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Published Version:
Regional and stock-specific differences in contemporary growth of Baltic cod revealed through tag-recapture data / McQueen K.; Casini M.; Dolk B.; Haase S.; Hemmer-Hansen J.; Hilvarsson A.; Hüssy K.; Mion M.; Mohr T.; Radtke K.; Schade F.M.; Schulz N.; Krumme U.. - In: ICES JOURNAL OF MARINE SCIENCE. - ISSN 1054-3139. - STAMPA. - 77:6(2020), pp. 2078-2088. [10.1093/ICESJMS/FSAA104]

This version is available at: https://hdl.handle.net/11585/809186 since: 2021-02-28

Published:

DOI: http://doi.org/10.1093/ICESJMS/FSAA104

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ICES JOURNAL OF MARINE SCIENCE VOL 77. ISSN 1054-3139

Doi: 10.1093/ICESJMS/FSAA104

Regional and stock-specific differences in contemporary growth of Baltic cod revealed through tag-recapture data

Kate McQueen[1*], Michele Casini[2,3], Bodo Dolk[1,4], Stefanie Haase[1], Jakob Hemmer-Hansen[5], Annelie Hilvarsson[2], Karin Hüssy[5], Monica Mion[2], Thomas Mohr[6], Krzysztof Radtke[7], Franziska Maria Schade[1], Norbert Schulz[4], Uwe Krumme[1]

[1]Thünen Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, 18069 Rostock, Germany

[2]Swedish University of Agricultural Sciences, Department of Aquatic Resources, Turistgatan 5, 45330 Lysekil, Sweden

[3]University of Bologna, Department of Biological, Geological and Environmental Sciences, Via Selmi 3, 40126 Bologna, Italy

[4]Fisch & Umwelt (FIUM) GmbH & Co. KG., Fischerweg 408, 18069 Rostock, Germany.

[5]Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, 2800 Kgs. Lyngby, Denmark

[6]Landesforschungsanstalt für Landwirtschaft und Fischerei Mecklenburg-Vorpommern, Fischerweg 408, 18069 Rostock, Germany.

[7]National Marine Fisheries Research Institute, Ul. Kołłątaja 1, 81-332 Gdynia, Poland

*Corresponding author: E-Mail: kate.mcqueen@thuenen.de, Tel: +49 381 66099 118, Fax: +49 381 66099 199

Abstract

The use of growth estimation methods which depend on unreliable age data have previously hindered quantification of perceived differences in growth rates between the two cod stocks inhabiting the Baltic Sea. Data from cod tagged in different regions of the Baltic Sea during 2007-2019 were combined, and general linear models were fit to investigate inter-regional (defined as area of release) and inter-stock (assigned to a subset of recaptures using genetic and otolith shape analysis) differences in individual growth. An average-sized cod (364 mm) caught in the western Baltic Sea and assigned to the western Baltic cod stock grew at more than double the rate (145 mm yr^{-1}) on average than a cod of the same size caught in the eastern Baltic Sea and assigned to the eastern Baltic cod stock (58 mm yr^{-1}), highlighting the current poor conditions for growth of cod in the eastern Baltic Sea. The regional differences in growth rate were more than twice as large (63 mm yr^{-1}) as the stock differences (24 mm yr^{-1}). Although the relative importance of environmental and genetic factors cannot be fully resolved through this study, these results suggest that environmental experience may contribute to growth differences between Baltic cod stocks.

Keywords: mark-recapture, individual growth rate estimation, stock assignment, Baltic Sea, Atlantic cod, fish stock productivity

Introduction

Understanding the dynamics of individual fish stocks, particularly parameters contributing to productivity such as growth rates, is key to sustainable fisheries management (Policansky and Magnuson, 1998; Crozier *et al.*, 2004). Individual growth rates of fish can be considered the integrated result of a variety of conditions experienced by the fish, including food availability and temperature (Jobling, 2002), as well as genetic variation (Gjedrem, 2000; Law, 2000). Demographically-independent stocks of the same fish species may differ in average individual growth rates and productivity, even when their distribution and habitat use overlaps to some extent. Such situations create fisheries management challenges, as mixed-stock fisheries run the risk of over-exploiting less-productive stocks (Ricker, 1958, 1973; Policansky and Magnuson, 1998; Heath *et al*., 2014). An understanding of average growth rates of fish in different stocks is therefore key to developing appropriate fisheries management strategies, and exploring whether differences are driven by environmental experience or genetic diversity can provide insight into the long-term dynamics of stock resilience to fishing pressure and environmental change (ICES, 2006).

Two exploited cod (*Gadus morhua*) stocks inhabit the Baltic Sea, referred to as the western Baltic cod (WBC) and eastern Baltic cod (EBC). The stock areas defined for stock assessment purposes are ICES subdivisions (SDs) 22-24 for the WBC, and SDs 24-32 for the EBC (Figure 1) (ICES, 2019a). The cod stocks are in close proximity geographically, with partially overlapping areas of distribution and some stock mixing (Hemmer-Hansen *et al.*, 2019; Weist *et al.*, 2019). Despite this, they differ in their environmental experience, status, and intrinsic population parameters (Bagge *et al.*, 1994; ICES, 2019b).

Growth of Baltic cod has traditionally been estimated by combining age data, gained through otolith interpretation, with size data (Bagge *et al.*, 1994). However, both cod stocks in the Baltic Sea have suffered from age estimation problems of differing severity (ICES, 2014).

