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Increasing the biological knowledge of Baltic Sea cod: growth, movements and reproductive potential from historical and contemporary data

Monica Mion

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Monica Mion
Faculty of Natural Resources and Agricultural Science
Department of Aquatic Resources
Lysekil

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Cover: Example of a cod tagged during the TABACOD (TAgging BAltic COD) project.
(photo: A. Hilvarsson)

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Abstract

Knowledge about life-history traits of commercially exploited fish stocks and their possible changes over time is essential for implementing a sustainable management. Biological parameters such as growth rate, fecundity and movement patterns are in fact, underlying determinants for stock responses to environmental forcing and fishing exploitation.

Historically, the Eastern Baltic cod (EBC) has been one of the most important commercial stocks in the Baltic Sea but currently is one of the most severely threatened fish stocks in Europe. During the past two decades, a number of changes in biology and ecological conditions has affected the EBC stock, raising concerns among fisheries scientists and managers. One of the main biological changes has been the contraction in the size structure of the stock towards smaller fish. However, due to the large uncertainties in age estimations, it was unclear whether this change was the result of reduced growth or increased mortality of older individuals, or a combination of both. This has led to the failure of the analytical stock assessment between 2014 and 2018. The contracted size distribution of the stock could have important implications also for its potential fecundity, affecting recruitment, and movement patters.

The aim of this thesis was to increase the knowledge on key biological parameters of EBC, including growth, fecundity and movement patterns. To this end, I collated data from historical and contemporary tagging experiments, to estimate EBC individual growth using length-based methods. The results revealed that the current growth of cod is the lowest observed in the past 7 decades indicating very low productivity. These estimations have contributed to the re-establishment of the EBC analytical stock assessment since 2019. In addition, the thesis showed that the currently low growth that lead to smaller fish sizes, together with the observed decline in condition, is expected to negatively affect the fecundity and thus the reproductive output of the stock.

The re-analyses of historical data confirmed the presence of different movement behaviours, stationary and migratory, with larger distances covered by cod released in the northern and central Baltic areas compared to cod released in the southern Baltic. In addition, larger fish seemed to move over larger distances than smaller fish, underlying the importance of having larger fish with higher potential of dispersion in the stock. Furthermore, data from the recent tagging experiment indicate enduring resident strategy in the southern Baltic area.

This thesis presents methods and results that increased the understanding of the EBC biology, relevant for its management and that could be applied for future monitoring.

Keywords: Baltic cod, mark-recapture, historical data, time-series, growth modelling, potential fecundity, movement patterns.

Author’s address: Monica Mion, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Lysekil, Sweden

Förbättrad kunskap om Östersjöntorkens biologi, tillväxt, rörelsemönster och reproduction – från historiska och nutida data

Sammanfattning

Kunskap om de livshistoriska egenskaperna hos kommersiellt exploaterade fiskbestånd och hur dessa kan förändras över tid är avgörande för att kunna bedriva en hållbar fiskförvaltning. Biologiska parametrar som tillväxt, fekunditet och rörelsemönster är viktiga underliggande faktorer som styr hur populationer svarar på miljöförändringar och fiske.

Historiskt har torsken i östra Östersjön (Eastern Baltic Cod, EBC) varit ett av de kommersiellt viktigaste bestånden i Östersjön. I dag är beståndet istället ett av de mest hotade i Europa.

Under de senaste två decennierna har ett antal förändringar i biologi och ekologiska förhållanden påverkat EBC-beståndet, vilket väcker oro bland fiskeriforskare och förvaltare. En av de viktigaste biologiska förändringarna är förändringen i beståndets storleksstruktur, torskarna har blivit allt mindre. På grund av stora osäkerheter vid åldersbestämning av torsken har det dock varit oklart om den här förändringen berott på försämrad tillväxt, en ökad dödlighet hos äldre individer eller en kombination av båda dess orsaker. Detta ledde till att den analytiska beståndsuppskattningen misslyckades mellan 2014-2018. Den förändrade storleksfördelningen kan dessutom få konsekvenser för beståndets potentiella fekunditet, vilket kan påverka torskens rekrytering och rörelsemönster.

Syftet med denna avhandling är att öka kunskapen om viktiga biologiska parametrar för EBC, inklusive tillväxt, fekunditet och rörelsemönster. Genom att använda längdbaserade metoder på data som jag samlat in och sammanställt från såväl historiska som nutida märkningsexperiment har jag uppskattat den individuella tillväxten hos EBC. Resultaten visar att den nuvarande tillväxten för torsken i östra Östersjön är den lägsta som observerats under de senaste sju decennierna, vilket indikerar en mycket låg produktivitet. Dessa uppskattningar har bidragit till att man sedan 2019 återigen kan göra analytiska beståndsuppskattningar av EBC. Avhandlingen visar också att den nuvarande låga tillväxten som lett till att fiskarna blivit mindre, i kombination med torskens låga kondition, påverkar torskbeståndets reproduktion negativt.

Mina analyser av historiska märkningsdata bekräftar att det förekommer skillnader i rörelsebeteenden - stationära och migrerande - där torsk som efter märkning släpptes i norra och centrala Östersjön rörde sig över större avstånd än torskar som släpptes i södra Östersjön. Dessutom verkade större fiskar röra sig över större avstånd än mindre fiskar, vilket visar på den betydelse större fiskar kan ha för att skapa en större geografisk spridning av beståndet. Data från nyligen genomförda märkningsexperiment visar att de historiska rörelsemönstren hos torsk i södra Östersjön upprätthållits över tid.

Denna avhandling presenterar metoder och resultat som ökar förståelsen för den östra Östersjötorskens biologi, kunskap som är relevant för förvaltningen och som kan användas i framtida övervakning.

Nyckelord: Östersjön torsk, märkning-återfångst, tillväxtmodellering, historiska data, tidsserie, potentiell fekunditet, rörelsemönster.

Författarens adress: Monica Mion, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Lysekil, Sweden

Dedication

To my family

The hero, Gadus morhua … is built to survive. Fecund, impervious to disease and cold … it was the perfect commercial fish.

Mark Kurlansky, 1997

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Mion, M., Hilvarsson, A., Hüssy, K., Krumme, U., Krüger-Johnsen, M., McQueen, K., Mohamed, E., Motyka, R., Orio, A., Plikshs, M., Radtke, K. and Casini, M. (2020). Historical growth of Eastern Baltic cod (*Gadus morhua*): Setting a baseline with international tagging data. *Fisheries Research*. 223, 105442.

II. Mion, M., Haase, S., Hemmer-Hansen, J., Hilvarsson, A., Hüssy, K., Krüger-Johnsen, M., Krumme, U., McQueen, K., Plikshs, M., Radtke, K., Schade, F.M, Vitale, F. and Casini, M. (2021). Multidecadal changes in fish growth rates estimated from tagging data: A case study from the Eastern Baltic cod (*Gadus morhua*, Gadidae). *Fish and Fisheries*. 22, 413-427

III. Mion, M., Thorsen A., Vitale., F., Dierking, J., Herrmann J.P., Huwer, B., von Dewitz, B. and Casini, M. (2018). Effect of fish legth and nutritional condition on the fecundity of distressed Atlantic cod *Gadus morhua* from the Baltic Sea. *Journal of Fish Biology*. 92, 1016-1034

IV. Mion, M., Griffiths, C.A., Bartolino, V., Haase, S., Hilvarsson, A., Hüssy, K., Krüger-Johnsen, M., Krumme, U., Lundgreen, R.B.C., Lövgren, J., McQueen, K., Plikshs, M., Radtke, K. and Casini, M. New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data. (manuscript).

Papers I-III are reproduced with the permission of the publishers.

The contribution of Monica Mion to the papers included in this thesis was as follows:

I. Participated in planning and designing of the study, conducted the statistical analyses, primary author of the manuscript and handled the review process.

II. Participated in planning, designing of the study and data collection, conducted the statistical analyses, primary author of the manuscript and handled the review process.

III. Participated in planning, designing of the study and data collection, conducted the laboratory analyses and the statistical analyses, primary author of the manuscript and handled the review process.

IV. Participated in planning, designing of the study and data collection, conducted the statistical analyses, primary author of the manuscript.

1. Introduction

1.1 Life history traits are the backbone of sustainable management

Fisheries have the potential to deplete fish populations and seriously impact ecosystems and biodiversity (Pauly *et al*., 2002). To avoid such detrimental changes and to fish within sustainable levels the life history traits determining the population structure and dynamics of exploited fish populations need to be well understood and carefully monitored. Life history traits are in fact, the underlying determinants for stock responses to environmental forcing and fishing exploitation (King and McFarlane, 2003).

It is vital to consider life-history of a population and possible changes when attempting to make predictions about a fish stock and to implement sustainable fisheries management. This is mainly due to the intrinsic connection between life-histories and population growth rates, and thus productivity of a fish stock. For example, a decrease in growth, may delay maturity (Hutchings, 2002), thus making fish particularly vulnerable to unsustainable fishing, being at higher risk of removal before a successful reproduction.

Body growth rate and fecundity are key life-history traits that are plastic and evolve in response to a range of trade-offs between genetic, ecological, environmental and physiological variables. For example, in an adult fish, the amount of energy assimilated through feeding that is allocated to survival behaviours (e.g. migration, foraging), growth and reproduction will depend on a number of factors, some intrinsic (genetic, physiological) while others environmentally driven (e.g. temperature and feeding) (Saborido-Rey and Kjesbu, 2005).

Many ecosystems have undergone large changes during the past decades, sometimes referred to as regime shifts, driven by overfishing and climate changes (Sguotti and Cormon, 2018 and references therein). Threats, such as increasing temperature (Barnett *et al*., 2005), acidification (Orr *et al*., 2005), reduced dissolved oxygen (Garcia *et al.*, 2005), pollution (Moore, 2008), overfishing (Jackson *et al*., 2001) and habitat loss (Yan *et al*., 2021) are posing serious challenges to the environment and fish stocks, often acting in concert.

