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Increasing biological knowledge for a better management of the Eastern Baltic Sea cod

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Front cover: A tagged cod from the project TABACOD. Photo: Magnus Andersson

Abstract

Stock assessment is the synthesis of information on life history, fishery monitoring, and resource surveys. It is a critical management tool for monitoring the abundance of commercial fish populations, as well as for predicting the consequences of policy decisions. However, without the key biological reference parameters, e.g., growth rate and age, the estimation of spawning stock biomass and fishing mortality rate is unpredictable.

During the past two decades, a number of changes in biology and ecological conditions has affected the Eastern Baltic cod stock, raising concerns among fisheries scientists and managers. Deteriorated quality of key biological parameters for stock assessment, such as true age, growth rates, and reproductive traits, in combination with changes in environmental and ecological conditions, has led the failure of the analytical stock assessment in 2014, leaving the present stock status unclear. Currently, it is unknown whether the drop in mean size and the disappearance of large individuals is due to a decrease in growth rates or by increased natural mortality. Therefore, whether the stock has suffered a decrease in productivity or an increase in mortality (fishing pressure or other natural causes) is an open dilemma, with large implication for fisheries management.

During my PhD, I will make use of results from historical tagging experiments, as well as new international tagging program to provide the necessary information on growth and mortality of Eastern Baltic cod to aid solving the issues with stock assessment. In addition, I will investigate the effects of the changes in growth and condition on cod reproductive potential. Finally, I will try to integrate all the gained biological knowledge (growth, mortality and reproductive potential) in new assessment models for a better management of the Baltic Sea cod.

Keywords: Eastern Baltic cod (*Gadus morhua*), tagging, life history, growth, fishing mortality, natural mortality, potential fecundity, stock assessment.

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1 Introduction

Fishery management depends on scientific advice based on stock assessment. Life history traits, along with fishery dependent as well as fishery independent data are included in the analytical models to assess the status of the stock. The knowledge of key biological reference parameters, e.g., growth rate and age, is fundamental for the estimation of, for example, spawning stock biomass and fishing mortality rate.

Assessing the status of the Eastern Baltic cod stock and providing management advice are presently challenged by a number of changes in the biology and the ecological conditions, which include reduced nutritional condition of fish (Fig. 1), maturation at a smaller size, increased parasite infestation and decline of larger individuals (Eero *et al.,* 2015). This could be due to low growth and/or high mortality, but this has hitherto been almost impossible to disentangle due to lack of reliable age information on cod to determine growth. As a consequence, since 2014, there is a lack of analytical stock assessment for Eastern Baltic cod. Thus, biological understanding of processes potentially affecting changes in growth and natural mortality is required to clarify the direction of these changes and possibly quantify their magnitude. In addition, given the large biological changes observed in the stock, effects on reproductive capacity could be also hypothesised.

The aim of this essay is to summarize the current issues with providing an analytical stock assessment for Eastern Baltic cod and to present possible methods to help providing the necessary biological information for cod management in the Baltic Sea. The essay contains an introductory chapter about the importance of life histories traits (such as growth, natural mortality and reproductive capacity) on stock assessment. Subsequently, I will describe the situation of Eastern Baltic cod along with the present knowledge regarding possible changes on life histories parameters. Finally, I will describe how tagging data can be used to inform stock assessment models. In the last sections of this essay, I will briefly introduce the international tagging project TABACOD (Tagging Baltic Cod) and my research questions.

Figure 1. Example of Eastern Baltic cod in low nutritional condition. © Peter Ljungberg.

2 Life history traits in fishery stock assessment

Life history traits (e.g. individual growth rates, age at maturation, maximum body length, mass, and adult rates of natural mortality) are the underlying determinants for population responses to environmental forcing and fishing exploitation (King and McFarlane, 2003). These biological characteristics greatly differ among different species and plays an important role for understanding and managing populations and ecosystems. A central assumption of life history theory is that the evolution of the biological traits is determined in part by trade-offs between these traits (Roff and Fairbairn, 2007). Accordingly, an increase in one life history trait, such as an increase in fecundity, is countered by a change in another trait that decreases fitness (e.g. decrease in survival´s rate when the fecundity increase; Roff, 1992). Life histories determine the individual´s fitness, the population´s persistence, growth rate and the ability of an exploited stock to sustain the exploitation, thus their consideration is fundamental in stock assessment and fisheries management (Hart and Reynolds, 2002).

The main objective of fish stock assessment is to predict what will happen in terms of future biomass levels and yields at different levels of fishing intensity and to provide advice on the optimum exploitation of aquatic living resources (Sparre and Venema, 1998). The knowledge of the stock life histories traits is a key aspect in analytical stock assessment. In fact, a stock has a unique set of dynamics (e.g., growth, maturity, mortality) that influence its current and future status (Fig. 1). Fishery stock assessment models are the synthesis of these informations on life histories in addition to fishery monitoring, and resource surveys for estimating stock size and harvest rate relative to sustainable reference points (Cadrin and Dickey-Collas, 2015). These models are designed to forecast the response of the resource to alternative management scenarios (Hilborn and Walters, 1992; Quinn and Deriso, 1999) and the framework for these analyses is provided by modelling the stock size fluctuations (in a closed population) accounting for four key processes: additive processes (growth and recruitment) and subtractive processes (fishing mortality and natural mortality). Where, the total biomass is increased by growth and recruitment, and reduced by natural and fishing mortality (Fig. 2).

