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Multidecadal changes in fish growth rates estimated from tagging data: A case study from the Eastern Baltic cod (*Gadus morhua*, Gadidae)

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1 **Multidecadal changes in fish growth rates estimated from tagging data: a case study from**
2 **the Eastern Baltic cod (*Gadus morhua*, *Gadidae*).**

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25

26 **Running title:** Changes in fish growth from tagging data.

27

28 **Abstract**

29 Long time-series of reliable individual growth estimates are crucial for understanding the status
30 of a fish stock and deciding upon appropriate management. Tagging data provide valuable
31 information about fish growth, and are especially useful when age-based growth estimates and
32 stock assessments are compromised by age determination uncertainties. However, in the
33 literature there is a lack of studies assessing possible changes in growth over time using tagging
34 data. Here, data from tagging experiments performed in the Baltic Sea between 1971-2019
35 were added to those previously analysed for 1955-1970 to build the most extensive tagging
36 dataset available for Eastern Baltic cod (*Gadus morhua*, *Gadidae*), a threatened stock with
37 severe age-determination problems. Two length-based methods, the GROTAG model (based
38 on the von Bertalanffy growth function) and a Generalized Additive Model, were used to assess
39 for the first time the potential long-term changes in cod growth using age-independent data.
40 Both methods showed strong changes in growth with an increase until the end of the 1980s
41 (8.6-10.6 cm·year⁻¹ for a 40 cm cod depending on the model) followed by a sharp decline. This
42 study also revealed that the current growth of cod is the lowest observed in the past 7 decades
43 (4.3-5.1 cm·year⁻¹ for a 40 cm cod depending on the model), indicating very low productivity.
44 This study provides the first example of the use of tagging data to estimate multidecadal
45 changes in growth rates in wild fish. This methodology can also be applied to other species,
46 especially in those cases where severe age-determination problems exist.

47

48 **Keywords:** Baltic cod, Generalized Additive Model, growth modelling, mark-recapture, time-
49 series, von Bertalanffy growth function.

50

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76 **1. Introduction**

77 Growth describes how body size changes with time, and variation in growth can have
78 substantial consequences for survival, age at sexual maturity, reproductive success and
79 movements, modulating the response of populations to environmental changes and
80 anthropogenic pressures including fisheries (Peters, 1983; Dortel et al., 2014). Therefore, long
81 time-series of reliable growth estimates are crucial for evaluating the present and past status of
82 a fish stock and deciding upon appropriate fisheries management actions under ecosystem
83 changes (Kell and Bromley, 2004; Dortel et al., 2014; Vincenzi et al., 2014; Aires-da-Silva et
84 al., 2015).

85 For temperate teleost fish species, growth estimates and stock assessment generally rely on age
86 determination through the interpretation of otolith annual increments. However, numerous
87 examples of severe age-reading uncertainties and inconsistencies causing highly inaccurate
88 estimates of population dynamics exist (Campana, 2001; Kestelle et al., 2017), resulting in
89 extreme cases in the abandonment of age-based analytical stock assessments (e.g. de Pontual
90 et al., 2006; ICES, 2014a and 2015). By contrast, tagging methods provide valid data for
91 length-based growth modelling for many fish families, including gadoids (e.g. cod; Shackell et
92 al., 1997, Tallack, 2009, McQueen et al., 2019a). Those data have also been integrated into
93 stock assessment as in the case of some tuna species (e.g. Hearn and Polacheck, 2003, Restrepo
94 et al., 2010, Ailloud et al., 2014, Aires-da-Silva et al., 2014, Dortel et al., 2014), and hake (de
95 Pontual et al., 2013). However, to the best of our knowledge, tagging data has never previously
96 been used for assessing possible changes in growth over long time periods.

97 The Baltic Sea is one of the largest brackish water areas in the world, where severe changes in
98 biotic and environmental conditions have occurred in the past hundred years (Reusch et al.,
99 2018). Historically, cod (*Gadus morhua*, *Gadidae*) has been one of the most important
100 commercial species in the Baltic Sea (Bagge et al., 1994; ICES, 2014b) and, as a major

101 piscivorous fish, has important structuring roles in the ecosystem (Casini et al., 2009). During
102 the past hundred years, the Eastern Baltic cod (EBC) stock size has changed considerably, with
103 a peak in the early 1980s when the stock yielded the third-largest landings of all cod stocks in
104 the North Atlantic (ca. 200.000 t). Since then, the stock has been in decline and is currently one
105 of the most severely threatened fish stocks in Europe (ICES, 2020a). From 2019, the advice for
106 EBC is for a closure of the fisheries (ICES, 2020b).

107 Concurrent with the decline in stock size, a number of changes have been observed in the EBC
108 stock, which include reduced body condition, maturation at a smaller size, increased parasite
109 infestation and thiamine deficiency (Eero et al., 2015; Horbowy et al. 2016; Engelhardt et al.,
110 2020). Additionally, a decline in relative abundance of larger individuals (i.e. >35–40 cm) and
111 a drop in maximum length has occurred (Eero et al., 2015; Orio et al., 2017, ICES 2019a).
112 However, due to the lack of reliable age determination for this stock (ICES, 2014; Hüsey et al.,
113 2016b), it is unclear whether the change in size structure of the stock is the result of reduced
114 growth or increased mortality of older individuals, or both.

115 The existence of ageing problems in the EBC stock has been known since the implementation
116 of an analytical stock assessment in the beginning of the 1970s (ICES, 1972; Hüsey et al.,
117 2016b). To overcome this problem, stock assessment models that can handle length-based data
118 are currently used (e.g. Sock Synthesis; ICES, 2019b). However, such approaches still require
119 information on individual growth, especially if growth is changing. Accurate information on
120 temporal patterns in growth is therefore required (ICES, 2018; Eero et al., 2015).

