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Historical growth of Eastern Baltic cod (*Gadus morhua*): setting a baseline with international tagging data

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Abstract

Understanding the growth of commercially exploited fish is crucial in fisheries biology. Correct estimations of growth and its change over time are paramount for the evaluation of stock status development.

Mark-recapture experiments represent a reliable method to estimate growth when age determination based on otolith reading is uncertain, as is the case of the Eastern Baltic cod stock. In this study, historical data (1955-1970) from tagging experiments on Eastern Baltic cod performed by Sweden, Poland, Denmark, Latvia and Germany were digitised and collated for the first time in a unique dataset to estimate historical von Bertalanffy growth function (VBGF) parameters based on fish length increments using GROTAG model.

The estimated VBGF parameters were L_∞ = 98.22 cm and k = 0.14 for the period 1955-1964 (n = 1151), L_∞ = 123.61 cm and k = 0.09 for 1965-1970 (n = 2612), and L_∞ = 125.60 cm and k = 0.09 for the aggregated period (n = 3763). A seasonal growth signal was detected for all the periods, with a peak after the spawning season in early autumn. These estimates are the most thorough historical growth baseline now available for the Eastern Baltic cod and can be compared to ongoing and future tagging experiments contributing to the development of stock assessment models for this stock.

Keywords: Baltic cod, historical data, baseline, mark-recapture, growth modelling, von Bertalanffy growth function.

1. Introduction

A fundamental aspect of ecology and fisheries research is to pursue a thorough understanding of how fish grow. Variation in growth can have substantial consequences for populations, since it affects survival, age at sexual maturity, reproductive success and movement, modulating the response of populations to environmental changes and anthropogenic pressure, including fisheries (Peters, 1983; Dortel et al., 2014). Specifically, in fish stock assessment, reliable growth estimates are needed to assess the present and past stock status for sound fisheries management decisions (Kell and Bromley, 2004; Dortel et al., 2014; Vincenzi et al., 2014; Aires-da-Silva et al., 2015).

Sustainable management highlights the importance of ‘reference points’ in fisheries, to constrain harvesting within safe biological limits while accounting for the major sources of uncertainty (Hilborn, 2002). Many marine ecosystems have undergone large changes during the past decades, sometimes referred to as regime shifts, driven by overfishing and hydro-climatic changes (Möllmann et al., 2014; Rocha et al., 2014). Therefore, information on historical time-periods, used as anchor points that describe the status of a stock before increases in fishing efforts or changes in its biology and environment, are essential for understanding the long-term changes in exploited stocks. Pauly (1995) highlighted the risks associated with a shifting perception of the stock´s status or the health of marine ecosystems (i.e., “shifting baseline syndrome”) when not accounting for historical data. Reliable information on historical baselines have been demonstrated to be essential to avoid overly optimistic or misleading assessments of the status of fished populations that may affect management decisions (Pinnegar and Engelhard, 2008; Cardinale et al., 2009 and 2011). Thus, without the knowledge of historical baselines of key life history traits, such as growth, a context to interpret current stock condition and its change over time is lacking (McClenachan et al., 2012).

Atlantic cod (*Gadus morhua*) is a key species in the North Atlantic, both economically and ecologically (Hamilton and Butler 2001; Frank et al., 2007). In the Baltic Sea, the Eastern Baltic cod stock size has fluctuated during the last decades, reaching a peak in the early 1980s, after which a major decline occurred (MacKenzie et al., 2011). Concurrently, the stock has suffered a number of changes in its biology, which include changes in nutritional condition, size at maturation, spawning time, parasite infestation, presumed decrease in individual growth and changes in length distribution (Wieland et al., 2000; Eero et al., 2011; Eero et al., 2015) that have challenged the management of this stock. Moreover, the lack of reliable age determination for this stock contributed to the failure of the analytical assessment in 2014 (ICES, 2014), hampering the reliability of management advice in the last few years. However, the existence of ageing problems in the eastern Baltic cod has been known since the implementation of an age-based assessment in the beginning of the 1970s (ICES, 1972). Models that can handle length-based data can be used to overcome the uncertainty of age estimations. However, such approaches still require information on individual growth, especially if this is likely to have changed as in the case of eastern Baltic cod. Thus, accurate growth information is urgently required (ICES, 2018; Eero et al., 2015).

Tagging experiments are one of the most reliable methods to validate age determination and directly estimate growth rates in wild fish (Campana, 2001; Kohler and Turner, 2001). Tagging data have been used to estimate growth rates for many fish families (e.g. in scombrids, serranids, labrids), including gadoids (e.g. cod; Shackell et al., 1997; Tallack, 2009 and references therein; McQueen et al., 2018), and are also integrated into the stock assessment of, for instance, some tuna species (e.g. Ailloud et al., 2014; Dortel et al., 2014; Aires-da-Silva et al., 2015) and hake (e.g. Mellon-Duval et al., 2010; de Pontual et al., 2013).

For Baltic cod, tagging experiments have been performed in the past, with around 50-60000 cod tagged by the countries bordering the Baltic Sea since the late 1950s (Bagge et al., 1994).

These historical data have been mainly used to analyse cod movements over the Baltic seascape (reviewed in Aro, 1989 and 2002), while they have been underutilized for growth analyses. Although some estimates of growth based on the historical tagging data exist, they are limited to single national surveys and cover limited periods. The growth estimates in Draganik and Netzel (1966) are based on southern Baltic tagging experiments conducted in 1957-1963, while Sjöblom et al. (1980) presented growth estimates based on Finnish tagging experiments in 1974-1978. However, the compilation of historical tagging data would provide a unique opportunity to estimate the historical growth of cod covering much larger areas and periods in order to set baselines for future growth analyses.

In our study, we have digitised and collated the existing archived data from the nations that have performed cod tagging experiments in the Baltic Sea between 1955 and 1970. The objectives of our study were: (1) to create a common and quality-checked historical tagging database for cod in the Baltic Sea, and (2) to estimate the historical growth of cod in the eastern Baltic over the whole area of its distribution.

2. Material and methods

2.1. Data overview

For this study, historical data from cod tagging experiments performed between 1955 and 1970 by Sweden, Poland, Denmark, Latvia and Germany in the Baltic area (ICES subdivisions, SDs, 23-30; Fig. 1) have been collected from the respective national archives, digitised and collated in a common database. A total of 7837 tagging records of fish releases with corresponding recaptures were available (Table 1).

The compiled database includes, for most of the records, information on individual fish release and recapture dates, total length, spatial coordinates and rarely information on total weight, sex and maturity stage. In total, there were 7646 records with clear information on both release and recapture dates, locations (ICES SD) and length measurements. The historical tagging activities were performed mostly in quarter 1, 2 and 4 (i.e. 97%; Fig. 2a), when the temperature differences between the water layers are moderate and tolerated by cod at release (Otterlind, 1984). Overall, the main tagging areas were the ICES SDs 25-29 (Fig. 2b) and the time between release and recapture (days at liberty, DAL) ranged between 0 and 3650 days (Fig. 2c)

Additional information about tagging technique and recapture method were also included in the database. Around 95% of the records had information on the tags type used. The most frequently used tags were the Lea´s hydrostatic tags (82%; i.e. a small celluloid cylinder, which remains hermetically sealed and contains information for the finders; Fig. 3a), followed by t-bars (10%; i.e. cylindrical markers, which are anchored between the spines at the base of the second dorsal fin; Fig. 3b), and Carlin tags (2%; i.e. a plastic labels attached to the back of the fish by braided nylon thread; Fig. 3c). Less than 1% of fish were tagged with the Peterson disc (i.e. a tag attached to the base of the pectoral fin that consists of two celluloid discs attached to the body by a wire; Fig. 3d). Around 51% of the recaptures contained information about the recapture gears (43% active gears, i.e. trawls; 8% passive gear, i.e. gillnets, longlines, traps and pots).

