
Determinants of growth and selective mortality in anchovy and sardine in the Bay of Biscay

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Abstract :

In many exploited marine fish species, older individuals within cohorts often have slower growth rates at age than their younger counterparts, a process generally attributed to fishing. However, environmental changes might also contribute to the selective disappearance of faster growing individuals because of the increasing constraints acting on growth in suboptimal environments. Using otoliths of anchovy and sardine collected each year in spring since 2000 in the Bay of Biscay, we measured individuals' growth during age-0 and catch-up growth during age-1, and followed their changes in time from 2000 to 2018 to quantify the magnitude of selective mortality. We then determined whether the variations in growth and selective mortality were related to seasonal temperature, food quantity, stock biomass or stock harvest rate. In both species, there was a decline in growth during age 0 over time and a catch-up growth declined in anchovy. Density-dependence had a strong effect on growth in anchovy. In both species, there was a systematic selective disappearance of individuals with large growth at age-0 within each cohort and selection has changed over time to favour individuals with large catch-up growth in anchovy. Moreover, diversifying selection occurred for growth at age-0 in both species and catch-up growth in anchovy. In anchovy, years with high selective disappearance of large individuals, high catch-up growth and high diversifying selection were those in which the harvest rates were high (environmental variables having more limited effect). In sardine, the selective disappearance of large individuals was stronger in years with low food quantity and the magnitude of selection acting on growth was unrelated to this stock's harvest rate. Though fishing exerted strong selection pressure in anchovy, selective mortality against large growth still occurred even at low harvest rates in both species, suggesting that this might be a natural process affecting these small pelagic forage fish species. Although anchovy and sardine have a similar trophic position, their selection regimes differed due to differences in their stock dynamics, environmental sensitivity, and fishing rate. It might therefore be hazardous to extrapolate the responses of single species to environmental and anthropogenic factors onto others.

Highlights

► Individuals' life-time growth trajectory is determined by early growth. ► Age-0 growth has declined and is density-dependent for anchovy and sardine. ► Large fish disappear within cohorts and this occurs even with low harvest rates. ► Environmental variables have little effect of the magnitude of selection. ► Different stock histories explain the different selection regimes both of species.

Keywords : Catch-up growth, Growth, Otolith, Mortality, Size-at-age

57 **1. Introduction**

58 In many exploited marine fish species, body size-at-age are declining over time
59 (e.g. Baudron et al., 2014, 2011; Edeline et al., 2007; Jørgensen, 1990). Two non-
60 independent processes can explain this pattern: a decline in age-specific growth, and a
61 selective mortality of individuals with rapid growth. In marine species living in optimal
62 environmental conditions, natural selection favours large individuals that have greater
63 survival rates because of their greater energetic reserves and foraging capacities
64 (Kenchington, 2014; Kissner & Weatherhead, 2005; Lorenzen, 1996; Olsen et al., 2004) and
65 higher reproductive success (Fleming & Gross, 1994). In degraded environmental
66 conditions, individuals set up a physiological stress response whose lasting energetic costs
67 might induce declines in growth and reproductive investments (Korte et al., 2005; McEwen
68 & Wingfield, 2003; Romero et al., 2009; Wingfield, 2002). However, individuals may recover
69 from a period of limited growth, in a process called catch-up growth (Ali et al., 2003;
70 Metcalfe & Monaghan, 2001; Wright et al., 2007). This process has primarily been shown in
71 the context of experimental studies in which a period of limited growth was induced
72 through food shortages and differences in subsequent growth dynamics were characterized
73 between control and treatment groups (Hector & Nakagawa, 2012). Yet, patterns akin to
74 catch-up growth can be observed in natural populations and describe the negative
75 correlation between growth rates in consecutive ages (e.g. Bertram et al., 1993). Individuals
76 with slow growth in their first year (either because of environmental constraints or hatched
77 late in the reproductive season) can therefore have a higher growth rate in their second
78 year and declines in catch-up growth might also contribute substantially to the overall
79 decline in body size of marine fish species.

80 Declines in size-at-age can also be explained by the selective disappearance of large
81 individuals within cohorts (Conover & Munch, 2002; Law, 2000). Indeed, old individuals
82 have typically smaller growth rates than their younger counterparts suggesting a trade-off
83 between survival and growth (Lee, 1912). As growth is a heritable character, the shorter
84 lifespan of large individuals might lead to evolutionary changes towards smaller growth
85 rates and size-at-age (Dieckmann & Heino, 2007; Heino & Dieckmann, 2008; Laugen et al.,
86 2014; Swain et al., 2007). The selective disappearance of individuals with rapid growth has
87 often been attributed to fishing which, by targeting large individuals, increases the
88 mortality rate of fast growing individuals (Allendorf & Hard, 2009; Ernande et al., 2004;
89 Essington et al., 2015; Heino & Dieckmann, 2008; Law, 2000, 2007; Matsumura et al., 2011;
90 Swain et al., 2007). However, environmental changes have also the potential to exert a
91 particularly strong constraint on individuals with rapid growth (Korte et al., 2005; Metcalfe
92 & Alonso-Alvarez, 2010; Metcalfe & Monaghan, 2003; Ohlberger, 2013). Therefore,
93 understanding the declines in size-at-age in natural populations requires quantifying the
94 concomitant changes in growth patterns and selective mortality as well as identifying the
95 biotic, abiotic and anthropogenic factors that underpin these changes.

96 Many studies have investigated the effect of fisheries' induced selective mortality and the
97 subsequent declines in growth in exploited marine species (e.g. Olsen et al., 2004; Edeline et
98 al., 2007; Kuparinen & Merilä, 2007), but the effects of environmental variations on growth
99 and selective mortality have often been limited to a few easily estimated variables (e.g. sea

100 surface temperature, Daufresne et al., 2009; Baudron et al., 2014; Forster et al., 2011;
101 Ohlberger, 2013). Density-dependent processes or the amount of food available may have
102 critical effects on individuals' growth and survival rates (Dieckmann & Heino, 2007;
103 Jørgensen et al., 2007; Metcalfe & Monaghan, 2003; Swain et al., 2007). Moreover, most
104 previous studies focused on single populations of emblematic marine fish species with long
105 life cycles (e.g. Edeline et al., 2007; Matsumura et al., 2011). However, species with short life
106 cycles may have more acute responses to the selective disappearance of large individuals
107 due to fishing and/or environmental changes, and the consistency in the response of
108 populations' of different species facing the same environmental constraints and/or
109 selective pressures has rarely been considered (Hendry et al., 2009; Kaeuffer et al., 2012).
110 Furthermore, the process of selective mortality has often been estimated using directional
111 selection because of the expected selectivity of fishing gear toward large individuals (Nusslé
112 et al., 2009; Swain et al., 2007). Yet, changes in the variance in growth rate arising through
113 non-linear selection may also occur (Johnson et al., 2012), particularly in response to the
114 variance in environmental conditions that can constrain (balancing selection) or strengthen
115 phenotypic changes (disruptive selection associated to directional selection; Johnson et al.,
116 2014). Finally, measurements of fishing intensity in many exploited fish species are
117 inaccurate because of the unknown or inaccurate amount of discards (Allen et al., 2002;
118 Machias et al., 2001). To bypass this issue, past studies often defined broad categories (high
119 vs low intensity; Nusslé et al., 2009) but these are very crude measures of the variance in
120 fishing intensity limiting the accuracy of the relationship between fishing and selective
121 mortality. Understanding the processes underpinning changes in growth and thus selective
122 mortality requires estimating the relative importance of each of these factors and assess
123 their consistency between species or populations.

124 In this study, we used otolith growth data of the European anchovy *Engraulis encrasicolus*
125 and the European sardine *Sardina pilchardus* of the Bay of Biscay, collected during fisheries
126 research surveys conducted each year from 2000 to 2018. In both survey data and fishery
127 catches the size-at-age of these species has declined during this period (Doray et al., 2018;
128 Véron et al., 2020) which is a concern for the fishing industry and the ecosystem
129 functioning. Indeed, a decline in size-at-age of anchovies and sardines might lead to a
130 decline in the foraging efficiency of their predators (Ainley & Blight, 2009; Smith et al.,
131 2011) but might also have major consequences for the entire ecosystem through the
132 regulation of planktonic communities (Nikolioudakis et al., 2012, 2014). Anchovies and
133 sardines are sensitive to environmental changes (Chavez et al., 2003; Hsieh et al., 2008;
134 Petitgas et al., 2013), have relatively short life cycles as fish mature in their first year and
135 ages 1 and 2 contribute the most to the biomass of these stocks (Chavez et al., 2003; Doray
136 et al., 2014, 2018; ICES 2019; Motos, 1996; Petitgas et al., 2012). The decline in size-at-age
137 in anchovy and sardine in the Bay of Biscay is similar to the one observed in the Gulf of Lion
138 (Van Beveren et al., 2014) that has been attributed to changes in the composition of the
139 plankton community and an increasing competition with the European sprat (*Spratus*
140 *spratrus*; Bacha et al., 2010; Costalago et al., 2015; Van Beveren et al., 2014). As exploitation
141 rates of anchovy and sardine had been particularly low for a long time in the Gulf of Lion,
142 fishing *per se* was not associated with the decline in size-at-age but the lack of sufficient
143 time series describing measurements of individuals' growth based on otolith increments
144 prevented a direct measure of size selective mortality and its changes over time (Saraux et

145 al., 2019). Contrary to the anchovy and sardine of the Gulf of Lion, in this study we can
146 quantify the magnitude of selective mortality and the effect of fishing and the
147 environmental factors on this process as otolith data have been collected for a longer time
148 span, detailed environmental variables are available, and the harvest rate is estimated by
149 ICES. Furthermore, the anchovy and sardine stocks in the Bay of Biscay have experienced
150 important and contrasting changes, making their comparison worthwhile to understand the
151 drivers of change in size-at-age. More specifically, the anchovy stock experienced high
152 fishing mortality in the early 2000s, collapsed in 2005 and fishing was banned between
153 2005 and 2009 (ICES 2019). Subsequently the harvest rate of this stock has remained low,
154 its biomass increased but size-at-age continued to decline (Doray et al., 2018; ICES 2019;
155 Petitgas et al., 2010). Conversely, the harvest rate of sardine was relatively small until 2010
156 and increased substantially during the last decade (ICES 2018).

157 The combination of individual growth data collected over multiple generations,
158 environmental data and the variation in harvest rate estimates will allow us to quantify the
159 relative contribution of environmental changes and fishing to the variation in growth and
160 selective mortality of anchovy and sardine. To this end, we will therefore first quantify
161 yearly variations in growth during age 0, catch-up growth, and both directional and non-
162 directional selections differentials in these two growth characteristics. We will then identify
163 the factors explaining these temporal variations focusing on the effects of density-
164 dependence, water temperature, food quantity, and harvest rates. More specifically, we
165 expect that high temperature or high food quantities are associated with increasing growth
166 during age 0 and catch-up growth, that growth is negatively associated with population
167 abundance because of intra-specific competition. Finally, we will investigate whether the
168 magnitude of directional and non-directional selection indices are related to low food
169 quantity, high temperature and harvest rate if fishing is selective.

