Exploring the role of temperature in observed inter-population differences of Atlantic cod (*Gadus morhua*) growth with a 4-dimensional modelling approach

Nadezhda Sokolova [1,3]*, Martin Butzin [1], Flemming Dahlke [1], Karl Michael Werner [2], Daniel Balting [1], Gerrit Lohmann [1,3], and Hans-Otto Pörtner [1,3]

[1]*Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany*
[2]*Thünen Institute of Sea Fisheries, Bremerhaven, Germany*
[3]*University of Bremen, Bremen, Germany*

*Corresponding author: tel: +49 471 48 31 18 80; e-mail: nadezhda.sokolova@awi.de.

Atlantic cod (*Gadus morhua*) is one of the most commercially important fish species in the North Atlantic. Environmental factors, such as water temperatures, influence growth of individuals over time, thus forming population-specific growth patterns across climatic regions. Here we develop an integrative approach to investigate the role of temperature in shaping geographic differences of cod growth in the Celtic Sea, North Sea, Iceland, and Barents Sea. We combine a physiology-based growth model and 50-years observational temperature data of $0.5 \times 0.5°$ spatial resolution to simulate continuous growth of cod. The model generated weight-at-age data for the period 1959–2007 which we compared to observational data from fishery-independent scientific surveys. In the Celtic and the northern North Sea, simulated growth matches well observational data. We also show that relatively warm temperatures in the Celtic Sea facilitate maximum growth rates; future warming is likely to have a negative impact on growth of these cod stocks. Growth simulations in Icelandic waters and the Barents Sea are less consistent with local observational data. More complex growth patterns in these regions are probably shaped by ontogenetic shifts in temperature regimes, feeding conditions and physiological adaptations. These findings should stimulate further research on critical processes to be considered in population-specific projections of growth of cod and productivity.

Keywords: Atlantic cod, ecophysiology, growth model, high-resolution temperature data, historical weight-at-age observations, Northeast Atlantic

Introduction

Atlantic cod (*Gadus morhua*) is widely distributed across the shelf regions of the North Atlantic between 40 and 80°N (Cohen, 1990; Chabot and Claireaux, 2019). Many studies investigated the effects of environmental conditions on the growth performance of Atlantic cod and suggested that water temperatures play a key role in shaping growth patterns across populations (Brander, 1995; Pörtner *et al.*, 2001; Rätz and Lloret, 2003; Drinkwater, 2005; Pörtner *et al.*, 2008; Rogers *et al.*, 2011; Chabot and Claireaux, 2019). Furthermore, additional factors such as food availability (Frater *et al.*, 2019; Link and Sherwood, 2019), oxygen demand and seawater oxygenation (Pörtner *et al.*, 2001, 2008), life-history and behaviour (Godø and Moksness, 1987; Tallack, 2009), genetic and physiological differences (Pörtner *et al.*, 2001; Petersen and Steffensen, 2003), population density (Weatherley, 1966; Thorsen *et al.*, 2010), and fishing efforts (Enberg *et al.*,
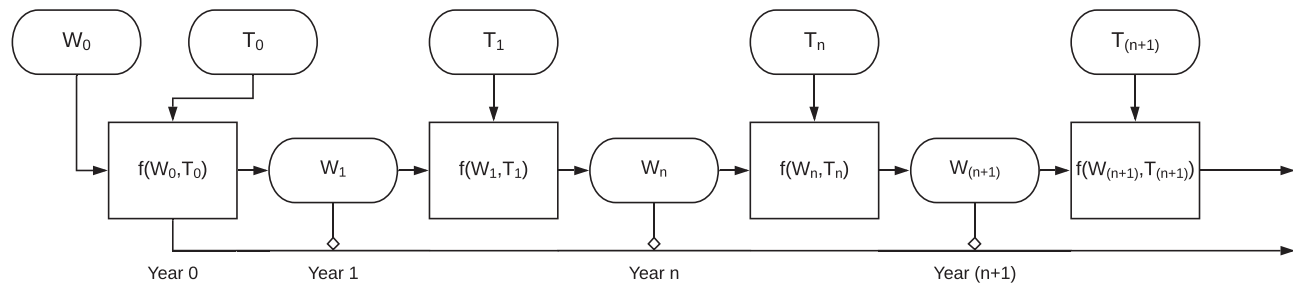
Figure 1. Schematic representation of the transient growth model setup: $f(W, T)$ – growth model function; W – weight-at-age output data that are also used as a subsequent input; T – 4-dimensional temperature input (horizontal boundaries are shown in Fig. 1; vertical boundaries are shown in Fig. 3, 4, 5).

2012) were found to affect the growth of cod. Physiological principles of growth imply a direct thermal response of an organism to changes in external temperatures through activating metabolic processes, i.e. turnover of energy and materials on molecular and cellular levels as well as on the organism level (Brown et al., 2004; Pörtner et al., 2017). Laboratory experiments show direct dependence of cod growth rates on temperature changes when food supply is unlimited (Jobling, 1988; Clark and Green, 1991; Björnsson and Steinarsson, 2002; Björnsson et al., 2007). In addition, these studies recorded optimal temperatures for maximized growth rates which are often difficult to extrapolate to a "real" environment (Weatherley, 1966; Godø and Moksness, 1987; Link and Sherwood, 2019). In contrast to laboratory experiments, observational studies provide information on biotic and abiotic factors, which may affect the growth of cod and reflect species' natural environment (Neat and Righton, 2007; Righton et al., 2010; Thorsen et al., 2010). These studies mainly focus on ecological interpretations of growth, whereas the underlying physiological mechanisms remain unclear. Although both laboratory and observational studies explore the role of temperature in the growth process, only a few of them connect experimental findings of temperature-dependent growth with the observed interpopulation differences in growth patterns (Pörtner et al., 2017).