2.2. Data manipulation

Prior to growth analyses, some data filters were applied in a stepwise approach. Days at liberty can affect growth estimates, especially when growth is slow compared to the precision of the measurements (Allioud et al., 2014; McQueen et al., 2018). In addition, high numbers of short-term recaptures, as in our case (Fig. 1c), may cause a downward bias in growth estimate (Tallack, 2009). Therefore, only fish with DAL ≥ 60 were included in the analyses to ensure enough time for measurable growth to occur (remaining data n = 5275). Previous cod growth analyses based on tagging data used DAL ≥ 60 for the Northwest Atlantic cod stock (Tallack, 2009) and DAL ≥ 50 for the Western Baltic cod (McQueen et al., 2018). The length distributions of fish with DAL ≥ 0 and DAL ≥ 60 were similar (Fig. S1). In an attempt to reduce the inclusion of Western Baltic cod individuals (inhabiting the SDs 22-24) in the growth analyses, only fish which were both released and recaptured within the boundaries of the Eastern Baltic cod management area (SDs 25-32) were used (remaining data n = 4016).

We then calculated the predicted average annual growth rate (G; Ailloud et al., 2014) of recaptured cod as:

(1) $G = (\Delta L / \Delta T) \times 365$

where ΔL indicates change in total length of fish and ΔT indicates DAL. The predicted average annual growth rate was then used to exclude fish with extreme growth rates likely caused by measurement errors. To identify an appropriate maximum annual growth threshold for our data, the estimates of the von Bertalanffy growth function (VBGF) for North Sea cod, based on Daan (1974), were used to calculate the maximum annual growth for this stock (25 $\text{cm}\cdot\text{year}^{-1}$). Thereafter, all the fish in our database with a growth $G > 25$ $\text{cm}\cdot\text{year}^{-1}$ were excluded from further analyses. We decided to take the North Sea cod as a reference because of its higher growth than the Eastern Baltic stock (Daan, 1974). In addition, McQueen et al. (2018) estimated G for a 25 cm Western Baltic cod to be around 14 $\text{cm}\cdot\text{year}^{-1}$. Thus, we are confident that by removing the fish with $G > 25$ $\text{cm}\cdot\text{year}^{-1}$ we removed only measurement errors and not individual variability. In order to remove the extreme negative growth values (i.e. recapture length << release length), the same percentile of fish growing above the cut-off of 25 $\text{cm}\cdot\text{year}^{-1}$ (i.e. 3%) was used to remove the data from the left-tail of the growth distribution (i.e. negative growth; Fig. S2).

After filtering for all these criteria, a total of 3763 tagged cod and correspondent recaptures were qualified for growth estimation.

2.3. Growth analyses

Length-based estimates of the von Bertalanffy growth function (VBGF) parameters L_∞ (i.e. the asymptotic length, the length at which growth rate is theoretically zero), and k (i.e. the Brody growth coefficient, which determines how fast the fish approaches its L_∞) were calculated using Francis´s (1988a) maximum likelihood GROTAG model in the R library "fishmethods" (Nelson, 2016) in R 3.5.0 (R Core Team, 2018).

The GROTAG model is a re-parametrization of the standard VBGF, which is most commonly applied to tagging data, and models growth (i.e., change in length) as a function of length at release (L_1) and time between release and recapture (ΔL):

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

where, ΔL is the change in length between L_1 and the length at recapture (L_2), and ΔT is the duration in fraction of years between time at release (T_1) and time at recapture (T_2) (Francis 1988a). T_1 and T_2 were measured in fraction of years from the 1st of January 1955, the year of the first tagged cod release.

This method was selected since it incorporates individual variation in growth rate and for its suitability to handle large datasets (Tallack, 2009). Moreover, the GROTAG model has been successfully applied previously to tagging data to estimate growth rates of cod in the Northeast Atlantic (Tallack, 2009) and Western Baltic Sea (McQueen *et al.*, 2018).

The GROTAG model includes parameters g_α and g_β, which are the mean annual growth rates at two release sizes (α and β, respectively, where $\alpha < \beta$). Reference lengths for α and β which were well represented by the tagging data were chosen (Francis, 1988a). In our study, the 5th percentile value of L_1 measurements was adopted for α (i.e. 25 cm) and the 95th percentile value of L_2 measurements was adopted for β (i.e. 55 cm; as in Tallack, 2009).

Francis´s model allows the inclusion of additional parameters that can improve model fit, including: 1) the standard deviation of the growth increment (*nu*), 2) the standard deviation of the measurement error (*s*), 3) the mean of the measurement error (*m*), 4) the outlier contamination probability (*p*; when $p > 0.05$ caution is required in interpreting the model fit since it indicates a high level of outliers; Francis, 1988a), 5) the seasonal growth (*w*; i.e. a proportion which describes when growth is at its maximum in relation to 1st January) and the amplitude of seasonal growth (*u*) that ranges from 0 to 1 (with $u = 0$ and $u = 1$ representing no seasonal growth and maximum seasonal growth effect, respectively). The ratio of maximum and minimum instantaneous growth rate is $(1 + u):(1 – u)$. The standard deviation (σ) of g (at each length class) was estimated as:

(3) $\sigma = nu \times g$

where, *nu* is a scaling factor, as deviation in individual growth from the mean growth increment is assumed to increase linearly with the size of the growth increment. Assuming that two thirds of the growth rates fall within one standard deviation of the mean, the majority of growth rates for a given size class would be expected to be within 1 - *nu* and 1 + *nu* times the estimated average growth per length class (Francis 1988a).

Model selection was done as in Francis (1988a), involving incremental combinations of the parameters (Table 2), with unfitted parameters held at zero. The best fitting model (i.e. final model) was selected through Akaike´s Information Criterion (AIC; Akaike, 1973), with improved model fit indicated by a ΔAIC value ≤ 6 (where, ΔAIC value is defined as the difference between the AIC values of the model with the lowest AIC and the remaining models with less parameters; Richards 2005, 2008). The model fit was also visually assessed by plotting the residuals (observed-expected growth) versus the predicted growth increments (McQueen et al., 2018).

Growth parameters were estimated for two different periods, i.e. 1955-1964 and 1965-1970, and for these periods combined, i.e. 1955-1970 (Table 3). The period selection was made considering the data availability and that the two periods correspond to two main groups of tagging events. The data available correspond to the period with medium stock size before the peak that occurred in the early 1980s. A preliminary analysis did not find regional differences in VBGF parameters comparing the northern-central (SDs 27-32) and southern (SDs 25-26) Baltic areas for the period 1965-1970, when most of the historical tagging experiments took place (Table S1). Therefore, for growth analyses the data available from the entire Eastern Baltic cod stock management area have been pooled (SDs 25-32).

For the period 1955-1964, L_1 ranged between 17 and 75 cm (median = 42 cm), L_2 between 22 and 97 cm (median = 47 cm; Fig. 4a), and DAL up to 3928 days (median = 258 days). For the period 1965-1970, L_1 ranged between 18 and 98 cm (median = 38 cm), L_2 between 18 and 110 cm (median = 43 cm; Fig. 4b), and DAL up to 2767 days (median = 252 days). For the periods combined, i.e. 1955-1970, L_1 ranged between 17 and 98 cm (median = 39 cm), L_2 between 18 and 110 cm (median = 45 cm; Fig. 4b), and DAL up to 3928 days (median = 254 days).