170 **2. Methods**

171 **2.1. Sampling protocol at sea**

172 Sardine and anchovy samples were collected onboard R/V Thalassa during the research
173 survey PELGAS (full description of the survey in Doray et al., 2018). The survey takes place
174 in May in each year since 2000 and covers the entire French shelf of the Bay of Biscay, from
175 coast to shelf-break. This spatial coverage encompasses most of sardine and the whole
176 anchovy populations in the Bay of Biscay (Doray et al., 2018; Gatti et al., 2017). PELGAS is
177 primarily an acoustic survey and pelagic trawl hauls are targeted on echotraces for their
178 identification and collecting fish biological parameters (Doray et al., 2014; Petitgas et al.,
179 2003). After each trawl haul, the catch is sorted and weighed by species. A random
180 subsample of each species is taken to establish length frequencies, from which a second
181 subsample is taken for individual measurements, covering the whole length range (Doray et
182 al., 2014; 2018). The individual measurements amount to extracting otoliths and measuring
183 individuals' total length, weight and further biological parameters. Forty individuals of
184 sardine and anchovy are individually analysed when the species are present in the catch.
185 This standard protocol is implemented within the data collection framework for the

186 assessment of fisheries resources managed at EU level (Doray et al., 2014). For each
187 individual the two otoliths sagittae are extracted on board, mounted in leukit for age
188 reading, and the growth pattern in their microstructure is analysed under binocular
189 microscope in the laboratory on land. The data span 19 years from 2000 to 2018 and
190 comprise 535 and 549 hauls for anchovy and sardine, respectively.

191 **2.2. Otolith growth increment measures**

192 In the laboratory, we imaged and analysed the otoliths with the image processing software
193 TNPC (Traitement Numérique des Pièces Calcifiées, Mahé et al., 2009). Under the binocular
194 microscope (x12.5) and natural light, the otoliths showed opaque portions corresponding
195 to growth (accretion of aragonite) and hyaline stripes corresponding to winter periods
196 without growth. We measured the segment lengths corresponding to annual growths at
197 ages 0 to 5 years along the longitudinal axis of the otolith between winter stripes (i.e., the
198 outer border of the stripe). We conformed to the standard way of interpreting otoliths by
199 ICES for anchovy (ICES 2009; 2017a; Uriarte 2016a) and for sardine (ICES 2011). The
200 survey is undertaken during spring-time, which is the reproductive season of anchovy and
201 the major reproductive season for sardine (Motos, 1996; Stratoudakis et al., 2007). Thus,
202 age-1 fish otoliths show a hyaline outer border corresponding to their first winter. In that
203 case, the segment length of the entire otolith from border to border corresponds to growth
204 during age-0 before the first winter and during winter. In some cases, the border of the
205 otolith is opaque, meaning that growth has resumed in spring. In these cases, the segment
206 length is measured to and from the outer border of the winter stripe. The ring diameter in
207 the first winter (growth during age-0) is named 'R1' (first growth ring) and to the following
208 winters 'R2' to 'R5'. The individuals' age-specific growth is therefore noted R1 (growth
209 during age-0), R2-R1 (growth during age-1), and so on. Age-specific growth was measured
210 for all hauls containing anchovy from 2000 to 2018 (N = 20,185). For sardine, we stratified
211 the Bay of Biscay according to its ecosystem spatial structure (Petitgas et al., 2018) and
212 selected hauls in each strata to cover the entire area in each year. The selected hauls
213 represented half of the hauls in which sardines were sampled during 2001-2018 (N = 8,264
214 individuals).

215 **2.3. Measurements of growth, catch-up growth and selective mortality**

216 There are multiple ways of measuring individuals' growth from their otolith (e.g. Swain et
217 al., 2007; Nusslé et al., 2009). Given the relatively short lifespan of anchovies and sardines
218 and the limited number of increments considered (R1 to R5) growth measurements were
219 based on otoliths' annual increments as their overall radius was strongly correlated to
220 individual length-at-age in both species (linear regression; anchovy: $\beta = 0.897$, p-value <
221 0.01; sardine: $\beta = 0.929$, p-value < 0.01). Growth increments during age-0 and age-1 (otolith
222 increments R1 and R2-R1, respectively) were by far the largest of all increments for both
223 anchovy and sardine; representing more than 90% of fish overall growth (Petitgas et al.,
224 2012; Uriarte et al., 2016a). Therefore, this study focused on these two growth increments.
225 Catch-up growth is an individual process describing the individual's ability to grow rapidly
226 following a period of slow growth (Dmitriew, 2011). In anchovy and sardine, there is a
227 negative correlation between their growth at age-0 (R1) and that at age-1 (R2-R1; Appendix

228 Figure A1; Petitgas et al., 2012; Uriarte et al., 2016a). We measured catch-up growth during
229 age-1 by the ratio (R2-R1)/R1, which therefore consisted in only individuals of age-2
230 (individuals with high values of this ratio had higher growth at age-1 relative to their
231 growth at age-0).

232 We then calculated the weighed means otolith growth R1 and catch-up growth (R2-R1)/R1
233 to have cohort level means. The weights were defined as the fraction of population biomass
234 at that station as follows:

$$235 \quad R = \frac{\sum_i (b_i \bar{R}_i)}{\sum_i (b_i)}$$

236 where i is the index of trawl hauls (in a given year), \bar{R}_i is the mean index R of the individuals
237 measured at station i and b_i is the mean fish concentration estimated in the surroundings of
238 station i . We estimated fish concentration surrounding each trawl haul by the mean of the
239 species' acoustic density estimates (one value per nautical mile along transects: Doray et al.,
240 2018) located up to 4 nautical miles (one hour trawling) from the trawl haul mid position.
241 The sums b_i correlated with population abundance over the series for both anchovy and
242 sardine (not shown), meaning that the trawl hauls sampled the populations of sardine and
243 anchovy over all their spatial distributions. The cohort level estimates of growth were
244 further used to estimate selection indices.

245 As the selection pressure is exerted on fish length rather than otolith size, indices of
246 selective mortality were estimated using fish back-calculated length. We therefore applied
247 the Scale Proportional Hypothesis (SPH) model (Francis, 1990; Whitney & Carlander, 1956)
248 from the r-package 'FSA' (Ogle et al., 2020) to estimate fish growth during age-0 (L1) and
249 during age-1 (L2). The SPH model was used under the assumption that the body-scale
250 relationship is linear (this is true in both species for the age considered). Selective
251 mortality was estimated following Johnson et al. (2012), who distinguished directional
252 selection applying on the mean of the trait considered (here L1, and (L2-L1)/L1) and
253 diversifying/stabilizing selection when the variance of the trait increases/decreases.
254 Cumulative directional selection differential for cohort j , S_j , was estimated as

$$255 \quad S_j = \frac{\sum_{i=\min(\text{age}+1)}^{\max(\text{age})} (T_{i,j} - T_{i-1,j})}{\sqrt{(\sigma_{T_{i-1,j}}^2)}}$$

256 where, T is the mean of the trait considered (either L1, or (L2-L1)/L1), j is the index of the
257 cohort, i the index of the age the, and $\sigma_{T_{i-1,j}}^2$ is the variance of trait inferred from cohort j at
258 age $i-1$. The index is a standardized differential in length-at-age within cohorts over the
259 years. The index S_j was estimated for the two traits, age-0 growth and age-1 catch-up
260 growth. As 88% of the cumulative directional selection was explained by the selection
261 occurring between ages 1 and 2, the index was estimated with these two ages only and
262 denoted $S_{1,2}$.

263 Diversifying selection acting on trait for cohort j , C_j , was estimated as

$$C_j = \sum_{i=\min(\text{age}+1)}^{\max(\text{age})} (\sigma_{(T_{i,j})}^2 - \sigma_{(T_{i-1,j})}^2) + S_{i,j}^2$$

265 where, j is the index of cohorts, i the index of age, $\sigma_{(T_{i,j})}^2$ the variance of trait T at age i in
 266 cohort j and $S_{i,j}$ is the directional selection index defined above. This index is the difference
 267 in variance between consecutive ages within cohorts. The index C_j was estimated for age-0
 268 growth and age-1 catch-up growth, which used ages 1 and 2 ($C_{1,2}$) and 2 and 3 respectively
 269 ($C_{2,3}$). As for S_j , the index C_j estimated for age-0 growth was initially calculated considering
 270 ages 1 to 3 in both species. But as 92% of the variance in C_j was explained by the difference
 271 in variance between the ages 1 and 2, the index considered here was estimated with ages 1
 272 and 2 only.

273 2.4. Indices of the environment, population abundance, and harvest 274 rate

275 We measured growth during age-0, catch-up growth and the two selection differentials
 276 acting on these two growth indices for the 18 cohorts available in the data set. We selected
 277 the factors most likely to influence these parameters based on biological knowledge. Many
 278 environmental variables are measured during PELGAS (Doray et al., 2018) but as the survey
 279 takes place in spring (during spawning). It therefore, only provides a snapshot of the
 280 environmental conditions that does not reflect on the environmental conditions
 281 experienced by anchovies and sardines during various stages of their growth (spring,
 282 summer and autumn are periods of growth while during winter energy reserves are used).
 283 We thus retrieved environmental conditions during these periods using operational
 284 oceanographic products. The MARC/Previmer project (<http://marc.ifremer.fr/>) offers daily
 285 satellite images of sea surface chlorophyll-a and temperature, in a standard format, ready
 286 for use and compatible with CMEMS (Copernicus Marine Environment Monitoring Service).
 287 These variables were averaged over the Bay of Biscay shelf, providing time series with daily
 288 values of surface temperature and chlorophyll-a, from 1999 to 2017. We first calculated
 289 seasonal averages by quarter of the year and carried out a Principal Components Analysis
 290 (PCA: function “pca” in R) to extract a few, uncorrelated synthetic variables characterising
 291 the environmental conditions. The two first principal components were retained, the first
 292 principal component (PC1) was correlated with chlorophyll-a in summer, autumn and
 293 spring, while the second (PC2) was correlated with temperature in winter (Figure A4 in
 294 appendix). As spring corresponds to the birth date of the individuals of each cohorts, the
 295 PCA was carried out on the set of spring, summer, autumn values in year $n-1$ and winter
 296 values in year n .

297 Because food is shared among congeners, population biomass might also affect individuals’
 298 growth through density-dependent mechanisms (e.g. Post et al., 1999). To estimate such a
 299 density-dependent effect, we used yearly estimates of anchovy and sardine population
 300 abundance as published by ICES (2019) for the Bay of Biscay. Finally, the harvest rates of
 301 both fish stocks were considered as proxies for fishing pressure. We retrieved these harvest
 302 rate estimates from ICES assessments working group reports (ICES 2019). As fishing

303 vessels use specific gear (pelagic trawls, purse seines and sonar) to target schools, the ICES
304 working group considers discards as negligible and measures of harvest rate in the Bay of
305 Biscay as accurate (ICES 2017b).

