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Understanding the response of the Western Mediterranean cephalopods to environment and fishing in a context of alleged winners of change

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Abstract :

Increasing impacts of both fisheries and climate change have resulted in shifts in the structure and functioning of marine communities. One recurrent observation is the rise of cephalopods as fish recede. This is generally attributed to the removal of main predators and competitors by fishing, while mechanistic evidence is still lacking. In addition, climate change may influence cephalopods due to their high environmental sensitivity. We aim to unveil the effects of different anthropogenic and environmental drivers at different scales focusing on the cephalopod community of the Western Mediterranean Sea. We investigate several ecological indicators offering a wide range of information about their ecology, and statistically relating them with environmental, biotic and fisheries drivers. Our results highlight non-linear responses of indicators along with spatial differences in their responses. Overall, the environment drivers have greater effects than biotic and local human impacts with contrasting effects of temperature across the geographic gradient. We conclude that cephalopods may be impacted by climate change in the future while not necessary through positive warming influence, which should make us cautious when referring them as generalized winners of current changes.

Highlights

► Effects of environmental, biotic and human drivers were investigated for ecological indicators of cephalopods. ► Dynamics of this taxon are mainly influenced by sea temperature, explaining geographical gradients in several metrics. ► Relationships with biotic variables could hint at the decrease of high trophic fishes. ► Fishing has little effect on cephalopods with β-diversity being the only indicator influenced by this variable. ► Potential negative effects of warming on indicators challenge the idea of cephalopods as a climate change winners.

Keywords : Cephalopods, ecological indicators, fishing, climate change, anthropogenic impact, ß-diversity

1. Introduction

Global change causes several negative impacts reported worldwide on marine ecosystems, while it can favour some taxonomic groups. Numerous studies on different areas and species have identified cephalopods as potential winners in the marine environment, while the generalization of this patten is still pending of conclusive proofs. This trend, observed at both regional (Keller et al., 2016; Veloy et al., 2022) and global scales (Doubleday et al., 2016), may be largely influenced by the favouring conditions of climate change (such as warming) and interspecific relationships with other diminishing and competing taxa such as fishes of higher trophic level. Cephalopods have a great ecological importance for their top-down control mechanisms due to their strong predatory role and high trophic levels (Anderson et al., 2011; Eddy et al., 2017). Therefore, an understanding of the factors that affect the cephalopod community, as well as the increase of dominance in the ecosystem, can aid to better understand of the current state and expected changes of marine ecosystems.

The overexploitation of fishes, as one of the main predators of cephalopods (Caddy and Rodhouse, 1998; Hastie et al., 2009; Staudinger et al., 2013), has been proposed as an important factor in the increase of this taxonomic group. Indeed, the decrease of fish production results in fishing fleets switching from declining fish stocks towards invertebrates, including cephalopods. In fact, the landings on cephalopods is rising worldwide (FAO, 2020; Ospina-Alvarez et al., 2022). The south of Europe, particularly Spain, is among the countries with more local cephalopod supply available per capita alongside Republic of Korea, Japan and Taiwan (Hunsicker et al., 2010; Ospina-Alvarez et al., 2022), which makes south European stocks potentially more at risk. In the Mediterranean Sea, while many assessed fish stocks are already heavily exploited the lack of generalized assessment of cephalopods limit the capacity to assess their current health status (FAO, 2022). Furthermore, for these invertebrates, metrics such as the Maximum Sustainable Yield (MSY) are not well adapted to them compared to fishes. This is mainly due to poor data as well as the problems their short life-strategy poses to modelling (Arkhipkin et al., 2021), which represent a long-lasting challenge for the current and future management..

