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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  $L_{\infty} = 98.22$  cm and  $k = 0.14$  for the period 1955-1964 ( $n = 1151$ ),  $L_{\infty} = 123.61$  cm and  $k = 0.09$  for 1965-1970 ( $n = 2612$ ), and  $L_{\infty} = 125.60$  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).

67 Atlantic cod (*Gadus morhua*) is a key species in the North Atlantic, both economically and  
68 ecologically (Hamilton and Butler 2001; Frank et al., 2007). In the Baltic Sea, the Eastern  
69 Baltic cod stock size has fluctuated during the last decades, reaching a peak in the early  
70 1980s, after which a major decline occurred (MacKenzie et al., 2011). Concurrently, the  
71 stock has suffered a number of changes in its biology, which include changes in nutritional  
72 condition, size at maturation, spawning time, parasite infestation, presumed decrease in  
73 individual growth and changes in length distribution (Wieland et al., 2000; Eero et al., 2011;  
74 Eero et al., 2015) that have challenged the management of this stock. Moreover, the lack of  
75 reliable age determination for this stock contributed to the failure of the analytical assessment  
76 in 2014 (ICES, 2014), hampering the reliability of management advice in the last few years.  
77 However, the existence of ageing problems in the eastern Baltic cod has been known since  
78 the implementation of an age-based assessment in the beginning of the 1970s (ICES, 1972).  
79 Models that can handle length-based data can be used to overcome the uncertainty of age  
80 estimations. However, such approaches still require information on individual growth,  
81 especially if this is likely to have changed as in the case of eastern Baltic cod. Thus, accurate  
82 growth information is urgently required (ICES, 2018; Eero et al., 2015).

83 Tagging experiments are one of the most reliable methods to validate age determination and  
84 directly estimate growth rates in wild fish (Campana, 2001; Kohler and Turner, 2001).  
85 Tagging data have been used to estimate growth rates for many fish families (e.g. in  
86 scombrids, serranids, labrids), including gadoids (e.g. cod; Shackell et al., 1997; Tallack,  
87 2009 and references therein; McQueen et al., 2018), and are also integrated into the stock  
88 assessment of, for instance, some tuna species (e.g. Ailloud et al., 2014; Dortel et al., 2014;  
89 Aires-da-Silva et al., 2015) and hake (e.g. Mellon-Duval et al., 2010; de Pontual et al., 2013).  
90 For Baltic cod, tagging experiments have been performed in the past, with around 50-60000  
91 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  $DAL \geq 60$  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  $DAL \geq 60$  for the Northwest Atlantic cod stock (Tallack, 2009) and  $DAL \geq 50$  for the Western Baltic cod (McQueen et al., 2018). The length distributions of fish with  $DAL \geq 0$  and  $DAL \geq 60$  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  $\Delta L$  indicates change in total length of fish and  $\Delta T$  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  $\ll$  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  $L_{\infty}$  (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  $L_{\infty}$ ) 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 ( $L_I$ ) and time between release and recapture ( $\Delta L$ ):

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

where,  $\Delta L$  is the change in length between  $L_I$  and the length at recapture ( $L_2$ ), and  $\Delta T$  is the duration in fraction of years between time at release ( $T_I$ ) and time at recapture ( $T_2$ ) (Francis 1988a).  $T_I$  and  $T_2$  were measured in fraction of years from the 1<sup>st</sup> 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  $g_{\alpha}$  and  $g_{\beta}$ , which are the mean annual growth rates at two release sizes ( $\alpha$  and  $\beta$ , respectively, where  $\alpha < \beta$ ). Reference lengths for  $\alpha$  and  $\beta$  which

were well represented by the tagging data were chosen (Francis, 1988a). In our study, the 5<sup>th</sup> percentile value of  $L_1$  measurements was adopted for  $\alpha$  (i.e. 25 cm) and the 95<sup>th</sup> percentile value of  $L_2$  measurements was adopted for  $\beta$  (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 1<sup>st</sup> 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 ( $\sigma$ ) 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  $\Delta AIC$  value  $\leq 6$  (where,  $\Delta AIC$  value is defined as the

217 difference between the AIC values of the model with the lowest AIC and the remaining  
218 models with less parameters; Richards 2005, 2008). The model fit was also visually assessed  
219 by plotting the residuals (observed-expected growth) versus the predicted growth increments  
220 (McQueen et al., 2018).

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

230 For the period 1955-1964,  $L_1$  ranged between 17 and 75 cm (median = 42 cm),  $L_2$  between 22  
231 and 97 cm (median = 47 cm; Fig. 4a), and DAL up to 3928 days (median = 258 days). For the  
232 period 1965-1970,  $L_1$  ranged between 18 and 98 cm (median = 38 cm),  $L_2$  between 18 and  
233 110 cm (median = 43 cm; Fig. 4b), and DAL up to 2767 days (median = 252 days). For the  
234 periods combined, i.e. 1955-1970,  $L_1$  ranged between 17 and 98 cm (median = 39 cm),  $L_2$   
235 between 18 and 110 cm (median = 45 cm; Fig. 4b), and DAL up to 3928 days (median = 254  
236 days).

237 To estimate the variance of the VBGF parameters, each dataset was bootstrapped 1000 times.  
238 The bootstrapping procedure involved random resampling with replacement from the original  
239 datasets, and then fitting the selected final model to this new dataset, thereby generating new  
240 estimates of  $L_\infty$  and  $k$  (Maria, 2008; Haddon, 2011). For each period, an approximate 95%  
241 confidence interval (CI) for  $L_\infty$  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 ( $\alpha$ ) and 55 cm ( $\beta$ ) cod were 9.39 cm·year<sup>-1</sup> and 5.54 cm·year<sup>-1</sup>, 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 cm·month<sup>-1</sup> for a 40 cm cod), and was around 2 times the minimum growth rate that occurred in March (e.g. 0.45 cm·month<sup>-1</sup> 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 ( $\alpha$ ) and 55 cm ( $\beta$ ) cod were 8.59 cm year<sup>-1</sup> and 5.97 cm year<sup>-1</sup>, 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.  $0.79 \text{ cm} \cdot \text{month}^{-1}$  for a 40 cm cod), and was around 2 times the minimum growth rate that occurred in March (e.g.  $0.42 \text{ cm} \cdot \text{month}^{-1}$  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 ( $-0.55 \text{ cm}$ ) and the standard deviation in measurement error ( $s$ ) was  $1.60 \text{ cm}$ , which is in accordance with the  $1 \text{ cm}$  precision of the length measurements recorded in the historical tagging data (Table 5). The VBGF parameters estimates were  $L_{\infty} = 123.61 \text{ cm}$  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 ( $\alpha$ ) and 55 cm ( $\beta$ ) cod were  $8.59 \text{ cm year}^{-1}$  and  $6.14 \text{ cm year}^{-1}$ , 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.  $0.79 \text{ cm} \cdot \text{month}^{-1}$  for a 40 cm cod), and was around 2 times the minimum growth rate that occurred in March (e.g.  $0.44 \text{ cm} \cdot \text{month}^{-1}$  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 ( $-0.54 \text{ cm}$ ) and the standard deviation in measurement error ( $s$ ) was  $1.50 \text{ cm}$ , which is in accordance with the  $1 \text{ cm}$  precision of the length measurements recorded in the historical tagging data (Table 6). The VBGF parameters estimates were  $L_{\infty} = 125.60 \text{ cm}$  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  $L_{\infty}$  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 owing 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 ( $L_{\infty} = 98.22$  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 ( $L_{\infty} = 120.40$  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  $L_{\infty}$  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  $L_{\infty}$  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  $L_{\infty}$  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; Hüseyin et al., 2016) that are currently under development.