306 2.5. Relating growth and selective mortality to explanatory variables

307 Overall, we aimed at identifying the factors underpinning the variation in six variables
308 (Table 1): growth during age-0 (R_1), catch-up growth during age-1 $((R_2-R_1)/R_1)$,
309 directional and non-directional selective differentials ($S_{1,2}$ and $C_{1,2}$) applied to growth
310 during age 0 (L1 measured and inferred from individuals of ages 1 and 2 respectively), and
311 directional and non-directional selective differentials ($S_{2,3}$ and $C_{2,3}$) applied to catch-up
312 growth during age 1 (measured on individuals of ages 2 and 3). Each of these variables for
313 sardine and anchovy was related to the following explanatory variables: population
314 abundance ('Biom', in tons) and harvest rate ('HR') as estimated by ICES (ICES 2019
315 report), and the two environmental PCA-based indices ('PC1' and 'PC2'). When relating the
316 dependent variables to the explanatory ones (covariates), a time lag was considered (Table
317 2), the time reference being the cohort year. In particular, we adjusted the timeframe over
318 which density-dependence and environmental effect acted. For growth at age 0, we
319 considered population biomass during the months during which such growth occurred
320 because it is the overall presence of conspecifics that creates density dependence. In the
321 case of the catch-up growth at age 1, we considered population abundance during the
322 period when the catch-up growth was active. No interaction was considered between
323 covariates due to the small number of cohorts considered (19 years). We carried out simple
324 linear regressions as their residuals showed no correlation over time for all our response
325 variables. All possible models were considered from the full model (all covariates) to the
326 null model (no covariate) and models were ranked from most to least probable given the
327 data, based on the corrected Akaike's Information Criterion (AIC; function dredge in R,
328 Barton, 2017). Model-averaged coefficient estimates with unconditional SE and
329 unconditional 95%CI were calculated for models with differences in AICc lower than 4
330 using the r-package 'MuMIn' v1.43.17 (Barton, 2017). This threshold was chosen so as to
331 quantify the relative contribution of the explanatory variables. All analyses were run in R
332 4.0.2 (R Core Team, 2014).

333 3. Results

334 3.1. Temporal changes in age-0 growth and catch-up growth

335 For the cohorts born from 1999 to 2017, the decline in R_1 (growth during age-0) measured
336 on age-1 individuals was significant for both anchovy and sardine (linear regressions ($\beta \pm$
337 SE); anchovy: -21.26 ± 6.60 , p-value < 0.01; sardine: -16.01 ± 3.62 , p-value < 0.01; Figure 1).
338 The decline was slightly greater for anchovy (14%) than sardine (11%). Similarly, catch-up
339 growth during age-1 showed a significant decline over time for anchovy (linear regression
340 ($\beta \pm$ SE); -0.01 ± 0.00 , p-value < 0.01; Figure 1C), with a decrease of 47%. Conversely, there
341 was no significant temporal change in catch-up growth for sardine over the same period
342 (linear regression ($\beta \pm$ SE); 0.00 ± 0.01 , p-value = 0.94; Figure 1D).

343 3.2. Directional selection differentials in age-0 growth and catch-up 344 growth

345 For both species, $S_{1,2}$ was almost always negative over the time series meaning that larger
346 individuals at age-1 (i.e., with larger growth during age-0) consistently disappeared from all
347 cohorts (mean \pm SE; anchovy: -1.18 ± 0.16 ; sardine: -0.75 ± 0.13 ; Figs. 2A and 2B). The
348 magnitude of the directional selection differentials decreased with time in anchovy (linear
349 regression ($\beta \pm$ SE): 0.06 ± 0.03 , p-value = 0.04; Figs. 2A) while there was no significant
350 temporal changes in $S_{1,2}$ in sardine (linear regression ($\beta \pm$ SE): 0.04 ± 0.02 , p-value = 0.13;
351 Figs. 2B). The selective disappearance of individuals with larger age-0 growth occurred
352 mainly during the first year of life for both anchovy and sardine, as the selection index
353 measured on individuals aged 1 and 2 was very close to that calculated with a larger age
354 range (Figs. 2A and 2B). In anchovy, the directional selection differential acting on catch-up
355 growth (i.e. $S_{2,3}$) increased from negative to positive values over time indicating that
356 individuals with higher catch-up growth disappeared in the beginning of the time series
357 while in later years, individuals with a lower catch-up growth disappeared (linear
358 regression ($\beta \pm$ SE); 0.07 ± 0.03 , p-value = 0.04; Fig. 2C). This index varied around zero in
359 sardines, indicating absence of directional selection for catch-up growth in this species
360 (linear regression ($\beta \pm$ SE); -0.01 ± 0.02 , p-value = 0.57; Fig. 2D).

361 3.3. Non-linear selection differential in age-0 growth and catch-up 362 growth

363 In both species, the non-linear selection differential index (C_j) applied on age-0 growth was
364 generally positive (mean \pm SE; anchovy: 4.08 ± 0.83 ; sardine: 1.10 ± 0.42 ; Figs. 3A and 3B),
365 meaning that the variance in age-0 growth increased with age within cohorts. For anchovy,
366 the amplitude of $C_{1,2}$ decreased over time (linear regression ($\beta \pm$ SE); -0.42 ± 0.13 , p-value =
367 0.01; Fig. 3A). In contrast for sardine, there was no significant temporal pattern in $C_{1,2}$
368 (linear regression ($\beta \pm$ SE); -0.04 ± 0.08 , p-value = 0.62; Fig. 3B). Most of the selection
369 differential takes place during age-1 as the selection index calculated on individuals aged 1
370 and 2 was close to that calculated on ages 1 to 3 (Fig. 3). As for $C_{1,2}$, the non-linear selection
371 differential for catch-up growth ($C_{2,3}$) was generally positive for both anchovy and sardine,
372 indicating that variance in catch-up growth increased with age within cohorts. There was
373 no pattern in the variation of the index ($C_{2,3}$) over time for both species (linear regression
374 ($\beta \pm$ SE); anchovy: 0.04 ± 0.04 , p-value = 0.25; sardine: -0.01 ± 0.01 , p-value = 0.36; Figs. 3C
375 and 3D).

376 3.4. Factors underpinning the variation in growth and selection 377 differential indices

378 The variation in the growth parameters R1 and $(R2-R1)/R1$, and their selection differentials
379 ($S_{1,2}$, $C_{1,2}$, $S_{2,3}$ and $C_{2,3}$) could be explained by several models, which had a Δ AICc less than 4
380 (Tables 3 and 4). These models showed different combinations of the explanatory variables,
381 meaning that there was uncertainty in their relative contribution and it is the reason why

382 we considered models with a ΔAICc less than 4. We averaged the parameters among these
383 retained models, resulting in more reliable parameter estimates that reproduced the time
384 series of each index (Fig. 4). Here, we outline the most important explicative variables in the
385 average models (Appendix Tables A1 to A7).

386 In anchovy, R1 was negatively related to population biomass (mean parameter \pm SE: -0.003
387 ± 0.001 , p-value = 0.04; Table 3a; Table A1, Fig. 4A) and catch-up growth was positively
388 related to harvest rate (mean parameter \pm SE: 0.34 ± 0.11 , p-value < 0.01; Table 3b; Table
389 A2, Fig. 4B). Directional selection acting on growth ($S_{1,2}$) in anchovy was negatively related
390 to harvest rate (mean parameter \pm SE: -3.22 ± 0.95 , p-value < 0.01; Table 3c; Table A3, Fig.
391 4C) indicating that the selective disappearance of individuals with high age-0 growth was
392 stronger in years with high harvest rate. The diversifying selection acting on growth ($C_{1,2}$)
393 tended to be positively correlated to harvest rate (mean parameter \pm SE: 10.34 ± 5.00 , p-
394 value = 0.06; Table 3d; Table A4, Fig. 4D). Anchovy directional selection acting on catch-up
395 growth ($S_{2,3}$) tended to be negatively related to harvest rate (mean parameter \pm SE: $-1.79 \pm$
396 0.9 , p-value = 0.07; Table 3e; Table A5, Fig. 4E) suggesting that the selective disappearance
397 of individuals with high catch-up growth was stronger in years with high harvest rate.

398 By contrast, we only found two significant effects in sardine. Growth during age-0 was
399 positively correlated to population abundance, which may be indicative of population
400 expansion into new habitats still not occupied, density-dependent effects having not yet
401 taken place (mean parameter \pm SE: 0.002 ± 0.001 , p-value = 0.01; Table 4a, Table A6, Fig.
402 4F). Directional selection acting on catch-up growth ($S_{2,3}$) was positively correlated to the
403 first principal component (PC1) of environmental indices (mean parameter \pm SE: $0.09 \pm$
404 0.05 , p-value = 0.06; Table 4e; Table A7, Fig. 4G) suggesting that the selective disappearance
405 of individuals with high catch-up growth was stronger in years with low food availability.

406 4. Discussion

407 4.1. Variations in growth at age-0 and catch-up growth

408 The decline in otolith growth (R1) in anchovy and sardine was consistent with the decline
409 in length and weight-at-age already observed in both species between 2000 and 2015
410 (Doray et al., 2018; Véron et al., 2020). The slightly less pronounced decline in otolith
411 growth for sardine than anchovy is similar to the pattern reported based on weight
412 measured at age 1 in Doray et al. (2018). R1 was negatively correlated with population
413 biomass in anchovy, while in sardine the opposite was observed. Since 2010 anchovy
414 biomass has increased substantially while R1 has been low suggesting that growth is
415 density-dependent in Bay of Biscay's anchovy, a process that has been reported in many
416 other anchovy populations around the world (Canales et al., 2020; MacCall, 1990) and could
417 be mediated by intraspecific competition (Grossman & Simon, 2020). The counter-intuitive
418 positive correlation between R1 and abundance in sardine might reflect an indirect effect of
419 fishing as the decline in R1 was parallel to that in population abundance while harvest rate
420 increased (ICES, 2019) or that there is a particularly strong bottom up effect leading to both
421 high biomasses and high R1.

422 The environmental conditions experienced by young fish determine the variance in their
423 growth rates (Metcalf & Monaghan, 2001). Over time, this variance may remain consistent,
424 increase (cumulative effect) or decrease (compensatory effects; Dmitriew, 2011). Catch-up
425 growth is one of the main processes underpinning compensatory effects, as the increase in
426 individuals' growth rate leads to a decrease of the variance in fish size in subsequent ages
427 (Ali et al., 2003; Bertram et al., 1993; Metcalfe & Monaghan, 2003). We found that catch-up
428 growth in anchovy (but not in sardine), measured as the ratio $(R_2 - R_1)/R_1$, decreased over
429 time meaning that growth at age-1 (i.e. $R_2 - R_1$) was greater than the decline in growth at
430 age-0 (R_1). Hence, the entire growth dynamics has changed in anchovy while only growth
431 at age-0 declined in sardines. Anchovy catch-up growth was positively correlated to harvest
432 rate, which can be interpreted by the interaction between density-dependent growth and
433 selective fishing mortality. Indeed, the selective disappearance of larger individuals due to
434 fishing (as was the case during the first part of the time series) might have allowed the
435 remaining smaller individuals at age to grow larger in the following year. In recent years,
436 when population biomass was high and harvest rate low, growth has decreased and catch-
437 up growth even more. The maintenance of catch-up growth in sardine might explain the
438 lower decrease in length-at-age in this species in comparison to anchovy (Doray et al.,
439 2018).

440 We found no major significant effect of the seasonal environmental parameters
441 (temperature and chlorophyll-a) on growth at age-0 and catch-up growth at age-1. This
442 result might be surprising as growth dynamics are linked to the amount of food available
443 and temperature in many wild marine fish species (Baudron et al., 2014; Costalago et al.,
444 2014; Daufresne et al., 2009; Ohlberger, 2013). However, models comprising the
445 environmental variables were still considered as plausible ($\Delta AIC < 4$) meaning that the
446 effect of temperature and food availability on anchovy and sardine growth were weaker
447 than that of biomass and/or harvest rate. Moreover, environmental conditions could also
448 influence fish growth indirectly through their effect on density-dependent processes (see
449 e.g. Baudron et al., 2014; Dmitriew, 2011; Ohlberger, 2013), but this effect is harder to
450 quantify in the present analysis due to the relatively small number of years in the time
451 series. Other parameters could also influence growth such as food quality or predators'
452 abundance but the data required to quantify these parameters at different seasons (or even
453 on a yearly basis) were not available and we could not consider them.

