

# Temperature exposure in cod driven by changes in abundance

Gotje von Leesen, Bjarte Bogstad, Einar Hjörleifsson, Ulysses S. Ninnemann, and Steven E. Campana

**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 (*Gadus morhua*) 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 ( $\delta^{18}\text{O}_{\text{otolith}}$ ). Linear mixed effect models were used to identify and quantify the density-dependent temperature exposure 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 ( $p < 0.001$ ). Our results suggest that thermal preferences and density-dependent effects can be used to forecast potential redistribution scenarios of fish as oceans warm.

**Résumé :** Les animaux choisissent activement les habitats de meilleure qualité sur le plan de l'aptitude, cette qualité étant en bonne partie modulée par la température. Nous avons reconstitué des chronologies d'abondance de la population, d'isotopes de l'oxygène et de températures pour les populations de morue (*Gadus morhua*) islandaise et de l'Atlantique du Nord-Est (ANE) afin de déterminer si leur sélectivité thermique au cours des 100 dernières années était modulée par la hausse des températures de l'eau ou encore des variations de l'abondance. Des zones de croissance annuelle pour différentes étapes immatures et matures du cycle biologique de morues prélevées du sud de l'Islande et de la région de Lofoten (Norvège) ont été obtenues par microabrasion d'otolithes d'adultes puis ont fait l'objet d'analyses d'isotopes stables de l'oxygène ( $\delta^{18}\text{O}_{\text{otolith}}$ ). Des modèles linéaires à effets mixtes ont été utilisés pour cerner et quantifier l'exposition à la température dépendante de la densité pour les deux populations de morue. Les résultats indiquent que les morues islandaises migraient vers des eaux plus chaudes quand leur abondance augmentait ( $p < 0,05$ ), alors que les morues de l'ANE migraient vers des eaux plus froides ( $p < 0,001$ ). Nos résultats semblent indiquer que les préférences de température et les effets dépendants de la densité peuvent être utilisés pour prédire d'éventuels scénarios de redistribution de poissons découlant du réchauffement des océans. [Traduit par la Rédaction]

## 1. Introduction

Habitat suitability is defined by a set of abiotic and biotic factors that determine the geographical distribution of organisms. Animals have a range of habitats that they can tolerate, but they actively select among habitats to maximize their evolutionary fitness (Swain and Wade 1993; Fretwell and Lucas 1969). Food availability, predator abundance, terrestrial humidity, pH, salinity, depth and temperature, or any combination thereof, may all differ among habitats. Temperature is one aspect of habitat selection that 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 range that 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

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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, Atlantic cod (*Gadus morhua*) 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 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, 1997). In recent years, both cod populations have increased again, with the spawning stock biomass of NEA cod still being high after a record high in 2013 (Kjesbu et al. 2014). The broad geographical distribution of cod implies a wide temperature range from below  $-1\text{ }^{\circ}\text{C}$  up to  $20\text{ }^{\circ}\text{C}$  with a critical annual mean bottom water temperature of  $12\text{ }^{\circ}\text{C}$ , 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 that are characterized by wider temperature fluctuations (Bardarson et al. 2017). Southern cod populations that are confined to relatively shallow waters ( $<100\text{ m}$ ) experience temperature changes of up to  $10\text{ }^{\circ}\text{C}$  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 that 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 of aragonitic calcium carbonate in a noncollagenous 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  $\delta^{18}\text{O}$  of otolith aragonite is negatively correlated to the ambient water temperature of the fish; the higher the water temperature, the lower the  $\delta^{18}\text{O}_{\text{Otolith}}$  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). In many cases, the ambient temperature experienced by a moving fish differs from that of the environmental temperature recorded at fixed locations, with the ambient temperature being the more accurate measure of temperature

exposure. Instrumental water temperature time series are further limited by data availability; sea-surface temperature time series began in the early 20th century, while temperature-at-depth time series only began much later 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 that 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. Materials 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) that 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 northern 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. Although the annual sample size was too small for adequate representation of a given year, it was considered sufficient for determining long-term trends.