Because ecosystems are changing, sometimes abruptly, and due to the plasticity of these biological traits, long time-series are crucial for monitoring and understanding the present and past stock status and decide upon correct fisheries management actions (Reid and Ogden, 2006; Poloczanska *et al*., 2013; Denechaud *et al*., 2020). Overlooking the long-term perspective when studying a population typically results in a more optimistic evaluation of the stock status, with fisheries quotas set higher than if relevant historical information were considered (shifting baseline syndrome; McClenachan *et al.,* 2012). Long time-series usually include larger contrasts and cover different combinations of natural conditions and anthropic pressures (Rose, 2004; Eero *et al*., 2011).

Thus, given the rapidly changing environment and the various selection pressures, it is crucial that biological traits of exploited fish populations are understood and carefully monitored, so that any changes in response to anthropogenic or environmental stressors can be detected in time to adapt management.

1.1.1 Growth

Body growth describes how body size changes with time and variation in growth can have substantial consequences for survival, age at sexual maturity, reproductive success and movements, modulating the response of populations to environmental changes and anthropogenic pressures including fisheries (Peters, 1983; Dortel *et al*., 2015). Hence, it is a fundamental component in fisheries research to pursue good understanding of fish growth. Somatic growth is the result of the energetic balance between assimilated and consumed energy and several physiological mechanisms play important roles in this balance. Individual growth rate is phenotypically plastic, and can vary in response to changes in biotic and abiotic conditions. Growth rates can thus be considered as the combined result of a variety of conditions experienced by the fish, including food availability and temperature (Jobling, 2002).

Most methods of fish stock assessment require some form of size-at-age or growth information to estimate the status of a fish stock, and to make predictions about changes in biomass in relation to different exploitation scenarios (Beverton and Holt, 1957). Size-at-age and growth information are essential for estimating recruitment, year-class strength, and natural mortality. Within the regular monitoring of many commercially exploited fish populations, data are routinely collected and used to estimate size-at-age or growth parameters.

In fisheries science, growth is frequently described using the von Bertalanffy growth model, which expresses the length as a function of time or the age of the fish:

$$L_t = L_\infty * [1 - \exp(-k\,(t - t_0))] \quad (1)$$

Where L_t is the expected length at time (or age) t, L_∞ is the average asymptotic length (the length at which growth rate is theoretically zero), k is the Brody growth coefficient which determines how fast the fish approaches its L_∞ and t_0 is the time when length would have been zero on the modelled growth trajectory.

There are three principal data sources available to fit growth models to data from wild fish: 1) direct aging of a fish of a known size from the periodic deposit growth increment in calcified tissues, such as otoliths (Campana and Thorrold, 2001; Panfili *et al.*, 2002), 2) modal progression in length frequency distributions obtained from commercial fisheries catches or scientific monitoring, using indirect modal decomposition techniques (Bhattacharya, 1967; Fournier *et al.*, 1998; Rosenberg and Beddington, 1988) and, 3) increase in fish length over time at liberty from tagging experiments (Fabens, 1965; Dortel *et al.*, 2015).

Estimating growth from tagging data

For temperate teleost fish species, growth estimates and stock assessment generally rely on age determination through the interpretation of otolith annual increments. However, in some cases the zone formation of fish otoliths does not clearly represent a reliable seasonal signal which can be related to age (e.g. Beamish and McFarlane, 2000; Hüssy, 2010). Even in situations where otoliths are considered legible, there is always the possibility that environmental changes may influence the correct interpretation of fish otoliths (e.g. Millner *et al*., 2011). Numerous examples of severe age-reading uncertainties and inconsistencies causing highly inaccurate estimates of population dynamics exists (Campana, 2001; Kastelle *et al*., 2017), resulting in extreme cases in the abandonment of age-based analytical stock assessment (e.g. de Pontual *et al*., 2006; ICES, 2014a; 2015).

Tagging experiments are one of the most reliable methods to directly estimate growth rates in wild fish (Campana, 2001; Kohler and Turner, 2001), and are particularly useful when the age of individuals is not easily determined (Fabens, 1965). This method provides valid data for length-based growth modelling for many fish families, including gadoids (e.g. cod; McQueen *et al*., 2019; Shackell *et al*., 1997; Tallack, 2009) and have also been integrated into analytical stock assessment as in the case of some tuna species (e.g. Ailloud *et al*., 2014; Aires-da-Silva *et al*., 2015; Dortel *et al*., 2015; Hearn and Polacheck, 2003; Restrepo *et al*., 2010; Hampton and Fournier, 2001; Francis *et al*., 2016) and hake (de Pontual *et al*., 2013).

Conventional tagging method involves marking wild fish with unique, external tags that identify individuals (i.e. displaying a printed ID number as well as information required for the return of a recaptured fish), then releasing them into the wild to be recaptured after some time at liberty.

Length measurements recorded at release and recapture of tagged fish can be used to calculate individual growth, and with data from enough recaptures, average individual growth functions for a population can be calculated (Fabens, 1965). One of the advantages of using tagging data to estimate fish growth, is that information on age of fish is not necessarily required. Thus, length-based growth functions can be estimated from tag-recapture data, modelling the increment in size over the time fish spent at sea before being recaptured (Fabens, 1965).

1.1.2 Fecundity

Reproduction is an energetically demanding process for fish, and can therefore cut into the energy budget. This means that reproduction can affect growth, usually slowed down at the time of maturation in fish (Roff, 1983; Folkvord *et al*., 2014). Once mature, fish invest variable amounts of energy acquired through feeding into reproduction, and one of the parameters that describes this investment is fecundity, defined as reproductive potential in terms of number of eggs released.

The size and number of eggs produced by individual fish are therefore determined by the predictability of survival and trade-offs in energy allocation to reproduction, growth, behaviour and maintenance (McBride *et al*., 2015).

Fish are able to compensate negative energy balances, by metabolic or activity compensation (Van Winkle, 1997). In fact, fish body condition (used as a proxy for total energy reserves) has been shown to have a significant effect on individual reproductive investment (Kjesbu *et al*., 1991; Kjesbu *et al*., 1998; Marshall *et al*., 1998; Dutil and Lambert, 2000; Marteinsdóttir and Begg, 2002). Fish with limited food supply may partly or fully sacrifice egg production to preserve body condition (Marshall *et al*., 1998; Rideout *et al*., 2000, and references therein), while others, may maintain investment in reproduction at the expense of body reserves (Roff, 1982). Skipped spawning, defined as mass atresia (resorption of oocytes), may occur in populations under various types of considerable stress (Marshall *et al*., 1998; Rideout and Tomkiewicz, 2011), such as reduced prey availability or low availability of specific types of prey.

Fecundity usually increases with body size in fish (Fudge and Rose 2008; Rideout and Morgan 2010) such that larger, older females tend to have a proportionally higher egg production than smaller females (Lambert *et al*. 2005; Barneche *et al*., 2018). Specifically, Hixon *et al* (2014) used the term BOFFFFs (big old fat fecund female fish) that not only produce more eggs than smaller female, but also eggs of higher quality and offspring of higher viability e.g. larger and better provisioned larvae with faster growth and higher survival rate.

Despite this biological knowledge, fisheries stock assessment models have traditionally been based on the assumption that the spawning stock biomass (SSB), estimated as the biomass of fish, which are capable of spawning in the population, is an adequate proxy of the stock reproductive potential. However, the use of the SSB in stock assessment as a proxy for egg production, based on the assumption that individual egg production is proportional to individual mass, has been increasingly questioned (Marshall *et al*., 1998, 2006, 2009; Kell *et al*., 2016). As such, there is mounting evidence that the SSB is a rather imprecise measure of stock reproductive potential, overlooking stock specific features, such as the stock length composition and individual condition, whose variations in time can produce different number of recruits at the same level of spawning biomass (Saborido-Rey *et al*., 2004; Marshall *et al*., 2006, 2009; Morgan *et al*., 2011). Routine estimations of fecundity should thus be made to follow potential future changes in the stock reproductive potential (Kraus *et al*., 2002; Lambert, 2008; Marshall, 2009).

The estimation of fecundity, specifically potential fecundity, usually refers to the determination of the number of vitellogenic oocytes (*i.e*. developing female germ cells with yolk deposition). Different methods for estimating fecundity exist, but their use will depend on the species under investigation, resources and laboratory facilities available (Murua *et al*., 2003). Traditionally, potential fecundity is determined by a gravimetric or volumetric method (Bagenal, 1978; Kjesbu and Holm, 1994). Although these methods are simple, and give reliable results, the work is time-consuming (Thorsen and Kjesbu, 2001). However, Thorsen and Kjesbu (2001) developed a method to measure oocyte density (number of oocytes/g) using an image analysis system to reduce the time and labor involved in measuring fecundity. This method could allow following the temporal and spatial changes in fecundity in relation to different physiological and environmental conditions experienced by the stock.

1.1.3 Movement patterns

Migration is a common feature of the life histories of many of the world's economically important species of fish. Fish often undertake regular migrations between areas of feeding and spawning to maximize the benefits available from certain habitats for a particular activity or life-stage (Metcalfe, 2006). As a consequence, knowledge on migration and dispersal behaviour, termed "movement patterns", is fundamental for managing commercially fished populations, especially in areas where population mixing takes place (Rose and Rowe 2015; Neat *et al*. 2014; Zemeckis *et al*. 2014) or where environmental conditions are subject to change (Drinkwater, 2005, 2015; Engelhard *et al*. 2014).

