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**Modelling temperature effects
on population-specific growth patterns
of Atlantic cod (*Gadus morhua*)**

by

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“A Golden Moment” by Victor Nizovtsev

Picture on page 5:

Original painting is hosted McBride Gallery, 215 Main Street Annapolis MD 21401

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CONTENTS

Acknowledgements	7
Summary	11
Zusammenfassung	13
Introduction	
1. Temperature effects on growth among other factors	15
2. Temperature-size rule and its effects on individual and populations' growth	20
3. Brief characteristics of four case study populations (Northeast Atlantic)	22
4. Climate change and its impacts on fish species at individual and population levels	25
5. Methodological aspects of growth studies in the frames of eco-physiological research	27
Publications with author's contribution statements	35
Results and discussion	37
Synthesis	47
Open questions and perspectives	51
Outlines	54
References	55
Supplements	71
Publications	87
1. Exploring the role of temperature in observed inter-population differences of Atlantic cod (<i>Gadus morhua</i>) growth with a 4-dimensional modelling approach	
2. Growth and reproductive potential of Atlantic cod (<i>Gadus morhua</i>) under future warming	
3. Atlantic cod growth models: open source Python package for numerical growth experiments	

Summary

Human-induced climate change has been affecting oceans' temperatures for several decades (IPCC, 2014). Temperature is one of the most important environmental factors influencing metabolic rates and therefore development, growth and reproduction of terrestrial and marine organisms (Clarke, 2017). Growth rates of ectotherms (e.g. fish species) are expected to be altered by climate-induced temporal and spatial changes in ocean temperatures (Pörtner, 2010; Pörtner et al., 2014). Studies suggest that warming will have differential effects on fish body size with the major trend of reduction in mean species size across latitudes (Forster et al., 2012; Cheung et al., 2013; Audzijonyte et al., 2020). The thesis aims to bridge advanced knowledge and methodology of various kinds of research, such as climate physics and climate modelling, theoretical, experimental and observational biology, and biophysical modelling in order to investigate temperature effects on fish growth from both historical and future climate perspectives. In particular, the study is dedicated to the main subject - the role of different thermal environments in shaping the growth patterns of Atlantic cod (*Gadus morhua*) with the focus on the Northeast Atlantic populations. Additionally, the author addresses methodological aspects, advantages and limitations of a modelling study in a context of eco-physiological research and introduces an open source modelling tool that can help link findings from experimental (physiology) and observational (ecology) studies.

The thesis structure includes *Introduction*, *Results and discussion* divided into three parts (*Publications 1-3*), *Synthesis* with concluding remarks, *Open questions and perspectives* for further studies and *Outlines*. *Supplements* provide figures that are not included in *Publications 1-3*.

In Part 1 (*Publication 1*) the author provides the results of the growth model simulations compared to observational data reported by the International Council for the Exploration of the Sea (ICES). In order to simulate continuous growth of Atlantic cod over their natural life cycles the growth model derived by Butzin and Pörtner (2016) was extended with a 4-dimensional ocean temperature data set. An extended version of the model generated 50-year weight-at-age data which were directly compared to observational data from fishery-independent scientific surveys. Growth curve inter-comparison was applied in order to depict temperature effects on population-specific growth patterns of Atlantic cod. Along with biological interpretations, efforts were made to develop a unified approach that extrapolates laboratory findings to a population level (ecological context) and enables direct linkage of experimental, modelling, and observational data.

Part 2 (*Publication 2*) involves AWI Earth System Model outputs, in particular, ocean temperatures projected over the next two centuries (Ackermann et al., 2020). Those data are used as a continuous environmental forcing in growth model simulations in order to provide possible scenarios of climate impacts on growth of Atlantic cod over centennial time scales. Shortly, the main purpose of the study was to assess the magnitude and direction of projected changes in weight of different age groups in the Celtic Sea and the Barents Sea populations inhabiting the southern- and the northernmost edges of the species distribution area. Additionally, historical and projected values of age-specific body weights were implemented in empirically derived weight-fecundity scaling to calculate long-term dynamics in potential egg production which represents a proxy for populations reproductive capacity (Lambert, 2008; Thorsen et al., 2010).

In Part 3 (*Publication 3*) the author focuses on development and management of transparent, reusable, and reproducible growth model software which can serve as a tool for testing temperature effects on growth rates under “controlled laboratory conditions”, on the one hand, and in “idealized open sea environments”, on the other hand. The tool incorporates multi-scale growth and weight-at-age data from growth model simulations, laboratory experiments, observations as well as input temperature data sets.

The *Results and discussion* introduces the main findings included in *Publications 1-3* that are summarized in the *Synthesis*. In *Open questions and perspectives* the thesis addresses issues and limitations as well as proposes directions for further research including integration of statistical and physiological modelling into a common framework of inter-disciplinary growth studies. The *Outlines* provides thesis conclusions in relation to the observed impact of global climate change on marine organisms.

Zusammenfassung

Der vom Menschen verursachte Klimawandel beeinflusst die Temperaturen der Ozeane seit mehreren Jahrzehnten (IPCC, 2014). Die Temperatur ist einer der wichtigsten Umweltfaktoren, die die Stoffwechselrate und damit die Entwicklung, das Wachstum und die Fortpflanzung von Land- und Meeresorganismen beeinflussen (Clarke, 2017). Es wird erwartet, dass die Wachstumsraten von Ektothermen (z. B. Fischarten) durch klimabedingte zeitliche und räumliche Änderungen der Meerestemperaturen verändert werden (Pörtner, 2010; Pörtner, 2017). Studien deuten darauf hin, dass die Erwärmung unterschiedliche Auswirkungen auf die Körpergröße von Fischen haben wird, wobei der Haupttrend zur Verringerung der mittleren Artengröße in allen Breitengraden führt (Forster et al., 2012; Cheung et al., 2013; Audzijonyte et al., 2020). Die Dissertation zielt darauf ab, fortgeschrittene Kenntnisse und Methoden verschiedener Arten von Forschung wie Klimaphysik und Klimamodellierung, theoretische, experimentelle und beobachtende Biologie sowie biophysikalische Modellierung zu verbinden, um Temperatureffekte auf das Fischwachstum sowohl aus historischer als auch aus zukünftiger Klimaperspektive zu untersuchen. Insbesondere widmet sich die Studie dem Hauptthema, nämlich der Rolle unterschiedlicher thermischer Umgebungen bei der Gestaltung der Wachstumsmuster des Kabeljaus (*Gadus morhua*) mit Schwerpunkt auf den Populationen im Nordostatlantik. Darüber hinaus geht der Autor auf methodische Aspekte, Vorteile und Grenzen einer Modellierungsstudie im Kontext ökophysiologischer Forschung ein und stellt ein beispielhaftes Open-Source-Modellierungstool vor, das dabei helfen kann, Erkenntnisse aus experimentellen (Physiologie) und beobachtenden (Ökologie) Studien zu verknüpfen.

Die Arbeit beginnt mit einer allgemeinen *Einführung*, gefolgt von einem in drei Teile gegliederten *Ergebnis- und Diskussionsteil (Publikationen 1-3)*. Weiter folgt eine *Synthese mit Bemerkungen und Outlines*. Der *Anhang* enthält Abbildungen, die nicht in den *Publikationen 1-3* enthalten sind.

In Teil 1 (Publikation 1) stellt der Autor die Ergebnisse der Wachstumsmodellsimulationen im Vergleich zu Beobachtungsdaten des International Council for the Exploration of the Sea (ICES) vor. Um das kontinuierliche Wachstum des Atlantischen Kabeljaus über seinen natürlichen Lebenszyklus zu simulieren, wurde das von Butzin und Pörtner (2016) abgeleitete Wachstumsmodell um 4-dimensionale Ozeantemperaturdaten verschiedener räumlicher und zeitlicher Auflösung erweitert. Eine erweiterte Version des Modells generierte 50-Jahres-Altersgewichtsdaten, die direkt mit Beobachtungsdaten aus fischereiunabhängigen

wissenschaftlichen Erhebungen verglichen wurden. Eine Wachstumskurvenanalyse wurde angewendet, um Temperatureffekte auf populationsspezifische Wachstumsmuster über Klimaregionen im Nordatlantik darzustellen. Neben biologischen Interpretationen wurden Anstrengungen unternommen, um einen einheitlichen Ansatz zu entwickeln, der Laborbefunde auf Populationsebene (ökologischer Kontext) extrapoliert und eine direkte Verknüpfung von experimentellen, Modellierungs- und Beobachtungsdaten ermöglicht.

Teil 2 (Publikation 2) verwendet Ergebnisse des AWI-Erdsystemmodells, insbesondere die für die nächsten zwei Jahrhunderte projizierten Meerestemperaturen (Ackermann et al., 2020). Diese Daten werden als kontinuierlicher Umweltantrieb in Wachstumsmodellsimulationen verwendet, um mögliche Szenarien der Klimaauswirkungen auf das Wachstum des Atlantischen Kabeljaus über Jahrhunderte hinweg bereitzustellen. Kurz gesagt bestand der Hauptzweck der Studie darin, das Ausmaß und die Richtung der prognostizierten Gewichtsänderungen verschiedener Altersgruppen in den Populationen der Keltischen See und der Barentssee zu bewerten. Die dabei betrachteten Kabeljaubestände leben an den südlichsten und nördlichsten Rändern des Artenverbreitungsgebiets. Darüber hinaus wurden historische und prognostizierte Werte des altersspezifischen Körpergewichts verwendet, um die langfristige Dynamik der potenziellen individuellen Eiproduktion zu berechnen (Lambert, 2008; Thorsen et al., 2010).

In Teil 3 (Publikation 3) konzentriert sich der Autor auf die Entwicklung und Verwaltung einer transparenten, wiederverwendbaren und reproduzierbaren Wachstumsmodellsoftware, die als Werkzeug zum Testen von Temperatureffekten auf Wachstumsraten dienen kann, einerseits unter kontrollierten Laborbedingungen und andererseits in idealisierter Form für Umgebungen auf offener See. Das Tool enthält Multiskalen-Wachstums- und Altersgewichtsdaten aus Wachstumsmodellsimulationen, Laborexperimenten, Beobachtungen sowie Datensätzen zur Meerestemperatur.

Die Ergebnisse der Studie sind in der *Synthese* zusammengefasst. In *Offene Fragen und Perspektiven* befasst sich die Arbeit mit verbleibenden Fragen und vorgeschlagenen Richtungen für die weitere Forschung, einschließlich der Integration statistischer und biomechanischer Modellierung in einen gemeinsamen Rahmen interdisziplinärer Wachstumsstudien. *Outlines* bietet eine Thesesschlussfolgerung im Rahmen der beobachteten Auswirkungen des globalen Klimawandels auf Meeresorganismen.

INTRODUCTION

This study focuses on fish growth under various thermal environments. Growth is one of the fundamental properties of life (Campbell et al., 2008). A diversity of internal, environmental and ecological factors influence growth performance on multiple time scales spanning hours, days, years and decades (Brett, 1979; Brander, 2006). However, environmental temperatures are suggested as a key factor driving metabolic rates and thus influencing the rates at which an organism grows (Clarke, 2017). The context of rapidly increasing ocean temperatures determines the need for studies investigating individual and population-specific growth strategies which in fact influence the whole population growth and productivity (Savage et al., 2004). Hence, growth studies provide valuable information for resource management and food security units connecting marine resources to the human needs (Lorenzen, 2016). The main objective of this thesis is to improve understanding of temperature effects on growth of Atlantic cod (*Gadus morhua*) - one of the most valuable commercial fish species which is widely distributed over the North Atlantic shelf regions (Rose, 2019). This modelling study aims at researching historically observed growth patterns of several cod populations (*Publication 1*) as well as testing the sensitivity of population-specific growth rates to future ocean warming (*Publication 2*). Besides, methodological aspects such as reusability and reproducibility of provided results and techniques are of particular interest, so in the final part the author provides a *Python growth-model package* designed as a publicly available software tool that can be used for conducting inter-disciplinary growth studies and in educational purposes (*Publication 3*).

As an exemplar of a multidisciplinary study the thesis involves various topics that are briefly introduced in sections 1-5.

1. Temperature effects on growth among other factors

This section describes mechanisms of growth in relation to temperature and additional factors such as nutrition, oxygen satiation, behavior etc. However, additional factors are not investigated and are mentioned only in relation to the main focus of the study which is temperature.

Growth is one of the fundamental life processes powered by metabolism with a “demonstrably plastic nature” responding strongly to environmental conditions such as temperature, water

chemical properties and food availability (Weatherley and Gill, 1987; Brown et al., 2004; Lorenzen, 2016). At an organism level “growth” is defined as a measurable increase of an organic system in size over a period of time, where size is represented in one or more physical dimensions such as length, volume or weight (von Bertalanffy, 1938; Weatherley and Gill, 1987; Lorenzen, 2016; Clarke, 2017). In other words, size is an end-product of growth (a physical state), while growth is a process (Lorenzen, 2016). In physical terms growth is work that requires energy and materials provided via metabolic processes (Campbell et al., 2008). At the cellular level growth is a “complex temperature-sensitive sequence of chemical and mechanistic processes” (metabolism) that provide “the energy an organism needs to power internal functioning” (Clarke, 2017). Individual growth in fish is rooted in physiological processes and is the net result of two antagonistic processes of anabolism (the building up of body materials) and catabolism (the breaking down of body materials) restated in energetic terms: $\text{growth} = \text{energy assimilation} - \text{energy loss}$ (von Bertalanffy, 1938; Katsanevakis and Maravelias, 2008; Lorenzen, 2016). To put it differently: total energy costs for growth is defined as “chemical potential energy used to build a new tissue and the metabolic costs of synthesizing that tissue” - metabolic costs (Clarke, 2017). Available chemical potential energy is mostly determined by nutrition levels, food processing capacity and an interplay between oxygen supply and demand (Clarke, 2017; Pörtner et al. 2017).

A combination of factors influence individual growth rates at all levels of biological organization – from molecules to ecosystems (Pörtner et al. 2014; 2017). The plastic nature of growth results in a highly variable organism response to internal (e.g oxygen demands or inheritance of growth rate potentials) and external (e.g. environmental) factors (Weatherley, 1966; Weatherley and Gill, 1987; Pörtner, 2001; Lorenzen, 2016). Complex interactions between those factors define an individual growth strategy and the resulting organism body size. Environmental factors such as water temperature and oxygen levels, nutrients composition, wind and ocean circulation patterns etc. shape growth of individuals in the natural environment (Link and Sherwood, 2019). Besides the surrounding environment, organism growth is influenced by ecological (“social”) factors such as species interactions at community, population and ecosystem levels; species migration patterns, spawning and feeding behavior (Andersen, 2019). Individual growth strategies are also driven by organism characteristics such as sex, body size (allometry) and maturity age (Weatherley and Gill, 1987). However, those ecological and physiology based factors are mainly determined by external thermal conditions (Pörtner and Farrell, 2008). Concepts such as the Oxygen- and capacity-limited

thermal tolerance theory (Fig. 1) – OCLTT (Pörtner, 2001; Pörtner, 2010; Pörtner et al., 2017) and Metabolic theory of ecology (Brown et al., 2004) provide a thorough discussion of growth performance from both physiological and ecological perspectives.

Temperature is stated as the major factor influencing individual growth rates in isolated laboratory environments as well as in the wild. It is commonly observed that organisms grow faster in a warmer environment while a colder environment causes slower growth of ectotherms (Clarke, 2017). On sub-organism level thermal sensitivity is reflected in protein synthesis (synthesis proceeds faster at higher temperatures) and in RNA concentration which is higher in fast-growing organisms (Clarke, 2017). Furthermore, temperature affects food intake and processing as well as oxygen supply and demand ration thus limiting energy gain by an organism (Brett, 1979; Pörtner, 2010). However, it is hard to disentangle the exact mechanisms at work that primarily drive growth performance when upscaling to an organism level.

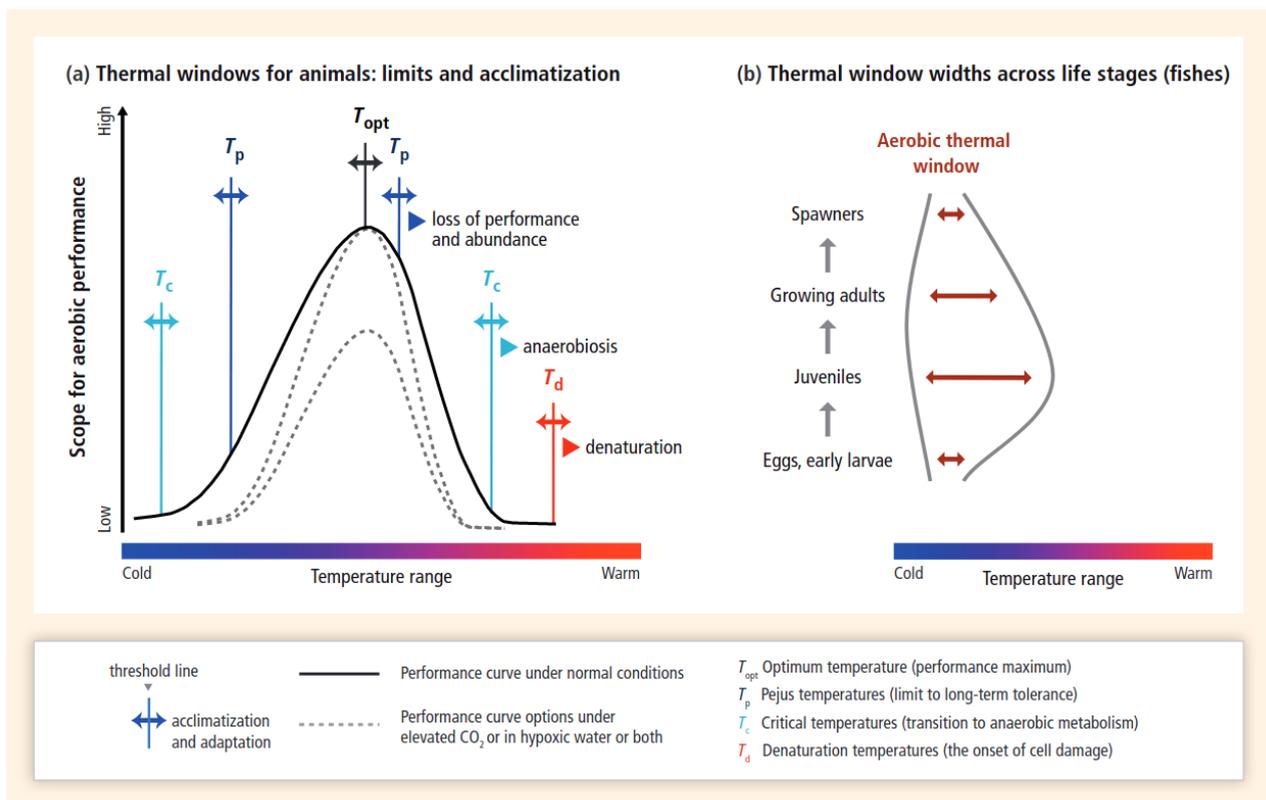


Fig. 1. (a) The thermal tolerance range and performance levels of an organism. Each performance (e.g., exercise, growth, reproduction) is maximal at its optimum temperature (T_{opt}), and becomes progressively constrained during cooling or warming. (b) thermal window changes with the life

stage of an individual. Blue to red color gradients illustrate the range between cold and warm temperatures. Source: Pörtner et al., 2014.

Despite the wide range of temperature environments that marine species experience across latitudes, experimental studies reveal species-specific temperatures that are optimal for growth (Fig. 2). These temperatures are directly related to an organism's energy budget defined by metabolic scope (Weatherley and Gill, 1987; Pörtner et al., 2017). Furthermore, the growth performance is shaped by the upper and lower temperature limits - thermal window (Fig. 1) - which is directly linked to aerobic capacity of an organism (Pörtner, 2001; Pörtner and Farrell, 2008; Pörtner et al., 2017; Link and Sherwood, 2019). Thermal limits are dependent on acclimation temperature and differ between species and/or populations (Pörtner et al., 2008). Atlantic cod growth rates increase with temperature, reaching a maximum between 8 and 10°C (Righton et al., 2010) where 10°C is considered as optimal regardless of a population (Poertner et al., 2001).

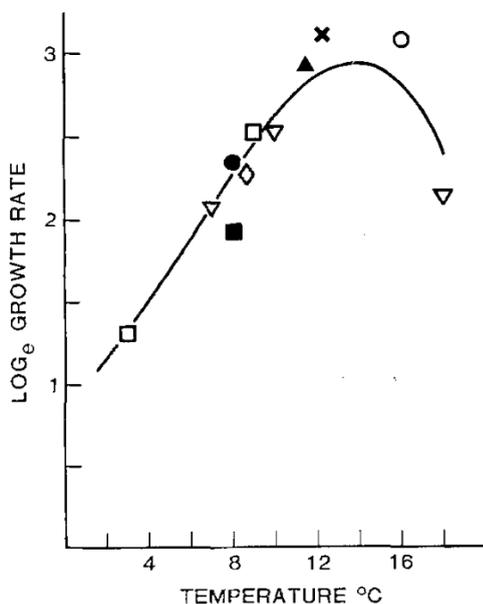


Fig. 2. One of the early studies on temperature effects on growth rates of cod, *Gadus morhua* calculated from the following sources: ○, Edwards et al. (1972); ◇, Braten (1984); ×, Jones and Hislop (1978); ▽, Hawkins et al. (1985); □, Jonsen (1981); ■, Lied et al. (1985); ▲, Jobling (1983); ●, Lie et al. (1986). Source: Jobling (1987).

Organisms growth rates in the wild are influenced by many other factors, where **availability of food** is one of the most critical ones as “the chemical energy stored in food powers the growth process” (Weatherley, 1966; Weatherley and Gill, 1987). Numerous experimental, ecological and statistical studies identified food availability as one of the primary factors shaping cod growth in its natural environment (Mehl and Sunnana, 1991; Dalpadado and Bogstad, 2004; Björnsson, 2018; Frater et al., 2019). Furthermore, ecological studies on the northern populations of Atlantic cod from Labrador, Greenland, Iceland regions, and the Barents Sea showed a positive correlation between cod growth and the availability of capelin, one of the main prey items for cod (Mehl and Sunnana, 1991). Nevertheless, consumption rate scales with temperature and body mass that control food intake so that the rate increases with increasing temperature, reaches a peak and then declines as temperature continues to increase (Lindmark et al., 2022). Thus, the amount of food available for growth is dependent on environmental temperature and maximized at an intermediate temperature when growth rates also peak (Brett, 1979). On a population level one of the confounding factors related to sufficient food availability is population density (Weatherley, 1966).

Last but not least, among the major physiological factors influencing growth are **oxygen** uptake levels in relation to demand which influence oxygen turnover within an organism and result in individual aerobic performance that determine the window for most of the organism functions including growth (Pörtner, 2010). Though investigations of physiological mechanisms underlying the growth process are outside of the study scope it is important to highlight oxygen limitation in light of the ongoing processes of ocean deoxygenation and potential increase in oxygen demands of marine organisms (Pörtner, 2001; 2010; Pörtner and Kunst, 2007; Pörtner and Farrell, 2008; Pörtner et al., 2010; 2017).

Overall, an **interplay** between temperature, body size, food availability and oxygen concentrations can be considered as a mixed forcing influencing growth rates. Direct effects of each factor combine with indirect effects thus adding non-linearity to the stressor-feedback relationships.

Besides, depending on a key factor, individual growth rates vary at different life stages and growth patterns change over the course of an organism’s life (Frater et al., 2019). Growth rates change over an individual's **life-history** as a result of changes in energy allocation between somatic growth and reproduction (Chamber and Trippel, 1997; Folkvord et al., 2014; Higgins et al., 2015). Growth rates are observed to cease at maturity as resources are invested in reproduction rather than in growth

(Jørgensen, 1976; Jørgensen and Fiksen, 2006). In turn, organism growth rate influences key life-history characteristics such as survival, development, and maturation size (Tallack, 2009; Lindmark et al., 2021). Besides, **behavior** factors such as changes in spatial distribution and migration (Tallack, 2009) or thermoregulatory behavior in a thermally stratified environment (Jobling, 1988; Björnsson, 2018) form a complex system of factors influencing growth performance.

Human effects on fish growth induced by fisheries (Enberg et al., 2012; Speirs et al., 2016) is partly addressed in *Publication 2* but is not a subject of discussion in the thesis.

2. Temperature-size rule and its effects on individual and populations' growth

In this section two topics are described: an interaction between size and temperature in relation to growth performance and the effects of individual size on populations' productivity.

Besides environmental temperatures most organisms' physiological rates are affected by **body size** which can be expressed by a power function: $Y = ax^b$ where, Y is measure of performance, x is a measure of size and a , b are species-specific coefficients (Brown et al., 2004; Clarke, 2017). This is called a principle of scaling: organism performance changes at a different rate during early life (smaller sizes) than later (larger sizes) (Chamber and Trippel, 1997). Both empirical and observational studies suggest direct temperature effects on the allometric exponent (b) of vital physiological rates and thermal tolerance (Peralta-Maraver and Rezende, 2021; Lindmark et al., 2022). For Atlantic cod it has been observed that smallest-sized individuals grow faster, have the highest optimal temperatures whilst the growth of larger fish is greater at lower temperatures (Jobling 1988; Pörtner et al., 2001; Bjoernsson and Steinarsson, 2002; Drinkwater, 2005). Both laboratory studies and multi-species statistical analyses show that optimal temperatures for growth decline with body size (Lindmark et al., 2021). For Atlantic cod the outcomes of aquatic experiments suggest variate optimal temperatures for growth depending on the size of individual: 15°C for a 10-g individual in contrast to 10°C for a 10-kg one (Fig. 3). Accounting for such size-temperature effects on organism growth is crucial because they impact biological processes at a population level.

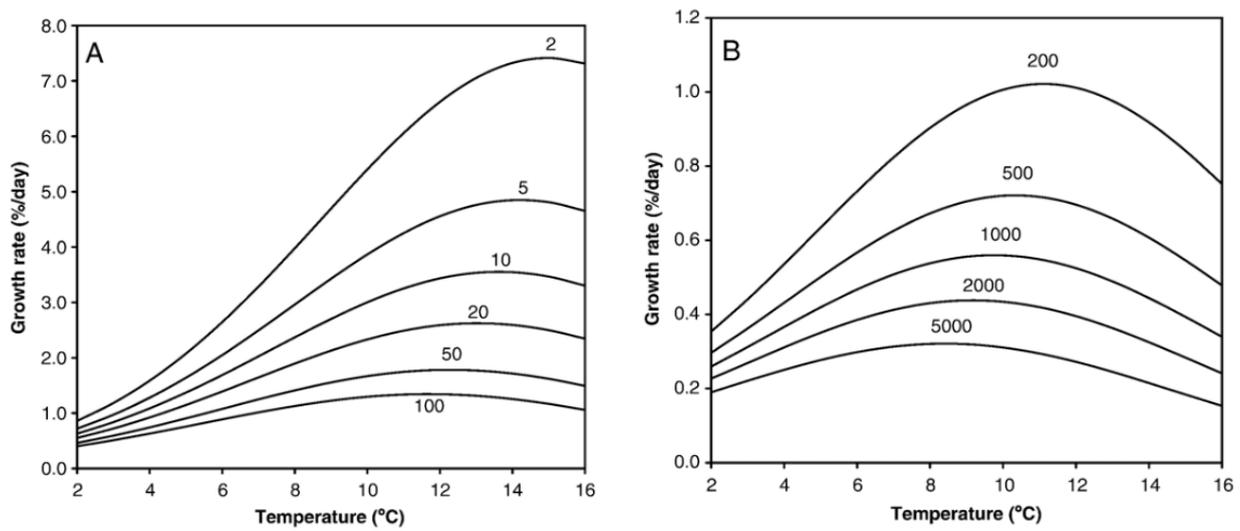


Fig. 3. Temperature effects on growth rates of Atlantic cod fed to satiation. Numbers above the curves represent the weight of individuals in gramm (g). Source: Björnsson et al., 2007.

Growth as a process and size as a final organism state have a significant impact on other organism properties as well as populations functioning (Weatherley and Gill., 1987; Grazer and Martin, 2012; Lindmark et al., 2021). Incorporating size-and temperature-scaled effects on growth of marine organisms is of fundamental importance when investigating population responses to changing environmental conditions. Because marine populations have species-specific demographic structure that comprises diverse age and size classes, organism responses to temperature regulate the whole population dynamics (Weatherley and Gill., 1987). Moreover, growth and underlying mechanisms are a key concept for fisheries management because particular characteristics of growth in fishes have impacts on population and ecosystem functioning (Weatherley and Gill., 1987; Frater et al., 2019). For example, the correlation between individual body weight and fecundity, which is a measure of organism capacity to produce offspring, plays a fundamental role in population replenishment. Both negative and positive effects on populations' reproductive potential due to changing environments are addressed in *Publication 2*.

3. Brief characteristics of four case study populations (Northeast Atlantic)

The four case study populations are: the Celtic Sea population, the North Sea population, the population from the Iceland shelf and the Barents Sea (NE Arctic) population (Fig. 4).

Atlantic cod is one of the world's largest fish populations - a demersal fish species that swim, forage and spawn near the bottom of the sea (Rose, 2019). It is a widely distributed commercially important fish species found across the shelf ecosystems of the North Atlantic displaying wide environmental tolerance, behavioral flexibility, and local adaptations (Righton et al., 2010; Brander, 2019; Rose, 20019). Cod is an important part of regional ecosystems - "a feeder with a broad diet consisting mainly of crustaceans and teleost fish" (Link and Sherwood, 2019). Wild cod occupy temperate to Arctic waters between -1.5°C in the Barents Sea and 20°C the Celtic Sea and the southern North Sea (Jobling, 1988; Righton et al., 2010; Neat et al., 2014; Brander, 2019).

Atlantic cod growth rates are observed to vary across populations and decrease at higher latitudes (Pörtner et al., 2001). Studies show that cod grow faster and mature earlier in the most southern regions of the Northeast Atlantic (Daan, 1974; Brander, 1995; Brander, 2019). The highest growth rates were found in cod from the Celtic Sea, the southern North Sea and Norwegian coast. The lowest growth rates are found for cod from sub-Arctic regions influenced by the cold temperature regime (Greenland and Iceland shelves, Barents Sea). However, high latitude populations are suggested to have higher capacity for growth than low latitude individuals, they grow slower but reach larger maxima in size in older age groups (Rose, 2019).

