**Faster or slower: Has growth of eastern Baltic cod changed?**

**Abstract**

Recent environmental changes have influenced the ecology and biology of eastern Baltic cod. Declining somatic condition, maturation at smaller size and restricted size distribution of the population suggest that growth rates have decreased between the early 2000s and the 2010s. Extensive age estimation problems have until now precluded testing of this hypothesis. This study presents evidence for a decrease in somatic growth rate of Baltic cod. Temporal patterns of growth, condition and maturation were analysed based on two complementary analyses: Length frequency mode progression derived from DATRAS bottom trawl survey data and known-age samples, where size at age was back-calculated from daily otolith growth patterns. In the known-age samples, growth was positively related to somatic condition at capture with maturity dependent differences. Immature individuals had experienced significantly lower growth and were in lower condition at capture than mature individuals. Growth rates in the known-age samples were estimated at 9.5, 7.8 and 5.7 cm per year for age classes 1, 2 and 3 respectively. Growth between age 2 and 3 decreased significantly from 8.8 cm in the 1997 year class to 7.6 cm in the 2010 year class. While the 2001 and 2004 known-age samples were representative for the population, the 2013 sample was biased towards individuals with a higher condition and growth. Complementary length frequency analysis following the length mode of fish from age 2 to age 3 confirmed growth estimates from the early 2000’s, while suggesting a 37.5% lower growth in 2013 compared to 2005.

**Key words**: Back-calculation, Baltic cod, growth, length frequency, maturation, otolith

**Introduction**

The eastern Baltic cod stock has been considered as one of the most data rich and best studied cod stocks worldwide, in particular owing to two large-scale EU projects (CORE 1997; STORE 2003). Between 1995 - 2015, substantial changes in the Baltic Sea environment (increasing temperatures, expansion of hypoxic areas, decreasing salinity) (HELCOM 2016) and ecosystem have occurred, which directly or indirectly, have influenced the ecology and population dynamics of eastern Baltic cod. Nutritional condition of cod in the Baltic has declined since the 1990s, which has been related to limited availability of sprat as a prey (Eero et al*.* 2012), increased parasite infestation (Horbowy et al. 2016), and density dependent mechanisms affecting productivity driven by an increasing restriction of the stock distribution area (Svedäng and Hornborg 2014; Bartolino et al. 2017) owing to an increased extent of hypoxic areas (Casini et al*.* 2016). Concurrently, size at first maturation of female cod has declined from approximately 40 cm in length in the 1990s down to 25 cm in the 2010s (Köster et al. 2017). Furthermore, both a prolonged spawning season and a shift in peak spawning time from spring to summer (Wieland et al*.* 2000; Bleil et al*.* 2009; Baranova et al*.* 2011; Köster et al. 2017) have occurred. The length distribution of eastern Baltic cod has also become increasingly truncated towards smaller fish (Eero et al. 2015). In a recent study, Svedäng and Hornborg (2017) suggested that this truncation may be the result of a reduction in somatic growth rate, and that fishing effort and trawl selectivity may exacerbate the decline in stock productivity. Prolonged size-selective mortality exposes fish stocks to the risk of evolutionary change towards permanently slower growing individuals (Swain et al. 2007) and earlier maturation (Chen and Mello 1999). Knowledge of the dynamics in somatic growth is thus of paramount importance for a precise assessment of stock status and sustainable management of the stock (Eero et al*.* 2015; ICES 2017). However, a prerequisite for estimating growth are accurate and precise estimates of the fish’s age, which have not been available to date.