A variety of modelling approaches have been developed to relate fish growth from different environments to fundamental physiological or ecological processes (Brander, 1995; Björnsson and Steinarsson, 2002; Jørgensen and Fiksen, 2006; Butzin and Pörtner, 2016; Neubauer and Andersen, 2019). However, there is a lack of studies that combine experimental and observational growth data to disentangle the temperature signal from other physiological, ecological, and environmental factors. Such an approach could help to find populations of Atlantic cod that follow experimentally derived temperature-dependent growth patterns. This would be the first step towards answering the question whether some populations of Atlantic cod may respond to increasing water temperatures due to climate change.

In this study, we combine simulations using a growth model derived from laboratory results and long-term observations from fishery-independent scientific surveys to identify areas where the observed growth patterns of cod are shaped by the direct effects of water temperatures. The growth model in this study is an extended version (Figure 1) of the growth model by Butzin and Pörtner (2016). The underlying theoretical framework was

motivated by the integrative concept of oxygen- and capacity-limited thermal tolerance theory that defines the upper and lower temperature limits for growth (Pörtner et al., 2017). The model is based on temperature-dependent reaction rate theory (Johnson and Lewin, 1946; Sharpe and DeMichele, 1977; Schoolfield et al., 1981) and assumes allometric growth (for a review, see White and Kearney, 2014). It generates growth curves based on spatial and temporal ranges of weight-at-age values which we compare to observational data for all ages reported by the International Council for the Exploration of the Sea (ICES) (Table 1).

To conduct such a comparative analysis, we chose four regions in the Northeast Atlantic with distinct oceanic conditions: the Celtic Sea, the North Sea, the Icelandic shelf, and the Barents Sea (Figure 2). Water temperatures in these regions range from sub-zero around Iceland and in the Barents Sea up to $19°C$ in the Celtic Sea and in the southern part of the North Sea (Neat and Righton, 2007; Righton et al., 2010; Neat et al., 2014). Although it is well known that growth of cod in the natural environment is affected by an interplay among physiological, ecological, and environmental factors (Lorenzen, 2016), we aim to identify cod populations showing growth patterns shaped by temperature effects only and not limited by other factors.

Methods
Growth model description
We employ a physiology-related growth model to simulate growth of Atlantic cod and to study size-dependent temperature effects on the growth of cod for different regions in the Northeast Atlantic. We use an extended transient version (Figure 1) of the growth model from Butzin and Pörtner (2016), which was calibrated with the results from growth experiments for Iceland cod (Björnsson and Steinarsson, 2002; Björnsson et al., 2007). The reason why we used the growth model derived from Iceland cod data is that experimental data on other cod populations that would be appropriate for calibration of the growth model are not available yet. Mathematical description, details on calibration, and procedure of model development are described in the study of Butzin and Pörtner (2016). The growth model relates temperature and growth rates based on the absolute reaction rate theory with growth inhibition at higher temperatures, including Arrhenius equation of temperature-dependent chemical reaction rates (Clarke, 2017). The growth model assumes that the rate at which an organism grows, depends on the value of its own body

Table 1. Field weight-at-age data (kg) from ICES surveys used in comparison analysis (Figures 3–5).

Area and division	Reference	Time frame	Age (years)	Description
Celtic Sea region(7e-k)	Report of the Working Group on Celtic Seas Ecoregion (WGCSE, 2019)	1979–2010	1–10	Data set 1: Catch/landings weight-at-age Data set 2: Stock weight-at-age = 1st quarter values
Southern North Sea (areas 4, 5,6) and northern North Sea (areas 1, 2, 3, 7)	Data ate openly accessible from ICES DATRAS website: http://datras.ices.dk/ (ICES Database of Trawl Surveys (DATRAS), Extraction 7 September 2020 of International Bottom Trawl Survey (IBTS). ICES, Copenhagen.)	1971–2010	1–10	Data collected from fishery-independent scientific trawl surveys
Iceland (5a)	Report of the North Western Working Group (NWWG, 2019)	1955–2010 1985–2010 1955–2010	3–14 1–9 3–14	Data set 1: Estimated mean weight at age in the catch Data set 2: Estimated survey weight-at-age in the spring survey (SMB) Data set 3: Estimated weight-at-age in the spawning stock
Barents Sea (1a-b)	Report of Arctic Fisheries Working Group (AFWG, 2019); Northeast Arctic Cod (Subareas 1 and 2)	1983–2010 1946–2010 1985–2010 1984–2010	2–14 3–14 5–11 1–12	Data set 1: Weight-at-age in landings Norway Data set 2: Estimated mean stock weight-at-age Data set 3: Weight-at-age in the Lofoten survey Data set 4: Weight-at-age from Russian surveys in November–December
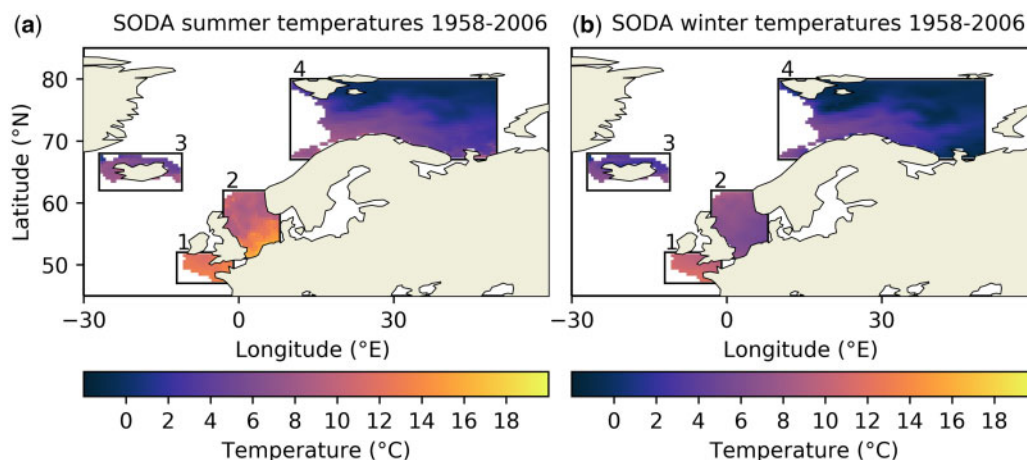
Figure 2. Water temperatures in the Northeast Atlantic during summer (a) and winter (b) averaged over 0–580 m: 1, Celtic Sea; 2, North Sea; 3, Iceland; and 4, Barents Sea. The same horizontal boundaries were used in growth model simulations. The white areas within each region indicate depths of >580 m. Time average, 1958–2006.

