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

3

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20

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22 **Abstract**

23 Understanding the growth of commercially exploited fish is crucial in fisheries biology.

24 Correct estimations of growth and its change over time are paramount for the evaluation of
25 stock status development.

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

32 The estimated VBGF parameters were $L_{\infty} = 98.22$ cm and $k = 0.14$ for the period 1955-1964
33 ($n = 1151$), $L_{\infty} = 123.61$ cm and $k = 0.09$ for 1965-1970 ($n = 2612$), and $L_{\infty} = 125.60$ cm and
34 $k = 0.09$ for the aggregated period ($n = 3763$). A seasonal growth signal was detected for all
35 the periods, with a peak after the spawning season in early autumn. These estimates are the
36 most thorough historical growth baseline now available for the Eastern Baltic cod and can be
37 compared to ongoing and future tagging experiments contributing to the development of
38 stock assessment models for this stock.

39

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

42 **1. Introduction**

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

51 Sustainable management highlights the importance of ‘reference points’ in fisheries, to
52 constrain harvesting within safe biological limits while accounting for the major sources of
53 uncertainty (Hilborn, 2002). Many marine ecosystems have undergone large changes during
54 the past decades, sometimes referred to as regime shifts, driven by overfishing and hydro-
55 climatic changes (Möllmann et al., 2014; Rocha et al., 2014). Therefore, information on
56 historical time-periods, used as anchor points that describe the status of a stock before
57 increases in fishing efforts or changes in its biology and environment, are essential for
58 understanding the long-term changes in exploited stocks. Pauly (1995) highlighted the risks
59 associated with a shifting perception of the stock’s status or the health of marine ecosystems
60 (i.e., “shifting baseline syndrome”) when not accounting for historical data. Reliable
61 information on historical baselines have been demonstrated to be essential to avoid overly
62 optimistic or misleading assessments of the status of fished populations that may affect
63 management decisions (Pinnegar and Engelhard, 2008; Cardinale et al., 2009 and 2011).
64 Thus, without the knowledge of historical baselines of key life history traits, such as growth,
65 a context to interpret current stock condition and its change over time is lacking
66 (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).

92 These historical data have been mainly used to analyse cod movements over the Baltic
93 seascape (reviewed in Aro, 1989 and 2002), while they have been underutilized for growth
94 analyses. Although some estimates of growth based on the historical tagging data exist, they
95 are limited to single national surveys and cover limited periods. The growth estimates in
96 Draganik and Netzel (1966) are based on southern Baltic tagging experiments conducted in
97 1957-1963, while Sjöblom et al. (1980) presented growth estimates based on Finnish tagging
98 experiments in 1974-1978. However, the compilation of historical tagging data would
99 provide a unique opportunity to estimate the historical growth of cod covering much larger
100 areas and periods in order to set baselines for future growth analyses.

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

106

107 **2. Material and methods**

108 2.1. Data overview

109 For this study, historical data from cod tagging experiments performed between 1955 and
110 1970 by Sweden, Poland, Denmark, Latvia and Germany in the Baltic area (ICES
111 subdivisions, SDs, 23-30; Fig. 1) have been collected from the respective national archives,
112 digitised and collated in a common database. A total of 7837 tagging records of fish releases
113 with corresponding recaptures were available (Table 1).

114 The compiled database includes, for most of the records, information on individual fish
115 release and recapture dates, total length, spatial coordinates and rarely information on total
116 weight, sex and maturity stage. In total, there were 7646 records with clear information on

117 both release and recapture dates, locations (ICES SD) and length measurements. The
118 historical tagging activities were performed mostly in quarter 1, 2 and 4 (i.e. 97%; Fig. 2a),
119 when the temperature differences between the water layers are moderate and tolerated by cod
120 at release (Otterlind, 1984). Overall, the main tagging areas were the ICES SDs 25-29 (Fig.
121 2b) and the time between release and recapture (days at liberty, DAL) ranged between 0 and
122 3650 days (Fig. 2c)

123 Additional information about tagging technique and recapture method were also included in
124 the database. Around 95% of the records had information on the tags type used. The most
125 frequently used tags were the Lea's hydrostatic tags (82%; i.e. a small celluloid cylinder,
126 which remains hermetically sealed and contains information for the finders; Fig. 3a),
127 followed by t-bars (10%; i.e. cylindrical markers, which are anchored between the spines at
128 the base of the second dorsal fin; Fig. 3b), and Carlin tags (2%; i.e. a plastic labels attached to
129 the back of the fish by braided nylon thread; Fig. 3c). Less than 1% of fish were tagged with
130 the Peterson disc (i.e. a tag attached to the base of the pectoral fin that consists of two
131 celluloid discs attached to the body by a wire; Fig. 3d). Around 51% of the recaptures
132 contained information about the recapture gears (43% active gears, i.e. trawls; 8% passive
133 gear, i.e. gillnets, longlines, traps and pots).

134

135 2.2. Data manipulation

136 Prior to growth analyses, some data filters were applied in a stepwise approach. Days at
137 liberty can affect growth estimates, especially when growth is slow compared to the precision
138 of the measurements (Allioud et al., 2014; McQueen et al., 2018). In addition, high numbers
139 of short-term recaptures, as in our case (Fig. 1c), may cause a downward bias in growth
140 estimate (Tallack, 2009). Therefore, only fish with $DAL \geq 60$ were included in the analyses
141 to ensure enough time for measurable growth to occur (remaining data $n = 5275$). Previous

142 cod growth analyses based on tagging data used $DAL \geq 60$ for the Northwest Atlantic cod
143 stock (Tallack, 2009) and $DAL \geq 50$ for the Western Baltic cod (McQueen et al., 2018). The
144 length distributions of fish with $DAL \geq 0$ and $DAL \geq 60$ were similar (Fig. S1). In an attempt
145 to reduce the inclusion of Western Baltic cod individuals (inhabiting the SDs 22-24) in the
146 growth analyses, only fish which were both released and recaptured within the boundaries of
147 the Eastern Baltic cod management area (SDs 25-32) were used (remaining data $n = 4016$).

