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## Integration of bioenergetics in an individual-based model to hindcast anchovy dynamics in the Bay of Biscay

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### Abstract :

The population of European anchovy of the Bay of Biscay collapsed at the beginning of the 21st century, causing the closure of its fishery between 2005 and 2010. In order to study both the human and environmental causes of the anchovy population dynamics, an approach coupling individual bioenergetics to an individual-based model was applied between 2000 and 2015. This modelling framework was forced with outputs from a physical–biogeochemical model. In addition to a base-case scenario with realistic forcing, alternative scenarios were run without inter-annual variability in either fishing mortality or environmental conditions. During the decrease in population biomass, a high fishing pressure coincided with a combination of environmental variables promoting the appearance of large individuals that could not survive severe winters because of their high energetic demands. The recovery of the population was favoured by a period of warm years with abundant food favouring the winter survival of age 1 individuals, in coincidence with the closure of the fishery. Our modelling approach also allows to test the consequences of a retrospective implementation of the current harvest control rule from 2000 which, according to our results, would have prevented the collapse of the population and avoided the fishery closure.

**Keywords :** anchovy, Bay of Biscay, Dynamic Energy Budget, fishery, harvest control rule, individual-based model, population collapse.

## Introduction

38 Like other small pelagic fish with a short lifespan, early maturation and high reproductive  
potential, the European anchovy (*Engraulis encrasicolus*) plays a pivotal ecological role due to  
40 its intermediate trophic position, high abundance, and energy content (Cury et al., 2000;  
Palomera et al., 2007). The population dynamics of small pelagic fish are often abrupt and  
42 tightly tied to environmental features by complex relationships (Checkley et al., 2009).  
Environmental forcing is known to affect population dynamics through both biological (e.g.  
44 changes in life history traits, physiological optima, behaviour, etc.) and physical (e.g. affecting  
survival, larval dispersion, feeding, etc.) pathways (Checkley et al., 2009).

46

In the Bay of Biscay (NE Atlantic), the anchovy population sustains a valuable fishery shared by  
48 France and Spain. The historical evolution of landings of anchovy peaked between 1960 and  
1965, with ca. 75,000 tonnes per year, while minimal landings occurred at the beginning of the  
50 21<sup>st</sup> century (ICES, 2018). In 2005, the population reached a historical minimum that forced the  
closure of the fishery between 2005 and 2010, entailing important socio-economic  
52 consequences (Vermard et al., 2008). The effect of fishing and environmental variables has  
been widely studied to understand both the drivers of this population and the causes of its  
54 collapse and, although a wide variety of approaches have been applied in this regard, few have  
succeeded in understanding the underlying biological or ecological mechanisms.

56

The literature on the effects of fishing and environment on the populations of small pelagic fish  
58 typically considers two levels of biological organization: populations and individuals  
(physiology). Among the first group, time-series correlation analyses have been used with  
60 different results. Hence, while the anchovy recruitment was not found to be related to  
zooplankton concentration (Irigoien et al., 2009), the East-Atlantic oscillation index successfully  
62 explained part of the recruitment failure at the beginning of the 21<sup>st</sup> century (Borja et al., 2008).  
Similarly, recruitment was found to be positively and negatively correlated to the magnitude of  
64 coastal upwelling and the degree of shelf stratification respectively (Allain et al., 2001). Other  
studies found that larval survival was related to anchovy spawning distribution (Allain et al.,  
66 2007). Using a Bayesian approach, Taboada and Anadón (2016) showed that changes in  
phytoplankton phenology and larval drift presented good prediction indicators for the dynamics  
68 of the population but, to explain the collapse of the population, fishing pressure needed to be

considered, improving considerably the skill of the models. At the individual/physiological level,  
70 several studies tried to determine the effect of environmental variables on life history traits such  
as growth (Cotano et al., 2008), mortality rates (Cotano et al., 2008; Uriarte et al., 2016) or  
72 reproduction (Motos, 1996; Somarakis et al., 2004). As far as we know, none of the previous  
works developed a mechanistic approach linking the effect of environmental conditions to the  
74 response of the population based on the physiology of individuals.

76 The Dynamic Energy Budget theory (DEB: Kooijman, 2010) is a metabolic-ecology theory  
describing the acquisition, use, and distribution of energy by individuals through metabolic  
78 reactions. In DEB theory, the energy from the environment is allocated through assimilation into  
three different compartments: structure, maintenance and reproduction/maturation, while  
80 temperature controls the velocity of all the metabolic reactions and fluxes of energy within the  
organism. Hence, the DEB theory facilitates understanding of the relationships between an  
82 individual's energy and life history traits such as growth, reproduction, and mortality rates. A  
model based on the DEB theory has recently been assembled for the anchovy in the Bay of  
84 Biscay, describing its bioenergetics at annual and life-cycle scales (Gatti et al., 2018). These  
kind of bioenergetic approaches are also useful to compare the life histories of individuals  
86 among geographic regions (Huret et al., 2018), and for understanding the variations in vital  
rates found in response to environmental fluctuations (Pethybridge et al., 2013; Politikos et al.,  
88 2015a; Politikos et al., 2015b). Integrating the information from different individuals, DEB  
models can further be scaled up to the population level using individual-based population  
90 models (IBMs, see Huse et al., 2002). The use of IBMs to infer the consequences of  
environmental changes on small pelagic fish populations has grown since the 1990's (e.g.  
92 Letcher et al., 1996; Rose et al., 1999,) but it was only after the inclusion of the full life cycle of  
fish (e.g. Jakobsen et al., 2009) that IBMs succeeded in capturing the effect of environmental  
94 variables on aspects such as reproduction and mortality (e.g. Fietcher et al., 2015; Politikos et  
al., 2018). In the case of anchovy, a plankton feeder, models considering low trophic levels  
96 (physical-biogeochemical models) provide the energy from the environment in the form of food  
(plankton) and temperature. In this manner, life history traits such as growth, reproduction,  
98 mortality or movement can be related to the environmental variables and, integrating these  
phenomena over an entire population, the response of the population can be simulated  
100 (Pethybridge et al., 2013, Politikos et al., 2015a).