454 **4.2. Directional and diversifying selection differentials**

455 In the evolutionary ecology literature, natural selection is widely expected to favour
456 individuals with larger body size because of their higher survival rates (Kissner &
457 Weatherhead, 2005) and reproductive success (Fleming & Gross, 1994). This general view
458 was confirmed by the review of selection differentials acting on early growth by Perez &
459 Munch (2010) which clearly showed that these differentials were mostly positive
460 (i.e. natural selection favours larger individuals). Yet, in the fisheries literature since Lee
461 (1912), mortality rates of larger sized fish within cohorts has often been reported to be
462 greater. We found that there is a consistent disappearance of individuals having large R_1 in
463 both anchovy and sardine as directional selection differentials for growth at age-0 (R_1)
464 were almost always negative. This process was particularly acute between ages 1 and 2

465 ($S_{1,2}$), where the majority of the cumulative selection differential (S_j) occurred in both
466 species. This difference in the direction of selection is due to the difference in the life stages
467 considered as the fish used in our study have already survived their first winter (hence
468 aged 1) preventing us from quantifying the effect of natural selection acting on growth at
469 age-0 before and after their first winter. Furthermore, studies focusing on the larval stage
470 have shown that the survival rates of anchovy and sardines's larvae increased with size
471 (Allain et al., 2003; Garrido et al., 2015). And a similar size-dependent survival was
472 reported by Escribano et al. (2019) for anchovy juveniles through winter, where survival
473 was also density-dependent. Thus, a reversal of selective mortality occurs in the life stages
474 ages involving reproduction.

475 The magnitude of directional selection can vary substantially among years and short
476 periods of strong selection can alternate with longer periods of weaker selection (Siepielski
477 et al., 2009). In both anchovy and sardine, we found that directional selection differentials
478 on growth ($S_{1,2}$) could vary substantially between consecutive years and that these
479 differences were slightly attenuated when using cumulative selection differentials (S_j). The
480 strongly negative directional selection differential on growth in anchovy became weaker
481 over time while the magnitude of the directional selection showed a similar trend in sardine
482 although weaker. Similarly, the directional selection differential on catch-up growth ($S_{2,3}$)
483 did vary substantially among years in anchovy (but not in sardine), the selective
484 disappearance of individuals with large catch-up growth being greater at the beginning of
485 the time series while there was a selective disappearance of individuals with small catch-up
486 growth towards the end of the time series.

487 Although catch-up growth is an important process explaining differences in growth
488 patterns, this study is the first, to our knowledge, to directly quantify selection on this trait.
489 Obviously, the measure of catch-up growth derived from these correlative data is very
490 different from those derived from lab experiment (e.g. Hector & Nakagawa, 2012) but these
491 suggest that there might be clear associations between individuals' catch-up growth and
492 survival. Inversions in the sign of the selection are not uncommon (Siepielski et al., 2009),
493 but the temporal patterns of $S_{1,2}$ and $S_{2,3}$ clearly showed that the selection regime has
494 changed in the anchovy probably because of the lack of individuals with rapid growth at
495 age-0 in the cohorts hatched towards the end of the time series. Such simultaneous changes
496 in the magnitude and direction of selection with the change of individuals' phenotype are
497 often linked to evolutionary changes (Kuparinen & Merilä, 2007; Law, 2007; Nusslé et al.,
498 2009; Swain et al., 2007) but could also be due to concomitant changes in other ecological
499 factors such as increased intra- or inter-specific competition (Van Beveren et al., 2014).
500 Consistent with the limited temporal trend in $S_{1,2}$ on sardine growth, values of $S_{2,3}$ on catch-
501 up growth in sardine varied around zero with no trend.

502 The variance in growth at age-0 increased within cohorts in both anchovies and sardines of
503 the Bay of Biscay (positive values of $C_{1,2}$), a result broadly consistent with the studies
504 reviewed in Perez & Munch (2010) that found diversifying selection to be more common
505 than stabilizing selection on fish early growth. Diversifying selection was particularly
506 strong in anchovy at the beginning of the time series meaning that selection led to an
507 increase in the proportions of individuals with small and large growth within cohorts. This

508 effect could result from fishing if catches comprised mostly individuals of a given size-at-
509 age, large enough but not necessarily the largest. Increasing variance could also occur
510 because of survey catch ability if fish with small growth at age-0 were less sampled in their
511 first year (e.g. being too close to shore) but better sampled in subsequent years a process
512 similar to a selective appearance of small individuals (van de Pol & Verhulst, 2006). This
513 might occur in a given year and contribute to the data's sampling variability but such a
514 sampling bias is however unlikely as this would lead to inconsistent biomass estimates at
515 age and it has been shown in these species that this is not the case (Escribano et al., 2019;
516 ICES 2019). Additional data will be necessary to determine whether non-linear selection
517 differentials could become negative (indicating stabilising selection) or fluctuate around
518 zero. In sardine, diversifying selection did not change significantly over time, which is
519 consistent with the directional selection differentials. Non-directional selection is generally
520 weaker than directional selection (Kingsolver et al., 2001) but we found that non-
521 directional selection differentials were often greater than directional selection differentials.
522 This might be due to the way selection is measured as selection differentials (based on
523 differences in mean and differences in variances) are by nature very different from
524 selection differentials gradient (based on linear and quadratic terms). The magnitude of
525 diversifying selection acting on catch-up growth ($C_{2,3}$) was substantially weaker in both
526 species and did not change over time suggesting that directional selection alone mattered
527 for this trait.

528 **4.3. Factors explaining directional and diversifying selection** 529 **differentials**

530 Identifying the factors underlying the temporal variations in selection differentials is
531 challenging as it requires collecting large-scale data over a sufficient number of years and
532 linking changes in estimates of selection to accurate ecological factors (Siepielski et al.,
533 2009). The selective disappearance of large individuals has been observed in many
534 exploited demersal, pelagic, marine and freshwater fish species (Taylor & Methot, 2013).
535 This process is typically interpreted as due to selective fishing but direct links between the
536 selective disappearance of large individuals and fishing are rare because of the difficulties
537 of quantifying accurately harvest rates and accounting for the potential effect of
538 environmental variables on the selective mortality. Here, we used harvest rates, population
539 biomass, and seasonal data describing sea surface temperature and a proxy of the amount
540 of food (concentration of chlorophyll-a) and found that the strongest correlate of
541 directional and non-directional selection differentials in anchovy (growth at age-0 and
542 catch-up growth) was the stock's harvest rate. Fishermen tend to target large enough
543 anchovies because of market price by fishing in particular areas in particular seasons. As
544 smaller anchovies at each age are more coastal (Petitgas et al., 2014), it is possible that
545 these fish are less likely to be captured by fishermen leading to the disappearance of large
546 individuals. The length distribution of anchovy fishery catches (ICES, 2019) included the
547 length of age 1 individuals with large growth at age-0 and remained consistent over time.
548 This agrees with the decline in the proportion of age-1 fish with large growth during age-0
549 across ages and hence the declines in directional and non-directional selection in anchovy
550 over time. Noteworthy, during the anchovy fishing ban, the directional selection
551 differentials for growth and catch-up growth remained negative meaning that the selective

552 disappearance of individuals with large growth at age-0 was not solely due to fishing.
553 Moreover, the selective disappearance of larger individuals in sardine also occurred even at
554 low harvest rates. Trophic interactions could explain the selective disappearance of larger
555 individuals for these forage species suffering high natural mortality rates (Uriarte et al.,
556 2016b) and fishing would then magnify this natural process.

557 In sardine, we only found that the directional selection acting on catch-up growth was
558 related to chlorophyll-a in summer, autumn and spring. Selection increased when this
559 proxy for food decreased. None of the other selection differentials were influenced by the
560 explanatory variables that we used. The harvest rate of this stock has increased
561 substantially since 2010 but the selective disappearance of large individuals remained at
562 levels similar to years in which the harvest rate was particularly small. This could suggest
563 that the harvest rate is still too low on sardine to lead to major changes in the selection
564 differentials or that sardine fisheries are less size-selective than for anchovy, sardine being
565 distributed over a greater range of habitats (ICES, 2010). The consistent disappearance of
566 large individuals in sardine and our inability to explain its variance suggests that this
567 process could be deeply rooted in small pelagic fish species' ecology and that selective
568 fishing might only increase its magnitude. Therefore, in spite of their broadly similar
569 ecological needs, selection patterns differed substantially between anchovy and sardine.
570 These differences might arise from differences in their environmental sensitivity due to
571 nutrition (Costalago et al., 2015; Garrido et al., 2008; Nikolioudakis et al., 2011) or their
572 spatial distribution (ICES, 2010) as anchovies and sardines considered in this study (ages 1-
573 3) are contained within the Bay of Biscay (ICES, 2010; Huret et al., 2020; Petitgas et al.,
574 2010). Furthermore, while the anchovies of the Bay of Biscay form a clearly genetically
575 distinct unit with very limited gene flow with other stocks (Huret et al., 2020), gene flow
576 might be more substantial between sardines of the Bay of Biscay, the English Channel and
577 the North sea (De Kooij & McKeown, personal communication).

578 **5. Conclusion**

579 In conclusion, we found that there was a consistent disappearance of large individuals
580 within cohorts in both anchovy and sardine of the Bay of Biscay and that this directional
581 selection was accompanied by a diversifying selection. In anchovy, these processes were
582 associated to fishing, environmental variable having a substantially smaller impact. In
583 sardine, we only found that the selective mortality of fish with high catch-up growth was
584 related to the amount of food available, but the disappearance of large individuals was
585 related to none of the variables that we used. The selective disappearance within cohorts of
586 larger individuals occurred even at low fishing rates in both species, suggesting that this is a
587 natural process in these forage species, which can be magnified by fishing. Furthermore, as
588 body growth is a well-studied heritable trait (see e.g. Domingos et al., 2013; Vandeputte et
589 al., 2004), smaller individuals within each cohort may have more opportunities to
590 reproduce and this could lead to an evolutionary decline in growth and body size. However,
591 the higher reproductive success of large individuals (Fleming & Gross, 1994) might
592 compensate for their shorter lifespans making their overall lifetime reproductive success
593 similar to their smaller but longer lived counterparts; both strategies would then coexist

594 within anchovy and sardine populations (Oliveira et al., 2008). Therefore, the next step to
595 this study will be to determine whether the selective disappearance of large individuals and
596 diversifying selections that we have reported here led to evolutionary changes towards
597 smaller body sizes or whether such changes are driven by changes in environmental
598 factors.