It is also known that cephalopods are highly sensitive to environmental factors (e.g. Arvanitidis et al., 2002; Forsythe, 2004; Pierce et al., 2008) (see list of references and associated mechanisms and observations reviewed and shown in the Supplementary Material Table S1). They also have a great degree of plasticity observed through their different life cycles and species (Arvanitidis et al., 2002; Otero et al., 2009; Pierce et al., 2008). This plasticity results in unexpected responses to certain environmental factors that vary by both taxa and study area with, for instance, differential responses in adult body size to warming across taxa and regions. Both increase in body size and younger maturation and, therefore, smaller adult size and shorter lifespan, have all been reported to be favoured by warming conditions (Forsythe, 2004; Hatfield, 2000; Pecl and Jackson, 2008). High sea surface temperatures (SSTs) generally benefits cephalopods at a population level allowing them to increase their abundance and even their spatial distribution range in some cases (van der Kooij et al., 2016). Primary production also plays a similar role benefitting cephalopod populations mostly related to upwelling processes, particularly in early life stages, allowing higher survival rates due to the associated increase in secondary production (Bakun and Csirke, 1998; Lauria et al., 2016; Otero et al., 2009; Puerta et al., 2016b). However, in some systems there is a negative relationship between certain species of cephalopods and primary production, mostly due to lagged responses, as paralarva are released during the less intense periods of upwelling (i.e. less productive) to ensure they remain near the coast (Otero et al., 2009), in agreement with the ‘optimal environmental window’ hypothesis (Cury and Roy, 1989).

The Mediterranean Sea is a semi-enclosed sea, characterized by oligotrophic nature and warming increasing temperatures (Coll et al., 2010). It is an important region as biodiversity hotspot (Coll et al., 2010; Costello et al., 2010), but with many marine resources still overexploited by fishing (FAO, 2022). The local marine ecosystem is also subjected to quick changes due to climate change (Hidalgo et al., 2018; Lejeusne et al., 2010), increased sensitivity to natural variability in primary production (Fu et al., 2018; Hidalgo et al., 2022a), the effects of invasive alien species such as the Lessepsian fauna (Galil et al., 2017) and of pollution (Danovaro, 2003; Pennino et al., 2020). Recent studies analysing marine biodiversity changes in space and time have shown divergent patterns according to the taxonomic groups investigated in this semi-enclosed sea (Carmezim et al., 2022; Pennino et al., 2024; Veloy et al., 2022). One example of these differences is the case of fishes and cephalopods: while the former have been shown to decrease with time, likely related to fisheries activity impacts (Farriols et al., 2020), cephalopods have been shown to be a prolific group (Ciércoles et al., 2018; Keller et al., 2017a; Puerta et al., 2016b; Quetglas et al., 2016).

In the Mediterranean Sea, some relationships between the different environmental drivers, the bathymetric gradient, and the cephalopod community have been already confirmed. For instance, the bathymetric pattern of species richness gradient has been shown to peak nearing the continental shelf break (Keller et al., 2017b). Environmental factors such as SST and primary production can have a positive relationship with species richness as well as biomass (Supplementary Material Table S1). In contrast, human impacts have been shown to have a negative influence on the cephalopod richness in non-target species, while a non-linear response (increasing richness at low and upper levels of exploitation) also observed (Navarro et al., 2015; Vilas et al., 2019). These findings are in line with reported higher biomass of cephalopods with lower levels of predators and higher levels of fishing (Coll et al., 2013), and in areas with relative warmer waters (Navarro et al., 2015). However, the responses of cephalopods to direct and indirect variables have been shown to differ depending on the studied species and region (Keller et al., 2017b; Puerta et al., 2016a, 2016b, 2015), in part due to short life cycle and their high capacity to adapt to local and regional environmental conditions (Moreno et al., 2002; Pierce et al., 2008).

Most of past and recent research has focused on direct quantitative approaches to study cephalopod populations taking biomass and abundance as main metrics (Hastie et al., 2009; Hatfield, 2000; Otero et al., 2009; Puerta et al., 2016b) (Supplementary Material Table S1), while little is known about other community and biodiversity indicators, or other indicators informing on their function on the ecosystems. In addition, the analyses of drivers causing variation on ß-diversity or other community and trophic-based indicators have not been widely investigated. The combination of these indicators may provide valuable information regarding the geographic and temporal evolution of this taxon, the mechanisms of change and potential implications on the ecosystem functioning attending to environmental and anthropogenic drivers in given areas.