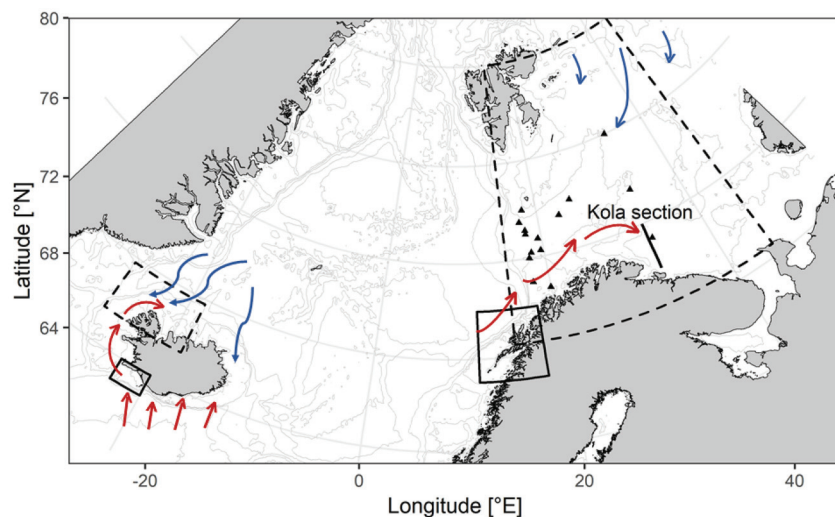
To avoid otolith breakage during preparation, otoliths were embedded in epoxy and then sectioned transversely through the core using a Buehler IsoMet 1000 Precision Saw (ITW Test & Measurement GmbH, Esslingen, Germany) equipped with a 15LC IsoMet Diamond Wafering blade to get otolith sections of  $\sim 1\text{ mm}$  thickness. Silicone EPDM (silicone combined with a synthetic rubber) molds, PolyLite 32032-20 resin and hardener Narpol

**Table 1.** Northeast Arctic cod otolith samples collected per gear-type aggregated by 5-year blocks.

Time period	Gear type						
	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

**Note:** Most 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 ( $n = 1$ ).

**Fig. 1.** Main spawning grounds (solid line) in southern Iceland and western Norway (Lofoten) and feeding grounds (dashed line) in northern Iceland and the Barents Sea. Mature, spawning cod migrate between the warmer waters of the spawning grounds off southern Iceland and the Lofoten, respectively, and the colder waters of the feeding grounds in northern Iceland and the Barents Sea, respectively. Locations of  $\delta^{18}\text{O}_{\text{seawater}}$  and salinity samples for the Norwegian salinity mixing curve (triangles). The line represents the Kola transect of in situ water temperature and salinity measurements. Arrows indicate the mean oceanographic currents around Iceland and the Norwegian ecosystem. Warm water originates from the Atlantic (red arrows) and cold water from Arctic inflow (blue arrows). The map was created based on the bathymetric (Amante and Eakins 2009) and shoreline (Wessel and Smith 1996) data.

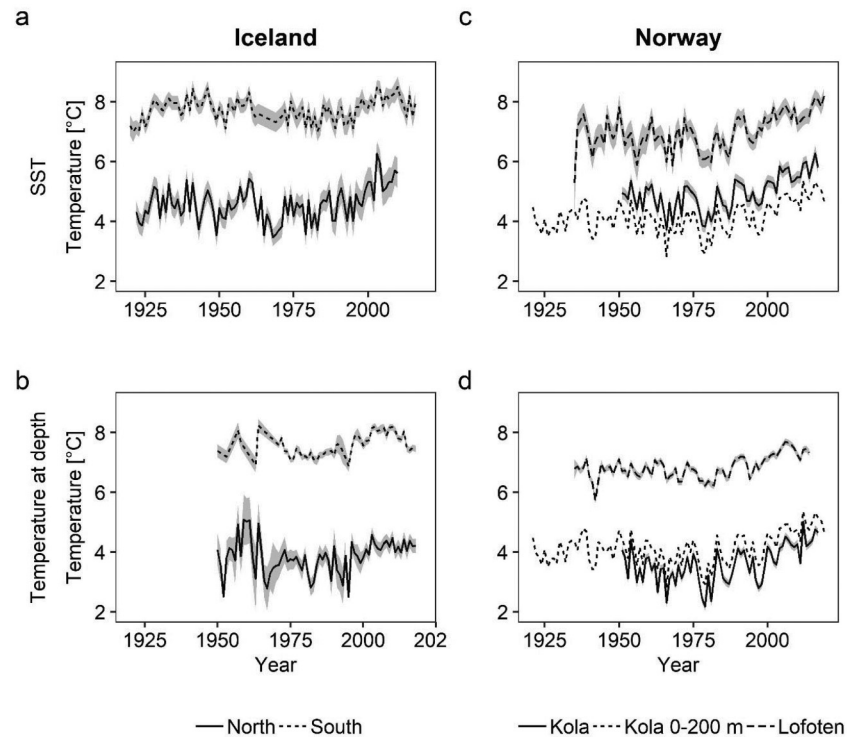


Peroxide 1 (a methyl ethyl ketone peroxide) were used for embedding. Otolith sections were imaged prior to milling with an Olympus DP 74 high-resolution (5760 × 3600 pixels (3 CMOS)) camera mounted on a Leica S8AP0 stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany) using CellSens Standard software (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 used to extract otolith material. Otolith sections were glued on glass slides using Crazy 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-year-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

**Fig. 2.** Sea surface temperature (SST) and water temperature at 150 m (Norway) or 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.