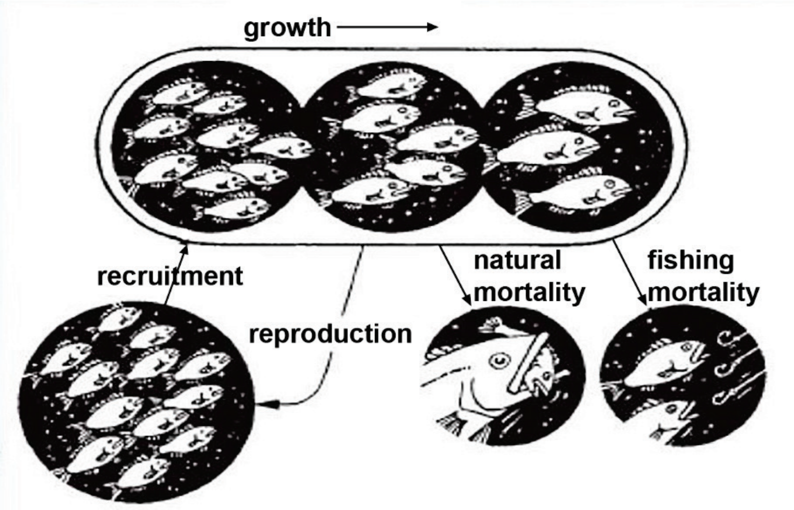

Figure 2. Stock biomass dynamics of an exploited fish stock (source: King, 1995)

2.1 Growth

A fundamental component in fisheries research is to pursue good understanding of fish growth. Growth and body weight are frequently related to survival, sexual maturity, reproductive success, movement and migration (Peters, 1983). Variation in growth can thus have substantial consequences on the stock status, regarding both ecological and evolutionary dynamics (Lomnicki, 1988). Moreover, changes in growth can also affect the estimation of vital rates and demographic traits, which may translate to incorrect predictions of population dynamics (Vincenzi *et al.,* 2014). As an example, changes in the mean length at age can have an impact on fishing mortality and biomass estimates and on derived references points for management as in the case of Eastern Pacific bigeye tuna (Aires-da-Silva *et al.,* 2015).

Growth of individual organisms within a population is generally characterized by an expression that is representative of individual growth of an “average” animal in the population. Individual growth is typically modelled by assuming a functional form describing body length or weight as a function of age, which can vary from less flexible (e.g. von Bertalanffy equation; Fig. 3) to more flexible growth curves (e.g. seasonal growth) depending on the growth aspect being modelled (Quinn and Deriso, 1999).

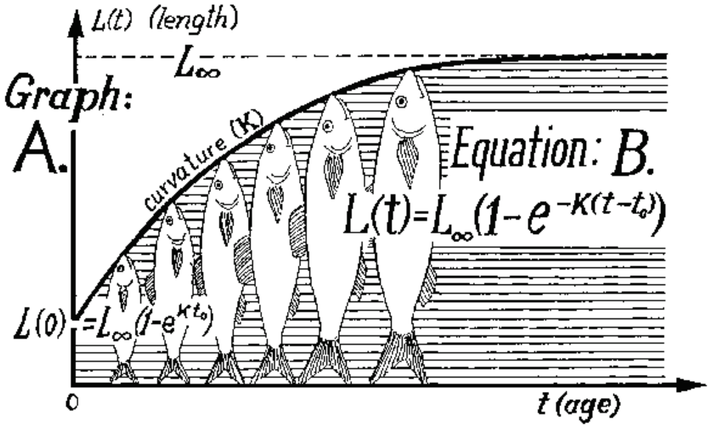

Figure 3. Graphical representation of the von Bertalanffy growth function (FAO, 1998)

The von Bertalanffy growth function (VBGF; Fig. 3), has become one of the keystones in fishery biology because it is used as a sub-model in more complex models describing the dynamics of fish populations.

The mathematical model for the VBGF expresses the length, L, as a function of time or the age of the fish:

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

Where L_t is the expected length at time (or age) t, L_∞ is the 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.

However, the VBGF assumes constant fish growth, i.e. the size increments with time, while it has been proved that growth varies greatly with food quality and availability, temperature and other environmental factors (Hamre *et al.,* 2014). In particular, the fish will reach the different stages in development more dependent on size than on age. A certain size or energy store is needed for metamorphosis in fish larvae (Amara & Lagardere, 1995; Aritaki & Seikai, 2004), smoltification in salmon (McCormick & Bjørnsson, 1994) and sexual maturation in fishes in general. Farmed cod grow faster and mature at an earlier age than wild cod (Braaten, 1984; Karlsen *et al.,* 1995). Therefore, since growth in fish is highly variable depending on food availability and environmental conditions, a growth function that is based on fish size would be in line with real fish growth and development, and would be preferred for calculation of yield in simulation models (Hamre *et al.,* 2014).

There are three principal data sources available to fit wild fish growth models: (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).

2.2 Natural mortality

The populations that we observe today are the result of life history manipulations through millions of years forced on by natural selection. In this sense, natural mortality is a selective force that drive the fishes to evolve, primarily in terms of life history and behavioural strategies (Jørgensen & Holt, 2013).

In fishery management, natural mortality is used to account for the loss of fish in a stock through death due to causes not associated with fishing (i.e. preda-tion, diseases, competition, cannibalism, age, etc.; Pauly, 1980) and it de-scribes flows of energy and mass through ecosystems. Thus, natural mortality is one of the most critical life history parameter, but is also the most difficult one to estimate (Pauly, 1980). Estimating natural mortality using mark-recapture sampling, cohort analysis, multispecies models of predation rates, or data-integrated stock assessment models is expensive, time-consuming and often requires major modelling assumptions. Conse-quently, since the 1950s, fisheries scientists have mostly treat natural mortality as an externally set parameter, usually equal to 0.2 (Jennings *et al.,* 2001), or have tried to assess it from the value of correlated life-history pa-rameters. However, so far no other drivers than predation have been formal-ly included in fish stock-assessment to account for natural mortality inter-annual variation (Casini *et al.,* 2016b). Therefore, in most fish stock assessments, estimates of current population status are generally based on age-structured models that assume a constant natural mortality for all ages and across time although it has been proved to be highly variable (Johnson et al 2014). Younger fish often experience higher predation rates (Lorenzen, 1996) while older fish may undergo senescence, cumulative reproductive stress (Mangel, 2003; Moustahfid *et al.,* 2009), or accumulate parasites as they grow older (Iyaji *et al.,* 2009).