An increasing number of studies suggest that the stock boundaries used to manage marine fish do not necessarily reflect the biological structure underlying population processes (Kritzer and Sale, 2004; Reiss *et al*. 2009; Ciannelli *et al*. 2013; Kritzer and Liu, 2013). A crucial element in understanding stock structure is defining movements and home range of the different population units. For example, populations that reside in small geographical areas year round may be the most prone to localized depletion. Conversely, if different populations mix widely outside the spawning period, they can be exploited as part of a separate stock (Block *et al*., 2005). A better understanding of the spatial ecology of the species provides a stronger basis for developing spatially explicit management measures that maintain each population unit at a safe level of abundance.

Patterns of movement between areas depend on trade-offs between the energetic costs of migration and energy used for other traits (e.g. reproduction and growth). Therefore, the characteristics of the migration (distances, routes, time spent in different habitats) will require that the benefits achieved by migrating, in terms of survival and reproductive success, outweigh the costs and risks related to the migration in order to be a successful life-history strategy.

Complexity in the physical and chemical marine environment gives rise to spatial diversity in both abiotic and biotic variables such as temperature, oxygen content, salinity and food availability. Habitat variables can vary widely, both in space and in time, particularly between seasons and different life-cycle stages, which often require different habitat conditions. Climate change, could reduce suitable habitat for reproduction through deteriorating hydrographic condition (e.g. decrease in salinity and oxygen dissolved), thus reducing the range of movements. Another factor potentially limiting the movement behaviour could be a decrease in individual size, since bigger individuals perform longer migrations due to higher energy reserves (Roff, 1988 and reference therein; Jørgensen *et al*., 2008). In addition, reduced muscle mass and body condition can negatively affect swimming performance, as seen in cod, who perform poorer in terms of prolonged swimming and implement energy efficient burst-and-coast swimming less frequently when starved (Martinez *et al*., 2003). Hypoxic conditions have also shown to reduce the swimming performance (maximum speed; Herbert and Steffensen 2005; Johansen *et al*. 2006; Dutil *et al*., 2007) and the overall level of swimming activity (Chabot and Dutil, 1999).

One of the most widely applied methods to study the movements of wild animals is to use individual markers. Particularly, conventional tagging experiments, which give information on release and recapture positions, are used for investigating broad-scale patterns, such as area of utilization and movement patterns of individuals (Righton and Metcalfe, 2019). The tagging of fish on a large scale began in the late nineteenth century (Harden Jones, 1968), and for some species (e.g. cod, see Robichaud and Rose, 2004 for a review) historical and new tagging data are available and could allow to detect possible changes in movement patterns over time.

1.2 Eastern Baltic cod in distress

The Baltic Sea is one of the largest brackish areas in the world, characterized by strong environmental gradients, where the low salinity makes it a challenging environment both for freshwater and marine species, causing low biodiversity (Hammer *et al*., 2008). Due to the peculiarity and fragility of its environment, the Baltic Sea is among the most actively and systematically investigated seas in the world (Leppäranta and Myrberg, 2009).

The ecosystem is relatively young and simple, supporting only a few dominant, commercially exploited fish species, most of which are not fully adapted to the low salinity environment (Snoeijs-Leijonmalm and Andrén, 2017). Historically, cod has been one of the most important commercial species in the Baltic Sea (Bagge *et al*., 1994; ICES, 2014b) and, as a large piscivorous fish, has important structuring roles in the ecosystem (Casini *et al*., 2009). Two genetically distinct cod populations are present in this area: the western Baltic cod (WBC) cod stock in the ICES (International Council for the Exploration of the Sea) subdivisions (SDs) 22-24, and the Eastern Baltic cod (EBC) stock in SDs 24-32 (Fig. 1). Traditionally, fish have been assigned to one of these stocks depending on the management area in which they were caught. However, since 2016 the mixing between stocks in SD 24 has been accounted for in stock assessment, based on otoliths shape analysis and genetics (ICES, 2015). In this extreme environment, the EBC have adapted to survive and successfully reproduce in the low salinity and oxygen conditions of the Eastern Baltic Sea (Andersen *et al*., 2009; Nissling *et al*., 1994), experiencing temperatures and salinities at the upper and lower limits of their tolerances, respectively (Köster *et al*., 2005; Mackenzie *et al*., 2007).

After the early 1990s, a regime shift has been identified in the Baltic, characterized by different biotic and abiotic conditions that can be regarded as "cod hostile" (Möllmann *et al*., 2009; Casini *et al*., 2009). In fact, in the last 40 years, the extent of hypoxic areas in the Baltic Sea has increased five-folds (Carstensen *et al*., 2014; Meier *et al*., 2018). Consequently, the Baltic

Sea has now became one of the largest anthropogenic "dead zones" in the world (Breitburg *et al*., 2018). The EBC stock size has also changed considerably, with a peak in the early 1980s when the stock yielded the third

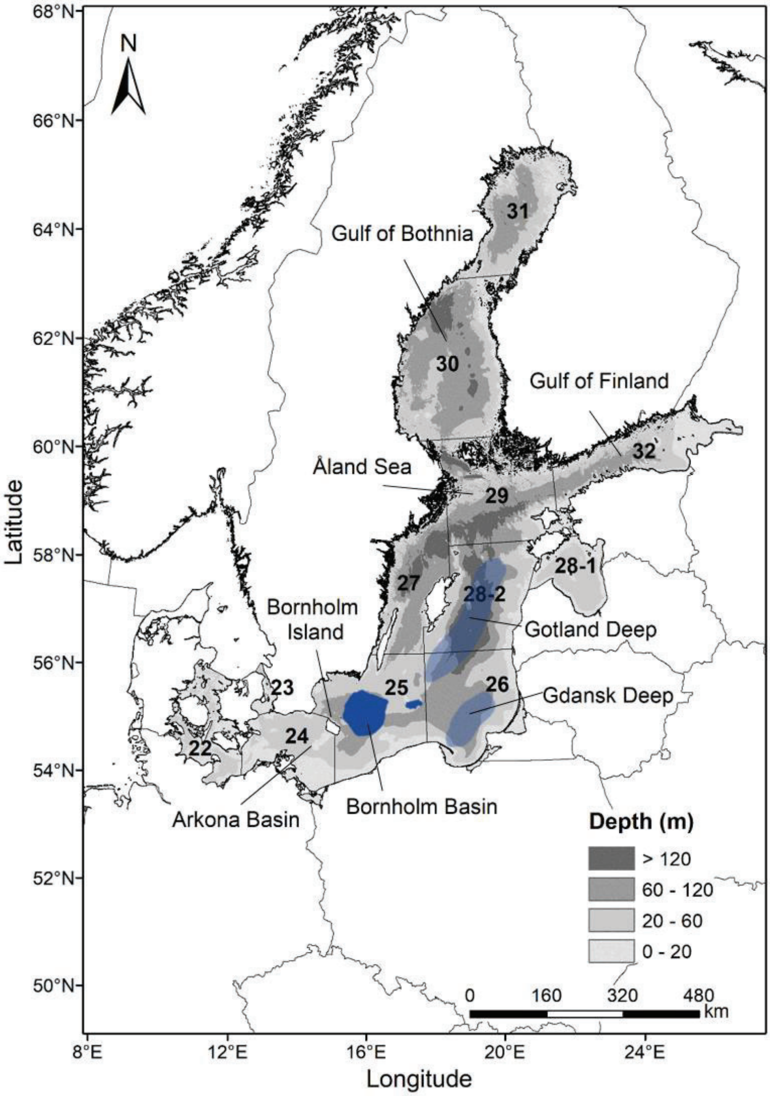

Figure 1. Map of the Baltic Sea divided in ICES subdivisions. Former spawning ground of the Gotland Deep and Gdansk Deep are shaded in blue, while the active spawning ground of the Bornholm Basin is marked in blue.

largest landings of all cod stocks in the North Atlantic (ca. 200.000 t). Since then, the stock has been in decline and is currently one of the most severely threatened fish stocks in Europe (ICES, 2020a). From 2019, the advice for EBC is for a closure of the fisheries (ICES, 2020b). Concurrent with the decline in stock size, a number of changes have been observed in the EBC stock, challenging its management. After the late 1980s, the majority of the EBC stock contracted spatially in the Bornholm Sea and surrounding areas (Eero *et al*., 2015; Orio *et al*., 2019). This contraction was likely linked to increased incidence of hypoxia in the north-eastern basins of the Baltic formerly occupied by EBC. Moreover, since the minimum salinity concentration required for the eggs to float is 11 PSU, and the minimum oxygen content for eggs' survival is 2 mL L^{-1} (Hinrichsen *et al*. 2017), the hydrographic conditions since the mid-1980s in the eastern spawning area (in SDs 26 and 28-2) were no longer suitable for survival of cod eggs. Thus, SD 25 has become the only area supporting successful reproduction of the EBC (Köster *et al*., 2017).

In addition, in the last decades a number of adverse biological developments, including reduced body condition (Casini *et al*. 2016a; Fig. 2a), maturation at a smaller size (Eero *et al*., 2015), increased infection loads with the seal-associated parasite *C. osculatum* (Horbowy *et al*., 2016; Sokolova *et al*., 2018) and thiamine deficiency (Engelhardt *et al*., 2020), indicate that the distress status of EBC has further worsened.