102 In this work, we integrate the bioenergetics of individual anchovies, using a DEB model forced

with the outputs of a coupled physical-biogeochemical model, into a population (IBM) model, in  
104 order to create a unique mechanistic framework enabling us to understand the causes of the  
rapid collapse and slow recovery of the population between 2000 and 2015. This approach goes  
106 a step beyond the historical complexity of models for anchovy in the Bay of Biscay, and is used  
to study the human and environmental effects on anchovy dynamics, by simulating different  
108 scenarios of environmental and fishing pressures. Finally, the implementation of the current  
harvest control rule from the beginning of the century is simulated, in order to test whether this  
110 measure could have prevented the collapse of the population between 2005 and 2010.

## Materials and methods

112 In order to scale up the effect of environmental variables on the anchovy's bioenergetics and  
evaluate the response at the population level, a joint modelling framework consisting of a DEB  
114 model and an IBM was assembled (Fig. 1). This approach used the outputs (temperature and  
zooplankton concentration) from a regional physical-biogeochemical model as forcing for the  
116 DEB model for the anchovy described in Gatti et al. (2017). Then, an IBM integrated the  
response of the different individuals considered within the population (in terms of growth,  
118 reproduction, and mortality), to infer the evolution of the population over time (Fig. 1). In this  
section we describe in more detail the different modules, parameters and processes considered.

### 120 Environmental forcing

The environmental forcing was provided by the regional coupled physical-biogeochemical  
122 POLCOMS-ERSEM model (Holt et al., 2001; Butenschön et al., 2016), using a 0.1° spatial  
resolution and 40 sigma layers over the period 1996-2015. The model was forced using  
124 reanalysis for the atmospheric interface (ERAinterim, Dee et al. 2011) and physical ocean  
boundary conditions (GLORYS2v4, product GLOBAL\_REANALYSIS\_PHY\_001\_025 from  
126 marine.copernicus.eu), with the biogeochemical boundary conditions and river inputs set using  
climatology (World Ocean Atlas, [www.nodc.noaa.gov/OC5/woa13/](http://www.nodc.noaa.gov/OC5/woa13/)),  
128 <https://www.nodc.noaa.gov/ocads/oceans/GLODAPv2/>), and GlobalNEWS2 (Mayorga et al.,  
2010). Temperature (°C) and zooplankton biomass (mg C m<sup>-3</sup>) outputs of this model were used  
130 to force the DEB-IBM model. Our model is not spatially explicit, so the forcing variables were  
averaged over the Bay of Biscay region from the coast to 48.0° N and 5.0° W (Fig. 2 and Figs.  
132 S1-S4), which covers the distribution of the population over its life-cycle. The depth considered  
for the temperature series was integrated between 0 and 150 m for adults, and between 0 and  
134 30 m for eggs, larvae and juveniles (Gatti et al., 2017), while the concentration of zooplankton  
in the first 50 m was used for the food density (Plounevez and Champalbert, 1999). Zooplankton  
136 biomass ( $X$ , mg C m<sup>-3</sup>) was then introduced as food concentration in the DEB model, being used  
to calculate the “scaled functional response” for food ( $f$ ) as a Holling type II function  $f = X / (X +$   
138  $K_f)$  (where  $K_f$  is the half saturation coefficient for food, see Table S1).

## 140 Individual bioenergetics modelling

The anchovy life cycle was described by means of a bioenergetic model based on the Dynamic  
142 Energy Budget (DEB) theory of Kooijman (2010) (DEB module). The values of the different  
parameters considered in this model are shown in Table S1, while the equations describing the  
144 main processes of the individual metabolism are presented in Table S2. Forcing the DEB  
module with a physical-biogeochemical model for the Bay of Biscay (Fig. 2) makes it possible to  
146 evaluate the impact of environmental variables on metabolic-dependent processes at the  
individual level such as growth, fecundity or mortality.

148

The DEB module used here was calibrated for the Bay of Biscay anchovy by Gatti et al. (2017).  
150 A simulation at the individual level using a daily environmental climatology of temperature and  
zooplankton from the period 1996-2015 ("individual run", Fig. S5), gave similar results to those  
152 of Gatti et al. (2017). However, because the coupled physical-biogeochemical model used as  
forcing was not the same than in their study, some minor adjustments to the maximum  
154 assimilation rate ( $p_{Am}$ ) and the fraction of energy allocated to growth ( $k$ ) were made (from 800 to  
820 J cm<sup>-2</sup> d<sup>-1</sup>, and from 0.71 to 0.80 respectively).

## 156 Population modelling

The DEB module was coupled to an individual based model (IBM). Super-individuals (SIs) were  
158 used as modelling units (Scheffer et al., 1995; Rose et al., 2015), in which each SI represented  
a large number of individuals born the same day and with identical life history and parameters.  
160 We integrated over all SIs to scale-up the response to environmental factors at the population  
level (IBM module). This consisted of the addition of the processes and state variables of the  
162 individuals forming each SI across the population (i.e. fecundity, biomass, growth, mortality,  
etc.), to infer the characteristics of the whole population. The population was initialised on April  
164 1<sup>st</sup> 1996 and the model was run until December 31<sup>st</sup> 2015, with years 1996 to 1999 used as a  
'spin-up' period to stabilize the population in terms of SI number. The initial number of  
166 individuals within each parental SI was derived from the age-structured data obtained in  
PELGAS surveys (Doray et al., 2018), while their size (g) and energy content on each of the  
168 DEB compartments (structural, reserve, and reproductive) were obtained from the individual run  
(Fig. S5). On this basis, the model started on April 1<sup>st</sup> 1996 with four adult SIs comprising  
170 different numbers of individuals ( $3.7 \times 10^9$ ,  $1.5 \times 10^9$ ,  $3.6 \times 10^8$ ,  $2.4 \times 10^7$ , respectively), with different  
age (1, 2, 3, 4 years, respectively), size (12.13, 16.20, 17.21, 17.56 cm, respectively), and

