increasing water temperature and decreasing sea ice cover are affecting Arctic communities on species, community, and food supply levels (Ingvaldsen et al. 2021). On Svalbard, the effect of these changes varies, as every single fjord has individual hydrographic and regional characteristics which have to be considered.

In comparison to other fjords on Svalbard, Isfjorden and Kongsfjorden on the west coast of Svalbard are well-studied fjord systems. For these fjords, the decline in sea ice cover has been connected to an increased inflow of warm Atlantic water masses (Cottier et al. 2007, Tverberg et al. 2019). Isfjorden, located slightly further south than Kongsfjorden is experiencing a positive trend with +1.5 °C water temperature per decade (Cottier et al. 2022) and an increase in sea-surface temperature (SST) as well as in advection of Atlantic water (AW) supported by wind forcing towards the fjord (Skogseth et al. 2020). Overall, a link between the wind-forced circulation pattern, wintertime inflow of AW into the fjords and the observed reduction of sea ice around Svalbard can be assumed (Skogseth et al. 2020). The effects of atmospheric forcing on the sea ice cover and sea-surface temperature are likely to be positively related (Cottier & Porter 2020).

In Kongsfjorden, it appears like the warming trend is unidirectional, and results only in warmer temperatures. But in fact, the interannual fluctuations and dynamics in the local hydrography seem to go in both ways, including heat and cold phases (Fig. 4). On the one hand, the general trend leads towards a warmer Arctic, on the other hand, fluctuations can also result in extreme cold short-time events as e.g., recorded in the shallow water zone in spring 2020. The cooling of the shallow water zone was in correlation with the above-average cold phase of the last decade and a result of an overall cold phase in the Svalbard area (see also Fig. 3). Interestingly, the cold phase of winter 2019/20 was followed by a heat phase and one of the warmest summers in the 121-year records of Longyearbyen airport (Norwegian Meteorological Institute 2021).

In chapter 3, temperature recordings show sub-zero degrees in the shallow water zone until mid-May, which is rather late compared to previous years. These cold temperatures might contribute to the absence of spawning attempts of Atlantic cod in Kongsfjorden or influenced the survival of early life stages. Cold surface temperatures were followed by the highest recorded shallow water temperature since the beginning of the recordings in 2012. Observations made in chapter 3 might indicate, in contrast to the absence of Atlantic cod eggs, that spawning of the long rough dab seems to have taken place either within the fjord or on the adjacent shelf. The long rough dab can be considered a boreo-arctic species, tolerating a wide

range of water temperatures. Short-term temperature fluctuations do not seem to have a negative impact on spawning, but general knowledge about early life stages and their survival along the west coast of Svalbard and within fjords is very limited.

The increase in volume transport of Atlantic water plays a key role in the warming Arctic and must be considered when it comes to changes in the distribution and movement of fish communities. Atlantic cod on Svalbard lives at the lower limit of their temperature range (Righton et al. 2010) and is therefore more affected by extreme cold phases. In contrast, heatwaves like in summer 2020 are more likely to be tolerated by boreal species as this temperature regime lies more within the optimal thermal range and might therefore be beneficial. The temperature of the surrounding water masses directly influences the recruitment of Atlantic cod and is linked to larval and juvenile growth (Ottersen & Sundby 1995, Vikebø et al. 2005). In addition, multidecadal processes like the NAO is reported in the past to have effects on the recruitment of Atlantic cod on a local scale within the Barents Sea area (Dippner & Ottersen 2001, Sundby & Nakken 2008). Thus, warmer years could have a positive effect on potential local recruitment in Kongsfjorden. Furthermore, it seems possible that cod might avoid non-tolerable temperatures by vertical or horizontal movement even though individual Atlantic cod has even been found up to the Central Arctic Ocean (CAO) and catches on the northern Yermak Plateau seem more common nowadays (Snøeijs-Leijonmalm et al. 2022).

The inflow of warm Atlantic water masses directly influences the seasonal hydrography of a fjord and therefore the timing of spring blooms and advection processes of zooplankton (Basedow et al. 2004, Hegseth & Tverberg 2013). The seasonal activity of plants and animals is driven by environmental factors and often triggered by temperature and light (Menzel & Fabian 1999). Phenological shifts, such as changes in the seasonal timing of life history events, are very valuable indicators of climate change (Zeng et al. 2013, Scranton & Amarasekare 2017). The timing of fish spawning e.g., must match with the timing of seasonal spring blooms, whereas a mismatch can lead to high mortality of the fish larvae due to starvation (Asch et al. 2019). Overall, the increased transport of heat into the fjord changes on the one hand the temperature regime which will affect the survival locally of fish species (Asch et al. 2019) and on the other hand interspecific interactions between species through changes in food supply or predation (Renaud et al. 2012, Hop et al. 2019b).

In combination, the inflow of Atlantic water masses, the level of sea ice concentration, sea-surface temperature, air temperature and local winds are likely to cause warming in the Svalbard fjord system, whereby year-to-year variability impacts the fjords on a local scale. Especially water temperature is the key driver of egg survival, recruitment, and growth of larvae and juveniles (Vikebø et al. 2005, Ottersen & Sundby 1995). Observations from previous years indicate that the hydrographic regime in Kongsfjorden is beneficial for the ecology of Atlantic cod, and that heat waves favour the settlement of boreal species.

