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RESEARCH ARTICLE

Shrinking body size of European anchovy in the Bay of Biscay

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Abstract

Decreased body size is often cited as a major response to ocean warming. Available evidence, however, questions the actual emergence of shrinking trends and the prevalence of temperature-driven changes in size over alternative drivers. In marine fish, changes in food availability or fluctuations in abundance, including those due to size-selective fishing, provide compelling mechanisms to explain changes in body size. Here, based on three decades of scientific survey data (1990–2021), we report a decline in the average body size—length and weight—of anchovy, *Engraulis encrasicolus* L., in the Bay of Biscay. Shrinking was evident in all age classes, from juveniles to adults. Allometric adjustment indicated slightly more pronounced declines in weight than in total length, which is consistent with a change toward a slender body shape. Trends in adult weight were nonlinear, with rates accelerating to an average decline of up to 25% decade^{-1} during the last two decades. We found a strong association between higher anchovy abundance and reduced juvenile size. The effect of density dependence was less clear later in life, and temperature became the best predictor of declines in adult size. Theoretical analyses based on a strategic model further suggested that observed patterns are consistent with a simultaneous, opposing effect of rising temperatures on accelerating early growth and decreasing adult size as predicted by the temperature-size rule. Macroecological assessment of ecogeographical—Bergmann's and James'—rules in anchovy size suggested that the observed decline largely exceeds intraspecific variation and might be the result of selection. Limitations inherent in the observational nature of the study recommend caution and a continued assessment and exploration of alternative drivers. Additional evidence of a climate-driven regime shift in the region suggests, however, that shrinking anchovy sizes may signal a long-lasting change in the structure and functioning of the Bay of Biscay ecosystem.

KEYWORDS

Bergmann's rule, body size, *Engraulis encrasicolus*, European anchovy, James' rule, metabolic theory, ocean warming, temperature-size rule

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1 | INTRODUCTION

Together with an altered phenology and shifts in spatial distribution, declines in species body size are often cited as the third major biological response to climate change (Gardner et al., 2011; Poloczanska et al., 2016; Sheridan & Bickford, 2011). Attention to body size reflects the impact that changes in this key biological trait exert on multiple aspects of the performance and life history of species, their role in food webs and their contribution to ecosystem functioning (Peters, 1983; Sibly et al., 2012). Shrinking body sizes are of particular concern in the marine realm (Daufresne et al., 2009; Forster et al., 2012), where food webs are strongly linked by size (Cohen, 1994; McGarvey et al., 2016), and where species are adapted to relatively narrow thermal niches (Fry, 1971). In the case of ectotherms, or "cold-blooded" species, like most marine fish, the impact of warmer conditions is clearly manifested through the temperature-size rule (TSR). The TSR establishes that, under controlled experimental conditions, individuals reared at warmer temperatures increase their initial growth rates with respect to conspecifics developing in colder waters, but emerge at a smaller adult body size (Atkinson, 1994; Atkinson & Sibly, 1997). Available estimates suggest an average shrinking of 3.65% in dry mass per degree of warming for aquatic species (Forster et al., 2012, based on experiments with 115 species including freshwater fish), which more than doubles comparable estimates for terrestrial ectotherms.

Despite extensive experimental data support TSR as a plastic response in most ectotherms (Clarke, 2017), its actual importance under natural conditions remains unclear (Audzijonyte et al., 2020; Huang, Ding, et al., 2021; Solokas et al., 2023; Verberk et al., 2021). In the field, size at age depends on the balance between individual growth and reproductive allocation, but also on selective survival. In the case of marine fish, lack of consensus is partly due to other processes affecting body size, like human exploitation (Sharpe & Hendry, 2009), fluctuations in population abundance (Rogers et al., 2011), or changes in food availability (Beveren et al., 2014; Lindegren et al., 2020). These alternative drivers add to the difficulty of adequately characterizing potentially weak responses to slowly varying environmental factors like temperature, and require extended monitoring efforts. The signature of TSR under natural conditions can be inferred, however, through biogeographical analysis of intraspecific variability in fish body size. For instance, metanalytical studies such as van Rijn et al. (2017) report an average decline of up to 10% in maximum length per degree of temperature increase for 74 fish species across the Mediterranean, while Saunders and Tarling (2018) found a decline in the standard length of 9 of the 11 most abundant mesopelagic fish species of the Southern Ocean as they moved from colder to warmer waters.

A complementary approach to TSR focuses on studying changes in species growth rates and body sizes through time. For instance, Thresher et al. (2007) analyzed otolith growth in the juveniles of eight long-lived fish species in the southwest Pacific. They found a strong positive association between temperature and growth rate in six species, with increased growth in species inhabiting rapidly warming near-surface waters and decreased growth in species experiencing cooling trends at depth. The experimental study by Huss et al. (2019) also found, as predicted by TSR, that artificial warming progressively enhances juvenile growth rates of Eurasian perch in the Baltic Sea, but not adult maximum size. Baudron et al. (2014) found trends toward an average decrease of 23% in yield per recruit over four decades in six of eight commercially exploited species associated with North Sea warming. The extensive study by Audzijonyte et al. (2020) found idiosyncratic changes in mean body length in relation to temperature in 335 coral reef fish species across the Australian continent, with a slight predominance of shrinking trends but no clear association with ocean warming.

Dissenting results demand further assessment of declines in fish body size and the potential role of climate warming. In this study, we develop an approach to analyze trends in fish body size over time and test the potential role of TSR compared to alternative candidate mechanisms such as changes in exploitation rates, resource availability and density-dependent effects. To this end, we take advantage of three decades (1990–2021) of careful scientific monitoring of body size at age of the anchovy population in the Bay of Biscay (ICES, 2021a, 2021b; Motos et al., 2005; Santos et al., 2018). Like other small pelagic fish species, anchovies play a key role in the functioning of coastal marine ecosystems and support important fisheries (e.g., Checkley et al., 2009). Their short lifespan makes them particularly vulnerable to changes in environmental conditions, and recent studies have revealed declines in growth and body size of anchovies and other small pelagics around the world (e.g., Albo-Puigserver et al., 2021; Canales et al., 2015, 2018; Lyashevska et al., 2020; Reum et al., 2013; Saraux et al., 2019), including the Bay of Biscay and areas nearby (Boëns et al., 2021; Doray, Petitgas, Huret, et al., 2018; Menu et al., 2023; Véron et al., 2020). Declines in anchovy size match a rebound to record population numbers after the closure of the fisheries between 2005 and 2010, providing an unpaired opportunity to assess the relative contribution of TSR to explain changes in body size with respect to intrinsic population mechanisms excluding fishing.

Our approach allowed us to reveal nonlinear trends in anchovy size through time and to characterize environmental and ecological correlates of size throughout the life cycle of anchovy, including the varying signature from juveniles to young and old adults that characterizes the TSR. We combined these analyses with a biogeographical assessment of TSR trends in the body size of different anchovy species and populations to frame our results in an eco-evolutionary framework. Finally, we developed a theoretical analysis to assess whether observed changes in size at age with temperature are consistent with observed variation among anchovy populations or across species in response to large scale ocean temperature gradients.

2 | MATERIALS AND METHODS

2.1 | Anchovy in the Bay of Biscay

European anchovy, *Engraulis encrasicolus* L., is a small pelagic fish species widely distributed along the coastal Mediterranean Sea and eastern Atlantic Ocean, from the North Sea to the Angola current

(Whitehead et al., 1988; see also www.fao.org/fishery/species/2106 and Figure 1). It is a short-lived (usually does not exceed 3 years of age) and fast growing species that reaches maturity during its first year of life. In the Bay of Biscay, anchovy spawning season extends from March to August, with a maximum intensity peak between May and July (Motos et al., 1996). From the tiny, characteristically rod-shaped anchovy eggs, larvae hatch with an initial length of 2.97 mm (Aldanondo et al., 2008). In about 2 months, surviving larvae metamorphose into juveniles with a length of ~30 mm (Aldanondo et al., 2011). During its first year of life, juveniles continue growing and mature into adults that, in the Bay of Biscay, reach a length of up to 150 mm, which is equivalent to ~75% of their maximum length (Uriarte et al., 2016).

As other Clupeoids, anchovy is a planktivorous fish that forms large migrating schools preyed upon a wide variety of predators, including other fish species, seabirds, and marine mammals (Astarloa et al., 2019; Corrales et al., 2022). It is also extensively exploited for food consumption and as live bait throughout its range. In the Bay of Biscay, it supports important fisheries operated by two fleets of purse-seiners and of pelagic trawlers—currently about 200 and 24 (12 pairs) vessels, respectively—that mainly capture the most abundant age 1 individuals on spawning aggregations and feeding shoals (ICES, 2021b; Uriarte et al., 1996). The fisheries peaked in the early 60s and then steadily decreased, which prompted the establishment of a long-term monitoring program in the late 80s following a period of extraordinarily low catches (Uriarte et al., 1996). Catches recovered in the 90s but anchovy declined again leading to the collapse and closure of the fisheries between 2005 and 2010. Fisheries reopened adopting a biomass-based catch bounded harvest strategy (up to 33×10^3 t), which currently corresponds to maximum harvest rates at or below 40% of the spawning biomass (see Uriarte et al., 2023, for a recent review). The population rebounded back to sustainable levels, with a historical highest abundance estimate above 200×10^3 t in 2021 (ICES, 2021b, see also Figure S1). Recent analyses, however, revealed a decline in anchovy size at age (e.g., Chust et al., 2022; Doray, Petitgas, Huret, et al., 2018; Menu et al., 2023). Shrinking anchovy size is becoming a major concern for the operation and profitability of the fisheries, and an indicator that is likely flagging changes in ecosystem functioning in the entire Bay of Biscay (Chust et al., 2022).