Beside the geographical factor such factors as inter-annual temperature variability, size of juveniles, plankton abundance and prey availability and population density influence growth rates of adult cod in the wild (Rätz and Lloret, 2003; Beaugrand and Kirby, 2010; Rogers et al., 2011). The growth data obtained by otolith analysis show a high inter-annual variability in growth rates within each population (Jørgensen, 1992). Furthermore, reduced food availability (mainly for younger individuals) affects many cod stocks, e.g. in the North Sea and the North-West Atlantic (Marshall & Frank, 1999; Yaragina & Marshall, 2000; Fischer, 2003).

Below is a description of the main physico-geographical and population-specific characteristics of four case study regions: the Celtic Sea cod, the North Sea cod, the Barents Sea cod, and Icelandic cod.

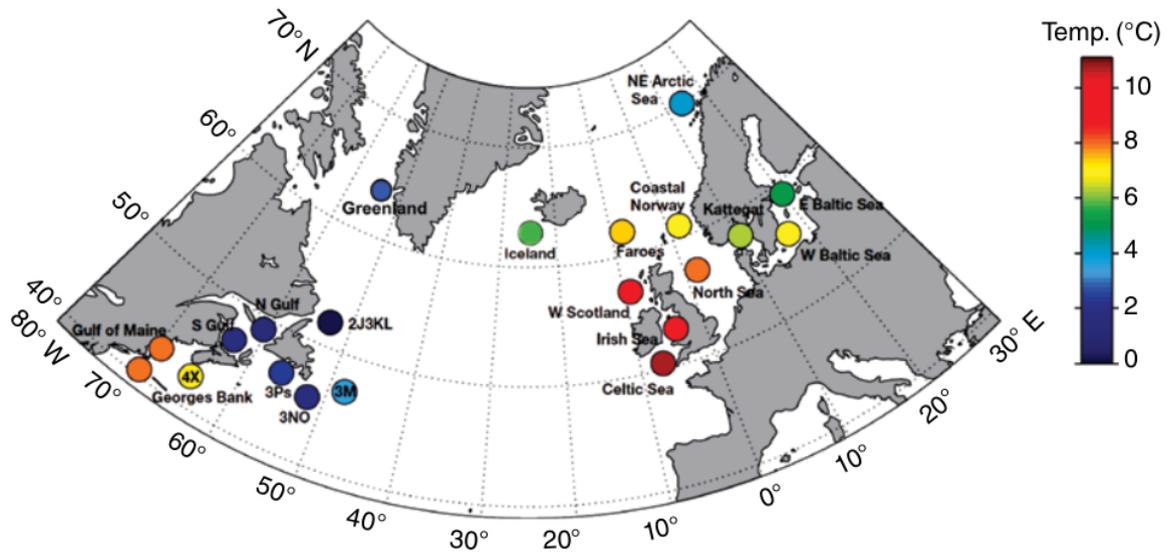


Fig. 4. Distribution of Atlantic cod across the North Atlantic coastal areas with marked averaged temperatures experienced by different populations. Source: Rose, 2019.

The Celtic Sea is an extensive shallow area bordering the eastern North Atlantic up to 200 m deep with the warm water brought to the region by the Gulf Stream (Cooper, 1961). Among the important physical characteristics of the area is the development of the seasonal thermocline at 17-40m depth and resulting vertical physical stability of the near surface water column (Davidson et al., 2013). The water column near the bottom never exhibits any significant degree of stratification and remains turbulent and vertically homogeneous in temperature structure (Pingree, 1980). **The Celtic Sea cod** is the fastest growing, the earliest maturing, and the smallest in comparison with the cod stocks elsewhere in the Northeast Atlantic (Du Buit, 1995; Righton et al., 2010; ICES, 2019). At an early immature life stage Celtic Sea cod inhabit shallow coastal waters characterized by the vertical temperature differences of 2°C between surface and bottom (Du Buit, 1995; ICES, 2019). Mature cod are found over the whole Celtic shelf but appear rarely on the southern limits of the shelf showing limited migrations to other areas (Du Buit, 1995; ICES, 2005).

The North Sea is a relatively shallow marginal sea between 51° and 61° north with highly heterogeneous hydrographic and biological conditions (ICES, 2005; Neat and Righton, 2007). It is

the shallowest in the southern North Sea (~ 30 m) and gradually deepens towards the Atlantic Ocean (> 200 m) (ICES, 2005). **The North Sea cod** population has a widespread distribution throughout the whole area with various thermal environments from 5° to 19°C (ICES, 2005; Neat and Righton, 2007; Neat et al., 2014). The population represents reproductively and to some extent genetically isolated cohorts with clear boundaries between the southern and northern parts of the North Sea (ICES, 2005; Neat et al., 2014). The temperatures that southern stocks experience vary between 6 and 16°C; in the northern part - from 5 to 13°C (ICES, 2005; Righton et al., 2010). In the southern and central areas of the North Sea cod occupy shallow <100 m waters (on average between 30 and 85 m), in the deeper northern North Sea – greater than 100 m (ICES, 2005; Neat et al., 2014). In some areas, at the age of 3 years cod move into deeper water and appear to stay in a constant thermal regime (ICES, 2005). Cod rests at the sea floor (Neat et al., 2014). There is no clear relationship between cod from distinct areas, thus migration of adult cod is restricted to limited areas between 11 and 200 km (ICES, 2005; Neat and Righton, 2007; Neat et al., 2014).

Iceland is located at a boundary between warm Atlantic water (around 5°C) and cold water from the Arctic (2-3°C) (Jochumsen et al., 2016). The hydrographical conditions around Iceland are characterized by a gradual decrease in temperatures along the coast from the north eastern part to the Southeast (Brander, 1995; Righton et al., 2010; J G. von Leesen et al., 2020). Differences in bottom temperature between areas around the island are much bigger than year-to-year variations (*Fig. 7 in Publication 1*). This temperature regime affects growth and distribution of **Icelandic cod** which is distributed over all of the continental shelf with the main spawning areas located close to the shore in Atlantic waters in the southeast of Iceland (ICES, 2005). Icelandic cod represents one of highly migratory cod populations with variable growth strategies depending on the area: cod in warm areas of the southeast and southwest coasts grow faster than cod of the north of Iceland (Righton et al., 2010). A specific shift in thermal habitats over the course of life is also observed for immature and mature cod (Pampoulie et al., 2008; Brander, 2019). Cod eggs drift to the colder northern waters where they develop and juveniles are observed to grow slow (Stensholt, 2001). When cod mature and migrate from colder offshore waters, which are sub-optimal for growth to warmer coastal areas for spawning they experience a change in temperature regime and feeding conditions (Grabowski et al., 2012).

Barents Sea cod is distributed over the area that consists of three oceanographic regimes: the ice-covered area to the north and northeast (low-saline Arctic water of < 1.5°C), the relatively warm

waters to the south and along the Norwegian coast (warm saline Atlantic water with temperatures of 4.5–6.5°C), and the boundary between the two (Ellingsen et al., 2008). The region is highly influenced by the inflow of the several extensions of Atlantic current bringing warm water northeastward (Hurdle, 1986). Such hydrological conditions cause specific life history patterns that influence cod growth strategy. Immature cod (until age 7-11) live in the open Barents Sea characterized by temperatures around 3-4°C and grow slowly (Nakken and Rakness, 1987). Mature cod (11+ years) move to the Norwegian coast and migrate substantial distances along stable thermal paths of warm Atlantic water ($T = 4.5 - 6.5\text{C}$) between northern feeding grounds in the Barents Sea (in summer) and southerly spawning grounds (Langangen et al., 2019; Stensholt, 2001; Godo and Moksness, 1987; Kristiansen et al., 2001; Ellingsen et al., 2008; Righton et al., 2010; Langangen et al., 2019; Rose, 2019). Furthermore, it is observed that the adult cod diet is highly dependent on the abundance of their main prey - capelin - which is the topic for further discussion (*Publication 1*).

4. Climate change and its impact on fish species at individual and population levels

This section includes description of historical and projected ocean temperatures specifically for the North Atlantic, general projections of climate change impacts on marine life at an organism and population levels.

Global and regional trends in ocean warming. Climate regulates physical and chemical properties of the ocean such as salinity, circulation, temperature, oxygen and nutrients (IPCC, 2014). The last few decades have reflected significant human impacts on the oceans and shown a rapid increase in global and regional ocean temperatures (at average rates of $> 0.1\text{C}$ per decade) with the strongest warming trends at high latitudes (IPCC, 2014; Deutsch et al., 2015). Moreover, by the end of the century climate models projections show even more pronounced global warming ($\sim 3^\circ\text{C}$ warmer than in 1990), deoxygenation and sea-ice loss throughout most of the upper ocean (IPCC, 2014; Deutsch et al., 2015). The Atlantic ocean is characterized by consequential climate events such as “the early Arctic warming in the 1930s, the pronounced North Atlantic cooling in the 1970s, and the ongoing warming over the last two decades” (Lohmann et al., 2020) and for the last decades the North Atlantic has experienced the highest rates of ocean warming (IPCC, 2014).

In *Section 3* current environmental conditions of four case study regions are described. Following are the main features of projected warming in the regions. Fig. 3 in *Publication 2* demonstrates temperature anomalies in the northeast North Atlantic in comparison to historical records (1960-1980). According to the RCP4.5 results by the end of the 21st (2100) and the 22nd (2200) centuries, a temperature increase of 1-3°C and 2-3°C is projected in the Celtic Sea. In the North Sea the model shows the same results, however, the amplitude of the temperature rise in the north is less pronounced (1-2°C) than in the south (2-3°C) by 2100. In contrast to the North Sea the projected temperature increase over the Iceland shelf is the opposite: 1-2°C in the south and 2-3°C in the north. The most remarkable temperature increase can be observed in the Barents Sea, where the temperature rises by 2-3°C (2-4°C) in the coastal areas and by 3-4°C (3-5°C) in the open areas by the end of the 21st (22nd) centuries. As for the RCP8.5 results at the same time periods, the model shows a higher temperature increase in comparison to RCP4.5. In the Celtic Sea the temperatures rise up to 2-4°C and 4-5°C by 2100 and 2200, respectively. In the North Sea the changes differ depending on the area: in the southern and central areas temperatures rise by 3-4°C, while in the open northern areas – 2-3°C by 2100. An even more pronounced increase is shown by 2200: 5-6°C in the south and 4-5°C in the north. Over the Iceland shelf the warming is 2-3°C except for the north-east where the temperatures increase by 3-4°C by 2100. By the end of the 22nd century overall temperatures rise by 4-5°C, however, in some areas they peak at 6°C. The Barents Sea is characterized with the most dramatic temperature increase in both coastal (Norwegian coast) and open areas: 3-4°C and 4-6°C by 2100, respectively. The sharpest rise is expected along the Norwegian coast (5-7°C) and over the open areas of the Barents Sea (> 7°C) by 2200.

Climate effects on marine organisms. Thermal sensitivity of an organism defines the boundaries of its bio-geographic distribution and determines its responses to changing environments (Pörtner et al., 2014). Long-term fossil records, recent laboratory findings as well as ecological studies state the direct link between key environmental factors and marine species (Pörtner et al., 2014; Brown et al., 2022). Recent effects of global warming on animal distribution, abundance and individual performance has been observed in many marine ecosystems (Pörtner et al., 2001; Pörtner et al., 2014; García Molinos et al., 2016). Further warming will impact organisms directly by changing physical and chemical environmental properties, as well as indirectly by changing organisms' behavior, life-history patterns, species interactions and population demographic structures as well as

by affecting primary or secondary production and the abundance of available prey species (Poertner and Peck, 2010; Brander, 2019; Clark et al., 2003).

Even small changes in temperature will directly influence species metabolic rates and life-history processes inducing growth performance at all life stages (Pörtner et al., 2001; Clark et al., 2003; Pörtner et al., 2008; Righton et al., 2010; Neubauer and Andersen, 2019; Dahlke et al., 2020). Ocean warming is projected to impact survival and development of marine species, individual growth rates, and asymptotic body size, as well as population productivity (Pörtner et al., 2014; Brander, 2019; Dahlke et al., 2020). Conceptual models predict that ocean warming will result in a global decrease of mean and maximum body mass of marine fishes (Audzijonyte et al., 2016; Lindmark et al., 2022). However, temperature is projected to have a differential impact on individual body size of younger and older organisms (Neuheimer et al., 2011; Audzijonyte et al., 2016; Lindmark et al., 2022). Firstly, warming might lead to faster development rates and larger initial size-at-age but smaller adult body size of ectotherms (Lindmark et al., 2022). Secondly, small individuals within a population may demonstrate increased growth with warming while the largest will experience direct negative effects such as decreased maximum body size and size-at-age of old fish (Lindmark et al., 2021). Finally, projected changes in size structure of populations will cause changes in fisheries productivity by affecting species reproductive potential (Brander, 2007; Barneche et al., 2018). The relationship between body mass and species fecundity and the impacts of warming on future reproductive capacity of Atlantic cod are addressed in *Publication 2*.

5. Methodological aspects of growth studies in the frames of eco-physiological research

This section provides a description of the following research methods: controlled experiments, observational studies, growth modelling approaches, and open source tools related to fish growth.

Growth studies are one of the basic areas of ecophysiological research. Investigation of growth involves such research fields as ocean physics, climate science, fisheries biology, marine ecosystem studies and ecophysiology, and to some extent archaeology, historical and social sciences. Studies on marine organisms response to future warming include theoretical background obtained from empirical growth data (laboratory experiments and aquatic studies), on the one hand, and growth

observations of wild populations (fisheries/scientific surveys, tagging studies etc.), on the other hand (Weatherley, 1966; Audzijonyte et al., 2020).

Growth of individual fish can be measured from different aspects such as growth increment counted at a particular size (relative growth) or attained asymptotic size (e.g. maximum asymptotic body weight) or size at a certain age (e.g. weight-at-age) (Lorenzen, 2016; Clarke, 2017; Neubauer and Andersen, 2019). Graphically growth performance can be described by a sigmoid growth curve approaching an upper asymptote with increasing time step (Beverton and Holt, 1957). Growth curves are used to identify individual growth strategies under various internal and external factors including temperature-dependent growth (Steinarsson, 2013; Lorenzen, 2016).

Controlled experiments. Growth is a complex system of interacting processes so to develop mechanism based concepts of growth the effects of different factors should be examined empirically (Clarke, 2017). In controlled experiments the response of an organism to different exposure factors (e.g. temperatures, oxygen, CO₂) is measured. Temperature-dependent growth rates have been described for a number of wild and harvested fish species (Jobling, 1988; Laurel et al., 2017). Most observations of cod thermal response have been made in laboratories or aquariums where all changes are measured at one fixed temperature (or other independent variable) at a time which gives pure cause-effect signals under certain assumptions (Schurmann and Steffessen, 1992; Claireaux et al., 1995). Organisms in laboratory experiments show higher metabolic rates than in the wild providing information about maximized growth performance in a given environment (Ursin et al., 1985; Brander, 1995; Svåsand et al., 1996; Righton et al., 2010; Claireaux et al., 2000; Lannig et al., 2004).

Observational (or field) studies. Observations of growth comprises data from scientific surveys, fisheries surveys and tagging studies that are researching fish growth in populations (Weatherley, 1966). Those data include values of individual growth histories of fish in large samples of particular “year-” or “age-classes” within a population (Weatherley and Gill, 1987). Thus, the subject of an observational study is “an individual or a cohort of individuals (a population) exposed to its natural environment”. A collection of other independent variables (e.g. size-at-maturity) and environmental measurements (e.g. temperature, salinity etc) accompany the main controlled variable (e.g. weight-at-age). The complications of the observational studies are the confounding factors that control size data besides temperature but they can be hardly disentangled (for example, the impact

of fishery). Another problem is mirrored by the significant differences in the size distribution within populations which complicates the direct comparison with laboratory data measuring growth on smaller temporal times scales (Weatherley, 1966).

Mathematical representation of growth. By definition, “a growth model is any quantitative description of growth”: theory based mathematical models, empirically based bio-mechanistic transformations or statistical representation of experimental/observational data (Lorenzen, 2016). A set of bioenergetic and mechanistic models describe biophysical and/or biochemical processes, in particular, energy and material flows in organisms (e.g. flows of chemical potential energy from food to growth and reproduction; Clarke, 2017). Bioenergetic models are based on the idea that growth is the net result of the antagonistic processes of anabolism (the building up of body materials) and catabolism (the breaking down of body materials) restated in energetic terms: “growth = energy assimilation – energy loss” (von Bertalanffy, 1938; 1957; Lorenzen, 2016; Clarke, 2017; Neubauer and Anderssen, 2019). In the history of growth model development the following models were consequently developed: the von Bertalanffy growth model which is the most commonly used; the Gompertz model; a power model that describes proportional increase in length with age; the logistic Yoshihara model that describes growth in length by a symmetrical sigmoid curve, etc (Fig. 5; Gompertz, 1815; von Bertalanffy, 1938; Hulme, Beverton and Holt, 1957; Lorenzen, 2016; Clarke, 2017). A detailed review on the individual based growth model approaches can be found in Koenigstein et al. (2016) and Lorenzen (2016).

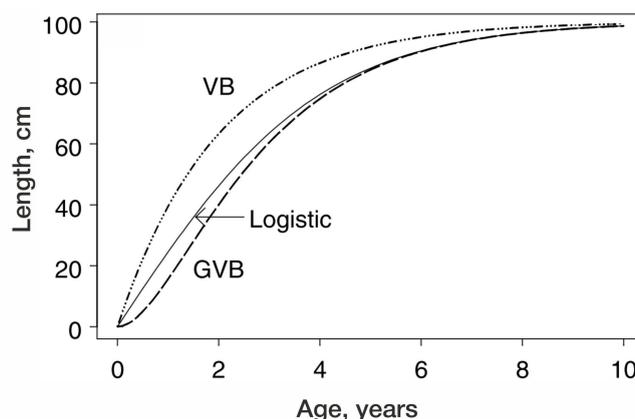


Fig. 5. Graphical comparison of three most commonly used growth curves: the von Bertalanffy (VB), logistic, and generalized von Bertalanffy (GVB) growth curves. Source: Laslett et al., 2002.

Growth models described above provide limited assumptions on species-specific individual life histories (Lorenzen, 2016; Wilson et al., 2018). Those uniphase (or uniphase) models (Wilson et al., 2018) describe lifetime growth as a single curve and do not incorporate shifts in growth rate resulting from reproductive investment or change in habitat/feeding regimes (Beverton and Holt, 1957; Katsanevakis and Maravelias, 2008; Wilson et al., 2018). In order to implement life-history trade-offs due to energy allocation between somatic growth and reproduction, biphasic models have been recently developed (e.g. Lester biphasic growth model) providing more biologically valid results than uniphase models (Lorenzen, 2016; Wilson et al., 2018).

In this study an empirical growth model derived from experimental data for Icelandic cod was implemented (Fig. 6, 7, 8). In the growth model equation temperature and weight of an individual are the main factors influencing growth rates. Initially the growth model was considered as a generalized von Bertalanffy model but in this study the growth model setup was extended in order to simulate continuous growth of cod over its life cycle.

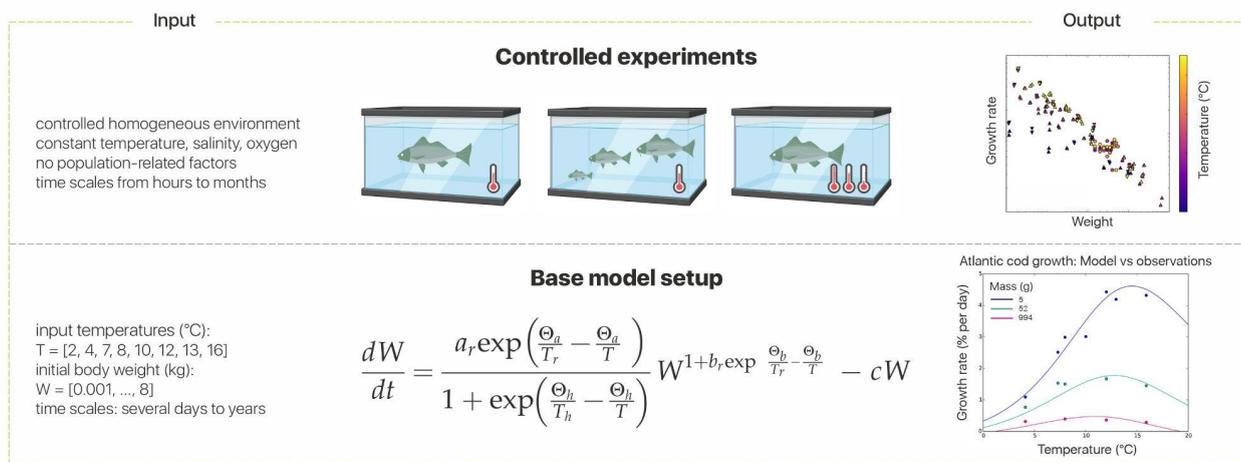


Fig. 6. Conceptual figure (from *Publication 3*) displaying the workflow of obtaining growth data from laboratory experiments and using these data to derive mathematical equations for growth - “laboratory simulations”. Equation: a_r (=8.660 % d 1 g 1/b) is the rate of uninhibited growth at a reference temperature T_r (=283 K), T_h (=286 K) is the limiting temperature, Θ_a (=18 145 K) and Θ_b (=25 234 K) are Arrhenius temperatures for the uninhibited and inhibited reaction kinetics; b_r

(=0.3055) is the allometric exponent at reference temperature T_r , Θ_b (=4258 K) - Arrhenius temperature, c - temperature-independent constant = 0.291 % per day. Source: Butzin and Pörtner, 2016.

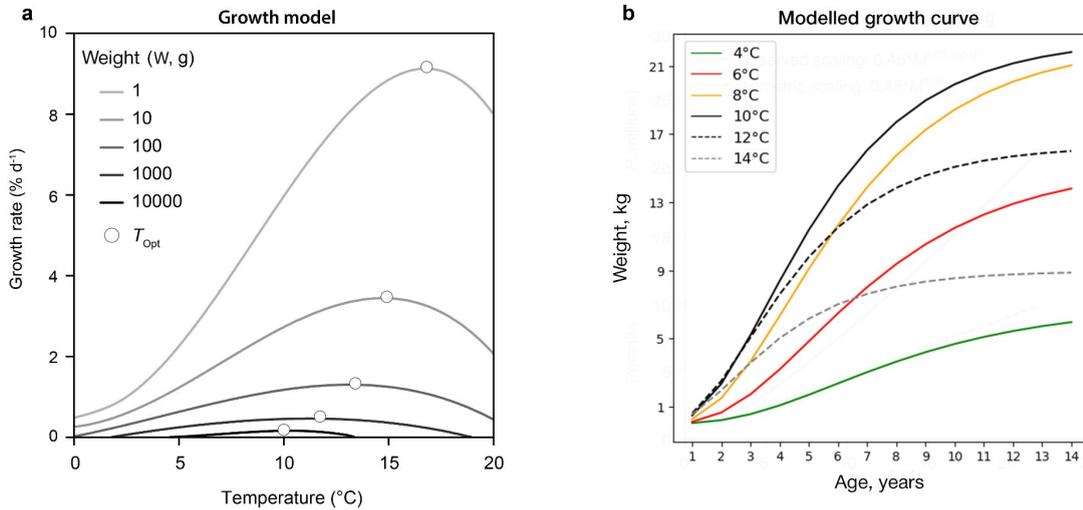


Fig. 7. Growth model results: (a) relationships between growth rates, temperature, and body weight; (b) growth rates converted into weight-at-age metrics and represented as growth curves; (a) is provided by Dr. Fleming Dahlke (from Publication 2).

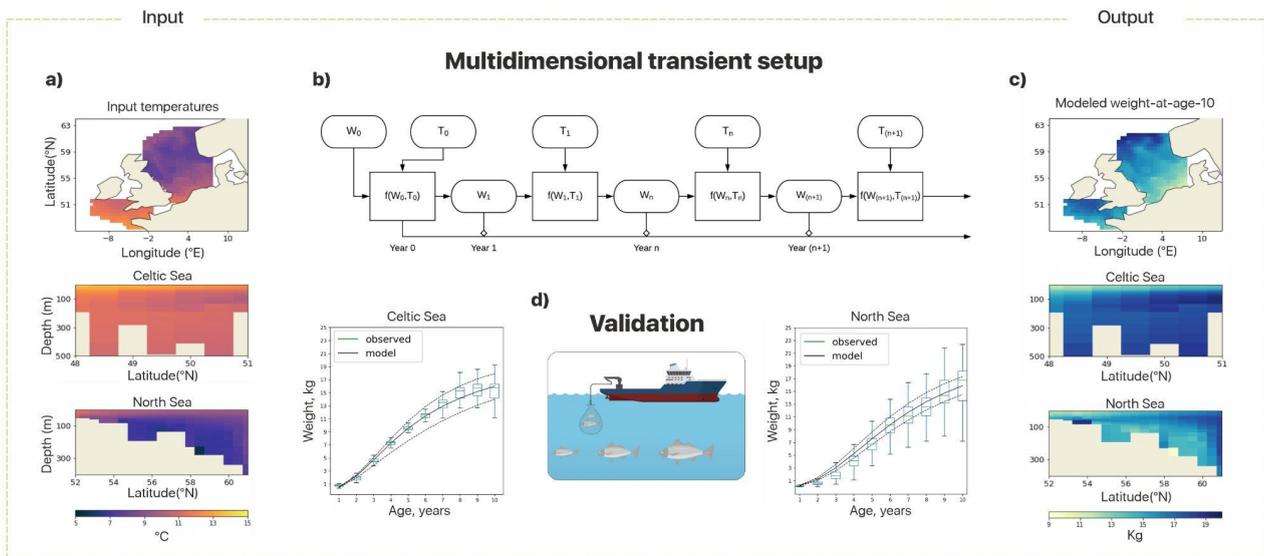


Fig. 8. Conceptual figure (from *Publication 3*) describing the workflow of multidimensional transient setup - “real-world simulations”; (a) the model uses a multi-dimensional input (e.g. lon, lat, depth, time) and (b) calculates growth rates for each year at a monthly time step; (c) the output data have the same resolution as the input data; (d) model outputs are converted to population growth curves and directly compared to observational data. Fish pictures are provided by Anja Rohner, Master student from Humboldt University of Berlin. The concept figures are included in *Publication 3*.

Multidimensional temperature data. This study involves space- and time-varying temperature data for historical and future time periods (1958-2014 and 2020-2200, respectively). Historical datasets include the Simple Ocean Data Assimilation (SODA) retrospective analysis data set (Carton et al., 2000; Carton and Giese, 2008) and outputs from a multi-scale AWI Earth System Model (AWI-ESM) equipped with an interactive Greenland Ice Sheet (Ackermann et al., 2020). Both SODA and AWI-ESM datasets provide 50 years of temperature data from 1958 to 2006 with monthly resolution; spatial resolution of 0.5x0.5 in the horizontal and 40 levels in the vertical dimensions. Projected ocean temperature datasets include high (RCP8.5) and intermediate (RCP4.5) emission scenarios (Ackermann et al., 2020). Historical and projected ocean temperatures over the European shelves of the Northeast Atlantic are of a main focus of this study (*Publications 1, 2*). In particular, temperature conditions in the Celtic Sea, the North Sea, the Barents Sea and over the Icelandic shelf are analyzed and used as the main forcing in growth model simulations.

Open science software as instruments for eco-physiological research. At present, society is facing an increasing amount of data, as well as a high pace of technical development and digitalization of all areas including science. More and more scientific studies are referring to databases, model codes, visualization and data analysis tools (Stodden et al., 2016; Powers and Hampton, 2019). Thus, it is becoming difficult to decide whether particular tools, types of information or data can be considered as valuable scientific outputs and published in scientific journals or on special platforms, e.g. GitLab, GitHub, Zenodo, Bitbucket etc. First examples of such platforms appeared by the end of 1990s when IT communities initialized the “Open Source Initiative” (<https://opensource.org/history>). It promoted the superiority of an open development process, as well as transparency, distributed peer review, higher quality, better reliability and greater

flexibility of software source code (<https://opensource.org/history>). In parallel to this, the Open Science movement appeared with the aim to make scientific products and processes accessible to a broader scientific community (Bezjak et al. 2018, Allen and Mehler, 2019). By borrowing philosophies, tools, and workflows primarily created for software development, scientists aimed to improve openness and reproducibility of science (Barnes, 2010, Lawndes et al., 2017). Open science strategy can increase the potential of trans- and interdisciplinary studies, since investment in development of high-quality, reusable scientific software accelerates scientific discoveries and enables broader communities to engage with research (Barnes, 2010; Kellogg et al., 2018).

In eco-physiological research software can be used for various purposes: storing, analyzing, visualizing and sharing experimental and observational data (e.g. Add-my-Pet; Size-based plankton simulator) as well as implementing mathematical equations and algorithms in order to run numerical experiments, test theoretical hypotheses, and predict organisms/ecosystems response to different “stressors” (e.g. Mizer). Among recently published software for growth studies there are: interactive software for growth models fitting (Growth II) and a Multi-Group Growth Model (growthmultifit) written in programming languages MatLab and R. There is a significant disadvantage of listed above software that they do not include spatial and long-term temporal dimensions.

In this study the growth model from Butzin and Pörtner (2016) and its extended multi-dimensional version (Sokolova et al., 2021) served as a basis for a Python package. The source code is stored on GitLab which allows version control tracking as well as adaptation of the software for interdisciplinary research and inter-institutional collaborations. The package includes several independent semi-dimensional settings that allow to simulate growth under controlled laboratory conditions as well as in an idealized open sea environment. The model can be used as an educational tool for studying temperature-dependent growth and testing research hypotheses by advanced undergraduate and graduate students (*Publication 3*).