It can be summarized that the ongoing climatic processes are the driver of movement and survival for Atlantic species that are invading the Arctic ecosystem. Therefore, short-term dynamics in hydrography and the variability of extreme temperature phenomena should be considered important factors for the Arctic ecosystem and the success of invading Atlantic species in Svalbard waters.

Ecotypes of Atlantic cod in Svalbard waters

Historical findings about the occurrence and distribution of Atlantic cod in Svalbard waters are sparse and often rely on reports of fishermen. The first documented cod fishery in Kongsfjorden started in 1874 and the earliest scientific reports date back to the 1920s when Norwegian fishery investigations reconvened after the first world war (Iversen 1923, 1934). Over the following decades, fluctuations in the abundance of Atlantic cod have been observed and assumptions were made concerning the origin of the Atlantic cod caught in Svalbard waters. The observed abundance increased in the 1920s - 1940s, which can be related to the reported period of Early Arctic warming (Drinkwater 2006, 2009). Interestingly, Iversen (1934) mentions in his report that 0+ individuals of Atlantic cod with a length of 3.5 - 6.0 cm have been found in Grønfjorden, an adjacent fjord of Isfjorden on the west coast of Svalbard. He states that these individuals might not originate from the known spawning grounds in the Lofoten and along the Norwegian coast. Further investigations on the origin of Atlantic cod in Svalbard waters are very limited and based mainly on single-site observations. Further, the harsh conditions in the Barents Sea prevented investigations in the past, as drift ice conditions stretched as far south as Bear Island and made passing into Svalbard waters often impossible (Iversen 1934). Only warming events allowed in the past for fishery on the Svalbard shelf.

Over the last decades, it was generally assumed that Atlantic cod in the Barents Sea and the adjacent Svalbard shelf belong to the ecotype of the Northeast Arctic cod (NEAC) (Brander

2005). Peak spawning occurs in March-April along the Norwegian coast from the Lofoten area in the north until the Møre region further south (Godø 1984a, b). From there, the eggs are advected with the Norwegian Coastal Current and the West Spitsbergen Current into the Barents Sea and onto the Svalbard shelf. The larvae and juveniles have approximately 5 months drift and are advected over a distance from 600 to 1200 km, which can be affected by interannual variation in wind-induced transport processes (Ådlandsvik & Sundby 1994). Atlantic cod larvae switch to a demersal lifestyle after their pelagic phase and remain in the settlement area for approx. 2 years (Wienerroither et al. 2011, Ottersen et al. 1998). The reported arrival of juvenile Gadidae in Kongsfjorden was observed with the COSYNA underwater observatory in August, the observed individuals had an average standard length of about 6.0 cm (Fischer et al. 2017). Individuals caught during the fishing campaigns performed in September could be assigned to the 0+ age group with an average length of approximately 8.6 cm (Brand & Fischer 2016).

Growth during this time is strongly dependent on water temperature and food availability. Results from chapter 1 show that the main food items of 0+ and 1+ cod consist of amphipods, whereas the food of 2+ individuals changes to a diet that also comprises fish tissue. This suggests predation on other fish species or cannibalism (Brand et al. 2022). The dietary composition of Atlantic cod in Kongsfjorden corresponds with the typical diet of juveniles in the Barents Sea, with crustaceans like amphipods being the main prey for age classes 0+ and 1+ and fish tissue for 2+ individuals (Dalpadado & Bogstad 2004). The age classes based on otolith analysis which have been calculated by Brand et al. (2022) correspond likewise with observed growth rates of Atlantic cod in the Barents Sea (Brander 2005) and imply that juvenile Atlantic cod finds an acceptable environment in the colder waters on Svalbard. Brown et al. (1989) also postulate that the 0+ age class can tolerate cold temperatures better than adult individuals, which would facilitate settlement in Svalbard fjords.

The spawning grounds along the Norwegian coast are not only occupied by NEAC, but also by the local, non-migrating Norwegian coastal cod (NCC) (Nordeide et al. 1998). This non-migratory ecotype of Atlantic cod does not perform long-distance movements in its life history and remains within the Norwegian coastal waters. Both ecotypes spawn almost simultaneously in the Lofoten area, but interbreeding is rarely observed, and mingling does not appear to take place randomly (Nordeide et al. 1998). In addition, the distribution of both ecotypes shows vertical overlapping, but NEAC was found more abundant in deeper waters than NCC

(Nordeide et al. 1998). Eggs of both ecotypes underlie the same hydrographic regime, therefore advection of NCC into the Barents Sea and onto the Svalbard shelf cannot be excluded. Mechanisms to retain NCC eggs within the origin fjord exist, such as the location of spawning and specific buoyancy characteristics, but this does not impede that all eggs remain in the fjord (Salvenes et al. 2004, Myksvoll et al. 2011, 2014). Therefore, individuals transported to Kongsfjorden might not only belong to NEAC but also to NCC. Observations with the underwater observatory documented the first gadoid individuals from August on, which most certainly belonged to *Gadus morhua* (Fischer et al. 2017). Unfortunately, the camera system does not allow a 100% identification to species level due to biotic constraints such as visibility, low light, but also position of the fish in front of the camera. Underwater, the differentiation between 0-group Atlantic cod and Polar cod can be challenging, as only small morphometric differences allow identification. Nevertheless, the arrival date in August/September is in accordance with known advection and transport mechanisms for Atlantic cod (Ottersen et al. 2014).

