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## 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.

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## 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:  $-21.26 \pm 6.60$ , p-value < 0.01; sardine:  $-16.01 \pm 3.62$ , 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);  $-0.01 \pm 0.00$ , 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);  $0.00 \pm 0.01$ , 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:  $-1.18 \pm 0.16$ ; sardine:  $-0.75 \pm 0.13$ ; Figs. 2A and 2B). The  
348 magnitude of the directional selection differentials decreased with time in anchovy (linear  
349 regression ( $\beta \pm$  SE):  $0.06 \pm 0.03$ , 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):  $0.04 \pm 0.02$ , 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);  $0.07 \pm 0.03$ , 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);  $-0.01 \pm 0.02$ , 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:  $4.08 \pm 0.83$ ; sardine:  $1.10 \pm 0.42$ ; 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);  $-0.42 \pm 0.13$ , 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);  $-0.04 \pm 0.08$ , 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:  $0.04 \pm 0.04$ , p-value = 0.25; sardine:  $-0.01 \pm 0.01$ , 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  $\Delta$ 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  $\Delta\text{AICc}$  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  $\pm 0.001$ , 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:  $0.34 \pm 0.11$ , 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:  $-3.22 \pm 0.95$ , 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:  $10.34 \pm 5.00$ , 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:  $0.002 \pm 0.001$ , 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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611 **References**

- 612 Ainley, D. G., & Blight, L. K. (2009). Ecological repercussions of historical fish extraction  
613 from the Southern Ocean. *Fish and Fisheries*, 10(1), 13–38. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-2979.2008.00293.x)  
614 2979.2008.00293.x
- 615 Ali, M., Nicieza, A., & Wootton, R. J. (2003). Compensatory growth in fishes: A response to  
616 growth depression. *Fish and Fisheries*, 4(2), 147–190. [https://doi.org/10.1046/j.1467-](https://doi.org/10.1046/j.1467-2979.2003.00120.x)  
617 2979.2003.00120.x
- 618 Allain, G., Petitgas, P., Grellier, P., & Lazure, P. (2003). The selection process from larval to  
619 juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by  
620 Lagrangian simulations and comparative otolith growth. *Fisheries Oceanography*, 12(4-5),  
621 407–418. <https://doi.org/10.1046/j.1365-2419.2003.00245.x>
- 622 Allen, M., Kilpatrick, D., Armstrong, M., Briggs, R., Course, G., & Pérez, N. (2002). Multistage  
623 cluster sampling design and optimal sample sizes for estimation of fish discards from  
624 commercial trawlers. *Fisheries Research*, 55(1), 11–24. [https://doi.org/10.1016/S0165-](https://doi.org/10.1016/S0165-7836(01)00308-3)  
625 7836(01)00308-3
- 626 Allendorf, F. W., & Hard, J. J. (2009). Human-induced evolution caused by unnatural  
627 selection through harvest of wild animals. *Proceedings of the National Academy of Sciences*,  
628 106(Supplement\_1), 9987–9994. <https://doi.org/10.1073/pnas.0901069106>
- 629 Bacha, M., Moali, A., Benmansour, N.-E., Brylinski, J.-M., Mahe, K., & Amara, R. (2010).  
630 Relationships between age, growth, diet and environmental parameters for anchovy  
631 (*Engraulis encrasicolus* L.) in the Bay of Bénisaf (SW Mediterranean, west Algerian coast).  
632 *Cybium*, 34(1), 47–57. <https://archimer.ifremer.fr/doc/00011/12212/9046.pdf>
- 633 Barton, K. (2017). *MuMIn: Multi-Model Inference; 2017; R package version 1.40. 0.*
- 634 Baudron, A. R., Needle, C. L., & Marshall, C. T. (2011). Implications of a warming North Sea  
635 for the growth of haddock *Melanogrammus aeglefinus*. *Journal of Fish Biology*, 78(7), 1874–  
636 1889. <https://doi.org/10.1111/j.1095-8649.2011.02940.x>
- 637 Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming  
638 temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes.  
639 *Global Change Biology*, 20(4), 1023–1031. <https://doi.org/10.1111/gcb.12514>
- 640 Bertram, D., Chambers, R., & Leggett, W. (1993). Negative correlations between larval and  
641 juvenile growth rates in winter flounder: Implications of compensatory growth for  
642 variation in size-at-age. *Marine Ecology-Progress Series*, 96, 209–209. [https://www.int-](https://www.int-res.com/articles/meps/96/m096p209.pdf)  
643 res.com/articles/meps/96/m096p209.pdf
- 644 Canales, T. M., Delius, G. W., & Law, R. (2020). Regulation of fish stocks without stock-  
645 recruitment relationships: The case of small pelagic fish. *Fish and Fisheries*, 21(5), 857–871.  
646 <https://doi.org/10.1111/faf.12465>

- 647 Chavez, F. P., Ryan, J., Lluch-Cota, S. E., & Ñiquen, M. (2003). From anchovies to sardines and  
648 back: Multidecadal change in the Pacific Ocean. *Science*, 299(5604), 217–221.  
649 <https://doi.org/10.1126/science.1075880>
- 650 Conover, D. O., & Munch, S. B. (2002). Sustaining fisheries yields over evolutionary time  
651 scales. *Science*, 297(5578), 94–96. <https://doi.org/10.1126/science.1074085>
- 652 Costalago, D., Palomera, I., & Tirelli, V. (2014). Seasonal comparison of the diets of juvenile  
653 European anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* in the Gulf of  
654 Lions. *Journal of Sea Research*, 89, 64–72. <https://doi.org/10.1016/j.seares.2014.02.008>
- 655 Costalago, D., Garrido, S., & Palomera, I. (2015). Comparison of the feeding apparatus and  
656 diet of European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters:  
657 Ecological implications. *Journal of Fish Biology*, 86(4), 1348–1362.  
658 <https://doi.org/10.1111/jfb.12645>
- 659 Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in  
660 aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106(31), 12788–  
661 12793. <https://doi.org/10.1073/pnas.0902080106>
- 662 Dieckmann, U., & Heino, M. (2007). Probabilistic maturation reaction norms: Their history,  
663 strengths, and limitations. *Marine Ecology Progress Series*, 335, 253–269.  
664 <https://doi.org/10.3354/meps335253>
- 665 Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate?  
666 *Biological Reviews*, 86(1), 97–116. <https://doi.org/10.1111/j.1469-185X.2010.00136.x>
- 667 Domingos, J. A., Smith-Keune, C., Robinson, N., Loughnan, S., Harrison, P., & Jerry, D. R.  
668 (2013). Heritability of harvest growth traits and genotype–environment interactions in  
669 barramundi, Lates calcarifer (Bloch). *Aquaculture*, 402–403, 66–75.  
670 <https://doi.org/10.1016/j.aquaculture.2013.03.029>
- 671 Doray, M., Badts, V., Massé, J., Duhamel, E., Huret, M., Doremus, G., & Petitgas, P. (2014).  
672 *Manual of fisheries survey protocols. PELGAS surveys (PELagiques GAScogne)*. 26.  
673 <https://archimer.ifremer.fr/doc/00191/30259/28714.pdf>
- 674 Doray, M., Petitgas, P., Huret, M., Duhamel, E., Romagnan, J. B., Authier, M., Dupuy, C., & Spitz,  
675 J. (2018). Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators  
676 from an integrated survey. *Progress in Oceanography*, 166, 168–188.  
677 <https://doi.org/10.1016/j.pocean.2017.12.004>
- 678 Edeline, E., Carlson, S. M., Stige, L. C., Winfield, I. J., Fletcher, J. M., James, J. B., Haugen, T. O.,  
679 Vollestad, L. A., & Stenseth, N. C. (2007). Trait changes in a harvested population are driven  
680 by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National  
681 Academy of Sciences*, 104(40), 15799–15804. <https://doi.org/10.1073/pnas.0705908104>
- 682 Ernande, B., Dieckmann, U., & Heino, M. (2004). Adaptive changes in harvested populations:  
683 Plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society of*

684 *London. Series B: Biological Sciences*, 271(1537), 415–423.  
685 <https://doi.org/10.1098/rspb.2003.2519>