172 energy in the different compartments of the DEB models: structure (20625, 45958, 50914,  
58395 J, respectively), and reserve buffer (7548, 20676, 26693, 34644 J, respectively). The  
174 energy of the reproductive buffer was the same for each initial SI: 12026 J. The SIs were  
allowed to spawn every 3 days between April and September, creating new generations of SI  
176 during the “spin-up” period. All eggs spawned within 3 days by all adult SI were gathered in a  
unique new SI. The population variability in the model is generated by the effect of the different  
178 environmental variables experienced by SIs born at different moments of the year. In this  
manner, a pool of life histories during the spin-up period was originated, giving rise to a  
180 diversified population of 130 SIs on January 1<sup>st</sup> 2000, when the calibration period started (see  
below). The frequency for creating new SIs, which in turn controls the number of SIs in the  
182 model, was subject to a sensitivity analysis prior to the simulations. The objective was to find the  
lowest number of SIs which allowed faster simulations without effects on the model results, i.e.  
184 allowing enough variability to be simulated based on the different life history trajectories of each  
SI.

186

Four sources of mortality were considered within the DEB-IBM framework. These mortalities are  
188 dependent on the energetic requirements, size, and stage of the fish, while the fishing mortality  
is considered as an external (fixed by semester) source of mortality. The mortality by energetic  
190 deprivation ( $Z_{DEB}$ ) is explicitly included in the DEB module. It occurs when a fish cannot supply  
the required energy for somatic maintenance costs, neither from its reserve or from emergency  
192 maintenance processes (reallocation from reproduction). This kind of mortality essentially  
occurs in late winter within our model in the Bay of Biscay.

194

Second, the natural mortality ( $Z_N$ ) considers implicitly the effects of predation and decreases  
196 with individual size (Fig. S6):

$$Z_N = Z_a + (Z_e - Z_a) e^{-z(L_T - L_{egg})} \quad \text{Eq. 1}$$

198 with  $Z_a$  and  $Z_e$  the instantaneous mortality rate of adults and eggs respectively, and  $z$  a  
decreasing coefficient of natural mortality.  $L_T$  is the individual length at a given time, and  $L_{egg}$  is  
200 the average size of an anchovy egg in the Bay of Biscay (0.0854 cm, Huret et al., 2016). These  
parameters ( $Z_a$ ,  $Z_e$ , and  $z$ ) are optimized during the calibration process (see below).

202

The third source of mortality is a density-dependent relationship between egg concentration and  
204 larval mortality established following the relationship by Somarakis and Nikolioudakis (2007) set  
in the Aegean Sea (Fig. S6):

206  $Z_{DD} = -0.154 + s \log(A)$  Eq. 2

with  $Z_{DD}$  the larval density-dependent mortality (applied until individual size = 2.81 cm, Fig. S6) and  $A$  the concentration of eggs, expressed in number  $m^{-2}$  (we considered 50,000  $km^2$ , more or less half of the area of study, representing the potential spawning area of anchovy). The value of the slope ( $s = 0.205$ , according to Somarakis and Nikolioudakis, 2007) was also optimized during the calibration process (see below).

212

Finally, the fishing mortality ( $Z_F$ , Fig. S6) was introduced as a constrained external parameter with an updated value for every semester between 2000 and 2015 (data from ICES, 2018). Fishing mortality is considered as:

216  $N_{t+\Delta t} = N_t e^{(-Z_F \Delta t)}$  Eq. 3

where  $N_t$  and  $N_{t+\Delta t}$  are the fish abundances at time  $t$  and  $t+\Delta t$  respectively, being  $\Delta t$  the length of time step (1 hour). This mortality rate was applied to adults and juveniles (not yet matured) during the first semester of the year, and to actively reproducing adult individuals during the second semester of the year.

### Model calibration with optimization of mortality parameters

222 The outputs from a Bayesian two-stage biomass-based model (CBBM, Ibaibarriaga et al., 2008) were considered as reference for anchovy biomass in the Bay of Biscay between 2000 and 224 2015. These estimations are provided for the 1<sup>st</sup> of January. CBBM is the standard population assessment provided by ICES and considers two kinds of individuals in the population: adults participating in reproduction (spawning stock biomass, SSB), and recruits (age 1 adults that do not participate in reproduction). 1<sup>st</sup> January biomass values were obtained from the model based on individual weight, the total number of individuals, and their age. The differences between the outputs of the IBM model and the CBBM model were then computed as a cost function:

$$\sum_i \sum_y \left( \frac{B_{i,y} - B'_{i,y}}{\sigma_i} \right)^2$$

Eq. 4

232 where  $B_{i,y}$ , and  $B'_{i,y}$ , are the simulated and observed (CBBM) biomass of class  $i$  (SSB and recruits) respectively at time  $y$  (year), and  $\sigma_i$  is the standard deviation of  $B'_{i,y}$ . The cost function was calculated iteratively using a Nelder-Mead simplex optimisation method (Nelder and Mead, 1965) considering different combinations of the following four parameters: the daily mortality rate of eggs ( $Z_e$ , Eq. 1), the mortality rate of adults ( $Z_a$ , Eq. 1), the coefficient of natural mortality

236



scaling the decrease in mortality with size ( $z$ , Eq. 1), and the slope of the density-dependent  
238 relationship between egg concentration and larval mortality ( $s$ , Eq. 2). The choice of these  
parameters for optimization was based on the difficulty of assessing mortality values in the field  
240 and the scarcity of the related literature.

242 As described above, our modelling approach allows to assess the impact of the mortality  
caused by winter starvation on the population ( $Z_{DEB}$ ). This parameter is often disregarded in fish  
244 population modelling due to the empirical difficulties of estimation. By running a simulation  
where this source of mortality is disregarded, we were able to highlight its relevance for the  
246 population, which can be seen as an added value of our work. To make a simulation with no  
death by starvation -making sense when compared to the base-case simulation- it was  
248 necessary to consider a new calibration of the mortality parameters  $Z_a$ ,  $Z_e$ ,  $z$ , and  $s$ , in the same  
manner as described above.