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

150

$$151 \quad (1) \quad G = (\Delta L / \Delta T) \times 365$$

152

153 where ΔL indicates change in total length of fish and ΔT indicates DAL. The predicted
154 average annual growth rate was then used to exclude fish with extreme growth rates likely
155 caused by measurement errors. To identify an appropriate maximum annual growth threshold
156 for our data, the estimates of the von Bertalanffy growth function (VBGF) for North Sea cod,
157 based on Daan (1974), were used to calculate the maximum annual growth for this stock (25
158 $\text{cm}\cdot\text{year}^{-1}$). Thereafter, all the fish in our database with a growth $G > 25 \text{ cm}\cdot\text{year}^{-1}$ were
159 excluded from further analyses. We decided to take the North Sea cod as a reference because
160 of its higher growth than the Eastern Baltic stock (Daan, 1974). In addition, McQueen et al.
161 (2018) estimated G for a 25 cm Western Baltic cod to be around $14 \text{ cm}\cdot\text{year}^{-1}$. Thus, we are
162 confident that by removing the fish with $G > 25 \text{ cm}\cdot\text{year}^{-1}$ we removed only measurement
163 errors and not individual variability. In order to remove the extreme negative growth values
164 (i.e. recapture length \ll release length), the same percentile of fish growing above the cut-off
165 of $25 \text{ cm}\cdot\text{year}^{-1}$ (i.e. 3%) was used to remove the data from the left-tail of the growth
166 distribution (i.e. negative growth; Fig. S2).

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

169

170 2.3. Growth analyses

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

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

179

$$180 (2) \Delta L = (L_\infty - L_I)[1 - \exp(-k\Delta T)]$$

181

182 where, ΔL is the change in length between L_I and the length at recapture (L_2), and ΔT is the
183 duration in fraction of years between time at release (T_I) and time at recapture (T_2) (Francis
184 1988a). T_I and T_2 were measured in fraction of years from the 1st of January 1955, the year of
185 the first tagged cod release.

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

190 The GROTAG model includes parameters g_α and g_β , which are the mean annual growth rates
191 at two release sizes (α and β , respectively, where $\alpha < \beta$). Reference lengths for α and β which

192 were well represented by the tagging data were chosen (Francis, 1988a). In our study, the 5th
193 percentile value of L_1 measurements was adopted for α (i.e. 25 cm) and the 95th percentile
194 value of L_2 measurements was adopted for β (i.e. 55 cm; as in Tallack, 2009).

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

205

$$206 \quad (3) \sigma = nu \times g$$

207

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

213 Model selection was done as in Francis (1988a), involving incremental combinations of the
214 parameters (Table 2), with unfitted parameters held at zero. The best fitting model (i.e. final
215 model) was selected through Akaike's Information Criterion (AIC; Akaike, 1973), with
216 improved model fit indicated by a ΔAIC value ≤ 6 (where, ΔAIC 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_∞ and k (Maria, 2008; Haddon, 2011). For each period, an approximate 95%
241 confidence interval (CI) for L_∞ and k was then constructed using the bootstrap variance.

242

243 **3. Results**

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

248 During the period 1955-1964, the mean growth rates for a 25 cm (α) and 55 cm (β) cod were
249 $9.39 \text{ cm}\cdot\text{year}^{-1}$ and $5.54 \text{ cm}\cdot\text{year}^{-1}$, respectively, as estimated from the growth model
250 parameters (Table 4). The growth variability parameter (nu) was estimated as 0.69, indicating
251 that individuals within the population could be expected to grow between 0.31 and 1.69 times
252 the estimated average growth per length class. The timing of peak growth rate (w) and
253 amplitude of seasonal variation (u) indicated that a peak in growth rate occurred in the
254 beginning of September (e.g. $0.80 \text{ cm}\cdot\text{month}^{-1}$ for a 40 cm cod), and was around 2 times the
255 minimum growth rate that occurred in March (e.g. $0.45 \text{ cm}\cdot\text{month}^{-1}$ for a 40 cm cod) (Fig.
256 5a). The contamination probability (p) was negligible (0.01), indicating that the occurrence of
257 outliers was scarce, and the model did not detect outliers after the data cleaning. The standard
258 deviation of measurement error (s) was 1.34 cm, which is in accordance with the 1-cm
259 precision of the length measurements recorded in the historical tagging data. The VBGF
260 parameters estimates were $L_{\infty} = 98.22 \text{ cm}$ and $k = 0.14$ (Table 4). The growth trajectories and
261 the fitted growth curve for the period 1955-1964 are presented in Fig. 6a.

262 During the period 1965-1970, the mean growth rates for a 25 cm (α) and 55 cm (β) cod were
263 $8.59 \text{ cm year}^{-1}$ and $5.97 \text{ cm year}^{-1}$, respectively, as estimated from the growth model
264 parameters (Table 5). The growth variability parameter (nu) was estimated as 0.74, indicating
265 that individuals within the population could be expected to grow between 0.36 and 1.74 times
266 the estimated average growth per length class (Table 5). The timing of peak growth rate (w)

267 and amplitude of seasonal variation (u) indicated that a peak in growth rate occurred in the
268 beginning of September (e.g. $0.79 \text{ cm}\cdot\text{month}^{-1}$ for a 40 cm cod), and was around 2 times the
269 minimum growth rate that occurred in March (e.g. $0.42 \text{ cm}\cdot\text{month}^{-1}$ for a 40 cm cod) (Fig.
270 5b). The contamination probability (p) was negligible (0.00), indicating that the occurrence of
271 outliers was scarce, and the model did not detect outliers after the data cleaning. The mean
272 measurement error (m) was low (-0.55 cm) and the standard deviation in measurement error
273 (s) was 1.60 cm , which is in accordance with the 1 cm precision of the length measurements
274 recorded in the historical tagging data (Table 5). The VBGF parameters estimates were $L_{\infty} =$
275 123.61 cm and $k = 0.09$ (Table 5). The individual growth trajectories and the fitted growth
276 curve for the period 1965-1970 are presented in Fig. 6b.

