



HAL
open science

New scale analyses reveal centenarian African coelacanth

Kelig Mahe, Bruno Ernande, Marc Herbin

► **To cite this version:**

Kelig Mahe, Bruno Ernande, Marc Herbin. New scale analyses reveal centenarian African coelacanth. Current Biology - CB, 2021, 31 (16), pp.3621–+. 10.1016/j.cub.2021.05.054 . hal-03451171

HAL Id: hal-03451171

<https://hal.umontpellier.fr/hal-03451171v1>

Submitted on 16 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **New scale analyses reveal centenarian coelacanths *Latimeria chalumnae***

2

3 Kélig Mahé¹, Bruno Ernande^{2,3}, Marc Herbin⁴

4

5 1 IFREMER, Fisheries Laboratory, Boulogne sur mer, France.

6 2, MARBEC, Univ. Montpellier, IFREMER, CNRS, IRD, Montpellier, France

7 3 Evolution and Ecology Program, International Institute for Applied Systems Analysis

8 (IIASA), Schlossplatz 1, A-2361 Laxenburg, Austria

9 4 Mécanismes Adaptatifs et Evolution (MECADEV, UMR7179) Muséum national d'histoire
10 naturelle de Paris, CNRS, CP 55, 57 rue Cuvier 75005 Paris, France.

11

12 Lead Contact : Kélig Mahé

13

14 **Summary**

15 **The extant coelacanth was discovered in 1938¹; its biology and ecology remain poorly**
16 **known due to the low number of specimens collected. Only two previous studies^{1,2} have**
17 **attempted to determine its age and growth. They suggested a maximum lifespan of 20**
18 **years placing the coelacanth among the fastest growing marine fish. These findings are**
19 **at odds with the coelacanth's other known biological features including low oxygen-**
20 **extraction capacity, slow metabolism, ovoviviparity, and low fecundity, typical of fish**
21 **with slow life-histories and slow growth. In this study, we use polarized light microscopy**
22 **to study growth on scales based on a large sample of 27 specimens. Our results**
23 **demonstrate for the first time nearly imperceptible annual calcified structures (circuli)**
24 **on the scales and show that maximal age of the coelacanth was underestimated by a**
25 **factor of 5. Our validation method suggests that circuli are indeed annual thus**
26 **supporting that the coelacanth is among the longest-living fish species, its lifespan being**
27 **probably around 100 years. Like deep-sea sharks with a reduced metabolism, the**
28 **coelacanth has amongst the slowest growth for its size. Further reappraisals of age at**
29 **first sexual maturity (in the range 40 to 69 years old) and gestation duration (of around**
30 **5 years) show that the living coelacanth has one of the slowest life histories of all marine**
31 **fish and possibly the longest gestation. As long-lived species with slow life histories are**

32 **extremely vulnerable to natural and anthropogenic perturbations, our results suggest**
33 **that coelacanths may be more threatened than previously considered.**

34 **Keywords :**

35 Scalimetry, Growth patterns, Polarized light, long-lived species, life-history traits

36

37 **Results and Discussion**

38 **A new ageing methodology**

39 Extant coelacanths were discovered in 1938 and are the only surviving members of an
40 extinct lineage³. The coelacanths are large lobe-finned fish (sarcopterygians). The African
41 coelacanth *Latimeria chalumnae*^{3,4} is considered critically endangered. This species is
42 characterized by a large body size that can reach up to two meters in length and weigh up to
43 105 kg⁵, with large length at maturity (around 150 cm^{6,7}). These animals are ovoviviparous,
44 produce a relatively small number of offspring, and have a large size at birth (around 35 cm).
45 The coelacanth is thought to be a nocturnal languid drift-hunter and its unique locomotory
46 movements are generally slow⁸, though it can exhibit fast-start escape responses⁹. These fish
47 have a slow metabolism^{10,11} often thought to be associated with its energy-saving mode of life,
48 typical of deep water species. African coelacanths are found most commonly at water
49 temperatures between 15 to 19°C where their oxygen uptake capacity is optimal¹⁰. These life-
50 history, physiological and behavioural traits initially positioned coelacanths at the slow end of
51 the slow-fast life-history continuum¹². Growth estimates presented in two previous studies^{1,2}
52 using the same dataset of 12 specimens, however, placed coelacanths among the fastest
53 growing fishes, comparable to tunas¹³. The inconsistency between a suggested fast body
54 growth and other life-history traits indicative of slow life-history prompted us to revisit the
55 age and body growth estimations of coelacanths. In this study, age and growth were estimated
56 from scales collected from 27 coelacanths captured of the coast of the Comoros Islands (13

57 females, 11 males, 1 juvenile, and 2 embryos) with total length ranging from 30.5 to 180 cm.
58 These specimens were captured between 1953 and 1991 (See also Table S1). The scales of
59 coelacanths present an anterior field with ridges radiating from the apex and concentric
60 macroscopic circuli¹ (called macro-circuli hereafter) observable under transmitted light
61 microscopy (Figure 1). Both previous ageing studies interpreted these macro-circuli as marks
62 of growth rate variation with alternating translucent and opaque bands suggesting fast and
63 reduced growth, respectively; however, these studies did not agree on the periodicity of band
64 formation. The earliest study suggested that macro-circuli were seasonal with two being laid
65 down each year in association with the alternation of two wet and two dry seasons annually in
66 the tropics¹, whereas the most recent study interpreted macro-circuli as annual, only one being
67 laid down each year², arguing that, as for the majority of fish¹⁴, tropical fish exhibit a
68 circannual rhythm despite climate seasonality.

69 Following these earlier studies, we analysed our extended sample under transmitted
70 light microscopy to count the macro-circuli along the longest growth axis of each scale
71 (Figure 1a). The age of the individuals was estimated to range between 0 to 8 years and
72 between 1 to 17 years under the hypothesis that macro-circuli are seasonal and annual,
73 respectively (See also Table S1). These age ranges and the total length range of our sample
74 are comparable to those of the previous ageing studies, thus suggesting an equally fast body
75 growth inconsistent with other life-history traits. We therefore decided to use another
76 observation method, namely polarized-light microscopy. As expected, polarized light revealed
77 much more detail on scale topography than transmitted light^{15,16} (Figure 1b), the quality of the
78 image being equivalent to micro-computed tomography (See also Figure S1). More
79 specifically, we identified new circuli that were thinner and more numerous than the macro-
80 circuli observed under transmitted light (Figure 1b vs. Figure 1a). These circuli were also
81 formed by alternating thin translucent and opaque bands suggestive of growth rate variation.

82 Counting circuli in the same manner as macro-circuli and under the assumption that they are
83 annual, we obtained individual ages ranging from 5 to 84 years (See also Table S1).
84 Comparing our results under transmitted and polarized light, the number of circuli appeared
85 linearly related to the number of macro-circuli ($P = 0.009$; $R^2=0.84$) with a slope of 5.16,
86 which indicates the appearance of a macro-circulus roughly every five circuli.

87 **Validation of coelacanth age**

88 Only direct validation methods, i.e., those using individual-level temporal reference
89 marks on scales relative to natural marks to assess the periodicity of the latter, would allow
90 indisputable confirmation of the interpretation of circuli as annual growth marks. The main
91 direct validation methods are (i) mark-recapture of wild individuals tagged externally and
92 labelled with a chemical depositing a mark on their scales and (ii) captive rearing of either
93 chemically-labelled fish of unknown age or of fish of known age (e.g. produced in controlled
94 conditions). These methods are, however, not applicable to coelacanths due to conservation
95 and ethical issues.

96 Instead, we used indirect validation methods. The most widely used method is Marginal
97 Increment Analysis (MIA), which assesses the periodicity of increments in calcified
98 structures, here macro-circuli and circuli. When growth has a circannual rhythm, increments
99 are formed during the growth period of the year. The size of the increment under formation,
100 named the marginal increment and measured as the distance between the last fully formed
101 (macro-) circulus and the edge of the scale, should thus exhibit some intra-annual periodic
102 pattern when plotted against the month at which the individual was captured. Applying MIA
103 to macro-circuli, no such intra-annual periodic pattern was evident ($P = 0.61$; Figure 1 lower
104 panel) suggesting that they are not formed annually. In contrast, the application of MIA to
105 circuli allowed detection of intra-annual variation in their growth ($P < 0.001$; Figure 1 upper
106 panel), revealing a circannual rhythm in circuli formation.

107 A second indirect validation method is to assess the internal and/or external consistency
108 of the population-level mean body growth pattern, or length-at-age data, obtained for each
109 scale. Three growth models are widely used in ecology to describe length-at-age data for
110 species with indeterminate growth because they conform to the observed shape of growth
111 curves: the von Bertalanffy, Gompertz, and logistic growth models. For both macro-circuli
112 and circuli ageing, the von Bertalanffy growth model appeared to best described the resulting
113 length-at-age data based on minimization of the small-sample bias-corrected AIC (See also
114 Table S2). The body growth curve estimated from length-at-age data obtained using macro-
115 circuli for ageing (Figure 2 dashed blue curve) was characterized by a combination of a large
116 asymptotic length ($TL_{\infty} = 296.1$ cm) reached at a fast rate ($K = 0.05 \text{ year}^{-1}$; note that
117 coefficient K in the von Bertalanffy model represents the rate at which asymptotic length is
118 reached and not size change per unit of time). Consequently, the largest ($TL = 180$ cm) and
119 oldest (17 years) specimen of our sample appeared as being still in a fast growth phase and at
120 about only 61% of the estimated asymptotic length TL_{∞} . Moreover, TL_{∞} was estimated to be
121 much larger than both the largest individual ever captured¹⁷ ($TL = 190$ cm) and the maximum
122 length ($TL_{\text{max}} \pm \text{c.i.} = 199 \pm 24$ cm) estimated independently from length-at-age data using
123 extreme value theory². The same holds when using length-at-age data obtained by the
124 previous ageing study assuming annual macro-circuli (Figure 2 dashed dark blue curve). In
125 contrast, the body growth model fitted to length-at-age data obtained using circuli (Figure 2
126 red curve) estimated a smaller asymptotic length ($TL_{\infty} = 203.8$ cm) reached at a slower rate
127 ($K = 0.02 \text{ year}^{-1}$) such that the largest ($TL = 180$ cm) and oldest (85 years) individual in the
128 data set is in a slow growth phase and much closer to its asymptotic length (88%). In addition,
129 TL_{∞} is in much better agreement with the length of the largest individual ever captured and
130 with the previously independently estimated maximum length. The growth pattern obtained
131 using circuli ageing appears thus to outperform other estimates.