686 Escribano, A., Aldanondo, N., Cotano, U., Boyra, G., Urtizberea, A., (2019). Size- and density-  
687 dependent overwinter mortality of anchovy juveniles in the Bay of Biscay. *Continental Shelf*  
688 *Research*, 183: 28-37. <https://doi.org/10.1016/j.csr.2019.06.006>

689 Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., Siple,  
690 M. C., & Stawitz, C. C. (2015). Fishing amplifies forage fish population collapses. *Proceedings*  
691 *of the National Academy of Sciences*, 112(21), 6648–6652.  
692 <https://doi.org/10.1073/pnas.1422020112>

693 Fleming, I. A., & Gross, M. R. (1994). Breeding competition in a Pacific salmon (coho:  
694 *Oncorhynchus kisutch*): Measures of natural and sexual selection. *Evolution*, 48(3), 637–657.  
695 <https://doi.org/10.1111/j.1558-5646.1994.tb01350.x>

696 Forster, J., Hirst, A. G., & Woodward, G. (2011). Growth and development rates have  
697 different thermal responses. *The American Naturalist*, 178(5), 668–678.  
698 <https://doi.org/10.1086/662174>

699 Francis, R. I. C. C. (1990). Back-calculation of fish length: A critical review. *Journal of Fish*  
700 *Biology*, 36(6), 883–902. <https://doi.org/10.1111/j.1095-8649.1990.tb05636.x>

701 Garrido, S., Ben-Hamadou, R., Oliveira, P., Cunha, M., Chícharo, M., & Lingen, C. van der.  
702 (2008). Diet and feeding intensity of sardine *Sardina pilchardus*: Correlation with satellite-  
703 derived chlorophyll data. *Marine Ecology Progress Series*, 354, 245–256.  
704 <https://doi.org/10.3354/meps07201>

705 Garrido, S., Ben-Hamadou, R., Santos, A. M. P., Ferreira, S., Teodósio, M. A., Cotano, U.,  
706 Irigoien, X., Peck, M. A., Saiz, E., & Ré, P. (2015). Born small, die young: Intrinsic, size-  
707 selective mortality in marine larval fish. *Scientific Reports*, 5(1), 17065.  
708 <https://doi.org/10.1038/srep17065>

709 Gatti, P., Petitgas, P., & Huret, M. (2017). Comparing biological traits of anchovy and sardine  
710 in the Bay of Biscay: A modelling approach with the Dynamic Energy Budget. *Ecological*  
711 *Modelling*, 348, 93–109. <https://doi.org/10.1016/j.ecolmodel.2016.12.018>

712 Grossman, G. D., & Simon, T. N. (2020). Density-dependent effects on salmonid populations:  
713 A review. *Ecology of Freshwater Fish*, 29(3), 400–418. <https://doi.org/10.1111/eff.12523>

714 Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up  
715 growth in diverse taxa: Compensatory and catch-up growth. *Journal of Animal Ecology*,  
716 81(3), 583–593. <https://doi.org/10.1111/j.1365-2656.2011.01942.x>

717 Heino, M., & Dieckmann, U. (2008). Detecting fisheries-induced life-history evolution: an  
718 overview of the reaction-norm approach. *Bulletin of Marine Science*, 83(1), 69–93.  
719 <https://www.ingentaconnect.com/content/umrsmas/bullmar/2008/00000083/00000001>  
720 /art00005

721 Hendry, A. P., Bolnick, D. I., Berner, D., & Peichel, C. L. (2009). Along the speciation  
722 continuum in sticklebacks. *Journal of Fish Biology*, 75(8), 2000–2036.  
723 <https://doi.org/10.1111/j.1095-8649.2009.02419.x>

724 Hsieh, C.-h., Reiss, C. S., Hewitt, R. P., & Sugihara, G. (2008). Spatial analysis shows that  
725 fishing enhances the climatic sensitivity of marine fishes. *Canadian Journal of Fisheries and*  
726 *Aquatic Sciences*, 65(5), 947–961. <https://doi.org/10.1139/f08-017>

727 Huret, M., Lebigre, C., Iriondo, M., Montes, I., & Estonba, A. (2020). Genetic population  
728 structure of anchovy (*Engraulis encrasicolus*) in North-western Europe and variability in  
729 the seasonal distribution of the stocks. *Fisheries Research*, 229, 105619.  
730 <https://doi.org/10.1016/j.fishres.2020.105619>

731 ICES. 1990. Report of the Working Group on the assessment of the stocks of Sardine, Horse  
732 Mackerel, and Anchovy, 20–29 June 1990, Copenhagen, Denmark. ICES C.M.1990/Assess:24.  
733 169 pp.

734 ICES. 2006. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel,  
735 Sardine and Anchovy (WGMHSA), 5 - 14 September 2006, Galway, Ireland. ICES CM  
736 2006\ACFM:36. 601 pp.

737 ICES. 2009. Report of the Workshop on Age Reading of European Anchovy (WKARA), 9-13  
738 November 2009, Sicily, Italy. ICES CM 2009/ACOM:43. (International Council for the  
739 Exploration of the Sea (ICES): Copenhagen) .

740 ICES. 2010. Life-cycle spatial patterns of small pelagic fish in the Northeast Atlantic. ICES  
741 Cooperative Research Report, N° 306. <http://doi.org/10.17895/ices.pub.5408>

742 ICES. 2011. Report of the Workshop on Age Reading of European Atlantic Sardine  
743 (WKARAS) , 14-18 February 2011, Lisbon, Portugal. ICES CM 2011/ACOM:42. 91 pp.

744 ICES. 2017a. Report of the Workshop on Age estimation of European anchovy (*Engraulis*  
745 *encrasicolus*). WKARA2 2016 Report 28 November - 2 December 2016. Pasaia, Spain. ICES  
746 CM 2016/SSGIEOM:17. 223 pp.

747 ICES. 2017b. Report of the Working Group on Southern Horse Mackerel, Anchovy and  
748 Sardine (WGHANSA), 24–29 June 2017, Bilbao, Spain. ICES CM 2017/ACOM:17. 640 pp.

749 ICES. 2018. Report of the Working Group on Southern Horse Mackerel, Anchovy and  
750 Sardine (WGHANSA), 26–30 June 2018, Lisbon, Portugal. ICES CM 2018/ACOM:17. 659 pp.

751 ICES. 2019. Working Group on Southern Horse Mackerel, Anchovy and Sardine  
752 (WGHANSA). ICES Scientific Reports. 1:34. 441 pp. <http://doi.org/10.17895/ices.pub.4983>

753 Johnson, D., Grorud-Colvert, K., Rankin, T., & Sponaugle, S. (2012). Measuring selective  
754 mortality from otoliths and similar structures: a practical guide for describing multivariate  
755 selection from cross-sectional data. *Marine Ecology Progress Series*, 471, 151–163.  
756 <https://doi.org/10.3354/meps10028>