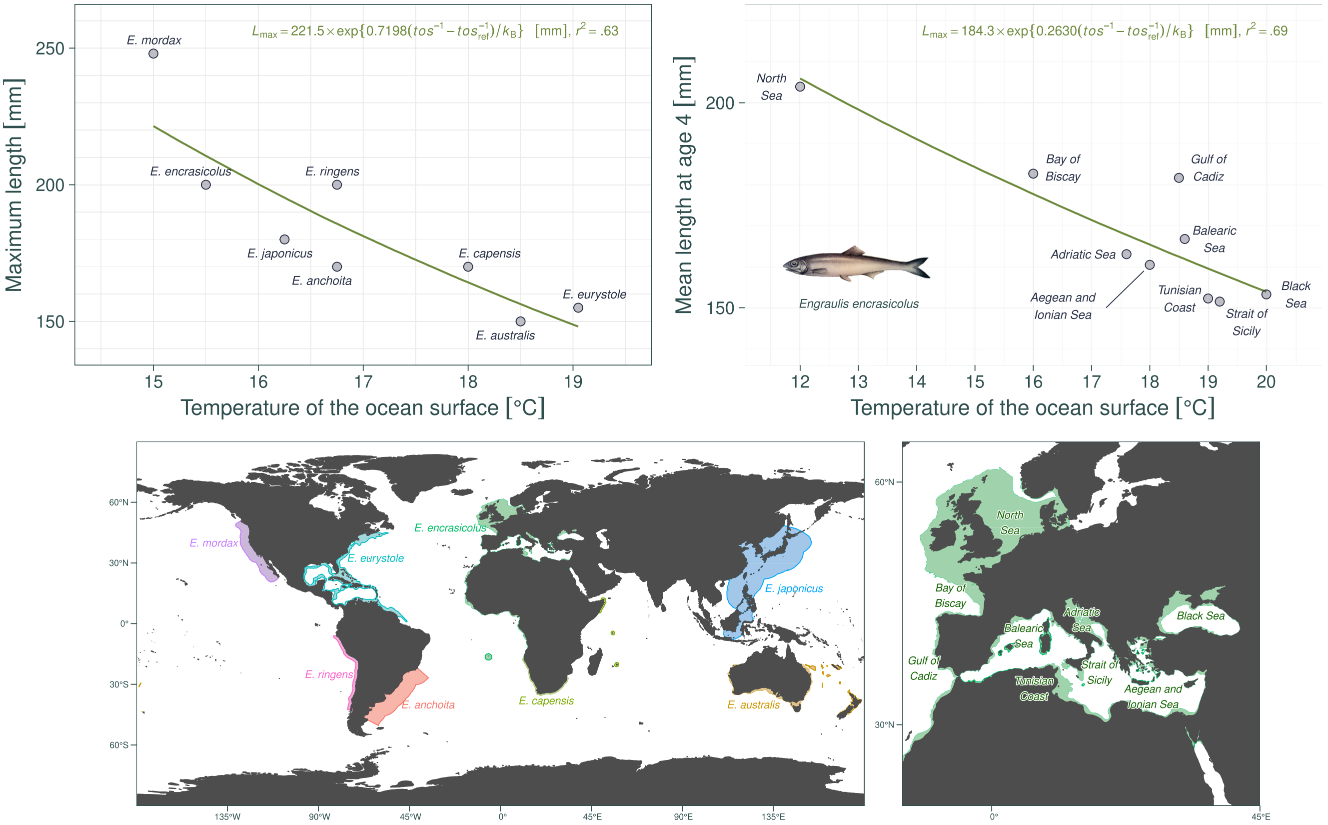


FIGURE 1 Ecogeographical patterns in the variation of anchovy body size with temperature. *Top left*: the maximum length of anchovies from the genus *Engraulis* decreases with temperature in agreement with Bergmann's rule, which states a tendency toward a larger body size in colder environments when comparing a set of closely related species. *Top right*: the mean body size of age 4 individuals from European anchovy, *E. encrasicolus*, populations distributed along the northeast Atlantic and Mediterranean coasts also decreases with temperature. This second pattern aligns with the predictions of James' rule, which states that the same tendency predicted by Bergmann's rule can be found when analyzing intraspecific clines in body size in relation to environmental temperature. The label on each panel shows posterior medians for each parameter on the natural scale after back-transformation of the intercept. *Maps*: the global map at the bottom left shows the distribution of the species featured in the analysis of Bergmann's rule. The detail map on the bottom right shows the approximate location of each of the populations featured in the analysis of James' rule. Distribution maps were retrieved from FAO (2022). Background cartography made with Natural Earth. See Section 2.3.1 for further details.

2.2 | Time series of anchovy size at age

Scientific monitoring of Bay of Biscay anchovy population extends traditional approaches with a set of dedicated surveys conducted each year in spring (May) and fall (September–October) (Figure S2; ICES, 2021b). These surveys gather careful measurements of anchovy body size (length and fresh weight) that, together with estimates of population abundance, allowed the assessment of trends in anchovy size at age. The text below summarizes the main characteristics of the surveys, though Section S3.1 provides full details about the surveys.

Fall surveys are named *Juvena* (2003–present) because they target the assessment of the abundance and size structure of young of the year anchovy juveniles using acoustic methods (Boyra et al., 2013). Survey design consists of a series of transects between coastal and open ocean waters along the entire Bay of Biscay (Doray et al., 2021; ICES, 2015). The vessels record acoustic targets up to a depth of 200 m, and tow 2–3 pelagic trawl hauls per day to account for changes in species composition and size structure along the transects (Doray et al., 2021; Simmonds & MacLennan, 2005). The latter involve sorting the catches by species as well as measurements of total length and fresh weight.

Spring surveys target the assessment of spawning biomass and involve two independent approaches; acoustic surveys (Doray, Petitgas, Romagnan, et al., 2018) and the daily egg production method (DEPM; Motos et al., 2005; Santos et al., 2011, 2018; Somarakis et al., 2004). We analyzed here data gathered during *Bioman* surveys (Biomass of Anchovy; 1987–present, Santos et al., 2023) to apply the DEPM. Additional analyses developed by Uriarte (2015) enable estimation of numbers- and size-at-age based on otolith readings, sexing and measurements of total length and fresh weight (Uriarte et al., 2016).

Available *Juvena* surveys have comprised between 7 and 57 hauls positive for juvenile anchovy per survey, which provide an independent sample of juvenile size throughout the Bay of Biscay (Figure S2). Surveys have been conducted each fall since 2003 with no gaps (i.e., 19 surveys in total). Available *Bioman* surveys have comprised between 21 and 94 hauls per year distributed along coastal and open waters of the Bay of Biscay (Figure S2). A lack of appropriate metadata restricted the analysis to the period 1990–2021, though there are four surveys in between lacking some data on anchovy adults (1993, 1996, 1999 and 2000), resulting in a total of 28 surveys providing adequate data to conduct our analyses. Both surveys recorded length and fresh weight at age together with estimates of relative abundance at age for each fishing haul, providing appropriate weighting factors to estimate the mean size of anchovy by age at the population level, as further detailed below (see Section 2.3.2).

2.3 | Statistical analyses

Analyses comprised three separate stages. A first stage targeted the characterization of biogeographical patterns of variation in anchovy body size with temperature to later infer eco-evolutionary constrains. A second set of analyses focused on the assessment of trends toward reduced mean sizes at age for the anchovy population in the Bay of Biscay based on data gathered during *Juvena* and *Bioman* surveys, including the potential occurrence of a change in the rate of decline in recent years. A third set of analyses targeted the assessment of the potential drivers underlying changes in anchovy size in the Bay of Biscay. These analyses considered the potential effect of environmental temperature, resource availability and the biomass of conspecifics on anchovy individual size.

All computer codes and data necessary to replicate the analyses and produce the figures and tables that appear in the manuscript are available at the sizanc repository (Taboada et al., 2023).

2.3.1 | Ecogeographical patterns in anchovy body size

Declining anchovy body sizes could be a direct response to ocean warming and the progressive exposure of anchovy to higher ambient temperatures. In ectotherms, such a response would be consistent with phenotypic plasticity, specifically, with the TSR (Atkinson, 1994; Atkinson & Sibly, 1997). At larger scales, two major ecogeographical rules provide a baseline to assess the response of adult size in marine fish to changes in temperature (e.g., Blackburn et al., 1999); Bergmann's rule states a tendency toward larger size in colder environments when comparing a set of closely related species, while James' rule states that the same tendency can be found when analyzing variation in body size across populations of the same species.