mass, i.e. allometric growth (White and Kearney, 2014) and considers immediate organismic response to changes in temperatures. The model disregards larval growth variations, vertical, or horizontal movements and does not expect ontogenetic habitat shifts. The model expects unlimited food availability and a homogeneous thermal environment during growth (based on Björnsson and Steinarsson, 2002; Björnsson *et al.*, 2007). The output of the growth model is the weight of an individual at a given age (weight-at-age in kilograms).

Growth model setup

As an input to the growth model, we used space- and time-varying temperature data from the Simple Ocean Data Assimilation (SODA) retrospective analysis data set (Carton *et al.*, 2000; Carton and Giese, 2008). SODA provides 50 years of temperature data from 1958 to 2006 with monthly resolution. Spatial resolution is $0.5° \times 0.5°$ in the horizontal and 40 levels in the vertical dimensions. We extracted temperature data for 0–
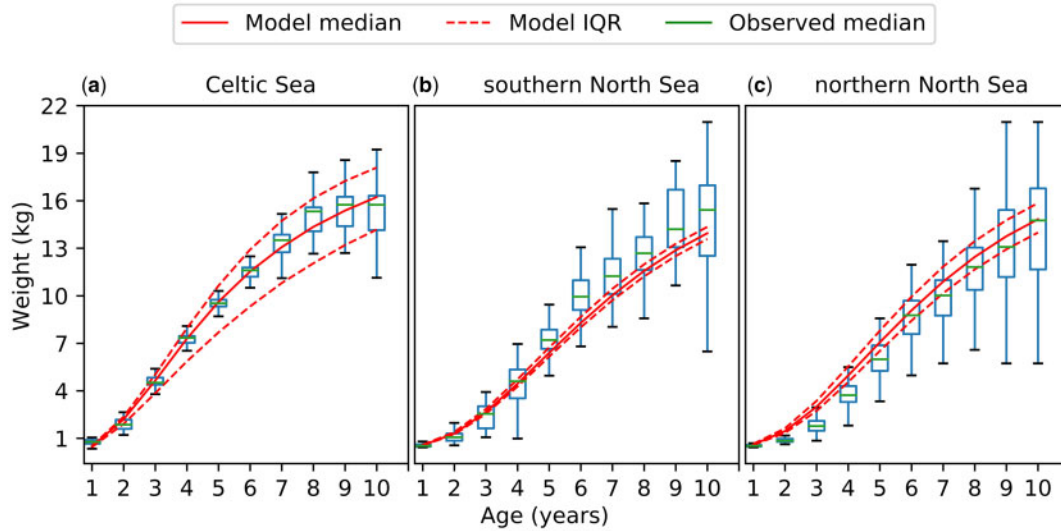
Figure 3. Modelled versus observed weight-at-age of Atlantic cod in the Celtic Sea (a), the southern North Sea (b), and the northern North Sea (c). Modelled weight-at-age time-series output was averaged for the period 1958–2006. The moving averaging window for simulated weights at every age class covers 36 years. Median and IQR of model results were estimated for each region including horizontal distribution and 21 vertical levels. ICES time-series data cover years described in Table 1 and represent horizontal, vertical, and temporal variability of weight-at-age values. ICES data are displayed as blue boxes (IQR), green line (median), and whiskers (minimum and maximum values); the outliers (minimum and maximum values) are removed from the analysis. The length of the whiskers is set to 1.5 × IQR.

580 m (0–21 vertical levels in SODA) which represent the observed depth range of cod distribution (Cohen *et al.*, 1990). In addition, we excluded areas in the Barents Sea with temperatures below 1.5°C according to the observed temperature preferences of the Northeast Arctic cod population (Svåsand *et al.*, 1996; Stensholt, 2001; Righton *et al.*, 2010). The core of our approach is a transient growth model setup, which estimates weights-at-age for the period 1959–2007 starting every year between at an initial weight of 1 g and using a time step of 1 day (Figure 1). We used data from ICES assessment reports (Table 1) for the validation of the model results at age classes 1–10 in the Celtic Sea and North Sea and ages 1–14 on the Iceland shelf and the Barents Sea. In accordance with observational age data provided by ICES, the model calculates individual growth over up to 10 years in the Celtic Sea and the North Sea, and up to 14 years for Iceland and the Northeast Arctic.

Comparison of modelling results with observational data

The model results are weight-at-age, i.e. the mass (kg) of an individual cod at a certain age. We simulated weight-at-age for the period 1959–2007 using monthly input temperatures for the period 1958–2006. We show latitudinal and vertical distributions of the modelled weight-at-age-10 as an example of the three-dimensional growth model output. This is the maximum age recorded by ICES for the Celtic Sea and North Sea populations and the age when 100% of Icelandic and Northeast Arctic populations become mature (ICES, 2005). The moving averaging window for weight at every age class covers 36 years. We compare the median of simulated weight-at-age values to the median in measurements reported by ICES surveys (Table 1). Observational data available for the North Sea allowed us to perform separate analysis in the southern and northern North Sea. As the modelling data are not normally distributed, we use the interquartile range (IQR) as a measure of the effects of temperature variability

(spatial and temporal) on the simulation results. To compare the simulated growth patterns across regions, we represent modelled weight-at-age values as growth curves. As shown in the previous studies and assessment reports, the North Sea cod consists of distinct reproductively isolated population components which do not show movements over great distances (ICES, 2005; Neat and Righton, 2007). Thus, we analysed simulated and observed weight-at-age data separately for the northern and the southern regions of the North Sea (Table 1). It was not possible to evaluate the uncertainty range of weight-at-age in observations arising due to different procedures of age determination, imprecise sampling information regarding location and sample size, and unknown ambient temperatures. To analyse the growth pattern of cod from the observational data, we apply box plots and calculate the median and IQR over given time periods (not <30 years), excluding weight minima and maxima from the study.

