Set in stones: the influence of long-term environmental changes on Northeast Arctic cod viewed through the analysis of otoliths

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Thesis for the degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
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“The road to wisdom?
Well, it's plain and simple to express:
Err and err and err again
but less and less and less.”

Piet Hein

Scientific environment

The work in this thesis was carried between 2017 and 2020 at the Institute of Marine Research, Demersal fish research group, and at the University of Bergen, Department of Biological Sciences. This PhD was part of the RANNIS project "Long-term otolith and bivalve growth chronologies in relations to cod stock dynamics and climate in the Northeast Atlantic", funded by the Icelandic Research Fund and lead by Dr. Steven Campana (University of Iceland).

Preface

The epigraph to this thesis is perhaps one of Danish scientist Piet Hein's most famous *grooks*, the trademark aphoristic poems he became renown for alongside his scientific work. *Err and err but less and less*, what better way to describe the endeavor that is a PhD and research in general? On both a scientific and a personal level, I could think of no quote more accurate to define what the experience of these last years as a PhD student has been. Not at all because I was lacking a purpose, but rather because each step forward, each "errancy" made it clearer for me to define a course and forge myself an identity as a young researcher.

I erred when I first accepted this PhD offer, leaving the tropical warmth of the Indian Ocean for the wet coldness of western Norway, throwing myself into something that felt dreadfully overwhelming. How not to give my deepest thanks to my supervisors Audrey, Jane and Steve then, whose guidance and patience quickly swept my worries away and turned wander into wonder?

Audrey, you have always been here to keep me focused and motivated, supporting my work with the same intensity throughout these three years despite the challenges of having moved to another country. You were central to the conception and realization of this thesis, and I will forever be thankful for your fresh ideas, your abilities to make sense of results in a biological context, and your never-ending reservoir of life and scientific advices. Jane, your daily involvement and supervision has been a huge part of what made this thesis such a good experience: you made me feel welcome in a large research group whose language was all but foreign to me, and three years later I am so grateful to be able to discuss and work with all of you as colleagues, in what I can only call my homebrewed Franco-Norwegian dialect. Finally Steve, you provided me the opportunity and funding to join a huge international research project where I got to work with many talented scientists from a large panel of expertise, attended international conferences across the world, and could always count on your advice, all the way down from Iceland.

Szymon, for the most part of this adventure you became a colleague, a co-author and a close friend, besides being certainly a much greater wanderer than myself. Your analytical skills, your boundless curiosity and your dedication to dig the slightest details had a huge impact on my PhD, but it would be reductive not to mention your constant good mood, our weekly volleyball practices, evening beers or hikes (be it atop Sandvisksfjellet or deep in a Croatian forest hut in Paklenica). I hope to keep working closely with you in the years to come, and hopefully get to travel around at your side even more! The same goes to all my colleagues at IMR Bunnfisk, UiB BIO, and everyone from the RANNIS project, I am so grateful you welcomed me from the first day and helped me whenever I needed. Listing everyone would be too long but know that I deeply appreciated your company.

My wanderings were not only scientific but personal, having moved to a country that was all but unknown to me. Then again, *err and err but less and less*, as I quickly spun my apprehension around and discovered a beautiful land filled with breathtaking landscapes and amazing people. *"Only those not bound can live like a true wanderer, able to answer the unknown's call without giving a glance to what they abandon"* wrote Sylvain Tesson, a French adventurer and philosopher whose stories had a seminal role in shaping my love of nature and traveling. I am so glad I took the leap and can now call Norway my home, thanks to the many friends I've met along the way.

To the most important of all: Mette, it will soon be three years since we met, and I would have never expected the path my life would take before I met you. You made me feel loved and welcome here, showed me your culture from the inside, and supported me through this crazy journey that was a thesis. Thank you for everything.

Finally, thanks to my family and friends in France, for your continued support despite the distance. Mom, Dad, you've always supported me in my choices, and I would not be here without you. A final thought goes to you Papou, even though you did not live to see the end, I will always be glad you got to meet Mette and I know you'd be proud.

Err and err but less and less. Like the cod at the heart of this thesis, "skrei", the Old Norse "wanderer".

Abstract

The living conditions of marine ecosystems are currently changing rapidly under the influence of human exploitation and contributions to climate change, especially in high latitude regions such as the Arctic. Predicting their future response and developing appropriate management strategies requires a good understanding of the factors influencing their biology and life history at different spatial and temporal scales, which may be enabled by long-term reconstructions and analyses of past populations. The Northeast Arctic cod is currently one of the largest and most commercially important Atlantic cod (*Gadus morhua*) populations in the world, although it experienced significant variability throughout the past century. Given the fast-changing nature of the Barents Sea region, there is therefore an increasing need to determine the response of cod to environmental changes.

In this thesis, I used century-long biological records and multiple modelling approaches to investigate the influence of changes in climate, fish population trends and human exploitation on cod growth and life history throughout the last 100 years, using otoliths as a proxy of individual life history.

Significant variations in cod growth and an earlier maturation trend throughout the past century could be related to changes in density-dependent competition and warming sea temperatures, providing evidence of synergistic influences of climate, exploitation and population dynamics. Contrasting effects of climate change at different temporal scales suggested that, while increasing temperatures benefit faster growth and earlier maturation, longer term warming may cause ecosystem-level changes that could be detrimental. Finally, although fishing mainly influenced cod biology through density-dependent release, the only partial reversal of maturity trends after exploitation pressure decreased may be indicative of fishing-induced evolution, which could have unforeseen consequences for the future response of NEA cod to climate change.

List of Publications

Paper I

Denechaud, C., Smoliński, S., Geffen, A. J., & Godiksen, J. A. (2020). Long-term temporal stability of Northeast Arctic cod (*Gadus morhua*) otolith morphology. *ICES Journal of Marine Science*, *77*(3), 1043-1054. doi: 10.1093/icesjms/fsz259.

Paper II

Denechaud, C., Smoliński, S., Geffen, A. J., Godiksen, J. A., & Campana, S. E. (2020). A century of fish growth in relation to climate change, population dynamics and exploitation. *Global Change Biology*, *26*(10), 5661-5678. doi: 10.1111/gcb.15298.

Paper III

Denechaud, C., Geffen, A. J., Smoliński, S. and Godiksen, J. A. (*In prep.*). Otolith "spawning zones" across multiple Atlantic populations: do they accurately record maturity and spawning? *(Manuscript).*

Other papers realized during this thesis or in preparation but not included:

Smoliński, S., **Denechaud, C.**, von Leesen, G., Geffen, A. J., Grønkjær P., Godiksen, J. A. and Campana, S.E. (in review). Variation of carbon isotopic composition in otoliths of Atlantic cod (*Gadus morhua*). (*Submitted to PLOS One)*

Butler, P.G., Andersson, C., Alexandroff, S.J., Campana, S.E., **Denechaud, C.**, Grønkjær, P., Hátún, H., Mette, M.J., Otterå, O.H., Smoliński, S. (*In prep.*). Links between oceanographic modes and ecosystem regime shifts in the northeast Atlantic Ocean over the past 100 years.

Smoliński, S., **Denechaud, C.**, Godiksen, J. A. and Geffen, A. J. (*In prep.*). Environmental changes affect otolith annual increment visibility - a long-term perspective from two Atlantic cod populations.

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List of abbreviations

ICES	International Council for the Exploration of the Sea
IMR	Institute of Marine Research
NEA	Northeast Arctic cod
NCC	Norwegian Coastal cod
AMO	Atlantic Multidecadal Oscillation
NAO	North Atlantic Oscillation
AIC	Aikaike Information Criterion
BLUP	Best Linear Unbiased Predictor

Contents

1. Introduction

1.1 External factors of variability in marine fish populations

1.1.1 Influence of climate change and fishing

Global climate has warmed at unprecedented rates in recent history, and anthropogenic contributions during the last 200 years are now unequivocal (IPCC and Stocker, 2014). The associated effects on Earth's habitats and ecosystems are recognized as a major threat to global biodiversity (Parmesan and Yohe, 2003; Thomas *et al.*, 2004). With temperatures rising in all projected scenarios (IPCC and Stocker, 2014) there is an increasing focus on forecasting and mitigating its further impacts. In particular, climate warming has measurable and increasing consequences on marine ecosystems and fish populations worldwide, affecting individual physiology and survival as well as population dynamics, species distribution, productivity or ecological diversity (Hoegh-Guldberg and Bruno, 2010; Cheung *et al.*, 2013; García-Reyes *et al.*, 2015).

The effects of ocean warming are however not restricted to temperature alone and can be extended to changes in the circulation of water masses, sea level, pH, salinity, vertical stratification and local weather (i.e. Francis and Vavrus, 2012), as well as changes in prey-assemblages and availability, which can in turn have significant impacts on fish populations. The associated response of phenotypic traits such as growth rate, maturation and timing of reproduction to rising water temperatures will however vary within populations, among populations and between species and locations due to plasticity and genetic variability (Crozier and Hutchings, 2014). For example, Ong et al. (2017) found contrasting patterns of growth variation in relation to environmental factors in different local populations of the coral reef fish *Lutjanus bohar*, highlighting the importance of characterising the local oceanographic and biological conditions when exploring species' response to climate change. Forecasting the potential response of fish to future change has become a central topic in marine research in the early 21st century (see for example Hollowed *et al.*, 2013), but accurate predictions remain challenging when inferred from theory or laboratory experiments alone. Instead, our ability to identify and predict these impacts is dependent on a comprehensive understanding of how fish populations respond to change, which can best be supported by first identifying, quantifying and contextualizing their long-term responses to past changes (Reid and Ogden, 2006; Poloczanska *et al.*, 2013).

In addition, many marine fish populations are subjected to another significant stressor in the form of human exploitation. It has long been debated whether fish population trends are mostly driven by fishing or the effects of climate change (Hidalgo *et al.*, 2011). Indeed, harvesting can gradually reduce population complexity (Hilborn et al., 2003), resulting in important changes in life-history (Jørgensen, 1990; Law, 2000) and demography (Ottersen et al., 2006). Increased mortality rates and selectivity for certain size-classes can then lead to diminished biomass and often select for faster growth and earlier maturation (Enberg *et al.*, 2012). However, the current consensus is that fishing-induced life history alterations in-turn erode population resilience to environmental changes and can magnify their impacts (Planque *et al.*, 2010; Hidalgo *et al.*, 2011; Morrongiello *et al.*, 2019). This is particularly important since the ability of a population to buffer and adapt to the effects of environmental change is often directly related to its age structure and specific life history traits. At larger spatial scales, this is called the "portfolio effect" and results in meta-populations being more resilient to changes than their isolated components (Schindler *et al.*, 2010). Because the potential loss of biocomplexity associated with on-going fishing could amplify the effects of climate change, identifying and quantifying the synergistic impacts of past exploitation and environmental conditions in important fish populations can help better understand future trends and changes.

1.1.2 The Barents Sea: a climate change hotspot and an ideal case study to examine the effects of climate warming and exploitation

Considered one of the most productive marine environments in the world, the Barents Sea is a shallow sea (230m average depth) situated to the north of Norway (Jakobsen & Ozhigin, 2011), bordering the Norwegian Sea to the west and the Arctic Ocean to the north (**Figure 1**). It is a major pathway for the flow of warm, saline Atlantic water into the Arctic Ocean and, at the same time, it directly receives cold and less saline water returning south from the Arctic (Smedsrud *et al.*, 2013). By splitting and transforming the water masses, the Barents Sea consequently acts as a complex hydrogeographic buffer zone at the interface between the Atlantic and the Arctic, and is a major source of variability for the entire Arctic ocean-atmosphere-ice system (Schauer *et al.*, 2002). This dynamic divides the Barents Sea into two distinct regions: the north with a cold climate and ice-associated ecosystems, and the south with warmer conditions and a richer biodiversity (Jakobsen and Ozhigin, 2011). Due to its mixed nature, the Barents Sea therefore shows large spatial and temporal variability in temperature regimes, extent of sea ice cover, timing of phytoplankton blooms, zooplankton abundance and magnitude of fish recruitment (Dalpadado *et al.*, 2012).

The Barents Sea ecoregion is home to nearly 100 fish species of which many have been or are currently exploited, including cod (*Gadus morhua*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) and redfish (*Sebastes sp.*) (ICES, 2018). Between 1955 and 2007 the international catches totalled around 128 million tonnes and averaged 2.4 million tonnes per year, with Norway and Russia dominating the fishing effort at respectively around 58% and 30% of the catches (Jakobsen and Ozhigin, 2011). Industrialization of fishing practices and increasing pressure throughout the second half of the 20th century led to significant changes in the Barents Sea fish stocks, starting with the herring collapse during the 1960s (Holst *et al.*, 2002). Since then, the capelin population has also seen three major collapses in the mid-1980s, the mid-1990s and the early 2000s (Gjøsæter *et al.*, 2009), and the cod population was driven to a very low biomass until the early 1990s, before changes in stock assessment and management practices brought it back to 1950s levels by 2010 (Institute of Marine Research, 2019). This increased variability in fish abundances since the 1970s has been associated with higher fishing pressure but also with the overall increasing trend in ocean temperature, which has led scientists to question the role of climate change in these fluctuations (Dippner and Ottersen, 2001; Drinkwater, 2011; Johannesen *et al.*, 2012).

The Barents Sea was recently defined as an “Arctic warming hotspot” (Lind et al., 2018) due to its fast-changing hydrography in response to climate warming. On one hand, the increase in heat transport via warmer Atlantic water flow causes a reduction in the sea-ice extent and a northward retreat of the sea-ice cover (Årthun *et al.*, 2012). On the other, the recent sharp increase in temperature and salinity can be associated with a decline in Artic sea ice import and an enhanced vertical mixing, which could transform the cold, stratified northern Barents Sea into an Atlantic-dominated regime (Lind *et al.*, 2018). This accelerating “Atlantification” could have significant consequences for the Barents Sea ecosystem, including the many commercially important fish stocks currently exploited. A growing effort is now being dedicated to predict the response of the Barents Sea ecosystems to future changes (e.g. Drinkwater, 2005; Michalsen *et al.*, 2013; Årthun *et al.*, 2018), which makes the Barents Sea a particularly suited system to study the synergistic effects of climate and exploitation on fish populations. One approach to answer these questions is to analyse and quantify the long-term biological variability of fish populations in response to past changes throughout the 20th and early 21st centuries.

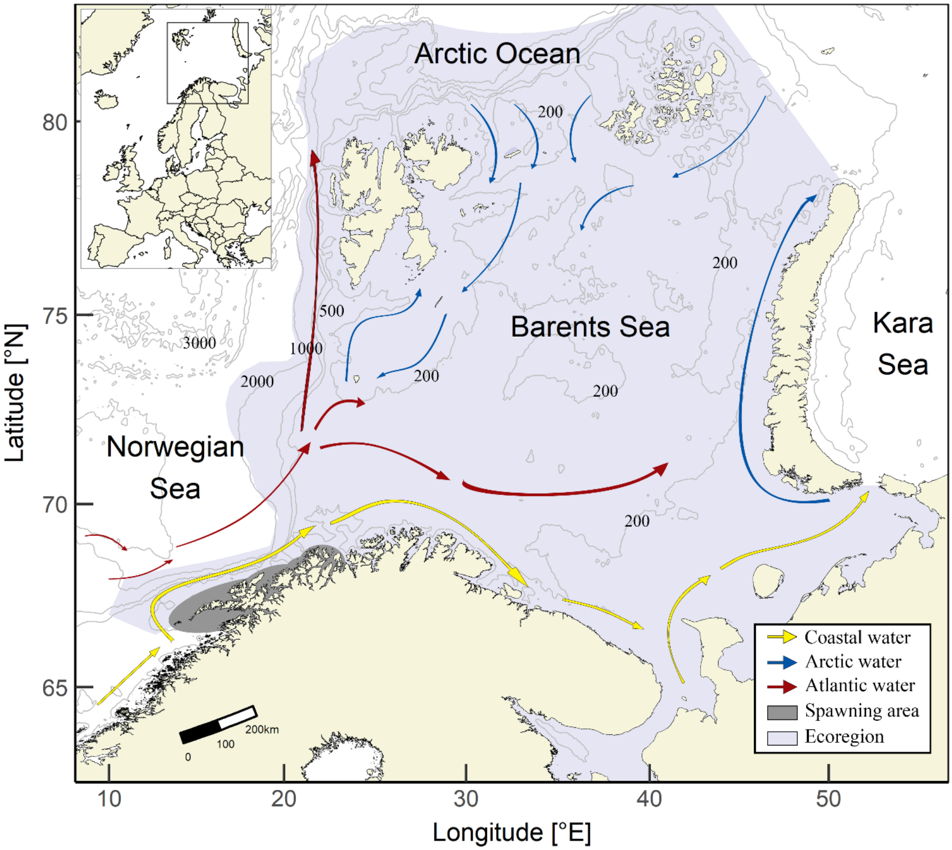

Figure 1: Map of Northeast Atlantic area and Barents Sea ecoregion, showing the bathymetry and main circulation of water masses.

1.2 The Northeast Arctic cod as a model population

1.2.1 General biology and plasticity: a species responsive to change

The Atlantic cod is a demersal predatory fish widely distributed throughout the North Atlantic, from north east coast of North America to the northern Barents Sea near Norway and Russia, and has been extensively studied for the past century (Brander, 1994a). The Northeast Arctic (NEA) cod is a migratory cod population that resides and feeds in the Barents Sea (Hylen *et al.*, 2008), where it is considered an apex predator with an essential role in the food-web dynamics notably through its high predation on small pelagic fish such as capelin (Bogstad *et al.*, 2015; Holt *et al.*, 2019). Every winter sexually mature cod migrate several hundred kilometres southward to spawn along the Norwegian coast, mostly around the Lofoten archipelago (**Figure 1**) where the main fishery has also historically taken place (Sundby and Nakken, 2008; Höffle *et al.*, 2014). The spawning area extent has recently increased north along the north-western Norwegian coast, suggesting a possible response to changes in the environment and demography (Sandø *et al.*, 2020).

Fish from the family Gadidae are known for their plasticity, exhibiting phenotypic variations in morphology and physiology across a wide range of environments. Atlantic cod also exhibits considerable inter-populations differences throughout its spatial range in terms of longevity, growth rates, sexual maturity and migratory behaviour (Brander, 1994a, 2005). For example, cod populations inhabiting the North Sea region experience warmer conditions with significant seasonal variations, which are associated with a fast life history where maturation occurs as early as age 3 and lifespan seldom exceeds 10 years (Engelhard *et al.*, 2014). In comparison, the NEA cod population experiences colder, less contrasted conditions and shows a much slower life history, where fish only become mature at age 7 to 8 and may live several decades (Hylen *et al.*, 2008). Atlantic cod populations are therefore highly plastic and diverse both physiologically and genetically (Hemmer-Hansen *et al.*, 2013), which makes cod a very responsive species to changes either at long term (i.e. slow genetic divergence) or at the year-class level when experiencing fast-changing conditions.

Studies increasingly highlight the significant influence of environmental changes and exploitation on the biology and demography of cod populations across the North Atlantic (e.g. Brander, 2000; Eero et al., 2011; Mieszkowska et al., 2009), which are now associated with the multiple collapses that occurred in the western Atlantic cod populations since the 1990s (Bavington, 2011; Pershing *et al.*, 2015). Because the Barents Sea is one of the fastest changing marine systems in the world, NEA cod is therefore a particularly informative population to study the long-term impacts of past climate and exploitation changes on fish.

1.2.2 Long-term exploitation and monitoring of NEA cod

The NEA cod population has a long history of exploitation, with the Lofoten area winter fishery going back millennia (Jakobsen and Ozhigin, 2011). NEA cod (also referred to as "skrei") is culturally and economically important to many countries in the area and especially Norway, where its large-scale exploitation and commerce can be traced back as early as the Viking era in the 10th century (Sicking and Abreu-Ferreira, 2008; Hufthammer *et al.*, 2010; Geffen *et al.*, 2011). Although catches have seen large fluctuations throughout the last century, the NEA cod stock is currently considered the largest cod stock in the world and yearly catches are estimated to range between 750 000 and 1 million tonnes (Hylen *et al.*, 2008; ICES, 2018).

In the late 19th and early 20th century, the work of Georg Ossian Sars (1867) and Johan Hjort (1914) on cod population dynamics paved the way for modern fisheries science and stock management, which led to NEA cod becoming one of the most monitored fish populations in the world. As a result, near century-scale time series of cod population age and size structure data derived from both fishing and surveys are now available (ICES, 2018). In addition, cod otoliths, or ear stones, became routinely used for ageing purposes following the publication of Rollefsen (1933), which also marked the beginning of an extensive collection program by the Norwegian Institute of Marine Research (IMR). The IMR archive now contains millions of fish otoliths going back as far as 114 years, and more than 80 000 fish otoliths are collected and aged every year (of which 30 000 are cod, mainly from the Barents Sea and the North Sea). This offers a valuable window to the past that allows scientists to trace back almost a century of cod changes, especially since otoliths can be used as individual life history recorders.

1.3 Otoliths as recorders of fish life history

1.3.1 Structure and interest for fisheries research

The inner ear of most teleost fish consists of a succession of semi-circular canals (the vestibular system) filled with endolymph fluid that connect to three organs (saccule, utricle and lagena) (Ladich and Schulz-Mirbach, 2016). Each organ comprises a sensory epithelium, the macula, and a calcified body, the otolith (Straka and Baker, 2011). Movement, sound, and pressure are transmitted to the brain through movement of the otoliths against the sensory hairs of the macula, the kinocilia. This complex sensory structure enables the fish to perceive sounds but also to sense pressure and motion to adapt its position and balance as it navigates in the water column (Mosegaard and Morales-Nin, 2000).

