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Contribution to the Special Issue: “MEDiterranean International Acoustic Survey (MEDIAS)”

Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species

Tarek HATTAB[1], Ali GUCU[2], Ana VENTERO[3], Andrea De FELICE[4], Athanassios MACHIAS[5], Claire SARAUX[1,6], Denis GAŠPAREVIĆ[7], Gualtiero BASILONE[8], Ilaria COSTANTINI[4], Iole LEONORI[4], Jean-Hervé BOURDEIX[1], Magdalena IGLESIAS[3], Marco BARRA[9], Marianna GIANNOULAKI[5], Rosalia FERRERI[8], Salah El AYOUBI[10], Sara MALAVOLTI[4], Simona GENOVESE[8], Stelios SOMARAKIS[5], Tea JURETIĆ[7], Vjekoslav TIČINA[7] and Grégoire CERTAIN[1]

[1] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Avenue Jean Monnet, Sète, France
[2] Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey
[3] Instituto Español de Oceanografía, Centro Oceanográfico de Baleares, Palma de Mallorca, Spain
[4] National Research Council (CNR), Institute of Marine Biological Resources and Biotechnologies, Largo Fiera della Pesca, Ancona, Italy
[5] Hellenic Centre for Marine Research (HCMR), Institute of Marine Biological Resources and Inland Waters, Iraklion, Greece
[6] IPHC UMR 7178, University of Strasbourg, CNRS, DEPE, Strasbourg, France
[7] Institute of Oceanography and Fisheries, Split, Croatia
[8] National Research Council (CNR), Institute for the Study of Anthropogenic Impacts and Sustainability in the Marine Environment, Torretta Granitola, Italy
[9] National Research Council (CNR), Institute of Marine Sciences, Napoli, Italy
[10] Instituto Español de Oceanografía (IEO), Balearic Islands Oceanographic Centre, Palma de Mallorca, Spain

Corresponding author: Tarek HATTAB tarek.hattab@ifremer.fr

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Abstract

In this study we consider the applicability of Bergmann’s rule to the populations of small pelagic fish species in the Mediterranean Sea. Under Bergmann’s rule, body size increases with decreasing temperature and increasing latitude. Although this macroecological pattern in body sizes is well established for many taxa of endotherms and ectotherms, it does not remain universal, and the proposed mechanisms underlying it are multiple and still lack consensus. Here we explored the occurrence of geographical body size clines using measurements of average body sizes of 10 species collected in pelagic trawl hauls carried out during acoustic surveys in the Mediterranean Sea. Bergmann’s rule was evaluated by correlating body sizes with latitude and temperature for each species while accounting for potential confounding variables and sampling bias. For 5 species, namely anchovy, sardine, Atlantic chub mackerel, bogue and blue jack mackerel, we demonstrate that they follow Bergmann’s rule, with a decline in average body size by about 3.01, 3.43, 3.67, 3.82 and 3.76 % per 1°C of warming, respectively, although this did not translate with an increase in size with latitude. The adherence of these 5 pelagic fish to Bergmann’s rules strongly suggest that temperature is a major determinant of their body sizes and enables them to act as sentinel species for identifying the drivers and consequences of warming in the Mediterranean ecosystems.

Keywords: Small pelagic fish; body size; Bergmann’s rule; temperature-size rule; Mediterranean Sea.

Introduction

The various traits of species often vary substantially across geographical gradients (Gaston *et al.,* 2008). Among them, body size is a key functional trait that influences the fitness of organisms (Brown *et al.,* 2004) and is of central importance because it relates directly to several ecological and physiological processes, such as respiration, growth, maturation, reproduction, and longevity (Blueweiss *et al.,* 1978; Calder, 1996). Geographical gradients of body size are evident across multiple faunal taxa and have been observed in both terrestrial and aquatic environments (Walters & Hassall, 2006; Blanck & Lamouroux, 2007; Fisher *et al.,* 2010a; Fisher *et al.,* 2010b).

Such gradients are thought to rely on a relation between size and temperature. Bergman's rule (Bergmann, 1848) states that larger individuals should be favored in cold environment through decreased heat perdition (reduced surface-to-volume ratio), resulting in a macroecological gradient of increasing size at higher latitudes. While this was originally developed for endotherms, it has quickly expanded to all organisms (Blanckenhorn & Demont 2004). This pattern was particularly prevalent in the strongly body size-structured aquatic communities, such as pelagic fishes and zooplanktons (Blueweiss *et al.,* 1978; Angilletta *et al.,* 2004; Blanchard *et al.,* 2009; Ohlberger, 2013; Evans *et al.,* 2020). Furthermore, according to the temperature-size rule, ectotherms should achieve smaller size at maturity at higher temperature through phenotypic plasticity (Atkinson, 1994; Blackburn *et al.,* 1999). Laboratory experiments and meta-analyses have revealed that across a broad range of taxonomic groups (from bacteria to vertebrates), body sizes of aquatic ectotherms strongly co-vary with temperature (Atkinson, 1994; Angilletta *et al.,* 2004; Forster *et al.,* 2012; Hoefnagel & Verberk, 2015; Horne *et al.,* 2015) and decline by about 3% per 1°C. The general trend for animal sizes to increase with cold temperature or high latitude, has been extensively studied from a biogeographic perspective and has been validated to marine fishes such as blennies (Gilligan, 1991), syngnathids (Wilson, 2009) and mesopelagic fishes (Saunders & Tarling, 2018) at broad taxonomic levels and large spatial scales (Fisher *et al.,* 2010b).

Recently, Audzijonyte *et al.* (2020) analyzed the body sizes of 335 reef fish species using a multi-decadal dataset spanning the whole Australian continent and multiple decades confirming that temperature is a major determinant of reef fish body sizes in the wild. Additionally, this study shows that the direction of a species' response to warming through space was generally consistent with its response to warming through time at any given location, suggesting that spatial trends could help forecast fish responses to long-term warming. However, many other studies considering adult body sizes in other marine fish species have found little evidence of Bergmann's rule (Macpherson & Duarte, 1994; Choat & Robertson, 2002; Smith & Brown, 2002), which could possibly be attributed to overfishing through size-selective harvesting that eliminates the faster-growing genotypes (Conover & Munch, 2002) and climate change homogenizing latitudinal patterns (Fisher *et al.,* 2010a).