Differences in interpretation of WBC otoliths by different age-readers have been previously detected (ICES, 2005, 2014), though recent age validation studies provide the information on the correct interpretation of zone structure necessary to avoid such issues in the future (McQueen *et al*., 2019a, Krumme *et al*., under review). Conversely, EBC otoliths are notoriously difficult to interpret (Hüssy, 2010) and low levels of precision and accuracy in age estimation are well documented (ICES, 2014; Hüssy *et al.*, 2016a). The lack of reliable age information for the EBC stock has hindered the estimation of growth and mortality rates, and contributed to the failure of the analytical age-based stock assessment in 2014 (Eero *et al.*, 2015) and the recent move to stock assessment methods with reduced reliance on age estimates (ICES, 2019b).

Studies on growth of Baltic cod have been conducted since at least the 1970s, with results revealing slower average growth rates of cod in the eastern versus the western Baltic Sea (reviewed in Bagge *et al*., 1994). Average length-at-age data were predominantly used for past Baltic cod growth studies. The use of such data for estimating growth can introduce biases stemming from sampling methods (e.g. via the use of gears which do not effectively sample all sizes), and will be particularly vulnerable to biases associated with the ageing uncertainties of Baltic cod (Bagge *et al.*, 1994). More recent studies which have included comparisons of growth rates of cod from different populations, including the Baltic cod stocks, have again relied on average weight-at-age data collected through routine sampling (Brander, 2000; Köster *et al.*, 2013). Although these studies provide insights into overall trends, the use of methods which rely on uncertain age information are unlikely to accurately quantify the differences in growth between cod from different regions or stocks in the Baltic Sea.

Within the past 20 years the body condition of EBC has declined (Eero *et al.*, 2015; Casini *et al.*, 2016) and there are indications that the growth rates of EBC have also decreased (Hüssy *et al*., 2018; ICES, 2019b). Key indicators of a decrease in growth rate include a noticeable lack of large cod in the eastern Baltic Sea, which cannot be attributed to fishing mortality alone (Eero *et al.*, 2015; Orio *et al.*, 2017, ICES, 2019a), and a reduction in size at maturation (Vainikka *et al.*, 2008; ICES, 2019b). Meanwhile, there is no indication that WBC growth rates have decreased in the past few decades (McQueen *et al.*, 2019b). Differences in growth rates between the two stocks may be increasing, as an outcome of the integrative effects of differing biotic, abiotic and anthropogenic pressures experienced by the two stocks, but the lack of reliable age data for the EBC has so far hindered a quantitative comparison.

Differences in the environmental experience of cod inhabiting the eastern and western Baltic Sea could contribute to perceived differences in growth rates. The WBC stock mainly inhabits the shallow western Baltic Sea (SDs 22-23, Figure 1, ICES, 2019b), which is strongly influenced by highly variable inflows of saline water from the North Sea (Matthäus and Franck, 1992; Schinke and Matthäus, 1998). The EBC stock mainly inhabits the less saline Bornholm Basin and surrounding areas (SDs 25-26, Figure 1, Eero *et al*., 2012; ICES, 2019a). This environment is characterised by strong thermohaline stratification that results in deep-water stagnation and occurrence of anoxic bottom conditions (Møller and Hansen, 1994), the extent of which have increased dramatically since the mid-1990s (Casini *et al.*, 2016). Tagging studies and genetic analysis have shown that the greatest amount of stock mixing occurs in the Arkona Sea (SD 24, Figure 1) (Bagge and Steffensen, 1989; Hemmer-Hansen *et al*., 2019; Weist *et al*., 2019).

A genetic basis to differences in growth between cod inhabiting different regions, or belonging to different populations, has been proposed previously (Purchase and Brown, 2001; Imsland and Jónsdóttir, 2003; Salvanes *et al.*, 2004; Hutchings *et al.*, 2007). However, the relative contribution of environmental and genetic influences for explaining differences in growth rates between the genetically distinct Baltic cod stocks has never been investigated.

Therefore, the influence of environment and genetics on growth potential of Baltic cod warrants further investigation, to better understand the capacity for the stocks to persist and recover under current and future environmental conditions.

Tag-recapture studies allow individual growth of wild fish to be directly measured, and can therefore be a useful approach when age estimation is problematic (e.g. de Pontual *et al*., 2006). Baltic cod tagging data has recently been used to estimate contemporary growth rates of WBC (McQueen *et al.*, 2019b), and growth of EBC during historical periods (Mion *et al.*, 2020). Tagging data from studies that encompass the distribution range of a fish stock are especially valuable, as they can be used to explore regional variation in life-history traits such as growth (Shackell *et al.*, 2019).

In this study, the compilation of data from recent tagging studies conducted in different regions of the southern Baltic Sea provided the opportunity to compare the current individual growth rates of wild Baltic cod. These tagging datasets provide the only contemporary, directly measured growth information presently available for Baltic cod, independent from unreliable age data. By assigning recaptured cod to their stock of origin using genetics and otolith shape analysis, it was possible to explore stock- and region-specific differences in individual growth. Estimation of the differences in growth rates of Baltic cod from different stocks and regions using tagging data is a first step towards exploring the relative importance of environmental and genetic influences on Baltic cod growth rates, though without fully resolving the issue.