The analysis of individuals caught during sampling campaigns over the last few years also showed that a morphometric differentiation between small larvae, as well as juvenile individuals of Atlantic cod and Polar cod can be challenging. Colour and dotting, the shape of the mouth and the overall body shape give an indication, but require experience for correct differentiation. Therefore, a more profound analysis was used in chapter 2 to clearly differentiate species and ecotypes.

Even more challenging than the identification of Gadidae species is the differentiation of Atlantic cod ecotypes, as outer morphometric characteristics such as body shape and colour cannot always be used with certainty for the differentiation between NEAC and NCC. Thus, another identification method is necessary for the evaluation of Atlantic cod ecotypes in Svalbard fjords. It is known that coastal cod can be separated into genetically distinguishable subpopulations along the Norwegian coast (Mork et al. 1985, Jorde et al. 2007, Dahle et al. 2018). This provides the genetic basis to identify a local ecotype in Svalbard waters. Chapter 2 describes the population structure of Atlantic cod in Svalbard fjords based on *Pan* I and SNP analysis. Both methods are accepted to discriminate between ecotypes (Johansen et al. 2018) and are used for the analysis of species composition. Results from chapter 2 show a clear differentiation between NEAC and coastal cod (CC) sampled in Svalbard fjords. In addition, the coastal cod sampled in Svalbard fjords showed significant genetic differences in comparison to reference samples of NCC from the Norwegian coast (Fig. 5). Therefore, a new ecotype, the Svalbard coastal cod (SCC) was introduced in the framework of this thesis.

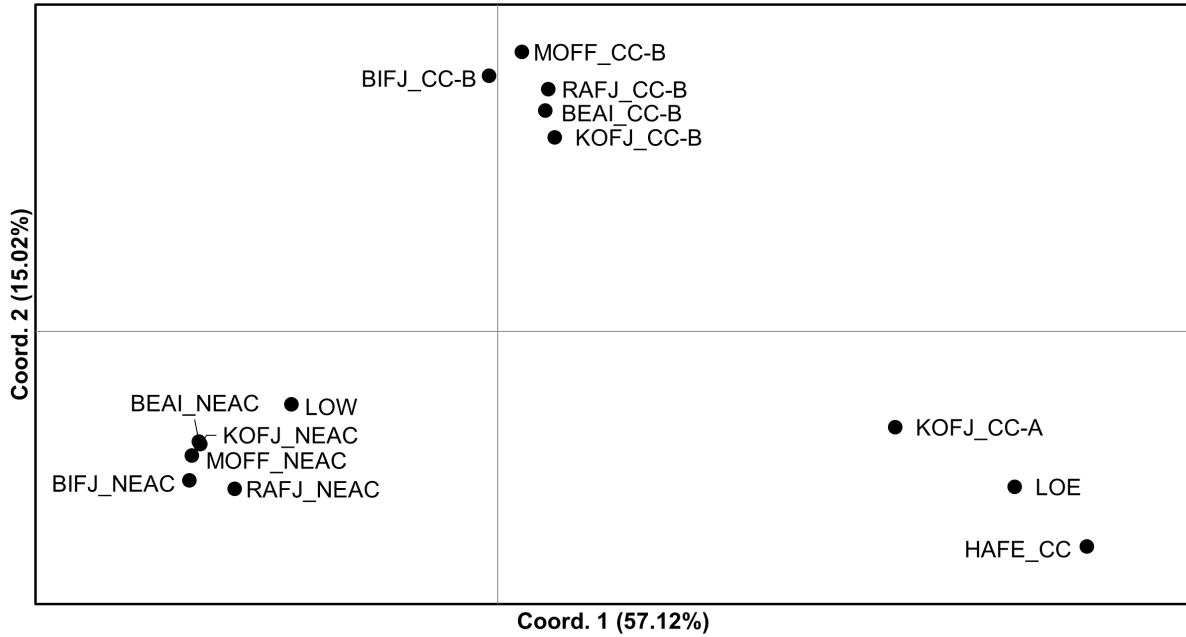


Figure 5 Principal coordinate analysis (PCoA) of Atlantic cod from Norway, Bear Island and Svalbard divided into Northeast Arctic cod (NEAC) and the coastal cod types CC-A (NCC) and CC-B (SCC) based on the software STRUCTURE 2.3.4. Reference samples from Lofoten East (LOE; CC) and Lofoten West (LOW; NEAC) were included. Axis 1 explains 57.12 % of the variance and 15.02 % at axis 2. Abbreviation of sampling sites: BEAI - Bear Island, BIFJ - Billefjorden, HAFE - Hammerfest, KOFJ - Kongsfjorden, MOFF - Moffen, RAFJ - Raudfjorden

This is the first time that Atlantic cod could be assigned to different ecotypes in Svalbard waters, and the results show that SCC can potentially live in a generally colder environment. The survival of cod eggs plays a key role in the establishment of a local Arctic spawning ground. Even though the water temperature shows a clear upwards trend, cod eggs still can experience temperatures much colder than they would undergo along the Norwegian coast. In addition, already observed cold phases might have a strong effect on egg survival when the eggs are exposed to ice and sub-zero temperatures. Cod eggs do not contain any antifreeze proteins but can tolerate minus degrees down to the freezing point of seawater (Valerio et al. 1992). In contrast to eggs which do not contain any antifreeze proteins, adult cod can produce antifreeze glycoproteins to overcome cold water temperatures down to -2 °C (Ruzzante et al. 1996).