## 250 Model validation

The model validation consisted of the comparison of the model outputs to independent data  
252 from scientific surveys for the stock assessment. Acoustic surveys for the stock assessment of  
anchovy in the Bay of Biscay are carried out during PELGAS spring surveys by the Institut  
254 Français de Recherche pour l'Exploitation de la Mer, IFREMER (France) (Doray et al., 2018). A  
second dataset comes from BIOMAN spring surveys conducted by AZTI-Tecnalia (Spain),  
256 which use the daily egg production method (DEPM) for an independent stock assessment of  
anchovy in the Bay of Biscay. In the validation of our model both the number of individuals and  
258 their weight are taken into account to obtain the equivalent of the population SSB provided by  
the surveys. The outputs of our model were extracted in spring (May 15<sup>th</sup>) for comparison with  
260 these surveys. In order to obtain a statistical measurement of the model validation, we  
estimated the significance of the slope ( $H_0$ : slope = 0) from the linear regression between the  
262 model and both independent time series (PELGAS and BIOMAN).

## Hypotheses and scenarios

264 In order to study the separate effects of fishing mortality and environmental variables on  
population dynamics, different scenarios combining fishing pressure and environmental forcing  
266 were defined (Table 1). Scenarios were defined based on different hypotheses about the  
relationship between external forcing and population response. First, in order to show the effect  
268 of fishing, the interannual variability of the environment was disregarded and instead, a daily

climatology of temperature and zooplankton computed over the period under study was used  
 270 (Scenario 1). Similarly, to study the effect of the environment on the population, fishing mortality  
 (Z<sub>F</sub>) was set constant (as the average of the whole time-series) over the full period of study  
 272 (Scenario 2), or just during the fishing ban (Scenario 3), aiming at understanding the effects of  
 fishing over the entire period and the consequences of the fishing ban between 2005 and 2010.

274

Our modelling approach can also test the effect of different harvest rates or control rules on the  
 276 stock performance. The current harvest control rule (HCR) has been implemented since 2010  
 (ICES, 2018), and is used to define a total allowable catch (TAC, in tonnes) of anchovy in a  
 278 given year in the Bay of Biscay. This TAC, implemented from January to December of year  
 y+1, is calculated based on the SSB at the end of the first semester of year y+1 as follows:

- 280 - TAC<sub>y+1</sub> = 0 t; if SSB<sub>y+1</sub> ≤ 24,000 t
- TAC<sub>y+1</sub> = -2,600 + 0.40 \* SSB<sub>y+1</sub>; if 24,000 t < SSB<sub>y+1</sub> ≤ 89,000 t
- 282 - TAC<sub>y+1</sub> = 33,000 t; if SSB<sub>y+1</sub> > 89,000 t

SSB<sub>y+1</sub> is estimated by the assessment group on December of year y based on a recruitment  
 284 prediction for year y+1. As we cannot make this projection in our model, we calculate the TAC  
 based on the modelled SSB on May 15<sup>th</sup> of the current year, and apply it from that date to the  
 286 same date of the following year.

288 To include the HCR in the DEB-IBM model, it was necessary to translate it to an instantaneous  
 mortality rate as Z<sub>F</sub>. To do this, we extracted the SSB from our model on May 15<sup>th</sup> each year and  
 290 the corresponding TAC was calculated according to the rules presented before. Then, using the  
 average individual weight of adults and juveniles, we transformed the TAC into the number of  
 292 individuals that can be captured (TAC') during the season, obtaining the instantaneous fishing  
 mortality (Z<sub>F</sub> in year<sup>-1</sup>) corresponding to the TAC' as:

$$294 \quad Z_F = -\ln\left(\frac{N_m - TAC'}{N_m}\right) \quad \text{Eq. 5}$$

where N<sub>m</sub> is the number of individuals on 15<sup>th</sup> May in the population. To investigate if the  
 296 application of the HCR would have avoided the collapse of the population, we defined a  
 scenario where this strategy was applied since 2000 (Scenario 4).

298

**Table 1.** Hypotheses on the influence of environment and fishing on the anchovy's population dynamics  
 300 between 2000 and 2015, with scenarios proposed for testing them.

Hypothesis	Scenario
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Hindcasted environmental variables and historical fishing mortality replicate the past dynamics of the population.	Sc0) Historical environmental forcing + historical fishing pressure.
Fishing pressure drives population dynamics.	Sc1) Historical fishing pressure + average environmental forcing (as daily climatology) in the period 2000-2015
Environmental variables drive population dynamics.	Sc2) Historical environmental forcing + constant fishing pressure.
The closure of the fishery was necessary for the recovery of the population.	Sc3) Historical environmental forcing + historical fishing pressure except between 2005 and 2010, when set constant.
The implementation of the current HCR in the beginning of the time series would have prevented the collapse of the population.	Sc4) Historical environmental forcing + HCR fishing pressure.

## 304 Results

### Environmental variables

306 The environmental forcing variables used to run the model between 1996 and 2015 are shown  
in Figs. S1, S2, and S3. These figures also show the daily climatologies used for the calibration  
308 of the individual DEB and to run scenario 2, while in Fig. S4 a summary of four descriptors are  
shown for each year: annual mean temperature between 0 and 30 m, annual mean temperature  
310 between 0 and 150 m, annual mean zooplankton concentration, and the day of the year when  
the highest concentration of zooplankton occurs. Years 2003, 2014, and 2006 showed summer  
312 surface temperatures well over the daily 2000-2015 climatology (Figs. S1, S2, and S4). These  
years, except of 2006, presented also an earlier zooplankton bloom (Fig. S3), albeit the annual  
314 maximum could happen later in the year (Fig. S4). Year 2011 showed high spring temperature  
(Fig. S1), with an advanced zooplankton bloom (Figs. S3 and S4), but summer temperature was  
316 colder than the climatology. Years 2002, 2010, and 2013 were colder than the average in winter  
and spring, while no special feature was identified in zooplankton production during these years.  
318 (Figs. S1, S2, S3, and S4). No clear temporal patterns were found within the environmental  
forcing variables apart from an increasing mean zooplankton concentration (Fig. S4C, p-  
320 val.=0.0535).