277 For the combined period, 1955-1970, the mean growth rates for a 25 cm (α) and 55 cm (β)
278 cod were $8.59 \text{ cm year}^{-1}$ and $6.14 \text{ cm year}^{-1}$, respectively, as estimated from the growth model
279 parameters (Table 6). The growth variability parameter (nu) was estimated as 0.74, indicating
280 that individuals within the population could be expected to grow between 0.36 and 1.74 times
281 the estimated average growth per length class (Table 6). The timing of peak growth rate (w)
282 and amplitude of seasonal variation (u) indicated that a peak in growth rate occurred in the
283 beginning of September (e.g. $0.79 \text{ cm}\cdot\text{month}^{-1}$ for a 40 cm cod), and was around 2 times the
284 minimum growth rate that occurred in March (e.g. $0.44 \text{ cm}\cdot\text{month}^{-1}$ for a 40 cm cod) (Fig.
285 5c). The contamination probability (p) was negligible (0.00), indicating that the occurrence of
286 outliers was scarce, and the model did not detect outliers after the data cleaning. The mean
287 measurement error (m) was low (-0.54 cm) and the standard deviation in measurement error
288 (s) was 1.50 cm , which is in accordance with the 1 cm precision of the length measurements
289 recorded in the historical tagging data (Table 6). The VBGF parameters estimates were $L_{\infty} =$
290 125.60 cm and $k = 0.09$ (Table 6). The individual growth trajectories and the fitted growth
291 curve for the period 1955-1970 are presented in Fig. 6c.

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

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

298

299 **4. Discussion**

300 In the last two decades, the interest in the recovery, digitisation and analysis of fish and
301 fisheries historical data has greatly increased in the framework of historical fisheries ecology
302 (Zeller et al., 2005; Fortibuoni et al., 2017). Data recovery has been demonstrated to be a
303 valuable contribution in countering the ‘shifting baseline’ syndrome (Pauly, 1995) providing
304 early time period reference points for analyses of the stock status (Zeller et al., 2005).
305 Furthermore, these data can be used to extend time series that are used as input data for stock
306 assessments (Richards and Schnute, 1998; Cox et al., 2002), and are also highly valuable for
307 understanding changes in exploited stocks over long time periods (Christensen et al., 2003;
308 Cardinale et al., 2014). However, collating historical information is often time-consuming
309 and difficult, as records are often reported in different languages and only accessible in the
310 national archives in paper format (McClenachan et al., 2012; Fortibuoni et al., 2017). The
311 digitisation of these archival data is an important process that would ensure increased
312 exposure and use of data that otherwise are vulnerable to be ‘forgotten’ (Zeller et al., 2005).
313 Traditionally, size at age data have been widely used to study growth in fish species that
314 consistently deposit growth increments in calcified tissues, such as otoliths (Campana, 2001;
315 Panfili et al., 2002). However, for stocks where age information is not available or unreliable
316 owing to severe age reading problems, tagging experiments have produced valid data for

317 length-based growth modelling, as for example for the north-east Atlantic tope shark (Dureuil
318 and Worm, 2015), for the Northwest Atlantic halibut (Shackell et al., 2019) and for Atlantic
319 cod in Gulf of Maine (Shackell et al., 1997) and in the Scotian Shelf (Tallack, 2009).

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

325 The VBGF parameters estimated in this study for the Eastern Baltic cod during the period
326 1955-1964 ($L_{\infty} = 98.22$ cm and $k = 0.14$) differed slightly from the estimates presented by
327 Draganik and Netzel (1966) from fish released in the years 1957-1963 in the Polish waters
328 ($L_{\infty} = 120.40$ cm and $k = 0.13$). This difference can be potentially attributed to the different
329 length frequency distributions and sample sizes of the fish available. Although no
330 information about the sample size or fish length range used for analysis was reported in
331 Draganik and Netzel, (1966), it is unlikely that it was as large and comprehensive as our
332 dataset.

333 In our analyses the VBGF parameter estimates differ between periods, with higher L_{∞} and
334 lower k for the period 1965-1970 compared to the period 1955-1964. Explaining these
335 differences is outside the scope of this study, however variations in both abiotic and biotic
336 factors as well as harvesting can shape the growth of fish (Lambert *et al.*, 1994; Lambert and
337 Dutil 2001; Krohn *et al.*, 1997; Lorenzen et al., 2016) and thus the combined effect of these
338 multiple pressures can be potentially the reason of the temporal changes in growth observed
339 in our case. In addition, the difference in VBGF parameters between the periods may be also
340 the result of the different fish length ranges available in our analysis. For the period 1955-
341 1964, the lack of released cod larger than 75 cm, compared to the maximum release length of

342 95 cm for the period 1965-1970, is likely the main reason for the lower estimate of L_{∞} in the
343 former period. The coverage of the length range is an important aspect when assessing
344 growth with tagging data since the estimation of the L_{∞} requires extrapolation from the
345 available data when large individuals are lacking in the sample (Knight, 1968).

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

356 Growth modelling using tag-recapture data provides estimates of growth in relation to length,
357 which can be converted to relative age. Therefore, auxiliary data, such as length frequency
358 data and age readings from otoliths or other hard parts, will be required to anchor our
359 estimated growth curve to an absolute age axis (Eveson et al., 2015; McQueen et al., 2018).
360 Moreover, the estimates of VBGF parameters based on age data are not directly comparable
361 with the estimates based on length data because the parameters change in definition (Francis,
362 1988b).

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

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

374

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380 (Sweden).

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624 **Figure captions**

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

626

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

630

631 Fig. 3. Different types of tag used in the Baltic cod tagging experiments during 1955-1970.
632 Lea's hydrostatic tag (a); t-bar (b); Carlin tag (c); Peterson disc tag (d).

633

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

637

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

640

641

642 Fig. 6. Seasonal changes in growth rate (solid line) and growth variability (dashed lines) of a
643 40 cm cod for the periods 1955-1964 (a), 1965-1970 (b), and the periods combined, 1955-
644 1970 (c).