Interestingly, coastal cod subpopulations originating from different latitudes along the Norwegian coast show differences in growth rates. The 1+ age class of high-latitude populations might have a higher growth potential due to local adaptations when the environment is potentially disadvantageous, e.g., related to temperature (Salvanes et al. 2004). These adaptations may be a higher food consumption and improved competitive ability with an active feeding strategy (Salvanes et al. 2004). In higher latitudes, higher food consumption

can be the result of an extended time for visual feeding during summer (Suthers & Sundby 1993). It can be assumed that Svalbard coastal cod might have adopted a life history strategy which is beneficial to survive in the local colder environment of a sub-Arctic fjord.

Changes in the environment are therefore not always unfavourable if the organism can cope with these changes. Phenotypic plasticity enables in response to a rise in sea temperatures a northward shift of cold-adapted Atlantic cod (Righton et al. 2010). The formation of phenotypic plasticity reflects therefore the short-term response of a population to changing environmental conditions (Oomen & Hutchings 2015). In general, temperature-induced phenotypic plasticity might affect life history, whereas temperature during early life stages drives phenotypic plasticity and allows organisms to cope better with conditions that they are expected to encounter later in life (Jonsson & Jonsson 2019). According to Oomen & Hutchings (2015), the thermal plasticity in early life stages is crucial to respond successfully to temperature fluctuations and indicates that, e.g., spawning in winter and spring might be more beneficial than autumn spawning.

Temperature and food density have been likewise found to be related to body shape, whereas the genetic differences in phenotypic plasticity between populations can affect morphology (Marcil et al. 2006). In the framework of this thesis, it was out of scope to analyse body shape or the effects of temperature on the early life stages of Atlantic cod. Nevertheless, single observations of differences in body shape might indicate local plasticity as a result of temperature changes. It would require further research to evaluate the level of phenotypic plasticity needed for SCC to survive in Svalbard fjords.

Unfortunately, knowledge about the temporal scale to develop phenotypic plasticity traits in Atlantic cod is lacking, whereby it was not possible within this thesis to conclude a potential time frame for the settlement and establishment of the local SCC ecotype.

Otolith formation in Svalbard fjords

The former assumption that only NEAC inhabits Svalbard waters is mainly based on its known long-distance migration patterns and a life history in the Barents Sea (Brander 2005), which demonstrates survival in colder environments. Further, the assumption is based on a relatively low frequency of adequate sampling in the Arctic region. Scientific sampling was performed mainly in deeper areas by trawling and line fishing, whereby the coastal zone was often neglected. This thesis provides therefore important key information about Atlantic cod in Svalbard fjords which have not been investigated before.

The formation of otoliths plays an important role to understand which ecotypes of Atlantic cod are inhabiting Svalbard fjords. Interestingly, due to the underlying mechanisms in the formation of otoliths towards a specific type, the results do not always match the results of a genetic analysis. Otoliths have been used extensively as a reliable tool to discriminate between Atlantic cod ecotypes (Campana & Thorrold 2001, Berg et al. 2005, Stransky et al. 2008). In general, a classification of 5 different otolith types is proposed (Jakobsen 1987, Mjanger et al. 2000) with 3 types describing the typical CC (type 1), otoliths from the Bear Island and Svalbard area (type 3) and typical NEAC (type 5). Based on this classification, Atlantic cod caught in Svalbard waters have been mostly assigned to the types 3 and 5 in the past. Although the use of otoliths is a reliable discriminant tool, it also has limits when it comes to individual adaptation to new habitats.

Results from chapter 2 show the discrepancy in ecotype determination based on otolith structure and genetic analysis. It shows that ecotype identification by otoliths on individuals from Svalbard might have been inaccurate in the past. In this case, otolith morphology seems to rather reflect a habitat type and growth, which can be linked to water temperature and food intake (Neat et al. 2008, Denechaud et al. 2020). In this study, Atlantic cod caught in Svalbard waters have been genetically identified as SCC but showed morphometric/phenotypic characteristics of NEAC. In addition, cod assigned to the Svalbard otolith type which is based on a distinct alteration of the NEAC otoliths have been likewise identified as genetically belonging to SCC (see Fig. 6). It became obvious that a discrepancy between otolith shape and genetic assignment exists, which might have led in the past to misleading interpretation of ecotype affiliation.

The morphology of otoliths is strongly affected by habitat, surrounding temperature, food availability and light (Chevin et al. 2010, Hüsey 2008). In contrast, genetic belongings are based on more profound underlying processes and reflect distinctively the origin. A key parameter which expresses the effect of the environment on life history parameters is phenotypic plasticity. The development of phenotypes, such as otolith shape, is directly influenced by environmental parameters (Chevin et al. 2010). The outer shape of otoliths is a main parameter to discriminate ecotypes. The formation of the otolith shape, especially the development of the lobes, can be correlated to food intake (Hüsey 2008). Thus, the previously mentioned similarities in food consumption between the sampled individuals from Kongsfjorden and the reference ones from the Barents Sea provide similar environmental information even though the habitat is far away from each other.