The sagitta is typically the largest of the otoliths (Campana and Neilson, 1985) and has been extensively used in fisheries research since the mid-20th century (Campana, 2005; Nash and Geffen, 2014). Indeed, the deposition rate and mineralization process of calcified structures such as scales or otoliths are often affected by the environment and physiology of a fish, making them effective life history recorders. Otoliths in particular have the advantage of being metabolically inert and therefore less subject to resorption than scales (Campana and Neilson, 1985). Because otoliths are formed through the accretion of both aragonitic calcium carbonate crystals and an organic matrix (Wright *et al.*, 2002), variability in resource incorporation rates or metabolic processes leads to optical differences between opaque (more organic) and translucent (more mineral) zones that can be associated with periods of high and low growth. At the macrostructural level, these increments may correspond to growth patterns linked to environmental seasonality and reflect age in years (Reibisch, 1899). Otoliths often present clear annual banding in fish inhabiting environments with high seasonal variation (Albuquerque *et al.*, 2019) and consequently provide reliable estimates of individual fish age and growth. These estimates are central to fisheries science, where the data produced can be used to study population structure and adapt management practices in consequence (Yaragina *et al.*, 2009; Morales-Nin and Geffen, 2015).

However, otoliths can be used beyond ageing purposes. Increment widths provide information on growth rates throughout the life of an individual, and outer shape comparison can be conducted to separate between species or populations. The most recent decades have also seen a diversification of studies involving otoliths and the development of additional approaches to extract information from them (Campana, 2005), such as otolith microstructures to study early growth (Morales-Nin, 1992; Geffen, 1995; Fox *et al.*, 2003) or infer mortality rates (Bunnell *et al.*, 2003); isotopic composition to evaluate environmental exposure (Devereux, 1967; Kennedy *et al.*, 2002) and metabolic activity (Chung *et al.*, 2019; Martino *et al.*, 2019); or trace elements to track migrations (Morales-Nin *et al.*, 2012) and mixing of fish populations (Gemperline *et al.*, 2002; Sturrock *et al.*, 2012; Macdonald *et al.*, 2013).

1.3.2 Otolith shape and growth in relation to population and environment

Due to its morphologic diversity, the outer shape of otoliths (referred to as otolith shape thereafter) is specific to species and often populations within species, which supports its use for species identification and for the assignment of individuals to (sub-populations (Cadrin *et al.*, 2014). Campana and Casselman (1993) first showed the potential of otolith shape to accurately distinguish between different populations of Atlantic cod, and the method has since been widely used to investigate fish population structure and inform fishery management (Stransky *et al.*, 2008; Higgins *et al.*, 2010; Hüssy *et al.*, 2016).

Like growth increments formed within the otolith, shape is closely related to the complex biophysical processes that regulate fish somatic growth. However, while otolith increments are mostly understood and the features are biologically interpretable, the determinants of otolith shape at both the intra- and inter-population levels remain less clear. Overall shape is generally considered to be genetically constrained and species-specific (Lombarte and Castellón, 1991; Tuset *et al.*, 2006; Vignon and Morat, 2010), but ontogenetic and environmental factors also induce significant inter- and intra-population differences (Cardinale *et al.*, 2004). For example, variability of otolith shape between fish from the same population has been associated with individual-specific factors such as age, sex, allometry or year-class (Castonguay *et al.*, 1991; Begg and Brown, 2000; Monteiro *et al.*, 2005; Hüssy, 2008). This ontogenetic component may induce significant inter-individual and intra-population shape variability, which was demonstrated in different species of gadoids (Brown *et al.*, 2001; Irgens *et al.*, 2017). This issue is often controlled for in shape studies by restricting the analysis to samples from similar ages, length groups or maturity stages, as well as limiting the samples' temporal range to prevent strong year-class effects (Castonguay *et al.*, 1991; Begg and Brown, 2000).

Environmental factors may also have a significant influence on otolith shape by altering both the somatic growth and the otolith biomineralization processes. Abiotic factors such as temperature, depth or salinity may therefore affect otolith shape both indirectly through changes in fish and otolith growth, or directly through changes in material deposition (Campana and Casselman, 1993; Lombarte and Lleonart, 1993; Cardinale *et al.*, 2004; Capoccioni *et al.*, 2011). Biotic factors such as food quantity (Gagliano and McCormick, 2004; Hüssy, 2008) and specific composition (Mille *et al.*, 2016) may also exert a strong influence on otolith macrostructure and shape by affecting the metabolism of the fish and consequently the growth and mineralization processes in the otolith. Otolith growth and thus shape can therefore be considered as the cumulative result of many interacting intrinsic and extrinsic factors throughout the life of an individual, as opposed to the yearly variability expressed within a single annual otolith growth increment. Large-scale spatial variability in the genetic and environmental factors will often be greater than the local variation, which may support the use of otolith shape as a tool for population discrimination. Recent studies have nonetheless shown the significant contribution of local conditions to otolith shape variability (Vignon, 2015, 2018), which highlights the need for a deeper understanding of the processes that affect otolith growth.

1.3.3 Reconstructing individual growth histories

A key property of otoliths is that they grow continuously throughout the life of an individual even when somatic growth slows (Casselman, 1987), whereas other calcified structures with a skeletal function such as bones can stop growing or be resorbed during periods of low growth or poor feeding. This specific trait gives otoliths the ability to record complete individual growth histories and accurate fish age for the majority of species investigated, as opposed to other structures (such as scales) in which ageing errors and discrepancies are more prevalent, especially as fish get older (Boxrucker, 1986; Beamish and McFarlane, 1995).

Analysis of fish growth derived from otolith information has typically relied on two methods. First, estimates of fish maximum size and growth rates at the population level can be generated with specific equations such as the von Bertalanffy growth curve (von Bertalanffy, 1938) using fish size and age-at-capture (see for example Pilling *et al.*, 2002; He and Bence, 2007; Baudron *et al.*, 2014). Second, otolith increment widths and size-at-capture can be used to back-calculate an individual's length at the time of formation for each increment (Francis, 1990; Li *et al.*, 2008). This method necessarily assumes a proportional relationship between fish and otolith length and requires the incorporation of a biological intercept, which can be defined as the combination of fish and otolith lengths corresponding to the onset of proportionality between fish and otolith growth (Campana, 1990). Otolith back-calculation can be an effective method to analyse individual fish growth and has often been used in an ecological context (Sinclair *et al.*, 2002a, 2002b; Tonkin *et al.*, 2011), but it is susceptible to significant biases when the relationship between somatic and otolith growth breaks down or is estimated incorrectly (Campana, 1990; Hare and Cowen, 1995), or when the fish is subject to growth-selective survival.

A limitation to traditional approaches is that growth is a complex biological response dependent on many processes, and methods relying solely on population-level data such as size-at-capture may fail to represent ongoing processes that elicit individual responses. Because these processes are controlled by both intrinsic (ontogenetic or individual-specific) and extrinsic (environment or population-specific) factors affecting the accessibility and allocation of necessary resources (Enberg *et al.*, 2012), it is critical to partition the sources of growth variation to address ecological and environmental influences (Morrongiello and Thresher, 2015). Linking multiple individual growth histories across different cohorts (year-classes) can provide a better understanding of the different sources of growth variation and aid in interpreting historical growth patterns, which can in turn be applied to population-level questions. To that end, newer approaches using mixed-effect modelling have been developed since the early 2010s to better consider the hierarchical structure of repeated growth measurements within individuals, years and cohort (Weisberg *et al.*, 2010). This method has the advantage of investigating both intrinsic and extrinsic effects simultaneously (Morrongiello and Thresher, 2015), which is more appropriate for species where growth trends might be subject to greater inter-individual variability (Black *et al.*, 2019). Mixed-effects modelling has been successfully applied to analyse otolith growth chronology from a wide range of species and environments, on time scales ranging from a decade to nearly a century (e.g. Australian black bream over 14 years in Doubleday *et al.*, 2015; Alaskan rockfish over 59 years in Matta *et al.*, 2018; Baltic Sea herring over 66 years in Smoliński, 2019).

1.3.4 Markers of life history events

Otoliths record annual growth patterns that are used in age estimation of individual fish, but they also act as recorders of life history events. At the microstructural level, daily increments can be used to infer growth at the daily scale (Campana and Jones, 1992). Some of these increments have been shown to record the precise timing of important life history events, which can in turn be used to compare the early life history of different species or populations (Marui *et al.*, 2001). Because otolith growth is affected by both fish physiology and its environment, significant alterations in environmental conditions, body ontogeny or somatic growth will often create specific features in the otolith structure, referred to as checks (Geffen *et al.*, 2002). Life history events are often characterized by such alterations, which makes otolith checks an important evidence of life history changes in fish, especially in the first year of life. For example, checks in the otolith microstructures have been shown to accurately reflect metamorphosis (Modin *et al.*, 1996; Geffen *et al.*, 2007), settlement (Wilson and McCormick, 1999; Hüssy *et al.*, 2003), and hatching or first feeding (Campana and Neilson, 1985; Grønkjær and Schytte, 1999). A significant limitation of otolith microstructures is that they become harder to read when the fish grows older, particularly in long-lived species (Pannella, 1971), as the increments become narrower and appear to coalesce unless seen at high magnification. This limits the ability of daily increment analysis to detect specific life history events that might happen later in an individual's life, such as migration or spawning.

Checks in the otolith macrostructure can also appear in response to significant life history events irrespective of fish age, such as sudden changes in otolith growth patterns associated with the onset of sexual maturity, for example in plaice (Rijnsdorp and Storbeck, 1995) and orange roughy (Francis and Horn, 1997). These so-called "spawning zones" were first identified in Atlantic cod by Rollefsen (1933), who described a transition in the appearance of the annual growth zones of NEA and Norwegian coastal cod wherein outer growth rings were narrower and more regular than inner growth rings. It was proposed these zones likely reflected years where spawning took place, and they have since become routinely recorded alongside age estimates as indications of the number of spawning events in NEA cod (Yaragina *et al.*, 2009). However, the mechanism of formation of these spawning zones has not been determined, and their validity as a spawning marker is still under debate. It was proposed that spawning zones might reflect trade-offs in growth and reproduction (Folkvord *et al.*, 2014), but recent studies have showed that physiological changes associated with maturation and spawning are not sufficient to consistently induce spawning zones in cod otoliths (Irgens *et al.*, 2019). It is therefore likely that other factors associated with spawning, such as the long-distance migration and/or changes in food intake and energy use, could be of importance for the formation of distinct zones.

2. Aim of the thesis

Given the current pressure on the world's marine environments, there is an increasing interest in identifying and quantifying the impacts of climate change and human exploitation on the ecosystems, and especially on fish populations. In particular, the insight from analysis of past populations can help identify the influence of past changes and improve our understanding of current and future trends in fish populations.

Through the lens of century-long biological records of an Atlantic cod population from a particularly sensitive and fast-changing area, this thesis investigates how fish growth and life history respond to long-term changes in climate, fish population trends and human exploitation.

The work presented in this thesis is based on the IMR historical archive, which constitutes one of the longest and largest collection of NEA cod samples available. Utilizing the property of otoliths to record individual fish life history, I collected and processed several thousand NEA cod otoliths from both the modern and pre-scientific surveys period to reconstruct the biology of NEA cod over the last 100 years, using specific otolith features such as shape (**Paper I**), annual growth increment (**Paper II-III**) and macro-structures (**Paper III**). Through these sclerochronological reconstructions of past populations, I explored the century-scale variability of cod growth (**Paper I-II**) and sexual maturity (**Paper III**), two traits known to respond to environmental changes and important predictors of population dynamics and productivity (the rate of production of new biomass). Further, I used multiple modelling approaches to investigate and partition the combined influence of climate change, fish population dynamics and fishing pressure on NEA cod biology throughout the last 100 years

Cod otolith shape during the last 90 years was explored in **Paper I**, to identify whether environmental influences such as temperature and cod population dynamics had affected fish and otolith growth. This work also provided the first long-term exploration of otolith shape stability within a single population to detect whether any population replacement had occurred, which further contributes towards a consensus on the biological interpretation of shape differences. In **Paper II**, I then focused on individual growth increments to investigate and disentangle the potential factors influencing fish growth variability at a finer scale. By combining two modelling approaches, I explored the interacting effects of climate change, fish population dynamics and fishing pressure on cod growth throughout nearly a century. Finally, in **Paper III**, I utilized specific zonation patterns within the otolith traditionally related to individual spawning to explore long-term trends in NEA cod maturity in relation to fishing pressure. This study was also the first investigation of spawning zone occurrence in multiple cod populations associated with different environmental conditions and life history traits, which explored its validity as recorder of life history events and maturity (**Figure 2**).

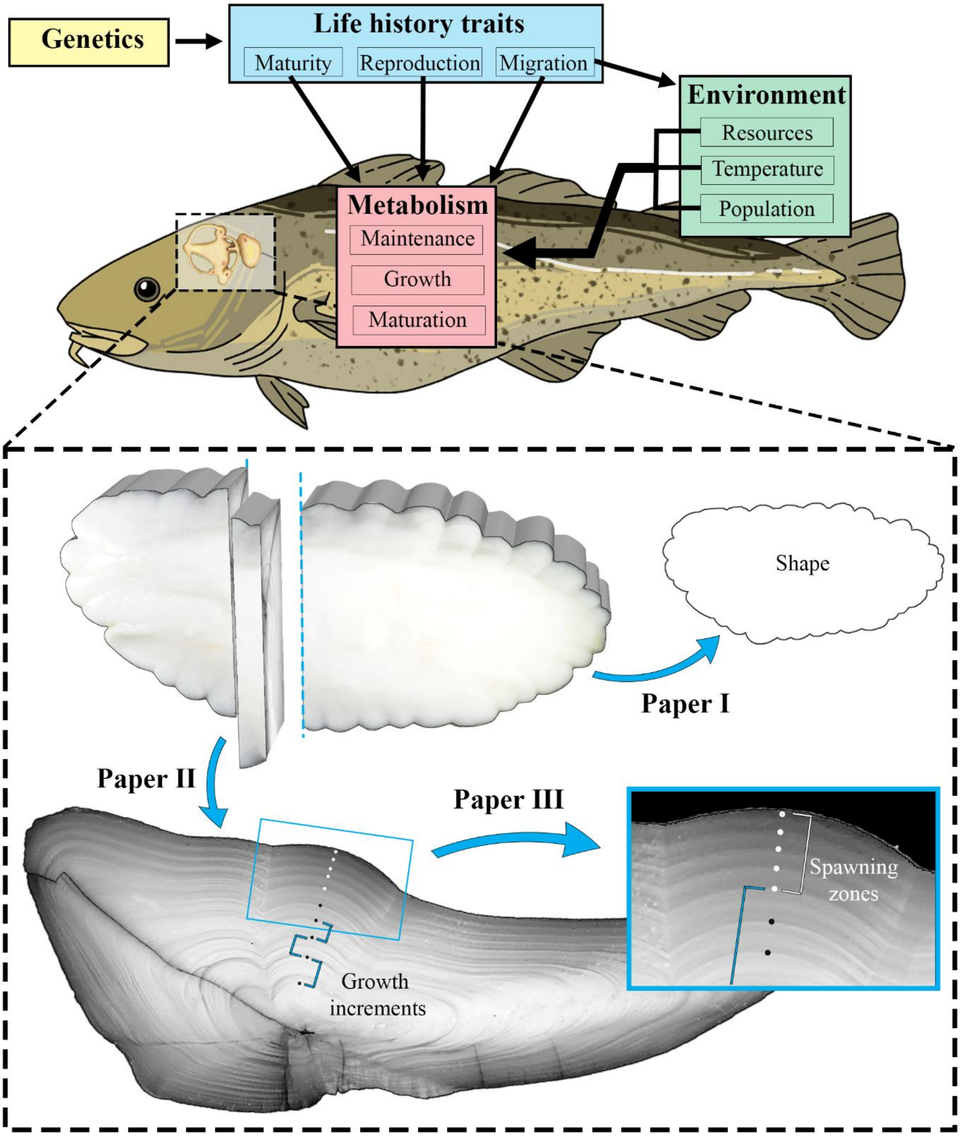

Figure 2: Main influences of life history and environment on fish metabolism and consequently otolith formation as explored in this thesis.

3. Summary of papers

Paper I

Long-term temporal stability of Northeast Arctic cod (*Gadus morhua*) otolith morphology.

C. Denechaud, S. Smoliński, A. J. Geffen, and J. A. Godiksen

NEA cod otoliths sampled from archived material were utilized to evaluate the temporal variability of otolith shape over a near-century. Otoliths from 2968 mature fish of the same age class and collected on the spawning grounds between 1933 and 2015 were described using elliptical Fourier descriptors. Series of hierarchical multivariate models were then developed to relate shape differences to environmental factors and their identified optimal time windows. Otolith shape of NEA cod was found to be temporally stable, as differences between years accounted for <3% of the observed variation and no significant differences were found between the average cohort shapes. Models confirmed shape differences were mainly caused by differences in growth rates, but also revealed effects of temperature and biomass-related variables at different life stages. Extrinsic factors described only a small fraction of the observed variance, which indicates that environmental changes over time likely account for less than the natural inter-individual variability in otolith shape. Our results bring evidence that otolith shape remains relatively stable through time, but that environmental influences on fish growth at different life stages can induce significant changes in shape. These results further contribute towards a consensus on the biological interpretation of shape differences.

Paper II

A century of fish growth in relation to climate change, population dynamics and exploitation.

C. Denechaud, S. Smoliński, A. J. Geffen, J. A. Godiksen and S. E. Campana

The impact of human activities and contributions to climate change on marine ecosystems and fish populations is significant, especially in high-latitude regions such as the Arctic. In order to investigate the response of NEA cod to these influences, 3894 archival otoliths were collected and the otolith increments were used as proxy for individual growth. The century-long growth reconstruction (1924-2014) was then modelled in relation to the selected climate, population and fishing-related factors using mixed-effects modelling and path analysis. Models revealed that density-dependent effects were the main source of growth variability, mainly due to competition for resources. Cod growth was positively correlated with warming sea temperatures but negatively correlated with the Atlantic Multidecadal Oscillation (AMO), suggesting contrasting effects of climate warming at different spatial scales. The addition of path analysis revealed significant interactions between factors that were not directly evident in the mixed-effects modelling, such as the positive influence of increasing temperature on capelin biomass, a key prey of NEA cod. Together, these results give a better long-term understanding of how multiple interacting factors have shaped cod growth throughout a century, both directly and indirectly.

Paper III

Otolith "spawning zones" across multiple Atlantic populations: do they accurately record maturity and spawning?

C. Denechaud, A. J. Geffen, S. Smoliński, and J. A. Godiksen

Specific changes identified in the otolith macrostructure of NEA cod are presumed to be representative of spawning events, but recent experimental studies have challenged this assumed relationship. Because these zones have never been investigated outside of Norway, otoliths from multiple Atlantic cod populations with different life history and environmental traits were first examined to see if spawning zones could be identified as a general characteristic of cod. Then, a large archival collection of more than 300 000 NEA cod otoliths was used to investigate temporal changes in the occurrence of spawning zones and test for correlations between otolith spawning zones and gonad development stages. Spawning zones could be reliably identified in all cod populations regardless of their individual environmental and life history characteristics. The long-term reconstruction of NEA cod maturity ogives using spawning zones showed trends consistent with those obtained from gonads, although they may not accurately record the first year or two following maturity. Changes in NEA cod maturity throughout the last 100 years were associated with significant changes in cod growth during the same period, likely in response of sustained high fishing pressure. This study brings new insights on the nature of spawning zones in cod otoliths and is the first to qualify their occurrence in multiple populations, which opens up interesting perspectives for species or populations with limited maturity data.

4. Synthesis and general discussion

Investigating and understanding the response of marine ecosystems to environmental changes has been central to marine science. For many fish populations, these changes include not only the fast warming and alteration of their habitats, but also the added contribution of human exploitation and selective fishing. In light of this complex web of interactions between climate, fish populations dynamics and fishing pressure, our ability to accurately foresee future changes relies in part on our ability to understand what factors drove historical variations. This doctoral thesis investigates the long-term variability of an Atlantic cod population in response to changes in its environment over a century, using specific otolith features such as shape (**Paper I**), annual growth increments (**Paper II-III**) and macro-structures (**Paper III**) as proxies of life history changes. This work shows that cod growth has varied significantly throughout the last 100 years in response to climate change at multiple scales, revealing contrasting effects of local warming (positive, **paper I & II**) and large-scale climatic alterations in the North-Atlantic (negative, **paper II & III**). Similarly, the increasing fishing pressure in the second half of last century and its effects on population dynamics were identified as important causes of variability in growth (**paper I & II**) and maturity (**paper III**). This thesis therefore highlights how multiple interacting factors have shaped cod variability throughout a century and provides a long-term perspective on the influence of environmental changes on fish biology and life history. Finally, it also discusses the value of historical reconstructions and how they might contribute to more accurate predictions of future changes.