132 We further used a double logarithmic plot of the von Bertalanffy rate coefficient K
133 versus asymptotic length TL_{∞} (so-called auximetric plot), and the growth performance index
134 ϕ' to compare the global body growth of coelacanths with other marine fish species (1383
135 populations distributed across 1313 species extracted from FishBase¹⁸) for each ageing
136 method. Ageing based on macro-circuli would position the coelacanth among the fastest
137 growing fishes with a similar asymptotic length (Figure 3A) and above the 90th percentile of
138 the growth performance index ϕ' distribution across all marine fish (Figure 3B). Such high
139 body growth capacity is almost equivalent to that of tunas¹³ (Figure 3) that have evolved
140 unique morphological: streamlined body and fin shapes, large mass-specific gill surface area,
141 and physiological: high oxygen-affinity blood, combined with endothermy, high proportion of
142 red muscle, high cardiac performance¹³, characteristics to support their high growth
143 performance and very active lifestyle. These traits differ strongly from those of coelacanths,
144 which are typical of fish with low growth performance and high longevity¹⁹ like deep-sea fish
145 with low metabolic rates. In contrast, the body growth pattern obtained from circuli would
146 place *L. chalumnae* among the slowest growing fish within the same range of asymptotic
147 length (Figure 3A) and close to the mode of the growth performance index ϕ' distribution
148 (64th percentile, Figure 3B). This growth is similar to that of deep-sea sharks, concurring with
149 the morphological and physiological traits of the living coelacanth, as well as its lifestyle.

150 These results suggest that ageing coelacanths by interpreting circuli as annual growth
151 marks provides the most realistic estimates of seasonal scale formation and lifelong body
152 growth, with the longevity of the coelacanth estimated to be close to one century. This
153 observed longevity is five times greater than previously estimated. Only one study had
154 hypothesised such an extended lifespan⁶ but with no direct evidence. Our study unequivocally
155 demonstrates for the first time the coelacanth exceptional longevity and positions it as one of
156 the most long-lived fish species. The factor of five between longevity estimates originates

157 from the fact that the macro-circuli used by the previous studies for ageing do not exhibit a
158 circannual formation rhythm and appear with an approximately 5-year periodicity throughout
159 the lifespan of both males and females (See also Figure S2). Two hypotheses may explain the
160 presence of these macro-circuli, the first one being of exogenous origin, namely periodic
161 environmental events, and the other of endogenous origin, i.e. periodic
162 physiological/behavioural events. Regarding the former, strong variations in environmental
163 conditions such as salinity or temperature are known to leave marks on scales and large-scale
164 climate oscillations such as the Indian Ocean Dipole (IOD) or the El Niño-Southern
165 Oscillation (ENSO)²⁰ could produce periodic scale marks. However, an exogenous origin
166 would imply a mark deposition on scales that is synchronized across individuals. This
167 synchrony is not observed in the years of appearance of the macro-circuli for the different
168 individuals in our sample (See also Figure S2A). The hypothesis of an endogenous origin
169 (periodic physiological or behavioural stresses) seems thus more likely. Periodic events that
170 affect both sexes equally, as macro-circuli are found in both females and males, such as
171 migration or reproductive behaviour are potential candidates. Unfortunately, knowledge on
172 the biology and behaviour of the coelacanth remains too fragmented to address this hypothesis
173 further.

174 **Implications for life history and conservation**

175 In addition to longevity and body growth, two other aspects the coelacanth's life-history can
176 be reappraised with our new age estimation method: the duration of gestation and the age at
177 first sexual maturity. The early life of coelacanth is not well known and developmental stages
178 available in collections are rare. In our sample, two different *pre-partum* embryos (CCC29.5
179 and CCC162.21), one early *post-partum* juvenile (CCC94), and another slightly older juvenile
180 were available (See also Table S1). The age of both *pre-partum* specimens is estimated at 5
181 years based on circuli whereas that of the two *post-partum* individuals is estimated at 9 and 12

182 years, respectively. This indicates that the gestation duration is at least five years contrary to
183 the 1 to 2 years suggested by earlier studies. The length at birth is uncertain but the size of the
184 largest observed *pre-partum* individual from a litter of 26 near-term embryos²¹ ranging from
185 30.8 to 35.8 cm total length found in a gravid female could be a good estimation. Based on
186 our estimate of the von Bertalanffy growth model and under the assumption that embryos
187 follow the same growth pattern as post-partum individuals, such length at birth would also
188 give a gestation period close to five years. The earlier hypothesis of a long gestation is thus
189 confirmed² but largely extended, placing the coelacanth among the vertebrates with the
190 longest gestation period, alongside the deep-sea frilled shark *Chlamydoselachus anguineus*
191 (three years)²².

192 The length at first sexual maturity was estimated to range between 120 and 129 cm for
193 males and between 160 to 179 cm for females^{6,7}. These values were obtained from the
194 anatomical and morphological differences between juveniles and matures specimens. In light
195 of our ageing data (See also Table S1), these length ranges would correspond to ages at first
196 maturity ranging from 40 to 69 years for males and from 58 to 66 years for females. These
197 new estimates of age at first maturity are also close to those of the frilled shark and
198 correspond to an onset of maturation much later in life (ratio of age maturity to maximum
199 longevity: 0.47-0.81 for males and 0.68-0.78 for females) than in teleost fishes (range: 0.16-
200 0.39 and typical values: 0.25-0.30²³). This pattern is consistent with the reproductive strategy
201 of both coelacanth and elasmobranches²⁴. Species that rely on internal fertilization and
202 produce a few large fully-developed offspring after a long gestation, especially ovoviviparous
203 and viviparous ones, tend to mature later in life than species that lay very large number of
204 eggs, rely on external fertilization and produce undeveloped larvae (most teleost fishes²⁵).
205 This conforms to life-history theory which predicts that an increased survival probability of
206 immature life-stages, such as in case of ovoviviparity and viviparity, favours the evolution of

207 delayed maturation²⁶. The delayed maturity of the coelacanth relative to its longevity also
208 implies a shorter relative reproductive lifespan than teleost fishes. This results in very
209 different benefits and demographic consequences of extreme longevity. In teleost, long-lived
210 species have an extended reproductive lifespan and thus “sample” multiple reproductive
211 events. In a variable environment resulting in fluctuating recruitment, this allows taking
212 advantage of occasional favourable environmental conditions to produce strong year classes
213 literally “stored” in the adult population until conditions for strong recruitment return, a type
214 of bet-hedging strategy also called “storage effect”²⁷. In contrast, the coelacanth demography
215 is likely to rely on a continuous influx of weak recruitment insured by very high survival rates
216 of a few offspring per individual whatever the environmental conditions.

217 Based on our re-appraisal of time-related life-history traits of the coelacanth, namely
218 growth rate through the von Bertalanffy rate coefficient K , maximum observed longevity, age
219 at first sexual maturity and gestation duration, we assessed its location along the slow-fast
220 life-history continuum in marine fish. A Principal Component Analysis was performed on
221 these four life-history traits across 147 populations in 131 marine fish species extracted from
222 FishBase¹⁸. By focusing on life-history traits with time dimensionality, we avoided the
223 problem of heterogeneous dimensions across traits that may prevent correct interpretation of
224 life-history strategies in terms of the slow-fast continuum¹². Ideally, the phylogenetic
225 relatedness between species should have been accounted for in this analysis. However, as far
226 as we are aware, no phylogeny relating the coelacanth, Actinopterygii and Chondrichthyes
227 with a sufficiently fine granularity, i.e. including most species of our life-history dataset, is
228 currently available. In addition, past analyses in other taxa have shown that phylogenetic
229 inertia does not affect strongly the detection and strength of the slow-fast continuum¹². The
230 first Principal Component observed trades-off high longevity and late maturity against fast
231 rate of approach towards asymptotic size, and thus can be considered as the main component

232 of the slow-fast life-history continuum, whereas the second one is mostly determined by
233 gestation duration (inversely related to spawning frequency used in the analysis; Figure 4A).
234 The estimation of life-history traits based on macro-circuli ageing places the coelacanth in the
235 main bulk of marine fish, close to the cluster formed by tunas (Figure 4A). In contrast, life-
236 history traits estimated from circuli position the coelacanth towards very slow life-histories,
237 close to deep-sea sharks and roughies (Figure 4A). Taking the first PC as a metric of the slow-
238 fast life-history continuum, ageing based on circuli places the coelacanth among the slowest
239 life-histories (0th percentile) together with roughies and deep-sea sharks whereas ageing based
240 on macro-circuli would correspond to a faster, moderate pace of life (26th and 13th percentile
241 for macro-circuli ageing of our data and previous data, respectively; Figure 4B).