- 757 Johnson, D. W., Grorud-Colvert, K., Sponaugle, S., & Semmens, B. X. (2014). Phenotypic  
758 variation and selective mortality as major drivers of recruitment variability in fishes.  
759 *Ecology Letters*, 17(6), 743–755. <https://doi.org/10.1111/ele.12273>
- 760 Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B.,  
761 Gardmark, A. G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A.,  
762 Dieckmann, U., Heino, M., & Rijnsdorp, A. D. (2007). Ecology: Managing evolving fish stocks.  
763 *Science*, 318(5854), 1247–1248. <https://doi.org/10.1126/science.1148089>
- 764 Jørgensen, T. (1990). Long-term changes in age at sexual maturity of Northeast Arctic cod  
765 (*Gadus morhua* L.). *ICES Journal of Marine Science*, 46(3), 235–248.  
766 <https://doi.org/10.1093/icesjms/46.3.235>
- 767 Kaeuffer, R., Peichel, C. L., Bolnick, D. I., & Hendry, A. P. (2012). Parallel and nonparallel  
768 aspects of ecological, phenotypic, and genetic divergence across replicate population pairs  
769 of lake and stream stickleback. *Evolution: International Journal of Organic Evolution*, 66(2),  
770 402–418. <https://doi.org/10.1111/j.1558-5646.2011.01440.x>
- 771 Kenchington, T. J. (2014). Natural mortality estimators for information-limited fisheries.  
772 *Fish and Fisheries*, 15(4), 533–562. <https://doi.org/10.1111/faf.12027>
- 773 Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang,  
774 A., Gibert, P., & Beerli, P. (2001). The strength of phenotypic selection in natural  
775 populations. *The American Naturalist*, 157(3), 245–261. <https://doi.org/10.1086/319193>
- 776 Kissner, K. J., & Weatherhead, P. J. (2005). Phenotypic effects on survival of neonatal  
777 northern watersnakes *Nerodia sipedon*. *Journal of Animal Ecology*, 74(2), 259–265.  
778 <http://www.jstor.org/stable/3505614>
- 779 Korte, S. M., Koolhaas, J. M., Wingfield, J. C., & McEwen, B. S. (2005). The darwinian concept  
780 of stress: Benefits of allostasis and costs of allostatic load and the trade-offs in health and  
781 disease. *Neuroscience & Biobehavioral Reviews*, 29(1), 3–38.  
782 <https://doi.org/10.1016/j.neubiorev.2004.08.009>
- 783 Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries-induced evolution.  
784 *Trends in Ecology & Evolution*, 22(12), 652–659.  
785 <https://doi.org/10.1016/j.tree.2007.08.011>
- 786 Laugen, A. T., Engelhard, G. H., Whitlock, R., Arlinghaus, R., Dankel, D. J., Dunlop, E. S.,  
787 Eikeset, A. M., Enberg, K., Jørgensen, C., Matsumura, S., Nusslé, S., Urbach, D., Baulier, L.,  
788 Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F., Pardoe, H., Therkildsen, N. O., ...  
789 Dieckmann, U. (2014). Evolutionary impact assessment: Accounting for evolutionary  
790 consequences of fishing in an ecosystem approach to fisheries management. *Fish and*  
791 *Fisheries*, 15(1), 65–96. <https://doi.org/10.1111/faf.12007>
- 792 Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*,  
793 57(3), 659–668. <https://doi.org/10.1006/jmsc.2000.0731>

- 794 Law, R. (2007). Fisheries-induced evolution: Present status and future directions. *Marine*  
795 *Ecology Progress Series*, 335, 271–277. <https://doi.org/10.3354/meps335271>
- 796 Lee, R. M. (1912). An investigation into the methods of growth determination in fishes by  
797 means of scales. *ICES Journal of Marine Science*, 1(63), 3–34.  
798 <https://doi.org/10.1093/icesjms/s1.63.3>
- 799 Lorenzen, K. (1996). The relationship between body weight and natural mortality in  
800 juvenile and adult fish: A comparison of natural ecosystems and aquaculture. *Journal of Fish*  
801 *Biology*, 49(4), 627–642. <https://doi.org/10.1111/j.1095-8649.1996.tb00060.x>
- 802 MacCall, A. D. (1990). *Dynamic geography of marine fish populations*. Seattle, WA:  
803 Washington Sea Grant Program.
- 804 Machias, A., Vassilopoulou, V., Vatsos, D., Bekas, P., Kallianiotis, A., Papaconstantinou, C., &  
805 Tsimenides, N. (2001). Bottom trawl discards in the northeastern Mediterranean Sea.  
806 *Fisheries Research*, 53(2), 181–195. [https://doi.org/10.1016/S0165-7836\(00\)00298-8](https://doi.org/10.1016/S0165-7836(00)00298-8)
- 807 Mahé, K., Bellail, R., Dufour, J. L., Boiron-Leroy, A., Duhamel, E., Elleboode, R., Félix, J.,  
808 Grellier, P., Huet, J., Labastie, J., Roy, D. L., Lizaud, O., Line, M., Martin, S., Metral, L., Nédelec,  
809 D., & Vérin, Y. (2009). *Système d'Informations Halieutiques Action Paramètres Biologiques*.  
810 78.
- 811 Matsumura, S., Arlinghaus, R., & Dieckmann, U. (2011). Assessing evolutionary  
812 consequences of size-selective recreational fishing on multiple life-history traits, with an  
813 application to northern pike (*esox lucius*). *Evolutionary Ecology*, 25(3), 711–735.  
814 <https://doi.org/10.1007/s10682-010-9444-8>
- 815 McEwen, B. S., & Wingfield, J. C. (2003). The concept of allostasis in biology and  
816 biomedicine. *Hormones and Behavior*, 43(1), 2–15. [https://doi.org/10.1016/S0018-](https://doi.org/10.1016/S0018-506X(02)00024-7)  
817 [506X\(02\)00024-7](https://doi.org/10.1016/S0018-506X(02)00024-7)
- 818 Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later?  
819 *Trends in Ecology & Evolution*, 16(5), 254–260. [https://doi.org/10.1016/S0169-](https://doi.org/10.1016/S0169-5347(01)02124-3)  
820 [5347\(01\)02124-3](https://doi.org/10.1016/S0169-5347(01)02124-3)
- 821 Metcalfe, N., & Monaghan, P. (2003). Growth versus lifespan: Perspectives from  
822 evolutionary ecology. *Experimental Gerontology*, 38(9), 935–940.  
823 [https://doi.org/10.1016/S0531-5565\(03\)00159-1](https://doi.org/10.1016/S0531-5565(03)00159-1)
- 824 Metcalfe, N. B., & Alonso-Alvarez, C. (2010). Oxidative stress as a life-history constraint: The  
825 role of reactive oxygen species in shaping phenotypes from conception to death. *Functional*  
826 *Ecology*, 24(5), 984–996. <https://doi.org/10.1111/j.1365-2435.2010.01750.x>
- 827 Motos, L. (1996). Reproductive biology and fecundity of the Bay of Biscay anchovy  
828 population (*Engraulis encrasicolus L.*). *Scientia Marina*, 60, 195–207.  
829 <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.470.5338&rep=rep1&type=pdf>

- 830 Nikolioudakis, N., Palomera, I., Machias, A., & Somarakis, S. (2011). Diel feeding intensity  
831 and daily ration of the sardine *Sardina pilchardus*. *Marine Ecology Progress Series*, 437, 215–  
832 228. <https://doi.org/10.3354/meps09275>
- 833 Nikolioudakis, N., Isari, S., Pitta, P., & Somarakis, S. (2012). Diet of sardine *Sardina*  
834 *pilchardus*: An ‘end-to-end’ field study. *Marine Ecology Progress Series*, 453, 173–188.  
835 <https://doi.org/10.3354/meps09656>
- 836 Nikolioudakis, N., Isari, S., & Somarakis, S. (2014). Trophodynamics of anchovy in a non-  
837 upwelling system: Direct comparison with sardine. *Marine Ecology Progress Series*, 500,  
838 215–229. <https://doi.org/10.3354/meps10604>
- 839 Nusslé, S., Bornand, C. N., & Wedekind, C. (2009). Fishery-induced selection on an alpine  
840 whitefish: quantifying genetic and environmental effects on individual growth rate.  
841 *Evolutionary Applications*, 2(2), 200–208. [https://doi.org/10.1111/j.1752-](https://doi.org/10.1111/j.1752-4571.2008.00054.x)  
842 [4571.2008.00054.x](https://doi.org/10.1111/j.1752-4571.2008.00054.x)
- 843 Ogle, D. H., Wheeler, P., & Dinno, A. (2020). *FSA: Fisheries Stock Analysis*. R package version  
844 0.8. 30.9000. <https://github.com/droglenc/FSA>
- 845 Ohlberger, J. (2013). Climate warming and ectotherm body size - from individual physiology  
846 to community ecology. *Functional Ecology*, 27(4), 991–1001.  
847 <https://doi.org/10.1111/1365-2435.12098>
- 848 Oliveira, R. F., Taborsky, M., & Brockmann, H. J. (2008). *Alternative reproductive tactics: an*  
849 *integrative approach*. Cambridge University Press.
- 850 Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., & Dieckmann, U.  
851 (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern  
852 cod. *Nature*, 428(6986), 932–935. <https://doi.org/10.1038/nature02430>
- 853 Perez, K. O., & Munch, S. B. (2010). Extreme selection on size in the early lives of fish.  
854 *Evolution*, 64(8), 2450–2457. <https://doi.org/10.1111/j.1558-5646.2010.00994.x>
- 855 Petitgas, P., Doray, M., Huret, M., Massé, J., & Woillez, M. (2014). Modelling the variability in  
856 fish spatial distributions over time with empirical orthogonal functions: anchovy in the Bay  
857 of Biscay. *ICES Journal of Marine Science*, 71(9), 2379–2389.  
858 <https://doi.org/10.1093/icesjms/fsu111>
- 859 Petitgas, P., Grellier, P., Duhamel, E., Masse, J., & Doray, M. (2012, January). Variability and  
860 controls of otolith growth in the anchovy of the Bay of Biscay. *ICES Annual Science*  
861 *Conference*. <https://archimer.ifremer.fr/doc/00114/22550/20236.pdf>
- 862 Petitgas, P., Huret, M., Dupuy, C., Spitz, J., Authier, M., Romagnan, J. B., & Doray, M. (2018).  
863 Ecosystem spatial structure revealed by integrated survey data. *Progress in Oceanography*,  
864 166, 189–198. <https://doi.org/10.1016/j.pocean.2017.09.012>
- 865 Petitgas, P., Massé, J., Beillois, P., Lebarbier, E., & Le Cann, A. (2003). Sampling variance of  
866 species identification in fisheries-acoustic surveys based on automated procedures