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## References

- Ailloud, L.E., Lauretta, M.V., Hoenig, J.M., Walter, J.F., and Fonteneau, A. 2014. Growth of Atlantic Bluefin tuna determined from the ICCAT tagging database: a reconsideration of methods. *Collect. Vol. Sci. Pap. ICCAT*. **70**(2): 380–393.
- Aires-da-Silva, A. M., Maunder, M. N., Schaefer, K. M. and Fuller, D. W. 2015. Improved growth estimates from integrated analysis of direct aging and tag–recapture data: An illustration with bigeye tuna (*Thunnus obesus*) of the Eastern Pacific Ocean with implications for management. *Fish. Res.* **163**: 119–126.

391

392 Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle.  
393 International Symposium on Information Theory. *In* Proceedings of the 2<sup>nd</sup> International  
394 Symposium on Information Theory. *Edited by* B. N. Petrov and F. Csaki. Budapest:  
395 Akademiai Kiado. pp. 267-281.

396

397 Aro, E. 1989. A review of fish migration patterns in the Baltic. *Rapp. P.-v. Réun. Cons. int.*  
398 *Explor. Mer.* **190**: 72-96.

399

400 Aro, E. 2002. Fish migration studies in the Baltic Sea: a historical review. *ICES Marine*  
401 *Science Symposia.* **215**: 361-370.

402

403 Bagge, O., Thurow, F., Steffensen, E. and Bay, J. 1994. The Baltic cod. *Dana.* **10**: 1–28.

404

405 Bradley, D., Conklin, E., Papastamatiou, Y.P., McCauley, D.J., Pollock, K., Kendall, B.E., et  
406 al. 2017. Growth and life history variability of the grey reef shark (*Carcharhinus*  
407 *amblyrhynchos*) across its range. *PLoS ONE.* **12**(2): e0172370.  
408 doi:10.1371/journal.pone.0172370

409

410 Campana, S. 2001. Accuracy, precision and quality control in age determination, including a  
411 review of the use and abuse of age validation methods. *J. Fish Biol.* **59**: 197–242.  
412 doi:10.1111/j.1095-8649.2001.tb00127.x.

413

Cardinale, M., Linder L., Bartolino V., Maiorano L. and Casini M. 2009. Conservation value of historical data: reconstructing stock dynamics of turbot during the last century in the Kattegat-Skagerrak. *Mar. Ecol. Prog. Ser.* **386**: 197–206.

Cardinale, M., Bartolino, V., Llope, M., Maiorano, L., Sköld, M. and Hagberg, J. 2011. Historical spatial baselines in conservation and management of marine resources. *Fish Fish.* **12**: 289-298. doi:10.1111/j.1467-2979.2010.00393.x

Cardinale M., Bartolino, V., Svedäng, H., Sundelöf, A. Poulsen, R. T., Casini, M. 2014. A centurial development of the North Sea fish megafauna as reflected by the historical Swedish longlining fisheries. *Fish Fish.* doi: 10.1111/faf.12074

Casini, M., Hjelm, J., Molinero, J.C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A. and Kornilovs, G. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **106**: 197–202.

Christensen, V., Guénette, S., Heymans, J.J., Walters, C.J., Watson, R., Zeller, D., Pauly, D. 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish Fish.* **4**: 1-24

Cox, S.P., Essington, T.E., Kitchell, J.F., Martell, S.J.D., Walters, C., Boggs, C.H., Kaplan I. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Can J Fish Aquat Sci.* **59**(11): 1736-1747

Daan, N., 1974. Growth of North Sea Cod, *Gadus morhua*. *J. Sea Res.* **8**(1): 27-48.

439

440 Draganik, B., and Netzel, J. 1966. An attempt to estimate the growth of cod in the Southern  
441 Baltic on the Basis of Tagging Experiments. ICES. CM 1966/D:12.

442

443 de Pontual, H., Jolivet, A., Garren, F., and Bertignac, M. 2013. New insights on European  
444 hake biology and population dynamics from a sustained tagging effort in the Bay of Biscay.  
445 ICES J. Mar. Sci. **70**: 1416–1428.

446

447 Dortel, E., Sardenne, F., Bousquet, N., Rivot, E., Million, J., Le Croizierc, G., Chassot, E.,  
448 2014. An integrated Bayesian modeling approach for the growth of Indian Ocean yellowfin  
449 tuna. Fish. Res. **163**: 69-84.

450

451 Dureuil, M. and Worm, B. 2015. Estimating growth from tagging data: an application to  
452 north-east Atlantic tope shark *Galeorhinus galeus*. J. Fish Biol. **87**: 1389-1410.

453

454 Eero, M., MacKenzie, B.R., Köster, F.W. and Gislason, H. 2011. Multi-decadal responses of  
455 a cod (*Gadus morhua*) population to human-induced trophic changes, exploitation and  
456 climate variability. Ecol. Appl. **21**: 214–226.

457

458 Eero, M., Hjelm, J., Behrens, J., Buckmann, K., Cardinale, M., Casini, M., Gasyukov, P.,  
459 Holmgren, N., Horbowy, J., Hüsey, K., Kirkegaard, E., Kornilovs, G., Krumme, U., Köster,  
460 F., Oeberst, R., Plikss, M., Radtke, K., Raid, T., Schmidt, J. O., Tomczak, M., Vinther, M.,  
461 Zimmermann, C. and Storr-Paulsen, M. 2015. Eastern Baltic cod in distress: biological  
462 changes and challenges for stock assessment. ICES J. Mar. Sci. **72**: 2180–2186.  
463 <https://doi.org/10.1093/icesjms/fsv109>.

464

465 Eveson, P.J., Million, J., Sardenne, F., and Le Croizier, G. 2015. Estimating growth of  
466 tropical tunas in the Indian Ocean using tag-recapture data and otolith-based age estimates.  
467 Fish. Res. **163**: 44-57

468

469 Fortibuoni, T., Libralato, S., Arneri, E., Giovanardi, O., Solidoro, C., and Raicevich, S. 2017.  
470 Fish and fishery historical data since the 19th century in the Adriatic Sea, Mediterranean. Sci.  
471 data. **4**: 170104. doi:10.1038/sdata.2017.104

472

473 Francis, R.I.C.C. 1988a. Are growth parameters estimated from tagging and age-length data  
474 comparable? Can. J. Fish. Aquat. Sci. **45**(6): 936–942. doi:10.1139/f88-115.