Results

Modelled weights compared to historical data across populations

Celtic Sea

The growth model results in the Celtic Sea closely track ICES survey data (Figure 3a). Similar to observations, modelled values increase exponentially during the first three simulated years, showing rapid growth until the age of 4 years. Model median values are in line with the observational median at each age group except for 10 years, which is the maximum simulated age for Celtic Sea cod. The model IQR shows a spread of 0.5 kg for weight-at-age-1 and 1.4–1.6 kg for weight-at-age-2. Observed weight-at-age varies around 0.6–0.9 kg for 1 year and 1.2–1.6 kg for 2 years.
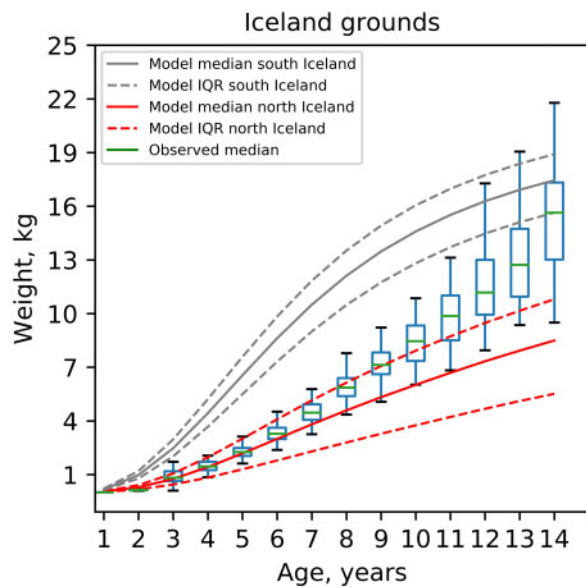
Figure 4. Modelled versus observed weight-at-age of Atlantic cod around Iceland. Modelled weight-at-age time-series output was averaged for the period 1958–2006. The moving averaging window for simulated weights at every age class covers 36 years. Median and IQR of model results were estimated for each region including horizontal distribution and 21 vertical levels. ICES time-series data cover years described in Table 1 and represent horizontal, vertical, and temporal variability of weight-at-age values. Modelled median and IQR calculated from the southern areas are shown in grey, from the northern areas—in red. ICES data are shown as blue boxes (IQR), green line (median), and whiskers (minimum and maximum values); the outliers (minimum and maximum values) are removed from the analysis. The length of the whiskers is set to 1.5 × IQR.

North Sea

In the southern North Sea, the model reflects the observed weight-at-age values at 1–4 years (Figure 3b). At ages of 5+ years, the model underestimates the observed values. The difference between the model median and the observational median data in the southern North Sea increases with age with the largest absolute difference of 2 kg at the age of 10 years (Figure 3b). In the northern North Sea, the model overestimates weight-at-age values at 2–4 years and captures observational values at 5–10 years (Figure 3c). Despite the difference between simulated and observed weight-at-age values, the model captures the shape of the growth curve in both areas of the North Sea. The spread of the model results is smaller than in the observational data at all age classes.

Iceland

Modelling results were calculated separately for the southern and northern parts of the Iceland shelf. The modelled weight-at-age values calculated for the southern area overestimate the growth of Icelandic cod at 1—13 years (Figure 4). Weight-at-age values calculated from the northern areas are similar to observations at 1–7 years. The most pronounced mismatch in the northern area occurs at 11–14 years (up to 5 kg higher than observed weight-at-age values). The modelling results calculated for the southern part of the area are closest to the observational values at 14 years (observed, 16 vs. 14 kg). The model results from both southern
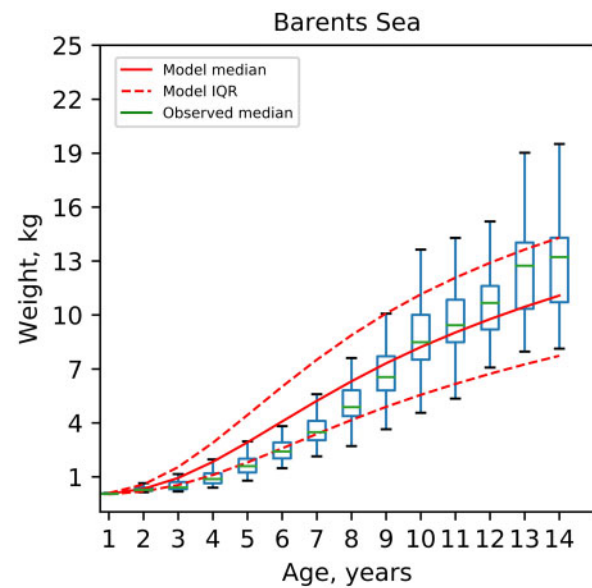

Figure 5. Modelled versus observed weight-at-age of the Northeast Arctic cod. Modelled weight-at-age time-series output was averaged for the period 1958–2006. The moving averaging window for simulated weights at every age class covers 36 years. Median and IQR of model results were estimated for each region including horizontal distribution and 21 vertical levels. ICES time-series data cover years described in Table 1 and represent horizontal, vertical, and temporal variability of weight-at-age values. ICES data are shown as blue boxes (IQR), green line (median), and whiskers (minimum and maximum values); the outliers (minimum and maximum values) are removed from the analysis. The length of the whiskers is set to 1.5 × IQR.

and northern areas have a smaller spread than the observational data at age classes of 10–14 years. The IQRs in weight-at-age 1-10 years are similar in both modelled and observed values.