4.1 Climate influences cod biology at multiple spatial and temporal scales

4.1.1 Cod productivity under warming local conditions

The influence of temperature on fish growth has been well studied and is known to affect growth rates through changes in both direct (i.e., metabolism, individual fitness, duration of the growth season) or indirect (i.e., food availability) processes (Brander, 1995; Neuheimer and Grønkjær, 2012). The direction of these changes is however variable between species and populations within species (Brander, 2000; Baudron *et al.*, 2014; Lyashevska *et al.*, 2020). The response of NEA cod to warming temperatures throughout the last 100 years appears to be positive, as growth increased significantly by up to 8.5% with sea temperature (**paper I & II**). While this had been mainly observed in the most recent decades, the reconstructed growth chronology highlights for example a period of higher than average growth during the 1920s and 1930s (**paper II**), which corresponds to a time when the North Atlantic underwent a significant warming period with important repercussions on the ecosystems (Johannessen *et al.*, 2004; Drinkwater, 2006). These result are in line with several studies predicting a higher productivity of certain cod populations such as NEA cod under warming trends (Brander, 1995; Drinkwater, 2005).

From prey availability and feeding to metabolism and protein synthesis, growth is a succession of complex processes that can be directly or indirectly affected by temperature at every stage (Brander, 1994b; Enberg *et al.*, 2012). The term “temperature effect” therefore often refers to the combined result of these individual influences but does not necessarily identify and disentangle the sources of the observed variation. Similarly, otolith growth is directly dependant on fish metabolism but is also under the additional, direct influence of temperature on biomineralization (Casselman, 1990; Campana and Casselman, 1993; Lombarte and Lleonart, 1993). Here, the influence of temperature on fish and otolith growth is evidenced at both the yearly level (growth increments, **paper II**) and at the level of an individual's life (otolith shape, **paper I**).

As demonstrated by Cardinale *et al.* (2004), individuals from a genetically homogenous population but living at different temperatures display significant enough differences in otolith shape with respect to growth rate to be accurately discriminated from one another. In NEA cod, changes in temperature over time induce slight changes in otolith shape between cohorts of the same population (**paper I**). This result is important, as **paper I** shows for the first time that otolith shape is temporally stable within a single population unit (less than 3% of shape differences attributed to year effect), but that variations can still be related to temporal changes in the environmental conditions. The identification of an optimal environmental window indicates that this temperature signal is the strongest during the juvenile life stage, when both fish and otolith growth are maximal, and has a lasting effect throughout the adult life (**paper I**). Likewise, the growth chronology constructed using otolith growth increments shows that the population-level variability in growth most closely reflects the variations in mean size-at-age observed for the age classes 1 through 6, the juvenile period (**paper II**). It seems therefore likely that temperature effects on growth are especially significant during the juvenile life stages and may alter the entire growth trajectory of individuals. The present results are in agreement with previous findings on cod (Brander, 1995; Björnsson *et al.*, 2001) and in line with the commonly accepted paradigm that temperature increase leads to faster juvenile growth and smaller adult body size.

This positive relationship between temperature and NEA cod growth may express itself through direct metabolic changes but also through indirect effects on prey assemblages and food availability that benefit cod. For example, the abundance of capelin was identified as having a significant positive influence on NEA cod growth, increasing by up to 4.7% (**paper II**). This is not surprising as capelin is known to be a key prey item of adult cod in the Barents Sea, and capelin population fluctuations can influence cod growth and recruitment success (Gjøsæter *et al.*, 2009; Fall *et al.*, 2018). However, integrating these results into a structural model also reveals significant interactions between temperature and capelin abundance, which were not evident in the separate analysis of growth and temperature or growth and capelin abundance (**paper II**). Warmer conditions therefore likely have a positive direct influence on fish growth (i.e. faster metabolism, longer growth season) but also an indirect one by favouring higher abundances of preys such as capelin.

Increased productivity in warming conditions is expected for a population such as NEA cod that has generally been described as having a “slow” life history: fish grow slowly but have a large theoretical maximum size, natural lifespan reaches up to 25 years, and maturation generally does not start before ages 6 to 10 (Hylen *et al.*, 2008). Atlantic cod have a plastic biology that allows the different populations to live in a large panel of environmental conditions. Because the Barents Sea population lives near the colder limit of their range it is therefore likely that it will respond positively to higher sea temperatures and the associated increased metabolic activity and ocean productivity (Holt and Jørgensen, 2014). On the other hand, this warming trend might be detrimental for cod populations inhabiting warmer waters further south, such as the Celtic Sea, Irish Sea and southern North Sea. Because they already live close to the upper limit of their thermal range these populations are likely to decline or even disappear if temperatures increase above 12°C, owing to thermal stress and reductions in recruitment (Planque and Frédou, 1999; Drinkwater, 2005; Heath *et al.*, 2012). Likewise, this thesis also reveals some negative influences of climate change on NEA cod which may be important for understanding how the population has responded to long-term changes.

4.1.2 Contrasting effects of large-scale climate change

Incremental warming of the environment in the Barents Sea has so far been correlated with an increased productivity of NEA cod, likely in response to increased prey availability and metabolic activity. However, this thesis also demonstrates negative effects of climate warming through the large, low frequency variations that happened toward the end of last century. **Paper II** demonstrates that NEA cod growth was significantly and inversely related to the AMO, a multidecadal oscillation alternating between warm and cold phases and defined as a running mean of North Atlantic sea surface temperature anomalies (Kerr, 2000; Alexander *et al.*, 2014). The negative effect of AMO decreased cod growth by as much as -7.2%, which is nearly the same magnitude as the positive relationship previously identified with temperature (**paper II**). This pattern illustrates how a similar warming trend can have opposing effects on organisms depending on the scale at which it is explored. The positive relationship between cod productivity and temperature discussed previously is limited to "local" and progressive warming, where the impacts are more direct and easier to interpret. On the other hand, large-scale and low frequency climatic changes such as the AMO phase are likely to be indicative of much larger modifications of the environment, such as the strength and direction of the water masses circulating the North Atlantic associated with numerous biological changes (Alheit *et al.*, 2014).

An important clue to this suggested negative relationship between growth and low frequency warming is the significant and abrupt drop in population-level growth observed between 1993 and 1999 in the reconstructed growth chronology (**paper II**). The concept of ecological and climatic regime shift - an ensemble of large, persistent changes in the structure and function of a system - has grown out of numerous studies showing significant ecosystem-level changes during the late 1980s and the mid-1990s in the Northern Hemisphere (Reid *et al.*, 2001; Beaugrand, 2004; Beaugrand *et al.*, 2015). In particular, the mid-1990s saw a significant shift in marine ecosystems throughout the North Atlantic which has been associated with a complex series of atmosphere–ocean changes characterized by a significant weakening of the NAO and a switch of the AMO from a cold to a warm phase (Robson *et al.*, 2012; Alheit *et al.*, 2019). While no such persistent change has been observed in the Barents Sea ecosystem (Johannesen *et al.*, 2012), the temporal correspondence between the observed drop in cod growth (**paper II**) and the mid-1990s regime shift is indicative that significant changes took place during that period and affected the productivity of NEA cod.

Since the direct relationship between cod growth and temperature is positive, the negative influence of low-frequency variations in sea temperature is likely more representative of their broader consequences in terms of hydrography and fish population dynamics (**paper II**). The "Atlantification" of the Barents Sea in response to warming is characterized by a decrease in sea-ice extent and sea-ice import, as well as more prevalent warm Atlantic water flow resulting in an enhanced vertical mixing (Årthun *et al.*, 2012; Lind *et al.*, 2018). This could in turn have significant consequences for the ecosystem and the NEA cod population, primarily by altering the food web structure, expanding or contracting species geographical range, and introducing new constraints related to warming temperature at depth (Hollowed *et al.*, 2013; Rutterford *et al.*, 2015). Year-to-year temperature increase might be beneficial for the NEA cod population by increasing growth rates, extending feeding areas and relaxing intra-population early-life competition (Brander, 1995; Holt and Jørgensen, 2014; Kjesbu *et al.*, 2014), but the results from **paper II** show that low frequency, large-scale changes might in the long term be detrimental.

Because warming of the near-Arctic areas such as the Barents Sea may create more favourable conditions year-round, recent studies have highlighted the rapid northward extension of many species' range and the associated borealization of the ecosystem (Fossheim *et al.*, 2015). Since warming conditions sustained over many years are required to enable the gradual colonisation and establishment of these species within the Barents Sea ecosystem, the recently observed borealization is probably the result of decades of temperature increase and its effects may only now become significant as directly observable consequences of climate warming. The associated changes are predicted to have considerable implications for the ecosystem (Kortsch *et al.*, 2015; Frainer *et al.*, 2017), and while Atlantic cod is considered a boreal species likely to benefit from increased temperatures, the consequences of larger changes in the food web structure and competition could be detrimental. For example, non-linear climate-driven interactions between species were shown for cod and haddock in the Barents Sea, where temperature anomalies over a certain threshold can cause the otherwise co-varying populations to start competing with one another (Durant *et al.*, 2020). It is therefore plausible that continued warming conditions also change the dynamic of other fish populations, which could lead to increased competition or decreased food availability for NEA cod (see for example Hjermann *et al.*, 2004; showing indirect negative effect of temperature on capelin when the herring population is large).

These contrasting effects of climate change over longer time scales are in line with the findings of Årthun *et al.* (2018), who used oceanographic data to reconstruct long-term variations of the NEA cod population and predicted a gradual decline in population size in the future, despite the overall positive relationship between temperature and cod productivity. Of interest is the fact that their modelled retrospective predictions not only reproduced most of the observed interannual variability, but were particularly successful in capturing the lower-frequency, decadal variations of population size and recruitment. In addition, multidecadal climate oscillations are also associated with spatial shifts in spawning locations of NEA cod between periods of cold or warm temperature anomalies (Sundby and Nakken, 2008). NEA cod has seen a large decrease in age at maturity from age 10 to age 6-7 since the 1950s (**paper III**), which has mostly been linked to selective pressure associated with high fishing mortality (Heino *et al.*, 2002). However, other studies have hypothesized that environmental influences were also driving these changes (Marshall and McAdam, 2007), and that disentangling phenotypic plasticity in maturation could be challenging when fishing pressure and environmental change happen simultaneously. The sclerochronological record is therefore a useful approach to evaluate the importance of fishing-induced effects on population, biology and life history changes in NEA cod over the last 100 years, in light of the climate influences presented here.

4.2 Cod response to population dynamics and human exploitation

Climate change is likely to be one of the most significant factors of change in marine ecosystems, but many fish populations are also subjected to another stressor in the form of human exploitation. Whether population trends are driven primarily by climate or fishing has long been debated (Hidalgo *et al.*, 2011), but the current consensus is that they both affect fish populations synergistically. In the previous section, I discussed the contrasting influence of climate change on cod biology at different time scales and how its effects may be both direct and indirect. Similarly, the consequences of fishing pressure are generally manifested directly in the population dynamics, which can in turn have significant repercussions on fish life history and biology.

Intra-population competition is one of the key factors regulating many fish populations, either through density-dependent juvenile survival or through competition for limited resources (Beverton and Holt, 1957; Lorenzen and Enberg, 2002). In this thesis, the variability in cod growth throughout the last 100 years was also found to be largely density-dependent (**paper I & II**). Like the temperature effect discussed previously, density-dependent growth is evidenced at both the yearly level (growth increments, **paper II**) and at the level of an individual's life (otolith shape, **paper I**). Food availability is one of the primary factors driving somatic and otolith growth rates, and it has consequently been proposed as an important source of variability in otolith shape (Hüssy, 2008). The significant influence of cod population size found on otolith shape in **paper I** may therefore be more representative of changes in growth rates driven by density-dependent effects on prey availability. Further evidence of this is found when investigating the optimal window for the effect, which identified the strongest signal during the late juvenile to early mature stage when cod diet shifts to a higher proportion of fish (Link and Garrison, 2002; Jaworski and Ragnarsson, 2006). Because otolith shape is the cumulative product of an entire individual's life, the stronger effect of cod population size on otolith shape during this specific window highlights how density-dependent competition for food may be the most prevalent for juveniles and adults feeding on fish, and how it affects their growth trajectories. Likewise, in **paper II,** density-dependent effects were the largest factor influencing year to year variations of cod growth, with a decrease of nearly 22% in growth between the periods of observed lowest and highest biomass. The period 1960 to 1990, which was characterized by a declining cod biomass down to its lowest historical value by 1980, was also associated with a sustained period of higher than average growth. This suggests that density-dependent effects were less significant during this period of lower cod biomass, and that cod growth benefited from relaxed competition.

The prevalence of density-dependent effects can in turn be related to the positive relationship between capelin biomass and cod growth discussed previously. After the collapse of the NSS herring population at the end of the 1960s and the subsequent increase in capelin biomass (Lees *et al.*, 2006), capelin has become an essential item in the diet of cod, in particular for late juvenile and adult fish where it accounts for up to 40% of the diet by weight (Holt *et al.*, 2019). The optimal signal of population size on shape identified in **paper I**, from age 2 to 7, may therefore indicate that competition is the highest during the life stages where capelin is the most important prey. As a key prey item, capelin collapses such as those that occurred in 1985, 1993 and 2003 (Gjøsæter *et al.*, 2009) likely negatively affected cod feeding, as reflected in **paper II** by sudden declines in cod growth during these same periods. In addition, the mid-1980s saw a simultaneous collapse of capelin and other fish populations resulting in a temporary suboptimal diet for cod (Reid et al., 2000), which is well reflected in the growth reconstruction from **paper II** with a sharp decline in growth between 1986 and 1988. The observed variability in cod growth during the period could thus reflect changes in prey availability and competition consistent with large fluctuations in capelin abundance (Gjøsæter *et al.*, 2009; Eriksen *et al.*, 2017; Holt *et al.*, 2019).

Fishing pressure is mainly regarded as the most important factor regulating the population of commercial species, despite the traditional view that environmental conditions determine recruitment success. With the large collapses of multiple fish stocks around the turn of the century, it has however become clear that harvested populations are more susceptible to large fluctuations than non-exploited ones, and that the effects of harvesting and climate change are synergetic (Planque *et al.*, 2010; Shelton and Mangel, 2011). Size selective fishing generally means that the adult, mature portion of the population suffers a significantly higher mortality and a reduced life span, which may have evolutionary consequences by changing the frequency of certain genes within the population (Hutchings, 2005; Jørgensen *et al.*, 2007; Kuparinen and Merilä, 2007). A multitude of studies have shown that the response of populations to this added pressure can go in two directions: in some cases growth rates may slow down to increase survival with age (e.g. Edeline *et al.*, 2007), or alternatively life history may accelerate through faster growth and maturation to compensate for increasing fishing mortality (Olsen *et al.*, 2004). Enberg *et al.* (2012) concluded that selection pressures associated with fishing are likely to act in both directions simultaneously, and that the response of organisms will depend on the relative strengths of these pressures. They also pointed out that the existence of fishing-induced evolution may be difficult to disentangle from other factors when using growth signals alone, due to the inherent plasticity of growth. The century-long reconstructions presented in this thesis provide a platform for discussion of the parallel changes in both cod growth (**paper I & II**) and maturation (**paper III**), two traits commonly associated with fishing-induced changes.

Atlantic cod is a well-known case when it comes to the consequences of overfishing: by the late 1980s and 1990s many cod populations were overexploited and consequently collapsed, and recovery trends in the following decades varied between populations (Brander, 2007). One of the most striking examples is probably the contrasting trajectories of “northern cod” in the western Atlantic and NEA cod in the Barents Sea, after they both collapsed between the late 1980s and early 1990s (Lilly *et al.*, 2013). Starting 1960 the northern cod stock decreased steadily and then collapsed in the early 1990s, but recently started showing signs of a slow recovery in the 2000s. On the other hand, the NEA cod stock reached a critical low in the mid-1980s and nearly collapsed, but then saw a remarkable recovery after a brief fishing moratorium as well as new harvesting rules and managing strategies were implemented (Hylen *et al.*, 2008; ICES, 2020).

Following the widespread development of trawling and the return of international fishing in the Barents Sea after the Second World War (Hylen *et al.*, 2008), fishing mortality of NEA cod increased consistently between the 1950s and the late 1980s, well beyond the previous levels of mortality experienced by the population (ICES, 2020). In addition, the technological shift from traditional longline to trawling and gillnets led to fishing becoming increasingly size-selective toward bigger fish. This was associated with a large decrease in cod biomass and the progressive disappearance of older fish (age classes 12+) from the population (**paper III**). As discussed above, **paper II** shows that this period of declining biomass is associated with a sustained period of higher growth, which is most likely a direct consequence of density-dependence release from competition. Similarly, the maturity time series reconstructed in **paper III** indicates a drastic decline in median age at maturity during this period, with a median age of maturity declining from 9-11 in earlier period compared to 6-8 in more recent decades. These results provide more evidence supporting previous studies of NEA cod suggesting that sustained high fishing pressure over several decades can be associated with faster growth and earlier maturation (Jørgensen, 1990, 1992; Durant *et al.*, 2013).

The effects of fishing on the biology and life history of fish populations can generally be explained by two potential mechanisms. First, the selective removal of certain individuals and the associated reduction in biomass leads to relaxed density-dependent competition and increased food availability, which is generally met with faster growth and earlier maturation (Jørgensen, 1990; Heino and Godø, 2002). This “phenotypic response” occurs quickly after fishing mortality increases and often follows rather closely the variations in biomass associated with changes in fishing pressure. Second, the sustained selective removal of some individuals can favour certain genotypes more likely to survive and reproduce, which at terms leads to changes in the genetic structure of the population (Law, 2000; Jørgensen *et al.*, 2007). While these survivors would usually be the slower-growing fish more likely to survive fishing, the harvesting of slow-growing and therefore late-maturing individuals before they reach maturity over a sufficiently long period may also favour faster growth and early maturation genotypes in the population (Law, 2000). This "evolutionary response" is likely to have larger consequences in the long-term, as it may drastically alter population dynamics and is expected to be substantially harder to reverse than the "plastic response" even when fishing is interrupted (Enberg *et al.*, 2009). Distinguishing between the two mechanisms and their respective importance is however difficult when relying on observational phenotypic data like growth, due to the multitude of other factors affecting growth rates (Enberg *et al.*, 2012).

The analyses presented in this thesis suggest that the changes in NEA cod biology and life history in relation to high fishing mortality throughout the second half of last century involve mainly a phenotypic response, where density-dependence release allowed for faster growth and earlier maturation (**paper II & III**). The cohort-based reconstruction of age at maturity shows that it varied around age 10 until the onset of high fishing mortality in the 1950s, after which an almost linear decline in age at maturity from year-class to year-class took place until the collapse of the population in the 1980s. However, despite drastic changes in exploitation pressure in the following decades (fishing mortality back to 1960s level by 2000) and a population biomass nearly as high in 2015 as it was in the early 1950s, maturity remained low for a sustained period and has only shown signs of slow increase since 2010 (**paper III**). This suggests that both mechanisms were acting in the NEA cod population in response to fishing pressure. The decline in age at maturity and higher growth observed in NEA cod is therefore a phenotypic response to release from density-dependent factors, as well as a result of genetic changes caused by selective fishing. The action of fishing-induced evolution is supported since changes in age at maturity were not immediately reversed once earlier maturation had been selected in the population (Law and Grey, 1989; Law, 2000). Theoretical work has demonstrated how both mechanisms can be active in combination, by modelling the role of density-dependence when investigating fishing-induced evolution of growth and maturation in NEA cod (Eikeset *et al.*, 2016).

When assuming weak density-dependence, as observed for the period 1930-1950, models predicted significant fishing-induced evolution to explain the observed past trends in growth and maturation. But when growth was highly density dependent (as observed for the period 1978 to 2005) model results predicted a more prominent role of the phenotypic response to density-dependence release to explain the observed trends. My reconstruction based on otolith analyses in this thesis shows that both mechanisms have probably acted in parallel in NEA cod over the past century. While the initial response was mainly driven by density-dependence release due to the decrease in population size and competition, some fishing-induced evolution is necessary to explain that faster life history traits were maintained even after fishing pressure decreased and population size recovered.

The respective influences of fishing and climate change on NEA cod biology are hard to disentangle, especially during a period where increasing fishing pressure and warming conditions occur together (Marshall and McAdam, 2007). If each factor is taken independently, growth rates should increase both as a response to density-dependence release and warming conditions additively (**paper II & III**). However, selective harvesting not only removes biomass but can also gradually reduce population complexity (Hilborn *et al.*, 2003), resulting in changes in life-history (Law, 2000; Anderson *et al.*, 2008) and demography (Ottersen *et al.*, 2006) that can in-turn erode population resilience to environmental changes. For example, a recent study on purple wrasse by Morrongiello *et al.* (2019) used a similar otolith-based approach to show that fishing caused a significant reduction of variability (and thus plasticity) in individual responses. While both fishing and warming conditions had an expected positive influence on purple wrasse growth, the study showed that selective harvesting also removed those very individuals who grew faster in response to higher temperatures. This selection pattern in the fishery could significantly weaken the population's ability to adapt to future warming conditions. The variation in cod growth and maturation presented in this thesis confirms that fishing had a significant influence on NEA cod biology throughout the second half of the 20th century, but also that climate change had contrasting effects at different time scales (**Figure 3**). It is therefore reasonable to question whether decades of overexploitation may have altered the plasticity of NEA cod, and thus their ability to adapt to future changes. Identifying this kind of indirect, non-additive interactions is one of the challenges that face ecologists and modelers, as predictions may drastically differ from reality if there are incorrect assumptions about the relationships between factors. The response of ecosystems to changes in their environment is likely the result of numerous complex influences interacting at multiple temporal and spatial scales, and as such is incredibly hard to predict with precision. In the next part, I will therefore discuss the value and limits of long-term historical reconstructions of fish populations to improve our predictive abilities.