475

476 Francis, R.I.C.C. 1988b. Maximum likelihood estimation of growth and growth variability  
477 from tagging data. N.Z. J. Mar. Freshw. Res. **22**: 43–51.  
478 doi:10.1080/00288330.1988.9516276.

479

480 Frank, K.T., Petrie, B. and Shackell, N.L. 2007. The ups and downs of trophic control in  
481 continental shelf ecosystems. Trends Ecol. Evol. **22**: 236–242.

482

483 Haddon, M. 2011. Modelling and quantitative methods in fisheries. Chapman Hall/CRC,  
484 Boca Raton, USA.

485

486 Hamilton, L.C. and Butler, M.J. 2001. Outport adaptations: social indicators through  
487 Newfoundland's cod crisis. Hum. Ecol. **8**: 1–11.

488

Hilborn, R. 2002. The dark side of reference points. Bull. Mar. Sci. **70**(2): 403-408.

Hüssy, K., Radtke, K., Plikshs, M., Oeberst, R., Baranova, T., Krumme, U., Sjöberg, R.,  
Walther, Y. and Mosegaard, H. 2016. Challenging ICES age estimation protocols: lessons  
learned from the eastern Baltic cod stock. ICES J. Mar. Sci. **73**: 2138–2149.  
doi:10.1093/icesjms/fsw107.

ICES. 1972. Report from the Meeting of the Working Group on Assessment of Demersal  
Stocks in the Baltic. 21–26 February 1972, Gdynia, Poland. ICES CM 1972/F:5. 35 pp.

ICES. 2006. Report of the Study Group on Ageing Issues of Baltic Cod (SGABC). ICES CM  
2006/BCC: 08. 49 pp.

ICES. 2014. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). 3–10  
April 2014, ICES HQ, Copenhagen, Denmark. ICES CM 2014/ACOM: 10.

ICES. 2018. Report of the Workshop on Evaluation of Input data to Eastern Baltic Cod  
Assessment. 23–25 January 2018, ICES HQ, Copenhagen, Denmark. ICES CM/ACOM:  
36.68 pp.

Kell, L. T. and Bromley, P. J. 2004. Implications for current management advice for North  
Sea plaice (*Pleuronectes platessa* L.). Increased biological realism in recruitment, growth,  
density dependent sexual maturation and the impact of sexual dimorphism and fishery  
discards. J. Sea Res. **51**: 301–312.

514 Knight, W. 1968: Asymptotic growth: an example of nonsense disguised as mathematics. J.  
515 Fish. Res. Board. Can. **25**(6): 1303-1307.  
516

517 Kohler, N. E. and Turner, P.A. 2001. Shark tagging: a review of conventional methods and  
518 studies. Environ. Biol. Fish. **60**: 191–223.  
519

520 Krohn, M.M., Reidy, S.P., and Kerr, S.R. 1997. Bioenergetic analysis of the effects of  
521 temperature and prey availability on growth and condition of northern cod (*Gadus morhua*).  
522 Can. J. Fish. Aquat. Sci. **54**(1): 113–121.  
523

524 Lambert, Y. and Dutil, J-D. 2001. Food intake and growth of adult Atlantic cod (*Gadus*  
525 *morhua*) reared under different conditions of stocking density, feeding frequency and size-  
526 grading. Aquac. **192**: 233-247  
527

528 Lambert Y, Dutil J-D. and Munro J. 1994. Effects of intermediate and low salinity  
529 conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). Can. J. Fish.  
530 Aquat. Sci. **51**: 1569-1576  
531

532 Lorenzen, K. 2016. Toward a new paradigm for growth modelling in fisheries stock  
533 assessments: Embracing plasticity and its consequences. Fish. Res. 180: 4–22. Elsevier B.V.  
534 <https://doi.org/10.1016/j.fishres.2016.01.006>.  
535

536 Maria, L. R. 2008. Statistical Computing with R. Chapman and Hall/CRC.  
537



McClenachan, L., Ferretti, F. and Baum, J. K. 2012. From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. *Conservation Letters*, 5, 349-359. doi:10.1111/j.1755-263X.2012.00253.x

McQueen, K., Eveson, J. P., Dolk, B., Lorenz, T., Mohr, T., Schade, F. M. and Krumme, U. (2018). Growth of cod (*Gadus morhua*) in the western Baltic Sea: estimating improved growth parameters from tag recapture data. *Can. J. Fish. Aquat. Sci.* [doi:10.1139/cjfas-2018-0081](https://doi.org/10.1139/cjfas-2018-0081)

Mellon-Duval, C., de Pontual, H., Metral, L., and Quemener, L. 2010. Growth of European hake (*Merluccius merluccius*) in the Gulf of Lions based on conventional tagging. *ICES J. Mar. Sci.* **67**(1): 62–70

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M. and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Glob. Chang. biol.* **15**: 1377–1393.

Möllmann, C., Folke, C., Edwards, M. and Conversi, A. 2014. Marine regime shifts around the globe: Theory, drivers and impacts. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **370**(1659): 20130260.

Nelson, G.A. 2016. fishmethods: fishery science methods and models in R. R package version 1.10-626 0. <https://CRAN.R-project.org/package=fishmethods>.

563 Otterlind, G. 1984. Cod migration and transplantation experiments. ICES HQ, Copenhagen.  
564 ICES C.M./J:13.  
565  
566 Panfili, J., H. De Pontual, H. Troadec, and P. Wright. 2002. Manual of Fish  
567 Sclerochronology. Co'edition Ifremer-IRD.  
568  
569 Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol.  
570 Evol. **10**: 430.  
571  
572 Pedersen, T. and Jobling, M., 1989. Growth rates of large, sexually mature cod, *Gadus*  
573 *morhua*, in relation to condition and temperature during an annual cycle. Aquac. **81**: 161-168.  
574  
575 Peters, R.H. 1983. The ecological implications of body size. *Cambridge University Press*.  
576 <http://books.google.com/books?id=OYVxiZgTXWsC>.  
577  
578 Pinnegar J.K. and Engelhard G.H. 2008. The “shifting baseline” phenomenon: a global  
579 perspective. Rev. Fish Biol. Fisher. **18**: 1–16.  
580  
581 R Core Team. 2018. R: a language and environment for statistical computing. R Foundation  
582 for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.  
583  
584 Richards, S.A. 2005. Testing ecological theory using the information- theoretic approach:  
585 examples and cautionary results. Ecol. **86**: 2805-2814  
586

587 Richards, S.A. 2008. Dealing with over dispersed count data in applied ecology. J. Appi.  
588 Ecol. **45**: 218  
589

590 Richards, L.J. and Schnute, J.T. 1998. A strategy for advancing stock assessment. *In*  
591 Reinventing fisheries management. *Edited by* T.J. Pitcher, P.J.B. Hart, and D. Pauly. Kluwer  
592 Academic Publishers, London. pp. 399-406.  
593

