Temperature selectivity in Icelandic and Northeast-Arctic cod

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Dissertation submitted in partial fulfillment of a
Philosophiae Doctor degree in Biology

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Abstract

Increasing water temperatures are predicted worldwide, with high amplitudes in the Arctic and sub-Arctic regions exceeding predictions for other regions. An understanding how Atlantic cod (*Gadus morhua*) reacted to changing environmental conditions in the past is essential for predicting re-distribution under climate change. In this thesis, I examined the temperature selectivity of Icelandic and Northeast-Arctic (NEA) cod in response to fluctuating temperature conditions and changes in the stock dynamics. Multiple century-long data time series and linear mixed-effect models were used to investigate the effect of fluctuating water temperatures and changes in stock dynamics on the temperature selectivity of cod, using stable oxygen isotope composition in otoliths as a proxy of ambient temperature. Icelandic cod $\delta^{18}O_{otolith}$ values were significantly correlated with water temperature time series, indicating that they were exposed to fluctuating water temperatures during the past 100 years and did not move appreciably in response to increasing ocean temperatures. Furthermore, abundance changes have affected the temperature selectivity of Icelandic and NEA cod as a density-driven response; however, the response of the two populations was different. Increasing abundance resulted in increasing intraspecific competition and decreasing individual fitness levels, which expanded the distribution area of both cod stocks into previously unfavorable thermal habitats. To validate the accuracy of high-resolution otolith isotopic records as a temperature proxy, stable oxygen isotope records of wild, free-swimming Icelandic cod tracked with data-storage tags (DST) were analyzed with high-resolution secondary-ion mass spectrometry (SIMS). Results demonstrated that the method is well-suited as a relative index of temperature exposure, although maximum ambient temperatures were often overestimated. Using century-long data time series and oxygen isotope chronologies of cod otoliths have markedly improved our understanding of the Icelandic and NEA cod temperature selectivity. Thus, this thesis provides important information that helps to predict how two commercially important cod stocks might respond to global warming and fluctuating stock dynamics.

Útdráttur

Hækkandi sjávarhita er nú spáð um allan heim og á norðurslóðum er auk þess búist við meiri hitasveiflum en annars staðar. Betri skilningur á viðbrögðum Atlantshafsþorsks (*Gadus morhua*) við breyttum umhverfisaðstæðum á liðnum áratugum opnar möguleika á að spá fyrir um mögulega breytta dreifingu þorskins á tímum loftslagsbreytinga. Hér er greint frá rannsóknum þar sem leitast var við að skýra hvort og hvernig þorskar af íslenska stofninum og norðaustur heimsskautsstofninum bregðast við breytingum á hitastigi sjávar og stofnstærð. Gagnasett með mælingum 100 ár aftur í tíman ásamt línulegum líkönum með blönduðum áhrifaþáttum voru notuð til þess að meta hvort stofnstærð og sjávarhiti hafi áhrif á hitastigsval einstaklings, sem hægt er að meta með stöðugum ísótópum súrefnis. Marktæk fylgni fannst milli δ^{18}O gilda íslenska þorskins og sjávarhita yfir tíma, sem bendir til þess að þorskurinn hafi verið útsettur fyrir sveiflukenndum sjávarhita síðastliðin 100 ár, en virðist ekki hafa hörfað að marki frá hækkandi hitastigi. Aukinn stofnþéttleiki á svæðum með kjörhita getur leitt til aukinnar samkeppni og minnkandi hæfni einstaklinga en slíkt getur valdið því að sumir einstaklingar leiti á önnur óhagstæðari hitastigs mið. Gögn okkar benda til þess að slíkt hafi átt sér stað í báðum stofnunum, þrátt fyrir ólík viðbrögð. Til frekari staðfestingar á notagildi kvarna til að varpa ljósi á hitastig sjávar á mismunandi stigum lífsferils voru ísótópar súrefnis mældir í kvörnum þorska sem á voru fest gagnasöfnunarmerki (DST-tag) sem mæla hitastig og dýpi. Í þessu tilfelli voru ísótópar í vaxtarhringjum kvarna mældir með meiri upplausn í nákvæmum massalitrófsgreini (SIMS) sem staðfesti að þessar aðferðir eru vel til þess fallnar að meta hitastig sjávar sem fiskar hafa dvalið í aftur í tíman, þó svo að hámarks hiti sé gjarnan ofmetin. Rannsóknirnar sýna hvernig nota má mælingar á ísótópum súrefnis í árhringjum kvarna ásamt sambærilegum langtímagögnum um hitastig sjávar og stofnsveiflur til þess að greina hvernig þessir þættir hafa áhrif á hitastigsval þorsks. Slíkar upplýsingar munu reynast gagnlegar við að spá fyrir um hvernig þorskstofnar bregðast við hnattrænni hlýnun og stofnsveiflum.

For Mama and Papa

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List of Papers

This thesis consists of three original papers. In the text, the papers are referred to with their respective numbers as follows:

Paper I: von Leesen, G., Ninnemann, U.S., and Campana, S.E. (2020). *Stable oxygen isotope reconstruction of temperature exposure of the Icelandic cod* (Gadus morhua) *stock over the last 100 years.* ICES Journal of Marine Science 77(3): 942-952. https://doi.org/10.1093/icesjms/fsaa011

Paper II: von Leesen, G., Bogstad, B., Hjörleifsson, E., Ninnemann U.S., and Campana S.E. *Temperature selectivity in cod driven by changes in abundance*. Canadian Journal of Fisheries and Aquatic Sciences. In review

Paper III: von Leesen, G., Bardarson, H., Halldórsson S.A., Whitehouse, M.J. and Campana, S.E. *Accuracy of otolith oxygen isotope records analyzed by SIMS as an index of temperature exposure of wild Icelandic cod* (Gadus morhua). Frontiers of Marine Science. In review

Peer-reviewed paper not included in the thesis:

Smoliński, S., Denechaud, C., von Leesen, G., Geffen, A. J., Grønkjær, P., Godiksen, J. A., and Campana, S. E. (2021). *Differences in metabolic rate between two Atlantic cod* (Gadus morhua) *populations estimated with carbon isotopic composition in otoliths*. PLoS One, 16: e0248711. https://doi.org/10.1371/journal.pone.0248711

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Abbreviations

AICc	Akaike information criterion corrected
$\delta^{13}C$	Stable carbon isotope ratio [‰]
$\delta^{18}O$	Stable oxygen isotope ratio [‰]
DST-tag	Data-storage tag
GLM	General linear model
ICC	Intraclass correlation coefficient
ICES	International Council for the Exploration of the Sea
IRMS	Isotope-ratio mass spectrometry
NBS-18	Standard reference material for $\delta^{18}O$ IRMS measurements (limestone)
NBS-19	Standard reference material for $\delta^{18}O$ IRMS measurements (carbonatite)
NEA cod	Northeast-Arctic cod
NC cod	Norwegian Coastal cod
S	Salinity
SBB	Spwning stock biomass
SST	Sea surface temperature
SIMS	Secondary-ion mass spectrometry
T	Temperature [°C]
T at 200 m	Temperature at 200 m depth [°C]
VPA	virtual population analysis
VPDB	Vienna Pee Dee Belemnite
VSMOW	Vienna Standard Mean Ocean Water

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1 Introduction

Temperature is the most important abiotic factor impacting fish population dynamics and habitat selectivity. Every organism can tolerate a specific-temperature range, although there is an optimum temperature that is most favorable in terms of fitness with potential differences in temperature and salinity tolerances between life stages and seasons (Pörtner and Peck, 2010). The optimum temperature range can be broad or narrow, depending on the species. Changing environmental conditions, population density or a combination of both can drive the temperature selectivity of fish. When temperature conditions change, mobile organisms can either change their distribution area and migrate vertically (i.e., into deeper waters) or horizontally to remain in their preferred temperature range. Distribution changes may alter feeding patterns, cause prey-predator mismatches, and exclude spawners from favorable larval retention and nursery areas (deYoung and Rose, 1993; Welch et al., 1998; Sanford, 1999; Brander, 2003). If organisms cannot move to optimum temperatures, their fitness decreases, and in some cases, regional populations might go extinct due to the high mortality at temperatures outside their thermal range. Moreover, it is metabolically costly to remain in water temperatures above the thermal optimum (Pörtner et al., 2001). Responses to changing water temperatures can differ between life stages, as the thermal window width varies between seasons and life stages (Pörtner and Peck, 2010).

Density-dependent habitat selection has been observed in many organisms, including fishes (Rosenzweig, 1991). Habitat suitability is generally defined by a set of abiotic and biotic factors, such as food availability, predator abundance, salinity, temperature, or any combination that determines the geographical distribution of organisms. Animals have a range of habitats that they can tolerate, but they actively choose habitats with optimum temperature in order to maximize their evolutionary fitness (Fretwell and Lucas, 1970; Swain and Wade, 1993). Temperature selectivity is governed by the principles of optimal foraging and intraspecific competition (Fretwell and Lucas, 1970; Swain and Wade, 1993). As a response, organisms expand their distribution range into previously unfavorable thermal habitats as the population abundance increases. Therefore, the fitness of some individuals decreases due to the increasing intraspecific competition. At a low population size, organisms should only occupy habitats within their optimal thermal range.

Increasing water temperatures are predicted worldwide, with high amplitudes in the Arctic and sub-Arctic regions exceeding predictions for other regions (Drinkwater, 2005; IPCC, 2013). Increasing water temperatures can result in large- and small-scale distribution changes of marine fish. Long-term population reconstructions combined with temperature exposure histories are needed to provide an insight into how fish stocks reacted to changing temperature regimes in the past. Understanding their reaction in the past is necessary to predict their response to changing environmental conditions in the future. Biological archives of otoliths and other calcified structures indirectly record the environmental conditions through their stable oxygen isotope composition and thus are valuable to reconstruct long-term temperature exposure chronologies.

1.1 Goal of the thesis

The overall objective of this thesis was to improve our understanding of the temperature selectivity of Atlantic cod (*Gadus morhua*) populations. Using the oxygen isotopic record of otoliths to reconstruct past temperature exposure, it was possible to develop a temperature exposure chronology of Icelandic and Northeast-Arctic (NEA) cod stocks over the last 100 years. The reconstruction of these temperature chronologies was the subject of **Papers I** and **II**. In **Paper I**, I focused on the relationship between the reconstructed ambient temperatures of Icelandic cod and the overall environmental temperature time series to determine if Icelandic cod moved in response to fluctuating environmental conditions over the last 100 years. Continuing the theme in **Paper II**, I broadened the analysis to stock dynamics to determine if and how the temperature selectivity of two large cod stocks was driven by density changes (**Paper II**). In contrast, **Paper III** was a more application-based paper to validate the accuracy of high-resolution otolith isotopic records as a temperature proxy of wild, free-swimming cod. Secondary-ion mass spectrometry was used to develop this application.

The remainder of the thesis is structured as follows. I begin with some relevant background on the temperature exposure and stock dynamics of the Icelandic and NEA cod stocks. The ecology of these two cod stocks is summarized. Later sections discuss stock dynamics and marine ecosystems in order to provide context for temperature selectivity issues. Background information about the use of otoliths as biorecorders and their potential to reconstruct ambient temperatures of fish is discussed, focusing on stable oxygen isotopes in otoliths. I subsequently explain the sample selection protocol, conclude with suggestions for further research and highlight pressing issues that remain.

1.2 Icelandic and Northeast-Arctic cod as model stocks

Despite overexploitation and significant declines in stock biomass, Atlantic cod remains one of the commercially most important species in the North Atlantic (Hutchings and Myers, 1994; Rose, 2004; Hutchings, 2005; Worm et al., 2006) (Fig. 1). The Icelandic and Northeast-Arctic (NEA) cod stocks are two of the largest cod stocks in the world and hence, of particular importance for fisheries management. Atlantic cod can reach an age of up to 25 years and show differences in life-history traits between stocks, including migratory types (ecotypes) (Salvanes et al., 2004; ICES, 2005; Thorsteinsson et al., 2012). Cod diet changes with size; small cod primarily feed on crustaceans, while larger cod on fish (Frank et al., 2005), with prey preferences being stock-dependent. The main prey of Icelandic and NEA cod is capelin and declines in capelin abundance have previously been linked to decreasing cod condition (Astthorsson et al., 2007; Link et al., 2009).

Figure 1: Sketch of Atlantic cod (Gadus morhua) (msc.org).

1.2.1 Temperature exposure (ambient temperature)

Climate change is increasing ocean temperatures with particularly high amplitudes of warming in Arctic and Sub-Arctic regions. Increasing water temperatures have already been recorded around Iceland and in the Barents Sea (Hanna et al., 2006a; Hanna et al., 2006b; Boitsov et al., 2012), and climate prediction models (IPCC, 2013) forecast a continued increase of mean annual water temperatures in both areas. Therefore, a movement of cod towards the pole or cooler waters is expected (Drinkwater, 2005). Cod has a broad geographical distribution ranging from the Irish and Celtic Sea in the south to Greenland, Iceland, and the Barents Sea in the north over a wide temperature range (Myers et al., 1997; Drinkwater, 2005). Cod are not usually found in waters above the critical mean annual bottom temperature of 12°C (Dutil and Brander, 2003). However, juveniles have a broader thermal window and can inhabit water masses up to 22.5°C, and thus, they are more tolerant to increasing water temperatures (Zanuzzo et al., 2019). Eggs, larvae, and spawners with an optimum spawning temperature of 7 to 8°C have a narrower thermal window, and hence, are most vulnerable to temperature changes (Brander, 1997; Pörtner and Peck, 2010).

The 22 cod stocks in the North Atlantic Ocean are exposed to different levels of climate change. It is difficult to generalize the reaction of cod to global warming, but stock-specific predictions can be made. The recruitment of cold- (mean annual bottom temperature < 7°C) and warm- (> 7°C) water stocks is expected to respond differently to temperatures changes. Cold-water stocks are expected to show increasing recruitment, while declining recruitment is expected for warm-water stocks (Drinkwater, 2005).

Temperature is the most important abiotic factor influencing fish population dynamics, including stock production, recruitment, and abundance. Growth, reproduction rate, production, and distribution of cod are directly affected by temperature, whereas temperature indirectly impacts prey and predator abundance (Drinkwater, 2005). Warmer temperatures lead to faster growth rates and better conditions but can lead to reduced growth rates at the extreme ends of the temperature range due to reduced feeding rates. Abundance changes in cod stocks also depend on temperature increase with contrasting reactions ranging from increasing abundance to stock collapses. The cod stocks most sensitive to temperature increase are the Celtic, Irish, and North Sea cod, which are already at the upper end of the temperature range (Drinkwater, 2005).

The effect of temperature on growth rate could be even larger than that on recruitment and abundance. Up to the species' tolerance extremes, warmer temperatures can directly lead to faster growth rates, but only if increasing amounts of food are also available (Pedersen and Jobling, 1989; Brander, 1995; Vikebø et al., 2005). Temperature also indirectly affects the growth rate through changes in productivity of lower levels. The production of copepods, which are the main prey of cod larvae and juveniles, is linked to the spring bloom of phytoplankton in the Subarctic Gyre of the northern North Atlantic. Through advection by the Norwegian Atlantic Current, copepod production extends to the shelf off Norway and the Barents Sea (Vikebø et al., 2005). For adult cod, mean bottom water temperatures can explain up to 90% of observed differences in growth rates among stocks (Brander, 1994; Brander, 1995). Large sexually mature cod grow better at lower temperatures, whereas juveniles perform better in warm waters (Pedersen and Jobling, 1989; Brander, 2003).

1.2.2 Stock dynamics

The Icelandic and NEA cod stocks have a long history of exploitation, which may explain their major cultural and socio-economic importance. The spawning areas have been the traditional focus of the fisheries since the Viking Age in Norway. The Icelandic cod stock has fluctuated considerably in the past and might have been collapsed in the 17th century due to temperature variations (Jónsson, 1994; Ólafsdóttir et al., 2014). In both stocks, the abundance declined, and recruitment fluctuated in the last century (Myers et al., 1997, 2001). Both cod populations have increased in recent years, with record-high spawning stock biomass of the NEA cod (Kjesbu et al., 2014). Recent (cod) stock collapses are usually linked to the industrialization of commercial fisheries in the 1950s, leading to overexploitation, with unfavorable temperatures possibly exacerbating the stock declines (Stenevik and Sundby, 2007).

Stock sizes may vary over annual to century-scales due to changes in recruitment (see Bailey (2019)). Recruitment is defined as the abundance of a year-specific cohort (year-class) at an age corresponding to its entry into the harvestable population. At this point, the year-class size has been largely determined by spawning and environmental effects, but fisheries have not yet had an effect. The predator abundance and spatial-temporal overlap of prey and predator species cause variability in recruitment. A poor recruitment success usually leads to low abundance levels, whereas high larval production leads to strong year-classes. Cannibalism or a focus-shift in feeding due to a high prey abundance are two density-dependent mechanisms impacting juvenile abundance.

The Icelandic and NEA cod populations have fluctuated considerably during the last 100 years, with a general decline in population size in recent years (Fig. 2). Recent increases in population abundance were probably due to a combination of improved fisheries management, better fishing practices, and environmental effects. Improvements in fisheries management include the introduction of quotas, minimum mesh size, and gear type limitations. NEA cod might be one of the few cod stocks that have benefited from global warming. Historically, cold years have never been associated with a strong NEA cod year-class (Sætersdal and Loeng, 1987; Ellertsen et al., 1989). In contrast, recruitment has increased when warmer, prey-rich Atlantic water masses from the southwest have flown into the Barents Sea (Sundby, 2000). One of the explanations for increased productivity of NEA cod in response to warming is the retreat and melting of sea ice resulting in larger ice-free areas, which allow for higher primary productivity. The inflow of zooplankton from the south into the Barents Sea has been higher in warmer years, and higher temperatures have led to higher biological activity (Sakshaug, 1997; Ottersen et al., 2006).

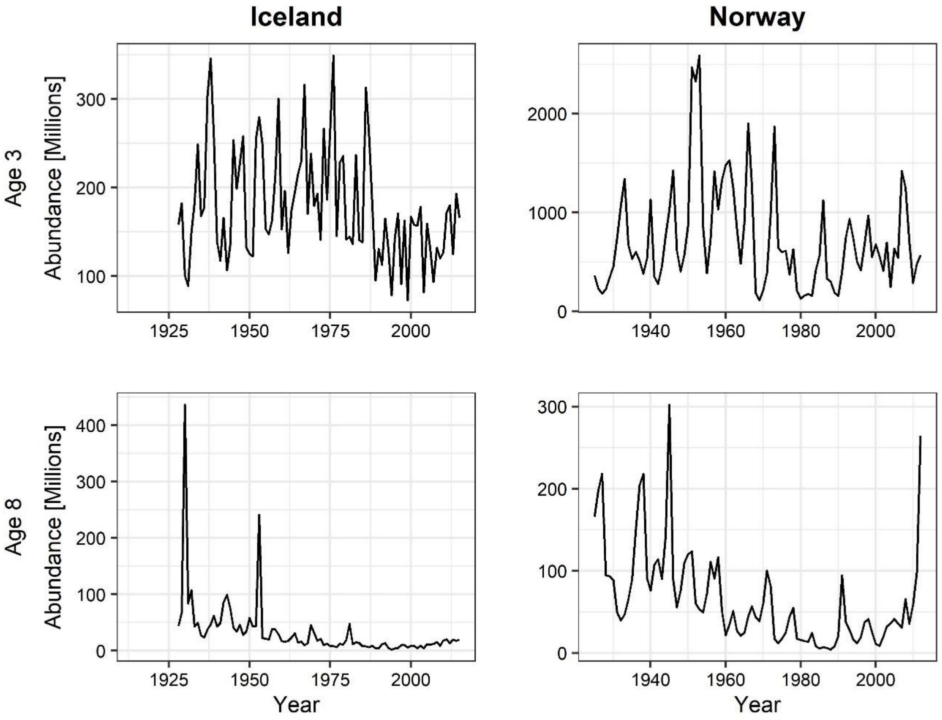

Figure 2: Abundance of Icelandic and NEA cod at the age of 3 and 8 years. The Marine and Freshwater Research Institute provided stock dynamics data for Icelandic cod (Einar Hjörleifsson, pers.comm.). The stock dynamics time series of NEA cod, starting in 1946, was provided by ICES - Arctic Fisheries Working Group. The development of the pre-1946 time series was described in Paper II.

One characteristic of Icelandic stock dynamics is the mixing of the Icelandic and Greenlandic cod stocks due to periodic immigration of cod from Greenland to Iceland (Bonanomi et al., 2015; Bonanomi et al., 2016). Icelandic cod larvae and juveniles spawned in Iceland sometimes drift towards Greenlandic waters, where they settle and form part of the basis of the Greenlandic fisheries. Due to their homing behavior, mature cod from this immigration might return to Icelandic waters for spawning (Christensen, 1996). During the last century, 15 immigration events have been detected in stock dynamics data, with the most prominent immigration events of mature cod taking place in the years 1930, 1933, 1953, 1969, and 1990. This connection between Icelandic and Greenlandic cod stocks appears to have benefited both stocks. High recruitment events in the Icelandic cod stock prior to 1950 were partly driven by immigration events from Greenland (Schopka, 1994; Astthorsson and Vilhjálmsson, 2002), while the Greenlandic cod stock benefited from the successful transport of Icelandic larvae and juveniles to Greenlandic waters (Stein and Borovkov, 2004; Therkildsen et al., 2013). Thus, the Iceland-Greenland transport connection helps explain peaks in the abundance of age 8 Icelandic cod, which are not evident in abundance at age 3 before the immigration event. The early life-history drift towards Greenland and the return migration of mature cod from Greenland to Iceland have been reduced since the 1970s, possibly due to reduced stock size (Schopka, 1994) or temperature-induced changes of the oceanographic currents (Dickson and Brander, 1993). The Iceland-Greenland connection is of importance when studying the temperature selectivity of Icelandic cod. Immigrants from Greenland have been exposed to colder temperatures prior their return to Iceland as water temperatures off eastern Greenland are at least 2°C colder than those off northern Iceland (Bacon et al., 2014).

Cannibalism in cod

Cannibalism is a density-dependent mechanism and is a common phenomenon in cod. Cannibalism has been reported in several stocks, including the Icelandic (Pálsson, 1983) and the NEA cod (Mehl, 1989, 1991). The overall quality of the NEA cod assessment and the accuracy of the recruitment estimation have improved since the incorporation of cod cannibalism into the cod VPA (virtual population analysis) model (Kovalev and Korzhev, 2004), highlighting its importance for stock dynamics. Cannibalism is suspected to influence recruitment to the fishery and thus, affects year-class strength. Cannibalism appears to be an important, variable cause of natural mortality for NEA cod of age 1 to 4, and thus, can influence recruitment to the fishery and perceived year-class strength (Bogstad et al., 1994; ICES, 2007). Cod up to 6 years of age can be eaten by bigger cod, but cannibalism of age 5 and 6 cod appears to be very low (ICES, 2007). Reasons for interannual variability in cannibalism are not clear, but one possible explanation might be that of varying year-class strength. Moreover, the frequency of cannibalism appears to increase with the abundance of juvenile cod and is inversely related to abundance of another prey source, that of capelin (Yaragina et al., 2009). Another possible reason for fluctuating cannibalism is the abundance at length/age, and thus, it is limited to 50% of predator size (Bogstad et al., 1994). The geographical overlap of prey (young) and predator (old) cod is a prerequisite for cannibalism. However, the distribution of NEA cod in the Barents Sea is driven mainly by temperature conditions (Nakken and Raknes, 1987; Ottersen et al., 1998). Therefore, changing environmental conditions might also impact fluctuating cannibalism levels.

In Icelandic waters, cannibalism mainly occurs in waters off the northern and northwestern coast and at reduced levels off east and south Iceland. The frequency of cannibalism appears to decrease from inshore to offshore areas (Bogstad et al., 1994). In contrast, cannibalism of NEA cod occurs mainly within the 200 m isobath and most frequently in the eastern part of the Barents Sea and in the Svalbard area where the spatial overlap of small and large cod is most pronounced. The contribution of cannibalized cod to the diet of adult cod increases with the size of the adult. The relationship between lengths of prey and predators is similar for both stocks, whereby cannibalism first becomes evident in adult cod above 30 cm which prey on young cod from 5 to 40 cm (Bogstad et al., 1994).

Cod fisheries

Cod is one of the most commercially important species in Icelandic and Norwegian waters. Past population collapses have resulted in substantial socio-economic and ecological impacts in Iceland (Hutchings and Myers, 1994; Hammerschlag et al., 2019). Although catches of NEA cod have seen large fluctuations, the NEA cod stock is currently among the largest in the world and is currently considered to be in good condition. The industrialization of commercial fisheries since the 1950s resulted in a continuous increase in fishing effort and led to a greater influence of harvest rates on population abundance (Schopka, 1994). The spawning stock biomass (SSB) of Icelandic cod declined from the 1950s to the 1980s due to the increasing fishing effort and decreasing yield (Jakobsson and Stefánsson, 1998). Larger, older individuals were selectively removed from the stock by fisheries, leading to a truncated age distribution and a corresponding reduction in the stock's reproductive potential (Schopka, 1994; Jakobsson and Stefánsson, 1998).

Age-at-sexual maturity

Industrial fishing has been identified as a cause of life-history changes in many commercially harvested stocks, mainly due to high fishing mortality and size selectivity of the gear. Fishing can change the ecological life history of fish via at least two different mechanisms (Sharpe and Hendry, 2009). Firstly, fishing can potentially induce plastic changes in life-history traits. High fishing pressure often causes drastic declines in stock abundance, leading to reduced intraspecific competition, and thus, the growth rate of the remaining fish can increase (Policansky, 1993). Higher growth rates can lead to maturity at a younger age, which is also associated with changes in size at maturity (Heino and Godø, 2002; Kuparinen and Merilä, 2007). Secondly, fishing pressure can induce evolutionary (genetic) changes in fish stocks by selecting particular life histories, e.g., by size-selective commercial fisheries (Heino and Godø, 2002; Sharpe and Hendry, 2009).

The proportion of sexually mature Icelandic and NEA cod at age 8 increased during the last 100 years. For Icelandic cod, it increased from 0.82 in 1928 to 0.91 in 2018, with year-to-year variations ranging from 0.53 to 0.92. The proportion of sexually mature NEA cod at age 8 was 0.7 in 2015 with year-to-year variations ranging from 0.02 to 0.94 in the last century (Fig. 3). The age at 50% maturity of Icelandic cod is 5.9 years for cod from south Iceland and 6.6 years for cod from north Iceland (Marteinsdottir and Begg, 2002). The age at 50% maturity of NEA cod declined from 10.5 to 8 years from 1923 to 1976 (Rollefsen, 1953; Jørgensen, 1990). Additionally, Norwegian otolith readers determine the age of first spawning of each NEA cod by “spawning zones” which are visible in the otolith sections (Rollefsen, 1933; Folkvord et al., 2014; Irgens et al., 2019). “Spawning zones” describe the change in appearance from broader annual growth bands in juvenile fish to narrower, denser growth after sexual maturation.

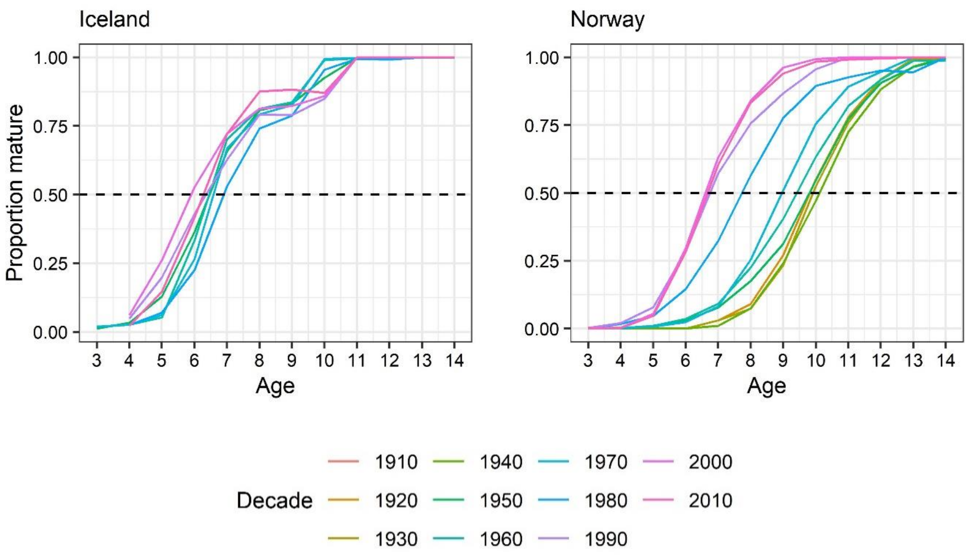

Figure 3: The proportion of sexually mature Icelandic and NEA cod at age 8 shown by decade.

1.3 Stock structure

1.3.1 Multiple migratory types (ecotypes)

A common feature of North Atlantic cod is the existence of multiple migratory types. The genetic diversity of cod is high, shown by the extensive divergence of local genomic regions despite extensive gene flow between ecotypes (Hemmer-Hansen et al., 2013). A selective sweep linked to the characteristic life history of the migratory ecotype favors using high productivity niches in the Arctic for feeding (Stensholt, 2001; Grabowski et al., 2011). Additionally, specialized adaptations to different temperature regimes are likely linked to the different life-history strategies (Righton et al., 2010; Grabowski et al., 2011; Hemmer-Hansen et al., 2013). Despite two different behavioral types, so-called ecotypes, the Icelandic cod stock is managed as a single unit. Differences in vertical migration and habitat choice in feeding migrations characterize the Icelandic ecotypes. However, both ecotypes are not sexually isolated, and genetic analyses of the *Pan* I gene have revealed inbreeds of coastal and frontal cod (Pampoulie et al., 2008). Icelandic ecotypes have been discriminated via genetic discontinuities (pantophysin locus *Pan* I), otolith shape analysis (Jónsdóttir et al., 2006; Pampoulie et al., 2006; Bardarson et al., 2017), and temperature and depth profiles recorded by DST tags (Pálsson and Thorsteinsson, 2003; Grabowski et al., 2011). Norway manages the Norwegian coastal (NC) and NEA cod separately, with Norwegian cod otoliths usually discriminated based on the shape of the otolith core.

Genetic analysis (*Pan* I) of Icelandic cod revealed that individuals carrying the *Pan* I^{AA} genotype are likely to display coastal cod behavior with shallow water feeding migrations. *Pan* I^{BB} carriers show frontal cod behavior characterized by deep water migration and foraging near thermal fronts. Heterozygotes (i.e., *Pan* I^{AB}) exhibit both behavioral types (Pampoulie et al., 2008). Additionally, limited gene low between in- and offshore spawning areas in the southwest off Iceland suggests the existence of two subpopulations within the Icelandic cod stock (Pampoulie et al., 2006). However, the exact function of this gene locus and the potential selective pressure explaining the observed genetic patterns are not yet understood (Pampoulie et al., 2008). The two ecotypes of Icelandic cod show characteristic temperature and depth-profiles. Frontal cod experience colder waters than the more stationary coastal cod due to depth stratification and feeding migration into the colder waters off northern Iceland. Adult frontal cod migrate between the spawning ground and the deeper, colder waters of the main feeding area northwest of Iceland (Jónsson, 1996). During spawning season, coastal and frontal cod can share their depth range, but the remaining time of the year, coastal cod spend at least 70% of their time in shallow waters, typically in the southwest and southeast off Iceland. In contrast, frontal cod move into deeper waters (250-600 m) for spawning migration (Thorsteinsson et al., 2012).