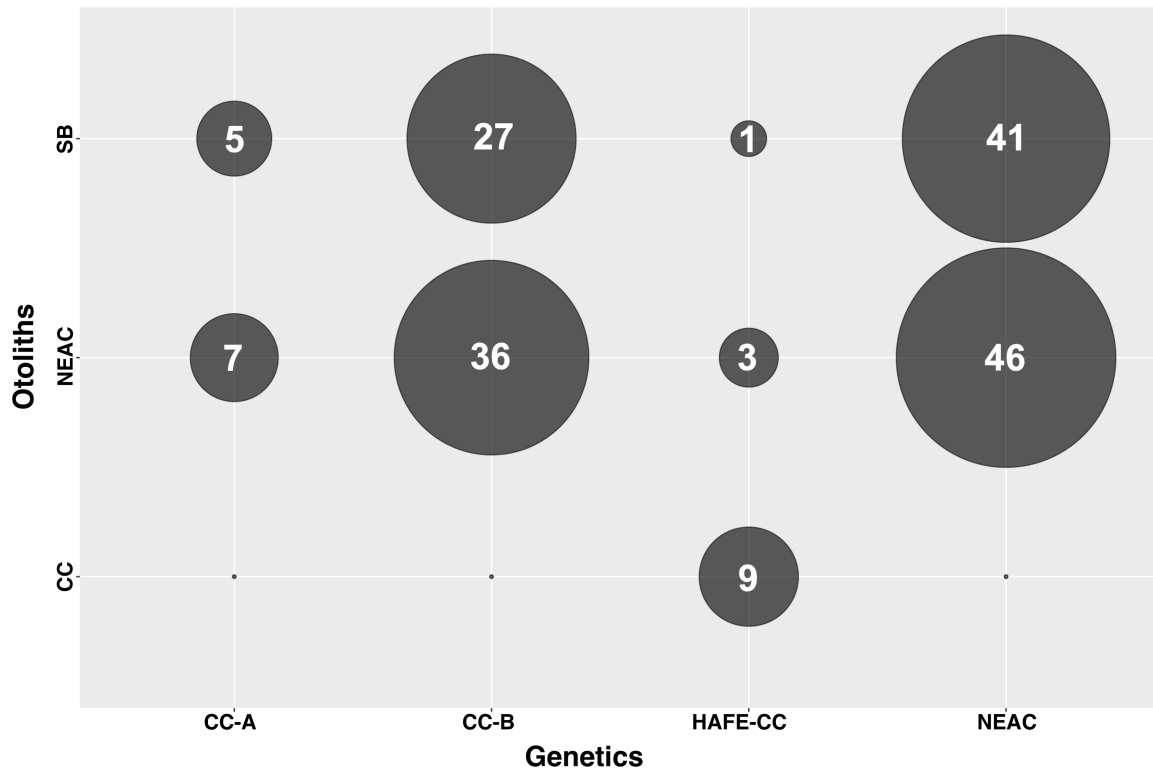


Figure 6 Comparison of classification results for inner otolith shape versus genetic assignment for NEAC and CC. For otolith typing CC = type 1-2, Svalbard type (SB) = type 3, NEAC = type 4+5

Similarities in feeding thereby provide information about an apparent NEAC ecotype whereas the CC ecotype inherited life history traits which have been known previously only from NEAC. In this case, the temporal stability of otolith shapes must be considered. Even though the overall otolith shape of NEAC remains stable over decades, temperature, and food intake might still affect the otolith shape (Denechaud et al. 2020). The effect of temperature is not only reflected in overall growth but also in the material deposition within the otoliths (Campana 1999). The chemical composition of otoliths can be therefore likewise used as a proxy, giving additional information about movement and settlement (Campana et al. 2000). Andrade et al. (2020) used this proxy to reveal the movement of Atlantic cod in Svalbard fjords and could identify movement pattern typical for NEAC and CC. Based on these results, the chemical analysis of SCC otoliths might provide in the future more insight into the movement of these individuals compared to simple ecotype discrimination based on their otolith shape.

Berg et al. (2005) highlight the reliability of separation techniques which are either based on otolith readings or classification with genetic data and conclude that both methods can be considered sufficient to separate between NEAC and NCC. However, otolith readings are always subject to the interpretation of the reader and require experience. The genetic analysis

with *Pan* I, therefore, provides a useful additional tool which also allows revealing subpopulations of coastal cod (Fevolden & Pogson 1997).

In the future, a methodical requirement for the analysis of Atlantic cod in Svalbard waters should be a holistic approach including both, phenotypic identification tools such as otoliths and also a more profound genetic analysis based on e.g., SNP's. Otolith chemistry might be an alternative tool which is more cost-efficient and requires less methodical resources but provides similar information about ontogenetic movement and life history. Overall, fishery management in the Svalbard area requires proper identification for the sustainable management of fish resources.

Implications of Atlantification and warming for the Arctic fish community

With extensive warming events, Atlantic cod seem to have expanded to the Northern Seas and the Svalbard archipelago (Drinkwater 2009). The movement of adult NEAC towards Svalbard waters implies only a temporal use of local fjords as foraging grounds based on the life history of NEAC performing long-distance migration (Brander 2005), whereas adult individuals sampled in the deeper parts of Svalbard fjords do not necessarily perform long-distance migration but originate from the local shallow water zone. Based on the results of chapter 2, juvenile NEAC have been caught likewise in Svalbard waters, which indicates a passive drift of NEAC eggs into Svalbard fjords.