867 associating acoustic images and trawl hauls. *ICES Journal of Marine Science*, 60(3), 437–445.  
868 [https://doi.org/10.1016/S1054-3139\(03\)00026-2](https://doi.org/10.1016/S1054-3139(03)00026-2)

869 Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K.,  
870 Drinkwater, K., Huret, M., & Nash, R. D. M. (2013). Impacts of climate change on the complex  
871 life cycles of fish. *Fisheries Oceanography*, 22(2), 121–139.  
872 <https://doi.org/10.1111/fog.12010>

873 Petitgas, P., Secor, D. H., McQuinn, I., Huse, G., & Lo, N. (2010). Stock collapses and their  
874 recovery: Mechanisms that establish and maintain life-cycle closure in space and time. *ICES*  
875 *Journal of Marine Science*, 67(9), 1841–1848. <https://doi.org/10.1093/icesjms/fsq082>

876 Post, J. R., Parkinson, E., & Johnston, N. (1999). Density-Dependent processes in structured  
877 fish populations: Interaction strengths in whole-Lake experiments. *Ecological Monographs*,  
878 69(2), 155–175. [https://doi.org/10.1890/0012-9615\(1999\)069\[0155:DDPISF\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0155:DDPISF]2.0.CO;2)

879 R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna,  
880 Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>

881 Romero, L. M., Dickens, M. J., & Cyr, N. E. (2009). The reactive scope model — a new model  
882 integrating homeostasis, allostasis, and stress. *Hormones and Behavior*, 55(3), 375–389.  
883 <https://doi.org/10.1016/j.yhbeh.2008.12.009>

884 Saraux, C., Van Beveren, E., Brosset, P., Queiros, Q., Bourdeix, J.-H., Dutto, G., Gasset, E., Jac, C.,  
885 Bonhommeau, S., & Fromentin, J.-M. (2019). Small pelagic fish dynamics: A review of  
886 mechanisms in the Gulf of Lions. *Deep Sea Research Part II: Topical Studies in Oceanography*,  
887 159, 52–61. <https://doi.org/10.1016/j.dsr2.2018.02.010>

888 Siepielski, A. M., DiBattista, J. D., & Carlson, S. M. (2009). It's about time: The temporal  
889 dynamics of phenotypic selection in the wild. *Ecology Letters*, 12(11), 1261–1276.  
890 <https://doi.org/10.1111/j.1461-0248.2009.01381.x>

891 Smith, A. D., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-  
892 Montes, H., Mackinson, S., Marzloff, M., Shannon, L. J., & others. (2011). Impacts of fishing  
893 low-trophic level species on marine ecosystems. *Science*, 333(6046), 1147–1150.  
894 <https://doi.org/10.1126/science.1209395>

895 Stratoudakis, Y., Coombs, S., Lanzós, A. L. de, Halliday, N., Costas, G., Caneco, B., Franco, C.,  
896 Conway, D., Santos, M. B., Silva, A., & others. (2007). Sardine (*Sardina pilchardus*) spawning  
897 seasonality in European waters of the northeast Atlantic. *Marine Biology*, 152(1), 201–212.  
898 <https://doi.org/10.1007/s00227-007-0674-4>

899 Swain, D. P., Sinclair, A. F., & Mark Hanson, J. (2007). Evolutionary response to size-selective  
900 mortality in an exploited fish population. *Proceedings of the Royal Society B: Biological*  
901 *Sciences*, 274(1613), 1015–1022. <https://doi.org/10.1098/rspb.2006.0275>

902 Taylor, I. G., & Methot, R. D. (2013). Hiding or dead? A computationally efficient model of  
903 selective fisheries mortality. *Fisheries Research*, 142, 75–85.  
904 <https://doi.org/10.1016/j.fishres.2012.08.021>

- 905 Uriarte, A., Rico, I., Villamor, B., Duhamel, E., Dueñas, C., Aldanondo, N., Cotano, U., 2016a.  
906 Validation of age determination using otoliths of the European anchovy (*Engraulis*  
907 *encrasicolus* L.) in the Bay of Biscay. *Marine and Freshwater Research*, 67, 951-966.  
908 <https://dx.doi.org/10.1071/MF15092>
- 909 Uriarte, A., Ibaibarriaga, L., Pawlowski, L., Massé, J., Petitgas, P., Santos, M., & Skagen, D.  
910 (2016b). Assessing natural mortality of Bay of Biscay anchovy from survey population and  
911 biomass estimates. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(2), 216–234.  
912 <https://dx.doi.org/10.1139/cjfas-2015-0096>
- 913 Van Beveren, E., Bonhommeau, S., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Brosset, P.,  
914 Roos, D., & Sarau, C. (2014). Rapid changes in growth, condition, size and age of small  
915 pelagic fish in the Mediterranean. *Marine Biology*, 161(8), 1809–1822.  
916 <https://doi.org/10.1007/s00227-014-2463-1>
- 917 van de Pol, M., & Verhulst, S. (2006). Age-dependent traits: A new statistical model to  
918 separate within-and between-individual effects. *The American Naturalist*, 167(5), 766–773.  
919 <https://doi.org/10.1086/503331>
- 920 Vandeputte, M., Kocour, M., Mauger, S., Dupont-Nivet, M., De Guerry, D., Rodina, M., Gela, D.,  
921 Vallod, D., Chevassus, B., & Linhart, O. (2004). Heritability estimates for growth-related  
922 traits using microsatellite parentage assignment in juvenile common carp (*Cyprinus carpio*  
923 *L.*). *Aquaculture*, 235(1), 223–236. <https://doi.org/10.1016/j.aquaculture.2003.12.019>
- 924 Véron, M., Duhamel, E., Bertignac, M., Pawlowski, L., & Huret, M. (2020). Major changes in  
925 sardine growth and body condition in the Bay of Biscay between 2003 and 2016: temporal  
926 trends and drivers. *Progress in Oceanography*, 182, 102274.  
927 <https://doi.org/10.1016/j.pocean.2020.102274>
- 928 Whitney, R. R., & Carlander, K. D. (1956). Interpretation of body-scale regression for  
929 computing body length of fish. *The Journal of Wildlife Management*, 20(1), 21–27.  
930 <https://doi.org/10.2307/3797243>
- 931 Wingfield, J. C. (2002). Endocrine responses to unpredictable environmental events: Stress  
932 or anti-stress hormones? *Integrative and Comparative Biology*, 42(3), 600–609.  
933 <https://doi.org/10.1093/icb/42.3.600>
- 934 Wright, H. A., Wootton, R. J., & Barber, I. (2007). Compensatory growth in threespine  
935 sticklebacks (*Gasterosteus aculeatus*) inhibited by experimental *Schistocephalus* infections.  
936 *Canadian Journal of Fisheries and Aquatic Sciences*, 64(5), 819–826.  
937 <https://doi.org/10.1139/f07-056>

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
$\beta$	Slope of linear regression
SE	Standard Error