In this study, we consider the applicability of Bergmann's rule to the populations of 10 small pelagic fish species in the Mediterranean Sea. These species represent key components of Mediterranean marine ecosystems and fisheries and they have recently experienced a lasting decrease in individual size and weight in several regions [e.g., anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus*, see Brosset *et al.* (2017)], making the study of geographical and temporal patterns of variation of their body size an important study topic to unravel the influences of fisheries and climate change. Indeed, the adherence of small pelagic fish to Bergmann's rule enables such species to act as sentinels for identifying signs and consequences of warming for the Mediterranean ecosystem. Here we employ empirical data on pelagic fish assemblages from many locations to investigate the intraspecific body size structure over a regional scale. Specifically, we aim to: 1) establish whether latitudinal body size clines can be observed on 10 pelagic fish species across the Mediterranean Sea; 2) quantitatively examine size-temperature trends in space and their intensities (i.e., slope estimates) while accounting for potential confounding variables (i.e., extraneous determinant such us bathymetric differences, which could influence both dependent and independent variables) and sampling bias (i.e., differences in sample sizes and timing of surveys).

Material and Methods

Biological sampling

Small pelagic fish were collected during acoustic surveys carried out on continental shelves of the Mediterranean Sea in the June-September period. The surveys were conducted along acoustic transects over the continental shelf from 15/20 m to 200 m (the border of the continental shelf, where the abundance of most small pelagic fish species drops critically). These surveys enabled us to monitor fish body size in the following geographical subareas (GSA, as established by GFCM 2009): the northern (GSA 01) and southern (GSA 03) Alboran Sea, northern Spain (GSA 06), the Gulf of Lions (GSA 07), the Ligurian and Tyrrhenian Seas (GSA 9-10), southern Sicily and Malta (GSA 16-15), the northern (GSA 17) and southern (GSA 18) Adriatic Seas, the western Ionian Sea (GSA 19), the eastern Ionian Sea (GSA 20), the Aegean Sea (GSA 22) and the south of Turkey (GSA 24). Length-frequency distributions (in terms of abundance and mass) of all species in the pelagic community were measured to 0.5 cm total size classes on board the research vessels. Biological sampling was made using pelagic trawl gears suitable to catch representative samples of the fish population in terms of species composition and size distribution. Trawl hauls were conducted during daytime in all GSAs except for the western GSA 17, GSA 18, 20 and 22, where daytime/ nighttime sampling was carried out (i.e., as it has been shown that there are no significant differences between day and night sampling (Machias *et al.*, 2013)). Still, trawl nets were not the same between areas and surveys, e.g., some used a covered cod end and accessed smaller fish than others. To obtain comparable size distributions among areas, we consequently set a common minimal total length of 72 mm for all areas (i.e., defined as the maximum value of the minimum sizes caught in each survey) above which we kept data.

In the present analysis, we selected only the most abundant pelagic species in catches (those representing 98% of total catches). Thus, 10 species were selected, namely anchovy (*Engraulis encrasicolus)*, sardine (*Sardina pilchardus)*, Atlantic chub mackerel (*Scomber colias)*, sprat (*Sprattus sprattus)*, Atlantic horse mackerel *(Trachurus trachurus)*, round sardinella (*Sardinella aurita)*, Mediterranean horse mackerel (*Trachurus mediterraneus)*, Atlantic mackerel *(Scomber scombrus)*, bogue (*Boops boops)*, and blue jack mackerel (*Trachurus picturatus)*.

A georeferenced dataset was compiled and included 1721 pelagic trawl hauls collected in 7 annual surveys carried out between 2012 and 2018 where catch weights and mean body size of all fish species were recorded (Fig. 1).

Temperature data

Temperature data were extracted from the Mediterranean Sea physical reanalysis system (Simoncelli *et al.*, 2019) which includes 3D monthly fields at 1/16° horizontal resolution (which for the Mediterranean basin ranges from 5 km at 45°N to 6 km at 30°N) and 72 unevenly spaced vertical layers. These reanalyses include a variational data assimilation scheme of *in-situ* and satellite observations (Simoncelli *et al.*, 2019). These data were averaged vertically by calculating the mean temperature value in each grid cell by considering only vertical layers located in the upper 200 meters (i.e., the vertical layers covered by survey data) (Fig. 1). A spatio-temporal match-up was subsequently performed between monthly fields of temperature and pelagic trawl hauls based on geographic coordinates of hauls and their corresponding year and month (Fig. 2).

Statistical analyses

All analyses were conducted using R software (3.6.3).

Bergmann's rule is traditionally evaluated by linearly correlating body size with temperature and latitude. Significant negative correlations with temperature or positive correlations with latitude can be interpreted as evidence for Bergmann's rule. Given that the body-size dataset was compiled from different surveys, there were some limitations that needed to be considered in the analyses. First, even though all surveys were carried out in the same season, they were spread over 4 months, between June and September, a variability that might create a source of bias (i.e., a four-month period may result in important ontogenetic variations in body sizes of these fast growing and short-lived species). Second, the nature of acoustic surveys prevented from a balanced sampling design. Indeed, hauls number per survey varied across regions and years as this largely depended on fish spatial distribution and abundance. Consequently, some temperature values had a lower or higher sampling probability than others, which could potentially lead to distortions of the outcomes since the considered sample will not be equally representative of all populations' body sizes at all environmental conditions. Finally, the size-specific bathymetric patterns of distribution, frequently observed in pelagic fish, may cause spurious associations in temperature-size relationships because both dependent and independent variables are confounded by depth (i.e., given the strong correlation between the mean temperature of the water column and the bathymetry on one side (Fig. S1), and the known ontogenetic differences in the bathymetric distribution between different ages and sizes in pelagic species on the other side). The presence of confounding variables may affect the variables under study so that the results might not reflect the actual relationships.