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  $\mu\text{m}$  depth (20–25 passes with a drill depth of 30  $\mu\text{m}$  per pass), which was usually adequate to collect the intended 50  $\mu\text{g}$  of sample material. A minimum of 15  $\mu\text{m}$  was required by the isotope-ratio mass spectrometer (IRMS).

Measurements of calcium carbonate samples for oxygen isotope content were conducted at EARLAB 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  $\leq 0.08\text{‰}$  and  $\leq 0.04\text{‰}$  for  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ , respectively, for sample sizes greater than 13  $\mu\text{g}$  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 Vienna Pee Dee Belemnite (VPDB) scale calibrated using NBS-19 and NBS-18.

There was no evidence of epoxy contamination on the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  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. Study area

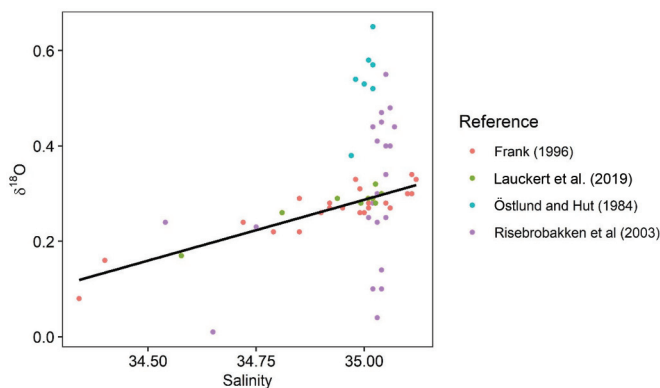
Icelandic waters were characterized by two warming events in the last century (Jakobsson and Stefánsson 1998; Malmberg and Valdimarsson 2003) (Fig. 2). Natural variation caused the first warming event that started in the 1920s and temperatures remained high until cooling began in the 1960s. The second

warming event started in the 1990s due to the increasing release of greenhouse gases in the atmosphere (Hanna et al. 2006). 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  $\leq 0$  °C. The warm and saline Atlantic water along the south coast is a downstream branch of the North Atlantic Current. 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 sea surface temperature (SST) and water temperatures at 200 m depth is greater in the north than in the south, where the seawater forms a homogeneous and thick layer extending to several hundred metres depth (Jónsson 1999; Malmberg and Valdimarsson 2003).

## 2.3. Salinity and water temperature time series

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  $\delta^{18}\text{O}_{\text{seawater}}$  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 (GLMs). 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).

**Fig. 3.** Salinity– $\delta^{18}\text{O}$  mixing line (3) (see Section 2.3) excluding the data points by Östlund and Hut (1984) and Risebrobakken et al. (2003) for the Barents Sea between 50 and 400 m depth.



The ambient temperature reconstruction of the Norwegian samples followed an approach similar to that used for Iceland. As  $\delta^{18}\text{O}_{\text{seawater}}$  is needed for the reconstruction of ambient temperatures from carbonate samples but was not available for the years represented by our samples, we estimated  $\delta^{18}\text{O}_{\text{seawater}}$  values from salinity using a salinity mixing curve for the Barents Sea. Salinity and  $\delta^{18}\text{O}_{\text{seawater}}$  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  $\delta^{18}\text{O}_{\text{seawater}}$  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. 3):

$$(1) \quad \delta^{18}\text{O}_{\text{seawater}} = 0.37 \times S - 12.46$$

where  $\delta^{18}\text{O}_{\text{seawater}}$  is the oxygen isotope content (‰ on the standard mean ocean water (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  $\delta^{18}\text{O}_{\text{seawater}}$ –salinity relationship due to its impact on the salinity with much smaller fractionation of  $\delta^{18}\text{O}$  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  $\delta^{18}\text{O}_{\text{seawater}}$  that cod experienced, and thus the sea ice related spread of salinity has only minor influence on  $\delta^{18}\text{O}_{\text{otolith}}$  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):

$$(2) \quad \delta^{18}\text{O}_{\text{seawater}} = 0.34 \times S - 11.47$$

( $n = 38$ ,  $R^2 = 0.3$ , 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:

$$(3) \quad \delta^{18}\text{O}_{\text{seawater}} = 0.26 \times S - 8.64$$

( $n = 32$ ,  $R^2 = 0.83$ , intercept and salinity:  $p < 0.001$ ). An error analysis was performed to quantify possible uncertainties in the reconstructed ambient temperatures of NEA cod caused by a high