We gathered data on adult size for species from the genus *Engraulis* to assess Bergmann's rule, and from different populations of *E. encrasicolus* in the northeast Atlantic and the Mediterranean Sea to assess James' rule (see Figure 1 for more details on the species and populations featured in the analysis and their spatial distribution). We sought data on adult maximum size to assess potential constraints on idealized growth. We found data on the maximum standard length of all extant *Engraulis* species in FishBase (Froese & Pauly, 2022), except for the recently described *E. maeoticus* (see Bonhomme et al., 2022). Annual temperatures experienced by each species were calculated from the data gathered by Reid (1967), except in the case of *E. eurystole*, for which data came from AquaMaps (Kaschner et al., 2019). However, analyses of James' rule leveraged on the predictions of mean standard length at age 4 and temperature data assembled by Uriarte et al. (2016) for *E. encrasicolus* populations. We implicitly assumed these data represented changes in adult size independent of gradients in fishing pressure and other factors, and that the ratio between maximum and adult size did not vary across populations.

Analyses proceeded by fitting a simple exponential model featuring an Arrhenius term to estimate the magnitude of changes in anchovy body size with temperature as an activation energy (Sibly et al., 2012), either among *Engraulis* species (Bergmann's rule) or among populations of *E. encrasicolus* (James' rule). The model took the form $L = L_0 \exp\{-E_a / k_B T_{os}\}$, where L [mm] is total length (maximum or mean length depending on the analysis), L_0 [mm] is a baseline length at a reference temperature (here we set $T_0 = 288.15\,\text{K}$), E_a [eV] is the activation energy, $k_B = 8.617 \times 10^{-5}\left[\text{eV K}^{-1}\right]$ is Boltzmann constant, and T_{os} [K] is environmental temperature. After taking the natural logarithm of anchovy lengths, we fitted the models using Bayesian simple linear regression with the R package rstanarm (Goodrich et al., 2022), setting default, weakly informative prior distributions (e.g., Gelman et al., 2020). Lack of data prevented a detailed assessment of phylogenetic constraints in the analyses of ecogeographical rules, so we regarded the data for each species and population as independent observations. Exploratory analyses suggested that including phylogenetic effects may change parameter estimates only slightly, consistent with the dominant effect of ecological constraints over common ancestry in explaining size variation in Clupeiforms (Bloom et al., 2018). The exponential model fits provided reference estimates to assess whether observed declines in anchovy size at age in the Bay of Biscay are more consistent with plastic and genetic variation among populations or with an evolutionary response to ocean warming, as further detailed in Section 2.4.

2.3.2 | Trends in anchovy size and identification of distinct regimes

The second set of analyses targeted the assessment of the presumed declining trends in the size at age of *E. encrasicolus* in the Bay of Biscay, including an eventual change point toward accelerated declines in recent years. Data gathered during *Juvena* and *Bioman* surveys provide time series records of anchovy mean total length, $l_{a,t,h}$ [mm], and wet weight, $m_{a,t,h}$ [g], at age $a \in \{0, 1, 2, 3+\}$ in year t for each haul h grouped into the strata $s[h]$. Analyses based on survey data further provide estimates of the relative abundance of age class a during year t for the stratum $s[h]$ of each haul, which were normalized to calculate the weighting factors $\omega_{a,t,s[h]}$, by the condition $\sum_j \omega_{a,t,j} = 1$. These weights enable proper weighting of haul level data to estimate population level averages for each survey year. Note that $a = 0$ and $h \equiv s[h]$ for *Juvena* surveys, where echosounder data allow simultaneous retrieval of body size and estimates of relative abundance. In the case of *Bioman* surveys, $a \in \{1, 2, 3+\}$ and each strata $s[h]$ includes one or more nearby hauls. Data on adult size and status need to be combined with observed egg production at the regional scale to assess spatial changes in relative abundance while applying the DEPM (Uriarte, 2015).

To estimate trends in mean size at age for the population, we applied a set of nested hierarchical Bayesian models featuring: (i) a data model layer to link model predictions with size observations gathered during the surveys, (ii) a process model layer predicting trends in anchovy size at age at the population level as a function of time, and (iii) a set of priors that, in the case at hand, just contributed weak information. We separately fitted models to length or weight observations for each age class *a*. This approach allowed us to later compare time trends and environmental effects based on posterior estimates of size at age. Differences in trend estimates among size measures follow in principle from simple allometric scaling. In a logarithmic scale, the magnitude of changes in weight through time are expected to approximately triple the changes in length because $m \propto l^3$ for anchovy according to available data at FishBase (Froese & Pauly, 2022) (i.e., $d\log(m)/dt = 3\,d\log(l)/dt$). Note that estimates based on survey data suggest an exponent close to 3.26 (Figure S13). Deviations from the 1:3 ratio between trends might point changes in individual shape (i.e., the so called fish body condition factor, $K = 100\,mL^{-3}$; see Jones et al., 1999). Importantly, in the following we just refer to size and omit subscripts for age to simplify the notation.

All the hierarchical models shared the same data model, which accounts for survey stratification by weighting the likelihood function based on available $\omega_{a,t,s[h]}$ estimates;

$$\log y_{t,h} \sim \omega_{t,s[h]} \times \mathcal{N}(u_t, \sigma), \tag{1}$$

where we assume that the natural logarithm of observed mean length or weight at age per haul, $y_{t,h}$, follows a Gaussian distribution with unknown underlying mean, u_t, and standard deviation σ.

The process model predicts a latent time series of the mean size at age at the population level x_t using a deterministic model (i.e., Equation 2), where x again corresponds either to length or weight for a given age. Predicted mean sizes are related to the underlying population mean u_t through a Gaussian sampling model; $u_t \sim \mathcal{N}(x_t, \nu)$, where the standard deviation ν accounts for deviations between model predictions and the underlying "true" mean, which were assumed to be of similar magnitude during the entire study period. The complexity of the process model for x_t ranges from a null model assuming a constant mean trend (i.e., no change in size at age), to a model featuring temporal autocorrelation and a change in the magnitude of trends in anchovy size:

$$x_t = \mu_x + \rho_{AR}(u_{t-1} - x_{t-1}) + (\beta + \delta_\beta[t \geqslant \tau]) \times (t - \bar{t}), \tag{2}$$

where predicted means combine an intercept μ_x, an autoregressive (AR) term to dampen deviations from the underlying population mean at age u_t at a rate ρ_{AR}, and a linear trend with slope β increased by an amount δ_β just after the change point year τ. The latter component will flag the presence of a shift between distinct regimes in the series when $\delta_\beta \neq 0$, which we loosely define as a period with a marked change in the trend. Later in the manuscript, slope parameters will be conveniently redefined as $\beta_1 = \beta$ and $\beta_2 = \beta + \delta_\beta$ to ease comparisons of the linear trend defining regimes before and after the change point τ, respectively. Time indices t were centered by subtracting their mean ($\bar{t}$) to interpret the intercept μ_x as the grand mean halfway through the series. As further detailed in Tables S1 and S2 in Section S2.3.2, setting one or more model parameters to zero results in alternative process models of varying complexity (e.g., when $\beta = \delta_\beta = 0$, the resulting constant autoregressive model simplifies to the null, red noise model proposed by Rudnick and Davis (2003) to discard spurious regime shifts; if $\delta_\beta = 0$, the model contemplates no regime shift).

Alternative models were fitted using Markov chain Monte Carlo methods (e.g., Gelman et al., 2014) in stan (Stan Development

Team, 2023). We extended the default formulation of multiple change point models developed by Lindeløv (2020) to account for the additional uncertainty due to the estimation of annual mean size (the data layer of our hierarchical model). We kept default uninformative priors for model coefficients and change points (Lindeløv, 2020), and for error terms (Gelman et al., 2020, see also Section S2.3.2 for further details). Inference was based on 5000 posterior samples following 45,000 iterations for adaptation from four parallel chains to ensure convergence. We calculated the median and 90% central, quantile-based intervals to summarize posterior parameters distributions taking advantage of the R interface rstan (Stan Development Team, 2022). Model selection proceeded based on the leave-one-out (LOO) criterion implemented in R package loo (Vehtari et al., 2022), which uses approximate cross-validation to assess models based on their out-of-sample prediction accuracy (Vehtari et al., 2017), and stacking to estimate the relative weights $\omega_{\mathrm{LOO}} \in [0,1]$ assigned to each model to maximize leave-one-out predictive density when combining their predictions (Yao et al., 2018).