Our hypothesis is that cephalopods, being short-lived organisms, respond more profoundly to the environment than to other drivers, although they can be influenced by local human activities such as fishing (Navarro et al., 2015; Nieblas et al., 2014; Puerta et al., 2016b). Furthermore, these factors could influence competition as well as food availability represented by the predatory fishes and crustaceans, respectively (Puerta et al., 2016a). Thus, the main objective of this study is to investigate local and regional scale drivers of spatial change in the cephalopod community of the West Mediterranean Sea in terms of a set ecological indicators and relate them to environmental, human and biotic drivers. This study follows the results of a regional analysis that showed important increases of cephalopods indicators in the region (Veloy et al., 2022), selecting those indicators that have shown most significant spatial variation.

2. Materials and Methods

a) Sampling and study area

We used cephalopods data collected from annual trawling surveys performed within the Mediterranean International Trawl Survey (MEDITS) program between 2013 and 2019 with 1296 unique sampling points (Supplementary Material Table S2), as this period allowed us to get a complete time series of the forcing variables of interest. A common sampling protocol was used in the entire study area, standardizing duration of the hauls as well as gear type and its specifications (Bertrand et al., 2002; Spedicato et al., 2020).

The General Fisheries Commission of the Mediterranean (GFCM) adopted several divisions of the surveyed area denominated Geographical Sub-Areas (GSAs). We focused on continuous area of the Western Mediterranean, ranging from the Alboran Sea to the Gulf of Lion, corresponding to GSA1 (Northern Alboran Sea), GSA6 (Northern Spain) and GSA7 (Gulf of Lion) (Fig. 1). These three areas display a continuous geographic area with contrasting hydrographical characteristics: i) the northern Alboran Sea is an area influenced by the influx of Atlantic waters and thus has a high and variable primary production; ii) the Northern Spain, including Valencia Channel, Ebro Delta and North Catalan Sea, is characterized by low values of chlorophyll-a concentration (although the Ebro Delta receives nutrients from continental sources) and high temperature but differ in the width of their continental shelves; and iii) the Gulf of Lion, a shallow area with an extended continental shelf as well as lower SST characterized by variable but high productivity due to its local oceanography (Rhone river input and wind induced coastal upwelling) (Bosc et al., 2004; Estrada, 1996; Nieblas et al., 2014). These subareas division have been used in previous studies (Veloy et al., 2022). Because the depth range between 25 and 500 m is the one with most diversity of taxa, only sample points from those depth ranges (corresponding to the continental shelf and upper slope area) were considered.