594 Rocha, J., Yletyinen, J., Biggs, R., Blenckner, T. and Peterson, G. 2014. Marine regime  
595 shifts: Drivers and impacts on ecosystems services. Philos. Trans. R Soc. Lond. B Biol. Sci.  
596 **370**(1659): 20130273.  
597

598 Shackell, N.L., K.J. Ferguson, C.E. den Heyer, D. Brickman, Z. Wang, and K.T. Ransier.  
599 2019. Growing degree-day influences growth rate and length of maturity of Northwest  
600 Atlantic halibut (*Hippoglossus hippoglossus* L.) across the southern stock domain. J. Northw.  
601 Atl. Fish. Sci. **50**: 25–35. doi:10.2960/J.v50.m716  
602

603 Shackell, N.L., Stobo, W.T., Frank, K.T., and Brickman, D. 1997. Growth of cod (*Gadus*  
604 *morhua*) estimated from mark–recapture programs on the Scotian Shelf and adjacent areas.  
605 ICES J. Mar. Sci. **54**: 383–398. doi:10.1006/jmsc.1996.0173.  
606

607 Sjöblom, V., Aro, E., and Suuronen, P. 1980. Migrations, mortality and growth of cod in the  
608 northern Baltic Sea. ICES CM 1980/J:8. 15 pp.  
609

610 Tallack, S.M.L. 2009. Regional growth estimates of Atlantic cod, *Gadus morhua*:  
611 applications of the maximum likelihood GROTAG model to tagging data in the Gulf of  
612 Maine (USA/Canada) region. Fish. Res. **99**: 137–150. doi:10.1016/j.fishres.2009.05.014.  
613  
614 Vincenzi, S., Mangel, M., Crivelli, A.J., Munch, S. and Skaug, H. J. 2014. Determining  
615 individual variation in growth and its implication for life-history and population processes  
616 using the empirical Bayes method. PLOS Comput. Biol. **10**: e1003828.  
617  
618 Wieland, K., Jarre-Teichmann, A., and Horbowa, K. 2000. Changes in the timing of  
619 spawning of Baltic cod: possible causes and implications for recruitment. ICES J. Mar. Sci.  
620 **57**: 452–464.  
621  
622 Zeller, D., Froese, R. and Pauly, D. 2005. On losing and recovering fisheries and marine  
623 science data. Mar Policy. **29**: 69–73.

## 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  $L_{\infty}$  and  $k$ . Blue dots represent the median of the bootstrapped von Bertalanffy parameters, blue vertical lines represent the 95% confidence interval. Violin plots

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

1   **Tables**

2   Table 1. Overview of historical tagging data (number of releases for which there was a  
3   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

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

GROTAG model	Estimated parameters	7
Model 1	$g_{\omega} \ g_{\beta}, \ s$	8
Model 2	$g_{\omega} \ g_{\beta}, \ s, \ nu$	
Model 3	$g_{\omega} \ g_{\beta}, \ s, \ nu, \ m$	9
Model 4	$g_{\omega} \ g_{\beta}, \ s, \ nu, \ m, \ p$	10
Model 5	$g_{\omega} \ g_{\beta}, \ s, \ nu, \ m, \ p, \ u, \ w$	
		11



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

Country	Release period		
	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
<b>Total</b>	<b>1151</b>	<b>2612</b>	<b>3763</b>

Table 4. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates  $\pm$  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 $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE
Mean growth rates (cm·year <sup>-1</sup> ) $g_{25}$	10.67 $\pm$ 0.29	7.42 $\pm$ 0.25	8.53 $\pm$ 0.37	9.27 $\pm$ 0.43	<b>9.39 <math>\pm</math> 0.42</b>
Mean growth rates (cm·year <sup>-1</sup> ) $g_{55}$	2.95 $\pm$ 0.20	5.36 $\pm$ 0.20	6.14 $\pm$ 0.28	5.74 $\pm$ 0.29	<b>5.54 <math>\pm</math> 0.27</b>
Amplitude of seasonality $u$	-	-	-	-	<b>0.31 <math>\pm</math> 0.08</b>
Timing of peak growth $w$	-	-	-	-	<b>0.70 <math>\pm</math> 0.03</b>
Growth variability $nu$	-	0.86 $\pm$ 0.04	0.75 $\pm$ 0.04	0.68 $\pm$ 0.04	<b>0.69 <math>\pm</math> 0.04</b>
Standard deviation of measurement error (cm) $s$	5.00 $\pm$ 0.09	1.19 $\pm$ 0.12	1.09 $\pm$ 0.12	1.23 $\pm$ 0.12	<b>1.34 <math>\pm</math> 0.11</b>
Mean measurement error (cm) $m$	-	-	-0.55 $\pm$ 0.13	-0.56 $\pm$ 0.13	<b>-0.28 <math>\pm</math> 0.15</b>
Outliers probability $p$	-	-	-	0.01 $\pm$ 0.01	<b>0.01 <math>\pm</math> 0.01</b>
VBGF asymptotic length (cm) $L_{\infty}$	66.48	133.18	132.15	103.83	<b>98.22</b>
VBGF Brody coefficient (year <sup>-1</sup> ) $k$	0.30	0.07	0.08	0.13	<b>0.14</b>
AIC	7146	6566	6550	6531	<b>6519</b>

Table 5. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates  $\pm$  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 $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE
Mean growth rates (cm·year <sup>-1</sup> ) $g_{25}$	9.77 $\pm$ 0.17	7.09 $\pm$ 0.17	8.19 $\pm$ 0.26	8.39 $\pm$ 0.30	<b>8.59 <math>\pm</math> 0.29</b>
Mean growth rates (cm·year <sup>-1</sup> ) $g_{55}$	3.89 $\pm$ 0.15	5.53 $\pm$ 0.16	5.97 $\pm$ 0.19	5.97 $\pm$ 0.19	<b>5.97 <math>\pm</math> 0.19</b>
Amplitude of seasonality $u$	-	-	-	-	<b>0.33 <math>\pm</math> 0.05</b>
Timing of peak growth $w$	-	-	-	-	<b>0.71 <math>\pm</math> 0.02</b>
Growth variability $nu$	-	0.90 $\pm$ 0.03	0.81 $\pm$ 0.03	0.77 $\pm$ 0.04	<b>0.74 <math>\pm</math> 0.04</b>
Standard deviation of measurement error (cm) $s$	5.00 $\pm$ 0.06	1.52 $\pm$ 0.10	1.39 $\pm$ 0.10	1.44 $\pm$ 0.10	<b>1.60 <math>\pm</math> 0.09</b>
Mean measurement error (cm) $m$	-	-	-0.67 $\pm$ 0.10	-0.70 $\pm$ 0.11	<b>-0.55 <math>\pm</math> 0.11</b>
Outliers probability $p$	-	-	-	0.00 $\pm$ 0.00	<b>0.00 <math>\pm</math> 0.00</b>
VBGF asymptotic length (cm) $L_{\infty}$	74.81	161.51	136.03	129.10	<b>123.61</b>
VBGF Brody coefficient (year <sup>-1</sup> ) $k$	0.22	0.05	0.08	0.08	<b>0.09</b>
AIC	16459	15157	15090	15089	<b>15038</b>