242 The new ageing method developed in this study shows that the African coelacanth, *L.*
243 *chalumnae*, may live for about a century, making it one of the most long-lived fish species.
244 Alongside its exceptional longevity, this study showed that the African coelacanth has one of
245 the slowest life histories among marine fish, and possibly all vertebrates, characterized by a
246 slow body growth relative to its size, very late age at first sexual maturity, and exceptionally
247 long gestation time, which is in concord with its ovoviviparity, relatively small clutch size,
248 and reduced metabolism. These life-history and physiological characteristics are partly similar
249 to those observed in the human fish (*Proteus anguinus*)²⁸, a small cave salamander with one
250 of the slowest life-histories among vertebrates. Long-lived species characterized by slow life
251 history and relatively low fecundity are known to be extremely vulnerable to perturbations of
252 a natural or anthropic nature due to their very low replacement rate²⁹. Ignoring such
253 characteristics has been shown to be detrimental to conservation and management as
254 exemplified by some deep-sea fisheries³⁰. The African coelacanth is assessed as critically
255 endangered (Red List of Threatened Species of IUCN). Our results suggest that it may be
256 even more threatened than expected due to its peculiar life history. Further studies on the

257 biology and ecology of the coelacanth, especially on its reproductive biology and behaviour,
258 are needed to be able to preserve this unique component of life on Earth.

259 **Acknowledgements**

260 We are grateful to R. Elleboode and G. Bled Defruit for age readings. We thank C. Bens and
261 A. Verguin of the Collection de Pièces anatomiques en Fluides at the Muséum National
262 d'Histoire Naturelle (MNHN) for their help, E. Sultan of UMR LOCEAN CNRS-MNHN for
263 providing the Comoros climatic data, and L. Poloni, S. Couette and C. Toti Lutet for micro-
264 computed tomography scanning of scales of one specimen at MorphOptics of the UMR
265 CNRS uB EPHE 6282 Biogéosciences. We would especially thank M. Etherton, W.
266 McCurdy, A. Herrel and K. M. MacKenzie for their valuable help in editing this manuscript.
267 We are extremely grateful to the two anonymous referees, J.M. Gaillard and the Editor for
268 their especially helpful and constructive comments to improve the manuscript. The MNHN
269 gives access to its collections in the framework of the RECOLNAT national Research
270 Infrastructure.

271 **Author contributions**

272 M.H., K.M. and B.E. contributed conception and design of the study. M.H. performed the
273 sampling. K.M. organized the image acquisition and ageing data collection. K.M.. performed
274 the analysis of growth patterns and the marginal increment analysis and B.E. the auximetric
275 analysis and the slow-fast life-history continuum analysis. All authors provided inputs for the
276 results and discussion. K.M. wrote the first draft of the manuscript and B.E. wrote sections of
277 the manuscript. All authors provided critical comments and were involved in the revision and
278 editing of the manuscript. All authors accepted the final version of the manuscript.

279 **Declaration of interests**

280 The authors declare no competing interests.

281

282 **Figure Legends**

283 **Figure 1: Analysis and periodicity of the circuli and macro-circuli of the African**
284 **coelacanth scale.** The same scale of *L. chalumnae* CCC4 (female of 109 cm caught in
285 January 1954) is analysed based on a reconstructed image under either transmitted light
286 microscopy (a.) or polarized light microscopy (b.) (Horizontal white scale bar = 1 mm).
287 Macro-circuli (a.) and circuli (b.) are marked (dots) along the longest growth axis (red line).
288 For each type of circuli, temporal dynamics of monthly marginal increments (mm) on scales
289 of *L. chalumnae* (n = 27) based on the hypothesis of annual circuli (red) or annual macro-
290 circuli (blue) are shown. The bottom and top of each box are the first and the third quartiles of
291 the marginal increment distribution for the considered month (x-axis), the horizontal segment
292 and the diamond inside the box are respectively the median and the mean, and whiskers
293 represent the most extreme data point within 1.5 interquartile range. For three specimens
294 (CCC162.21, CCC29.5 and CCC42.5), only macro-circuli could be identified and no
295 individual was collected in November and December so that no marginal increment was
296 available for month 10 and 12. The thin continuous curve in each panel represents the fit of a
297 sinusoidal regression of marginal increments against month with a period of 12 month to test
298 for annual periodicity. Under the hypothesis of annual circuli, a significant intra-annual
299 periodicity of marginal increment growth is detected by the sinusoidal regression. In contrast,
300 under the assumption of annual macro-circuli, no evidence of a periodic pattern is found (See
301 also Figure S1 and S2).

302

303

304

305

306

307

308 **Figure 2: Body growth pattern of the African coelacanth according to different scale**
309 **interpretations.** Observed length-at-age data for different scale interpretations for age are
310 shown (red solid circles: circuli ageing, blue open squares: macro-circuli ageing, dark blue
311 crosses: previous age interpretation²) together with the corresponding fitted von Bertalanffy
312 growth models (dashed light blue curve: macro-circuli, continuous red curve: circuli, dashed
313 dark blue curve: previous age interpretation). TL_{∞} and K are the asymptotic total length (cm)
314 and the rate coefficient, i.e. the rate at which the asymptotic length is reached (year^{-1}),
315 respectively, estimated from the von Bertalanffy growth models and $\phi' = \log(K) +$
316 $2 \log(TL_{\infty})$ is the growth performance index ($\text{cm} \cdot \text{year}^{-1}$) that allows overall growth
317 performance comparison across populations or species. The grey area represents embryos *in*
318 *utero*. The black horizontal line indicates the size of the largest specimen ever captured (See
319 also Table S1 and S2).

320 **Figure 3: Comparison of the African coelacanth growth rate characteristics to other**
321 **marine fish under the various ageing hypotheses. A.** Auximetric plot of the coelacanth
322 under the various ageing hypotheses (red diamond: annual circuli, light blue diamond: annual
323 macro-circuli from present study; dark blue diamond: annual macro-circuli from previous
324 study) relative to other taxonomic groups of marine fish species (solid circles; orange: tunas;
325 purple: deep-sea sharks; green: roughies; grey: other fish species). The auximetric plane is the
326 plane defined by two logarithmic axes representing the von Bertalanffy rate coefficient K
327 versus asymptotic total length TL_{∞} where a population characterized by a set of von
328 Bertalanffy growth parameters (TL_{∞}, K) is represented by a point. Populations of a given
329 species or species having similar growth characteristics will tend to form clusters of points
330 that delimit the growth space of that species or group of species. 95% ellipses, i.e. contours
331 enclosing 95% of the data points under the assumption of a bivariate-normal distribution, are
332 drawn to illustrate the growth space of tunas (orange circle), deep-sea sharks (purple circle)
333 and roughies (green circle) for better comparison. The auximetric plot allows comparison of
334 species according to their speed of growth at a given asymptotic size (vertical direction) and
335 according to their body size for a given speed of growth (horizontal direction). It also allows
336 comparison of species in terms of their global growth capacity by superimposing isolines of
337 the growth performance index $\phi' = \log(K) + 2 \log(TL_{\infty})$ since these have a known slope of
338 2 (dashed black lines labelled with the corresponding ϕ' value). **B.** Growth performance
339 index $\phi' = \log(K) + 2 \log(TL_{\infty})$ of the coelacanth (diamonds) under the various ageing
340 hypotheses (same colors as in A) relative to other taxonomic groups of marine fish species
341 (boxplots; same colors as in A). Labelled vertical lines give the percentiles of the distribution
342 of ϕ' values across all marine fish species corresponding to the ϕ' values of the African
343 coelacanth under the various ageing hypotheses. Boxplots are defined as in Figure 1. Von

344 Bertalanffy growth parameters for other marine fish were extracted from FishBase in June
345 2020 (1383 populations distributed across 1313 species).

346

347 **Figure 4: Locating the African coelacanth along the slow-fast life-history continuum in**
348 **marine fish under the various ageing hypotheses. A.** Biplot of the two first axes of a
349 Principal Component (PC) analysis on time-related life-history traits (von Bertalanffy rate
350 coefficient K , sexual maturity age, maximum observed longevity and spawning
351 frequency/inverse of gestation time) of marine fish after log₁₀-transformation, removal of the
352 effect of body size, centering and scaling. The coelacanth projection (diamonds) on the PC
353 plane under the various ageing hypotheses (same colors as in Figure 3) can be compared to
354 the projections of other taxonomic groups of marine fish species (solid circles; same colors as
355 in Figure 3). The percentage of variance explained by the PCs is indicated between
356 parentheses in axis labels. Arrows indicate how much each life-history trait contributes to
357 each PC according to its projection on each PC axis and the angle between the arrows is
358 indicative of the correlation between life-history-traits, orthogonality meaning independence
359 and opposite directions meaning negative correlations. Clearly, the first PC corresponds to the
360 slow-fast life-history continuum as it trades-off high longevity and late maturation on the left
361 hand side against fast approach rate towards asymptotic length on the right hand side whereas
362 the second PC mainly involves spawning frequency. **B.** Position of the coelacanth (diamonds)
363 under various ageing hypotheses (same colors as in Figure 3) relative to other taxonomic
364 groups of marine fish species (boxplots; same colors as in Figure 3) along the slow-fast life-
365 history continuum (scores along PC1, panel A). Labelled vertical lines give the percentiles of
366 the distribution of the scores along PC1 of all marine fish species that correspond to the scores
367 of the coelacanth under the various ageing hypotheses. Boxplots are defined as in Figure 1.