These three limitations could not be tackled simultaneously with a single linear mixed model because the structure of the random effects for such a model was too complex to be supported by the data and produced singular fits which is often an indication of over-fitting. We then addressed these limitations in separate steps using more parsimonious models. First, to account for the variability in the sampling period, linear mixed models were fitted using restricted maximum likelihood estimation, by considering mean body size in trawls hauls as a response variable, temperature and latitude as fixed-effect predictor variables, and season (i.e., month) as a random effect variable which includes a random intercept and a random slope of temperature. These mixed effects models were fitted using the lmer function in lme4 R package (Bates, 2005). By

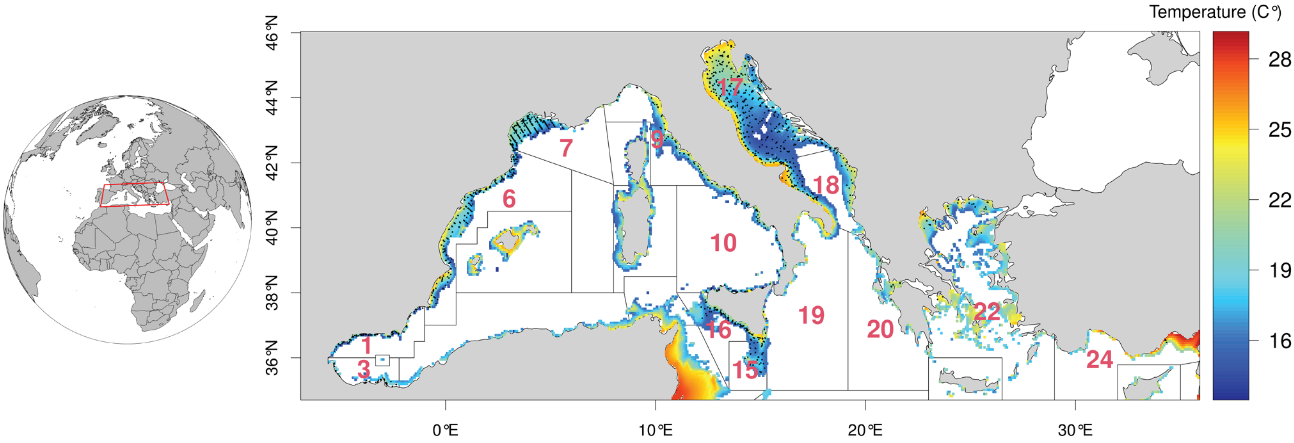

Fig. 1: Map of the Mediterranean Sea geographical sub-areas (GSAs): northern (GSA 01) and southern (GSA 03) Alboran Sea, northern Spain (GSA 06), Gulf of Lions (GSA 07), Ligurian and Tyrrhenian Seas (GSA 9-10), southern Sicily and Malta (GSA 16-15), northern (GSA 17) and southern (GSA 18) Adriatic Sea, western Ionian Sea (GSA 19), eastern Ionian Sea (GSA 20), Aegean Sea (GSA 22) and the south of Turkey (GSA 24). Black dots represent the location of the trawl hauls. The color scale represents summertime climatology of mean temperature of the water column along the continental shelf (0-200 m depth).

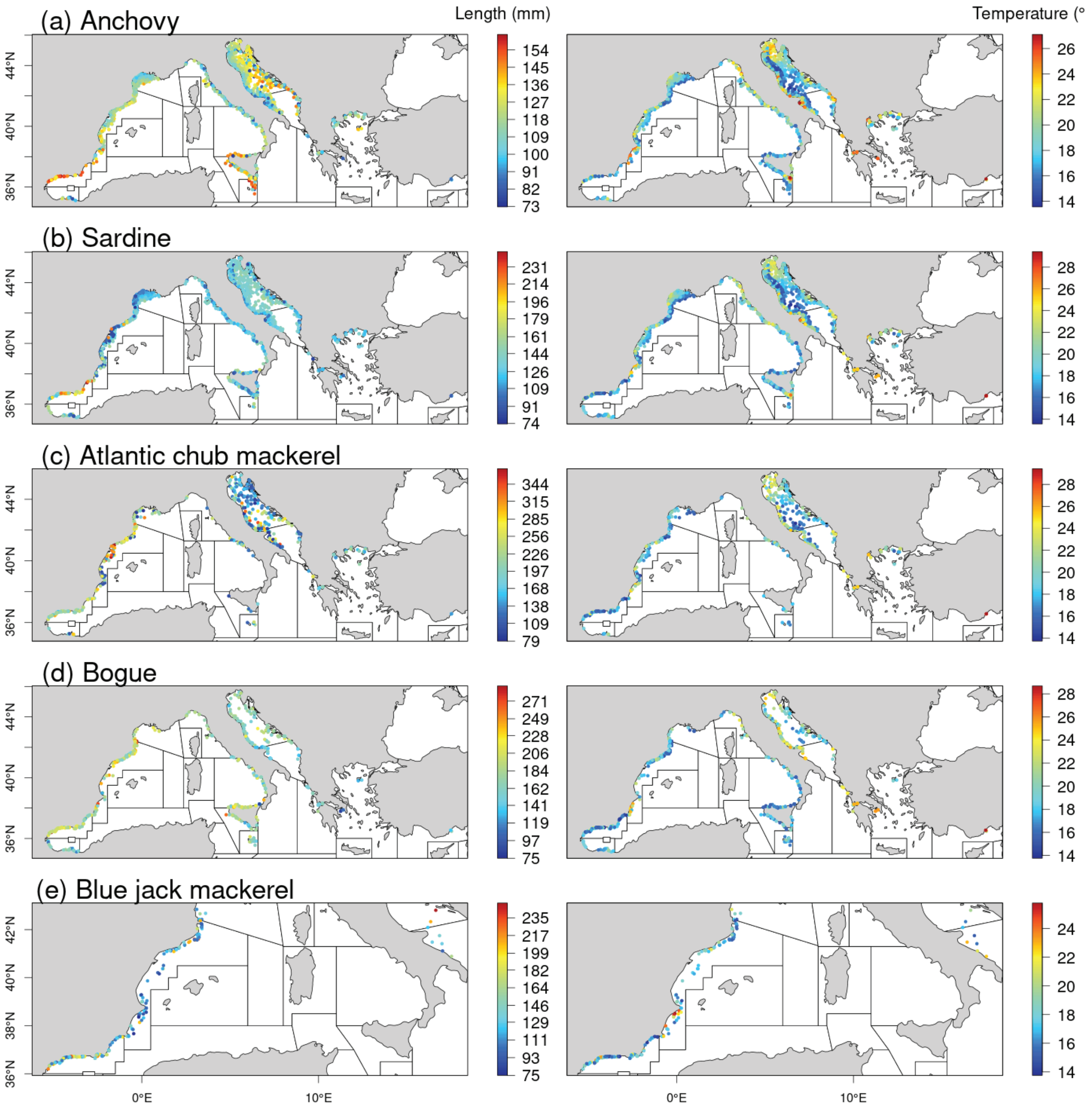

Fig. 2: Maps indicating the location of the trawl hauls and their corresponding temperature value and showing the geographic patterns of body size for five species. The color gradient indicates the mean total body size in mm (left panels) and temperature in °C (right panels).

comparing the residual variance and the variance associated with the random effect, we identified species for which survey-related variability (i.e., month) was not significant, and those were retained for further analyses.