Methods

Cod tagging data

During 2007 to 2019, 40463 cod were tagged in the southern Baltic Sea through three separate projects (the Fehmarn, Nienhagen reef, and TABACOD projects). These projects were conducted in different regions (Figure 1) and during slightly different periods, but overlapped considerably in methodologies (Table 1), and covered the current main areas of distribution of the two Baltic cod stocks. The Fehmarn and Nienhagen Reef projects were German national tagging programmes, and all cod tagged for these studies were released in SD 22 in the western Baltic Sea (Figure 1). Cod for these studies were captured in shallow waters using stationary pound nets or cod pots (McQueen *et al.*, 2019b, Krumme *et al.*, under review). Cod tagged within the international TABACOD project (TAgging BAltic COD) were released in Danish, German, Polish and Swedish national waters in SDs 24-26 (Figure 1). Fish for this tagging experiment were mainly caught by short (5-30 minutes) bottom trawls from research or commercial vessels. A subset (<10%) were captured using other gear types, such as fish traps, pound nets and angling. All cod were tagged with T-bar tags, and most cod from the Fehmarn and TABACOD projects additionally received an intraperitoneal injection of tetracycline-hydrochloride to induce a permanent mark on the otoliths (Stötera *et al.*, 2018, Table 1). A subset of cod for the TABACOD project were also surgically implanted with data storage tags (Table 1). It was assumed that tagging type did not influence the fish growth rate, an assumption that is partially justified by previous experiments (Righton *et al.*, 2006; Stötera *et al.*, 2018).

The tagging studies and a reward for each recapture were publicised. Recaptured cod and recapture information were provided by commercial and recreational fishers, or scientists involved in the studies. The total numbers of cod recaptured from the Fehmarn, Nienhagen Reef and TABACOD projects were 75, 1030, and 375, respectively.

For growth analysis, reliable data on date and total length at release ($TL_{release}$) and recapture (recorded to the nearest centimetre in the Nienhagen Reef project, and to the nearest millimetre in the TABACOD and Fehmarn projects) of cod were required. The number of days between release and recapture were recorded as the days-at-liberty (DAL). An overview of the relevant data is summarised in Table 1.

The majority of recaptures from the Fehmarn (52%) and TABACOD (85%) projects were frozen before measurement. A subset of the fresh measurements from the TABACOD (16%) and Fehmarn (21%) projects were provided by the fisher who recaptured the cod. Of the recaptures from the Nienhagen Reef project, 80% were recaptured live in cod pots at the reef by scientists involved in the study, and were measured and then re-released. The remainder of recaptured cod from the Nienhagen Reef project were captured by commercial and recreational fishers who provided length and recapture measurements.

The majority of cod tagged in SD 22 were recaptured within the same subdivision. There was extensive transfer of tagged cod across the borders of SDs 24-26. Few cod tagged in SDs 24-26 were recaptured in the Kattegat (SD 21) and the western Baltic Sea (SDs 22-23, Table 2).

Data preparation for growth analysis

Fish at liberty for <50 days were excluded from growth analysis. Fish at liberty for short time periods can bias growth estimates downwards (Tallack, 2009) and introduce high variability in growth estimates (Francis, 1988), if enough time has not passed for observable growth to occur. A threshold of 50 days has been demonstrated to be appropriate for growth estimation of cod from tagging data (50 day threshold used in McQueen *et al*., 2019b, 60 day threshold used in Mion *et al*., 2020, and Tallack, 2009). After removing individuals which lacked information necessary for growth estimation, or which were at liberty less than 50 days, the total sample size was 1012, with 36 from the Fehmarn project, 704 from the Nienhagen Reef project and 273 from the TABACOD project (Table 1).

As frozen storage of fish generally induces shrinkage (e.g. Halliday and Roscoe, 1969; Buchheister and Wilson, 2005; Ogle, 2009; McQueen *et al*., 2019c), the total or gutted length of recaptured cod which were stored in a freezer before measurement was converted to predicted fresh total length using shrinkage conversion factors developed for Baltic cod (McQueen *et al.*, 2019c). The freezing shrinkage correction factors were applied to 52% of the Fehmarn project recaptures and 85% of the TABACOD recaptures available for growth analysis, 30% of which were gutted before freezing.

Estimation of individual growth

Absolute growth (*G*) was estimated as:

$$G = \frac{\Delta L}{DAL} * 365$$

where ΔL indicates change in total length in millimetres of fish between release and recapture and *DAL* indicates time-at-liberty in days. The estimated daily growth rate was multiplied by 365 to estimate predicted annual growth of each recapture, assuming constant, stable growth throughout the year.

The assumption of constant growth may not be valid if there are strong seasonal variations in growth (Ailloud *et al.*, 2014). Previous growth modelling has indicated that seasonal variation in growth of tagged cod from Nienhagen Reef is relatively small, with the peak in average growth rate only 1.35 times the minimum growth rate (McQueen *et al.*, 2019b).

To explore the potential bias that may be introduced by including fish at liberty for only part of a year, statistical analyses were repeated using only data for fish at liberty for 275-455 DAL (i.e. close to one year at liberty). This resulted in a dataset of only 226 individuals (Supplementary Figure S1), including 11, 143, and 72 recaptures from the Fehmarn, the Reef Nienhagen and the TABACOD projects respectively.

Stock assignment

Different methods were applied to assign the recaptured individuals to their likely stock of origin. The cod tagged in Fehmarn were assumed to be WBC, as the majority of cod tagged were juveniles (Krumme *et al*., under review), and therefore were assumed to have been spawned in a nearby WBC spawning ground. This assumption is supported by the genetic relationship between juveniles and adults sampled from the same geographic regions of the Baltic Sea, which suggests local origin and retention of juveniles (Nielsen *et al*., 2005). However, there may be some error associated with this stock assignment, especially given that spawning EBC individuals have occasionally been detected in SD 22 (Stroganov *et al.,* 2017; Weist *et al.* 2019). Without conducting additional genetic analyses it is not possible to assess the accuracy associated with this assumption.

For the cod tagged in the Nienhagen reef project, the stock assignment through otolith shape analysis described in McQueen *et al*. (2019b) and Schade *et al*. (2019) was used. This method of stock assignment has a classification accuracy of approximately 83% for Baltic cod (Schade *et al.*, 2019), and has been used in the stock assessment since 2019 (ICES 2019b). This analysis was only conducted on the small sub-sample of recaptures for which otoliths were available (n=33).