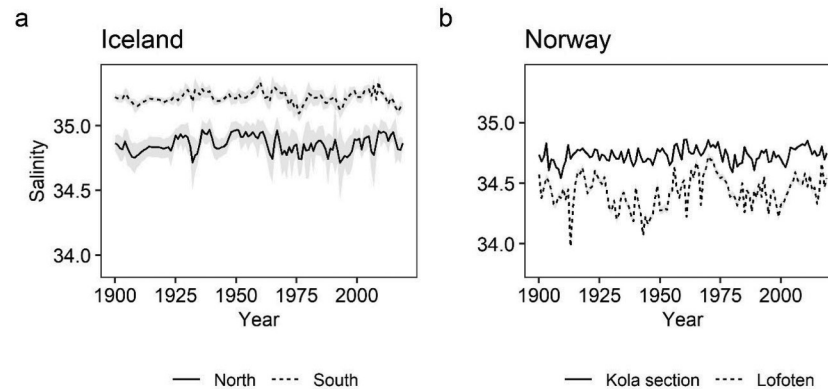
variance of  $\delta^{18}\text{O}_{\text{seawater}}$  at high salinities in the salinity mixing line (eq. 1).

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. 4). 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).

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 109 v4.2.1 dataset (Good et al. (2013); version EN4.2.1; downloaded from <http://apdr.csoest.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 larger area (grid size  $1^\circ \times 1^\circ$ ) and thus do not capture local salinity fluctuations. The small data range of salinity values ( $\sim 1.25$ ) in the Lofoten area is an additional explanation of the weak correlation of modelled and measured salinity time series in that area.

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 northwards 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 nonspawning mature cod are found in the Barents Sea all year around.

**Fig. 4.** Modelled salinity time series for (a) Iceland (depth range of 50–200 m for southern and northern Iceland) and (b) Norway (depth range Lofoten: 50–150 m, Kola section: 50–200 m). Standard deviation indicated by shading. Hadley EN4.2.1 analyses I09 data downloaded from APDRC LAS7 for public.



As was done with the salinity time series, standardized SST (depth < 50 m) 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.

#### 2.4. 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):

$$(4) \quad T(^{\circ}\text{C}) = -(\delta^{18}\text{O}_{\text{otolith}} - \delta^{18}\text{O}_{\text{seawater}}) \times 0.206^{-1} + 18.010$$

where  $\delta^{18}\text{O}_{\text{otolith}}$  is the oxygen isotope composition of the otolith aragonite and  $\delta^{18}\text{O}_{\text{seawater}}$  is the oxygen isotope composition of the ambient seawater. All isotope values for  $\delta^{18}\text{O}$  (and  $\delta^{13}\text{C}$ ) otolith carbonate are reported in ‰ on VPDB scale. Seawater values were corrected from SMOW 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  $\delta^{18}\text{O}_{\text{seawater}}$  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. 2020). When an age 9+ fish had not spawned by age 8, the sample was considered a non-spawner that did not migrate to the Lofoten. Samples of age 3 were always defined as nonspawners. 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, 2020).

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 area 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 that showed spawning checks migrated to the Lofoten area for spawning.

## 2.5. Population dynamics

### 2.5.1. NEA cod

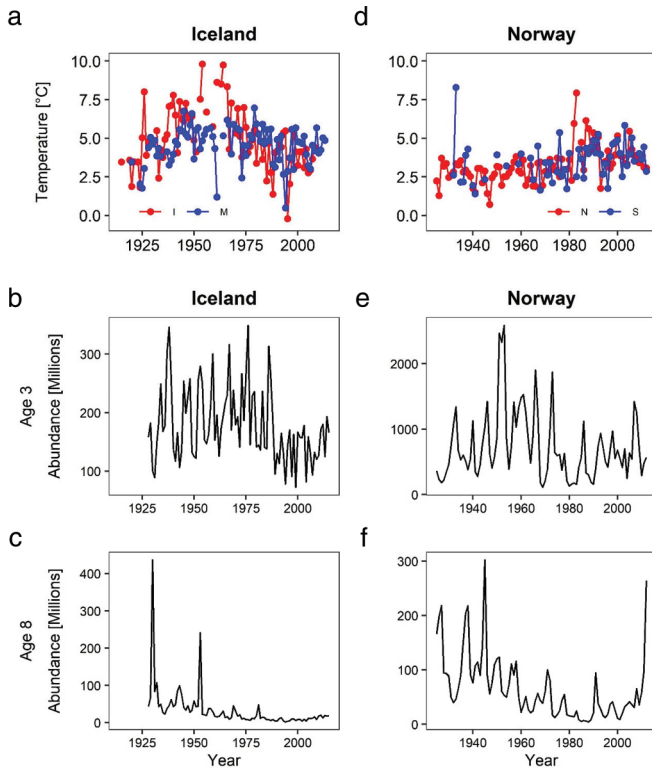
During the last 100 years, the population of NEA cod underwent major fluctuations with an overall decline in population size. In recent years, the population size increased again (Fig. 5). Abundance at age 3 tended to be higher prior to 1970 in each population compared to afterwards. The official stock dynamics time series used by ICES – Arctic Fisheries Working Group starts in 1946 and some changes were applied to make the pre-1946 series (virtual population analysis (VPA) back to 1913 reconstructed by Hysten (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 Hysten (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. For this study, we used age 3 and age 8 abundance data from the most recent stock assessment (ICES 2020).