In addition, predator–prey dynamics can change over time (Tyrrell *et al.,* 2011), and different environmental conditions or intense fishing pressure may lead to life history adaptations (Swain, 2011; Jørgensen and Holt, 2013). Moreover, an association between poor condition/growth and natural mortality has been reported for a number of species in the wild and experiments setups (Jørgensen and Holt, 2013 and references therein). Experimental studies performed on Atlantic cod have also found a negative relationship between body condition and natural mortality (Dutil & Lambert, 2000). Thus, in cases where strong time trends exists in some biological or eco-system parameters that are expected to influence natural mortality, efforts should be made to take this into account in stock assessment.

2.3 Productivity and recruitment

The spawning stock biomass (SSB) is the combined weight of all individuals in a fish stock that are capable of reproducing. To calculate the SSB, is needed the estimates of the number of fish by age group, the estimates of the average weight of the fish in each age group and an estimate of the amount of fish in each age group that are mature.

Current advice from the ICES (International Council for the Exploration of the Sea) on stocks is given on the basis of Maximum Sustainable Yield (MSY) and the Precautionary Approach (PA; ICES, 2017a). MSY means fishing at a level that takes the maximum catch (yield) that can safely be removed from a fish stock, on a continuous basis, whilst maintaining its long-term reproductive capacity. The PA is aimed at keeping the stock in a state where fishing do not affect reproduction. If fishing affects the fish populations' reproduction, it is described as 'recruitment overfishing'. If the SSB is below biomass set from the PA, managers are expected to take measures to reduce fishing mortality aiming at exploiting the stock at MSY. If the SSB is below the biomass limit (Blim, i.e. a deterministic biomass limit below which a stock is considered to have reduced reproductive capacity) the stock suffers of 'recruitment overfishing', or there is insufficient reproductive capacity to produce enough recruits to sustain a fishery (i.e. the stock is outside safe biological limits and risks collapse).

However, the use of the SSB in stock assessment as a proxy for the egg production, based on the assumption that individual egg production is proportional to individual mass, has been increasingly questioned (Marshall *et al.,* 2006; Kell *et al.,* 2016). There is in fact 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 can produce different number of recruits at the same level of spawning biomass (Saborido-Rey *et al.,* 2004; Marshall *et al.,* 2006; Morgan *et al.,* 2011). In fact, alterations in the size composition of the spawning component of a fish stock can also lead to changes in reproductive output because usually larger and older individuals may produce a higher number of eggs g−1 body mass than smaller and younger individuals

(Solemdal, 1997; Trippel *et al.,* 1997). Specifically, larger females can be more fecund than expected from the isometric scaling law for which the volume of a fish is equal to the cubic of its length. Elaborating on this concept, Hixon *et al.* (2014) used the term of BOFFFFs (big old fat fecund female fish) that not only produce more eggs than smaller females, but also offspring of higher viability e.g. larger and better provisioned larvae with faster growth and higher survival.

3 Eastern Baltic Cod

The Baltic fish community is dominated by cod, herring, and sprat which together constitute about 95% of the commercial catch of fish in the Baltic. 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 & Myrberg, 2009).

In the Baltic Sea (ICES subdivisions 22–32; Fig. 4), Atlantic cod (*Gadus morhua*) is economically the most important fisheries resources since prehistoric time (Olson, 2008), where nowadays the majority are caught by the trawl fishery (ICES, 2017b). Baltic cod populations are assessed and managed as two distinct stocks, the Eastern Baltic cod in SDs 25–32, and the Western Baltic cod in SDs 22–24 (Bagge *et al.,* 1994; Fig. 4). Traditionally, fish have been assigned to one of these stocks depending on the management area in which they were caught. Nevertheless, 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; ICES 2017b).

From the late 1980s to the 1990s, there was a distinct decline in the stock biomass (Fig. 5). After two decades of low biomass and productivity, the stock seamed to recover, mostly due to a reduced fishing mortality that reached the management objectives in 2009 (the Polish fishing fleet was paid to stay in harbour; Cardinale and Svedäng 2011; Eero *et al.,* 2012; ICES 2013). However, despite this increase in abundance, the main catches in the Baltic now consist of smaller and malnourished cod with a decline in the mean landing size by 30% between 2006 and 2011 (Svedäng and Hornborg, 2014). The lack of cod available for fisheries in the Eastern Baltic Sea can be linked to a possible loss of growth potential, resulting in a steep drop in numbers of fish of fishable size and, furthermore, poor individual status. As a consequence to the variability over time in Eastern Baltic cod productivity, large efforts have been spent trying to improve the state of this stock. Stock assessment for Eastern Baltic cod has been provided by ICES since the 1960s (Eero *et al.,* 2015) with an increasing trend in the quality of data used combined with the introduction of the data collection regulation (EC, 2000) and framework (EC, 2008) in Europe.

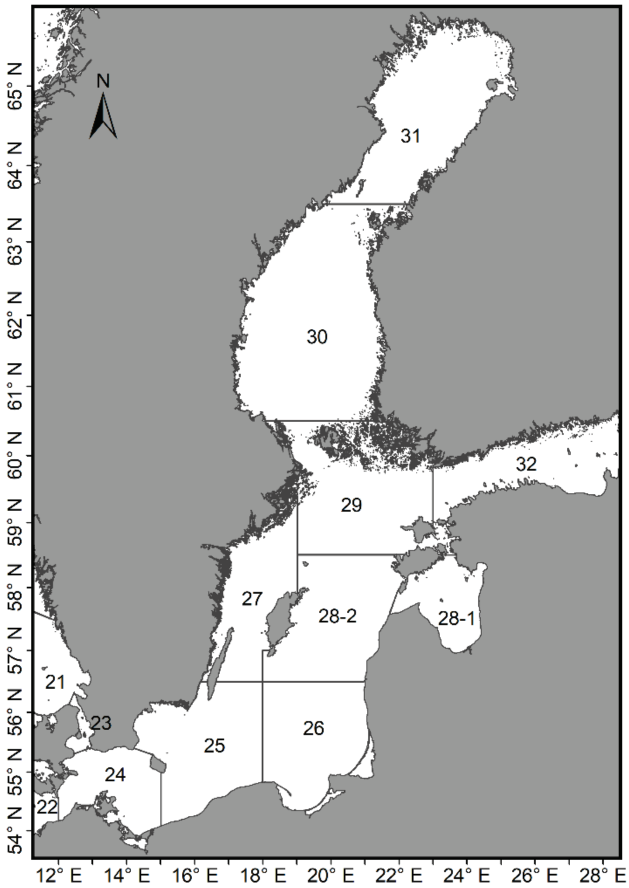

Figure 4. The Baltic Sea with the ICES subdivisions.