For the TABACOD recaptures, most cod were assigned genetically to their stock of origin. Tissue samples were collected during analysis of recaptured cod, stored in ethanol (95%) and were genotyped using 39 single nucleotide polymorphism markers following the procedures described in Hemmer-Hansen *et al*. (2019). A subset of the individuals that could not be genetically assigned were assigned to their stock of origin using otolith shape analysis (Schade *et al.*, 2019).

Statistical analyses

Statistical analyses were carried out to explore the relative importance of length at release (in millimetres), release region (SD 22, 24, 25, 26) and assigned stock (WBC, EBC) on explaining the variability in individual growth rates of the tagged fish.

The variable $TL_{release}$ was mean centred ($TL^{*}_{release_i} = TL_{release_i} - \overline{TL}_{release}$) prior to statistical analysis, to allow for easier, biological meaningful interpretation of the main effects (Schielzeth, 2010). A general linear model (GLM) was used to explore variation in the $TL^{*}_{release}$ and growth rate (*G*) relationship between regions of release. Given the extensive exchange of recaptures across subdivision boundaries, with high proportions of cod tagged in SD 24 recaptured in SDs 25-26 and vice-versa (Table 2), these three SDs were pooled together for statistical analysis. Few cod tagged in SD 22 were recaptured in any of the other SDs, and few cod tagged in SD 24-26 were recaptured in SD 22 (Table 2), so it was judged reasonable to consider SD 22 separately. The region variable therefore splits the data into two groups: cod which were released in SD 22, and cod which were released in SDs 24-26. The following model (GLM1) was fit to the data:

$$G_i = \alpha + \beta_1 region_i * \ \beta_2\, TL^{*}_{release_i} + \varepsilon_i \text{ where } \varepsilon_i \sim N(0, \sigma^2) \qquad (1)$$

i represents individual, and "*" denotes that the fixed effects and interaction between them were included in the model.

In addition, to explore the combined influence of assigned stock and region of release on individual growth, a GLM was fit to the growth data for individuals which had been assigned to a stock of origin. As less than one third of the recaptured individuals were assigned to a stock (n=325, Table 1), this model was considered in addition to GLM 1, which was fit to the entire available dataset (n=1012). This approach was used to maximise the use of the available tagging data for exploring regional and stock specific differences in growth. The following model (GLM 2) structure was used:

$$G_i = \alpha + \beta_1 stock_i * \beta_2 region_i * \beta_3\, TL^{*}_{release_i} + \varepsilon_i \text{ where } \varepsilon_i \sim N(0, \sigma^2) \qquad (2)$$

i represents individual, and "*" denotes that the fixed effects and interactions between them were included in the model. For both models, the significance of each of the interaction terms and fixed effects were assessed using *F*-tests, and non-significant terms were subsequently removed from the final model. All statistical analyses were conducted using R v3.5.0 (R Core Team, 2018), with the package "stats" used to fit the models (function: "lm") and calculate predicted mean growth rates and standard errors (function: "predict.lm"), and the package "jtools" (Long, 2019) used to create plots of results.

Results

Stock assignment of recaptures

In total, 202 of the TABACOD recaptures used in growth analysis were genetically assigned to a stock, with 16 recaptures assigned to the WBC stock and 186 recaptures assigned to the EBC stock. An additional 56 of the TABACOD recaptures used in growth analysis were assigned to a stock using otolith shape analysis, with 41 assigned to the EBC stock and 15 to the WBC stock (Figure S2). The remaining 31 recaptured cod from the TABACOD project were not assigned to a stock due to the fish not being returned to a research institute, or the sample being lost (Table 1).

Of the recaptured cod that could be assigned to a stock, 13% (n=10) that were tagged in the western Baltic Sea (SD 22) were assigned to the EBC stock. Of cod released in SD 24, which is recognised as a mixing zone for the two stocks, 17% (n=22) of stock-assigned recaptures were WBC, and 83% (n=109) were assigned as EBC. An even smaller percentage of recaptures which were released in the eastern Baltic Sea (SD 25-26) were assigned to the WBC stock (7%, n=9) (Supplementary Figure S2).

Regional differences in growth

Including fixed effects and the interaction term significantly improved the fit of GLM 1 to the full dataset of recaptures (Supplementary Table S1).

The relationship between $TL^*_{release}$ and growth rate was significantly negative, with average growth rate decreasing as fish length at release increased. The slope of the relationship between $TL^*_{release}$ and growth rate was steeper for cod released in SDs 24-26 than for those released in SD 22 (Table 3, Figure 2). This suggests that the decrease in growth with increasing fish length at release is more pronounced in the region SD 24-26. The average growth rate of an average-sized cod from this dataset ($TL_{release}$=364 mm) released in SD 22 was significantly higher (G=126 ± 2 mm yr^{-1}) than the average growth of a cod of the same size released in SDs 24-26 (G=63 ± 3 mm yr^{-1}).

The same analysis, including only fish at liberty for 275-455 days, gave similar results, suggesting that seasonality in growth did not bias the analysis (Supplementary Table S2).