To estimate the variance of the VBGF parameters, each dataset was bootstrapped 1000 times. The bootstrapping procedure involved random resampling with replacement from the original datasets, and then fitting the selected final model to this new dataset, thereby generating new estimates of L_∞ and k (Maria, 2008; Haddon, 2011). For each period, an approximate 95% confidence interval (CI) for L_∞ and k was then constructed using the bootstrap variance.

3. Results

GROTAG model parametrisation was undertaken for the two periods selected. The full model (i.e. the one including all the parameters, model 5) was selected as final model for each period. The distribution of the model residuals for the final model selected for each period is presented in Fig. S2.

During the period 1955-1964, the mean growth rates for a 25 cm (α) and 55 cm (β) cod were 9.39 $\text{cm}\cdot\text{year}^{-1}$ and 5.54 $\text{cm}\cdot\text{year}^{-1}$, respectively, as estimated from the growth model parameters (Table 4). The growth variability parameter (nu) was estimated as 0.69, indicating that individuals within the population could be expected to grow between 0.31 and 1.69 times the estimated average growth per length class. The timing of peak growth rate (w) and amplitude of seasonal variation (u) indicated that a peak in growth rate occurred in the beginning of September (e.g. 0.80 $\text{cm}\cdot\text{month}^{-1}$ for a 40 cm cod), and was around 2 times the minimum growth rate that occurred in March (e.g. 0.45 $\text{cm}\cdot\text{month}^{-1}$ for a 40 cm cod) (Fig. 5a). The contamination probability (p) was negligible (0.01), indicating that the occurrence of outliers was scarce, and the model did not detect outliers after the data cleaning. The standard deviation of measurement error (s) was 1.34 cm, which is in accordance with the 1-cm precision of the length measurements recorded in the historical tagging data. The VBGF parameters estimates were $L_\infty = 98.22$ cm and $k = 0.14$ (Table 4). The growth trajectories and the fitted growth curve for the period 1955-1964 are presented in Fig. 6a.

During the period 1965-1970, the mean growth rates for a 25 cm (α) and 55 cm (β) cod were 8.59 cm year^{-1} and 5.97 cm year^{-1}, respectively, as estimated from the growth model parameters (Table 5). The growth variability parameter (nu) was estimated as 0.74, indicating that individuals within the population could be expected to grow between 0.36 and 1.74 times the estimated average growth per length class (Table 5). The timing of peak growth rate (w)

and amplitude of seasonal variation (*u*) indicated that a peak in growth rate occurred in the beginning of September (e.g. 0.79 cm·month^{-1} for a 40 cm cod), and was around 2 times the minimum growth rate that occurred in March (e.g. 0.42 cm·month^{-1} for a 40 cm cod) (Fig. 5b). The contamination probability (*p*) was negligible (0.00), indicating that the occurrence of outliers was scarce, and the model did not detect outliers after the data cleaning. The mean measurement error (*m*) was low (-0.55 cm) and the standard deviation in measurement error (*s*) was 1.60 cm, which is in accordance with the 1 cm precision of the length measurements recorded in the historical tagging data (Table 5). The VBGF parameters estimates were L_∞ = 123.61 cm and k = 0.09 (Table 5). The individual growth trajectories and the fitted growth curve for the period 1965-1970 are presented in Fig. 6b.

For the combined period, 1955-1970, the mean growth rates for a 25 cm (α) and 55 cm (β) cod were 8.59 cm year^{-1} and 6.14 cm year^{-1}, respectively, as estimated from the growth model parameters (Table 6). The growth variability parameter (*nu*) was estimated as 0.74, indicating that individuals within the population could be expected to grow between 0.36 and 1.74 times the estimated average growth per length class (Table 6). The timing of peak growth rate (*w*) and amplitude of seasonal variation (*u*) indicated that a peak in growth rate occurred in the beginning of September (e.g. 0.79 cm·month^{-1} for a 40 cm cod), and was around 2 times the minimum growth rate that occurred in March (e.g. 0.44 cm·month^{-1} for a 40 cm cod) (Fig. 5c). The contamination probability (*p*) was negligible (0.00), indicating that the occurrence of outliers was scarce, and the model did not detect outliers after the data cleaning. The mean measurement error (*m*) was low (-0.54 cm) and the standard deviation in measurement error (*s*) was 1.50 cm, which is in accordance with the 1 cm precision of the length measurements recorded in the historical tagging data (Table 6). The VBGF parameters estimates were L_∞ = 125.60 cm and k = 0.09 (Table 6). The individual growth trajectories and the fitted growth curve for the period 1955-1970 are presented in Fig. 6c.

The distribution of the model residuals (observed – expected growth) plotted against predicted growth increment was fairly symmetrical for the final model selected for each period (Fig. S3).

The bootstrapped estimates of the mean L_∞ and k for the period 1955-1964 and 1965-1970, and for these periods combined, i.e. 1955-1970 (Table 7 and Fig. 7) were in line with the estimates from the original dataset (Tables 4, 5 and 6)

4. Discussion

In the last two decades, the interest in the recovery, digitisation and analysis of fish and fisheries historical data has greatly increased in the framework of historical fisheries ecology (Zeller et al., 2005; Fortibuoni et al., 2017). Data recovery has been demonstrated to be a valuable contribution in countering the ‘shifting baseline’ syndrome (Pauly, 1995) providing early time period reference points for analyses of the stock status (Zeller et al., 2005). Furthermore, these data can be used to extend time series that are used as input data for stock assessments (Richards and Schnute, 1998; Cox et al., 2002), and are also highly valuable for understanding changes in exploited stocks over long time periods (Christensen et al., 2003; Cardinale et al., 2014). However, collating historical information is often time-consuming and difficult, as records are often reported in different languages and only accessible in the national archives in paper format (McClenachan et al., 2012; Fortibuoni et al., 2017). The digitisation of these archival data is an important process that would ensure increased exposure and use of data that otherwise are vulnerable to be ‘forgotten’ (Zeller et al., 2005).

Traditionally, size at age data have been widely used to study growth in fish species that consistently deposit growth increments in calcified tissues, such as otoliths (Campana, 2001; Panfili et al., 2002). However, for stocks where age information is not available or unreliable owning to severe age reading problems, tagging experiments have produced valid data for length-based growth modelling, as for example for the north-east Atlantic tope shark (Dureuil and Worm, 2015), for the Northwest Atlantic halibut (Shackell et al., 2019) and for Atlantic cod in Gulf of Maine (Shackell et al., 1997) and in the Scotian Shelf (Tallack, 2009).

In this study, the available historical tag-recapture data of Baltic cod, collected over time by the states bordering the Baltic Sea during national tagging experiments, were digitised, quality-screened and collated for the first time in a unique dataset. These data were then used to estimate the historical growth of the Eastern Baltic cod stock based on length increments, since age determination based on otoliths is uncertain for this stock (ICES, 2014).

The VBGF parameters estimated in this study for the Eastern Baltic cod during the period 1955-1964 (L_∞ = 98.22 cm and k = 0.14) differed slightly from the estimates presented by Draganik and Netzel (1966) from fish released in the years 1957-1963 in the Polish waters (L_∞ = 120.40 cm and k = 0.13). This difference can be potentially attributed to the different length frequency distributions and sample sizes of the fish available. Although no information about the sample size or fish length range used for analysis was reported in Draganik and Netzel, (1966), it is unlikely that it was as large and comprehensive as our dataset.