121 Previous studies based on weight-at-age data from commercial landings suggested changes in
122 growth for EBC with an increase between 1980 and the early 1990s and a subsequent decline
123 (Brander, 2007; ICES, 2013). However, the severe age-determination uncertainties and
124 inconsistencies (Hüsey, 2016b) have put into question the trend observed. In addition, caution
125 is needed when using weight-at-age data (especially those from commercial landings) as proxy

126 for growth since they are also affected by size-selective fishing mortality and high-grading
127 practices, besides changes in individual body condition. The study by Hüsey et al. (2018), based
128 on otolith daily increment and year classes identification from length frequency data, suggested
129 a decline in growth rates also of young cod from the early 2000s, but the potential magnitude
130 of change in growth of older cod was not assessed since the methodologies used are not suitable
131 for older individuals (Hüsey et al., 2018).

132 Extensive tagging experiments on Baltic cod have been performed by the countries bordering
133 the Baltic Sea from the late 1950s to the 1980s (Bagge, 1994) and have continued more
134 sporadically thereafter. These historical tagging data were mainly used to analyse cod
135 movements over the Baltic seascape (reviewed in Aro, 1989 and 2002), but they have been
136 underutilized for growth analyses. Although some estimates of growth based on the historical
137 tagging data exist, they are mainly limited to single national surveys and cover limited periods
138 (Draganik and Netzel, 1966; Sjöblom et al., 1980; Mion et al., 2020).

139 In this study, we extended the historical database used in Mion et al. (2020), which is based on
140 tagging data collected during 1955-1970, by collating and digitising the existing archived data
141 from the countries that have performed tagging experiments in the Baltic Sea between the
142 1970s and the 1990s. In addition, data from international tagging experiments carried out in
143 the southern Baltic Sea in the 2000s and in recent years (2016-2019) have also been integrated
144 with the collated historical data. With this extensive dataset, which represents the longest
145 available time series of tagging data for the EBC over the whole area of its distribution, we
146 reconstructed for the first time growth pattern in cod over the past 7 decades. This study is an
147 example of the potential of tagging data for assessing time-series of growth, which is especially
148 important for those stocks and species suffering from age estimation problems.

149

150 **2. Material and methods**

151 **2.1 Data overview**

152 For this study, data from (1) historical tagging experiments carried out in the Baltic Sea, and
153 the more recent projects (2) CODYSSEY (Cod spatial dynamics and vertical movements in
154 European waters and implications for fishery management) and (3) TABACOD (Tagging
155 Baltic Cod) were combined in a common database.

156

157 *Historical data*

158 The historical tagging database of Baltic cod compiled in Mion et al. (2020) covering the period
159 1955-1970 was extended by digitising and collating additional historical data from tagging
160 experiments between the 1970s and the 1990s by Sweden, Poland, Latvia, Finland, Denmark
161 and Germany within ICES Subdivisions (SDs) 23-32 (Fig. 1). Data for a total of 10143
162 recaptured cod were available, covering a release period between 1955 and 1993 (Table 1).

163 The records in the compiled database of all recaptured cod included information on release and
164 recapture location, date and total length, as well as occasional information on total weight, sex
165 and maturity stage that were not considered in this analysis. In total, there were 8622 records
166 with clear information on both release and recapture dates, geographical position at least at the
167 ICES SD resolution and length measurements. The historical tagging activities were performed
168 year-round, except for the warmest months in the 3rd quarter which were less sampled, when
169 the thermocline is more pronounced and less tolerated by cod at release (Otterlind, 1984; Fig.
170 2a).

171 Information about the historical tagging procedures was available from literature for all tagging
172 experiments (Swedish experiments: Otterlind, 1969 and 1984; Danish tagging experiments:
173 Bagge, 1969 and 1970; Polish tagging experiments: Netzel, 1976; Latvian tagging
174 experiments: Kondratovich, 1980; German tagging experiments: Berner, 1962 and 1967;
175 Bingel, 1981; Finnish tagging experiments: Sjöblom et al., 1980). In the Swedish, Danish,

176 Polish, Latvian and German tagging experiments cod were fished with bottom trawl hauls from
177 chartered fishing cutters or research vessels. To enhance survival, fish were placed in a flow-
178 through tank with surface seawater before the tagging procedures and only fish not damaged
179 during capture were tagged. After tagging cod were immediately released at the surface at the
180 same location where they were caught, with the exception of two tagging experiments in 1968
181 where the fish were released at the bottom using a release cage (Otterlind, 1969; Otterlind,
182 1984). All the tagged cod, which were unable to swim, were retrieved and removed from the
183 tagging list. In the Finnish experiments, cod were mainly caught with gillnets and longline. In
184 the Gulf of Finland (SD 32) cod were held some days in tanks before tagging and subsequent
185 release, while in the Åland Sea (SD 29) cod were tagged and released immediately after capture
186 (Sjöblom et al., 1980).

187 Overall, the main release areas for the recaptured fish were within ICES SDs 25-32 (Fig. 2b).
188 The individual measurements (i.e. total length and total weight) and other information (e.g.
189 location) of the recaptured fish were reported mainly by the fishers through letters addressed
190 to the research institutes involved in the tagging project (Fig. 3). The length of recaptured cod
191 ranged from 140 to 1100 mm (median: 440 mm) and the time between release and recapture
192 (days at liberty, DAL) ranged between 0 and 3928 days (median: 128 days; Fig. 2c). The return
193 rate (i.e. the % of tagged cod that were recaptured and reported to the research institutes) for
194 the historical tagging experiments were on average 11.8% (Table 1). Around 75% of the
195 recaptures had information on the tag type used. Most of the recaptured tags were Lea's
196 hydrostatic tags (54%), followed by T-bars (15%), and Carlin tags (5%), while less than 1% of
197 fish were tagged with Peterson discs (for description of the tags used in the historical Baltic
198 cod tagging experiments see Mion et al., 2020). Around 59% of the recaptures contained
199 information about the recapture gear (43% active gears, i.e. trawls; 16% passive gear, i.e.
200 gillnets, longlines, traps and pots).