As juveniles remain in the area of settlement for the first two years, it can be assumed that eggs and larvae of NEAC arrived passively in Kongsfjorden where they inhabit the shallow water zone for a limited time before initiating first migrations in the form of dummy runs towards the Norwegian coast (Woodhead 1959, Ottersen et al. 1998). As individuals older than 3+ have not been found in the shallow water, a migration towards deeper waters can be assumed. A reason for the vertical migration can be a change in diet (Ingvaldsen et al. 2017) and the change towards another temperature regime. In general, NEAC is known to inhabit deeper water layers than CC (Pampoulie et al. 2008) and adult Atlantic cod is known for a preference for warmer temperatures compared to juveniles (Nakken & Raknes 1987, Brown et al. 1989).

The temperature preference of adult Atlantic cod can likewise affect its prey-predator interactions with the native Polar cod, which prefers much colder water than Atlantic cod. Benoit et al. (2010) report a diel vertical migration of small Polar cod for feeding on zooplankton, which leads them into water masses inhabited by Atlantic cod. Older individuals remain in greater depth once spawning occurred (Lønne & Gulliksen 1989). Feeding of Atlantic cod on Polar cod was observed during the research cruises with RV Heincke and

confirms Polar cod as potential prey. This might happen especially in the cold mixed layer of 0 - 3 °C water temperature that is used, according to their temperature range by both species. This behaviour might likewise increase the feeding pressure on Polar cod.

An establishment of a local, non-migrating cod ecotype could exacerbate the situation for the native Arctic fish community. The overall increase in temperature and therefore abundance of Atlantic cod seems to lead to a permanent presence of coastal cod in Svalbard fjords. Even though there is no concrete proof for the presence of Atlantic cod eggs or larvae in the framework of this thesis, indications are given which can lead to the resilient assumption of a permanent establishment of coastal cod in Svalbard. In this study, juvenile cod with a minimal standard length (SL) of 4 cm could be caught in the shallow water zone of Kongsfjorden and the length of these individuals indicates that hatching might have occurred within the fjord as it does not coincide with the growth of Atlantic cod eggs and larvae originating from the Norwegian coast. In addition, the genetic assignment to the SCC ecotype showed a clear separation from the local NCC, which only inhabits Norwegian coastal waters. The establishment of the local SCC could follow an invasion process which was not existent before, and which is nowadays supported by an unseen event of Arctic amplification. Climate fluctuations and co-occurring water temperature rise might have led in the past to an increase in the abundance of Atlantic cod in Svalbard fjords, but following cooling events might have detained the enduring settlement and successful survival of Atlantic cod.

It is unknown to which extent climate variability and global warming have to occur to affect the permanent migration of fish species towards the Arctic, but warming is reported to change the northern distribution limits of boreal species (Fossheim et al. 2015). In addition, boreal species like Atlantic cod experience likewise augmented pressure on southern spawning grounds with a potential loss if warming scenarios become reality (Butzin et al. 2016, Dahlke et al. 2018). Therefore, warming affects the survival of Atlantic cod on the higher and lower temperature limits, which leads to a displacement following its thermal optimum. It is unclear to which extent the northward migration and the loss of southern spawning sites are coupled and if future warming will affect the regions to a similar level, but it appears to be obvious that the intrusion of boreal species towards the Arctic will likely affect the local habitat and community.

An increase in the abundance of Atlantic cod in the Arctic could influence the diet of local sea mammals such as ringed seals. In the past, Polar cod was one of the most important food items, the overall average size of consumed fish was between 5 - 10 cm (Weslawski et al. 1994). The

diet of harbour seals likewise includes Polar cod and Atlantic cod (Hop et al. 2002). Other effects of borealization on the Arctic community occur on other trophic levels, which might affect the abundance of cod species. Copepods play a key role in the pelagic food web and provide an important food source (Kwasniewski et al. 2003). Ongoing Atlantification can also be observed within the zooplanktonic community. Boreal species such as the copepod *Calanus finmarchicus* are on the rise in Atlantic-influenced fjords such as Kongsfjorden and converge with the local *Calanus glacialis*. Interestingly, *Calanus finmarchicus* is smaller and stores lower quantities of valuable lipids compared to *C. glacialis* (Renaud et al. 2018). The availability of copepods is crucial for the early life stages of both, Atlantic and Polar cod. Moreover, the effects of the NAO are reported to have effects on the biogeographical boundaries of *Calanus* spp. as likewise observed in Atlantic cod distribution (Fromentin & Planque 1996).

Overall, it seems like nowadays local Arctic species must share habitat and its resources due to an increasing number of Atlantic competitors, which might lead to limited or decreasing resources for the local native community (Ottersen et al. 2023). The increase in water temperature seems to be a key factor for ongoing Atlantification and increased concurrence in habitat use.

Fluctuations occur on a seasonal, as well as multi-decadal scale. Small-scale seasonal changes have been observed e.g., during the winter warming event of 2005/2006 (Cottier et al. 2007) or, in contrast, as a cold phase which could be measured in early 2020 (own observation; Fischer et al. unpublished). These fluctuations might not only affect the abundance of Atlantic cod or Atlantic copepods, but also other fish species. In general, the introduction of boreal Atlantic species in the Arctic ecosystem might destabilize the local community and contribute to an enforcement of pressure on, e.g., the Polar cod population (Renaud et al. 2012).