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610

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938 *Table 1: List of abbreviations.*

Abbreviation	Definition
R1	Otolith growth during age 0
R2-R1	Otolith growth during age 1
(R2-R1)/R1	Catch-up growth during age 1
$L1_{(i,j)}$	Mean length at age 1 estimated on individuals of age i ($i>1$) within cohort j and derived their R1
$L1_{(i-1,j)}$	Mean length at age 1 estimated on individuals of age $i-1$ ($i>1$) within cohort j and derived their R1
S_j	Directional linear selection within cohort j
C_j	Non-linear selection differentials within cohort j
$S_{1,2}$	Directional linear selection applied to age-0 growth and calculated using $L1_{(i=2,j)}$ and $L1_{(i=1,j)}$ within cohorts
$C_{1,2}$	Non-linear selection differentials applied to age-0 growth and calculated using $L1_{(i=2,j)}$ and $L1_{(i=1,j)}$ within cohorts
$S_{2,3}$	Directional linear selection applied to catch-up growth and estimated using $L2_{(i=3,j)}$, $L1_{(i=3,j)}$, $L2_{(i=2,j)}$ and $L1_{(i=2,j)}$ within cohorts
$C_{2,3}$	Non-linear selection differentials applied to catch-up growth and estimated using $L2_{(i=3,j)}$, $L1_{(i=3,j)}$, $L2_{(i=2,j)}$ and $L1_{(i=2,j)}$ within cohorts
Biom_N	Biomass in year n of sardine or anchovy
Biom_N1	Biomass in year $n+1$ of sardine or anchovy
PC1	First principal component (PC1) when applying Principal Components Analysis on environmental indices
PC2	Second principal component (PC2) when applying Principal Components Analysis on environmental indices
β	Slope of linear regression
SE	Standard Error

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941 *Table 2: Time lag considered to relate dependent with explicative variables. Abbreviation of*
 942 *variables are detailed in Table 1.*

Dependent Variable	Cohort	Explicative variables			
		Environmental index (PC1)	Environmental index (PC2)	Biomass (Biom)	Harvest rate (HR)
Growth during age 0 (R1)	N	N	N	N	
Catch-up growth during age 1 ((R2-R1)/R1)	N	N+1	N+1	N+1	N+1
Selective differentials ($S_{1,2}$, $C_{1,2}$) applied to growth during age 0	N	N+1	N+1	N	N+1
Selective differentials ($S_{2,3}$, $C_{2,3}$) applied to catch-up growth during age 1 and measured on ages 2 and 3	N	N+1	N+1	N+1	N+1

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945 *Table 3: Fitted models explaining anchovy growth and selective mortality indices. Models are fitted using explanatory variables*
 946 *and ranked by decreasing values of the corrected Akaike's information criterion. Abbreviations: logLik : log likelihood; AICc :*
 947 *Akaike's information criterion with correction; $\Delta AICc$: difference in AICc values between the current model and that having the*
 948 *lowest AICc; W_i : model weight; Cum. W_i : cumulative model weight.*

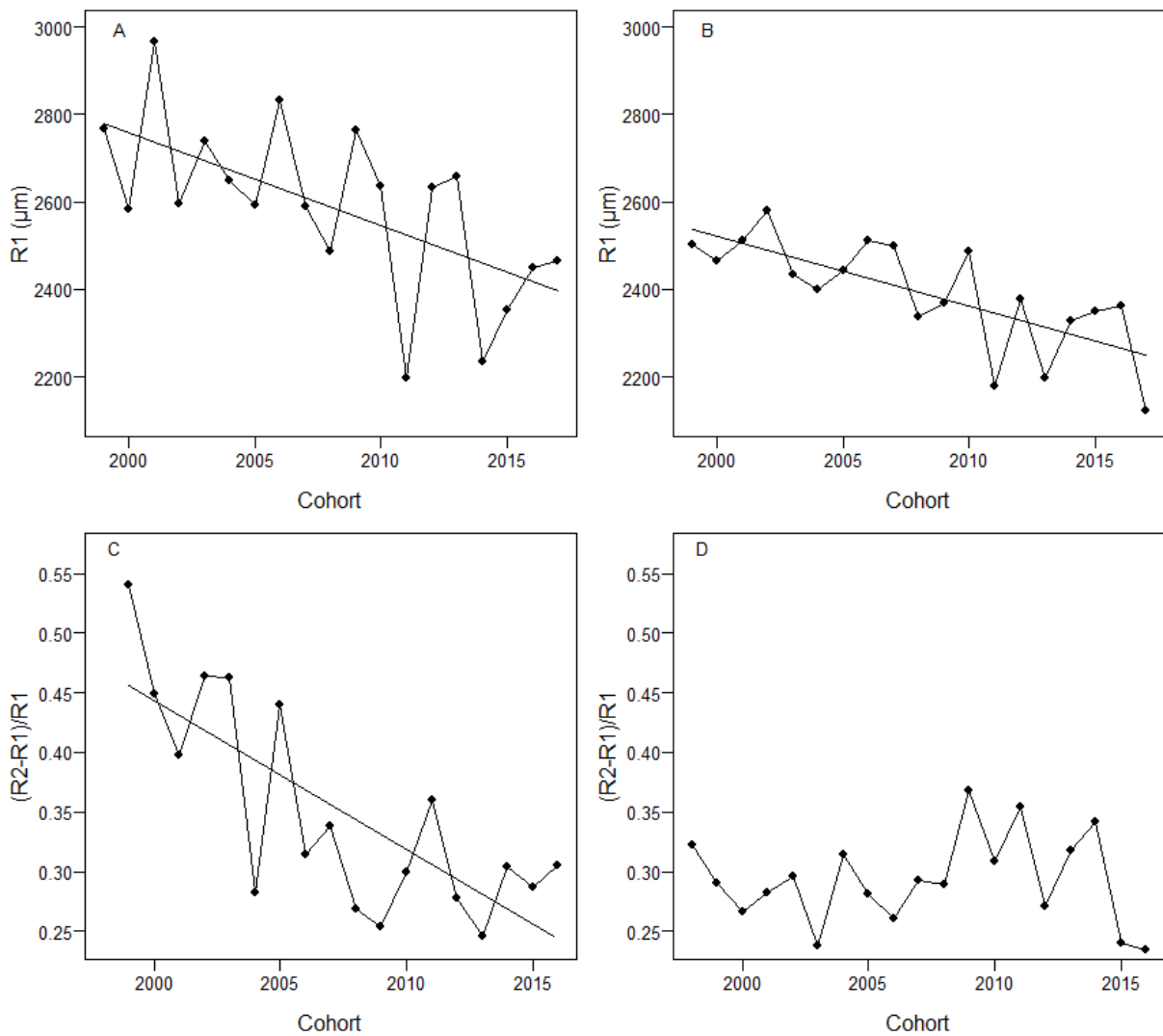
	Dependent variable	Model	logLik	AICc	$\Delta AICc$	W_i	Cum. W_i
a)	Growth during age-0 (R_1)	Biom_N	-117.92	243.55	0.00	0.41	0.41
		Biom_N + PC1	-116.72	244.51	0.96	0.25	0.66
		Intercept	-120.18	245.15	1.60	0.18	0.84
		PC1	-119.52	246.75	3.20	0.08	0.92
		Biom_N + PC2	-117.87	246.82	3.28	0.08	1.00
b)	catch-up growth during age-1 (R_2-R_1)/ R_1	Harvest.rate	21.85	-35.85	0.00	0.57	0.57
		Biom_N1 + Harvest.rate	22.50	-33.67	2.18	0.19	0.76
		PC1 + Harvest.rate	22.18	-33.02	2.83	0.14	0.90
		PC2 + Harvest.rate	21.89	-32.44	3.41	0.10	1.00
c)	Directional selection acting on growth during age-0 ($S_{1,2}$)	Harvest.rate	-15.25	38.35	0.00	0.55	0.55
		Biom_N + Harvest.rate	-14.51	40.35	2.00	0.20	0.75
		PC1 + Harvest.rate	-14.78	40.89	2.54	0.15	0.90
		PC2 + Harvest.rate	-15.25	41.83	3.48	0.10	1.00
d)	Selection differential acting on growth during age-0 ($C_{1,2}$)	Harvest.rate	-43.82	95.48	0.00	0.32	0.32
		PC1 + Harvest.rate	-42.46	96.26	0.77	0.22	0.54
		Intercept	-45.94	96.75	1.26	0.17	0.71
		PC1	-44.93	97.71	2.23	0.11	0.82

	PC2 + Harvest.rate	-43.76	98.85	3.37	0.06	0.88
	Biom_N + Harvest.rate	-43.77	98.87	3.39	0.06	0.94
	Biom_N	-45.59	99.02	3.54	0.06	1.00
e)	Directional selection acting on catch-up growth ($S_{2,3}$)					
	Harvest.rate	-14.48	36.80	0.00	0.37	0.37
	Intercept	-16.47	37.80	1.00	0.23	0.60
	Biom_N1 + Harvest.rate	-14.17	39.68	2.87	0.09	0.69
	PC2 + Harvest.rate	-14.35	40.04	3.24	0.07	0.76
	PC1 + Harvest.rate	-14.40	40.14	3.34	0.07	0.83
	PC2	-16.36	40.56	3.76	0.06	0.89
	Biom_N1	-16.41	40.66	3.86	0.05	0.94
	PC1	-16.41	40.66	3.86	0.05	0.99
f)	Selection differential acting on catch-up growth ($C_{2,3}$)					
	Intercept	-18.16	41.17	0.00	0.45	0.45
	Harvest.rate	-17.54	42.93	1.76	0.19	0.64
	Biom_N1	-17.82	43.48	2.31	0.14	0.78
	PC2	-17.94	43.73	2.56	0.12	0.90
	PC1	-18.14	44.12	2.95	0.10	1.00

949 *Table 4: Fitted models explaining sardine growth and selective mortality indices. Models are fitted using explanatory variables and*
950 *ranked by decreasing values of the corrected Akaike's information criterion values. Abbreviations: logLik : log likelihood; AICc :*
951 *Akaike's information criterion with correction; $\Delta AICc$: difference in AICc values between the current model and that having the*
952 *lowest AICc; W_i : model weight; Cum. W_i : cumulative model weight.*