201

202 *CODY SSEY project*

203 The aim of the CODY SSEY project was to study the behaviour and environmental experience
204 of larger cod (>45 cm) over periods of 9-12 months using external electronic data storage tags
205 (DSTs). Detailed information about the project and tagging methodology can be found in
206 Neuenfeldt et al. (2007). From 2002 to 2006, 446 fish tagged with DSTs were released in the
207 southern Baltic (SDs 24 and 25), and between 2003 and 2006, 234 cod recaptures were reported
208 (52.5% return rate; Table 1; Fig. 2a, b). The length of recaptured cod ranged from 450 mm to
209 985 mm (median: 524 mm) and DAL ranged between 1 and 607 days (median: 47 days; Fig.
210 2c). All cod were stored in a freezer after recapture until they were processed at the Danish
211 Fisheries Research Institute (now DTU Aqua, Denmark).

212

213 *TABACOD project*

214 The aim of the TABACOD project was to collect data on growth rates and otolith formation of
215 EBC. A total of 25352 cod were tagged by Denmark, Germany, Sweden and Poland in the
216 current main distribution area of the EBC stock (SDs 24-26) between 2016 and 2019. Fish were
217 mainly caught by bottom trawling from commercial and research vessels, using mainly short
218 hauls of 5–30 minutes' duration at 12-74 m depth. 10% of the cod were captured using fish
219 traps, pound nets and angling. In order to enhance survival and to select the fish in good health
220 (i.e. not showing injuries or barotrauma caused by trawling), fish were placed in a tank supplied
221 with flowing seawater prior to tagging procedures.

222 Fish in good health were tagged externally using numbered T-bar anchor tags inserted across
223 the pterygiophores below the first dorsal fin, and internally through intraperitoneal injection of
224 tetracycline-hydrochloride (following Stötera *et al.*, 2018). In addition, a subset (5%) of cod
225 was tagged with surgically implanted DSTs and marked externally with two T-bar anchor tags.

226 After individual measurements (total length to the lowest millimetre and total weight to the
227 nearest gram) and tagging procedures, fish were usually retained in tanks supplied with flowing
228 seawater for up to 1 hour, to recover from the tagging procedure before being released at the
229 location of capture. Fish caught with a trawl were mainly released using a cage at
230 approximately the same depth of capture both for acclimatization and for avoiding predation
231 from seagulls. Fish caught by other gear types were released at the surface. The length range
232 of cod tagged for this study was 148 to 652 mm (median: 355 mm).

233 By November 2019, 375 recaptured cod were reported (Table 1; i.e. 1.5% return rate).
234 Information about the recapture gears were available for 94% of the recaptures; 66% active
235 (i.e. commercial trawls) and 34% passive (i.e. commercial gillnets, longlines, traps and pots).
236 In addition, 8 cod were recaptured by recreational fishers. For 358 recaptures length and weight
237 measurements were recorded. The length of recaptured cod ranged from 253 to 617 mm
238 (median: 422 mm) and the DAL ranged between 0 and 876 days (median: 174 days).

239

240 ***2.2 Data preparation***

241 Before undertaking growth analyses, some data filters were applied in a stepwise approach
242 following Mion et al. (2020; Supplementary Fig. S1). In the Baltic, two cod stocks occur, i.e.
243 EBC and Western Baltic cod (WBC), located in ICES SDs 24–32 and 22–24, respectively (Fig.
244 1), with a main mixing area in SD 24 (Hüssy et al., 2016a). In order to identify the recaptured
245 individuals which most likely belonged to the EBC stock, different methods were applied: (i)
246 for the historical and CODYSSEY data, no information on the stock of origin was available
247 and thus a regional assignment has been applied. Following Mion et al. (2020), to reduce the
248 inclusion of WBC individuals in the growth analyses, only fish which were both released and
249 recaptured within the SDs 25-32 were included, excluding the main mixing area of the stocks
250 (i.e. SD 24). This procedure is supported by the lower exchange of the WBC towards the

251 eastern area (Berner, 1967; Hüsey et al., 2016a; Hemmer-Hansen et al., 2019). (ii) For the
252 TABACOD data, for 70% of the recaptures the stock of origin was assigned genetically, using
253 SNP genotyping of tissue samples from jaw, muscle or gill stored in ethanol (95%), following
254 the method described in Hemmer-Hansen et al. (2019). Where genetic analysis was not
255 possible, for 30% of the recaptures, otolith shape analysis was applied using a genetically
256 validated baseline of stock-specific shapes derived from Schade et al. (2019). These analyses
257 revealed that 285 fish recaptured in the TABACOD project belonged to the EBC stock. Another
258 44 fish were excluded from the analyses due to lack of genetic or otolith samples. In addition,
259 a sensitivity analysis on the growth estimates (see below) was done for the TABACOD data
260 assigning the stock of origin through the same regional assignment method used for the
261 historical and CODYSSEY data.

262 The measurements of the recaptured cod during the historical period were assumed to be taken
263 from fresh fish since no detailed information was available and most of the recaptures were
264 reported directly by fishers or anglers. For the recaptures of CODYSSEY and TABACOD,
265 when fish were stored in a freezer and the measurements taken after thawing, a shrinkage
266 conversion factor, developed for Baltic cod was applied (McQueen et al., 2019b).

267 Only fish with $DAL \geq 60$ were included in the analyses to ensure enough time for measurable
268 growth to occur. To exclude fish with unrealistically high growth rates, likely caused by
269 measurement errors, all fish in the database with predicted annual growth $> 25 \text{ cm} \cdot \text{year}^{-1}$ were
270 excluded from further analyses (Mion et al., 2020). To remove extreme negative growth values
271 (i.e. recapture length \ll release length), the same percentile of fish growing above the cut-off
272 of $25 \text{ cm} \cdot \text{year}^{-1}$ (i.e. 3%) was used to remove the data from the left-tail of the growth
273 distribution (i.e. negative growth; Supplementary Fig. S2). After filtering using these criteria,
274 4407 cod qualified for growth estimation for the historical data, 34 for CODYSSEY and 219
275 for TABACOD.