368 Life-history traits for other marine fish were extracted from FishBase in June 2020 (147
369 populations distributed across 131 species).

370

371

372

373 **STAR METHODS**

374 **RESOURCE AVAILABILITY**

375 **Lead contact**

376 Further information and requests for resources should be directed to and will be fulfilled by
377 the Lead Contact, Kélig MAHE (kelig.mahe@ifremer.fr)

378 **Materials availability**

379 This study did not generate any reagents or other materials.

380 **Data and code availability**

381 All data on coelacanth specimens are available in the Supplementary Material. Data on the
382 other marine fish species were extracted from FishBase in June 2020 (see Key resources
383 table). All data extracted and R codes supporting the current study have been deposited in
384 SEANOE (<https://doi.org/10.17882/80498>).

385 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

386 Between 2 and 5 scales were sampled from the basal part of the first dorsal fin of coelacanth
387 specimens from public natural history collections: two specimens of the Zoologischen
388 Staatssammlung München (ZSM; The Bavarian State Collection of Zoology) and 25 of the
389 Collections des pieces anatomiques en fluide from the Muséum National d'Histoire Naturelle
390 de Paris (MNHN; The French National Museum of Natural History). For each specimen, we
391 provide its inventory number of the institution that houses the collection and the Coelacanth
392 Conservation Council (CCC) number¹⁷ (See also Table S1). The specimens of the MNHN and
393 ZSM are stored in 10% formalin and 70° alcohol, respectively. The MNHN's specimens are

394 conserved in the formalin since their capture and, with time, the un-buffered conservative
395 solution became acid, which could have damaged the structure of some scales.

396 METHOD DETAILS

397 Sclerochronology

398 The coelacanth has an elasmoid-type scale that has evolved several times independently in the
399 evolutionary history of fish. All scales were rehydrated and cleaned. After this preliminary
400 step, they were photographed under transmitted light using a Zeiss microscope equipped with
401 a camera to observe the series of concentric macroscopic circuli (macro-circuli). In a second
402 step, they were photographed under polarized light microscopy in order to increase the
403 contrast between structures. Polarized light microscopy reveals topographical details on
404 anisotropic materials, including bio-calcified structures such as scales, which are difficult to
405 observe under transmitted light. Polarized light revealed more numerous circuli, thinner than
406 the macro-circuli and formed by alternating translucent and opaque bands suggestive of
407 growth rate variation. Several scales were scanned using a micro-computed tomography
408 scanner (CT scan) providing a high resolution 3-dimensional representation of the object. In a
409 few cases, the structures on the scale were not distinguishable due to degradation by the
410 formalin solution and thus scale interpretation was not possible in the corresponding
411 specimens (See also Table S1).

412 The image processing was performed using the image analysis system TNPC (Digital
413 processing for calcified structures) for pictures under both transmitted and polarized light.
414 Two sclerochronology experts analyzed each scale by identifying macro-circuli under
415 transmitted light and circuli under polarized light along the longest growth axis, i.e. from the
416 proximal to the distal end of the scale (Figure 1). Several scales per specimen were used to
417 obtain a robust estimate of the number of (macro-) circuli and thus of the age of the specimen
418 under the assumption of an annual growth periodicity (see age validation method below).

419 Age validation method: Marginal Increment Analysis

420 Calcified structures in fish have the potential to grow throughout the life of the individual
421 without resorption. Variations in the individual's body growth are translated into variations in
422 the growth of the calcified structures. These variations are revealed by the optical properties
423 of the bio-calcified material that appears either opaque or translucent. Hence, circannual
424 rhythm in body growth and calcified structure formation produces an alternation of
425 translucent and opaque bands on the latter. Pairs of translucent-opaque bands correspond to
426 annual increments and can thus be used for ageing individuals. However, for using observed
427 increments on calcified structures (here macro-circuli and circuli on coelacanth scales) to age
428 individuals, it is necessary to validate their annual frequency of formation as any event
429 affecting growth may produce such a mark (e.g. transition from endogenous to exogenous
430 nutrition in larvae, migration, gestation, thermal shock). Such age validation is required for
431 establishing the accuracy of an age estimation method³¹.

432 Marginal Increment Analysis (MIA) is the most commonly used age validation method
433 and allows assessing the periodicity of increment formation in bio-calcified structures³². It is a
434 quantitative approach that relies on a measure of the size of the increment under formation
435 (named the marginal increment), i.e., the distance between the most recently formed (macro-)
436 circuli and the edge of the scale, relative to the size of the last fully formed increment, i.e., the
437 distance between the last-but-one and the most recently formed (macro-) circuli. In
438 mathematical notation, the relative measure of the marginal increment, MI, is given by:

439
$$MI = \frac{R_0 - R_n}{R_n - R_{n-1}}$$

440 Where R_0 is the radius of the scale measured from its focus to the edge (Figure 1), R_n is the
441 distance between the focus and the last (macro-) circuli formed n , and R_{n-1} is the distance
442 between the focus and the last-but-one (macro-) circuli $n - 1$. If (macro-) circuli are formed

443 annually, the marginal increment MI will thus exhibit an intra-annual periodic pattern that can
 444 be observed by plotting its measure against the date of its origin, i.e. the month at which the
 445 specimen was captured. MI was measured for each specimen using macro-circuli under
 446 transmitted light and circuli under polarized light and plotted against the month of capture. A
 447 sinusoidal regression of MI against the month of capture m with a period of 12 months was
 448 used to test for the annual periodicity of (macro-)-circuli formation after linearization:

$$449 \quad MI \sim a + b \sin\left(\frac{2\pi}{12}m + c\right) = a + b \sin(c) \cos\left(\frac{2\pi}{12}m\right) + b \cos(c) \sin\left(\frac{2\pi}{12}m\right) \quad (1a)$$

450

451 so that,

$$452 \quad MI \sim \alpha_0 + \alpha_1 \cos\left(\frac{2\pi}{12}m\right) + \alpha_2 \sin\left(\frac{2\pi}{12}m\right) \quad (1b)$$

453

454 with $a = \alpha_0$, $b = (\alpha_1^2 + \alpha_2^2)^{1/2}$, and $c = \arctan\left(\frac{\alpha_1}{\alpha_2}\right)$.

455 The global significance of the linear regression provided a statistical validation for an intra-
 456 annual pattern in (macro-) circuli MI. The classical assumptions of the linear models
 457 (normality of, homoscedasticity of, and absence of trends in the residuals) were verified and
 458 met.

459 [Body growth models](#)

460 The mean body growth patterns of the sampled specimens obtained by interpreting scales
 461 using macro-circuli and circuli were described using three different growth models including:

462 a) the von Bertalanffy³³ model:

$$463 \quad TL_t = TL_\infty - (TL_\infty - TL_1) \cdot e^{-K \cdot (t-1)} \quad (2)$$

464 b) the Gompertz³⁴ model:

$$465 \quad TL_t = TL_\infty \cdot e^{\ln\left(\frac{TL_1}{TL_\infty}\right) \cdot e^{-K \cdot (t-1)}} \quad (3)$$

466 c) the logistic model³⁵:

$$467 \quad TL_t = \frac{TL_\infty}{1 + \left(\frac{TL_\infty}{TL_1} - 1 \right) * e^{-K \cdot (t-1)}} \quad (4)$$

468 Where TL_1 , TL_t , and TL_∞ are respectively the length at age 1, at age t and the asymptotic
469 length, and K is the rate at which the asymptote is reached, called the rate coefficient in this
470 paper. Notice that the models started at age 1 as no data was available for age 0 individuals,
471 hence the age offset of 1 in the exponential: $t - 1$.

472 [Auximetric plot and growth performance comparison](#)

473 The body growth patterns obtained for coelacanth macro-circuli and circuli were compared
474 with those of other marine species using two complementary approaches.

475 First, an auximetric plot³⁶, which is a double logarithmic plot (base 10) of the von Bertalanffy
476 growth model parameters K versus TL_∞ , was produced. Given that K represents the rate at
477 which TL_∞ is reached in inverse time units whereas TL_∞ represents the size range of the
478 species in size units, it is difficult to compare multiple growth patterns while accounting for
479 both dimensions at the same time. In addition, the fact that K and TL_∞ are negatively
480 correlated complicates the matter. The auximetric plot allows circumventing these difficulties.
481 A population characterized by a set of von Bertalanffy growth parameters (TL_∞, K) is
482 represented by a point and populations of a given species or species having similar growth
483 characteristics will tend to form clusters of points that delimit the growth space of that species
484 or group of species. Moreover, the auximetric plot allows the comparison of species according
485 to their speed of growth at a given asymptotic size (vertical direction) and according to their
486 body size for a given speed of growth (horizontal direction).

487 Second, the “growth performance index”³⁶ was computed:

$$488 \quad \phi' = \log_{10} K + 2 \log_{10} TL_\infty \quad (5)$$

489 This index has the interesting property of having the same dimension as a growth rate, i.e. size
490 per unit time, and thus allows to compare the global growth performances across species. A

491 very high growth index would correspond to species growing fast to large sizes relative to
492 species with a low one. Empirically, the index ϕ' is shown to be distributed normally for
493 populations of the same species or phylogenetically close species. Isolines of the index ϕ' can
494 be superimposed to the auximetric plot since these have a known slope of 2, thus allowing
495 both approaches to be used at the same time.