Table 6. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates  $\pm$  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 $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE	Estimate $\pm$ SE
Mean growth rates ( $\text{cm} \cdot \text{year}^{-1}$ ) $g_{25}$	$10.04 \pm 0.15$	*	$8.40 \pm 0.21$	$8.39 \pm 0.30$	<b><math>8.59 \pm 0.29</math></b>
Mean growth rates ( $\text{cm} \cdot \text{year}^{-1}$ ) $g_{55}$	$3.53 \pm 0.12$	*	$6.14 \pm 0.16$	$6.14 \pm 0.16$	$6.14 \pm 0.16$
Amplitude of seasonality $u$	-	-	-	-	<b><math>0.30 \pm 0.04</math></b>
Timing of peak growth $w$	-	-	-	-	<b><math>0.71 \pm 0.02</math></b>
Growth variability $nu$	-	*	$0.78 \pm 0.02$	$0.74 \pm 0.03$	<b><math>0.74 \pm 0.02</math></b>
Standard deviation of measurement error (cm) $s$	$5.00 \pm 0.05$	*	$1.34 \pm 0.08$	$1.40 \pm 0.08$	<b><math>1.50 \pm 0.07</math></b>
Mean measurement error (cm) $m$	-	-	$-0.68 \pm 0.08$	$-0.72 \pm 0.08$	<b><math>-0.54 \pm 0.09</math></b>
Outliers probability $p$	-	-	-	$0.00 \pm 0.00$	<b><math>0.00 \pm 0.00</math></b>
VBGF asymptotic length (cm) $L_{\infty}$	71.28	*	136.41	127.43	<b>125.60</b>
VBGF Brody coefficient ( $\text{year}^{-1}$ ) $k$	0.24	*	0.08	0.09	<b>0.09</b>
AIC	23656	*	21710	21710	<b>21639</b>

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

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

37

FIG1

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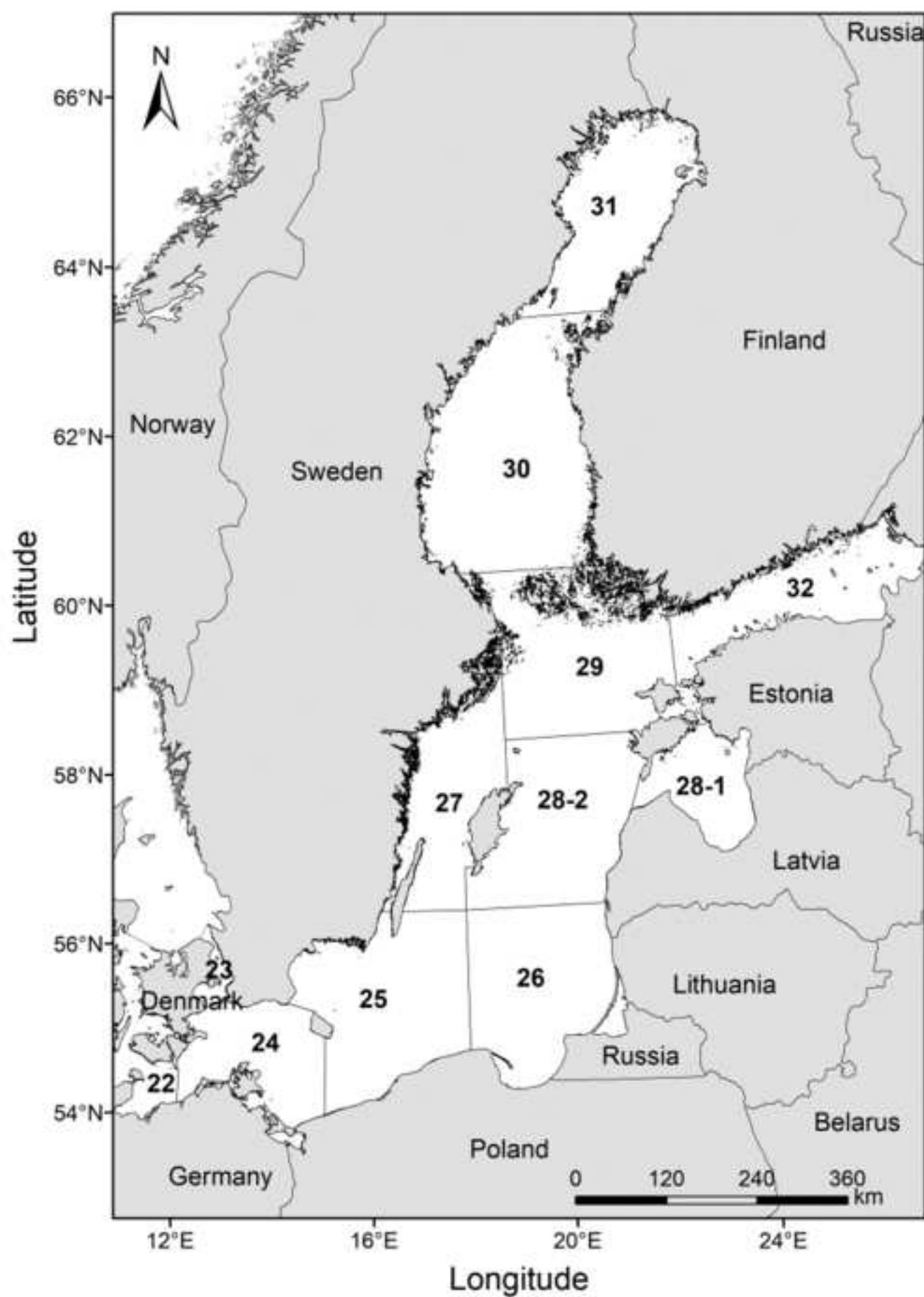
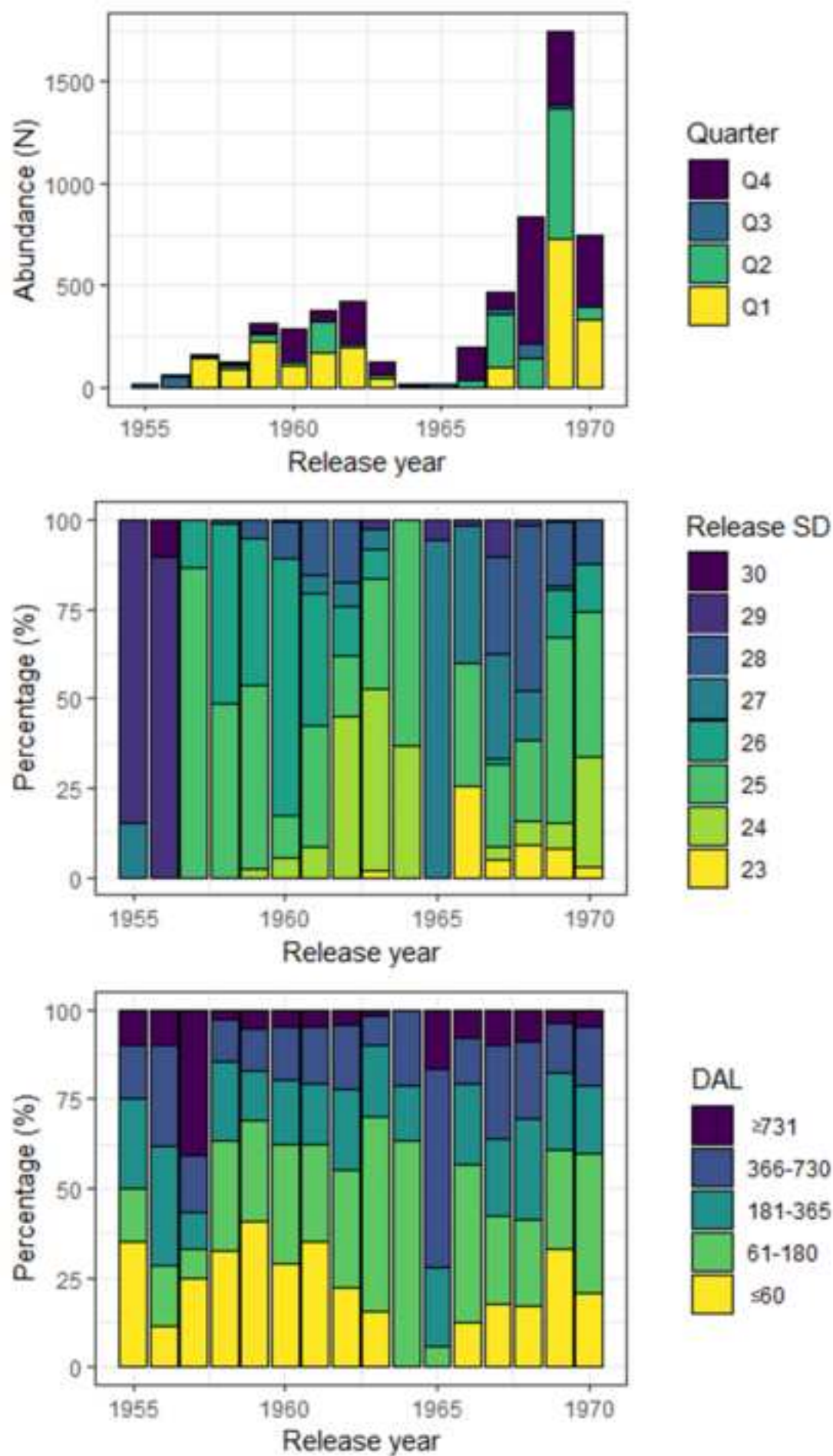