Barents Sea

The model reproduces observational values at 1–2 years (0.5–0.8 kg) and at 10–12 years (8–10 kg), but tends to overestimate weight-at-age 3–9 and underestimate values for the age group of 13–14 years (Figure 5). The biggest absolute differences are found at 7 years where the simulated median is 5 kg (IQR = 3–8 kg), whereas the median of the field data is 2.8 kg (IQR = 2.8–3.2 kg).

Our modelling results indicate the differences in absolute values of weights-at-age between the southern (Celtic Sea and North Sea) and northern populations (Iceland and the Northeast Arctic) as well as within the southern populations (between the Celtic cod and the North Sea cod). The best agreement of our simulation results with the observational data is found in the Celtic Sea and the northern North Sea and the strongest disagreement around Iceland, respectively.

Simulated horizontal and vertical distribution of weight-at-age-10

Celtic Sea

The modelled weight-at-age-10 values over the area vary from 11 to 19 kg (Figure 6b) with a minimum found in the South (48°N) between 2° and 6°W and a maximum—in the North (50–52° N) between 6° and 10°W. Vertically weight-at-age values increase
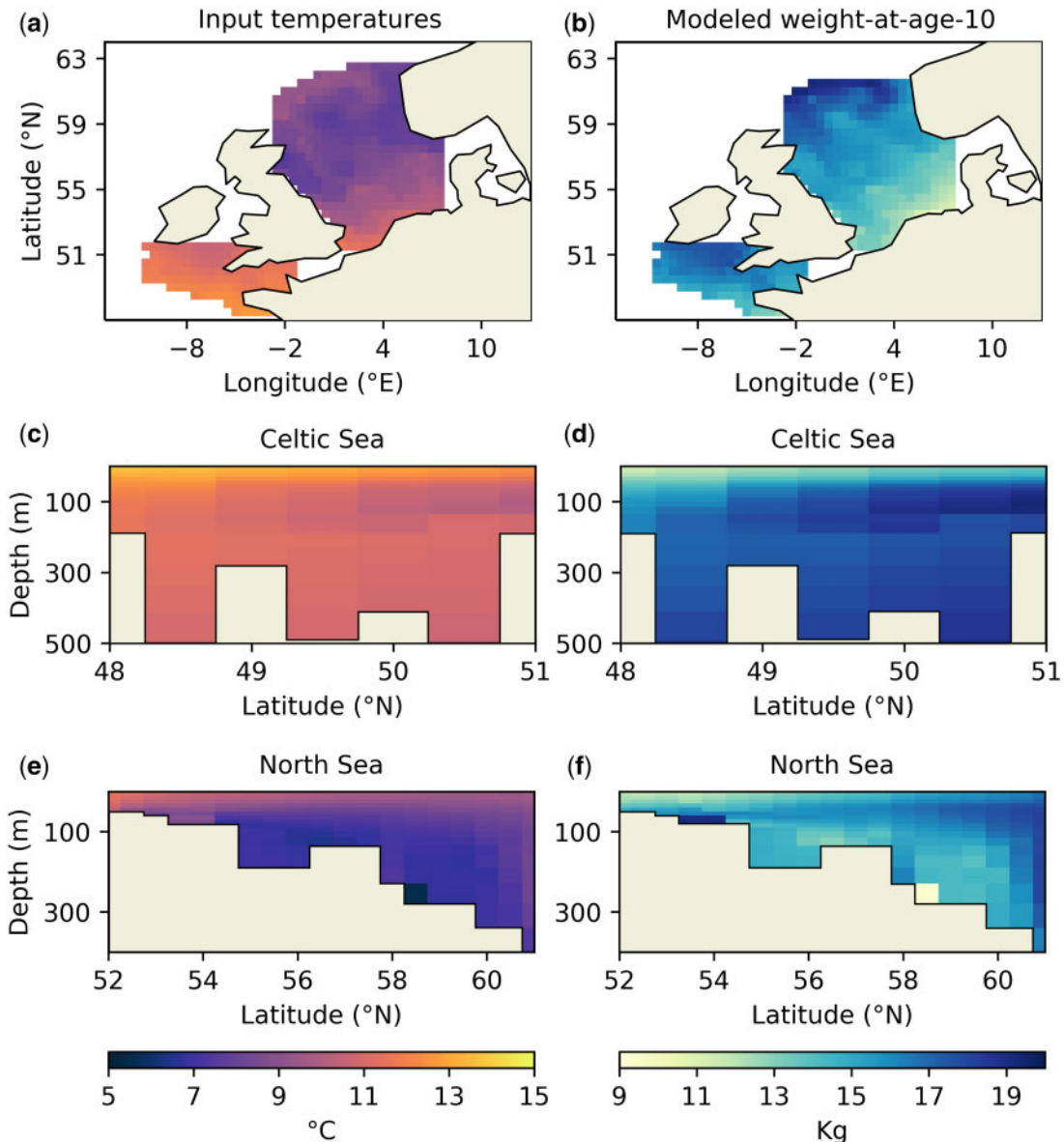
Figure 6. Simulated weight-at-age-10 and annual mean input temperatures in the Celtic Sea and North Sea: (a) Input temperatures in the Celtic and North Sea are averaged over depths 0–580 m and cover the period 1958–2002; (b) Weight-at-age-10 values in the Celtic and North Sea are averaged over depths 0–580 m, averaging window for 10 years covers the period 1968–2003; (c) Input temperatures in the Celtic Sea are averaged over longitude and the period 1958–2002; (d) Weight-at-age-10 values in the Celtic Sea are averaged over longitude, averaging window for 10 years covers the period 1968–2003; (e) Input temperatures in the North Sea are averaged over longitude and cover the period 1958–2002; (f) Weight-at-age-10 values in the North Sea are averaged over longitude, averaging window for 10 years covers the period 1968–2003. The beige areas indicate land (a, b) and the bottom of the ocean (c–f).

with depth with minimum values distributed at depths 0–50 m and maximum—at depths below 50 m (Figure 6d). Minimum weight-at-age-10 values relate to annual temperatures above 14°C and maximum values to temperatures of 10–11°C (Figure 6a and c).