The age of fish can be estimated from the otoliths, on which visually distinct growth bands reflect the seasonality of the environment the fish experiences in terms of temperature and prey availability (Neat et al. 2008). Age estimation of eastern Baltic cod has always been considered difficult and suffering from lack of precision (Hüssy et al. 2016, and references therein). A complete review of over 40 years of efforts to solve this issue may be found in Hüssy et al*.* (2016). The ageing problems arise from low visual contrast between otolith growth zones (Berner 1968; Stötera and Krumme 2016) resulting from the seasonal patterns in salinity and thermal stratification of the Baltic Sea and also the cod’s spawning biology and migration behaviour (Hüssy et al*.* 2009; Hüssy 2010). As a result, a mismatch between winter zones and translucent growth zones normally associated with winter (annual rings) (Beckman and Wilson 1995) frequently occurs (DECODE 2009; Hüssy 2010; Hüssy et al*.* 2010). Also the Baltic cod’s maturation cycle with spawning in summer contributes to less distinct growth zones as spawning leads to an additional hyaline zone formation in summer (false rings) (Berner 1968; Baranova and Sics 1999; Hüssy et al*.* 2009; Baranova et al*.* 2011).

While until now no known-age samples for older Baltic cod have existed, a technique to estimate the age of young fish is available (Hüssy et al. 2010). Otoliths of fish grow on a daily basis, where daily growth layers are visible throughout the first years of a fish’s life (Waldron and Kerstan 2001; Cermeño et al*.* 2003; Paul and Horn 2009). In eastern Baltic cod, the width of these daily growth increments is linked to the annual cycle in environmental temperature experienced by the cod (Hüssy et al. 2010). This results in distinct patterns where periods with clearly discernible increments formed during summer are interrupted by zones without regular increment structure during winter (DECODE 2009; Hüssy et al*.* 2010). Counting these zones thus provides an estimate of the fish’s age. Additionally, measurements of otolith growth between these zones allow back-calculation of fish growth from hatch to capture (Campana 1990; Francis 1990; Li et al*.* 2008). In the present study, we utilized this technique to determine age and estimate individual growth patterns for eastern Baltic cod.

The objectives of this study are to test 1) whether growth of young Baltic cod has changed since the beginning of the 2000’s, 2) to what extent maturation influences growth and 3) whether somatic condition is an indicator of growth rate.

**Material and methods**

***Population data***

In order to obtain growth estimates complementary to those derived from known-age samples, data on length frequency distributions of the eastern Baltic cod population were obtained from the Baltic International Bottom Trawl Surveys (BITS) for ICES Subdivision (SD) 25. Data were downloaded from ICES’ database of trawl surveys (DATRAS) (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx).

Length frequency distributions were used to obtain an indication of growth of selected year classes to compare with growth estimated from back-calculation of size at age from otoliths. Modes in length distribution data representing certain age groups are only discernible for young ages and are best detectable in years when stronger year classes are present, next to weaker ones. In the 2000s, strong year classes occurred in 2003 and 2011 (Köster et al. 2017), visible in the survey length distributions as 2 year olds in the first quarter of 2005 and 2013 and as 3 year olds in 2006 and 2014, respectively. The distance between modes in the length distributions (based on average length of the 3 highest cpue values) representing a given year class in subsequent years, was used as an approximation of average growth of this year class from age 2 to age 3.

Additionally, data on length (*L*) and total weight (*W*) of individual fish in the size range 15 - 35 cm from the first quarter of the years 2001, 2004 and 2013 were obtained from DATRAS. These data thus correspond to the known-age samples with respect to fish size and sampling time. Since the traditionally used Fulton’s *K* index is not independent of fish size, we here used le Cren’s condition index, which is designed to avoid any bias related to fish size (le Cren 1951). First, the parameters *a* and *b* of the length-weight relationship of the population (all three years combined) were estimated:

where *W* = fish total weight and *L* = fish length. Subsequently, for each individual fish *i* of both the population sample and the known-age samples le Cren’s condition index *K* was calculated as the ratio between its weight and the population average weight at the same length:

These data are representative of the population, and the known-age samples should ideally be a random and representative sub-sample of thereof.

***Known-age samples***

*Sample selection*

To establish samples of known-age cod, individuals in the size range 15 - 35 cm were selected randomly from the Danish samples collected during the Baltic International Trawl Survey (BITS) from the first quarter of the years 2001, 2004 and 2013 in ICES Subdivision (SD) 25 (Fig. 1). Fish length (*L*) and fish total weight (*W*) were measured to the nearest cm and weighed (g) on board. Le Cren’s condition index was calculated as above.