However, no analytical assessment has been produced by ICES for the Eastern Baltic stock since 2014. This is mainly due to lack of information about growth rates and natural mortality caused by the deteriorating quality of age determination. Thus, ICES is currently recommending that the European Commission sets fishing quotas for Eastern Baltic cod according to the principle of caution, which means not increasing the previous year's quota by more than 20 percent to avoid overfishing. Nevertheless, this principle does not ensure that fishing stays within sustainable limits. In addition, consequently to the missing analytical stock assessment, the Marine Stewardship Council, which certifies sustainable fisheries, suspended its sustainability certification of Baltic Sea cod.

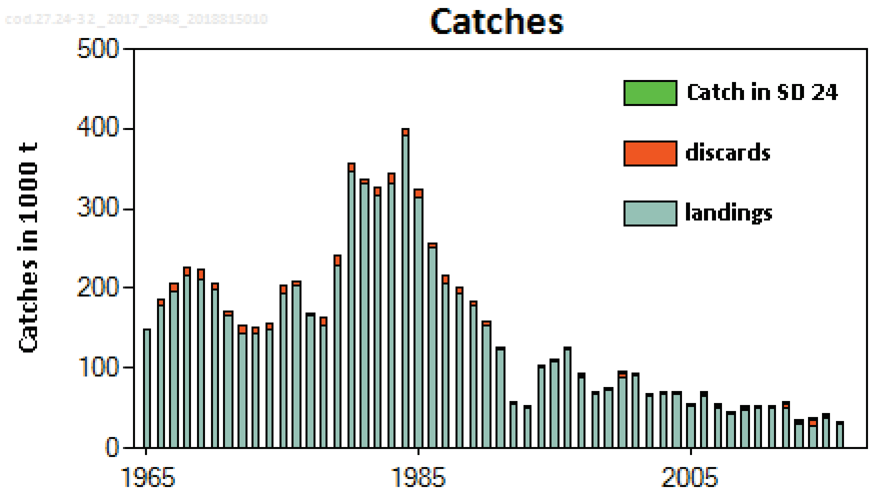

Figure 5. Catches of cod in subdivisions 25-32 (in thousand tonnes), divided in ICES estimated landings and discards, and catches of the Eastern Baltic cod stock taken in subdivision 24. (In ICES, 2017c)

3.1 Eastern Baltic cod in distress

Before the late 1980s, cod was widely distributed in the entire Baltic area (Aro 2000; Eero *et al.,* 2007). Thereafter, the prolonged overfishing in the 1990s and 2000s in addition to the deteriorated condition in two out of three spawning ground, led to poor reproductive success (Fig. 6.; Vallin et al 1999; Lindegren *et al.,* 2014), and have altered the population structure of Eastern Baltic cod with implication for the total stock productivity. The hydrographic conditions in the Eastern spawning area (in SDs 26 and 28), are in fact, no longer suitable for survival of cod eggs, and since the mid-1980s, SD 25 has become the only area supporting successful reproduction of the Eastern Baltic cod (Köster *et al.,* 2017). The collapse in cod biomass from the late 1980s to the 1990s (Casini *et al.,* 2009; Möllmann *et al.,* 2009) involved also a contraction of the stock to SD 25 in the southern Baltic Sea (Eero *et al.,* 2012).

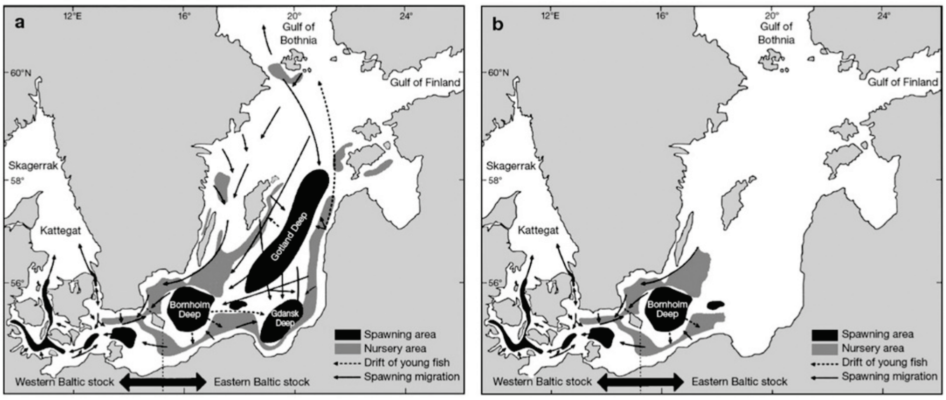

Figure 6. Changes in the historical main spawning areas of cod in the western Baltic, Eastern Baltic and Danish Belt Sea. (a) Cod spawning in the Gotland Deep and Gdansk Deep as it was depicted in the 1980s; (b) cod reproduction still occurs in the Bornholm Deep, but it is negligible nowadays in the Gotland and Gdansk Deeps. From Cardinale and Svedäng (2011), redrawn from Bagge *et al.* (1994).

A number of changes in Eastern Baltic cod biology have been observed, which include reduced nutritional condition, maturation at a smaller size, increased parasite infestation and declined in relative abundance of larger individuals (Eero *et al.,* 2015; Fig. 7). The decline in mean population size is one of the most significant stock developments observed in recent year and the reasons for this are unclear. It could be due to low growth and/or high mortality, which has not been possible to disentangle due to the lack of reliable age information on cod. In fact, the age estimates determined with otoliths became more and more uncertain and probably one of the causes is the poor cod condition in the last decades (ICES, 2014). Such uncertainty in age put into question the estimation of key biological parameters for assessments (i.e. estimation of spawning stock biomass and fishing mortality rate; ICES, 2014), since the stock assessment for cod rely on accurate knowledge of fish ages.