North Sea
Simulated weight-at-age-10 vary between 10 and 18 kg (Figure 6b) with the associated annual temperatures of 6–12°C (Figure 6a). The minimum weight-at-age-10 values are found in southeast (5–6°E; 53–54°N) and the maximum values in the

northern North Sea between 59 and 61°N (Figure 6b). Vertically minimum weight-at-age-10 are simulated at depths of 0–50 m where the annual temperature exceeds 11°C and rarely—at the bottom at 6°C (Figure 6e and f). Below 100 m, the model simulated the maximum weight-at-age-10 values at annual temperatures of 8–10°C (Figure 6e and f).

Iceland
The simulated weight-at-age-10 values range between 2 and 16 kg (Figure 7b and d) at annual temperatures from 0 to 12°C (Figure 7a and c). The maximum values are found in both
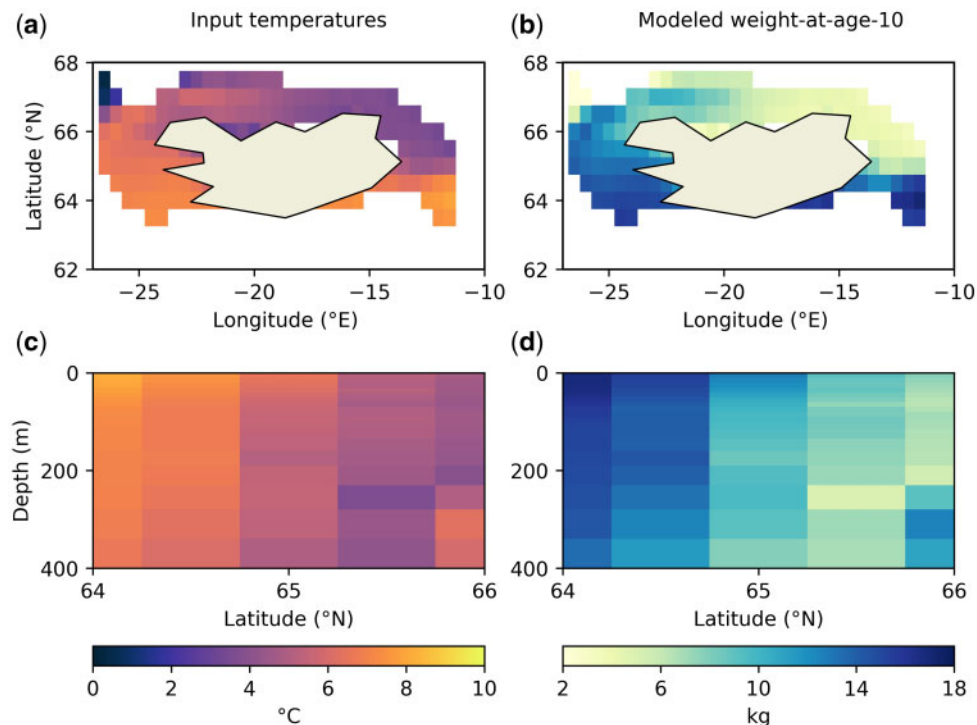
Figure 7. Simulated weight-at-age-10 and annual mean input temperatures around Iceland: (a) Input temperatures are averaged over depths 0–580 m and cover the period 1958–2002; (b) Weight-at-age-10 values are averaged over depths 0–580 m, averaging window for 10 years and covers the period 1968–2003; (c) Input temperatures are averaged over longitude and cover the period 1958–2002; (d) Weight-at-age-10 values are averaged over longitude, averaging window for 10 years and covers the period 1968–2003. White areas indicate missing values in areas with depths of >580 m. The beige areas indicate land (a, b).

southwest and southeast of Iceland at temperatures above 6°C. The minimum weight-at-age-10 values (Figure 7b) are found north of 65°N at temperatures below 2°C (Figure 7a). The vertical distribution of simulated weight-at-age-10 reveals maximum values at 0–100 m in the entire area and the minimum values are found below 300 m north of 65° N (Figure 7d).

Barents Sea
The modelled values of weight-at-age-10 range between 4 and 14 kg (Figure 8b). The maximum values of 10–13 kg are associated with the surface waters along the Norwegian coast and temperatures of 6–7°C. Minimum weight-at-age-10 values are simulated in the open Barents Sea at temperatures of 1.5–3°C.

Discussion
Using a physiology-related growth model, we found the best agreement of our modelling results with observational data in the Celtic Sea and the northern North Sea (Figure 3). We suggest that in these regions the growth of cod follows a temperature-dependent pattern with unlimited food supply.