Sagittal otoliths were removed, cleaned, and stored individually in labelled paper bags. The samples from 2001 and 2004 have previously been used to identify winter zones in the otoliths based on daily growth increment patterns in the context of DECODE, a project aiming at developing new age estimation methods for Baltic cod (DECODE 2009; Hüssy 2010; Hüssy et al*.* 2010). The 2013 samples were used for an age reading exchange by the Working Group for Baltic Fisheries Assessment (ICES 2014a). Following the BITS manual (ICES 2014b), individuals with a maturity stage of “1” were considered immature, and stages > “1” mature. Length and age distributions of the samples are similar between sampling years (Table I). Average size and age was somewhat smaller in the 2013 sample because age estimation became unreliable at a smaller size and age than in the other two years (see explanation below).

[Fig. 1 and Table I near here]

*Identification of winter zones*

A segment was cut from the central transverse plane of the known-age otoliths (ISOMET 1000 Buehler), fixed on a microscope slide with thermoplastic glue (Buehler Thermoplastic Cement no. 40-8100), and ground to the central plane on a rotating disc with abrasive paper (grit 30 µm to 0.3 µm) to a thickness of approximately 200 µm and polished with 1.0 µm alumina paste. Otolith sections were viewed under a microscope (Leica DMLB) and the images digitized (Leica DFC320) using a standard set-up (8 bit/channel with a frame of 2048 × 1536 pixels, exposure 100 - 500 ms) and a magnification of 0.08 µm pixel–1. The otolith sections revealed series of zones with clearly distinguishable increments, with increasing/decreasing widths in a dome-shaped pattern, interrupted by zones where there was no visible regular increment structure (Fig. 5 in Hüssy et al. 2010). The latter zones correspond to the time of the year when water temperatures are lowest (Hüssy 2010; Hüssy et al*.* 2010) and are henceforward referred to as winter zones. The distance from the midpoint of the winter zones to the core of the otolith was measured along the dorsal axis of the otolith. Since the samples used here were collected during the first quarter of the year and winter zones are formed during January to March (Hüssy et al*.* 2010), otolith growth from the last fully formed winter zone to the edge of the otolith therefore corresponds to an entire year’s growth – the last in the life of the fish. This resulted in otolith growth profiles for each individual fish. The count of winter zones, including the edge, corresponds to the fish’s age. Each sampling year thus consist of three year classes.

It is important to note, that only otoliths with clearly identifiable growth and winter zones can be used for this type of analysis. Otoliths without clearly defined zones were discarded, corresponding to 22, 25 and 47% of sectioned otoliths for the sampling years 2001, 2004 and 2013, respectively. A total of 31, 30 and 67 known-age fish were analysed for growth in the years 2001, 2004 and 2013, respectively (Table I).

*Back-calculation of size-at-age*

In cod, otolith size and fish size are strongly correlated so that otolith growth serves as a proxy for fish growth, allowing for accurate back-calculation of fish size (Campana 1990; Francis 1990; Li et al*.* 2008). Here, fish size at previous ages was back-calculated based on the measurements of otolith size at the centre of each winter zone using the ”biological intercept” back-calculation approach (Campana 1990; Francis 1990):

where *L* = fish length *O* = otolith size and superscripts *age* and *catch* denote the time the measurement was taken and where *L*0 = 4.3 mm and *O*0 = 10 m are the fish and otolith size of eastern Baltic cod at hatch (Nissling et al*.* 1998; Grønkjær and Schytte 1999).