Publications with author's contribution statements

1. Exploring the role of temperature in observed inter-population differences of Atlantic cod (*Gadus morhua*) growth with a 4-dimensional modelling approach. Nadezhda Sokolova, Martin Butzin, Flemming Dahlke, Karl Michael Werner, Daniel Balting, Gerrit Lohmann, Hans-Otto Pörtner (2021). ICES Journal of Marine Science, Volume 78, Issue 4, August 2021, Pages 1519–1529, <https://doi.org/10.1093/icesjms/fsab043>

NS collected weight data from the reports, set up growth model experiments, analyzed and visualized model outputs and drafted the manuscript. MB provided support to the model development and evaluation as well as contributed to drafting. FM and KMW contributed comments, additions and corrections to the manuscript and reviewed the final version. DB provided statistical analysis and data interpretation. GL and HOP guided the general concept of the paper. All authors as well as anonymous reviewers made comments and suggestions to all versions of the submitted manuscript.

2. Growth and reproductive capacity of Atlantic cod (*Gadus morhua*) under future warming. Nadezhda Sokolova, Fleming Dahlke, Martin Butzin, Lars Ackermann, Benjamin T. Schwertfeger, Hans-Otto Pörtner, Gerrit Lohmann (manuscript)

NS prepared input temperature data and set up growth model simulations, analyzed and visualized growth model results, conceived and wrote a draft. LA provided ocean temperature data and a paragraph about climate model setup in the methods section. FD prepared demographic concept and egg production data, designed Fig. 1 and Fig. 5. MB contributed to the model development and conceptual writing of the draft. BTS provided Python scripts and Figures for the Supplements. HOP and GL contributed conceptually, as well as with critical comments and suggestions.

3. Atlantic cod growth models: open source Python package for numerical growth experiments. Nadezhda Sokolova, Anja Rohner, Martin Butzin, Hans-Otto Pörtner, Gerrit Lohmann (submitted to the Journal of Open Research Software on 28th of June, 2022)

NS conceived and wrote the text as well established and developed the model repository. AR contributed to the development of an open source package and partly wrote an introduction section and package workflow. MB, HOP, GL provided suggestions during the development of the model. All authors provided comments and suggestions on the final manuscript.

Related work

1. Published data:

Ackermann, Lars; Sokolova, Nadezhda; Gierz, Paul; Lohmann, Gerrit (2022): Historical and projected (RCP4.5, RCP8.5) temperatures simulated with the AWI-ESM earth system model in the North Atlantic. PANGAEA, <https://doi.pangaea.de/10.1594/PANGAEA.943546> (dataset in review)

2. Growth model source code:

Nadezhda Sokolova, Anja Rohner, Martin Butzin, Thomas Foerster, & Benjamin Wolff. (2022). Atlantic-cod-growth-model-version1.0.1 (1.0.1). Zenodo. <https://doi.org/10.5281/zenodo.6705793>

Model development history and a list of available versions can be found on gitlab: https://gitlab.hzdr.de/awi_paleodyn/growth-model-atlantic-cod

3. Outreach:

https://www.awi.de/fileadmin/user_upload/AWI/Forschung/Klimawissenschaft/Dynamik_des_Palaeoklimas/Growth_Model/index.html

RESULTS AND DISCUSSION

This section provides a brief description of the main findings of the thesis and their extended discussion. For the convenience of the readers the discussion is divided into three sections following the order of publications.

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

This study investigated combined effects of body size and temperature on individual growth of Atlantic cod, on the one hand, and related growth model results to observed growth patterns, on the other hand. The aim of the study was to examine whether a temperature based growth model can capture cod growth patterns at a population level thus showing that temperature is the major factor influencing growth on decadal time scales. A continuous transient growth model setup, developed for this study, combined with multi-dimensional ocean temperature data allowed to simulate population growth curves over decadal time scales. The growth curve modelling is rarely used to analyze growth of individuals in Atlantic cod populations. In this study the author shows how growth curve analysis can be used as one of the key methods to capture observed growth patterns as it was proposed for farmed cod by Steinarsson (2013). By comparing the simulation results with observations one can clearly see that changes in growth patterns are linked to changes in regional temperature regimes. The results and their discussion are supported by the supplementary information including a list of numerical experiments, documented growth model settings, and visualized experimental results.

The **Celtic Sea** represents a case study region where temperature and feeding conditions are close to optimal ($T_{\text{median}} \sim 11^{\circ}\text{C}$) (*Publication 1, 2*). Our numerical experiments depict the observed growth patterns of the Celtic Sea cod with the following growth model setup: temperature range $9\text{-}16^{\circ}\text{C}$ (with monthly variations), feeding-to-satiation conditions (indirectly incorporated based on growth data), and low temperature gradients (relatively homogeneous environment represented by the multidimensional temperature dataset). Besides, our results demonstrate that juvenile and adult growth rates are maximized in the available natural environment and the growth strategy remains

the same over a 10-year life cycle which can be described by a uniphase (or uniphasic) growth curve (Fig. 9a).

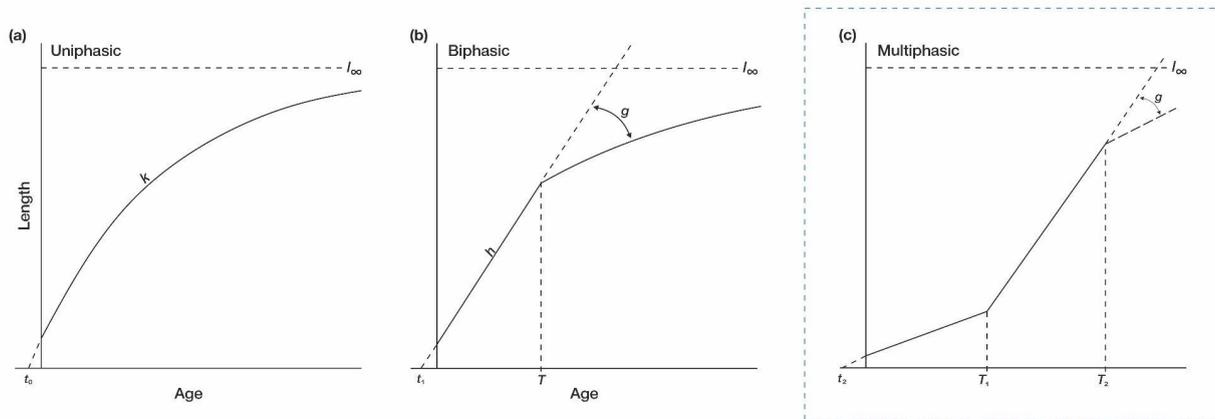


Fig. 9. Comparison of (a) uniphasic von Bertalanffy growth curve, (b) Lester biphasic curve, and (c) multiphasic curve proposed by the thesis author. The Lester model assumes that growth leading up to maturity (h) is linear, and that growth shifts when individuals mature (T) due to energetic investment in reproduction (g). Source for (a) and (b): Wilson et al., 2018.

The **Barents Sea** shows that relative thermal heterogeneity and complexity of the region influence cod growth patterns determining multiphase (or multiphasic, Fig. 9c) shape of population growth curve (habitat shift). Here the monophasic model setup doesn't work (*Supplement 2*) whereas incorporating habitat shift in thermal regimes allows to render observed decadal scaled growth patterns (*Fig. 2b in Publication 2*). Such a way of using the growth model setup is a conceptually new perspective of the population growth modelling studies. It doesn't require changes of any parameters of the growth model itself which means that temperature remains the main factor influencing growth rates. Detailed information on the setup and graphical representation of simulation results can be found in *Publications 1-2* and *Supplement 3*.

Despite utter differences in oceanic conditions, life-history, and behavioral characteristics of the Celtic Sea and the Barents Sea populations, the author suggests that their growth patterns are entirely shaped by the decadal mean temperature regimes and that food availability does not impose a major constraint on growth performance in those areas (Fig. 10). This approach, however, can not be used to explain interannual variability in growth rates and/or body size in different age groups

which is rather the task for complex multivariate statistical analyses requiring high quality long-term observations (ambient temperatures, primary and secondary productivity levels, prey availability etc.).

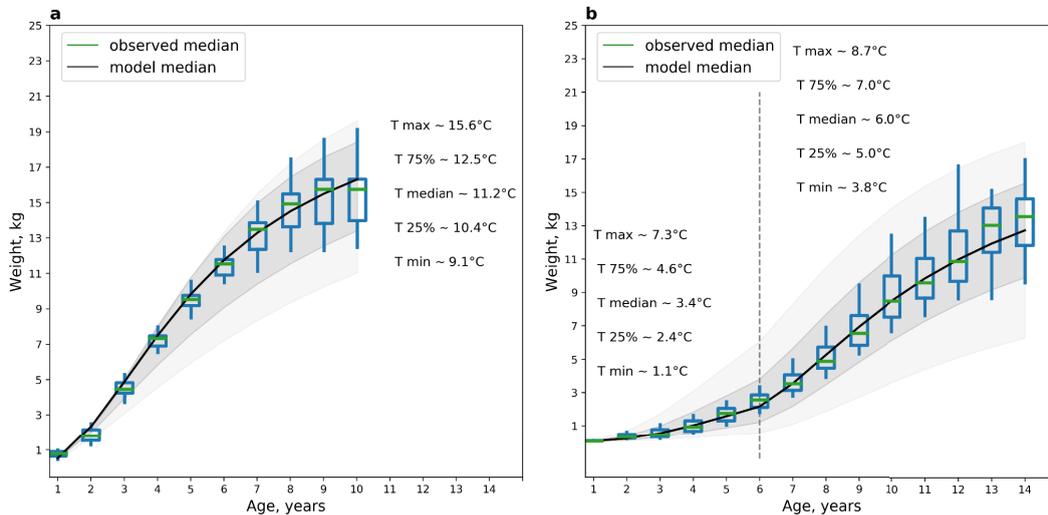


Fig. 10. Modeled weight-at-age of Atlantic cod in comparison with observations for two case study regions: the Celtic Sea (a, c) and the Barents Sea (b, d). Modeled temperature-shaped growth curves (a - Celtic Sea, b - Barents Sea) are represented by the median weight-at-age values (black lines), IQR (dark gray) and the 5th/95th percentiles (light gray). Observed weight-at-age values in (a) and (b) are displayed as box-plots where green lines are medians, blue boxes - IQR, and the upper/lower whiskers - 5th/95th percentiles (percentiles are calculated from the time series data reported by ICES). The input temperature range used in the simulation setups are represented in (a) and (b) by T max (95th percentile), T 75% (75th percentile), T median (50th percentile), T 25% (25th percentile), and T min (5th percentile). Percentiles are calculated from the 4-dimensional temperature datasets. The dashed gray line in (b) divides the 14-year life-cycle of the BarentsSea cod into two simulation phases (*Supplement 3*). Source: *Publication 2, Fig. 2a,b*.

Apart from the successful model implementation to the Barents Sea and the Celtic Sea regions, we revealed more populations where the model can not fully capture or even fail to depict the growth pattern.

The **North Sea** experiments show that available growth model settings don't completely capture the observed growth pattern (*Supplement 4*). Although the observational data follow the shape of the simulated temperature-dependent growth curves, there is a pronounced mismatch between model

results and observations at age 1-3 years. This means that temperature can not explain growth of younger cod and there might be other factors that have additional and more pronounced effects on growth rates such as food limitation or the effects of thermal environment on early larval development stages (Árnason et al., 2022). Literature sources comprising laboratory and field data as well as statistical interpretation of ecological data conclude that juvenile growth rates of North Sea cod are highly related to quantity and quality of available prey and food consumption rates (Daan, 1973; Ursin, 1984; Peck et al., 2003). In particular, Ursin (1984) and Ursin et al. (1985) reported that satiation level in age group 0-1 is twice as low as in other groups which might be related to the size of prey available for smaller cod (Daan, 1973). The author assumes that growth of the North Sea juveniles might be under influence of interrelated factors - distinct early thermal environments influencing not only growth rates but also consumption and food conversion rates as well as prey available for juveniles (Brander, 2005; Árnason et al., 2022) - which should be the topic for further research.

As for **Icelandic cod**, the temperature based growth model is limited to fully explain population growth performance. There is evidence that cod might experience the same thermal shift as in the Barents Sea (*Publication 1*) but the growth model setup incorporating habitat shift captures growth only for younger individuals (ages groups 1-7 years) while the growth pattern of older cod can not be fully depicted (*Supplement 5*). For older stages the model simulates asymptotic shape of the growth curve while observations show exponential growth. The author assumes that such a mismatch can be explained by the complexity of cod regional life-history and observed migration behavior exposing individuals to highly variable temperature and feeding conditions (Rose, 2019). In other words, it is observed that larvae and juveniles are exposed to cold temperature regimes in the northern part of the Icelandic shelf while the older mature adults migrate around the island and spend spawning seasons mostly in the southwestern part. However, the setup mimicking this shift in thermal environments didn't give reliable results. Thus, further model developments are required in order to understand the reasons for such large mismatches: incorporation of food availability as one of possible limiting factors, on the one hand, and implementation of higher resolution regional temperature datasets, on the other hand.

The current version of the model is geographically limited to the Northeast Atlantic. For a broader picture of how physiological and ecological factors interact and influence growth patterns of cod in its natural environment, further populations from regions in western North Atlantic should be

included. So far, the model has failed to stimulate growth patterns in the Northwest Atlantic which indicates that there might be another hierarchy of the factors (genetic, food limitation) where the temperature is not the major one (*Supplement 6*). This suggestion should be tested along with implementation of higher resolution temperature datasets.

There are some further limitations of the growth model that were identified during the study. Firstly, maturity artifacts of the laboratory growth data indirectly influence the behavior of the model (e.g. almost all individuals in controlled experiments became mature (Björnsson and Steinarsson, 2002; Björnsson et al., 2007) which might have influenced the growth rates of laboratory cod and affected the asymptote phase of the growth model curve (Árnason et al., 2022). Secondly, inter-population physiological effects on growth found in laboratory experiments can not be investigated due significant differences in size data within populations (Weatherley, 1966). Fourth, the model disregards larval growth and development that might affect the growth model results for yearly age groups (e.g. in the North Sea). And last but not least, the relative impacts of additional factors might be included in the observed interquartile spread of field data if their weight is proportionally much smaller than the impact of temperature so without thorough statistical analysis it is impossible to detect any of them.

To sum up, our modelling approach, which meets the needs of long-term climatic studies, captures temperature-shaped growth patterns on climatological time scales (>30 years). Projected changes in size structure of Atlantic cod populations as well as relationship between body mass and species fecundity and the impacts of warming on future reproductive capacity of Atlantic cod are addressed in *Publication 2*.

Growth and reproductive capacity of Atlantic cod (*Gadus morhua*) under future warming

The second study explored how projected increase in ocean temperatures may affect growth rates and consequently reproductive capacity of Atlantic cod. The author focused on two case study regions - the Barents Sea and the Celtic Sea - with historically observed distinct population growth patterns (discussed in previous section). Growth model projections show size-specific responses in growth rates in both populations. The younger juvenile cod (age groups 1-2 years) from both regions will most probably benefit from increased ocean temperatures with an exception for the

Celtic Sea under RCP8.5 scenario where pronounced 3-4-degree warming will cause reduction in body size of all age groups. As for the older and larger groups, the Celtic Sea cod might shrink up to 30% (60%) by 2100 (2200) whereas the Barents Sea individuals will experience increased growth performances becoming two to four times larger than historically observed. Though those results are mostly in line with published studies (Pörtner et al., 2001; Forster et al., 2012; Cheung et al., 2013; Audzijonyte et al., 2020) there are two main findings that may add new perspectives to the research field. First, a growth curve analysis shows that there is no potential for the Celtic Sea cod to grow larger under increasing temperatures, only decline in growth performance can be expected (Fig. 11). This conclusion is supported by the discussions drawn in *Publications 1 and 2* (and briefly addressed in the previous section) on optimal “aquarium” environments in the Celtic Sea altering historically observed maximized growth rates and setting the upper limits for future growth performance. Secondly, projected enhanced warming in the Barents Sea (up to 6°C) will cause a shift in population growth strategy: currently observed slow growth and later maturation at ages 7-10 years old and high potential to growth larger by the end of life will be switched to a fast exponential growth of juvenile and younger adults, potentially lower size at maturity and maximum asymptotic weights. This assumption is backed up by the latest finding on the growth performance of the farmed Arctic Charr that show that if the yolk and larvae are exposed to warmer thermal environments it causes precocious maturation and long-term growth depression of adult individuals (Árnason et al., 2022).

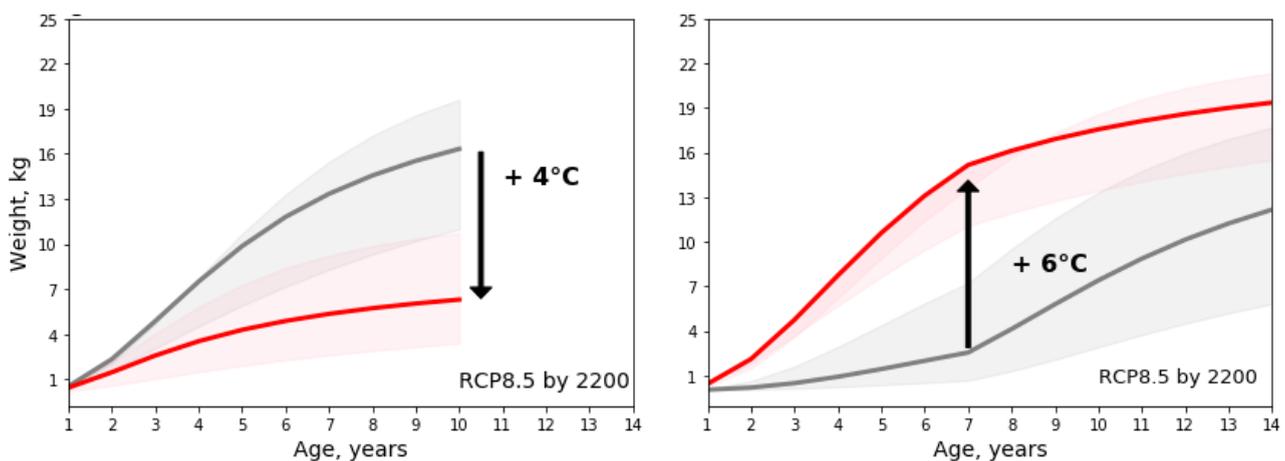


Fig. 11. Projected changes in the growth curve shapes for the Celtic Sea (left panel) and the Barents Sea cod (right panel). Gray lines represent growth curves simulated by the growth model with temperature time series for 1958-2007, red lines - projected growth curves with temperature time

series for 2020-2200, gray and red shadowing - the 5th/95th percentiles range in weight-at-age values produced by the model for each region for 1958-2007 and 2020-2200, respectively. The arrows indicate the direction of changes in weight-at-age (increase or decrease) under every specified warming scenario. Temperature values display projected magnitude of warming in each region (spatially averaged values include depth range 0-580m). Source: *Publication 2, Fig. 4g, h.*

As body size is an essential factor that impacts almost all the biological traits (Brown et al., 2004; Clarke, 2017) changes in growth strategies and adult body size under future warming are expected to influence population's growth. Therefore, in this study size-specific temperature effects projected for the next two centuries (by 2200) were related to weight-fecundity scaling to estimate populations' reproductive capacities (*Fig. 5 in Publication 2*). Thus, an attempt to integrate the growth model output (weight-at-age) into a more complex population-related framework was made.

The main uncertainty in studying such fundamental organism processes as growth and reproduction is the difficulty to pick out a particular factor and research it without taking into consideration the complex system of other interdependent factors. Furthermore, it is difficult to assess future ecosystem responses as a result of ecosystem complexity, different vulnerabilities of species, and ecosystem-specific critical thresholds associated with nonlinear responses to environmental change. Numerical climate change scenarios are analogous to the lab experiments run with different settings (e.g. elevated water temperatures, increased CO₂ levels etc) and under a specified set of assumptions (Brander, 2013). Because of those numerous interactions, projecting the potential outcomes of environmental change on fish populations is not straightforward (Clark et al., 2003; Planque, 2016; Sinclair et al., 2016; Freer et al., 2017). Thus, studies of life-history (Bohn et al., 2004; Tallack, 2009), nutrition (Townhill et al. 2021), eco-physiology (Pörtner et al., 2017) etc. need to join forces in order to improve scenarios of potential impacts of climate change on marine organisms as well as estimate possible individual and population feedback mechanisms to changes in fundamental organism functions.

As a basis for further research the growth model developed during the study was introduced as an open source tool with flexible settings. The package architecture, functionality and applications are described in *Publication 3*.

Atlantic cod growth models: open source Python package for numerical growth experiments

In *Publication 3* the author addressed the issue of developing transparent, extensible, and reusable modelling approaches (Lopez et al., 2013) which is one of the key topics of Open Science concept (Bartling and Friesike, 2014). Publishing an open source scientific code is a necessary practice especially in the field of climate research which is a multidisciplinary scientific field (Lohmann et al., 2020).

The study used advanced programming and software management technologies to share a developed model code and simulation protocols as an open source software project. The published structured repository provides different versions of a growth model setup, input and output data as well as documentation of a simulation procedure. Thus, the repository can be used for external testing and review of previously published results from *Publications 1* and *2*, further developments in terms of current model limitations (addressed in *Discussion 1*) and/or integration into more complex ecological modelling structures, in particular, in eco-physiological studies investigating complex physiological and ecological mechanisms to embed experimental findings and observational studies into broad theoretical concepts (Pörtner et al., 2017).

The main advantage of developed software is that it comprises independent model configurations of different complexity levels enabling users to set up both “laboratory” and “real-world” numerical experiments thus providing solid technical support for integrated ecophysiological research. Besides, the tool can meet the needs of several audience groups (experimental and theoretical biologists, model developers, graduate students etc.) who might be interested in such routines as model development, model testing and validation, or model application (experiments, hypothesis testing). There are numerous practical applications of the developed growth model package (not limited to the listed ones): 1. development/hypothesis testing platform; 2. a module for more complex eco models; 3. single-species studies; 4. integrative methodology / scientific methods.

The growth model may be also used for educational purposes, such as: 1. broadening students’ experience in computational biology; 2. communicating scientific issues related to climate and biological processes; 3. providing a case study of multidisciplinary research.

The model code has been already translated into JavaScript and presented as an outreach web-page: https://www.awi.de/fileadmin/user_upload/AWI/Forschung/Klimawissenschaft/Dynamik_des_Palaeoklimas/Growth_Model/index.html.

To sum up, the focus of *Publication 3* is technical integration and development of a flexible independent open source tool which can help save scientists time, improve reproducibility of research results as well as point out errors that might be overlooked during the research process and even lead to misinterpretation of data. Though developing software is a continuous process, this also enables scientists to efficiently share their work while it is ongoing rather than only post-published (Lowndes et al., 2017). Further developments such as integration of interactive parametrization and restructuring to the class based architecture are planned.

SYNTHESIS

Coupled effects of temperature and body size on growth: historical and future climate perspectives. The thesis comprises several research topics which concern one of the fundamental research issues - consequences of human-induced climate change for marine life at all levels of biological organization (Pörtner et al., 2017). For several decades scientists have been observing tremendous effects of ongoing climate warming on marine organisms in all biogeographic zones (Pörtner et al., 2014). In particular, warming ocean temperatures have been influencing such fundamental physiological traits as organism growth and reproduction (Brander, 2000; 2005; 2006). Historical observations and experimental data show that variations in water temperatures play a major role in regulating the growth performance of ectotherms (e.g. fishes) - marine organisms whose body temperature “mirrors” surrounding water temperatures. However, the temperature effects are often mixed and confused with multiple additional factors such as food availability, oxygen saturation levels, migration, habitat shifts etc. that can be hardly disentangled.

Thus, the first aim of the study was to depict the temperature signal in Atlantic cod population growth patterns and show to what extent size-specific temperature effects shape populations growth curves on decadal time scales. A combined implication of the growth model, that was derived from high quality empirical data, and multidimensional ocean temperature datasets of high spatial and temporal resolution allowed developing a transient simulation setup as well as modelling continuous growth of cod in the “real-world” environment. This approach helped extrapolate laboratory findings of temperature- and size-dependent growth to those found on a population level. Growth curve analysis was used in order to compare observed and modeled growth patterns. The results show that two out of four case study populations (the Celtic Sea and the Barents Sea) demonstrate temperature-dependency in population growth curves while growth in the other two populations (Icelandic and the North Sea cod) is shaped by temperature only at specific life stages (*Discussion, Publication 1*). Furthermore, the temperature environment in the Celtic Sea and the Barents Sea are found to shape the growth curves in different ways. On the one hand, a rather small area of the Celtic Sea with relatively low spatial, vertical and seasonal temperature gradients ranging around 8-12°C (temperatures optimal for maximized growth) combined with an absence of population-specific behavior/habitat shifts determines a uniphasic shape of the growth curve (Fig. 9a) which is often described with the help of von Bertalanffy growth model (*Introduction, Section 5, Fig. 5*). On the other hand, highly heterogeneous Barents Sea environment with distinct thermal

regimes and temperature gradients ranging from sub-zero to 10°C features population-specific habitat shift during lifetime: larvae, juveniles and young immature individuals dwell in colder south-eastern region while older mature cod move to warmer Norwegian waters. This shift characterizes population related multi-phasic shape of the growth curve (Fig. 9c) that the author was able to depict with a “thermal shift based” setup (*Discussion, Publications 1-2, Supplement 3*).

The author also showed how population-specific temperature-shaped growth patterns will change under projected temperature increase at the example of two populations - the Celtic Sea (8-12°C) and the Barents Sea (0-10°C) - populations at the southern and northern-most species distribution limits (*Publication 2*). The growth model simulations provided two opposite scenarios: critical declines in weight of cod in the Celtic Sea (30% - RCP4.5 and 60% - RCP8.5) and two to four times increase in weight of the Barents Sea cod. The two findings are to be highlighted here: a complete shift in the growth pattern from multiphasic to uniphase continuous growth which is now observed in the southern populations is expected in the Barents Sea if temperatures increase by more than 6°C; in the Celtic Sea the 4-degree warming will reduce the growth rates to minimum bringing the mean weights (age groups 1-10 years) close to those currently measured in cold water populations (*Fig. 4 in Publication 2*).

Size-specific temperature effects on species reproductive capacities. As most physiological and ecological rates depend on species body size (Brown et al., 2014), hindcasting temperature- and size-dependent growth patterns and understanding effects influencing growth in nature are a key to revealing the potential impacts of ocean warming on structure and functioning of marine communities, populations, and ecosystems (Lindmark et al., 2021). *Publication 2* demonstrates differential response of various age groups to projected temperature increase which might lead to reordering of the mean size spectrum of younger and older individuals in a population. In particular, the following changes in mean weight of older cod are projected: increase in the Barents Sea and decline in the Celtic Sea. Furthermore, a temperature threshold of 6°C was identified in the Barents Sea which may completely change cod growth strategies there and induce shifts in maximized growth performance towards high latitudes. Assuming observed scaling between adult body weight and fecundity (Thorsen et al., 2010), those changes are expected to influence species capacity to reproduce. Thus in the final part of *Publication 2* the authors related projected changes in individual weight to empirically derived weight-fecundity scaling in order to estimate the magnitude of potential changes in populations’ reproductive capacity (calculations provided by Dr. Fleming

Dahlke). The results show that the Barents Sea cod will benefit in body size from temperature-dependent increase if fishing pressure remains sustainable whereas the Celtic Sea cod will experience losses assuming any fishing pressure level (*Fig. 5 in Publication 2*). Inferring to the complexity of interrelated factors that affect growth and reproduction at both individual and population levels, further incorporation of proposed scenarios into a bigger ecosystem framework is necessary in order to investigate potential feedback mechanisms that can moderate projected changes.

Open research software as an assistant in a multidisciplinary research. Technologies have induced the speed of scientific software development, revolutionized nature sciences and become a critical part of modern research. Due to the fact that climate change boosts trans-disciplinary studies and connects climate researchers, physicists and biologists, more and more scientists refer to modelling as an essential tool to link scientific fields. Building an integrative eco-physiological approach requires open, reusable tools that should be published on open source platforms. Those tools can help a researcher save time and focus on their goals due to the absence of necessity to develop software from scratch and a possibility to adjust available tools. A growth model tool that was developed in particular in this study (*Publications 3*) integrates experimental and observational data into a unified methodological framework (Fig. 12). It is a Python package that includes different settings of the growth model scaled from dimensionless to multidimensional versions. Differential software architecture that comprises independent parts of various functionality (equations, input parameters, supporting functions etc) allows modification of the model according to specific tasks. The simplicity of the software and user friendly documentation make it comprehensible for users with various programming and research backgrounds.

Concluding remarks: eco-physiological study from a modelling perspective. Marine ecosystems provide vital resources for humanity as even slight changes in them lead to significant changes in populations nutrition levels. Growth curve modelling (GCM) may serve as a tool implemented in fish stock assessment and resource management that provide information about available food resources (Steinarsson, 2013). Although, integrating physiological findings into an ecological context is a challenging task to accomplish (Pörtner et al., 2017), the study made an attempt to build a bridge between experimental and observational data by providing a simplified, flexible, easy-to-reproduce modelling framework with incorporated multidimensional ocean temperature datasets. Additional efforts were made for thorough analysis of strengths and limitations of the

growth model within an eco-physiological framework. The study did not aim to explain mechanisms of growth as the ability of the growth model to downscale to physiological level is very limited. However, it covers various temporal and spatial scales thus being a useful tool that can support both physiological and ecological studies. It gives access to the input and output data as well as to the integrated parameters related to individual (laboratory) level, and to the model setup related to the ‘real-world’ level. Finally, the method was initially developed for Atlantic cod but can be parameterized for other fish species.