Two different migratory types of cod also occur in Norwegian waters: NEA cod and Norwegian coastal cod (NCC). NCC is not a discrete population but rather includes genetically distinct groups within the NCC, and thus, the stationary type is better defined as “not NEA, not migratory”. Both NEA and NCC stocks are managed separately and are distinguished through otolith morphology (Mjanger et al., 2000; Stransky et al., 2008). During migration and spawning, NEA and NC cod overlap spatially. In contrast to NEA, NC cod display less migratory behavior and are typically found within fjords along the Norwegian coast (Berg and Pedersen, 2001). Although both populations may simultaneously be at the same spawning grounds, they usually do not mix due to the different depth distribution, with NEA cod being more abundant in deeper waters (Nordeide and Båmstedt, 1998). Moreover, NEA and NC cod show different life-history characteristics displayed by different growth rates resulting in higher length-at-age for NC cod and earlier maturity, body shape differences, and different otolith sizes at a given length (Otterlei, 2001). This thesis used only otoliths from NEA cod.

The Icelandic cod otoliths used in **Papers I** and **II** were of unknown ecotype, and hence, samples might include both ecotypes. All Norwegian otoliths (**Paper II**) belong to the NEA cod stock. The ecotype of DST-tagged cod otoliths (**Paper III**) was previously determined by temperature and depth profiles (see Thorsteinsson et al. (2012)).

1.3.2 Spawning migration of Icelandic and Northeast-Arctic cod

Migration of mature, spawning cod between colder feeding areas and warm water spawning grounds is a common characteristic of Icelandic and NEA cod. The ambient temperature reconstructions of Icelandic cod (**Paper I,** Fig. 4) assumed that Icelandic cod spawned in the warmer waters of the southwest off Iceland between March and May and then migrated to the colder waters of feeding grounds in the northwest. After spawning off the southwest coast in spring, pelagic eggs and larvae drift to the main nursery grounds off the northwest coast as facilitated by the Irminger Current and the Icelandic Coastal Current. Juveniles are found on the nursery grounds all year-round (Astthorsson et al., 1994; Begg and Marteinsdottir, 2000; Begg and Marteinsdottir, 2002). In contrast, coastal cod do not undergo pronounced feeding migrations, and their spawning takes place in smaller spawning grounds all around Iceland (Begg and Marteinsdottir, 2000).

NEA cod migrate between the spawning grounds in Lofoten and the main feeding grounds in the Barents Sea (Bergstad et al., 1987; Kjesbu et al., 2014) (Fig. 4; **Paper II**). In the Lofoten, spawners mainly occur in the boundary layer between the cool coastal and the warm Atlantic water at temperatures between 4 and 6°C at 50 to 100 m depth (Bergstad et al., 1987). The spawning period of NEA cod in the Lofoten is typically between March and April when they experience significantly higher temperatures than they do when they are in the Barents Sea (Ellertsen et al., 1989; Ottersen et al., 1998). The spawning migration can start as early as December, and spawners leave the spawning area immediately afterwards and return to the Barents Sea as early as May (Bergstad et al., 1987). In June and July, the eggs and early larvae have reached the cool (3 to 4°C) coastal waters of the southwestern Barents Sea (Bergstad et al., 1987). Every year NEA-spawning cod return to the place of first spawning (Godø and Sunnanå, 1984), while immature and non-spawning mature NEA cod remain in the Barents Sea all year-round. Juveniles undergo less pronounced seasonal migration as they follow their main prey, capelin, towards the coast of Russia and northern Norway (Mehl et al., 1985). Juveniles are found in the cold water masses of the Barents Sea and start to migrate into the warmer waters of the western Barents Sea with age (Bergstad et al., 1987).

Individuals which skip reproductive events despite maturation (skipped spawning) to maximize their lifetime fitness have been described in several cod stocks, including NEA cod (Skjæraasen et al., 2012). NEA cod that had skipped spawning grew significantly faster than mature NEA cod, which migrated to the spawning grounds indicating a trade-off between reproduction and growth (Folkvord et al., 2014). The extent of skipped spawning is challenging to measure, but it has been estimated that about 24% for females of 60 – 100 cm length in 2008 (Skjæraasen et al., 2012). A comparison of reconstructed ambient temperatures of NEA cod spawners with migration-adjusted environmental temperature time series might derive incorrect conclusions if the individual fish had skipped spawning in that year.

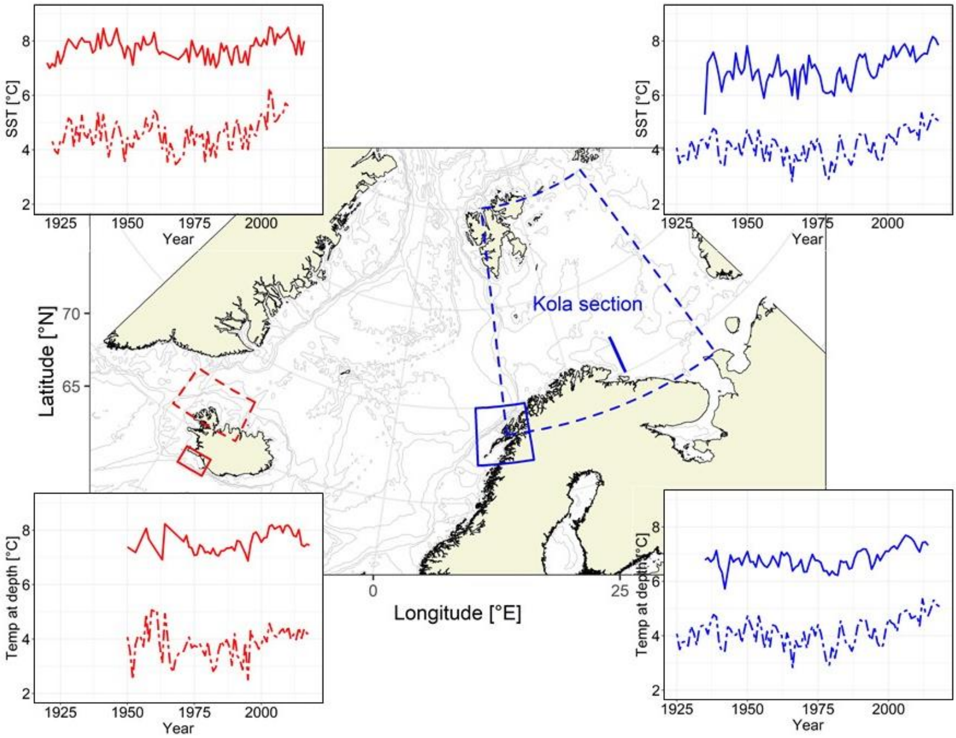

Figure 4: Map of the Northeast Atlantic Ocean showing the sample locations on the main spawning grounds (solid line) in southern Iceland and western Norway (Lofoten). Feeding grounds (dashed line) are visible in northern Iceland and the Barents Sea. The plots show SST and water temperature at depth (Norway: 0-200 m; Iceland: 200 m) at the main spawning (solid lines) and feeding grounds (dashed line).

1.4 Marine ecosystems

The Icelandic and the Barents Sea marine ecosystems experienced fluctuating water temperatures over the last century, as evidenced by alternating warm- and cold-water periods. One major difference between both ecosystems is the absence of sea ice in the Icelandic marine ecosystem. In contrast, the Barents Sea is seasonally covered by sea ice, thus limiting NEA cod distribution (Ogilvie and Jónsdóttir, 2000; Onarheim and Årthun, 2017).

1.4.1 Ocean circulation around Iceland

The North Atlantic experienced a regime shift in the 1920s and 1930s due to warming of air and ocean temperatures. Atlantic cod and other boreal species, e.g., haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*) expanded their range further north, whereas cold-water species such as capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) retreated northward. Species typically found in southern waters, e.g., witch (*Glyptocephalus cynoglossus*), turbot (*Scophthalmus maximus*), basking sharks (*Cetorhinus maximus*), tunny (*Thunnus thynnus*), and Atlantic mackerel (*Scomber scombrus*) first immigrated to the Icelandic waters during the warm period in the 1920s (Drinkwater, 2006).

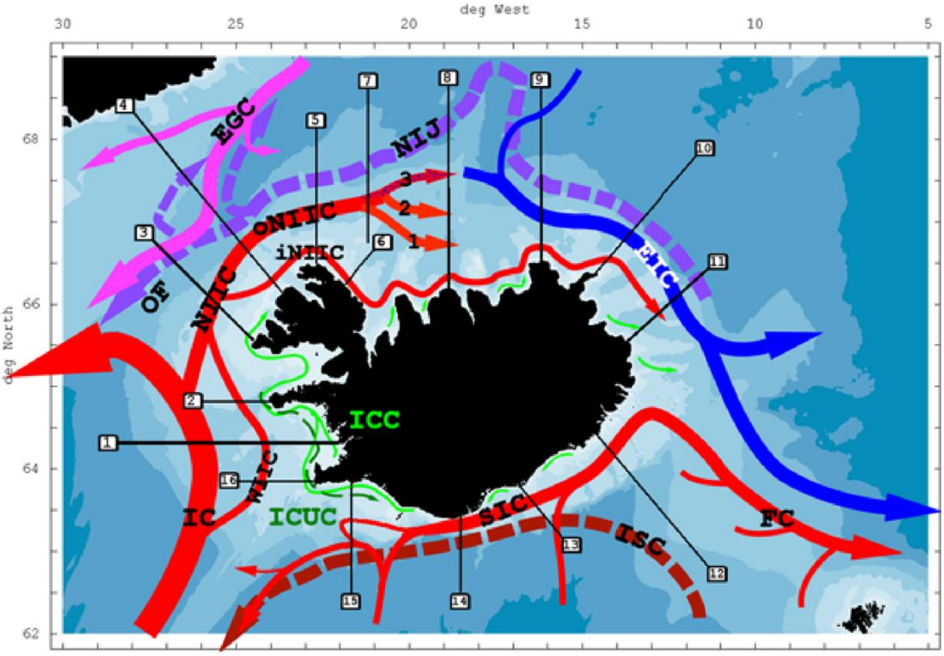

Figure 5: Proposed three-dimensional circulation scheme of Icelandic waters with locations of the 16 analysis sections. Dashed arrows denote deep currents. The abbreviations are: EGC – East Greenland Current, EIC – East Icelandic Current, FC – Faroe Current, IC – Irminger Current, ICC – Icelandic Coastal Current, ICUC – Icelandic Coastal Undercurrent, iNIIC – inner NIIC, ISC – Icelandic Slope Current, NIJ – North Icelandic Jet, NIIC – North Icelandic Irminger Current, OF – Overflow, oNIIC – outer NIIC, SIC – South Icelandic Current, WIIC – West Icelandic Irminger Current. Image and caption are taken from Logemann et al. (2013).

Iceland is part of the Mid-Atlantic Ridge and is located at the juncture of the North Atlantic and the Arctic Ocean. Thus, Iceland's oceanographic currents are highly dynamic due to the interacting two primary water masses (Fig. 5). Polar water in the north originates as the East Greenland Current entering from the Arctic Ocean with a salinity < 34.5, a temperature of ≤ 0°C, and low in nutrients. The warm and saline Atlantic water along the south coast is a branch of the Gulf Stream. It forms a homogenous and thick water layer extending to several hundred meters depth. This water mass flows westwards as the Irminger Current and eventually northwards, where the water cools down, and the salinity decreases (Stefánsson and Ólafsson, 1991; Jónsson, 1999; Malmberg and Valdimarsson, 2003). Due to their contrasting oceanographic properties, the Icelandic marine ecosystem is heavily impacted by the mixing of both water masses, resulting in higher primary production in the warm, nutrient-rich Atlantic waters off southern Iceland (Astthorsson and

Vilhjálmsson, 2002; Astthorsson et al., 2007; Valdimarsson et al., 2012). In contrast, the primary and secondary production in northern Icelandic waters depends strongly on the ratio of warm, nutrient-rich Atlantic water and cold, nutrient-poor Arctic water, which varies interannually (Astthorsson and Gislason, 1998; Valdimarsson et al., 2012).

During the last 100 years, temperature and salinity conditions of Icelandic waters were mainly characterized by two warming events (Jakobsson and Stefánsson, 1998; Malmberg and Valdimarsson, 2003). The first warming event started in the 1920s, presumably due to natural climatic variation, and water temperatures remained high until water began to cool in the 1960s. During the 1920s warming period, water temperatures were 1 to 1.5°C higher compared to the late 19th century (Hanna et al., 2006b). Rising greenhouse gas levels caused the second warming event, which began in the 1990s and is still ongoing (Hanna et al., 2006b). Salinity around Iceland declined in the 1960s due to the "Great Salinity Anomaly", returning to normal levels in 1976 (Dickson et al., 1988; Belkin et al., 1998).

1.4.2 Norwegian and Barents Sea

The Barents Sea showed substantial climate variability with increasing temperatures in recent years and has been recently defined as an “Arctic warming hotspot” (Lind et al., 2018). Sea ice retreat and the corresponding loss of freshwater, linked to the increase in ocean temperatures and salinity, lead to changing oceanographic conditions. These changes have weakened ocean stratification and increased vertical mixing, preventing sea ice formation (Lind et al., 2018). In recent years, the extent of warm Atlantic water has increased, resulting in expanded thermal habitats for juvenile cod, haddock, and herring (Eriksen et al., 2012). Simultaneously, the extent of cold Arctic water has declined, causing a reduction in zooplankton (Dalpadado et al., 2012). These thermal changes might be expected to cause altered migration patterns and distributional range shifts but could also affect the spatiotemporal overlap of prey and predator species. In warm years, cod and capelin distribution were partially segregated while cod migrated into the colder waters of the eastern Barents Sea (Orlova et al., 2005).

The Barents Sea is a relatively shallow ocean with an average depth of ~ 300 m. Below 100 m depth, water temperatures are stable with only small seasonal variations of 1 to 3°C (Ottersen and Ådlandsvik, 1993). It is strongly influenced by the inflow of warm Atlantic water and coastal water from the Norwegian Sea (Loeng, 1991) (Fig. 6). The Norwegian Coastal Current and North Atlantic Current meet in the Norwegian Sea. Due to its origin from a mixture of freshwater run-off from Norwegian rivers, the outflow of the Kattegat and North Sea coastal water, the Norwegian Coastal Current is less saline than the North Atlantic Current (Albretsen et al., 2011).

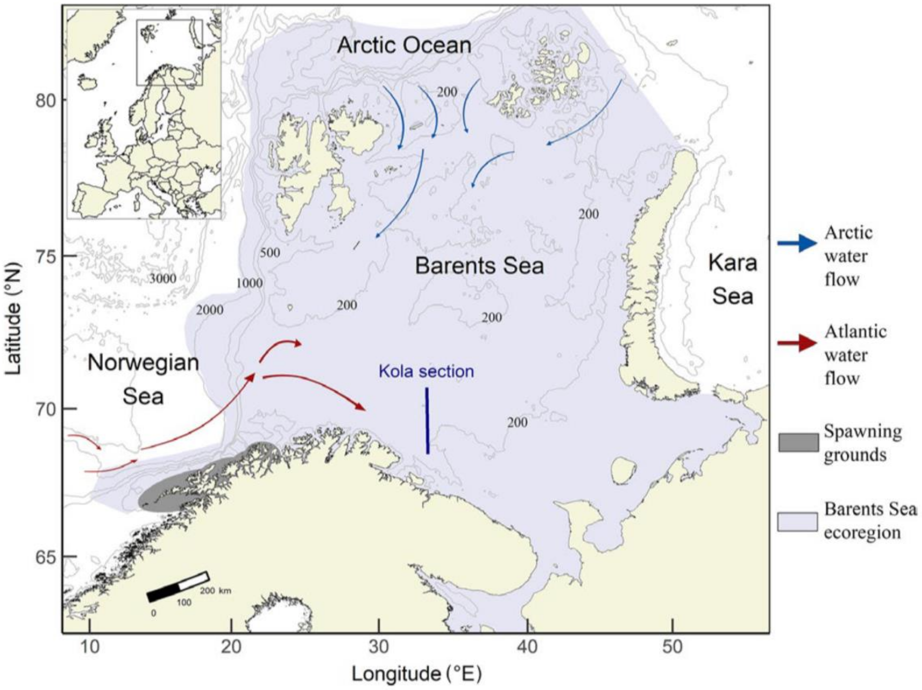

Figure 6: The Barents Sea ecoregion with the main oceanographic currents. Warm, saline Atlantic water flows along the Norwegian coast before entering the Barents Sea, where it mixes with cold, less saline Arctic water. The bathymetry data shows that the Barents Sea is a relatively shallow sea with an average depth of about 300 m. Map taken from Denechaud et al. (2020).

Water temperatures in the Barents Sea fluctuated markedly during the last century (Boitsov et al., 2012). Similar to the cold- and warm water events around Iceland, cold air and water temperatures and high ice coverage dominated the Barents Sea until the late 1920s, followed by a warm water period until 1961. Water temperatures of the 0–200-m layer in the Murmansk Current of the Barents Sea were about 0.4°C higher than the long-term average during the 1950s (Boitsov et al., 2012). Afterwards, the Barents Sea cooled until the more recent increase of air and water masses began in the late 1980s. Large quantities of sea ice characterized the cold 1980s. In warmer years, the Barents Sea is covered by less sea ice (Orlova et al., 2005). Water temperatures rose especially since 2000, with the highest measured temperatures in 2006 (Boitsov et al., 2012). The Kola section is commonly monitored as an indicator of water temperatures in the Barents Sea (Tereshchenko, 1996).

1.5 Otoliths as biorecorders

Otoliths (ear stones) are paired calcified (aragonitic) structures used for hearing and/or balance and can be found in all teleost fish (Campana, 1999). Coupled with age or date of catch, they provide chronological records that can be used to reconstruct a fish's life and temperature history as otoliths grow continuously from hatching to death (Campana and Thorrold, 2001). Each individual annulus (annual growth increment) can be assigned a year of formation and a calendar year when the date of catch is known (Fig. 7). The stable oxygen isotope composition of otoliths can be used to reconstruct ocean temperatures. These temperature reconstructions can be carried out using otolith archives even when instrumental records are missing, such as in the early 1990s. Thus, otoliths are also well suited for paleoenvironmental studies (West et al., 2012; Wang et al., 2013).

For **Papers I** and **II**, two stable oxygen isotope samples were micromilled from each otolith section. These two annuli, formed at age 3 and 8, respectively, represent two different life stages. Annuli of age 3 were formed at the immature, while age 8 was formed at the mature life stage.

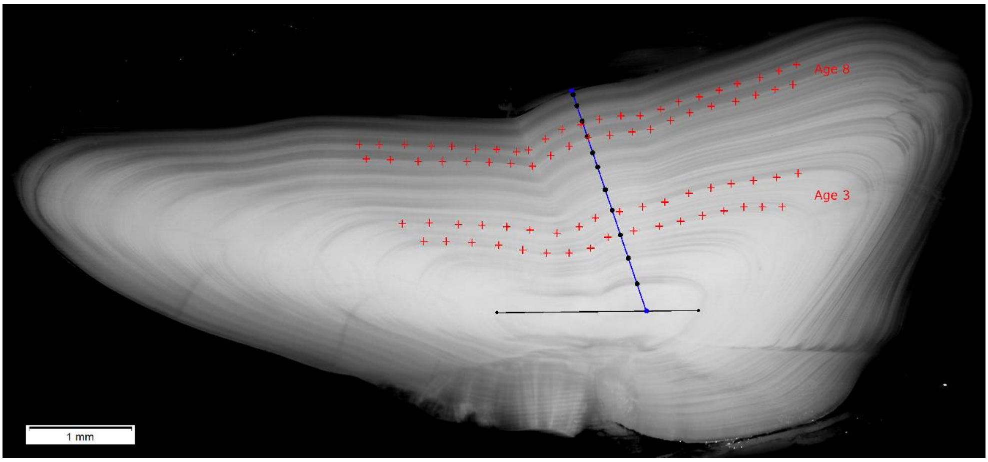

Figure 7: Otolith section showing the distal axis of growth measurements and the annuli (growth bands) formed at age 3 and 8, which were micromilled for $\delta^{18}O_{otolith}$.

1.5.1 Stable oxygen isotopes in otoliths

Isotopes are atoms of a given element whose nuclei contain the same number of protons but a different number of neutrons and thus, have a different weight. The electronic structure of an element determines its chemical behavior, whereas the nucleus defines the physical properties. Therefore, all isotopes of one element have a far-reaching similarity in chemical behavior. Due to mass differences, they show certain differences in physicochemical properties. Isotope fractionation describes processes between two isotopes of the same substance that result in different isotope ratios. Differences in the isotope abundance of one element are caused by isotope exchange reactions (equilibrium isotope distribution), kinetic processes, and metabolic effects (Hoefs, 2015). Fractionation process of stable oxygen isotopes in biogenic calcium carbonate is temperature-dependent with decreasing $\delta^{18}O$ when temperature increases (Watkins et al., 2013).

Isotopic composition is commonly expressed in terms of "delta" – (δ) values:

$$\delta = \left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) \times 1000(\%) \tag{1}$$

where R is the respective ratio measurements of the heavy versus the light isotope different to a standard.

Oxygen is the most abundant element on Earth, naturally occurring in gaseous, liquid, and solid compounds. There are three different stable isotopes of oxygen with different natural abundances: ^{16}O: 99.757%, ^{17}O: 0.038%, and ^{18}O: 0.205% (Rosman and Taylor, 1998). The $^{18}O/^{16}O$ ratio is the easiest to determine analytically.

Oxygen in otoliths is incorporated in an isotopic ratio nearly identical to that of the ambient water (Campana, 1999), highlighting that the stable oxygen isotopes originate primarily from the water. $\delta^{18}O_{otolith}$ is correlated with both temperature and salinity. Variations of $\delta^{18}O$ in the seawater are explained by the hydrological cycle; when water evaporates from the ocean's surface, the water vapor is enriched in ^{16}O because $H_2{}^{16}O$ has a higher vapor pressure than does $H_2{}^{18}O$ (Hoefs, 2015). Thus, the $\delta^{18}O$ value of seawater results from evaporation, atmospheric vapor transport, and subsequent return of freshwater into the ocean via precipitation or freshwater run-off from rivers (Nile, Amazon) or by melting glaciers (e.g., Antarctica).

For this thesis, two different mass spectrometry techniques were used to measure stable oxygen isotopes in otoliths. Isotope-ratio mass spectrometry (IRMS) is the most widely applied measurement technique for carbonates. In contrast, secondary-ion mass spectrometry (SIMS) has not been widely applied in otolith research but provides considerably improved spatial and temporal resolution over that of IRMS. IRMS is well suited for reconstructing annual mean ambient temperatures from otoliths (**Papers I** and **II**), while SIMS enables higher spatial-temporal resolution within the otolith (**Paper III**).

Isotope-ratio mass spectrometry (IRMS)

Isotope-ratio mass spectrometry measures the relative abundance of isotopes in each sample. Stable isotope ratios can be used as proxies for temperature ($\delta^{18}O$, Kalish (1991b); Patterson et al. (1993); Thorrold et al. (1997)), metabolism ($\delta^{13}C$, Chung et al. (2019)), or trophic levels ($\delta^{15}N$, Rowell et al. (2010)).

Secondary-ion mass spectrometry (SIMS)

SIMS uses an internally generated beam of positive (e.g., caesium) or negative (e.g., oxygen) ions (primary beam) focused on a smooth sample surface to generate ions that are then transferred across a high electrostatic potential. These secondary ions, which are emitted by the surface of the sample, are measured with a mass spectrometer. SIMS is considered the most sensitive of elemental and isotopic surface analysis techniques (Mueller and Verwoort, 2017).

SIMS assays offer a high spatial resolution compared to classical IRMS measurements, enabling high spatial-temporal resolution and the investigation of sub-annual temperature variations. IRMS requires a large amount of sample material generally acquired through micromilling. IRMS samples must be drilled to a depth sufficient to obtain the required amount of material. Different accretion layers can be mixed in the resulting sample due to the three-dimensional growth structure of the otolith. Temperature reconstructions based on IRMS-analyzed $\delta^{18}O_{otolith}$ often represent mean annual temperatures, although sub-annual milling is possible. Thus, intra-annual temperature peaks are often not well represented in IRMS-analyzed $\delta^{18}O_{otolith.}$ In contrast, the small spot size of 20 µm of SIMS measurements can reflect temperature exposure of several days to months, depending on the sampling age and growth rate of the fish.

1.5.2 Ambient temperature reconstruction using $\delta^{18}O_{otolith}$

Otoliths are metabolically inert and composed of aragonitic calcium carbonate in a non-collagenous matrix. The oxygen isotope values of otoliths reflect those of the water from which the oxygen is sourced but with a temperature-dependent offset (fractionation) (Campana, 1999). The change in $\delta^{18}O$ of otolith aragonite is negatively correlated to water temperatures; the higher the water temperature, the lower the $\delta^{18}O$ value (Kim and O'Neil, 1997). Kinetic, metabolic, or physiological effects are generally not considered to impact the otolith $\delta^{18}O$ (Thorrold et al., 1997; Høie et al., 2003), while "vital" effects strongly influence $\delta^{13}C$ (Kalish, 1991a; Geffen, 2012). Experimental studies have shown that otolith $\delta^{18}O$ is in equilibrium with that of the water, while some studies suggested differences in the temperature-$\delta^{18}O$ fractionation between life-stages, species, stocks, and across temperature-salinity combinations (Kalish, 1991a; Thorrold et al., 1997; Høie et al., 2004; Ghosh et al., 2007; Storm-Suke et al., 2007; Geffen, 2012; Darnaude et al., 2014).

In this study, ambient water temperatures corresponding to individual annuli were based on $\delta^{18}O_{otolith}$ using the equation by Jones and Campana (2009) (adapted from Kim and O'Neil (1997)):

$$T\,(°C) = -(\delta^{18}O_{otolith} - \delta^{18}O_{seawater}) \times 0.206^{-1} + 18.010 \qquad (2)$$

where $\delta^{18}O_{otolith}$ is the oxygen isotope composition of the otolith aragonite and $\delta^{18}O_{seawater}$ is the oxygen isotopic composition of the ambient seawater. All isotope values for $\delta^{18}O$ (and $\delta^{13}C$) were reported in ‰ on the V-PDB (Vienna Pee Dee Belemnite, international standard reference for carbon isotopes). Seawater values were given relative to the VSMOW (Vienna Standard Mean Ocean Water) standard and were corrected by subtracting 0.27‰ (Bemis et al., 1998; Grossman, 2012; Marchitto et al., 2014). Direct $\delta^{18}O_{seawater}$ measurements are not available in many regions but can be back-calculated using geographically specific salinity mixing curves, which describe the relationship between $\delta^{18}O_{seawater}$ and the salinity of the specific area (**Papers I** and **II**).

1.6 Sample selection

Archived otoliths stored dry in envelopes were accessed from the Marine and Freshwater Research Institute, Reykjavík, Iceland (**Papers I** and **II**), and the Institute of Marine Research, Bergen, Norway (**Paper II**), respectively. Three otolith samples with a minimum fish age of 10 years were collected for each calendar year and stock. The minimum age of 10 years ensured that the immature and mature life stage carbonate samples could be extracted for stable isotope analysis. If no otoliths of age 10 were available, otoliths of fish aged 9 were collected. For **Papers I** and **II,** increments of age 3 and 8 were micromilled, representing the immature and mature life stage, respectively.

Samples for **Paper III** were also provided by the Marine and Freshwater Research Institute but were extracted from DST-tagged cod. More details about these samples can be found in the respective manuscripts.

1.6.1 Icelandic sample selection

The Icelandic otolith archive consists of a collection of almost 150,000 cod otolith samples collected between 1928 and 2015. In total, 238 Icelandic otoliths were selected for stable isotope analysis from 1929 to 2015, which were derived from cod caught in the main spawning area in the southwest of Iceland. No otolith samples could be located for the years 1928, 1953, 1959, 1963, 1972, and 1984.

If the sample would be sampled with a size-selective gear, it is possible that the resulting oxygen isotope values would be similarly biased. Therefore, the mean-length-at-age between different fisheries gear types was compared to determine if there was any size selectivity bias. Gillnet samples showed consistently higher mean-length-at-age than the other gear types and thus, were excluded from subsequent analysis. Icelandic samples analyzed in this thesis were mainly caught by longline and (research) bottom trawls which had similar size selectivity.

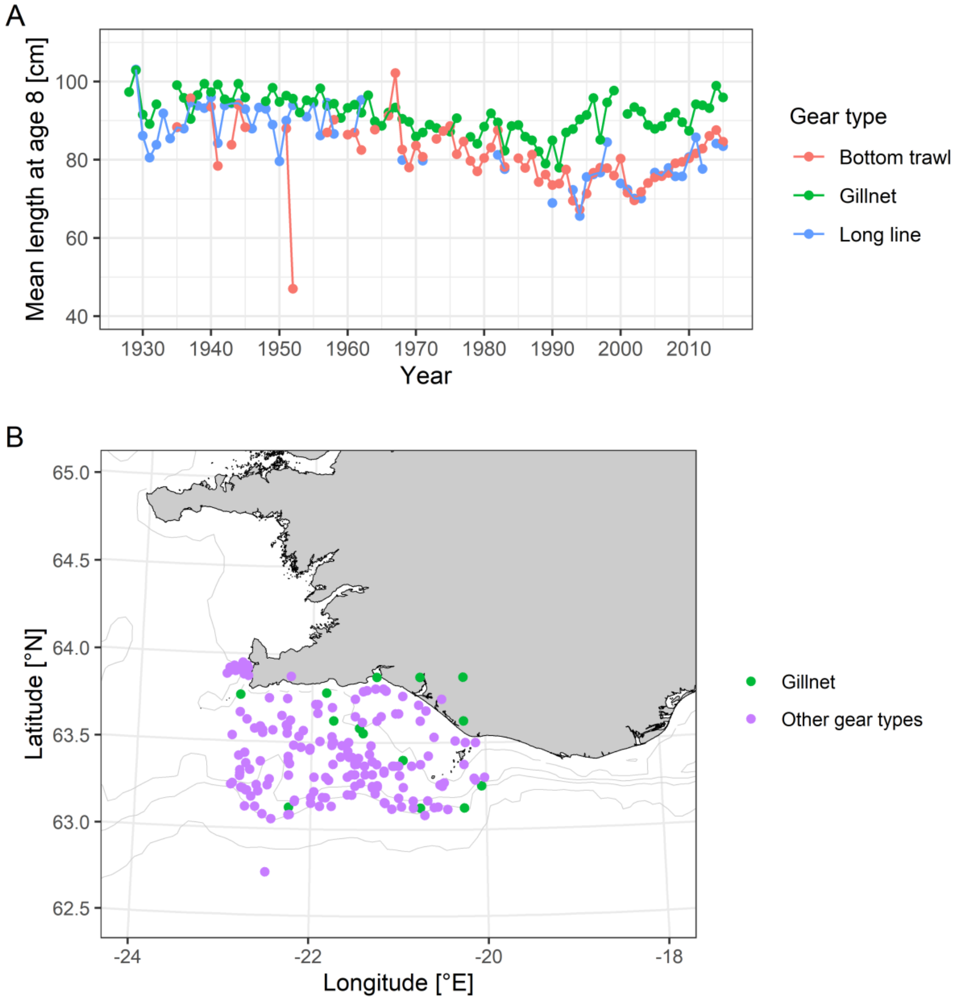

Figure 8 (previous page): (A) Mean length-at-age of cod caught by different gear types in southwest Iceland between 1928 and 2015 during the spawning season. (B) Spatial distribution of gillnet and other gear type samples in the main spawning grounds southwest off Iceland. Locations on land are errors in the otolith database.