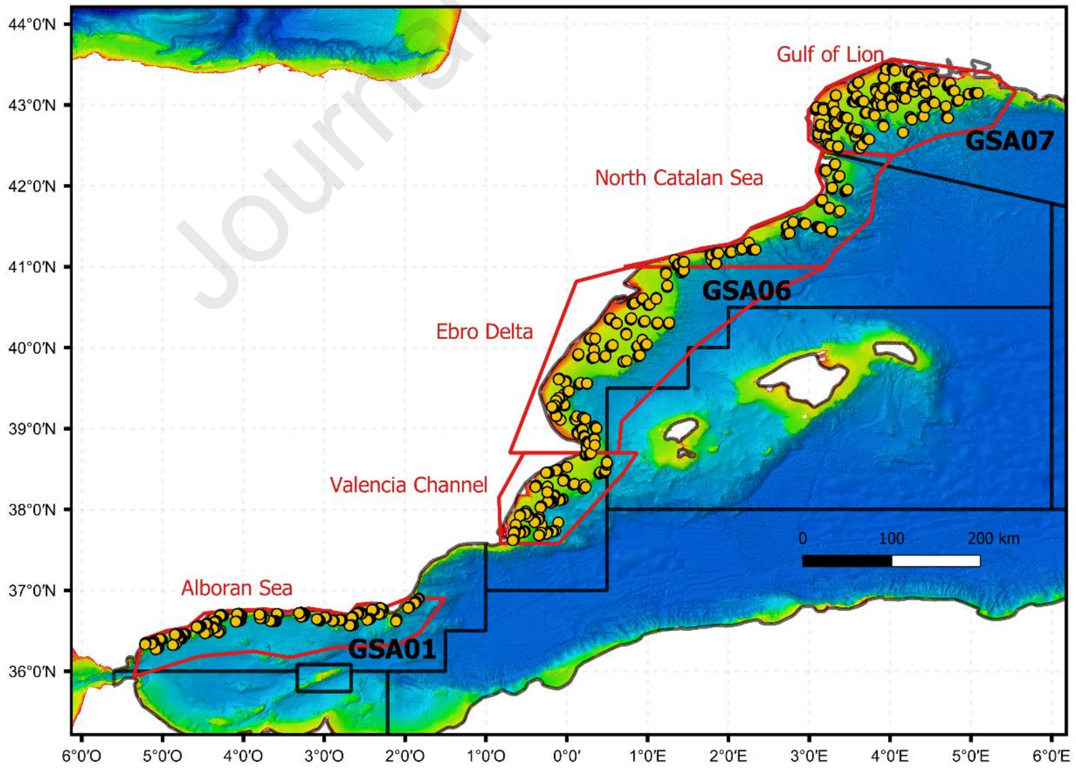

Figure 1: Western Mediterranean area with the considered subregions (in red), GSA areas (in black) and sampling points of the MEDITS trawling survey used in this study.

b) Indicators and drivers of change

We used three groups of indicators: (a) traditional biodiversity indicators such as species richness and β- diversity (Jaccard index); (b) community indicators such as biomass, mean size (both of these transformed into logarithm in this study) and relative biomass of predators within the cephalopods (B_{pred}); and (c) trophic level indicators as $TL_{3.25}$ and TL_4 (Table 1). These indicators were selected based on criteria used in previous studies (Veloy et al., 2022) and the Indiseas project (Coll et al., 2016; Shannon et al., 2014; Shin et al., 2018), such as measurability and data availability (must be estimated routinely and have time-series available), ecological significance and sensitivity to different drivers.

To calculate B_{pred} we labelled as “predator” those species of cephalopods with Trophic Level (TL) above 3.5 that were reported as having maximum sizes larger than 20 cm of total length or equivalent measurements. Trophic levels were obtained from different online databases (Froese and Pauly, 2021; Palomares and Pauly, 2021). After assigning this trait data, those species present in less than 80% of the temporal series were discarded from the study (Supplementary Material Table S3).

The drivers (independent variables) (Table 2, Fig. 2) were classified into four categories depending on the information they provided: (a) depth as a structural and static driver (note that geographic smoother were explicitly avoided; see explanation below) (b) dynamic environmental variables (Sea Surface Temperature (SST), and Chlorophyll-a (Chl-a), (c) dynamic human drivers (Fishing effort) and (d) dynamic biotic variables (Relative biomass of predatory fishes (Fish B_{pred}) and crustacean biomass as a prey indicator). These independent variables were selected because they have shown to be very influential on cephalopod populations, as well as they allow to explore different types of change (anthropogenic and natural) (Supplementary Material Table S1).

Environmental and human drivers were obtained from reanalysis data of physic and biochemistry parameters of the Mediterranean provided by COPERNICUS (2021) with a resolution of 0.04 degrees and from Global Fishing Watch (2019) data with a resolution of 0.01 degree, respectively. The study period selected within the databases is between 2013 to 2019. In the case of the environmental drivers, data was used to calculate yearly means per sample point (i.e. grid cell), while for fishing effort the daily data was processed to get the yearly sum of the total fishing hours per grid cell using previously established methods (Taconet et al., 2019). While the use of lagged variables, specially for the environmental ones, have been featured in other studies (Keller et al., 2017a), we only used data from the same year beacuse the focus of the study was to understand the spatial variation of the community and adding a temporal dimension could complicate the interpretation of the results attending to the spatiotemporal dependence of processes and data.

Lastly, biotic data was extracted from the data available in a previous study (Veloy et al., 2022). The Fish B_{pred} considered a similar criterion of predator as it was described previously for predatory cephalopods (i.e., *Octopus vulgaris*, *Loligo forbesii*). Both fishing effort and the biomass of crustaceans was transformed using the logarithm.

The biotic data derived from MEDITS and the drivers investigated were interpolated into a grid with a resolution of 0.25 degrees over the study area (Fig. 2).