This resulted in a growth curve (length at previous age) for each individual fish from hatch to capture. These growth curves were linearized by log-transforming length at previous age. Differences between sampling years were tested statistically by fitting Linear Mixed Effects Models from the nlme R package (Pinheiro et al. 2015) with previous age as dependent variable, and sampling year as fixed effect and individual fish as random effect. Subsequently, the analysis was repeated with year class instead of sampling year as fixed effect:

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The most complex model being one with a year effect on both intercept and slope of the size – age regression. This model was then tested against hierarchical sub-models using ANOVA and the Akaike Information Criterion (AIC), where the sampling year effect was successively removed. These sub-models also included different random effects models testing whether the intercept and slopes of individuals within years differed. The model with the lowest AIC was selected as the most appropriate. Subsequently, pairwise comparison of growth curves between years was performed using Tukey Contrasts with the multcomp R package (Hothorn et al. 2008).

For each individual fish, year class was calculated as: Year class = sampling year – fish age, and the above analysis repeated using year class instead of sampling year as fixed effect. For comparison with the growth estimates from population length-frequency analysis, growth between age 2 and 3 was calculated for each year class by subtracting the sample means of age 2 from age 3.

*Linking growth and condition*

The relationship between growth and condition of the known-age fish was examined using a two-step approach. First, growth since the last winter zone (*L*catch – *L*age -1) was regressed on age of the fish for each sampling year separately. The residuals of this regression identify whether an individual has grown faster or slower compared to the average. Positive residuals are indicative of faster than average growth, while negative residuals are the result of slower growth. An ANCOVA was used to test whether year had a significant effect on the growth – age regression. Since year did have a significant influence, residual growth was calculated from separate regressions for each year. Subsequently this residual growth was regressed against le Cren’s condition index. This analysis thus tests whether growth during the year prior to capture was correlated with the condition at capture.

All analyses were carried out using R ver. 3.3.2 (R Development Core Team 2009).

**Results**

***Condition comparison of population and known-age samples***

Prior to any growth analyses, we tested whether the known-age samples were representative of the population with respect to somatic condition within the same size rangeBy comparing the average le Crenindex of the known-age fish with the average in the population. This comparison showed that in 2001 and 2004, the average condition of the known-age fish and the population were similar (ANOVA, df = 1, p > 0.05). In contrast, the known-age sample from 2013 was biased towards individuals with a significantly higher condition than the population average within the same size range (ANOVA, df = 3, p < 0.05)(Fig. 2).

[Fig. 2 near here]

***Known-age samples***

*Growth*

*Sampling year effect*: In the LME Model based on back-calculated size at previous age used for this analysis, the intercepts correspond to the size at age 0 while the slopes represent estimates of growth rate over the rest of the fish’s life. In the analysis testing sampling year effect on growth, the best model (lowest AIC) resulted in significantly different intercepts between sampling years, but no difference in slopes (LMEM, n = 368, individuals = 134) (Fig. 3, Table II). The random effect (individuals within years) included separate intercepts and slopes for each individual, showing that individuals within a year may experience different growth rates. While the intercepts of the growth curves of fish from 2001 and 2013 did not differ statistically from each other, they were both lower than the intercept of the growth curve for 2004 (Tukey Contrasts, both p < 0.001). Thus, individuals from the three sampling years were of different starting size, but did not experiencing different growth rates over the rest of their lives (Table II). Average growth rates were estimated at 9.5, 7.8 and 5.7 cm per year for age classes 1, 2 and 3 respectively. However, it is important to note here, that the 2013 samples are not representative of the population, see paragraph above.

Statistical testing of growth differences between sexes and immature/mature individuals simultaneously was not possible owing to the limited sample size of mature females (Table I). However, growth patterns were seemingly similar between sexes (Fig. 4). Males and females were therefore pooled and only the effect of maturity stage tested. In samples from all three years, the individuals that were immature at capture had grown significantly slower than the individuals that were mature at capture (LMEM, statistics see Table II).