1.6.2 Norwegian sample selection

The fish represented by the Norwegian otoliths were caught on the main spawning ground in the Lofoten region of western Norway and were selected based on gear type. Samples from 1932 to 1950 only include cod caught in the inner Lofoten; sampling in the outer Lofoten started in 1980. A potential selectivity bias of gillnets towards bigger, faster-growing fish was detected, and thus, the otolith selection was limited to bottom trawl, longline, and seine samples (Fig. 9). The selectivity bias of gillnet samples was smaller for Norway than for Iceland, but to ensure data comparability, fish caught by gillnet in both stocks were not included in this thesis. Due to missing otoliths in the archive, no samples were located for 1965, 1966, 1980, 1981, 1983, 1984, 1986, and 1989. Altogether, 219 otoliths from the years 1933 to 2016 were collected from the Norwegian otolith archive.

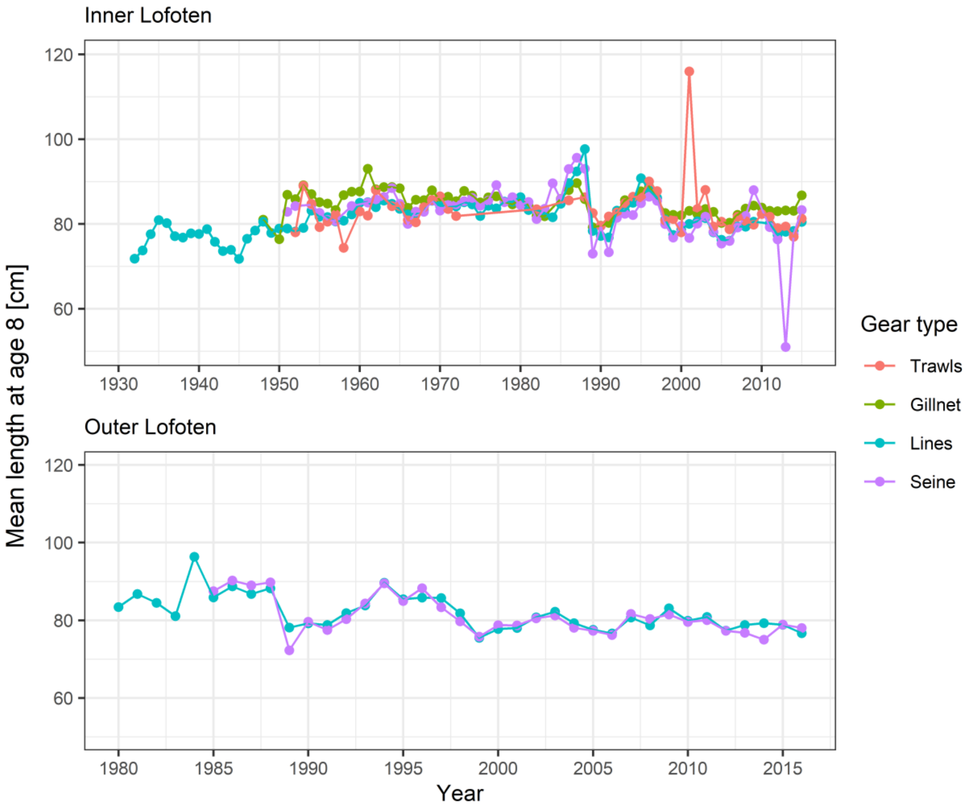

Figure 9: Mean length at age 8 of NEA cod caught by different gear types in the Inner and Outer Lofoten between 1933 and 2016 during the spawning season.

2 Results and discussion

2.1 Temperature exposure of Icelandic and NEA cod (Papers I and II)

Cod is known to be a temperature-tolerant and adaptable species, capable of surviving and growing in a wide temperature range (Righton et al., 2010). The reconstructed ambient temperatures of the Icelandic and NEA cod are well within the physiological tolerance of cod, with NEA cod being exposed to colder temperatures than those of Iceland. The mean reconstructed ambient temperature of NEA cod was 3.3°C and thus, at the lower edge of the thermal range, which goes as low as -1°C (Woodhead and Woodhead, 1965; Mehl et al., 1985). NEA cod spawners had a mean ambient temperature of 3.7, ranging from 0.8 to 8.3°C. Non-spawning NEA cod experienced colder ambient temperatures with a mean of 3.1°C (-0.4 to 7.9°C). Icelandic cod experienced higher temperatures with a mean ambient temperature of 4.8°C: 4.9°C (-0.8 to 11.7°C) for juveniles and 4.6°C (-1.7 to 10.6°C) for adults.

The temperature exposure of Icelandic and NEA cod differed significantly between life stages, as indicated by previous studies (Astthorsson et al., 1994). NEA cod spawners were exposed to higher temperatures than immature and non-spawning NEA cod as they migrate into the warmer waters of the Lofoten for spawning. The reconstructed ambient temperatures of mature Icelandic and spawning NEA cod were well within the preferred temperature range for spawning of 1 to 8°C (Righton et al., 2010). Despite the spawning migration to the warmer waters off south Iceland, juvenile Icelandic cod were exposed to slightly warmer ambient temperatures than mature cod, which is probably due to different depth ranges and the closer proximity to the coast of the immature Icelandic cod. Studies have shown that immature cod can tolerate temperatures of up to 22.5°C (Zanuzzo et al., 2019). Generally, juvenile cod are more tolerant to temperature shifts than adults as they have a broader thermal window width than early ontogenetic life stages or spawners (Pörtner and Peck, 2010).

2.2 Response of Icelandic cod to increasing water temperatures (Paper I)

The reconstructed data on individual temperature exposure indicates that Icelandic cod have not moved appreciably in response to increasing water temperatures during the last 100 years. Linear mixed-effect models confirmed that stable oxygen isotope values of otoliths are significantly correlated with environmental water temperature time series. The mean ambient temperature reconstructed for Icelandic cod was 4.8°C which is well within the physiological tolerances of cod which is limited by the critical mean annual bottom water temperature of 12°C (Dutil and Brander, 2003). Poleward distribution shifts of cod have been observed in other cod populations with higher mean annual temperatures than Icelandic cod (Perry et al., 2005), but never at an individual level. Previously reported northward distribution shifts of cod might have been due to changes in recruitment, settlement, or abundance, or changes in local sub-stocks distribution were mistakenly interpreted (Neat and Righton, 2007). Remaining in unfavorable warm water temperatures is metabolically costly (Pörtner et al., 2001). However, if fish change their distribution as a response to increasing water temperatures, they simultaneously move away from otherwise favorable conditions (e.g., main spawning grounds). Furthermore, thermoregulatory movements can result in prey-predator mismatches. Additional to temperature, density-dependent effects (**Paper II**; Swain and Wade (1993); Swain (1999); Swain et al. (2003)), demographic changes (Ottersen et al., 2006), and behavior (Righton et al., 2010) are important drivers of habitat selection.

Physical factors, such as gear selectivity, length-at-age, migration patterns, and growth rate variations, were excluded as alternative explanations for the significant correlation of Icelandic cod $\delta^{18}O_{otolith}$ and water temperature time series. Prior to the sample collection, the mean length-at-age between gear types was compared, and gillnet samples were excluded as they were consistently bigger. Gear types can be size-selective, and gillnet samples targeted bigger cod, but no difference in $\delta^{18}O_{otolith}$ was visible among the remaining gear types. The growth rate of cod is strongly influenced by temperature, and thus, long-term trends in growth rate could have affected the interpretation of reconstructed ambient temperatures. However, the mean length of Icelandic cod of age 8 did not vary significantly over the last 100 years; hence, a possible correlation between length at age and temperature exposure was considered negligible.

The effect of uncertainty in salinity estimation and its potential to explain the offset between reconstructed and environmental temperature was tested for a series of migration pattern scenarios. Information about the respective ecotype of each sample was not available. Thus, it was assumed that all Icelandic samples were frontal cod, migrating between the main spawning ground in the southwest and the main feeding area in the northwest off Iceland. Five different possible migration pattern scenarios with their respective salinities were tested but could not explain the observed offset. Even when assuming a fixed salinity of 35.3, which is the highest salinity measured avround Iceland, the ambient temperature and environmental temperature time series diverged.

The observed divergence in ambient and reconstructed water temperatures in some parts of the time series could be explained by temperature stratification with depth. Frontal cod around Iceland is found at a depth of up to 600 m (Bardarson et al., 2017). The temperature stratification around Iceland varies between regions and seasons but can be up to 5°C between 200 and 600 m (H. Valdimarsson, pers. comm.). Water masses in southwestern Iceland form a homogenous, thick layer, but waters off northern Iceland are characterized by strong depth stratification, especially in the summer.

2.3 Density-dependent temperature selectivity of Icelandic and NEA cod (Paper II)

Changes in abundance drive the temperature selectivity of Icelandic and NEA cod. However, the resulting responses varied between populations. When abundance increased, NEA cod migrated into colder, more northward waters of the Barents Sea, including sub-optimal temperature conditions. The temperature selectivity likely changed as a density-driven response due to increasing intraspecific competition and decreasing fitness levels (Laurel et al., 2007). At low densities, individuals live in the highest quality habitat within their optimal temperature range (Fretwell and Lucas, 1970; Rosenzweig, 1991). When abundance increases, fish expand their habitat into previously unfavorable thermal habitats, which became equally attractive. Temperatures at the lower or higher end of the thermal range are considered unfavorable in terms of growth performance and fitness. Colder temperatures decrease foraging and fecundity, alter metamorphosis, affect endocrine homeostasis and migratory behavior, slow down digestion and reduce growth due to lower food supply (Barton and Barton, 1987; Donaldson, 1990; Pörtner et al., 2001; Orlova et al., 2005). In recent years, range shifts of NEA cod into the colder waters of the eastern and northern Barents Sea were observed (Ottersen et al., 1998). Increasing water temperatures reduce sea ice coverage and cause the expansion of suitable feeding areas for NEA cod in the Barents Sea, which reduces potential density-dependent effects on cod (Kjesbu et al., 2014). Furthermore, the distribution of NEA cod spread to its maximum in especially warm years (Prokhorova, 2013; Mehl et al., 2014).

In contrast, Icelandic cod moved into warmer waters with increasing abundance. Warmer water temperatures generally increase the growth, but when cod are exposed to temperatures above their stock-specific optimal temperature, mortality and reproduction success decrease (Brander, 2003; Dahlke et al., 2020). The spatial distribution of Icelandic cod seems to be mainly controlled by habitat characteristics and not just temperature and depth (Marteinsdottir and Begg, 2002), although, temperature and depth, among other abiotic and biotic factors, define habitat characteristics.

The temperature selectivity of both cod populations changed with abundance; however, Icelandic and NEA cod responded differently to increasing density levels. Different responses to stock dynamic and temperature changes within the same species highlight the importance of area- and stock-specific studies to improve our understanding of climate change effects (McFarlane et al., 2000). In particular, cod stocks with their broad geographical range and different stock-specific thermal optimums likely react differently to changing environmental conditions.

2.4 Accuracy of the otolith isotopic record as an index of temperature exposure (Paper III)

Otoliths are well-suited as temperature proxies for the temperature exposure of wild, free-swimming cod. SIMS-measured and predicted $\delta^{18}O_{otolith}$ corresponded well, especially for mean and maximum $\delta^{18}O_{otolith}$ values. However, measured $\delta^{18}O_{otolith}$ values were generally higher than predicted values (mean (±SD) predicted $\delta^{18}O_{otolith}$ 2.48 ± 0.47‰; mean measured $\delta^{18}O_{otolith}$ 2.32 ± 0.60‰) implying an overestimation of ambient temperatures. This coincides with previous studies that IRMS measurements generally overestimate reconstructed temperatures (Weidman and Millner, 2000; Geffen, 2012).

The matrix effect of the SIMS method and the lack of a reliable aragonite standard for SIMS measurements potentially explain the small divergence between measured and predicted $\delta^{18}O_{otolith}$. The different chemical compositions and structures of the otolith relative to the standards can introduce a bias (Hane et al. (2020) and references therein). The minor protein component of otoliths can influence the instrumental mass fractionation, resulting in lower SIMS-analyzed $\delta^{18}O_{otolith}$ values. A matrix-matched standard could avoid this effect. As there is no reliable aragonitic SIMS-standard, calcite is used as a standard for biogenic calcium carbonate measurements. Calcite and aragonite are polymorphs of the same mineral, but their atoms are stacked in different configurations. Calcite behaves differently than aragonite under a caesium (Cs) ion beam due to the high strontium (Sr) content in calcite. Although absolute temperature estimations are not correct when $\delta^{18}O_{otolith}$ values are measured against a calcite standard, relative temperature changes are valuable for many studies (M. Whitehouse, pers.comm.). Moreover, the aragonite-calcite bias can be corrected by applying an offset factor. However, this approach is not perfect as inherent mass-balance and growth rate issues are not considered. However, in the absence of a reliable aragonite standard for SIMS-measurements, alternative options are not apparent.

The estimation of ambient salinity can introduce potential errors in temperature reconstructions. The accuracy of the otolith isotopic record as an index of temperature exposure was higher for frontal than for coastal cod. Despite the migration between spawning and feeding areas, the match of measured and predicted $\delta^{18}O_{otolith}$ values was better for frontal than for coastal cod. Due to their characteristic differences in spawning migration and depth distribution, it was easier to assume the environmental conditions experienced by frontal cod. As revealed by the name, coastal cod is found closer to the shore. Local salinity fluctuations are more pronounced inshore; however, these were not represented in the salinity measurements used for temperature reconstructions. Freshwater run-off causes salinity fluctuations, which are especially pronounced along the south coast of Iceland, where most fish were tagged and recaptured (Thórdardóttir, 1986).

In contrast to $\delta^{13}C_{otolith}$ values, which are strongly influenced by physiological processes (Kalish, 1991a; Geffen, 2012), $\delta^{18}O_{otolith}$ values are mainly driven by ambient temperatures and are independent of fish metabolism and thus, commonly applied to reconstruct ambient temperatures (Thorrold et al., 1997; Høie et al., 2003). On the other hand, differences in the extent of temperature-$\delta^{18}O$ fractionation have been reported across life stages, species, stocks, and across temperature-salinity combinations (Kalish, 1991a; Thorrold et al., 1997; Høie et al., 2004; Ghosh et al., 2007; Storm-Suke et al., 2007; Geffen, 2012; Darnaude et al., 2014). Physiological, kinetic, or metabolic processes (i.e., "vital) potentially impact the temperature-$\delta^{18}O$ fractionation, but to minimize the effect of these potential error sources, all samples belonged to the same species and were mature fish. Moreover, the different ecotypes were considered in the respective data analysis. Additionally, $\delta^{18}O_{otolith}$ values were predicted using the equation by (Høie et al., 2004), but predicted $\delta^{18}O_{otolith}$ values were higher by 0.22‰ resulting in a loss of accuracy of predicted $\delta^{18}O_{otolith}$ values.

Incorrect ambient salinity estimations can be a source of error in otolith-based temperature reconstructions. Wrongly assigned geolocations could cause incorrect salinity estimations resulting in inaccurately predicted $\delta^{18}O_{otolith}$ values (Darnaude et al., 2014). However, a salinity sensitivity analysis showed that the assumed salinity had the best correspondence between measured and predicted $\delta^{18}O_{otolith}$ values.

3 Future research

Different responses to changing environmental temperatures highlighted the importance of local and stock-specific studies of climate change responses. Cold-water cod stocks were expected to be less affected by global warming, with some stocks even benefitting from rising water temperatures. Thus, it is important to extend similar studies to warm-water cod stocks, which are predicted to decline or even disappear due to rising water temperatures. North Sea plaice, autumn spawning herring in Norway, and sand lance are potential candidates for future studies as they are presumably more heavily affected by global warming than Icelandic or NEA cod (Petitgas et al., 2013). It is already known that North Sea plaice will be affected by the loss of suitable spawning habitats due to increasing water temperatures. Moreover, fewer North Sea plaice recruits are produced in years of warm winter sea-surface temperatures, probably linked to changes in phytoplankton levels which larvae feed (Cook and Heath, 2005).

Some species will move to remain in their preferred thermal habitat as a response to warming ocean waters. These thermoregulatory movements may lead to changing prey-predator interactions. Thus, exploring the thermal habitats of other fish species around Iceland and in the Barents Sea, particularly of cod's main prey capelin, would further increase our understanding of climate change responses within an ecosystem. If capelin move into colder waters, cod will have to react by changing its prey preference or following its main prey. Furthermore, modeling the possible response of cod (and other fish species) under different climate change scenarios (IPCC, 2013) would further improve our understanding of fish's temperature selectivity.

The proposed future research projects could all be done based on reconstructed ambient temperatures derived from stable oxygen isotopes of otoliths. Currently, methodological limitations often restrict the sample size and/or the spatial-temporal resolution. Micromilling, which is the most common method to collect calcium carbonate samples of otoliths, is time-consuming and has a limited spatial-temporal resolution. SIMS circumvent some of these limitations and enables the measurements of whole transects reflecting the fish's entire temperature life history at a high spatial-temporal resolution. However, the lack of a reliable biogenic aragonitic standard and the resulting offset is subject to further research. SIMS will likely become the standard $\delta^{18}O_{otolith}$ assay method once this challenge is solved. SIMS can analyze more $\delta^{18}O_{otolith}$ samples in a given time than IRMS due to a higher degree of automatization and the discontinuation of the time-consuming process of micromilling.

Moreover, changes in seawater geochemistry might become a pressing issue in the near future, with serious consequences for the $\delta^{18}O_{otolith}$ application as a temperature proxy. The sea ice retreat in the Barents Sea will change the isotopic composition of the seawater and the salinity resulting in incorrect temperature reconstructions (Rohling, 2013). Salinity values usually drop due to melting sea ice. Thus, $\delta^{18}O_{seawater}$ is also affected, resulting in a changing salinity-$\delta^{18}O_{seawater}$ relationship making currently established salinity mixing lines for the Barents Sea unusable and $\delta^{18}O_{otolith}$ of NEA cod less reliable as temperature proxies.

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Paper I

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Stable oxygen isotope reconstruction of temperature exposure of the Icelandic cod (*Gadus morhua*) stock over the last 100 years

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Stable oxygen isotope reconstruction of temperature exposure of the Icelandic cod (*Gadus morhua*) stock over the last 100 years

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Increasing water temperatures are predicted around the globe, with high amplitudes of warming in Subarctic and Arctic regions where Atlantic cod (*Gadus morhua*) populations currently flourish. We reconstructed oxygen isotope and temperature chronologies from Icelandic cod otoliths, one of the largest cod stocks in the world, to determine if cod moved or migrated over the last 100 years to avoid increasing water temperatures. For $\delta^{18}O_{otolith}$ analysis, individual annual growth increments from immature and mature life history stages were micromilled from adult otoliths, which were collected in southern Iceland. Linear mixed-effect models confirmed that stable oxygen isotope time series of immature and mature cod differ significantly between both life stages ($p < 0.001$). Overall, cod otolith $\delta^{18}O$ was significantly correlated with water temperature (sea surface temperature: $p < 0.001$, temperature at 200 m depth: $p < 0.01$), indicating that Atlantic cod were exposed to fluctuating water temperatures during the past 100 years and did not move as a response to increasing ocean temperatures. All of the alternate physical factors that were considered for the isotope-based variation in the temperature exposure of Icelandic cod were rejected.

Keywords: ambient temperature, Atlantic cod, Iceland, stable oxygen isotopes

Introduction

Global warming is causing a rise in sea level, decrease in sea ice cover in polar regions, and range shifts across all taxa (e.g. IPCC, 2013). Rising water temperatures will force many taxa of marine aquatic organisms to move to areas outside their current distribution area. However, some marine mammals such as the narwhal (*Monodon monoceros*) or the polar bear (*Ursus maritimus*) are dependent on sea ice and cannot change their habitat (Simmonds and Isaac, 2007). Marine fish, in contrast, do not have physical boundaries when migrating but are limited by their physiological thermal tolerance (Comte and Olden, 2017). Rising water temperatures have already led to distributional changes on several different scales in marine ecosystems (e.g. Welch *et al.*, 1998; Castonguay *et al.*, 1999). For example, in the North Sea, cod, anglerfish (*Lophius piscatorius*), and snake blenny (*Ophidion barbatum*) showed climate-related latitudinal changes >25 years, but fish can also change their depth range rather than their latitudinal distribution [e.g. plaice (*Pleuronectes platessa*) in the North Sea; Perry *et al.*, 2005].

Despite overexploitation, significant declines in stock biomass, and, in some cases, stock collapse (Hutchings and Myers, 1994; Rose, 2004; Hutchings, 2005; Worm *et al.*, 2006), Atlantic cod (*Gadus morhua*) is still one of the most commercially important species in the North Atlantic. The Icelandic cod stock is one of the largest cod stocks in the world. Due to declining harvest rates, the spawning-stock biomass has increased in recent years (MFRI, 2019). Icelandic cod spawn in spring, and pelagic eggs and larvae drift clockwise from the main spawning grounds off the southwest coast to the main nursery grounds off the north coast where juveniles are found year-round (Astthorsson *et al.*, 1994;

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Begg and Marteinsdottir, 2000, 2002a). Adult cod migrate between the spawning ground and the deeper waters of the main feeding area northwest of Iceland (Jónsson, 1996). The migration pattern must be known to be able to correctly reconstruct the temperature history of Icelandic cod.

Temperature is the most important abiotic factor influencing fish population dynamics (Myers *et al.*, 2001). It is necessary to understand the past behaviour of cod to predict their response to changing environmental conditions in the future. Natural variation caused a warming event in the northern North Atlantic in the 1920s to 1940s, leading to regime shifts and northward movement of several fish species, including cod (Rose, 2005; Drinkwater, 2006). Icelandic waters showed many salinity and temperature variations during the last century, particularly two warming events (Jakobsson and Stefánsson, 1998; Malmberg and Valdimarsson, 2003). The first warming event started in the 1920s, and temperatures remained high until cooling started in the 1960s. The second warming event started in the 1990s due to the increasing release of greenhouse gases in the atmosphere (Hanna *et al.*, 2006). Rising water temperatures are expected to cause the disappearance of certain cod stocks, while others will decrease or most likely spread northwards (Drinkwater, 2005). The IPCC (2013) predicts an increase in the annual mean water temperature of ~1.4–5.8°C in the distributional area of Icelandic cod by 2100. Therefore, a future northward movement of Atlantic cod is expected (Drinkwater, 2005). Mobile species such as cod have two options in responding to changing environmental conditions. One possibility is to undertake small-scale migrations (horizontal or vertical) to avoid unfavourable environmental conditions and thus remain within their preferred temperature regime. However, they simultaneously move away from otherwise favourable conditions such as the main spawning ground and prey–predator interactions may change (Brander, 2003). Alternatively, they could acclimate to the new temperature regime, which is metabolically costly (Pörtner *et al.*, 2001). Cod have a broad geographical distribution, implying a wide temperature range, and are usually not found in waters above the critical annual mean bottom water temperature of 12°C (Myers *et al.*, 1997; Drinkwater, 2005). If this temperature is reached, a cod stock would either have to move into colder water masses or disappear due to high mortality (Dutil and Brander, 2003). However, juveniles have a broader thermal window and can inhabit water masses up to 20°C, while spawners, eggs, and larvae have a narrower thermal window and are most vulnerable to temperature changes (Brander, 1997; Pörtner and Peck, 2010).

Otoliths (ear stones) can be found in all teleost fish and are paired calcified structures used for balance and/or hearing (Campana, 1999). Coupled with age or date, they provide chronological records that can be used to reconstruct a fish's life or temperature history as it grows continuously from hatching to death (Campana and Thorrold, 2001). Each individual annulus (annual growth increment) can be assigned an age of formation as well as a calendar year of formation. Otoliths are metabolically inert and composed of aragonitic calcium carbonate in a non-collagenous organic matrix. The oxygen isotope values of otoliths reflect those of the water from which the oxygen is sourced, but with a temperature-dependent offset (fractionation) (Campana, 1999). The change in ^{18}O of otolith aragonite is negatively correlated to water temperature; the higher the water temperature, the lower the $\delta^{18}O_{\mathrm{otolith}}$ value (Kim and O'Neil, 1997). Stable oxygen isotopes allow temperature reconstructions even in the absence of temperature measurements, such as early in the 1900s. Furthermore, instrumental time series record the environmental temperature, which is the temperature measured at one station, not the ambient temperature experienced by the fish. Otoliths are well suited as environmental recorders, and the mean annual ambient water temperature can be calculated by using stable oxygen isotopes of an otolith, when the isotopic composition of the ambient seawater can be determined (e.g. Jones and Campana, 2009).

We used otoliths to reconstruct a 100-year temperature exposure history of Icelandic cod to determine if Icelandic cod altered their microhabitat to avoid non-preferred temperatures as a result of increasing ocean temperatures due to climate change. If Icelandic cod did not move to avoid unfavourable conditions, the reconstructed ambient temperatures should have increased over the last 100 years. The alternative hypothesis is that Icelandic cod actively migrated away from warming regions to remain in their optimal temperature habitat, in which case the otolith oxygen isotope time series would show no change or trends over time. Since cod associate with different temperature ranges at different ages, we did not necessarily expect to see comparable temperature reconstructions between immature and mature cod.

Material and methods

Sampling

Archived cod otoliths ($n = 238$ from 1929 to 2015) stored dry in envelopes were accessed from the Marine and Freshwater Research Institute (Hafrannsóknastofnun), Iceland (Table 1). The fish represented by the otoliths were caught in the main spawning ground southwest of Iceland (Figure 1) and were selected based on gear type. Gillnet samples appeared to show size selectivity, relative to other gears, with a continuously larger mean length-at-age of 8 than the length-at-age of other gear types. Differences in length-at-age were not caused by differences in spatial distribution as mapping the catch locations of all cod did not show any spatial differences between gillnet samples and other gear types. When possible, we collected three otoliths, with a minimum fish age of 10 years, for each calendar year of sampling. Due to excluded gear types, no samples were available from 1928, 1953, 1959, 1963, 1972, and 1984.

To avoid otolith breakage during preparation, otoliths were embedded in epoxy and cut through the core using a Buehler IsoMet 1000 Precision Saw (ITW Test & Measurement GmbH, Esslingen, Germany) equipped with a 15LC IsoMet Diamond Wafering blade to get otolith sections of ~1-mm thickness. Silicone EPDM (silicone combined with a synthetic rubber) moulds, Polylite 32032-20 resin, and hardener Narpol Peroxide 1 Methyl Ethyl Ketone Peroxide were used for embedding. Otolith sections were imaged prior to milling with an Olympus DP 74 high-resolution [5760 × 3600 pixels (3 CMOS)] camera mounted on a Leica S8AP0 stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany) using CellSens Standard software (Olympus Europa SE & Co. KG, Hamburg, Germany). Images were processed with Adobe Photoshop CS2 (Version 9.0) and aged along the distal axis of growth.

For stable oxygen isotope analysis, a micromilling approach was applied to extract otolith material. Otolith sections were glued on glass slides using Krazy Glue or Super Glue Liquid Control. Sample vials were decontaminated by rinsing with Milli-Q water (Millipore, Merck KGaA, Darmstadt, Germany) and

Table 1. Otolith samples collected per gear type aggregated by 5-year blocks.

Years	Longline	Handline	Danish seine	Bottom trawl	Research survey bottom trawl
1929	3	–	–	–	–
1930–1934	15	–	–	–	–
1935–1939	13	–	–	2	–
1940–1944	6	–	–	9	–
1945–1949	15	–	–	1	–
1950–1954	9	–	1	2	–
1955–1959	10	–	–	2	–
1960–1964	2	1	–	6	–
1965–1969		–	3	8	–
1970–1974	2	–	–	9	–
1975–1979		–	–	13	–
1980–1984	2	–	–	10	–
1985–1989		–	–	3	12
1990–1994	3	–	3	1	8
1995–1999		–	–	4	11
2000–2004	1	–	–	3	7
2005–2009	2	–	2	5	6
2010–2015	8	–	2	3	20

All samples were caught in southwestern Iceland between March and May 1929–2015. Usually three otoliths per year were collected except for the most recent years (2010–2015) when six samples per year were collected.

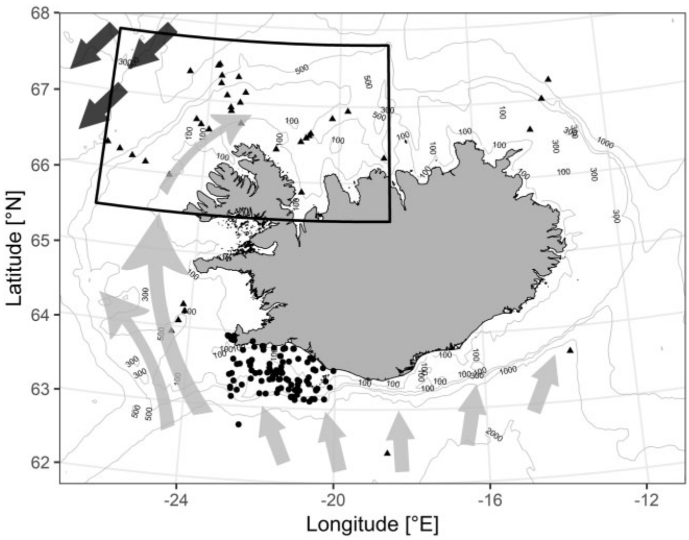

Figure 1. Sampling locations of otoliths (black circles) in the south off Iceland (main spawning ground) and locations of δ^{18}O seawater and salinity samples for the salinity mixing line (triangles). The polygon shows the main feeding and nursery area in the north and northwest of Iceland. The major currents are the North Atlantic Drift (light grey arrows), which flows northwards as the Irminger Current, and the East Greenland Current (dark grey arrows) coming from the north.

then air dried. A high-precision, computer-controlled Merchantek New Wave MicroMill (Elemental Scientific, Omaha, NE, USA) equipped with a Leica GZ6 camera (Komet/Gebr. Brassler GmbH & Co. KG, Lemgo, Germany) and a 360-µm drill bit was used to mill two samples of carbonate powder; age 3 represented the immature life stage of cod and age 8 represented the mature cod. In general, the third and eighth annuli from age 10 fish were micromilled, but in years where 10-year-old fish were unavailable, age 9 fish were collected and ages 3 and 7 sampled, respectively. We did not sample close to the edge so as to prevent any contamination of the calcium carbonate sample with epoxy. No differences in temperature exposure were expected between ages 7 and 8 as age at 50% maturity has been shown to be 5.9 years for cod from south of Iceland and 6.6 years for cod from north Iceland (Marteinsdottir and Begg, 2002). To maximize the weight of milled material, the drill path was offset by the radius (180 µm) of the drill bit. Furthermore, a “discharge” scan was run to remove some coarse material next to the year of interest to prevent any contamination of the actual sample material. To prevent contamination between samples, the otolith section, drill bit, and sampling tweezers were cleaned with compressed air and ethanol between samples. The samples were drilled up to 750-µm depth (20–25 passes with a drill depth of 30 µm/pass), which was usually adequate to collect the intended 50 µg of sample material. A minimum of 15 µm was required by the isotope ratio mass spectrometer (IRMS).

Measurements of calcium carbonate samples for oxygen and isotope content were conducted at FARLAB in the Department of Earth Sciences, University of Bergen, Norway. Otolith carbonate was transferred to glass vials and reacted with an automated Keil IV carbonate device and analysed using a coupled MAT 253 mass spectrometer. The long-term reproducibility (or 1-sigma precision) of the mass spectrometer was $\leq 0.8‰$ and $\leq 0.4‰$ for δ^{18}O and δ^{13}C, respectively, for sample sizes >13 µg, based on replicate measurements of an internal carbonate standard run in parallel with the samples over a period of months. Isotope values are reported on the VPDB scale calibrated using NBS-19 and NBS-18.