496 Both approaches were used for the comparison of the coelacanth with other marine fish
497 species. Von Bertalanffy parameters for the other marine fish species were extracted from
498 FishBase in June 2020 (Popgrowth table¹⁸). Only populations for which size was measured as
499 total length were kept for comparison, resulting in 1383 populations distributed across 1313
500 species.

501 [Slow-fast life-history continuum analysis](#)

502 The location of the coelacanth along the slow-fast life-history continuum¹² in marine fish was
503 assessed using estimates of time-related life-history traits obtained from both macro-circuli
504 and circuli ageing: the von Bertalanffy rate coefficient K (yr^{-1}), the maximum observed
505 longevity (yr), the age at first sexual maturity (yr), and the gestation duration (yr) transformed
506 into a spawning frequency (yr^{-1}). These four traits were extracted for other marine fish species
507 from FishBase in June 2020 (Popgrowth, Species, Maturity, Fecundity and Spawning tables¹⁸)
508 and were available together for 147 populations distributed across 131 species.

509 [QUANTIFICATION AND STATISTICAL ANALYSIS](#)

510 [Body growth models](#)

511 For both macro-circuli and circuli ageing, the best growth model was identified as the one
512 minimizing the small-sample, bias-corrected form of the Akaike Information Criterion
513 ($\text{AICc}^{37,38}$). The AICc balances the trade-off between the quality of fit and the number of
514 parameters used³⁸ while accounting for small-sample bias and is defined as:

$$515 \quad \text{AICc} = 2k - 2 \ln(L) + \frac{2k(k+1)}{n-k-1} \quad (6)$$

516 where n is the sample size, k is the total number of parameters of the model and L is its
517 likelihood.

518 Slow-fast life-history continuum analysis

519 As time-related life-history traits are known to be affected by body size¹², the four traits were
520 regressed against asymptotic total length TL_{∞} after log10-transformation of the five variables.
521 A Principal Components (PC) analysis was then carried out on the residuals of the regressions
522 of the four life-history traits after centering and scaling. The two first PCs explained 78.9% of
523 the variation. A biplot on the plane defined by the two first PCs was produced in order to
524 identify the slow-fast life-history continuum and to position the coelacanth life-history as
525 estimated by the two ageing methods. The biplot represents both populations' projection on
526 the PC plane as dots and life-history trait projection as arrows.

527 Statistical analyses and plots were performed using the following packages in the statistical
528 environment R: Rfishbase³⁹, ade4⁴⁰, ggplot2⁴¹, factoextra⁴², ggpubr⁴³.

529 ADDITIONAL RESOURCES

530

531 References

- 532 1. Hureau, J. C. and Ozouf, C. (1977). Determination de l'âge et croissance du coelacanthé
533 *Latimeria Smith*, 1939 (poisson, crossopterygian, coelacanthide). *Cybium*. Ser. 3, 129–137.
- 534 2. Froese, R., and Palomares, M.L.D. (2000). Growth, natural mortality, length weight
535 relationship, maximum length and length-at-first-maturity of the coelacanth *Latimeria*.
536 *Environ. Biol. Fish* 58, 45–52. <https://doi.org/10.1023/A:1007602613607>.
- 537 3. Smith, J.L.B. (1939). A living fish of Mesozoic type. *Nature* 143, 455–456.
538 <https://doi.org/10.1038/143455a>.

- 539 4. Fricke, H. Hissmann, K., Schauer, J., Reinicke, O., and Ksang, L. (1991). Habitat and
540 population size of the coelacanth *Latimeria chalumnae* at Grand Comoro. Environmental
541 Biology Fishes. 32, 287–300. <https://doi.org/10.1007/BF00007462>
- 542 5. Smith, C. L., Rand, C. S., Schaeffer, B., and Atz, J.W. (1975). *Latimeria*, the living
543 coelacanth, is ovoviviparous. Science 190, 1105–1106.
544 <https://doi.org/10.1126/science.190.4219.1105>
- 545 6. Fricke, H., Hissmann, K., Froese, R., Schauer, J., Plante, R., and Fricke, S. (2011). The
546 population biology of the living coelacanth studied over 21 years. Mar. Biol. 158(7), 1511-
547 1522. <https://doi.org/10.1007/s00227-011-1667-x>.
- 548 7. Bruton, M. N., and Armstrong, M. J. (1991). The demography of the coelacanth *Latimeria*
549 *chalumnae*. Environ. Biol. Fish. 32, 301–311. <https://doi.org/10.1007/BF00007463>.
- 550 8. Hissmann, K., Fricke H., and Schauer, J. (2000). Patterns of time and space utilisation in
551 coelacanths (*Latimeria chalumnae*), determined by ultrasonic telemetry. Mar. Biol. 136, 943-
552 952. <https://doi.org/10.1007/s002270000294>.
- 553 9. Décamps, T., Herrel, A., Ballesta, L., Holon, F., Rauby, T., Gentil, Y., Gentil, C., Dutel, H.,
554 Debruyne, R., Charrassin, J.-B., *et al.* (2016). The third dimension: a novel set-up for filming
555 coelacanths in their natural environment. Methods in Ecol. Evol. 8: 322-328.
556 <https://doi.org/10.1111/2041-210X.12671>.
- 557 10. Hughes, G.M. (1995). The gills of the coelacanth, *Latimeria chalumnae*, a study in
558 relation to body size. Philosophical Transactions of the Royal Society of London B. 347, 427-
559 438. <https://doi.org/10.1098/rstb.1995.0034>.
- 560 11. Fricke, H., and Hissman, K. (2000). Feeding ecology and evolutionary survival of the
561 living coelacanth *Latimeria chalumnae*. Mar. Biol. 136, 379-386.
562 <https://doi.org/10.1007/s002270050697>.

- 563 12. Gaillard, J. M., Lemaître, J. F., Berger, V., Bonenfant, C., Devillard, S., Douhard,
564 M., Gamelon, M., Plard, F., and Lebreton, J. D. (2016) Life history axes of variation. In
565 The Encyclopedia of Evolutionary Biology, R. Kliman, ed. (Cambridge : Academic Press), pp.
566 312–323.
- 567 13. Murua, H. Rodriguez-Marin, E. Neilson, J. D. Farley, J. H., and Juan-Jordá, M. J. (2017).
568 Fast versus slow growing tuna species: age, growth, and implications for population dynamics
569 and fisheries management, *Rev. Fish Biol. Fisher.* 27(4), 733-773.
570 <https://doi.org/10.1007/s11160-017-9474-1>.
- 571 14. Vitale, F., Worsøe Clausen, L., and Ní Chonchúir, G. (2019). Handbook of fish age
572 estimation protocols and validation methods. *ICES Coop. Res. Rep.* 346, 1-180
573 <http://doi.org/10.17895/ices.pub.5221>.
- 574 15. Treble, M. A., Campana, S. E., Wastle, R. J., Jones, C. M., and Boje, J. (2008). Growth
575 analysis and age validation of a deepwater Arctic fish: the Greenland Halibut (*Reinhardtius*
576 *hippoglossoides*). *Can. J. Fish. Aquat. Sci.* 65, 1047–1059. <https://doi.org/10.1139/F08-030>.
- 577 16. Le Cren, E. D. (1947).The determination of the age and growth of the perch (*Perca*
578 *fluviatilis*) from the opercular bone. *J. Anim. Ecol.* 16, 188 – 204.
579 <https://doi.org/10.2307/1494>.
- 580
- 581 17. Nulens, R., Scott, L., and Herbin, M. (2011).An updated inventory of all known
582 specimens of the coelacanth, *Latimeria* spp. *Smithiana Special Publication* 3, 1–52.
- 583 18. Froese, R., and Pauly. D. Editors. FishBase. World Wide Web electronic publication.
584 www.fishbase.org (12/2019)
- 585 19. Cailliet, G. M., Andrews, A.H., Burton, E.J., Watters, D.L., Kline, D.E., and Ferry-
586 Graham, L.A. (2001). Age determination and validation studies of marine fishes: do deep-

587 dwellers live longer, *Exper. Gero.* 36, 739-764. <https://doi.org/10.1016/S0531->
588 5565(00)00239-4.

589 20. Sinha, M., Jha, S., and Chakraborty, P., (2020). Indian Ocean wind speed variability and
590 global teleconnection patterns. *Oceanologia*, Preprint at
591 <https://doi.org/10.1016/j.oceano.2019.10.002>.

592 21. Heemstra, P.C., and Greenwood. P.H. (1992). New observations on the visceral anatomy
593 of the late term foetuses of the living coelacanth fish and the oophagy controversy.
594 *Proceeding of the Royal Society of London B.* 249, 49-55.
595 <https://doi.org/10.1098/rspb.1992.0082>.

596 22. Tanaka, S., Shiobara, Y., Hioki, S., Abe, H., Nishi, G., Yano, K., and Suzuki, K., (1990).
597 The reproductive biology of the frilled shark, *Chlamydoselachus anguineus* from Suruga Bay,
598 Japan. *Jap. J. Ichthyol.* 37(3), 273-291. <https://doi.org/10.11369/jji1950.37.273>.

599 23. Beverton, R. J. H. (1992). Patterns of reproductive strategy parameters in some marine
600 teleost fishes. *J. Fish Biol.* 41(sB), 137–160. <https://doi.org/10.1111/j.1095->
601 8649.1992.tb03875.x

602 24. Conrath, C. L., and Musick, J. A. (2012). Reproductive Biology of Elasmobranchs. In
603 *Biology of Sharks and Their Relatives*, J.C. Carrier, J.A. Musick, and M.R. Heithaus, eds.
604 (Florida : CRC Press), pp. 307–328.