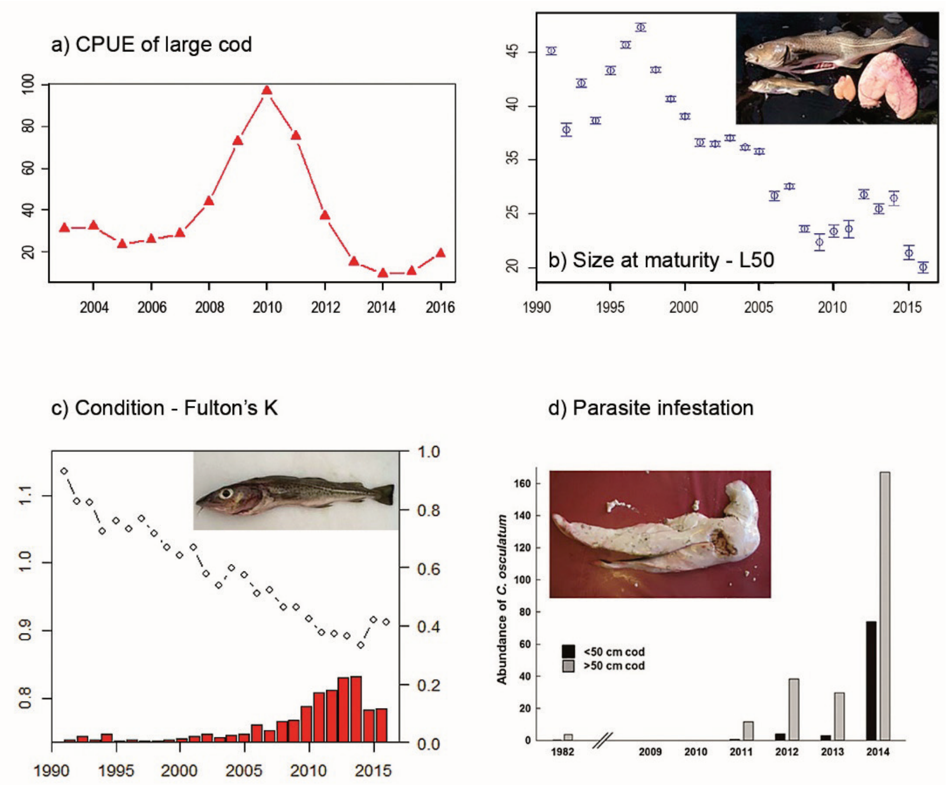

Figure 7. Changes in a) CPUE of large cod (>45 cm in length) from BITS survey, b) size at first maturity for female and males combined, from BITS Q1 survey, c) mean Fulton´s condition factors (K) for 40-60 cm cod from BITS Q1 survey; the red bars show the proportion of cod at K<0.8 and d) parasite infestation (Eero *et al.*, 2015, and ICES, 2007d)

Some attempts are being made to reproduce quantitative stock assessment based on length information instead of using age (ICES, 2018). However, such approaches still require information on growth of the fish and natural mortality. Thus, a review of the biological processes potentially affecting variations in growth and natural mortality has been recently made (ICES, 2017d) to elucidate the direction of changes in these variables and possibly quantify their magnitude. Additionally, given the large biological changes observed in the stock, effects on reproductive capacity could be hypothesised, which is important to consider in the context of future stock development and management advice (ICES, 2017b).

3.2 Potential signals of changes in growth

Large changes in fish stocks regularly occur, and the recent developments with Eastern Baltic cod are not unique in this respect. For example, a rapid increase in natural mortality and absence of larger individuals has been recorded for several demersal stocks in the Northwest Atlantic (Swain and Benoit, 2015).

Possible reasons for the potential change in cod growth in SD 25 can be related to climate change, food limitation, density-dependence mechanism (Eero *et al.,* 2012) and an increased selectivity in mesh size (Svedäng and Hornborg; 2014). Low condition has been suggested as one of the causes of the recent disappearance of large cod individuals, via decreased growth (ICES, 2017b; Fig. 7). The changes in cod condition, as shown in Casini *et al.* (2016b), are related to feeding opportunities, driven either by density-dependence or food limitation, and to the fivefold increase in the extent of hypoxic areas in the most recent 20 years.

Increased population densities may lead to a decreased condition and lower growth as seen for example in North Sea plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) after the increased in population during the period of reduced fishing effort due to the World War II (Beverton & Holt, 1957). Density-dependent growth as a result of competition in recruited (late juvenile and adult) fishes is in fact a common and important mechanism regulating population dynamics (Lorenzen and Enberg, 2002; and references therein). Furthermore, the example of Pacific halibut (*Hippoglossus stenolepis*) demonstrates that the large changes in growth are density-dependent responses to changes in stock size (Clark and Hare, 2002).

The contraction of the stock to SD 25 in the southern Baltic Sea due to unfavourable environmental conditions (i.e. increased hypoxic areas), has in the last years resulted in the highest cod abundance recorded in this area since the 1970s (Eero et al. 2007). In this case, the habitat compression has been concomitant with an increase in cod population abundance since the mid-2000s, potentially worsening the density-dependent response, such as a decline in condition. Moreover, the study of Svedäng and Hornborg (2014) showed that the increased selectivity has induced a steady increase in number of small-sized fish, which in turn might have led to density-dependent growth.

The growth of Eastern Baltic cod has also been related to the relative availability of clupeid prey (Baranova 1992). The stocks of the main pelagic prey for cod, sprat and herring, have in fact decreased in the southern Baltic, main cod´s distribution area, and increased in the northern Baltic since the early 1990s (Casini *et al.,* 2011; 2016a). In addition to clupeid prey, cod also fed upon benthic invertebrates, and adult cod is cannibalistic (Uzars 1994). Utilization of benthic food resources by cod is believed to be reduced at low oxygen concentrations in deeper water layers, with a consequent change in cod behaviour probably feeding proportionally more on pelagic prey (Schaber *et al.,* 2009). However, at present ecological conditions, the alternative food resources seem not to be able to compensate for the shortage of clupeids in SD 25. This is indicated by an increasing proportion of individuals with empty stomachs and a close correspondence between the availability of sprat and herring and the weight of adult cod in this area (Eero *et al.,* 2012).