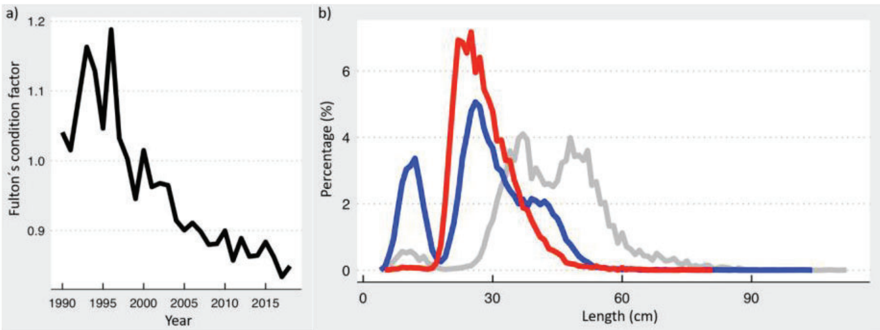

Figure 2. Changes in a) mean Fulton's body condition factor, and b) length frequency distribution (grey, blue and red lines represent the years 1991, 2001 and 2018 respectively) of Eastern Baltic cod. Data from the Baltic International Trawl Survey (BITS). (Modified from: Bergenius *et al*., 2019)

One of the most significant stock developments observed in recent years is the decline in relative abundance of larger individuals (i.e. >35–40 cm; Fig. 2b) and a drop in maximum length (Eero *et al*., 2015; ICES, 2019a; Orio *et al*., 2017). However, due to the lack of reliable age determination for this stock (Hüssy *et al*., 2016a; ICES, 2014a, 2014b), it was unclear whether the change in size structure of the stock was the result of reduced growth or increased mortality of older individuals, or a combination of both. Being able to disentangle these two processes (increased natural/fishing mortality or reduced growth) is essential for adequate management advice.

The stock assessment methods used for many fish species, including the EBC stock, depend on age-classified data (such as catch, relative abundance index, length, weight, maturity etc.). Thus, the lack of reliable age determination contributed to the failure of the analytical stock assessment for EBC between 2014 and 2018 (ICES, 2014a, 2015, 2019a). The existence of ageing problems in the EBC stock has been known since the implementation of an analytical stock assessment in the beginning of the 1970s (ICES, 1972; Hüssy *et al*., 2016a). To overcome this problem, stock assessment models that can handle length-based data are currently used (e.g. Stock Synthesis; ICES, 2019b, 2020b). However, such approaches still require information on individual growth, especially if growth is changing. Accurate information on temporal patterns in growth is therefore required (Eero *et al*., 2015; ICES, 2014a, 2015, 2017, 2018). Tag-recapture studies are an effective means for gaining information on the growth of Baltic cod.

Tagging experiments on Baltic cod have been performed from the late 1950s to the 1980s (Bagge *et al*., 1994) and have continued more sporadically thereafter. The results from recent tagging studies together with information from the historical tagging experiments can thus provide the urgently required measurements of growth of wild cod in the Baltic Sea and assess possible changes over time.

Another key question related to the production of the stock is whether the reproductive potential of EBC has been reduced given the decline in condition, small size at maturation, and a population consisting mainly of smaller individuals. It could also be hypothesized that a fraction of the stock would skip spawning, if in poor condition (Rideout *et al*., 2006; Rideout and Tomkiewicz, 2011). From a management point of view, an increasing number of studies have shown that SSB fails to accurately account for stock specific features that can produce different number of recruits at the same spawning biomass level, such as length composition (Kell *et al*., 2016; Marshall *et al*., 2006, 2009). Consequently, when a stock is dominated by small individuals, this leads to an overestimation of the reproductive potential. Thus, the worsened status of EBC calls for an improved understanding of the possible effects that change in size composition and body condition may have on the reproductive potential of the stock, in order to gain a better understanding of its current productivity (Murawsky *et al*., 2001; Morgan and Brattey, 2005).

Finally, pattern of movements between areas depends on energetic trade-off between migration, reproduction and body size together with habitat availability. The dramatic changes in the biology of EBC stock together with the deteriorated conditions of the Baltic Sea and loss of spawning areas (Köster *et al*., 2017), suggest a change also in the movement patterns of the stock. The possible changes in movement patterns that could lead to an increase in mixing with the neighboring WBC stock need to be taken in account when managing this distress stock to avoid further depletion. Re-analyses of the historical Baltic cod tagging data can provide important insight into characteristic patterns of movement that can be compared with contemporary tagging data increasing the biological knowledge of the stock to inform future management.

2. Goals of the thesis

The aim of this thesis was to increase the knowledge on key biological parameters of EBC, including growth, fecundity and movement patterns, in light of the detrimental status of EBC stock and its environment.
To achieve this aim, the following specific objectives were addressed:

I. Create a common and quality checked historical tagging database for cod in the Baltic Sea to estimate an historical age-independent growth baseline of EBC over the whole area of its distribution to be compared with ongoing and future tagging experiments (**Paper I**).

II. Combine the historical tagging database, collated in **Paper I***,* with contemporary tagging experiments to study the long term changes in growth rate of EBC using age-independent data (**Paper II**)

III. Improve the understanding of possible effects that decline in size composition and body condition may have on the reproductive potential of the EBC (**Paper III**).

IV. Update our understanding on EBC movement patterns, and explore possible differences in the seasonal movement behaviour of cod in different areas of the Baltic Sea between historical and contemporary periods using tagging data collated in **Paper I** and **II** (**Paper IV**).

3. Material and methods

3.1 Tagging data

Tagging data play an important role in fisheries assessment and management because they can provide information on the species dynamics in terms of growth, mortality and behaviour (Sippel *et al*., 2015). Tagging of Atlantic cod has been carried out for almost a century (Robichaud and Rose, 2004), and tagging of cod in the Baltic Sea has been carried out since at least the 1950s (**Paper I** and **II**). Seventy years later, there are still new insights to be gained from tagging experiments of cod in the Baltic Sea.

In this thesis, the data from historical and more recent large scale tagging studies were used to provide the urgently required estimations of growth for the EBC stock (**Paper I** and **II**) and to analyse possible changes in seasonal movement patterns (**Paper IV**).

3.1.1 Historical Tagging data

In **Paper I** and **II** historical data from cod tagging experiments performed between the 1950s and 1990s by Sweden, Poland, Latvia, Finland, Denmark and Germany in the Baltic area have been collected from the respective national archives, digitized and combined in a common database (n = 10,143 recaptures). To this common historical tagging database, data from the more recent project CODYSSEY (Cod spatial dynamics and vertical movements in European waters and implications for fishery management), performed between 2002 and 2006, have been also added (234 recaptures).

The records in the compiled database of all recaptured cod included information on release and recapture location, date and total length, as well as occasional information on total weight, sex and maturity stage. A summary of the different tags used and tagging procedures regarding releases and recaptures for the historical data can be found in **Paper I** and **II**. For the CODYSSEY project, detailed information about tagging methodology can be found in Neuenfeldt *et al*. (2007).

From the 10,143 recaptures, there were 8,856 records with clear information on both release and recapture dates, length measurements and geographical position at least at the SD level (Fig. 3a). The length of recaptured cod ranged from 140 to 1100 mm (median: 440 mm) and the time between release and recapture (days at liberty, DAL) ranged between 0 and 3,928 days (median: 128 days). The return rate (i.e. the % of tagged cod that were recaptured and returned to the research institutes) for the historical tagging experiments were on average 11.8%.

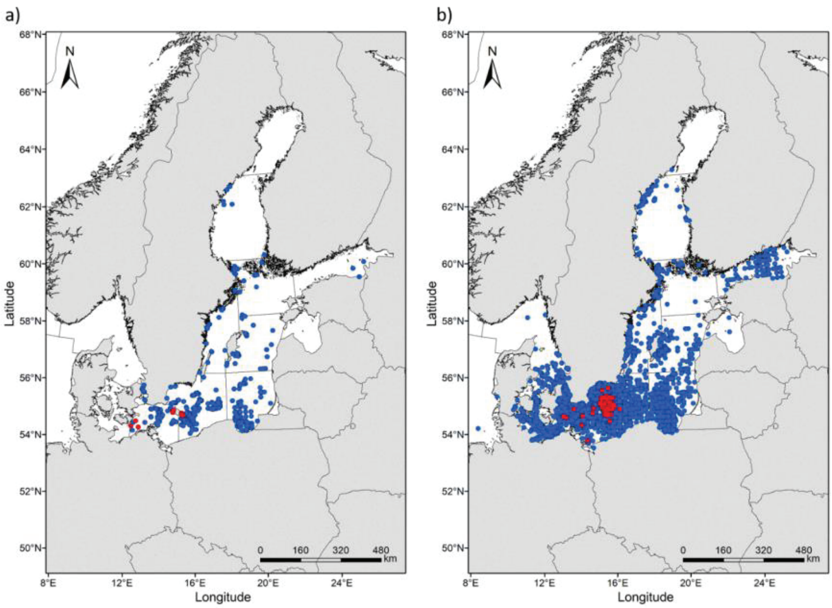

Figure 3. Maps of the Baltic Sea with release positions (a) and recapture positions (b) for the historical tagging experiments and CODYSSEY project combined (blue dots), and the contemporary tagging project TABACOD (red dots).

3.1.2 Contemporary tagging data:

A new tagging project of Baltic cod (TABACOD, TAgging BAltic COD) was carried out between March 2016 and May 2019. In total 25,352 cod were tagged in Danish, German, Polish and Swedish national waters in SDs 24-26

(Fig. 3b), covering the main, current distribution of the EBC stock (Eero *et al.*, 2012; Orio *et al.*, 2019; ICES, 2020a,b).

All cod were tagged externally with T-bar anchor tags (Hallprint TBA) into the dorsal musculature of the fish, where the tag is interlocked with the interneural bones (Fig. 4), and internally through intraperitoneal injection of a dose of tetracycline (following Stötera *et al.*, 2018). A subset (5%) of cod were additionally tagged with internal data storage tags (DSTs) surgically implanted, and were marked with two T-bar tags. A summary of the tagging procedures regarding releases and recaptures for these data can be found in **Paper II** and Hüssy *et al*. (2020).