### Simulation at the individual level

322 The bioenergetic model captured successfully the dynamics of individual growth and energy  
density when using the daily 2000-2015 climatology as environmental forcing (Fig. S5, see also  
324 Gatti et al., 2017). Individual growth in weight and length, and energy density of individuals (see  
Gatti et al., 2017 for details on calculation) matched the observations from the surveys (dots in  
326 Fig. S5, see Gatti et al., 2017 for data origin). According to these simulations, individual length  
and weight reached an asymptote at around 18 cm and 37 g respectively. The model captured  
328 the variations in weight and energy density occurring on a seasonal scale based on the  
reproductive cycle and food availability.

### 330 Reconstruction of the past population dynamics

The IDEB-IBM model was able to capture the main features of the population dynamics of the  
332 European anchovy between 2000 and 2015 in the Bay of Biscay (Fig. 3A). This includes the

collapse of the population in 2005 and the recovery afterwards. Four parameters were optimized  
334 (see methods): the daily adult mortality coefficient (Eq. 1,  $Z_a=0.000001$ ), the daily egg mortality  
coefficient (Eq. 1,  $Z_e=0.2494$ ), the coefficient parameterising length-decreasing natural mortality  
336 (Eq. 1,  $z=0.3491$ ), and the slope of the density-dependent mortality of larvae (Eq. 2,  $s=0.1418$ ).  
Similarly to the CBBM values, the biomass predicted by our model (Fig. 3A) decreased in the  
338 first few years of the simulation, with minimum values in 2005-2006 and two main drops in 2004  
and 2007. After 2008, however, the population followed a steady and slow recovery until the  
340 end of the simulation, with a drop in 2014 (Fig. 3A). The regression between the simulated and  
CBBM biomass values is significant ( $r^2 = 0.40$ ; p-val. = 0.0039).

342  
The model was validated using biomass and weight-at-age values from biomass estimation  
344 surveys PELGAS and BIOMAN (see methods). As on January 1<sup>st</sup> (Fig. 3A), the population  
biomass on May 15<sup>th</sup> reached a minimum in 2005 and recovered afterwards (Fig. 4A). A second  
346 important drop was also found in 2012. These dynamics are broadly coincident with the results  
from the research cruises, including the drop near the end of the time series (Fig. 4A). The  
348 regression between observations and the model outputs showed significant relations (p-val. =  
0.020 PELGAS; p-val. = 0.0563 BIOMAN, although the fit was poor ( $r^2 = 0.327$  PELGAS;  $r^2 =$   
350  $0.236$  BIOMAN) (Fig. 4B). Additionally, the weight-at-age on May 15<sup>th</sup> for the different ages in  
the population agreed with the survey data, albeit the interannual variability in the model outputs  
352 was lower (not shown).

354 From the DEB-IBM simulations, a variety of ecological indicators can be extracted to understand  
the mechanisms underlying the population dynamics (Fig. 5). The age-structure of the  
356 population in terms of number of individuals can be obtained at different times of the year. On 1<sup>st</sup>  
of January, the proportion of age 1 individuals was found to be around 80% (Fig. 5A), while on  
358 May 15<sup>th</sup> it decreased to around 50% (Fig. 5B). DEB-mortality, at the end of winter, is hence  
largely responsible for the loss of a high percentage of simulated age 1 individuals (Fig. 6), 2014  
360 being the year with the highest drop in the proportion of age 1 individuals between January 1<sup>st</sup>  
and May 15<sup>th</sup> (Fig. 5B). This can be also appreciated in Fig. S7A and B, where the number of  
362 recruits on January 1<sup>st</sup> and May 15<sup>th</sup> is shown. Similarly, the age structure in terms of biomass  
(Fig. 5C, 1<sup>st</sup> of January), shows that age 1 individuals are not so dominant as in terms of  
364 numbers of individuals, and that the proportion corresponding to the different age classes did  
not vary significantly during the time series.

366 Different ecological indicators obtained from the DEB-IBM model show a drop in the  
performance of the population in 2004 (Fig. S7): egg survival, fertility, mean weight gain  
368 between January and May, Fulton's index as the condition factor, average adult weight, and the  
energy content of individuals in different DEB compartments. The energy density of age 1  
370 individuals on January 1<sup>st</sup> did not show any special characteristic between 2004 and 2005, but  
dropped significantly in 2013 and 2014 (Fig. S7E). The average size at age did not vary  
372 significantly between 2000 and 2015 (Fig. S7H), with the highest inter-annual variation found for  
age 1.

374

The contribution of each source of mortality to the total mortality was estimated with the DEB-  
376 IBM model (Fig. 6). The starvation mortality ( $Z_{DEB}$ ) affected age 1 individuals only. It happens at  
the end of winter when the recruits have insufficient resources and therefore die. Fishing  
378 mortality ( $Z_F$ ) was more important than natural mortality for ages 2, 3, and 4, affecting age 1 as  
well. Natural mortality ( $Z_N$ ) decreases in importance as fishes grow (Fig. S6). Within the  
380 hindcasted period,  $Z_{DEB}$  was found to be especially high in 2004 and 2007. After 2008,  $Z_{DEB}$   
dropped for age 1 individuals, until 2014 when it suffered a sudden increase.

382

The simulation where  $Z_{DEB}$  was not included in the DEB model (additional simulation, Fig. 3B)  
384 required a different calibration of the mortality parameters ( $Z_a = 0.0004$ ,  $z = 1.045$ ,  $Z_e = 0.950$ ,  
 $s=0.172$ ). In this simulation, the population was found to drop from the beginning of the period  
386 until 2005, recovering afterwards and dropping again by the end of the simulation (Fig. 3B). Part  
of the interannual variability was lost, and many indicators were substantially different from  
388 scenario 0 (Fig. S8). The proportion of individuals dying by fishing mortality was increased,  
while the energetic minima of 2004, 2007, and 2014 were also captured under this simulation.