Celtic Sea
We suggest that the agreement between our modelling results and observational data occurs because the boundary conditions of our simulations accurately reflect the environmental conditions in the Celtic Sea. The characteristics of the Celtic Sea environment—a homogeneous temperature structure (Figure 6a and c) and high food availability with a wide range of suitable forage species—are

optimal for maximized growth of cod. (Du Buit, 1995; Link and Sherwood, 2019). At depths below 50 m, we found the best match of our modelling results with observational data. The temperature range behind the model simulations (annual mean, 10–12°C) corresponds to ambient temperatures reported in the studies of Celtic Sea cod [water temperatures of 11°C according to Brander, 1995; temperatures at 70–110 m depth were around 9.0–10.5°C (Neat et al., 2014)]. The Celtic Sea homogeneous water temperature structure and cod-feeding conditions coincide with limited latitudinal movements to other areas (Du Buit, 1995; ICES, 2005; Neat et al., 2014). This closely reflects the boundary conditions and growth model assumptions in our simulations (see section Growth model description). We propose that the combination of a homogeneous temperature regime, high prey availability within a relatively small-sized area and limited migrations are the main factors shaping the growth of cod in the Celtic Sea. The same factors—limited migration, stability of the environment, and high food availability—were suggested to enhance the growth of cod in the Inshore Gulf of Maine (Tallack, 2009). Tallack (2009) suggested that in such areas the "variability in growth rate then becoming a function of size/age and/or genetics," which we propose as a possible explanation for the growth pattern of cod in the Celtic Sea.

North Sea
Our comparison analysis shows that the simulated growth curves have the shapes similar to the observed in both regions, which indicates that temperature is a key driver of the growth of cod in the North Sea. Numerous studies investigated food availability in relation to growth rates, examining consumption rates, stomach
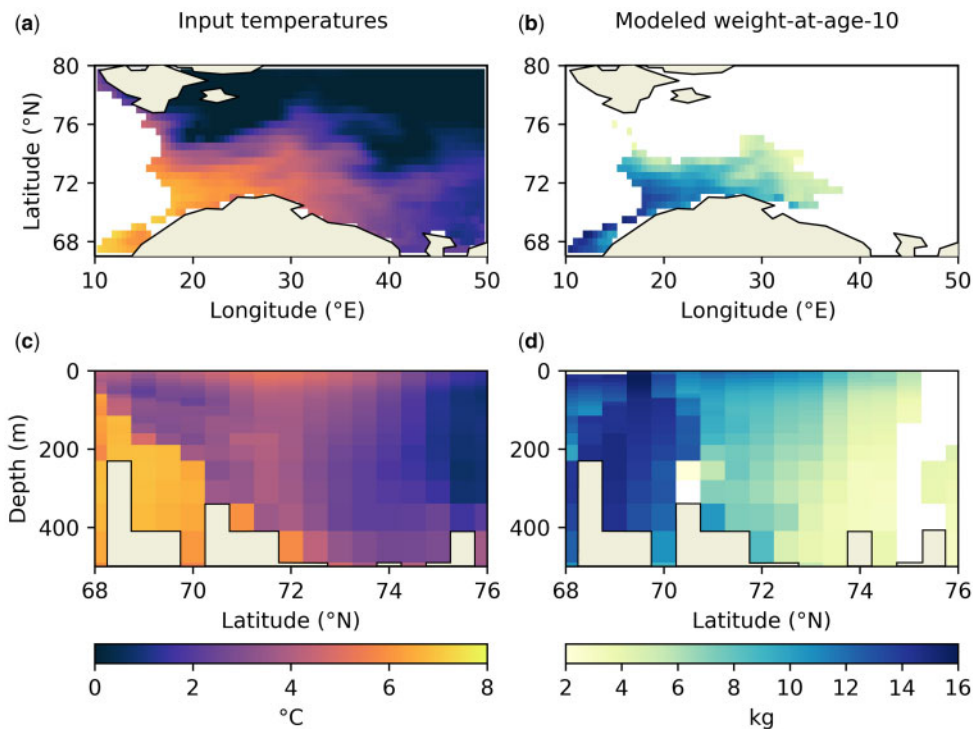
Figure 8. Simulated weight-at-age-10 and annual mean input temperatures in the Barents Sea: (a) Input temperatures are averaged over depths 0–580 m and cover the period 1958–2002; (b) Weight-at-age-10 values are averaged over depths 0–580 m, averaging window for 10 years covers the period 1968–2003; (c) Input temperatures are averaged over longitude and cover the period 1958–2002; (d) Weight-at-age-10 values are averaged over longitude, averaging window for 10 years and covers the period 1968–2003. Areas with temperatures below 1.5°C were excluded from calculations. White areas indicate missing values in areas with depths of >580 m or temperatures <1.5°C. The beige areas indicate land (a, b) and the bottom of the ocean (c, d).

contents, and satiation levels of cod in the southern and northern North Sea (Ursin, 1984; Ursin *et al.*, 1985; Daan, 1973, 1974, 1978) but our results do not show any evidence of food-limited growth in these regions. Daan (1974) has shown differences in the growth of cod from the northern and the southern North Sea with faster growth in the young age classes (Daan, 1978). Our model captures reasonably well the rapid growth of the southern North Sea cod at 1–4 years (Figure 3b). However, neither observed nor simulated growth curves show distinct differences in growth rates between the southern and the northern populations except for 2–4 years (Figure 3b and c). These results support earlier studies (Ursin, 1984; Ursin *et al.*, 1985), which showed relatively small differences in length-at-age between southern and northern North Sea cod at all age groups except for the age group of 2 years where cod in the northern region were significantly smaller than in the south. We found a relatively small discrepancy between simulation results and observations at 6+ years in the southern region (Figure 3b), which might be explained by the limited resolution of the temperature data used in our simulations and reflected by the low IQR of the simulated weight-at-age values. In general, our analysis shows that the growth of cod in the southern and the northern North Sea is similar to that found in the Celtic Sea, with a key role for environmental temperatures in shaping the growth curves of these populations.