In total, 375 cod had been recaptured (Fig. 3b), corresponding to a return rate of 1.5%. DAL of recaptured cod ranged from 0 to 927 days (mean: 216 days). Individuals were assigned to a stock through genetic analysis (Hemmer-Hansen *et al*., 2019) or using otolith shape analysis (Schade *et al*., 2019): 76% of recaptured cod were assigned to the Eastern Baltic stock, while 12% were assigned to the Western Baltic stock, and 12% could not be assigned to a stock.

Figure 4: Example of a cod tagged during the TABACOD project with an orange nylon T-bar tag anchored between the spines at the base of the second dorsal fin. The tag displays a unique ID number, as well as the phone number to call if the fish is recaptured. (Photo by Annelie Hilvarsson)

3.2 Growth analyses

Before undertaking the growth analyses, some data filters were applied in a stepwise approach (e.g. shrinkage correction and stock assignment). A full description of these steps can be found in **Paper I** and **II**.

In **Paper I** the historical length-based estimates of growth were calculated using Francis's maximum likelihood GROTAG model (Francis, 1988). This model is a re-parametrization of the VBGF and models growth as a function of length at release (L_1) and time between release and recapture:

$$\Delta L = (L_\infty - L_1)[1 - \exp(-k\Delta T)] \quad (2)$$

where, ΔL is the change in length between L_1 and the length at recapture, and ΔT is the time between release and recapture (Francis, 1988).

The GROTAG model was selected because it has been successfully applied previously to estimate growth of cod from tagging data (Tallack, 2009; McQueen *et al*., 2019). Moreover, this method incorporates individual variation in growth and can handle large datasets (Tallack, 2009).

In **Paper II** both the GROTAG model and a Generalized Additive Model (GAM), were used to estimate growth and investigate possible changes over time. Several authors have questioned the use of the VBGF (which is at the base of the GROTAG model) to describe growth (e.g. Day and Taylor, 1997; Marshall and White, 2019; Roff, 1983; Schnute, 1981). The VBGF was developed from bioenergetics principles (von Bertalanffy, 1938) with the assumption that growth slows down with fish size because the rate at which resources are acquired cannot balance with the rate at which resources are required. However, this assumption does not take into account reproduction. In addition, k and L_∞ are negatively correlated and uncertainties in the estimation of one parameter will bias the other (Andersen, 2019). Here, GAMs, which are not based on any a priori assumption on growth trajectory, were used as additional models to estimate EBC time series of growth.

3.3 Fecundity and atresia analyses:

Data for assessing potential fecundity and atresia (i.e. process of down-regulating fecundity through resorbing oocytes) have been collected in the Arkona and Bornholm Basins (SDs 24 and 25, respectively) during five demersal-trawl surveys covering the pre-spawning and spawning seasons in

2015 and 2016. In total 168 ovaries for fecundity and 121 ovaries for atresia estimation were collected (see full description in **Paper III**).

In order to estimate a calibration curve for the autodiametric method for rapid estimation of potential fecundity based on the oocyte density-diameter relationship (see Fig. 5), fecundity samples were measured in whole-mount analysis (Kjesbu, 1991) using an image analysis program as detailed in Thorsen and Kjesbu (2001). A full description of the auto-diametric method to estimate potential fecundity can be found in **Paper III.**

The current potential fecundity of EBC was analysed in relation to the length and indices of nutritional status such as body condition and hepato-somatic index using generalized linear models (McCullagh and Nelder, 1989). In addition, histological analyses were performed to assess the presence of atretic oocytes that could cause a down-regulation of fecundity.

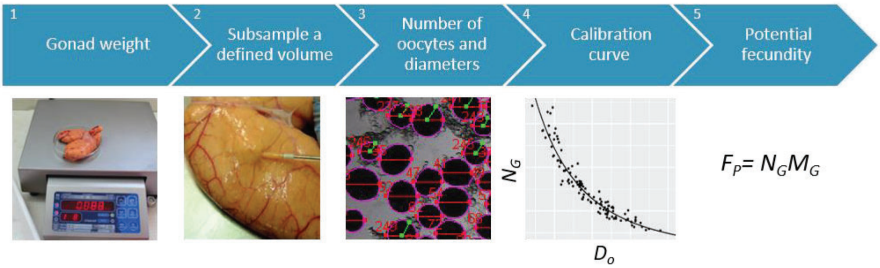

Figure 5. Procedure for auto-diametric method. (1) Measure the gonad weight. (2) Take a subsample of a defined volume with a capillary pipette. (3) For the defined volume of subsample, oocytes number (N_S) and average oocytes diameter (D_O) are measured with an image software. (4) The oocyte density (N_G), defined as N_S divided by the subsample mass (i.e. 0.026 g), and D_O are used to estimate the auto-diametric fecundity relation. (5) When the calibration curve is established, only D_O is measured per individual and with that value, N_G is estimated through the auto-diametric fecundity relation. By multiplying the weight of the gonad with N_G the individual potential fecundity is calculated. (Modified from Örey, 2008).

3.4 Analyses of fish movement

Data from historical Baltic cod tagging experiments performed between the 1950s and 1980s covering the main distribution area of the EBC stock (SDs 24-32) and the modern dataset (2016-2019; SDs 24-26) were extracted from the database compiled in **Paper I** and **II**. All records were quality checked for movement analyses (**Paper IV**). The distance that cod travelled between release and recapture positions (*d*) was calculated as Euclidean distance (Fig. 6).

A common method to study the area of utilization from terrestrial individuals is trough Kernel Density Estimation (KDE; Worton, 1989; Seaman and Powell 1996) that has become popular also for marine species within tagging studies (Parra, 2006; Righton *et al*., 2007; Svedäng *et al*., 2007; Espeland *et al*., 2008). The KDE method consists on substituting a recapture position with a probability distribution (a kernel). By summarising all the individual probability distributions, it is then possible to calculate the overall probability distribution for recapturing a tagged individual (Worton, 1989).

In **Paper IV,** KDE analyses were used to estimate the main distributional areas for cod tagged in different SDs of the Baltic Sea, during spawning and feeding seasons for the historical and modern datasets. This was done in order to assess if changes in the species main distributional areas occurred through time and across seasons.

For the KDE analyses, records were grouped into seasons without accounting for the effects of DAL on *d* (e.g., cod that were at liberty for two months were considered alongside cod that were at liberty for two years). Previous studies on North Atlantic cod stocks described for some groups a linear relationship between *d* and DAL, while for other groups a non-linear relationship linked with seasonality pattern was found (Rogers *et al.,* 2014; Espeland *et al.,* 2008). Therefore, to explore further the movement patterns of EBC, a GAM was applied to the relationship between *d* and DAL. The prior expectation was that *d* standardized by DAL, would be affected by where cod have been released. Thus, *d* would change according to the proximity of the SD of release to spawning and feeding areas (e.g. with shorter *d* for cod recaptured during the spawning period and released in an area closer to the spawning ground). The length at release was included as an additional explanatory variable to assess possible effects of ontogeny on distance moved by cod (**Paper IV**).

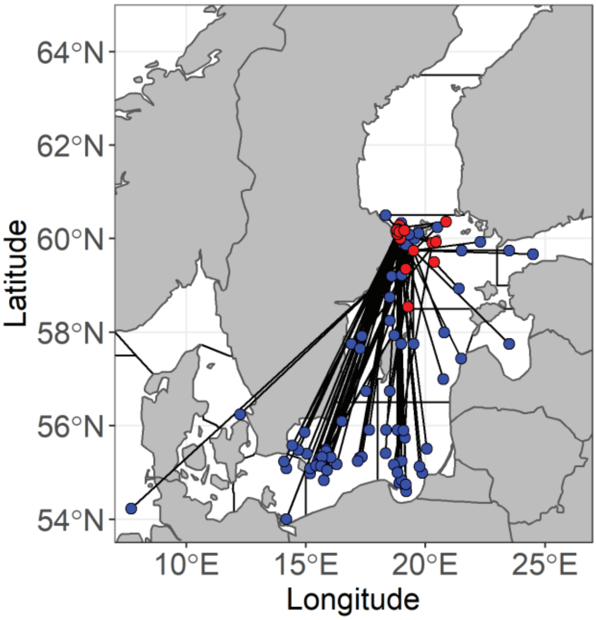

Figure 6. Example of Euclidean distance trajectories (black lines) between release (red dots) and recapture (blue dots) positions for fish released in SD 29 during the historical tagging experiments.

4. Results and discussion

4.1 Eastern Baltic cod growth estimates

In this thesis, the digitisation and collation of historical and recent data from several tagging experiments performed in the Baltic Sea over 7 decades allowed to estimate the longest existing time series of age-independent growth, based on tagging data, for the EBC stock.

Two methods, the GROTAG model (based on the von Bertalanffy growth function) and a Generalized Additive Model, were used to assess for the first time the potential long-term changes in cod growth using age-independent data. The growth curves based on the von Bertalanffy growth function from the GROTAG analyses are shown in Fig. 7. Both methods showed strong changes in growth with an increase until the end of the 1980s (8.6–10.6 cm/year for a 40 cm cod depending on the model) followed by a sharp decline (Fig. 8). Results from **Paper II** also revealed that the current growth of cod is the lowest ever observed in the past 7 decades (4.3–5.1 cm/year for a 40 cm cod depending on the model; Fig. 8), indicating very low productivity. This information is an additional indicator of the current distressed status of this stock, along with the declined body condition, reduced size at maturity, contracted spatial distribution and increased parasite infestation (Eero *et al*., 2015).

Paper II demonstrates that the shifted size structure towards smaller fish during the past two decades has been at least partially due to a strong decline in growth, although an increased natural mortality of larger individuals (e.g. Casini, *et al*., 2016a; Horbowy *et al*., 2016) can also have contributed.