2.3.3 | Environmental and ecological correlates of anchovy size

The third set of analyses attempts to unravel the possible drivers of observed changes in anchovy body size in the Bay of Biscay. To do that, we used linear regression to analyze the association between the natural logarithm of anchovy size at age and three covariates representing environmental temperature, resource availability and the abundance of conspecifics. The rationale to test the association between environmental temperature and body size was extensively detailed in Section 2.3.1 though it can be succinctly summarized as "hotter is smaller" (Kingsolver & Huey, 2008). Besides the expected effect of temperature, years of resource shortage may depress growth and tend to be associated with smaller individual sizes at age, just like a string of years of bonanza would result in larger average sizes. Recent analyses suggest however the opposite trend. For instance, Bachiller et al. (2013) found a positive trend in the relative weight of anchovy stomachs from 2003 to 2010. Further, conditions in the Bay of Biscay have become more favorable for anchovy, at least in terms of the abundance of prey (see e.g., Valdés et al., 2021, for a recent review of trends in zooplankton biomass), while extensive analyses based on imaging samples reveal a stable taxonomic composition and spatial structure of the mesozooplankton community (Grandremy, Romagnan, et al., 2023). In that context, we also considered the potential impact of changes in population abundance through density-dependence. On the one hand, higher abundances may prompt declines in size through reduced per capita resource availability. On the other hand, increased abundance may be a consequence of relaxed selection pressures, which might allow the survival of individuals of a smaller size compared to those persisting under less favorable conditions as predicted, for instance, under growth-selective predation (Takasuka et al., 2003, 2017). Both hypotheses predict a decline in size at high population abundances.

We extracted temperature of the ocean surface data from National Oceanic and Atmospheric Administration (NOAA) Optimum interpolation 0.25° daily sea surface temperature analysis (*oiSST* version 2.1), which is available since September 1981 (Banzon et al., 2016; Huang, Liu, et al., 2021). We calculated annual average temperatures based on the AVHRR-only version of the product. To represent potential changes in resource availability, we retrieved satellite based estimates of chlorophyll *a* concentration produced by ACRI-ST for Copernicus Global Ocean Satellite Observations (OCEANCOLOUR_GLO_BGC_L4_MY_009_104). It is important to stress that anchovy is predominantly zooplanktivorous, and that chlorophyll acted here as an indirect proxy of food availability. We calculated an annual time series between 1998 and 2021 based on the monthly, "cloud free" 4 km data product, generated by CMEMS using space–time interpolation to merge SeaWiFS, MODIS, MERIS, and VIIRS-SNPP daily retrievals. Finally, to assess density-dependent effects, we retrieved a time series of anchovy spawning stock biomass estimates from the 2021 assessment conducted by ICES (2021b). In all cases, we applied a moving average filter rolling over the year in which each age class was born and the year of each survey to average covariate data for the each age class. There was a low correlation between covariates ($r < .5$) that, together with variance inflation factors below 2, suggested a low risk of multicollinearity. Use of subannual averages did not alter the results. In the case of temperature and resource availability, we averaged data over the Bay of Biscay continental shelf, defined here by the bottom depths below 500 m based on GEBCO Compilation Group (2022) bathymetry data, within the quadrangle defined by the coordinates 6° W 43° N and 0° 47° N, to approximately match anchovy distribution. Figure S1 displays raw time series data for each covariate.

Analyses related covariates representing temperature, resource availability and density-dependence, with posterior estimates of anchovy length and weight at age, u_t, resulting from the analyses of trends in anchovy size described above (Section 2.3.2). Uncertainty from the estimation of u_t was propagated to the regression analyses using Zellner's G priors (e.g., Hoff, 2009) to reduce the computation burden. We fitted seven alternative models (ranging from simple regression models with a single covariate to the full model with the three covariates), for four age classes and two size measurements (length and weight). These 56 combinations (Figure S8) were assessed for the 20,000 posterior parameter estimates resulting from second stage analyses. Retained outputs included regression slopes and the coefficient of determination (r^2) with uncertainty summaries (90% central quantile intervals). We relied on a simple goodness of fit metric like r^2 to assess model performance to avoid nuances due to lack of covariate data for some years and imbalances in sample size.

2.4 | Temperature and anchovy size at age

To further assess the potential contribution of the TSR to observed changes in anchovy body size in the Bay of Biscay, we compared estimates of the relative change in size at age with temperature resulting from the analyses of survey data described above, with theoretical predictions based on the metabolic theory of ecology (Brown et al., 2004; Sibly et al., 2012). As discussed by Atkinson and Sibly (1997), the TSR may reflect a trade-off among early growth and mature size (see also Angilletta & Dunham, 2003; Forster & Hirst, 2012; Sibly et al., 2015). To capture such behavior, we extended the ontogenetic growth model of West et al. (2001) to incorporate the effect of temperature on early growth and final adult size (see Section S3.5 for full details)

$$m(t,T)=M_{\infty}(T)\left[1-\left(1-\left(\frac{m_0}{M_{\infty}(T)}\right)^{1-\alpha}\right)\exp\{-k(T)t\}\right]^{\frac{1}{1-\alpha}}, \quad (3)$$

where m is body mass in grams at age t for an organism growing at temperature T. The model is completed with newborn mass, m_0, adult asymptotic mass, M_{∞}, the growth parameter k $[\text{year}^{-1}]$, and the universal metabolic exponent $\alpha = 3/4$ proposed by the metabolic theory of ecology (e.g., Sibly et al., 2012). The dependence of the asymptotic biomass M_{∞} and the growth parameter k on temperature was featured through Arrhenius factors with activation energies $E_{g,M_{\infty}}$ and $E_{g,k}$ [eV], respectively. Use of Arrhenius factors restricts the model to normal, non-harmful temperature conditions, and it also presumes a linear scaling with inverse temperature that may only hold over a limited temperature range (Knies & Kingsolver, 2010). Typically, these activation energies have opposite signs, with $E_{g,M_{\infty}} < 0$ and $E_{g,k} > 0$, which result in faster growth rates at early stages but smaller adult sizes under warmer conditions; patterns that characterize the TSR and match the expected trade-off.

As further detailed in Section S3.5, it is possible to derive from Equation (3) a general, two-component expression for the expected relative change in mass at age with respect to temperature

$$\begin{aligned}\frac{\partial \log m}{\partial T} = {} & \frac{E_{g,M_{\infty}}}{k_B T^2}\left\{1-\left(\frac{m_0}{m}\right)^{1-\alpha}\exp\{-kt\}\right\} \\ & + \frac{E_{g,k}}{k_B T^2}\frac{1}{1-\alpha}\left(\frac{m}{M_{\infty}}\right)^{\alpha-1}\left(1-\left(\frac{m_0}{M_{\infty}}\right)^{1-\alpha}\right)tk\exp-\{kt\},\end{aligned} \quad (4)$$

in which the first term in the right hand side captures the contribution due to changes in asymtotic size M_{∞} with temperature, and the second term represents changes in the growth rate parameter k. Depending on the relative magnitude of the activation energies $E_{g,k}$ and $E_{g,M_{\infty}}$ (Figure S11), the model predicts that changes in size at age with increasing temperature will range from (*a*) a rapid convergence toward a constant negative log ratio over the entire lifespan [as $(\partial k/\partial T) \rightarrow 0$], to (*b*) a pattern featuring an increase in size with temperature at early ages followed by a slower convergence toward declines in adult size due to $E_{g,M_{\infty}} < 0$.

We parameterized the allometric growth model (Equation 3) for anchovy based on estimates of average weight at age resulting from the analyses described above (Section 2.3.2). The fit returned estimates of k and M_{∞} under average conditions in the Bay of Biscay (see Section S3.5.3; Figure S13). Then we used Equation (4) to calculate the expected relative change in mass at age with respect to temperature, and compared the predictions with estimates based on observed changes in anchovy size. To do that, we set $E_{g,k} = 0.65$ [eV] based on estimates of the activation energy of heterotrophic respiration in marine ecosystems (López-Urrutia, San Martín, et al., 2006). The activation energy $E_{g,M_{\infty}}$ is more uncertain, so we assessed predictions based on the output of the analysis of ecogeographical rules (Section 2.3.1) with an estimate directly derived from on our data. We retrieved estimates of observed changes in anchovy size with temperature from the multiple regression models described in Section 2.3.3 to account for potential confounding due to the effect of resource availability and the abundance of conspecifics.

It is important to note that Equation (4) provides a strategic model for assessing the effect of temperature on size at age. The approach also presumed that the effects of three covariates considered were additive and independent, and that the analyses described in Section 2.3.3 returned reliable estimates of the partial effect of temperature on size. Section S3.5.4 briefly outlines other sign combinations that we found implausible, like growth depression at warmer temperatures (i.e., $E_{g,k} > 0$), and the expected effect of other environmental effects.

3 | RESULTS

3.1 | Anchovy body size and temperature: Ecogeographical rules

Analyses of biogeographical variation in anchovy body size in relation to temperature revealed patterns that are consistent with major ecogeographical rules (Figure 1). As predicted by Bergmann's rule, the maximum length of the eight anchovy species from genus *Engraulis* analyzed here declined in parallel with increases in water temperature. Their maximum lengths ranged from the 250 mm of *E. mordax* found in the cold waters of the California Current, to the 150 mm of the tiny *E. australis* that inhabits warm waters around the Australian continent, corresponding to a difference of 4°C in annual temperature. Exponential model fits suggested a decline close to a 10% per degree of increase in temperature in the maximum length of *Engraulis* species, corresponding to an activation energy $E_a = -0.72\,\text{eV}\,[-1.02, -0.39]_{90\%}$ (Figure 1 top left).