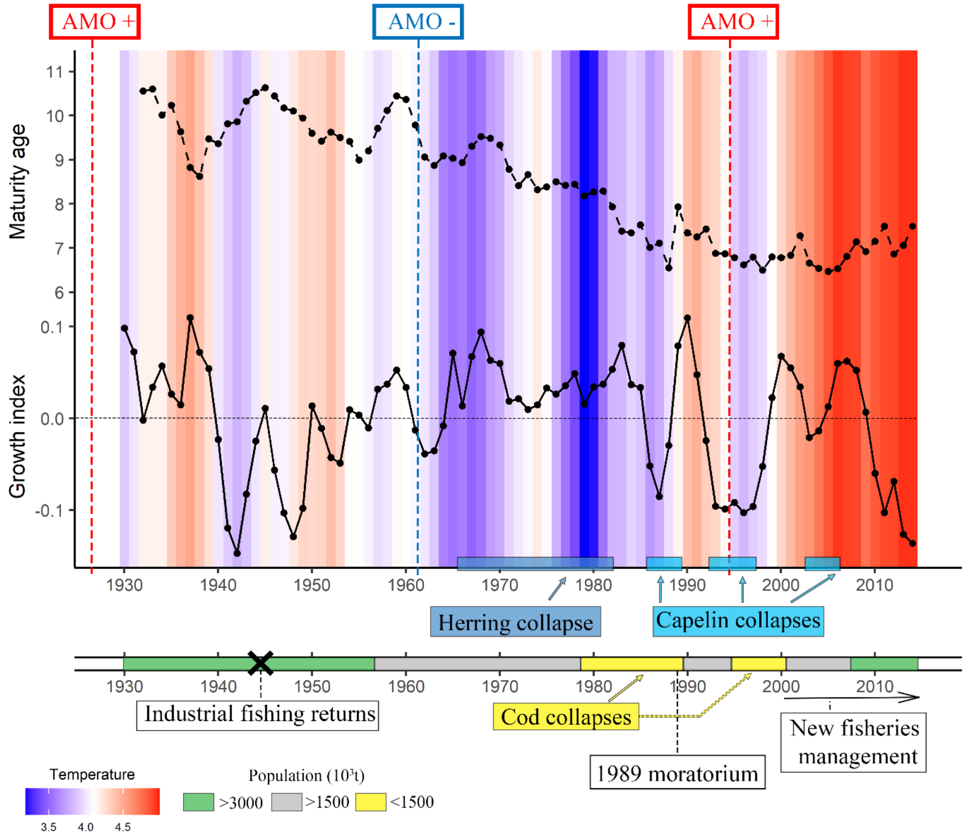

Figure 3: illustrated timeline of the past century, with long-term reconstructions of median age at maturity (**paper III**, top dashed curve) and growth index (**paper II**, bottom curve) built in this thesis. Background gradient represents the 5-years rolling

average of the Kola section 0-200m sea temperature. Bottom axis displays variations in the NEA cod population size and important changes in exploitation.

4.3 Perspectives: can long-term reconstructions help better forecast future changes in fish populations?

In a context of the accelerating rate of environmental change, predictive modelling studies have become a very significant part of modern marine research. The challenges of accurate predictive modelling are many, and more so when one attempts to integrate a large variety of factors whose concurrent effects may be additive, multiplicative, cancel each other or interact in ways that defy expectations from a straightforward analysis of each factor independently (Lehodey *et al.*, 2006). The main goal of this thesis has been a long-term exploration of population-level changes in NEA cod biology and life history in relation to environmental influences, against the backdrop of the extensive literature on cod and fish biology to form a narrative for the observed past variations. Although I did not directly attempt to model the future response of NEA cod to its environment, the results of this thesis were used to formulate a set of hypotheses which, in turn, can be tested more quantitatively in future studies focused on a predictive modelling approach. I advocate that long-term biological reconstructions, such as presented in this thesis, are an essential step toward more accurate predictions and mitigation of future changes, and will therefore use this last section to discuss their value and the challenges for modern marine research and predictive modelling.

Aquatic ecosystems have long been under-studied in comparison to land ecosystems, in part due to the inherent difficulty to observe and collect data underwater, and as a result there is a significant lack of long-term historical information (Richardson and Poloczanska, 2008; Brown *et al.*, 2011). While early investigations of the relationship between fish populations and environmental conditions date as far back as the late 19th and early 20th century (Baird, 1889; Helland-Hansen and Nansen, 1909), fish stocks were long thought to be inexpungible and variations in catches were mostly associated with population migration. One of the consequences is that the regular collection of biological data on fish began quite late, with few databases extending prior to the second half of the 20th century (see for example Pacific halibut in Clark and Hare, 2002; or Atlantic cod in Hylen *et al.*, 2008). This poses a significant challenge in evaluating and predicting the response of fish to its environment, as data over sufficiently long periods of time is seldom available. In addition, this lack of long-term monitoring is particularly problematic for exploited fish populations, as it means that the available data seldom extends beyond the beginning of industrial fishing and its associated effects of fish populations and biology. In a seminal essay at the turn of last century, Pauly (1995) first coined the term “shifting baseline syndrome” (SBS) to describe the gradual shift in the perception of what the baseline conditions of a fish population are, between generations of scientists that often use their early-career as a reference point. This concept has since been expanded to describe the “gradual change in the accepted norms for the condition of the natural environment due to a lack of experience, memory, and/or knowledge of its past condition” (Pinnegar and Engelhard, 2008). The lack of long-term data for most fish populations not only means that SBS is likely to affect our perception of their baseline biological conditions, but also that it is difficult to evaluate what these conditions were prior to the direct influence of human exploitation and anthropogenic contributions to climate change.

The sclerochronological reconstructions central to this thesis show that a useful alternative may be to use archival materials such as otoliths, scales or bones to generate long-term biological data. These “hard parts” have seen an increasing use in modern marine research in the recent decades, owing to the diversity of information regarding individual growth, fish condition, migratory behavior or environmental exposure that can be extracted from them (see section 1.3 for more details). Hard parts of marine organisms, mostly bivalve shells and corals, have been traditionally used to reconstruct past climate variability (e.g. Lough and Cooper, 2011; Butler *et al.*, 2013; Mette *et al.*, 2016). This approach can give an appreciation of long-term climatic variability, but the selection of mostly sessile organisms and the customary standardization/detrending of growth or isotope signals necessarily comes at the expense of capturing population-level responses to change. For mobile organisms like fish there is also an added layer of uncertainty and difficulty due to more complex factors regulating fish biology, and the direct influence of human harvesting.

I used the characteristics of otoliths from a large collection started in the 1930s as a tool to reconstruct NEA cod growth (**paper I & II**) and maturity (**paper III**) over a century, when survey monitoring of the population only goes back to the 1970s. As shown by the relatively good agreement both between otolith growth chronology and length-at-age time series (**paper II**), and between maturity inferred from spawning zones and gonad development stages (**paper III**), these reconstructions are effective proxies of fish life history which can be used in parallel with traditional data or as alternative sources for periods with poor or missing data. Many universities, institutes and museums worldwide have similar archives, some of them going back centuries, which may hold an enormous amount of information that is currently underutilized (Rivers and Ardren, 1998; Campana and Thorrold, 2011). Archives therefore make a compelling resource to reconstruct long-term fish biology in many populations, including those that lack data prior to the more contemporary period. This can be especially true for long-lived species where individual otoliths can represent decades of fish life history.

Since the end of the 20th century, Global Climate Models (GCMs) have been developed as a tool to simulate and predict the evolution of climate around the world. With technological progress GCMs have become an incredibly complex web of interactions between atmosphere, oceans and land, which in turn provides essential insights into possible future changes in the environmental conditions (IPCC and Stocker, 2014). However, scale remains one of the main challenges of coupling GCMs with biological models for marine organisms such as fish: while GCMs utilize data over broad geographic areas, predicting the response of a given ecosystem frequently needs to be evaluated at more local and regional scales and therefore requires a “downscaling” of the environmental factors of interest (Hollowed *et al.*, 2009; Brown *et al.*, 2016). In addition, forecasting ecological responses based on what we currently observe or have empirically established is challenging for many reasons. First, no matter the time scale of the predictions we are always limited to observe changes happening in real time, and as a result it may be difficult to confirm whether or not past reconstructions are correct. For example, observed short term trends may be similar to those predicted but diverge significantly over longer time periods if the environmental influences were not properly understood or, alternatively, may appear non-related to a factor of interest because the signal is hidden behind the effects of other covariables (e.g. Myers, 1998; Oliveira and Butterworth, 2005; Francis *et al.*, 2006). A direct consequence is that scientists may lack a broader context to establish cause and consequence when comparing the original predictions to the present observations, with incorrect assumptions of causality.

The principle that correlation does not necessarily imply causality is well-known, especially in the context of climate change and ecology. Causality can be wrongly assumed between two (or more) covarying variables although there are no causal links, for example if a third parameter is in reality driving both. A widespread example is the difficulty to model stock-recruitment relationships of fish populations in the context of a changing environment, where linear direct relationships are unlikely to hold and spurious correlations may be wrongly interpreted (Sugihara *et al.*, 2012; Pierre *et al.*, 2018). In addition, predictions based on empirical relationships often necessarily assume uniformity and stationarity, which implies that the biological processes involved in the response of organisms to a given environmental factor is always of the same direction and magnitude. Such assumptions may limit the accuracy of predictions, as most biological traits have an inherent tolerance threshold and their response is likely to change under environmental conditions beyond those on which the empirical relationships were drawn (Ciannelli *et al.*, 2012). Therefore, one of the priorities for improving predictive models is to identify the linkages between environmental forcing and fish biology at the process level and not only in terms of general correlations, such that environmental factors can be selected to reflect known physiological tolerances or optima (Morrongiello *et al.*, 2011, 2012).

The limitations and challenges faced by scientists when attempting to predict future changes based on empirical relationships are numerous, but they do not necessarily invalidate the current knowledge drawn from them. As Lehodey *et al.* (2006) concluded in their review of climate and fisheries, “until now, correlations have been useful to demonstrate that climate-related variability of fish populations is the rule rather than the exception”. In that sense, empirical correlations and experimental work have laid the foundations for understanding some of the environmental influences driving fish populations, and have often proved to be useful to assess, at least qualitatively, the potential consequences of future environmental change. Long-term reconstructions can therefore be valuable, as they reveal the responses of organisms to multiple environmental and anthropogenic influences over large spatial and temporal scales (Pyke and Ehrlich, 2010). By drawing from past observations and experimental work, long-term reconstructions like those generated in this thesis can explore the effects of various factors of interest with the advantage of having the full knowledge of what happened before, during and after, both at the level of fish populations and environmental conditions. In turn, this information may be a stepping-stone toward better modelling of responses to future changes, as it provides a broader appreciation of the mechanisms behind empirical correlations between the environment and biological changes in fish populations.

5. Conclusion

This thesis has explored the long-term response of NEA cod to environmental changes, through the prism of the otolith as a proxy of individual life history. Using various modelling approaches, the different papers show that cod growth and maturation varied significantly in the last 100 years, mostly in response to the release of density-dependent competition and to the effects of warming sea temperatures. Altogether, this work provides evidence of contrasting and synergistic influences of climate change, population dynamics and harvesting on cod biology throughout the past century. While warming conditions seemed beneficial to growth and maturation, the evidence of low-frequency negative relationships suggests that larger ecosystem-level changes tied to the Atlantification of the Barents Sea may be detrimental in the future. Likewise, the prevalence of density-dependent effects in NEA cod was evident in the response of the population to high fishing mortality throughout the second half of the 20th century. Changes in growth and maturity that were only partly reversed after the implementation of new management strategies may be indicative of fishing-induced evolution, which could have unforeseen consequences for the future response of NEA cod to climate change.

Besides these general results, this thesis includes unique applications and approaches to long-term biological reconstructions. Using otoliths as a proxy to study growth is an increasingly popular method, but the century-scale growth chronology constructed in **paper II** constitutes one of the longest continuous and annually resolved biological time series available for Atlantic cod, as well as one of the most extensive otolith-derived fish biochronology. In addition, **paper I** provides the first assessment of within-population otolith shape temporal stability as well as a novel approach to decompose sources of shape variability and to integrate optimal environmental signals, which further contributes towards a consensus on the biological interpretation of shape differences. Finally, **paper III** provides the first multi-population examination of the occurrence of spawning zones in Atlantic cod otoliths and their validity as a proxy of individual maturity, which may open new perspectives for the reconstruction of past maturity in other species.

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7. Papers

Paper I

Paper II

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PRIMARY RESEARCH ARTICLE

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A century of fish growth in relation to climate change, population dynamics and exploitation

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Abstract

Marine ecosystems, particularly in high-latitude regions such as the Arctic, have been significantly affected by human activities and contributions to climate change. Evaluating how fish populations responded to past changes in their environment is helpful for evaluating their future patterns, but is often hindered by the lack of long-term biological data available. Using otolith increments of Northeast Arctic cod (*Gadus morhua*) as a proxy for individual growth, we developed a century-scale biochronology (1924–2014) based on the measurements of 3,894 fish, which revealed significant variations in cod growth over the last 91 years. We combined mixed-effect modeling and path analysis to relate these growth variations to selected climate, population and fishing-related factors. Cod growth was negatively related to cod population size and positively related to capelin population size, one of the most important prey items. This suggests that density-dependent effects are the main source of growth variability due to competition for resources and cannibalism. Growth was also positively correlated with warming sea temperatures but negatively correlated with the Atlantic Multidecadal Oscillation, suggesting contrasting effects of climate warming at different spatial scales. Fishing pressure had a significant but weak negative direct impact on growth. Additionally, path analysis revealed that the selected growth factors were interrelated. Capelin biomass was positively related to sea temperature and negatively influenced by herring biomass, while cod biomass was mainly driven by fishing mortality. Together, these results give a better understanding of how multiple interacting factors have shaped cod growth throughout a century, both directly and indirectly.

KEYWORDS
Atlantic cod, climate change, fish growth, fisheries, *Gadus morhua*, mixed-effects modeling, otolith chronology, structural equation model

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1 | INTRODUCTION

Climate change is affecting marine ecosystems worldwide and there have been measurable and increasing consequences to populations over the past century, affecting individual physiology and survival as well as population dynamics, species distribution, productivity or ecological diversity (Cheung et al., 2013; García-Reyes et al., 2015; Hoegh-Guldberg & Bruno, 2010). Temperatures are predicted to increase in all projected scenarios (Stocker et al., 2014) and ocean warming has consequently been at the center of research. However, its future consequences for fish populations remain difficult to predict given the scarcity of long-term biological chronologies for certain marine ecosystems or communities (Poloczanska et al., 2013). Additionally, many fish populations are subject to other significant stressors, especially fisheries exploitation. Selective harvesting can gradually reduce population complexity (Hilborn, Quinn, Schindler, & Rogers, 2003), resulting in changes in life history (Jørgensen, 1990; Law, 2000) and demography (Ottersen, Hjermann, & Stenseth, 2006). These alterations, in turn, erode population resilience to environmental changes and magnify their impacts (Hidalgo et al., 2011; Morrongiello, Sweetman, & Thresher, 2019; Planque et al., 2010). In this context of significant stressors, there is a need to evaluate the past variability of fish populations to identify, quantify and contextualize the causes of observed changes and forecast their future impacts accordingly (Reid & Ogden, 2006).

Fish somatic growth is an ideal proxy which responds to both environmental changes and exploitation pressure. Spatial or temporal changes in growth have been associated with different environmental factors such as temperature (Campana, Mohn, Smith, & Chouinard, 1995) or prey availability (Graeb, Dettmers, Wahl, & Cáceres, 2004) but also to population-specific effects such as density dependence (Lorenzen & Enberg, 2002) or harvesting (Enberg, Jørgensen, Dunlop, Heino, & Dieckmann, 2009). Small changes in growth rates within a population can not only influence individual fitness but also population mortality, productivity and reproductive success (Audzijonyte, Kuparinen, Gorton, & Fulton, 2013; Hixon, Johnson, & Sogard, 2014; Lorenzen, 2016). As a result, long-term growth chronologies can be valuable indicators of population response to the combined effects of environment and exploitation (Morrongiello et al., 2019) and associated changes in fitness over time (Morrongiello, Walsh, Gray, Stocks, & Crook, 2014).

Fish growth data are often derived directly from size-at-age data as a population index, using growth functions to estimate theoretical maximum size and the rate at which it is reached (e.g., Pilling, Kirkwood, & Walker, 2002). However, growth processes are controlled by both intrinsic (individual-specific) and extrinsic (environment-specific) factors affecting the accessibility and allocation of necessary resources. In particular, resources acquired by an individual are distributed between basal metabolism, structural growth and reproduction (Enberg et al., 2012), which means growth rates are directly dependent on multiple processes fluctuating throughout an individual's life. Methods relying solely on population data such as age-length keys may therefore only represent the "final" state of fish individuals and fail to capture the importance of inter- and intra-individual variability in growth trajectories. Linking individual growth histories from different cohorts can instead provide a better understanding of the different sources of growth variation and aid in interpreting historical growth patterns. Individual growth patterns can then be applied to population-level questions through biochronological reconstructions. Such growth chronologies based on calcified tissues have been successfully developed for both bivalves and fish, and show promising potential to study long-term, ecologically relevant data at fine-scale resolution (Morrongiello, Thresher, & Smith, 2012). Incremental growth of these hard structures is typically closely related to somatic growth (Black et al., 2019; Doubleday et al., 2015) and often identifiable at fixed temporal scales (i.e., daily, seasonal or yearly), thus providing continuous time-resolved growth histories of individuals and populations (Black, von Biela, Zimmerman, & Brown, 2013; Morrongiello, Crook, King, Ramsey, & Brown, 2011).

In particular, large numbers of fish otoliths are collected worldwide every year (Campana, 2001), making it a widespread and easily accessible resource for developing long-term individual-based growth chronologies across a wide range of environments and fish taxa (Morrongiello et al., 2012). Otolith-derived biochronologies have been developed in diverse contexts, with a strong focus on the influence of climatic factors on growth. For example, classical detrending approaches directly derived from tree rings analysis (dendrochronology) have been successfully applied to fish studies to reconstruct population-level variability in growth based on otolith increment widths (Black et al., 2013; Matta, Black, & Wilderbuer, 2010; Ong et al., 2018). However, more modern statistical approaches such as mixed-effect modeling allow for in-depth investigation of how fish growth varies in response to different factors (Weisberg, Spangler, & Richmond, 2010). A key advantage of mixed-effects models is that they do not detrend or standardize growth time series to maximize relationships at the population level. Rather, they partition and investigate both biological and environmental effects simultaneously by utilizing all available biological information and accounting for the hierarchical structure of the data within individuals, years and cohort (year-classes, i.e., year of hatching; Morrongiello & Thresher, 2015). This provides a broader and more comprehensive understanding of how fish respond to particular factors of interest, as well as being more appropriate for the study of species where growth variations might be subject to high inter-individual variability (Black et al., 2019).

The Barents Sea is a highly productive shallow area situated to the north of Norway, bordering the Norwegian Sea to the west and the Arctic Ocean to the north (Jakobsen & Ozhigin, 2011). Described as the "Arctic warming hotspot" (Lind, Ingvaldsen, & Furevik, 2018), this region at the interface between the Atlantic and the Arctic is an ideal system to study the effects of global warming on ecosystems due to its fast changing hydrography. It is also home to one of the largest populations of the commercially important Atlantic cod (*Gadus morhua*; ICES, 2018), the Northeast Arctic (NEA) cod, a large migratory population with a long history of human exploitation. NEA cod lives and feeds in the Barents Sea, where it is considered an apex predator with an essential role in the food-web dynamics, notably through its high predation on small pelagic fish such as capelin (Holt, Bogstad, Durant, Dolgov, & Ottersen, 2019). Every winter it migrates southward to spawn around the Lofoten archipelago (Höffle et al., 2014), where the main fishery has also historically taken place (Sundby & Nakken, 2008). Spawning has recently been taking place north of the traditional area along the north-western Norwegian coast, suggesting a possible reaction to changes in the environment and demography (Opdal & Jørgensen, 2015). Multiple studies have highlighted the significant influence of environmental changes and exploitation on the biology and demography of cod across the North Atlantic (e.g., Brander, 2000; Eero, MacKenzie, Köster, & Gislason, 2011; Mieszkowska, Genner, Hawkins, & Sims, 2009). NEA cod is therefore a particularly attractive population to study the long-term impacts of climate change and exploitation, especially in light of the multiple collapses that occurred in the western Atlantic cod stocks since the 1990s (Bavington, 2011; Pershing et al., 2015).

In this study, we used a large archive of otoliths collected from commercial catches and scientific surveys to develop a near century-long biochronology for the NEA cod. Using a hierarchical mixed-effects modeling approach, we related the observed growth variability to selected climatic, demographic and fishing factors which have been considered to have an important influence on cod growth. We hypothesized that warming conditions and increasing prey availability likely had a positive influence on cod growth. We also hypothesized that fishing can selectively remove either fast or slow growing fish from a population (Enberg et al., 2012; Sinclair, Swain, & Hanson, 2002) but also alter density-dependent processes that, in turn, influence growth (Lorenzen & Enberg, 2002). We then applied path analysis to test hypothesized causality between the different factors tested within the growth modeling and identify their respective direct and indirect effects on cod growth. The results provide a long-term and integrated perspective on the different factors that have influenced NEA cod growth during the 20th and beginning of the 21st centuries.