In our analyses the VBGF parameter estimates differ between periods, with higher L_∞ and lower k for the period 1965-1970 compared to the period 1955-1964. Explaining these differences is outside the scope of this study, however variations in both abiotic and biotic factors as well as harvesting can shape the growth of fish (Lambert *et al.*, 1994; Lambert and Dutil 2001; Krohn *et al.*, 1997; Lorenzen et al., 2016) and thus the combined effect of these multiple pressures can be potentially the reason of the temporal changes in growth observed in our case. In addition, the difference in VBGF parameters between the periods may be also the result of the different fish length ranges available in our analysis. For the period 1955-1964, the lack of released cod larger than 75 cm, compared to the maximum release length of

95 cm for the period 1965-1970, is likely the main reason for the lower estimate of L_∞ in the former period. The coverage of the length range is an important aspect when assessing growth with tagging data since the estimation of the L_∞ requires extrapolation from the available data when large individuals are lacking in the sample (Knight, 1968).

In our study, a seasonal growth signal was detected by the GROTAG model. The peak in growth rate was estimated in all periods analysed to occur in the beginning of September, while the minimum growth rate occurred in March. The unbalanced number of fish released among quarters (e.g. lower tagging effort during the summer) might potentially have affected the seasonality leading to wider confidence intervals (Fig. 5). However, the seasonal growth pattern revealed by the model conforms to the timing of spawning for the Eastern Baltic cod that in the late 1960s peaked at the end of April (Wieland et al., 2000). After spawning, compensatory growth occurs in fish, and the peak in growth rates estimated in this study at the beginning of autumn reflects this recovery growth, as also seen in laboratory experiments (Pedersen and Jobling, 1989).

Growth modelling using tag-recapture data provides estimates of growth in relation to length, which can be converted to relative age. Therefore, auxiliary data, such as length frequency data and age readings from otoliths or other hard parts, will be required to anchor our estimated growth curve to an absolute age axis (Eveson et al., 2015; McQueen et al., 2018). Moreover, the estimates of VBGF parameters based on age data are not directly comparable with the estimates based on length data because the parameters change in definition (Francis, 1988b).

In the Baltic Sea, two different ecosystem regimes (pre- and post-1991) have been identified in the last 50 years characterized by different biotic and abiotic conditions, which have greatly affected the Eastern Baltic cod stock (Möllmann et al., 2009; Casini et al., 2009).

This study made use of international mark-recapture data covering the whole distribution of this stock, to provide the most thorough VBGF parameters for the historical period between the post–World War II, when a targeted cod fishery developed (Eero et al., 2008), and the Baltic Sea regime shift. New tagging experiments are currently ongoing in the Baltic Sea and the growth estimates from our study provide the historical baselines to be used for comparison. Moreover, the historical growth parameters estimated in our study can also be used as corroboration of new age determination methods based on otoliths (e.g. otolith microchemistry; Hüssy et al., 2016) that are currently under development.

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Figure captions

Fig. 1. Map of the Baltic Sea divided in ICES subdivisions.

Fig. 2. Overview of historical tagging data (fish releases for which there was a corresponding recapture; n= 7646) available by year and (a) quarter of release, (b) release subdivision (SD) in percentage, (c) days at liberty (DAL) in percentage.

Fig. 3. Different types of tag used in the Baltic cod tagging experiments during 1955-1970. Lea´s hydrostatic tag (a); t-bar (b); Carlin tag (c); Peterson disc tag (d).

Fig. 4. Length distributions at release and recapture of tagged cod for the periods 1955-1964 (a), 1965-1970 (b) and the periods combined, 1955-1970 (c). Bars representing release length are shaded grey, and recaptured lengths are shaded blue.

Fig. 5. Individual growth trajectories (black) and fitted curve (red) of the final model (model 2) for the periods 1955-1964 (a), 1965-1970 (b), and the periods combined, 1955-1970 (c).

Fig. 6. Seasonal changes in growth rate (solid line) and growth variability (dashed lines) of a 40 cm cod for the periods 1955-1964 (a), 1965-1970 (b), and the periods combined, 1955-1970 (c).

Fig. 7. Distribution of bootstrap replicates for each period, and the periods combined, of the VBGF parameters L_∞ and k. Blue dots represent the median of the bootstrapped von Bertalanffy parameters, blue vertical lines represent the 95% confidence interval. Violin plots

shows the probability distribution of the estimates. Red dots represent the von Bertalanffy parameters calculated from the GROTAG final models.

Tables

Table 1. Overview of historical tagging data (number of releases for which there was a corresponding recapture) available by release country and release period used in this study.

Release country	Release period	Number of releases with corresponding recaptures
Sweden	1955-1970	4740
Poland	1957-1970	2207
Denmark	1957-1970	519
Latvia	1958-1970	257
Germany	1959-1962	114
All	1955-1970	7837

Table 2. Parameter combinations estimated by the GROTAG model: five models were applied to the dataset to evaluate optimal model parameterization.

GROTAG model	Estimated parameters
Model 1	g_{α}, g_{β}, s
Model 2	g_{α}, g_{β}, s, nu
Model 3	g_{α}, g_{β}, s, nu, m
Model 4	g_{α}, g_{β}, s, nu, m, p
Model 5	g_{α}, g_{β}, s, nu, m, p, u, w

Table 3. Amount of data available (number of releases for which there was a corresponding recapture) per country and selected period after the data filtering.

	Release period		
Country	1955-1964	1965-1970	1955-1970
Sweden	391	1922	2313
Poland	639	355	994
Denmark	87	328	415
Latvia	32	7	39
Germany	2	-	2
Total	**1151**	**2612**	**3763**

Table 4. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates ± standard error (SE) for the estimated model parameters calculated for the period 1955-1964 (n = 1151). AIC value is reported for each model. Bold: final model; “-”: parameter fixed to 0 in the model.

	Model 1	Model 2	Model 3	Model 4	**Model 5**
Description	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	**Estimate ± SE**
Mean growth rates (cm·year^{-1}) g_{25}	10.67 ± 0.29	7.42 ± 0.25	8.53 ± 0.37	9.27 ± 0.43	**9.39 ± 0.42**
Mean growth rates (cm·year^{-1}) g_{55}	2.95 ± 0.20	5.36 ± 0.20	6.14 ± 0.28	5.74 ± 0.29	**5.54 ± 0.27**
Amplitude of seasonality *u*	-	-	-	-	**0.31 ± 0.08**
Timing of peak growth *w*	-	-	-	-	**0.70 ± 0.03**
Growth variability *nu*	-	0.86 ± 0.04	0.75 ± 0.04	0.68 ± 0.04	**0.69 ± 0.04**
Standard deviation of measurement error (cm) *s*	5.00 ± 0.09	1.19 ± 0.12	1.09 ± 0.12	1.23 ± 0.12	**1.34 ± 0.11**
Mean measurement error (cm) *m*	-	-	-0.55 ± 0.13	-0.56 ± 0.13	**-0.28 ± 0.15**
Outliers probability *p*	-	-	-	0.01 ± 0.01	**0.01 ± 0.01**
VBGF asymptotic length (cm) L_∞	66.48	133.18	132.15	103.83	**98.22**
VBGF Brody coefficient (year^{-1}) *k*	0.30	0.07	0.08	0.13	**0.14**
AIC	7146	6566	6550	6531	**6519**

Table 5. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates ± standard error (SE) for the estimated model parameters calculated for the period 1965-1970 (n = 2612). AIC value is reported for each model. Bold: final model; “-”: parameter fixed to 0 in the model.