[Fig. 3, Fig. 4and Table II near here]

*Year class effect*: In the analysis testing year class effect on growth, samples were restricted to year classes > age 3. Year class 2009 was discarded as it consisted of only 2 individuals. Year classes included in the analysis were 1997 (7), 1998 (15), 1999 (5), 2000 (5) 2001 (19), 2002 (6), 2010 (36) and 2011 (29), with number of individuals in brackets. The model with the lowest AIC had significantly different intercepts and slopes between year classes (LMEM, n = 352, individuals = 122). Post-hoc comparison of growth curves found that the year class 1997 grew significantly faster than 2002 (Tukey Contrasts, all p < 0.001). The year classes 2009 and 2010 had significantly slower growth rates than both 1997, 2001 and the 2002 (Tukey Contrasts, all p < 0.001). In all other pairwise comparisons of year classes there were no significant differences in growth.

For comparison with the growth estimates from population length-frequency analysis, growth between age 2 and 3 was calculated for each year class. Growth decreased significantly from 8.8 cm in the 1997 year class to 7.6 cm in the 2010 year class (growth = 165 – 0.1 · year class, p < 0.05, df = 5, r2 = 0.67). From this regression, growth of the two year classes used in the length frequency analysis was estimated as 8.3 cm for the 2003 year class and 7.7 cm for the 2011 year class.

*Linking growth and condition*

Le Cren’s condition index of the known-age fish ranged between 0.7 and 1.25 (Fig. 5). Both year and maturity had a significant effect on condition (GLM, df = 122, p < 0.05), with immature individuals having a lower condition than mature ones (Fig. 5) and with different average condition for 2001 (0.99), 2004 (1.02) and 2013 (1.05). Condition of both immature and mature males was significantly lower than females in 2004 and 2013 but higher in 2001. In all years sampled, immature individuals had thus experienced lower growth rates and were also in lower condition than mature individuals.

Growth over the last year (*L*catch – *L*age -1) was linearly related to the age of the fish (Fig. 6) but with significant differences in the intercept between years (ANCOVA, df = 4 and 121, p < 0.001, r2 = 0.89). Slopes of the regression did not differ between years. Residual growth was therefore calculated separately for each year based on the year specific regression for 2001: *G* = 13.38 – 2.26 ∙ *age*, (df = 30, p < 0.001, r2 = 0.18), 2004: *G* = 15.61 – 2.60 ∙ *age* (df = 29, p < 0.001, r2 = 0.23), and 2013: *G* = 11.63 – 2.52 ∙ *age*, (df = 66, p < 0.001, r2 = 0.19). Residual growth was positively related with le Cren’s condition index of the fish without significant difference between years (ANCOVA, df = 1 and 126, p < 0.05, r2 = 0.034) (Fig. 7). Even though the regressions were statistically significant, the variability explained is limited (only 3.4%).

[Fig. 5, Fig. 6 and Fig. 7 near here]

***Population data***

*Growth estimates from population length frequency analysis*

The length distribution of the population, following the 2003 year class, showed a peak at 23 cm at age 2 (in 2005) and at 31 cm at age 3 in the following year (Fig. 8), corresponding to an average growth of 8 cm. For the 2011 year class, the peak in length distribution at age 2 was at 24 cm and at 29 cm at age 3, corresponding to an annual growth of 5 cm. Size at age 2 was thus similar between the two year classes. However, growth from age 2 to age 3 decreased from 8 to 5 cm in the 2011 year class - a decrease in growth of 37.5 %. Growth of the 2003 year class estimated from the population length frequency corresponded with growth estimated from the known-age samples’ 2003 year class (8.3 cm). However, for the 2011 year class, the length distribution derived growth of 5 cm is considerably lower than the estimates from the 2011 known-age year class (7.7 cm). This supports the hypothesis that the 2013 known-age sample was biased towards individuals with faster growth.

[Fig. 8 near here]

**Discussion**

The results from this study suggest that the growth rates of eastern Baltic cod at least from age 2 to 3 have decreased from the early 2000’s to 2013. The potential magnitude of change in growth of cod older than age 3 remains unclear, as back-calculating growth from daily increment patterns of the otoliths is not possible for older cod, in which year classes cannot be identified from length frequency data either. With increasing age and size, cod successively occupy deeper water (Pihl and Ulmestrand 1993; Oeberst 2008), migration behaviour changes in association with sexual maturation (Bagge et al*.* 1994; Hüssy et al*.* 2009; Nielsen et al*.* 2013) and feeding preference (Bagge 1981; Bagge and Bay 1987; Bagge et al*.* 1994; Maczassek 2006). Extrapolation of the observations from this study to the entire adult population is therefore not warranted. This study nevertheless presents evidence for recent changes in juvenile growth of eastern Baltic cod, hypothesised by Eero et al. (2015) and Svedäng and Hornburg (2017), at least in cod < 35 cm.