645

646 Fig. 7. Distribution of bootstrap replicates for each period, and the periods combined, of the
647 VBGF parameters L_{∞} and k . Blue dots represent the median of the bootstrapped von
648 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

4

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	$g_{\omega} g_{\beta} s, nu, m, p, u, w$	

- 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
Total	1151	2612	3763

15 Table 4. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates \pm
 16 standard error (SE) for the estimated model parameters calculated for the period 1955-1964
 17 ($n = 1151$). AIC value is reported for each model. Bold: final model; “-”: parameter fixed to 0
 18 in the model.
 19

	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 ⁻¹) g_{25}	10.67 \pm 0.29	7.42 \pm 0.25	8.53 \pm 0.37	9.27 \pm 0.43	9.39 \pm 0.42
Mean growth rates (cm·year ⁻¹) g_{55}	2.95 \pm 0.20	5.36 \pm 0.20	6.14 \pm 0.28	5.74 \pm 0.29	5.54 \pm 0.27
Amplitude of seasonality u	-	-	-	-	0.31 \pm 0.08
Timing of peak growth w	-	-	-	-	0.70 \pm 0.03
Growth variability nu	-	0.86 \pm 0.04	0.75 \pm 0.04	0.68 \pm 0.04	0.69 \pm 0.04
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	1.34 \pm 0.11
Mean measurement error (cm) m	-	-	-0.55 \pm 0.13	-0.56 \pm 0.13	-0.28 \pm 0.15
Outliers probability p	-	-	-	0.01 \pm 0.01	0.01 \pm 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

20

21

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

26

	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 ⁻¹) g_{25}	9.77 \pm 0.17	7.09 \pm 0.17	8.19 \pm 0.26	8.39 \pm 0.30	8.59 \pm 0.29
Mean growth rates (cm·year ⁻¹) g_{55}	3.89 \pm 0.15	5.53 \pm 0.16	5.97 \pm 0.19	5.97 \pm 0.19	5.97 \pm 0.19
Amplitude of seasonality u	-	-	-	-	0.33 \pm 0.05
Timing of peak growth w	-	-	-	-	0.71 \pm 0.02
Growth variability nu	-	0.90 \pm 0.03	0.81 \pm 0.03	0.77 \pm 0.04	0.74 \pm 0.04
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	1.60 \pm 0.09
Mean measurement error (cm) m	-	-	-0.67 \pm 0.10	-0.70 \pm 0.11	-0.55 \pm 0.11
Outliers probability p	-	-	-	0.00 \pm 0.00	0.00 \pm 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

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29 Table 6. GROTAG and von Bertalanffy growth function (VBGF) parameter estimates \pm
 30 standard error (SE) for the estimated model parameters calculated for the period 1955-1970
 31 ($n = 3763$). AIC value is reported for each model. Bold: final model; “-”: parameter fixed to 0
 32 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 (cm·year ⁻¹) g_{25}	10.04 \pm 0.15	*	8.40 \pm 0.21	8.39 \pm 0.30	8.59 \pm 0.29
Mean growth rates (cm·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	-	-	-	-	0.30 \pm 0.04
Timing of peak growth w	-	-	-	-	0.71 \pm 0.02
Growth variability nu	-	*	0.78 \pm 0.02	0.74 \pm 0.03	0.74 \pm 0.02
Standard deviation of measurement error (cm) s	5.00 \pm 0.05	*	1.34 \pm 0.08	1.40 \pm 0.08	1.50 \pm 0.07
Mean measurement error (cm) m	-	-	-0.68 \pm 0.08	-0.72 \pm 0.08	-0.54 \pm 0.09
Outliers probability p	-	-	-	0.00 \pm 0.00	0.00 \pm 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

33

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_{∞}	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

37

FIG1

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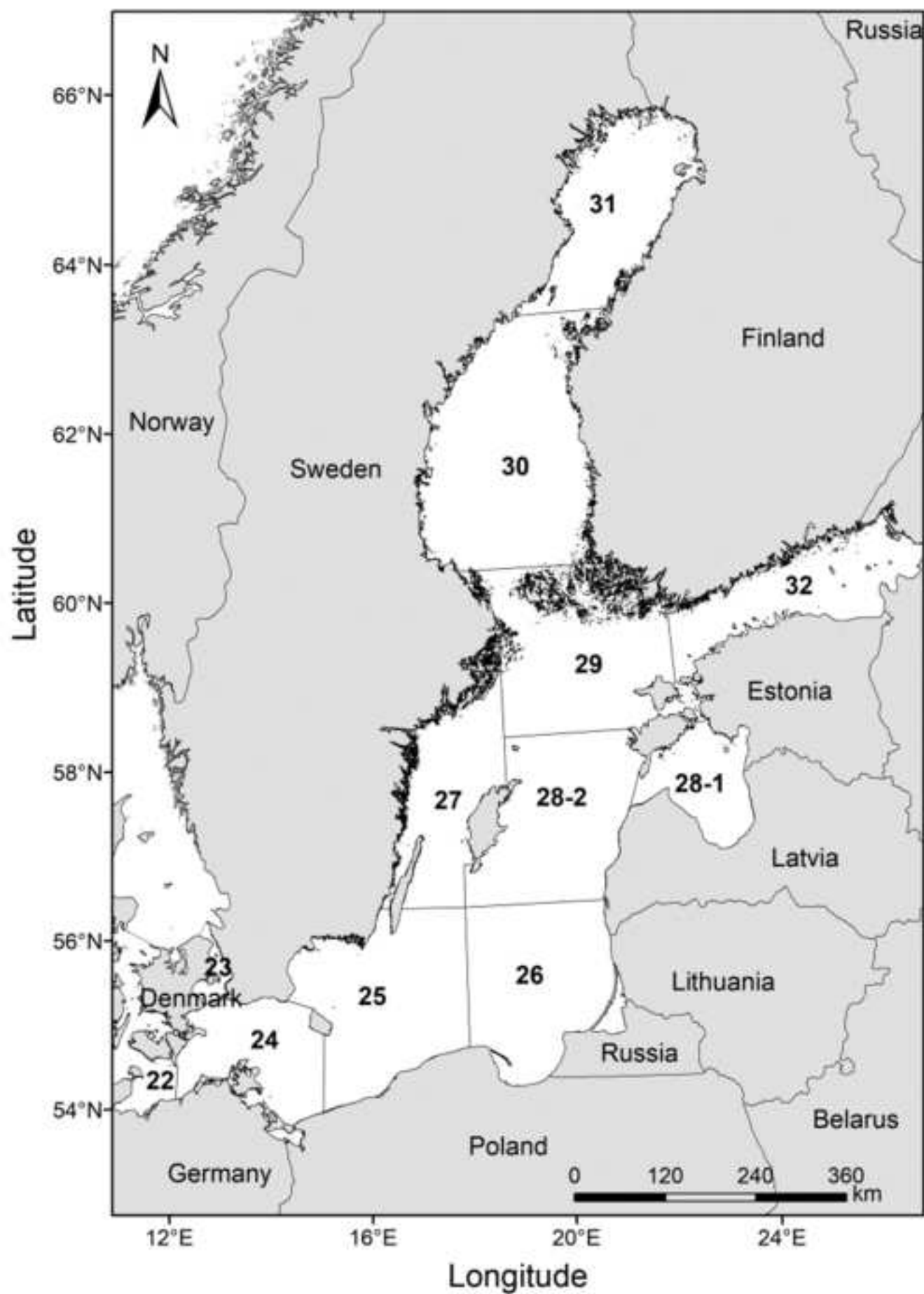