There was no evidence of epoxy embedding medium contamination on the δ^{13}C and δ^{18}O values. As a test for contamination, epoxy samples were added to in-house marble standards. Within the standard two-sigma uncertainty of replicates, none of the samples containing epoxy were isotopically distinct from the samples without epoxy (in addition, five of the six samples were within one-sigma of the mean).

Salinity and water temperature

As $\delta^{18}O_{seawater}$ is needed for the reconstruction of ambient temperatures from carbonate samples but was not available for our samples, we estimated δ^{18}O values from salinity using a salinity mixing curve. Salinity and $\delta^{18}O_{seawater}$ data were derived from NASA GISS Global Seawater Oxygen-18 Database (Schmidt *et al.*, 1999; Smith *et al.*, 2005; J. Ólafsson and Á. Sveinbjörnsdóttir, unpublished data). The salinity mixing curve describes the relationship between $\delta^{18}O_{seawater}$ and salinity for the Icelandic shelf at depths between 50 and 400 m, the typical depth range of cod around Iceland. Water samples for oxygen isotope assays had been collected at multiple locations around Iceland in several years (1972–2012). A simple linear regression through these points produced the following salinity mixing curve (Figure 2):

$$\delta^{18}O_{seawater} = 0.58 \times S - 20.12, \quad (1)$$

where $\delta^{18}O_{seawater}$ is the oxygen isotope content [‰ on the standard mean ocean water (SMOW) scale] of seawater and S is the salinity. Our salinity mixing curve is almost identical to published salinity mixing lines for the Greenlandic–Icelandic–Norwegian seas and the North Atlantic (LeGrande and Schmidt, 2006).

Measured salinity data were available from 1950 onward at several locations. To account for differences between time (month, year), depth, and stations, these variables were treated as factors in general linear models (GLM) to derive an overall salinity time series. We estimated a salinity time series for the south (Selvogsbanki) and the north (Látrabjarg, Kögur, Hornbanki, Húnafloi, and Siglunes) based on these measured salinity data (depth range: 50–200 m, data downloaded from https://sjora.hafro.is/ on 29 June 2019). Modelled salinity values from 1900 onward were derived from the Hadley Centre subsurface temperature and salinity objective analyses I09 v4.2.1 dataset (Good *et al.*, 2013; version EN4.2.1; depth range 50–200 m; Table 2). Measured and modelled salinity time series for both areas were statistically compared to justify the use of the modelled data. Modelled and measured salinity time series were correlated in both areas and showed similar trends ($r^2 = 0.7$ for the south and $r^2 = 0.55$ for the north). However, modelled and measured salinity time series showed offsets of up to 0.1 south of Iceland, whereas the offset for northern Iceland was smaller. Due to frequently changing oceanographic conditions, salinity models for the Icelandic shelf are challenging to build and unavoidably include an uncertainty that might explain the offset. Therefore, we decided to use the modelled salinity timeline for the entire time period rather than using the modelled salinity time series prior to 1950 and the measured time series from 1950 onward. In that way, we avoided potential influences (bias) related to change in the data source when comparing the two time windows.

Salinity values used for ambient temperature reconstruction need to account for the annual migration pattern of Icelandic cod between northern and southern Icelandic waters (Jónsson, 1996). The timing of annual migration can vary slightly but has not changed significantly during the studied time period. The time series for juvenile cod only considers northern salinity values, as immature cod are found in the main nursery grounds along the north and northwest year-round. Due to the migration between the spawning and feeding areas, mature cod are exposed to intra-annual salinity variation. Therefore, the salinity time series for mature cod integrated salinity values from the south for January–June and the north for July–December.

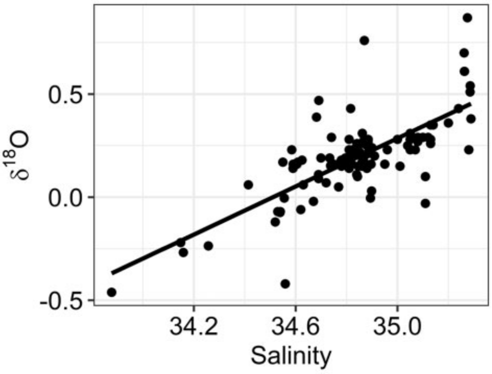

Figure 2. The relationship between the oxygen isotope content ($\delta^{18}O_{seawater}$) of seawater and salinity for the Icelandic shelf at depth 50–400 m ($n = 100$, $p < 0.001$, $r^2 = 0.55$).

Table 2. Location information of stations considered for salinity time series.

Stations	Longitude	Latitude
Hadley-North	−24	66
	−22	67
Hadley-South	−21	63

Salinity data were derived from Hadley EN4.2.1 analyses l09 data downloaded from APDRC LAS7 for public (Good *et al.*, 2013). Just one station was considered for the south, as all stations in that area basically have the same salinity.

Table 3. Stations considered for general linear models calculating the SST and water temperature (*T*) at 200-m depth south and north of Iceland.

Measurements	**South**	**North**	**Years**
SST	Grindavík, Stórhöfði, Vestmannaeyjabær	Grænhóll í Árneshreppi, Hraun á Skaga, Kjörvogur, Litla-Ávík, Suðureyri	S: 1878–2016 N: 1922–2010
T at 200 m	Selvogsbanki	Hornbanki, Húnafloi, Kögur, Látrabjarg, Siglunes	1950–2018

Years: time period in which measurements were conducted. SST derived from Jónsson (2003) and temperature data at 200-m depth from Hafro (data downloaded from https://sjora.hafro.is/ on 29 July 2019).

Comparable to the salinity approach, sea surface temperature (SST) and water temperature time series at 200 m depth were created by generalized linear models to produce an overall temperature time series applicable to cod from our study area. Year and stations were used as factors for the SST time series. Month, year, depth (179–210 m), and stations (same as for the salinity time series) were considered as factors in the general linear model, which estimated the temperature time series at 200-m depth (Table 3). For both sets of water temperatures, we created one generalized linear model for the north and one for the south. SST data were available since 1922 (Jónsson, 2003), whereas measurements at 200 m started in 1950 (downloaded from https://sjora.hafro.is/ on 29 June 2019). Assuming the same migration pattern as for the salinity time series and the reconstruction of ambient water temperatures, SST and water temperature at 200 m were calculated and matched with the measured stable oxygen isotope value by year and life stage.

Temperature reconstruction

Ambient water temperatures were reconstructed using the equation of Jones and Campana (2009) (adapted from Kim and O'Neil, 1997):

$$T\ (^{\circ}\mathrm{C}) = -(\delta^{18}\mathrm{O}_{\mathrm{otolith}} - \delta^{18}\mathrm{O}_{\mathrm{seawater}}) \times 0.206^{-1} + 18.010, \tag{2}$$

where $\delta^{18}\mathrm{O}_{\mathrm{otolith}}$ is the oxygen isotope composition of the otolith aragonite and $\delta^{18}\mathrm{O}_{\mathrm{seawater}}$ is the oxygen isotope composition of the ambient seawater. All isotope values for $\delta^{18}\mathrm{O}$ (and $\delta^{13}\mathrm{C}$) otolith carbonate are reported in ‰ on the VPDB scale. Seawater values were corrected from SMOW by subtracting 0.27‰ (Bemis *et al.*, 1998; Grossman, 2012; Marchitto *et al.*, 2014).

Linear mixed-effect modelling

Linear mixed-effect models were fitted to model the oxygen isotope content of cod and to account for the repeated measurements (two life stages measured within the same otolith) for the same individual (Zuur *et al.*, 2009). Life stage and year of formation were treated as fixed factors. Year was modelled as a fixed effect to obtain a prediction for every year rather than just a trend over time. A random intercept for individual fish was included to correct model estimates for differences among fish.

Two additional linear mixed-effect models were applied to assess the relationship between $\delta^{18}\mathrm{O}_{\mathrm{otolith}}$ and seawater temperatures (SST and seawater temperature at 200 m, respectively) as an extrinsic effect using the same random-effect structure as in the first model. As these temperatures already accounted for differences between life stages and their migration patterns, life stage was not included as an intrinsic factor in these models.

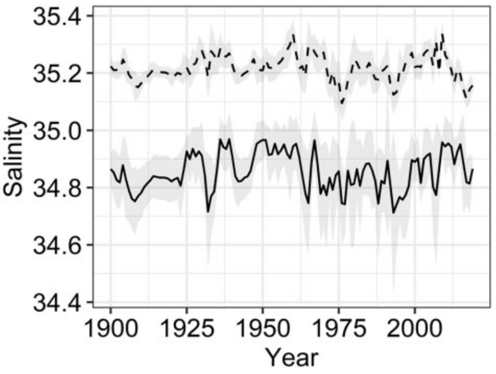

Figure 3. Mean salinity time series in southern (dashed) and northern (solid) Iceland at depths of 50–200 m. Standard deviation indicated by shading. Hadley EN4.2.1 analyses l09 data downloaded from APDRC LAS7 for public.

Mixed models with different levels of complexity were compared using the Akaike information criterion corrected (AICc) for the small sample sizes. The first step of analysis involved selection of the optimal random-effect structure. Second, the optimal fixed-effect structure was selected by the comparison of models fitted using maximum likelihood and previously identified random structure. Alternative models were again compared using AICc, and the best-ranked model was refitted with REML, allowing unbiased model estimates (Zuur *et al.*, 2009). Assumptions of the final model were checked and satisfied with standard diagnostics. Interclass correlation was calculated to assess the level of consistent between-individual and between-year differences in otolith trait values. The conditional and marginal r^2 metric was calculated for all models to assess the variance in otolith traits explained by both fixed and random effects.

Statistical analysis and graphical outputs were produced using R 3.6.0 (R Core Team, 2019).

Results

Environmental conditions

The salinity timelines for northern and southern Iceland showed year-to-year variations, which were less pronounced in the south than in the north (Figure 3). The last 100 years were characterized by interannual salinity variations; in the 1960s, salinity dropped due to the "Great Salinity Anomalies", returning to normal levels in 1976 (Dickson *et al.*, 1988; Belkin *et al.*, 1998).

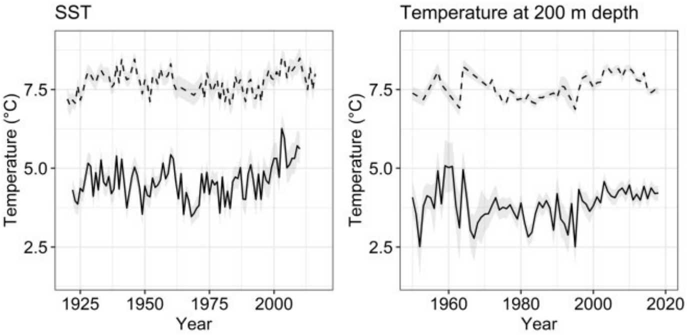

Figure 4. Modelled SST and water temperature at 200 m in the south (dashed) and north (solid) of Iceland. Standard deviation indicated by shading.

Water temperatures in the south were warmer than in the north (Figure 4). The difference between SST and water temperature at 200 m in the south is small, as it forms a homogeneous and thick water layer extending to several hundred metres (Jónsson, 1999; Malmberg and Valdimarsson, 2003). The temperature difference is more pronounced in the north where water at 200 m depth is notably colder. The warming trend that started in the late 1990s was more pronounced in the north.

Otolith isotopes and ambient temperature reconstruction

We built a century-long temperature chronology for cod around Iceland using stable oxygen isotopes in otoliths. The assayed annuli had a mean $\delta^{18}O_{otolith}$ of 2.60‰; the mean $\delta^{18}O_{otolith}$ for immature cod was 2.51‰ (1.06–3.61‰), while that for mature cod was 2.68‰ (1.44–4.02‰). The change in ^{18}O of otolith aragonite is negatively correlated to the water temperature; the higher the water temperature, the lower the $\delta^{18}O_{otolith}$ value.

Catch depth was shallower at the beginning of the time series than later indicating that cod caught before 1970 were exposed to different temperature regimes than cod fished thereafter. The mean fishing depth was 115 m (37–209 m; $n = 6$ fish) prior to 1970 and 152 m (22–549 m; $n = 85$ fish) afterwards. Deeper waters could be due to redirected fishing effort into deeper offshore waters with the introduction of larger vessels since the 1950s (Jakobsdóttir *et al.*, 2011) but could also indicate a deepening of Icelandic cod due to increasing water temperatures. However, the 1970s were characterized by rather cold water temperatures around Iceland, and a vertical migration to deeper, colder waters would have to be a delayed response to the warming period that lasted until the early 1960s. To support this assumption, further fishing depth information would be needed.

Five different scenarios with different complexities of migration patterns were tested to exclude the possibility that incorrect salinity assumptions explained the temperature variations (Table 4):

(i) Cod (mature and immature) stayed in southern (1.1)/northern (1.2) Iceland year-round, with one constant salinity value over the entire time period.

(ii) Mature cod migrated between southern and northern Iceland, and immature cod stayed in the north, but both areas had one fixed salinity value.

(iii) Cod did not migrate, and all stayed in southern Iceland, but interannual salinity variations were assumed.

(iv) The most complex scenario that was used for the final ambient temperature reconstructions; immature cod spent all year in the north(west), and mature cod migrated between the south and north; both areas showed interannual salinity variability.

(v) Mature cod stayed in the south year-round (5.1)/migrated between both areas (5.2), but instead of year-to-year salinity variation, long-term salinity trends (three blocks of ~20 years) were assumed.

These different scenarios resulted in temperature offsets between the different migration assumptions, but the temperature trend over time was always the same.

Reconstructed temperature time series based on $\delta^{18}O_{otolith}$ showed differences in temperature exposure between immature and mature cod (Figure 5). The overall trend over time was the same for both life stages, but immature cod were exposed to warmer temperatures than mature cod until 1980, when the ambient temperature of juveniles decreased. Since then, mature and immature cod have experienced similar water temperatures. The mean ambient temperature of all samples was 4.8°C: 4.9°C (−0.8 to 11.7°C) for juveniles and 4.6°C (−1.7 to 10.6°C) for adults.

Linear mixed-effect models showed that stable oxygen isotope time series were significantly different ($p < 0.001$) between life stages (Table 5). The effect of sex was also tested with male and female (unknown sex was excluded from analysis) as a fixed factor but was not significant ($p = 0.6$, $n = 365$). $\delta^{18}O_{otolith}$ was significantly related to SST ($p < 0.001$). An additional linear mixed-effect model estimated the effect of water temperatures at 200-m depth, which was also significantly related to $\delta^{18}O_{otolith}$ ($p < 0.01$; Figure 6). Both water temperature time series (SST and water temperature at 200 m) are correlated ($r^2 = 0.84$), which explains why both are significantly related to $\delta^{18}O_{otolith}$. Since cod $\delta^{18}O_{otolith}$ was significantly correlated with water temperature, cod were exposed to changing temperatures during the last 100 years.

Table 4. Ambient water temperature reconstructed assuming different migration patterns.

		Salinity		Temperature (°C)			Temperature (°C)—immature			Temperature (°C)—mature		
Scenario	Migration scenario	South	North	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
1.1	Just south	35.2	–	5.5	−1.4	13.0	6.0	0.1	13.0	5.1	−1.4	11.2
1.2	Just north	–	34.9	4.7	−2.2	12.1	5.1	−0.7	12.1	4.3	−2.2	10.3
2	Six months in the south, 6 months in the north	35.2	34.9	4.9	−1.8	12.1	5.1	−0.7	12.1	4.7	−1.8	10.7
3	South all year	Year-to-year variability	–	5.6	−1.1	13.2	6.0	0.2	13.3	5.2	−1.1	11.1
4	Six months in the south, 6 months in the north	Year-to-year variability	–	4.8	−1.7	11.7	5.0	−0.8	11.7	4.7	−1.7	10.6
5.1	Just south	Long-term trends (three blocks: 1950–1974, 1975–1994, 1995–2017)	–	5.3	−1.5	13.0	5.6	−0.1	13.0	5.0	9.5	−1.5
5.2	Six months in the south, 6 months in the north			4.7	−2.0	12.2	4.9	−0.8	12.2	4.6	9.2	−2.0

The different migration patterns are described in detail in the article.

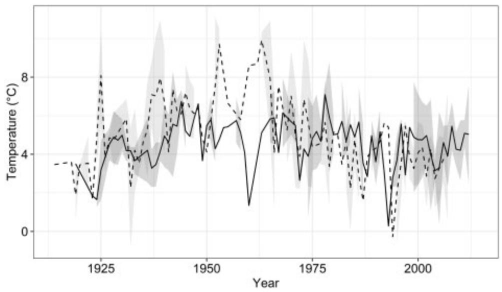

Figure 5. Reconstructed ambient water temperature of immature (dashed) and mature (solid line) Icelandic cod. Standard deviation indicated by shading.

Discussion

Icelandic cod have not moved appreciably in response to increasing water temperatures during the last 100 years. As cod is an adaptable and tolerant species, capable of surviving and growing in a wide temperature range, it can easily tolerate fluctuations in environmental conditions (Righton *et al.*, 2010). Nevertheless, the $\delta^{18}O_{otolith}$ of our samples was significantly correlated with measured water temperatures, suggesting that cod were indeed exposed to water temperature variations over the past century and did not move to avoid it. Several studies support this conclusion. First, the critical annual mean bottom water temperature of 12°C limits the geographical distribution of cod globally (Dutil and Brander, 2003). However, the mean ambient temperature reconstructed for Icelandic cod is 4.8°C, well within physiological tolerances. Second, our finding that cod did not move is consistent with a previous study reporting that North Sea cod remained in warmer waters, which were suboptimal for growth, even though they were theoretically capable of finding colder waters (Neat and Righton, 2007). Northward distribution shifts of cod have been observed in other locations (Perry *et al.*, 2005) but never at an individual level. Shifts in overall cod distribution were actually through changes in recruitment or settlement, or were mistaken interpretations of changes in abundance and distribution of local substocks (Neat and Righton, 2007). Life in unfavourably warm waters is metabolically costly (Pörtner *et al.*, 2001), but biotic factors such as prey availability, density-dependent effects (Swain, 1999; Swain *et al.*, 2003), demographic changes (Ottersen *et al.*, 2006), and behaviour (Righton *et al.*, 2001) have been shown to be important drivers of habitat selection. Third, a previous analysis using fisheries data concluded that Icelandic cod did not shift their large-scale distribution in response to the most recent water temperature increase (Drinkwater, 2009). However, ambient individual temperatures provide a more accurate picture of individual fish movement in response to warming oceans than do aggregated measures such as stock dynamics. Fourth, the most recent temperature increase was limited to sea surface waters, but cod are mainly found in deeper waters, which did not exhibit rising temperatures (Pálsson and Thorsteinsson, 2003). Therefore, we conclude that Icelandic cod did not shift their location, either vertically or horizontally, to follow their preferred temperature range when water temperatures increased or fluctuated over the past 100 years.

Alternative explanations for the isotope-based variation in temperature exposure of Icelandic cod were rejected. Physical factors, such as gear selectivity, length-at-age, and migration patterns, were considered:

(i) Gear can be size selective, resulting in a systematic difference in size at age across fishing gears (Butler, 1992). However, gillnet samples were excluded from this study due to size selectivity and there were no visible differences in $\delta^{18}O_{otoliths}$ among the remaining gear types.

(ii) Since water temperature accounts for 90% of observed differences in growth rate in Atlantic cod across its global range (Drinkwater, 2005), long-term trends in growth rate could have affected the interpretation of the temperature reconstructions. However, length-at-age 8 in our samples

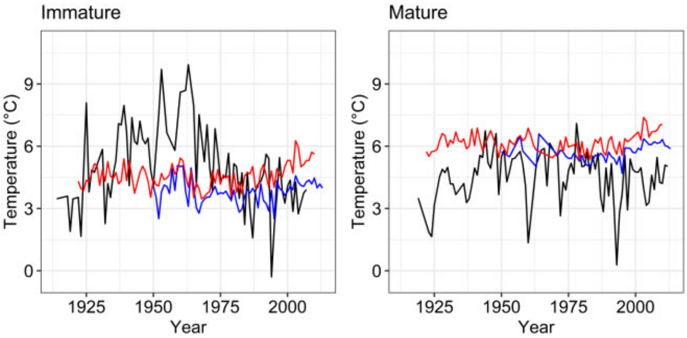

Figure 6. Reconstructed ambient water temperature of Icelandic cod (black), SST time series (red), and water temperatures at 200-m depth (blue). Temperatures for mature cod were adjusted for migration.

Table 5. Fixed and random effects estimates and s.e. of the optimal model for otolith δ^{18}O.

Models	**Life stages**			**SST**			***T* at 200 m**		
Fixed effects	**Estimate**	**s.e.**	***p***	**Estimate**	**s.e.**	***p***	**Estimate**	**s.e.**	***p***
Intercept	2.87	0.33	<0.001	2.01	0.10	<0.001	2.35	0.10	<0.001
Life stage	0.19	0.03	<0.001	–	–	–	–	–	–
Temperature	–	–	–	0.107	0.02	<0.001	0.056	0.02	<0.01
Random effects		**Fish ID**			**Fish ID**			**Fish ID**	
Residual variance σ^2		0.087			0.118			0.134	
Variance associated with tested effects τ_{00}		0.029			0.051			0.057	
ICC		0.301			0.301			0.302	
Number of observations		471			446			279	
Marginal/conditional r^2		0.338/0.504			0.062/0.346			0.019/0.311	

Residual variance (σ^2), the variance associated with the tested effects (τ_{00}), and their ICC are given. The lower number of observations for SST and water temperature at the 200-m model is explained by missing values in the relevant temperature timeline.
ICC, intraclass correlation coefficient.

did not vary significantly over time, so there was no correlation between ambient temperature and length-at-age.

(iii) Errors in the assumed migration pattern could have introduced artefacts into the assumed temperature field. Although cod are characterized by spatially structured stocks with highly individual migration behaviour (Pálsson and Thorsteinsson, 2003), we assumed the same migration pattern for the entire time series. A different migration pattern of Icelandic cod could imply higher salinity values, which, in turn, could result in higher ambient temperatures, but even when the highest oceanographically justifiable salinity value of 35.3 is assumed for mature cod until the year 1940, the ambient temperatures still diverge from the measured water temperatures by an average of 1.5°C (compared to an offset of 2.1°C when using the GLM-based salinity time series).

In summary, the significant correlation of $\delta^{18}O_{otolith}$ and water temperature time series cannot be explained by alternate physical factors.

Otolith growth rate varies over the year and is, therefore, another possible alternative explanation for the observed difference between reconstructed ambient and exposed temperatures. Seasonal variations in otolith growth rate result in the over- or underrepresentation of calcium carbonate accretion in certain months and can thus introduce artificial differences between the reconstructed annual mean temperature and the actual water temperature. We assumed a linear otolith growth across months of the year, but Icelandic waters are characterized by temperature seasonality. Since temperature influences the otolith accretion rate, the latter probably varies during the year resulting in non-linear otolith growth. For example, if 90% of the otolith growth occurred in the 6 months of summer (May–October), and the remaining 10% of the otolith accretion occurred in the 6 months of winter, our reconstructed ambient temperatures based on $\delta^{18}O_{otolith}$ would be higher than the mean annual water temperatures. To demonstrate the difference between non-linear and linear otolith growth rate, we examined temperature profiles from Vestmannæyjar in southern Iceland from 1999. The measured annual mean was 8.0°C (summer mean 9.3°C, winter mean 6.7°C), but the predicted ambient temperature assuming non-linear otolith growth over the year would be 9°C. This might explain why our reconstructed ambient temperatures for immature cod were higher than the SST and 200 m temperatures. However, ambient temperatures for mature cod were colder than both water temperature time series. Therefore, a non-linear accretion rate could explain the offset between our reconstructed ambient temperatures and the measured water temperatures for immature cod, but not for mature cod.

Temperature stratification with depth could explain the divergence in ambient and measured water temperatures in our study.

Ambient water temperatures of mature cod were lower than measured water temperatures at the beginning of the time series (until the 1940s) and again at the end (from the 1980s onwards). Cod are found in waters of up to 600-m depth around Iceland (Bardarson *et al.*, 2017). The offset between ambient and actual water temperatures in certain periods of the time series suggests that cod, at least temporarily, occupied waters $<$200 m, which are colder. The temperature stratification with depth varies locally and seasonally, with a differential of $\sim$2°C between 200 and 400 m and up to 5°C between 200 and 600 m, respectively (H. Valdimarsson, pers. comm.). Temperature stratification is lowest in winter but increases towards summer. Moreover, temperature stratification is higher in northern Iceland due to a more pronounced seasonality. Of all the alternate physical factors that were considered, deviations between observed and measured water temperatures of mature cod seem most likely to have been due to depth assumptions, whereas gear selectivity, length-at-age, migration patterns, and otolith growth rate effects were implausible.

Our study suggests that immature and mature cod might react differently to increasing water temperatures in the future due to differing thermal ranges. Life stage-dependent temperature exposure is indicated by the significant difference of $\delta^{18}O_{otolith}$ values between juvenile and adult cod and is consistent with previous studies (Astthorsson *et al.*, 1994). First, juveniles are known to inhabit higher temperatures than adult cod (Lafrance *et al.*, 2005). Immature cod can inhabit water masses up to 20°C (Brander, 1997), whereas the preferred water temperature for spawning is between 1 and 8°C (Righton *et al.*, 2010). Second, the thermal window width of cod varies between different life stages, with a broader thermal window for juveniles, which are thus more tolerant of temperature shifts (Pörtner and Peck, 2010; Righton *et al.*, 2010). Off the Eastern Scotian Shelf, juvenile cod experienced a wider temperature range than mature cod (Jones and Campana, 2009). Early ontogenetic stages and spawners, in turn, are more sensitive to changing temperatures as they have the narrowest thermal window width. To compensate for temperature fluctuations and to maintain their optimum temperature range of 2–8°C, mature cod often migrate along routes of preferred ambient temperatures (Mountain and Murawski, 1992; Rose, 1993; Begg and Marteinsdottir, 2002b).

This study used $\delta^{18}O_{otolith}$ to build a century-long temperature chronology for Atlantic cod around Iceland and would be expected to increase our understanding and knowledge of the response of cod (and their fisheries) to rising water temperatures. Use of a cod-specific $\delta^{18}O$ fractionation temperature equation and a geographically specific salinity mixing curve (which provides an accurate correction for seawater isotope composition) limits the uncertainties around the temperature exposure estimates for cod. However, accurate temperature reconstructions require both local salinity mixing curves and a salinity time series. In our study, long-term salinity time series were not available prior to 1950; consequently, salinity models were used instead, which could have introduced some error. Nevertheless, wrongly assumed salinity values and alternative migration patterns were not a likely explanation for the observed temperature exposure variations in the cod. The absolute reconstructed ambient water temperatures varied only slightly when different salinity values were assumed, but the trend over time (and the conclusions) remained unchanged. The reconstructed ambient temperatures for each year are more variable than temperature itself. This does not imply that one fish experienced such variable temperatures but shows that Icelandic cod are exposed to variable water temperatures depending if they are found near- or offshore and their depth range, but data storage tags have shown that Icelandic cod are exposed to high temperature variations of up to 10°C within 1 year due to seasonal variations and thermal stratification of the seawater.

To our knowledge, this is the first study to present such a long temperature chronology for any fish species. Data storage tags are now giving detailed insights into temperature habitat (e.g. Bardarson *et al.*, 2017) but were developed too recently to provide any long-term perspective. The advantage of data storage tags is that depth and temperature are recorded several times a day, whereas otolith-based reconstructions are annual means. Our understanding of the response of cod to rising water temperatures could be further improved by increasing the temporal sampling resolution. However, subannual sampling was not possible in this study due to the weight requirement of the IRMS. With the advent of ion microprobe-based isotope assays, future temperature reconstructions could well offer seasonal or even monthly resolution (e.g. Matta *et al.*, 2013).

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Paper II

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Temperature selectivity in cod driven by changes in abundance

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Temperature selectivity in cod driven by changes in abundance

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Abstract

Animals actively select the most suitable habitat in terms of fitness, much of which is mediated by temperature. We reconstructed population abundance, oxygen isotope and temperature chronologies for the Icelandic and the Northeast Arctic (NEA) cod populations to determine if their temperature selectivity over the last 100 years was driven by rising water temperatures and/ or changes in abundance. Individual annual growth increments from immature and mature life history stages of cod collected in southern Iceland and the Lofoten area (Norway) were micromilled from adult otoliths and then assayed for stable oxygen isotopes ($\delta^{18}O_{otolith}$). Linear mixed effect models were used to identify and quantify the density-dependent temperature selectivity of both cod populations. The results indicated that Icelandic cod migrated into warmer waters with increasing abundance ($p < 0.05$), whereas NEA cod moved into colder waters ($p < 0.001$). Global warming effects on fish can be used to forecast potential re-distribution scenarios as oceans warm, making them important tools for sustainable management plans.

Keywords: ambient temperature, Atlantic cod, temperature selectivity, stable oxygen isotopes, population dynamics

1 Introduction

Habitat suitability is defined by a set of abiotic and biotic factors which determine the geographical distribution of organisms. Animals have a range of habitats which they can tolerate, but they actively select among habitats to maximize their evolutionary fitness (Swain and Wade, 1993, Fretwell and Lucas, 1970). Food availability, predator abundance, terrestrial humidity, pH, salinity and temperature, or any combination thereof, may all differ among habitats. Temperature is one aspect of habitat selection which directly affects the physiology of organisms through regulation of chemical reactions and the physical properties of water (Reynolds and Casterlin, 1980, Cossins, 2012). Hence, every organism has a temperature tolerance range, but there is also an optimum temperature which is most favourable in terms of individual's lifetime reproductive success which is used as a proxy for estimating fitness. Not surprisingly, temperature is also the most important abiotic factor influencing fish population dynamics (Myers et al., 2001). When temperature conditions change, organisms either acclimate to the new conditions, or avoid or minimize the impact of the temperature change through thermoregulatory movement (Reynolds and Casterlin, 1980, Angilletta et al., 2002). When temperature increases, fish can migrate to colder waters, usually poleward or into deeper waters to remain in their preferred temperature regime. In doing so however, they also move away from otherwise favourable conditions, such as their main spawning ground, and their feeding grounds may change due to temporal and/or spatial prey-predator mismatches (Brander, 2005, Durant et al., 2007). Alternatively, they could acclimate to the new temperature regime, which is metabolically costly (Pörtner et al., 2001). Global warming has already forced many taxa of marine aquatic and terrestrial organisms to move outside their previous distribution area (IPCC, 2013). While terrestrial organisms often have physical boundaries, marine fish are often limited by their physiological thermal tolerance (Comte and Olden, 2017).

Changes in temperature selectivity - the temperature organisms actively select - can be driven by changes in environmental temperature (Gibson, 1994), population or prey density (e.g. food resources (Swain and Kramer, 1995)) or an interaction of both (Ottersen et al., 1998). When population density increases due to naturally varying environmental conditions and/ or anthropogenic impact, temperature selectivity decreases as a response to the associated increase in intraspecific competition and the decreasing relative reproductive success between individuals. Thus, the distribution area expands into habitats previously considered outside the optimal thermal range, which have now become attractive due to reduced competition relative to the former habitat (Swain and Wade, 1993, Laurel et al., 2007). For example, cod in the southern Gulf of St. Lawrence tend to occupy colder water in years of high abundance, possibly to reduce competition for food (Swain and Kramer, 1995). Distributional range shifts have often been observed in both terrestrial and aquatic organisms in response to rising atmospheric and water temperatures, respectively.