Regional and stock differences in growth

Including the variables $TL^*_{release}$, region, and assigned stock significantly improved the fit of GLM 2 to the reduced dataset of recaptures with stock assignment. None of the interaction terms included in the initial model were significant (Supplementary Table S3). This indicates that across the length range of data available, the relationship between release length and growth did not vary between stocks or regions, though the intercepts of the model did. Therefore, the interaction terms were removed and the model was refit (GLM 3) as:

$$G_i = \alpha + \beta_1 region_i + \beta_2 stock_i + \beta_3 TL^*_{release_i} + \varepsilon_i \text{ where } \varepsilon_i \sim N(0, \sigma^2) \quad (3)$$

In GLM 3, there was again a significant negative relationship between $TL^*_{release}$ and growth rate, with both region of release and assigned stock significantly influencing the individual growth rate (Table 4, Figure 3). Overall, a WBC tagged and released in either region was predicted to grow significantly faster (24 ± 8 mm yr^{-1}) than an EBC of the same size tagged and released in the same region (Table 4). An even greater difference was predicted between cod of the same stock tagged in different regions, with cod of either stock tagged and released in SD 22 predicted to grow significantly faster (63 ± 9 mm yr^{-1}) than a cod of the same size and stock tagged and released in SDs 24-26 (Table 4). The lowest average growth rates were therefore predicted for EBC in SDs 24-26 ($TL_{release}$ = 364 mm: 58 ± 3 mm yr^{-1}), and the highest growth rates for WBC in SD 22 ($TL_{release}$ = 364 mm: 145 ± 6 mm yr^{-1}). Intermediate growth rates were predicted for EBC tagged in SD 22 ($TL_{release}$ = 364 mm: 121 ± 9 mm yr^{-1}) and WBC tagged in SDs 24-26 ($TL_{release}$ = 364 mm: 81 ± 7 mm yr^{-1}).

The effect sizes for regional differences in growth were similar between GLM 3 and GLM 1, as was the slope of the relationship between $TL^{*}_{release}$ and growth rate (Tables 3, 4), suggesting that the reduced dataset of recaptures with stock assignment still captured the regional differences apparent in the full dataset.

The same analysis could not be conducted including only fish at liberty for 275-455 days, as sample sizes per group became too small (Supplementary Table S4).

Discussion

The analysis of the combined data from three recent tagging studies of cod in the Baltic Sea revealed clear regional differences in the current growth rates of Baltic cod, with cod tagged in the eastern Baltic Sea growing at approximately half the rate of those tagged in the western Baltic Sea. The striking differences in growth may be due to differences in environmental experience, genetic differences between cod of the different stocks, or a combination of these factors. While it was not possible to conclusively disentangle genetic and environmental effects with the tagging dataset of wild cod used in this study, some insight was gained into the relative importance of stock and region on the growth rates of Baltic cod. The model fit to the reduced dataset of individuals with stock assignment information reproduced the regional growth differences apparent from analysis of the full dataset, and revealed a smaller, though still significant, effect of stock assignment. EBC grew significantly slower than WBC, and the slowest growth rates were predicted for EBC inhabiting the eastern Baltic Sea region. These findings are in line with the growing body of evidence that growth of EBC has been relatively low in recent years, one of several indicators that this cod stock is in distress (Eero *et al.*, 2015).

Drivers of regional differences in growth rates of Baltic cod

The observed slow growth rates of cod in the eastern Baltic Sea region coincide with numerous indications that changes in the ecosystem and environment in the eastern Baltic Sea in recent years have had negative impacts on EBC. An observed decrease in nutritional condition of EBC since the early 1990s is likely linked to the documented decline in food quality and availability in the eastern Baltic Sea (Eero *et al.*, 2012; Casini *et al.*, 2016), which has detrimental consequences on feeding level and energy intake (Neuenfeldt *et al.*, 2019). The extent of hypoxic bottom regions has greatly increased within the known habitat of EBC since the mid-1990s (Casini *et al.*, 2016). Hypoxia may cause direct habitat loss of benthic organisms, consequently reducing access of cod to important benthic prey (Neuenfeldt *et al.*, 2019). A decline in the proportion of benthic organisms such as *Mysis* spp. and *Saduria entomon* in EBC stomachs during the past decade has already been observed (Kulatska *et al.*, 2019; Neuenfeldt *et al.*, 2019). Low oxygen levels can also directly restrict the growth potential of cod by decreasing food consumption rates (Chabot and Dutil, 1999). This mechanism has been proposed as an alternative explanation for the apparent decrease in growth rates of smaller cod in the eastern Baltic Sea (Brander, 2020). Additionally, an increase in infestation of cod livers in the eastern Baltic Sea with larvae of anisakid worm *Contracaecum osculatum* has been observed during the past decade (Mehrdana *et al.*, 2014;

Horbowy *et al.*, 2016; Sokolova *et al.*, 2018). It is assumed that high levels of infestation can be partially linked to a diet dominated by fish, which act as transport hosts to the parasite (Sokolova *et al.*, 2018). Recently, thiamine deficiency has also been suggested as a possible mechanism contributing to the low growth and body condition of the EBC (Engelhardt *et al.*, 2020).

Conditions for growth of cod are apparently better in the western than the eastern Baltic Sea. The longitudinal environmental gradients present in the Baltic Sea (Snoeijs-Leijonmalm and Andrén, 2017) create differences in environmental experience of cod inhabiting different regions. Atlantic cod is a marine species, and therefore the higher salinities of the western Baltic Sea are closer to the salinity experience of cod in most other regions. The less saline eastern Baltic Sea can be considered a marginal ecosystem for this species (Johannesson and André, 2006). The average bottom water temperatures in the western Baltic Sea are higher than those in the eastern Baltic Sea (Snoeijs-Leijonmalm and Andrén, 2017), so given the relationship between temperature experience and growth rate of cod (Pedersen and Jobling, 1989; Brander, 1995), the warmer western Baltic Sea environment may contribute to faster growth of cod. However, summer temperatures in the shallow western Baltic may be above optimal for growth of cod, contributing to the low amplitude of seasonality in growth rates (McQueen *et al.*, 2019b). It has been postulated that these conditions may contribute to slightly slower growth rates of cod in the western Baltic Sea compared to cod in the nearby Irish and southern North Sea (Thorsen *et al*., 2010; McQueen *et al.*, 2019b).