Besides feeding opportunities on pelagic fish, the extent of low-oxygen bottoms is also an important factor to explain the decrease in cod condition, and consequently a possible decrease in growth. Variations in cod growth have been linked also to hydrological conditions as in the case of North Atlantic cod (Swain et al. 2003 and references therein). The oxygen concentration has been shown to affect cod metabolism with impacts on growth and condition (Hinrichsen *et al.,* 2011; Casini *et al.,* 2016a and references therein).

Climate changes can also affect cod´s growth, e.g. Icelandic experiments on individual fish fed to satiation show that the growth rate increases with temperature, but then declines again at high temperatures when the metabolic costs outweigh the somatic gains (Bjornsson *et al.,* 2001; Bjornsson & Steinarsson, 2002). Surface waters in the Baltic Sea have warmed in all seasons since 1985 (HELCOM, 2013). The annual mean sea-surface temperature has been estimated to have increased by up to 1 °C/decade from 1990 to 2008. Moreover, future warming is expected to increase hypoxia given that temperature controls the stratification of the water column, the respiration of organisms, and the solubility of oxygen (HELCOM, 2013).

3.3 Potential signals of changes in natural mortality

As discussed previously, poor condition can been associated with a decrease in growth, but also an increase in natural mortality for several species (Casini *et al.,* 2016b).

Experimental studies performed on Atlantic cod have found a negative relationship between body condition and mortality (Dutil and Lambert, 2000). Therefore, with the current stock´s status, an increase in natural mortality could be expected also for the Baltic cod. Natural mortality (an instantaneous annual rate for age groups 2 and older) of EB cod has been assumed constant and relatively low (0.2) in the entire time-series since 1966 (Eero *et al.,* 2015). However, the study of Casini *et al.* (2016b), relating natural mortality with critically low condition (Fulton's K, based on fork length and gutted weight ≤ 0.65), estimated for larger cod (35-50 cm) an increased in mortality by approximately 0.1 a year since the second half of 2000s. There are also evidences of a shift in the sex ratio towards females (only 20% of cod in the size rage 50.55 cm are currently males). Thus, there seems to be an increased mortality of males relative to females possibly as a result of the decline in length at first maturation (ICES, 2017d).

In addition, since the beginning of the 2000s, the grey seal population has increased threefold in the entire Baltic (Härkönen *et al.,* 2013), likely increasing the predation mortality on cod (ICES, 2017d). Moreover, cod is a transport host for two seal parasite species: cod worm (*Pseudoterranova decipiens*) and liver worm (*Contracaecum osculatum*; Mehrdana *et al.,* 2014). Recent investigations have documented a marked increase in prevalence and intensity of infestation for both parasites compared with the 1980s when seal abundance was lower, possibly increasing even further natural mortality (Horbowy *et al.,* 2016; ICES 2017d).

3.4 Potential signals of changes in reproductive capacity

One of the key questions in relation to reproductive capacity is whether or not the reproductive potential of the stock has been reduced given the poor condition of the fish, small size at maturation, and a population consisting mainly of smaller individuals. New analyses are ongoing on the relation between potential fecundity and condition for Baltic cod, and a recent study shows that fish in low conditions have lower fecundity (Mion *et al.,* 2018), as observed in other cod stocks. It could also be hypothesized that a fraction of the stock would skip spawning, if in poor condition (Rideout & Tomkiewicz, 2011).

It has also been documented that larger females not only produce more eggs and offspring of higher viability, but also produce larger eggs, which have a higher survival probability due to differences in egg buoyancy (Hinrichsen *et al.,* 2016). Thus, it could be expected that the eggs of the current spawning stock consisting of small individuals have reduced survival probability compared to the previous situation with in average larger spawners.

From a management point of view, the SSB relationships are presently not used for Eastern Baltic cod advice, since there is no analytical assessment (ICES 2018). 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 and condition (Kell *et al.,* 2016; Marshall *et al.,* 2006). Consequently, when a stock is dominated by small individuals and/or with low condition, this leads to an overestimation of the reproductive potential. In the case of Eastern Baltic cod, Mion *et al.* (2018) showed that condition is already accounted for in the estimation of SSB (an increase in condition, and thus weight, is linearly related by an increase in potential fecundity), while length-structure of the spawning fish is not. Therefore, correcting SSB by the length distribution of the spawning component of the populations would provide a better estimate of stock reproductive potential and thus better prediction of recruitment.

4 Use of tagging data for stock assessment

Explaining the absence of larger cod and being able to quantify growth and mortality are essential for understanding the present ecology of the Baltic Sea ecosystem. 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, spatial distribution and behaviour (Sippel *et al.,* 2015).

4.1 Growth

Although tagging studies primarily focus their research on distribution and movement, these studies can also provide information on a variety of biological aspects, including growth (Kohler & Turner, 2001). Approaches for estimating growth based on mark–recapture tagging data use differential length measurements (Gulland & Holt, 1959; Fabens, 1965; Francis, 1988b) and have been applied for many species, including scombrids, gadoids, labrids and elasmobranchs (Tallak, 2009 and references therein). The "mark and recapture" technique involves marking a number of individuals in a natural population with an external, easily identifiable tag, returning them to that population, and subsequently recapturing some of them.

Tag and recovery data can be analysed by the GROTAG maximum likelihood method (Francis, 1988b; Tallack, 2009), a re-parameterisation of the Fabens growth model (Fabens, 1965) based on the VBGF for estimating growth from length increment data. The usual von Bertalanffy parameters, K and $L\infty$, are replaced by two alternative parameters, g_α and g_β, which represent mean annual growth increments (mm/yr) of chosen reference length α and β (Francis, 1988b). These parameters have better statistical properties than K and $L\infty$, particularly when the entire size range of the species is not represented in the data (Francis, 1988a, b). This modelling approach has the capacity to allow for individual variation in growth increment around the population mean and to detect seasonal growth variations (Francis, 1988). In addition, GROTAG is also well suited to data collected by multiples individuals (e.g. fishermen and scientists) since it estimates measurement error and the proportion of outliers in the dataset (Meyer *et al.,* 2014).