FIG2  
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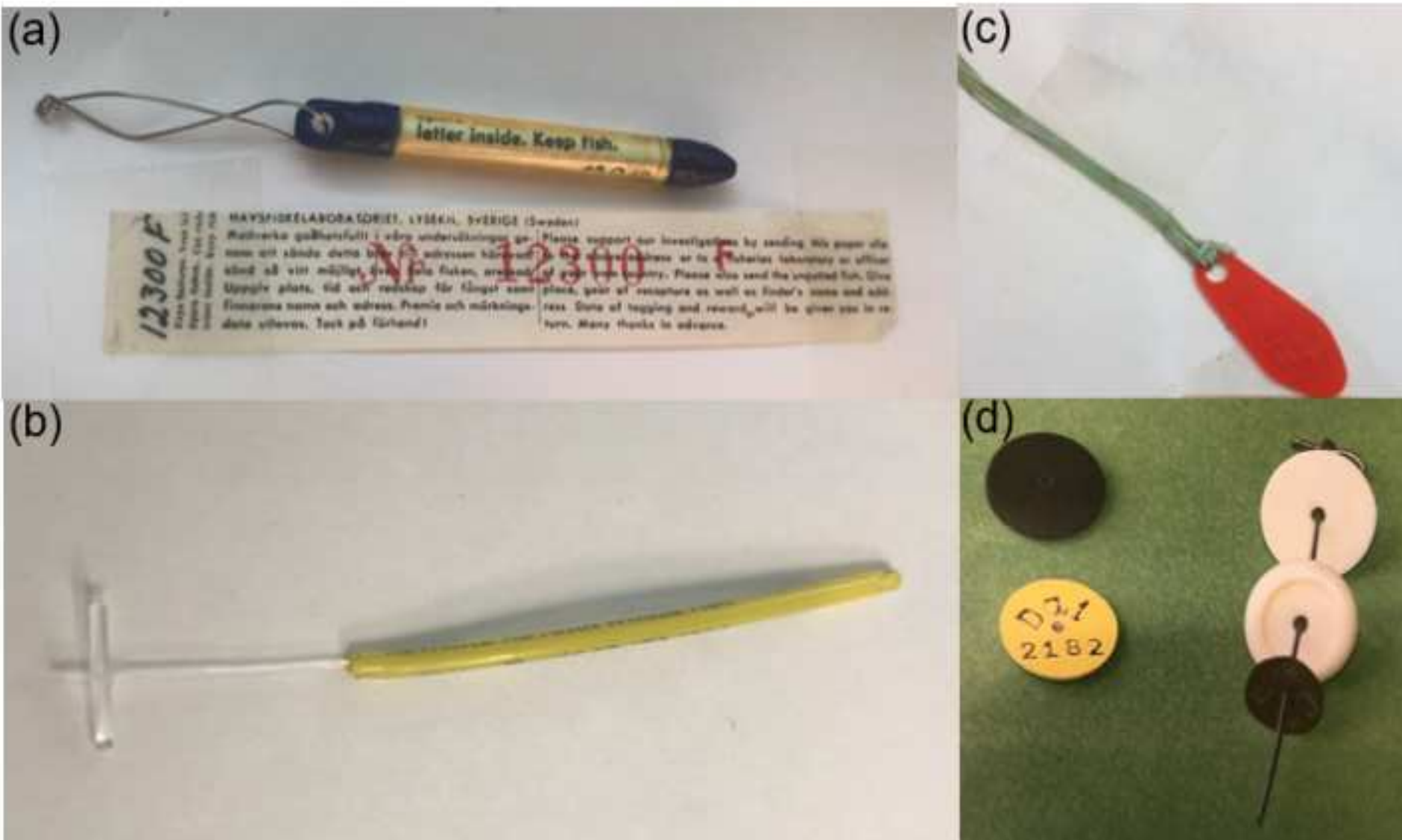