FIG2

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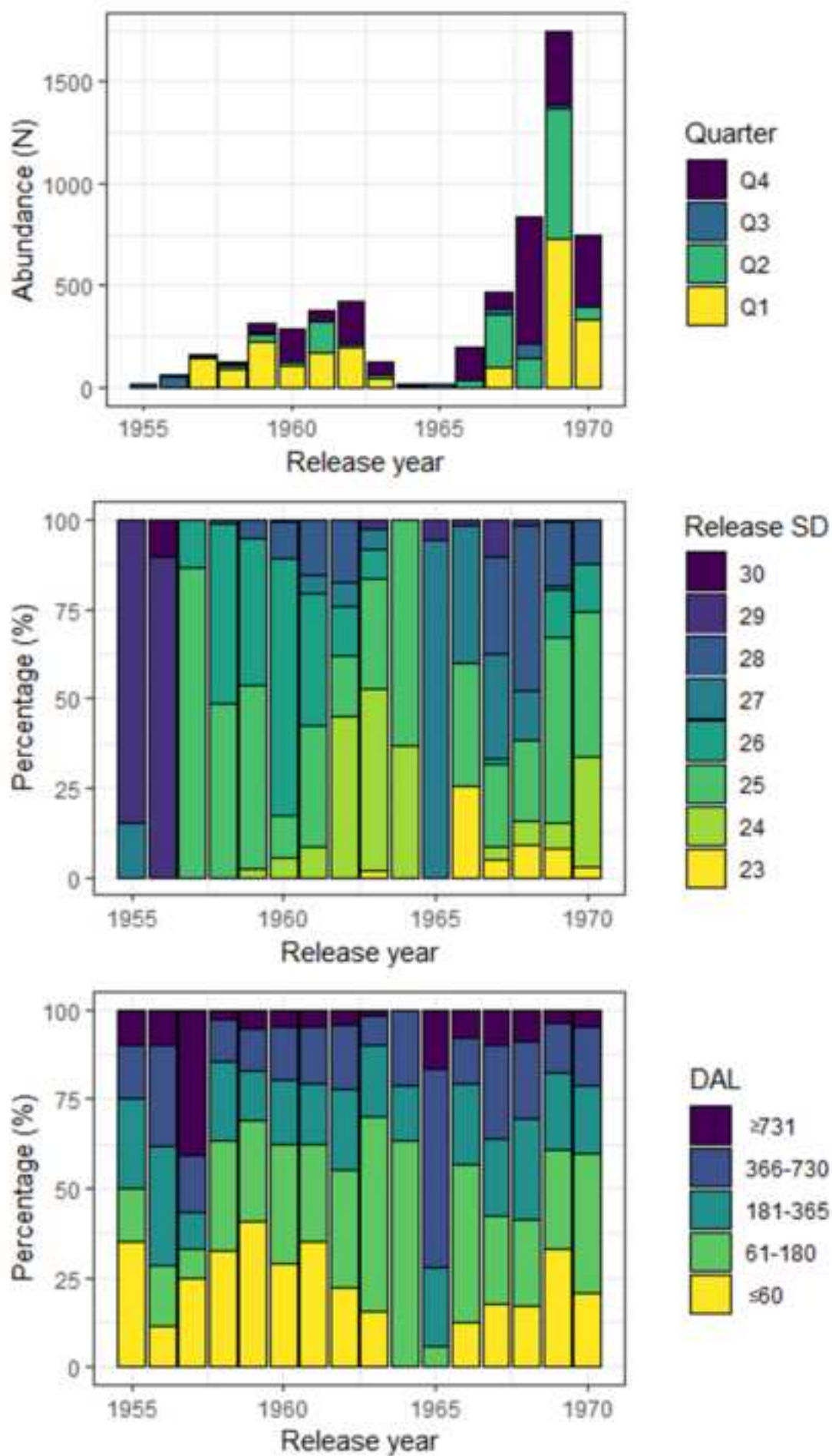