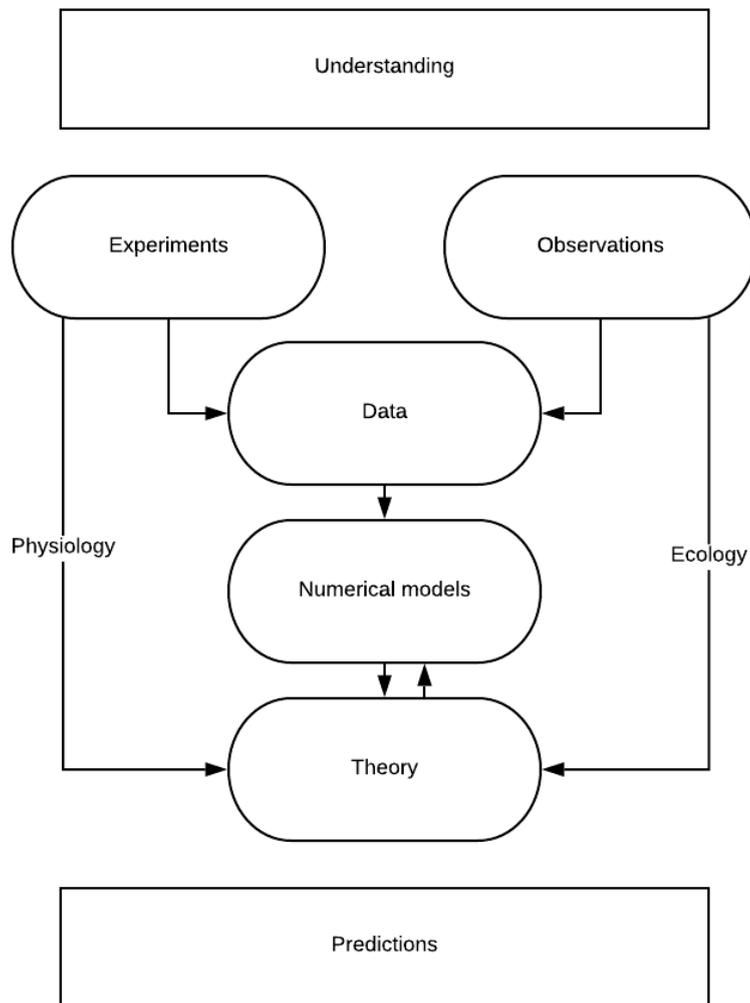


Fig. 12. A unified methodological framework, which integrates theoretical biology, experimental and observational data, and numerical modeling, as a basis for projecting species response to environmental changes.

OPEN QUESTIONS AND PERSPECTIVES

First of all, growth studies investe multiscale physiological and ecological processes. Therefore, experimental data describe growth of fish over a short period of life cycle (days to several months) whereas observational data keep track of growth on a population level over the entire lives of individuals. An implication of various methods measuring growth at different time scales might cause a misleading interpretation when comparing experimental findings to observational data because for comparison short-term data is directly interpolated to some intermediate or longer time-scales. This might introduce scaling error because short-term physiological responses depicted in aquatic experiments do not include other forces working on larger scales. This issue has been addressed in statistical physics and climate research, in particular in “weather versus climate” studies (Lohmann et al., 2020; Lohmann, 2020). Therefore it should be more often discussed in eco-physiological research. In this study an attempt to overcome the scaling issue was made by developing a modelling approach that allows integration of both types of data into a common framework in order to explore laboratory based findings in the natural environment. The model allows exploration of current capacities and limitations of thermal environments available for fish species among populations. In a context of future climate research the approach helps identify temperature thresholds that may transform growth strategies of aquatic animals and induce shifts in maximized growth performance towards high latitudes. Another problem is mirrored by significant differences in size distribution within wild populations which complicates direct comparison with laboratory data capturing inter-population differences in growth rates on smaller temporal times scales (Weatherley, 1966).

Secondly, the study involves growth curve modelling and analysis which has been rarely used among methods studying fish growth on a population level. In most ecological research so far growth data have been demonstrated quantitatively whereas this study emphasizes the importance of visual data representation and comparison. Growth curve modeling is introduced by Steinarsson (2013) as a tool to simulate growth of farmed cod. It can be also used as one of the main tools in eco-physiological research aiming to extrapolate experimental findings of fish growth to a population level.

Thirdly, most of the growth studies use the von Bertalanffy growth equation which represents uniphase growth - continuous growth under a stable external environment - and does not take into

account changes in thermal conditions over a fish life cycle. The idea has been already debated in various scientific articles (Katsanevakis and Maravelias, 2008; Higgins et al., 2015; Lorenzen, 2016; Wilson et al., 2018). This study shows that growth models of a von Bertalanffy type can not be implemented for fish with observed thermal habitat shift. The study proposes an alternative setup which integrates observed shifts in growth patterns (e.g for the Barents Sea cod). As the von Bertalanffy growth model is most commonly used in ecosystem modelling approaches and stock assessments it should be reconsidered and upgraded with settings that simulate habitat shifts. Alternatively, the growth model represented in the study can be implemented in ecosystem and fisheries models as it has more flexible architecture.

Fourth, the model developed in this study is concentrated on temperature as the main factor influencing growth and doesn't take into account other ones. However, the model concept can be used as a basis for developing models focusing on other factors and later possibly unified in one complex system that will allow more detailed and flexible simulations of population growth curves. Though to investigate the impact of other factors such as food and oxygen limitation, further calibration of the model with experimental data is necessary. One of the biggest challenges that growth studies have been facing is nonlinearity and underlying structural (or hierarchical) nature of growth process as well as difficulties to disentangle direct causal effects from confounding factors and their interrelations (*Introduction, Section 1*). Thus, multivariate statistical analysis of time series observational data along with consideration of non-quantitative categorical variables obtained from expert knowledge (e.g. migration patterns or specific spawning behavior) should accompany further experimental and modelling studies. Among one of the most critical factors that should be taken into account is a combined effect of temperature and different nutrition levels (in experimental studies) or food availability (in ecological studies) on growth. Ideally, both bio-mechanistic and statistical approaches should be combined in a coupled modelling architecture (Fig. 13) that would comprise: 1. modules for covariate factors (oxygen, food, salinity etc.) that can be added or excluded depending on statistical model output; 2. growth strategy selection based on categorical parameters (thermal heterogeneity of the region, presence/absence of migration pattern, observed habitat shift etc.) such as expert scorings provided by Kjesbu et al. (2022); 3. parameters of population-specific deviations in growth rates based on laboratory data. Basically, statistical time-series analysis and multivariate modelling can serve as a “decision-making tool” (if-approach)

for choosing for a growth strategy whereas bio-physical empirically based models would provide underlying physiological mechanisms.

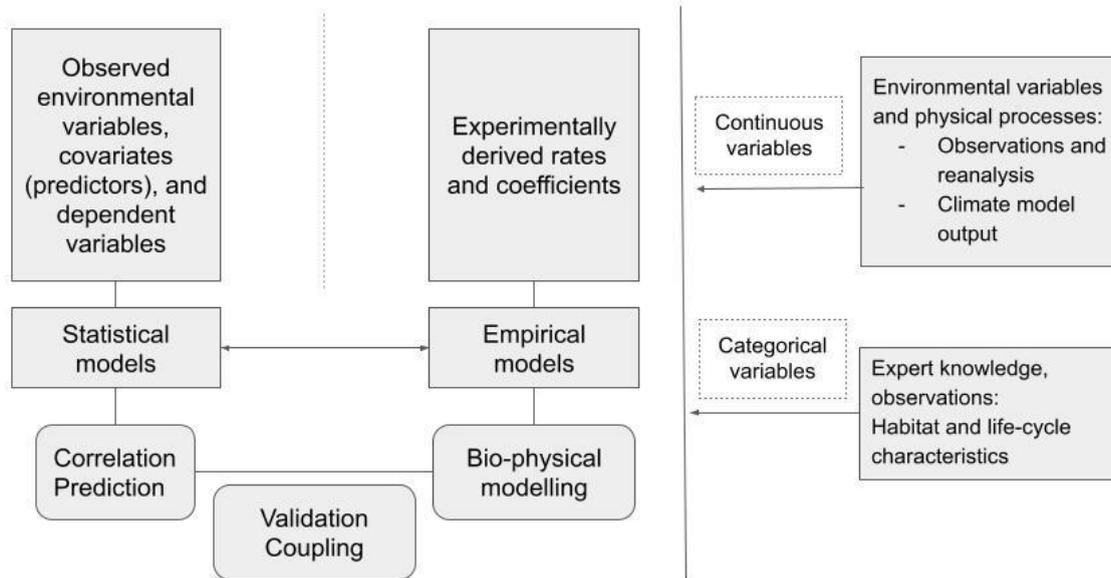


Fig. 13. Modelling framework that includes both statistical models (ecology) and empirical¹ models (physiology).

Nowadays, the scientific community progresses towards diverse collaborative teams which leads to popularization of open source software that can be used for solving complex transdisciplinary problems. While the development of sustainable, reusable, high-quality scientific software is a challenge, it is crucial to foster these practices in academia. Open source codes - as it is presented in the study - shall be considered as an integrated part of eco-physiological research as they are developed by scientists and for scientists, and therefore have practical significance and allow to increase and simplify the process of cross-validation of experimental, observational and modelling data.

¹ By the term “empirical” the author means models built upon experimental data.

OUTLINES

Growth studies help improve understanding of climate impacts on aquatic animals at all organizational levels: from individual organisms to marine ecosystems. The thesis results show that observed and projected poleward distribution shifts and changes in species abundance (Poloczanska et al., 2013; Hollowed and Sundby, 2014; García Molinos et al., 2016; Pinsky et al., 2020) will be accompanied by induced growth rates and changes in populations' size structures. Increasing regional temperatures as well as changing hydrographic conditions will cause a northward shift of species thermal windows and therefore changes in individual growth strategies. In other words, southernmost populations, that are at the peak of their growth performance (e.g. the Celtic Sea cod or other species: Neuheimer et al., 2011), will be exposed to sub-optimally warm environmental conditions while species that are currently at the northern edges of the thermal window (e.g. the Barents Sea cod) will show maximized growth performance.

Growth performance underlines many individual, population and ecosystem processes such as survival, maturation, reproduction and prey-predator interactions (Howell and Filin, 2014; Stige et al., 2017). Thus, such physiological constraints as decreased or increased growth rates will influence individual life histories (faster or slower maturation), local food web structures, species reproductive potential, total species biomass and therefore fisheries catch potential and fishing efforts that provide valuable resources for mankind (Worm et al., 2006; Free et al., 2019; Burraco et al., 2020). As a result projected shifts in individual growth performance will cause cross-latitudinal changes in mean population size.

Despite the major effects of temperature, there are other significant factors such as food availability and oxygen limitations that regulate growth processes. Changes in spatial distribution and abundance of prey as well as invasion of tropical species are projected across the Northeast Atlantic and Arctic shelf (Fossheim et al., 2015) which will influence the amount of food available for growth. On the other hand, changes in mean population size will induce restructuring of local food webs causing deviations in prey-predator hierarchies. Finally, declining levels of dissolved oxygen (IPCC, 2014) which is the key factor regulating organism aerobic performance (Pörtner, 2001; 2010; Pörtner and Kunst, 2007; Pörtner and Farrell, 2008; Pörtner et al., 2010; 2017) will set additional limits to projected species-specific thermal windows and shape both individual and populations' size.

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SUPPLEMENTS

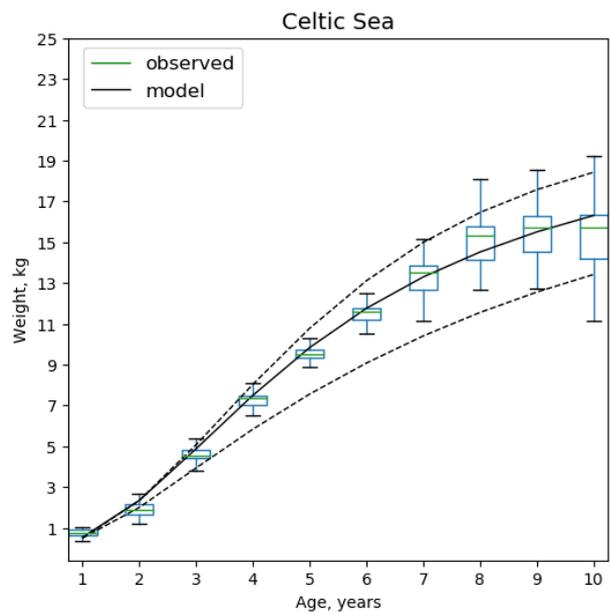
Supplement 1

The Celtic Sea simulation results with two depth settings: depth layers masked over 0-580 m and 30-580 m. Hereafter: a solid black line indicates model median, a dashed black line - model IQR, box plots - observed median (green), IQR (blue), min/max (black).

Coordinates: 47°N; 52°N; 12°W; 1°W

Temperature mask: no masking, whole regional temperature range is considered

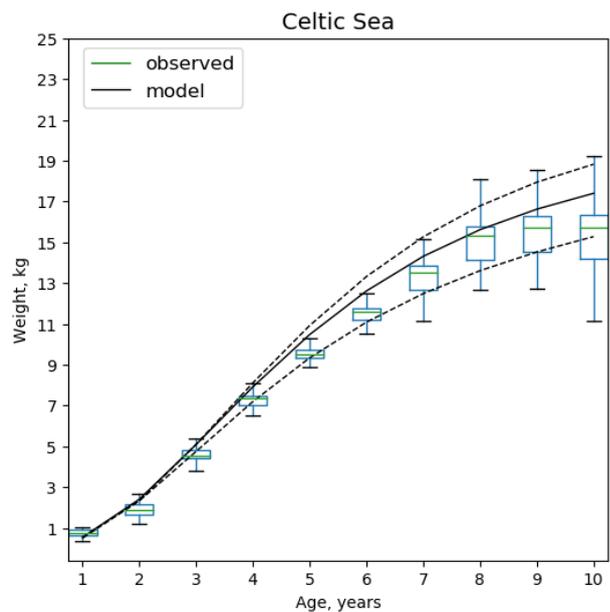
Depth levels: 0-580 m



Coordinates: 47°N; 52°N; 12°W; 1°W

Temperature mask: no masking, whole regional temperature range is considered

Depth levels: 30-580 m



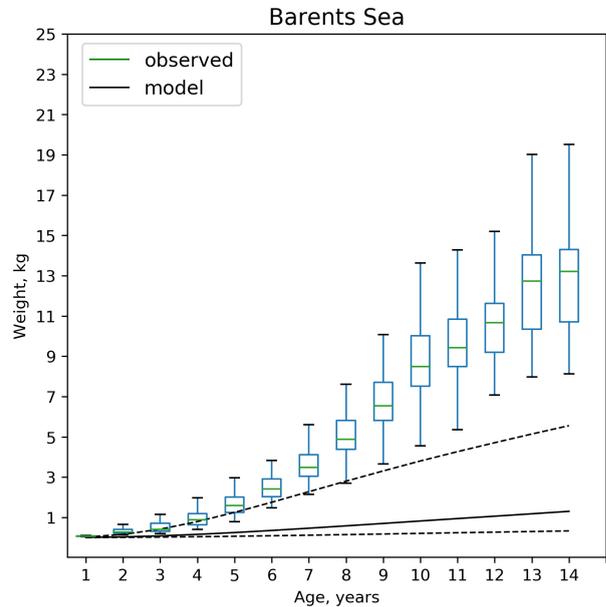
Supplement 2

The Barents Sea simulation results with various geographic boundaries (lon, lat, depths) and temperature ranges.

Coordinates: 67°N; 80°N; 10°E; 50°E

Temperature mask: no masking, whole regional temperature range is considered

Depth levels: 0-580 m

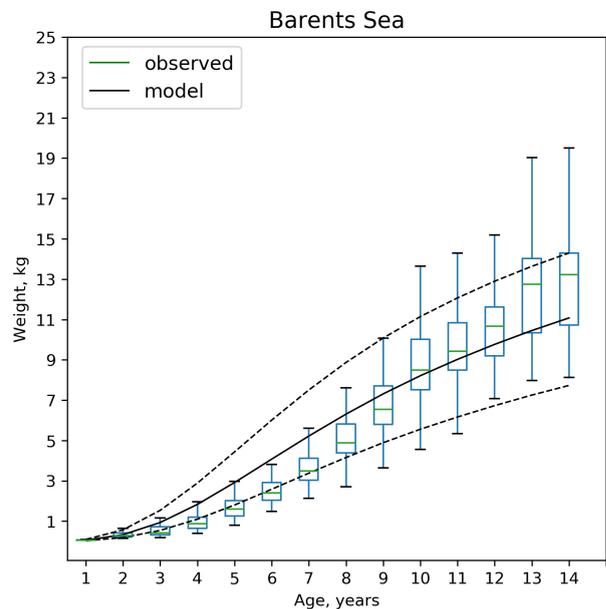


Coordinates: 67°N; 80°N; 10°E; 50°E

Temperature mask: areas beyond 1.5-12°C are blanked out

Depth levels: 0-580 m

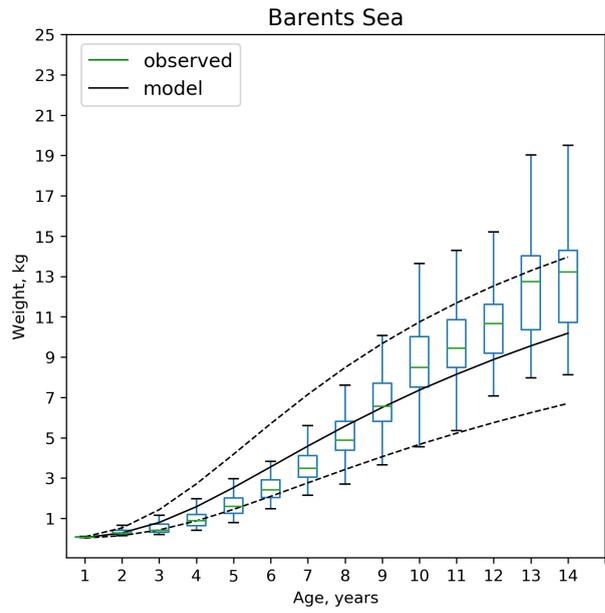
(from *Publication 1*)



Coordinates: 67°N; 80°N; 10°E; 50°E

Temperature mask: areas below 0°C are blanked out

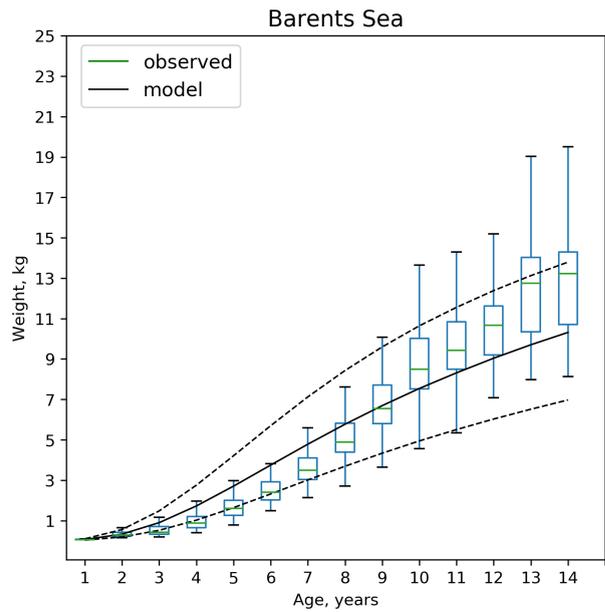
Depth levels: 0-580 m



Coordinates: 68°N; 74°N; 10°E; 40°E

Temperature mask: areas below 0°C are blanked out

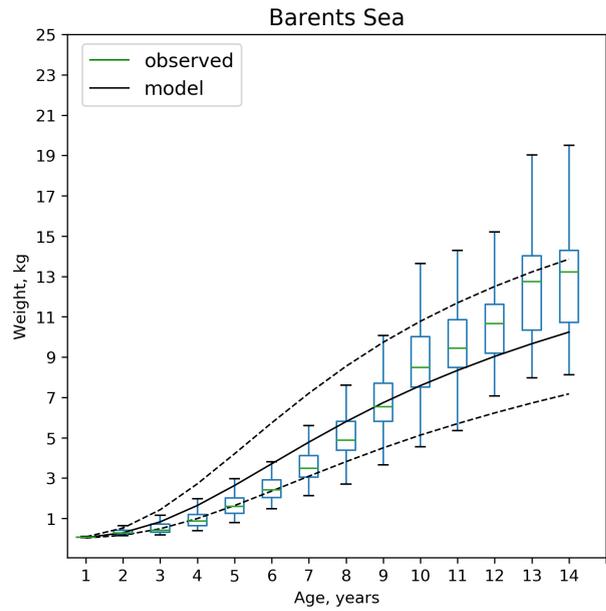
Depth levels: 0-580 m



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Temperature mask: areas beyond 1.5-12°C are blanked out

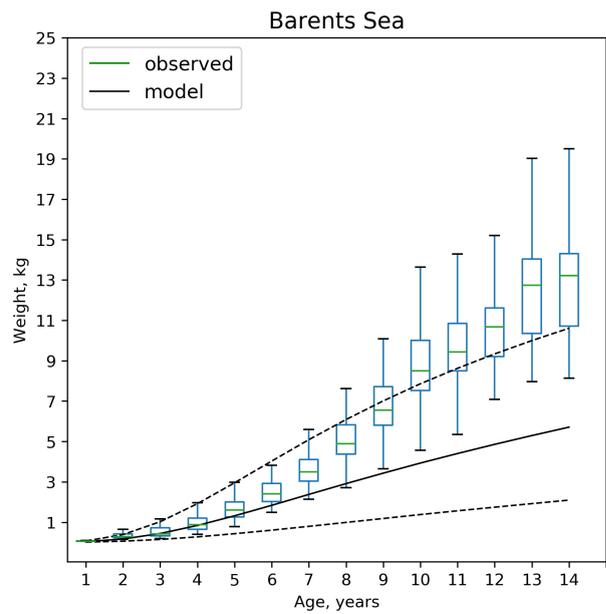
Depth levels: 30-580 m



Coordinates: 68°N; 74°N; 10°E; 40°E

Temperature mask: no masking, whole regional temperature range is considered

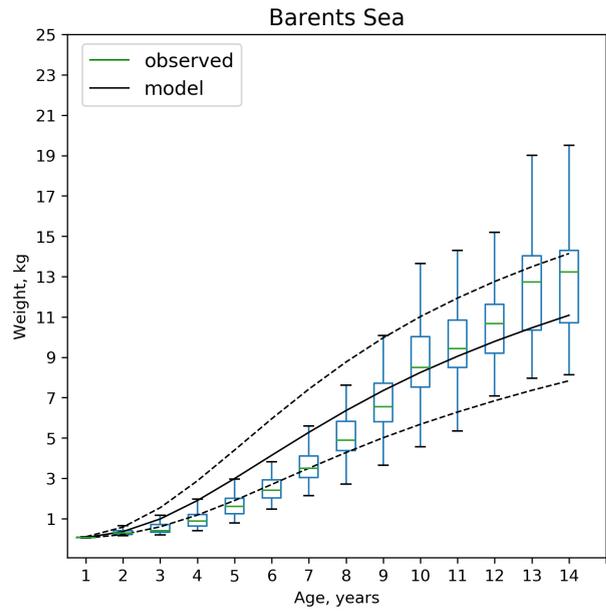
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Coordinates: 68°N; 74°N; 10°E; 40°E

Temperature mask: no masking, whole regional temperature range is considered

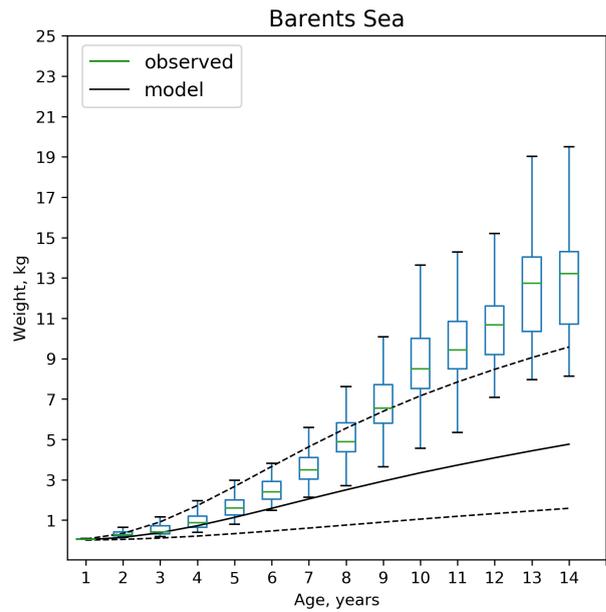
Depth levels: 0-580 m



Coordinates: 68°N; 74°N; 10°E; 40°E

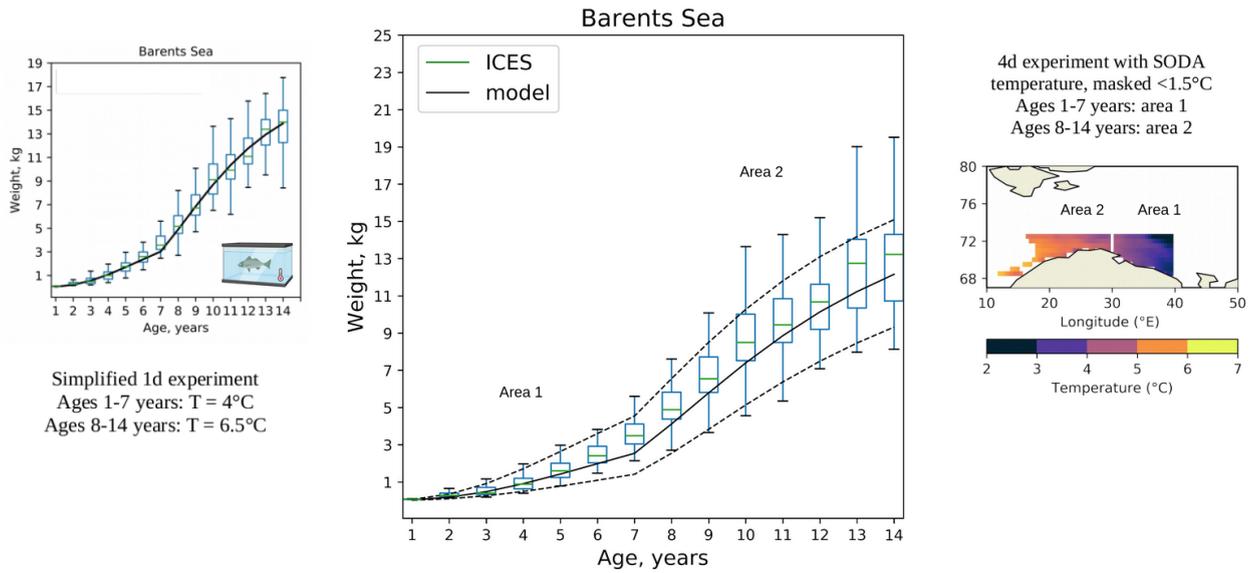
Temperature mask: no masking, whole regional temperature range is considered

Depth levels: 30-580 m



Supplement 3

Implementation of thermal shift in the Barents Sea (simulation setup): area 1 (ages 1-7 years) incorporates temperatures from the eastern Barents Sea (68°N, 72°N, 30°E, 40°E) while area 2 - temperatures from the area along the Norwegian coast (68°N, 72°N, 10°E, 30°E).



Supplement 4

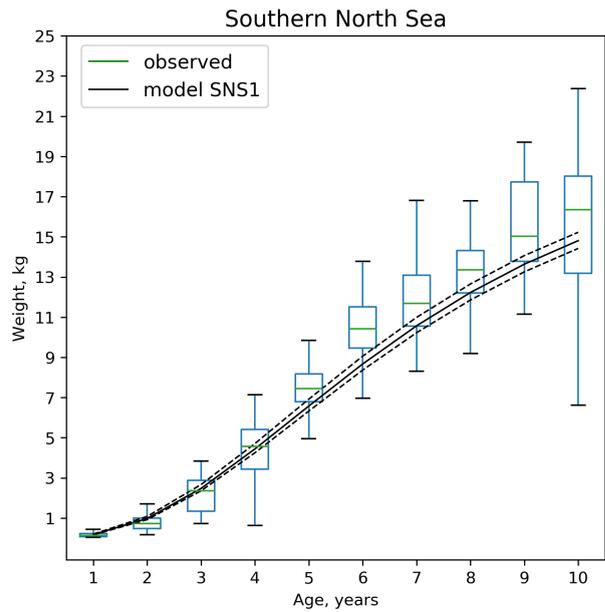
The North Sea simulation results with various geographic boundaries (lon, lat, depths) and temperature ranges.