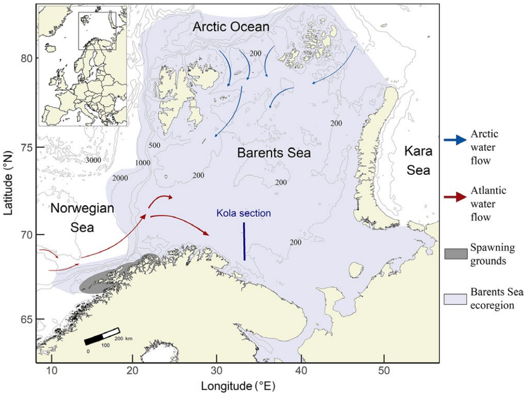

FIGURE 1 Map of Northeast Atlantic area and Barents Sea ecoregion. Arrows represent the main circulation of water masses. Dark grey area represents the main Northeast Arctic cod spawning grounds along the Norwegian coast. Blue line represents the Kola transect of temperature measurements. Top left insert shows the location of the study area [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Sample selection

An extensive archive of cod otoliths exists at the Institute of Marine Research in Bergen (Norway), where about one million Atlantic cod otoliths from both research surveys and commercial fishing have been archived since 1920. Age readers have routinely aged cod from otoliths since 1932, and location, date, fishing gear and biological information (length, weight and sex) has been collected for most of the fish. For this study, sagittal otoliths of adult fish were randomly selected for each year between 1933 and 2015. Following the multiple cohort approach advocated by Morrongiello et al. (2012), these subsamples consisted, whenever possible, of 50 fish per year. Sampling of overlapping cohorts can better capture the range of growth phenotypes as well as within-population variations. Sample selection was limited to fish caught by bottom trawl, longline and seine, to avoid selectivity bias toward bigger, faster-growing fish in gillnet catches. To sample otoliths from sexually mature individuals only, our selection was limited to fish collected from the Lofoten spawning grounds and consisted of a mixture of survey and fishery-caught fish (Figure 1). Mean age-at-maturity has decreased from 10.8 to 6.1 since 1920 due to fishing selectivity (Jørgensen, 1990; Nash, Pilling, Kell, Schön, & Kjesbu, 2010), and as a result the archive for the recent decades comprises relatively few fish older than 9. Conversely, the archive for the earliest decades has fewer samples available from fish caught during the spawning season, which limited the age classes available for collection of a reasonable sample depth. We consequently collected mainly fish of age 8 or older to provide enough samples of mature fish in the more recent decades while trying to minimize the effects of faster growth and maturation in the earlier period. The resulting growth chronology was nonetheless potentially biased toward earlier maturing fish and faster juvenile growth for the earlier years. Due to the limited availability of older fish in 1988, 1990, 1991 and 1996, some samples of age 7 were included (respectively 22, 2, 1 and 15 otoliths). A total of 4,096 fish of age 7–21 were retrieved, of which 3,023 were age 8.

2.2 | Otolith processing and measurement

Otoliths were embedded in black epoxy (NM Laminering 275, Nils Malmgren AB with NM Svart Pasta pigment paste) to enhance contrast around the edges. They were sectioned transversely (~800 μm thickness) through the core, which was identified during embedding by a distinctive narrow and hourglass-shaped depression near the sulcus, on the proximal surface of the otolith. Images of the sectioned otoliths were digitalized using a high-resolution (5,616 × 3,744 pixels) mounted DSLR system comprising a Canon EOS 5D Mark II body and a Canon MP-E 65 mm f/2.8 1–5× lens. The imaging process was standardized at 3× magnification, 1/50 s exposure, f/6.3 and ISO 100 to ensure consistency in the captured pictures. The otolith images were then enhanced in Adobe Photoshop CC 2019 using a standardized macro that converted them to greyscale to remove color aberrations, adjusted levels/brightness/contrast to enhance the transition between opaque and translucent zones and added a sharpening mask to increase clarity and readability.

An open-access, dedicated set of ObjectJ macros was developed for the software ImageJ (Schneider, Rasband, & Eliceiri, 2012) to annotate the otolith sections following a standardized workflow (Supporting Information B). Otolith radius is often linearly correlated with fish total length (Francis, 1990; Harvey, Loughlin, Perez, & Oxman, 2000), and a strong relation between otolith and fish growth has been experimentally confirmed in Atlantic cod (Hüssy & Mosegaard, 2004; Li et al., 2008). Changes in increment widths can therefore be used directly as a proxy for changes in somatic growth (Campana, 1990). Because our study used mostly fish of age 8 and older, we verified this relationship by including a wider range of age and length classes from Høie et al. (2009) in the correlation analysis (Figure S2).

Northeast Arctic cod form an annual otolith growth increment comprising a translucent zone formed from December to April and an opaque zone formed from May to November (Høie et al., 2009), and increment growth can thus be used as a proxy for annual somatic growth. Increments widths (µm) were measured on the distal side of the otolith along a single linear axis. Because the quality of the core was variable depending on the precision of the sectioning, we marked the largest diameter of the first increment and defined our measurement axis as the line in the distal direction that intersected perpendicularly the maximum number of increments from the otolith edge to the intersection with the drawn diameter (Figure 2). Each increment width was assigned to a year of formation by counting back from date of capture and accounting for marginal increment interpretation. These measurements then provided subsequent estimates of annual growth, yearly age, age-at-capture and year-class for each individual. One otolith from each pair had previously been broken for age estimation by experienced otolith readers, and the age provided was consequently used as verification. The high agreement (95.76%) and low coefficient of variation (3.70%) between both readings indicated no important differences between age estimates of sectioned and previously broken otoliths. Age-bias cross-tabulation (Table S1) and plot (Figure S4) indicated that most of the discrepancies were mainly associated with a difference of 1 year (positive or negative). Measurements from aberrant, crystalline or damaged otolith sections were removed from the analysis. Additionally, otoliths from fish older than 12 were removed after initial model exploration, as the scarcity of data points for these age classes created convergence issues during modeling. A total of 3,894 samples were consequently retained in the final analysis (Figure S1). Finally, both the core (growth between hatching and first winter ring) and the marginal (residual growth between last winter ring and outer edge) increments were excluded from the analysis as they did not comprise a whole year of growth. In total, the measurements of 28,504 increments ranging from age 2 to 12 were included in the analysis (Figure S3).

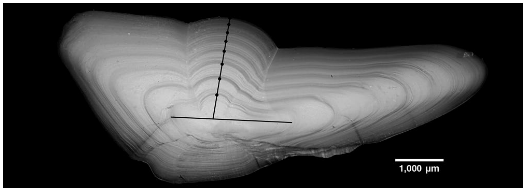

FIGURE 2 Cod (*Gadus morhua*) otolith transverse section of an 8-year-old male caught in 1956, viewed under reflected light. The vertical line identifies the axis along which age was estimated from its intersection with the core radius (horizontal line), and the points identify where increments were annotated and measured

2.3 | Growth factors

Possible sources of inter-annual growth variation were identified and selected for analysis (Table 1). Intrinsic variables representing individual-specific factors included Age (to account for age-related trends in growth) and Sex (to account for possible sex-specific variability in growth rates), as well as an interaction (Age × Sex). Furthermore, Year (calendar year of increment formation) and Cohort (year-class) were included to investigate inter-annual and between year-class growth differences.

Extrinsic variables were then included to investigate the influence of the environment on cod growth. Since temperature is known as one of the most significant factors influencing fish growth due to its effects on metabolism and prey availability (Brander, 1995; Michalsen, Ottersen, & Nakken, 1998), we first included the yearly Barents Sea average temperatures of the 0–200 m layer, represented by the Kola section in situ records (KolaT) provided by the Russian Polar Research Institute of Marine Fisheries and Oceanography (PINRO; Bochkov, 1982; Tereshchenko, 1996). Additionally, two large-scale hydro-climatological indices were included: the winter North Atlantic Oscillation (NAO) calculated as the standardized NAO from December to March (Hurrell, 1995), and the Atlantic Multidecadal Oscillation (AMO; Enfield, Mestas-Nuñez, & Trimble, 2001; Kerr, 2000). Both indices are derived from temperature anomalies but usually reflect larger changes in the hydrology, the circulation and the distribution of the water masses of the North Atlantic, which have been shown to cause large-scale fluctuations in many fish populations including cod, affecting for example spatial distribution, prey availability or recruitment (Alheit et al., 2014; Drinkwater et al., 2003; Stige, Ottersen, Brander, Chan, & Stenseth, 2006). Given the temporal range covered by our chronology, the AMO index could additionally provide insights on the response of cod growth to lower frequency changes (20–40 years) in the environmental conditions.

TABLE 1 Description of variables used in the mixed effect and structural equation modeling

Parameter	Description	Mixed-effects model^a	Structural equation model	Data range
Increment	Width of increment (µm)	Response	+	
FishID	Unique identifier of fish individual	R		
Year	Calendar year of otolith growth increment formation	R	+	
Cohort	Year-class of fish born in the same spawning year	R		
Age	Age of fish when increment was formed	R, F		
Sex	Sex of individual fish	F		
KolaT	Mean sea temperature of the Kola section 0–200 m layer (°C)	F	+	1924–2014
AMO	Mean Atlantic Multi-decadal Oscillation index	F	+	1924–2014
NAO	Mean winter North Atlantic Oscillation index (Dec-Mar)	F	+	1924–2014
Stock	Total cod biomass age 3+ (10^3 tons)	F	+	1924–1945^b 1946–2014^b
Fbar5.10	Average cod fishing mortality from ages 5 to 10	F	+	1946–2014
Cap_ts	Total capelin biomass age 1+ (10^3 tons)	F	+	1973–2014
Her_ts	Total young herring biomass age 1–2 (10^3 tons)		+	1973–2014

[a] Designates whether the predictor was used as a random (R) or a fixed (F) effect in the mixed-effect modeling.

[b] For cod biomass, two time series were available: 1946–2014 from official ICES estimates and 1924–1945 from the reconstructed time series by Hylen (2002).

Total NEA cod (Stock) and capelin (Cap_ts) biomass obtained from the International Council for the Exploration of the Sea (ICES) Working Group for Arctic Fisheries (ICES, 2018) were included to investigate the effects of intra-specific competition and prey availability on cod growth. Finally, fishing mortality (Fbar5.10) time series obtained from ICES (2018) were included to investigate the potential influence of fishing pressure on individual growth, either due to the selective removal of specific individual growth trajectories or due to release of density-dependent pressures.

2.4 | Statistical analysis

Hierarchical linear mixed-effects modeling (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) was used to model increment width (Increment) in relation to the selected factors. This approach helps partition different sources of variability while taking into consideration repeated measurements within individuals (Morrongiello & Thresher, 2015; Weisberg et al., 2010). Prior to analysis, increment width (referred as growth in the manuscript) and Age were log transformed to linearize the relationship and meet model assumptions. All intrinsic and extrinsic factors were mean-centered to aid model convergence and interpretation (Morrongiello & Thresher, 2015; Morrongiello et al., 2014). Models with random intercept and age slope for each individual (FishID) were tested to allow individual-specific growth trajectories. These models were then extended to incorporate the effects of sex (intrinsic fixed effect), calendar year of formation and cohort (random effects), and the effects of both climatic and population variables (extrinsic fixed effects). The most complex model can be represented by:

$$y_{ijkl} = \left(\alpha_0 + \alpha_i^F + \alpha_k^Y + \alpha_l^C\right) + \left(\beta_0 + \beta_{ij}^F + \beta_{jk}^Y + \beta_{jl}^C\right) x_{ijkl} + f(\cdot) + \varepsilon_{ijkl},$$

$$\begin{bmatrix} \alpha_i^F \\ \beta_{ij}^F \end{bmatrix} \sim N(0,\ \Sigma_i), \begin{bmatrix} \alpha_k^Y \\ \beta_{jk}^Y \end{bmatrix} \sim N(0,\ \Sigma_k), \begin{bmatrix} \alpha_l^C \\ \beta_{jl}^C \end{bmatrix} \sim N\left(0,\ \Sigma_l\right), \varepsilon_{ijkl} \sim N(0,\ \sigma^2),$$

where y_{ijkl} is the increment width relative to age at formation (x_{ijkl}) for the ith fish at age j from year k and cohort l; α_0 and β_0 are the fixed mean intercept and slope describing population-wide decline in increment width in relation to age; α_i^F and β_{ij}^F are the fish-specific random intercept and slope describing individual growth trajectories in relation to age; α_k^Y and β_{jk}^Y are the year-specific random intercept and slope in relation to age; α_l^C and β_{jl}^C are the cohort-specific random intercept and slope in relation to age; and $f(\cdot)$ represents additional fixed factors (e.g., intrinsic factor sex, and extrinsic factors described in Section 2.3).

2.4.1 | Base model and intrinsic sources of growth variation

Initially, different random effects were tested in combination to optimize the random structure of the base model (Table S2). Random intercepts for individual fish (FishID), year of increment formation (Year) and fish year-class (Cohort) were tested to control for correlations among growth increments within individual fish, year or cohort. Random by-FishID, by-Year and by-Cohort slopes for the Age effect were also examined to test for differences in age-dependent growth trajectories among individuals, years and year-classes. Models were fitted to the entire growth time series from 1924 to 2014 (n = 28,504 increments, 3,894 FishID) with the full intrinsic fixed-effect structure (Age × Sex) and restricted maximum likelihood estimation (REML; Morrongiello & Thresher, 2015; Zuur et al., 2009). Models were ranked using Akaike's information criterion corrected for small sample sizes (AICc) and the optimal model was selected (Burnham & Anderson, 2004). If the difference in AICc (ΔAICc) between the highest and a second highest ranked model was <2, the two were considered to be equally supported (Burnham & Anderson, 2004).

To explore the optimal intrinsic fixed-effect structure, combinations of Age, Sex and Age × Sex interaction were fitted with the maximum likelihood (ML) method with the previously selected random structure and compared using AICc (Table S3). The optimal model was then refitted with REML to obtain unbiased estimates (Zuur et al., 2009). For each model, the marginal (variance explained by intrinsic effects alone) and conditional (variance explained by both intrinsic and extrinsic effects) R^2 metrics were calculated (Nakagawa & Schielzeth, 2013). Growth synchrony between individuals from a given year or a given year-class was estimated by calculating the intra-class correlation coefficients (ICC) for optimal Year-only and Cohort-only models. These coefficients estimated the correlation of fish growth within years and year-classes by measuring the relative similarity as proportions (Koch, 2006).

The master growth chronology was developed by extracting the best linear unbiased predictor (BLUP) for the Year random effect from an optimal intrinsic-only model to visualize mean inter-annual variations in growth at the population level (Morrongiello & Thresher, 2015). This Year random effect essentially represents the yearly variation in growth which can be associated with the extrinsic environmental factors, after accounting for age and sex effects. BLUP for the Year random effect was compared with mean size-at-age and growth rates derived from survey data from 1981 to 2014 (ICES, 2018). A sequential t test analysis (STARS) was applied to the extracted chronology to identify significant shifts in mean population growth. This method provides an estimation of statistically significant changes in the mean level and magnitude of fluctuation in a time series and their probability (Lindegren, Diekmann, & Möllmann, 2010; Rodionov, 2004, 2006). The cut-off length (i.e., the minimum length of a shift for which its magnitude remains intact) was set to 5 years with a significance level to .05 so that shifts in cod growth were identified only when the shift lasted at least 5 years. "Prewhitening," a process that eliminates or reduces short-term autocorrelation to enable the detection of trend changes, was implemented prior to the sequential t test analysis to remove the red noise component of the growth time series (Rodionov, 2006; Smoliński & Mirny, 2017).

2.4.2 | Influence of extrinsic factors on cod growth

External factors influencing fish growth were assessed through a series of model comparisons by adding potential extrinsic factors to the best intrinsic structure previously selected. First, the influence of environmental conditions on annual growth was investigated by fitting combinations of sea temperature (KolaT), NAO and AMO index to the entire growth time series from 1924 to 2014 (n = 28,504 increments, 3,894 FishID; Table S4a). Second, the effects of cod biomass (Stock), capelin biomass (Cap_ts) and fishing mortality (Fbar5.10) were evaluated by comparisons of optimal growth models refitted to a more limited time period, from 1973 to 2014, due to the temporal limitations of the capelin and fishing mortality time series (n = 12,171 increments, 1,837 FishID; Table S4b). Finally, global extrinsic models incorporating combinations of both environmental, population and fishing factors were refitted to data from 1973 to 2014 (n = 12,171 increments, 1,837 FishID; Table S4c) and compared to investigate the influence of all extrinsic factors on cod growth. Potential collinearity between explanatory variables in the final models was investigated by calculating their variance inflation factors (VIF), with a more conservative threshold defined at VIF < 2 (Borcard, Gillet, & Legendre, 2018). Assumptions of normality and homoscedasticity were evaluated visually by inspecting model residuals. Linear trends in mean growth over the years and age-dependent effects of extrinsic variables on growth were also explored but were found to be negligible and are therefore not presented.

2.4.3 | Mechanistic modeling of cod growth and extrinsic factors

To unravel simultaneous direct and indirect effects of environmental factors on growth and their potential interactions, a structural equation model (SEM) was developed using the BLUP for the Year random effect refitted from the optimal intrinsic-only model to represent the pooled growth variation over time at the population level. Confirmatory path analysis based on the piecewise fitting of component hierarchical models was conducted to model hypothesized causal relationships between climate, population dynamics and fish growth (Lefcheck, 2016; Shipley, 2009). It was first hypothesized that capelin biomass could be modeled in response to changes in temperature and larger climatic modes (NAO and AMO) known to affect recruitment success. Additionally, because strong herring year-classes have been linked to capelin recruitment failure (Hallfredsson & Pedersen, 2009; Hjermann et al., 2010), juvenile Norwegian spring-spawning (NSS) herring biomass time series obtained from ICES (2018) were included as a factor of capelin biomass. Cod biomass was also modeled in response to these same environmental factors, as well as to fishing mortality to account for the significant effect of human exploitation on population size. Finally, population-level cod growth was modeled as a response to population, climate and fishing factors together. Predator–prey interactions were also tested by sequentially fitting the SEM with a bottom-up (cod biomass depends on capelin biomass variability) or a top-down (capelin biomass depends on cod biomass variability) control and comparing fit. During model optimization, non-significant relationships were removed, and missing pathways identified by the analysis were considered. If a missing relationship was significant, was biologically realistic and generated a lower AIC score when included, it was added to the models and the SEM was further optimized. Goodness-of-fit of the final optimized SEM was evaluated using a chi-square test on the Fischer's C statistic, wherein lack of significance ($p > .05$) indicated an overall good fit to the data. In addition, individual R^2 were calculated to measure the variation explained by each component model within the SEM. Finally, SEM estimates for all significant pathways were reported and used to compare the direction and strength of direct and indirect effects between tested variables, where indirect effects were described as one variable affecting another through a simultaneous response of a third.

All analyses were conducted using the R scientific computing language (R Core Team, 2019) with the packages *tidyverse* (Wickham, 2017), *AICcmodavg* (Mazerolle, 2019) and *MuMIn* (Bartoń, 2019). Linear mixed-effect modeling was performed using the *lme4* (Bates, Mächler, Bolker, & Walker, 2015) and *effects* (Fox, 2003; Fox & Weisberg, 2018, 2019) packages. SEM was developed using the package *piecewiseSEM* (Lefcheck, 2016) and the result flowcharts were constructed using *DiagrammeR* (Iannone, 2019).

3 | RESULTS

3.1 | Temporal variations in growth

The 28,504 increments used in the analysis resulted in a 91-year long biochronology spanning 1924–2014 (Figure 3a). The consistent sampling of around 50 mature individuals per year allowed a large overlap in growth measurements, and multiple age classes associated with the different life stages were consequently represented in every year across most of the time series (Figure 3b). As commonly found in fish otoliths, increment width declined significantly with age, indicating that growth was age-dependent (Figure 4a).

The growth time series extracted from the BLUP for the Year random effect showed significant interannual variation of NEA cod population growth (Figure 5a). Periods of peak growth were seen in 1937, 1969, 1985, 1990 and 2000, while periods of lowest growth were observed in 1942, 1948, 1987, 1993 and 2010. The STARS analysis conducted on the BLUP for the Year random effect identified onsets of sharp declines in growth in 1941, 1993 and 2010 (Regime Shift Index = −0.53, −1.20 and −1.09), and positive shifts in 1957 and 1999 (Regime Shift Index = 0.15 and 0.96). The cohort-specific growth time series (BLUP for the Cohort random effect) also showed significant interannual variability and shifts throughout the time period (Figure 5d). However, cohorts with higher than average growth were usually evident during years of significantly poorer growth. Both the temporal growth synchrony across individuals over the same year or within a cohort was generally low, based on the calculated ICC for Year (0.046) and Cohort (0.019). Population-level growth variation extracted from the BLUP for the Year random effect showed similar trends to survey age-length keys and was correlated to the mean size-at-age (Figure S5) and growth rates (Figure S6) time series derived from survey data (1981–2014).

