



# Comparing biological traits of anchovy and sardine in the Bay of Biscay: A modelling approach with the Dynamic Energy Budget



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## ABSTRACT

Similar or very contrasted puzzling population dynamics between anchovy and sardine occur worldwide. Underlying factors are not well understood, but insights towards different biological traits are suggested, in particular trophic specialisation, leading to different responses to environmental conditions. Based on most striking differences in biological and life history traits, i.e. size, spawning and feeding, we calibrated a bioenergetics model, based on the Dynamic Energy Budget theory, for *Engraulis encrasicolus* and *Sardina pilchardus* in the Bay of Biscay. Starting from the anchovy model, differences in traits were successively integrated to build the sardine model through a novel exploratory approach by scenarios. We used a robust method for parameter estimation, the Evolution Strategies, with a large dataset of length and mass at age, as well as energy density, which is the first time in such a model calibration. Energy density data proved to be particularly well suited to assess the quality of DEB model predictions and parameter set estimates. Insights in respective physiology were drawn from analysis of parameter values and predictions of the model. We showed that anchovy and sardine have distinct strategies with respect to energy acquisition and especially to allocation to spawning. Anchovy are characterised by higher metabolic rates and requirements. This species is more likely to benefit from periods of high food availability to carry out both growth, spawning and reserve storage. Sardine have less demanding food requirements and metabolic costs. Sardine take advantage of larger reserves storage capacity to decouple spawning and prey blooms and to lengthen spawning period, and thus display a more capital breeding spawning behaviour. Overall, our model outputs distinguish between anchovy that tend towards an almost “all or nothing” energetic strategy, and sardine that tend to carry out lower metabolic activities but on a more regular basis. This first modelling demonstration of a bioenergetics difference between these two species, and the explanation it brings in the understanding of their respective reproduction strategies, opens new perspectives in the interpretation of their differential responses at the population scale to environment variability.

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## 1. Introduction

Anchovy and sardine populations often co-occur around the world and have displayed out-of-phase fluctuations in the Pacific Ocean (Schwartzlose et al., 1999). Several hypotheses may explain such a pattern, e.g. trophic specialization (Canales et al., 2016; Fiechter et al., 2015; Van der Lingen et al., 2006) or temperature preferences (Fiechter et al., 2015; Takasuka et al., 2008). These fluctuations of biomass are probably rather due to slightly different biological traits and sensitivity to environmental conditions rather

than competition for habitat (Barange et al., 2009) or food (Van der Lingen et al., 2006).

In European waters, to our knowledge, no biomass alternations of stock biomass occurred, sometimes affecting one species and sometimes both. Since the mid-1990s anchovy and sardine abundances in the North Sea increased probably due to higher summer temperature (Alheit et al., 2012), enabling the expansion of local remnant populations (Petitgas et al., 2010). Bay of Biscay (BoB) anchovy collapsed in 2005 and has been in a state of recovery since 2010 (ICES, 2012). Sardine and anchovy in the Gulf of Lion display, since 2000s, poor fish condition associated with the depletion of older (and also bigger) individuals (Brosset et al., 2015). It is thus challenging to anticipate such dramatic changes in abundance, condition and distribution of both species in European waters.

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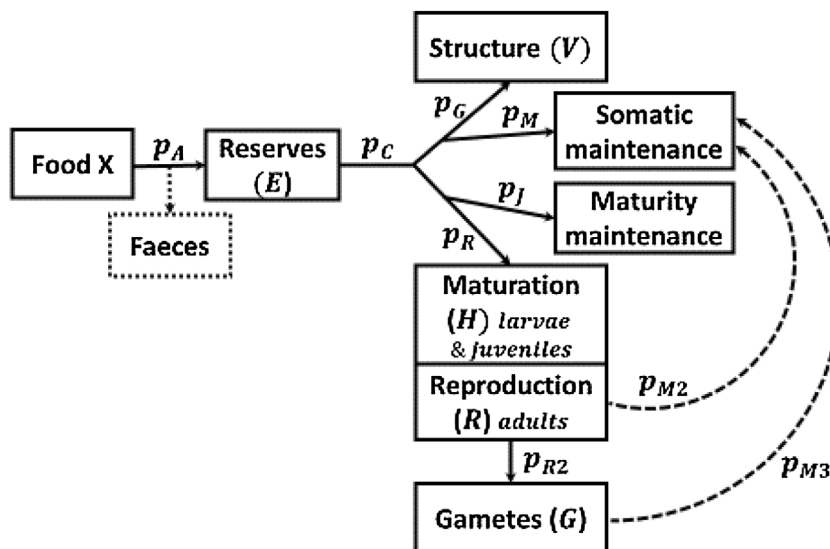


Fig. 1. Schematic representation of the structure of the DEB model and energy fluxes.