276

277 **2.3 Growth analyses**

278 To analyse growth, two length-based models were used: 1) the maximum likelihood GROTAG
279 model (Francis 1988a; applied for EBC in Mion *et al.* 2020), which is based on the von
280 Bertalanffy growth function (VBGF), and 2) a generalized additive model (GAM), which does
281 not assume any *a priori* growth trajectory.

282

283 *GROTAG model*

284 Growth parameters were estimated for four periods which were selected considering the data
285 availability, and which also corresponded to the main changes in the EBC stock size based on
286 Eero *et al.* (2007): 1) 1971-1980 (increase in stock size), 2) 1980-1990 (peak in stock size and
287 subsequent decline), 3) 2003-2006 (stock size at the lowest level observed in the time-series
288 since the 1950s), and 4) 2016-2019 (stock in poorest body condition level detected so far). The
289 earlier periods 1955-1964 and 1965-1970 were analysed by Mion *et al.* (2020) using the same
290 data filters and the same method as in the present study. The length frequency distribution for
291 length at release (L_1) and length at recapture (L_2) for the different periods are presented in
292 Supplementary Fig. S3.

293 The VBGF is commonly used to describe individual fish growth, modelling fish length as a
294 function of age. The VBGF parameters are L_∞ (i.e. the asymptotic length at which growth rate
295 is theoretically zero), k (i.e. the Brody growth coefficient, which determines how fast the fish
296 approaches L_∞) and t_0 that is the theoretical age at zero length. To model growth as a function
297 of length at release (L_1) and time between release and recapture, we used a re-parametrization
298 of the age-based VBGF, which is commonly applied to tagging data (Fabens, 1965):

299

$$300 \Delta L = (L_\infty - L_1)[1 - \exp(-k\Delta T)] \quad (1)$$

301

302 Where, ΔL is the change in length between L_1 and L_2 , and ΔT is the time between release (T_1)
303 and recapture (T_2) (Francis, 1988a). To standardize the dates, T_1 and T_2 were measured in
304 fraction of years from the 1st of January of the year of the first tagged cod release.

305 The growth parameters were estimated applying the maximum likelihood GROTAG technique
306 (Francis, 1988a) using the function “grotag” from the R package “fishmethods” (Nelson, 2016)
307 in R 3.5.0 (R Core Team, 2018). The GROTAG model includes the parameters g_α and g_β , that
308 are the mean annual growth rates at two release sizes (α and β , respectively, where $\alpha < \beta$).
309 Parameters g_α and g_β can be used to estimate the conventional parameters L_∞ and k of the VBGF
310 by the equations (Francis, 1988b):

311

$$312 \quad L_\infty = (\beta g_\alpha - \alpha g_\beta) / (g_\alpha - g_\beta) \quad (2)$$

313

$$314 \quad k = -Ln [1 + (g_\alpha - g_\beta / \alpha - \beta)] \quad (3)$$

315

316 Reference lengths for α and β which are well represented by the length distribution of the
317 tagging data should be chosen (Francis, 1988a). In our study, the 5th percentile value of L_1
318 measurements was adopted for α and the 95th percentile value of L_1 measurements was adopted
319 for β (as in Tallack, 2009; see also Mion et al., 2020).

320 Francis’s model allows the inclusion of additional parameters that can improve model fit,
321 including: 1) the standard deviation of the measurement error (s), 2) the standard deviation of
322 the growth increment (nu), 3) the mean of the measurement error (m), 4) the outlier
323 contamination probability (p); when $p > 0.05$ caution is required in interpreting the model fit
324 since it indicates a high level of outliers (Francis, 1988a); 5) the seasonal growth, which
325 includes a proportion that describes when growth is at its maximum in relation to the 1st of

326 January (w), and the amplitude of seasonal growth (u) that ranges from 0 to 1 (with $u = 0$ and
327 $u = 1$ representing no seasonal growth and maximum seasonal growth effect, respectively). The
328 ratio of maximum and minimum instantaneous growth rate is $(1 + u):(1 - u)$.

329 The GROTAG model was selected since it incorporates individual variation in growth rate, is
330 suitable for handling large datasets (Tallack, 2009) and has been successfully applied to tagging
331 data to estimate growth rates of cod (Tallack, 2009; McQueen et al., 2019a; Mion et al., 2020).
332 Model selection was done as in Francis (1988a), involving incremental combinations of the
333 parameters (Table 2), with unfitted parameters held at zero. The best model (i.e. final model)
334 was selected through Akaike's Information Criterion (AIC; Akaike, 1973), with improved
335 model fit indicated by a ΔAIC value ≤ 6 to select the most parsimonious model (where ΔAIC
336 value is defined as the difference between the AIC values of the model with the lowest AIC
337 and the remaining models with less parameters; Richards 2005, 2008). The model fit was also
338 visually assessed by plotting the residuals (observed-expected growth) versus relative age at
339 the time of tagging and time at liberty (Ailloud *et al.*, 2014). Residual deviation was expected
340 to decrease as relative age increases, because the likelihood function assumes an allometric
341 relationship between individual growth variation and mean growth, and the latter declines with
342 length and thus relative age (Francis, 1988a; Bradley *et al.*, 2017). Relative age is calculated
343 by inverting the VBGF (Ailloud *et al.*, 2014).

344 To estimate the variance of the VBGF parameters, each period's dataset was bootstrapped 1000
345 times following Mion et al. (2020). For each period, an approximate 95% confidence interval
346 for L_∞ and k was then constructed using the bootstrap variance.