4.2 Fishing mortality

Fishing mortality can be estimated by releasing a known number of tagged fish and determining the proportion harvested by fishers (i.e. recapture´s rate). However, the results of tagging studies can be compromised if tags are lost or not reported, leading to underestimation in tag return rates, which create a negative bias in fishing mortality estimates, rates of fishery interactions, and movement. These sources of error should be carefully reviewed and, if possible, corrected before exploitation rate estimates are applied to management (Miranda *et al.,* 2002).

There are two types of tag losses: the first reduces the number of tags initially put out (immediate tag shedding and immediate tagging mortality), the second occurs steadily over time (long term shedding; Beverton and Holt, 1957). In addition, the recapture´s rate can be underestimated if the fishermen are not reporting the tagged fish.

Short-term tag shedding and short-term tagging induced mortality are commonly estimated by observing tagged fish under controlled laboratory conditions or in field cages (Brattey & Cadigan, 2004; Pollock and Pine, 2007). However, post release mortality estimates derived under these circumstances may be biased because captive fish are in general not affected by post-release predation as wild fish. On the other hand, restraining fish in confined conditions can have lethal or sub-lethal effects.

Long-term tag loss can instead be estimated by double-tagging (Muoneke 1992), or applying a permanent mark for comparison with a temporary mark (Brewin et al. 1995). These estimates can be obtained from changes over time in the proportion of double tagged cod that are returned with one or two tags (Seber 1982; Wetherall 1982; Barrowman and Myers 1996).

Reporting rates of tagged fish by fishers, beside by scientists, have usually been assessed with escalating-value rewards (Nichols et al. 1991; Pollock *et al.,* 2001). In addition, to estimate the reporting rates during commercial surveys can be used a seeding experiment (Hampton, 1997; Leroy *et al.,* 2013). To implement these experiments a member of the vessel crew or a fishery observer, without the knowledge of any other crewmember, discretely tags a small number of fish prior to their placement in the fish wells on a commercial vessel. The proportions of these tags that are recovered are then used to infer, with appropriate statistical treatment, the reporting rate of the regular tags for use in stock assessment (e.g. Hoyle, 2011). Tag seeding experiments are generally only implemented on vessels that allow to seed tagged fish unobserved (i.e. purse-seine vessels for tuna; Leroy *et al.,* 2015). These experiments should ideally cover all the fleets involved in the area or at least targeting the fisheries with a high fishing effort on the stock, and they should continue throughout all the tagging activities so that reporting rates can be monitored through time (Leroy *et al.,* 2015).

4.3 Migration and mixing

In recent year, integrated stock assessment models (Mauder and Punt, 2013) that extract information about biological and fishery processes from multiple data sources, including tagging data, have become increasingly common (Goethel *et al.,* 2011; Sippel *et al.,* 2014 and references therein). However, while conventional tagging is particularly useful in assessment models with regard to estimating mortality rates and stock abundances, it is hard to use the data collected by this method to inform spatially structured models (Sippel *et al.,* 2014). One of the main reasons is that conventional tag methods depend on recapture of the tagged fish, no information is provided for the time between the fish is tagged until it is recaptured, and no information about the geographical position is provided for the fish not being recaptured. Moreover, the distribution of recaptures will be highly influenced by the distribution and intensity of the fishing effort. Therefore, the conventional tags usually provide only snapshot information, and less accurate information on the continuous long-term fish behaviour, dispersal and habitat use.

Recent developments in technology now offer a variety of methods to identify behaviour and migration routes of individual fish in their natural environment providing fishery independent locations (Robichaud and Rose, 2001; Thorrold *et al.,* 2001; Neuenfeldt *et al.,* 2009; Nielsen *et al.,* 2013). Environmental information obtained by Data Storage Tags (DSTs), also known as archival tags, from recaptured fish can provide a considerable amount of information which can be used to directly estimate the geographical position of individual fish throughout the time they were at liberty (e.g. Block *et al.,* 2001; Svedäng *et al.,* 2007). However, it is important to consider that these tags might affect fish behaviour or swimming performance (Mellas et al., 1985; Thorstad et al., 2013).

Geolocation is a technique that can relate the movements of individuals directly to environmental parameters like temperature, salinity, light, and additional information such as bottom depth and tidal patterns (e.g. Hunter *et al.,* 2003; Svedäng *et al.,* 2007). The precision of estimates of geographic position can be improved by combining more than one variable in the analysis (Block *et al.,* 2001). DSTs can be used to investigate on individual basis horizontal and vertical migrations in relation to spawning, nursery and feeding grounds (Heffernan *et al.,* 2004). These investigations will serve to estimate population rates of migration and dispersion in different localities and seasons in relation to hydrographic features.

5 TABACOD (Tagging Baltic Cod)

The objectives of the project TABACOD (Tagging Baltic Cod; http://www.tabacod.dtu.dk/), financed by BalticSea2020, are to provide information on growth and mortality of the Eastern Baltic cod to contribute in solving the issues with stock assessment and establish a solid scientific basis for cod management in the Baltic Sea. To do that a large-scale tagging program covering all Baltic cod stock components has been designed involving the major countries with a targeted fishery: Sweden, Denmark, Poland and Germany. The tagging areas (Fig. 8) has been assigned to each country based on the stock distribution from fishery dependent and independent surveys (e.g. BITS, Baltic International Trawl Surveys). The entire size range of cod is tagged, ensuring that both the smallest (15-25 cm) and largest (>45 cm) size groups are well represented.