3.2 | Intrinsic sources of growth variation

Age had the greatest influence on growth among the tested variables, with predicted increment widths strongly declining as fish

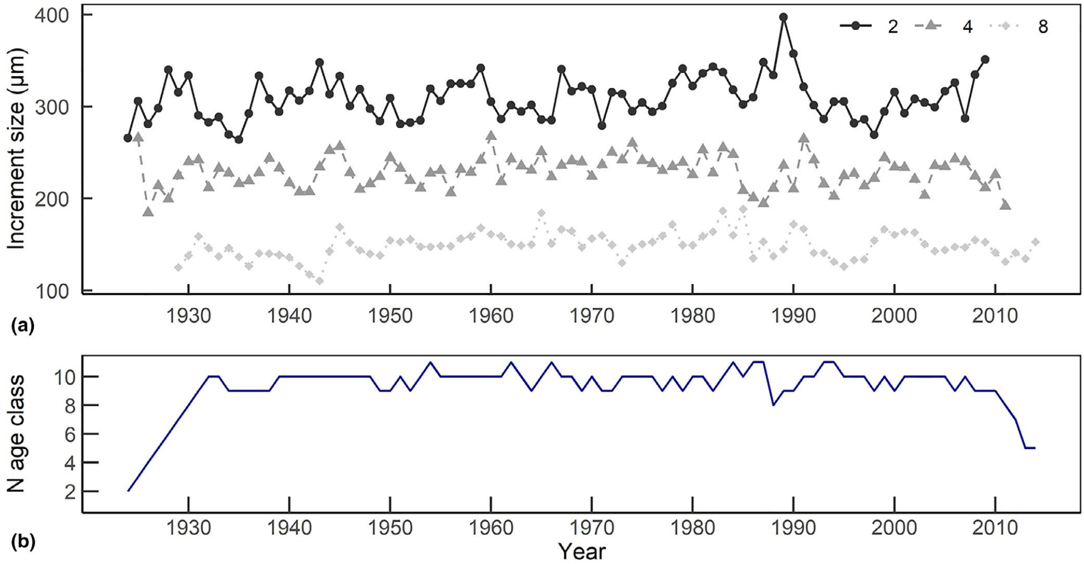

FIGURE 3 Unfiltered time series of mean increment widths for ages 2, 4 and 8 (a); number of distinct age classes represented across all increments for each year (b) [Colour figure can be viewed at wileyonlinelibrary.com]

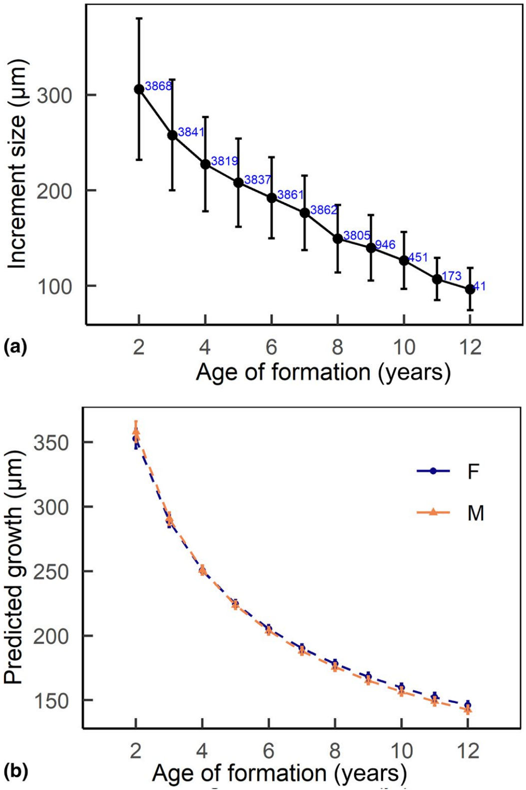

FIGURE 4 Differences in the observed and predicted increment widths in relation to age. Observed mean increment widths (with *SD*) relative to age of formation (a). Values in blue indicate the total number of increments representing each age class in the chronology. Model predicted mean increment widths (with 95% CI) in relation to age and sex (b) [Colour figure can be viewed at wileyonlinelibrary.com]

aged (Table 2). A significant Age × Sex interaction showed that males older than 6 years old grew slightly slower than females, which corresponds to the onset of maturity (Figure 4b). Calculated AICc values for the different model random structures indicated the strongest support for the incorporation of a random intercept and Age slope for FishID and Year, and a random intercept for Cohort (Table S2). The optimal intrinsic fixed-effect structure consisted of Age in interaction with Sex (Table S3). The associated conditional R^2 (.66) indicated that intrinsic and random factors together explained around 66% of the observed variance in cod growth.

3.3 | Influence of extrinsic factors on cod growth

The inclusion of climatic factors (temperature, NAO and AMO indices) to the optimal base model fitted to data from 1924 to 2014 revealed significant effects on growth. Model predictions revealed that growth was positively correlated with temperature and weakly correlated with NAO, while AMO had a significant negative effect on cod growth (Table S5). Comparisons of AICc showed the strongest support for models incorporating temperature, and the optimal identified model incorporated both temperature and AMO index (Table S4a). Because there was similar strong support for the model including all three factors (ΔAICc < 2), it was used to estimate the predicted effects on growth. Second, the addition of population factors (cod and capelin biomass) and fishing mortality to the optimal base model refitted to data from 1973 to 2014 significantly improved model fit and revealed significant relationships to growth (Table S4b). In models restricted to population factors for the period 1973–2014, both cod biomass and fishing mortality had a significant negative influence on growth, while capelin biomass had a positive effect (Table S6).

Finally, all factors (climatic, demographic and fishing) were added together to the optimal base model refitted to data from 1973 to 2014. Model predictions revealed a strong negative influence of cod biomass on growth, as well as a positive influence of capelin biomass (Table 2; Figure 6a–c). Growth was also positively correlated with temperature but negatively correlated with AMO (Table 2; Figure 6d,e). Within the ranges of the environmental variables experienced by fish individuals, the predicted change in growth associated with variations of cod biomass was the strongest with a decrease of −21.78% (Table 3). Variability of the AMO was also associated with a significant decrease in growth (−7.20%). Increased growth was associated with variations of temperature (8.48%) and capelin biomass (4.67%). Comparison of AICc showed the best fit for the model comprising all factors except fishing mortality and NAO (Table S4c). However, the inclusion of fishing mortality had a similar statistical support and the variable was significant in the models previously refitted without climatic factors (Table S4b). Fishing mortality was consequently retained in the final model, where we found a significant but weak negative influence on growth (−2.78%; Table 2; Figure 6a–c). The associated marginal R^2 (.48), the proportion of variance explained by fixed effects alone, indicated that the inclusion of environmental variables explained more of the growth variance than the intrinsic-only model (.45) refitted to the same period (Table S3).

3.4 | Mechanistic modeling of cod growth and extrinsic factors

Structural equation models built with a bottom-up or a top-down relationship between cod and capelin biomasses had similar final optimized structures, although the latter did not support the inclusion of temperature as a factor influencing capelin biomass. Comparison of model fit yielded a stronger support for a bottom-up control (AICc = 41.67 for bottom-up and AICc = 50.55 for top-down) and this model structure was consequently chosen as the optimal SEM ($\chi^2 = 17.67$; $p = .13$).

Both temperature and herring biomass had a significant influence on capelin biomass (respectively, positive and negative;

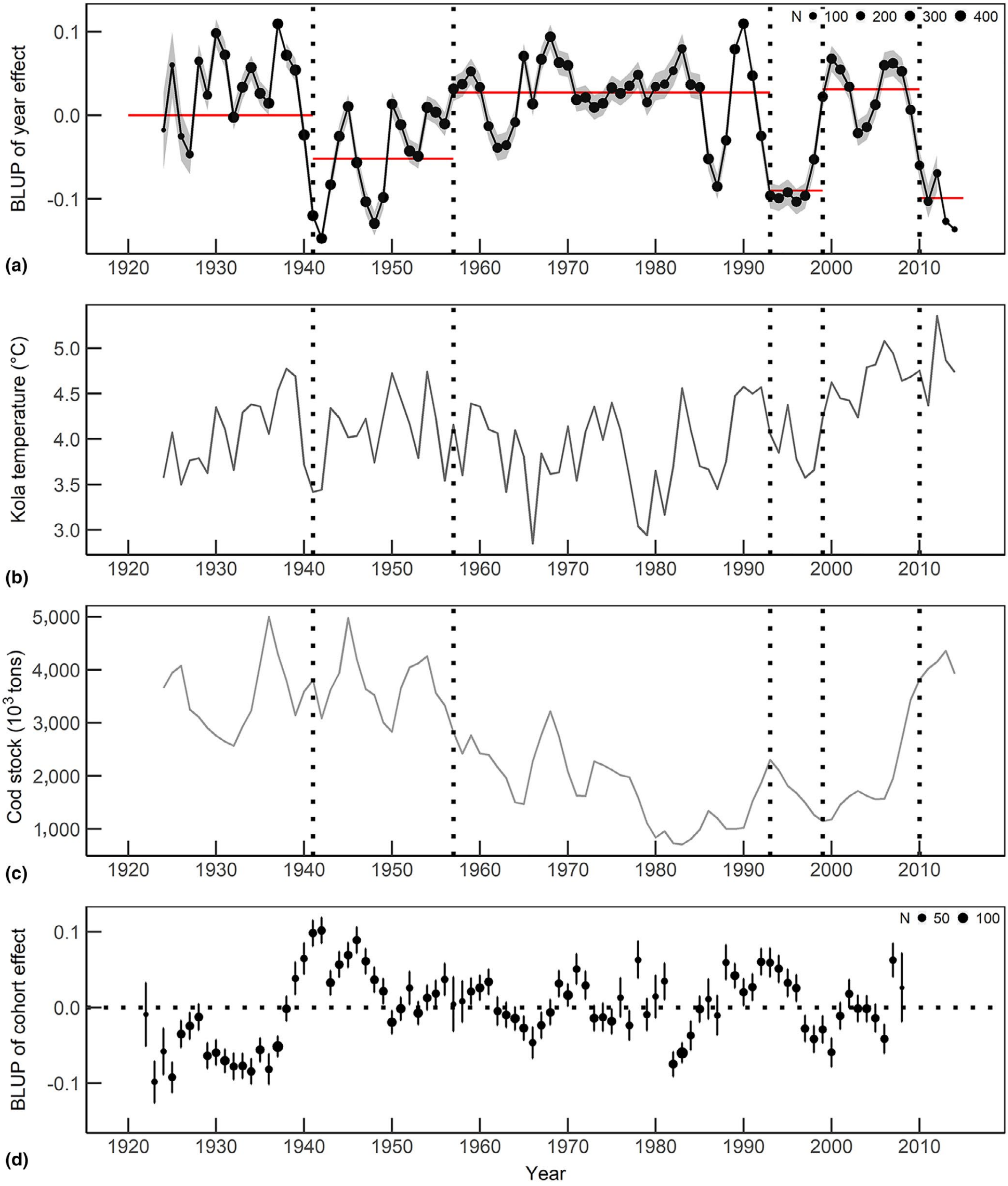

FIGURE 5 Best linear unbiased predictor (BLUP) for the Year random effect (a), mean sea temperature of the 0–200 m layer of the Kola section (b), cod stock (c) time-series, and BLUP for the Cohort random effect (d) between 1924 and 2014. Standard errors are indicated by the grey shaded area (a) and the error bars (d). Significant shifts in yearly population growth detected by sequential *t* test analysis on the BLUP for Year random effect are shown as vertical dotted lines, with mean growth deviation associated to each period as horizontal thin red lines in (a) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Parameter estimates of random (a) and fixed (b and c) effects for the final optimal growth model (M7d) fitted to data from 1973 to 2014 (12,171 increments, 1,837 FishID). Random age slopes are denoted by "|". Age, cod and capelin biomass are log-transformed in the model

(a)		
Random effects	**Variance (±*SD*)**	**Correlation**
FishID	0.007 (0.084)	
Age|FishID	0.020 (0.142)	.22
Year	0.001 (0.034)	
Age|Year	0.007 (0.085)	.66
Cohort	0.010 (0.101)	
Residuals	0.040 (0.201)	
(b)		
Intrinsic effects	**Estimate (*SE*)**	***t* value**
Intercept	5.275 (0.017)	315.16
Age	−0.487 (0.016)	−31.01
Sex (male)	−0.003 (0.006)	−0.51
Age:Sex (male)	−0.026 (0.011)	−2.40
(c)		
Extrinsic effects	**Estimate (*SE*)**	***t* value**
KolaT	0.032 (0.015)	2.18
AMO	−0.093 (0.042)	−2.24
Stock	−0.127 (0.024)	−5.39
Cap_ts	0.011 (0.006)	1.68
Fbar5.10	−0.035 (0.050)	−0.69
R^2 marginal	.48	
R^2 conditional	.68	

standardized coefficients = 0.33 and −0.48), whereas cod biomass was strongly influenced by fishing mortality alone (standardized coefficient = −0.72; Figure 7). While the two climatic indices were not significant within the SEM, NAO tended to exert a negative influence on cod biomass (standardized coefficient = −0.22; $p = .079$), indicating that the relationship between the two factors was potentially relevant despite not being significant here. Cod growth at the population level was positively related to temperature and capelin biomass (standardized coefficients = 0.34 and 0.50), but cod biomass was the strongest factor and had a direct negative influence on growth (standardized coefficient = −0.77).

4 | DISCUSSION

We used an otolith-based approach to reconstruct a 91-year-long continuous and annually resolved growth history of the NEA cod population. After accounting for intrinsic effects such as the age-dependent decline in growth, we identified density dependence associated with cod population size as the strongest extrinsic factor influencing cod growth throughout the time period. Our analysis also highlighted significant variability in cod growth which was associated with fluctuations in prey availability, as well as with environmental changes at both the local (i.e., temperature) and large (i.e., AMO) scales. Potential negative effects of fishing mortality on cod growth were also identified, although the relationship was weak and hard to disentangle from density dependence.

The growth biochronology extracted from the BLUP for the Year random effect was successful in reconstructing population-level variations of NEA cod growth, as shown by the correlation with mean size-at-age and growth rate time series extractedacapelin biomass and cod growth within our models is in line with recent studies on the importance of capelin in the diet of NEA cod (Bogstad, Gjøsæter, Haug, & Lindstrøm, 2015). After the collapse of the NSS herring population at the end of the 1960s and the subsequent increase in capelin biomass (Lees, Pitois, Scott, Frid, & Mackinson, 2006), capelin

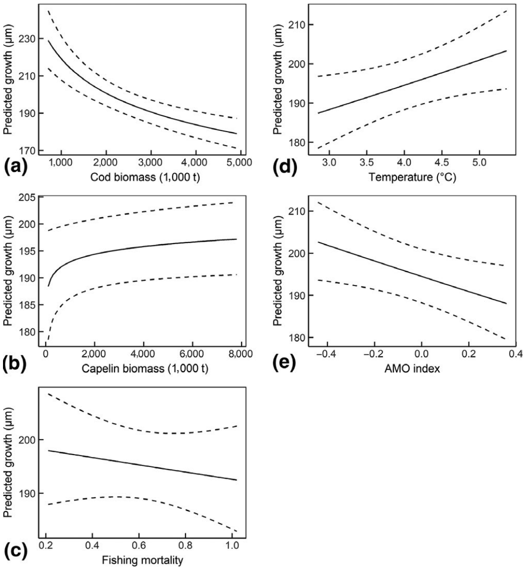

FIGURE 6 Predicted effects with 95% confidence interval of cod biomass (a), capelin biomass (b), fishing mortality (c), temperature (d) and Atlantic Multi-decadal Oscillation index (e) on cod growth

TABLE 3 Predicted percentage change in cod growth in relation to the selected extrinsic factors in the final optimal growth model

Extrinsic factor	Predictor range	Predicted effect (%)
Kola temperature	2.85–5.36°C	8.48
AMO	−0.44 to 0.36	−7.20
Cod biomass	707–4,999 $\times 10^3$ tons	−21.78
Capelin biomass	101–7,806 $\times 10^3$ tons	4.67
Fishing mortality	0.21–1.02	−2.78

Abbreviation: AMO, Atlantic Multi-decadal Oscillation.

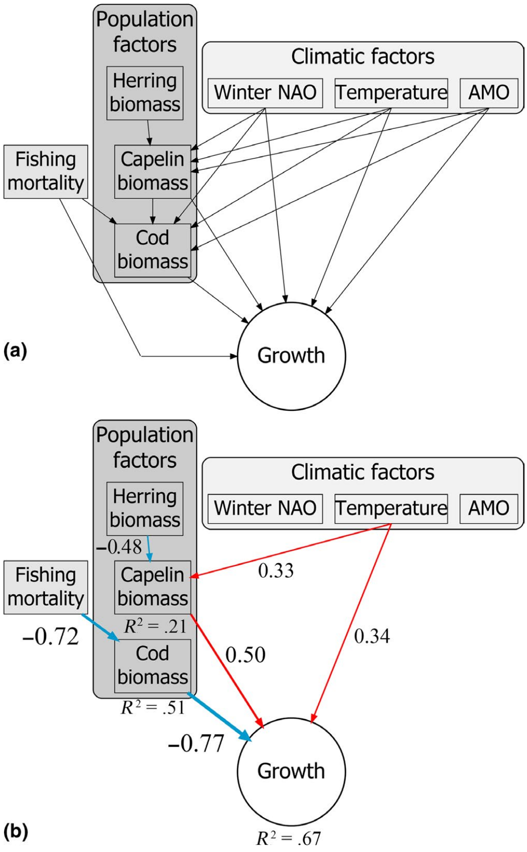

FIGURE 7 Structural equation models (SEMs) of climatic, population and fishing factors with Northeast Arctic cod growth extracted from the BLUP for the Year random effect. Hypothesized path diagram (a) and results of the final optimized SEM (b). Arrows represent the unidirectional relationships among factors and only significant paths ($p < .05$) are shown. Positive and negative influences with their associated standardized estimated coefficients are represented as red and blue arrows respectively, where the thickness of the path is scaled to the magnitude of the relationship. R^2 are indicated for the three factors modeled as response variables within the SEM. AMO, Atlantic Multi-decadal Oscillation [Colour figure can be viewed at wileyonlinelibrary.com]

has become an essential item in the diet of cod (Holt et al., 2019). The three capelin collapses that occurred in 1985, 1993 and 2003 (Gjøsæter, Bogstad, & Tjelmeland, 2009) may have negatively affected cod feeding, which is likely reflected in our chronology by sudden drops in cod growth during these periods. In addition, it has been hypothesized that particularly strong herring year-classes might be a key factor in capelin recruitment failure due to their predation on capelin larvae (Hallfredsson & Pedersen, 2009; Hjermann et al., 2010). Our study did not include herring biomass as a direct factor influencing cod growth but it was tested as a factor of capelin biomass within the SEM, where we found a strong and significant negative effect. It appears likely that large herring year-classes were partly responsible for capelin collapses, which, in turn, led to a lower prey availability and a significant decrease in cod growth. Furthermore, a collapse of the capelin population and a low herring biomass occurred simultaneously in the mid-1980s and resulted in a temporary shift in cod diet toward less-preferred prey such as Euphausiids and Hyperiids (Reid, Battle, Batten, & Brander, 2000). The abrupt decrease in cod growth we observed between 1985 and 1988 likely reflects the reduction in growth associated with this temporary sub-optimal diet, although the duration was too short to be identified as a significant shift in growth within the STARS analysis. In addition, cannibalism is known to occur in many cod populations and is especially prevalent in NEA cod (Bogstad, Lilly, Mehl, Palsson, & Stefánsson, 1994; Yaragina, Bogstad, & Kovalev, 2009). The observed variability in cod growth after 1980 could thus reflect changes in prey availability and cannibalism consistent with large fluctuations in capelin abundance (Eriksen, Skjoldal, Gjøsæter, & Primicerio, 2017; Gjøsæter et al., 2009; Holt et al., 2019). Density dependence would therefore be important even during the period of relatively lower cod biomass due to increased cannibalism and lack of alternative prey.

Temperature was the second strongest extrinsic factor identified in our study. Cod growth increased significantly with sea temperature in all of our models, which is in agreement with our initial hypothesis that it is positively influenced by warming conditions. Sea temperature is known to significantly influence fish growth and may correlate with growth rates through changes in direct (i.e., metabolism, individual fitness, duration of the growth season) or indirect (i.e., food availability) processes (Brander, 1995; Neuheimer & Grønkjær, 2012). Temperature signals in growth have already been identified in multiple otolith-based biochronologies, although the strength and direction vary between species and locations (Gillanders, Black, Meekan, & Morrison, 2012; Izzo et al., 2016; Martino et al., 2019). We are confident in the relationship found here since our analysis is based on the Kola section temperature time series, which has been shown to accurately represent temperature variability in the southwestern regions of the Barents Sea where Atlantic water masses are prevalent (Dippner & Ottersen, 2001). We also used in situ measurements averaged for the 0–200 m depth layer which constitutes a closer proxy of the environment experienced by a demersal species such as NEA cod than SST. Our temperature time series thus provides an accurate coverage of the areas where both the juvenile and adult cod life stages are found.

The positive relationship with temperature is also evident in the significantly higher growth observed in the earliest parts of the chronology. During the 1920s and 1930s, the North Atlantic underwent a significant warming that had important environmental and ecosystem effects (Drinkwater, 2006; Johannessen et al., 2004). The Barents Sea in particular showed a drastic increase in primary and secondary production, which likely created favorable conditions for fish growth (Drinkwater, 2006). This also coincided with high recruitment, high population size, and a northward expansion of the feeding and spawning grounds observed for NEA cod during the same period (Hylen, 2002; Sundby & Nakken, 2008). However, while our analysis indicates a positive correlation between growth and warming conditions, it must be noted that cod growth has decreased despite record warming of the Barents Sea in the most recent decade (Levitus, Matishov, Seidov, & Smolyar, 2009; Lind et al., 2018). The ongoing warming trend has been associated with significant changes in the ecosystems and the hydrography of the region (see e.g., Fossheim et al., 2015; Lind et al., 2018; Smedsrud et al., 2013), which could eventually affect the productivity of cod under the continued warming projected for the next decades (Stocker et al., 2014). The fast alteration of the Barents Sea conditions combined with the highest cod biomass recorded in more than 50 years could consequently explain the sharp decline in growth observed since 2008, although edge effects were likely in effect as these years only comprised fish from the same cohort and thus were represented by increasingly older individuals.