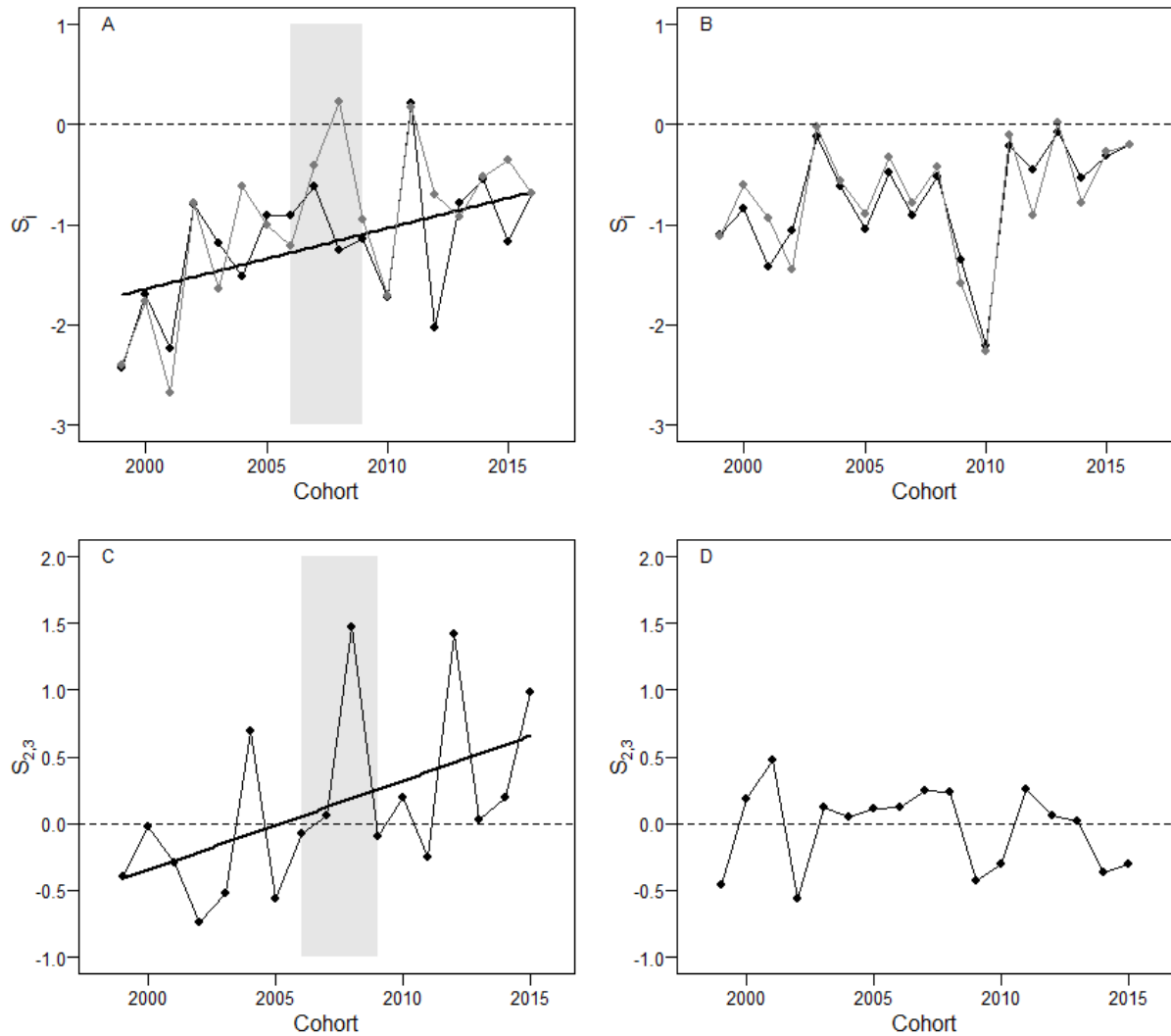
	Dependent variable	Model	logLik	AICc	$\Delta AICc$	W_i	Cum. W_i
a)	Growth during age-0 (R_1)	Biom_N	-99.44	206.72	0.00	0.66	0.66
		Biom_N + PC1	-98.76	208.86	2.14	0.23	0.89
		Biom_N + PC2	-99.41	210.15	3.43	0.12	1.01
b)	catch-up growth during age-1 (R_2-R_1)/ R_1	Intercept	30.21	-55.50	0.00	0.57	0.57
		PC2	30.42	-52.83	2.67	0.15	0.72
		PC1	30.41	-52.82	2.68	0.15	0.87
		Biom_N1	30.32	-52.63	2.87	0.13	1.00
c)	Directional selection acting on growth during age-0 ($S_{1,2}$)	Intercept	-14.36	33.64	0.00	0.40	0.40
		Harvest.rate	-13.51	35.02	1.38	0.20	0.60
		PC1	-13.85	35.70	2.06	0.14	0.74
		PC2 + Harvest.rate	-12.27	36.18	2.54	0.11	0.85
		PC2	-14.26	36.53	2.89	0.09	0.94
		PC1 + Harvest.rate	-12.95	37.53	3.89	0.06	1.00
d)	Selection differential acting on growth during age-0 ($C_{1,2}$)	Intercept	-34.16	73.23	0.00	0.58	0.58
		Harvest.rate	-33.93	75.85	2.62	0.16	0.74
		PC1	-34.08	76.15	2.92	0.14	0.88
		PC2	-34.15	76.30	3.07	0.13	1.01

e)	Directional selection acting on catch-up growth ($S_{2,3}$)	PC1	-0.49	8.99	0.00	0.47	0.47
		Intercept	-2.60	10.11	1.12	0.27	0.74
		PC1 + Harvest.rate	-0.15	11.93	2.94	0.11	0.85
		PC1 + PC2	-0.49	12.62	3.63	0.08	0.93
		Harvest.rate	-2.33	12.66	3.67	0.08	1.01
f)	Selection differential acting on catch-up growth ($C_{2,3}$)	Intercept	15.21	-25.49	0.00	0.58	0.58
		PC1	15.44	-22.89	2.61	0.16	0.74
		Harvest.rate	15.26	-22.52	2.97	0.13	0.87
		PC2	15.21	-22.43	3.07	0.13	1.00

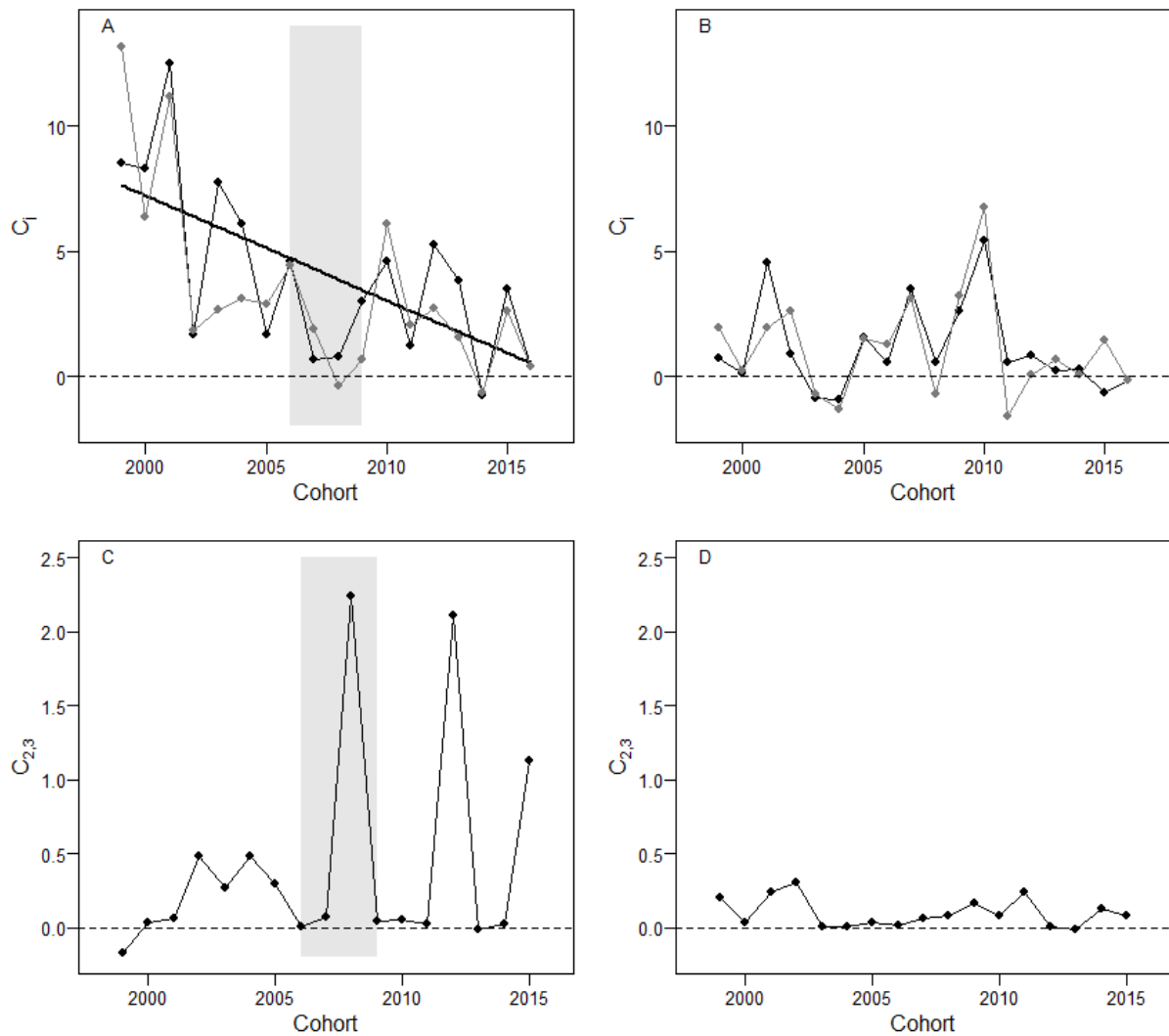


954

955 *Figure 1: Temporal changes in mean age-0 growth (R1 otolith growth increment, panels A and*
 956 *B) and catch-up growth during age-1 ($(R2-R1)/R1$; panels C and D) for anchovy (A, C) and*
 957 *sardine (B, D). Otolith R1 increments are measured in age-1 individuals and $(R2-R1)/R1$ is*
 958 *measured in age-2 individuals and is defined as the otolith growth increment during age-1*
 959 *relative to the growth increment during age-0. Linear regression lines are drawn when the*
 960 *regression is significant.*