939

940

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

943

944

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.*

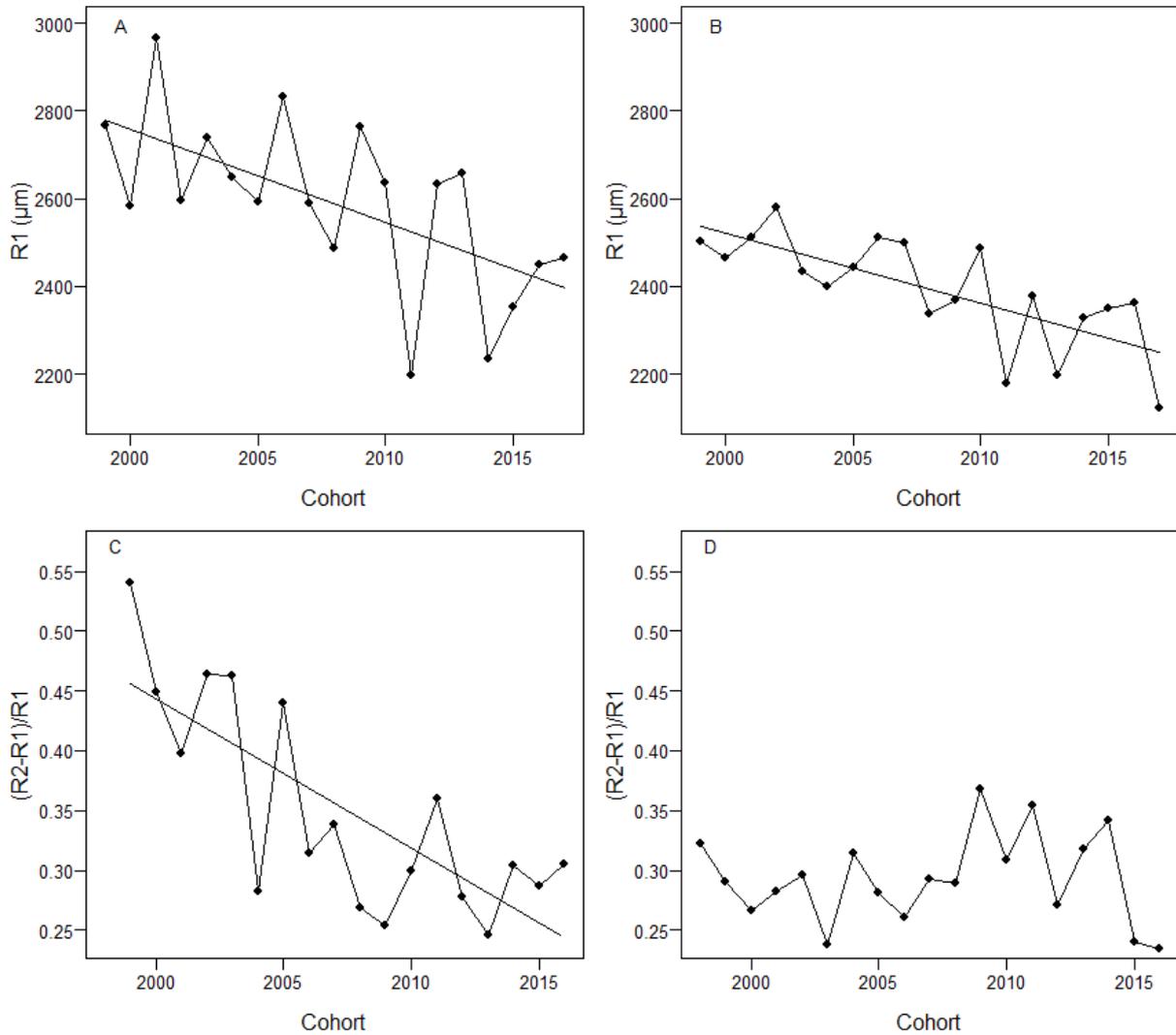
	Dependent variable	Model	logLik	AICc	$\Delta AICc$	$W_i$	Cum. $W_i$
a)	Growth during age-0 ( $R_1$ )	Biom_N	-117.92	243.55	0.00	0.41	0.41
		Biom_N + PC1	-116.72	244.51	0.96	0.25	0.66
		Intercept	-120.18	245.15	1.60	0.18	0.84
		PC1	-119.52	246.75	3.20	0.08	0.92
		Biom_N + PC2	-117.87	246.82	3.28	0.08	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.*

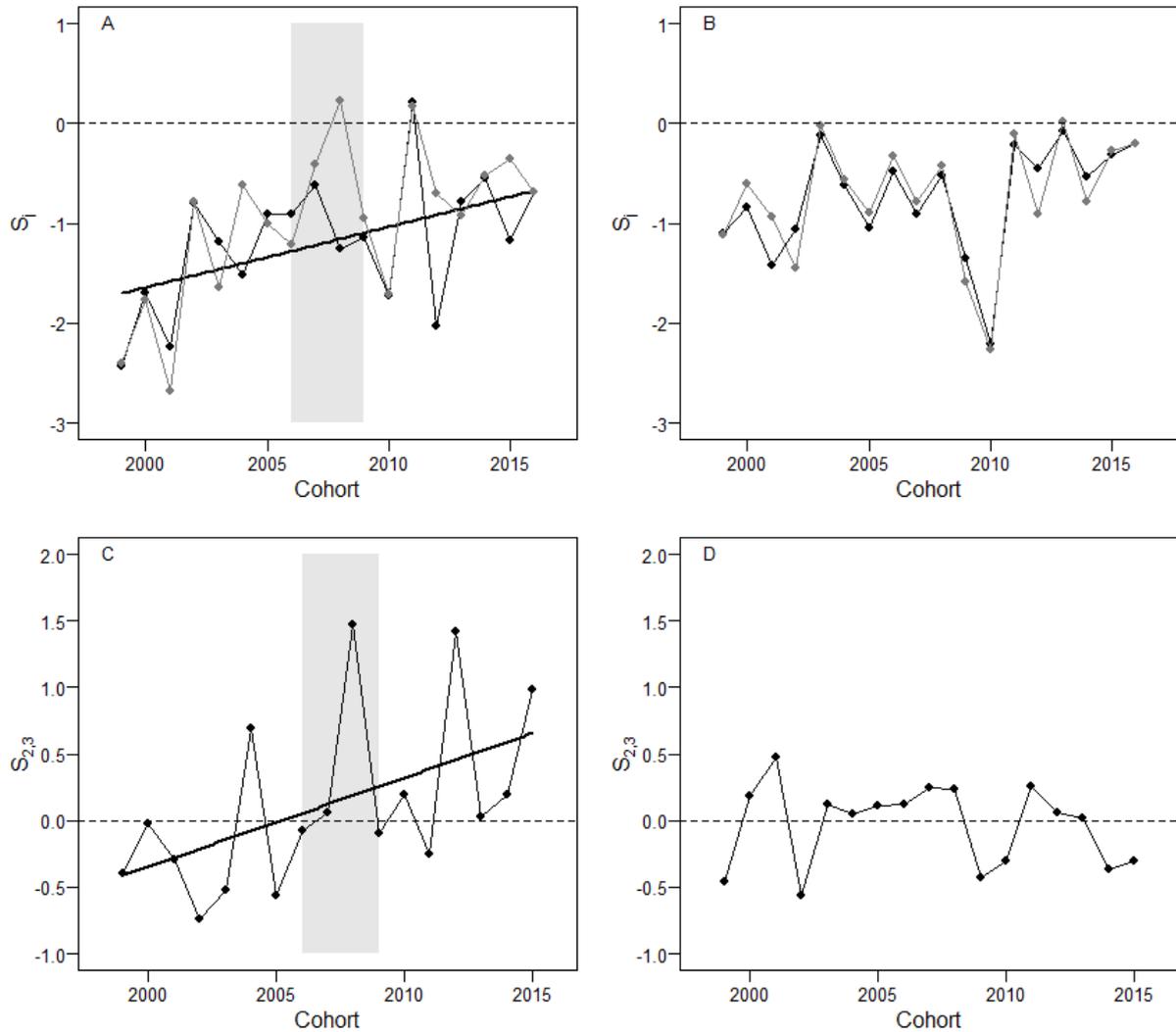
	Dependent variable	Model	logLik	AICc	$\Delta AICc$	$W_i$	Cum. $W_i$
a)	Growth during age-0 ( $R_1$ )	Biom_N	-99.44	206.72	0.00	0.66	0.66
		Biom_N + PC1	-98.76	208.86	2.14	0.23	0.89
		Biom_N + PC2	-99.41	210.15	3.43	0.12	1.01
b)	catch-up growth during age-1 ( $R_2-R_1$ )/ $R_1$	Intercept	30.21	-55.50	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