Analyses of variation in the body size of *E. encrasicolus* populations along the northeast Atlantic and the Mediterranean Sea also revealed a decline in average size with temperature (Figure 1 top right), which is consistent with the predictions of James' rule. Average length at age 4 declined from 200 mm in the North Sea, to 150 mm in the Black Sea, which corresponds to a difference in annual temperature of 8°C. The relationship for James' rule was however weaker than for Bergmann's rule, suggesting up to a 4% decrease in length per degree of increase in temperature among populations ($E_a = -0.26\,\text{eV}\,[-0.37, -0.15]_{90\%}$, Figure 1). The relationships for Bergmann's and James' rules explained more than half of the observed variation in anchovy body size across species and among populations, respectively.

3.2 | Shrinking anchovy in the Bay of Biscay

Analyses of time series of size at age data gathered during *Juvena* and *Bioman* surveys confirmed a decline in the length and weight of *E. encrasicolus* in the Bay of Biscay (Figure 2; see also Figure S3). Anchovy body size was larger before the closure of the fishery and continued to decline during the closure and after the reopening (Table S1). Shrinking trends, however, differed among age classes and among body size measures (i.e., length and weight). We detected a change point for trends in the body size of adult age classes but not for juveniles (the change point detected in juvenile length bears almost no change in the trend). The length of anchovy juveniles steadily declined at a rate close to 10% decade^{-1} (30% decade^{-1} for weight) according to model selection (Table S2). These estimates are less reliable due to the comparatively short span of the *Juvena* series (2003–2021) (i.e., as can be seen from the wide confidence intervals for the slope parameters β in Figure 2, which even contain zero in the case of length).

Adult anchovy size time series based on *Bioman* surveys extend back one more decade (1990–2021). Model selection results primarily differed among the two body size measures considered, length and weight at age (Figure 2; Table S2; Figure S3). Analyses of changes in adult length suggested a steady decline close to 4% decade^{-1} for age classes 1 and 3+, and only suggested a shift in the trend for age 2 adults, with rates of decline increasing from 2% decade^{-1} to 7.6% decade^{-1} after year 2002. In contrast, analyses of anchovy weight favored models featuring a change in trend for all adult age classes, depicting an initial period with almost no change in the mean weight of adults up to the early 2000s, followed by a steady decline of up to 27% decade^{-1} for age 2 individuals. Estimates of the exact timing of the shift from a flat trend to a fast decline in the size of adult anchovies are difficult to assess and the resulting estimates were highly uncertain. Our approach situated the regime shift circa 2001 for age 1 individuals, depicting the propagation to older age classes in subsequent years (see the rug plot in Figure 2). The magnitudes of estimated rates of decline for adults were smaller than those calculated for juveniles. The ratios between trends in length and in weight at age also deviated from those expected under constant allometric scaling (1/3), and were closer to 1/4 (Table S2; Figure S3). Such ratios suggest a decline in body condition toward slender body shapes due to a proportionally faster decline in weight than in length at age.

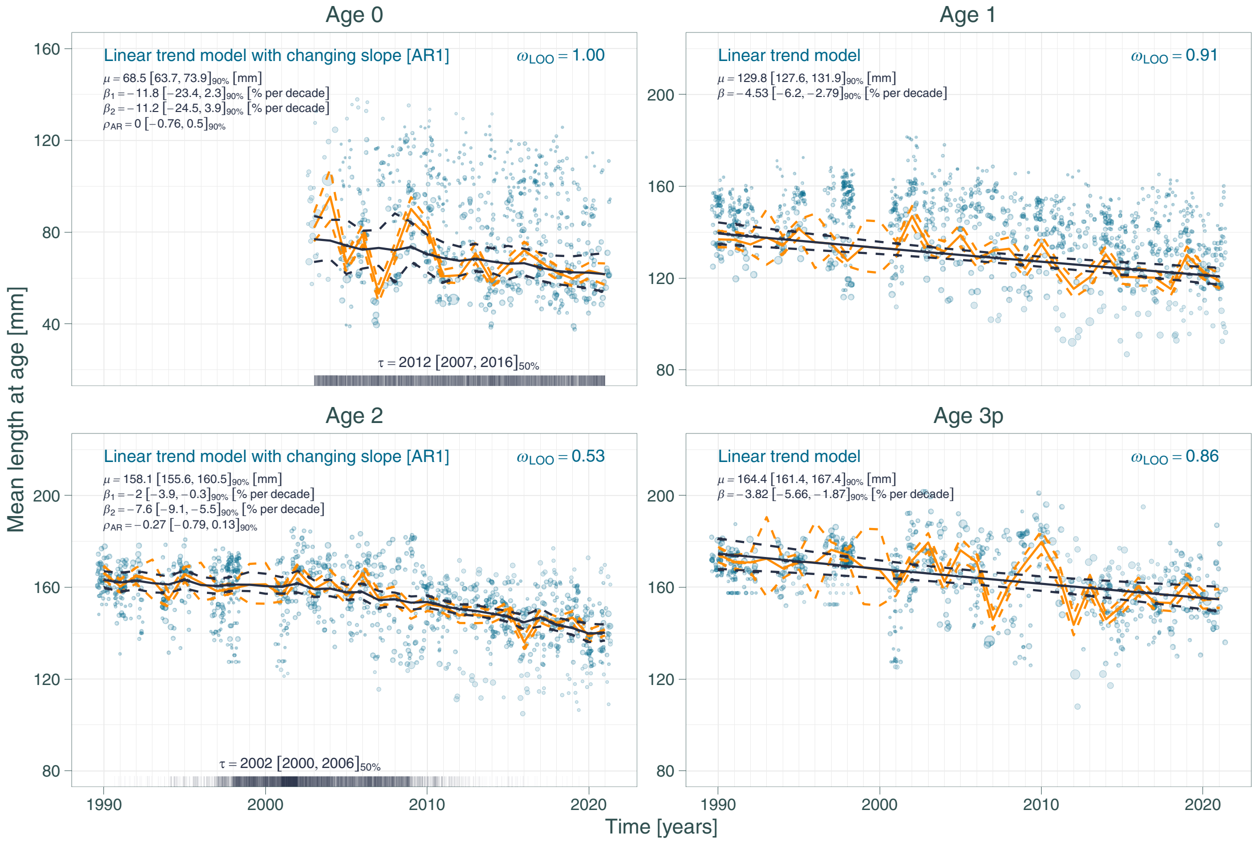
3.3 | Environmental and ecological drivers of declines in anchovy size

Analyses of variability in anchovy size revealed patterns of association with covariates representing temperature, resource availability and density-dependent effects, which were consistent for both length and weight at age (Table S3; Figures S4–S8). Figure 3 summarizes the results showing scaled, partial regression coefficients. The degree of association varied between covariates and across anchovy age classes, though they remained qualitatively unaffected by the analyzed body size measure (i.e., the ratio of the magnitude of estimates based on weight and on length again exceeded three, which is consistent with temperature induced changes in body shape as commented in Section 3.2). As above, the shorter time span of *Juvena* surveys hinders the analyses for juveniles.

Simple and multiple linear regression models featuring two or three covariates provided consistent results on the effect of each covariate across age classes (Table S3; Figure S8). For juveniles, no combination of covariates beat the simple regresssion model featuring the effect of density-dependence, with a decline in the average juvenile length of 10% when population biomass increases by a factor ~2.78, a quantity that doubled the corresponding decline found for adult age classes. Temperature and food availability were weakly associated with juvenile size. Indeed, simultaneous consideration of density-dependent effect reduced the estimated magnitude of the association between temperature and size (from 15% to 5% in length, and from 40% to 18% in weight per degree of increase in temperature, respectively).

For adult age classes, the saturated model featuring all three covariates explained more variance than any other combination, though most of the predictive power arose from complementarity between the effects of temperature and adult biomass, especially for age classes 1 and 3+. These two covariates alone explained between 35% to 70% of variability in anchovy adult size (with slightly larger r^2 in the case of analyses targeting weight), which was more than 80% of the explanatory power reached by the saturated model. The importance of the two covariates, however, was reversed with age. Detected associations between temperature and size, for instance, became more apparent for adult age classes than for juveniles (i.e., from explaining one tenth to more than one third of variability in

FIGURE 2 Trends in anchovy body size at age. Blue dots correspond to mean anchovy length (four panels above) or fresh weight (four panels below) per haul during *Juvena* (age 0) and *Bioman* (ages 1–3+) surveys. The area of each dot is proportional to anchovy relative abundance at age during each survey year in the region where each haul was towed. Each panel features the best model selected for each size metric and age class among a set of alternative, hierarchical Bayesian models allowing for a change point in the trend (see Section 2.3.2). Labels on the top left corner of each panel detail the name of the best model and provide the median and 90% quantile-based, central interval of the posterior parameters. Labels on the top right give the relative weight $\omega_{\mathrm{LOO}} \in [0, 1]$ assigned to each model, which were calculated using the leave-one-out (LOO) criterion. Orange lines correspond to posterior estimates of the population level mean size at age during each survey year. Dark blue lines give estimates based on the best fitting model. Solid lines give the posterior median, and dashed lines delimit a 90% quantile-based, central interval. If the selected model features a change point, the rug plot at the bottom of the plot enables visualizing the posterior distribution of the specific date τ [year] of the change point through alpha blending (i.e., transparency; the darker the hue, the larger is the posterior density in a given interval due to the greater overlap of rugs). The label on top of the rugs gives the median and 50% quantile-based, central interval of τ (the choice of narrower, 50% levels for the confidence interval responds to the wide uncertainty on the estimation of this parameter). See Figure S3 for the full set of alternative models assessed.