347 Recaptures released in 1993 ($n=33$) and during 2003 and 2006 (CODYSSEY project; $n=34$)
348 were excluded from the GROTAG analyses, as for these years only small sample sizes, with
349 only large-sized cod, were available (Supplementary Fig. S3e).

350 In order to compare the growth estimates between periods, the parameters g_α and g_β were used
351 to estimate the mean annual growth of cod for the same selected length γ for each period using
352 the following equation (Francis, 1988a):

353

$$354 \quad g_\gamma = ((\gamma - \alpha) g_\beta + (\beta - \gamma) g_\alpha) / (\beta - \alpha) \quad (4)$$

355

356 The corresponding 95% confidence intervals were estimated from the standard errors
357 calculated as in Francis (1988a).

358

359 *Generalized Additive Model*

360 Cod growth ($\Delta L = L_2 - L_1$) in different periods was modelled using a generalized additive model
361 (GAM) with a restricted maximum likelihood approach (Wood, 2006). The periods considered
362 were the same used in the GROTAG analyses in Mion et al. (2020; i.e. periods 1955-1964 and
363 1965-1970) and the present study (i.e. periods: 1955-1964, 1965-1970, 1971-1980, 1981-1990,
364 and 2016-2019). The following equation was used:

365

$$366 \quad \Delta L = a + te(L_1 * DAL, by(Period)) + \varepsilon \quad (5)$$

367

368 where a is the intercept, te is the tensor product smoothing function and ε an error term.

369 An interaction was used between the continuous variables L_1 and DAL since the shape of the
370 effect of fish size at release (L_1) on ΔL can be affected by how long the fish has been at sea
371 before being recaptured (DAL). This interaction can change between periods, therefore, the
372 factor *Period* was also put in interactions with ($L_1 * DAL$).

373 In addition, we parametrized a second model replacing the factor *Period* with the continuous
374 variable year at release ($Year_1$) using the following equation:

375

$$376 \quad \Delta L = a + te(L_l * DAL * Year_l) + \varepsilon \quad (6)$$

377

378 In this model, the periods were not set *a priori* and ΔL was therefore allowed to change
379 annually.

380 For both GAM formulations, a gamma distribution with a logarithmic link function was used
381 because it best represented the distribution of ΔL frequencies according to the skewness–
382 kurtosis plot for continuous data (i.e. lognormal distribution; Supplementary Fig. S4; Cullen &
383 Frey, 1999). The models (equations 5 and 6) were used to predict the mean annual growth and
384 95% confidence interval of cod from 25 to 45 cm (by 5 cm steps), for each *Period* and *Year_l*
385 respectively, using the `predict.gam` function from the package `mgcv` (Wood, 2006) in R v3.5.2
386 (R Development Core Team 2018). Due to the low availability of recaptured cod that have
387 been out for a longer time, we excluded all the recaptures with $DAL > 1300$ days from the
388 GAM analyses (remaining data $n = 4558$). In addition, for larger fish the predicted ΔL of the
389 individuals with $DAL > 1300$ declined, contrary to the expectation that an asymptote should
390 be reached.

391

392 **3. Results**

393 **3.1 GROTAG model**

394 For the period 1971-1980, model 4 (i.e. including g_α , g_β , s , nu , m and p) was selected as the
395 final model (Supplementary Table S1). For the periods 1981-1990 and 2016-2019, a simpler
396 model (i.e. including g_α , g_β , s , nu , model 2) was selected according to the AIC values
397 (Supplementary Table S2 and S3). The best fitting models for the periods selected did not
398 include the seasonality parameters. The distribution of the model residuals for the final model
399 for each period is presented in Supplementary Fig. S5.

400 During the period 1971-1980, the mean growth rates for a 31 cm (α) and 72 cm (β) cod were
401 9.26 cm·year⁻¹ and 4.31 cm·year⁻¹, respectively (Supplementary Table S1). The growth
402 variability parameter (nu) was estimated as 0.57, indicating that individuals within the
403 population could be expected to grow between 0.43 and 1.57 times the estimated average
404 growth (Supplementary Table S1). The contamination probability (p) was negligible (0.01),
405 indicating that the occurrence of outliers was scarce, and the model did not detect outliers after
406 the data cleaning. The mean measurement error (m) was close to zero (0.08 cm) and the
407 standard deviation in measurement error (s) was 1.13 cm, which is in accordance with the 1 cm
408 precision of the length measurements recorded in the historical tagging data (Supplementary
409 Table S1). The VBGF parameter' estimates derived from the GROTAG function were $L_{\infty} =$
410 107.73 cm and $k = 0.13$ (Supplementary Table S1).

411 During the period 1981-1990, the mean growth rates for a 26 cm (α) and 63 cm (β) cod were
412 11.78 cm·year⁻¹ and 3.43 cm·year⁻¹, respectively (Supplementary Table S2). The growth
413 variability parameter (nu) was estimated as 0.61, indicating that individuals within the
414 population could be expected to grow between 0.39 and 1.61 times the estimated average
415 growth (Supplementary Table S2). The standard deviation of measurement error (s) was higher
416 than the 1 cm precision of the length measurements recorded in the historical tagging data (i.e.
417 4.07 cm), probably due to the low number of data available for this period and the fact that in
418 this simpler model, p and m are not included, therefore the variability is accounted mainly by
419 s (Supplementary Table S2). The VBGF parameter' estimates derived from the GROTAG
420 function were $L_{\infty} = 78.21$ cm and $k = 0.26$ (Supplementary Table S2).

421 During the period 2016-2019, the mean growth rates for a 28 cm (α) and 47 cm (β) cod were
422 6.57 cm·year⁻¹ and 4.18 cm·year⁻¹ respectively (Supplementary Table S3). The growth
423 variability parameter (nu) was estimated as 0.66, indicating that individuals within the
424 population could be expected to grow between 0.34 and 1.66 times the estimated average

425 growth (Supplementary Table S3). The standard deviation of measurement error (s) was 0.69
426 cm (Supplementary Table S3). The VBGF parameter estimates derived from the GROTAG
427 function were $L_{\infty} = 80.12$ cm and $k = 0.13$ (Supplementary Table S3).