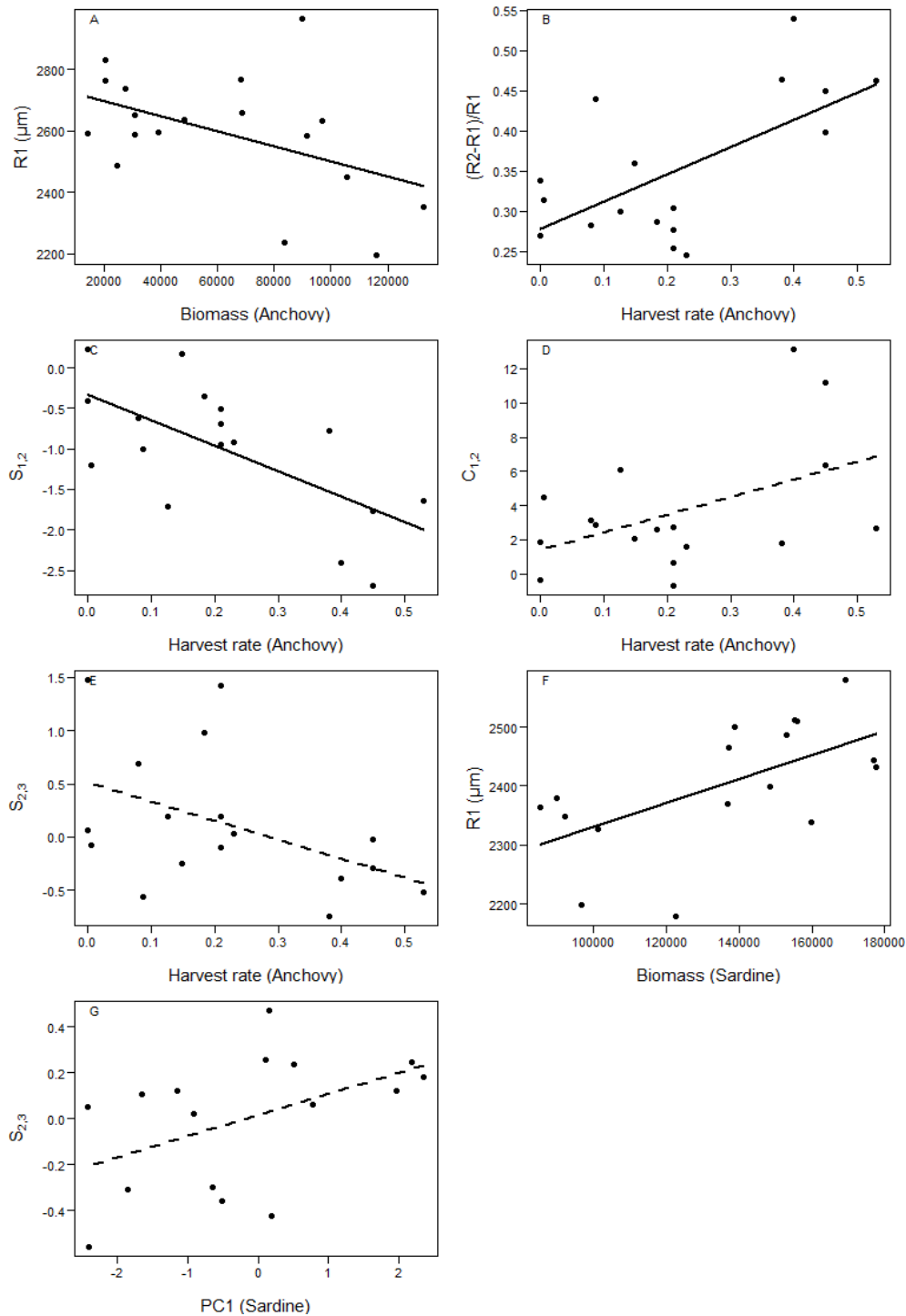


961
 962 *Figure 2: Temporal variations in directional linear selection in growth during age-0 (S_j , panels*
 963 *A and B) and catch-up growth during age-1 ($S_{2,3}$, panels C and D) for anchovy (A, C) and*
 964 *sardine (B, D). Horizontal dotted lines correspond to the absence of directional selection*
 965 *differentials. For R1, the gray lines represent the selection index computed on individuals aged*
 966 *1 and 2 within cohorts ($S_{1,2}$) while the black curve represents the cumulative index calculated*
 967 *for ages 1 to 3 (S_j). Linear regression lines are drawn when the regression is significant. The*
 968 *shaded grey areas denote the period of anchovy fishing ban.*



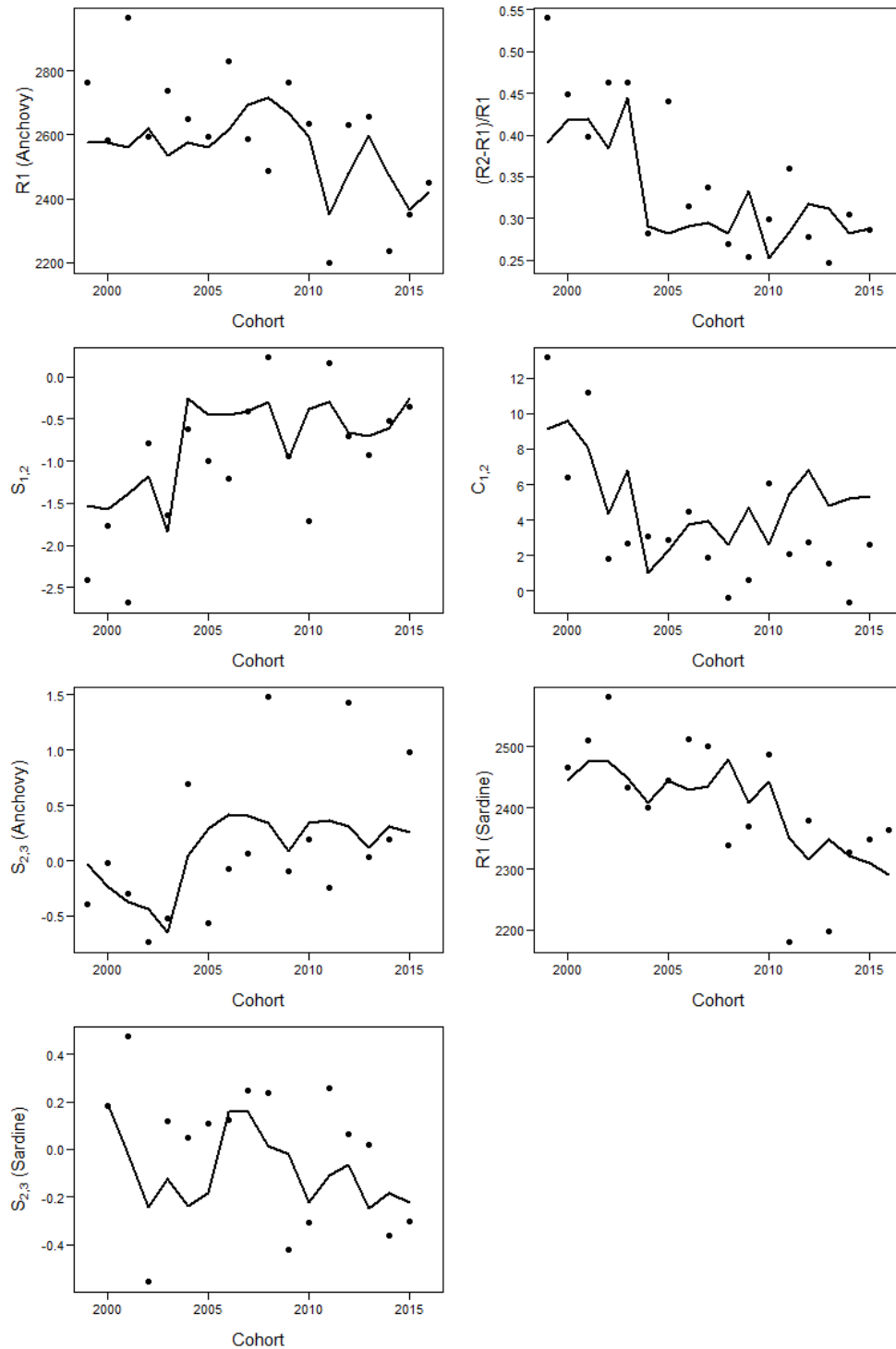
969

970 *Figure 3: Temporal variation in non-linear selection differential in age-0 growth (C_j ; panels A*
 971 *and B) and catch-up growth during age-1 ($C_{2,3}$; panels C and D) for anchovy (panels A and B)*
 972 *and sardine (panels B and D). Horizontal dotted lines correspond to the absence of non-linear*
 973 *selection differential. For R1, the selection differential index was calculated on individuals*
 974 *aged 1 and 2 within cohorts ($C_{1,2}$, gray line) and for ages 1 to 3 (C_j , black line). Linear*
 975 *regression lines are drawn when the regression is significant. The shaded grey areas denote*
 976 *the period of anchovy fishing ban.*



977
 978 *Figure 4: Effects of the most important explanatory variables on each of the growth (R_1 ;*
 979 *growth during age-0, $(R_2-R_1)/R_1$; catch-up growth during age-1) and selective mortality*
 980 *parameters ($S_{1,2}$; directional selective differentials between ages 1 and 2, $C_{1,2}$; non-linear*
 981 *selection differentials between ages 1 and 2, $S_{2,3}$; directional selective differentials between*

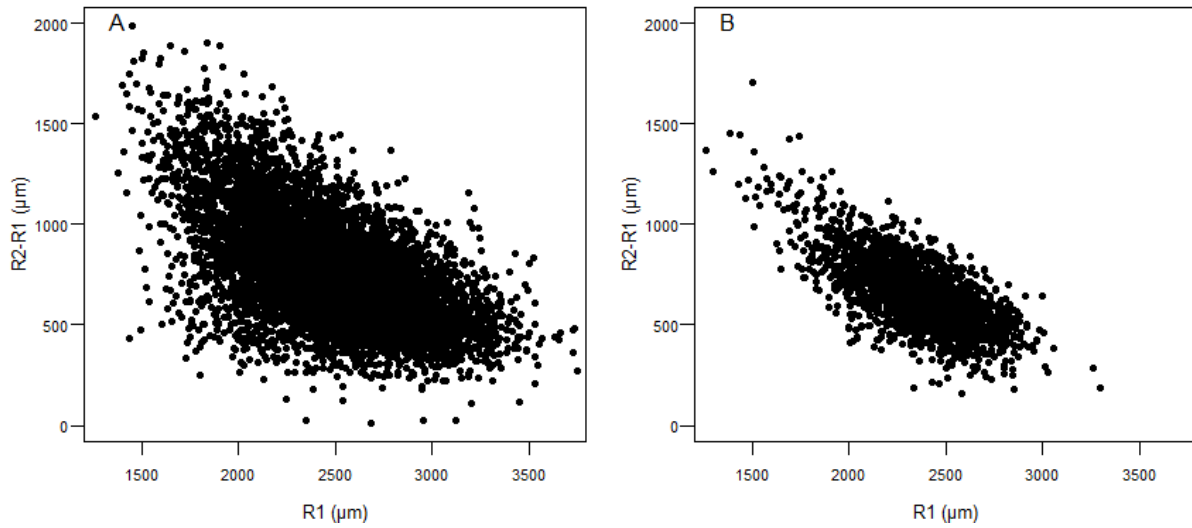
982 *ages 2 and 3). Solid linear regression lines are drawn when the averaged coefficients are*
 983 *significant*



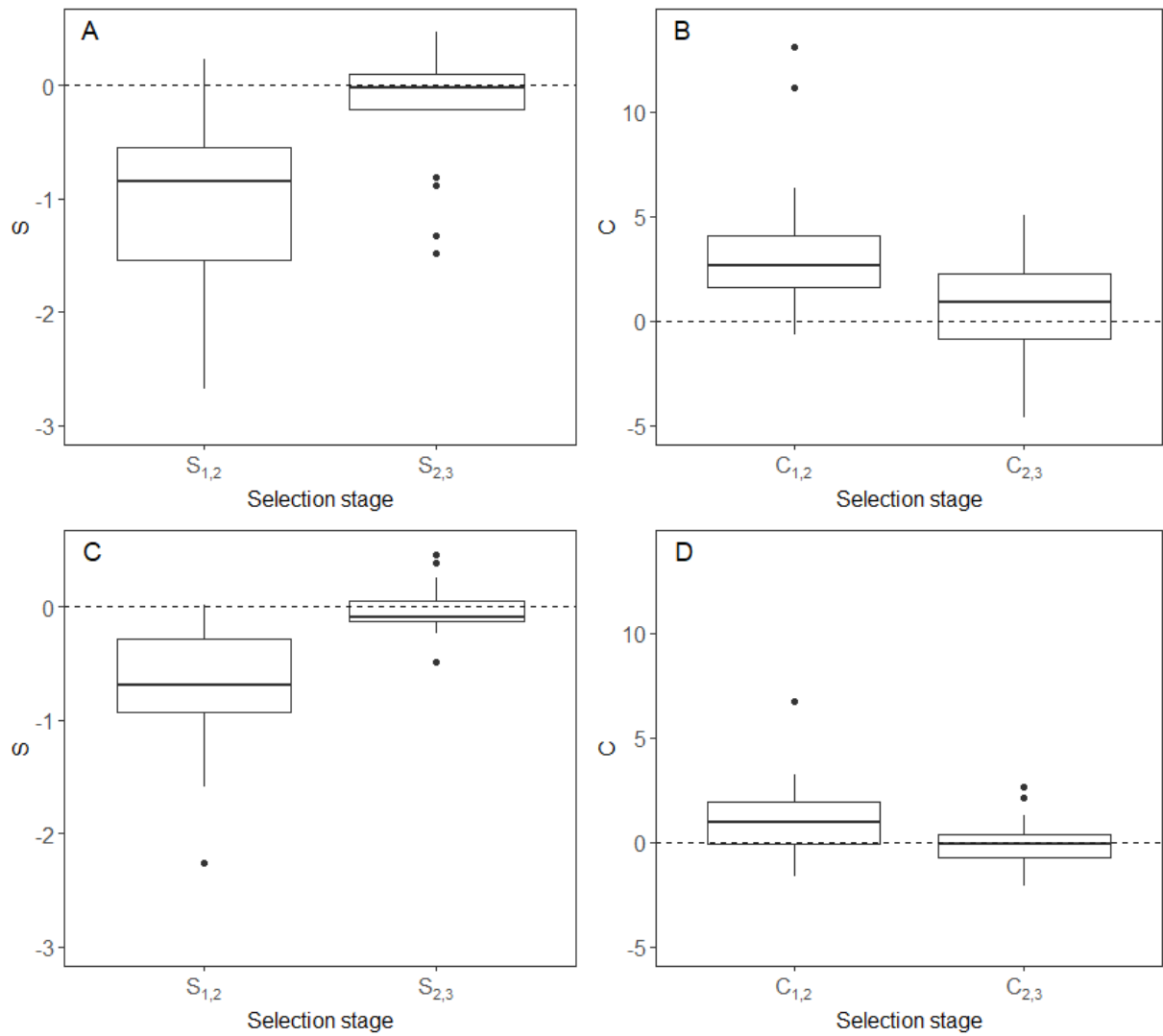
984
 985 *Figure 5: Modelled (lines) and observed (points) time series of growth (R_1 : growth during age-*
 986 *0, $(R_2-R_1)/R_1$: catch-up growth during age-1) and selective mortality indices ($S_{1,2}$: directional*