Despite overexploitation, significant declines in population biomass, and in some cases fisheries collapse (Worm et al., 2006, Hutchings, 2005, Hutchings and Myers, 1994, Rose, 2004), Atlantic cod (*Gadus morhua*) is still one of the most important commercial species in the North Atlantic Ocean. For most parts of the last century, marked declines in abundance and fluctuating recruitment have been observed for the two largest cod populations in the Northeast Atlantic, Icelandic and Northeast Arctic (NEA) cod (Myers et al., 2001, Myers et al., 1997). In recent years, both cod populations have increased again. The spawning stock biomass of NEA cod was at a record high in 2013 and is still high (Kjesbu et al., 2014). The broad geographical distribution of cod implies a wide temperature range from below -1°C up to 20°C with a critical annual mean bottom water temperature of 12°C, which is the maximum temperature cod can tolerate over an extended period (Myers et al., 1997, Drinkwater, 2005, Woodhead and Woodhead, 1965, Mehl et al., 1985). Juvenile cod can inhabit water masses at the upper thermal range, while spawners and embryos have a narrower thermal window and are more vulnerable to temperature changes (Brander, 1997, Pörtner and Peck, 2010, Dahlke et al., 2020). The geographical distribution of cod is also limited by depth. Cod can be found in depths of 600 m, sometimes even 850 m, but also in shallower waters which are characterized by wider temperature ranges (Bardarson et al., 2017). Southern cod populations which are confined to relatively shallow waters (< 100 m) experience temperature changes of up to 10°C within one day, whereas cod in deeper, northern ecosystems have smaller average temperature fluctuations per day (Righton et al., 2010). Cod populations are expected to react differently to future global warming depending on their current position within the species' thermal range. At temperatures above their thermal range, cod must either move into colder water masses or die as opposed to cod populations at the lower range which will probably benefit from rising water temperatures (Drinkwater, 2005, Dutil and Brander, 2003).

Otoliths (ear stones) can be found in all teleost fish and are paired calcified structures used for balance and/ or hearing (Campana, 1999). Coupled with age or date of capture they provide chronological records which can be used to reconstruct the entire life or temperature history of the individual fish, since they grow continuously from hatching to death (Campana and Thorrold, 2001). Analogous to tree rings, each individual otolith annulus (annual growth increment) can be assigned an age of formation as well as a calendar year of formation (Jensen, 1970). Otoliths are metabolically inert and composed from aragonitic calcium carbonate in a non-collagenous organic matrix. The oxygen isotope values of calcium carbonate in otoliths reflect those of the water, from which the oxygen is sourced, but with a temperature dependent offset (fractionation) (Campana, 1999). The change in ^{18}O of otolith aragonite is negatively correlated to the ambient water temperature of the fish; the higher the water temperature, the lower the $\delta^{18}O_{otolith}$ value (Kim and O'Neil, 1997). Thus, the mean ambient water temperature can be calculated, when the isotopic composition of the seawater is also known (e.g. Jones and Campana (2009)). The ambient temperature experienced by moving fish might differ from the environmental temperature, which is the temperature at fixed locations recorded by instrumental water temperature time series. Sea-surface temperature time series began in the early 20th century, while temperature-at-depth time series only began in the mid-20th century.

In this study, we used two extensive collections of cod otoliths to build century-long ambient temperature chronologies for both the Icelandic and NEA cod populations. Mixed effect models were then used to identify and quantify the density-dependent temperature selectivity of cod. We would predict that the stable oxygen isotope time series should have changed over the last 100 years if abundance significantly impacted the temperature exposure of Icelandic and NEA cod. However, water temperatures around Iceland and in the Norwegian and Barents Sea alternated between warm and cold periods over the last century and could also have impacted the ambient water temperature of cod. Although von Leesen et al. (2020) investigated the ambient temperature of Icelandic cod in response to the physical environment, the influence of stock dynamics remained unexplored. The current study expands the scope of the investigation to include both temperature effects and stock dynamics, both in Iceland and for the NEA cod stock. Despite certain similarities in population dynamics, we did not necessarily expect the same response in both populations. Icelandic cod is defined as a cold-water population (Drinkwater, 2005), but its current mean bottom water temperature is close to the tipping point of being classified as a warm-water population which would be negatively impacted by global warming, whereas the ambient temperature of NEA cod is lower and will probably benefit from rising water temperatures. Hence, the response of Icelandic and NEA cod to rising water temperatures and increasing abundance would be expected to differ.

2 Material and methods

Details on the sample selection and ambient temperature reconstruction of Icelandic cod have previously been described (von Leesen et al., 2020). In brief, Icelandic otoliths (n=238 from the years 1929 to 2015) were sampled from the main spawning grounds in the south off Iceland. Ambient temperatures of Icelandic cod were reconstructed assuming a spawning migration from the main feeding ground off northwest Iceland to the warmer spawning ground in the south where mature cod were found from January until June. Sample selection, stable oxygen isotope assays and temperature reconstruction were otherwise similar to what is described below for NEA cod.

2.1 Sampling of Norwegian otoliths

Archived cod otoliths (n=219 from the years 1933 to 2015) which were stored dry in envelopes were accessed from the Institute of Marine Research in Bergen, Norway (Table 1). The fish represented by the otoliths were caught on the main spawning ground in the Lofoten region of western Norway (Fig. 1) and were selected based on gear type. A preliminary analysis showed a potential selectivity bias of gillnets towards bigger, faster-growing fish, thus the otolith selection was limited to bottom trawl, longline and seine samples. Due to missing otoliths in the archive, no samples were collected in 1965, 1966, 1980, 1981, 1983, 1984, 1986 and 1989. When possible, we collected three otoliths with a minimum fish age of 10 years for each calendar year of sampling between 1933 and 2015. Just four otoliths with a fish age of 9 years were collected.

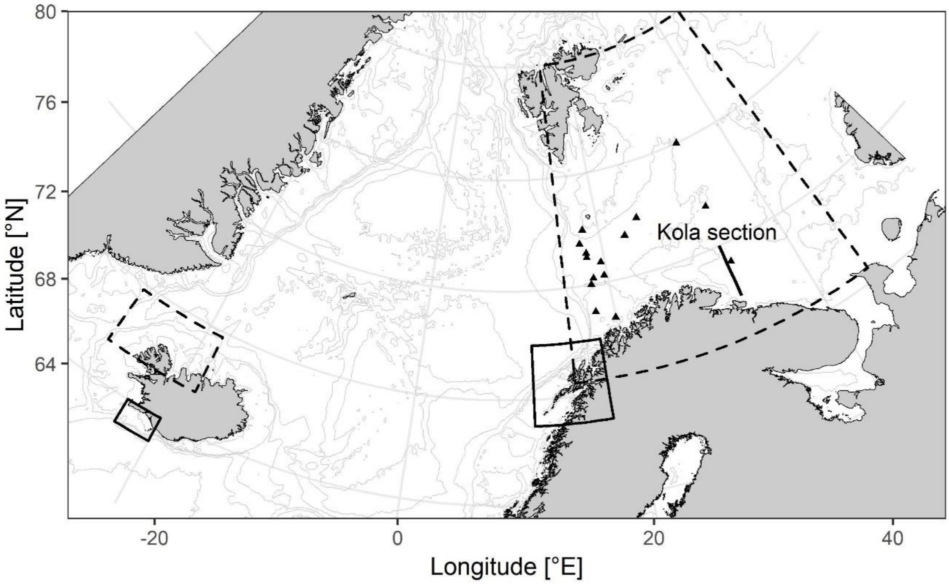

Figure 1: Sampling locations of otoliths on the main spawning grounds (solid line) in southern Iceland and western Norway (Lofoten). Feeding grounds (dashed line) in northern Iceland and the Barents Sea and locations of $\delta^{18}O_{seawater}$ *and salinity samples for the Norwegian salinity mixing curve (triangles). The line represents the Kola transect of in situ water temperature and salinity measurements.*

Table 1: Northeast Arctic cod. Otolith samples collected per gear-type aggregated by 5-year blocks. All samples were caught in the Lofoten area between February and April 1933-2015; some otoliths were sampled in January (n=2), May (n=3) and October (n=1).

	Gear-types						
Years	Bottom trawl	Handline	Longline	Shrimp trawl	Purse seine	Seine	Floating trawl
1933-1934	-	-	6	-	-	-	-
1935-1939	-	-	15	-	-	-	-
1940-1944	-	-	15	-	-	-	-
1945-1949	-	-	15	-	-	-	-
1950-1954	-	1	12	-	2	-	-
1955-1959	-	-	15	-	-	-	-
1960-1964	-	-	10	-	5	-	-
1965-1969	-	1	5	-	2	1	-
1970-1974	-	-	9	-	6	-	-
1975-1979	-	-	9	-	4	2	-
1980-1984	-	-	3	-	-	-	-
1985-1989	-	-	2	-	2	3	2
1990-1994	-	1	7	7	-	-	-
1995-1999	-	-	9	1	-	5	-
2000-2004	1	1	8	2	-	2	1
2005-2009	-	-	4	4	-	5	1
2010-2015	-	1	2	10	-	2	2

To avoid otolith breakage during preparation, otoliths were embedded in epoxy and then sectioned transversely through the core using a Buehler IsoMet 1000 Precision Saw (ITW Test & Measurement GmbH, Esslingen, Germany) equipped with a 15LC IsoMet Diamond Wafering blade to get otolith sections of ~1 mm thickness. Silicone EPDM (silicone combined with a synthetic rubber) molds, Polylite 32032-20 resin and hardener Narpol Peroxide 1 Methyl Ethyl Ketone Peroxide were used for embedding. Otolith sections were imaged prior to milling with an Olympus DP 74 high resolution (5760x3600 pixels (3 CMOS)) camera mounted on a Leica S8AP0 stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany) using CellSens Standard software (Olympus Europa SE & Co. KG, Hamburg, Germany). Images were processed with Adobe Photoshop CS2 (Version 9.0) and aged along the distal axis of growth.

For stable oxygen isotope analysis, a micro-milling approach was used to extract otolith material. Otolith sections were glued on glass slides using Krazy Glue or Super Glue Liquid Control. Sample vials were decontaminated by rinsing with Milli-Q water (Millipore, Merck KGaA, Darmstadt, Germany) and then air-dried. A high-precision, computer-controlled Merchantek New Wave MicroMill (Elemental Scientific, Omaha, Nebraska, USA) equipped with a Leica GZ6 camera (Komet/Gebr. Brassler GmbH & Co. KG, Lemgo, Germany) and a 360 µm drill bit was used to mill two samples of carbonate powder from each otolith; age 3 representing the immature life stage of cod, and age 8 representing the mature cod. In general, the 3rd and 8th annuli from the fish of age 10 were micromilled but in years where 10-yr old fish were not available, fish of age 9 were collected and age 3 and age 7 sampled, respectively. We did not sample close to the edge so as to prevent any contamination of the calcium carbonate sample with epoxy. To maximize the weight of milled material the drill path was offset by the radius (180 µm) of the drill bit. A "discharge" scan was run to remove some coarse material next to the year of interest to prevent any contamination of the actual sample material. To prevent contamination between samples, the otolith section, drill bit and sampling tweezers were cleaned with compressed air and ethanol between samples. The samples were drilled up to 750 µm depth (20-25 passes with a drill depth of 30 µm/pass) which was usually adequate to collect the intended 50 µg of sample material. A minimum of 15 µm was required by the isotope-ratio mass spectrometer (IRMS).

Measurements of calcium carbonate samples for oxygen isotope content were conducted at FARLAB at the Department of Earth Sciences, University of Bergen, Norway. Otolith carbonate was transferred to glass vials and reacted with an automated Keil IV carbonate device and analyzed using a coupled MAT 253 mass spectrometer. The long-term reproducibility (or 1-sigma precision) of the mass spectrometer was ≤ 0.8‰ and ≤ 0.4‰ for $\delta^{18}O$ and $\delta^{13}C$, respectively for sample sizes greater than 13 micrograms based on replicate measurements of an internal carbonate standard run in parallel with the samples over a period of months. Isotope values are reported on the VPDB scale calibrated using NBS-19 and NBS-18.

There was no evidence of epoxy contamination on the $\delta^{13}C$ and $\delta^{18}O$ values. As a test for contamination, epoxy samples were added to in-house marble standards. Within the standard 2-sigma uncertainty of replicates, none of the samples containing epoxy were isotopically distinct from the samples without epoxy (in addition, five of six samples were within 1-sigma of the mean).

2.2 Salinity and water temperature

Details on the Icelandic salinity mixing curve, salinity and measured water temperature time series, and the reconstruction of ambient temperature of the Icelandic cod are described in von Leesen et al. (2020). In brief, a salinity mixing curve was constructed for the continental shelf around Iceland using measured salinity and $\delta^{18}O_{seawater}$ data. Annual salinity and measured water temperature time series (SST: 1922 - 2010; temperature at 200 m depth: 1950 - 2015) were reconstructed for the south and north off Iceland using general linear models (GLM). As was done for Norway, modelled salinity values from 1900 onwards were derived from the Hadley Centre subsurface temperature and salinity objective analyses I09 v4.2.1 dataset ((Good et al., 2013); depth range: 50-200 m).

The ambient temperature reconstruction of the Norwegian samples followed an approach similar to that used for Iceland. As $\delta^{18}O_{seawater}$ is needed for the reconstruction of ambient temperatures from carbonate samples but was not available for the years represented by our samples, we estimated $\delta^{18}O_{seawater}$ values from salinity using a salinity mixing curve for the Barents Sea. Salinity and $\delta^{18}O_{seawater}$ data were derived from NASA GISS Global Seawater Oxygen-18 Database (Schmidt et al., 1999) and Laukert et al. (2019). The salinity mixing curve describes the relationship between $\delta^{18}O_{seawater}$ and salinity for the Barents Sea at depths between 50 and 400 m, the typical depth range of NEA cod. A simple linear regression through these points produced the following salinity mixing line (Fig. 2):

$$\delta^{18}O_{seawater} = 0.37 \times S - 12.46 \tag{1}$$

where $\delta^{18}O_{seawater}$ is the oxygen isotope content (‰ on the SMOW scale) of seawater and S is salinity (n=62, R^2=0.2, intercept and salinity: $p < 0.001$). The Barents Sea is a highly dynamic region with multiple water masses mixing (Laukert et al., 2019), and the influence of sea ice alters the $\delta^{18}O_{seawater}$ – salinity relationship due to its impact on the salinity with much smaller fractionation of $\delta^{18}O$ during freezing (Toyota et al., 2013) than during evaporation and precipitation related to freshwater fluxes (Craig and Gordon, 1965). Thus, while sea ice influences salinity, it has little influence on the $\delta^{18}O_{seawater}$ that cod experienced, and thus the sea ice related spread of salinity has only minor influence on $\delta^{18}O_{otolith}$ values. Measurements performed in 1980 (Östlund and Hut, 1984) and 1995 (Risebrobakken et al., 2003) contribute to the high variance. Although there is no obvious reason to exclude these data points, the following salinity mixing line was produced after the exclusion of the data points by Risebrobakken et al. (2003):

$$\delta^{18}O_{seawater} = 0.34 \times S - 11.47 \tag{2}$$

(n=38, R^2=0.3, intercept and salinity: $p < 0.001$).

The remaining variance of about 0.3‰ at high salinities is caused by measurements reported by Östlund and Hut (1984). An alternative salinity mixing line without these data points was built for an error analysis:

$$\delta^{18}O_{seawater} = 0.26 \times S - 8.64 \tag{3}$$

(n=32, R^2=0.83, intercept and salinity: $p < 0.001$).

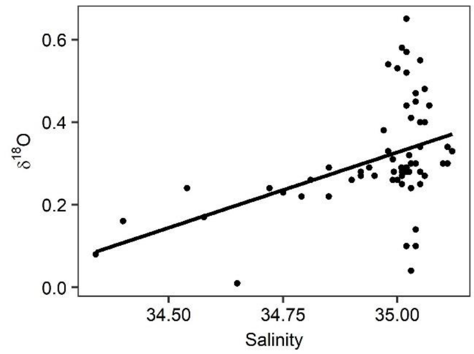

Figure 2: Salinity mixing curve for the Barents Sea between 50 and 400 m depth.

Standardized salinity time series for the Lofoten and the Kola section (Barents Sea) were reconstructed using GLMs to account for salinity differences between time (month, year), depth, and stations (Fig. 3). Measured salinity time series for Eggum and Skrova, representing the Lofoten, started in 1935 (depth range: 50 – 150 m, data downloaded from http://www.imr.no/forskning/forskningsdata/stasjoner/view/initdownload on 12 November 2019). The Kola section represents the hydrology of the Barents Sea (Tereshchenko, 1996) and provides unique long-term salinity temperature time series from 1951 onwards which are not available for any other part of the Barents Sea (depth range: 0 – 200 m, data downloaded from http://www.pinro.ru/labs/hid/kolsec22.php?lang=e on 12 November 2019).

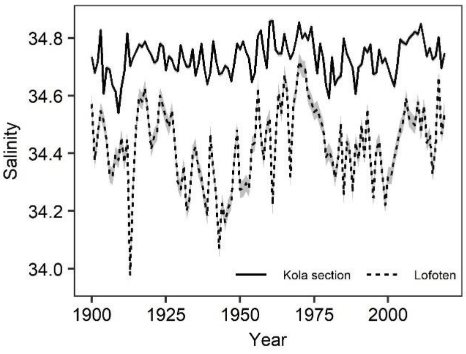

Figure 3: Modelled salinity time series for the Lofoten (depth range: 50 – 150 m) and the Kola section (depth range: 50 – 200 m). Standard deviation indicated by shading. Hadley EN4.2.1 analyses I09 data downloaded from APDRC LAS7 for public.

Instrumental salinity measurements started in 1935/1951 and thus did not cover the entire time period of the stable oxygen isotope chronology. Therefore, we decided to use the modelled salinity timeline for the entire time period to avoid potential influences (bias) related to change in the data source when comparing the two time windows. Modelled salinity values from 1900 onwards were derived from the Hadley Centre subsurface temperature and salinity objective analyses l09 v4.2.1 dataset (Good et al. (2013); version EN4.2.1; downloaded from http://apdrc.soest.hawaii.edu on 3 December 2019). Measured and modelled salinity time series for both areas were statistically compared to justify the use of the modelled values. Modelled values for the Barents Sea were highly correlated with measured salinity data from the Kola section (depth range: 0 – 200 m; $R^2=0.8$, $p < 0.001$). The mean salinity difference between the measured and modelled salinity time series of the Kola section was only 0.05. Modelled and measured salinity time series of the Lofoten were more weakly correlated ($R^2=0.3$, $p < 0.01$). The Lofoten area is an archipelago and both oceanographic stations, Eggum (68.3°N, 13.7°E) and Skrova (68.2°N, 14.7°E), are located near the shore and were compared with two near-by locations from the Hadley model (68°N, 14°E and 68°N, 15°E). The offset between both salinity time series was up to 0.4. Freshwater run off along the shore probably explains lower measured salinity values which are not reflected in the modelled data as they cover a bigger area (grid size 1° x 1°) and thus do not catch local salinity fluctuations.

Salinity values used for ambient temperature reconstruction of cod migrating to the spawning grounds need to account for the months spent in different areas. Spawning-NEA cod migrate between the Lofoten and the Barents Sea (Bergstad et al., 1987, Kjesbu et al., 2014). The spawning period of NEA cod in the Lofoten is typically in March and April (Ellertsen et al., 1989), but the spawning migration starts as early as December. The timing of the annual migration has not changed significantly during the studied time period, although the feeding grounds in the Barents Sea expanded northward when the NEA cod population started to increase in 2007 (Kjesbu et al., 2014). The spawning population is known to leave the main spawning ground immediately after spawning and has been recorded on the feeding grounds in the Barents Sea from May onwards (Bergstad et al., 1987). Therefore, the salinity time series for spawning cod integrated salinity values from the Lofoten for March and April and from the Barents Sea for the remaining time of the year. Swimming back and forth to the spawning ground takes one to two months, but the migration is mainly through the waters of the Barents Sea. As cod usually return to the place of first spawning (Godø and Sunnanå, 1984), we assumed that our sampled cod spawned in the Lofoten. Immature and non-spawning mature cod are found in the Barents Sea all year around.

As was done with the salinity time series, standardized sea surface (SST; depth <50m) and water temperature time series at 0 to 200 m depth representative of NEA cod in the Lofoten area were reconstructed with GLMs to account for differences across month, year, depth and station. Due to limited data availability, the standardized temperature time series for the Kola section was reconstructed using only month and year as factors (temperature data was downloaded from http://www.pinro.ru/labs/hid/kolsec22.php?lang=e). Predicted water temperatures were matched with the measured stable oxygen isotope value by year and spawning activity.

2.3 Temperature reconstruction – NEA cod

Ambient water temperatures were reconstructed from otolith carbonate using the equation of Jones and Campana (2009) (adapted from Kim and O'Neil (1997)) :

$$T\ (°C) = -\ (\delta^{18}O_{otolith} - \delta^{18}O_{seawater})\ x\ 0.206^{-1} + 18.010 \qquad (4)$$

where $\delta^{18}O_{otolith}$ is the oxygen isotope composition of the otolith aragonite and $\delta^{18}O_{seawater}$ is the oxygen isotope composition of the ambient seawater. All isotope values for $\delta^{18}O$ (and $\delta^{13}C$) otolith carbonate are reported in ‰ on VPDB scale. Seawater values were corrected from SMOW (standard mean ocean water) by subtracting 0.27‰ (Grossman, 2012, Bemis et al., 1998, Marchitto et al., 2014).

Icelandic and NEA cod spawners both migrate annually into warmer waters for spawning. Year-specific salinity values were used to back-calculate the $\delta^{18}O_{seawater}$ values which were needed for ambient temperature reconstructions. These were based on the spawning age, which is routinely determined for NEA cod by otolith readers based on the number of spawning checks (Rollefsen, 1933, Folkvord et al., 2014, Irgens et al., 2019). When an age 9+ fish had not spawned by age 8, the sample was considered a non-spawner which did not migrate to the Lofoten. Samples of age 3 were always defined as non-spawners. Median age at maturity declined from 10.5 to 8 years from 1923 to 1976 (Rollefsen, 1953, Jørgensen, 1990) and further declined to 6.8 years in the 2010s. Maturity-at-age data for both populations were derived from the population assessment models and the mean maturity-at-age for each decade and population were calculated (ICES, 2018, ICES, 2020).

2.4 Population dynamics

2.4.1 NEA cod

During the last 100 years, the population of NEA cod underwent major fluctuations with an overall decline in population size. In recent years, the population size increased again (Fig. 5). Abundance at age 3 tended to be higher prior to 1970 in each population compared to afterwards. The official stock dynamics time series used by ICES/ Arctic Fisheries Working Group starts in 1946 and some changes were applied in order to make the pre-1946 series (virtual population analysis (VPA) back to 1913 reconstructed by Hylen (2002)) consistent with the present series used in the assessment from 1946 onwards (ICES, 2020), as some revisions have been made to the time series since 2002.

The changes were as follows: Natural mortality for ages 3-5 for the years from 1946 onwards has recently been updated, based on available data for cod cannibalism (Yaragina et al., 2018). Natural mortality for the years prior to 1946 was in these calculations set to the 1946-1983 average, i.e., 0.410 for age 3, 0.274 for age 4 and 0.219 for age 5. Number at age in 1946 was taken from the most recent assessment (ICES, 2020). Number at age in previous years was calculated using Pope’s approximation. For the years prior to 1946 terminal N values by year for the oldest true age group (14) were the same as used by Hylen (2002), and the F for the plus group (15+) was set equal to that of the oldest true age group. Weight and maturity were unchanged.

2.4.2 Icelandic cod

The abundance of age 3 Icelandic cod was relatively constant over the period 1928 to the 1980s, abruptly declined in the 1980s with potentially some minor increase in recent years (Fig. 5). Abundance of age 8 declined until the 1990s with some increase in the past 20 years. The reconstruction of the stock dynamics of the Icelandic cod stock was based on combining the catch at age (age 3-14) matrix for years 1928-1954 (Schopka, 1994) and 1955-2017 (ICES 2019). The assessment model used was a statistical catch-at-age model with constant selectivity assumption for 6 periods (years 1928-1937, 1938-1949, 1950-1975, 1976-1993, 1994-2003, 2004-2017). Immigration was estimated for the following years and ages: 1930-8, 1933-9, 1953-8, 1958-9, 1959-9, 1960-10, 1962-9, 1964-10, 1969-8, 1970-8, 1972-9, 1980-7, 1981-8, 1990-6 and 2009-6. The estimates of the year and age of immigration after 1955 is the same as in NWWG 2019, while the three immigration prior to 1955 are only estimated for superabundant cohorts (1922, 1924 and 1945), the year and the age of the immigration based on anomalies in the catch at age information. The immigration of the 1922 and 1924 year also supported by tagging studies by Hansen et al. (1935). The natural mortality was scaled to 0.2 for all age groups.

2.5 Linear mixed effect modelling – Iceland and Norway

Linear mixed effect models were fitted to model the oxygen isotope content of cod and to account for the repeated measurements within the same individual (two life stages measured within the same otolith) (Zuur et al., 2009). A random intercept for individual fish was included in order to correct model estimates for differences between fish.

A linear mixed effect model with life stage as a factor variable with two levels (immature and mature), and abundance at age and water temperature at 0 - 200 m depth as covariates was built to explain the temperature exposure of NEA cod. In order to meet model assumptions, abundance at age data of NEA cod were scaled to mean-life stage abundance by dividing the observed abundance by the mean abundance of immature and mature cod, respectively. For Iceland, abundance at age and temperature at 200 m depth were treated as covariates. For both populations, a random intercept for individual fish was included in order to correct model estimates for differences between fish. Due to limited data availability, the water temperature time series around Iceland started in 1950 which resulted in a smaller sample size for the linear mixed effect model (n=279). Yearclass strength at age 3 (as a proxy for productivity) did not have a significant effect on either population models.

Mixed models with different levels of complexity were compared using the Akaike information criterion corrected (AICc) for the small sample sizes. The first step of analysis involved selection of the optimal random effect structure. Secondly, the optimal fixed effect structure was selected by comparison of models fitted using maximum likelihood and the previously identified random structure. Alternative models were again compared using AICc and the best-ranked model was refitted with REML allowing unbiased model estimates (Zuur et al., 2009). Assumptions of the final model were checked and satisfied with standard diagnostics. Interclass correlation was calculated in order to assess the level of consistency between-individual and between-year differences in otolith trait values. The conditional and marginal R^2 metric was calculated for all models to assess the variance in otolith traits accounted for both fixed and random effects.

Statistical analysis and graphical outputs were produced using R 3.6.0 (R Core Team 2019).

3 Results

3.1 Environmental conditions – Iceland and Norway

Salinity was higher in the Kola section than in the Lofoten area with more pronounced year-to-year fluctuations in the Lofoten area. Temperature patterns were similar in both regions with colder temperatures measured in the Kola section than in the Lofoten area (Fig. 4). The Barents Sea was subject to marked temperature fluctuations during the last century (Boitsov et al., 2012). Until the late 1920s the Barents Sea was characterized by cold water and air temperatures, and high ice coverage, followed by a period of warmer waters until 1961. From 1962 onwards the Barents Sea was relatively cold again until the most recent warming of air and water masses which began in the late 1980s.

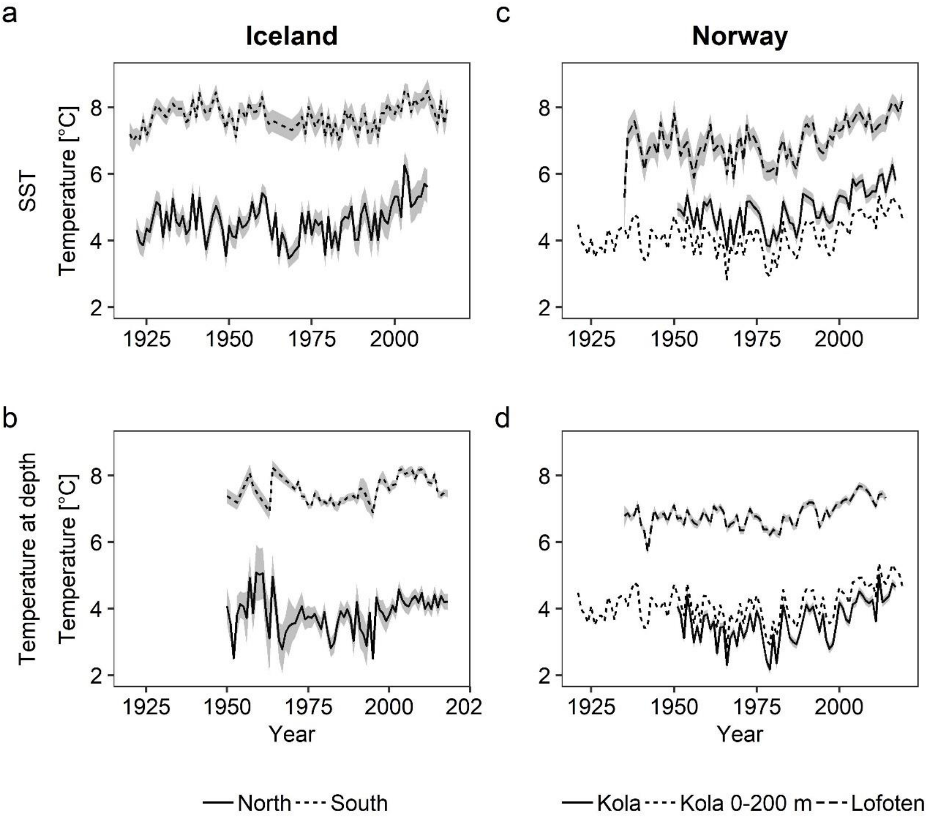

Figure 4: SST and water temperature at 150 m (Norway) / 200 m (Iceland) depth at the main spawning grounds of Iceland (South) and in the Lofoten along the west coast of Norway. Temperature time series were also estimated for northern Iceland and in the Kola section (150 – 200 m and 0- 200 m) in the Barents Sea. For Norway, the averaged water temperature of the Kola section between 0 – 200 m is shown to compare it with (c) SST and (d) temperature at depth data. Water temperatures at 0 – 200 m were lower than SST, but higher than temperatures at 150 – 200 m depth. Standard deviation is indicated by shading.

Icelandic waters were characterized by two warming events in the last century (Jakobsson and Stefánsson, 1998, Malmberg and Valdimarsson, 2003) (Fig. 4). Natural variation caused the first warming event which started in the 1920s and temperatures remained high until cooling started in the 1960s. The second warming event started in the 1990s due to the increasing release of greenhouse gases in the atmosphere (Hanna et al., 2006). Salinity was higher in southern Iceland than in the north. Water temperatures were higher in the main spawning grounds of southern Iceland and colder in the main feeding grounds of northern Iceland. Polar water in the north originates from the Arctic Ocean as the East Greenland Current entering with a salinity < 34.5 and a temperature of ≤ 0°C. The warm and saline Atlantic water along the south coast is a branch of the Gulf Stream. This water mass flows westwards as the Irminger Current and eventually northwards, where the water cools down, and the salinity decreases. Water temperatures off southern and northern Iceland showed a similar temporal trend with more pronounced warming in the north. The difference between SST and water temperatures at 200 m depth is greater in the north than in the south, where the seawater forms a homogenous and thick layer extending to several hundred meters depth (Jónsson, 1999, Malmberg and Valdimarsson, 2003).

The observed low-frequency variability in air and sea temperatures and sea ice in the northern North Atlantic is consistent with the Atlantic Multidecadal Oscillation (AMO) (Drinkwater et al., 2014). Temperature variability in the Barents Sea is linked to the strength and thermohaline conditions of the Atlantic water inflow. The 2.5-3°C difference in water temperatures in the Barents Sea between the last cold water period (1978-1982) and the most recent warming period (since 2002) can be explained by the multidecadal variability (Levitus et al., 2009). The water temperature increase of 2.5-3°C is well in line with observations for the Kola section.