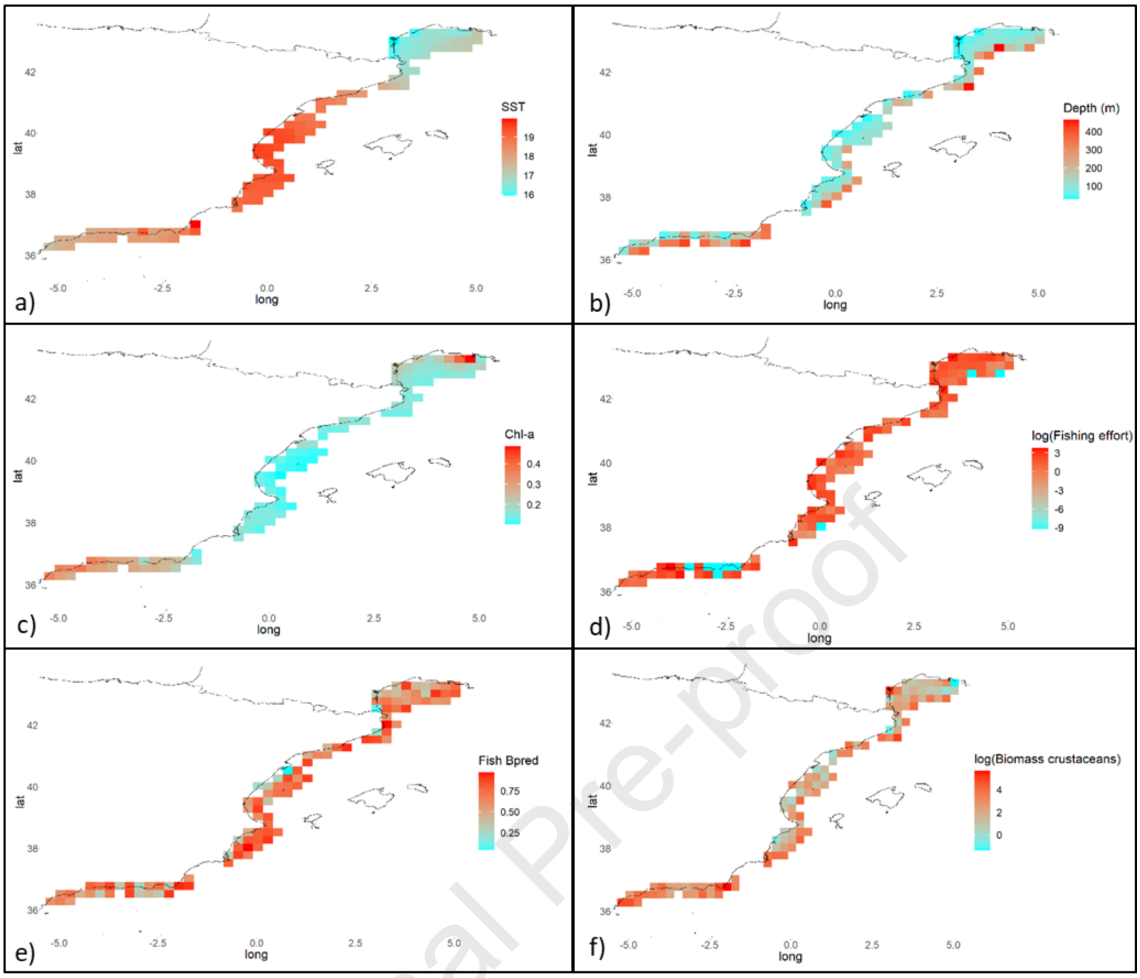

Figure 2: Spatial variation of the different independent variables considered for this study. Values represent the mean of the time period. a) SST (ºC), b) Depth (m), c) Chl-a (mg/m3), d) log (Fishing Effort), e) Fish B_{pred}*, f) log (Biomass crustaceans).*

c) Data analysis

Firstly, correlation matrices were used to preliminary check the correlation between drivers and all the ecological indicators. The final selection of independent variables (Table 2) featured indicators of each category (environment, human or biological) that were complementary: SST, Chl-a, Fishing Effort, Fish B_{pred} and Biomass of crustaceans.