Other species, such as the boreal long rough dab, are known to occur normally in the Barents Sea and on the Svalbard shelf. The abundance and distribution are likewise considered to be affected by warm Atlantic water inflow, resulting in stronger year-classes (Albert et al. 1994). Even though long rough dab is the most abundant flatfish in the Barents Sea, essential information about its life history parameters such as spawning in the Svalbard zone is lacking. Long rough dab is known in Svalbard coastal waters (Albert et al. 1994, Dolgova & Albert 2011), but the observations of chapter 3 are therefore particularly interesting as they indicate that spawning grounds of long rough dab seem to have shifted towards Svalbard waters, too. So far, the role of long rough dab in the Arctic ecosystem is unknown, but doesn't seem to be

detrimental. A reason for the lack of knowledge is its low value in fisheries, as long rough dab is not considered as a commercially important fish species.

In addition to climate variability and temperature fluctuations, fishing pressure plays another key role in the evolvement of species distribution and abundance of fish populations in the Barents Sea and Svalbard region (Bergstad et al. 2018). Fisheries of boreal species move poleward and increase the risk for local Arctic species to end up as bycatch (Christiansen et al. 2014), provoking the disruption of the Arctic ecosystem functioning. The borealization of Arctic fish communities could be observed on the species level over the last 20 years (Fossheim et al. 2015) and seems to expand even towards the Greenland shelf. Advection processes from the Barents Sea seem to transport boreal fish species like Atlantic cod, but also other species such as the beaked redfish and deep-sea shrimp towards Northeast Greenland (Andrews et al. 2019). These observations indicate that the Northeast Greenland shelf might also become a potential settlement region for Atlantic cod (Strand et al. 2017). The widespread dispersion of Atlantic cod towards potential new habitats also demands an adapted management of cod fisheries in Arctic waters. Interestingly, the recent warming of the Barents Sea already results in improved management actions (Kjesbu et al. 2014) because of an increasing abundance of Atlantic cod. Management strategies for high-latitude fisheries must be adapted in the future to follow-up seasonal and decadal changes in populations strengths as well as shifts in spatial distribution following the species-specific thermal ranges for survival, spawning and successful settlement.

Improvements for a more profound understanding of Atlantic cod distribution in the Arctic

The Arctic moved progressively into focus since climate observations show an alarming rise in sea and surface air temperature (SST; Chylek et al. 2022, Rantanen et al. 2022). To track these changes, it is necessary to install instruments and sensor-carrying platforms which allow long-term observation even during the harsh conditions of the polar night (Sørensen et al. 2020). Due to its location, the Arctic remains a place with limited access to satellite coverage, even though the Svalbard Satellite Station (SvalSat; Skatteboe & Kjeldsen 2004) provides nowadays unique opportunities for pole coverage. A stable remote infrastructure for measurement instruments is likewise crucial for permanent observation. Thus, it is very challenging to cover wide parts of the Arctic and thereby also Svalbard. Many of the more permanent installations can be found in and around Kongsfjorden. First research activities

started in the late 1960s and early 1970s in Ny-Ålesund after mining activities had been terminated (Hanoa 2016). Since then, Ny-Ålesund and Kongsfjorden became one of the best-studied regions in the Arctic, providing today infrastructure for an international consortium of researchers from many disciplines (Wiencke & Hop 2016). Nowadays, the research activities are divided into 4 flagships: Atmosphere, Glaciology, Kongsfjorden system and Terrestrial ecosystems (The Research Council of Norway 2019). Since access to Kongsfjorden was mainly limited to the summer months, only nowadays, due to accelerated sea-ice loss, it is possible to extend research under the water surface to e.g., polar night (Smith et al. 2019).

Autonomous marine observatories such as moorings have been installed in Kongsfjorden since 2002 (Hop et al. 2019a). Depending on the design, moorings can remain in the field of observation for several months (commonly a year) and cover most of the water column. A disadvantage of moorings is the fact that they do not cover the first 10 - 15 m of the water column and that access to data is only possible after the recovery of the whole system. One step to improve data availability of the shallow water community was done in 2012 with the installation of the underwater observatory in the proximity of the Old Pier in Ny-Ålesund, Kongsfjorden. With this system, it is possible to monitor the hydrographic parameters of the upper 10 m of the water column in the coastal area (Fischer et al. 2017). First observations of the overall fish community provided insight into the abundance of Gadidae in shallow water. Over the last few years, observations of the underwater camera system have been complemented with additional sampling campaigns (Brand & Fischer 2016, Brand et al. 2022) as it improved overall species identification, especially concerning differentiation between Atlantic cod and Polar cod.

Unfortunately, this observation is limited to Kongsfjorden and cannot be transferred easily to other fjords on Svalbard, as each fjord has different and specific hydrographic properties which makes every fjord and its fish assemblages unique. Kongsfjorden e.g., is strongly affected by warm Atlantic water masses and only shows low amounts of the cold local winter water. Sampling campaigns which could be performed in the framework of this thesis with the RV Heincke gave valuable additional insight into the hydrographic conditions of other Svalbard fjords. The observations from these research cruises indicate that Svalbard fjords are impacted differently by either warm Atlantic water masses or cold Arctic water (see cruise reports RV Heincke; Mark 2018). Different hydrographic properties suggest that every fjord on Svalbard will react individually to the effects of warming. Overall, surveys performed from research vessels are sparse and can only record a few weeks per year. Thus, the data availability of other

fjord systems is limited but still very valuable for the understanding of long-term changes. It has to be noted that research cruises are rarely performed during polar night and often focus on hydrography, phyto- and zooplankton as well as fisheries in the deeper parts of the fjords. The shallow water zone is often neglected. Interestingly, ichthyoplankton surveys are generally rare in Svalbard waters.