3.2 Otolith isotopes and ambient temperature reconstruction

The NEA cod temperature reconstruction based on otolith oxygen isotopes showed a gradual increase over almost an entire century (Fig. 5). The assayed increments had a mean $\delta^{18}O_{otolith}$ of 3.17‰ (2.12-3.91‰), with the mean for immature cod being 3.22‰ (2.12-3.91‰) and that for mature cod was 3.12‰ (2.32-3.68‰). The mean for non-spawners (immature and non-spawning mature cod) was 3.21‰ (2.19-3.91‰) while that for spawners was 3.07‰ (2.12-3.68‰). The sample size of non-spawners was higher than for spawners as the proportion of mature cod at age 8 was just 0.03 in 1933. There was a clear trend towards decreasing age at first maturity in NEA cod (our data and Bergstad et al. (1987)). The proportion increased to 0.7 in 2015 with year-to-year variations ranging from 0.02 to 0.94 (Fig. S1).

Oxygen isotopes of Icelandic cod otolith annuli had a mean $\delta^{18}O_{otolith}$ of 2.60‰ (1.06-4.02‰); the mean $\delta^{18}O_{otolith}$ for immature cod was 2.51‰ (1.06-3.61‰), while that for mature cod was 2.68‰ (1.44-4.02‰) (von Leesen et al., 2020). As expected from the paleotemperature equation (equation 2), the change in ^{18}O of otolith aragonite was negatively correlated to the water temperature; the higher the water temperature, the lower the $\delta^{18}O_{otolith}$ value. Age at 50% maturity is 5.9 years for cod from southern Iceland and 6.6 years for cod from northern Iceland throughout the period from 1985 to 1999 (Marteinsdottir and Begg, 2002). The proportion of mature cod at age 8 increased from 0.82 in 1928 to 0.91 in 2018 with year-to-year variations ranging from 0.53 to 0.92 (Fig. S1).

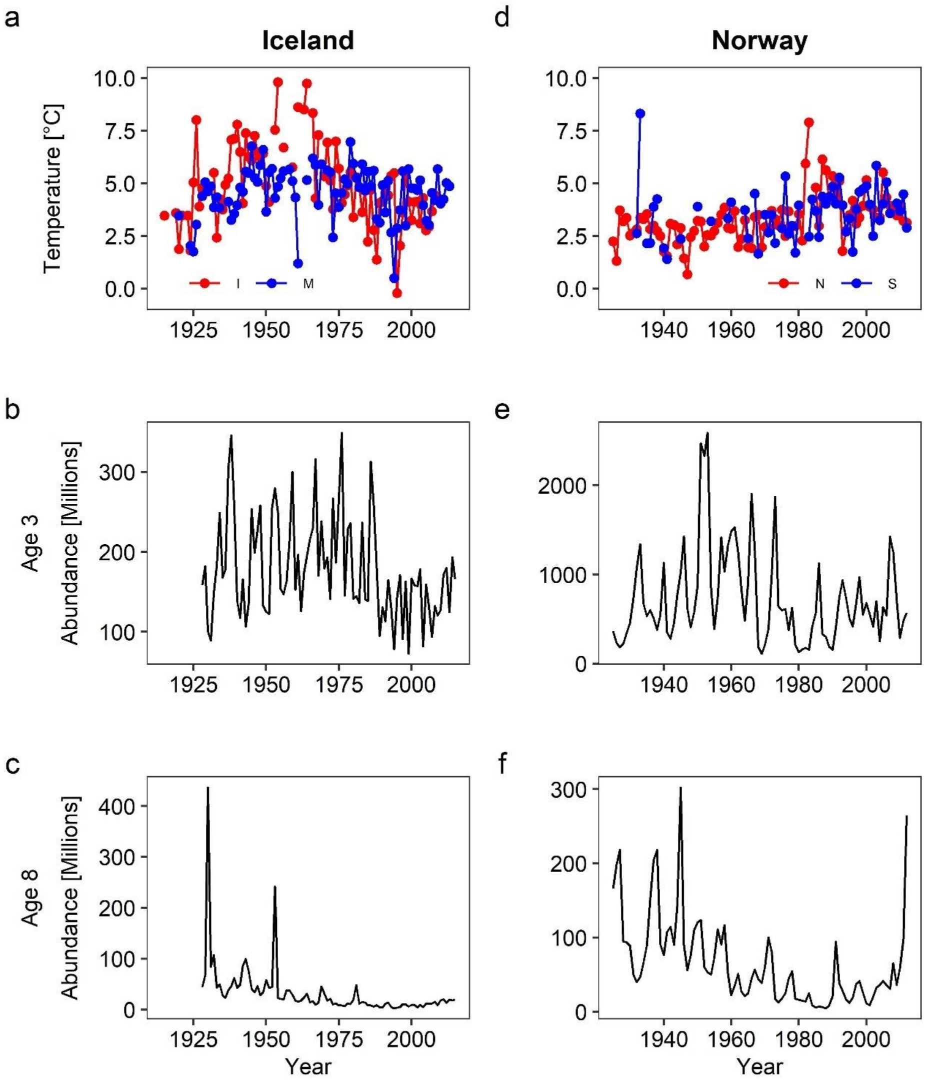

Figure 5: Reconstructed ambient temperature of (a) Icelandic and (d) NEA cod and abundance at age 3 and 8 of Icelandic (b & c) and NEA (e & f) cod. Reconstructed ambient temperatures of (a) immature cod and (d) non-spawners are shown in red, (a) mature cod and (d) spawners in blue.

The reconstructed temperature time series for mature and spawning NEA cod tended to be warmer than that of immature NEA cod. The mean reconstructed ambient temperature using all samples and using salinity mixing line (1) was 3.3°C with warmer temperatures for spawners (3.7°C, ranging from 0.8 to 8.3°C) than for non-spawners (3.1°C, ranging from -0.4 to 7.9°C). Since incorrect assumptions about the proportion of mature cod would distort our ambient temperature reconstructions (spawning NEA cod migrate between the different salinities of the Barents Sea and the Lofoten), two different scenarios were tested:

(i) Cod of age 3 were immature and all age 8 cod were mature and migrated to the Lofoten for spawning.

(ii) Cod of age 3 (immature) and cod of age 8 without spawning marks stayed in the Barents Sea all year around but only those age 8 cod which showed spawning checks migrated to the Lofoten for spawning.

Of the two scenarios, the second scenario appeared to be more accurate, since the reconstructed ambient temperatures corresponded well with the water temperature time series at 150 m depth (Fig. 6). The mean offset between the reconstructed and environmental temperature time series was 0.06°C, but was 0.90°C between the ambient water temperature and the 0 – 200 m time series and 1.40°C between the ambient water temperature and the SST time series, respectively. Since the temperature time series at 150 m depth only started in 1951, the water temperature time series at 0 – 200 m was used for further data analysis.

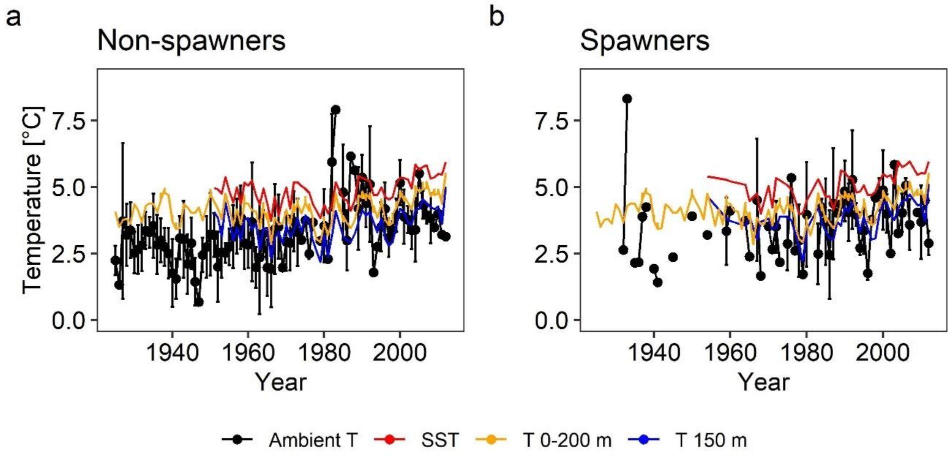

Figure 6: Reconstructed ambient water temperature of NEA cod with error bars indicating standard deviation, SST time series and water temperature time series 0 to 200 m and 150 to 200 m depth. Temperatures for spawners were adjusted for migration. Non-spawners included immature (age 3) and non-spawning mature (age 8) NEA cod.

An error analysis was performed to quantify possible uncertainties in the reconstructed ambient temperatures of NEA cod caused by a high variance of $\delta^{18}O_{seawater}$ at high salinities in the salinity mixing line (1). Reconstructed ambient temperatures were slightly colder when excluding the data points by Risebrobakken et al. (2003) and slightly warmer when excluding Risebrobakken et al. (2003) and Östlund and Hut (1984). The mean difference between reconstructed ambient temperatures using salinity mixing lines (1) and (2) is 0.25°C, 0.02°C between salinity mixing lines (1) and (3) and 0.23°C between salinity mixing lines (2) and (3) (Table 2). Salinity mixing line (1) was used for ambient temperature reconstructions in this paper. Samples and depths-areas where sea ice has had a strong influence explain the high variance at high salinities.

Table 2: Reconstructed ambient temperatures (mean, minimum and maximum) of NEA cod using three different salinity mixing lines for the Barents Sea.

	Reconstructed ambient temperatures using different salinity mixing line [°C]		
	Equation (1)	Equation (2)	Equation (3)
All samples	3.3	3.0	3.2
Non-spawning NEA cod	3.1 (-0.4 – 7.9)	2.8 (-0.6 – 7.7)	3.1 (-0.4 – 8.0)
Spawning NEA cod	3.7 (0.8 – 8.3)	3.5 (0.6 – 8.1)	3.7 (0.8 – 8.3)

3.3 Impact of population dynamics on temperature selectivity

3.3.1 NEA cod

The linear mixed effect model that best described the temperature exposure of NEA cod included life stage, abundance at age and the measured water temperature at depths between 0 and 200 m. Compared to a linear mixed effect model without population dynamics data, the inclusion of abundance at age significantly improved the fit of the model (Δ AICc > 2). Stable oxygen isotope time series differed significantly between the life stages ($p < 0.05$; Table 3). Moreover, the oxygen isotope time series was significantly correlated with the abundance of cod ($p < 0.001$) and measured water temperature times series ($p < 0.001$) (Fig. 7). The interaction between life stage and measured water temperatures ($p < 0.05$) was also significant, but not the interaction term between abundance and life stage, indicating that immature and mature NEA cod reacted differently to changing water temperatures.

Table 3: Fixed and random effects estimates and confidence interval (CI) of the optimal model for Norwegian $\delta^{18}O_{otolith}$. Residual variance σ^2, the variance associated with the tested effects τ_{00} and their ICC (intraclass correlation coefficient) is given. Significant p-values are bold.

		$\delta^{18}O_{otolith}$	
Predictors	*Estimates*	*CI*	*p*
(Intercept)	3.94	3.64 – 4.25	**<0.001**
Abundance	0.10	0.06 – 0.13	**<0.001**
Temperature	-0.20	-0.28 – -0.13	**<0.001**
Life stage	-0.56	-0.98 – -0.13	**<0.05**
Temperature : Life stage	0.12	0.01 – 0.22	**<0.05**
Random Effects			
σ^2	0.05		
$\tau_{00\ Fish\_ID}$	0.02		
ICC	0.29		
N_{Fish_ID}	223		
Observations	437		
Marginal R^2 / Conditional R^2	0.148 / 0.397		

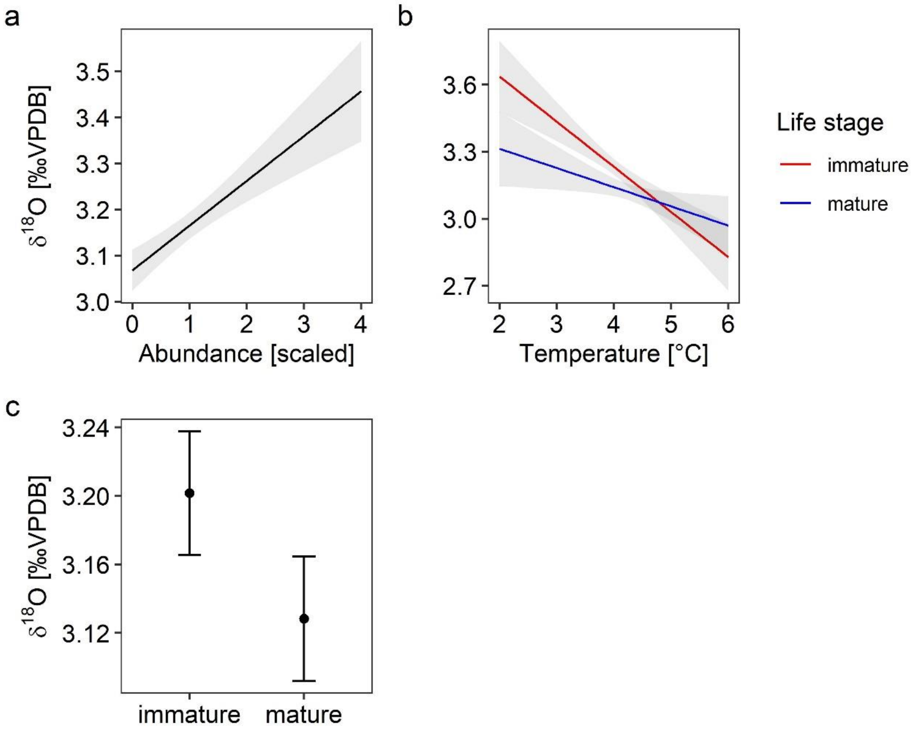

Figure 7: Predicted effects of cod abundance and temperature on $\delta^{18}O_{otolith}$ *of the NEA cod.*

3.3.2 Icelandic cod

The temperature exposure ($\delta^{18}O_{\mathrm{otolith}}$) of the Icelandic cod population was significantly correlated with abundance at age ($p < 0.5$), but not with the measured water temperature at 200 m depth in the region (Table 4, Fig. 8). This indicates that the ambient temperature of Icelandic cod increased with increasing abundance but not with water.

Table 4: Fixed and random effects estimates and confidence interval (CI) of the optimal model for Icelandic $\delta^{18}O_{otolith}$. Residual variance σ^2, the variance associated with the tested effects τ_{00} and their ICC (intraclass correlation coefficient) is given. Significant p-values are bold.

		$\delta^{18}O_{otolith}$	
Predictors	*Estimates*	*CI*	*p*
(Intercept)	2.82	2.41 – 3.22	**<0.001**
Abundance	-0.010	– 0.013 – -0.006	**<0.05**
Temperature at 200 m	-0.02	-0.09 – 0.05	0.554
Random Effects			
σ^2		0.13	
$\tau_{00\ Fish\_ID}$		0.06	
ICC		0.30	
N_{Fish_ID}		163	
Observations		286	
Marginal R^2 / Conditional R^2		0.033 / 0.321	

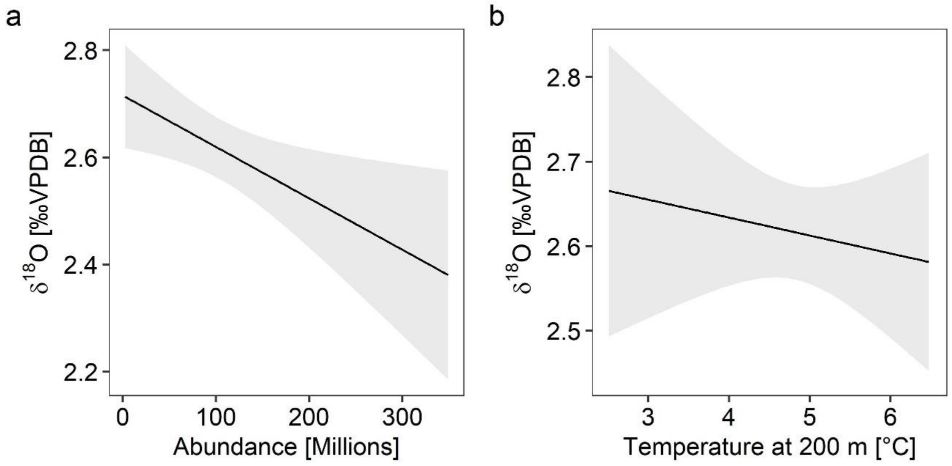

Figure 8: Effects of the variables predicted by the model of $\delta^{18}O_{otolith}$ of the Icelandic cod. Values of $\delta^{18}O_{otolith}$ were significantly correlated with (a) abundance at age ($p < 0.05$), but not with (b) temperature at 200m.

3.3.3 Comparison between Icelandic and NEA cod

Our results indicate that the temperature exposure of both Icelandic and NEA cod was mainly driven by abundance. The reconstructed ambient temperatures of Icelandic and NEA cod both increased with increasing water temperatures. When the abundance of Icelandic cod doubled, the ambient temperature increased by 1°C. With increasing abundance, the ambient temperature of NEA cod decreased. Over the abundance range (age 3: 111 – 2,588 thousand; age 8: 4 – 302 thousand) of the last 100 years, the ambient temperature of NEA cod decreased by 1.9°C.

4 Discussion

Stable oxygen isotope assays suggested that the temperature selectivity of cod was driven by changes in abundance, but the resulting reaction varied between populations. The interplay of climate fluctuations and population dynamics has previously been documented in long-term studies of taxa as varied as birds, reptiles, plants and fish (Stenseth et al., 2002, McCarty, 2001). At low densities, individuals live in the highest quality habitat within their optimal temperature range (Fretwell and Lucas, 1970, Rosenzweig, 1991). When abundance increases, fish expand their temperature exposure to previously unfavourable thermal habitats which have now become equally attractive. The ambient temperature of NEA cod decreased with increasing abundance and thus, also included sub-optimal temperature conditions. We suggest that the temperature selectivity changed as a density-driven response due to increasing intraspecific competition and decreasing fitness levels (Laurel et al., 2007). Even if in the species' thermal range, colder environments can decrease foraging and fecundity, alter metamorphosis, affect endocrine homeostasis and migratory behaviour, slow digestion and lower food supply cause reduced growth (Pörtner et al., 2001, Barton and Barton, 1987, Donaldson, 1990, Orlova et al., 2005). In periods of increasing abundance, distributional range extension of NEA cod into the colder waters of the eastern and northern Barents Sea has been observed (Ottersen et al., 1998). Higher water temperatures resulted in the increase of the suitable feeding area for NEA cod in the Barents Sea and thus, likely reduced density-dependent effects on cod (Kjesbu et al., 2014). In especially warm years when sea ice coverage was reduced, cod moved into colder waters. The distribution of NEA cod was at its greatest in autumn 2013 extending as far north as 81°N and to the areas southeast of Franz Josef Land, where large cod was found at 79°30N/66°-69°E in the middle of October. The most eastern observation of cod in the area that year was east of St. Anna Through at 79°E, which is an easterly record for cod distribution (Prokhorova, 2013). In the 1920s, NEA cod extended its distribution to Bear Island Bank and further east to Novaya Zemlya and north off West Svalbard as a response to warming (Beverton and Lee, 1965). This suggests that NEA cod penetrate to these regions in high abundance and warm years. Moreover, a general eastward movement of immature NEA cod has been observed in the 1990s along with increasing population abundance and temperature (Ottersen et al., 1998, Drinkwater, 2005). NEA cod will extend its distribution into colder waters further north and east in high abundance years in combination with the observed increase of water temperatures. In contrast, our results indicate that Icelandic cod moved into warmer waters with increasing population density. Increasing water temperatures can lead to increased growth but when cod migrate into waters warmer than the population-specific optimal water temperature, mortality will increase and the reproduction success will decrease as spawners, eggs and larvae are particularly vulnerable to temperature changes (Dutil and Brander, 2003, Pörtner and Peck, 2010, Dahlke et al., 2020). Stable oxygen isotope assays of Icelandic cod were not significantly correlated with temperature, consistent with previous findings that the relative abundance and spatial distribution of mature Icelandic cod was mainly explained by habitat characteristics, rather than by temperature and depth (Begg and Marteinsdottir, 2002). Abundance of Icelandic cod (at age 8) was high in the 1920s and 1930s and is increasing again (albeit to lower levels) in the most recent years, which also corresponds to warming events. Previous distribution shifts of Icelandic cod resulted in spawning sites to northern shelf areas around Iceland, when they had previously been restricted to the warmer waters off southwestern Iceland (Sæmundsson, 1934, Vilhjálmsson, 1997). However, this range shift was caused by warming waters and not by high abundance. The temperature selectivity of both cod populations changed with abundance, but the direction varied between populations. Confounding responses to changing environments highlight the importance of population- and area-specific research on the effects of global warming (McFarlane et al., 2000). Furthermore, the scale and direction of density-dependent temperature selectivity provides a more accurate indication of the temperature range of a population than experimentally determined temperatures, which often differ from temperature exposure in the wild.

Atmospheric changes may impact oceanographic conditions, including circulation patterns, the strength of the mixing, and stratification, resulting in ocean temperature changes (Drinkwater, 2005). These factors were not included in this data analysis as there is much greater uncertainty about changes in physical oceanography than in water temperatures. However, changes in atmospheric or oceanographic circulation can certainly influence cod distribution. First, atmosphere-driven circulation changes caused warming in the North Atlantic in the 1920s changing cod distributions (Rogers, 1985) such as Greenlandic cod, which extended its distribution by 1200 km in less than 20 years (Jensen et al., 1931, Hansen, 1949). Icelandic cod spawning spread to northern Iceland due to increasing water temperatures (Sæmundsson, 1934, Vilhjálmsson, 1997). Circulation changes can also directly affect the distribution of cod larvae. If the direction or strength of oceanographic currents changes, cod larvae will drift to new areas which might not be well-suited as nursery grounds due to altered temperature conditions. One characteristic of Icelandic cod stock dynamics is the periodic mixing of the Icelandic and Greenlandic cod stocks due to periodic immigration of cod from Greenland to Iceland (Bonanomi et al., 2016, Bonanomi et al., 2015). Icelandic cod larvae and juveniles spawned in Iceland can also drift towards Greenlandic waters. Due to their homing behaviour, mature cod from this immigration might return to Icelandic waters for spawning (Christensen, 1996). However, since the 1970s the Iceland-Greenland transport has been reduced, possibly due to reduced stock size (Schopka, 1994) or temperature-induced changes associated with oceanographic conditions (Dickson and Brander, 1993). In the Barents Sea the combination of a warmer climate, the warmer North Atlantic Current and less cooling in the Barents Sea results in warmer waters flowing out the Barents Sea, affecting oceanographic currents globally. Increasing water temperatures in the Barents Sea are expected to shift the distribution of cod and other fish species into the colder waters of the eastern Barents Sea (Skagseth et al., 2020).

The reconstructed ambient temperatures of both cod populations placed them well within physiological tolerances, but at different positions within the species' thermal range. With a mean ambient temperature of 3.3°C, NEA cod was at the lower edge of the species thermal range, which can be found in waters down to -1°C (Woodhead and Woodhead, 1965, Mehl et al., 1985). The mean ambient temperature of Icelandic cod was 4.8°C and thus higher than that of NEA cod. The temperature exposure of NEA cod differed significantly between life stages which is consistent with previous studies for Icelandic cod (Astthorsson et al., 1994, von Leesen et al., 2020). Reconstructed ambient temperatures for mature, spawning NEA cod were well within the preferred temperature range for spawning of 1 to 8°C (Righton et al., 2010). Due to the migration to the warmer spawning grounds in the Lofoten (with annual mean temperatures of 6 to 8°C) (Aure and Østensen, 1993, Bergstad et al., 1987), spawners had higher reconstructed ambient temperatures than non-spawners. Immature cod are found in the colder Barents Sea all year around where they feed on their main prey, capelin (Ottersen et al., 1998). However, juvenile cod can inhabit waters up to 20°C and are more tolerant to temperature shifts as they have a broader thermal window compared to early ontogenetic stages and spawners (Brander, 1997, Pörtner and Peck, 2010). With increasing age (independent of the stage of maturity), NEA cod gradually move westwards in the Barents Sea where they are exposed to higher water temperatures (Bergstad et al., 1987, Nakken and Raknes, 1987).

Direct $\delta^{18}O_{seawater}$ measurements would limit the uncertainties in reconstructed ambient temperatures. However, direct measurements are rarely available, and area-specific salinity mixing lines are a standard approach to overcome this issue. Some variation in $\delta^{18}O_{seawater}$ observed at high salinity in the Barents Sea is not surprising given the mixture of Atlantic and Arctic water masses with different processes influencing the flux of freshwater and its isotopic value. A small divergence in reconstructed ambient temperatures using alternative salinity mixing lines showed that the relatively small uncertainties around our reconstructed ambient temperatures do not change the main conclusions of this paper. Moreover, linear-mixed effect models were applied to investigate if density changes drove the temperature selectivity of Icelandic and NEA cod.

Comparisons of reconstructed ambient temperatures and instrumentally recorded water temperatures indicate that NEA cod were, at least partly, exposed to increasing water temperatures in the Lofoten and Barents Sea during the last 100 years. Rising water temperatures can cause either horizontal or vertical distributional shifts (Castonguay et al., 1999). In some cases however, cod remain in warmer waters which are considered sub-optimal, even if colder waters are available (Neat and Righton, 2007). Ontogeny and fisheries exploitation could also explain the deepening of fish (Frank et al., 2018), but this was not investigated in this study. The Barents Sea is relatively shallow with an average depth of around 300 m, extending as deep as 500 m in the northwest entrance to the Barents Sea and with stable water temperatures below 100 m (Ottersen and Ådlandsvik, 1993). Although vertical migration of NEA cod has been observed (Ingvaldsen et al., 2017), it does not seem to be a response to increasing water temperatures. Density-dependent effects to avoid competition for food (Kjesbu et al., 2014) and high-risk takers surpassing the limitations of the demersal environment (Sih et al., 2004) possibly explain the observed vertical movement of NEA cod. Vertical movement of NEA cod into deeper depth seemed to occur at certain times of the diel cycle, randomly or for longer period e.g., during the spawning migration between the Barents Sea and the spawning grounds along the Norwegian coast (Michalsen et al., 2014). NEA cod have a depth range between 50 and 150 m at the spawning grounds and below 100 m in the Barents Sea with the exception of the shallower (< 100 m) Southeast Barents Sea (Pechora Sea) where cod are found in summer-autumn (Korsbrekke et al., 1995). Instead, NEA cod moved poleward and have already extended their distribution range into the previously unsuitable northern regions of the Barents Sea which used to be covered by sea ice with temperatures below their thermal range (Orlova et al., 2005). Just 35% of the Barents Sea had suitable conditions for cod in the late 1970s/ early 1980s, while more than 70% of the Barents Sea were suited for cod in recent years (Kjesbu et al., 2014).

This study used $\delta^{18}O_{otolith}$ to build a century long chronology of temperature exposure for NEA cod off Norway and used the previously published Icelandic cod chronology (von Leesen et al., 2020) to investigate the effect of changing population dynamics and rising water temperatures on the temperature exposure of both cod populations. Use of cod-specific $\delta^{18}O$ fractionation temperature equations and geographically specific salinity mixing curve limits the uncertainties around our temperature estimates for cod. However, accurate temperature reconstructions require both local salinity mixing curves and salinity time series. For both Icelandic waters and the Barents Sea, long-term salinity time series were not available prior to 1950/1951; consequently, salinity models were used instead which could have introduced some error. However, the strong correlation between measured and modelled salinity time series justified the use of modelled salinity time series. Nevertheless, more $\delta^{18}O_{seawater}$ measurements, especially for the Norwegian and Barents Sea, would further improve the salinity mixing curves and their spatio-temporal variability. Spawning checks were helpful in determining the age at first spawning and improved the accuracy of the Norwegian ambient temperature reconstruction but were not available for Icelandic cod. Nevertheless, the divergence between reconstructed ambient temperature and measured water temperature in Icelandic mature cod cannot be explained by incorrect maturity assumptions. In fact, the divergence would increase even further as the reconstructed ambient temperatures of Icelandic mature cod would be even colder if it was assumed that they were in the colder, less saline waters off northern Iceland all year around.

Global warming will cause changes in population dynamics with divergent responses in different cod populations. Increasing abundance is predicted for the Icelandic and NEA cod population if the temperature increase is limited to 2°C (Drinkwater, 2005). NEA cod seem to benefit from rising water temperatures as they migrated poleward and inhabited cold water masses of the northern and eastern Barents Sea where Atlantic cod were previously not found (Mehl et al., 2014, Prokhorova, 2013). The Icelandic cod is also considered to be a cold-water population, but its annual mean bottom water temperature is close to the tipping point of being a warm-water population. Populations at the upper temperature range show negative relationships between temperature and recruitment and thus it is expected that the Icelandic cod population will remain static or even decline with increasing water temperature (e.g. Drinkwater (2009)). Generally, fish populations in arctic and arctoboreal ecosystems (at the lower edge of their temperature range) benefit from moderately increasing water temperatures, leading to increased growth and reproduction. In contrast, cod populations at the upper edge of the temperature range are expected to collapse and be replaced by invading new species from the south. Thus, the species composition in these regions will change and favourable environmental conditions will lead to increased abundance of more southern species (Stenevik and Sundby, 2007). We suggest that the use of long-term stable oxygen isotope and ambient temperature chronologies can be a powerful tool to predict fish re-distribution in warming ocean as population abundances change.

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Author contributions

The study was conceived, designed and coordinated by GvL and SEC. All authors contributed to lab work, data collection and/or data interpretation. GvL drafted the paper with contributions from all authors.

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Competing interests

The authors declare there are no competing interests.

Data availability

Fish data, stable oxygen isotope data and the R code are available from the corresponding author on reasonable request. Population dynamics data of Icelandic and NEA cod are available from the latest ICES report of the North-Western Working Group and Arctic Fisheries Working Group, respectively. Records of Kola section temperature and salinity are publicly available at PINRO from 1951 onwards, while data prior 1951 has restricted sharing agreements outside the Institute of Marine Research (IMR). Salinity records of the Norwegian Sea are publicly available at IMR. Records of Icelandic water temperatures and salinity are publicly available from the Marine and Freshwater Research Institute. Hadley modelled salinity data is publicly available from the Asia-Pacific Data-Research Center.

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Supplementary Material

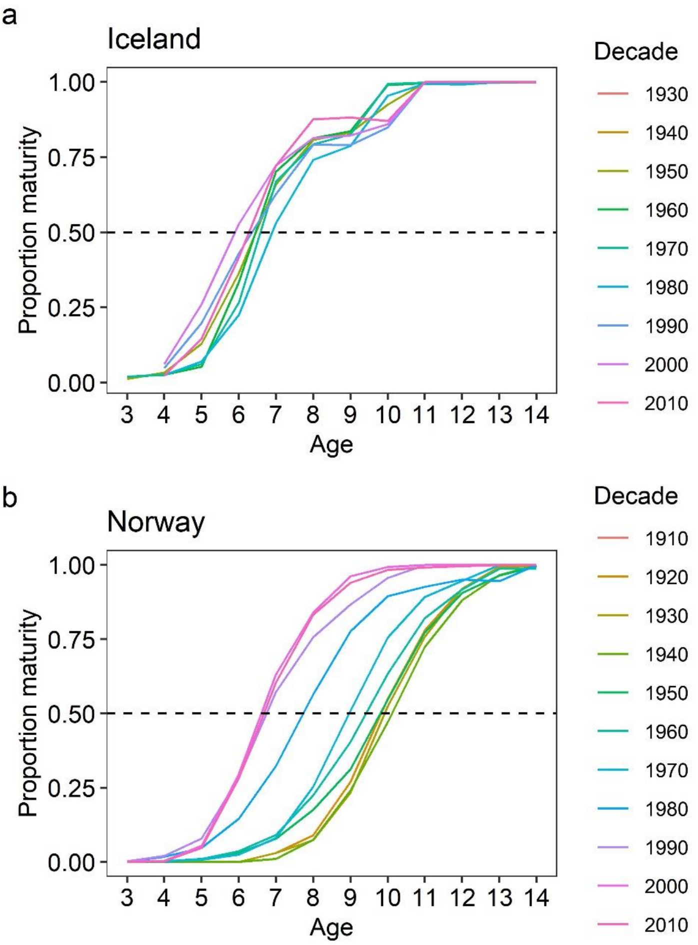

Figure S1: Age at 50% maturity of (a) Icelandic and (b) NEA cod shown by decade.