987 selective differentials between ages 1 and 2, $C_{1,2}$: non-linear selection differentials between
988 ages 1 and 2, $S_{2,3}$: directional selective differentials between ages 2 and 3) for sardine and
989 anchovy.

990 **Appendix**

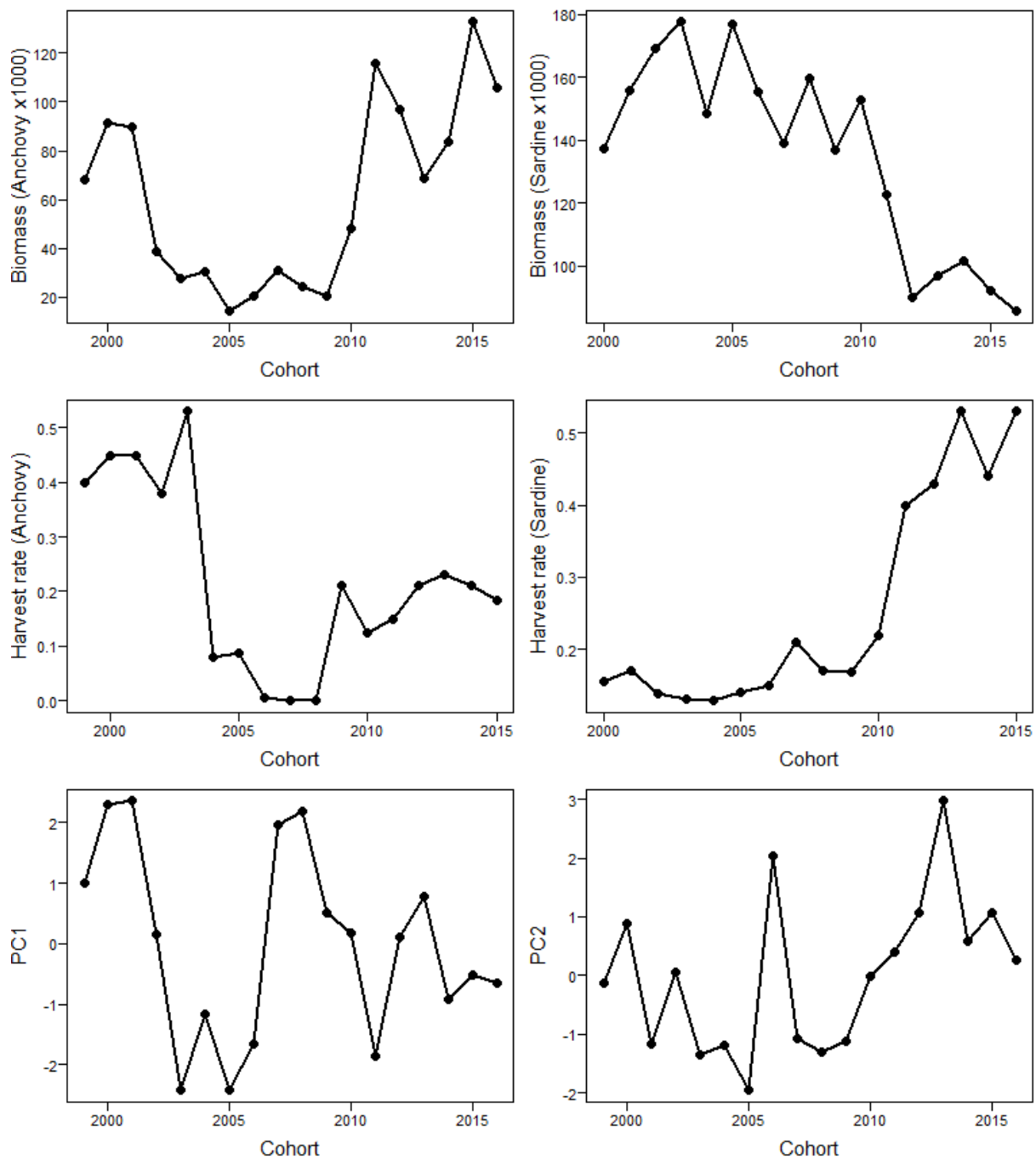


991
992 *Figure A1: Relationship between growth during age-0 (R_1) and age-1 ($R_2 - R_1$) for anchovy (A)*
993 *and sardine (B).*

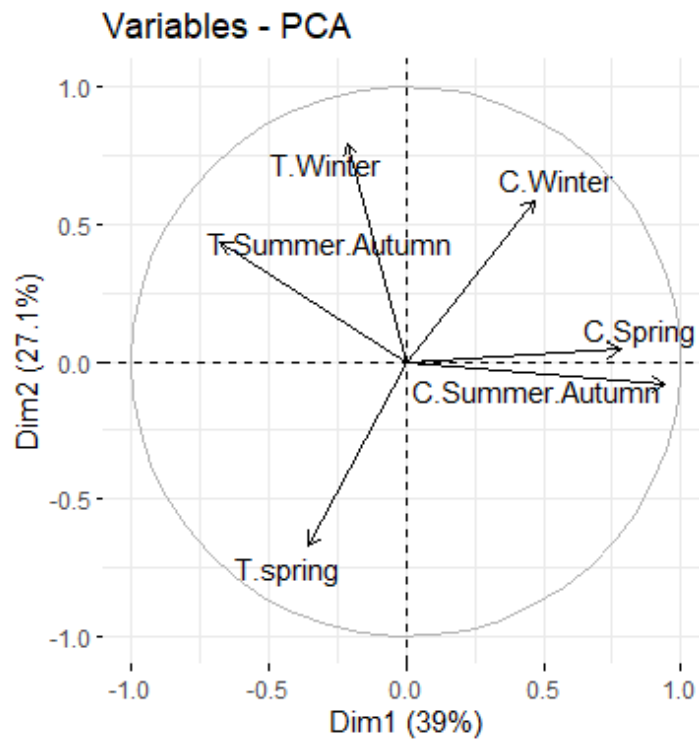


994

995 *Figure A2: Magnitude of selective mortality indices (S and C) acting on age-0 growth for*
 996 *anchovy (A and B) and sardine (C and D) measured on individuals aged 1 and 2, and 2 and 3.*



997
 998 *Figure A3: Time series of the explanatory indices considered for modelling the growth and*
 999 *mortality indices in anchovy and sardine. (PC1; the horizontal axis PC1, PC2; the vertical axis*
 1000 *PC2)*



1001

1002 *Figure A4: Principal Components Analysis on the environmental indices. Abbreviations C and T*
 1003 *correspond to surface chlorophyll-a and temperature*

1004

1005

1006 *Table A1: Average model statistics for anchovy growth during age-0 (R1) (Biom_N; biomass of*
 1007 *year n, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2710.38	101.91	25.42	0.00
Biom_N	-2.5e-03	1.2e-03	2.01	0.04
PC1	37.81	27.84	1.25	0.21
PC2	10.47	38.72	0.25	0.80

1008
 1009 *Table A2: Average model statistics for anchovy catch-up growth during age-1 ((R2-R1)/R1)*
 1010 *(Biom_N1; biomass of year n+1, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.28	0.03	8.09	0.00
Harvest.rate	0.34	0.11	2.94	0.00
Biom_N1	-4.9e-07	4.6e-07	0.97	0.33
PC1	0.01	0.01	0.68	0.50
PC2	-3.5e-03	0.01	0.23	0.82

1011
 1012 *Table A3: Average model statistics for anchovy directional linear selection ($S_{1,2}$) (Biom_N;*
 1013 *biomass of year n, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.38	0.28	1.23	0.22
Harvest.rate	-3.22	0.95	3.09	0.00
Biom_N	5e-06	4.4e-06	1.03	0.30
PC1	-0.09	0.1	0.82	0.41
PC2	-0.01	0.12	0.06	0.95

1014
 1015 *Table A4: Average model statistics for anchovy non-linear selection differentials ($C_{1,2}$)*
 1016 *(Biom_N; biomass of year n, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.09	1.65	1.20	0.23
Harvest.rate	10.34	5	1.90	0.06
PC1	0.78	0.53	1.37	0.17
PC2	0.21	0.65	0.29	0.77
Biom_N	1.3e-05	2.6e-05	0.48	0.63

1017
 1018 *Table A5: Average model statistics for anchovy catch-up growth directional linear selection*
 1019 *(S_{2,3}) (Biom_N1; biomass of year n+1, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.34	0.3	1.07	0.28
Harvest.rate	-1.79	0.9	1.82	0.07
Biom_N1	2.3e-06	4.2e-06	0.51	0.61
PC2	0.05	0.12	0.42	0.68
PC1	0.03	0.1	0.32	0.75

1020
 1021 *Table A6: Average model statistics for sardine growth during age-0 (R1) (Biom_N; biomass of*
 1022 *year n, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2121.79	102.83	18.93	0.00
Biom_N	2.1e-03	7.4e-04	2.56	0.01
PC1	14.94	13.9	0.98	0.33
PC2	4.54	21.77	0.19	0.85

1023
 1024 *Table A7: Average model statistics for sardine catch-up growth directional linear selection*
 1025 *(S_{2,3}) (Biom_N1; biomass of year n+1, PC1; the horizontal axis PC1, PC2; the vertical axis PC2)*

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.02	0.09	0.24	0.81
PC1	0.09	0.05	1.86	0.06
Harvest.rate	-0.35	0.48	0.66	0.51
PC2	-3.9e-03	0.05	0.07	0.95

1026