FIG3

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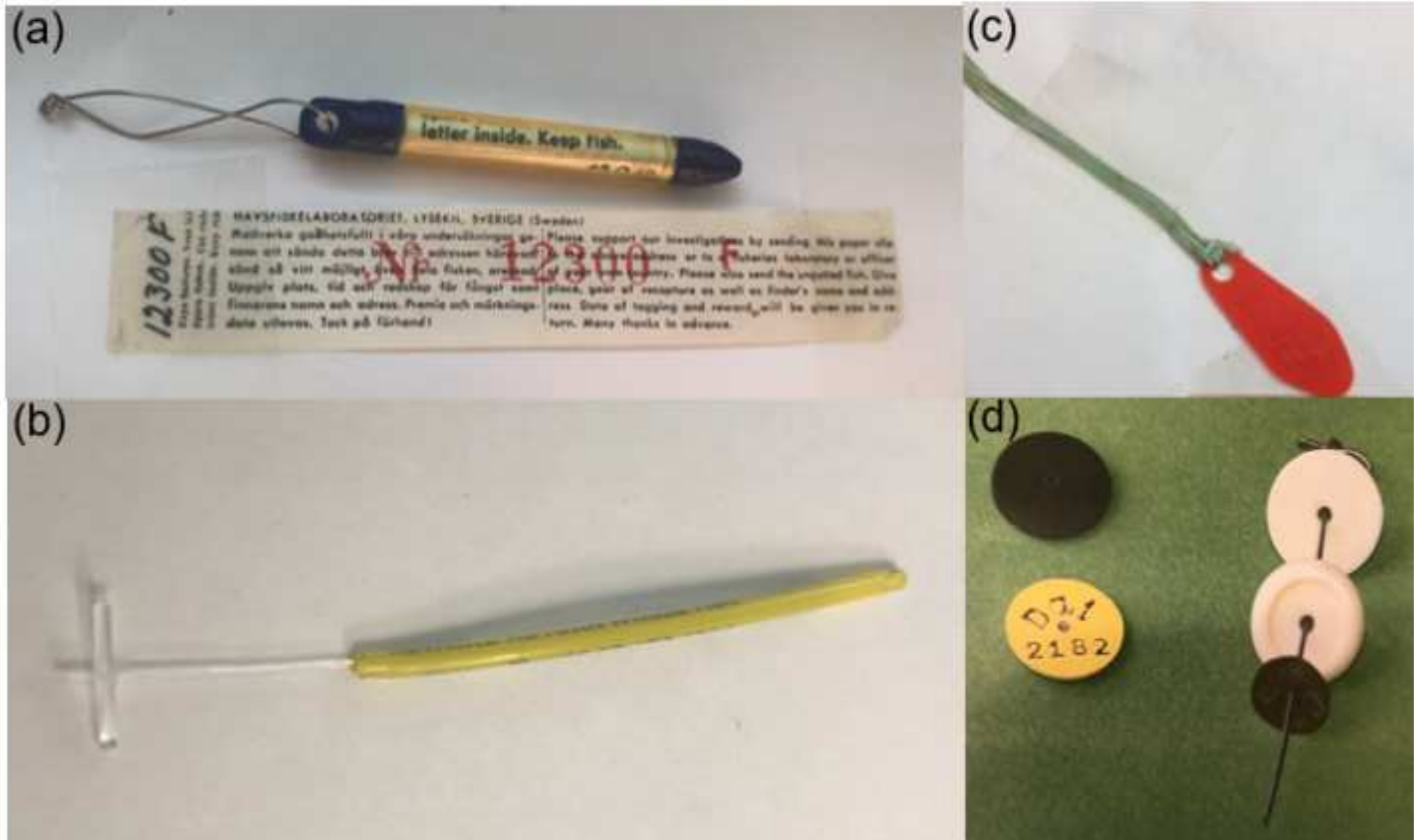


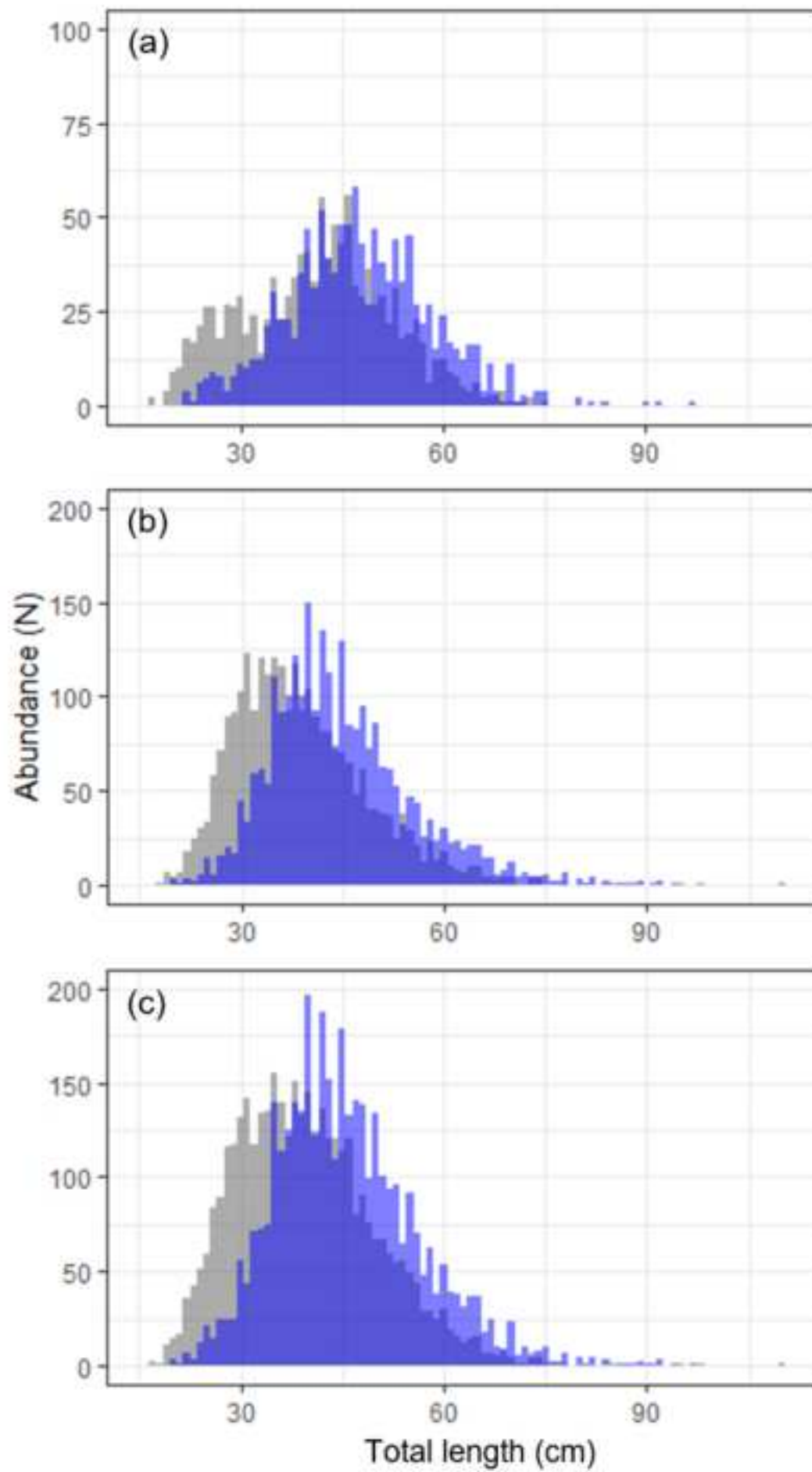