	Model 1	Model 2	Model 3	Model 4	**Model 5**
Description	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	**Estimate ± SE**
Mean growth rates (cm·year^{-1}) g_{25}	9.77 ± 0.17	7.09 ± 0.17	8.19 ± 0.26	8.39 ± 0.30	**8.59 ± 0.29**
Mean growth rates (cm·year^{-1}) g_{55}	3.89 ± 0.15	5.53 ± 0.16	5.97 ± 0.19	5.97 ± 0.19	**5.97 ± 0.19**
Amplitude of seasonality u	-	-	-	-	**0.33 ± 0.05**
Timing of peak growth w	-	-	-	-	**0.71 ± 0.02**
Growth variability nu	-	0.90 ± 0.03	0.81 ± 0.03	0.77± 0.04	**0.74 ± 0.04**
Standard deviation of measurement error (cm) s	5.00 ± 0.06	1.52 ± 0.10	1.39 ± 0.10	1.44 ± 0.10	**1.60 ± 0.09**
Mean measurement error (cm) m	-	-	-0.67 ± 0.10	-0.70 ± 0.11	**-0.55 ± 0.11**
Outliers probability p	-	-	-	0.00 ± 0.00	**0.00 ± 0.00**
VBGF asymptotic length (cm) L_∞	74.81	161.51	136.03	129.10	**123.61**
VBGF Brody coefficient (year^{-1}) k	0.22	0.05	0.08	0.08	**0.09**
AIC	16459	15157	15090	15089	**15038**

Table 6. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates ± standard error (SE) for the estimated model parameters calculated for the period 1955-1970 (n = 3763). AIC value is reported for each model. Bold: final model; “-”: parameter fixed to 0 in the model; “*”: no fitting of the model.

	Model 1	Model 2	Model 3	Model 4	**Model 5**
Description	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	**Estimate ± SE**
Mean growth rates (cm·year^{-1}) g_{25}	10.04 ± 0.15	*	8.40 ± 0.21	8.39 ± 0.30	**8.59 ± 0.29**
Mean growth rates (cm·year^{-1}) g_{55}	3.53 ± 0.12	*	6.14 ± 0.16	6.14 ± 0.16	6.14 ± 0.16
Amplitude of seasonality *u*	-	-	-	-	**0.30 ± 0.04**
Timing of peak growth *w*	-	-	-	-	**0.71 ± 0.02**
Growth variability *nu*	-	*	0.78 ± 0.02	0.74 ± 0.03	**0.74 ± 0.02**
Standard deviation of measurement error (cm) *s*	5.00 ± 0.05	*	1.34 ± 0.08	1.40 ± 0.08	**1.50 ± 0.07**
Mean measurement error (cm) *m*	-	-	-0.68 ± 0.08	-0.72 ± 0.08	**-0.54 ± 0.09**
Outliers probability *p*	-	-	-	0.00 ± 0.00	**0.00 ± 0.00**
VBGF asymptotic length (cm) L_{∞}	71.28	*	136.41	127.43	**125.60**
VBGF Brody coefficient (year^{-1}) *k*	0.24	*	0.08	0.09	**0.09**
AIC	23656	*	21710	21710	**21639**

Table 7. Bootstrapped (1000 simulations) von Bertalanffy growth parameters' estimates for each period selected and the periods combined. Median estimates and 95% confident intervals (CI) are shown.

Period	Parameter	Median	95% CI
1955-1964	L_∞	98.89	84.2 - 128.00
	k	0.14	0.09 - 0.19
1965-1970	L_∞	117.38	92.8 - 155.00
	k	0.11	0.07 - 0.15
1955-1970	L_∞	117.49	98.3- 142.00
	k	0.11	0.07 - 0.14