### 390 Fishing and climate scenarios

Following the scenarios approach shown in Table 1, applying a constant fishing mortality rate  
392 with the historical environmental forcing should demonstrate the real impact of environmental  
forcing alone (scenario 1; Fig. 7A). In this simulation, the population dropped during the first  
394 years but to a lower extent than when the real fishing mortality was applied (Fig. 3A and the  
grey line in Fig. 7A). Then, the population reached two minima, in 2003 and 2005, dropping  
396 again in 2008. At the end of the simulation the population did not increase as much as under  
scenario 0. The interannual variability was found to be higher in scenario 1 than in scenario 0  
398 (Fig. 7A). Fig. S9 shows the different ecological indicators extracted from this simulation. The

age composition of the population was similar to scenario 0, while the recruitment was higher in  
400 the beginning of the time series, but lower in the end. The drop of indicators found in 2004  
402 under scenario 0 was also found for the weight gain between January and May, the Fulton's  
condition factor, the egg survival, and the fecundity. According to the energetics of individuals,  
important drops were also registered in 2004, 2007, and 2014.

404

In scenario 2 (fishing alone drives population dynamics: Table 1, Fig. 7B) the population was  
406 found to suffer a drastic increase after the closure of the fishery in 2005, stabilizing at the end.  
The interannual variability was found to be much lower than in scenarios 0 and 1, which is also  
408 evident in a range of ecological indicators (Fig. S10). The drop of performance found in  
scenarios 0 and 1 in 2004 was not so evident, but still present in this scenario, mainly referring  
410 to the Fulton's condition factor and the fecundity of individuals, while the survival of eggs  
decreased by the end of the simulation (Fig. S10 G, I, J).

412

Under scenario 3 (closure necessary for the recovery: Table 1, Fig. 7C), the population did not  
414 recover after the collapse of 2005, keeping minimal values until the end of the simulation.  
Ecological indicators showed the same patterns as in scenario 0, but with lower values by the  
416 end of the simulation. This is especially evident for the recruitment and for the proportion of age  
1 individuals in terms of numbers and biomass (Fig. S11).

418

The simulation of the application of the current HCR from the beginning of the period (scenario  
420 4), showed that the population did not drop at the beginning, being sustained well over the limit  
of 24,000 tonnes established in the HCR to close the fishery (Fig. 7D). The interannual  
422 variability was found to be coincident with scenarios 0, 1, and 3, while the final period, on the  
other hand, did not show the increase in population found in the scenario 0 simulation: instead,  
424 it was more or less stable around 100,000 tonnes. Ecological indicators also show similar  
patterns as those for scenario 1, with drops of individual performance in 2004, 2007, and 2014  
426 and with lower recruitment values in 2003, 2005, 2008, and 2012 (Fig. S12).

## Discussion

430 We integrated for the first time a bioenergetics model into a population model for the Bay of  
 Biscay anchovy. This coupling framework successfully replicated the main patterns of the  
 432 population dynamics between 2000 and 2015 (Fig. 3A), including the initial drop, the collapse of  
 2005, and the recovery after 2008. Additionally, by combining this approach with simulations  
 434 based on different scenarios of environmental and fishing pressure, we provide new insights  
 into the causes of the collapse of 2005 and on the recovery afterwards. Our results provide  
 436 evidence that the interannual variability of the anchovy population was mostly driven by  
 environmental conditions, while the effect of fishing was more evident on a longer time scale.  
 438 We also investigated the relevance of the closure of the fishery between 2005 and 2010 for the  
 recovery of the population, as well as the likely consequences of the implementation of the  
 440 current HCR before the collapse.

442 Including the effect of mortality associated with individual bioenergetics improved the hindcast  
 ability of the model (Fig. 4A vs 4B). The calibration considering  $Z_{DEB}$  (scenario 0; Fig. 3A)  
 444 provided estimates of egg ( $Z_e$ ), and adult ( $Z_a$ ) mortality rates consistently lower than values in  
 the literature (Uriarte et al., 2016). This result was expected as natural mortality measured in the  
 446 literature should be comparable to the sum of  $Z_{DEB}$  and  $Z_N$  in our modelling framework. On the  
 other hand, the values of  $Z_a$  and  $Z_e$  when  $Z_{DEB}$  was not taken into account (Fig. 3B) were much  
 448 higher. Further, the interannual variability was better captured when  $Z_{DEB}$  was considered. This  
 source of mortality could be very important for the recruitment success at the end of the first  
 450 winter as it affects age 1 individuals. A negative (but non-significant) relationship between the  
 number of recruits on May 15<sup>th</sup> and the proportion of dead individuals by  $Z_{DEB}$  in the previous  
 452 winter (both estimated from our model) was found ( $p\text{-val.}=0.091$ ;  $r^2=0.19$ ). Hence, according to  
 our results, this potential source of mortality establishes a direct link between the environmental  
 454 variability and the resulting population dynamics. Due to inherent methodological difficulties, few  
 references on natural mortality by starvation during winter for early stages of pelagic fish are  
 456 available (but see Pepin, 2015a, 2015b).

### Population dynamics related to environmental and fishing

458 Simulating the anchovy population under different scenarios (Table 1) allowed us to study the  
 effects of fishing and environment on the population dynamics. Hence, while scenario 1



460 (population subject to constant fishing mortality, Fig. 7A) captured the interannual variability of  
the simulation of reference, it failed to replicate the drop and recovery of the population. On the  
462 other hand, under scenario 2 (no interannual variability of the environment, Fig. 7B) the  
simulation did not capture the interannual variability of the population, but rather, the longer-  
464 term pattern of increase-decrease in biomass. These findings suggest a short-term control of  
the population by environmental drivers, while the effect of fishing would have effect on a longer  
466 time scale. This is probably because of the autorreccorrelation of the fishing pressure showing a  
clear temporal trend: high at the beginning of the simulation, minimal or null between 2005 and  
468 2010, and intermediate between 2010 and 2015. In fact, the response of the population to the  
closure of the fishery under scenario 2 (constant environment) was immediate in 2005,  
470 demonstrating that fishing pressure could affect population dynamics in a short temporal scale  
as well.