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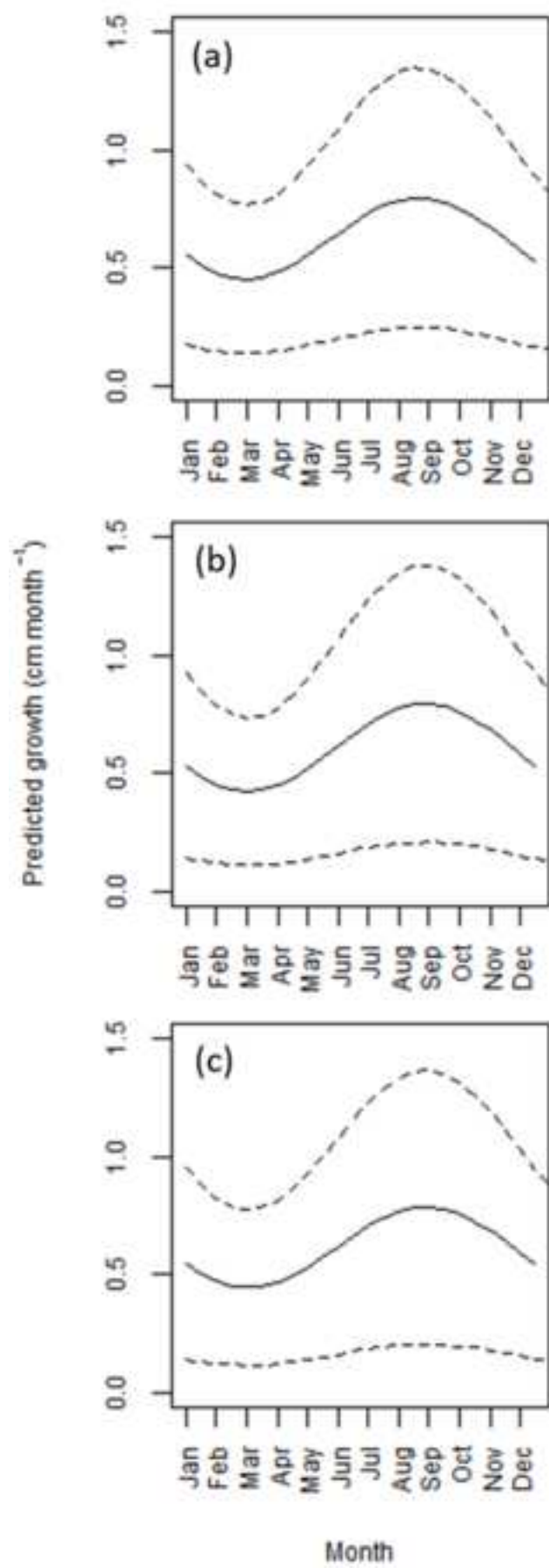
FIG5[Click here to download high resolution image](#)