South North Sea

Coordinates: 50°N; 57°N; 3°W; 8°E

Temperature mask: 0-10°C

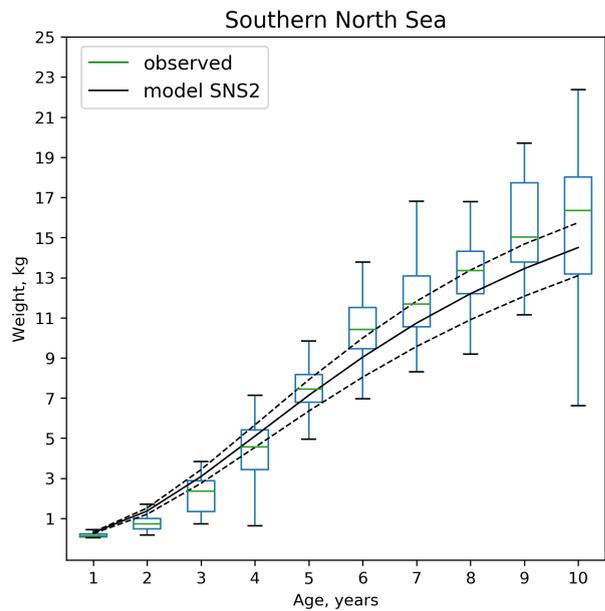
Depth levels: 0-580 m



Coordinates: 50°N; 57°N; 3°W; 8°E

Temperature mask: no mask

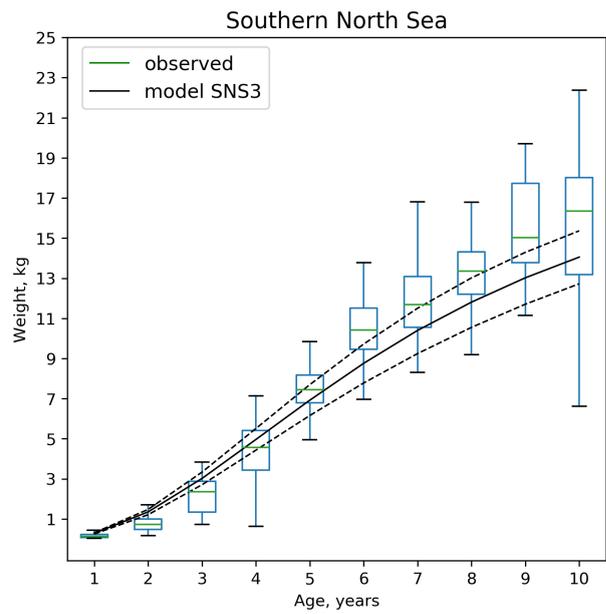
Depth levels: 0-580 m



Coordinates: 51°N; 56°N; 3°W; 8°E

Temperature mask: no mask

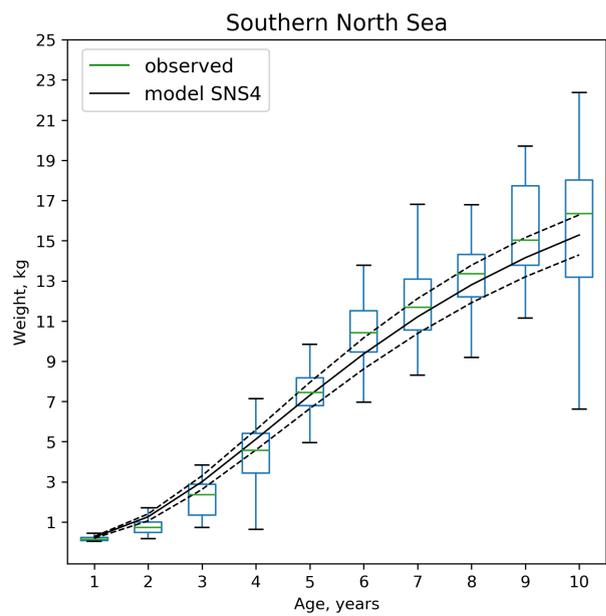
Depth levels: 0-580 m



Coordinates: 50°N; 57°N; 3°W; 8°E

Temperature mask: no mask

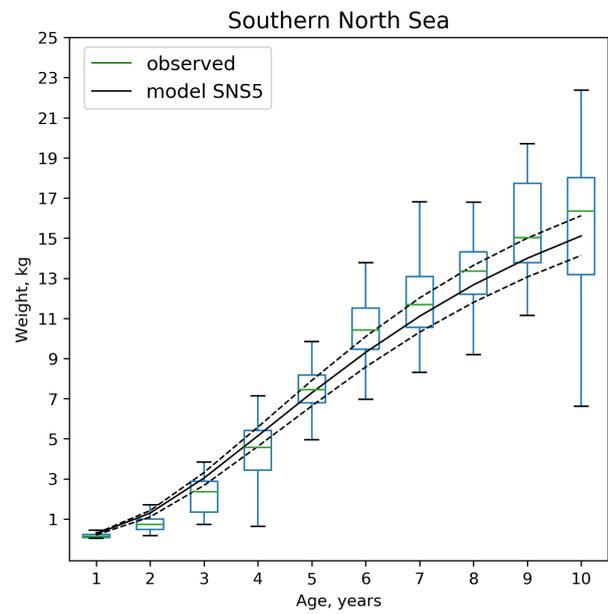
Depth levels: 30-580 m



Coordinates: 51°N; 56°N; 3°W; 8°E

Temperature mask: no mask

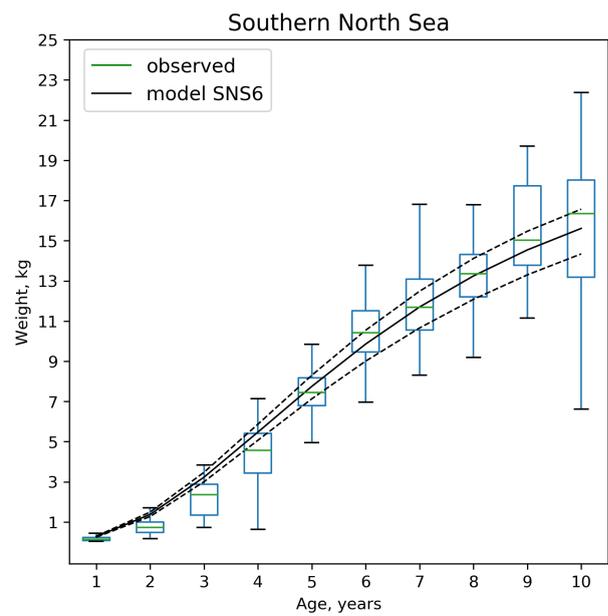
Depth levels: 30-580 m



Coordinates: 50°N; 57°N; 3°W; 8°E

Temperature mask: no mask

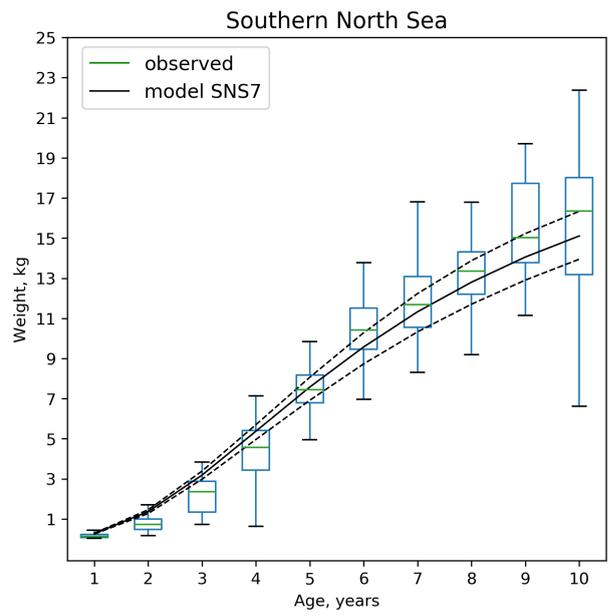
Depth levels: 30-50 m



Coordinates: 51°N; 56°N; 3°W; 8°E

Temperature mask: no mask

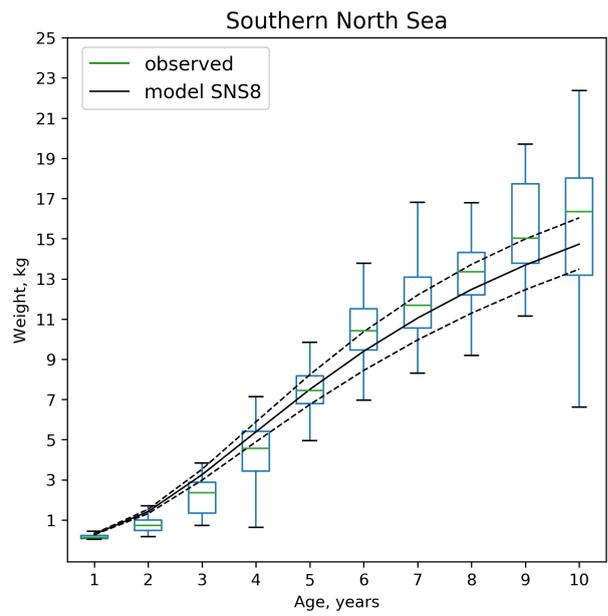
Depth levels: 30-50 m



Coordinates: 50°N; 57°N; 3°W; 8°E

Temperature mask: no mask

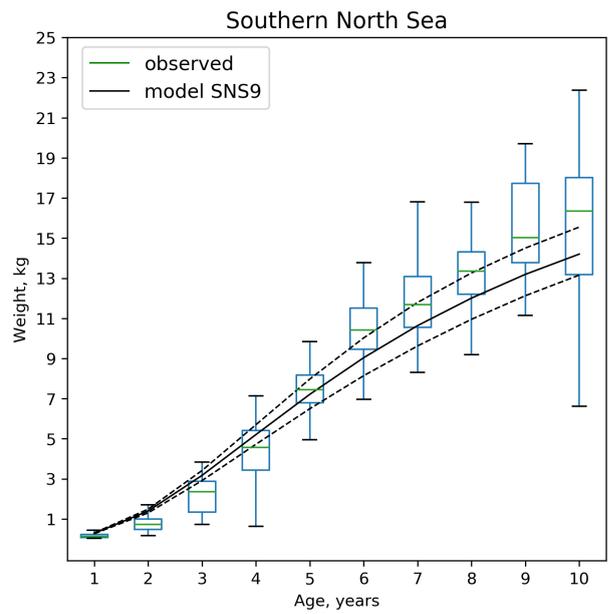
Depth levels: 20-40 m



Coordinates: 51°N; 56°N; 3°W; 8°E

Temperature mask: no mask

Depth levels: 20-40 m

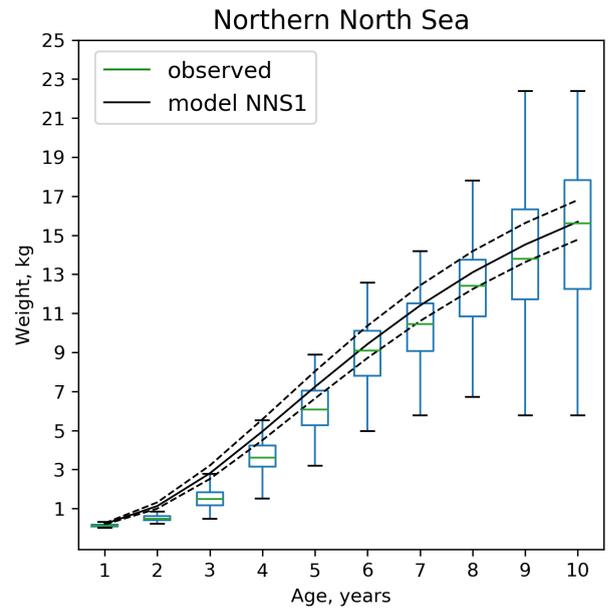


North North Sea

Coordinates: 56°N; 62°N; 3°W; 8°E

Temperature mask: 0-10°C

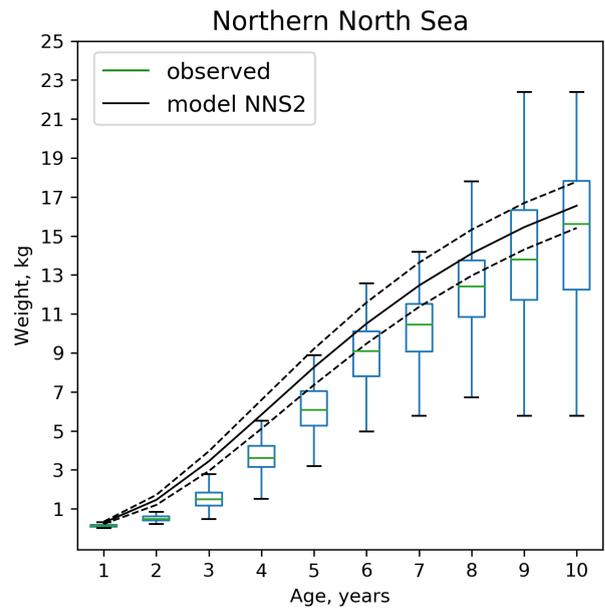
Depth levels: 0-580 m



Coordinates: 56°N; 62°N; 3°W; 8°E

Temperature mask: no mask

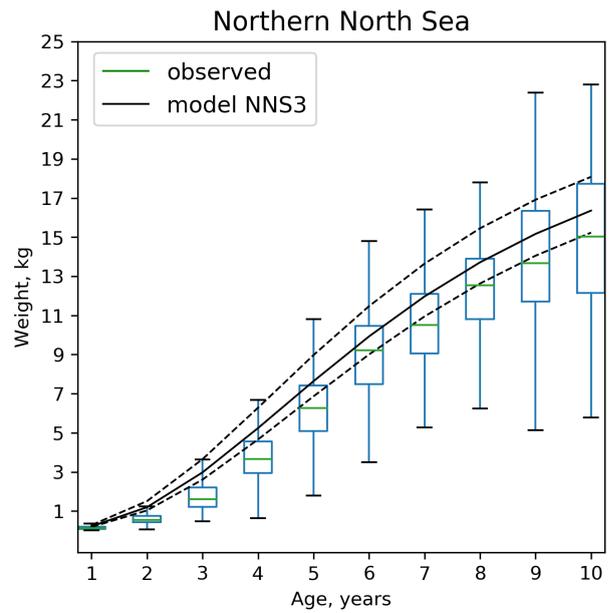
Depth levels: 0-580 m



Coordinates: 56°N; 62°N; 3°W; 8°E

Temperature mask: no mask

Depth levels: 60-580 m



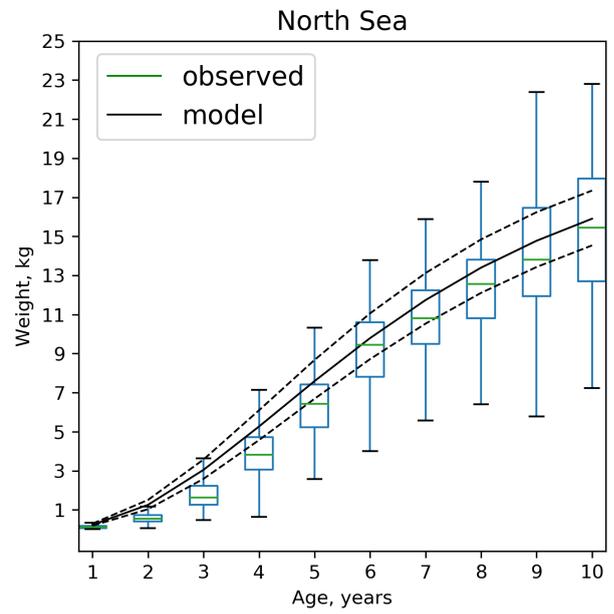
North Sea + Skagerrak Channel

Coordinates: 51°N; 62°N; 3°W; 13°E

Temperature mask: no mask

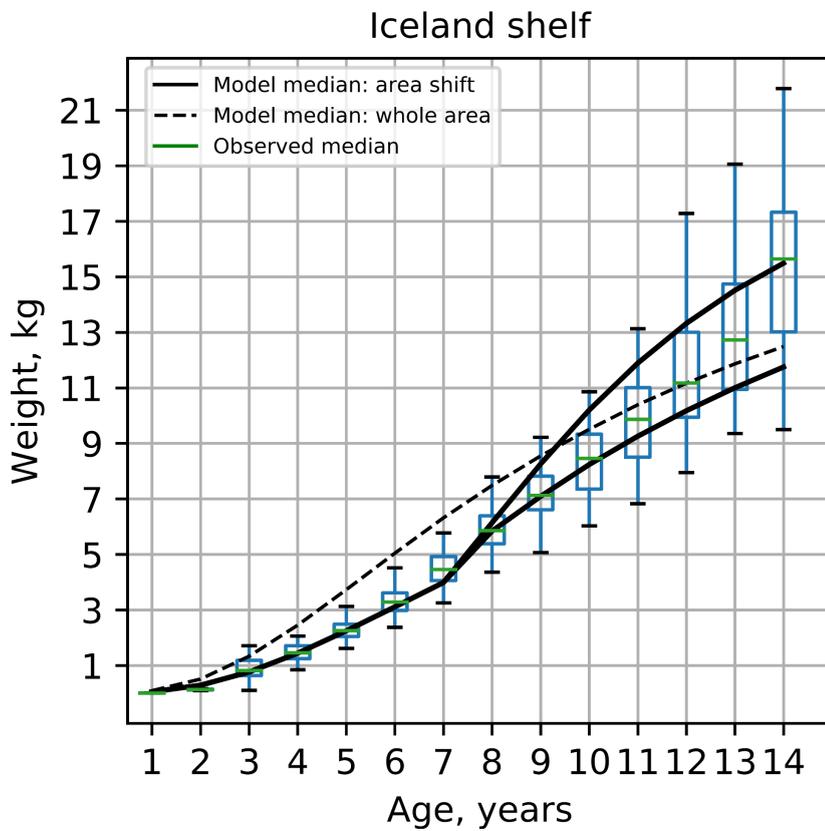
Depth levels: 30-580 m

Observations: DATRAS areas 1-9



Supplement 5

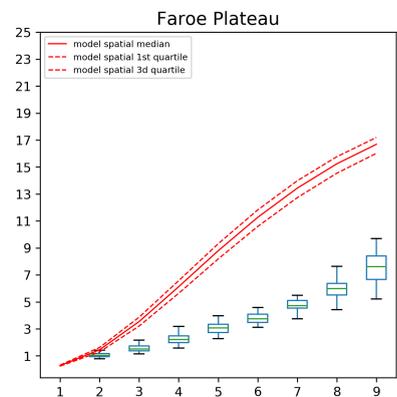
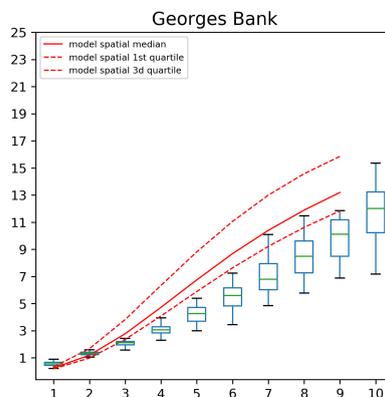
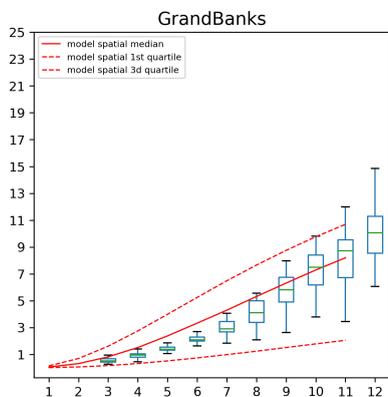
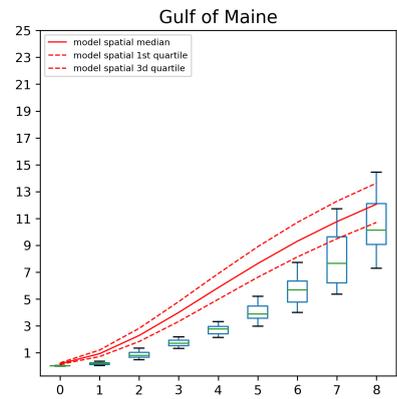
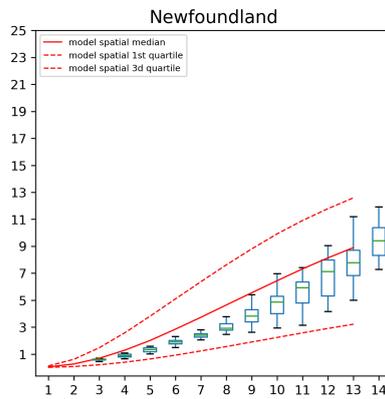
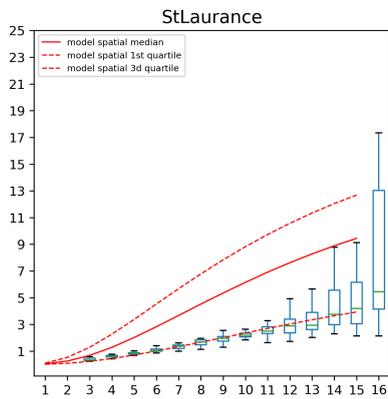
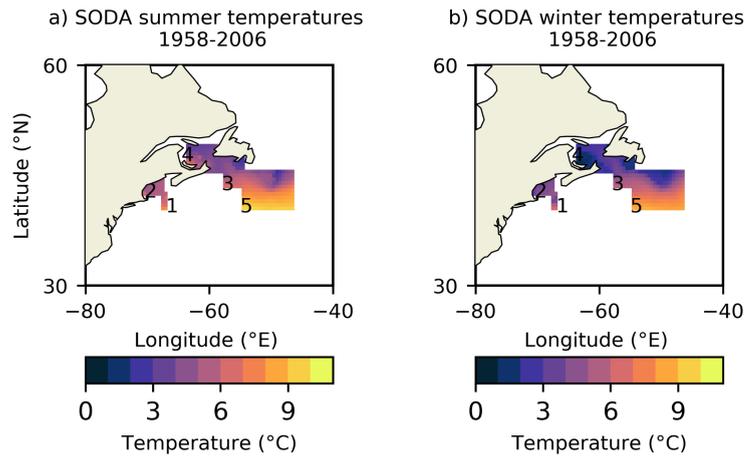
Comparison of continuous growth (dashed black line) and thermal shift (solid black lines) setups for the Iceland shelf. The black line for ages 1-7 years represents northern area off Iceland (65°N, 68°N, 27°W, 11°W), the upper black line (from age 7 and above) represents southern area off Iceland (62°N, 65°N, 27°W, 11°W), the lower black line (from age 7 and above) - the whole area around Iceland (62°N, 68°N, 27°W, 11°W).



Supplement 6

The simulation results for the Northwest Atlantic (+ Faroe Plateau) cod populations. Red lines - growth model medians and IQRs, box plots - observed medians and IQRs.

1 – Georges Bank, 2 – Gulf of Maine, 3 – Newfoundland, 4 – St. Lawrence, 5 – Grand Banks



PUBLICATIONS

PUBLICATION 1

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

N Sokolova, M Butzin, F Dahlke, K M Werner, D Balting, G Lohmann & H-O Pörtner

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

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Sokolova, N., Butzin, M., Dahlke, F., Werner, K. M., Balting, D., Lohmann, G., and Pörtner, H.-O. Exploring the role of temperature in observed inter-population differences of Atlantic cod (*Gadus morhua*) growth with a 4-dimensional modelling approach. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsab043. Received 10 June 2020; revised 8 February 2021; accepted 9 February 2021.

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 $0.5 \times 0.5^\circ$ 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.*,

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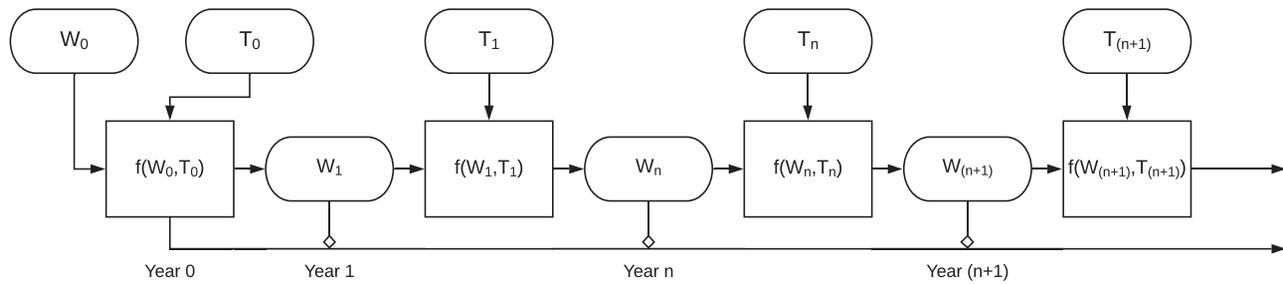


Figure 1. Schematic representation of the transient growth model setup: $f(W, T)$ – growth model function; W – weight-at-age output data that are also used as a subsequent input; T – 4-dimensional temperature input (horizontal boundaries are shown in Fig. 1; vertical boundaries are shown in Fig. 3, 4, 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 inter-population 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.

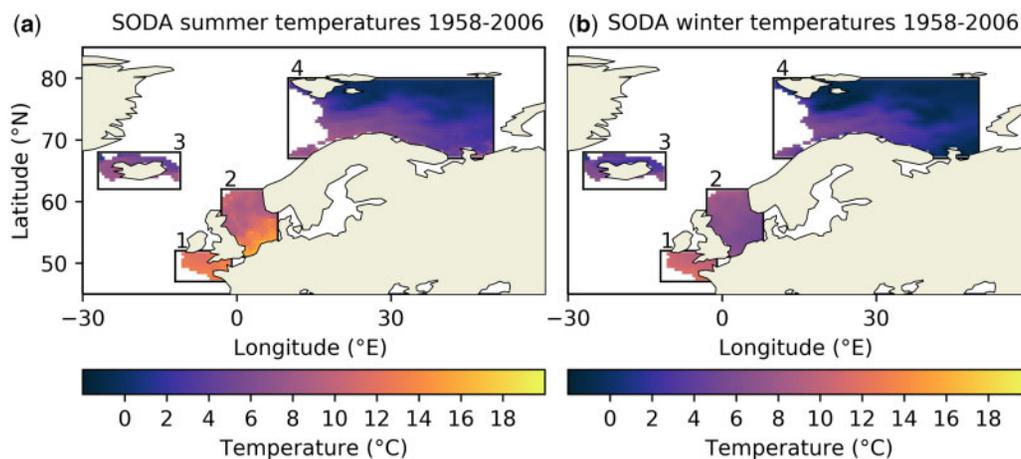
Methods

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 are 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	3–14	Data set 1: Estimated mean weight at age in the catch
		1985–2010	1–9	Data set 2: Estimated survey weight-at-age in the spring survey (SMB)
		1955–2010	3–14	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	2–14	Data set 1: Weight-at-age in landings Norway
		1946–2010	3–14	Data set 2: Estimated mean stock weight-at-age
		1985–2010	5–11	Data set 3: Weight-at-age in the Lofoten survey
		1984–2010	1–12	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 Steinarrson, 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 $0.5^\circ \times 0.5^\circ$ in the horizontal and 40 levels in the vertical dimensions. We extracted temperature data for 0–

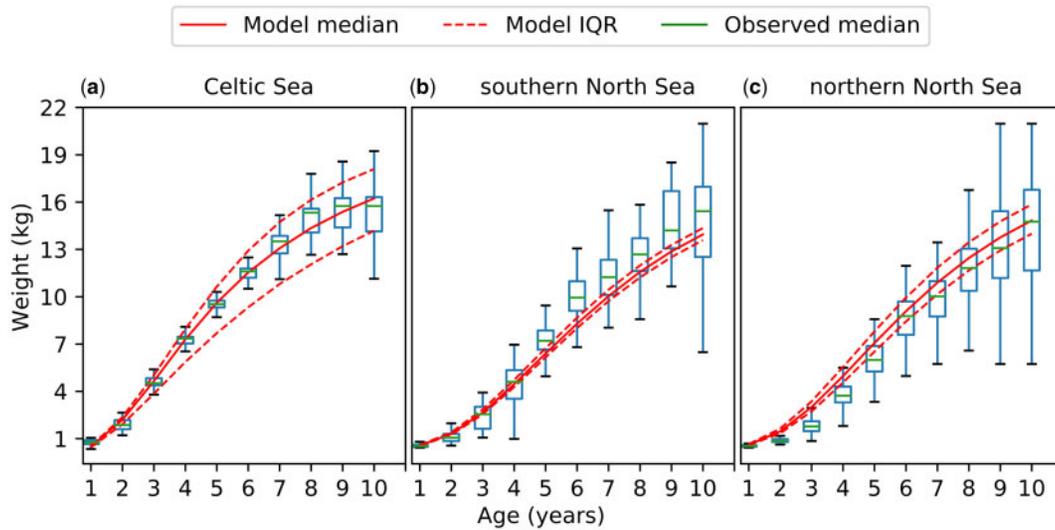


Figure 3. Modelled versus observed weight-at-age of Atlantic cod in the Celtic Sea (a), the southern North Sea (b), and the northern North Sea (c). Modelled weight-at-age time-series output was averaged for the period 1958–2006. The moving averaging window for simulated weights at every age class covers 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 $1.5 \times \text{IQR}$.

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.

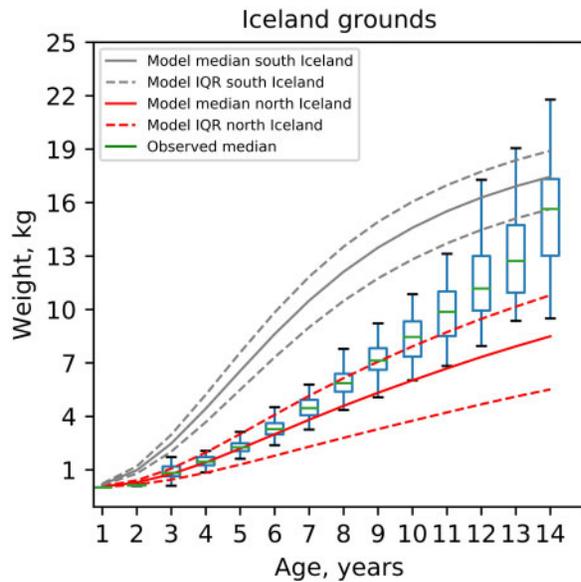


Figure 4. Modelled versus observed weight-at-age of Atlantic cod around Iceland. Modelled weight-at-age time-series output was averaged for the period 1958–2006. The moving averaging window for simulated weights at every age class covers 36 years. Median and IQR of model results were estimated for each 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 $1.5 \times \text{IQR}$.

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

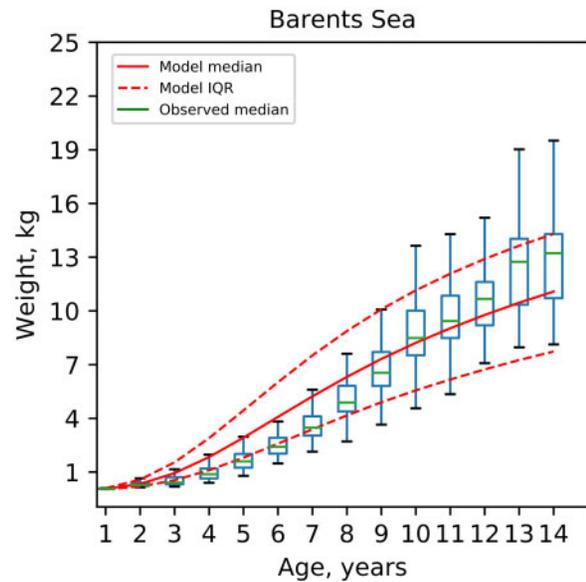


Figure 5. Modelled versus observed weight-at-age of the Northeast Arctic cod. Modelled weight-at-age time-series output was averaged for the period 1958–2006. The moving averaging window for simulated weights at every age class covers 36 years. Median and IQR of model results were estimated for each 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 $1.5 \times \text{IQR}$.