Age 0
Linear trend model with changing slope [AR1]
$\omega_{LOO} = 1.00$
$\mu = 68.5\ [63.7, 73.9]_{90\%}$ [mm]
$\beta_1 = -11.8\ [-23.4, 2.3]_{90\%}$ [% per decade]
$\beta_2 = -11.2\ [-24.5, 3.9]_{90\%}$ [% per decade]
$\rho_{AR} = 0\ [-0.76, 0.5]_{90\%}$
$\tau = 2012\ [2007, 2016]_{50\%}$
Age 1
Linear trend model
$\omega_{LOO} = 0.91$
$\mu = 129.8\ [127.6, 131.9]_{90\%}$ [mm]
$\beta = -4.53\ [-6.2, -2.79]_{90\%}$ [% per decade]
Age 2
Linear trend model with changing slope [AR1]
$\omega_{LOO} = 0.53$
$\mu = 158.1\ [155.6, 160.5]_{90\%}$ [mm]
$\beta_1 = -2\ [-3.9, -0.3]_{90\%}$ [% per decade]
$\beta_2 = -7.6\ [-9.1, -5.5]_{90\%}$ [% per decade]
$\rho_{AR} = -0.27\ [-0.79, 0.13]_{90\%}$
$\tau = 2002\ [2000, 2006]_{50\%}$
Age 3p
Linear trend model
$\omega_{LOO} = 0.86$
$\mu = 164.4\ [161.4, 167.4]_{90\%}$ [mm]
$\beta = -3.82\ [-5.66, -1.87]_{90\%}$ [% per decade]
Mean length at age [mm]
Time [years]
160
120
80
40
200
160
120
80
1990
2000
2010
2020

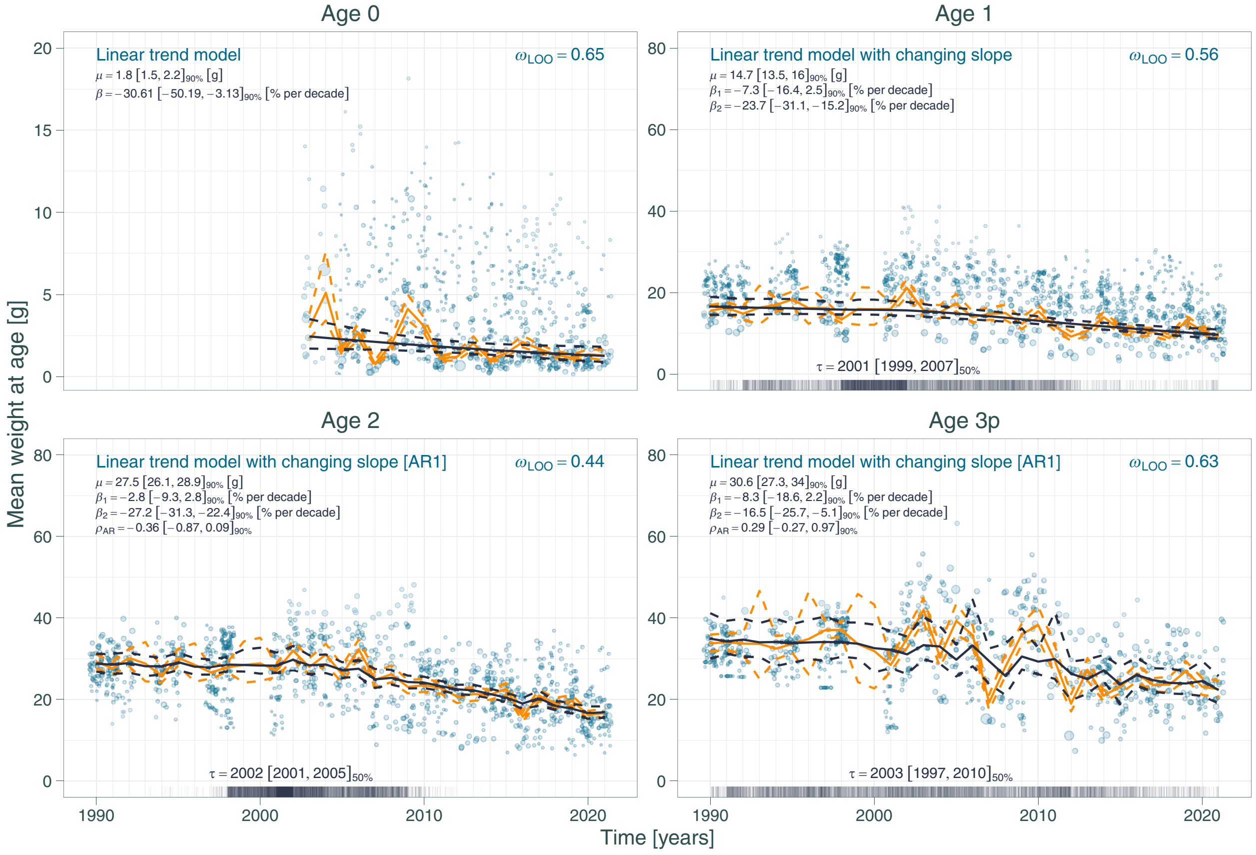

Age 0
Linear trend model
$\omega_{LOO} = 0.65$
$\mu = 1.8\ [1.5, 2.2]_{90\%}$ [g]
$\beta = -30.61\ [-50.19, -3.13]_{90\%}$ [% per decade]
Age 1
Linear trend model with changing slope
$\omega_{LOO} = 0.56$
$\mu = 14.7\ [13.5, 16]_{90\%}$ [g]
$\beta_1 = -7.3\ [-16.4, 2.5]_{90\%}$ [% per decade]
$\beta_2 = -23.7\ [-31.1, -15.2]_{90\%}$ [% per decade]
$\tau = 2001\ [1999, 2007]_{50\%}$
Age 2
Linear trend model with changing slope [AR1]
$\omega_{LOO} = 0.44$
$\mu = 27.5\ [26.1, 28.9]_{90\%}$ [g]
$\beta_1 = -2.8\ [-9.3, 2.8]_{90\%}$ [% per decade]
$\beta_2 = -27.2\ [-31.3, -22.4]_{90\%}$ [% per decade]
$\rho_{AR} = -0.36\ [-0.87, 0.09]_{90\%}$
$\tau = 2002\ [2001, 2005]_{50\%}$
Age 3p
Linear trend model with changing slope [AR1]
$\omega_{LOO} = 0.63$
$\mu = 30.6\ [27.3, 34]_{90\%}$ [g]
$\beta_1 = -8.3\ [-18.6, 2.2]_{90\%}$ [% per decade]
$\beta_2 = -16.5\ [-25.7, -5.1]_{90\%}$ [% per decade]
$\rho_{AR} = 0.29\ [-0.27, 0.97]_{90\%}$
$\tau = 2003\ [1997, 2010]_{50\%}$
Mean weight at age [g]
Time [years]
20
15
10
5
0
80
60
40
20
0
1990
2000
2010
2020

FIGURE 3 Environmental and ecological correlates of anchovy body size at age in the Bay of Biscay. Each panel shows scaled estimates (median and 90% quantile-based, central interval) of the relative change in anchovy size with temperature, spawning biomass, and chlorophyll *a* concentration, based on analyses of survey data. The estimates are partial regression coefficients based on the multiple regression model providing the most conservative estimates for each covariate (corresponding to the models *ssb*, *tos* and *ssb*, *tos*, *chl* in Table S3). To ease comparisons, predictors were rescaled by dividing them by the double of their standard deviations (Gelman, 2008).

size, attending to r^2 estimates, Figure S5). The importance of the association between abundance and size decreased for adult age classes, with scaled estimates suggesting that the effect was less than half that of the temperature (Figure 3). In the case of resource availability, associations between anchovy size and chlorophyll *a* concentration were in general negative and weak ($r^2 \leq .1$), except for a surprisingly high association only for age class 2, which we therefore deemed as spurious. We retained estimates based on model *ssb*, *tos* in Table S3 for the assessment of analytical predictions of the rate of change in size at age with temperature.