In addition to local changes in the environmental conditions, we identified significant shifts in cod growth which could be linked to large-scale changes in the Barents Sea, especially between 1993 and 1999. Significant shifts in fish population biomass and life history in the Northeast Atlantic have been historically correlated to large-scale climatic variations (Alheit et al., 2014; Hjermann, Stenseth, & Ottersen, 2004; Lehodey et al., 2006). The concept of regime shift has, in turn, grown out of a number of studies showing significant ecosystem-level changes during the late 1980s and the mid-1990s in the Northern Hemisphere (Auber, Travers-Trolet, Villanueva, & Ernande, 2015; Beaugrand et al., 2015; Reid, Borges, & Svendsen, 2001). The mid-1990s ecosystem shift in particular has been associated with a complex series of atmosphere–ocean changes characterized by a significant weakening of the NAO and a switch of the AMO from a cold to a warm phase (Alheit et al., 2019; Hughes, Holliday, & Gaillard, 2012; Robson, Sutton, Lohmann, Smith, & Palmer, 2012). Yet, despite periods of substantial alterations of both the climatic conditions and the abundances of several species during the last decades, no persistent ecological regime shift has been identified for the Barents Sea (Johannesen et al., 2012). Our model reveals that AMO had a strong negative influence on cod growth and that the abrupt decrease in growth rates between 1993 and 1999 correlates with the onset of its warmest phase. However, while AMO is defined as a detrended indicator of sea temperature anomalies (Kerr, 2000), its influence on the marine ecosystems seems to be primarily linked to large-scale changes in the strength and direction of the water masses circulating in the North Atlantic (Alheit et al., 2019). In particular, the dynamics of many small pelagic fishes vary significantly with the AMO phases, not directly due to the temperature anomalies but through complex changes in the coupled atmosphere–ocean system (Alheit et al., 2014). The significant negative relationship we found between AMO and cod growth, which contrasts with the positive influence of warming conditions discussed earlier, may thus be more representative of its indirect effect through large fluctuations in small pelagic fish assemblages and prey availability for NEA cod.

Finally, we found a significant but weak negative relationship between growth and fishing mortality. Fisheries-induced evolution is well studied and has been associated with changes in growth and maturity in many populations (Kuparinen & Merilä, 2007; Swain, Sinclair, & Mark Hanson, 2007), which makes growth signals an effective proxy to identify its presence in a given population. While the present relationship may indicate that multi-decadal fishing have caused a decline in cod growth through selective harvesting of faster-growing individuals (Enberg et al., 2012; Heino & Godø, 2002; Sinclair et al., 2002), the relationship was very limited and models that did not include fishing mortality had a similar statistical support. In contrast, it is possible that fishing mortality had an indirect positive influence on growth through its significant effect on cod biomass and consequently on density-dependent effects, as suggested by the optimized SEM. In the present study, it is therefore hard to disentangle the effects of fishing mortality and density dependence, and fisheries-induced effects on cod growth are ultimately difficult to interpret.

In addition to the interannual variability, our results showed cod growth variations at the year-class level, which indicate a persistent growth signal in fish born during the same spawning season. Cohort-specific growth variability is an important aspect of temporal variations in growth, as it likely reflects intrinsic differences in the systematic response to environmental conditions (Morrongiello & Thresher, 2015). This is often associated with carry-over effects (Murphy, Jenkins, Hamer, & Swearer, 2013) wherein the growth trajectory might be influenced by the early conditions, for example, individuals born in a particular year-class where environmental conditions were detrimental (or beneficial) for future growth. Our results showed that year-specific and cohort-specific growth extracted from the BLUP for each random effect were often negatively correlated, and cohorts born in years with poorer than average growth often displayed higher than average growth trajectories throughout their entire life. The two signals are not directly comparable: one represents the overall growth deviation from the population average pooled across all age-classes for a single year, the other the deviation from the population average in the entire growth trajectories of individuals born in a given year. However, this negative relationship could be the marker of some form of compensatory growth response, indicating that fish born in poor conditions grew faster following intervals of slow growth. Such compensatory growth is widespread in juvenile fish especially in an aquaculture context (e.g., Urbinati, Sarmiento, & Takahashi, 2014), and this response was shown to sometimes overshoot the “average” growth trajectory (Hayward, Noltie, & Wang, 1997). This hypothesis seems plausible for a near-arctic population of Atlantic cod, as Schultz, Lankford, and Conover (2002) showed that high-latitude populations in highly seasonal environments were prone to strong compensatory growth responses. It is however difficult to quantify this effect with precision without experimental data, especially as the growth synchrony within cohorts was ultimately minimal. Year-class strength can also have persistent effects on growth through competition for resources among same-age individuals (Amundsen, Knudsen, & Klemetsen, 2007). These results suggest that years with unfavorable conditions may have been correlated with weaker year-classes and therefore relaxed early-life competition, which is in line with the importance of density-dependent effects highlighted in our study.

The combination of mixed-effects models and SEM has only been used recently in fish studies (e.g., Taylor, Chinkin, & Meekan, 2020), yet it provides a powerful tool to investigate interrelated factors and their potential direct or indirect effects following a set of biologically sound hypotheses. In our study, the addition of SEM revealed significant pathways between growth and the investigated extrinsic factors but also between factors, which could not be revealed by the results of mixed-effect modeling alone. Warming conditions may influence cod growth both directly and indirectly through their positive effect on capelin biomass and consequently prey availability. Similarly, fluctuations in the cod population are largely driven by fishing mortality and increased fishing pressure may therefore indirectly profit growth by releasing density-dependent effects. However, while our modeling approach offers a robust method to investigate and quantify the influence of different factors on growth, there are some limitations to consider. Many factors are only annual or monthly proxies of the environmental conditions experienced at the individual scale and can seldom be correlated with individual-specific environmental exposure, which makes it difficult to properly account for inter-individual differences. It is also not always possible to include all the potentially important factors of NEA cod growth variability due to the scarcity of time series available at the relevant temporal or spatial scale. For example, finer-scale hydrographical data describing the complex and contrasting conditions of the Barents Sea and Lofoten spawning grounds could provide a more accurate description of the environment NEA cod experiences within years and between maturity stages. Similarly, the inclusion of time series for other important cod prey items such as Euphausiids (Holt et al., 2019) could better quantify the influence of diet and prey availability on growth at different life stages. In addition, many model-derived variables such as fishing pressure or stock biomass carry a non-negligible level of uncertainty as we progress back in the time series beyond the period covered by survey data, due to increased model assumptions.

The biological basis for the assumed proportionality between somatic and otolith growth is well accepted and has been experimentally verified (Hüssy & Mosegaard, 2004; Li et al., 2008; Yamamoto, Ueda, & Higashi, 1998). However, as shown in this study, this relationship can be more subtle due to inter-individual differences in otolith growth and mineralization rates that stem from different individual environmental and feeding conditions (Grønkjær, 2016). One advantage of the mixed modeling approach over traditional biochronology studies is that we partly controlled for this by including random FishID effects to account for this type of inter-individual variation (Morrongiello & Thresher, 2015; Weisberg et al., 2010). In the future, it would nonetheless be interesting to conduct experimental studies to quantify how these effects may influence sclerochronological reconstructions. Finally, the sampling strategy we adopted due to the uneven availability of older fish throughout the whole period means that our study could be biased toward earlier maturing, potentially faster growing individuals during the earliest parts of the growth chronology. This could have affected some of our results and more specifically the growth variation found during the earliest years. We nonetheless remain confident in our interpretations, as our hypotheses were based on relevant ecological knowledge of the NEA cod dynamics in the Barents Sea and our core results were focused on the period 1973–2014, where the available data and therefore our modeling approach were much more robust.

5 | CONCLUSION

Altogether, we provide evidence that NEA cod growth has responded to the joint effects of climate change, population dynamics and harvesting throughout the 20th and beginning of the 21st centuries. We found that density dependence had the strongest influence on cod growth, but that climatic factors also had important positive (temperature) or negative (AMO) effects. As a major diet component, capelin was also a strong factor of cod growth and we identified significant drops in growth likely associated with collapses of the Barents Sea capelin population. In addition, we demonstrated significant pathways between growth, climatic, population and fishing factors, illustrating how environmental predictors may be interrelated and exert their influence both directly and indirectly. Although recent studies using fossil samples collected from dig sites have evaluated the variability of cod growth over several centuries (NEA cod in Geffen et al., 2011; Icelandic cod in Ólafsdóttir, Pétursdóttir, Bárðarson, & Edvardsson, 2017), the present chronology constitutes one of the longest continuous and annually resolved biological time series available for Atlantic cod, as well as one of the most extensive otolith-derived fish biochronologies in the Northern hemisphere.

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CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

AUTHOR CONTRIBUTION

C.D., S.S., A.J.G. and S.E.C. conceived and designed the study with funding secured by S.E.C. C.D. collected and processed the samples then generated the data. C.D. conducted the statistical analysis and interpretation with additional input from S.S., A.J.G., J.A.G. and S.E.C. C.D. led the writing of the manuscript. All authors edited and provided critical contributions to drafts and gave final approval for publication.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare they have complied with ethical standards.

DATA AVAILABILITY STATEMENT

Fish data, otolith data and R scripts are available upon reasonable request from the authors. Fishing mortality and population data for cod, capelin and herring are available from the latest ICES report of the Arctic Fisheries Working Group. Records of Kola section temperature are publicly available at PINRO for the period 1951–2015, while the earlier period has restricted sharing agreements outside of the Institute of Marine Research. Winter NAO and AMO time series are publicly available at ClimateDataGuide from the National Centre for Atmospheric Research.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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ERRATUM

A century of fish growth in relation to climate change, population dynamics, exploitation
Côme Denechaud, Szymon Smoliński, Audrey J. Geffen, Jane A. Godiksen, and Steven E. Campana (2020)

In this article, the following text under the Discussion section was omitted in error from the published article:

"from survey data. Considering that otoliths collections often began far back in time, they could help produce accurate individual and population growth histories that extend well beyond the limited recent period covered by most surveys. In addition, growth chronologies modeled from otolith increments have the advantage of capturing the full growth history for every individual and therefore account for individual-specific variability in growth rates, as opposed to size-at-age data which only provides information on the sizes at capture.

Fish somatic and otolith growth is generally age-dependent (Campana, 1990; Lee, 1920) and this has been shown for different species in similar otolith-derived biochronologies (Doubleday et al., 2015; Izzo et al., 2016; Smoliński & Mirny, 2017). In this study, age was also, as expected, the strongest factor influencing growth of NEA cod, and growth decreased significantly as fish got older. We also highlighted small age-specific sexual differences in growth rates where males grew slightly slower than females as they got older. Because sexual differences in cod growth were small, this probably reflected the decrease in growth following sexual maturation since males tend to mature earlier and at a smaller size (Brander, 1994). Growth synchrony was higher across years, irrespective of age, than across cohorts (year-classes) but remained relatively low in both cases, which is a consistent pattern seen in other otolith chronologies based on mixed-effect modeling (Martino, Fowler, Doubleday, Grammer, & Gillanders, 2019; Morrongiello & Thresher, 2015; Smoliński, 2019). The lower level of inter-individual growth synchronicity in fish and more specifically NEA cod, as opposed to relatively static organisms such as bivalves or corals, may be caused by largescale migrations undertaken once they reach sexual maturity (Höffle et al., 2014).

Our growth chronology highlighted significant alterations of NEA cod growth that can be correlated to important fluctuations in fish populations, and in particular that abrupt shifts in cod growth since 1973 seemed to closely reflect variations in cod and capelin biomasses. Density-dependent decrease in growth as a result of enhanced competition for food and resources has been identified in many species and is known to be one of the key factors regulating fish populations (Beverton & Holt, 1957; Lorenzen & Enberg, 2002). A recent study showed that the importance of density-dependent processes in NEA cod had changed throughout the last century, and in particular that models based on contemporary data (1978–2005) showed better support for strong density-dependent growth (Eikeset et al., 2016). Despite a period of heavy exploitation and decreasing stock size between the 1950s and the 1980s, NEA cod biomass in the Barents Sea has since been rising steadily and in 2014 reached the highest biomass ever recorded (Kjesbu et al., 2014). Our model predictions also suggest strong density-dependent growth, as cod biomass was identified as the strongest extrinsic factor and was significantly correlated with a large decrease in cod growth (more than 20% between the lowest and highest recorded biomass). Since our final growth model was refitted to data from 1973 to 2014, it therefore likely captured a period of strong density dependence correlated to the significant increase in stock biomass.

Temporal variations in the strength of density-dependent growth have been observed when ecosystem conditions change significantly, and especially when resources become scarcer (Casini, Rouyer, Bartolino, Larson, & Grygiel, 2014; Rueda, Massutí, Alvarez-Berastegui, & Hidalgo, 2015). The significant positive relationship found between capelin biomass and cod growth within our models is in line with recent studies on the importance of".

We apologize for this error.

REFERENCE

Denechaud, C., Smoliński, S., Geffen, A. J., Godiksen, J. A., & Campana, S. E. (2020). A century of fish growth in relation to climate change, population dynamics and exploitation. *Global Change Biology*, *26*(10), 5661–5678. https://doi.org/10.1111/gcb.15298

SUPPLEMENTARY MATERIAL A

A century of fish growth in relation to climate change, population dynamics and exploitation

Running title: Cod growth variation over a century

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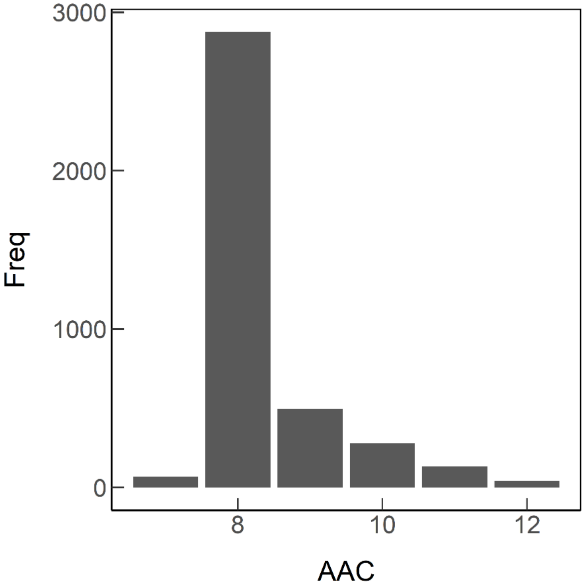

Figure S1: Age-at-capture distribution of the otoliths used in the analysis.

A few older fish up to age 21 were initially collected and measured but ultimately removed from the analysis because the sparse age data points hindered model convergence and created singularity issues.

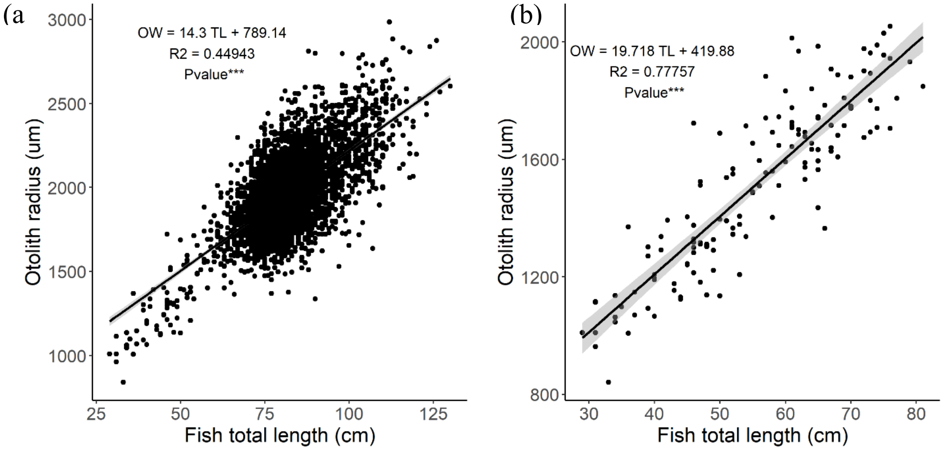

Figure S2: Relationship between otolith length and total length of fish for NEA cod. In order to have a larger range of size and age classes, younger cod sections collected for Høie et al. (2009) were measured and plotted in addition to the samples from this analysis (showed alone in (b), not included in the growth chronology analysis).

There was a significant correlation between otolith radius and fish length, although the fit was slightly low (R^2=0.45). However, this value can be justified by the very high number of fish from a single age class (8) used in this analysis, wherein the range of otolith radii was larger than the range of fish lengths due to inter-individual differences in growth and mineralization rates. Otolith radius/fish length correlations are more significant when investigating samples equally distributed throughout different age-classes (and therefore length groups), which was evident in the samples from Høie et al. (2009) as R^2 increased to 0.78.

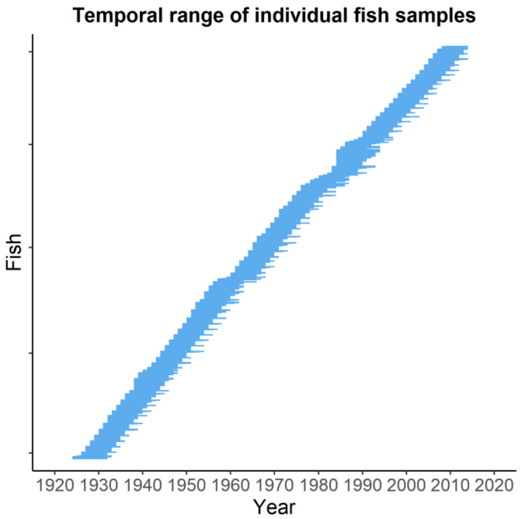

Figure S3: Temporal coverage of the samples used in the chronology. Each line represents one individual fish and its lifespan from hatch to year of fishing.

Table S1: crosstabulation of ages estimated between sectioned and initially read broken otoliths. Number of otoliths for each age are given, the green diagonal indicates agreement.

	Broken					
Sectioned	7	8	9	10	11	12
7	29	38	1			
8		2857	19	1		
9		80	414	4		
10		4	5	265	4	
11			1	6	124	1
12					1	40
	Agreement = 95.76%			CV = 3.70%		

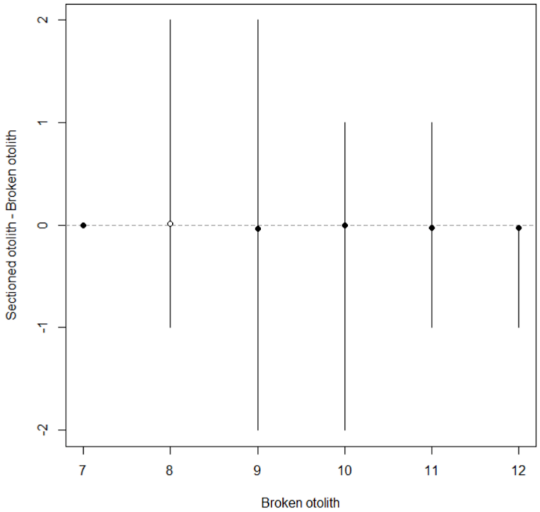

Figure S4: age-bias plot comparing estimated ages from the sectioned otoliths with the initial reading of the broken otolith.

These figures show a very high agreement between the aging of the sectioned otolith and the previous estimates from a broken otolith of the same pair. No significant trend or bias in specific age classes is evident, and most of the discrepancies concern differences of +1 or -1 year, likely due to the interpretation of the marginal increment at the edge.

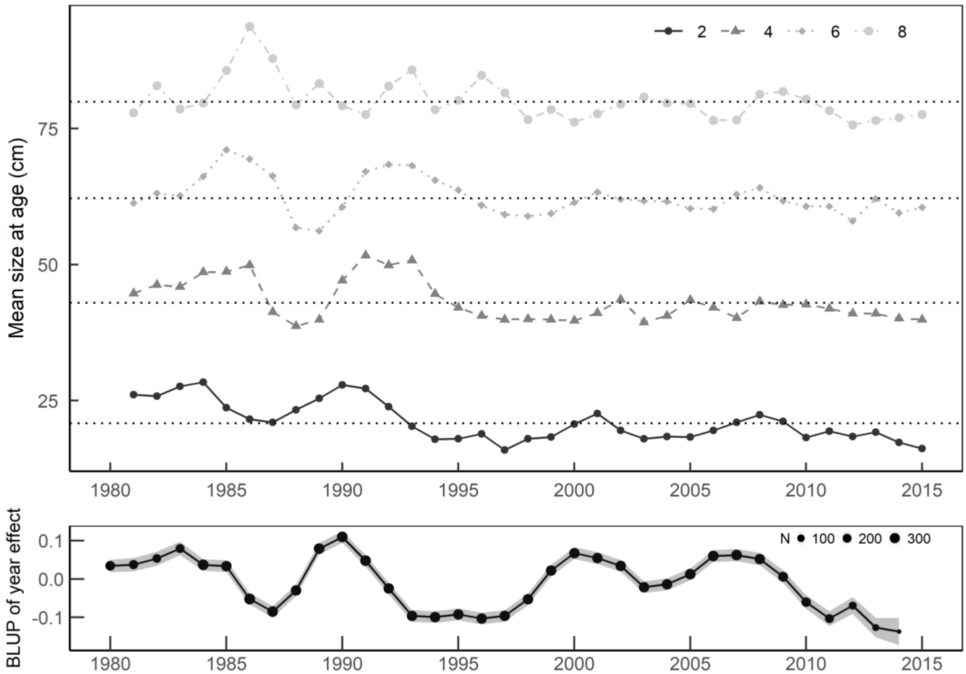

Figure S5: mean size-at-age 2, 4, 6 and 8 extracted from the ICES stock assessment report and BLUP for the Year random effect between 1980 and 2015.