Paper III

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Accuracy of otolith oxygen isotope records analyzed by SIMS as an index of temperature exposure of wild Icelandic cod (*Gadus morhua*)

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Accuracy of otolith isotopic record analyzed by SIMS as an index of temperature exposure of wild Icelandic cod (*Gadus morhua*)

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Abstract

Global warming is increasing ocean temperatures, forcing marine organisms to respond to a suite of changing environmental conditions. The stable oxygen isotopic composition of otoliths is often used as an index of temperature exposure, but the accuracy of the resulting temperature reconstructions in wild, free-swimming Atlantic cod (*Gadus morhua*) has never been groundtruthed. Based on temperatures from data storage tags (DST) and corresponding salinity values, the stable oxygen isotope ($\delta^{18}O$) value was predicted for each month of tagging and compared with $\delta^{18}O_{otolith}$ values measured *in-situ* with secondary-ion mass spectrometry (SIMS). Paired-sample Wilcoxon tests were applied to compare measured and predicted $\delta^{18}O$ values. The difference between measured and predicted mean and maximum $\delta^{18}O_{otolith}$ values was not significant, suggesting a good correspondence between SIMS-measured and DST-predicted $\delta^{18}O_{otolith}$ values. However, SIMS-measured and predicted minimum $\delta^{18}O_{otolith}$ values were significantly different (all samples: $p < 0.01$, coastal and frontal cod: $p < 0.05$). Our results confirm that otoliths are well-suited as proxies for mean ambient temperature reconstructions. However, maximum temperatures were often overestimated. Possible matrix effect and the absence of a reliable aragonite standard for SIMS measurements appeared to cause a small divergence between measured and predicted $\delta^{18}O_{otolith}$ values. However, the absolute accuracy of temperature estimates is often less important than the relative temperature changes which are accurately given by SIMS-analyzed $\delta^{18}O_{otolith}$ values.

Keywords: accuracy, Atlantic cod, DST-tags, SIMS, stable oxygen isotopes

1 Introduction

Global warming is increasing ocean temperatures, forcing marine organisms to respond to a suite of changing environmental conditions (IPCC, 2013). Mobile species like fish have two options on how to react to changing environmental conditions; they can either stay and be exposed to increasing water temperatures, or they can migrate (often poleward) to remain in their preferred temperature range. Thus, environmental temperatures measured at a fixed station may not reflect the ambient temperature exposure of the organism. Data storage (DST) tags and natural proxies in bioarchives record the ambient environment of organisms, and thus provide more accurate temperature exposures than do environmental temperatures. DST tags which record temperature and depth have allowed greater insight into the migration, distribution, feeding and spawning behavior, vertical and horizontal movement, and geographic location of many marine animals (Righton and Mills, 2008; Thorsteinsson et al., 2012; Darnaude et al., 2014; Bardarson et al., 2017). The disadvantage of DST tags is that they are costly, the recapture rate is low, and they cannot be used to reconstruct historical ambient temperatures. Biological and geochemical archives of otoliths and other calcified structures indirectly record the ambient conditions experienced by marine organisms, and thus are valuable in reconstructing long-term ecological time series.

The otoliths of fish (ear stones) are metabolically inert, paired calcified (aragonitic) structures used for balance and/or hearing (Campana, 1999). Their stable oxygen isotope composition provides a direct means of reconstructing the temperature exposure of the fish, at least in laboratory settings (Campana and Thorrold, 2001; Høie et al., 2004b). The oxygen isotope ratio of otoliths reflects that of the water from which the oxygen is sourced but with a temperature-dependent offset (fractionation) (Campana, 1999). Changes in $\delta^{18}O$ of otolith aragonite are negatively correlated to water temperature; the higher the water temperature, the lower the $\delta^{18}O_{otolith}$ value (Kim and O'Neil, 1997). Kinetic, metabolic, or physiological effects are generally not considered to impact the otolith $\delta^{18}O$ (Thorrold et al., 1997; Høie et al., 2003). However, a disequilibrium for oxygen isotope fractionation has been observed for some species, e.g., North Sea plaice (Geffen, 2012; Darnaude et al., 2014), especially at temperature extremes. Cod-specific temperature-dependent fractionation and the precision and accuracy of stable oxygen isotope signals of lab-reared cod have previously been demonstrated (Høie et al., 2004a; Høie et al., 2004b). Since otoliths form annual growth bands continuously throughout their lifetime, they also record the complete exposure history of environmental conditions. Coupling stable oxygen isotope values with age or date of catch, $\delta^{18}O_{otolith}$ can be used to provide chronological records of the ambient temperature of the fish. Some otolith archives go back to the early 1900s, while DST tags have been applied only in more recent years. Otoliths are also found in archaeological sites, which allows the investigation of temperature exposure in past times. Thus, the isotopic composition of oxygen in otoliths has not just been applied by ecologists (Jones and Campana, 2009; von Leesen et al., 2020) but also by paleontologists (West et al., 2012; Wang et al., 2013).

Due to its high commercial value and broad geographical distribution in the North Atlantic Ocean, Atlantic cod (*Gadus morhua*) has been extensively studied. In the large Icelandic cod stock, two ecotypes with distinct seasonal patterns of temperature exposure and depth distribution have been reported (Pampoulie et al., 2012; Thorsteinsson et al., 2012). The most distinct difference between both ecotypes is temperature fluctuation seen in frontal cod due to their feeding migrations towards thermal fronts. Frontal cod migrate between spawning and feeding areas and are found in waters up to 600 m depth (Thorsteinsson et al., 2012; Bardarson et al., 2017). In contrast, coastal cod occur in shallower waters and are characterized by a more uniform temperature exposure with steadily increasing temperatures during summer months and a decrease again towards the winter months. Both ecotypes show spawning site fidelity. They are usually found at different depths, and it seems that ecotypes exhibit different habitat selection during spawning season, but the possibility of mixing of frontal and coastal cannot be excluded (Grabowski et al., 2011). The main spawning ground is off southwest Iceland, but smaller spawning sites are found all around Iceland (Marteinsdottir et al., 2000). The main migration routes are from the spawning ground in southwest Iceland to the feeding areas in the north, either along the south and southeast coast to the northeast or along the (south-)west to northwest Iceland (Jónsson, 1996; Neuenfeldt et al., 2013). Frontal cod spawning in northeastern Iceland appear to be more sedentary than from southwest Iceland but can migrate to northwest Iceland in the winter; however, their contribution in the waters off northwestern Iceland depends on oceanographic conditions (Jónsson, 1996; Pampoulie et al., 2012).

The accuracy of the isotopic record of otoliths as an index of temperature exposure in wild, free-swimming cod has not previously been established. This study used high-resolution (weekly or even daily resolution depending on otolith growth rate) secondary-ion mass spectrometry (SIMS) to quantify the accuracy of the isotopic record in the otolith and confirm that stable oxygen isotope values are a reliable temperature proxy in wild, free-swimming cod. Thus, the intent was to determine if accurate temperature reconstructions were possible using routine otolith oxygen isotopic assays of wild cod otoliths.

2 Material and methods

2.1 Sampling

Otolith sections from 38 wild, DST-tagged cod were selected for stable oxygen isotope analyses (Suppl. Tab. 1). The majority (n=25) of the tagged cod were classified as coastal cod, while 12 were frontal cod, and one individual could not be clearly identified. Ecotypes were previously determined by temperature and depth profiles. Cod were tagged between April 2002 and April 2004 around Iceland in four different areas (west, southwest, southeast, and northeast; Fig. 1), with 22 cod being tagged in southeast Iceland. In most cases, tags were attached to the fish for about one year. Pampoulie et al. (2008) described the DST, DSTmilli and DSTcenti-ex tags (manufactured by Star Oddi) in detail. Temperature and depth were usually recorded in 10-minute intervals with a depth range of 0-700 m, a resolution of 0.21 m, and an accuracy of ±0.70%. These tags are capable of recording temperatures ranging from -2 to 39°C with a precision of 0.01°C, and accuracy of ±0.20°C. In 7 out of 38 cases, the recording time of water temperature and depth was shorter than the tagging time because the recording did not start directly after tagging or the DST battery ran out of power before recapture. The tagging procedure is described in detail on the following website:
https://www.hafogvatn.is/static/files/enska/merkingar_thorskur.pdf.
The license for operations on fish (No. 0304-1901) was issued by the Icelandic Committee for Welfare of Experimental Animals, Chief Veterinary Office at the Ministry of Agriculture, Reykjavik, Iceland.

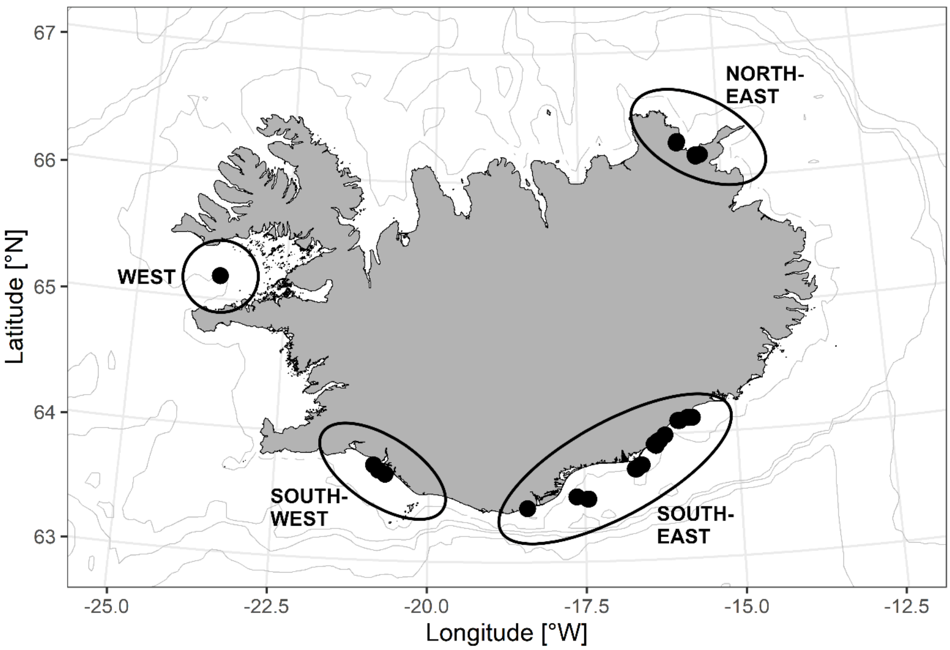

Figure 1: Release position of DST-tagged cod on spawning grounds between 2002 and 2004. In total, 38 fish were tagged: 1 in the west (W), 3 in southwest (SW), 22 in southeast (SE): 22, and 12 northeast (NE) off Iceland.

2.2 Otolith preparation

Stable oxygen isotopes ratios were analyzed by secondary ion mass spectrometry (SIMS), which is a high-spatial resolution method for determining the elemental and isotopic composition of solid materials (Campana, 1999). The otolith sections (~200 µm) were cut out of glass slides using a Buehler IsoMet 1000 Precision Saw (ITW Test & Measurement GmbH, Esslingen, Germany) equipped with a 15LC IsoMet Diamond Wafering blade. Sample mounts were prepared following the standard procedure for stable isotopes at NordSIMS. Five to 6 otoliths and 3 to 4 pieces of a calcite reference material were embedded in each epoxy mount, which dried overnight in a pressure pot. The surface of the sample mounts was ground with sandpaper (2000 microns) and polished using diamond or aluminum paste of 3 and 1 micron(s) to remove residual epoxy and resin. The sample mounts were cleaned in ethanol using an ultrasonic bath to remove any residue of polishing pastes.

The mounted otolith sections were imaged with an Olympus DP74 high resolution [5760 x 3600 pixel (3CMOS)] camera attached to a Leica S8AP0 stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany) using CellSens Standard software (Olympus Europe SE & Co. KG, Hamburg, Germany). Fish age was previously determined by experienced age readers, and growth was measured along the dorsal axis. The otolith material formed during the tagging period was determined by measuring the distance from the edge of the otolith (date of catch) back to the growth increment assumed to have been formed in the year of tagging.

2.3 Secondary Ion Mass Spectrometer (SIMS)

Sub-annual otolith $\delta^{18}O$ values were measured by SIMS at the NordSIMS laboratory, Department of Geosciences at the Swedish Museum of Natural History in Stockholm, Sweden. SIMS is a probe-based method for determining the elemental and isotopic composition of solid materials (in otoliths: e.g., Darnaude et al., 2014; Helser et al., 2018; Willmes et al., 2019). Polished mounts were gold-coated, and the stable oxygen isotopes were measured using a CAMECA ims1280 ion microprobe, an advanced high-sensitivity mass spectrometer that uses a focused beam of ions to sample *in situ* selected micrometer-sized areas of a sample for measurement of isotopic composition.

A critically focused Cs+ (caesium) primary beam with 20 keV impact was used to sputter the sample, and a low-energy electron flooding gun was used for charge compensation. The primary beam current was ca. 2.5 – 3 nA, which yielded ca. 15 µm analytical spots, including a 10 µm raster to homogenize the beam. Each analysis consisted of an initial pre-sputter over a rastered 20 µm area to remove the gold coating, followed by centering the secondary beam in the field aperture (field of view on the sample of 30 µm with 90x magnification transmission ion optics). For oxygen, the ^{16}O (ca. 3×10^9 cps) and ^{18}O ion beams were mass filtered at a mass resolution of ca. 2500 ($M/\Delta M$) and analyzed simultaneously using two Faraday detectors with amplifiers housed in an evacuated, temperature-stabilized chamber. The secondary magnet field was locked at high stability using an NMR field sensor operating in regulation mode. All pre-sputter, beam centering, and data acquisition steps were automated in the run definition. Fully automated sequences comprised regular measurements of the reference materials, bracketing measurements of unknown targets. Calcite was used as a standard to measure aragonitic otoliths. The calcite reference material was used largely to monitor instrument drift through the session and assess the external reproducibility. Instrumental mass bias was calibrated in each session using the calcite reference material S0161, which comes from a granulite facies marble in the Adirondack Mountains (kindly provided by R.A.Stern, University of Alberta). The value used for IMF correction was determined by conventional stable isotope ratio mass spectrometry at the Department of Geosciences, Stockholm University, using a Thermo Finnigan GasBench II and CTC PAL autosampler coupled to a MAT253 mass spectrometer. Dried and homogenized S0161 (0.2 mg) was put into a vial with phosphoric acid, without the two touching; the vial was then flushed with helium (He) before allowing the acid to contact and react with the carbonate. The long term (>10 years) standard deviation on the IAEA-CO-1, IAEA-CO-8 and NBS18 calcite standard is 0.15 ‰. Ten separate aliquots of the S0161 calcite yielded $\delta^{18}O = -5.62 \pm 0.11‰$ V-PDB (1 std. dev.).

2.4 Prediction of otolith δ^{18}O values during DST recording time

2.4.1 Calculation of predicted $\delta^{18}O_{otolith}$

Monthly otolith δ^{18}O values between release and recapture were predicted using the tag-recorded temperatures and geo-referenced water δ^{18}O values, and then compared with the SIMS-analyzed $\delta^{18}O_{otolith}$. Before comparing measured and predicted otolith δ^{18}O values, images with growth measurements and SIMS measurement spots were overlayed to verify that the SIMS samples were measured in the correct part of the otolith. Oxygen isotope ratios of the ambient seawater at the time and place of prediction were back-calculated using salinity measurements (derived from the Marine and Freshwater Research Institute: https://sjora.hafro.is/) matching the predicted geolocations and the salinity mixing curve for the Icelandic shelf (von Leesen et al., 2020):

$$\delta^{18}O_{seawater} = 0.58 \times S - 20.12 \tag{1}$$

where $\delta^{18}O_{seawater}$ is the oxygen isotope value of seawater [‰ on the standard mean ocean water (SMOV) scale], and S is the salinity. Salinity values were matched according to known migration patterns of the respective ecotype (Pampoulie et al., 2012; Thorsteinsson et al., 2012), tagging and recapture location, and the DST-recorded depth. All isotope values for δ^{18}O otolith carbonate are reported in ‰ on the VPDB scale. Seawater values were corrected from SMOW by subtracting 0.27‰ (Bemis et al., 1998; Grossman, 2012; Marchitto et al., 2014). Finally, $\delta^{18}O_{otolith}$ values were predicted using the equation of Jones and Campana (2009) (adapted from (Kim and O'Neil, 1997)) incorporating the corresponding temperatures recorded by the DST tag:

$$T\ (°C) = -(\delta^{18}O_{otolith} - \delta^{18}O_{seawater}) \times 0.206^{-1} + 18.010 \tag{2}$$

or the temperature fractionation equation by Høie et al. (2004b), respectively:

$$\delta^{18}O_{otolith} - \delta^{18}O_{seawater} = 3.90 - 0.20T\ (°C) \tag{3}$$

2.4.2 Offset factor to correct measured $\delta^{18}O_{otolith}$

Atlantic cod otoliths are aragonitic, but the stable oxygen isotope concentration was measured against a calcite standard as no reliable aragonite standard is available for SIMS measurements. The bias between aragonite and calcite was corrected using an offset factor which was estimated in this study using four different approaches (Table 2), and then added to all measured δ^{18}O values. The approaches used for calculating the offset were:

1. The last SIMS measurement of each otolith was subtracted from the last predicted $\delta^{18}O_{otolith}$ value. Since the known recapture position near the edge of the otolith enabled a close to reality temperature and salinity estimation, the predicted $\delta^{18}O_{otolith}$ should have been relatively accurate.
2. The offset between measured and predicted otolith δ^{18}O values for coastal cod (only) was calculated. Coastal cod have a less pronounced feeding migration than frontal cod, and thus, the estimation of the geolocation and the corresponding salinity should have been more accurate.
3. Analogous to (2), the offset of all but seven samples (including both coastal and frontal cod) was calculated. The water temperature and depth recordings of these

samples stopped at least 100 days before the fish was recaptured which makes the date-matching of measured and predicted $\delta^{18}O_{otolith}$ values more challenging.

4. Analogous to (3), but all 38 samples were included in calculating the offset factor.

Measured and predicted otolith $\delta^{18}O$ values were statistically compared using a paired-samples Wilcoxon Test. Outliers were excluded from the statistical analysis (i.e., DSTid 1C0426). Values above Q3 + 1.5xIQR or Q1 – 1.5IQR were considered outliers (Q3: third quartile, Q1: first quartile, IQR: interquartile range). All statistical analyses were performed in R (Team, 2019).

2.4.3 Salinity sensitivity analysis

Predicted $\delta^{18}O$ values were based on known DST-temperature records and salinity-derived $\delta^{18}O_{seawater}$ values. A sensitivity analysis was performed to test the effect of incorrect salinity estimations on the predicted $\delta^{18}O_{otolith}$ values (using the temperature fractionation equation by Jones and Campana (2009)). In total, five different salinity scenarios were tested in the sensitivity analysis:

1. Most probable salinity: Salinity values were matched with DST-recorded temperatures based on depth distribution, tagging and recapture position, and the known migration pattern of the ecotype.
2. Minimum salinity: Salinity measurements of the years 2002 to 2005 were used to calculate the lowest possible salinities in the geolocation area over a year (see Suppl. Table 2).
3. Maximum salinity: Analogous to (3), the highest possible salinities in the area were determined (see Suppl. Table 2).
4. Salinity 34.5: A fixed salinity value of 34.5 was assumed, which is the lowest salinity value in fully marine water around Iceland.
5. Salinity 35.2: Analogous to (4), a fixed salinity of 35.2 was assumed for all samples, which is the highest salinity measured around Iceland.

2.4.4 Otolith growth scenarios

SIMS-analyzed and predicted $\delta^{18}O_{otolith}$ timeseries of individual otoliths were aligned using QAnalySeries to achieve the best match in the position of inflection points (Kotov and Paelike, 2018).

Since water temperatures may influence the accretion rate of otolith growth, two different scenarios for otolith annual growth were tested.

- SC 1: otolith growth is constant throughout the year, i.e., linear otolith growth (equal weighting of 100% given to all months)
- SC 2: 90% of the otolith growth occurred in the 6 months of summer (May-October) and the remaining 10% of the otolith was formed during the 6 months of winter, i.e., non-linear otolith growth (see Pilling et al. (2007)).

3 Results

3.1 DST-recorded temperatures

Cod off south(western) Iceland were exposed to warmer temperatures than cod off northeastern Iceland (the mean difference between SE/SW and NE coastal cod: 3.4°C, frontal cod: 1.4°C; Table 3). A Two-Way ANOVA showed that DST-recorded temperatures varied significantly by region (F = 235.73, $p < 0.001$, df=1) and ecotype (F = 7.96, $p < 0.01$, df=1) with a significant interaction of both factors (F = 39.70, $p < 0.001$, df=1). The temperature amplitude across the year was highest in west Iceland and lowest in the northeast (Fig. 2). Frontal cod off south-eastern Iceland were exposed to fluctuating temperatures with the highest temperatures during the spawning season in April and May. The ambient temperature varied with depth (Suppl. Fig. 1) with colder temperatures in deeper waters, tagging/ recapture area, and ecotype (Table 1).

Table 1: Mean (± SD), minimum and maximum temperature recorded with DST tags by both ecotypes in the different tagging areas (W=west, SW=southwest, SE=southeast, and NE=northeast off Iceland) and the sample size (n). -: data not available.

		NE	**n(NE)**	**SE**	**n(SE)**	**SW**	**n(SW)**	**W**	**n(W)**
Coastal	Mean	3.8	5	7.3	16	7.1	3	7.1	1
	SD	1.7		1.6		1.6		2.8	
	Min	0.3		2.2		4.5		3.4	
	Max	7.7		9.6		11.4		11.3	
Frontal	Mean	3.1	6	4.5	6	-		-	
	SD	1.2		2.6		-		-	
	Min	0.5		-0.4		-		-	
	Max	6.3		8.2		-		-	

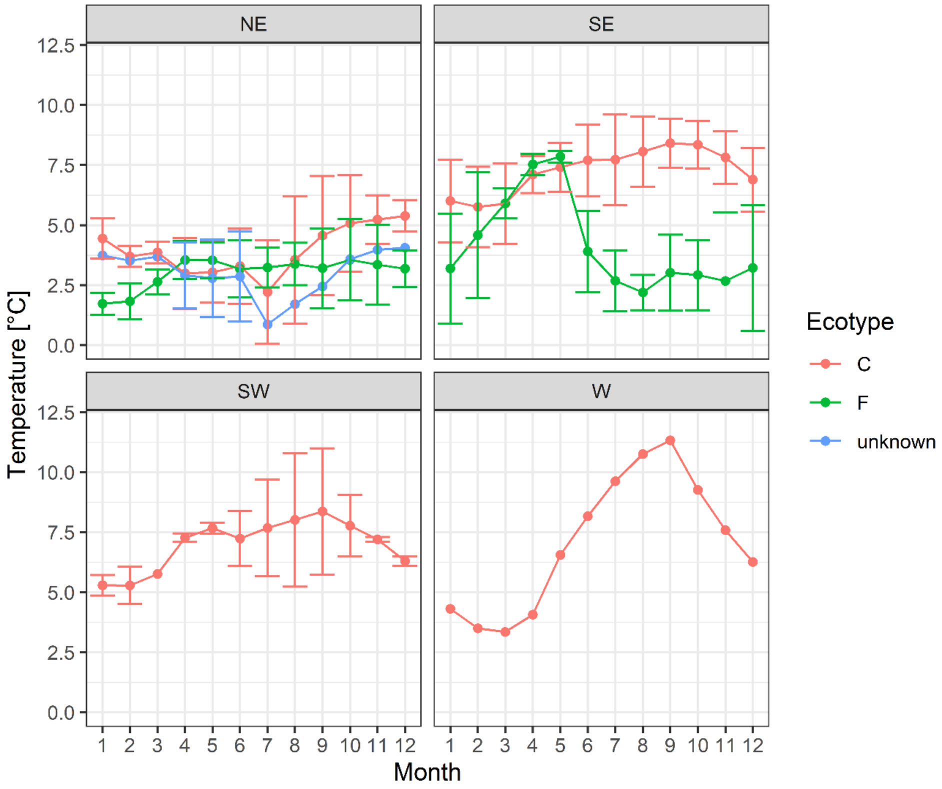

Figure 2: Mean monthly temperatures and standard deviation for each tagging area (W=west, SW=southwest, SE=southeast, and NE=northeast off Iceland) and ecotype (C = coastal, F= frontal) recorded by DST tags.

3.2 Comparison of SIMS-measured and predicted $\delta^{18}O_{otolith}$

The offset factor between SIMS-measured and predicted $\delta^{18}O_{otolith}$ was not sensitive to the method of calculation, with all four methods producing similar values (Table 2). A Kruskal-Wallis test showed that the four offset factors were not statistically different. Therefore, SIMS-measured $\delta^{18}O_{otolith}$ values were corrected applying the offset-factor of 1.62 which had the best correspondence between measured and predicted $\delta^{18}O_{otolith}$ values.

Table 2: Mean and standard deviation of the different offset calculations.

Scenario	**1**	**2**	**3**	**4**
Mean	1.58	1.62	1.56	1.63
Standard deviation	0.63	0.57	0.44	0.48

Predicted and measured $\delta^{18}O_{otolith}$ values were relatively similar after the offset factor was applied to the SIMS measurements. All means are reported ± SD. Predicted and measured $\delta^{18}O_{otolith}$ values were in the same range with often slightly higher predicted values, whereas the range of measured $\delta^{18}O_{otolith}$ values was broader than for predicted $\delta^{18}O_{otolith}$ (Suppl. Fig. 2): mean predicted $\delta^{18}O_{otolith}$ 2.48 ± 0.47‰, mean measured $\delta^{18}O_{otolith}$ 2.32 ± 0.60‰. We predicted the $\delta^{18}O_{otolith}$ values based on DST-recorded temperatures instead of calculating the ambient temperature based on SIMS-analyzed $\delta^{18}O_{otolith}$ values because the possible mismatch of $\delta^{18}O_{otolith}$ values and dates would add a potential error. The temporal resolution of SIMS measurements varied depending on sample resolution, the age of the fish, and the individual growth rate but was usually about one month based on mean spot size (20 µm) and growth rate. Hence, monthly DST-recorded temperatures were calculated to predict $\delta^{18}O_{otolith}$.

Both measured and predicted otolith $\delta^{18}O$ values of frontal cod were higher than those of coastal cod, resulting in colder ambient temperatures of frontal cod than coastal cod (Fig. 3). Coastal cod had a measured $\delta^{18}O_{otolith}$ mean of 2.12 ± 0.55‰ and a predicted mean of 2.26 ± 0.41‰; frontal cod had a measured $\delta^{18}O_{otolith}$ mean of 2.74 ± 0.45‰ and a predicted mean of 2.82 ± 0.35‰. Otolith $\delta^{18}O_{otolith}$ values varied significantly between ecotype ($F = 76.79$, $p < 0.001$, df =1), regions ($F = 107.02$, $p < 0.001$, df = 1; including just SE and NE Iceland where both ecotypes were present) and the interaction of both ($F = 20.85$, $p < 0.001$, df = 1). Statistical comparisons by paired-samples Wilcoxon test showed that the measured and predicted mean and maximum values did not vary significantly (Fig. 3). However, minimum $\delta^{18}O_{otolith}$ values differed significantly among all samples ($p < 0.01$), and when restricted to ecotype ($p < 0.05$).

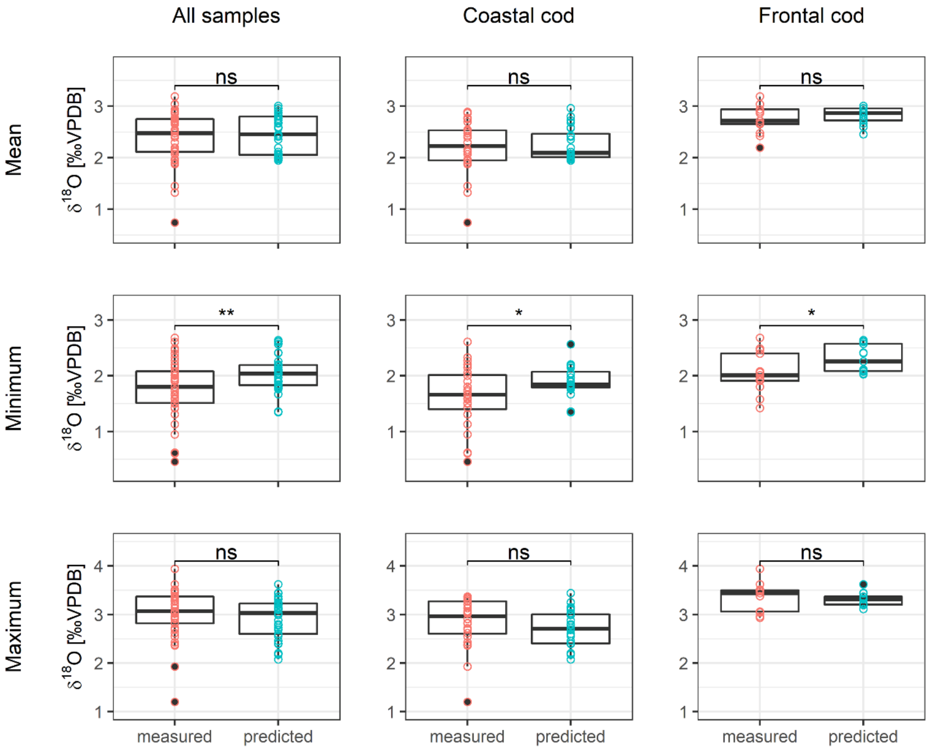

Figure 3: Differences between SIMS-measurements and predicted mean, minimum, and maximum $\delta^{18}O_{otolith}$ *values of all samples and distinguished between coastal and frontal cod. Significant differences, based on paired-samples Wilcoxon test, are shown at* $p < 0.001$ *(***),* $p < 0.01$ *(**),* $p < 0.05$ *(*) and ns for non-significant differences.*

The two different temperature fractionation equations produced predicted $\delta^{18}O_{otolith}$ which differed by about 0.22‰ which is equivalent to a temperature difference of 1.1°C (Table 3 and 4). The equation by Jones and Campana (2009) provided a more accurate prediction of the $\delta^{18}O_{otolith}$ values.

Table 3: Mean (±SD) predicted $\delta^{18}O_{otolith}$ values using the temperature fractionation equations by Jones and Campana (2009) and Høie et al. (2004b).