FIG6

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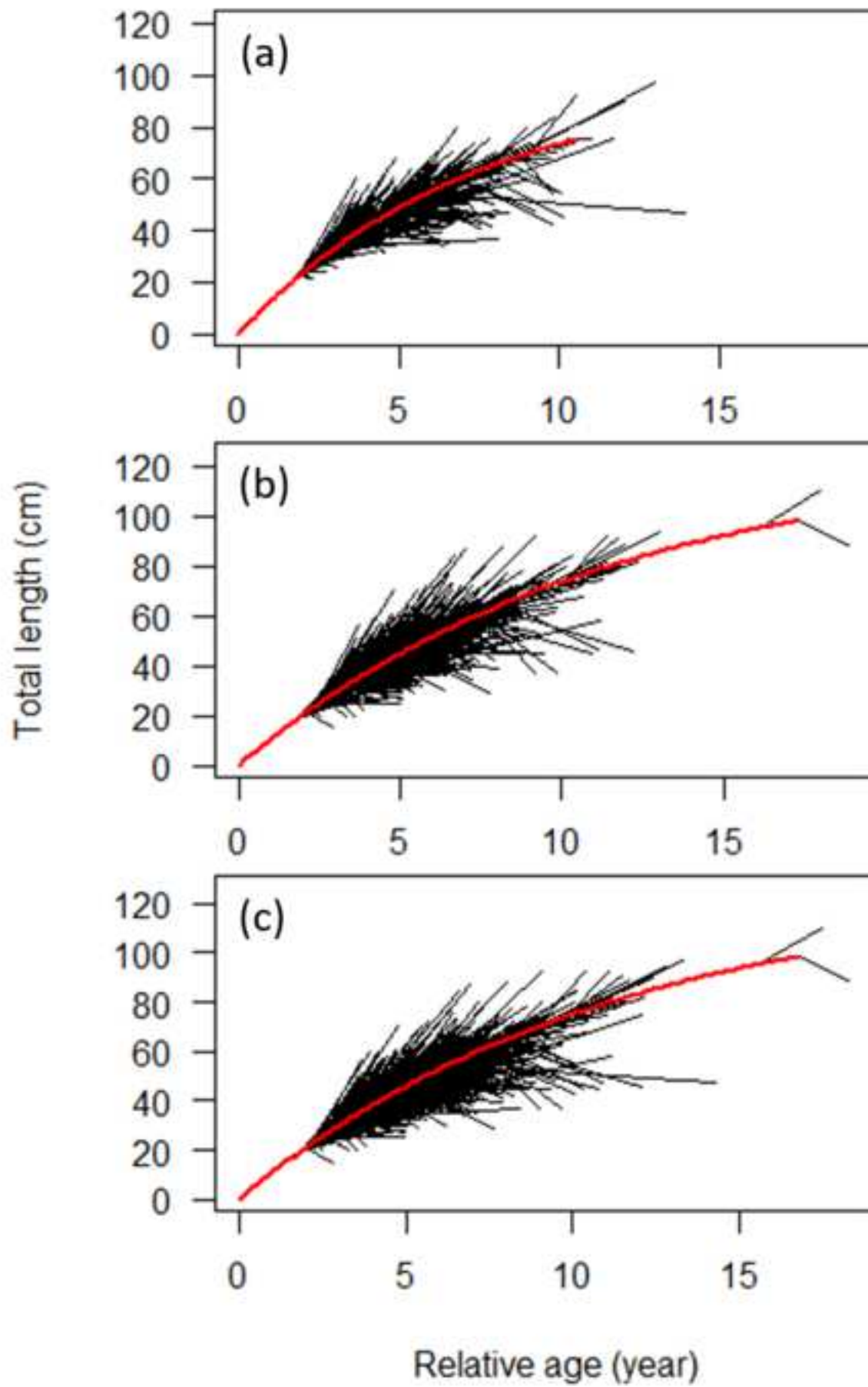
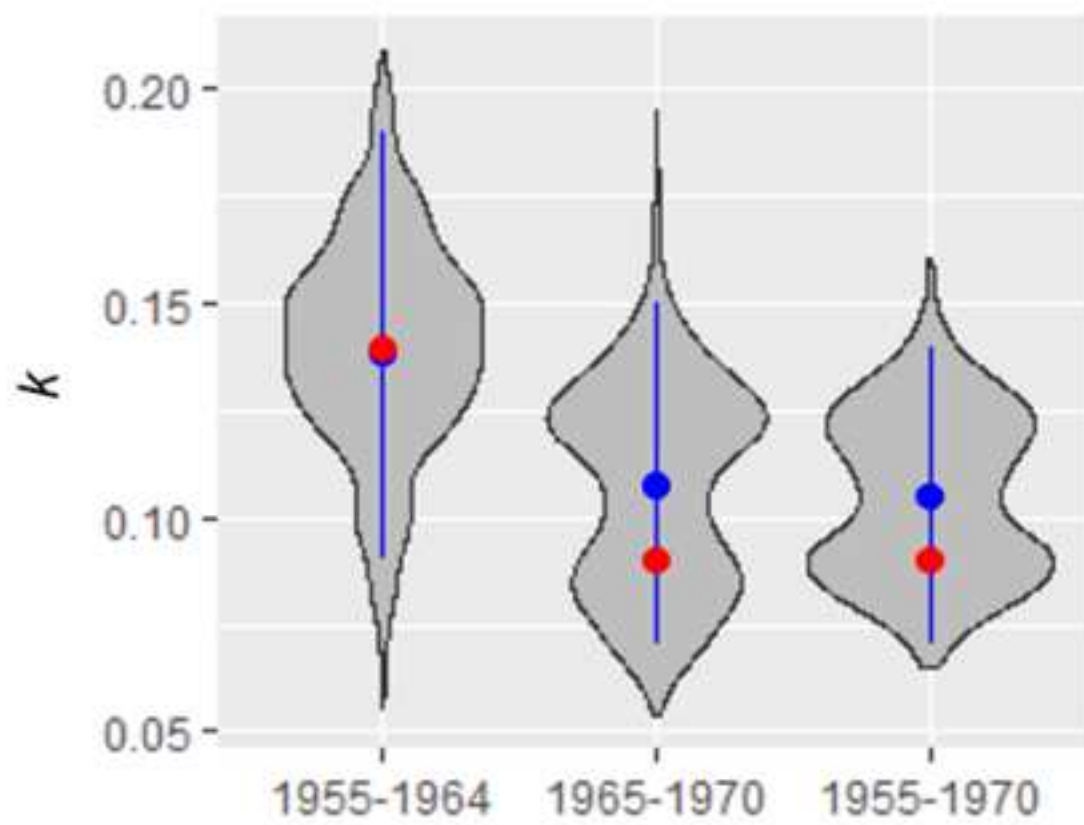
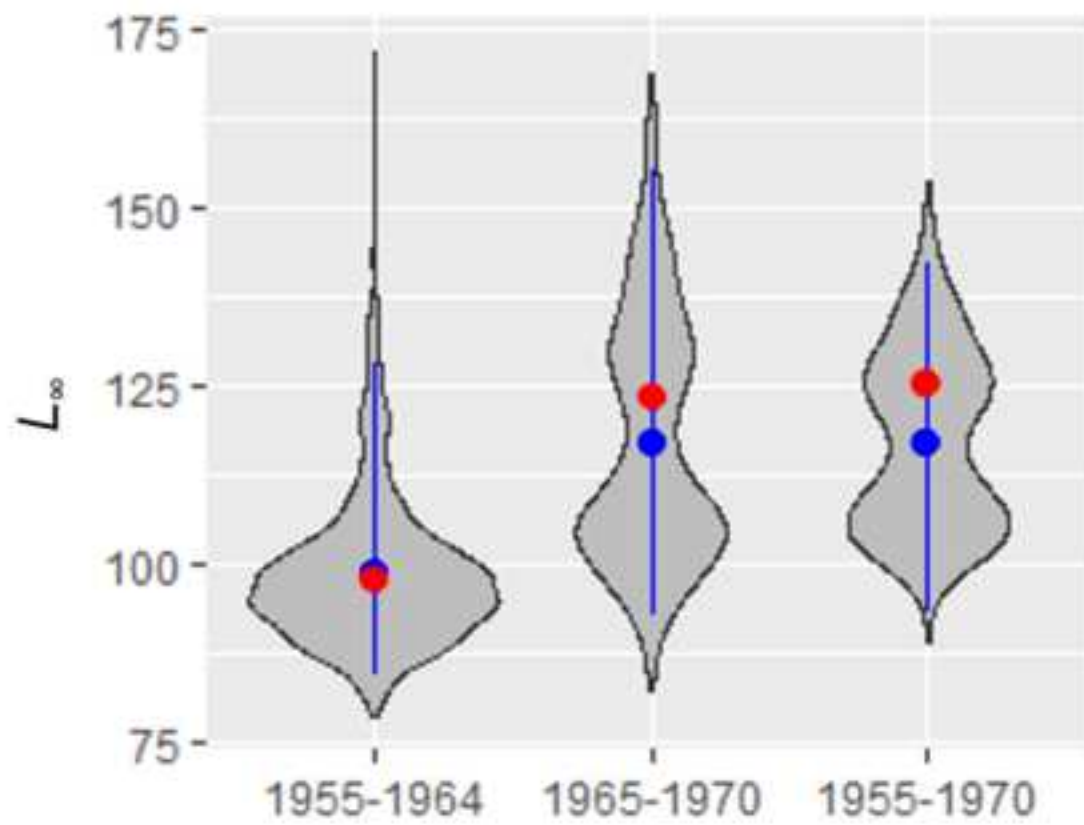


FIG7

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Period

Supplementary material for on-line publication only

[Click here to download Supplementary material for on-line publication only: Supplementary_revision.docx](#)