Secondly, we applied General Additive Modelling (GAM) (Wood, 2006) to each indicator to evaluate the regional influence of environmental and anthropogenic drivers as univariate smoother along with depth as a structural variable (i.e. persistent influence). GAM models were considered for the study due to their premise of non predefined functional form of the effect and their capacity to determine non-linear effects, allowing a more complete understanding of the effects and the response capacity of all the indicators. We also took into account the ease of interpretation of the relationships between each indicator and the drivers on an individual level as well as the efficiency to study the residuals, as opposed to other methods. One-dimensional non-parametric smoothing functions used included cubic splines with up to a maximum of 3 degrees of freedom (i.e. 4 knots) to avoid model overfitting and obtain meaningful functional forms of the effects. All the models were calculated using Gaussian distribution with the exception of the Richness model, where a Poisson distribution was used. Model selection was done comparing the models with all the independent variables with those where the non-statistically significant variables were sequentially removed (Supplementary Material Table S5). An important element in our modelling approach is that we explicitly avoided the use of a geographic bi-variate smoother (latitude, longitude) to allow environmental factors to capture the potential spatial variability.

To distinguish whether the drivers investigated were geographically structured or whether they represented a larger scale impact at the scale of the studied region, we investigated the partial residuals of all covariates and models according to the five distinct sub-regions continuously spread over the three contiguous GSAs: GSA1, GSA6 and GSA7. We indicate in the results when it is meaningful based on the overlapping of the residuals of different sub-regions. Finally, we present the spatial predictions of the models using the independent variables as predictors.

All indicators and analysis were calculated with R version 4.2.2 (R Core Team, 2022). Jaccard index and its components were calculated using the R package betapart (Baselga and Orme, 2012) and the GAM models were obtained using mgcv (Wood, 2011).

Table 1. Dependent variables used in the study and information they provide about the state of cephalopods and the communities they are part of.

Indicators	**Information about cephalopods/ecosystem**	**Data source**	**Indicator source**
Biodiversity indicators			
Richness	Number of cephalopod species present	MEDITS data; Veloy et al., 2022	McIntosh, 1967
B-diversity (Jaccard index)	Temporal change of the cephalopod subset of the ecosystem	MEDITS data; Veloy et al., 2022	Blowes et al., 2019; Dornelas, 2014
Biomass and size			
Total biomass of cephalopods (Biomass)	Weight of all cephalopods (transformed to logarithm)	MEDITS data; Veloy et al., 2022	Coll et al., 2016
Relative predatory cephalopod biomass (B_{pred})	Fraction of cephalopods that are considered predators	MEDITS data; Veloy et al., 2022	Coll et al., 2016
Mean Size	Weight of the average cephalopod as a proxy for size (transformed to logarithm)	MEDITS data; Veloy et al., 2022	Shin et al., 2018; Forsythe, 2004
Trophic level indicators			
$TL_{3.25}$	Mean trophic level of cephalopods above 3.25	MEDITS data; Veloy et al., 2022	Shannon et al., 2014
TL_4	Mean trophic level of cephalopods above 4	MEDITS data; Veloy et al., 2022	Shannon et al., 2014

Table 2. Independent variables used in the study and sources of origin.

Variable	Definition	Data source	Variable source
Structural driver			
Depth	Depth at sea bottom	MEDITS data	
Environmental drivers			
SST	Sea Surface Temperature	COPERNICUS, 2021	COPERNICUS, 2021
Chl-a	Primary production	COPERNICUS, 2021	COPERNICUS, 2021
Human impact drivers			
Fishing effort	Number of yearly hours that vessels spent fishing on an area, (human pressure) (transformed to logarithm)	Global Fishing Watch 2021	Anderson et al., 2011; Caddy and Rodhouse, 1998
Biotic drivers			
Fish B_{pred}	Fraction of fishes that are considered predators (competitors and predators of cephalopods)	MEDITS data; Veloy et al., 2022	Coll et al., 2016; Veloy et al. (2022)
Crustacean biomass	Weight of all sampled crustaceans from the order Malacostraca, excluding amphipods and isopods (cephalopod main prey) (transformed to logarithm)	MEDITS data; Veloy et al., 2022	Puerta et al., 2015; Veloy et al. (2022)