3.4 | Temperature and changes in anchovy size at age

As expected, the allometric growth model provided an acceptable fit to average anchovy weight at age (Figure S13), returning parameter estimates of $k = 1.48\,\text{year}^{-1}$ $[1.38, 1.59]_{90\%}$ and $M_\infty = 35.6\,\text{g}$ $[34.1, 37.1]_{90\%}$ for average conditions in the Bay of Biscay (i.e., here set just as $T_{\text{os}} = 15°\text{C}$). To predict changes in relative size at age with temperature, we tested predictions based on estimates of the activation energy E_{g,M_∞} returned from the analysis of ecogeographical rules (Figure 1). Adjusting these estimates by the length-weight scaling exponent $b = 3.26$ yielded $E_{g,M_\infty} = -2.34\,\text{eV}\,[-3.33, \ -1.27]_{90\%}$ for Bergmann's rule and $-0.86\,\text{eV}\,[-1.21, \ -0.50]_{90\%}$ for James' rule, respectively. Both estimates, particularly the one resulting from James' rule, yielded predictions that clearly felt short with respect to estimates of relative changes in size at age with temperature based on survey data (Figure 4). To reconcile analytical predictions with our estimates, we used the raw estimate $E_{g,M_\infty} \approx -3.32\,\text{eV}$, which is based on the observed association between anchovy weight and temperature (Figure S5). The adjusted value fell at the lower tail of E_{g,M_∞} estimates for Bergmann's rule. Adjusted analytical predictions showed a remarkable agreement with our estimates and reproduced the observed increase in the magnitude of shrinking rates with age.

The analyses also revealed a clear signature of the sensitivity of the early growth rate k to temperature (i.e., purple lines in the top row of plots in Figure 4 correspond to the predicted changes when k remains constant), and how this effect contributed to bring closer the growth trajectories of young anchovies (i.e., solid vs. dashed lines in the growth trajectory plots in Figure 4).

4 | DISCUSSION

Declines in species body size are among the main biological responses to climate change (McKenzie et al., 2021; Ohlberger, 2013; Pörtner & Peck, 2010; Scheffers et al., 2016; Sheridan & Bickford, 2011). Evidence for the emergence of climate-driven trends toward shrinking body sizes remains, however, contentious (e.g., Audzijonyte et al., 2020; Huang, Ding, et al., 2021; Huss et al., 2019; Solokas et al., 2023). Here, based on analyses of scientific survey data gathered during the last three decades, we found a decline in the body size of anchovy in the Bay of Biscay. Shrinking was evident in all age classes, from juveniles to adults, and when analyzing changes in total length or fresh weight. The two size metrics were, however, uncoupled, with more pronounced declines in weight that suggest an accelerating trend toward a slender body shape over the last two decades. Among candidate drivers, declines in the average size of juveniles were mainly associated with increases in population abundance, while water temperature turned the best predictor of declines in average adult size. Association between warmer conditions and declining sizes increased with age in a manner consistent with predictions of the TSR, but the magnitude of the responses exceeded expectations based on ecogeographical rules.

Several processes may combine to explain shrinking trends in fish body size, even in the absence of warming or marked fluctuations in abundance. Candidate processes include changes in exploitation rates (Jorgensen, 1990; Sharpe & Hendry, 2009), or in food availability (Lindegren et al., 2020). Here we found little support of a direct

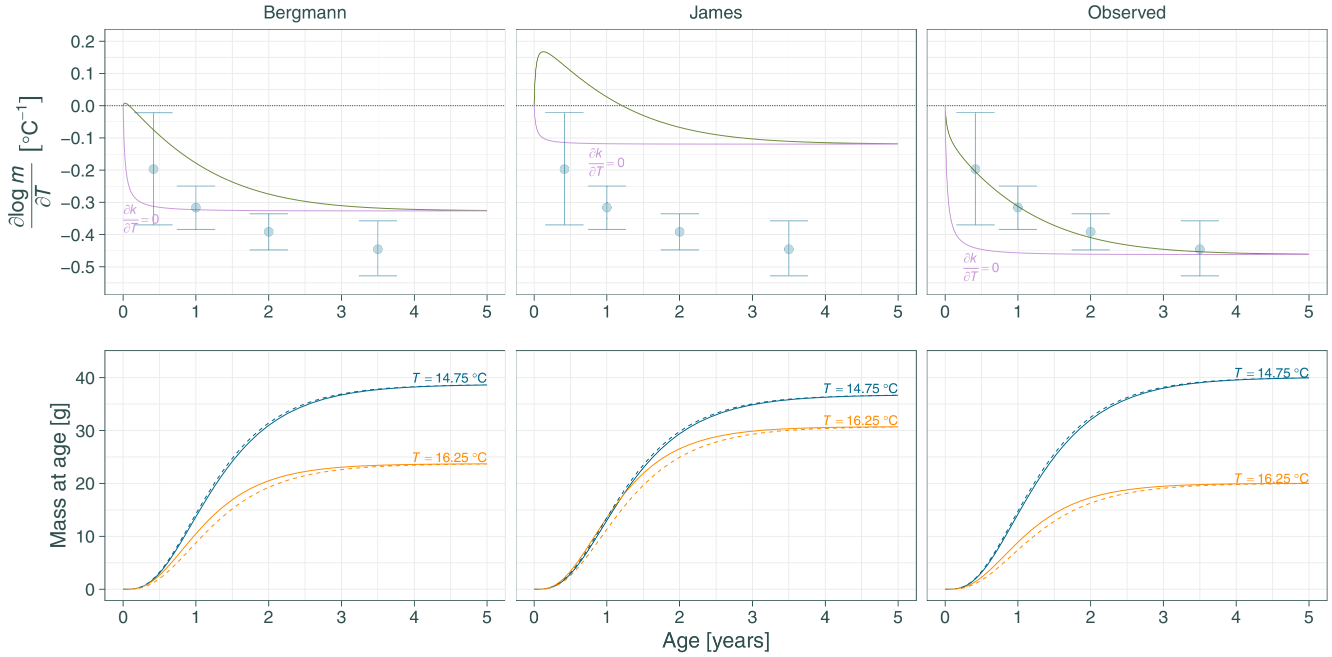


FIGURE 4 Analytical predictions for the expected relative change in anchovy mass at age with respect to temperature based on the allometric model discussed in Section 2.4. The plots in the top row show estimates of the relative change in anchovy size with temperature based on survey data (blue dots), along with theoretical predictions resulting from assuming that both M_∞ and k (green line), or just M_∞ (violet line) vary with temperature. As discussed in the text, estimates of the association between size and temperature come from a multiple regression model that also features a covariate to represent density-dependent effects (i.e., model *ssb*, *tos* in Table S3). Plots in the second row depict predicted growth trajectories for the maximum and minimum average annual temperatures observed in the Bay of Biscay during the study period (blue and orange lines, respectively). Solid lines correspond to predictions assuming that temperature modulates both M_∞ and k, while the dashed line correspond to the case of constant k. See the main text for further details, and Section S3.5 for a detailed account of the model and its parameterization.

association between resource availability and shrinking trends, and we also ruled out overfishing as a direct cause of shrinking, at least beyond the indirect impact of reduced catch levels on the rebound of the population following the closure of the fisheries. We can neither rule out that selective fishing favored the dominance of small sized anchovy before the closure of the fisheries. Previous studies have reported shrinking trends of a similar magnitude to those described here for anchovy, and for other small pelagics like sardine in the Bay of Biscay (Doray, Petitgas, Huret, et al., 2018; Véron et al., 2020). Selection gradients time series based on otolith growth analyzed by Boëns et al. (2021) favor such a hypothesis. These authors report consistent trends toward depressed growth in anchovy associated with high population densities and selective mortality, but also that selective harvest may be just reinforcing the natural disappearance of larger individuals from the population (Boëns et al., 2021). Shrinking trends have been also reported in nearby regions where anchovy and sardine have a much different exploitation history (Baudron et al., 2014; Beveren et al., 2014; Menu et al., 2023). Macroecological analyses further suggest that the effect of temperature on early growth varies between fish guilds and decreases with asymptotic size, with small pelagics among the groups showing a larger effect (van Denderen et al., 2020).

We are thus confident in the robustness of reported trends, and that the most likely explanation may involve an underlying environmental driver affecting large areas. The two independent surveys analyzed here yielded consistent trends and estimates, and although survey effort has varied over the years, the main results remain unaffected even to exclusion of entire survey years. In that respect, the study highlights the unique value of continued monitoring to assess the impact of global change in marine ecosystems. Adoption of a Bayesian approach also enabled us to probabilistically assess alternative hypotheses and to propagate uncertainty between sequential analyses (Gelman et al., 2014; Hobbs & Hooten, 2015). Other aspects deserve further attention and remain uncertain, starting with the detection of a change point for trends in adult body size. Previous studies have reported that declines in size accelerated following the reopening of the fisheries in 2010 (e.g., Doray, Petitgas, Huret, et al., 2018), but our analyses suggest instead that shrinking acceleration started earlier, before the closure. It is important to note in that respect that the series analyzed here extend back one more decade with respect to previous analyses. Besides, despite huge efforts to monitor anchovy in the Bay of Biscay (ICES, 2021b; Santos et al., 2018), large-scale sampling at sea always involves compromises. Practical constraints limit the surveys to yield snapshot, aggregated estimates of size at age. Pooling individuals into age classes enables meaningful estimation of size at age for the entire population (ICES, 2021b; Santos et al., 2011, 2018; Uriarte, 2015), but it may be problematic when assessing changes in size through time.