FIG4

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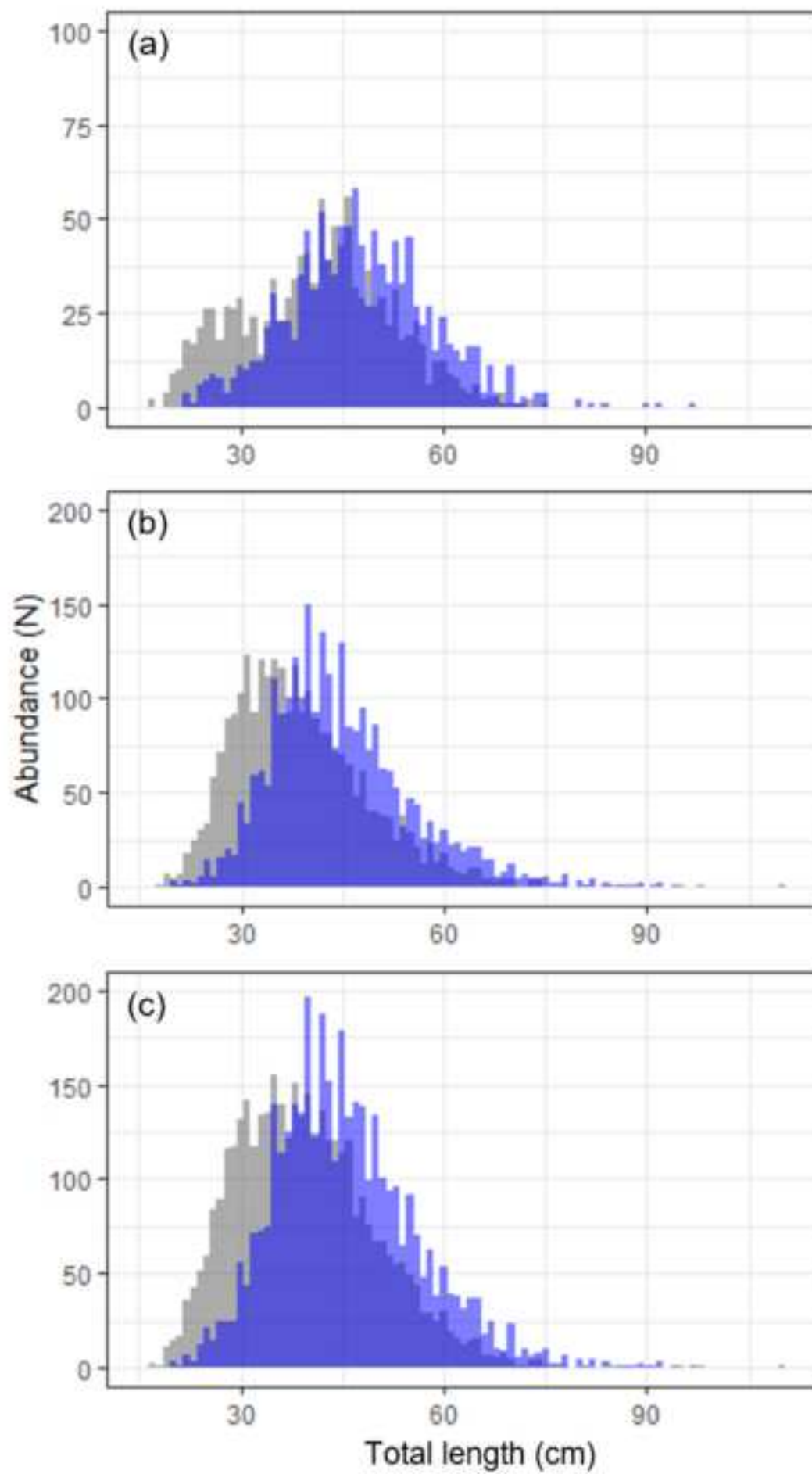


FIG5  
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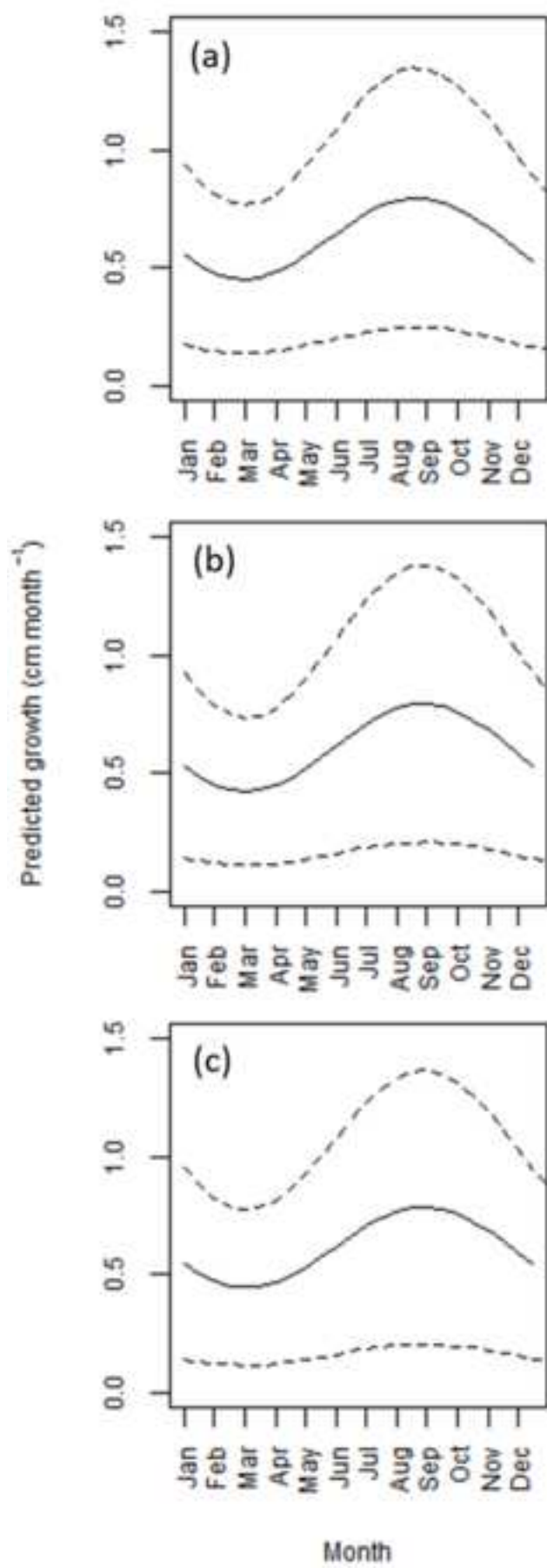