FIG1

Click here to download high resolution image

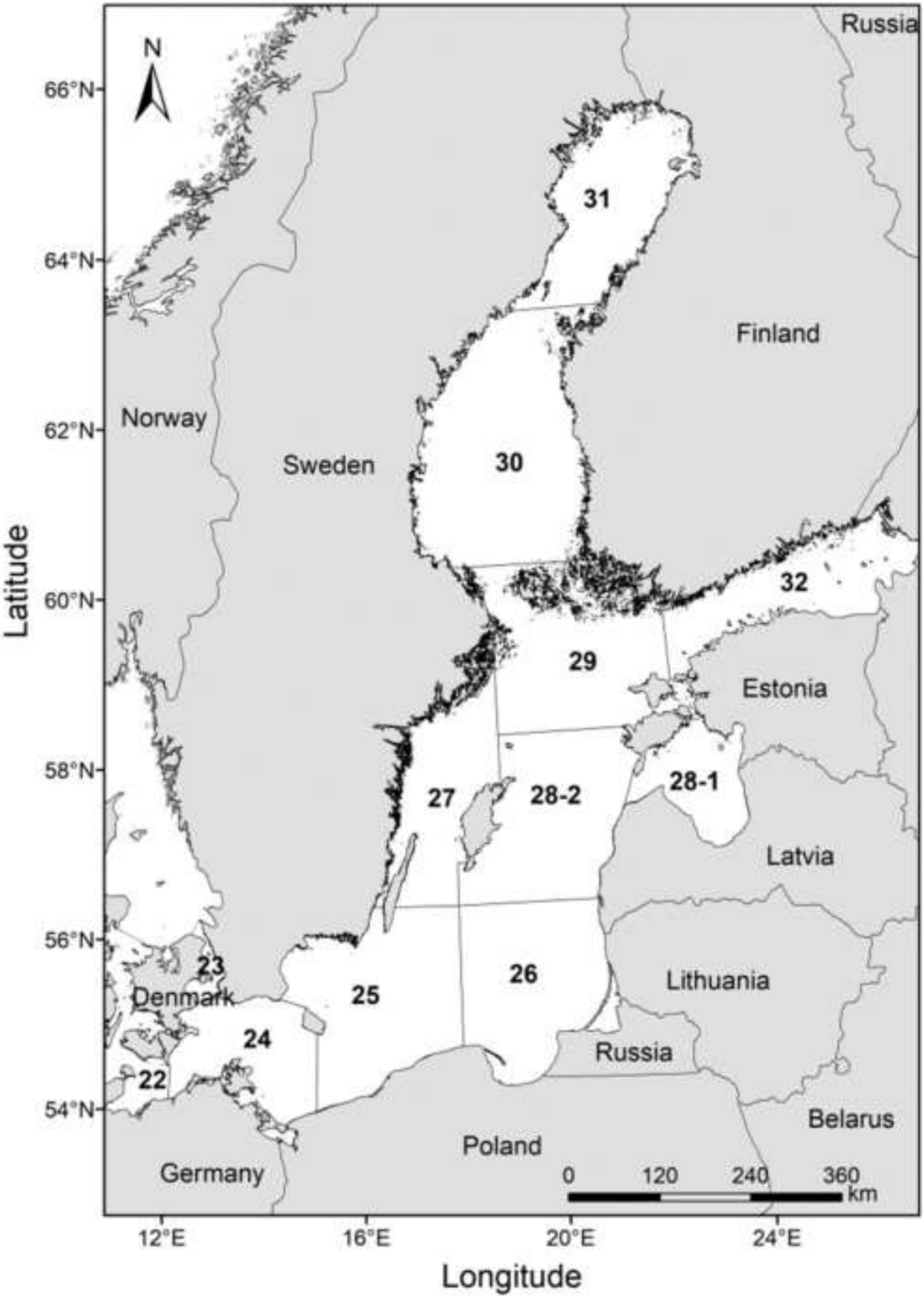


FIG2

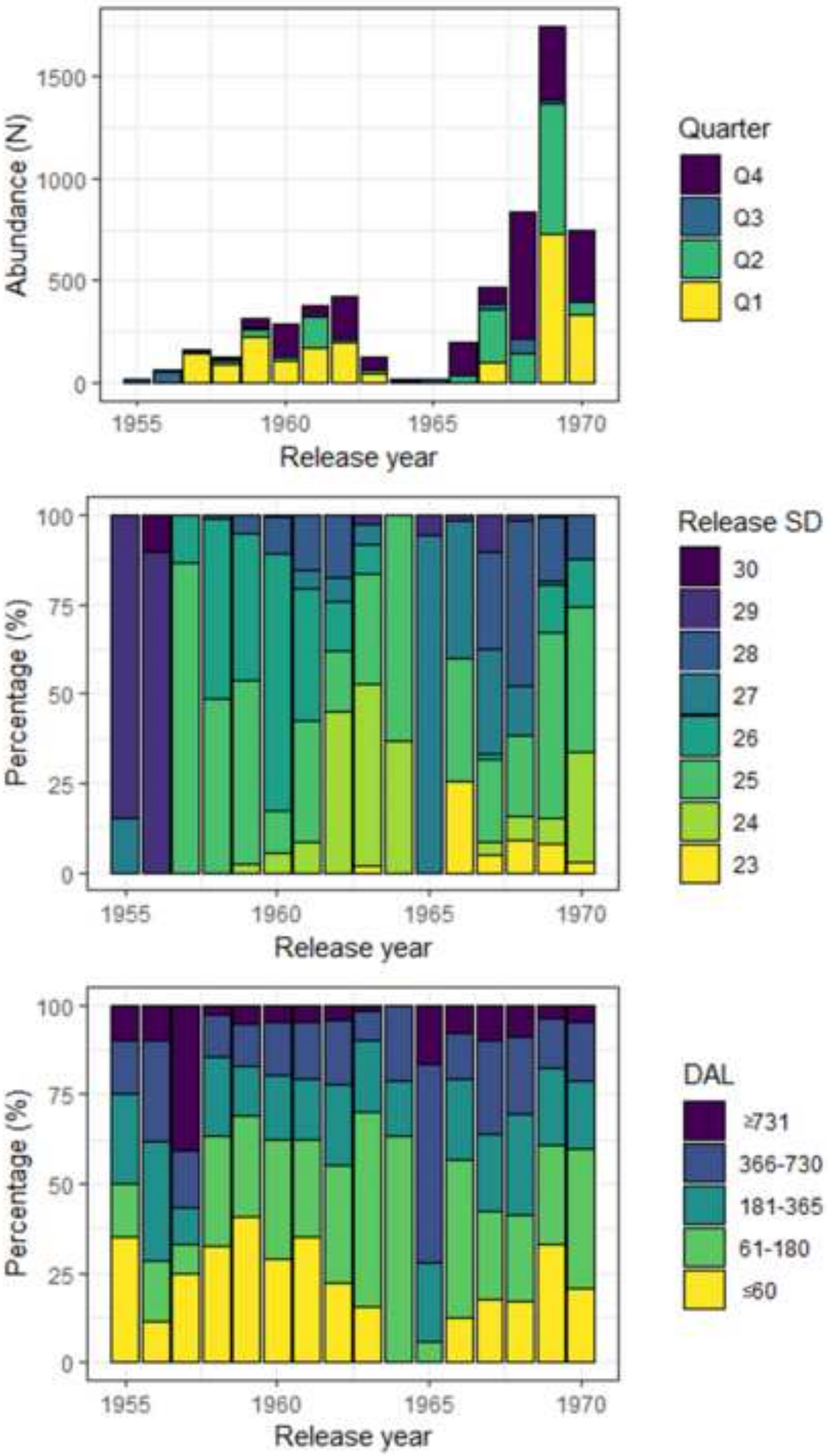

Abundance (N)
0
500
1000
1500
1955
1960
1965
1970
Release year
Quarter
Q4
Q3
Q2
Q1
Percentage (%)
0
25
50
75
100
1955
1960
1965
1970
Release year
Release SD
30
29
28
27
26
25
24
23
Percentage (%)
0
25
50
75
100
1955
1960
1965
1970
Release year
DAL
≥731
366-730
181-365
61-180
≤60