The population-level growth variability expressed by the BLUP for the Year random effect shows very similar variations to the available mean size-at-age time series derived from survey data in the Barents Sea for the period 1981-2014 (no data prior). Additionally, we calculated mean growth rates from ages 5 to 6 (adult growth before sexual maturity) and 1 to 2 (juvenile growth) and plotted them against the entire time series, which further shows that the trends in both time series are correlated.

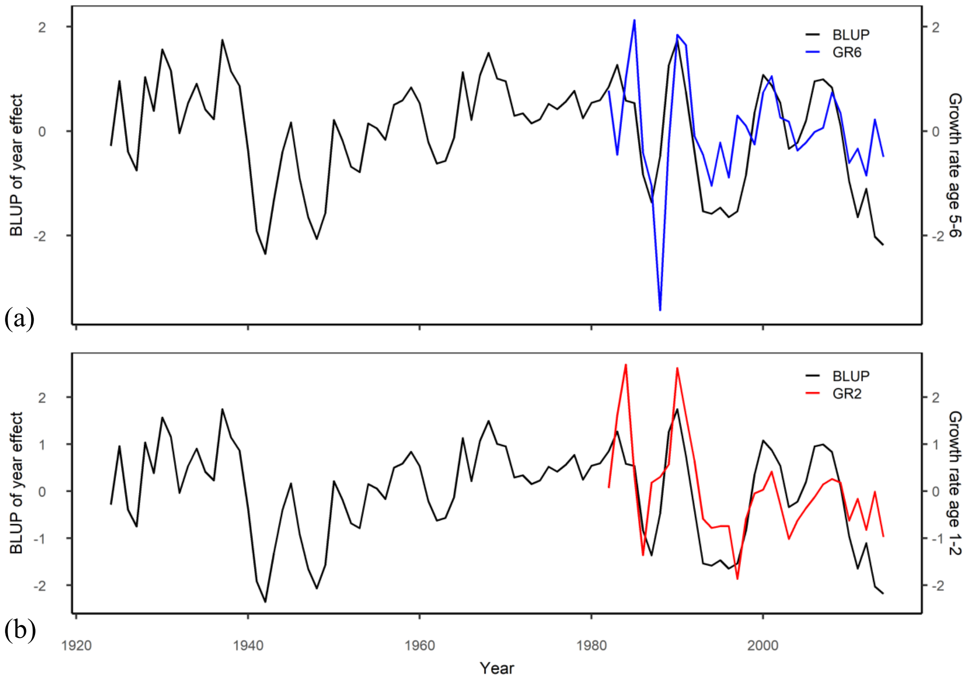

Figure S6: Scaled BLUP for the Year random effect and growth rates from ages 5-6 (a) and 1-2 (b) calculated from mean size-at-age against year.

Table S2: Random effects optimization fitted to data from 1924-2014 (28 504 increments, 3894 FishID) with full intrinsic structure. Random age slopes for FishID, Year and Cohort are denoted by "|". Best model (in bold) was selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; Res.LL = restricted log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects.

Model	Random intercept	Random slope	K	ΔAICc	Res.LL	Cond.R^2
M1a	FishID		6	2668.46	1858.09	0.57
M1b	FishID	Age|FishID	8	1783.39	2302.63	0.63
M2a	FishID, Year	Age|FishID	9	515.52	2937.57	0.65
M2b	FishID, Cohort	Age|FishID	9	1485.57	2452.54	0.63
M3a	FishID, Year	Age|FishID, Age|Year	11	86.72	3153.96	0.66
M3b	FishID, Cohort	Age|FishID, Age|Cohort	11	1105.42	2644.62	0.63
M4a	FishID, Year, Cohort	Age|FishID	10	281.07	3055.79	0.65
M4b	**FishID, Year,**	**Age|FishID, Age|Year**	**12**	**0**	**3198.33**	**0.66**
M4c	FishID, Year, Cohort	Age|FishID, Age|Cohort	12	124.72	3135.96	0.66
M4d	FishID, Year, Cohort	Age|FishID, Age|Year, Age|Cohort	Failed to converge			

While model M4d was the most complex structure, it failed to converge and created singularity issues, likely due to too low variance between Age specific slopes for each cohort and year. The analysis consequently discarded that model in the next steps and used model M4b instead.

Table S3: Intrinsic fixed-effects optimization fitted to data from 1924-2014 (28 504 increments, 3894 FishID) with full optimal random structure from Table S2. Best model (in bold) was selected based on ΔAICc. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects.

Model	Fixed terms	K	ΔAICc	LL	Marg.R^2	Cond.R^2
M4b1	Age	10	10.76	3207.62	0.514	0.66
M4b2	Age, Sex	11	7.78	3210.11	0.514	0.66
M4b3	**Age*Sex**	**12**	**0**	**3215.00**	**0.514**	**0.66**

When M4b3 is refitted to the period 1973-2014, R^2 marginal = 0.46 and R^2 conditional = 0.68

Table S4: Extrinsic fixed-effects optimization with full optimal structures from Table S2 & S3: a) environmental factors fitted to data from 1924-2014 (28 504 increments, 3894 FishID); b) population and fishing factors fitted to data from 1973-2014 (12 171 increments, 1837 FishID); c) all factors fitted to data from 1973-2014 (12 171 increments, 1837 FishID). Best models (in bold) were selected based on ΔAICc. Secondary best models with substantial support (ΔAICc<2) are highlighted in green. K = number of estimated parameters; ΔAICc= difference in AICc between a model and the model with the lowest AICc; LL = log likelihood; Cond.R^2= conditional R^2, assessing variance explained by both fixed and random effects.

a) Environmental factors fitted to data from 1924-2014 (28 504 increments, 3894 FishID)					
Model	Fixed terms	K	ΔAICc	LL	Cond.R^2
M5a	KolaT	13	1.90	3218.21	0.66
M5b	NAO	13	3.92	3217.20	0.66
M5c	AMO	13	6.49	3215.91	0.66
M5d	KolaT, NAO	14	2.23	3219.05	0.66
M5e	**KolaT, AMO**	**14**	**0**	**3220.16**	**0.66**
M5f	**KolaT, AMO, NAO**	**15**	**1.12**	**3220.60**	**0.66**
b) Population and fishing factors fitted to data from 1973-2014 (12 171 increments, 1837 FishID)					
M6a	Stock	13	9.88	966.96	0.68
M6b	Cap_ts	13	23.92	959.94	0.68
M6c	Fbar5.10	13	32.66	955.57	0.68
M6d	Stock, cap_ts	14	2.32	971.74	0.67
M6e	Stock, fbar5.10	14	1.14	972.20	0.67
M6f	Cap_ts, fbar5.10	14	25.42	960.19	0.68
M6g	**Stock, cap_ts, fbar5.10**	**15**	**0**	**973.91**	**0.67**
c) All factors fitted to data from 1973-2014 (12 171 increments, 1837 FishID)					
M7a	KolaT, stock, cap_ts, fbar5.10	16	3.53	976.24	0.67
M7b	KolaT, NAO, stock, cap_ts, fbar5.10	17	4.17	976.91	0.67
M7c	**KolaT, AMO, stock, cap_ts**	**16**	**0**	**978.00**	**0.67**
M7d	**KolaT, AMO, stock, cap_ts, fbar5.10**	**17**	**1.43**	**978.29**	**0.67**
M7e	KolaT, NAO, AMO, stock, cap_ts, fbar5.10	18	2.76	978.62	0.67

Notes: in (c), a total of 128 models with different combinations of factors were tested. Only 5 of them are displayed for readability: two combinations of climate factors with all the others (M7a & b), optimal supported models (M7c & d) and most complex structure (M7e)

Table S5: Parameters estimates of random (a) and fixed (b & c) effects for the climate optimal growth model (M5f) fitted to data from 1924 to 2014 (28 504 increments, 3894 FishID). Random age slopes are denoted by “|”. Age is log-transformed in the model.

a)

Random effects	Variance (± SD)	Correlation
FishID	0.006 (0.076)	
Age|FishID	0.020 (0.140)	0.17
Year	0.003 (0.050)	
Age|Year	0.007 (0.082)	0.54
Cohort	0.001 (0.034)	
Residuals	0.038 (0.200)	

b)

Intrinsic effects	Estimate (SE)	*t*-value
Intercept	5.312 (0.007)	764.19
Age	-0.493 (0.010)	-49.33
Sex (male)	-0.009 (0.004)	-2.53
Age:sex (male)	-0.021 (0.007)	-3.12

c)

Extrinsic effects	Estimate (SE)	*t*-value
KolaT	0.029 (0.012)	2.35
NAO	0.003 (0.003)	0.93
AMO	-0.055 (0.032)	-1.75

Table S6: Parameters estimates of random (a) and fixed (b & c) effects for the stock dynamic optimal growth model (M6g) fitted to data from 1973 to 2014 (12 171 increments, 1837 FishID). Random age slopes are denoted by "|". Age, cod and capelin biomasses are log-transformed in the model.

a)

Random effects	Variance (± SD)	Correlation
FishID	0.007 (0.084)	
Age|FishID	0.020 (0.143)	0.22
Year	0.001 (0.035)	
Age|Year	0.007 (0.085)	0.61
Cohort	0.008 (0.090)	
Residuals	0.040 (0.201)	

b)

Intrinsic effects	Estimate (SE)	*t*-value
Intercept	5.278 (0.015)	344.18
Age	-0.494 (0.015)	-32.16
Sex (male)	-0.003 (0.006)	-0.50
Age:sex (male)	-0.026 (0.011)	-2.37

c)

Extrinsic effects	Estimate (SE)	*t*-value
Stock	-0.125 (0.022)	-5.59
Cap_ts	0.012 (0.006)	1.86
Fbar5.10	-0.096 (0.046)	-2.10

ObjectJ: Marking Growth Rings in Fish Otoliths

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Sources

ObjectJ can be downloaded at: https://sils.fnwi.uva.nl/bcb/objectj/index.html

This plugin as well as example data and a video tutorial can be found at: https://sils.fnwi.uva.nl/bcb/objectj/examples/otoliths/MD/otoliths.html

Description

This tutorial is destined to help using the ObjectJ plugin "Marking Growth Rings in Fish Otoliths". Ageing and growth of fish based on otoliths has been adapted from the study of tree rings and is now widely used and developed in fisheries science. By measuring otolith increments, one can estimate past growth and correlate it with different environmental or population variables.

This plugin is designed to measure these increments in a standardized and straightforward way, as well as to provide a comprehensive output directly transferable for further use. Note that while it is flexible, the plugin was primarily developed to measure growth patterns in a straight line along the distal axis. Consequently, it might require a few changes to be adapted for ventral / dorsal axis measurements and other species whose standard methodologies require break points and multiple lines from the core to the edge of the otolith.

Setting up a project

- Loading data in ObjectJ

To start a new project, load the plugin version provided on this website. It contains the proper setup for measuring increments, as well as the necessary macros. The first step is to link the images to the project, either one by one or by directly linking all images from a folder.

Just open the Project Window > Linked Images > choose images one by one, or choose a location folder to link all images from. Images can also be dragged directly from Explorer to the project window.

ObjectJ works as an overlay, meaning it will fetch the images linked to it from a designed location but won't directly modify them. Instead, all the measurements will be saved inside the project file. This way, there is no risk for the pictures to be degraded with a wrong manipulation.

- Calibrating pictures

All linked images should now appear in the project window. If the pictures aren't calibrated or if they are in a format that doesn't contain metadata (such as .JPG), they can easily be calibrated in ObjectJ. In the project window, right click on the "px/unit" column and enter a scale and a unit. If multiple pictures were taken in a batch, the scale can be propagated to all of them by clicking the corresponding checkbox.

If the scale is not known, it can be measured using a calibration picture. In base ImageJ, measure the scale with the line tool and extract the corresponding value. It can then be used as a scale for the images, granted they were taken under the same conditions than the calibration picture.

- Project window

With a quick look at the rest of the project window, two more tabs can be noticed: “Objects” and “Columns”.

- “Objects” shows the items that will be created during the measuring process. The sequence is made of two lines called “core” and “vector” and finishes with a series of points called “increments”. The column “clones” indicates the number of items from one type: in this project, there will always be only one core line, one vector line, and up to 99 increment points. One can easily change these values but it is recommended to leave them as it is, since the number of increments can easily range from a few to several dozen. These items are essential to the measuring process and their names are tied to the macros coding: it is thus also recommended to leave them untouched, as any change will require to manually edit the macros correspondingly.

- “Columns” shows various values that will be displayed with “ObjectJ results”. However, the ring measurements won’t be displayed here but in a macro output. Because these columns names are also tied to the functioning of the macros, it is recommended to leave them untouched.

Measuring sequence

- Annotating images

Once the images are linked to the project and calibrated, the measuring sequence can start. Just open any image with a Double Click. The sequence can be started by clicking in ObjectJ > Start a sequence, or by simply pressing F1, which is the designed shortcut for this first macro.

This starts the sequence with the first item, a segment called “core”. Simply place the two extremities on the core edges so that it crosses the theoretical center. Determining with precision the core origin can be difficult and highly subjective, and therefore the first increment is often removed from chronologies. Drawing this arbitrary line will give a standardized distance that can then be used as an additional proxy for comparing first years of growth.

The sequence then automatically switches to a second item, another segment called “vector”. This segment is central to the plugin. It will act as both an axis and a measuring tool. Simply place two points, one at the theoretical core center and one at the otolith edge, to draw the corresponding axis.

It will then move on to the final item, a series of points called “increment”. Just place each point on its corresponding growth ring to mark it, and progressively move from one extremity to the other. If a point is misplaced, simply delete it by pressing Backspace. This will remove points by chronological order, starting from the most recent.

To delete specific items, go in the ObjectJ Tools window and select the Pistol tool. Keep Alt key down and click on one point to delete it or keep Shift down and click on a point to delete the entire associated item. Then, to resume annotating, select the Finger tool and double click on any point. The sequence will resume at the selected item type. To delete an entire object (i.e all three items), simply use the Pistol tool without pressing any action key.

While it is important to be precise when annotating growth increments, keep in mind that this macro also has a built-in function to pin dots on the measuring axis (see below). Consequently, it is not problematic if the points aren't exactly aligned, as long as the deviation isn't significant.

- Inputs for known year and quality

Once every item has been placed, the sequence can be ended by clicking on ObjectJ > Year and quality, or by pressing the F2 shortcut. This macro opens a dialog box with two fields.

- First, it requires a known year. A positive value assigns subsequent years from the core to the last increment, thus corresponding to a known cohort. A negative value can instead be used if only the collection date of the individual is known. The given year will there be attributed to the outermost increment and the ageing will go backwards down from the edge to the core center. Use the macro F4 to toggle on and off these values for reading purposes.

- Then, it asks for a quality value. This is an arbitrary scale of the sample quality, defined directly by the user. A suggested basic scale reads as follows. If the increments are clear, well contrasted and easy to read, mark the samples with quality “1” (Very Good). If the sample is readable as a whole but small issues hinder the measuring accuracy, a quality “2” (Good) can be chosen. On the other hand, if the sample is degraded or broken, if the picture is of poor quality, or if the increments are split and impossible to read, assign a quality 3 (Poor). This stamp makes it easy to manipulate the measurement data, for example to subset difficult otoliths from the dataset to remove uncertainties.

As mentioned before, this macro also pins the increment (blue dots) on the measuring axis to ensure every measurement is aligned from the core to the edge of the otolith. This is done automatically and will simply drag the points horizontally to the axis. This way the displacement will be minimal, and the measures won’t be impacted as long as the points were placed close to the axis.

Once done with the first image, simply close it and move on to the next one in the project window to repeat the annotation sequence.

Getting the output results

Once every sample in the project has been annotated, the output results can be generated by clicking on ObjectJ > Create output table, or once more by simply pressing the shortcut F3. This macro does several things:

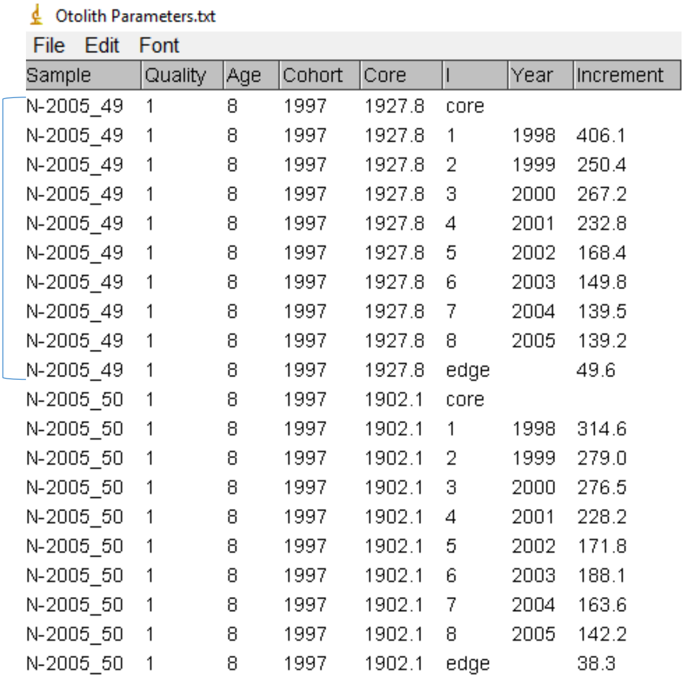
1) It arranges vector direction and ring sequence to facilitate increments measurement. First, distances between increments will always be calculated as an ascending path from the core to the edge, no matter which way the axis was drawn. Second, if the increments weren’t put in order or if some were noticed

and added later, it will correct their sequence so that they always rank from the core to the edge.

2) It measures the distance between each increment based on the axis' size. The first measurement will be from the core to the first increment (from the origin of the axis to the first dot). The following ones will be between consecutive increments. The final measurement will be the remaining distance between the last increment and the edge of the otoliths (end of the axis). This measure will correspond to the most recent growth over a period inferior to a year.

3) Finally, it groups the results in an output table organized in several columns:
    a. Sample: name of the image, minus the file extension
    b. Quality: quality stamp assigned with the second macro
    c. Age: age of the fish calculated with the number of increments measured
    d. Cohort: cohort of the fish, calculated with the known year and the number of increments
    e. Core: arbitrary core diameter
    f. I: sequence of the increments. Will always start with "core" and end with "edge", with any number of increments in between
    g. Year: year assigned to each increment based on the known year provided in macro 2
    h. Increment: measured width of each increment
    i. X & Y: coordinates in pixels of each point

This table displays each sample one under another in alphabetical order, and each measurement as an individual row. See figure below for illustration.



Sample	Quality	Age	Cohort	Core	I	Year	Increment
N-2005_49	1	8	1997	1927.8	core		
N-2005_49	1	8	1997	1927.8	1	1998	406.1
N-2005_49	1	8	1997	1927.8	2	1999	250.4
N-2005_49	1	8	1997	1927.8	3	2000	267.2
N-2005_49	1	8	1997	1927.8	4	2001	232.8
N-2005_49	1	8	1997	1927.8	5	2002	168.4
N-2005_49	1	8	1997	1927.8	6	2003	149.8
N-2005_49	1	8	1997	1927.8	7	2004	139.5
N-2005_49	1	8	1997	1927.8	8	2005	139.2
N-2005_49	1	8	1997	1927.8	edge		49.6
N-2005_50	1	8	1997	1902.1	core		
N-2005_50	1	8	1997	1902.1	1	1998	314.6
N-2005_50	1	8	1997	1902.1	2	1999	279.0
N-2005_50	1	8	1997	1902.1	3	2000	276.5
N-2005_50	1	8	1997	1902.1	4	2001	228.2
N-2005_50	1	8	1997	1902.1	5	2002	171.8
N-2005_50	1	8	1997	1902.1	6	2003	188.1
N-2005_50	1	8	1997	1902.1	7	2004	163.6
N-2005_50	1	8	1997	1902.1	8	2005	142.2
N-2005_50	1	8	1997	1902.1	edge		38.3

Sample 49, each increment is on an individual row

Because this table will display any number of measurements from all the images linked to the project file, is it recommended to first annotate every sample and then print out the results as a single, comprehensive table. Nonetheless, the table can be re-created every time a new image has been annotated or corrected: the output table will always display the samples in alphabetical order, and any image left unannotated simply won’t appear in the measuring table.

Another great functionality of this plugin is its ability to produce measurements that are easy to export and use. In Files, simply save the output table as a .csv document that can be effortlessly imported in Excel/R/Matlab or examined in a standard growth chronology model.

Finally, in case further image analysis is planned for the otolith sections, the final macro (shortcut F5) prints a second table comprising the scaling factor in pixel per unit for each sample. Combined with the coordinates from the previous table, this allows to accurately recreate the measurement transect and increment locations in any imaging software.

Final words

This ObjectJ project works as a simple and intuitive extension to annotate and measure growth from fish otoliths in a non-destructive way. Its ability to annotate increments in a few clicks and to deliver result tables that are both comprehensive and simple to export makes it a useful tool for any level, without requiring advanced knowledge of image editing software. ObjectJ's overlay also allows to annotate and later review JPG images without having to store them as TIF. Besides, it can be used on a wide range of species and organisms and could for example be adapted to measure daily growth in juveniles' hard structures with some slight changes to the embedded macros.

Paper III

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