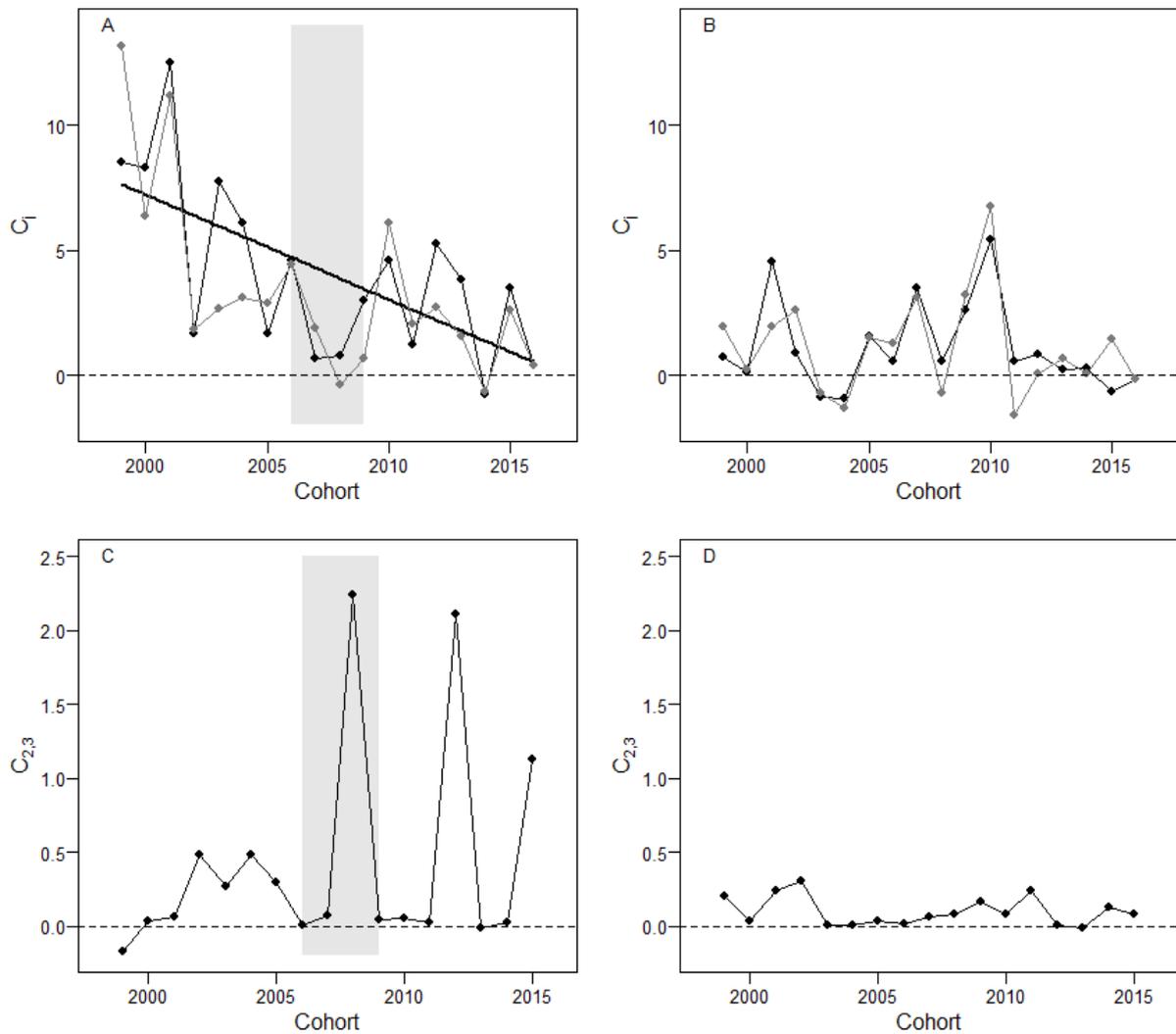


954

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.*

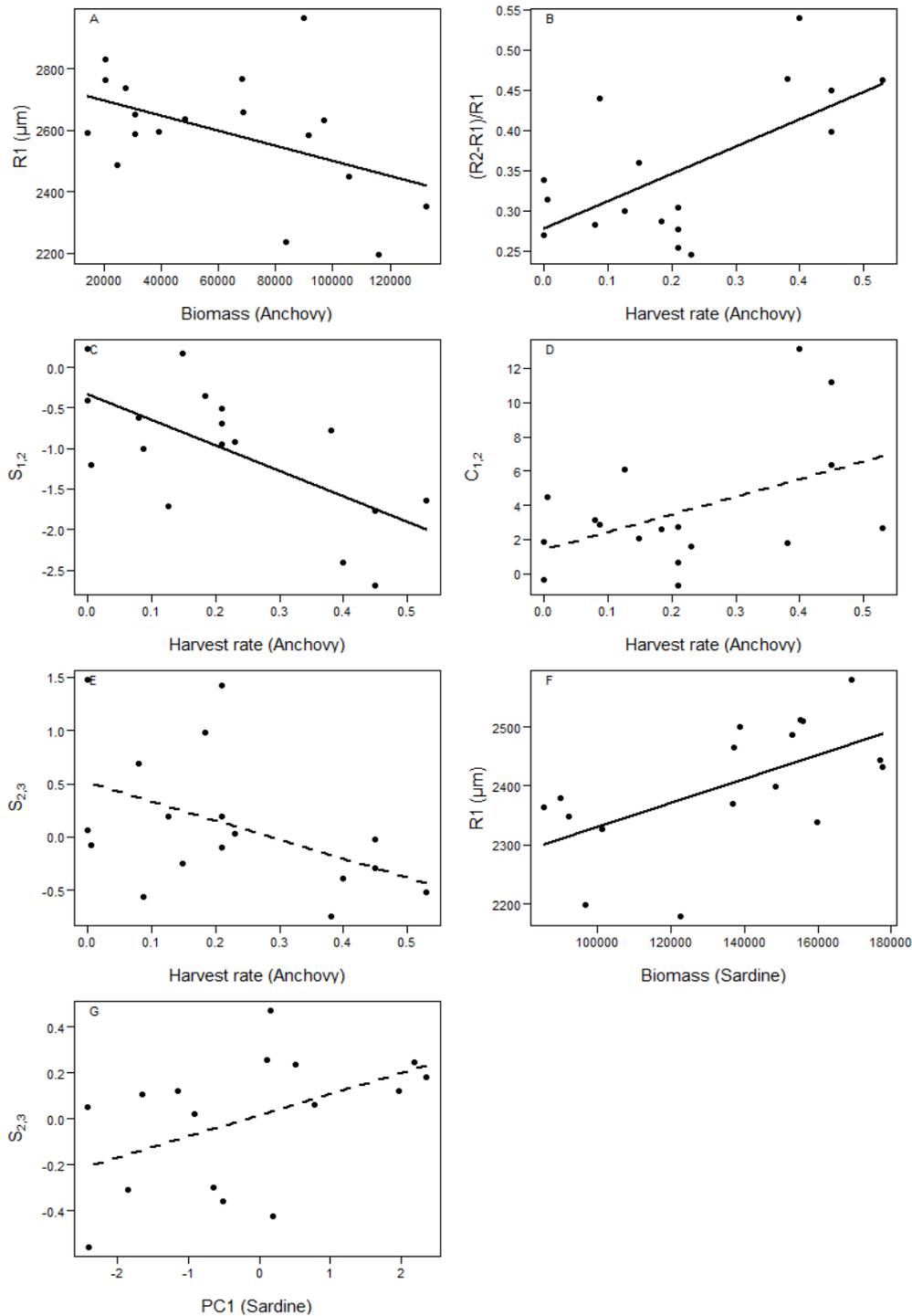


961  
 962 *Figure 2: Temporal variations in directional linear selection in growth during age-0 ( $S_j$ , panels*  
 963 *A and B) and catch-up growth during age-1 ( $S_{2,3}$ , panels C and D) for anchovy (A, C) and*  
 964 *sardine (B, D). Horizontal dotted lines correspond to the absence of directional 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.*