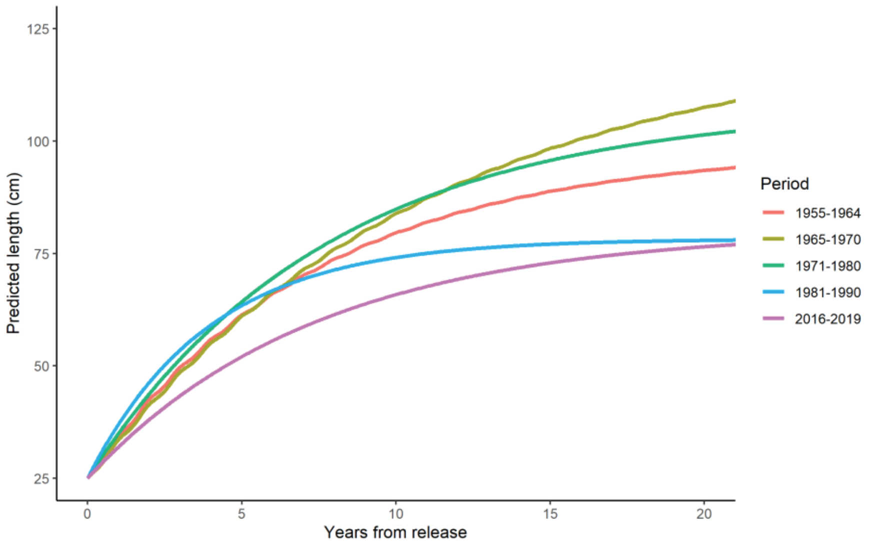

Figure 7. Fitted growth curves estimated from GROTAG model for the different periods.

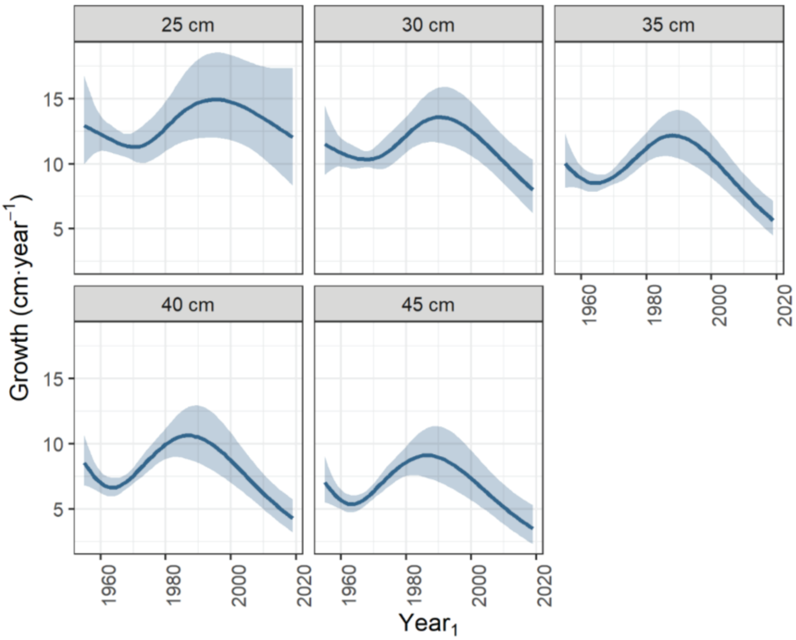

Figure 8. Predicted average growth rates (cm/year) for a 25, 30, 35, 40 and 45 cm cod for different years at release ($Year_1$) analysed with GAM (blue line). The shaded blue area represents the 95% confidence interval. Reproduced from **Paper II**

A seasonal signal in growth rates was analytically detected only for the historical baseline (1955-1970), with a peak in growth in the beginning of autumn and a minimum in spring during reproduction (**Paper I**). The absence of seasonality in growth in the more recent periods may be related to the lower number of recaptures compared to the period 1955–1970, or be a real biological change resulting from the overall contemporary low growth rates. Determinate spawners (i.e. species where the standing stock of oocytes, eventually becoming eggs, is fixed prior to the onset of spawning) such as cod, are often classified as capital breeders since they reduce feeding during the spawning season (Boulcott and Wright, 2008). After spawning, when they start feeding again, compensatory growth occurs (Pedersen and Jobling, 1989). For the EBC however, due to a decline in food availability and the overall decrease of feeding level and energy intake after the early 1990s (Casini *et al*., 2016b; Eero *et al*., 2011; Neuenfeldt *et al*., 2020), this compensatory growth may be too weak to be detected within the overall reduced growth context, explaining the recent absence of seasonality in growth.

The temporal changes in growth revealed in **Paper II** are generally in line with the patterns of weight-at-age presented in the literature (Brander, 2007a; ICES, 2013). However, the decline in weight-at-age since the mid-1990s, besides being an effect of a decline in growth, could also have been the result of size-selective removals by the high fishing pressure occurring at that time (ICES, 2020a) and therefore, a direct quantitative comparison is not possible. In addition, the results for the small fish during the most recent period are qualitatively consistent with the decline in growth of young cod from the early 2000s found by Hüssy *et al*. (2018) based on otolith daily increment and length-frequency analysis.

The decrease in growth found in **Paper II** is likely linked to the combined effects of several factors raised in literature to explain the observed concomitant decline in condition (Casini *et al*., 2016b; Eero *et al*., 2012), presumably driven by decreased food quality and availability (Eero *et al*., 2012; Rojbek *et al*., 2014; ICES, 2017), increased parasite infestation (Horbowy *et al*., 2016; Sokolova *et al*., 2018), and perhaps increased competition with flounder (Haase *et al*., 2020). The increase of hypoxic bottom water could have induced direct physiological stress (Chabot and Dutil, 1999; Casini *et al*., 2016b; 2021; Brander, 2020) and restricted the availability of cod´s benthic prey (Neuenfeldt *et al*. 2020), but focused studies should be performed to discern the relative role of the different drivers likely involved in changes of EBC growth.

In literature, there is a lack of studies investigating possible changes in growth of cod stocks over long time periods. Denechaud *et al*. (2020), using otolith increments data, revealed significant variations in Northeast Arctic cod growth over the last century, but no declining trend has been detected in the recent period. Long time series of weight-at-age data are available and routinely used for stock assessment for the other North Atlantic cod stocks. In several of these cod stocks a decline in average weight-at-age has occurred in recent periods (Northern cod: Morgan, 2019; Southern Newfoundland cod: Ings *et al*., 2019; North Sea cod: ICES, 2020c; West of Scotland cod: ICES, 2020d) and in particular for the Southern Gulf of St. Lawrence stock a strong decline in weight-at-age has occurred since the 1980s (Swain *et al*., 2019), potentially suggesting that growth could have declined also in these cod stocks.

To date, the growth estimates produced in this thesis, are incorporated in the Stock Synthesis model and contributed to the re-establishment of the EBC analytical stock assessment in 2019 (ICES, 2019a,b). The output of the latest stock assessments predicted a continuation of the decline in SSB and recruitment observed in recent years. Given the high natural mortality, low growth, low recruitment and therefore very low productivity of the stock, the scientific advice for 2020 and 2021 is to close the EBC fishery (ICES, 2019a, 2020b).

4.2 Eastern Baltic cod fecundity

The findings of **Paper III** showed a positive relationship between potential fecundity, length and different indices of nutritional status (Fig. 9), i.e. Fulton’s condition factor and hepato-somatic index, which reflect the fish total energy and lipid content (Lambert and Dutil, 1997a, 1997b), particularly stressing the negative influence that the current low condition of EBC has on oocytes production. Determinate spawners, such as cod, are in fact dependent on energy reserves to sustain gonad maturation and withdraw protein from the muscle and fat from the liver during the spawning period (Kjesbu *et al*., 1991). Some studies have shown that the inclusion of annual indices of lipid energy (Marshall *et al*., 1999) or food availability (Kraus *et al*., 2002) into fecundity models can significantly improve predictions of egg production. However, the influence of a combination of environmental factors on potential fecundity may be more complex than the simple cumulative effect of influential factors such as length and indices of nutritional status accounted for in **Paper III**, imposing some constraints on the possible patterns of energy allocation between maintenance, growth and reproduction (Lambert, 2008).

Considering the decrease in growth found in **Paper II** and the drop in individual body condition experienced by the stock during the past two decades (Casini *et al*., 2016a), it is evident that overlooking these specific biological features may lead to an overestimation of the stock reproductive potential.

Paper III demonstrates that changes in SSB, if these are due to variations in the length structure of the population, do not correctly picture the changes in population egg production and reproductive potential, while changes in reproductive potential due to variations in individual body condition are almost fully accounted for by changes in SSB.

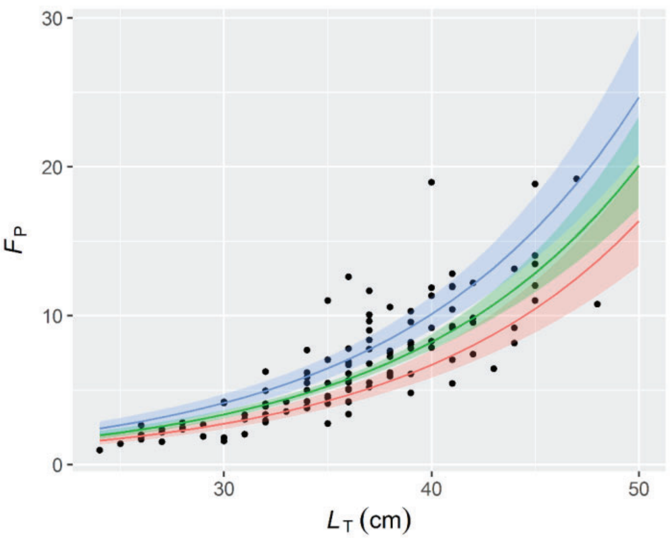

Figure 9. Plot of the predicted potential fecundity (F_P) from the final length model ($F_P \sim L_T + K + IH$, where the hepato-somatic index, IH, is set as mean IH of the samples. Observations (black dots); model predictions for Fulton's condition index K = 0.8 (red line), K = 1.0 (green line); K = 1.2 (blue line). The shaded areas represent the corresponding 95% C.I. Reproduced from **Paper III**.