FIG3

Click here to download high resolution image

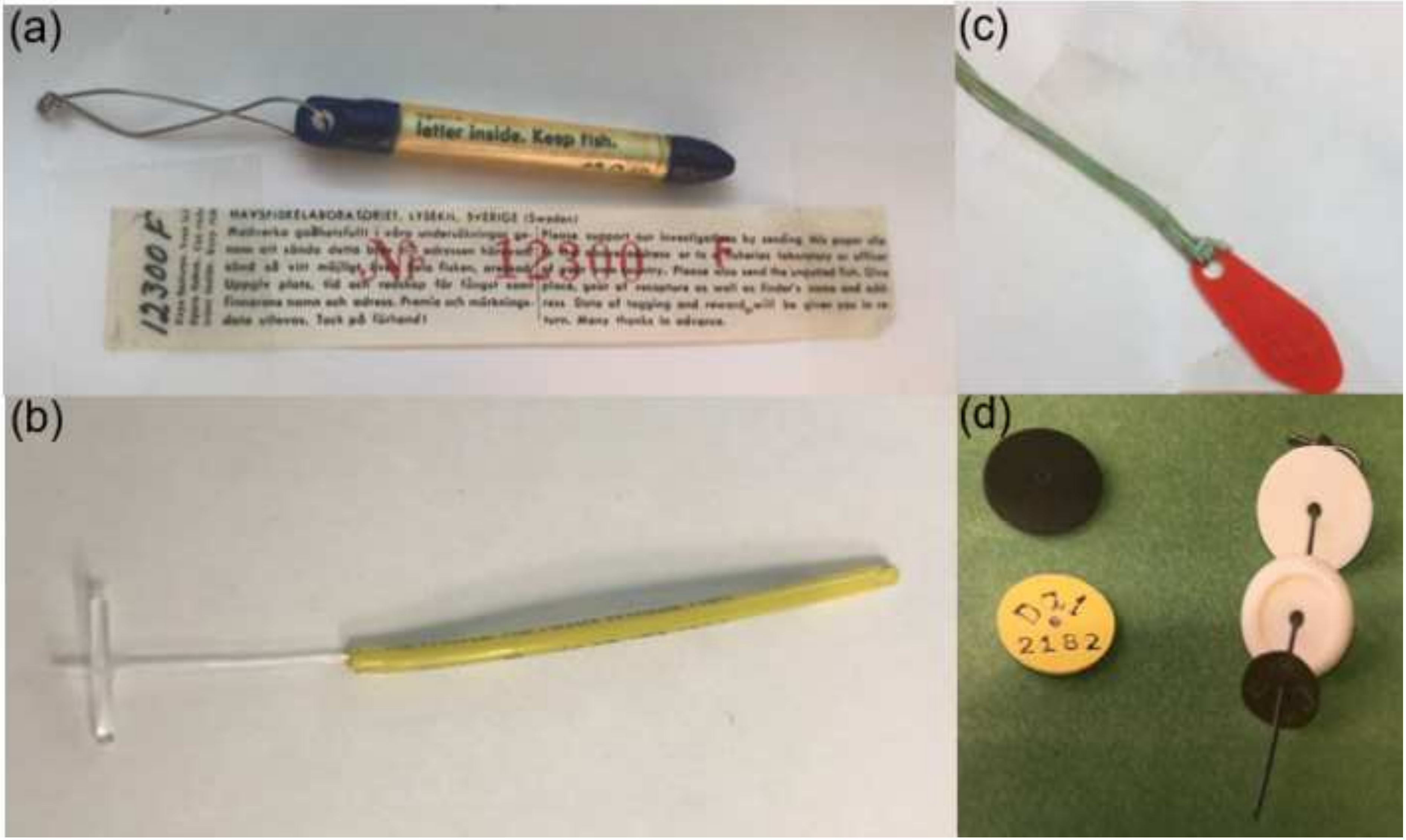


FIG4

Click here to download high resolution image

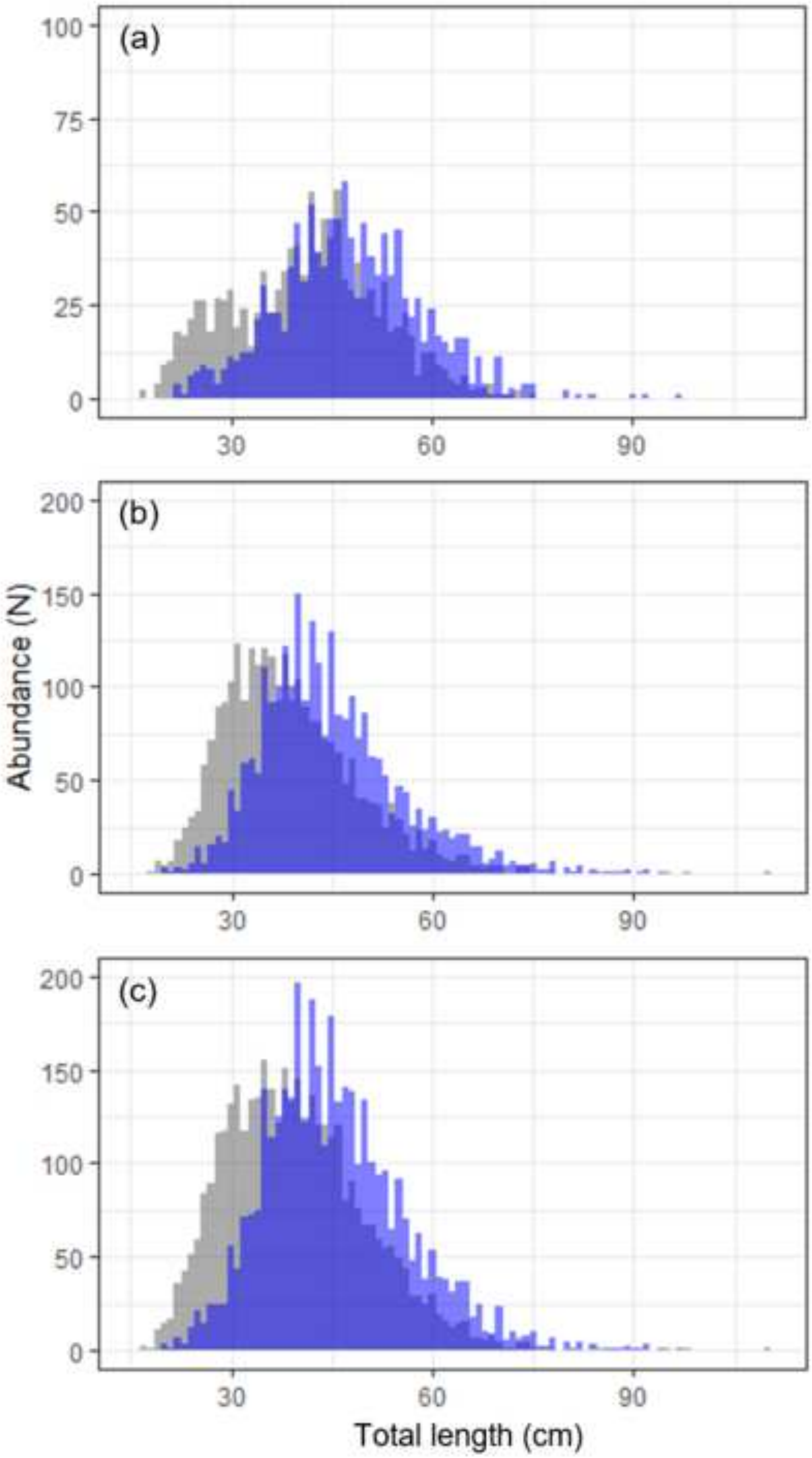


FIG5

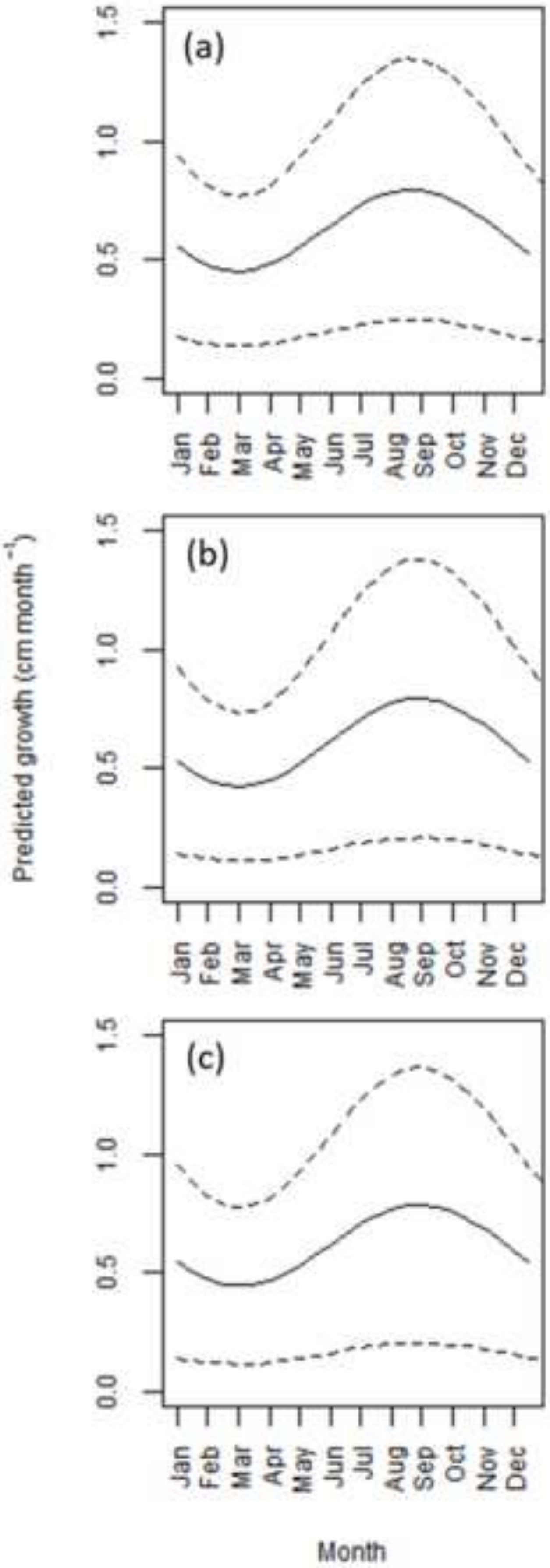

(a)
(b)
(c)
0.0
0.5
1.0
1.5
Predicted growth (cm month^{-1})
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