***Relationship between condition and growth***

In this study, we tested whether there was a relationship between condition at capture and growth over the last year of life. Measuring growth and condition in the field is inherently difficult since condition can only be measured at capture. Somatic condition indices are considered a good indicator for energy reserves (Lambert and Dutil 1997) and indicative of feeding conditions over the last weeks of the cod’s life only (Jobling 1988), whereas growth was measured over an entire year. The literature is somewhat inconclusive regarding whether faster growth is linked with higher somatic condition. Rowe and Thorpe (1990) for example, did not find a consistent pattern between growth and condition in Atlantic salmon. However, most other studies report a significant positive correlation in taxonomically distanced species such as largemouth bass (Adams and McLean 1985), Arctic charr (Tveiten et al*.* 1998) and cyprinids (Cui and Wootton 1988). Generally, earlier seasonal maturation is also associated with faster growth and higher condition (Rijnsdorp 1990, 1993; Tveiten et al*.* 1998; Rowe et al*.* 2008). The present study found a significant correlation between growth and condition despite little explanatory power.

***Temporal patterns in growth***

A number of earlier studies have documented a decline in condition of eastern Baltic cod stock since the 1990s (Eero et al*.* 2012; 2015; Casini et al. 2016), whereas concurrent changes in growth are hitherto untested due to the age reading issues. The observed reduction in nutritional condition can be hypothesised to coincide with a simultaneous decrease in growth of the fish, however direct evidence for this is limited (ICES 2017). Assuming that such a link is potentially present, the condition of the known-age fish selected for growth analyses should be similar to the average of the population, to be able to extrapolate the resulting growth estimates to the population.

Condition indices were compared between known-age samples and those of the population in order to test whether the known-age samples were representative of the population in terms of condition. Only total weight (contrary to the preferred somatic weight) were available, which may have contributed to the substantial variability in condition observed in all samples. This analysis found no difference between the two sample types in 2001 and 2004. In 2013 however, the known-age fish had a significantly higher condition than the population. Since growth and condition are correlated, these higher condition individuals also have faster growth rates. The 2013 known-age sample therefore seems biased towards individuals with faster growth and is therefore not representative of the whole population. The likely reason for this bias is that only individuals with visible daily otolith growth increments were selected for growth analyses (DECODE 2009; Hüssy et al*.* 2010), with a higher discard rate of unreadable otoliths in 2013 than the other two years supporting this hypothesis. Nevertheless, the analysis of growth by year class showed a decreasing trend in growth from the year class of 1997 over 2001/2002 to 2009 and 2010, decreasing on average by 0.1 cm per year. Owing to the sampling bias in the latter year classes, this decline in growth can be expected to be underestimated. From the present study it is evident, that unbiased sample selection is crucial for correct growth estimates. Furthermore, samples should not be analysed by sampling year but rather by year class in order to get a reliable picture of actual growth patterns.

In order to provide additional evidence for changes in growth, the combined information from back-calculation of individual growth and population length frequency data were considered. Cod smaller than 20 cm are generally caught in low numbers in the BITS surveys, and thus may not be representative of the population. Furthermore, older age groups are not detectable in the length distributions due to large variability in individual size at age. However, the length data provides useful insight into differences in growth for approximately 20 - 35 cm cod, representing ages 2 - 3, in particular in cases where strong year classes appear in the midst of weaker ones. The advantage of population length data is that these are based on much larger numbers of fish compared to the known-age samples.