Thereafter, in order to verify whether the observed patterns were due to spatial distribution along the bathymetric gradient, a second set of linear models were fitted including temperature and depth as predictor variables to control for bathymetric variation that may confound the temperature-size relationships. In these models, predictor variables were scaled to make the coefficient of each variable indicative of its influence in the regression equation. In addition, collinearity among the predictor variables was checked using the variance inflation factor (VIF), a measure of severity of multicollinearity. VIF values were calculated using the *car* R package (Fox & Weisberg, 2019).

Finally, to cope with the unbalanced sampling, we implemented, as a third step, a bootstrap sampling procedure among trawl hauls from over-sampled temperature conditions. The temperature range of the dataset was split into 13 equal bins of 1°C. For each bin we selected a random sub-sample of trawl hauls so as to get an equal number of observations in all temperature bins. The number of sub-samples was set as the minimum number of trawl hauls observed by temperature bins. Resampling was repeated 999 times, where at each run a linear model was fitted by considering mean size as the response variable, and temperature and depth as the predictor variable.

Results

Biogeographic patterns of body size in 10 small pelagic species

Among the 10 considered species, only bogue showed positive correlation with latitude. Five other species showed an opposite trend where a significant pattern of decreasing size with latitude was observed for anchovy, sardine, Atlantic chub mackerel, Atlantic mackerel, and blue jack mackerel (Table 1).

Size-temperature relationships in 10 small pelagic species

Linear mixed models results indicate that survey-related variability did not allow identifying clear spatial patterns of body size variation for sprat, Atlantic horse mackerel and Atlantic mackerel for which no reliable conclusion could be drawn. For example, in the case of sprat, temperature negatively affected body size, lowering it by 0.4 mm. However, the residual variance (i.e., variance outside our measured parameters) was considerably low (132 mm^2) in comparison with the random effect of seasonality which accounted for a variance of 446 mm^2 (Table 1, Fig. 3). Thus, only the 7 remaining species were selected for further analysis. Among the latter, only 5 species (anchovy, sardine, Atlantic chub mackerel, bogue, and blue jack mackerel) showed a significant negative effect of temperature on mean body size with a low random effect of seasonality compared with other possible factors (Table 1, Fig. 3). For round sardinella and Mediterranean horse mackerel, the residual variance was higher compared to the random effect of seasonality, however, no significant negative effect of temperature was observed, suggesting that these two species do not follow a temperature-size rule.

Among the 5 species showing a negative correlation with temperature, 3 species (anchovy, sardine, and bogue) showed bathymetric patterns of distribution with

Table 1. Parameter estimates for the linear mixed models relating mean body size to temperature and latitude while considering the season as a random effect variable (including a random intercept and a random slope of temperature). N is number of observations.

Species	**Scientific names**	**Fixed effect**				**Random effect**				
		Predictors	**(Intercept)**	**Latitude**	**Temperature**	**Residual variance (mm^2)**	**Month variance (mm^2)**	**Temperature (slope)**	**N**	**Marginal / Conditional R^2**
European anchovy	***Engraulis encrasicolus***	*Estimates*	206.45	-1.25	-2.07	227.38	62.90	0.07	1303	0.171/ 0.202
		p	**<0.001**	**<0.001**	**<0.001**					
		df	1296.00	1296.00	1296.00					
Sardine	***Sardina pilchardus***	*Estimates*	232.55	-1.67	-1.84	456.22	291.13	0.64	1228	0.101 / 0.166
		p	**<0.001**	**<0.001**	**<0.001**					
		df	1221.00	1221.00	1221.00					
Atlantic chub mackerel	***Scomber colias***	*Estimates*	440.68	-4.42	-3.43	3663.37	0.00	1.35	427	0.075 / 0.170
		p	**<0.001**	**0.001**	**0.005**					
		df	420.00	420.00	420.00					
Sprat	***Sprattus sprattus***	*Estimates*	113.05	-0.16	-0.40	132.41	446.75	1.08	423	0.005 / 0.313
		p	**<0.001**	0.768	0.532					
		df	416.00	416.00	416.00					
Atlantic horse mackerel	***Trachurus trachurus***	*Estimates*	191.08	-1.42	0.59	2058.11	5117.44	15.38	628	0.007 / 0.123
		p	**<0.001**	0.061	0.782					
		df	621.00	621.00	621.00					
Round sardinella	***Sardinella aurita***	*Estimates*	234.86	-2.27	1.05	1830.55	656.15	4.56	235	0.020 / 0.160
		p	**<0.001**	**0.049**	0.479					
		df	228.00	228.00	228.00					
Mediterranean horse mackerel	***Trachurus mediterraneus***	*Estimates*	243.80	-0.98	-1.18	2865.76	164.66	0.78	542	0.009 / 0.037
		p	**<0.001**	0.279	0.209					
		df	535.00	535.00	535.00					
Atlantic mackerel	***Scomber scombrus***	*Estimates*	310.15	-5.36	4.87	2095.35	4744.51	11.12	482	0.079 / 0.284
		p	**<0.001**	**<0.001**	**0.017**					
		df	475.00	475.00	475.00					
Bogue	***Boops boops***	*Estimates*	170.81	1.67	-3.14	875.40	141.75	0.43	474	0.084/ 0.171
		p	**<0.001**	**0.002**	**<0.001**					
		df	467.00	467.00	467.00					
Blue jack mackerel	***Trachurus picturatus***	Estimates	323.56	-2.64	-4.57	1568.27	191.09	0.60	170	0.094 / 0.096
		p	**<0.001**	0.057	**0.001**					
		df	163.00	163.00	163.00					