605 25 Gunderson, D. R. (1997). Trade-off between reproductive effort and adult survival in
606 oviparous and viviparous fishes. *Can. J. Fish. Aquat. Sci.* 54(9), 990-998.

607 26 Ernande, B., Dieckmann, U., and Heino, M. (2004). Adaptive changes in harvested
608 populations: Plasticity and evolution of age and size at maturation. *Proceedings of the Royal*
609 *Society of London Series B* 271, 415–423.

- 610 27 Warner, R. R., and Chesson, P. L. (1985). Coexistence Mediated by Recruitment
611 Fluctuations: A Field Guide to the Storage Effect. *The American Naturalist*, *125*(6), 769–787.
612 <https://doi.org/10.1086/284379>
- 613 28. Voituron, Y., de Fraipont, M., Issartel, J., Guillaume, O., and Clobert, J. (2011).
614 Evolutionary biology Extreme lifespan of the human fish (*Proteus anguinus*): a challenge for
615 ageing mechanisms. *Biol. Lett.* *7*, 105–107. <https://doi:10.1098/rsbl.2010.0539>.
- 616 29. Cheung, W.W.L., Pitcher, T.J., and Pauly, D. (2005) A fuzzy logic expert system to
617 estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological*
618 *Conservation*, *124*, 97–111. <https://doi.org/10.1016/j.biocon.2005.01.017>.
- 619 30. Norse, E. A., Brooke, S., Cheung, W. W. L., Clark, M. R., Ekeland, I., Froese, R., Gjerde,
620 K. M., Haedrich, R. L., Heppell, S. S., Morato, T., *et al.* (2012). Sustainability of deep-sea
621 fisheries. *Marine Policy*, *36*(2), 307–320. <https://doi.org/10.1016/j.marpol.2011.06.008>
- 622 31. Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation
623 in fisheries biology. *Trans. Am. Fish. Soc.* *112*, 735–743. <https://doi.org/10.1577/1548-8659>.
- 624 32. Campana, S. (2001). Accuracy, precision and quality control in age determination,
625 including a review of the use and abuse of age validation methods. *J. Fish Biol.* *59*(2), 197–
626 242. <https://doi.org/10.1111/j.1095-8649.2001.tb00127.x>
- 627 33. Von Bertalanffy, L. (1938). A quantitative theory of organic growth (Inquiries on growth
628 laws II). *Hum. Biol.* *10*, 181-213.
- 629 34. Gompertz, B. (1825). On the nature of the function expressive of the law of human
630 mortality and on a new mode of determining the value of life contingencies. *Philos. Trans. R.*
631 *Soc. Lond.* *115*, 515–585. <https://doi.org/10.1098/rspl.1815.0271>.
- 632 35. Verhulst, P. F. (1838). Notice sur la loi que la population poursuit dans son accroissement.
633 *Corresp. Math. Phys.* *10*, 113-121. <http://dx.doi.org/10.1371/journal.pbio.1001827>

634 36. Pauly, D. (1979). Gill size and temperature as governing factors in fish growth: a
635 generalization of von Bertalanffy's growth formula. PhD Thesis, Univ. Kiel and Institut für
636 Meereskunde.

637 37. Akaike, H. (1974). A new look at the statistical model identification. IEEE Trans. Autom.
638 Control. *19*, 716-723. <http://dx.doi.org/10.1109/TAC.1974.1100705>

639 38. Sakamo, Y., Ishiguro, M., and Kitagawa, G. (1986). Akaike Information Criterion
640 Statistics (Netherlands : Springer).

641 39. Boettiger, C., Lang D. T., and Wainwright, P. C. (2012). rfishbase: exploring,
642 manipulating and visualizing FishBase data from R. J. Fish Biol. *81*, 2030-2039. DOI:
643 10.1111/j.1095-8649.2012.03464.x

644 409. Chessel, D., Dufour, A., and Thioulouse, J. (2004). The ade4 Package - I: One-Table
645 Methods. R News, *4(1)*, 5-10. <https://cran.r-project.org/doc/Rnews/>

646 41. Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis (New York : Springer-
647 Verlag).

648 42. Kassambara, A., and Mundt, F. (2020). factoextra: Extract and Visualize the Results of
649 Multivariate Data Analyses. R package version 1.0.7. [https://CRAN.R-](https://CRAN.R-project.org/package=factoextra)
650 [project.org/package=factoextra](https://CRAN.R-project.org/package=factoextra).

651 43. Kassambara, A. (2020). ggpubr: 'ggplot2' Based Publication Ready Plots. R package
652 version 0.4.0. <https://CRAN.R-project.org/package=ggpubr>.

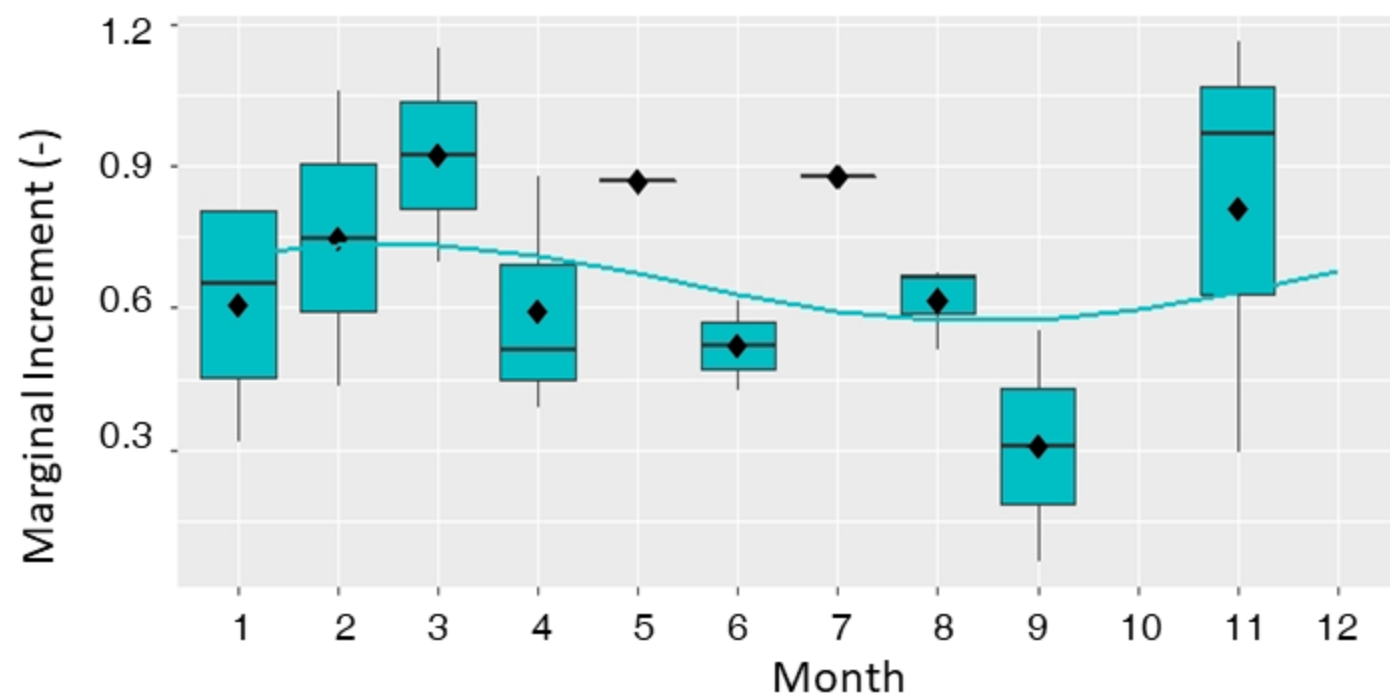
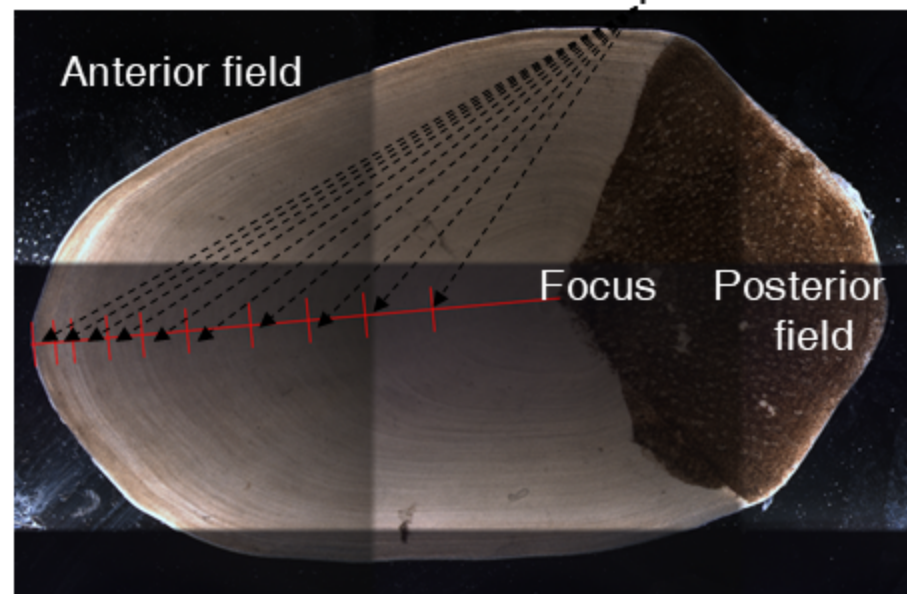
653