Analyses presented here implicitly assumed that, year after year, surveys captured and measured individuals of approximately the same age. Delayed spawning, for instance, may lead to fall surveys sampling younger, smaller juveniles than average. It is known, however, that anchovy spawning is tied to warmer spring temperatures (Ibaibarriaga et al., 2007; Motos et al., 1996). Reconstructions of anchovy reproductive niche suggest, indeed, an advance in the timing of the spawning peak in recent decades (Erauskin-Extramiana et al., 2019). This advance parallels reported changes in the seasonality of surface temperatures and plankton phenology in the Bay of Biscay (Taboada & Anadón, 2012, 2014). Those same analyses also suggest a prolonged warm season and a delayed fall, which leaves open the possibility of an extended reproductive season and even the occurrence of secondary spawning peaks (e.g., Motos et al., 1996). Fast growth during early development may lead to huge differences in size even for subtle changes in age at sampling between years, recommending a more detailed assessment based on growth reconstructions from otolith analyses (Aldanondo et al., 2010, 2011). Similarly, pooling adult individuals over 3 years of age into a terminal class may confound changes in size with changes in the relative abundance of older age classes. However, the negligible abundance of age 4+ individuals and reduced growth rates after maturation suggest a limited impact (Uriarte et al., 2016).

Lack of realism in the characterization of the environmental conditions experienced by individual anchovy during growth provides another opportunity for improvement. We adopted a relatively simple yet pragmatic approach to the problem, averaging data over time and space to empirically assess associations between candidate drivers and anchovy size. The approach obviated growth dynamics and spatial heterogeneity in habitat use along the Bay of Biscay (see Irigoien et al., 2007), but yielded seemingly associations between population density, temperature, and size, which are consistent with theoretical expectations and with previous work. Declines in individual size as population density rises are often explained in terms of depressed growth due to intraspecific competition for resources (Rose et al., 2001). This kind of effect is more likely manifested at the juvenile stage (Cowan & Shaw, 2002; but see also Rindorf et al., 2022), which has been proposed as a critical stage for recruitment (e.g., Myers, 2001). Lack of resources leads to larger differences in size at age early in life (e.g., Atkinson & Sibly, 1997, see also Section S3.5.4). Qualitatively, that response is consistent with the reduced association observed between population density and adult size. Such interpretation is at odds with the lack of association between juvenile size and phytoplankton biomass, with the observed increase in population biomass (ICES, 2021b), with trends in anchovy stomach weights (Bachiller et al., 2013), and with reported increases in the overall productivity of the Bay of Biscay (Bode et al., 2011; Chust et al., 2022; Valdés et al., 2021). Another important clue comes from the continued decline in size during the closure of the fisheries between 2005 and 2010. Shrinking precedes the 2005 collapse, with an acceleration of the decline of anchovy weight that we estimated to begin about 2001. Taken together, these facts rule out a direct effect of fishing on the decline in anchovy size, but leave open the possibility of an indirect, long-lasting effect due to size-selective mortality (i.e., Boëns et al., 2021, 2023), highlighting the need for further research on potential feedbacks between changes in size and population dynamics (e.g., de Roos & Persson, 2013).

There is room, however, to improve the characterization of changes in resource availability and their impact in anchovy size, including changes in prey capture efficiency (Ljungström et al., 2020), or a potential reduction in food quality (Brosset et al., 2017; Menu et al., 2023). There is evidence of changes in the structure of zooplankton communities in the Bay of Biscay, including an increase in warming tolerant copepod species (Valdés et al., 2021; see also Grandremy, Romagnan, et al., 2023). Potential changes in the size structure of plankton are another possibility worth considering (e.g., Grandremy, Bourriau, et al., 2023; Vandromme et al., 2014), given the well-known effect of prey sizes on the growth and dynamics of small pelagics (e.g., Rykaczewski, 2019; Rykaczewski & Checkley, 2008; Thoral et al., 2021). There have also been changes in the relative abundance of other small pelagics that may simultaneously act as anchovy competitors and predators (i.e., sardine, mackerel, and horse mackerel) (ICES, 2021b), as well as increases in the abundance of top predators like the common dolphin (e.g., Astarloa et al., 2021). Another possibility is that milder conditions relax selection pressures, allowing the survival of small-bodied individuals that would otherwise perish under average conditions. The display of alternative growth strategies depending on larvae retention or advection away from the shelf (Aldanondo et al., 2010), where anchovy find a refuge to escape from predators (Irigoien et al., 2007), and evidence for size-dependent juvenile mortality (Boëns et al., 2021; Escribano et al., 2019), favor the hypothesis of density-driven changes in size-dependent survival as a potential driver of changes in average juvenile size.

Anchovy size was also negatively associated with rising environmental temperatures, featuring a relationship consistent with the predicted impacts of ocean warming in marine ectotherms (Daufresne et al., 2009; Forster et al., 2012). The relationship was negative both for juvenile and adult age classes, and became more negative with age. Theoretical analyses suggest that the increase in the magnitude of the relationship results from opposite effects of warmer temperatures on accelerating early growth and reducing adult body size, as predicted by the TSR (Atkinson, 1994; Atkinson & Sibly, 1997; Forster & Hirst, 2012). The net effect of growth acceleration is to bring growth trajectories closer and to reduce variability in the size of young anchovies, in agreement with hypotheses stressing selection pressures toward faster growth during early development (Sibly et al., 2015) and its importance in determining the success of fish recruitment (Houde, 2008). In this respect, the framework presented here provides an approach to easily assess the generality of temperature effects on early growth modulation and its relative importance with respect to the effect of temperature on determining adult size.

The characterization of the thermal environment that anchovy experience in the field, however, also requires further refinement. Our estimates were robust to the choice of the averaging window for surface temperature, but it is important to highlight that anchovy migrates through the water column and even tends to overwinter at depth close to the continental slope (Uriarte et al., 1996), where they experience cooler temperatures and slower warming trends than in surface waters. On the other hand, the approach simultaneously smoothed out the potential impact of extremes like marine heatwaves, which have become more frequent in the region (Izquierdo et al., 2022), and of distinct rates of warming through the year that have probably affected the more vulnerable early stages (Dahlke et al., 2020).

Although marine ectotherms are particularly sensitive to temperature (Forster et al., 2012), the magnitude of changes in size with temperature for anchovy in the Bay of Biscay clearly exceeds estimates available in the literature (e.g., values up to 8% in weight per degree of increase in temperature under laboratory conditions, which are far from values above 20% reported here), probably due to the multiple stressors experienced by anchovy in the field. Estimates of relative changes in size with respect to temperature also exceed analytical predictions based on activation energies from ecogeographical rules considering either variation among populations (i.e., as inferred from James' rule) or, to a lesser extent, those expected under evolutionary divergence (i.e., as inferred from Bergmann's rule). The short time span and magnitude of change suggest a shift in local ecotypes due to selective mortality or earlier maturity rather than evolutionary innovation or invasion of foreign ecotypes. The anchovy population in the Bay of Biscay is well defined and virtually isolated from immigration from neighboring populations to the north and west (Petitgas et al., 2012), where cooler and more productive environments favor larger individuals. Analytical predictions based on ecogeographical rules also predicted a positive association between temperature and size early in life, which is consistent with previous studies on the impact of temperature on the growth of anchovy larvae (Urtizberea et al., 2008). Although the expected increase in size at early ages almost vanished after adjusting the activation energy E_{g,M_∞} to match our estimates of changes in size at age with temperature, the analytical model revealed that enhanced declines in size at older ages are a clear signature of a positive effect of temperature on early growth.

Other clues suggest that changes in temperature were the primary driver of observed declines in adult size, besides the strong association between size and temperature and the qualitative match with theoretical predictions. For instance, other studies have reported shrinking trends of a similar magnitude for other small pelagics species like sardine (Véron et al., 2020), whose abundance is declining in the Bay of Biscay, and for both anchovy and sardine in the Gulf of Lion (Menu et al., 2023). Synchronized responses in space, accompanied by opposite trends in population abundance, are often interpreted as the result of large-scale climate forcing. The trends toward a slender body size may be also interpreted in terms of a decline in body condition, but they can point as well a response toward increased surface-to-volume ratios (Scheffers et al., 2016). Finally, as commented above, declines in size continued in absence of exploitation and at low population densities, suggesting that the impact of density-dependence may be limited to juveniles. There are other candidate explanations that remain to be tested, ranging from the potential effect of pollutants to food web interactions, through the alternation in the dominance of different anchovy ecotypes (Montes et al., 2016). All these mechanisms might interact with fluctuations in population density and the effect of warming and contribute to explain observed changes in size. Additional evidence suggest, in any case, an undergoing, climate-driven regime shift (Chust et al., 2022), and that shrinking anchovy sizes may be just another signal of a long-lasting change in the structure and functioning of the Bay of Biscay ecosystem.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and codes that support the findings of this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.10090204.

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