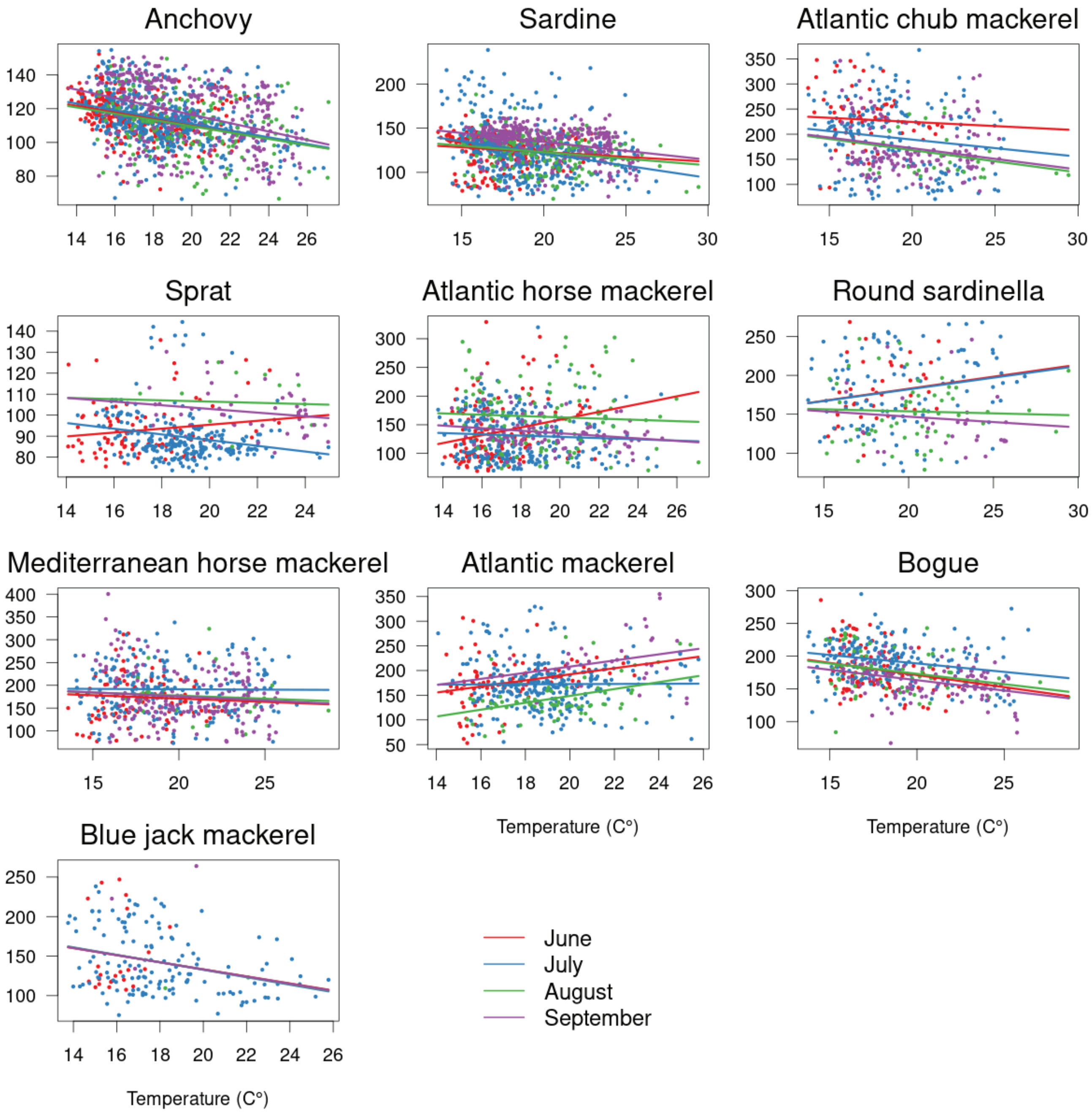

Fig. 3: Effect of survey-related variability on body size temperature relationship for the 10 considered species. The lines represent predictions based on linear mixed models relating body size to temperature and latitude while considering the season as a random effect variable including a random intercept and a random slope of temperature.

a significant increase in body size with depth (Table 2, Fig. 4) and 1 species (Atlantic chub mackerel) showed a negative correlation between body size and depth. However, the negative effect of temperature remained significant for all 5 species when controlling for depth in the model (Table 2), suggesting that the temperature-size rule observed was not an artifact resulting solely from their bathymetric distribution. Indeed, we observed a decrease in size with an increase in temperature at each given depth range (Fig. 5). Even more, the effect size of temperature was stronger than that of bathymetry in all species but bogue (Fig. 4 and Table 2).

Finally, the bootstrap-sampling procedure of trawl hauls within over-sampled temperature conditions showed that temperature-body size relationships were relatively stable against the sampling size. About 99 % of the slope values were still negative for sardine, Atlantic chub mackerel, bogue, and blue jack mackerel, while 98 % of the slope values remained negative for anchovy (Fig. 6). The bootstrap results confirmed that body size was affected by temperature, lowering it on average by -2.07 (± 0.09), -1.62 (± 0.03), -8.26 (± 0.24), -2.74 (± 0.04) and -6.80 (± 0.25) mm.° C^{-1} for anchovy, sardine, Atlantic chub mackerel, bogue and blue jack mackerel, respectively (Fig. 6), corresponding to a decline in the average body size by about 3.01, 3.43, 3.67, 3.82 and 3.76 % per 1° C of warming.

