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Original Article

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;

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 $\delta^{18}O_{otolith}$ 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.
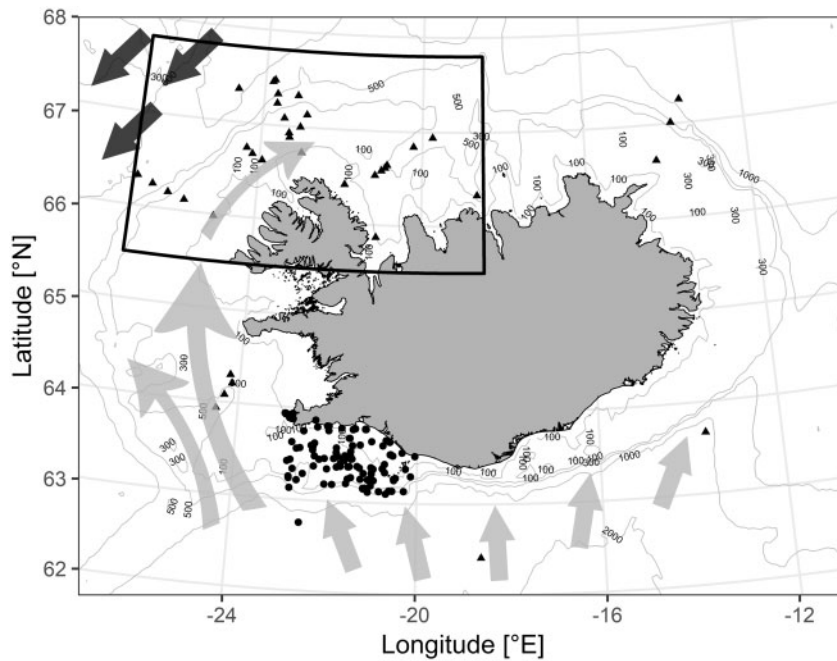

Figure 1. Sampling locations of otoliths (black circles) in the south off Iceland (main spawning ground) and locations of $\delta^{18}O$ seawater and salinity samples for the salinity mixing line (triangles). The polygon shows the main feeding and nursery area in the north and northwest of Iceland. The 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 $\leq 0.8\text{‰}$ and $\leq 0.4\text{‰}$ for $\delta^{18}O$ and $\delta^{13}C$, 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 $\delta^{13}C$ and $\delta^{18}O$ values. As a test for contamination, epoxy samples were added to in-house marble standards. Within the standard 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 $\delta^{18}O_{\text{seawater}}$ is needed for the reconstruction of ambient temperatures from carbonate samples but was not available for our samples, we estimated $\delta^{18}O$ values from salinity using a salinity mixing curve. Salinity and $\delta^{18}O_{\text{seawater}}$ 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 $\delta^{18}O_{\text{seawater}}$ 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):

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

where $\delta^{18}O_{\text{seawater}}$ 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, Húnaflói, 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
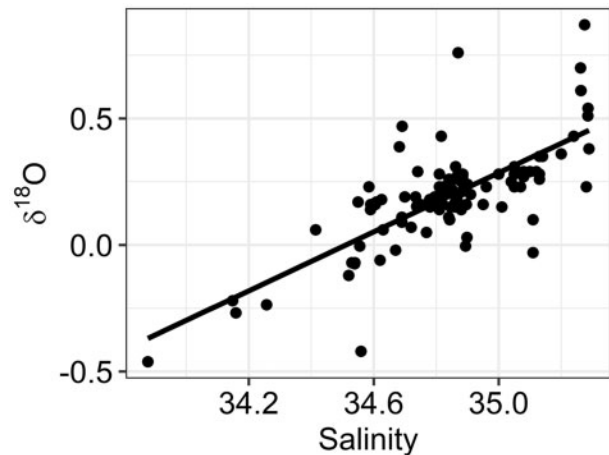

Figure 2. The relationship between the oxygen isotope content ($\delta^{18}O_{\text{seawater}}$) of seawater and salinity for the Icelandic shelf at depth 50–400 m ($n = 100$, $p < 0.001$, $r^2 = 0.55$).

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.

temperature and salinity objective analyses l09 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.