Working towards understanding such dynamics, we first need to accurately understand biology and life history strategies of both species. In the BoB, anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) obviously differ in size (sardine are larger than anchovy) and feeding strategy (anchovy feed more effectively on larger prey (Bachiller and Irigoien, 2015), while sardine feed more efficiently on smaller prey by filtering (Van der Lingen et al., 2006)). They also differ in terms of reproductive strategies, i.e. spawning season, frequency and fecundity per spawning event (Ganias et al., 2014). In the BoB, anchovy mainly spawn between May and July (Motos, 1996), whereas sardine seem to spawn earlier in spring, i.e. from March to June, as well as sporadically in autumn, i.e. from October to December (Coombes et al., 2006). There appear then to be two spawning peaks, but the occurrence of a continuous spawning through the winter cannot be rejected since no sampling effort was conducted during that season.

For a comprehensive understanding of the dynamics of these species, integrative approaches of the ecosystem may be required. Rose et al. (2015) developed an End-to-End approach by coupling a full life cycle model for anchovy and sardine in the California Current System, with a dynamic environment and a fleet model to simulate and understand past population dynamics of both species. However, disentangling the effects of internal and external processes on individuals of such similar species may become complex in such applications. Focussing on the biological traits and physiological processes at the individual level in response to the environment seems a reasonable first step. Bioenergetics theories quantitatively model energy flux inside the organism, from assimilation to latter allocation in different functions (e.g. growth, reproduction or maintenance). Among the bioenergetics approaches, the Dynamic Energy Budget (DEB) theory (Kooijman, 2010) has proved to be successful in reproducing patterns linked with size, through the “body size scaling relationship” (Pecquerie et al., 2011), temperature affinities (Freitas et al., 2010; Teal et al., 2012), habitat use (Teal et al., 2012) or food (Lavaud et al., 2014). The DEB model is generic and theoretically designed to suit a large variety of single organism. Parameter values for a given species are considered as indicators of its biological and physiological traits (Kooijman and Lika, 2014; Lika et al., 2011) and thus species can be compared with respect to their core parameterisation.

Our objective in this paper was to explore the respective biology and life history strategies of anchovy and sardine in the BoB using the DEB theory. Two DEB models have already been published for

anchovy (*Engraulis encrasicolus*), the first one in the BoB (Pecquerie et al., 2009) and the second one in the Gulf of Lion (Pethybridge et al., 2013). Our anchovy model is derived from those previous applications, but a new calibration based on an updated dataset was performed. To our knowledge no model has been published for sardine yet. The sardine model was built from the anchovy model by progressively integrating traits that appear of major importance to explain differences between the two species. These traits were size, reproductive and feeding strategies. Throughout the results and discussion sections, we first analysed and interpreted how the variations in those traits impacted the calibrated parameters values in both species. Then we relied on our model simulations to discuss biological and life strategy emergent properties with respect to species bioenergetics.

## 2. Material and methods

### 2.1. Fish data

An extensive data set was necessary to calibrate a full life cycle bioenergetics model covering the successive life stages (i.e. larvae, juveniles and adults). Length (cm), wet weight (g) and energy density ( $\text{kJ g}^{-1}$  wet weight) data at two seasons and over several years as well as for the different life cycle stages were compiled. The samples came from spring and autumn fisheries survey (PELGAS and EVHOE respectively from 2000 to 2014), dedicated surveys to larvae (PELGAS 2009–2012, ECLAIR 2008, SENTINELLE 2010 and PLAGIA 1999) and juveniles (JUVESU 1999, JUVAGA 2003 and 2005) as well as commercial landings.

Juveniles and adults samples were caught using pelagic or demersal trawls, measured and weighted respectively to the nearest 0.5 cm and 0.2 g and then frozen and stored for later age reading (in years) in laboratory by two experienced readers, following the ICES guidelines (ICES, 2011, 2009). Larvae were caught by towing the “Carré” net (Bourriau, 1991), an ichthyoplankton net with a one meter square aperture and 315  $\mu\text{m}$  mesh size, for 20 min at 2 knots between the bottom of the thermocline and the surface. Larval samples were then stored in ethanol and total length was corrected for shrinking following Somarakis and Nikolioudakis (2007). Daily age reading was performed following Allain et al. (2003).

Sexual maturity stages have been estimated routinely during surveys PELGAS and EVHOE and during commercial sampling

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