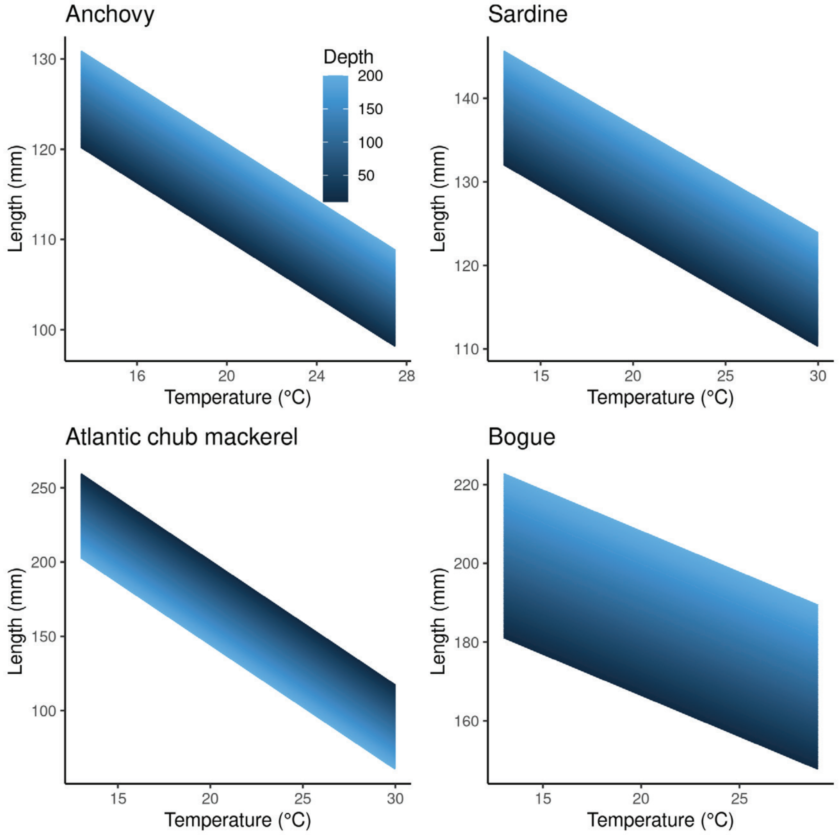

Fig. 4: Response surface graph of linear regressions showing the predicted mean body sizes as a function of temperature and depth.

Table 2. Parameter estimates for linear models relating mean body size to temperature and depth.

Species	Scientific names		Intercept	Temperature	Depth	Observations	VIF	R^2 / R^2 adjusted
European anchovy	*Engraulis encrasicolus*	*Estimates*	120.14	-21.35	10.61	1303	1.49	0.128 / 0.126
		p	**<0.001**	**<0.001**	**<0.001**			
		df	1300.00	1300.00	1300.00			
Sardine	*Sardina pilchardus*	*Estimates*	131.37	-20.29	13.54	1228	1.43	0.057 / 0.055
		p	**<0.001**	**<0.001**	**0.001**			
		df	1225.00	1225.00	1225.00			
Atlantic chub mackerel	*Scomber colias*	*Estimates*	253.16	-131.36	-56.28	427	1.45	0.094 / 0.090
		p	**<0.001**	**<0.001**	**0.003**			
		df	424.00	424.00	424.00			
Bogue	*Boops boops*	*Estimates*	179.58	-31.18	41.53	474	1.25	0.141 / 0.137
		p	**<0.001**	**<0.001**	**<0.001**			
		df	471.00	471.00	471.00			
Blue jack mackerel	*Trachurus picturatus*	*Estimates*	167.94	-61.49	-19.01	170	1.20	0.086 / 0.075
		p	**<0.001**	**<0.001**	0.226			
		df	167.00	167.00	167.00			

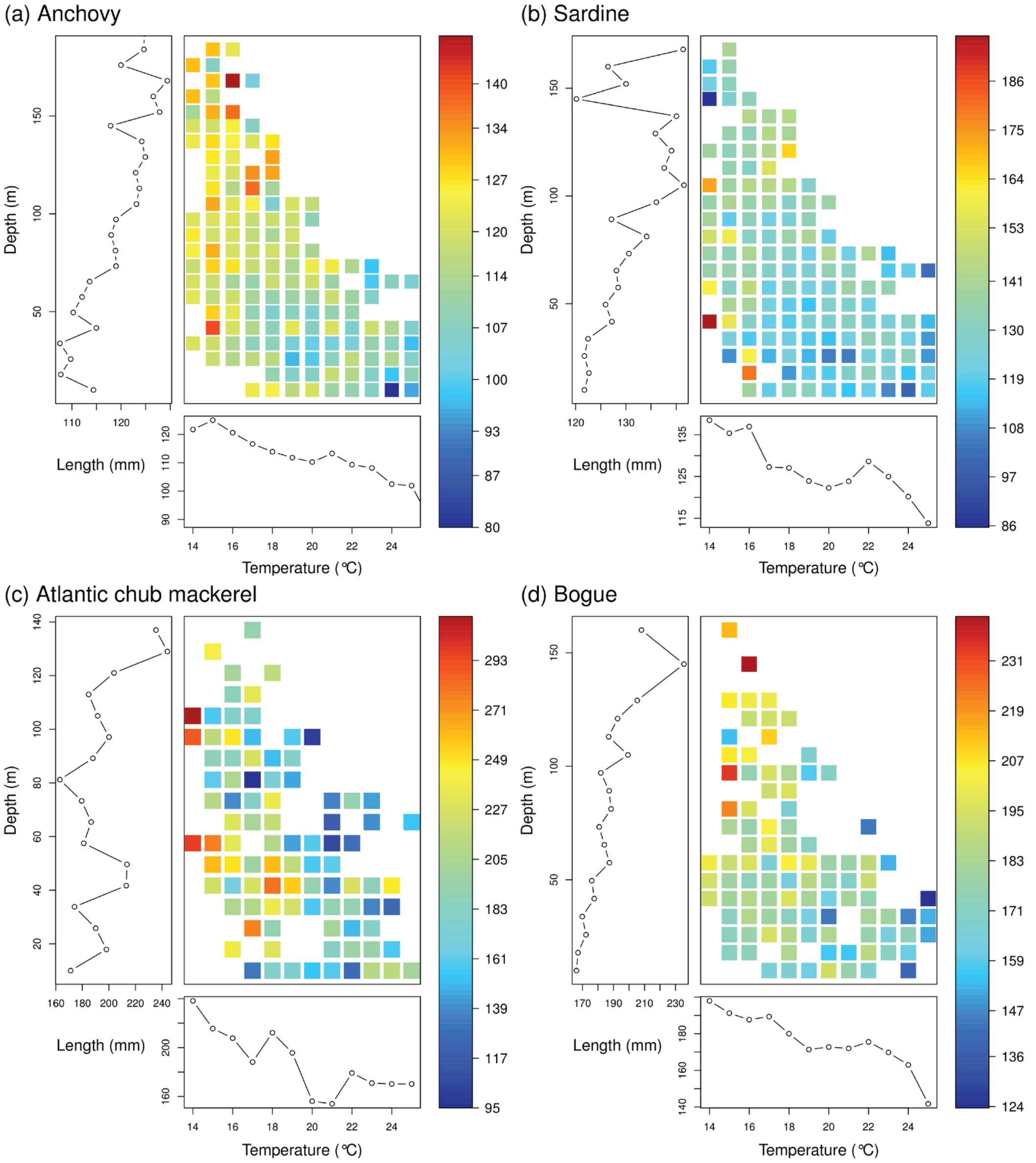

Fig. 5: Patterns of body size variation in relation to temperature and depth. The color gradient indicates the observed mean body sizes (in mm) for each combination of temperature and depth values.