Established environmental differences may have contributed to the difference in growth rates reported between western and eastern Baltic cod in the past (Bagge *et al.*, 1994). Perhaps more important for understanding the current, striking differences in cod growth between the eastern and western Baltic Sea, is that the key issues currently afflicting cod in the eastern Baltic are not apparent in the western Baltic to the same extent. Infection rates of parasitic liver worms are much lower in cod in the western Baltic (Sokolova *et al.*, 2018), and hypoxic areas, though present, are not as extensive and permanent as in the eastern Baltic Sea (Hansson *et al.*, 2019; Naumann *et al*., 2019).

The slow growth of cod in the eastern Baltic Sea appears to be symptomatic of an interconnected combination of deleterious factors and deteriorating habitat quality currently affecting cod in this region, which until now do not appear to be affecting the western Baltic to the same extent. The recent availability of contemporary tagging data allowed the estimation of the current growth rate of EBC and, likewise, the comparison of growth rates between neighbouring and partially overlapping cod stocks in the Baltic Sea.

Inter-regional growth comparisons beyond the Baltic Sea

Atlantic cod are widely distributed across relatively heterogeneous regions in the North Atlantic (Drinkwater, 2005), and comparative analysis between cod populations has proven an effective method of revealing general trends and patterns in population-specific differences in life-history traits such as growth rate (Brander, 1994; Righton *et al.*, 2010; Thorsen *et al.*, 2010). In particular, inter-regional comparisons have revealed a correlation between individual growth rates of cod and average ambient temperatures (Brander, 1994). The average annual bottom temperature in the Bornholm Basin has been ca. 7°C for the past five years (Naumann *et al*., 2019), similar to the average temperatures experienced by cod inhabiting the Western Bay of Fundy and Georges Bank regions of the Northwest Atlantic (Shackell *et al.*, 1997). Results from tagging studies carried out in this region revealed that the average annual growth rates of cod tagged with 400 mm total length in the Western Bay of Fundy (180 mm yr^{-1}) and Georges Bank (149 mm yr^{-1}) (Shackell *et al.*, 1997) were considerably higher than the average annual growth rate of cod tagged at the same length in the eastern Baltic Sea (from our study, 55 mm yr^{-1}), despite the similarity in thermal environments. Not only do cod in the eastern Baltic Sea grow slower than the cod in the neighbouring western Baltic Sea, but growth of cod in the eastern Baltic is also slow in comparison with the growth of cod inhabiting regions with a similar thermal environment outside the Baltic Sea.

Study limitations

The results of this study suggest that region, and hence the environment, may have a stronger influence on growth rate of Baltic cod than assigned stock. This interpretation is partially supported by the above mentioned environmental factors detrimental to cod growth present in the eastern Baltic Sea, but almost absent from the western Baltic. However, it should be stressed that the design of our study is not optimized for separating genetic from environmental effects on growth. While we are able to identify the genetic component, we have limited ability to accurately control for effects of environmental variation. Additional caveats are the limited number of tagged cod released in SDs 24-26 that were subsequently assigned to the WBC stock, and the limited number of individuals released in SD 22 assigned to the EBC stock, which reduces the power of the comparisons. Additionally, some error and uncertainty is associated with the non-molecular stock assignment methods used, though their classification accuracy can be assumed to be relatively high (see methods section and Schade *et al.,* 2019). Finally, the regional assignment could not account for potential movement between neighbouring regions during time-at-liberty, an issue that is difficult to avoid in tagging studies of mobile marine fish species (Tallack, 2009). Laboratory breeding experiments or common-garden experiments, such as those carried out to reveal population differences in cod larval growth, survival, and their reaction norms across varying environmental temperatures and food availability by Hutchings *et al*. (2007), would need to be carried out to test the hypotheses regarding environmental and genetic influences on growth arising from this study. However, as conducting the required common-garden experiments on a long-lived, broadcast spawning fish species such as cod can be particularly challenging (Hutchings *et al.*, 2007), this analysis of available tagging data is a useful first step towards addressing this research question.

Tagging data provided a valuable, age-independent source of growth information, with which to explore the current growth rates of cod in the Baltic Sea. The coincidence of several tagging projects in different regions of the Baltic allowed for quantification of the suspected divergence in growth rates between the two Baltic cod stocks, which had been previously hindered by the age reading uncertainties (Bagge *et al.*, 1994). However, although the use of tagging data avoids the age reading issues, additional limitations have to be considered when interpreting recapture results. Seasonality in growth is an important issue to consider when estimating growth from tagging data (Ailloud *et al.*, 2014). The results of our sensitivity analysis, and other recent growth analysis of Baltic cod (McQueen *et al*., 2019b), suggest that seasonal fluctuations in Baltic cod growth are currently low, which may be an outcome of overall low growth rates. Additionally, the sub-sample of length measurements used for growth analysis provided by commercial and recreational fishers will potentially have higher measurement error than measurements taken by trained scientific staff (Eveson and Million, 2008; McQueen *et al.*, 2019b). However, as measurements recorded by fishers were present in each of the project datasets, this should not have introduced a strong directional bias to the data.

An additional consideration specific to this study was that the tagging projects were not conducted simultaneously. In particular, the data collection for the Nienhagen Reef project ended the same year as the start of the TABACOD project, meaning that the majority of the data from the western Baltic Sea was collected several years before the data from the eastern Baltic. However, the growth rates of cod in the western Baltic Sea appear to have remained relatively stable for the past 40 years (McQueen *et al.*, 2019b), and the growth rates of cod tagged more recently at Fehmarn in the western Baltic Sea do not appear to diverge substantially from the growth rate of cod tagged at the reef several years earlier (Supplementary Figure S2). Therefore, it seems reasonable to assume that the differences in observed growth rates between cod in the western and eastern Baltic Sea represent a real difference between stocks and regions, and are unlikely to be due mainly due to the temporal differences in the study periods.