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

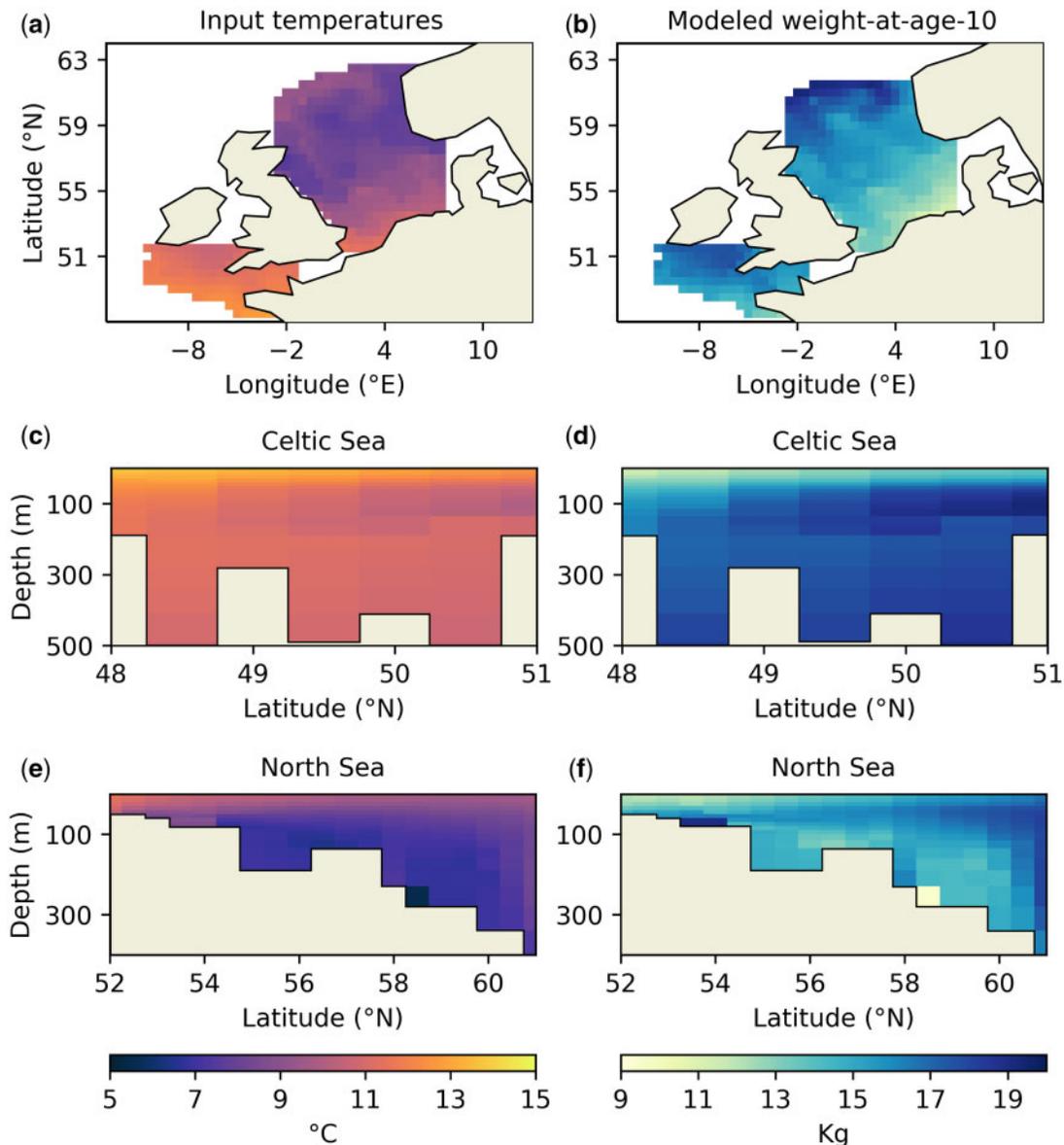


Figure 6. Simulated weight-at-age-10 and annual mean input temperatures in the Celtic Sea and North Sea: (a) Input temperatures in the Celtic and North Sea are averaged over depths 0–580 m and cover the period 1958–2002; (b) Weight-at-age-10 values in the Celtic and North Sea are averaged over depths 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

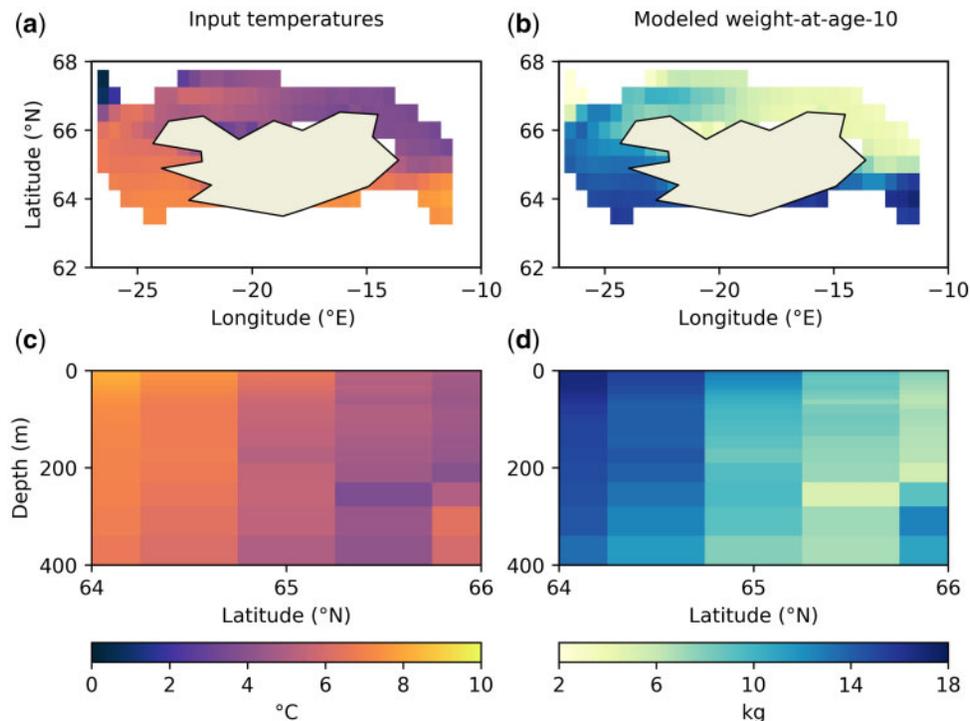


Figure 7. Simulated weight-at-age-10 and annual mean input temperatures around Iceland: (a) Input temperatures are averaged over depths 0–580 m and cover the period 1958–2002; (b) Weight-at-age-10 values are averaged over depths 0–580 m, averaging window for 10 years and covers the period 1968–2003; (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

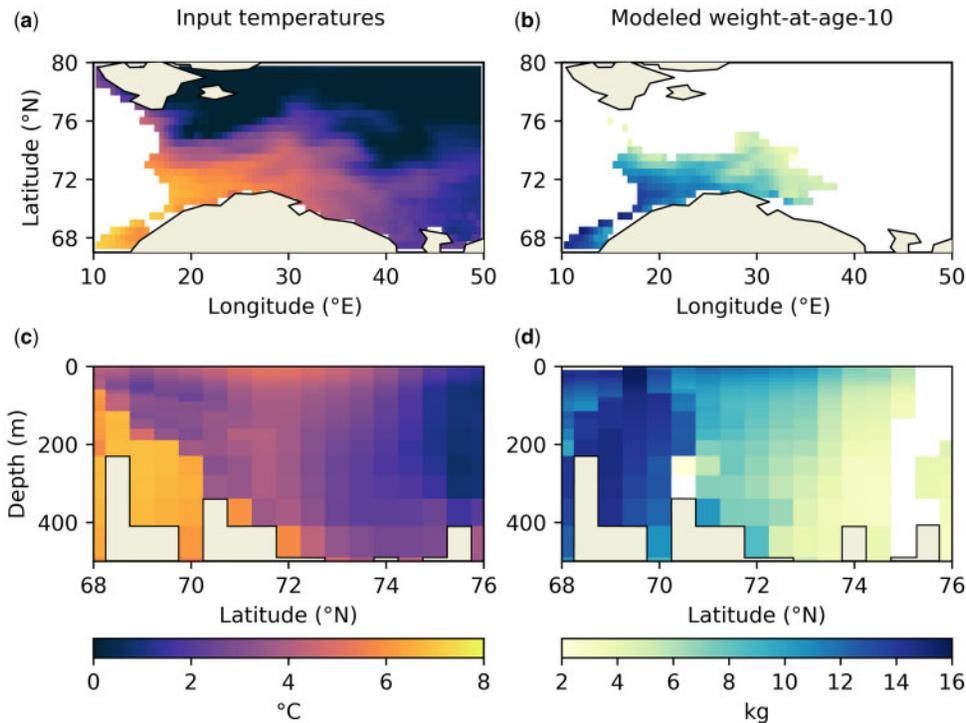


Figure 8. Simulated weight-at-age-10 and annual mean input temperatures in the Barents Sea: (a) Input temperatures are averaged over depths 0–580 m and cover the period 1958–2002; (b) Weight-at-age-10 values are averaged over depths 0–580 m, averaging window for 10 years covers the period 1968–2003; (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 Steinarrson,

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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PUBLICATION 2

Growth and reproductive potential of Atlantic cod (*Gadus morhua*) under future warming

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MANUSCRIPT

Growth and reproductive potential of Atlantic cod (*Gadus morhua*) under future warming

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Body size and temperature are two fundamental factors influencing almost all physiological rates and therefore the whole ecosystem functioning. Climate change is expected to alter changes in species body size and thus influence reproductive potential of many marine populations. In this study we introduce an integrated modeling concept that helps estimate potential impacts of ocean warming on growth and reproduction of Atlantic cod (*Gadus morhua*) - one of the largest fish stocks in the Northeast Atlantic. Our study suggests variable reactions in growth rates to future warming in different age groups: in the Celtic Sea only the youngest cod will benefit from warming while older and larger cod might shrink up to 30% (60%) by 2100 (2200) whereas the Barents Sea individuals will experience increased growth performance in all age groups becoming two to four times larger than historically observed. In terms of reproductive potential, the Barents Sea cod is expected to benefit from temperature-dependent increase in body size if fishing pressure remains sustainable in contrast to the Celtic Sea cod which is expected to experience losses under warming assuming any fishing pressure level.

The tight relationship between temperature, body size and many physiological processes has been observed in most terrestrial and marine organisms (Brown et al., 2014; Clarke, 2017; Glazier, 2021). Among the main organism functions that are affected by environmental temperatures and individual body size are growth and reproduction (Brown et al., 2014). Incorporating mechanisms of observed size-specific temperature effects on growth in eco-physiological studies is critical in a context of rapidly warming climate that has been affecting marine organisms at all organizational levels for decades (Pörtner et al., 2001; Pörtner et al., 2017; Lindmark et al., 2018). Climate change

is expected to alter growth rates and size structure of many marine populations by shifting the range of temperature regimes supporting individual organism growth rates (Pörtner et al., 2001). Studies suggest that warming will have differential effects on fish body size with the major trend of reduction in mean species size across latitudes (Cheung et al., 2013; Audzijonyte et al., 2020; Lindmark et al., 2021). Furthermore, warming environments will influence population size structure defined as abundance and size of individuals of each age group (Lindmark et al., 2018). Changes in population demography will shape the overall dynamics of fundamental ecological characteristics such as population reproductive potential (or population fecundity) which can be assessed as the quantity of eggs produced by mature individuals (Andersen et al., 2019). In our study we explore how projected warming will affect growth and reproductive potential of Atlantic cod (*Gadus morhua*) - one of the largest fish stocks in the Northeast Atlantic. We assess warming induced changes in body size of different age groups and estimate to what extent changes in size structure may alter shifts in reproductive potential at population level. Historically, the southern cod stocks show higher quantity and quality of offspring because they mature at larger size and larger individuals produce dis-proportionally more offspring than smaller ones (Lambert, 2008; Thorsen et al., 2010; Barneche et al., 2018). In light of projected effects of ocean warming on growth rates and population size structure it is expected that in warm waters cod reproductive potential will decrease while increasing in currently unfavorable colder areas (Alix et al., 2020). In this study we estimate the magnitude and direction of changes in body weight and reproductive potential of Atlantic cod by applying projected temperatures from a multi-scale Earth System Model (Ackermann et al., 2020), a temperature- and size-based mechanistic growth model (Butzin and Pörtner, 2016; Sokolova et al., 2021), and empirically derived weight-fecundity scaling (Thorsen et al., 2010; Kjesbu, 2016). In our estimations we also consider abundance data for all reported age groups and the effects of fishing pressure on population demographic structure (Fig. S1). Our study workflow is schematically represented in Fig.S2.

Study concept: integrated temperature effects on body size and reproductive potential

Over the wide range of temperature environments that Atlantic cod experience across latitudes, experimental studies revealed species-specific temperatures that are optimal for growth and vary with size and life-stage of individuals (Björnsson and Steinarsson, 2002; Björnsson et al., 2007). Fig. 1a displays an example of such a relationship between temperatures, growth rates, and individual body mass empirically obtained for Icelandic cod: the smaller individuals have higher optimal temperatures for growth than larger ones (e.g. 15°C for a 10-g cod in contrast to 10°C for a 10-kg cod). Those growth data were integrated in our growth model which allows us to simulate growth of cod over its entire life cycle (Butzin and Pörtner, 2016; Sokolova et al., 2021). We

convert model output (growth rates) into widely used fisheries metrics - weight-at-age - and represent temperature related growth patterns as growth curves (Fig. 1b). At temperature 10° the growth rates in our idealized simulations are maximized and cod reaches the largest size (Fig. 1b). This temperature is suggested as optimal for cod growth regardless of the population (Pörtner et al., 2001). Temperatures below 6°C and above 12°C limit growth performance and as a result, the shapes of the growth curves differ from the “optimal”. In this study we link temperature- and size-dependent growth described above with observed mass-fecundity scaling (Fig. 1c, d). Observed fecundity is one of the most widely used indicators of species reproductive fitness (Alix et al., 2020). Fecundity represents reproductive potential of an organism or population expressed in the number of eggs produced during the spawning season (Lambert, 2008; Thorsen et al., 2010). The relationship between body mass and fecundity plays a fundamental role in reproductive biology. It is observed that a high abundance of eggs is associated with a high proportion of older individuals in a spawning stock (Stige et al., 2017). In Atlantic cod, the weight-fecundity scaling exponent equals 1.25 (Fig. 1c) which is in line with inter-specific data compiled by Barneche et al. (2018). A combination of simulated weight-at-age data with weight-fecundity scaling provides us with a generalized fecundity-at-age metrics that helps estimate temperature effects on reproductive potential, or the amount of eggs produced by individuals of a certain age group at any given temperature range (Fig. 1d). In the following sections we apply the described concept to a wild cod population by simulating inter-annual monthly resolved growth over decades, integrating modeling results into a weight-fecundity scaling equation and extrapolating individual-based calculations with reported relative abundance data (Fig. S2).

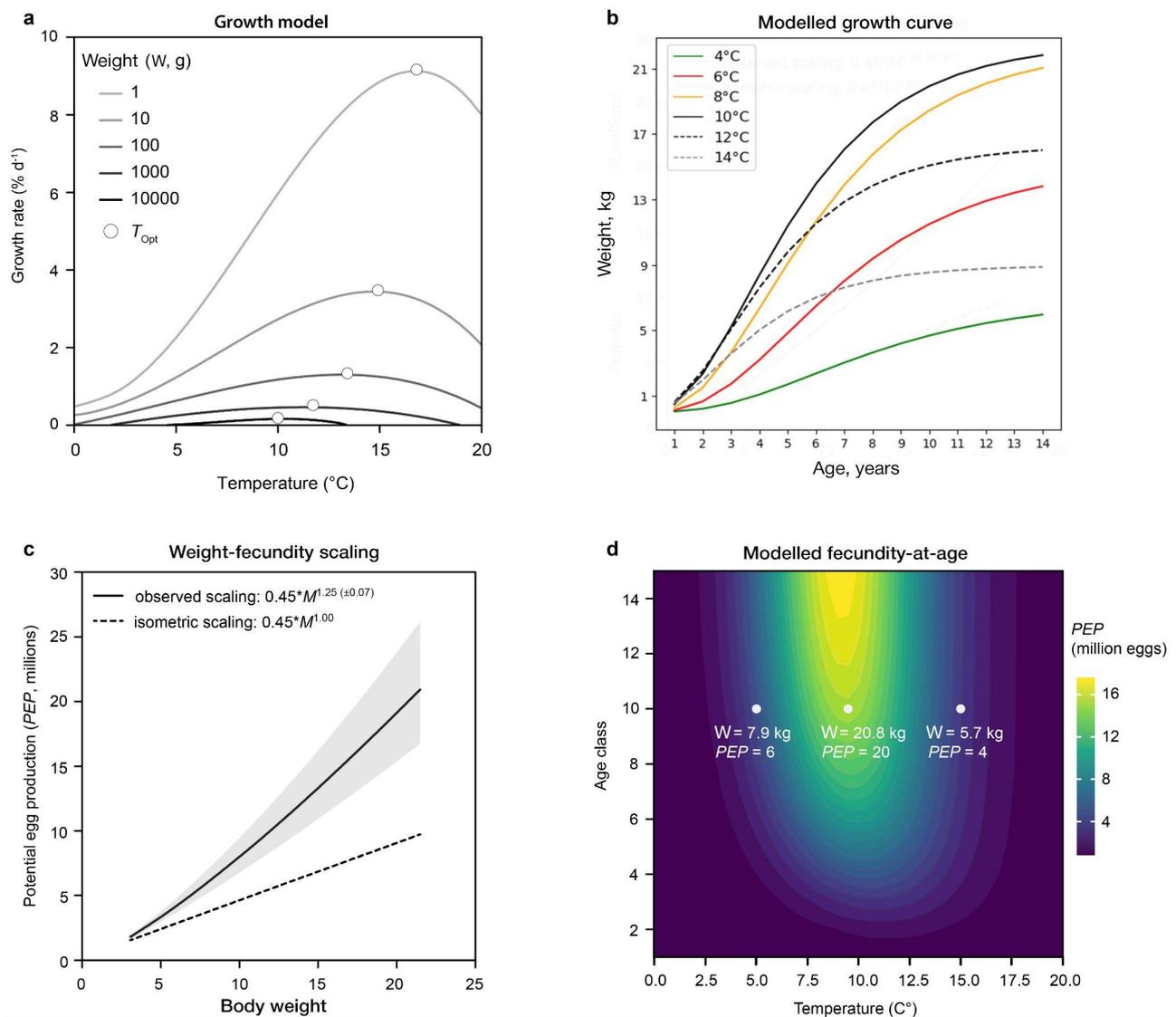


Fig. 1. Conceptual figure displaying (a) relationships between growth rates, temperature and body weight incorporated into the growth model; (b) growth model results converted into weight-at-age metrics and represented as growth curves; (c) empirically derived weight-fecundity scaling; (d) correlation between temperature, body weight, and fecundity at a specific age class. Fig. 1a is an extended version of Fig. 2a in Butzin and Pörtner (2016) that shows modeled temperature-dependent growth rates of Atlantic cod for a specific individual body weight in kg (lines). The optimal temperatures for each sample body weight are displayed by circles. Fig. 1b represents weight-at-age data estimated from simulated growth rates and displayed as individual growth curves; note, that the growth curves are idealized examples modeled under constant temperature values and exceed feeding ration. Fig. 1c represents empirically derived scaling of body weight (kg) and potential egg production (PEP, mln eggs) of Northeast Atlantic cod (solid line) in comparison to generalized isometric scaling (dashed line). Gray shading indicates standard error of the regression parameters. Observed scaling coefficient is based on field samples

(Kjesbu, 2016; Thorsen et al., 2010). Fig. 1d represents temperature-based fecundity-at-age that incorporates the growth model output - body weight (kg) at a specific age class - and calculated weight-dependent PEP values (mln eggs).

Temperature-shaped growth curves of Atlantic cod: historical perspective

Atlantic cod is one of the key commercial fish species distributed over a wide range of thermal habitats in the Northeast Atlantic (Link and Sherwood, 2019). Species temperature conditions range from sub-zero in the Barents Sea to around 20°C in the Celtic Sea (ICES, 2005; Righton et al., 2010). Such pronounced differences in thermal regimes influence individual growth rates resulting in population-specific body weights that cod achieve at a certain age (Link and Sherwood, 2019). In our previous study we showed that regional temperatures shape the growth curves of the northeast Atlantic cod populations over time periods longer than 30 years (Sokolova et al., 2021). This study focuses on cod populations from regions with distinctly different temperature regimes - the Celtic Sea and the Barents Sea – populations at the southern and northernmost species distribution limits (Pörtner et al., 2008; Link and Sherwood, 2019). We use observed and modeled weight-at-age values as a proxy for growth performance of wild populations.

The Celtic Sea provides environmental conditions that are considered as optimal for growth: a wide range of suitable forage species and a relatively homogeneous water structure covering temperature range 9 to 15°C (Fig. 2a). Observational data as well as modeling results show that the growth rates in the Celtic Sea environment are maximized, especially in the first years of life (age group of 1-4 years). This corresponds with temperature-dependent growth patterns depicted in laboratory experiments (Sokolova et al., 2021). The Barents Sea cod is observed to experience shifts in thermal environments over its life-cycle: young immature cod live in the open Barents Sea until age 7 years and grow slowly while mature cod of older age groups are found consistently in warmer waters (Link and Sherwood, 2019). Older mature individuals migrate substantial distances using warm flowing Atlantic water between spawning grounds along the Norwegian coast and feeding grounds in the Barents Sea (ICES, 2005; Righton et al., 2010; Link and Sherwood, 2019). In our growth experiments we mimic the observed life-history feature by applying two different thermal regimes for different life stages: an open sea thermal environment of ~ 4°C for the group of 1-6 years old individuals, and Norwegian coast temperatures of ~ 6°C for 7+ years old ones (Fig. 2b). This population specific simulation setup allowed us to capture the observed shape of the Barents Sea growth curve: uniform gradual increase in weight between 1-7 years and exponential increase in weight after age 7 years (Fig. 2b, d). Despite radical differences in environmental conditions, feeding and spawning behavior, as well as life-history characteristics, based on the growth curve

analysis of both populations we suggest that their growth performance is shaped by regional temperature gradients on scales over 30 years.

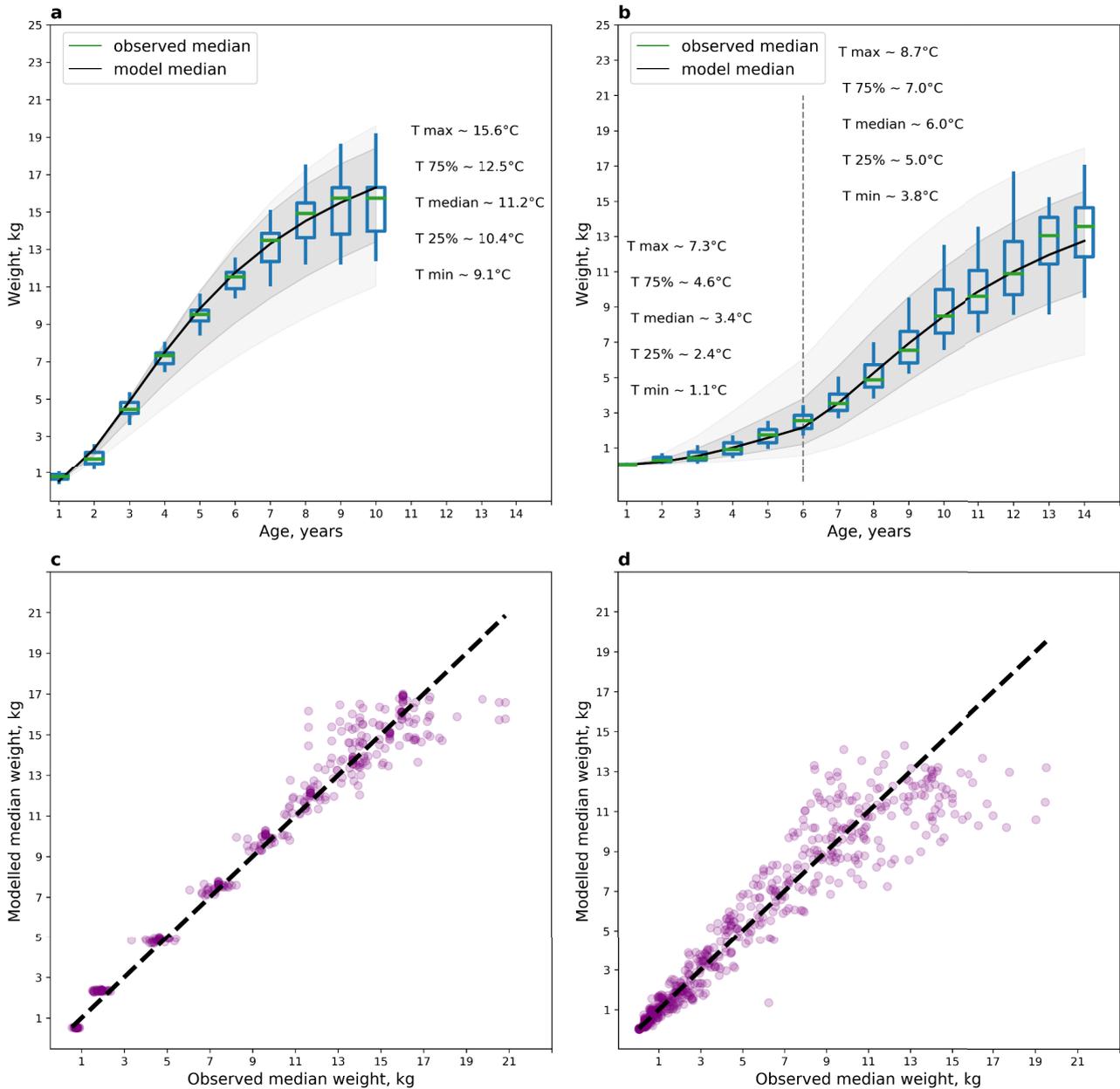


Fig. 2. Modeled weight-at-age of Atlantic cod in comparison with observations for two case study regions: the Celtic Sea (a, c) and the Barents Sea (b, d). (a, b) Modeled temperature-shaped growth curves are represented by the median weight-at-age values (black lines), IQR (dark gray shading) and the 5th/95th percentiles (light gray shading). Observed weight-at-age values in (a) and (b) are displayed as box-plots where green lines are medians, blue boxes - IQR, and the upper/lower whiskers - 5th/95th percentiles (calculated from ICES time series data). The setup input temperatures (calculated from 4-dimensional temperature data) are represented in (a) and (b) by T max (95th percentile), T 75% (75th percentile), T median (50th percentile), T 25%

(25th percentile), and T min (5th percentile). The dashed gray line in (b) divides the 14-year life-cycle of the Barents Sea cod into two simulation phases: phase 1 (ages 1-6 years) incorporates temperatures from the eastern Barents Sea (68°N, 72°N, 30°E, 40°E), while phase 2 - temperatures from the area along the Norwegian coast (68°N, 72°N, 10°E, 30°E). (c, d) Scatter plots (c - the Celtic Sea and d - the Barents Sea) show modeled versus observed weight-at-age medians for each age class: 1-10 years (Celtic Sea) and 1-14 years (Barents Sea). The weight-at-age time series data span 1971-2007 (Celtic Sea) and 1959-2019 (Barents Sea).

Impacts of warming on growth of Atlantic cod: future perspective (2100 and beyond)

Here we use ocean temperatures projected by the multi-scale AWI Earth System Model (AWI-ESM) equipped with an interactive Greenland Ice Sheet (GIS) forced under high (RCP8.5) and intermediate (RCP4.5) emission scenarios (Ackermann et al., 2020). Involving ice sheet dynamics captures the potential impacts of a melting GIS on the coastal habitats of Atlantic cod. To our knowledge, this is the first time such a comprehensive Earth system model has been used in eco-physiological studies. Fig. 3 shows differences between the projected temperature values and historical records (1960-1980) in the Northeast Atlantic; Fig. 4 - direction and magnitude of changes in cod growth patterns that might be potentially caused by ocean warming.

According to the RCP4.5 results by the end of the 21st (2100) and the 22nd (2200) centuries, a temperature increase of 1-2°C is projected in the Celtic Sea (Fig. 3a, b). Growth model projections show that such temperature changes will not affect age groups of 1- and 2-year-old individuals while a decrease in weight up to 30% is expected for age groups 3+ years old (Fig. 4 a, c; Fig. S3). In comparison to RCP4.5, RCP8.5 results for the same time periods show a higher temperature increase (Fig. 3c, d): ocean temperatures rise up to 3 and 4°C by 2100 and 2200, respectively. Such a pronounced warming reduces the weight of cod in all age groups (10-30% by 2100 and 50-60% by 2200; Fig. S3). The 4-degree warming reduces the growth rates to minimum and flattens the growth curve bringing the weight-at-age values close to those observed in the Barents Sea in the 20th century (Fig. 4 g, h).

The Barents Sea is characterized by the most dramatic temperature increase in both coastal (Norwegian coast) and open areas: 3-4°C (RCP4.5) and 4-6°C (RCP8.5) by 2100 (Fig. 3c, d). The warming peaks are projected along the Norwegian coast (5-7°C) and over the open areas of the Barents Sea (>6°C) by 2200. Growth model simulations reveal that all age groups will gain in weight under projected warming (Fig. 4b, d, f, h). The older age groups might become two to four times larger than historically observed (Fig. S3). A complete shift in the growth pattern (from

bi-phasic to one-phase continuous growth) is expected if the temperatures increase by more than 6°C (Fig. 4f, h).