		Equation	
		Jones and Campana (2009) [‰]	**Høie et al. (2004b) [‰]**
All samples	Mean	2.47 ± 0.37	2.70 ± 0.46
	Minimum	2.05 ± 0.32	2.28 ± 0.31
	Maximum	2.94 ± 0.42	3.13 ± 0.41
Coastal cod	Mean	2.28 ± 0.31	2.49 ± 0.39
	Minimum	1.91 ± 0.27	2.15 ± 0.26
	Maximum	2.72 ± 0.38	2.93 ± 0.36
Frontal cod	Mean	2.81 ± 0.16	3.03 ± 0.35
	Minimum	2.30 ± 0.25	2.53 ± 0.24
	Maximum	3.31 ± 0.14	3.51 ± 0.13

Table 4: Differences between predicted and measured means and extremes (minimum/ maximum) $\delta^{18}O_{otolith}$ values obtained for the DST-tagged cod when using either the temperature fractionation equation by Jones and Campana (2009) or the temperature fractionation equation for lab-reared Norwegian cod by Høie et al. (2004b). Statistical differences are based on paired-samples Wilcoxon test; ns = non-significant.

		Equation	
		Jones and Campana (2009) [‰]	**Høie et al. (2004b) [‰]**
All samples	Mean	0.07 ± 0.35 (ns)	0.29 ± 0.40 ($p < 0.0001$)
	Minimum	0.28 ± 0.46 ($p < 0.01$)	0.51 ± 0.48 ($p < 0.0001$)
	Maximum	-0.10 ± 0.35 (ns)	0.11 ± 0.41 (ns)
Coastal cod	Mean	0.07 ± 0.48 (ns)	0.30 ± 0.47 ($p < 0.01$)
	Minimum	0.29 ± 0.51 ($p < 0.05$)	0.57 ± 0.54 ($p < 0.0001$)
	Maximum	-0.14 ± 0.37 (ns)	0.13 ± 0.46 (ns)
Frontal cod	Mean	0.06 ± 0.21 (ns)	0.29 ± 0.21 ($p < 0.001$)
	Minimum	0.28 ± 0.36 ($p < 0.05$)	0.51 ± 0.36 ($p < 0.01$)
	Maximum	-0.02 ± 0.32 (ns)	0.18 ± 0.32 (ns)

The range of possible salinity environments for the tagged cod resulted in an overall uncertainty of 0.41‰ in the predicted $\delta^{18}O_{otolith}$ values (Fig. 4). Measured and predicted $\delta^{18}O_{otolith}$ values were most similar under the "most probable salinity" and "minimum salinity” scenarios. The correspondence between measured and predicted $\delta^{18}O_{otolith}$ was lower when applying the other salinity scenarios (difference between mean (±SD) predicted and measured $\delta^{18}O_{otolith}$ for the different salinity scenarios (Fig. 4); most probable salinity: 0.07 ± 0.35‰, minimum salinity: -0.03 ± 0.35‰, maximum salinity: 0.17 ± 0.35‰, salinity of 34.5: -0.19 ± 0.39‰, and salinity of 35.2: 0.21 ± 0.39‰).

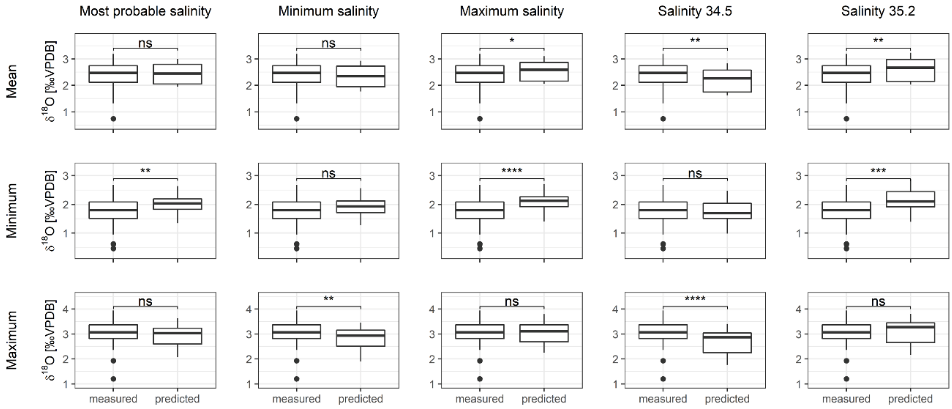

*Figure 4: Measured and predicted $\delta^{18}O_{values}$ in all DST-tagged cod otoliths assuming different salinity scenarios. Significance levels: ns = non-significant, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$ and ****: $p < 0.0001$.*

SIMS-measured and predicted mean and extremes (minimum and maximum) were generally correlated (Fig. 5, Suppl. Fig. 3). However, differences exceeded the SIMS measurement error for several tagged fish, irrespective of the ecotype. In the poorly correlated cases, the measured $\delta^{18}O_{otolith}$ values were lower than the predicted $\delta^{18}O_{otolith}$ values by a mean of 0.99‰. However, these measurements seemed to be implausible outliers as the required salinities (based on DST-recorded temperatures) have not previously been reported around Iceland. All of the outliers are from the (south)east and largely restricted to coastal cod.

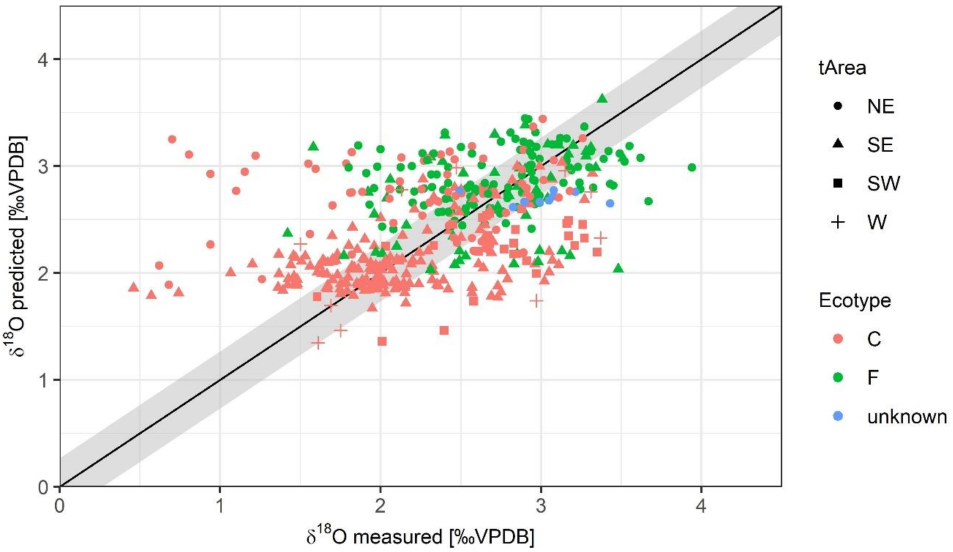

Figure 5: Predicted vs. measured $\delta^{18}O_{otolith}$ values for all DST-tagged cod assuming linear otolith growth by tagging area (tArea) and ecotype (C=coastal, F=frontal). The grey area around the 1:1 line represents the approximate analytical error of the SIMS measurement.

At maximum spatial resolution, measured and predicted $\delta^{18}O_{otolith}$ values corresponded well and showed similar fluctuations (Fig. 6). However, the predicted $\delta^{18}O_{otolith}$ time series appeared more smoothed due to a limited temporal resolution of salinity data relative to the measured $\delta^{18}O_{otolith}$.

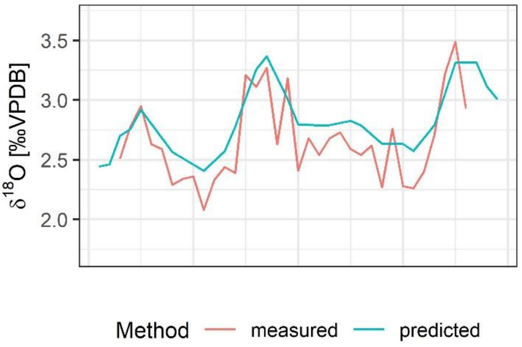

Figure 6: Example of the correspondence between measured and predicted $\delta^{18}O_{otolith}$ in one otolith specimen (frontal cod, tagging and recapture area: northeast off Iceland).

The correspondence of measured and predicted $\delta^{18}O_{otolith}$ values improved when accounting for non-linear otolith growth (SC 2), however a small divergence between measured and predicted $\delta^{18}O_{otolith}$ values remained (Fig. 7). The two growth scenarios SC 1 and SC 2 were significantly different when including both ecotypes (paired-sample

Wilcoxon-test: V = 498, n = 37, $p < 0.05$) and for coastal cod (V = 246, n = 24, $p < 0.01$), but not for frontal cod V = 45, n = 13, p = non-significant).

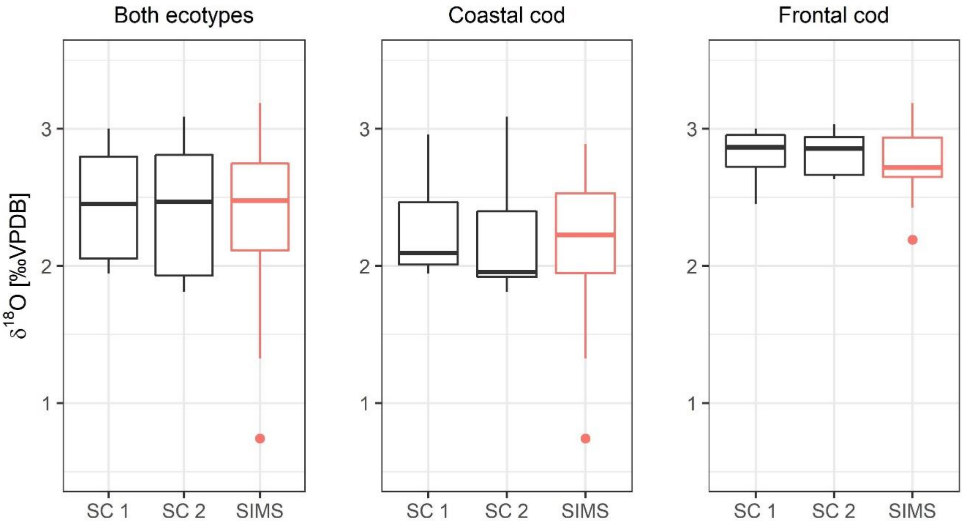

Figure 7: Predicted $\delta^{18}O_{otolith}$ *from each otolith growth scenario (SC 1, SC 2) compared with SIMS-analyzed* $\delta^{18}O_{otolith}$ *values by ecotypes.*

4 Discussion

Our results indicated that otoliths are well-suited as proxies for the temperature exposure of wild, free-swimming cod. Predicted $\delta^{18}O_{\mathrm{otolith}}$ values corresponded well with those measured *in-situ* by SIMS, especially for mean and maximum $\delta^{18}O$ values. On the other hand, measured and predicted minimum $\delta^{18}O_{\mathrm{otolith}}$ values differed significantly. In general, the SIMS-measured $\delta^{18}O_{\mathrm{otolith}}$ values were lower, implying that the SIMS measurements were overestimating the ambient temperature (Rollion-Bard et al., 2007; Shirai et al., 2018). Overestimated ambient temperatures based on isotope-ratio mass spectrometry (IRMS) measurements in previous studies provided similar results, suggesting that this is probably a bias endemic to both these analytical method (Weidman and Millner, 2000; Geffen, 2012).

There are two possible reasons for the analytical bias causing the small divergence between measured and predicted $\delta^{18}O_{\mathrm{otolith}}$ values. One could be the matrix effect of the SIMS method, whereby the different chemical compositions and structures of the otolith relative to the reference material can introduce a bias (Hane et al. (2020) and references therein). This matrix effect could have been avoided if a matrix-matched standard material had been available. Reliable biogenic aragonite references are not yet available, and calcite is used primarily to constrain the measurement reproducibility, accepting that as a reference material accuracy will be compromised. Aragonite may also behave differently than calcite under a caesium (Cs) ion beam due to its different trace element chemistry (e.g., aragonite is commonly strontium (Sr) enriched while calcite reference material is typically low in trace elements). While the calcite-based calibrations might be inaccurate, they are very precise, thus ensuring that all of the within-otolith differences are accurate. There is no standard approach to correcting SIMS-analyzed otolith δ^{18}O values for a calcite standard. However, the offset factor of 1.62 applied in this study appeared to be the best of the different approaches and performed better than the offset factor of 1.58 (Table 2, scenario 1 which had the highest accuracy of corresponding salinity estimations). This correction is not perfect as an average value is applied, which does not consider inherent mass-balance and growth rate issues.

The estimation of the ambient salinity and $\delta^{18}O_{seawater}$ composition can introduce potential errors in temperature reconstructions. Despite the feeding migration of frontal cod and the accompanying salinity changes, the match of DST-recorded temperatures and respective salinity values was more accurate for frontal cod than for coastal cod. Frontal cod are mainly found offshore and in deeper waters where salinity fluctuations are less pronounced than in coastal areas (Thorsteinsson et al., 2012). Although coastal cod do not undergo significant feeding migrations, they do migrate along the coast. The broader range of measured $\delta^{18}O_{otolith}$ values compared to predicted values suggested that cod experienced a broader range of environmental conditions than were assumed. This could be due to the fact that coastal cod are exposed to local salinity fluctuations, which are not represented in the quarterly salinity measurements conducted by the Marine and Freshwater Research Institute. Freshwater run-off by glaciers also causes salinity fluctuations, especially along the south coast of Iceland (Thórdardóttir, 1986).

Otolith stable oxygen isotopes are commonly applied to reconstruct the temperature exposure of fish, based on the assumption that the isotopic fractionation between otolith aragonite and the ambient water is in equilibrium (Kalish, 1991; Campana, 1999; Høie et al., 2003). Otolith δ^{13}C values are strongly influenced by physiological processes (Kalish, 1991; Geffen, 2012), but experimental studies have shown that otolith δ^{18}O values are driven mainly by ambient temperatures and is independent of fish metabolism (Thorrold et al., 1997; Høie et al., 2003). Other studies have suggested that physiological, kinetic, or metabolic processes (i.e., “vital effects”) influence temperature-dependent δ^{18}O fractionation. Differences in the extent of temperature-dependent δ^{18}O fractionation have been reported across life-stages, species, stocks, and across temperature-salinity combinations (Kalish, 1991; Thorrold et al., 1997; Høie et al., 2004b; Ghosh et al., 2007; Storm-Suke et al., 2007; Geffen, 2012; Darnaude et al., 2014). The use of the temperature equation by Jones and Campana (2009) has been shown to reconstruct the ambient temperature of Atlantic cod accurately (von Leesen et al., 2020). The cod-specific temperature equation of Høie et al. (2004b) resulted in a slightly lower correspondence. The mean difference between predicted $\delta^{18}O_{otolith}$ values obtained with the two equations was 0.22‰, corresponding to a temperature difference of 1.1°C, with higher predicted $\delta^{18}O_{otolith}$ values by Høie et al. (2004b). A possible reason for the difference in predicted values between the equations is that Høie et al. (2004b) was based on lab-reared juvenile cod at temperatures between 6 and 20°C. Although juvenile cod can tolerate temperatures of up to 20°C, the critical annual mean bottom temperature of cod is 12°C (Myers et al., 1997; Drinkwater, 2005). Icelandic cod, especially those off northern Iceland, are typically exposed to temperatures below 6°C all year around. Temperature-dependent fractionation of oxygen isotopes is close to that reported for inorganic aragonite at low temperatures, supporting the use of the Jones and Campana (2009) equation. Furthermore, all otoliths in this study were from mature fish and belonged to the same stock. Based on observations of vital effects in lab-reared fish, Darnaude et al. (2014) suggested that deviations between measured and predicted otolith $\delta^{18}O$ values in wild fish are more pronounced because of the greater variation in environmental exposure and metabolic uptake. However, our results showed that the isotopic composition of otoliths from wild, free-swimming cod is an accurate index of temperature exposure with no apparent evidence of vital effects.

Incorrect ambient salinity estimations can be a source of error in otolith-based temperature reconstructions. Geo-locations and migrations paths of individual fish were estimated based on known ecotype, their known migration paths, the tagging and recapture position, and the depth profile recorded by DST tags. Wrongly assigned geo-locations could cause incorrect salinity estimations resulting in inaccurately predicted $\delta^{18}O_{otolith}$ values (Darnaude et al., 2014). However, a salinity sensitivity analysis showed that the assumed ("most probable") salinity had the best correspondence between measured and predicted $\delta^{18}O_{otolith}$ values. A second potential source of error was the back-calculation of $\delta^{18}O_{seawater}$ values based on an area-specific salinity mixing line. Direct measurements of $\delta^{18}O_{seawater}$ are rarely available, and thus, the area-specific salinity mixing line is a well-established method to overcome the data limitation. Oceanographic conditions that influence the water chemistry change over long time periods and thus, were assumed to be negligible in this study. A third potential source of error was the influence of seasonal temperature variations on the otolith accretion rate, resulting in non-linear otolith growth and the over- or under-estimation of calcium carbonate accretion in certain months. The importance of intra-annual variation in otolith growth has been mentioned previously when predicting $\delta^{18}O_{otolith}$ values of wild fish (Darnaude et al., 2014). However, intra-population variations in otolith deposition rates and/or metabolic differences across populations (i.e., the occurrence of vital effects) were also observed. An assumption of non-linear otolith growth in our study generally improved the correspondence of measured and predicted $\delta^{18}O_{otolith}$, particularly of frontal cod. Our results suggested that intra-annual differences in the otolith accretion rate might be less pronounced in coastal cod. Ecotype-specific accretion rates could be due to their different temperature exposure with lower intra-annual temperature variation experienced by coastal cod, as temperature seems to drive the accretion rate of otolith growth.

To our knowledge, this is the first study that has groundtruthed the accuracy of temperature reconstructions based on routine *in-situ* SIMS otolith oxygen isotope assays of wild, free-swimming fish. Our results confirm that otoliths are well-suited as proxies for ambient temperature reconstructions. Although mean temperature exposures were accurately estimated in our study, the maximum temperatures were sometimes overestimated, an issue which affected absolute accuracy but not relative temperature changes. Although archival tags are also capable of providing temperature history, they can be limited by low or location-specific recapture rates, which is not an issue with otoliths. Indeed, the wide availability of otoliths makes them particularly suitable for paleotemperature studies.

IRMS and SIMS can provide $\delta^{18}O$-based temperature reconstructions, but both approaches have advantages and disadvantages. Although classical IRMS measurements are less expensive than SIMS assays, SIMS assays offer a higher temporal-spatial resolution of otoliths. SIMS measurements enable the investigation of weekly or even daily resolution (depending on otolith growth rate), while micromilling (IRMS) allows sub-annual (monthly) resolution at its best. Moreover, IRMS requires larger amounts of sample material than SIMS, resulting in unintended temporal averaging of IRMS $\delta^{18}O_{otolith}$ values. Furthermore, to obtain the required sample weight (usually ~ 50 µg), IRMS samples drill deeper, resulting in the mixing of different accretion layers due to the three-dimensional structure of otoliths. On the other hand, SIMS measurements suffer from the general lack of a reliable aragonite reference material, while IRMS does not. Thus, the use of SIMS is recommended when the calcite-aragonite bias can be corrected, as is the case here, or only relative temperature changes are of interest.

Conflict of Interest

All authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

Conceptualization: GvL, SEC
Formal analysis: GvL
Funding acquisition: SEC
Investigation: GvL, HB, MJW
Writing – original draft: GvL
Writing – review and editing: GvL, HB, SAH, MJW, SEC

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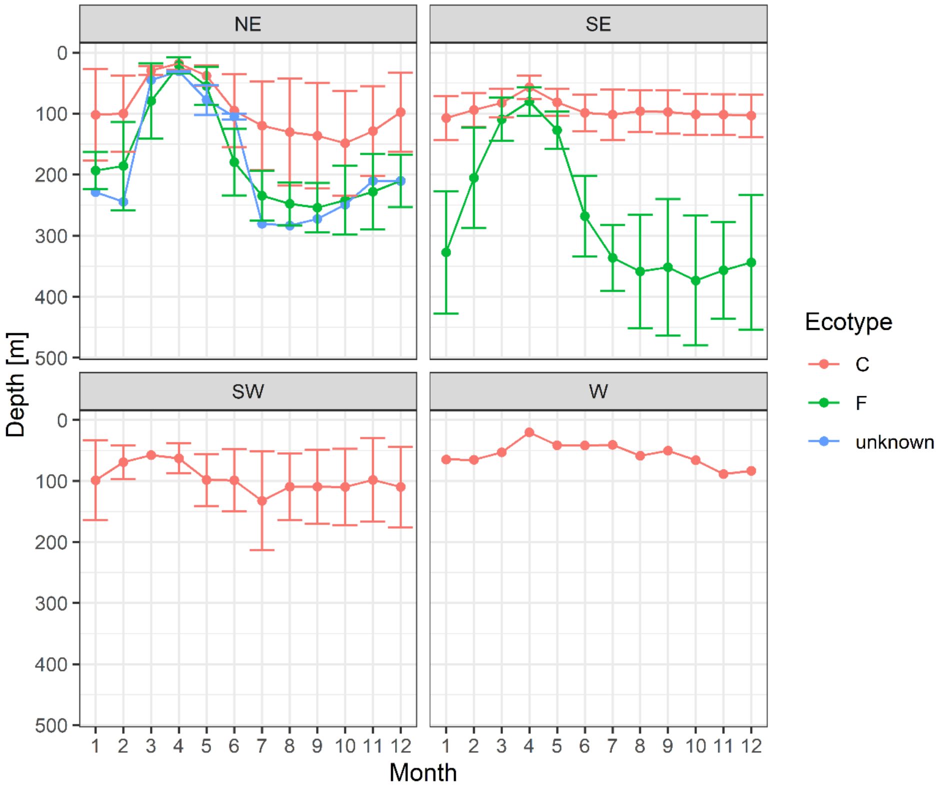
Supplementary Material

Supplementary Table 1: Details of DST-tagged cod analyzed for sub-annual $\delta^{18}O$ *signatures. Dates are given in dd/mm/yyyy format, Sex: M = male, F = female and behavior type: C = coastal, F = frontal, NA = data not available, tagging and recapture area: W = west, SW = southwest, SE = southeast, NE = northeast, N = north off Iceland, * = recapture area is offshore.*

DST ID	Release date	Recapture date	Days at liberty	Days DST	Age at tagging [yr]	Age at recapture [yr]	Sex	Behavior type	Tagging area	Recapture area
2C0526	15/04/2003	07/04/2004	358	358	10	11	M	C	SE	SE
1C0593	23/04/2003	06/03/2005	683	683	8	10	F	F	NE	NE
1C0595	23/04/2003	11/04/2005	719	719	7	9	F	F	NE	NE
1C1366	20/04/2004	08/04/2005	353	352	7	8	F	F	SE	SW
1C0605	24/04/2003	05/03/2005	681	681	7	9	M	F	NE	N
1C1270	19/04/2004	06/04/2005	352	352	6	7	F	C	SE	SE
3M1052	23/04/2002	27/10/2003	552	424	10	11	F	F	NE	E*
2M1056	23/04/2002	30/03/2005	1072	423	8	11	F	NA	NE	NE
2M1060	23/04/2002	31/03/2004	708	424	7	9	F	C	NE	NE
2M1061	23/04/2002	08/03/2004	685	424	8	10	F	C	NE	NE
2M1074	24/04/2004	20/01/2004	636	423	5	7	M	C	NE	NE
1M1085	24/04/2004	06/03/2004	682	422	7	9	F	C	NE	NE
1M1087	24/04/2004	08/11/2003	563	422	7	8	M	C	NE	N
1C1315	14/04/2004	31/03/2005	351	350	7	8	M	C	W	W
1C1279	19/04/2004	03/04/2005	349	348	8	9	M	C	SE	SE
1C0431	12/04/2003	05/09/2004	512	512	6	7	NA	C	SE	SE

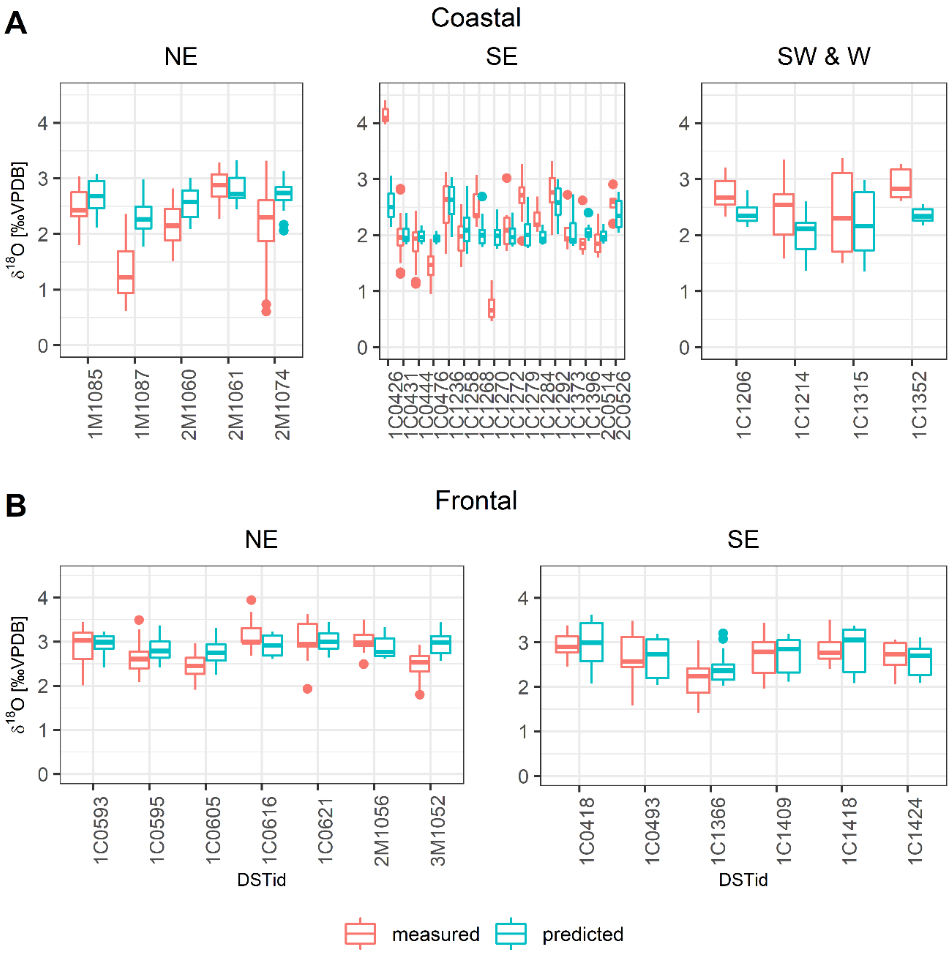
1C0444	12/04/2003	11/03/2005	699	699	5	7	M	C	SE	SE
1C0476	13/04/2003	12/06/2004	426	426	6	7	M	C	SE	SE
1C0493	14/04/2003	05/05/2004	387	387	9	10	M	F	SE	SE
2C0514	15/04/2003	02/09/2004	506	506	9	10	F	C	SE	SE
1C0418	12/04/2003	22/03/2004	345	345	9	10	M	F	SE	SE
1C1236	18/04/2004	29/03/2005	345	345	5	6	F	C	SE	NE
1C0426	12/04/2004	19/03/2004	342	342	7	8	F	C	SE	SE
1C1352	16/04/2004	18/03/2005	336	336	6	7	NA	C	SW	SW
1C1258	18/04/2004	16/05/2005	393	393	4	5	M	C	SE	SE
1C1272	19/04/2004	15/03/2005	330	330	6	7	F	C	SE	SE
1C0616	24/04/2003	15/03/2004	326	326	6	7	F	F	NE	NE
1C1396	22/04/2004	09/03/2005	321	321	6	7	M	C	SE	SW
1C1418	23/04/2004	08/03/2005	319	319	8	9	M	F	SE	SE
1C1284	19/04/2004	24/02/2005	311	309	12	13	M	C	SE	SE
1C1292	20/04/2004	25/02/2005	311	311	6	7	M	C	SE	SE/E
1C1214	16/04/2004	18/02/2005	308	308	4	5	F	C	SW	SW/W
1C1268	19/04/2004	21/02/2005	308	308	6	7	M	C	SE	E
1C1206	16/04/2004	13/02/2005	303	300	7	8	M	C	SW	SE
1C1373	21/04/2004	15/02/2005	300	299	6	7	M	C	SE	E
1C1409	22/04/2004	09/05/2005	382	382	9	10	M	F	SE	E*
1C1424	23/04/2004	04/05/2005	376	376	10	11	M	F	SE	SE
1C0621	24/04/2003	08/09/2004	503	503	9	10	F	F	NE	NE*



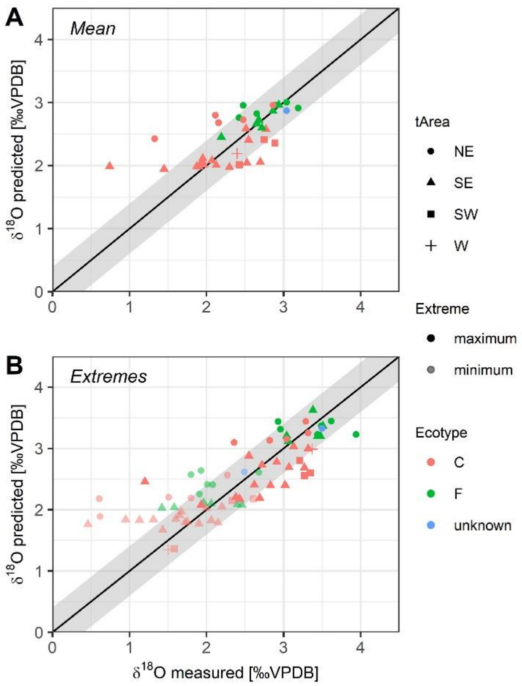
Supplemenary Figure 1: Mean monthly depth and standard deviation for each tagging area (W=west, SW=southwest, SE=southeast, and NE=northeast off Iceland) and ecotype recorded by DST tags.

Supplementary Table 2: Salinity variation around Iceland (W=west, SW=southwest, SE=southeast, and NE=northeast off Iceland) between 2002 and 2005. Season: 1=January-March, 2=April-June, 3=July-September, and 4=October-December.

		Season				
Area	**Year**	**1**	**2**	**3**	**4**	**Variation**
W	2002	35	35-35.1	35.1	35	0.1
	2003	35	35	35-35.1	35	
	2004	35	35	35.1	35	
	2005	35.1	35	35.1	35.1	
SW	2002	35.1	35.2	35.1-35.2	35.1	0.15
	2003	35-35.2	35.2	35.2	35.1-35.2	
	2004	35.2	35.2	>35.1	35-35.2	
	2005	35.1-35.2	35.2	35.3	35.1-35.2	
SE	2002	34.7-35.2	35.1-35.2	34.7-35.2	34.5-35.2	0.6
	2003	34.7-35.2	34.9-35.2	34.9-35.2	34.8-35.3	
	2004	34.9-35.2	34.8-35.2	35	34.8-35.3	
	2005	34.7-35.2	34.6-35.2	34.6-35.2	34.7-35.2	
NE	2002	34.6-34.7	34.6-34.7	34.7-34.8	34.5	0.25
	2003	34.7-34.9	34.8-34.9	34.9	34.7-34.8	
	2004	34.8	34.8-34.9	35	34.8	
	2005	34.8	34.6-34.7	34.6-34.8/9	34.7	



Supplementary Figure 2: Measured and predicted otolith δ^{18}O of (A) coastal and (B) frontal cod by tagging area (W=west, SW=southwest, SE=southeast, and NE=northeast off Iceland).



Supplementary Figure 3: Predicted vs. measured (A) mean and (B) minimum and maximum δ^{18}Ootolith values for all DST-tagged cod by tagging area (tArea) and ecotype (C=coastal, F=frontal). Extremes show minimum (50% color transparency) and maximum (full-color intensity). The grey area around the 1:1 line represents the approximate analytical error of the SIMS measurement.