The shallow water zone is known to be a nursery ground for many fish species (Teagle et al. 2017). In Kongsfjorden, larvae and juveniles of the most frequent fishes have been observed (pers. observation; see also Brand & Fischer 2016), such as shorthorn sculpins (*Myoxocephalus scorpius*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*) and Polar cod (*Boreogadus saida*). In this zone, Arctic species encounter their Atlantic relatives, and only little is known about how this is affecting the overall Arctic community. It is known that juvenile Atlantic cod is not threatening juvenile Polar cod, but adults of species such as the boreal Atlantic cod have a high predation potential which could impact the abundance of Polar cod (Renaud et al. 2012). Over the last few years, phyto- and zooplankton sampling campaigns in Kongsfjorden have been widely extended, whereas the ichthyoplankton sampling remains limited. A profound assessment of the ichthyoplanktonic community is needed to understand the spawning and settlement pattern of species which have shifted their area of distribution northwards. Effects must be observed on all trophic levels, and the fish assemblage has been neglected over the last decades.

If Arctic amplification continues to raise the water temperature, Atlantic cod could become even more abundant in Atlantic-influenced fjords and therefore could interfere in an unprecedented way with the Arctic community. Scenarios like the Early Arctic warming showed in the past the resilience of Atlantic cod and its fast adaptation to fluctuating aquatic systems. High levels of phenotypic plasticity and good chances of survival even at the lower temperature range make Atlantic cod a powerful invader in the Arctic that might be able to profit from future climate variability and warming.

Conclusion

This thesis contributes to a more profound understanding of the ongoing borealization processes in Svalbard fjords and highlights the effect of seasonal as well as decadal temperature fluctuations on the distribution of Atlantic cod. In addition, the determination of different ecotypes revealed the existence of a local Svalbard coastal cod ecotype.

The observation of the SCC ecotype in combination with warming Arctic waters indicates a permanent settlement of Atlantic cod in Svalbard. As nursing grounds for the early life stages, the shallow water zone seems to play an important role. The presence of migrating and non-migrating Atlantic cod ecotypes inhabiting Svalbard fjords demonstrated the importance of precise knowledge of fish communities, which is essential for a good fishery management in this area. Furthermore, the climate sensitivity of these communities shows the necessity to include climate data in future predictions of sustainable fishing activities.

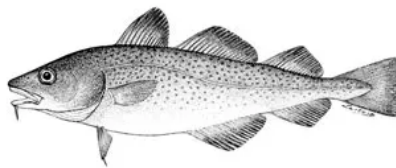
These climate data can only be gathered by a good infrastructure that is able to record temperature as well as other abiotic data on a long-term basis. Records of a single year might be relevant for a specific observation, but only the connection with previous years might reveal reappearing fluctuations which can be put into a larger context. The movement patterns of fish species such as Atlantic cod or long rough dab cannot be fully understood without these long-term hydrographic and atmospheric observations. Furthermore, long-term data is crucial for the understanding of future distribution shifts in the light of climate change.

In this context, this thesis contributes baseline information about the presence of Atlantic cod in Svalbard fjords and how its increasing abundance might affect the local Arctic species composition. The presence of Atlantic cod eggs in Kongsfjorden could not be proven in the framework of this thesis. Therefore, an increasing research effort with regular ichthyoplanktonic surveys is required in the future to evaluate the occurrence of Atlantic cod eggs in Svalbard fjords. The presence of a locally spawning Atlantic cod stock might influence other species, such as Polar cod. Those might be affected by predation pressure and food concurrency. Moreover, the local effects of Arctic amplification such as increasing water temperatures might result in a loss of suitable habitat. For specific species, e.g., the long rough dab, temperature changes might rather affect the early life stages and the overall spawning behaviour than the overall distribution of adult individuals. For others, it might influence the whole life cycle and spatial distribution.

In the past, the movement of Atlantic cod in the Barents Sea and the adjacent Svalbard shelf could be correlated to global warming and climate variability. Examples are the Early Arctic warming in the 1920s and 1930s, as well as the adjacent overall increase in temperatures attributed to climate change.

However, it was not possible within this thesis to give a timeframe for the settlement of SCC in Svalbard fjords. Furthermore, a distinct proof for SCC eggs and larvae is not given, but providing the baseline for future assessments of the Atlantic cod distribution in the Arctic might be a first step towards a better understanding of future warming scenarios.

As Atlantic cod lives at the lower temperature range in Svalbard fjords, the effects of cold phases might be of particular interest in future investigations. They also might be the explanation why no distinct proof for SCC eggs and larvae was possible in this study. The disappearance of cod stocks at high latitudes in the past could indicate that future temperature fluctuations might affect the distribution similarly. Starting now to deepen the knowledge about the SCC ecotype might help in the future to evaluate the stability of this local ecotype and how it will influence the local Arctic community.



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Credits for images

Atlantic cod

Retrieved from: <https://thefishsite.com/articles/cultured-aquatic-species-atlantic-cod>

Long rough dab

Retrieved from: <https://britishseafishing.co.uk/additional-rare-and-unusual-fish/>

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