### 2.5.2. Icelandic cod

The abundance of age 3 Icelandic cod was relatively constant over the period 1928 to the 1980s, abruptly declined in the 1980s followed by minor increases 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 from Greenland was estimated for the following years and ages: 1930: 8, 1933: 9, 1953: 8, 1958: 9, 1959: 9, 1960: 10,

**Fig. 5.** Reconstructed ambient temperature of (a) Icelandic and (d) Northeast Arctic (NEA) cod and abundance at age 3 and 8 of Icelandic (b and c) and NEA (e and f) cod. Reconstructed ambient temperatures of (a) immature cod and (d) nonspawners are shown in red, (a) mature cod and (d) spawners are in blue.



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 reported in ICES 2019; while the three immigration events prior to 1955 are only estimated for super-abundant cohorts (1922, 1924 and 1945), with the year and the age of the immigration based on anomalies in the catch at age information. The immigration events of the years 1922 and 1924 were also supported by tagging studies by Hansen et al. (1935). The natural mortality was scaled to 0.2 for all age groups. The estimated abundance-at-age based on the model results were used in subsequent analysis.

**2.6. 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 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. 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 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 ( $n = 279$ ). Year class 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 ( $AIC_c$ ) 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  $AIC_c$  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. 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**

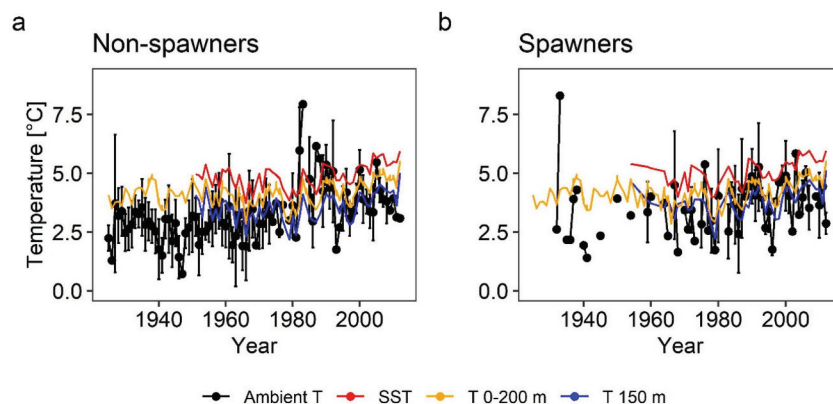
Salinity was higher in the Kola section than in the Lofoten area with more pronounced year-to-year fluctuations in the Lofoten area. Temperature patterns were similar in both regions with colder temperatures measured in the Kola section than in the Lofoten area (Fig. 2). The Barents Sea was subject to 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.

Icelandic waters were characterized by two warming events in the last century (Jakobsson and Stefánsson 1998; Malmberg and Valdimarsson 2003) (Fig. 2). 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  $\leq 0$  °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 homogeneous and thick layer extending to several hundred metres 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 2.5–3.0 °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 2.5–3.0 °C is well in line with observations for the Kola section.

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**Fig. 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. Nonspawners included immature (age 3) and nonspawning mature (age 8) NEA cod.



### 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  $\delta^{18}\text{O}_{\text{otolith}}$  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 nonspawners (immature and nonspawning mature cod) was 3.21‰ (2.19‰–3.91‰) while that for spawners was 3.07‰ (2.12‰–3.68‰). The sample size of nonspawners 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 of mature cod at age 8 increased to 0.7 in 2015 with year-to-year variations ranging from 0.02 to 0.94 (see online Supplementary Fig. S1<sup>1</sup>).

Oxygen isotopes of Icelandic cod otolith annuli had a mean  $\delta^{18}\text{O}_{\text{otolith}}$  of 2.60‰ (1.06‰–4.02‰); the mean  $\delta^{18}\text{O}_{\text{otolith}}$  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 (eq. 4, the change in  $^{18}\text{O}$  of otolith aragonite was negatively correlated to the water temperature; the higher the water temperature, the lower the  $\delta^{18}\text{O}_{\text{otolith}}$  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 (Supplementary Fig. S1<sup>1</sup>).