Iceland

As the growth model was calibrated with the results from growth experiments using Icelandic cod (Björnsson and Steinarsson,

2002; Björnsson *et al.*, 2007), we would expect that the model results agree with observational data. However, only simulation results from the northern part of the Icelandic shelf capture well the observed weight-at-age values at 1–8 years (Figure 4). Our analysis indicates a shift (or change) in growth strategy after 7 years. We suggest that the mismatch between modelling and observational data may arise from migration behaviour after cod mature or spatially separated in the region. The temperatures around Iceland are characterized by a gradual decrease from the highest values of the south and southwest coast to the lowest values of the northeast and east coast (Figure 7; Brander, 1995; Righton *et al.*, 2010). Our simulations (Figure 7b) confirm that cod in warm areas of the southeast and southwest coasts grow faster than cod of the north of Iceland (Righton *et al.*, 2010). Thus, when cod mature and migrate from colder offshore waters, which are sub-optimal for growth (Björnsson, 2019) to warmer coastal areas for spawning they experience a change in temperature regime and feeding conditions (Stensholt, 2001). The closest match of modelled values with observational data for cod at 1–7 years old is found in the northern part of Iceland shelf, whereas for cod older than 7 years this is the case in the southern areas at temperatures around 8°C (Figure 4). These results may support the observed differences in environmental conditions for immature and mature cod.

Barents Sea

Modelling results reflected the observed weight-at-age values for cod older than 7 years but the simulated values for cod between 1

and 7 years were overestimated ([Figure 5]). Similar to Iceland cod, we suggest that the difference between modelling results and observed values arises because of a shift in temperature regimes. Immature cod live in the open Barents Sea until 7–11 years and grow slowly ([Godø and Moksness, 1987]; [Kristiansen et al., 2001]). Our simulation results confirm this observed exposure of younger cod to a colder environment and show a minimum simulated weight-at-age in the open areas of the Barents Sea at temperatures of 3–4°C, which are sub-optimal for the growth of small cod ([Björnsson and Steinarsson, 2002]). Mature adult cod migrate substantial distances using warmer thermal paths of inflowing Atlantic water between spawning grounds in the Lofoten region along the Norwegian coast and feeding grounds in the Barents Sea ([Svåsand et al., 1996]; [Stensholt, 2001]; [ICES, 2005]; [Righton et al., 2010]). This thermal path with water temperatures between 4.5 and 6.5°C is close to the optimal temperatures for growth (5–6°C for cod of 5 kg, from [Björnsson and Steinarsson, 2002]) and might result in higher growth rates at older stages. Furthermore, [Nakken and Raknes (1987)] found that the Northeast Arctic cod of older age groups are found consistently in warmer waters. A better agreement between our modelling results and observations is found in fish of 10–14 years old. In support of this hypothesis, maximum weight-at-age-10 values ([Figure 8b]) are found in the areas of spawning migrations along the Norwegian coast.

As a next step, our modelling approach shall be extended with the findings from physiological and ecological studies on physiological adaptations to different temperatures ([Oomen and Hutchings, 2015]; [Pörtner et al., 2001]) and food limitation ([Björnsson, 2019]) as well as their interactions in defining the energy budget available for growth. The role of these factors in growth process is broadly discussed in various experimental and observational studies. Genetic and physiological adaptations to colder or warmer environments, such as differences in haemoglobin type and mitochondrial functional properties, modulate the growth performance of individuals ([Pörtner et al., 2001]). This could explain the overestimated growth of younger cod in the northern populations. To test this hypothesis, it would be necessary to calibrate the model with experimental data from the Barents Sea and the southern cod populations and to include relevant processes at the molecular level. In addition, experimental and ecological studies ([Mehl and Sunnana, 1991]; [Dalpadado and Bogstad, 2004]; [Björnsson, 2019]; [Frater et al., 2019]) identified food availability as one of the primary factors shaping growth in the natural environment. For example, [Mehl and Sunnana (1991)] found a positive correlation between the cod growth and the availability of capelin, one of the main prey items for cod in Iceland and Barents Sea ([Frater et al., 2019]). Our model assumes food-unlimited growth, leaving the option open that decreased growth rates through food-limitation led to lower weights-at-age in the natural environment, which might explain some of the disagreements between modelled and observational data, e.g. age group 2–4 years in the northern North Sea. Finally, variations in thermal reaction norms for larval growth should be considered in further modelling studies as they might influence the body size of cod in early life and differ among populations ([Oomen and Hutchings, 2015])*****. These variations are connected to the temperature environment and genetic variations in thermal reaction norms ([Oomen and Hutchings, 2015]) and thus influencing larval growth rates which in turn might impact the initial state of young cod in nature and lead to the discrepancies found in our study.

Conclusions

We relate the temperature-dependent results of our mechanistic growth model to observed population-specific differences in growth of Atlantic cod using highly resolved observational temperature data. First, we found that temperature-dependent growth patterns can explain the observed growth of Atlantic cod in areas where the natural environmental conditions are close to optimal as determined in laboratory experiments, e.g. in the Celtic Sea and the northern North Sea. In addition, our results show that cod in the natural environments such as the Celtic Sea and the North Sea may already show maximized growth rates and that with increasing water temperatures growth rates may decrease unless cod move to more suitable environment. Second, we propose that food availability does not impose a major constraint on growth performance in these areas. Finally, temperature-based physiological concepts are limited to completely explain the complex growth pattern of Atlantic cod in areas with distinct temperature regimes. Around Iceland and the Barents Sea, behaviourally induced shifts in temperature environments, including foraging and spawning behaviour, and feeding conditions at different life stages may contribute to shape more complex growth pattern. For a broader picture on how physiological and ecological factors interact and influence growth patterns of cod in its natural environment, further populations from regions in the eastern and western North Atlantic could be included. In addition, it is necessary to extend the model to incorporate the observed life-time events related to behaviour and associated shifts in temperature and feeding regimes ([Higgins et al., 2015]).

Our study is an important step towards addressing the primary factors that influence growth of different populations of Atlantic cod in their natural environment. Further development of such an integrative modelling approach, supported by additional experiments, surveys, and more detailed climate data, could help to determine how different populations of Atlantic cod may respond to increasing water temperatures under future climate change.

DATA AVAILABILITY STATEMENT

Data are available on request from the authors.

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