428 The median bootstrapped estimates of L_{∞} and k for the different periods (Supplementary Table
429 S4) were in line with the estimates from the original datasets (Supplementary Table S1, S2 and
430 S3). The joint bootstrapped estimates of L_{∞} and k for the different periods are shown in
431 Supplementary Fig. S6.

432 According to the GROTAG model (Fig. 4), for a smaller cod (25 cm) the average annual growth
433 increased between 1955-1970 and the 1980s by 28%, and then decreased by 42% in the recent
434 period (2016-2019). On the other hand, for a larger cod (45 cm) the average annual growth
435 oscillated during 1955-1990 and then decreased by 41% from the 1980s to 2016-2019 (Fig. 4).

436

437 **3.2 Generalized Additive Model**

438 The GAMs based on selected periods (equation 5) and year of release (equation 6) explained
439 47.2 and 47.7% of the deviance, respectively (see Supplementary Table S5 and S6 for the
440 statistics of the models). Visual inspection of the residuals of the models revealed, in some
441 cases, slight departures from the model assumptions, but we considered the overall quality of
442 the residuals to be satisfactory (Supplementary Fig. S7). The predicted average annual growth
443 for the GAM based on selected periods (equation 5) oscillated during 1955-1980 until it
444 reached a peak in the 1980s. In particular, for smaller cod (i.e. 25 cm) the growth in the 1980s
445 increased by 28% above the growth rates estimated from 1955-1970. For larger cod (i.e. 45
446 cm) higher growth rates were already apparent in the 1970s (Fig. 4) with a 42% increase above
447 1955-1970. In the latest period, after this peak, growth declined, especially for cod larger than
448 25 cm (e.g. 54% decline below the peak for a 45 cm cod). For smaller cod (i.e. 25 cm) the

449 decline from the peak in growth was less pronounced (i.e. 10% decline), with wider confidence
450 intervals and recent growth rates similar to 1955-1970.

451 The predicted average annual growth using GAM based on year of release (model 6) also
452 showed an increase during the 1980s with a subsequent decline, reaching a minimum in the
453 most recent decade for the size range considered in the study (Fig. 5). For larger cod (i.e. 45
454 cm) the decline from the peak was around 53%. For smaller fish (i.e. 25 cm) the declining trend
455 after the 1980s was less pronounced (19%), with wider confidence interval and with recent
456 growth similar to 1955-1970.

457 The sensitivity analyses using GAMs based on selected periods (equation 5) and years of
458 release (equation 6), revealed that the growth estimates for the 2016-2019 period based on the
459 regional assignment of the stock (n=97) did not differ from the estimates based on genetics and
460 otolith shape analysis (n=219; Supplementary Fig. S8 and S9). Except for smaller fish (i.e. 25
461 cm), growth estimates based on regional assignment were smaller than for the ones based on
462 genetics and otolith shape for both the models.

463

464 **4. Discussion**

465 In this study, the longest time series of age-independent growth estimates based on tagging
466 data has been provided for the first time for the EBC stock. Our analyses show that growth of
467 the EBC has changed over the past 7 decades, with an increase in the 1980s followed by a
468 prolonged decline. This study also demonstrates that EBC growth is currently the lowest ever
469 observed in the last 7 decades, indicating a very low current productivity. According to both
470 the methods used, a cod of 45 cm presently increases on average 4.2 cm in length per year,
471 which is 35% and 45% lower than the growth rate of the same size in the 1960s and 1980s,
472 respectively. Assuming constant condition, the average increase in weight per year for a cod of
473 45 cm with an average weight of 903 grams is presently 266 grams, which is 42% and 53%

474 lower than the growth rate in weight of the same size fish in the 1960s and 1980s, respectively.
475 This information is an additional indicator of the current distressed status of this stock, along
476 with the declined body condition, reduced size at maturity, contracted spatial distribution and
477 increased parasite infestation (Eero et al., 2015). Our results demonstrate that the shifted size
478 structure towards smaller fish during the past two decades has been at least partially due to a
479 strong decline in growth, although an increased mortality of larger individuals (e.g. Casini et
480 al., 2016a, Horbowy et al., 2016) can also have contributed.

481 Explaining the causes of the estimated changes in growth is beyond the scope of this paper.
482 However, the temporal growth patterns revealed by our analyses coincide with the decrease in
483 the 1980s and subsequent increase of hypoxic areas in the central Baltic Sea (Casini et al.,
484 2016b). Hypoxia may affect cod growth directly via physiological stress and loss of appetite
485 (Chabot and Dutil, 1999; Brander, 2020) and indirectly by reducing the availability of
486 important benthic prey (Neuenfeldt et al., 2020), or by contraction of suitable habitat which
487 induced density-dependent responses (Casini et al., 2016b). These factors have been advocated
488 in the literature to have also affected the body condition of EBC (Limburg et al., 2019; Casini
489 et al., 2016b), and indeed the long-term temporal trends in cod growth found in this study are
490 remarkably similar to concurrent changes in body condition (Casini et al., 2016b). Besides the
491 oxygen conditions, other factors could have contributed to the changes in cod growth. For
492 example, the sharp increase in growth in the 1980s could have been facilitated by the
493 corresponding stock collapse, potentially due to density-dependent mechanisms (Casini et al.,
494 2016a). Moreover, after the early 1990s the declined abundance of pelagic prey in the area of
495 cod distribution (Casini et al., 2016a; Neuenfeldt et al., 2020), and the increased parasite
496 infestation (Horbowy et al., 2016; Sokolova et al., 2018) could have contributed to the growth
497 decline, but focused studies should be performed to discern the relative role of the different
498 drivers likely involved in changes in EBC growth.