Conclusion

The comparison of growth rates estimated from recent tagging data revealed clear inter-stock and inter-regional differences in Baltic cod growth. The clear differences in this productivity-related trait presents challenges for the management of fisheries in areas where the two stocks mix, and research into mixing proportions and their consequences is therefore an active area relevant to the stock assessment process for Baltic cod (Eero *et al.*, 2014; Hüssy *et al.*; 2016b; ICES, 2019b; Hemmer-Hansen *et al*., 2019; Schade *et al*., 2019; Weist *et al*., 2019). The exceptionally slow growth rate of cod in the eastern Baltic Sea seems likely to be linked to the current detrimental ecosystem conditions for cod. Our results suggest that the differences in growth may be influenced by environmental factors, indicating that EBC growth rates, and thus stock productivity, would have the capacity to increase, but only if ecosystem and environmental conditions improved. The usefulness of combining data from several tagging studies to gain a more comprehensive understanding of the status and dynamics of wild fish stocks are exemplified in the inter-regional comparison presented here.

Acknowledgements

Thanks go to all technical staff involved in the tagging, collection and processing of samples used in this study. The Nienhagen Reef tagging experiment was undertaken by staff from the Research Centre for Agriculture and Fishery Mecklenburg-West Pomerania

(Landesforschungsanstalt für Landwirtschaft und Fischerei Mecklenburg-Vorpommern (LFA)) and the Institute of Fish and Environment (FIUM GmbH &Co. KG). The Fehmarn tagging experiment was carried out by staff from the Thünen Institute of Baltic Sea Fisheries. TABACOD tagging was carried out by staff from the National Marine Fisheries Research Institute, the Technical University of Denmark, the Swedish University of Agricultural Sciences and the Thünen Institute of Baltic Sea Fisheries. The tagging experiments were conducted under the following animal test permissions: Nienhagen Reef project: TVA 7221.3-1-060/15; Fehmarn project: V 244 – 7224.121.9-6 (84-6/14); German TABACOD T-bar tagging: AZ 7221.3.1-029/15; German TABACOD DST tagging: AZ 7221.3.1-007/18; Danish TABACOD T-bar and DST tagging: 016-15-0201-00929, Polish TABACOD T-bar tagging: Permission no 19/2016, dated 28.06.2016, Swedish TABACOD T-bar and DST tagging: Dnr 5.8.18-14823/2018

Funding

The Nienhagen reef tagging experiment was supported by the European Fisheries Funds (EFF) and the Ministry of Agriculture, Environment and Consumer Protection, Mecklenburg-Vorpommern (LU). The Fehmarn tagging experiment was funded by the European Commission's Data Collection Framework (DCF). The TABACOD tagging experiment was funded by BalticSea2020 (http://balticsea2020.org) through the project "*Tagging Baltic Cod*" (TABACOD). Additional funding was provided by the Swedish Agency for Marine and Water Management.

Data availability statement

The Fehmarn data were provided by the Thünen Institute of Baltic Sea Fisheries. The Nienhagen Reef data were provided by FIUM GmbH & Co. KG. These data may be shared on reasonable request with permission of the respective institutes. The TABACOD data are subject to an embargo of 5 years (i.e. until the end of 2025). Once the embargo expires, the data will be available upon reasonable request.

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Table 1: Overview of data used in growth analysis, from three different tagging projects in the Baltic Sea. Only individuals with ≥ 50 days at liberty (DAL), and with reliable data on date and total length at release ($TL_{release}$) and recapture were included in the analysis.

Project	Release SD	Study period	Number of releases	Tag type	Number of recaptures	Number of recaptures with stock assignment	$TL_{release}$ range (mm)	mean $TL_{release}$ (± s.d.)	DAL range	mean DAL (± s.d.)
Fehmarn	22	Oct 2014 - Oct 2018	9111	T-bar and intraperitoneal injection of tetracycline-hydrochloride	36	36	180 - 390	284 (±61)	56 – 835	251 (±159)
Nienhagen Reef	22	Feb 2007 – Aug 2016	6000	T-bar	704	33	200 - 690	362 (±75)	50 – 1312	226 (±180)
TABACOD	24-26	Mar 2016 – May 2019	25352	T-bar (100%);intraperitoneal injection of tetracycline-hydrochloride (79%); surgically implanted data storage tag (5%)	273	257	177 – 541	384 (±58)	51 – 927	270 (±173)

Table 2: Release and recapture regions (categorised by ICES subdivisions (SDs)) of the individuals used in growth analysis. SDs 22-24 are the WBC management area, SDs 24-26 are the EBC management area. SD 24 is recognised as a stock mixing area.