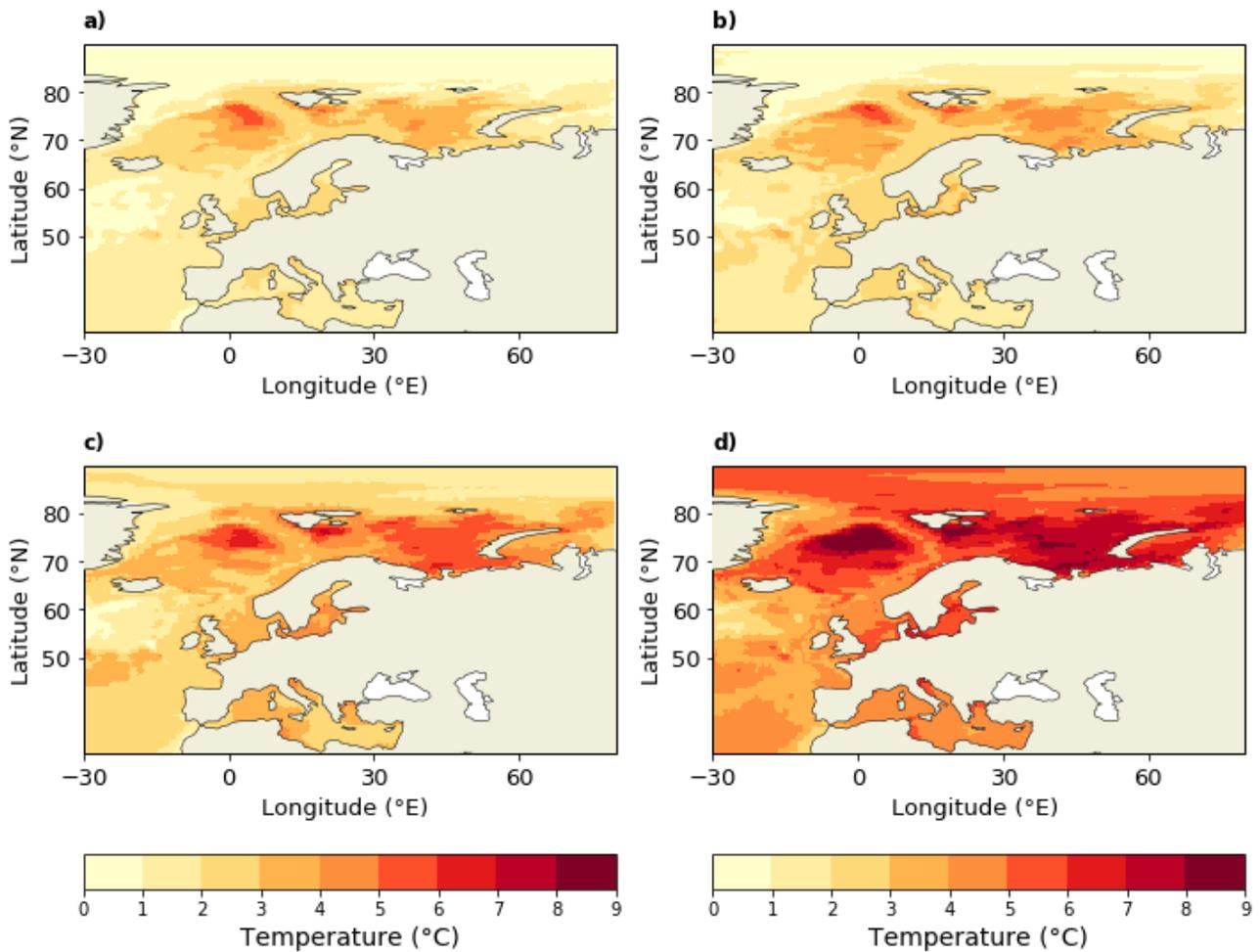


Fig. 3. Annual mean temperature differences between projected and historical data. Annual mean temperature differences between RCP4.5/RCP8.5 scenarios and SODA reanalysis dataset (Carton et al., 2000; Carton and Giese, 2008; here we use time mean over 1960-1980). Ocean temperatures are projected by the AWI-ESM global climate model: a) RCP4.5 time mean over 2080-2100; b) RCP4.5 time mean over 2180-2200; c) RCP8.5 time mean over 2080-2100; d) RCP8.5 time mean over 2180-2200. Values are averaged over the upper 580 m.

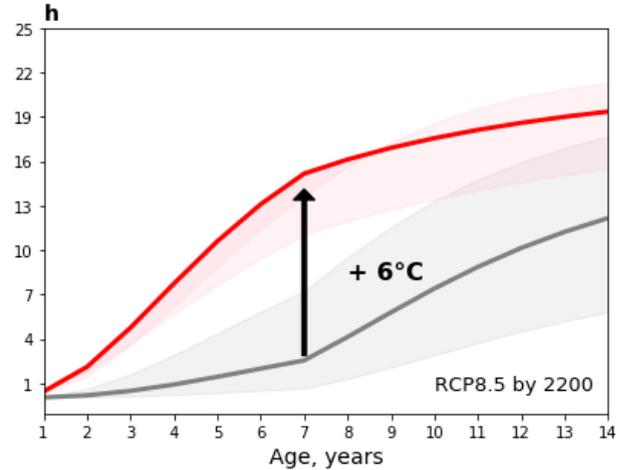
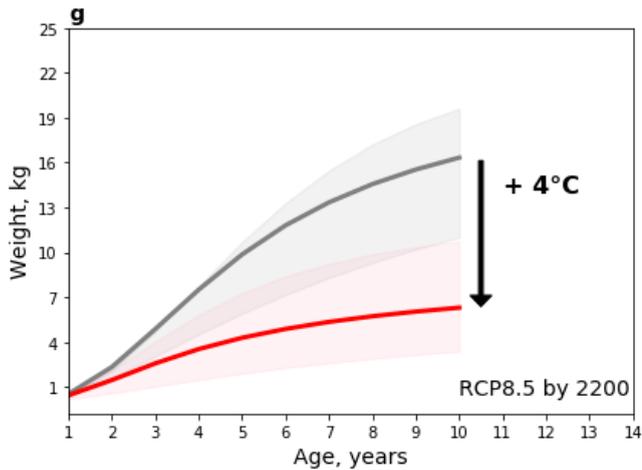
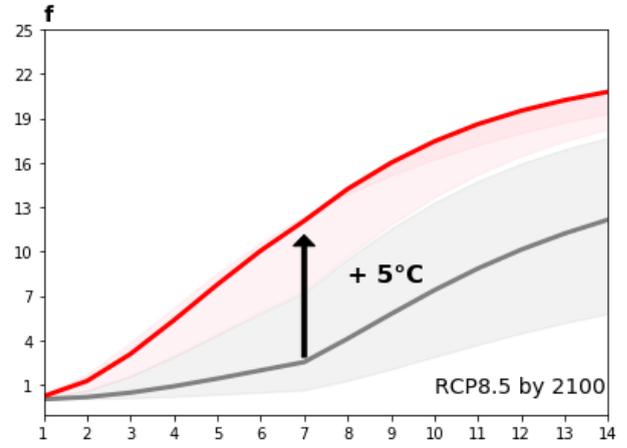
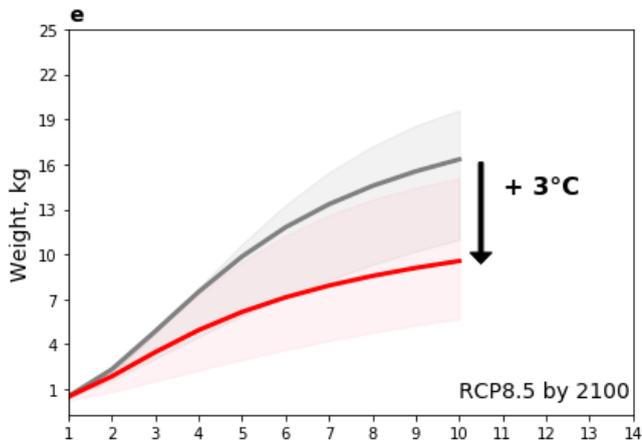
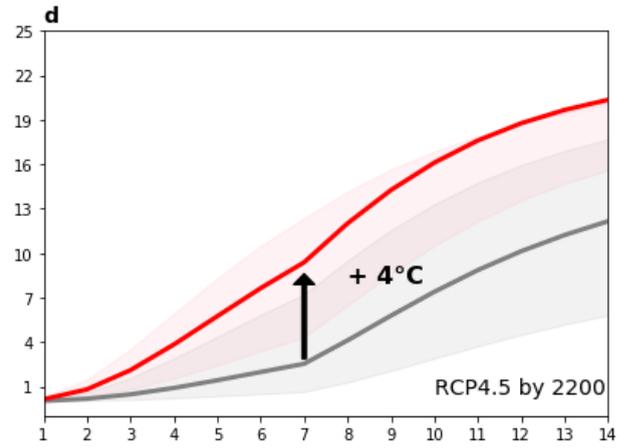
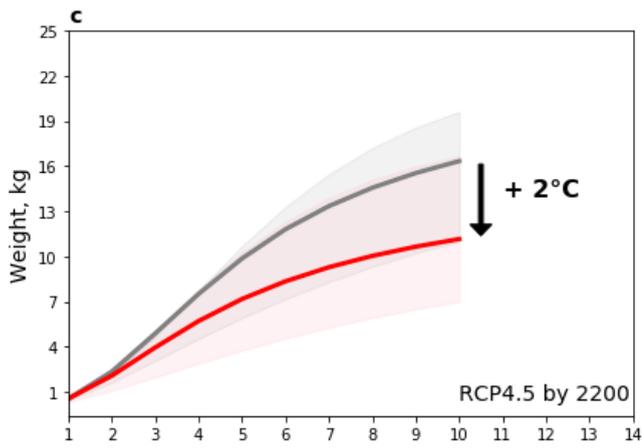
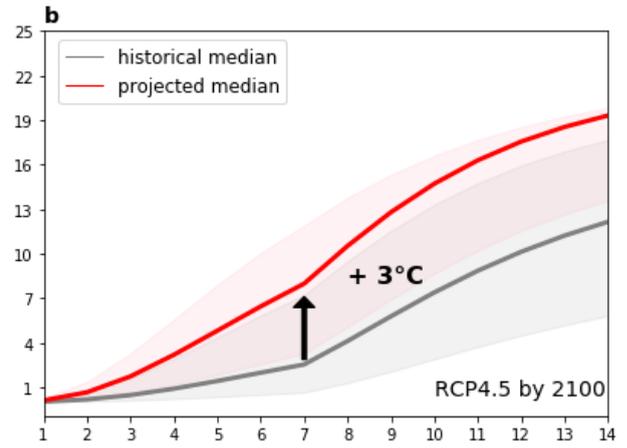
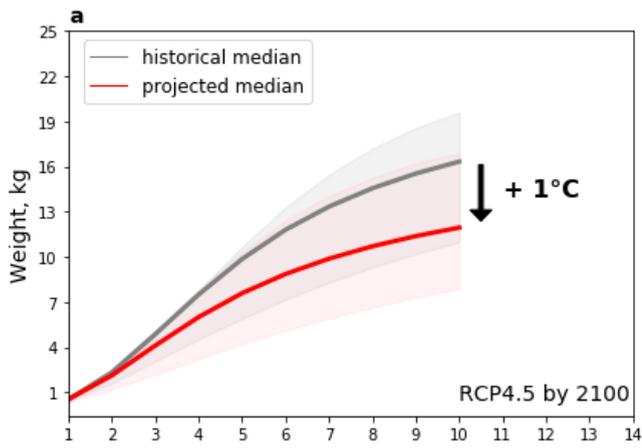


Fig. 4. Projected changes in the growth curve shapes for the Celtic Sea cod (left panel) and the Barents Sea cod (right panel). Gray lines represent growth curves simulated by the growth model with temperature time series for 1958-2007, red lines - projected growth curves with temperature time series for 2020-2200, gray and red shadowing - the 5th/95th percentiles range in weight-at-age values produced by the model for each region for 1958-2007 and 2020-2200, respectively. Arrows indicate the direction of changes in weight-at-age under each warming scenario. Temperature values display projected magnitude of warming in each region (spatially averaged values include depth range 0-580m).

Although our projections show variate reactions to future warming in different age groups two major trends are found in case study regions: dramatically reduced weight-at-age in the Celtic Sea and enlargement of Barents Sea cod accompanied by a diametrically opposite growth curve shapes in comparison to historical data (Fig. 4). Both trends are in line with published modeling and observational studies (Pörtner et al., 2001; Cheung et al., 2013; Audzijonyte et al., 2020). Projected temperature-related decline in weight of the Celtic Sea cod is expected and has been already observed (Alix et al., 2020). Warming of 1°C and more will narrow the habitat temperature range available for cod in the Celtic Sea and impair currently favorable conditions causing maximized growth to suboptimal environments. In this region other factors influencing growth rates, such as limited prey availability or oxygen supply, will exacerbate such a pronounced temperature effect (Pörtner et al., 2014). The northern cod population - the Barents Sea cod - will experience increased growth performance in all age groups. However, the following factors might limit the positive feedback to warming temperatures: limited prey availability due to food web perturbation; increased population density and competition for food. Conversely, physiological adaptation to warmer temperatures and restructuring of organism functions on molecular level might benefit growth.

Warming effects on reproductive potential in relation to population demography and fishing

When assessing reproductive potential on a population level we account for population demographic structure - relative abundance of younger/smaller individuals and older/larger ones in a population (Andersen et al., 2019). In other words, we estimate how much percent of each age class is present in a population which provides us with a quantity of big and old mature fish that can potentially produce larger amounts of offspring (Barneche et al., 2018). The demographic structure of many fish populations shows a reduced age range of spawners with more young and small individuals in contrast to fewer old and large fish (Stige et al., 2016). In particular, a decline in mean weight is observed in the Celtic Sea in association with decreased abundance of large fish and increased abundance of small fish (Blanchard et al., 2005). Historical data show that large old individuals (7+ years old) in the Celtic Sea make up substantially smaller proportions in comparison

to younger and smaller ones: 44% of 2-year-old individuals, below 10% of 4- to 6-year-old, and less than 1% of age groups 7-10 years old (WGCSE, 2019). The Barents Sea abundance data compose the following structure: 10-20% of age groups 4-7 years old, 10-25 of 8- to 10-year-old, and less than 1% of age groups 11-14 years old (AFWG, 2021). We use those demographic data to estimate the relative reproductive potential of all individuals in a population. Furthermore, for each RCP scenario we implement various fishing mortality coefficients to capture the potential effects of fishing on population age structure (Fig. S2). Studies state that fishing-induced loss of old and large spawners reduces reproductive potential of populations (Stige et al., 2017). Thus, we explore how various levels of fishing pressure impact projected reproductive potential. We assume a coefficient of F0.30 as a historical reference and assess changes in reproductive potential with lower (F0.15) and higher (F0.45) fishing pressure scenarios. As a proxy for reproductive potential we use potential egg production (PEP, mln per individual) that was calculated based on historical and projected weight-at-age values.

Fig. 5 shows historical and projected egg quantity per individual (potential egg production, PEP) where projected values incorporate both warming (RCP4.5/RCP8.5) and fishing effects (F0.15/F0.30/F0.45). In the Celtic Sea (Fig. 5a) historical PEP values fluctuate around 1-2 mln per individual. Projected model outcomes show decreasing egg production starting from 2020. Each level of fishing pressure substantially expands warming effects: both intermediate (F0.30) and high (F0.45) fishing coefficients halve egg production values. Interestingly, even under low fishing pressure egg production values decline rapidly (up to 1 mln per decade under RCP8.5; 0.5 mln - under RCP4.5). Both RCP4.5 and RCP8.5 show that under high fishing levels individuals will lose their capacity to produce offspring (Fig. 5a - red lines). Regardless of fishing pressure level, a pronounced rise in potential egg production can be observed in the Barents Sea (Fig. 5b). The highest egg production quantity can be seen under RCP8.5 scenario with the lowest (F0.15) fishing pressure level. Despite the positive effect of climate warming on fish growth, a high fishing coefficient (F0.45) impairs it. Overall, the Barents Sea cod is expected to benefit from temperature increase if fishing pressure remains sustainable whereas the Celtic Sea cod will experience losses under both warming scenarios and any fishing pressure level.

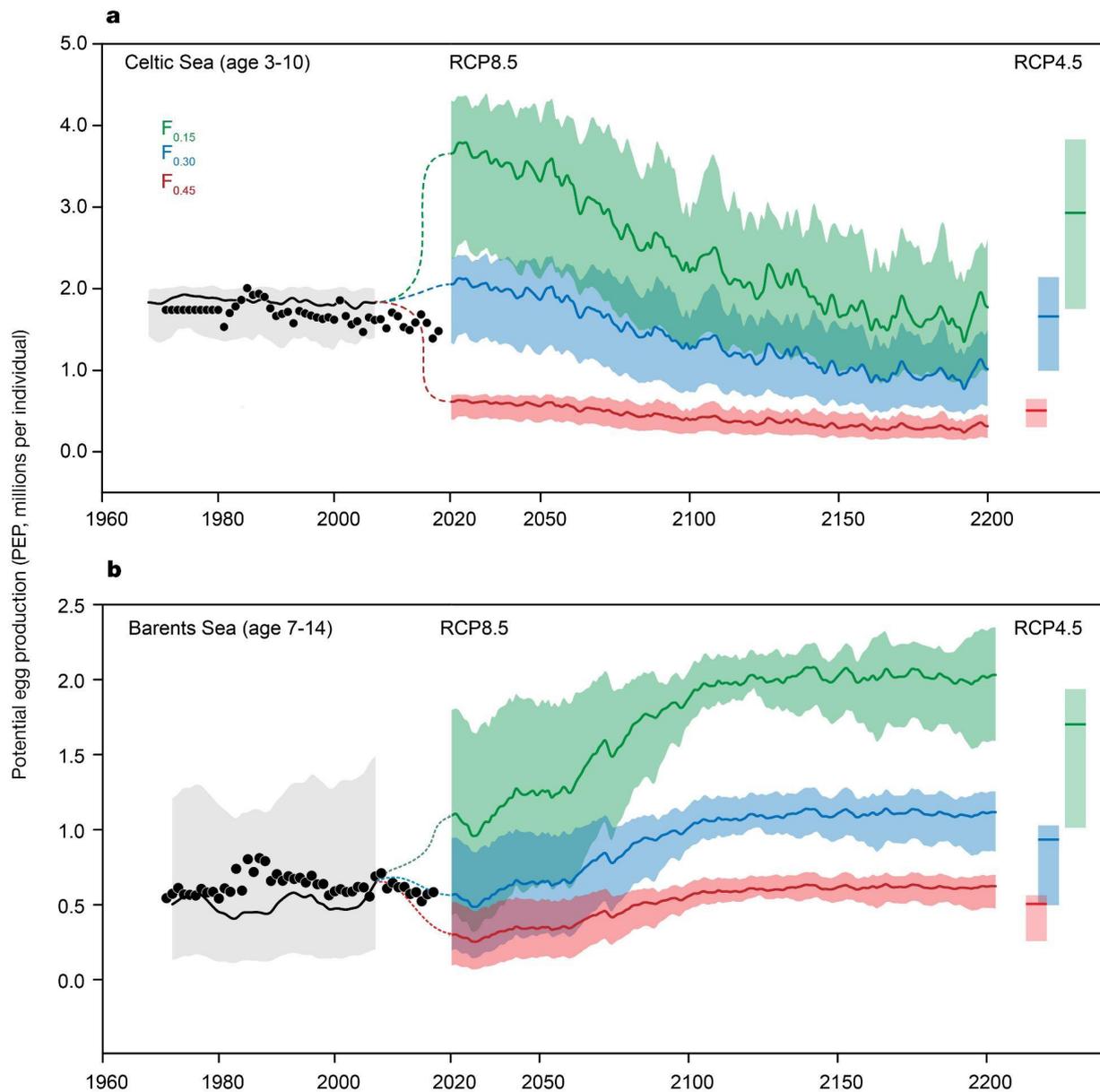


Fig. 5. Long-term projections of potential egg production (PEP) of the Northeast Atlantic cod populations under the RCP4.5 and the RCP8.5 emission scenarios. Black circles represent interannual variability in PEP based on observed weight-at-age values, population age structure (relative number of individuals at each age class), and empirically derived mass-fecundity scaling (assumed as constant over time); black lines - PEP variability based on modeled weight-at-age; gray shading - the 5th/95th percentile range of the modeled PEP values. Projected trends in PEP span 2020-2200 (colored solid lines - median values; colored shadings - the 5th/95th percentile range). PEP estimations incorporate temperature-dependent changes in weight-at-age, population size structure, empirically derived mass-fecundity scaling, and fishing pressure scenarios. Observed weight-at-age values, age structure and fishing pressure coefficients are collected from ICES reports.

Perspectives

Projecting the impact of climate change on marine organisms is inevitably challenged by several covariate factors. First of all, scaling problems caused by complexity of semi-level studies: experimental findings of organism physiological functions based on thermodynamic nature, on the one hand, should be scaled with the results of ecological studies researching organisms in interaction with each other and under the influence of external factors, on the other hand (Pörtner et al., 2017; Pinsky et al., 2020). Secondly, apart from influencing directly, the effects of climate change on organisms' growth and reproductive functions are also shaped by global restructuring of bio-geographical patterns: borealization of Arctic, changes in food web dynamics and population density (Fossheim et al., 2015; García Molinos et al., 2015). Third, climate induced changes in life history, such as boosted maturation, alter inhibited adult growth at earlier ages and thus lead to smaller adult body size (Audzijonyte et al., 2016). Finally, thermal adaptation to warmer temperatures accompanied by down-regulation of metabolic rate and physiological restructuring on molecular level change organism reaction rates to warmer temperatures (Pörtner et al., 2017). As growth and reproduction are fundamental organism functions which involve processes on all biological levels ranging from molecules to ecosystems, results provided in this study should be carefully interpreted in a context of described above covariate factors and their interplay.

Methods

Global Climate Model

AWI Earth System Model (AWI-ESM) provides climate change projections for years 2016-2200. The AWI-ESM model comprises atmosphere, ocean and sea ice components (Sidorenko et al., 2015). The atmosphere model ECHAM6 is run on a T63L47 grid which corresponds to about $1.85^\circ \times 1.85^\circ$ horizontal resolution and 47 vertical layers (Stevens et al., 2013). The ocean component FESOM1.4 employs an unstructured triangular grid which allows to increase the model output resolution in the range from 20 km in the North Atlantic up to 150 km in the open ocean (Wang et al., 2014). The output from the ocean model was interpolated to a horizontal resolution of $0.5^\circ \times 0.5^\circ$. The ice sheet model (PISM1.1) is dynamically coupled to the ocean and atmosphere components (Martin et al., 2011; Winkelmann et al., 2011).

We use the RCP4.5 and RCP8.5 scenarios following the Representative Concentration Pathway adopted by the IPCC for its fifth Assessment Report (AR5, Cubasch et al., 2013; Ackermann et al., 2020). The RCP8.5 scenario employs greenhouse gas concentrations (GHG) of 1231 ppm in 2100. Starting from 2100, GHG values are fixed. The GHG concentrations represent a combination of CO_2 , CH_4 and N_2O gasses including such anthropogenic factors as land-use change and aerosols emissions and has been applied for past, present and future scenarios (Brierley et al., 2020; Lohmann et al., 2020; Keeble et al., 2021; Kageyama et al., 2021).

Growth model setup

To simulate potential changes of Atlantic cod weight-at-age (the size of individual cod in kg at a certain age from 1 to 14 years) by the end of the 22nd century under the RCP8.5 scenario we use the growth model derived by Butzin and Pörtner (2016). The growth is defined as a function of the life-long experienced temperature of an individual. Estimates of historical changes in weight-at-age and the growth model behavior in comparison to observations were analyzed and discussed by Sokolova et al. (2021). In our projections, growth is determined by the bias-corrected temperature output from the AWI-ESM model surface, subsurface and bottom oceanic layers averaged over the upper 580 m. Our growth model calculates the weight-at-age of individual Atlantic cod in the Northeast Atlantic. We also use a time series of simulated temperatures to generate diagrams of projected variations in weight of different age groups through the 21st and the 22nd centuries (Fig. S2).

Weight – fecundity scaling

The relationship between female weight-at-age (W_a) and potential egg production at a given reproductive age ($E_a = 0.5081W^{1.25}$, Fig.1c) was derived based on observational data extracted from FishBase (www.fishbase.org). To account for natural variability in female fecundity and methodological inconsistencies (Lambert et al., 2008), observations were pooled across different Northeast Atlantic cod populations (Barents Sea, North Sea, Irish Sea and Iceland) and sampling years. Reported length-fecundity relationships were transformed based on the species-specific length-weight relationship provided by FishBase ($W = 0.0069 \cdot L^{3.08}$). Maturity ogives and maximum ages from recent ICES reports (ICES, 2019; 2021) were used to define reproductive age classes for cod from the Celtic Sea (age 3-10) and Barents Sea (age 7-14).

Population age structure and fishery scenarios

Population-level reproductive potential (R_p) was estimated as $\sum E_a N_a$, where E_a is the weight-dependent egg production of individual females at a given reproductive age a , and N_a is the relative abundance of reproductive age classes (age 3-10 for Celtic Sea and age 7-14 for Barents Sea). Historic demographic data of cod from the Celtic Sea and Barents Sea were extracted from ICES reports (ICES, 2019; 2021). Future demographic structure as a function of fishing pressure was calculated as $N_a = N_0 e^{-Za}$, where Z is the sum of natural mortality (M) and fishing mortality (F). Natural mortality was assumed to be $M = 0.2$, which is common practice in fish population dynamics (Andersen et al., 2019). Fishing mortality was set to $F = 0.15, 0.3$ and 0.45), representing realistic scenarios of low, intermediate and high fishing pressure, respectively (ICES, 2019; 2021).

Model availability

Global Climate Model AWI-ESM. Code for the AWI-ESM-PISM coupler SCOPE is available under <https://gitlab.awi.de/pgierz/scope>. The Parallel Ice Sheet Model PISM is available from this site (<https://github.com/pism/pism>). FESOM is also free software and available from this site (<https://github.com/fesom/fesom>). The atmosphere ECHAM6 is available after registration (<https://www.mpimet.mpg.de/en/science/models/availability-licenses>).

Atlantic cod growth model is written in Python and publicly available on https://gitlab.hzdr.de/awi_paleodyn/growth-model-atlantic-cod

Atlantic-cod-model-version-1.0.1 is archived on Zenodo (Sokolova et al., 2022).

Data availability

Climate model temperature outputs used in this study are provided via:

<https://doi.pangaea.de/10.1594/PANGAEA.943546>

https://gitlab.hzdr.de/awi_paleodyn/growth_model_atlantic_cod_inputs

Growth model weight-at-age sample outputs are provided via:

https://gitlab.hzdr.de/awi_paleodyn/atlantic_cod_growth_data

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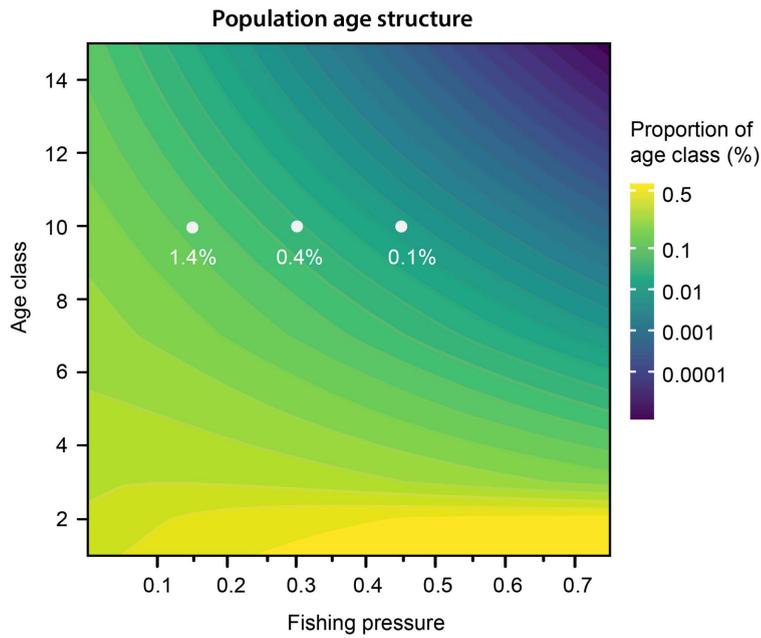


Fig. S1. Potential effects of different fishing pressure scenarios on population age structure: 0 represents “no fishing” scenario and 0.7 - maximized fishing pressure that shifts the age class distribution. Numbers represent relative abundance of age class 10 (old mature individuals) in a population at different fishing pressure levels. Fishing coefficients are collected from International Council for Marine Sciences (ICES) reports.

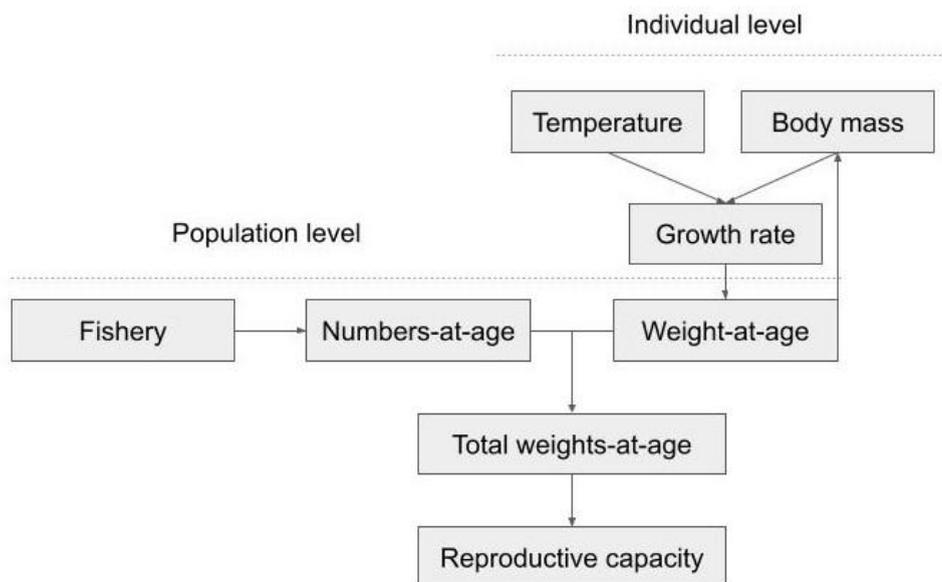


Fig. S2. Study concept in a schematic representation.