499 The temporal changes in growth revealed by this study are generally in line with the patterns
500 of weight-at-age presented in the literature (Brander, 2007; ICES, 2013). In particular, the
501 average decline in weight-at-age for the combined ages 2-4 (corresponding to lengths ~30-45
502 cm) from the peak in late 1980s-early 1990s to 2013 (i.e. last year where weight-at-age data
503 are available from stock assessments, ICES, 2013) was ~51%, while the average decreased in
504 weight, calculated from the decrease in length found in our study for the lengths 30-45 cm and
505 considering the changes in body condition, was ~46%. However, the decline in weight-at-age
506 since the mid-1990s, besides being an effect of a decline in growth, could also have been
507 facilitated by size-selective removals by the high fishing pressure occurring at that time (ICES,
508 2020a) and therefore, a direct quantitative comparison is not possible. Our results for the small
509 fish during the most recent period are qualitatively consistent with the decline in growth of
510 young cod from the early 2000s found by Hüseyin et al. (2018) based on otolith daily increment
511 and length frequency analysis.

512 In the literature, there is a lack of studies investigating possible changes in growth of cod stocks
513 over long time periods. Denechaud et al. (2020), using otolith increments data, revealed
514 significant variations in Northeast Arctic cod growth over the last century, but no declining
515 trend has been detected in the recent period. Long time series of weight-at-age data are
516 available and routinely used for stock assessment also for the other North Atlantic cod stocks.
517 In several of these cod stocks a decline in average weight-at-age has occurred in recent periods
518 (Northern cod: Morgan, 2019; Southern Newfoundland cod: Ings et al., 2019; North Sea cod:
519 ICES, 2020c; West of Scotland cod: ICES, 2020d) and in particular for the Southern Gulf of
520 St. Lawrence stock a strong decline in weight at-age has occurred since the 1980s (Swain et
521 al., 2019), potentially suggesting that growth could have declined also in these cod stocks.

522 In this study, growth has been analysed using two length-based models: the GROTAG model
523 is based on the VBGF, which is the most commonly used growth function in fisheries biology,

524 and has been previously used in other tagging studies, while the GAM has no *a priori*
525 assumption on growth trajectory. The VBGF was developed from bioenergetics principles (von
526 Bertalanffy, 1938) with the underlying assumption that growth slows down with fish size
527 because the rate at which resources are acquired cannot balance with the rate at which resources
528 are required. However, several authors have questioned its universal applicability and stressed
529 that it should not be considered as a growth ‘law’, since it does not take into consideration
530 reproduction (e.g. Roff 1983; Schnute, 1981; Day and Taylor, 1997; Marshall and White,
531 2018). In addition, k and L_{∞} are negatively correlated, therefore, uncertainties in the estimation
532 of one parameter will bias the other (Andersen, 2019; Supplementary Fig. S6). The GAM, on
533 the other hand, can be more sensitive to the number of observations available since it is not
534 based on any *a priori* assumption on growth. According to the GROTAG model, growth
535 increased between 1955-1970 and the 1980s and then decreased until the most recent period
536 (2016-2019). A similar declining trend towards the recent period was also predicted with the
537 GAMs, although for smaller cod (25 cm) this decline was less pronounced and had wider
538 confidence intervals. The wider confidence intervals estimated by GAMs for smaller fish may
539 be related to the lack of smaller size cod (≤ 25 cm) for the period 2016-2019 (see also
540 Supplementary Fig. S3f). Alternatively, the decline in length at first maturity (i.e. length at first
541 maturity has declined in the last 20 years down to 20 cm in the recent period; Reusch et al.,
542 2018) likely means that in the recent period fish of 25 cm may consist of both adults and
543 juveniles, while this size class in 1955-1990 likely consisted mainly of juvenile fish. Therefore,
544 the mixture of adults and juveniles in the smaller size classes may have increased the variability
545 in growth estimates in the GAM analyses for the recent period.

546 In our study, a seasonal growth signal was not analytically detected, contrary to the seasonality
547 found for the period 1955-1970, with a peak in growth in the beginning of autumn and a
548 minimum in spring during reproduction (Mion et al., 2020). The absence of seasonality in

549 growth in the more recent periods may be related to the lower number of recaptures compared
550 to the period 1955-1970, or be a real biological change resulting from the overall contemporary
551 low growth rates. Determinate spawners such as cod, are often classified as capital breeders
552 since they reduce feeding during the spawning season (Boulcott and Wright, 2008). After
553 spawning, when they start feeding again, compensatory growth occurs (Pedersen and Jobling,
554 1989). For the EBC however, due to a decline in food availability and the overall decrease of
555 feeding level and energy intake after the early 1990s (Eero et al., 2011; Casini et al., 2016a;
556 Neuenfeldt et al., 2020), this compensatory growth may be too weak to be detected within the
557 overall reduced growth context, explaining the absence of seasonality in growth in our analyses
558 in the more recent periods.

559 To reconstruct this long time-series of growth estimates, data from different tagging projects,
560 originally planned with different aims and tagging techniques have been compiled in our study,
561 potentially affecting the growth estimates. The tagging experiments used in our study for
562 example employed different tags, but previous experiments have shown that tagging type
563 (internal vs. external tagging) did not influence the fish growth rate (Righton et al., 2007). In
564 addition, Stötera et al. (2018) found no significant effect of injection with tetracycline (that was
565 used in the two most recent tagging periods, 2003-2006 and 2016-2019) on short-term growth
566 of Baltic cod. Another factor that could affect growth estimates is the selectivity of the
567 recapture gears, with passive gears and recreational angling with rod and line being selective
568 for boldness (Arlinghaus et al., 2017). However, in our study the majority of recaptures from
569 both the historical and current tagging experiments came from trawlers suggesting that the
570 growth estimates were not affected by possible differences in individual behaviour of the fish.
571 Finally, the length measurements used for growth analysis in the historical period, which were
572 reported by fishers or anglers, likely had higher measurement error than the measurements
573 taken by trained scientific staff in the more recent period (Eveson and Million, 2008; McQueen

574 et al., 2019a), but this potential source of bias has been partially accounted for in our analysis
575 by using a restrictive data filter procedure.