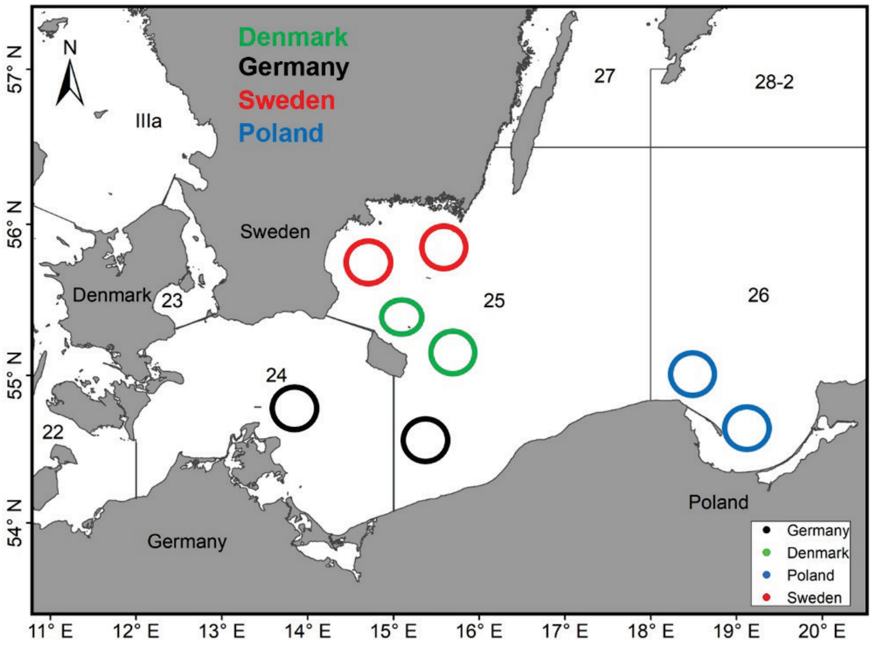

Figure 8. Map of the different TABACOD tagging areas divided by countries.

In order to provide the necessary growth and mortality data, as part of the TABACOD project, around 20 000 cod is caught and marked with traditional external tag (T-bar). Since traditional tagging and recapture data usually provide only snapshot information (i.e. they produce less accurate information on the continuous long-term fish behaviour, dispersal and habitat use), an additional 2000 cod is also tagged with electronic Data Storage Tags (DST).

In the case of Baltic cod stocks, as discussed previously, mixing of the Eastern and western Baltic cod stocks has become substantial in Subdivision 24 (Hüssy *et al.,* 2016). Moreover, the stock mixing within Subdivision 24 variates spatially and possibly also between seasons and age groups, introducing uncertainty in the allocation of catches to stock (ICES 2017c). In this sense, tagging data would be an important tool for understanding the Baltic stocks spatial distribution dynamics.

In addition to the current tagging data, extensive historical external tagging data from Sweden, Germany, Poland and Denmark is collate within TABACOD. These data is used to estimate directly the growth and mortality rates of Eastern Baltic Sea cod in 1960s-1980s, providing a baseline for comparisons with recent tagging surveys. Historical and contemporary tagging surveys will be use also to analyse the movements of cod across the Baltic and resolve the mixing between stocks. Collectively, the biological information gained from analysing historical tagging data will help develop new analytical stock assessment models and improve the advice for Baltic cod management. For a successful tagging study, a high reporting rate of the recaptured fish is necessary. Therefore, a comparison between the past and present reporting rates will be made to help improving future tagging studies.

6 Research questions

A number of questions regarding the recent developments in growth, mortality and reproductive potential of the Eastern Baltic cod have recently emerged. During my PhD I will try to answer some of these questions, including:

1. Are the present growth and mortality rates of Eastern Baltic cod different compared to the rates in the period between 1960s-1980s? Moreover, what are the possible drivers for these changes?
2. What is the present magnitude of stock mixing between Eastern and Western Baltic cod stocks? Are there any differences in the extent and seasonality of mixing between the present and the past (1960s-1980s)?
3. Are size and condition affecting the behaviour of Eastern Baltic cod in terms of vertical and horizontal migrations?
4. Is tagging a useful method to provide missing biological information to be integrated into stock assessment? How the experience gained from historical and present tagging of Eastern Baltic cod can help improving future tagging studies?
5. What are the consequences of low nutritional condition and low mean size for the reproductive output (e.g. potential fecundity) of Eastern Baltic cod?
6. Finally, I will investigate whether these results (growth, mortality and reproductive potential) can be combined in order to improve the stock assessment of Eastern Baltic Cod.

To answer the questions listed above, I will make use of results from historical and new tagging data, and histological analyses (Fig. 9).

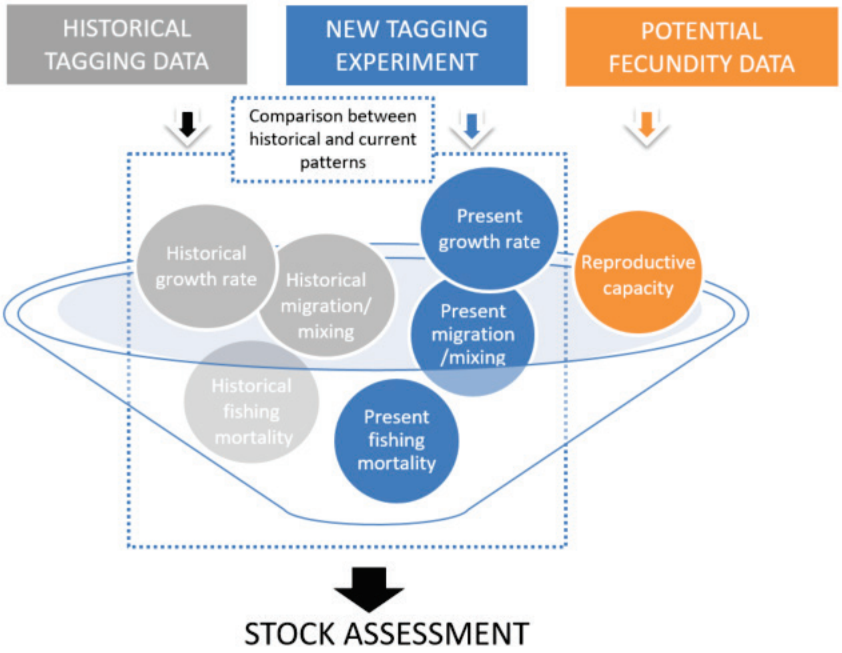

Figure 9. Schematic summary of the main data that will be used during this PhD with their possible inputs to the Eastern Baltic cod assessment.

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