Discussion

Small pelagic fish are fast growing, migratory and short-lived species relative to most marine fish species, often presenting rapid shifts in distribution related to oceanographic changes (Checkley *et al.*, 2009). Consequently, even though in this study we used a dataset collected during the summertime, the variability associated with the sampling period was relatively high for 3 species out of 10 (i.e., sprat, Atlantic horse mackerel and Atlantic mackerel) for which no reliable conclusion could be drawn. For round sardinella and Mediterranean horse mackerel, no significant and negative effect of temperature was observed. For the five (5) remaining species, we demonstrated that they follow the Bergmann's rule, with larger individuals being more common at lower temperature. In the case of anchovy, these results are consistent with previous investigations of the effect of temperature on their growth which showed a significant negative effect of temperature on asymptotic length (i.e., L_∞ the length at which growth rate is theoretically zero) (Basilone *et al.*, 2004). These negative correlations did not seem to be confounded by the sampling period or by the bathymetric variation of fish sizes. Indeed, when controlling for depth by adding it as a covariate in the model, all negative size-temperature relationships remained significant. Furthermore, except for bogue, the effect of temperature was stronger than the effect of depth. The output of the bootstrap-sampling procedure also showed that the negative correlations between temperature and body sizes were stable against sample-size variation. These analyses strongly suggest that temperature is a major determinant of pelagic fish body sizes. The rates of body size changes with temperature through space are in the same order of magnitude as those estimated by Audzijonyte *et al.* (2020) for reef fishes in the wild (~4% body size change per 1°C change through space) and those measured for marine ectothermic organisms in controlled experiments

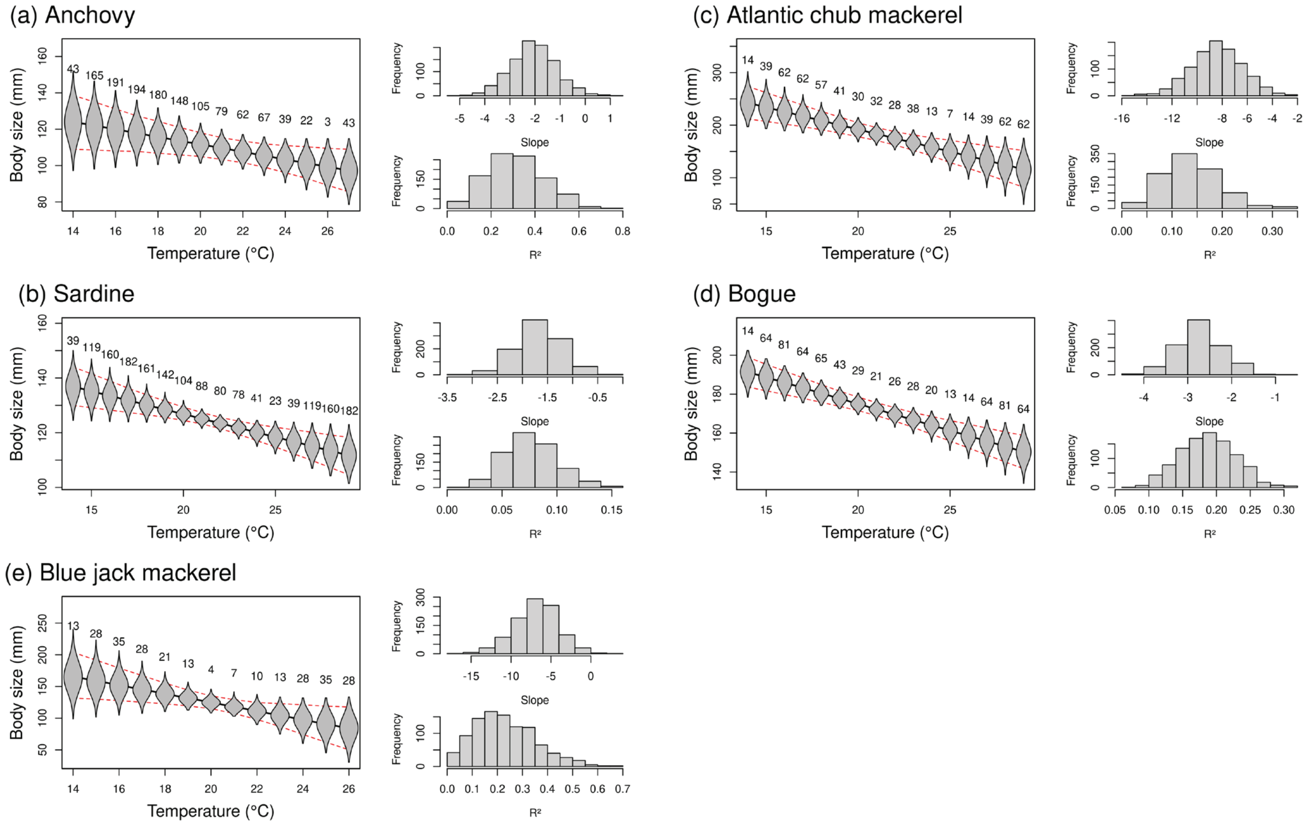

Fig. 6: Effect of sub-sampling on body size temperature relationships. Violin plots indicate the body size distributions in each bin of 1 °C. Numbers indicate the sample size (number of trawls) per temperature bin. The histograms represent the distributions of slopes and the R² of the 999 linear models fitted using the resampling procedure.

(−3.0% °C^{-1}; Forster *et al.*, 2012).