However, additional studies are needed to assess whether the decline in the condition of EBC also affects the size of the spawned eggs and the amount of yolk, as it has been seen for example in Icelandic cod (Marteinsdóttir and Steinarsson, 1998) and haddock (Jobling, 1994).

In addition, the low prevalence of atresia (5.8%) found in **Paper III**, compared with the higher prevalence (32%) found by Kraus *et al*. (2008), suggests that the current distressed status of EBC may have led to a shift in the fecundity regulation mechanism during the past two decades, from a down regulation based on atresia over the course of the spawning period to a down regulation of vitellogenic oocyte recruitment before the start of the spawning season. Thus leading to a less optimistic strategy, already reducing the number of oocytes at the onset of gonad development.

The results of **Paper III** can be used to correct SSB estimated by analytical models, using oocyte production accounting for the changes in fish length distributions. **Paper III** provides for the first time a calibration curve, based on the autodiametric method, for EBC that can be used for routine estimations of fecundity to follow potential future changes in stock reproductive potential (Kraus *et al.,* 2002; Lambert, 2008; Marshall, 2009).

4.3 Eastern Baltic cod movement patterns

The results from **Paper IV** are in line with the literature (Robichaud and Rose, 2004), showing that EBC historically exhibited two broad migratory strategies, one resident (i.e. cod recaptured year-round within the area of release) and one migratory (i.e. cod performing larger movements, probably linked to spawning), with distance travelled between release and recapture varying by season and area of release.

Recaptures from the historical period indicated long distance movements from the northern and central Baltic towards the southern Baltic area, probably linked to spawning in the Bornholm basin, but also sedentary groups were present all year round in the northern and central Baltic (Fig. 10). Conversely, shorter distances were covered by cod released in the southern Baltic area during both the historical and contemporary periods (Fig. 10) suggesting enduring resident strategy in the southern area (Fig. 10).

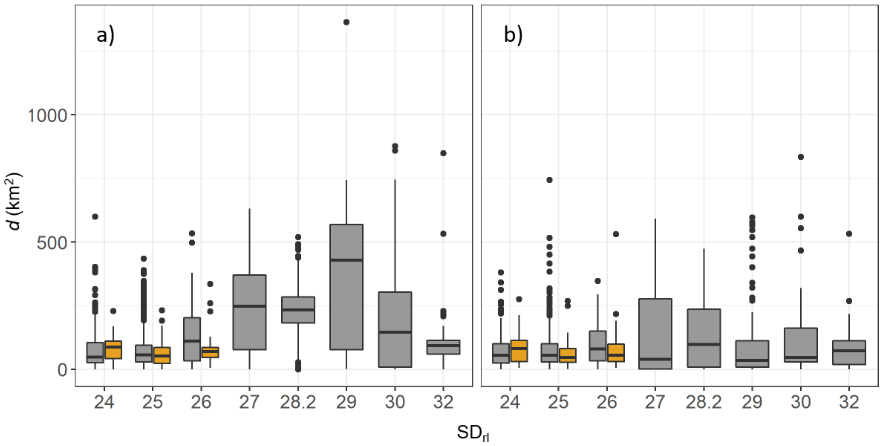

Figure 10. Box plots of the distance between release and recapture (*d*) during spawning (a) and feeding seasons (b) by subdivisions of release (SD_{rl}) for the historical (1955-1988; grey) and current periods (2016-2019; orange). Thick line: median; box: 25 and 75% percentiles; whiskers: 1.5 times the interquartile range above the 75% percentile and below the 25% percentile; black dots: outliers). Reproduced from **Paper IV**.

In **Paper IV**, the resident group in the northern Baltic area is suggested to be a subpopulation, i.e. a semi-independent, self-reproducing group of individuals within a larger population that undergoes some exchange of individuals with other areas within the population (Smedbol and Stephenson, 2001).

Because of the low salinity, fertilization of the eggs was deemed not possible in Åland Sea and farther north. Therefore, it was believed that recruitment to these northern areas took place mostly through larval drift and passive transport of young cod at times of strong influxes of water from the south (Otterlind, 1983, 1985), rather than being the results of a local subpopulation. Preliminary results indicate that some individuals from the Åland Sea have higher successful fertilization at lower salinities compared to cod from the Gotland and Bornholm areas (Bergström *et al*. unpublished). Thus, although the results of **Paper IV** for the northern area are restricted to the historical period, they could contribute to add evidence to the presence of a subpopulation of cod in the Åland Sea. More information is needed on genetics, oceanographic processes, larval drift and possible active adult migration from the southern Baltic area towards Åland Sea to understand the possible connectivity between these areas.

Paper IV shows that management boundaries between SD 24 and 25 are crossed all-year round both in the historical and in the contemporary data. However, the percentage of fish released in the eastern Baltic area (SD 25) and recaptured in the western area (SD 24) has particularly increased in the latest period. In the historical period on average 6 % and 7 % of fish released in the eastern Baltic area were recaptured in the western area during the spawning and feeding seasons, respectively. In the recent period, the 30 % and 41 % of fish released in the eastern Baltic area were recaptured in the western area during the spawning and feeding seasons, respectively.

Findings from **Paper IV**, using quantitative methods (i.e. Kernel Density Estimation analysis and Generalized Additive Model) to re-analyse historical tagging data combined with contemporary data, present additional information on general movement patterns, home ranges and mixing between different areas of the Baltic Sea, but caution is advised regarding some limitations of the analyses (Rijnsdorp and Pastoors, 1995; Bolle *et al*. 2005). Further work is needed to account for spatio-temporal patterns in fishing effort in the analysis, which might result in an overrepresentation of some recapture locations. Population movements derived from tagging studies rely on commercial fishermen and thus the results might present an integration of both fish behaviour and fishing activity, which could confound the interpretation of population movements (Rijnsdorp and Pastoors, 1995; Bolle *et al*. 2005). In addition, conventional data are restricted to information of release and recaptures but nothing is known about fish behaviours in between. Data-storage tags offer an advanced method for gathering high-resolution data on fish movements and behaviour that can be related to the physical environment. Combining results from conventional tagging data with fine-scale movement patterns of individual cod would allow to further study changes in migration related to changes in the environment.

Results from **Paper IV** show that re-analysing historical conventional tagging data can provide important insight into characteristic patterns of movement behaviour that can be compared with contemporary data and increase the biological knowledge of the stock to inform future management.

5. Conclusions

The digitization, collation and combination of historical and contemporary data from several tagging experiments performed in the Baltic Sea over 7 decades allowed to reconstruct for the first time a long time series of age-independent growth rates contributing to the re-establishment of the analytical stock assessment for the EBC stock. These data are fundamental for gaining a more complete understanding of the growth dynamics of the EBC. In particular, they revealed an increase in growth at the end of 1980s and a constant decline afterwards with an exceptionally slow contemporary growth rate.

The decline in growth of Baltic cod have both ecological implications and consequences for an appropriate management strategy of this stock. As shown by this thesis, the currently low growth that lead to smaller fish sizes, together with the observed decline in condition, is expected to negatively affect the fecundity and thus the reproductive output of the stock.

The re-analyses of historical data confirmed the presence of different movement behaviours, resident and migratory, with larger distances covered by cod released in the northern and central Baltic areas compared to cod released in the southern Baltic. Furthermore, data from the recent tagging experiment indicate enduring resident strategy in the southern area.

This thesis presented methods and results that increased the understanding of key biological traits that are relevant for the management of Baltic cod and that could be applied for future monitoring.

In addition, this thesis shows the importance of historical data mining and the great relevance of tagging experiments to analyse wild fish movements and to reconstruct potential changes in their growth rates, especially in those cases where severe age-determination problems exist.

6. Future perspectives

6.1 The future for the Eastern Baltic cod stock

The environmental conditions in the Baltic Sea are expected to continue to be affected by climate change (Belkin, 2009), with consequences for the EBC stock. The pressures of climate change and fishing affect fish populations in an interactive way, as size and age-truncated populations are particularly sensitive to changes in their environment (Brander, 2007b). In the Baltic Sea, these pressures triggered the ecosystem regime shift in the late 1980s (Lindegren *et al*., 2010; Möllmann *et al*., 2009). During this century, temperatures in the Baltic Sea are predicted to continue to increase (Andersson *et al*., 2015), while salinity and oxygen are predicted to decline (Meier *et al*., 2012, 2021).

The predicted environmental changes may be expected to affect Baltic cod biology in several ways, in particular in light of the decline in growth over the last decades found in **Paper II**, individual growth rates may also be expected to further decrease. On the other hand, studies suggest that Atlantic cod growth rates may increase in response to warming temperatures caused by climate change (Drinkwater, 2005). However, Baltic cod already subsist at the limit of its physiological tolerances, and are probably already experiencing above optimum temperatures for growth during summer (Haase *et al*., 2019; Righton *et al*., 2010; McQueen *et al.,* 2020). Additionally, the predicted environmental changes may therefore be further challenging for Baltic cod to tolerate, in particular due to direct and indirect consequences of concurrent increase in oxygen depletion.

For example, as hypoxic regions in the Baltic Sea are predicted to increase during this century (Meier *et al*., 2011), cod benthic prey availability is likely to be further affected, with negative repercussions for growth (Neuenfeldt *et al* 2020). In addition, decline in growth and condition of cod are expected to further negatively affect the fecundity and thus reproductive output of the EBC stock as shown in **Paper III** (Lindegren *et al*., 2010, Mackenzie *et al*., 2007). Moreover, additional studies are needed to assess whether the decline in length and condition status also affect the quality of the spawned eggs (e.g. size and the amount of yolk; Marteinsdóttir and Steinarsson, 1998; Jobling, 1994; Hixon *et al*., 2014).