Growth estimated from back-calculation of otolith measurements indicated no differences between sampling years, but a significant decrease with year class. Length frequency analysis of the population documented a notably lower growth from age 2 to age 3 for the 2011 year class (5 cm) compared to the 2003 year class (8 cm). Although based on a relatively simple approach, this appears to give a reasonable indication of average growth as the growth estimated for the 2003 year class is very similar to the corresponding 2003 known-age year class (8.3 cm). Growth of the known-age 2011 year class was considerably faster (7.7 cm) than the length frequency derived estimate, owing to the mentioned sample bias. Given 1) the sampling bias towards fish in higher condition in the known-age samples from 2013, 2) the observed decline in the populations condition (Casini et al*.* 2016) and 3) the observed positive relationship between previous growth and condition, the conclusion that growth of eastern Baltic cod within 20-35 cm length range has decreased since the early 2000’s is empirically supported. More specifically, the increase in the average size of cod is about 3 cm smaller between age 2 and age 3 – a decrease of 37.5 %. Given the moderate increase in population size observed in 2006-2007 accompanied by only a minor expansion of distribution range (Bartolino et al. 2017), density dependent mechanisms may indeed have played a role in the observed reduction in growth (Svedäng and Hornborg 2014).

***Influence of maturation***

Regardless of stock, faster growth of cod during the young ages tends to lead to earlier maturation both in the wild (Chen and Mello 1999; Godø and Haug 1999), and in captive individuals (Yoneda and Wright 2005). The faster back-calculated growth of the individuals that were mature at the time of capture is thus not an exceptional observation. In other species, energy is only allocated to surplus production (growth and maturation) when body reserves are above a certain threshold (Rijnsdorp 1990, 1993; Tveiten et al*.* 1998). As the mature individuals from our study also had higher condition than the immature ones, it seems reasonable to assume that a similar causality between condition, growth and maturation exists in eastern Baltic cod. Considering the general declining trend in condition of the Baltic cod stock (Casini et al*.* 2016), this link between condition, growth and maturation may have negative implications for future stock recruitment.

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**Figures**



Figure 1. Map of the sampling locations in ICES Subdivision 25 in the eastern Baltic Sea, where the colours represent different years and the circle size the number of cod selected by station. Years: 2001 (black), 2004 (dark grey) and 2013 (light grey). The inset shows the entire Baltic Sea, where the rectangle outlines SD 25.



Figure 2. Relationship between le Cren’s condition index and fish size of the known-age samples (grey symbols with 95% confidence interval band) and the average of the population in SD 25 in the first quarter of the same years (black symbols and line).



Figure 3. Growth patterns of Baltic cod, back-calculated from otolith measurements. Data shown are means ± confidence intervals, with x-values dodged for improved visibility of the growth curves. Years: 2001 (black), 2004 (dark grey) and 2013 (light grey).



Figure 4. Growth patterns of Baltic cod by sex and maturity for each year separately. Data shown are means ± confidence intervals, with x-values dodged for improved visibility of the growth curves, where colours and line types represent females (black) and males (grey) as immature (dashed line) and mature (solid line) individuals.



Figure 5. Boxplot of le Cren’s condition index for Baltic cod by sampling year, sex and maturity stage (immature= white, mature = grey). Horizontal lines indicate mean, box upper and lower limits the 25% and 75% percentiles, whiskers represent the highest and lowest values within 1.5 ∙ interquartile range and dots represent outliers.



Figure 6. Growth within the last year in relation to age observed in Baltic cod for the years 2001 (black), 2004 (dark grey) and 2013 (light grey). Data show means ± 95% confidence intervals.



Figure 7. Relationship between residual growth and le Cren’s condition index for Baltic cod. Positive residuals correspond to faster than average growth, negative values to slower growth. Data shown are means with 95% confidence interval bands. Years: 2001 (black), 2004 (dark grey) and 2013 (light grey).



Figure 8. Length distribution of the eastern Baltic cod population in selected years, following 2 relatively strong year classes (2003 and 2011), at the age of 2 years in 2005 and 2013, and age 3 in 2006 and 2014, respectively.