654

655

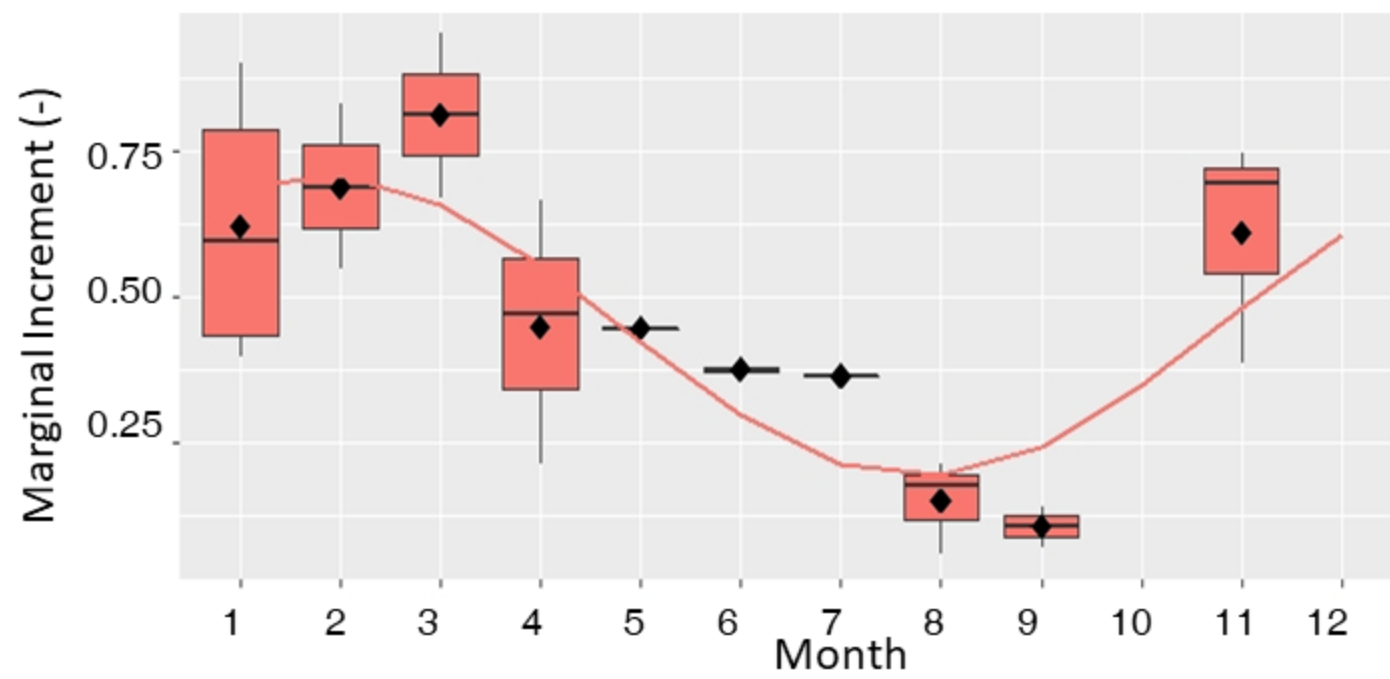
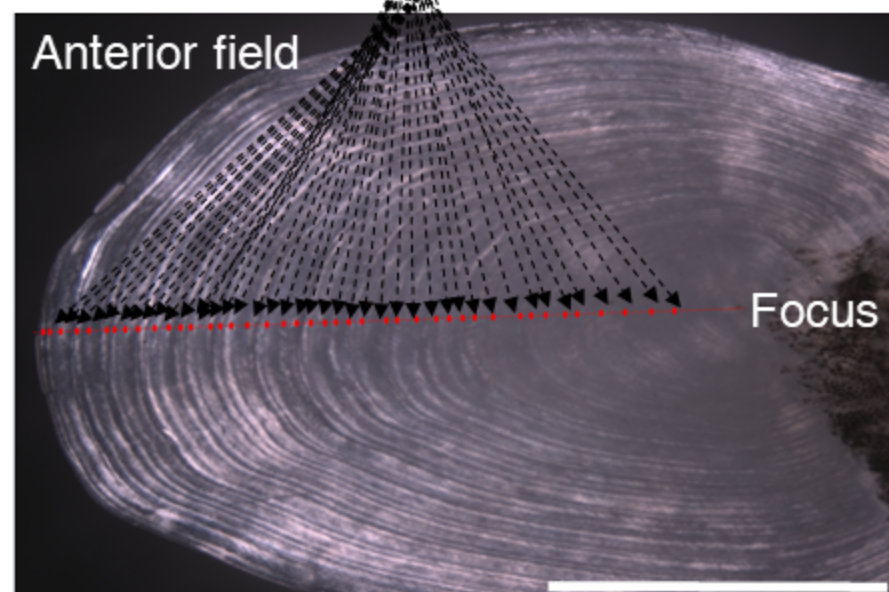
A