576

577 *Conclusions*

578 The digitisation, collation, and combination of historical and recent data from several tagging
579 experiments performed in the Baltic Sea over 7 decades allowed to reconstruct for the first time
580 a long time series of age-independent growth rates in a stock with severe ageing problems, and
581 therefore are now available to be integrated in assessment models (i.e. stock synthesis; ICES,
582 2019b). These data are fundamental for gaining a more complete understanding of the growth
583 dynamics of the Eastern Baltic cod. In particular, they revealed an increase in growth at the
584 end of 1980s corresponding to the stock collapse, and a constant decline afterwards with an
585 exceptionally slow contemporary growth rate. Our study provides an example of the use of
586 tagging data to estimate changes in growth rates in wild fish that can be also used for other cod
587 stocks and species, especially in those cases where severe age determination problems exist. In
588 addition, our study shows the importance of historical data mining and the great relevance of
589 tagging experiments, not only to analyse wild fish movements, but also to reconstruct potential
590 changes in their growth rates. Tag-recapture programs performed at regular time intervals (e.g.
591 every decade) or when surveys indicate substantial changes in the stock structure or in the
592 environment would ensure an age-independent time series of growth estimates to calibrate
593 stock assessment models.

594

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603

604 **Data Availability Statement**

605 The historical data may be shared on reasonable request with permission of the respective
606 institutes. The TABACOD data are subject to an embargo of 5 years (i.e. until the end of 2025).
607 Once the embargo expires, the data will be available upon reasonable request.

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969 **Tables**

970 Table 1. Overview of the available tagging data (number of released and recaptured cod) from
 971 the historical experiments and the projects CODYSSEY and TABACOD, by release country
 972 and release period. † Information about the total number of cod released by Finland was not
 973 available for the period 1979-1984. ‡ The return rate includes Finnish release only for the
 974 period 1974-1978 because the number of releases for the period 1979-1984 was not available.

975

Project	Release country	Release period	Number of released cod	Number of recaptured cod	Return rate (%)
Historical data	Sweden	1955-1993	43343	4981	11.5
	Poland	1957-1970	15183	2299	15.1
	Denmark	1957-1984	9824	1348	13.7
	Latvia	1958-1977	10552	762	7.2
	Germany	1959-1974	869	132	15.2
	Finland	1974-1984	6425†	621	9.7‡
All		1955-1993	86196†	10143	11.8‡
CODYSSEY	Denmark	2003-2006	446	234	52.5
TABACOD	Sweden	2016-2018	6386	62	1.0
	Poland	2016-2018	5409	60	1.1
	Denmark	2016-2018	5184	87	1.7
	Germany	2016-2019	8373	166	2.0
	All		2016-2019	25352	375

976

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

979

GROTAG model	Estimated parameters
Model 1	g_{α}, g_{β}, s

Model 2	g_α, g_β, s, nu	980
Model 3	$g_\alpha, g_\beta, s, nu, m$	981
Model 4	$g_\alpha, g_\beta, s, nu, m, p$	
Model 5	$g_\alpha, g_\beta, s, nu, m, p, u, w$	982

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985 **Figure legends**

986 Fig. 1. Map of the Baltic Sea, divided into ICES subdivisions. On top-right, a picture of a Baltic
987 cod (*Gadus morhua*, *Gadidae*; © Christina Waitkus).

988

989 Fig. 2. Overview of recaptured Baltic cod (fish releases for which there was a corresponding
990 recapture) by year of release and (a) quarter of release, (b) release subdivision (SD) in
991 percentage and (c) days at liberty (DAL) in percentage (n= 8622 for the historical data; n= 234
992 for CODYSSEY; n= 358 for TABACOD). Figure appears in colour in the online version only.

993

994 Fig. 3. (a) Example of an historical Swedish recapture letter sent by a fisherman in 1971
995 (sensitive data about the fisherman has been redacted). The recapture letter reported the species
996 (Fiskart), tag number (Nr), location of the recapture (Fångstplats), date of recapture (Datum),
997 depth (djup; it was not reported in this example), recapture gear (Redskap), total length
998 (Fiskens totala längd) and total/gutted weight (Vikt orensad/rensad). (b) Example of an
999 historical German recapture letter sent by the German research institute in Rostock to the
1000 Swedish research institute in Lysekil in 1964 (sensitive data about the fisherman has been
1001 redacted). The recapture letter reported the tag number (i.e. C 176), location of the recapture
1002 (i.e. Southeast Utklippan), date of recapture (i.e. 15/01/64), length (Fiskens totala längd) and
1003 gutted weight (Gewicht geöffnet).

1004

1005 Fig. 4. Predicted average annual growth rates ($\text{cm}\cdot\text{year}^{-1}$; dots) and 95% confidence intervals
1006 (vertical lines) for 25, 30, 35, 40 and 45 cm cod for different periods calculated from the
1007 GROTAG final models (red) and GAM (equation 5; blue). The predicted average growth rates
1008 ($\text{cm}\cdot\text{year}^{-1}$) for the periods 1955-1964 and 1965-1970 analysed with GROTAG are based on
1009 Mion et al. (2020). Figure appears in colour in the online version only.

1010

1011 Fig. 5. Predicted average growth rates ($\text{cm}\cdot\text{year}^{-1}$) for a 25, 30, 35, 40 and 45 cm cod for
1012 different years at release ($Year_t$) analysed with GAM (equation 6; blue line). The shaded blue
1013 area represents the 95% confidence interval. Figure appears in colour in the online version
1014 only.

1015