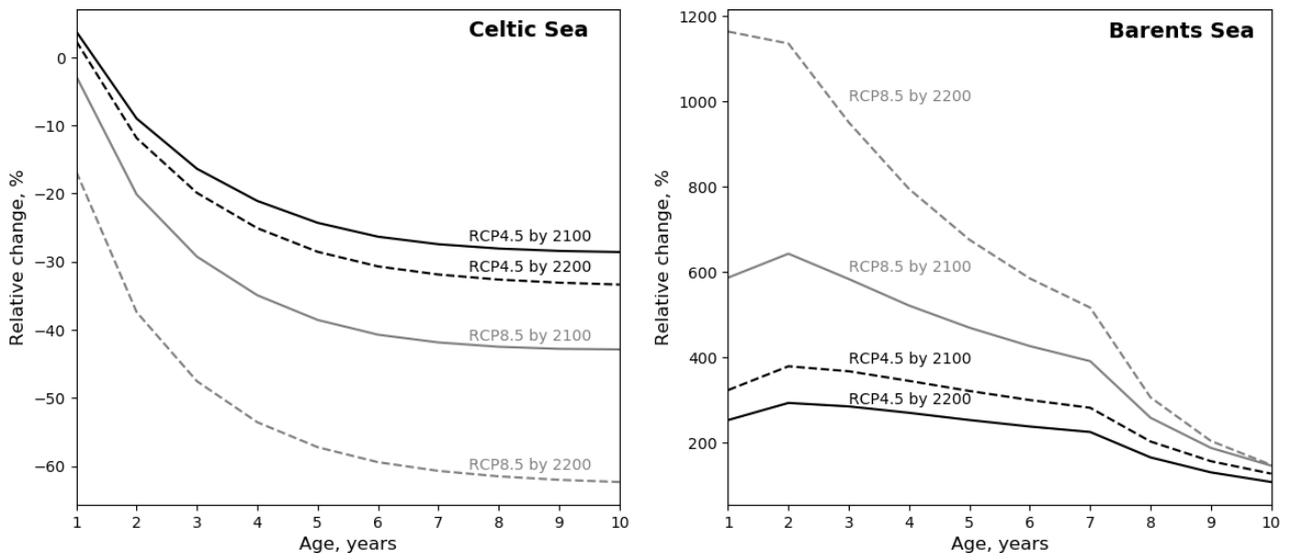


Fig. S3. Relative change in weight-at-age of the Celtic Sea cod and the Barents Sea cod.
 Reference periods: observed - 1970-1990; projected (RCP4.5/RCP8.5) - 2080-2100 and 2180-2200.

PUBLICATION 3

Atlantic cod growth models: open source Python package for numerical growth experiments

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(1) Overview

Title

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Abstract

In this article we provide an open source tool that is used to study growth of Atlantic cod (*Gadus morhua*) under different thermal conditions. It is a mechanistic physiology-based growth model that mimics growth under controlled laboratory conditions as well as in an idealised open sea environment. The model can be used as an educational tool for studying temperature-dependent growth and testing research hypotheses by advanced undergraduate and graduate students.

Keywords

Python, physiology-based growth model, temperature-dependent growth, Atlantic cod, ectotherms, biological data

Introduction

Growth is one of the main properties of life as well as a key physiological and ecological trait [3]. Growth of marine organisms is influenced by many interacting factors that differ across species and vary with time scales. Laboratory findings show a direct response of organism growth rate to temperature changes, especially in ectotherms - organisms whose body temperature depends on surrounding water temperatures (e.g. fishes). Studies show that fish growth rates will change under global ocean warming, in particular that maximum fish size may decrease if ocean temperatures continue rising [8]. Our growth model was primarily developed to test temperature effects on growth of Atlantic cod from different regions based on climatological time scales.

By definition, a “growth model” is any quantitative description of growth from theoretically informed mathematical equations to purely empirical or statistical models [17]. The most common growth models used for fishes are the following: von Bertalanffy growth model, Gompertz model, logistic and power models [27], [28], [17]. Some of those models, written in the programming language R, have been already introduced on open source platforms (e.g. [16], [26]). Our source code is written in Python and available on GitLab. It includes growth model equations derived by Butzin and Pörtner (2016) [4] and an extended version of the growth model [23].

Conceptual framework

A bio-physical mechanistic background of the model roots in controlled laboratory experiments for Icelandic cod [2], [1] where fish growth was measured in fish tanks with various constant temperature settings ($T = [2, 4, 7, 8, 10, 12, 13, 16]$ °C) for any given individual weight from 0.001 to 8.7 kg (Fig. 1a). Laboratory experiments are characterised by the regimes of constant temperature, salinity and oxygen. The time frame spans hours to months. Experimental output includes growth rates measured as increments in body weight in relation to temperature (Fig. 1b). Based on these data a mathematical equation was derived that includes a temperature dependent nonlinear reaction model with growth inhibition at 12°C (coefficient a) and temperature dependent allometric scaling exponent b (Fig. 1c; see Listing 5, 7 for Python code). As the model equations were derived from experimental data, the base model setup mimics the results of controlled laboratory experiments by simulating temperature-dependent growth for any given individual weight class (Fig. 1d). The base model could be considered as a generalised von Bertalanffy growth model. Details on calibration and procedure of model development are described in [4].

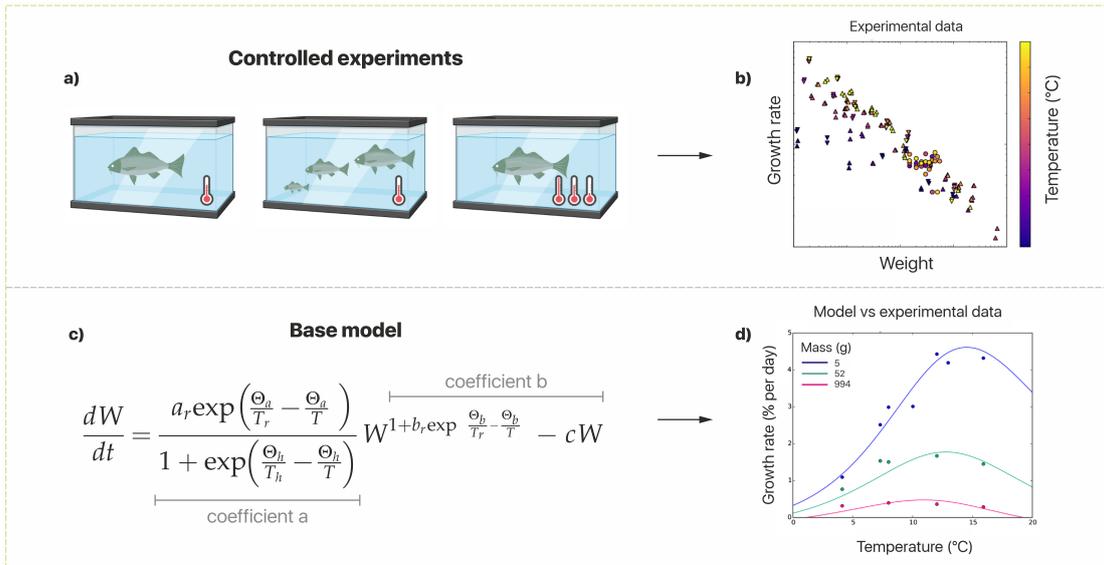


Figure 1: Conceptual figure depicting the workflow of obtaining growth data from laboratory experiments and using these data to derive the mathematical equation for growth.

Key model assumptions:

- growth rates scale with body size - allometric growth [29];
- immediate response of organisms to temperature changes [4];
- the growth response is accompanied by unlimited food supply (based on growth data from [2], [1]).

In order to simulate growth in the natural environment we incorporated multi-dimensional temperature datasets into the base model setup (Fig. 2). The multi-dimensional transient setup imitates continuous growth of cod over its life-cycle for any given time period in different locations of the North Atlantic. The model output (weight-at-age) is in the same format and provides the same temporal resolution as field data reported by the International Council for the Exploration of the Sea [13], [14], [15], which allows direct comparison of modelled and observed values.

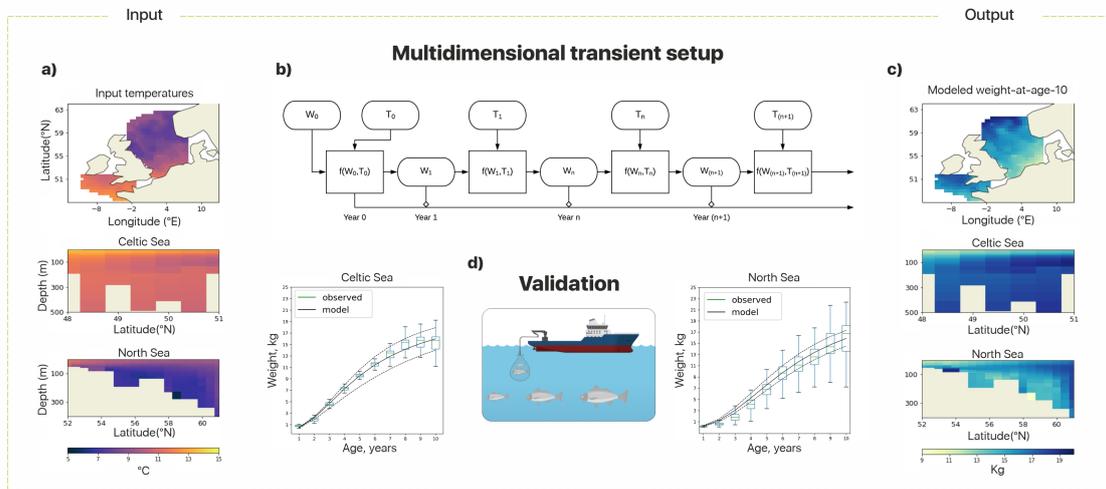


Figure 2: Conceptual figure describing the workflow of multidimensional transient setup. The model uses a multi-dimensional (e.g. lon, lat, depth, time) input (a) and calculates growth rates for each year at a daily time step (b). The output data have the same resolution as the input data (c). For each age class median weight-at-age values are calculated for each age class (d - black lines) and compared with ICES data (d - boxplots).

Implementation and architecture

The flowchart of the growth model is shown in Figure 3. It is implemented as a Python package with a simple user setup. The package structure is based on two central components: the source code written in Python (version 3.8, [25]) and user configuration files in the `.toml` format. The source code architecture comprises the following elements: growth model equations and constants (Listing 5); main executable file (Figure 3: main) that calls a certain function based on a given growth model configuration (Table 1, Table 2); growth model scripts (Figure 3: growth models); supporting functions ((Figure 3): utils). The main executable file incorporates parameters from the config file and arguments from the growth model functions.

Workflow

To work with the model it is necessary to clone the repository and build the package with the Python dependency management tool Poetry [19].

```
$ git clone git@gitlab.hzdr.de:awi_paleodyn/growth-model-atlantic-cod.git
$ cd growth-model-atlantic-cod && poetry build -f wheel && poetry install
```

Listing 1: Cloning and Setup

To set up a simulation a user chooses one of the available models. There are five model configurations a user can apply (Table 1, Table 2). In a given `config` file a user defines input parameters of the model - initial and boundary settings - and runs the model (Listing 1). The executable `cod-growth-model` is called via the terminal command line. Below is an example of the command line arguments that a user should give in to get the provided output for the base model.

```
cod-growth-model~$ ./config/base.toml ./output/growth_model_base.csv
```

Output:

```
Initial weight: 1000 g
Input temperature: 10 °C
Relative growth rate: 0.0046543 per day
Calculated weight: 1004.65432 g
```

Listing 2: Running the model

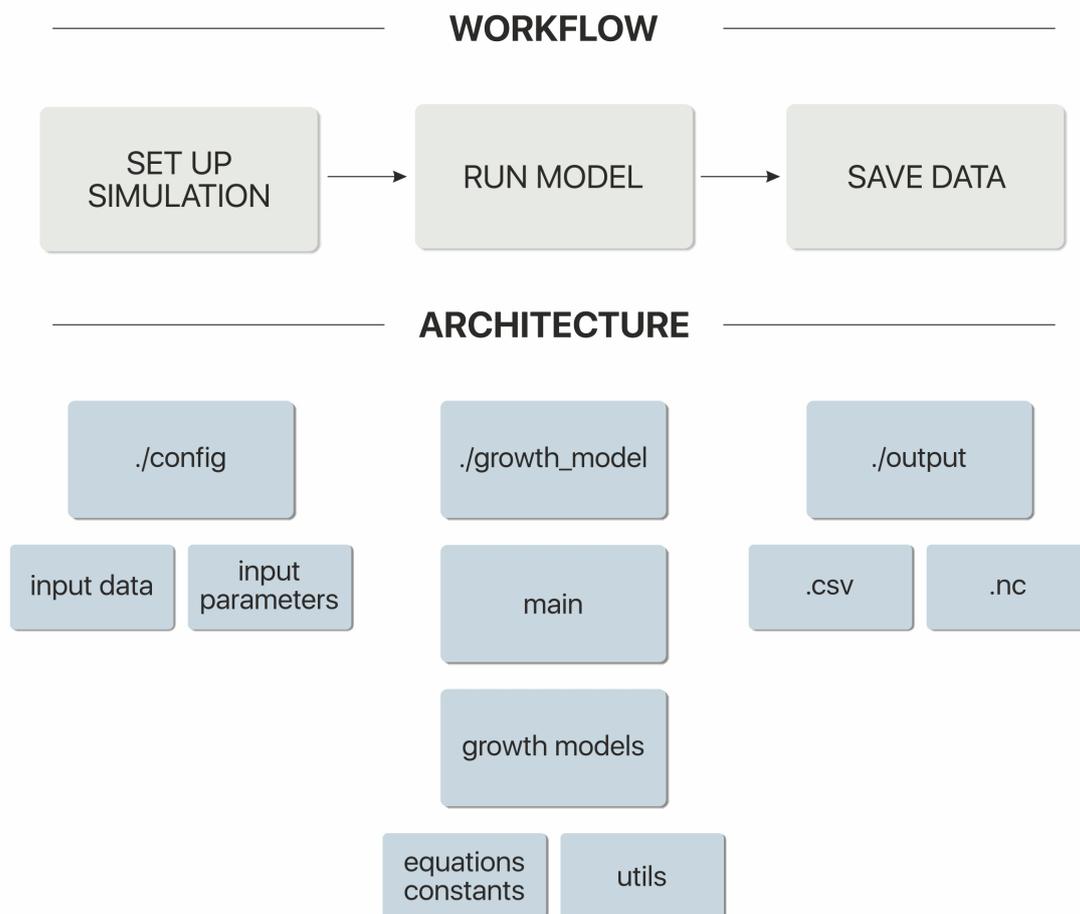


Figure 3: Workflow and package architecture. The workflow includes model setup, growth model simulation, and output data saving. A user sets up a simulation in a config file by specifying input data and parameters for a specific growth model. Growth simulation at runtime involves numerical calculations using growth model equations and constants. The growth model scripts are linked to the main executable file. Input and output data processing is supported by functions in utils. The outputs are saved in a directory specified by a user in a command line (.csv or .netcdf formats).

Based on a research question a user can choose any setting from the base model setup to the complex multidimensional configuration. Depending on a model configuration, a config file should provide information about input temperature values, geographical boundaries, biological parameters (e.g. max age in a life cycle, initial weight of individual), input and output directories. Parameters in a config file have various data types: integers or floating point numbers, lists, and strings.

Here we provide the description of the multidimensional model (`multi_dim`). An example config file is shown in Listing 3, a running command - in Listing 4 and output data structure - in Figure 4. The default configuration simulates growth of the Celtic Sea cod over a 5-year life cycle for the time period from 1980 to 1989. The model uses the Python `xarray` library [10] to create, process and save variables (`a_3d`, `b_3d`, `growth_rates_3d`, `weight_3d`, `weight_max`) in multidimensional

.netcdf files. The `multi_dim` model inputs and outputs are represented in the .netcdf format ([Unidata's Network Common Data Form](#)). This is a portable binary data format that supports creation, access, and sharing of array-oriented metadata. The default input dataset is stored in a repository folder named `input_data`. A user can run the model with an alternative dataset and provide the path to the input data in a related `multi_dim` config file. The output file names are created automatically based on a given variable, experiment name, region name, and simulation year.

```
model = "multi_dim"
'''
    Define coordinates (longitudes, latitudes) of your region
    These coordinates will be used for extracting input
    temperature data from netcdf file
    and saving output weight-at-age data to netcdf
'''

lat, lon = [
    47.25, 47.75, 48.25, 48.75, 49.25, 49.75, 50.25,
    50.75, 51.25, 51.75
], [
    -11.75, -11.25, -10.75, -10.25, -9.75, -9.25, -8.75,
    -8.25, -7.75, -7.25, -6.75, -6.25, -5.75, -5.25,
    -4.75, -4.25, -3.75, -3.25, -2.75, -2.25, -1.75, -1.25
]

# Define same depth levels as in your netcdf file
depth = [
    30, 40, 50, 60, 70, 80, 90, 100, 115,
    135, 160, 190, 230, 280, 340, 410, 490, 580
]

# Number of years in one life cycle of an individual
max_age = 5

'''
    Input dataset parameters
    Range of years in the input temperature dataset
    Initial year should be one year less than starting
    year in the dataset
'''
initial_year, final_year = 1980, 1989

# Referenced output folders
exp_name, region, output = "SODA", "CelticSea", "./output/"
```

Listing 3: Example config file for the multidimensional model

```
cod-growth-model ./config/multi_dim.toml ./output/
```

Listing 4: Command line arguments for the multidimensional model

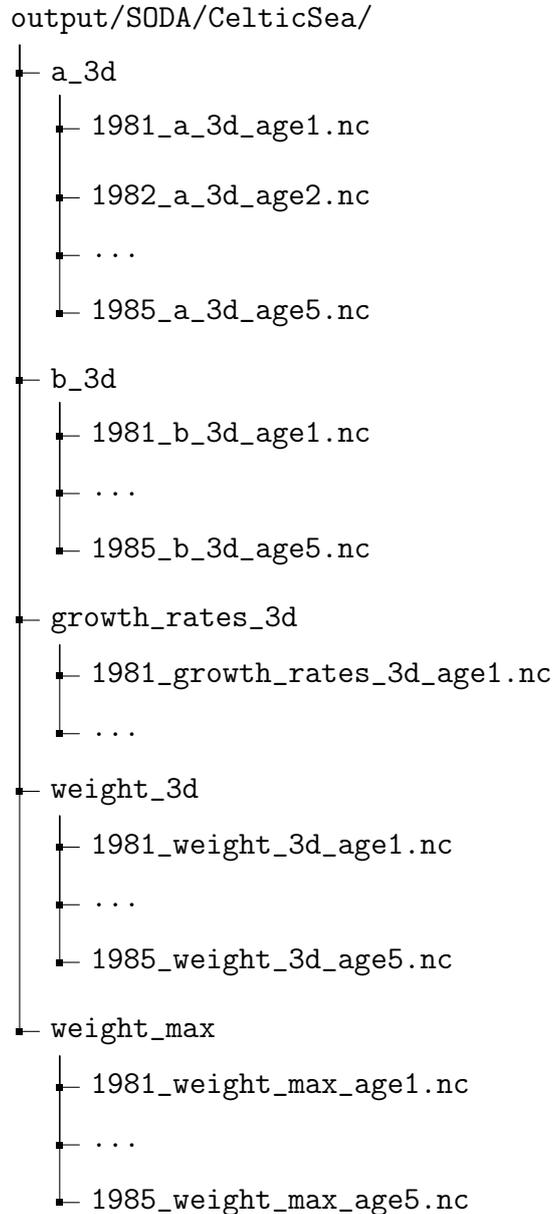


Figure 4: Output files tree

Depending on the model configuration outputs are saved in the “csv” (base, one_init_weight, one_temp_input, one_dim), or “netcdf” (multi_dim) formats. The growth model outputs are saved in an automatically created directory (./output) defined in a command line.

Quality control

The behaviour of the one_dim and multi_dim models versus experimental and observational data was validated in [4] and [23]. To test the model code we provide

a sample input dataset - SODA temperature dataset [5], [6] which can be replaced with any alternative data.

Alternative input datasets are available on GitLab: https://gitlab.hzdr.de/awi_paleodyn/growth_model_atlantic_cod_inputs

Additional datasets for model simulations with climate model outputs will be published on: <https://doi.pangaea.de/10.1594/PANGAEA.943546>

Sample output data are available on GitLab: https://gitlab.hzdr.de/awi_paleodyn/atlantic_cod_growth_data

(2) Availability

Operating system

Growth model runs were tested under Windows, macOS Monterey 12.4 and Linux operating systems. Preferable operating system is Ubuntu 20.03.4 LTS 64-bit.

Programming language

Python 3

Additional system requirements

At least 10 Mb of free disk space are required for the default model runs. For the current version of the model poetry-core 1.0.0 is used to build the package.

Dependencies

- $\geq 3.8, < 3.11$
- xarray 2022.3.0
- tomli 2.0.1
- netCDF4 1.5.8
- dask 2022.5.2

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Software location:

Archive

Name: Zenodo

Persistent identifier: <https://doi.org/10.5281/zenodo.6705793>

Licence: MIT License

Publisher: Nadezhda Sokolova

Version published: 1.0.1

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Code repository GitLab

Name: growth-model-atlantic-cod

Persistent identifier: https://gitlab.hzdr.de/awi_paleodyn/growth-model-atlantic-cod/

Licence: MIT License

Date published: 23/06/22

Language

English

(3) Reuse potential

Publicly available open source model code should facilitate model development and hypothesis testing in fish growth studies. Dimensionless versions (`base`, `one_temp_input`, `one_init_weight`) can be applied to test empirically derived growth parameters for Atlantic cod populations from different regions. Further development of the model will be focused on the effects of physiological adaptation on growth [20]. The multidimensional version (`multi_dim`) allows study growth on different spatial and temporal scales providing outputs that can be directly compared to field data. The source code can be also used as a practical teaching tool. The model code of `one_dim` version was translated to JavaScript and published on an institutional web site as an introduction tool to growth studies for undergraduate students. The preliminary version of the web page can be found on https://www.awi.de/fileadmin/user_upload/AWI/Forschung/Klimawissenschaft/Dynamik_des_Palaeoklimas/Growth_Model/index.html (see sample JavaScript code in Listing 8). The web page repository is published on GitHub: <https://github.com/btschwertfeger/Growth-Model-Website>. Overall, the model framework provides the end user with ultimate flexibility, can be used in species-specific comparison studies and integrated in more complex ecological or climate models.

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Competing interests

The authors declare that they have no competing interests.

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Supplements

```
'''
Definitions of growth models constants
from Butzin and Poertner, 2016
'''

A_R = 8.660      # Uninhibited growth rate at reference
temperature T_R (% d-1 g1/b)
B_R = 0.3055     # Value of allometric exponent at reference
temperature Tr
THETA_A = 18145  # Arrhenius temperature (K) for uninhibited
reaction kinetics = 17871.85°C
THETA_B = 4258   # Arrhenius temperature (K) = 3984.85°C
THETA_H = 25234  # Arrhenius temperature (K) for inhibited
reaction kinetics = 24960.85 °C
T_R = 283        # Reference optimum temperature (K) = 9.85°C
T_H = 286        # Temperature for inhibitive processes (K) =
12.85°C
C_AVG = 0.291   # Independent of temperature and weight
constant (%d-1)
```

Listing 5: Python code for constants from Eq. 2 and 3 in Butzin and Poertner (2016).

Supplements

```
'''
In this file functions for coefficients a and b are defined (Eq. 2
and 3 in Butzin and Poertner, 2016)
'''

from growth_model.constants import A_R, THETA_A, T_R, THETA_H, T_H,
    B_R, THETA_B, T0

from numpy import exp

def equation2(input_temp):
    """
    This function calculates parameter "a" (Eg. 2 in Butzin and
    Poertner, 2016)
    This is a nonlinear master reaction model of poikilotherm
    development
    with growth inhibition at higher temperatures.

    @param input_temp: input temperature for growth rate
    calculation ( C )
    @return: a
    """
    temperature_kelvin = input_temp + T0
    # Calculate a
    a_numerator = A_R * exp(THETA_A / T_R - THETA_A /
    temperature_kelvin)
    a_denominator = 1 + exp(THETA_H / T_H - THETA_H /
    temperature_kelvin)
    a = a_numerator / a_denominator
    return a

def equation3(input_temp):
    """
    This function calculates an allometric scaling exponent "b"
    (Arrhenius equation, Eg. 3 in Butzin and Poertner, 2016)

    @param input_temp: input temperature for growth rate
    calculation ( C )
    @return: b
    """
    temperature_kelvin = input_temp + T0
    # Calculate b
    b = B_R * exp(THETA_B / T_R - THETA_B / temperature_kelvin)
    return b
```

Listing 6: Python code for coefficients a and b from Eq. 2 and 3 in Butzin and Poertner (2016).

```

def main():
    """
    Entrypoint of the command line interface for interacting with
    cod-growth-models

    @return: exit code
    """

    # Initialize logger
    logger_config = pathlib.Path.cwd().joinpath('logger.conf')
    init_logger(logger_config)

    # Parse cli arguments
    args = _parse_args()
    settings = load_config(args.config_file)

    model = settings['model']
    output = pathlib.Path(args.output)

    models_output_dir = ['multi_dim']
    models_output_file = ['base', 'one_dim',
                          'one_temp', 'one_weight']

    if model in models_output_dir and output.is_file():
        sys.exit(f'Error:
        Output must be directory for models
        {models_output_dir}')
    if model in models_output_file and output.is_dir():
        sys.exit(f'Error:
        Output must be a file for models
        {models_output_file}')

    if model == 'base':
        logging.info
        (f'Calculating growth model with model "base"...')
        try:
            base(temp=settings['temp'],
                weight=settings['weight'],
                output=output)
        except KeyError:
            sys.exit(f'Error:
            Model-Settings for model "base" in config-file
            {args.config_file} are incomplete!')

    elif model == 'one_dim':
        logging.info
        (f'Calculating growth model with model "one_dim"...')
        try:
            one_dim(min_temp=settings['min_temp'],
                max_temp=settings['max_temp'],
                temp_step=settings['temp_step'],
                weight=settings['weight'],
                max_age=settings['max_age'],
                output=output)
        except KeyError:

```

```

        sys.exit(f'Error: Model-Settings for model "one_dim" in
        config-file {args.config_file}' f' are incomplete!')

elif model == 'one_temp':
    logging.info
    (f'Calculating growth model with model "one_temp"...')
    try:
        one_temp(temp=settings['temp'],
                 weight=settings['weight'],
                 output=output)
    except KeyError:
        sys.exit
        (f'Error: Model-Settings for model "one_temp" in
        config-file {args.config_file} are incomplete!')

elif model == 'one_weight':
    logging.info
    (f'Calculating growth model with model "one_weight"..')
    try:
        one_weight(temp=settings['temp'],
                  weight=settings['weight'],
                  output=output)
    except KeyError:
        sys.exit(f'Error:
        Model-Settings for model "one_weight"
        in config-file {args.config_file} are incomplete!')

elif model == 'multi_dim':
    logging.info
    (f'Calculating growth model with model "multi_dim"...')
    try:
        multi_dim(lat=settings['lat'],
                  lon=settings['lon'], depth=settings['depth'],
                  max_age=settings['max_age'],
                  first_year=settings['first_year'],
                  final_year=settings['final_year'],
                  exp_name=settings['exp_name'],
                  region=settings['region'],
                  input_data=settings['input_data'], output=output)
    except KeyError:
        sys.exit
        (f'Error:
        model "multi_dim" expects parameter-settings!')
else:
    logging.critical(f'Error: model "{model}" not available')
    sys.exit(1)

```

Listing 7: Sample code of mainpy that incorporates parameters from the config file and arguments from the growth model functions.

Table 1: Growth models and their configurations (Part 1)

Model/Config name	Description	Inputs	Outputs
<code>base</code>	a dimensionless model that calculates relative growth rate and final weight of one individual considering one constant temperature environment	temperature: single value (integer), initial weight: single value (integer)	relative growth rate: single value, final weight: single value, file format: csv
<code>one_temp_input</code>	a dimensionless model that calculates relative growth rate and final weight of several individuals considering one constant temperature environment	temperature: single value (integer), initial weight: several values (list)	relative growth rates: list, final weights: list, file format: csv
<code>one_init_weight</code>	a dimensionless model that calculates relative growth rate and final weight of one individuals considering several constant temperature environments	temperature: several values (list), initial weight: one value (integer)	relative growth rates: list, final weights: list, file format: csv

Table 2: Growth models and their configurations (Part 2)

Model/Config name	Description	Inputs	Outputs
<code>one_dim</code>	a 1-dimensional model that calculates continuous growth of several individuals over a given time period under several constant temperature regimes (Fig. 2b in Butzin and Pörtner, 2016).	temperature: minimum temperature (integer), maximum temperature (integer), temperature step (float); initial weight: single value (integer); maximum age of individual in years (integer)	relative growth rates and final weights: table, file format: csv
<code>multi_dim</code>	a multi-dimensional transient model (updated setup from Sokolova et al. (2021). The model immitates monthly growth and calculates weight at a certain age (weight-at-age) using multidimensional ocean temperature data (space-, depth- and time-varying)	temperature: multi-dimensional temperature dataset in netCDF format (minimum 10 years time series); temporal boundaries: first and last year in a dataset (integers); geographic boundaries: latitudes, longitudes, depths levels (lists); maximum age of individual in years (integer)	annual multi-dimensional datasets: <code>a_3d</code> , <code>b_3d</code> , <code>growth_rates_3d</code> , <code>weight_3d</code> , <code>weight_max</code> ; file format: netCDF

```

run_model = (
  data = null, parameters = null, initial_weight = null
) => {
  data = (data === null) ?
    window.process_data_simple : data;
  parameters = (parameters === null) ?
    window.default_input_simple : parameters;
  initial_weight = (initial_weight === null) ?
    parameters.initial_weight * 1000
    : parseFloat(initial_weight) * 1000;

  let
    a_fit = data.a_fit,
    b_fit = data.b_fit,
    c_avg = data.c_avg,
    itemp = 0,
    dt = 1,          // time step in days
    temperature_range = range(-2, 30.5 - .5, .5);

  /* weight at age (in g) for a given temperature
    && initial weight in kg
  */
  let weight_at_age = [...new Array(
    parameters.max_age
  )].map(
    (e, i) => [...new Array(
      a_fit.length
    )].map(() => (i === 0) ? initial_weight : 0)
  );

  // loop over temperatures, increasing values by 0.5°C
  temperature_range.forEach(() => {
    range(1, parameters.max_age - 1, 1).forEach((age) => {
      let growth_rate = .01 * (
        a_fit[itemp] * Math.pow(
          weight_at_age[age - 1][itemp], b_fit[itemp]
        ) - c_avg
      );
      weight_at_age[age][itemp] =
        weight_at_age[age - 1][itemp] * (
          1 + dt * growth_rate
        );
    });
    itemp++;
  });

  return {
    a_fit: a_fit, b_fit: b_fit,
    c_avg: c_avg,
    weight_at_age: weight_at_age,
    temperature_range: temperature_range,
  }
}

```

Listing 8: Growth Model in JavaScript

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