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, Húnaflói, 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):

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

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 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 $\delta^{18}O_{otolith}$ 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.
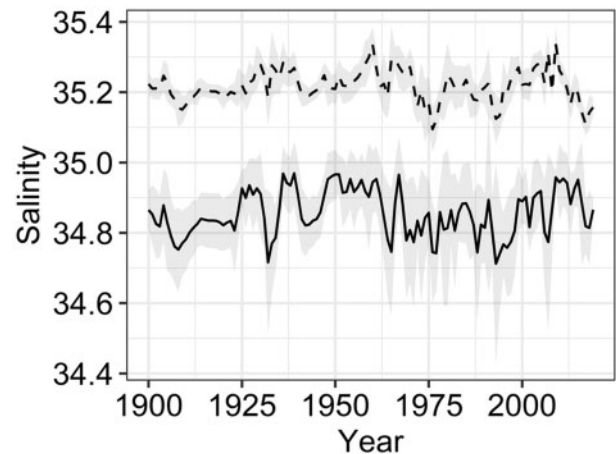

Figure 3. Mean salinity time series in southern (dashed) and northern (solid) Iceland at depths of 50–200 m. Standard deviation indicated by shading. Hadley EN4.2.1 analyses l09 data downloaded from APDRC LAS7 for public.

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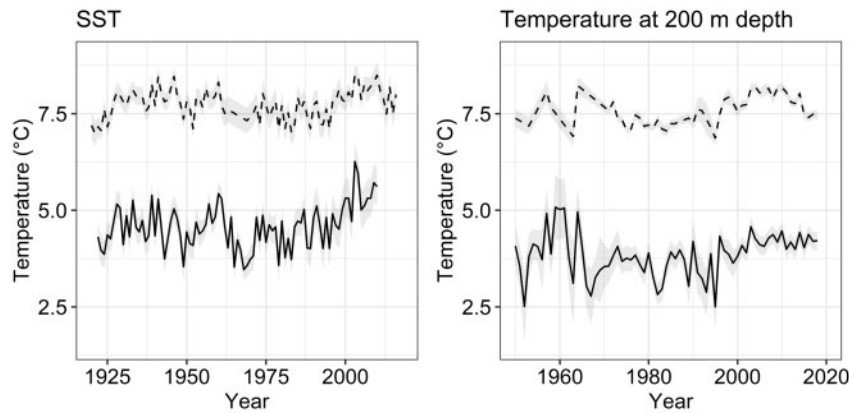
Figure 4. Modelled SST and water temperature at 200 m in the south (dashed) and north (solid) of Iceland. Standard deviation indicated by shading.

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.

Scenario	Migration scenario	Salinity South	North	Temperature (°C) Mean	Minimum	Maximum	Temperature (°C)—immature Mean	Minimum	Maximum	Temperature (°C)—mature 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

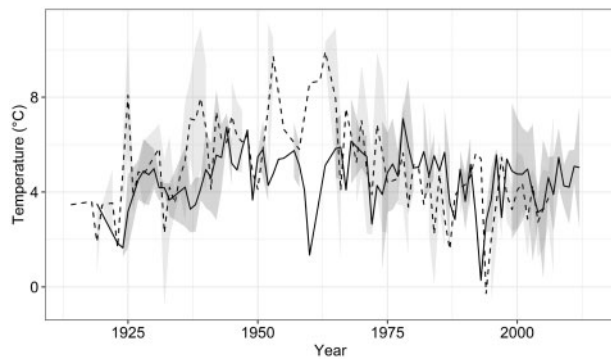The different migration patterns are described in detail in the article.

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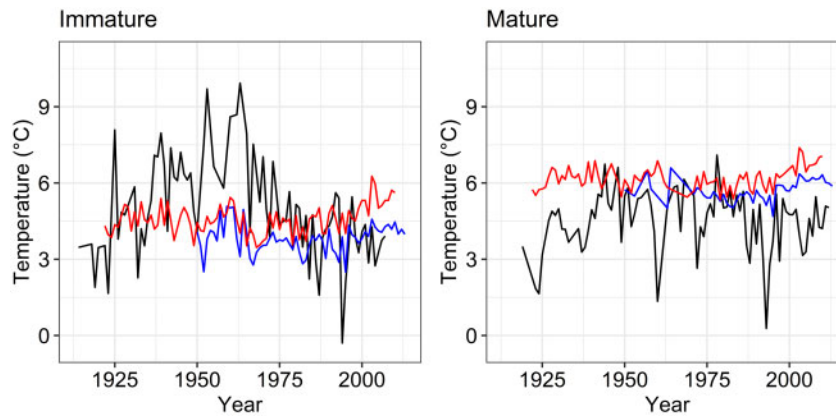
Figure 6. Reconstructed ambient water temperature of Icelandic cod (black), SST time series (red), and water temperatures at 200-m depth (blue). Temperatures for mature cod were adjusted for migration.

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

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 ~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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