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 (3) was 3.2 °C with warmer temperatures for spawners (3.7 °C, ranging from 0.8 to 8.3 °C) than for nonspawners (3.1 °C, ranging from –0.4 to 8.0 °C).

Of the two scenarios described in Section 2.3, 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 at 200 m was 0.08 °C, but was 0.92 °C between the ambient water temperature and the 0–200 m time series and 1.42 °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.

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

	Temperature (°C)		
	Eq. 1	Eq. 2	Eq. 3
All samples	3.3	3.0	3.2
Nonspawning NEA cod	3.1 (–0.4 to 7.9)	2.8 (–0.6 to 7.7)	3.1 (–0.4 to 8.0)
Spawning NEA cod	3.7 (0.8 to 8.3)	3.5 (0.6 to 8.1)	3.7 (0.8 to 8.3)

Reconstructed ambient temperatures were slightly colder when excluding the data points by Risebrobakken et al. (2003) and slightly warmer when excluding both 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 (3) was used for ambient temperature reconstructions in this paper. Sample and depth areas where sea ice has had a strong influence likely explain the high variance at a salinity of ~35.

### 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 ( $\Delta\text{AIC}_c > 2$ ). 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.

#### 3.3.2. Icelandic cod

The temperature exposure ( $\delta^{18}\text{O}_{\text{otolith}}$ ) of the Icelandic cod population was significantly correlated with abundance at age ( $p < 0.05$ ),

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2020-0424>.

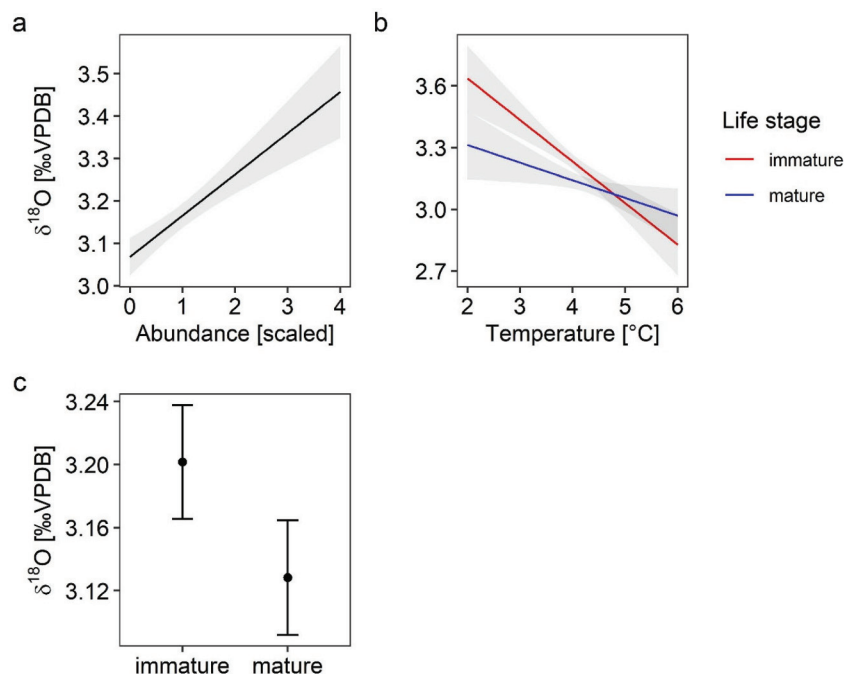


**Table 3.** Fixed and random effects estimates and confidence interval (CI) of the optimal model for Norwegian  $\delta^{18}\text{O}_{\text{Otolith}}$ .

Predictor	$\delta^{18}\text{O}_{\text{Otolith}}$		<i>p</i>	MAE	RMSE
	Estimate	CI			
<b>Fixed effects</b>					
(Intercept)	3.94	3.64 to 4.25	<b>&lt;0.001</b>	—	—
Abundance	0.10	0.06 to 0.13	<b>&lt;0.001</b>	0.221	0.279
Temperature	-0.20	-0.28 to -0.13	<b>&lt;0.001</b>	0.201	0.246
Life stage	-0.56	-0.98 to -0.13	<b>&lt;0.05</b>	0.223	0.304
Temperature × life stage	0.12	0.01 to 0.22	<b>&lt;0.05</b>	Immature: 0.219 Mature: 0.156	0.260 0.193
<b>Random effects</b>					
$\sigma^2$	0.05				
$\tau_{00}$ Fish_ID	0.02				
ICC	0.29				
$N_{\text{Fish\_ID}}$	223				
Observations	437				
Marginal $R^2$ / conditional $R^2$	0.148 / 0.397				

**Note:** Residual variance ( $\sigma^2$ ), the variance associated with the tested effects ( $\tau_{00}$ ) and their ICC (intraclass correlation coefficient) is given. Significant *p* values are bold. Mean absolute error (MAE) and root mean squared error (RMSE) are also shown.