Although the results from **Paper IV** did not indicate a substantial change in movement patterns in the southern Baltic area, an increase in mixing between stocks was suggested, as also highlighted by previous studies (Hüssy *et al*., 2016b; Stroganov *et al*. 2018). In addition, the study of Stroganov *et al*. 2018 found that recently EBC can temporarily spawn in the Belt Sea (i.e. main spawning area of EBC) showing that EBC can utilized for reproduction also this western Baltic area and that the overlap between the two stocks in the western Baltic area is expected to increase.

It is difficult to predict how the various interacting factors will affect Baltic cod biology. In general, there is high uncertainty associated with predictions of how Atlantic cod will respond to climate change, given the complex interactions between abiotic (e.g. oxygen, salinity and temperature), biotic (e.g. prey availability) and anthropogenic (e.g. fishing pressure) factors (Drinkwater, 2005). Thus, given the rapidly changing environment and the various selection pressures, a continuous monitoring of key biological parameters is crucial, so that any changes in response to anthropogenic or environmental stressors can be detected in time to adapt management.

6.2 The use of tagging data to inform Eastern Baltic cod stock assessment model

Tagging studies have the potential to deliver data relevant for assessment of fish stocks (Walters and Martell, 2004), but can be considered time-consuming and too expensive to be performed on a large scale. Growth estimated from tag-recapture data produced in **Paper I** and **II** has already informed the most recently applied stock assessment model for EBC (ICES, 2019a; ICES, 2020b).

The future implementations of tagging data into the Stock Synthesis model currently used in the EBC stock assessment can be multiple. Raw tagging data (number of releases and recaptures) can be included in Stock Synthesis models and used to estimate mortality within the model. In area-based Stock Synthesis models, raw tagging data can be also used to estimate movements and number of fish in the different areas. The development of a new Stock Synthesis version that can estimate growth within the model using raw tagging data (lengths at release and recapture and the days at liberty) is ongoing. However, due to the current low return rate (i.e. 1.5%) and the dependency on fishing activities, that recently have been strongly regulated for the EBC stock, recaptures from new potential tagging project are unlikely to become at the moment a data source that contribute to estimate stock mixing between different areas.

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Popular science summary

Knowledge about the biology of commercially exploited fish stocks and their possible changes over time is essential for implementing a sustainable management. Biological parameters such as growth rate, quantity of eggs produced and movement patterns are in fact, underlying determinants for stock responses to environmental forcing and fishing exploitation.

Historically Eastern Baltic cod (EBC) has been one of the most important species for the Baltic Sea, both as a top predator in the ecosystem and as a source of income for fisheries. However, now EBC is one of the most severely impacted stock in Europe.

During the past two decades, a number of changes in biology and ecological conditions has affected the EBC stock, raising concerns among fisheries scientists and managers. One of the main biological changes was the variation in size structure of the stock with the disappearance of larger fish. However, due to the large uncertainties in age estimations, it was unclear whether this change was the result of reduced growth or increased mortality of older individuals, or a combination of both.

The estimation of the individual growth is paramount in the management of fish populations. However, due to the difficulties in determining fish age, researchers have found increasingly difficult to estimate the growth of EBC. This has hindered a reliable evaluation of the stock status between 2014 and 2018, with consequences for the annual fishing quotas set by the European Commission. The contracted size distribution of the stock could have important implications also for its potential quantity of eggs produced, affecting recruitment (number of fish surviving to enter a fishery), and movement patterns.

The aim of this thesis was to increase the knowledge on key biological parameters of EBC, including growth, quantity of eggs produced and movement patterns.

Tagging data (from fish marked with a unique identification number, released and recaptured) are one of the best alternative way for assessing growth in case of age-determination problems, but there is a lack of studies assessing possible changes in growth over time using this type of data. Tagging experiments for cod have been performed extensively by the countries bordering the Baltic Sea since the mid-1950s and have continued intermittently until the present in different national and international projects.

In this thesis, the existing tagging data for Baltic cod have been collated to build an extensive dataset including ~ 10 000 recaptures from the historical and recent Baltic tagging experiments from 1955 to 2019.

The results revealed that the current growth of cod is the lowest ever observed in the past 7 decades, indicating very low productivity. These estimations have contributed to re-establish a robust evaluation of the EBC stock status since 2019. In addition, the thesis showed that the currently low growth, together with the observed decline in body condition (fish weight at a specific length), are expected to negatively affect the EBC egg production.

The re-analyses of historical data confirmed the presence of different movement behaviours, stationary and migratory, with larger distances covered by cod released in the northern and central Baltic areas compared to cod released in the southern Baltic. In addition, larger fish tended to be recaptured at more distant locations, whereas smaller fish tended to be recaptured closer to the point of release. Furthermore, data from the recent tagging experiment indicate that the historical movement patterns in the southern Baltic have been generally maintained over time.

This thesis presents methods and results that increased the understanding of the EBC biology, relevant for its management and that could be applied for future monitoring.

Populärvetenskaplig sammanfattning

Kunskap om biologin av kommersiellt exploaterade fiskbestånd och hur dessa kan förändras över tid är avgörande för att kunna bedriva en hållbar fiskförvaltning. Biologiska parametrar som individuell tillväxt (längd/ålder), äggproduktion och rörelsemönster är viktiga underliggande faktorer som styr hur populationer svarar på miljöförändringar och fiske.

Historiskt har torsken i östra Östersjön (Eastern Baltic Cod, EBC) varit ett av de kommersiellt viktigaste bestånden i Östersjön, både som rovdjur i ekosystemet och som inkomstkälla för fisket. I dag är beståndet istället ett av de mest hotade i Europa.

Under de senaste två decennierna har ett antal förändringar i biologi och ekologiska förhållanden påverkat EBC-beståndet, vilket väcker oro bland fiskeriforskare och förvaltare. En av de viktigaste biologiska förändringarna är variationen i beståndets storleksstruktur, torskarna har blivit allt mindre. På grund av stora osäkerheter vid åldersbestämning av torsken har det dock varit oklart om den här förändringen berott på försämrad tillväxt, en ökad dödlighet hos äldre individer eller en kombination av båda dess orsaker.

För fiskförvaltning behövs tillförlitliga uppskattningar om fiskbeståndens storlek och utveckling, och här är uppskattningar av fiskars individuella tillväxt en viktig parameter. På grund av svårigheter att bestämma åldern hos torsk i det östra beståndet har forskare emellertid haft svårt att uppskatta EBCs tillväxt, vilket skapar problem inte bara för forskare och förvaltare utan också för EU-kommissionen, som behöver säkra underlag när de fastställer de årliga fiskekvoterna. Detta ledde till att utvärderingen av beståndstatus ej var tillförlitlig mellan 2014-2018. Den förändrade storleksfördelningen kan dessutom få konsekvenser för beståndets potentiella äggproduktion, vilket kan påverka mängden torskar som blir stora nog för att fiskas upp.

Syftet med denna avhandling är att öka kunskapen om viktiga biologiska parametrar för EBC, inklusive individuell tillväxt, äggproduktion och rörelsemönster.

När bristande åldersdata gör det svårt att bestämma fiskars tillväxt så är det bästa alternativet att använda data från fiskmärkningar (individ märkta fiskar som släppts ut och återfångats)

Hittills har det dock saknats studier som visat hur den här typen av data kan användas för att bedöma fiskars tillväxt över tid. Omfattande märkningsexperiment på torsk har genomförts av länder runt Östersjön sedan mitten av 1950-talet, och både nationella och internationella märkningsprojekt har periodvis genomförts ända fram tills idag.

I den här avhandlingen har data från både historiska och nutida märkningsstudier på Östersjötorsk samlats och sammanställts. Datamängden innefattar ~ 10 000 återfångster från märkningsstudier genomförda mellan 1955 och 2019.

Resultaten visar att den nuvarande tillväxten för torsken i östra Östersjön är den lägsta som observerats under de senaste sju decennierna, vilket indikerar en mycket låg produktivitet. Dessa uppskattningar har bidragit till att man sedan 2019 återigen kan göra en trovärdig utvärdering av EBC beståndstatus. Avhandlingen visar också att den nuvarande låga tillväxten som lett till att fiskarna blivit mindre, i kombination med torskens låga kondition (fiskens vikt vid en visst längd) påverkar torskbeståndets äggproduktion negativt.

Analyserna av historiska märkningsdata bekräftar att det förekommer skillnader i rörelsebeteenden - stationära och migrerande - där torsk som efter märkning släpptes i norra och centrala Östersjön rörde sig över större avstånd än torskar som släpptes i södra Östersjön. Dessutom verkade större fiskar återfångas längre bort, medan mindre fiskar återfångades närmare den plats där de återutsattes. Data från nyligen genomförda märkningsexperiment visar att de historiska rörelsemönstren hos torsk i södra Östersjön upprätthållits över tid.

Denna avhandling presenterar metoder och resultat som ökar förståelsen för den östra Östersjötorskens biologi, kunskap som är relevant för förvaltningen och som kan användas i framtida övervakning av beståndet.

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Knowledge about biological traits of exploited fish populations is paramount for sustainable management. The Eastern Baltic cod has experienced a contraction of its size structure towards smaller fish, but the reasons were so far unclear. This thesis revealed that the current growth of cod is the lowest ever observed in the past 7 decades contributing to explain the size contraction. This together with the observed decline in condition, negatively affect cod fecundity and movement patterns.

Monica Mion received her graduate and undergraduate education in Italy at the University of Padua.

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