	Recapture SD						
Release SD	**21**	**22**	**23**	**24**	**25**	**26**	***Total***
22	0	734	0	6	0	0	*740*
24	2	6	0	76	50	0	*134*
25	0	1	1	34	55	1	*92*
26	0	1	0	2	12	32	*47*
Total	*2*	*742*	*1*	*118*	*117*	*33*	*1013*

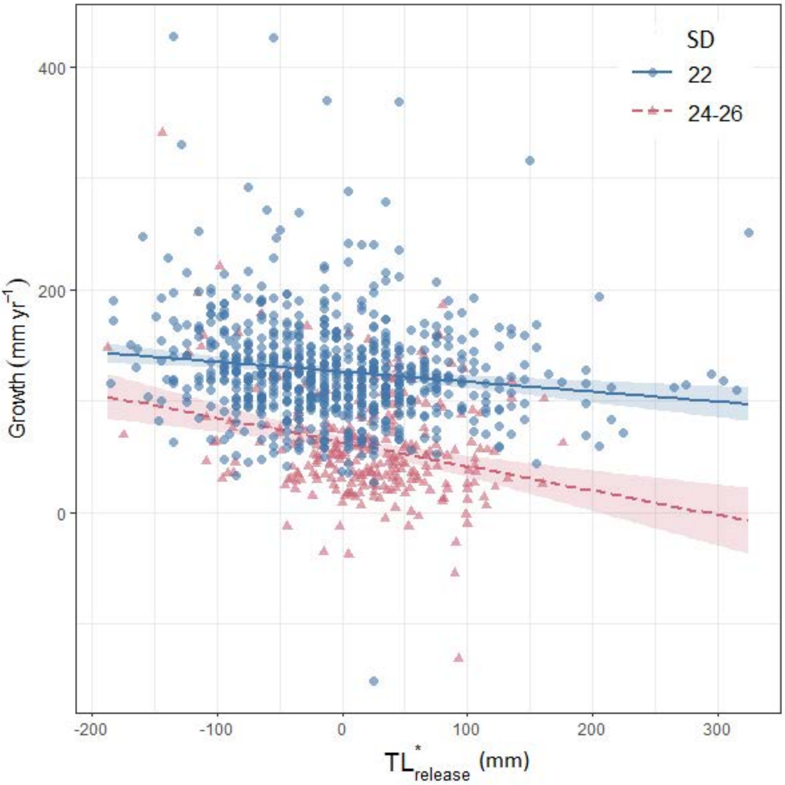
Table 3: Parameter estimates and standard errors for a general linear model of the inter-regional differences in individual growth (GLM 1) ($F_{3,1009}$=153.9, p<0.001). $TL^{*}_{Release}$=total length at release, mean centred (mean $TL_{Release}$ =364 mm). SD=subdivision of release.

Term	**Parameter estimate**	**Standard Error**	***t*-value**	***p*-value**
Intercept (***region*** = SD 22, $TL^{*}_{Release}$=0)	126.0	1.7	73.7	<0.001
$TL^{*}_{Release}$	-0.1	0.02	-4.0	<0.001
region = SD 24-26	-62.9	3.4	-18.6	<0.001
$TL^{*}_{Release}$: SD 24-26	-0.13	0.05	-2.4	0.02

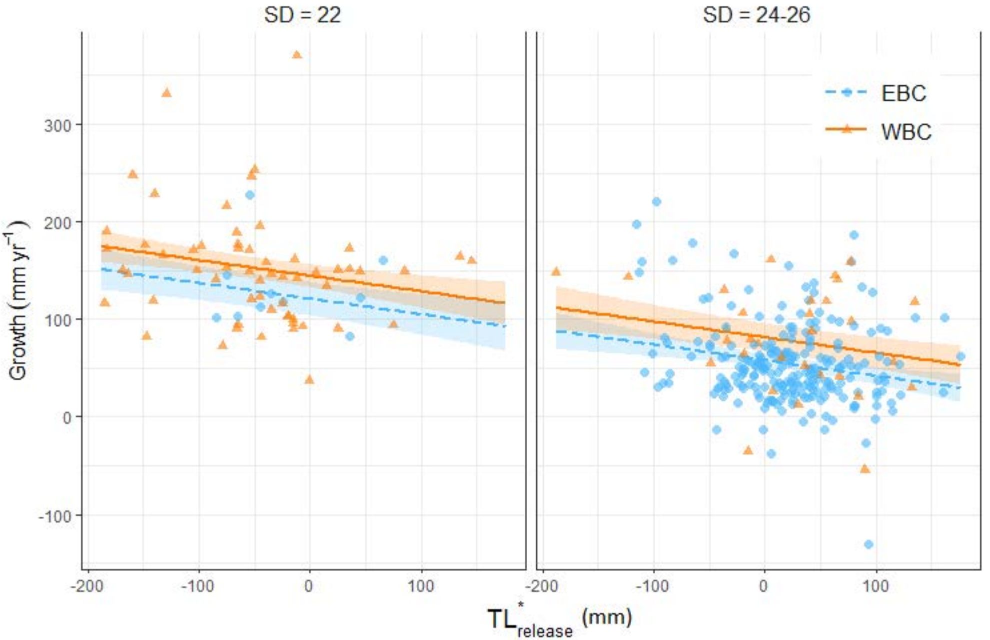
Table 4: Parameter estimates and standard errors for a general linear model of inter-regional and inter-stock differences in growth (GLM 3) ($F_{3,322}$=80.25, p<0.001). WBC= western Baltic cod; EBC = eastern Baltic cod. $TL^{*}_{Release}$=total length at release, mean centred (mean $TL_{Release}$ =364 mm). SD=subdivision of release.

Coefficient	**Parameter estimate**	**Standard Error**	***t*-value**	***P*-value**
Intercept (*stock* = EBC, *region* = SD 22, $TL^{*}_{Release}$=0)	120.9	8.7	13.9	<0.001
$TL^{*}_{Release}$	-0.16	0.04	-3.7	<0.001
***region* = SD 24-26**	-63.1	8.8	-7.2	<0.001
***stock* = WBC**	23.6	7.6	3.1	0.002

Source of elevation data: GEBCO Compilation Group (2019)



SD
22
24-26
400
200
0
Growth (mm yr⁻¹)
-200
-100
0
100
200
300
TL*release (mm)



SD = 22
SD = 24-26
EBC
WBC
Growth (mm yr-1)
300
200
100
0
-100
-200
-100
0
100
TL*release (mm)