Several partially competing hypotheses exist regarding the occurrence of thermal size clines in ectotherms (Atkinson *et al.*, 2006; Walters & Hassall, 2006; DeLong, 2012; Zuo *et al.*, 2012; Audzijonyte *et al.*, 2019). Oxygen limitation was originally proposed as a key mechanism to explain smaller ectotherm body size at higher temperatures (see e.g., Atkinson *et al.*, 2006; Audzijonyte *et al.*, 2019 for a review). The general body-size optimization hypothesis “maintain aerobic scope and regulate oxygen supply” states that ectotherms grow to a smaller final body size at higher temperatures to maintain their aerobic scope as oxygen concentrations decline with increasing temperature (Atkinson *et al.*, 2006). For marine fishes, the gill oxygen limitation hypothesis (Pauly, 1981) proposes that body size in fish is limited by the inability of gills (whose surface area is limited) to supply enough oxygen to meet the requirements of increasing metabolic costs that scale with body volume. According to Pauly & Cheung (2018), the gill oxygen limitation hypothesis provides the most parsimonious explanation for a range of responses including temperature dependence of maximal attainable body masses in ectotherms, prevalence of small fish in tropical waters, higher sensitivity of larger individuals to temperature, and lower food assimilation efficiency in larger individuals. However, it is important to note that this hypothesis is strongly debated, as recent criticisms were expressed about its validity and universality (see Lefevre *et al.*, 2018; Lefevre *et al.*, 2021; Pauly, 2021). Another main hypothesis used to explain the temperature–size rule is the mismatch, or difference in developmental rates versus growth rates thermal responses (Van der Have & De Jong, 1996; Forster *et al.*, 2012; Zuo *et al.*, 2012). This hypothesis considers that temperature responses of growth and development during ontogeny differ. An increase in development rate relative to growth rate at high temperature leads to smaller body sizes as a result of lower somatic growth following earlier sexual maturity (Zuo *et al.,* 2012). Furthermore, resource supply models state that the proximate cause for optimal body size is determined by the temperature-dependent interplay of resource supply from the environment versus demand, leading to smaller body sizes (higher resource demands) at higher temperatures (DeLong, 2012). Evidence of abiotic and biotic predictors of body size structure has been obtained from several studies showing that differences in productivity and taxonomic composition contribute to size differences (Jeppesen *et al.*, 2000; Emmrich *et al.*, 2011; Emmrich *et al.*, 2014). Thus, the realized size in marine ectotherms populations integrates growth, mortality, competition, predation risk and food availability simultaneously, and the interplay among these factors (Audzijonyte *et al.*, 2020). Several of these factors are modulated by temperature, which result in the occurrence of thermal body size clines in ectotherms, such as the 5 pelagic species of the present study.

Our results indicate that a positive correlation between body size and latitude can be observed only in bogue. The presence of negative correlations between body sizes and latitude can be explained by the geographical gradient of the temperature in the Mediterranean Sea which does not solely follow a latitudinal gradient. The averaged zonal surface temperature gradient over most of the Mediterranean Sea increases from north to south especially in the Gulf of Lions and in the northern Adriatic Sea where the temperature minima are located. However, a meridional gradient of temperature, partly due to the Mediterranean surface circulation, occurs also over the northern Tyrrhenian and the Levantine sub-basins where temperature increases from west to east (Shaltout & Omstedt, 2014). Moreover, the annual temperature in the northern Aegean sub-basin is much lower than in the northern Ionian sub-basin, although the two areas are at the same latitude. This is largely due to the input of less saline and colder water of Black Sea origin entering the northern Aegean Sea through the Dardanelles strait. Besides, here, we used a vertically integrated temperature dataset rather than only surface temperature. Thus, the local bathymetric variations of temperature may further increase the decoupling between temperature and latitude. The increase in fish body size with increasing latitude reported in several other studies at larger spatial scales, may thus be partially due to a greater latitudinal gradient of temperature than that encountered in the Mediterranean Sea (e.g., Fisher *et al.*, 2010b; Saunders & Tarling, 2018). In addition, it should be noted that, as the Mediterranean is classified as an oligotrophic Sea (d'Ortenzio & Ribera d'Alcalà, 2009), primary production can be considered as a limiting factor for fish growth in this area as demonstrated for anchovy (Basilone *et al.*, 2004). Thus, the Mediterranean west-east gradient of primary productivity (d'Ortenzio & Ribera d'Alcalà, 2009) could also explain the absence of positive correlations between body sizes and latitude observed for planktivorous fish species, namely anchovy, sardine, and blue jack mackerel.

In addition to the temperature, fishing is also an external driver that may alter the size structure of a fish population (Fisher *et al.*, 2010a; Tu *et al.*, 2018). Fishing represents size-selective removal of larger individuals that can truncate the size structure of a fish population (Berkeley *et al.*, 2004; Barnett *et al.*, 2017), which, in turn, may cause recruitment failure, reduce the reproductive outputs, and increase the size variability of fish populations (Rouyer *et al.*, 2012). This may also lead to evolutionary consequences and selection of slow-growing fish (Heino *et al.*, 2015) that start first maturation at a younger age and smaller size due to both genetic and plastic responses (Conover & Munch, 2002; De Roos *et al.*, 2006). Unfortunately, the exploitation status was available only for sardine and anchovy and not in all areas due to the absence of stock assessment for the other 8 species included in this study. The exploitation status of sardines and anchovies in the Mediterranean Sea varies greatly from one area to another. Stocks assessed were either sustainably exploited (for sardine in GSA 9 and anchovy in GSAs 6, 9 and 22), or in overexploitation (sardine in GSAs 1, 3, 6, 16, 17-18 and 22; anchovy in GSAs 17-18), or ecologically unbalanced (sardine in GSA 7), or at a low biomass level (anchovy in GSA 7) (GFCM 2019). Although, body size variations can be related to exploitation, we believe that the effects of the spatial patterns of exploitation on body size clines are unlikely to affect our overall conclusions. Fisheries targeting small pelagic in the Mediterranean Sea, which consists mainly of purse seine fleets (and pelagic trawler in GSA 7 and GSA 17), cannot be considered as large size-biased exploitation in comparison to other types of fisheries. For instance, in the Gulf of Lions (GSA 7), where the most drastic decrease in growth, condition and size of the two main exploited small pelagic fish species (e.g., sardine and anchovy) was observed (Van Beveren *et al.*, 2014; Brosset *et al.*, 2017), it has been shown that these decreasing trends did not appear to be mediated by a high fishing pressure (Saraux *et al.*, 2019) but rather by a bottom-up control (Feuilloley *et al.*, 2020).

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Supplementary Data

The following supplementary information is available online for the article:

Figure S1: Pearson's r ccorrelation between the mean temperature of the water column, depth, and latitude intrawl haul stations