FIG6

Click here to download high resolution image

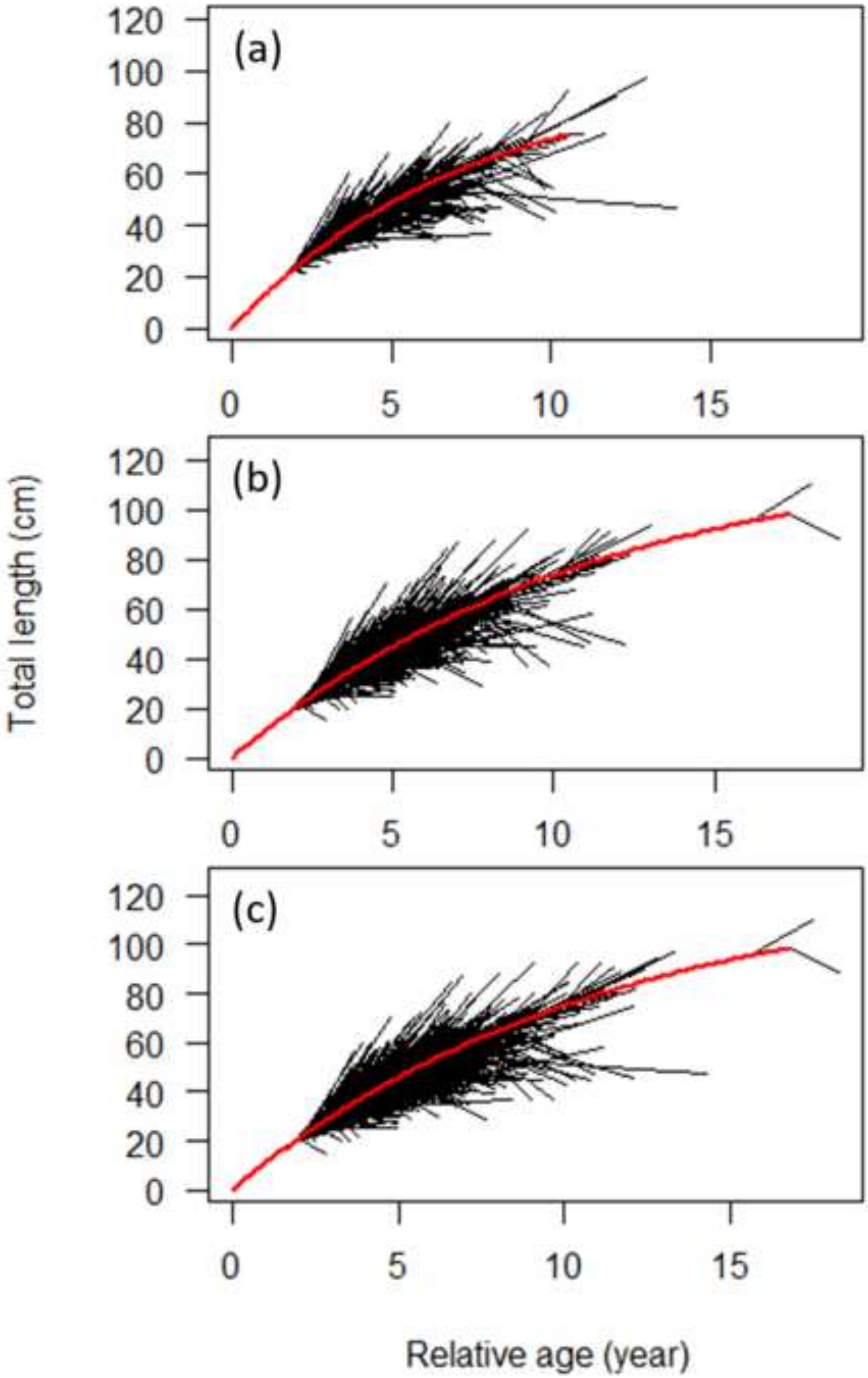
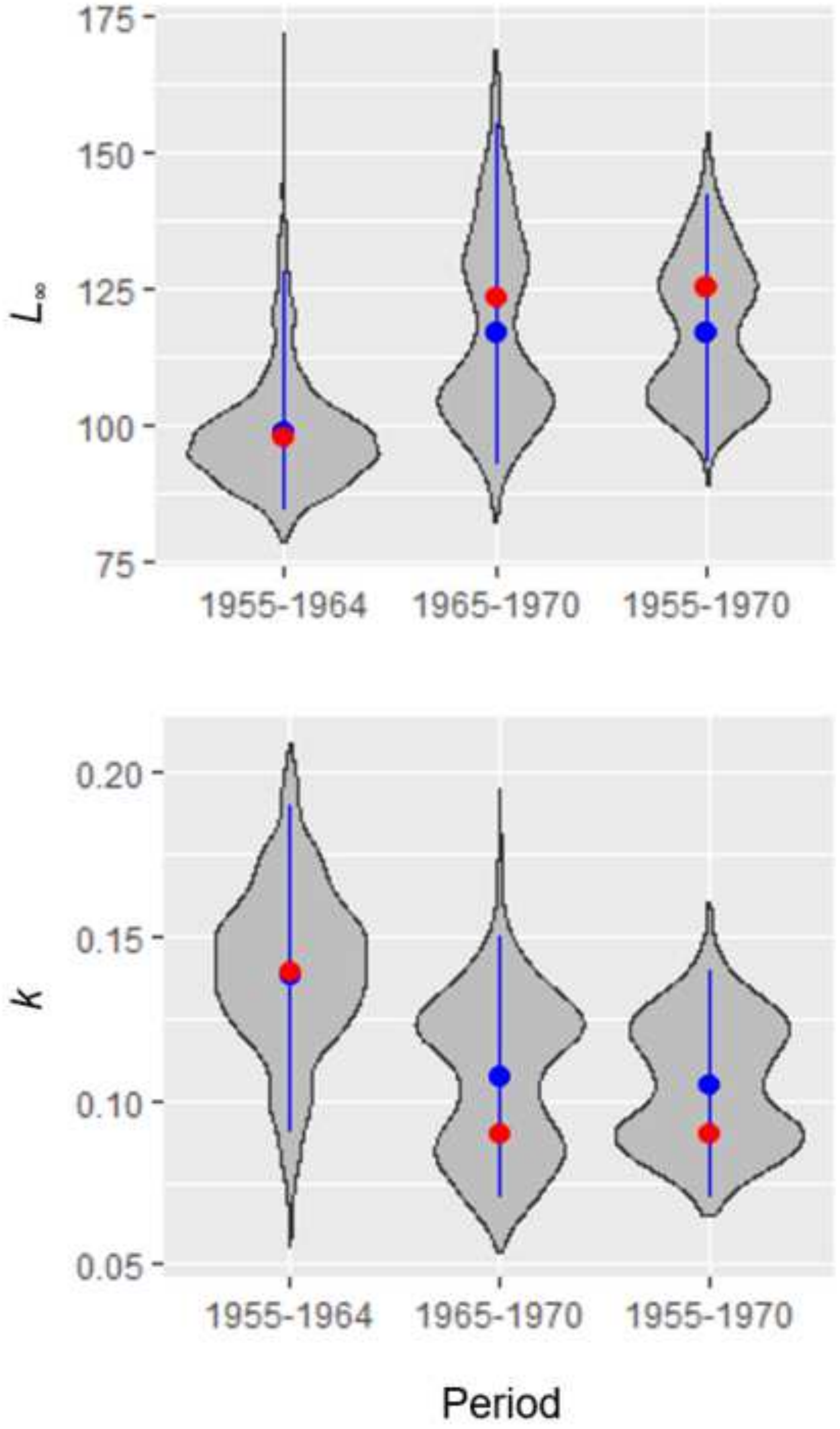


FIG7


175
150
125
100
75
L_∞
1955-1964
1965-1970
1955-1970
0.20
0.15
0.10
0.05
k
1955-1964
1965-1970
1955-1970
Period