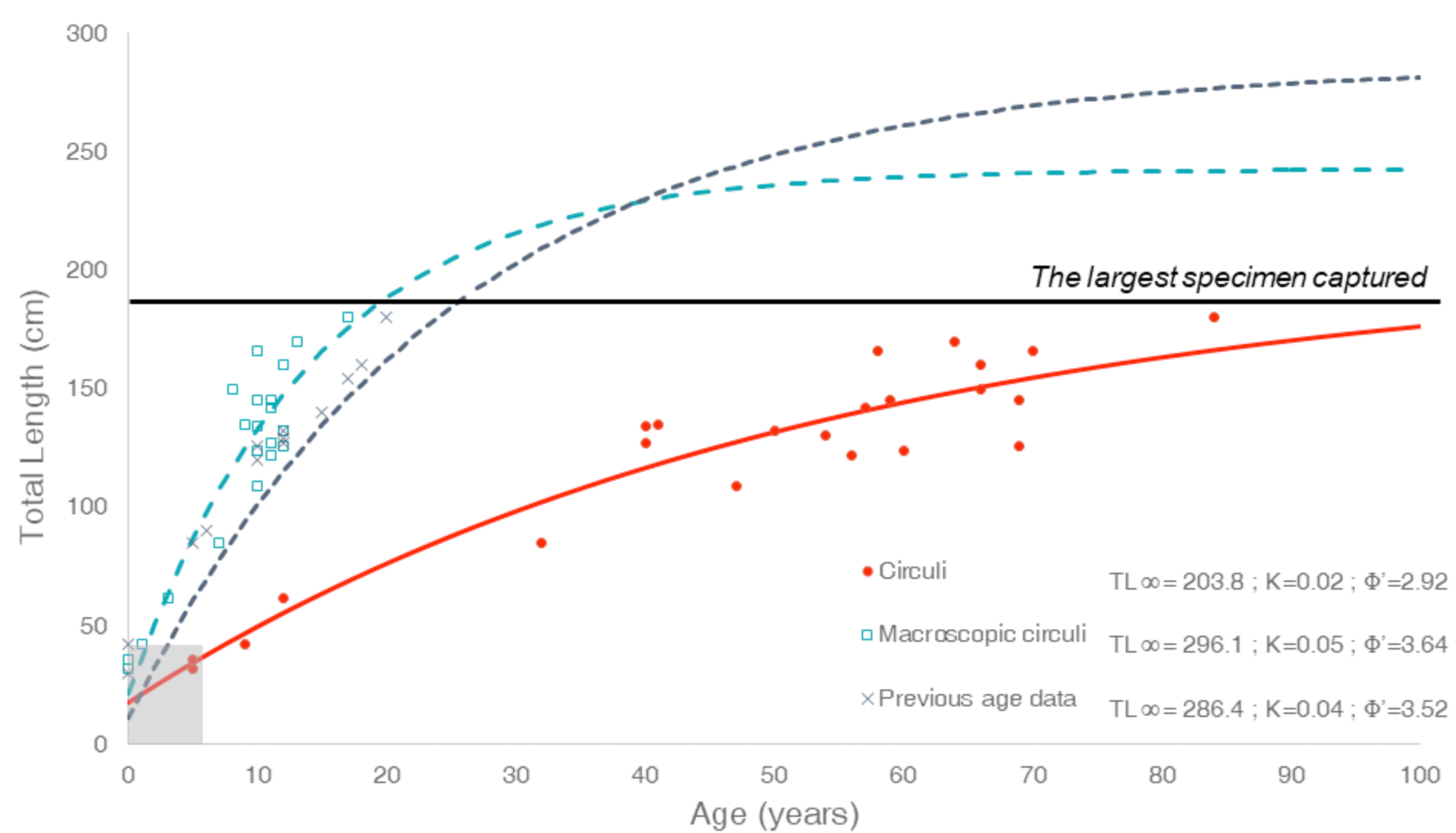
10 Macroscopic circuli

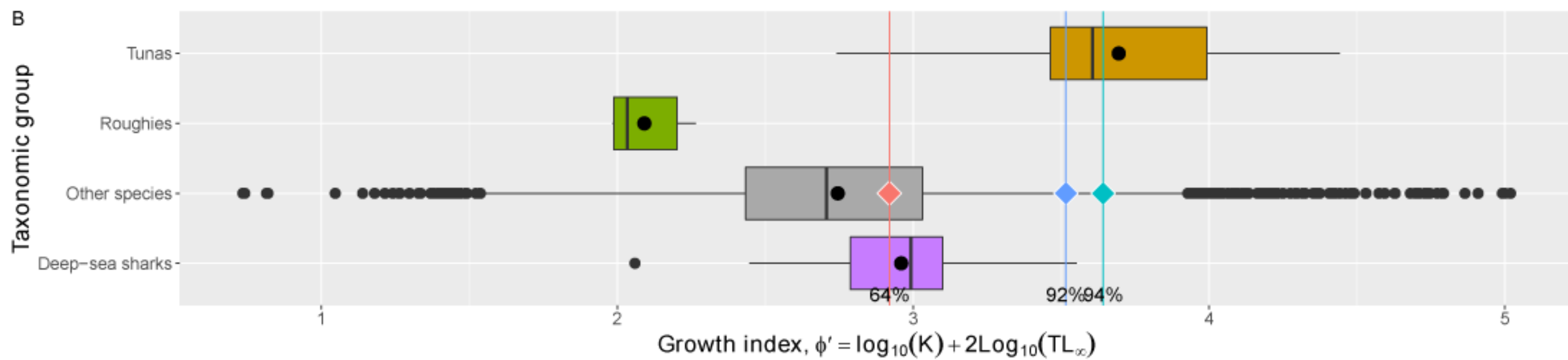
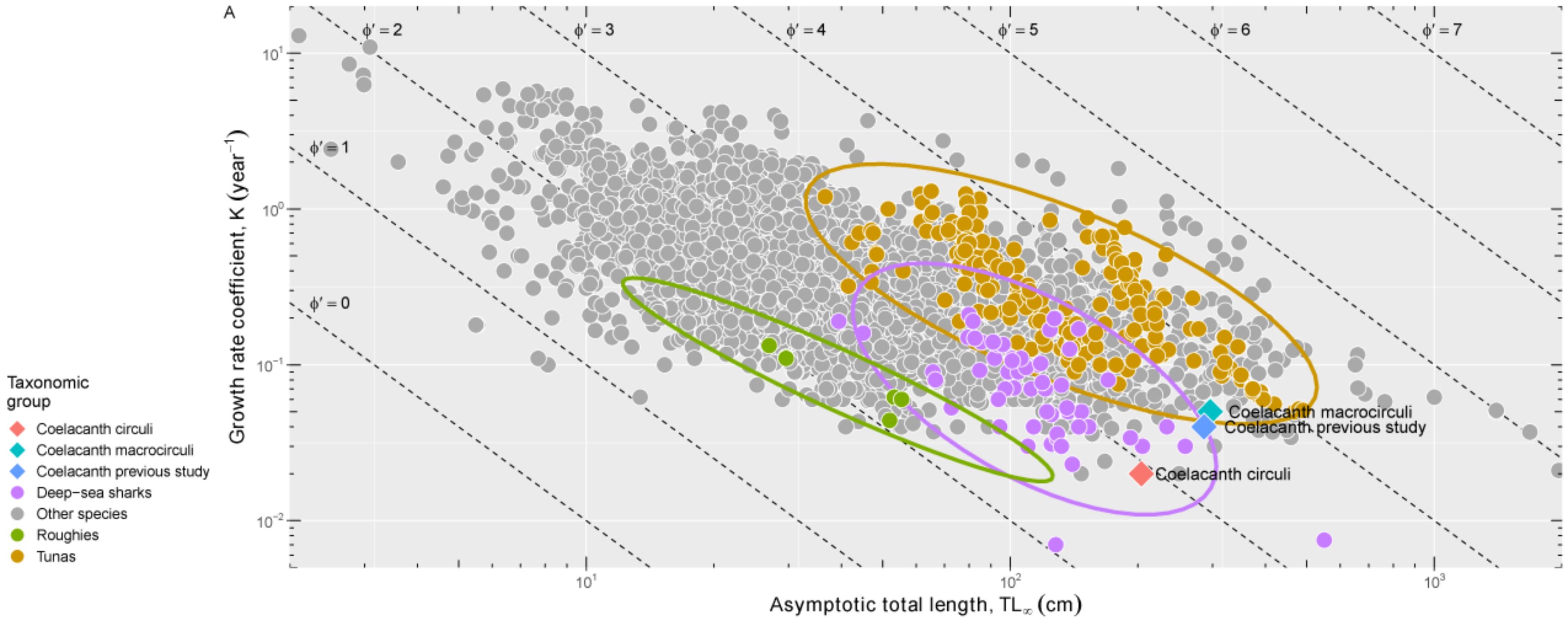


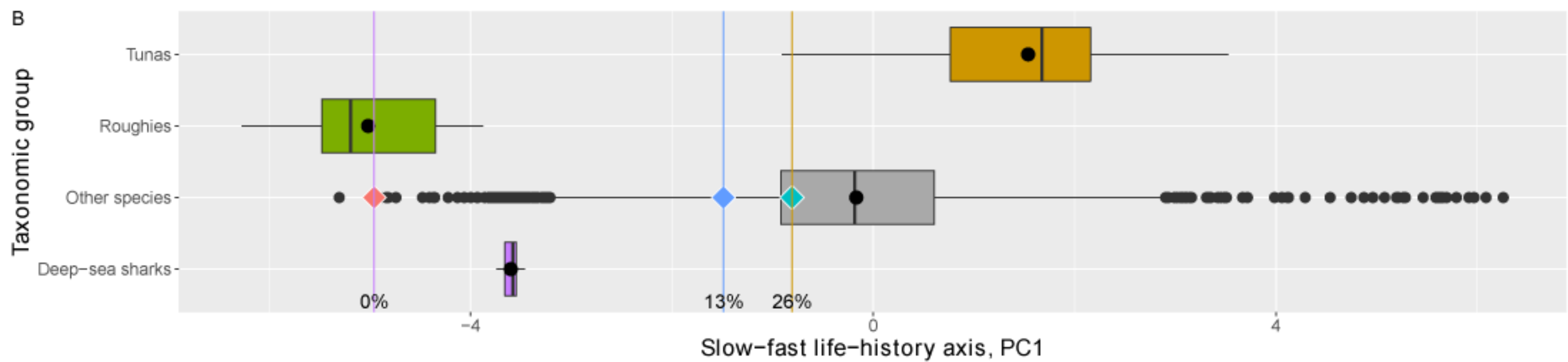
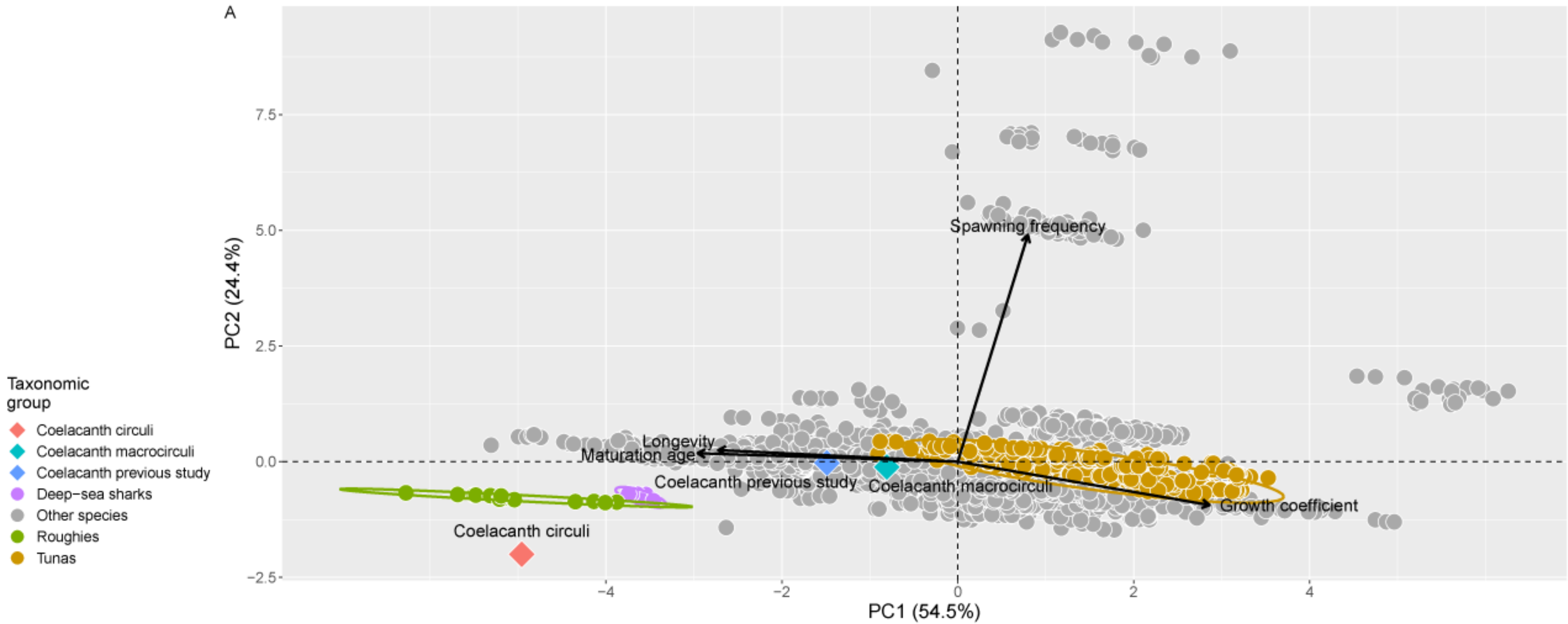
B

47 Circuli









Earlier ageing
Transmitted light



New ageing
Polarized light

Scale observation

Ageing validation

Life History Reappraisal

Length

190 cm

Slow growth

Long
gestation

Late
maturity

High
longevity

5 yr

40 yr

70 yr

100 yr

Age