472

Scenarios 1 (constant fishing) and 2 (constant environment) suggest a joint action of  
474 environmental and fishing on the drop and collapse of the population in the early 2000s. Hence,  
scenario 1 (and scenario 4, see below) showed that environment was unfavourable for the  
476 population during that period, and also, that a lower fishing mortality at the beginning of the time  
series would have prevented the collapse of the population (Fig. 7A). On the other hand, the  
478 constant environment simulated in scenario 2 indicated that fishing pressure alone was  
sufficient to cause a low population before 2005, close to the 24,000 t limit established by the  
480 HCR to close the fishery (Fig. 7B). The corollary of these simulations is that both factors  
contributed to the fall of the population, with the especially bad environmental conditions of 2004  
482 being the definitive drivers of the collapse of the population in 2005 (see below a mechanistic  
discussion on the specific causes). This finding is in agreement with the work of Taboada and  
484 Anadón (2016), which showed that fishing pressure was fundamental to explaining the collapse  
of the population in 2005, in addition to environmental variables such as the phytoplankton  
486 bloom phenology or the larval drift.

488 In a similar manner, the recovery of the population after 2008 in our model was probably  
triggered by a combination of low fishing pressure and favourable environmental conditions. Fig.  
490 6 showed that the recovery period of the simulation had the lowest proportion of  $Z_{DEB}$  of the time  
series, while the simulation of scenario 4 (with no closure of the fishery; Fig. 7D), demonstrated  
492 that the population would not have been able to recover if fishing had been kept constant  
between 2005 and 2010. Interestingly, as shown in the simulation of scenario 1 (constant

494 fishing), the effect of lower  $Z_{DEB}$  would have not been sufficient to trigger the recovery of the  
population (Fig. 7A), probably due to an increased fishing mortality in regards of scenario 0. By  
496 contrast, the closure of the fishery alone (scenario 2) would probably have been enough to allow  
the recovery of the population (Fig. 7B) which, comparing with scenario 0, could have been  
498 faster than under variable environmental forcing. Hence, both the closure of the fishery and the  
drop of  $Z_{DEB}$  were beneficial and coincident in time for the population, finally triggering its  
500 recovery. The environmental causes of the drop of  $Z_{DEB}$  in this period are discussed below.

### Mechanistic perspective of the population dynamics

502 The environmental features preceding the collapse of 2005 deserve special consideration to  
understand the mechanisms of action of environmental variables on the bioenergetics of  
504 individuals and populations. 2003 temperature was significantly high at both 0-30 and 0-150 m  
integrated depths (Figs. S1, S2) with an early bloom of zooplankton in spring and low  
506 zooplankton concentration during the second part of the year (Fig. S3), while in 2004  
temperature and zooplankton concentration were close to the average (Figs. S1, S2, S3). As a  
508 consequence of the higher temperature, different indicators extracted from our model on  
January 1<sup>st</sup> 2004 indicate good individual performance during 2003: a higher proportion of the  
510 time series of age 1 individuals (Fig. 5A), high proportion of age 1 individuals in terms of  
biomass (Fig. 5C), high recruitment of individuals (Fig. S7A), age 1 individuals with high energy  
512 density (Fig. S7E), and large adults (Fig. S7I), with high energy levels (Fig. S7J). Conversely,  
indicators from the model obtained on May 15<sup>th</sup> 2004 show a trend change, with the lowest  
514 weight gain between January and May (Fig. S7C), and a critical drop of energetics between  
2003 and 2004 (Fig. S7J). The drop of performance at the individual and population level is also  
516 in agreement with the high  $Z_{DEB}$  (Fig. 6) shown by the model. This mortality is expected to take  
place at the end of winter when individuals cannot pay maintenance costs from food or from  
518 reserves.

520 The high and low performance of the modelled population in 2003 and 2004 respectively can  
probably be explained from a bioenergetics perspective. The high temperature in 2003  
522 contributed positively to the growth and reproduction of individuals in our model. Yet, despite  
many indicators showing good performance of the population at the beginning of 2004, the  
524 lower food during the second part of 2003 was the reason why age 1 individuals and adults  
showed low energy density in 2003 (Figs. S7E). This led to insufficient accumulation of reserves  
526 to face the winter and caused the drastic drop of energy observed between 2003 and 2004 (Fig.

S7J). Furthermore, the high temperature of 2003 and the early zooplankton bloom could have  
528 favoured the growth of individuals in the first half of 2003, with a consequent increase of  
maintenance costs at the individual level (proportional to body volume). In this sense, the model  
530 predicts a trade-off along the size spectra, with lower predation-based mortality for bigger  
individuals but also higher risk to starve. This could make the population especially sensitive to  
532 subsequent 2003-2004 winter scarcity of food and explain the lowest-in-the-time-series weight  
gain as well as high bioenergetics mortality ( $Z_{DEB}$ ) at age 1 between January and May 2004 (Fig.  
534 S7C). All these phenomena, together with the lowest fecundity of the time series in 2004 as a  
consequence of the low food in the second part of 2003 (Fig. S7G), led to the collapse of the  
536 population in 2005.

538 After 2005, several indicators showed positive trends for the recovery of the population. The  
proportion of individuals dying because of energetic failure ( $Z_{DEB}$ ) in 2006 dropped and stayed  
540 low until 2012 (Fig. 6), except for 2007. These years were warm in general (Figs. S1, S2, S4),  
and with zooplankton in late autumn (Fig. S3), resulting in shortening of the winter period and  
542 thus decreasing starvation risk. In 2013  $Z_{DEB}$  rose again, which coincided with a delay in the  
bloom of zooplankton resulting in food scarcity at the end of winter, increasing the mortality of  
544 age 1 individuals by starvation. This truncated the recovery of the modelled population between  
2013 and 2014 according to our simulation. The observations from the CBBM, on the other  
546 hand, showed drastic drops of the biomass in 2011 and 2012. None of our simulations captured  
these features, but it is worth noting that CBBM estimates may be subject to considerable error  
548 as well.