FIG6

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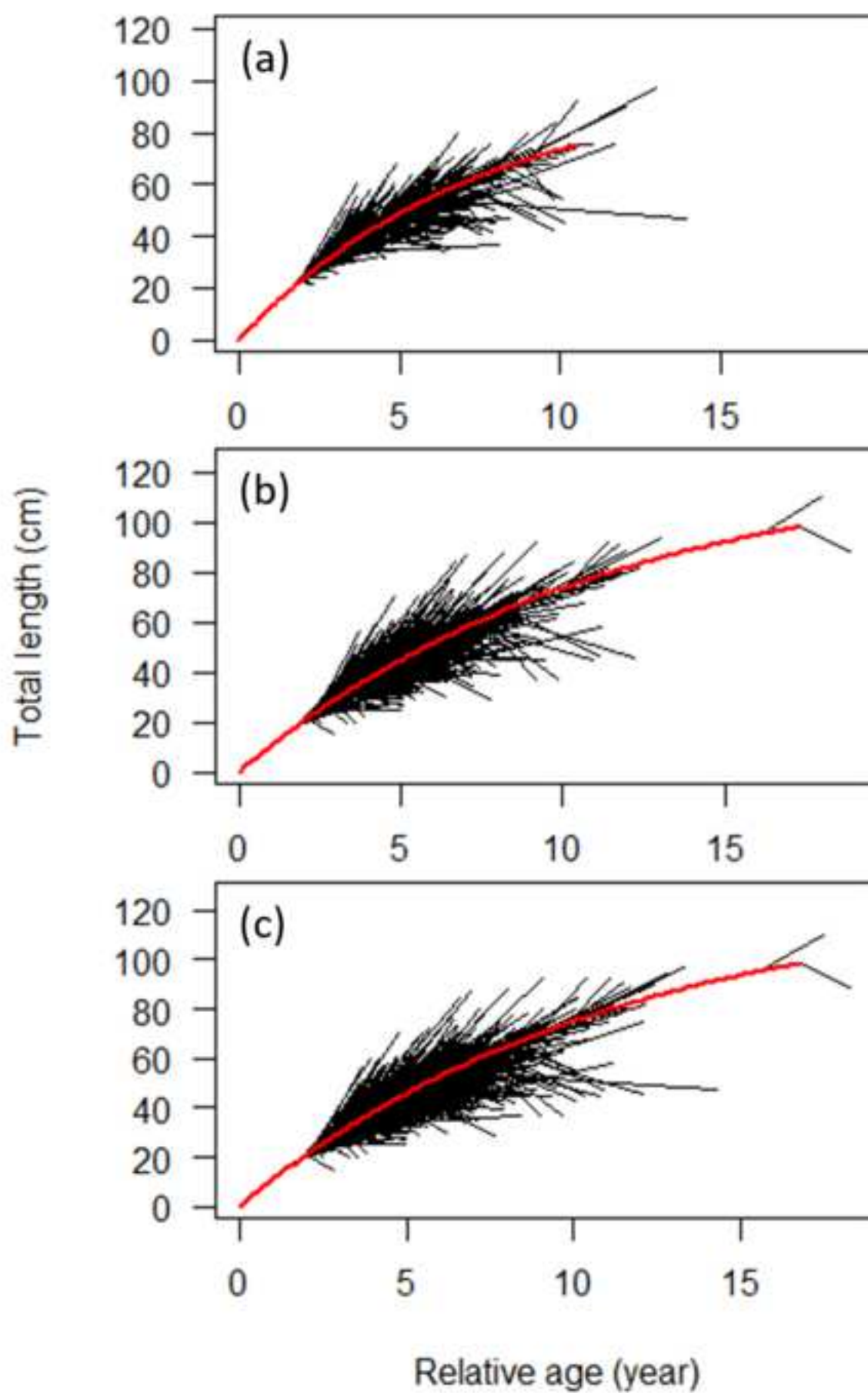
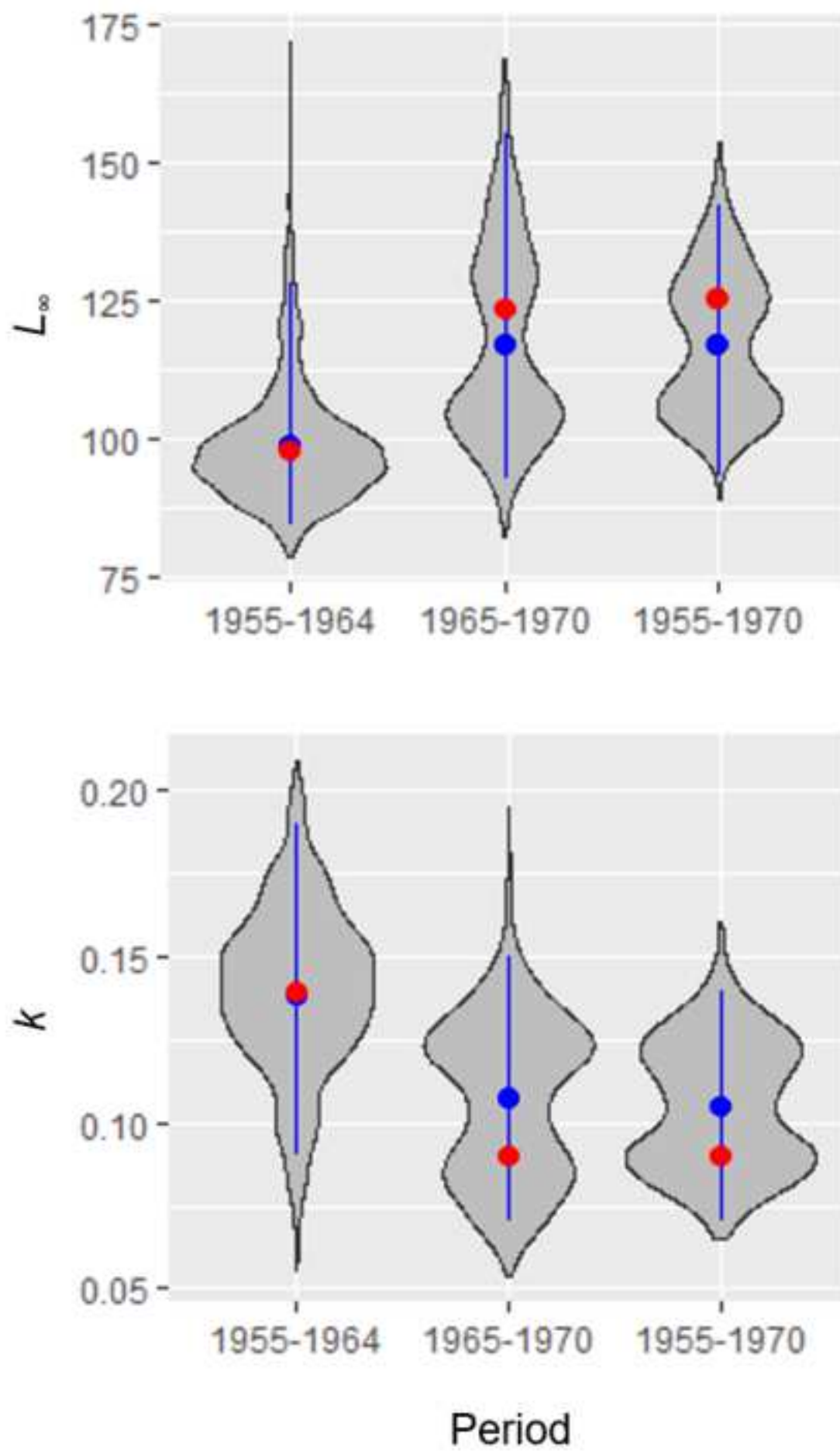


FIG7

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