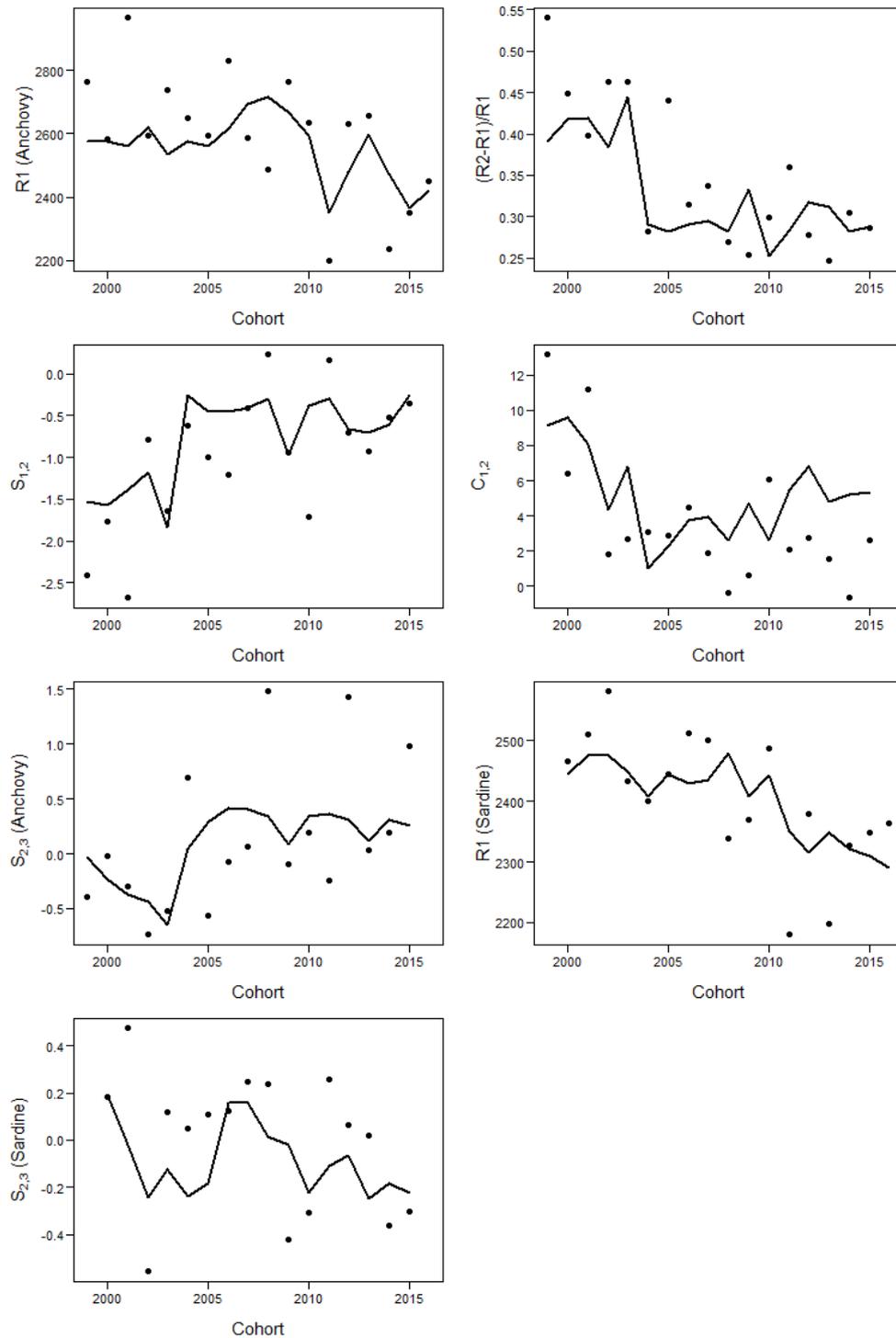
969

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*

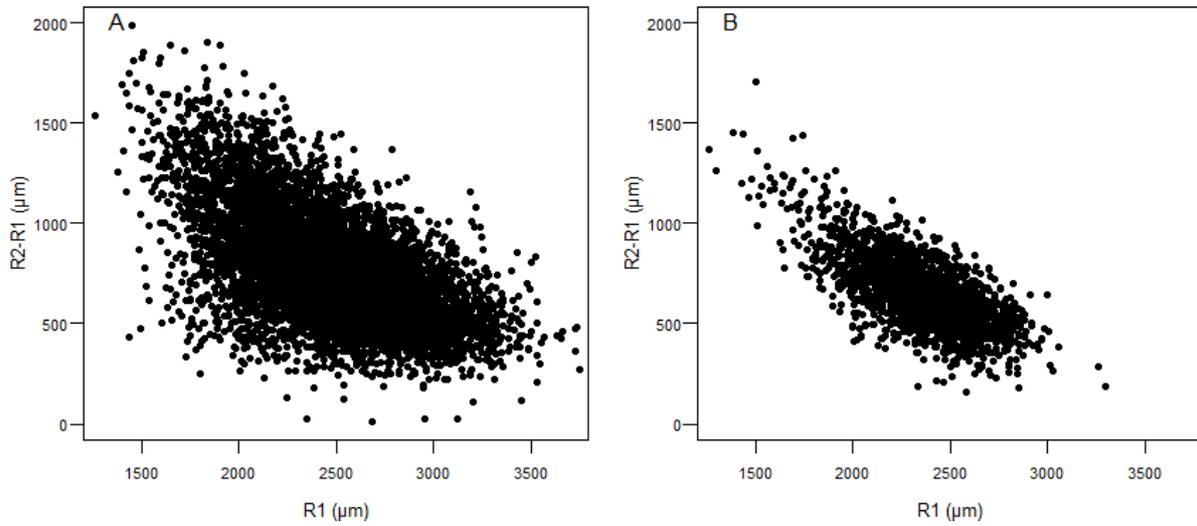


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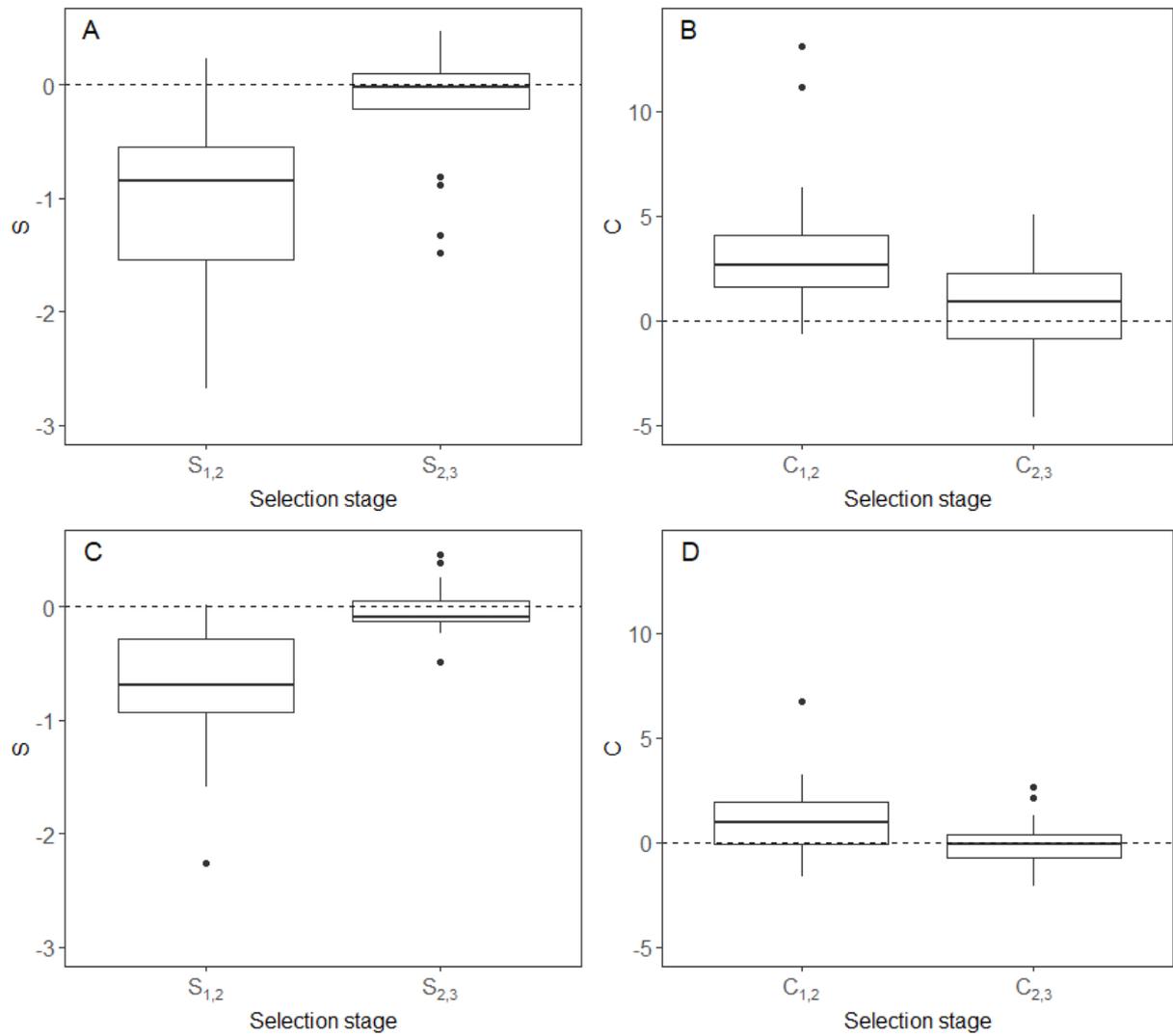
985 *Figure 5: Modelled (lines) and observed (points) time series of growth ( $R_1$ : growth during age-*  
 986 *0,  $(R_2-R_1)/R_1$ : catch-up growth during age-1) and selective mortality indices ( $S_{1,2}$ : directional*

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**

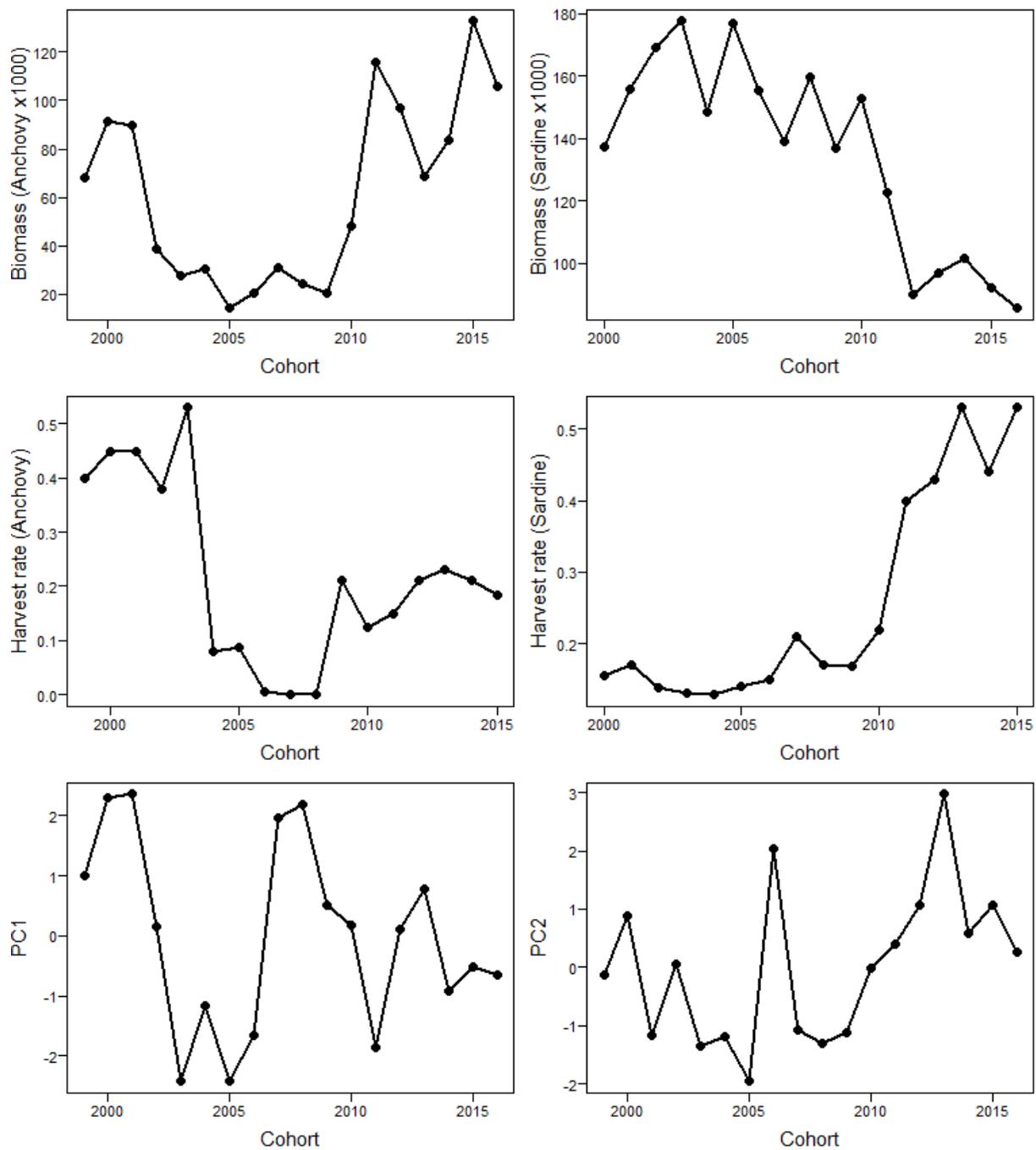


991  