### Retrospective application of the HCR

550 One of the consequences of the closure of the fishery between 2005 and 2010 was the  
subsequent implementation of the HCR to estimate the TAC of anchovy in the Bay of Biscay.  
552 This measure established a lower SSB boundary of 24,000 tonnes to close the fishery and a  
maximal catch of 33,000 tonnes if the estimated SSB was higher than 89,000 tonnes (see  
554 Materials and methods and Sánchez et al., 2019 for a deeper analysis of the HCR). Simulating  
this HCR from the beginning of the period is a direct application of the DEB-IBM approach, and  
556 is useful for evaluating the utility of this policy to prevent the collapse of the population. Also, it  
permits us to analyse whether the upper TAC limit of 33,000 tonnes is sufficiently restrictive to  
558 avoid situations of risk for the population. In this manner, under scenario 4, we found that the  
biomass of the population remained well over the lower boundary of 24,000 tonnes during the

560 whole simulation (Fig. 7D), and also, that the biomass minimum occurred in 2003, after which  
the population started to increase slightly. This result shows that the current HCR could be  
562 adequate to avoid the collapse of the population under similar circumstances, but also showed  
that the population would have been impeded from growing as much as under scenario 0,  
564 where the closure of the fishery for five years was pivotal for the increase of the population to  
current values of around 150,000 tonnes (Fig. 3A).

## 566 Model limitations and sensitivity analysis

The integrated DEB-IBM model presented here contains inherent noise related to model  
568 parametrization and estimated parameters. At the individual level, the genetic inter-individual  
variability within the population was not considered, instead the unique determinant of the  
570 individual life history trajectory and phenotype was the environmental conditions from the birth  
date. Also, the model is constructed based on more than 20 parameters within the IBM and  
572 DEB modules that are subject to estimation errors (see Gatti et al., 2017). These parameters  
were calibrated in regards of individual size, weight-at-age, seasonal data on energy density,  
574 and yearly time-series of population biomass which further introduced some error. The overall  
error associated with the calibration of our mortality parameters is difficult to assess since the  
576 CBBM biomass time-series used as reference is an estimation from an assessment model  
containing its own intrinsic uncertainties (Ibaibarriaga et al., 2008). The density-dependent  
578 mortality ( $Z_{DD}$ ), only applied to the larval stage in our model, likely affects juveniles and adults as  
well, introducing more error in the estimations of mortality. The initialization parameters used for  
580 the population in 1996 were also obtained from surveys (see Gatti et al., 2017), being subject to  
estimation errors as commented before and introducing some noise into the model as well.  
582 Initialization parameters always influence simulations, and the purpose of this work was to use  
the most realistic set of initial conditions available from data. Hence, we considered the  
584 population structure and energetics respectively from the surveys (see Gatti et al., 2017) and  
the individual run with climatological forcing (Fig. S5) as reliable data for initialization. Minor  
586 adjustments in DEB parameters ( $p_{Am}$  and  $K$ ) relative to the work of Gatti et al. (2017) were  
applied in order to stabilize the population during the spin-up period. These parameters were  
588 chosen because they had the highest uncertainty of estimation. The stabilization of the  
population during the spin-up period was measured in terms of the number of SIs conforming  
590 the population (around 130), but still there was an important gap between the modelled  
population biomass and CBBM data in 2000.

592

At the population level the model is not spatially explicit, which means that all the environmental  
594 variables are averaged over the area of study (Fig. 1). This limits the effectiveness of the model  
because spatial processes, such as the variability in spatial distribution throughout the life cycle,  
596 or variability in larval drift, may explain part of the unresolved variability between the  
observations and the historical evolution of the population. In any case, it is also worth to  
598 mention that while new model components such as spatial detail, or individual variability, could  
increase the resolution of the model, they could also make predictions more uncertain if poorly  
600 parameterized. Furthermore, the outputs from the physical-biogeochemical model providing  
environmental data (POLCOMS-ERSEM) contain their own sources of error. Improving both  
602 aspects in our model (individual variability and spatial detail) seems to be necessary to increase  
the resolution of the model, whereas they could lead to more uncertain predictions if poorly  
604 parameterized.

606 Finally, a sensitivity analysis was carried out in order to determine the importance of variations  
of the considered environmental variables on the behaviour of the DEB-IBM model. This  
608 consisted of simulations of population biomass evolution under conditions of  
increased/decreased zooplankton concentration and temperature (Fig. S13). Generally, the  
610 response of the population was found to be favoured both by increased temperature and  
increased zooplankton, which could be understood from a bioenergetics perspective of  
612 metabolic enhancement leading to improved individual performance.

## 614 Conclusions

This is the first time that a bioenergetics model for the Bay of Biscay anchovy has been coupled  
616 to an IBM with the purpose of hindcasting the period of the population collapse and recovery at  
the beginning of the century. Our modelling approach allowed us to study the effect of the  
618 environmental and human pressures on the population of anchovy, and showed that the  
environmental variability had immediate consequences on the population dynamics, while the  
620 effect of the fishery was apparent on a longer temporal scale. Moreover, the collapse of the  
population seems to have been a joint consequence of an elevated fishing pressure in the  
622 years preceding the collapse and unfavourable environmental conditions in the year before the  
collapse, with an exceptionally long winter (leading to food scarcity) causing a great natural  
624 mortality due to starvation. In the same manner, the recovery of the population was mainly  
triggered by the closure of the fishery for 5 years and favoured by warmer years with short

626 winters leading to the appearance of larger individuals with high fecundity. Finally, a simulation  
of a retrospective implementation of the current HCR showed that this measure could have  
628 avoided the collapse of the population and the closure of the fishery in 2005.

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