**Fig. 7.** Predicted effects of cod abundance and temperature on  $\delta^{18}\text{O}_{\text{Otolith}}$  of the NEA cod. VPDB, Vienna Pee Dee Belemnite.



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 temperature.

**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:

111–2588 million; age 8: 4–302 million) of the last 100 years, the ambient temperature of NEA cod decreased by 1.9 °C. The  $\delta^{18}\text{O}_{\text{Otolith}}$  values of NEA cod were significantly correlated with the environmental water temperature (depth range: 0–200 m), while they were not significantly correlated for Icelandic cod. Otolith  $\delta^{18}\text{O}$  values of both stocks decreased with increasing environmental water temperature due to the negative correlation of water temperature and stable oxygen isotopes.

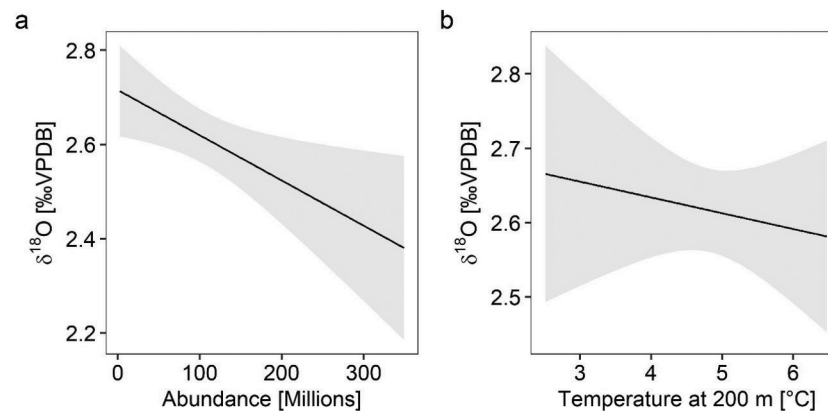
**4. Discussion**

Stable oxygen isotope records indicated that the temperature selectivity of cod was mainly driven by changes in abundance, but the resulting response varied between populations. The

**Table 4.** Fixed and random effects estimates and confidence interval (CI) of the optimal model for Icelandic  $\delta^{18}\text{O}_{\text{otolith}}$ .

Predictor	$\delta^{18}\text{O}_{\text{otolith}}$		<i>p</i>	MAE	RMSE
	Estimate	CI			
<b>Fixed effects</b>					
(Intercept)	2.82	2.41 to 3.22	<b>&lt;0.001</b>	—	—
Abundance	-0.010	-0.013 to -0.006	<b>&lt;0.05</b>	0.313	0.412
Temperature at 200 m	-0.02	-0.09 to 0.05	0.554	0.331	0.440
<b>Random effects</b>					
$\sigma^2$	0.13				
$\tau_{00}$ Fish_ID	0.06				
ICC	0.30				
$N_{\text{Fish\_ID}}$	163				
Observations	286				
Marginal $R^2$ /conditional $R^2$	0.033/0.321				

**Note:** Residual variance ( $\sigma^2$ ), the variance associated with the tested effects ( $\tau_{00}$ ) and their ICC (intra-class correlation coefficient) is given. Significant *p* values are bold. Mean absolute error (MAE) and root mean squared error (RMSE) are also shown.

**Fig. 8.** Effects of the variables predicted by the model of  $\delta^{18}\text{O}_{\text{otolith}}$  of the Icelandic cod. Values of  $\delta^{18}\text{O}_{\text{otolith}}$  were significantly correlated with (a) abundance at age ( $p < 0.05$ ), but not with (b) temperature at 200 m. VPDB, Vienna Pee Dee Belemnite.