992 *Figure A1: Relationship between growth during age-0 ( $R_1$ ) and age-1 ( $R_2 - R_1$ ) for anchovy (A)*  
993 *and sardine (B).*



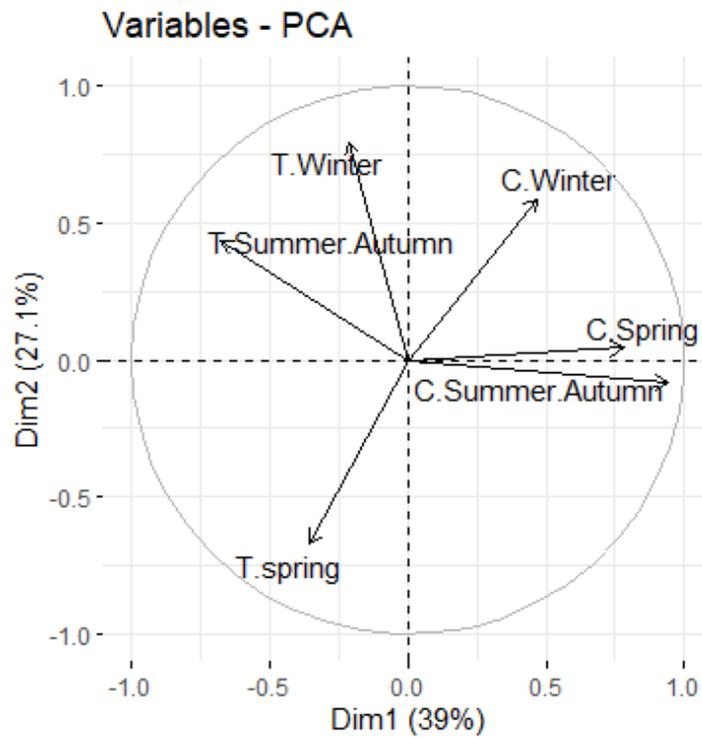
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995 *Figure A2: Magnitude of selective mortality indices (S and C) acting on age-0 growth for*  
 996 *anchovy (A and B) and sardine (C and D) measured on individuals aged 1 and 2, and 2 and 3.*



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<sub>2,3</sub>) (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<sub>2,3</sub>) (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