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 1969; Rosenzweig 1991). When abundance increases, fish expand their temperature exposure to previously unfavourable thermal habitats, which have now become equally attractive in terms of fitness. The ambient temperature of NEA cod decreased with increasing abundance and thus, also included suboptimal 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 contained within 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 causing reduced growth (Pörtner et al. 2001; Barton and Barton 1987; Donaldson 1990; Orlova et al. 2005). In periods of increasing abundance, a distributional range extension of NEA cod into the colder waters of the eastern and northern Barents Sea has been observed (Ottersen et al. 1998; Kjesbu et al. 2014). 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°30'N, 66°E–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 eastwards 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 already has and it appears likely to further extend its distribution into colder waters further north and east in high abundance years in combination with the observed increase of water temperatures (Ottersen et al. 1998; Kjesbu et al. 2014; Skagseth et al. 2020). 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, presumably due to the range of habitable depths in each stock area. As their population increased, NEA cod have been able to expand into the shallow areas in the northern and eastern Barents Sea. In contrast, Icelandic cod have had more limited expansion possibilities, as there were no uninhabited shallow areas to occupy. Therefore, Icelandic cod have mainly stayed in the same area although with some movement to the north, and thus have experienced warmer ambient temperatures (Campana et al. 2020). Complex 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.

The fixed effects in our model explained only a small percentage of the variance (3.3% and 14.8% for the Icelandic and NEA cod, respectively) with a higher percentage of the variance explained by the random effect (Fish ID, 25%–30%). Thus, the temperature exposure of Icelandic and NEA cod was mainly driven by individual (fish)-specific effects rather than by environmental factors (fixed effects). The selected three fish per calendar year might represent minimum and maximum temperature exposure and not the population level average. A higher samples size could possibly increase the percentage of variance explained by the fixed effects and simultaneously decrease the percentage of variance explained by the random effect. Prey abundance (food availability) and other environmental factors (e.g., depth, salinity, geolocation, spawning migration and maturity) may affect the habitat selection and thus, the temperature selection of cod, and would have undoubtedly increased the predictive power of our model. However, these data are very limited. Cod is a generalist feeder, with capelin (*Mallotus villosus*) being the main prey of Icelandic (Pálsson 1983) and NEA (Holt et al. 2019) cod. However, the capelin stock dynamic time series only started in the late 1970s, and thus, half of the  $\delta^{18}\text{O}_{\text{otolith}}$  time series would have been excluded in our data analysis.

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 with 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 that might not be well-suited as nursery grounds due to altered temperature conditions. Thus, next to environmental temperature and abundance, the distribution of cod is also driven by

the dispersal of their larvae influenced by (changing) oceanographic currents. 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 and Lassen 1996). The Iceland–Greenland transport helps explain peaks in abundance of age 8 Icelandic cod, which are not evident in abundance at age 3 before the immigration event. 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). The Iceland–Greenland connection is of importance when studying the temperature exposure of Icelandic cod. Immigrants from Greenland have been exposed to colder temperatures prior their return to Iceland as waters off eastern Greenland are at least 2 °C colder than those of northern Iceland (Bacon et al. 2014). 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 3.2 °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 nonspawners. 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).

This study used  $\delta^{18}\text{O}_{\text{otolith}}$  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. Various sources of error were identified that could impact the accuracy of the ambient temperature reconstructions. Use of cod-specific  $\delta^{18}\text{O}$  fractionation temperature equations, local salinity mixing line and salinity time series reduces the uncertainties around our temperature estimates for cod. Direct  $\delta^{18}\text{O}_{\text{seawater}}$  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  $\delta^{18}\text{O}_{\text{seawater}}$  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. Nevertheless, more  $\delta^{18}\text{O}_{\text{seawater}}$  measurements, especially for the Norwegian and Barents Sea, would further improve the salinity mixing lines and their spatiotemporal variability. 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. The offset of 0.4 between measured and modelled salinity time series in the Lofoten has only a small effect on reconstructed ambient water temperatures. The ambient temperatures of nonspawning NEA cod are not affected as they are in the Barents Sea all year around and spawning NEA cod are in the Lofoten for only two months a year. Thus, the salinity of the Lofoten only contributes 20% to the reconstructed mean annual ambient water temperatures. 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 become even lower if it was assumed that they remained in the colder, less saline waters off northern Iceland all year around.

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 suboptimal, even if colder waters are available (Neat and Righton 2007). Ontogeny and fisheries exploitation is another potential explanation for the deepening of fish (Frank et al. 2018), but this was not investigated in this study.

Vertical migration of NEA cod has been observed (Ingvaldsen et al. 2017), but it does not seem to be a response to increasing water temperatures. The Barents Sea is relatively shallow with an average depth of around 230 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). The observed vertical movement of NEA cod is possibly explained by density-dependent effects to avoid competition for food (Kjesbu et al. 2014) and (or) by cod, which shows high-risk behaviour surpassing the boundaries of their primary feeding area and thus, were observed in deeper waters (Sih et al. 2004). 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).

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 redistribution in warming ocean as population abundances change.

#### Author contributions

The study was conceived, designed and coordinated by Gotje von Leesen and Steven Campana. All authors contributed to lab work, data collection and (or) data interpretation. Gotje von Leesen 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 are publicly available from the Asia-Pacific Data-Research Center.

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