3. Results

Biodiversity indicators

Cephalopods’ richness showed positive relationships with SST above 18 °C, a linear influence of the biomass of crustaceans, as well as a maximum of species at depths of 150-300 m (Fig. 3, Table 3). Spatially, it presented lower values in northern areas, characterized by low temperatures and low values of crustacean biomass. Richness showed maximum values on the southernmost area of GSA6, where all those drivers show higher values. Interestingly, SST displayed a spatial segregation of partial residuals while the other drivers showed a regional effect (i.e. overlapping distribution, Supplementary Material Figure S2). Maximum species richness values were observed south the Ibiza Channel and a heterogeneous pattern emerged in the Alboran Sea and the Ebro delta.

β-diversity showed a nonlinear relationship with SST with a maximum value around 17 °C followed by a decrease (Fig. 3, Table 3). It showed a negative relationship with Chl-a until 0.4 mg/m^3 from which ß-diversity increased. It also showed a positive non-linear relationship with fishing effort and a negative relationship with fish B_{pred} and depth. Spatial patterns were roughly opposite to the ones found for richness, with the highest values found in the northern areas and the lowest on the south of GSA6 on the Valencia Channel. The partial residuals of the effects showed the highest values of this index in the Gulf of Lion and North Catalan Sea, which are areas with the lowest SST (Fig. 4).

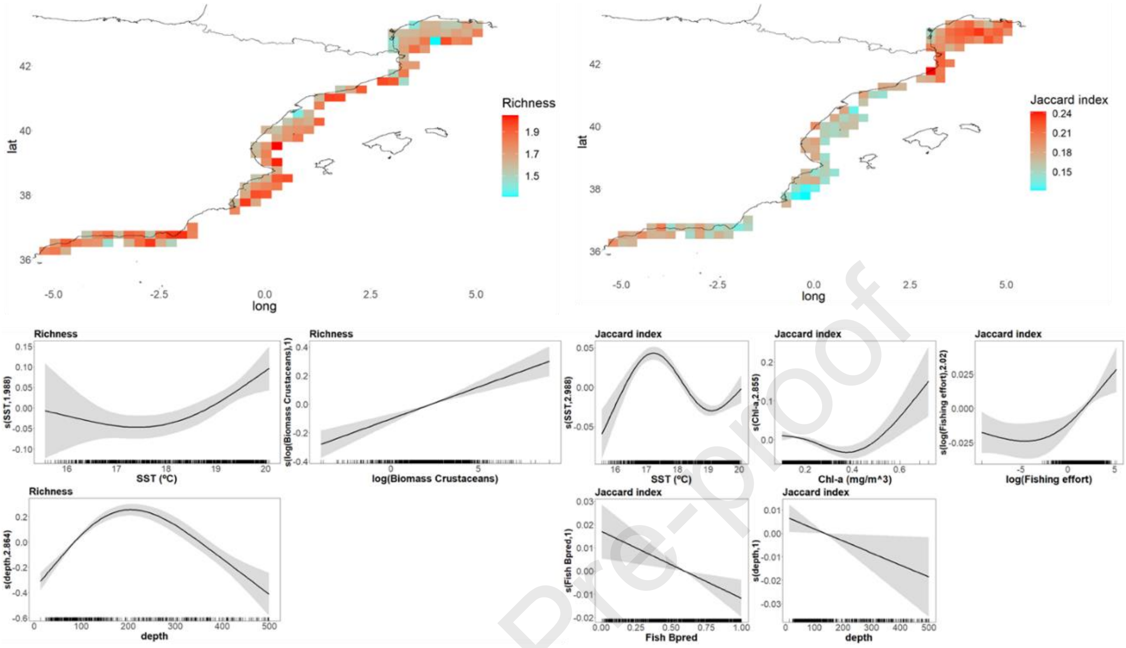

Figure 3: Spatial variation and smoothing effect of species richness (left) and ß-diversity (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

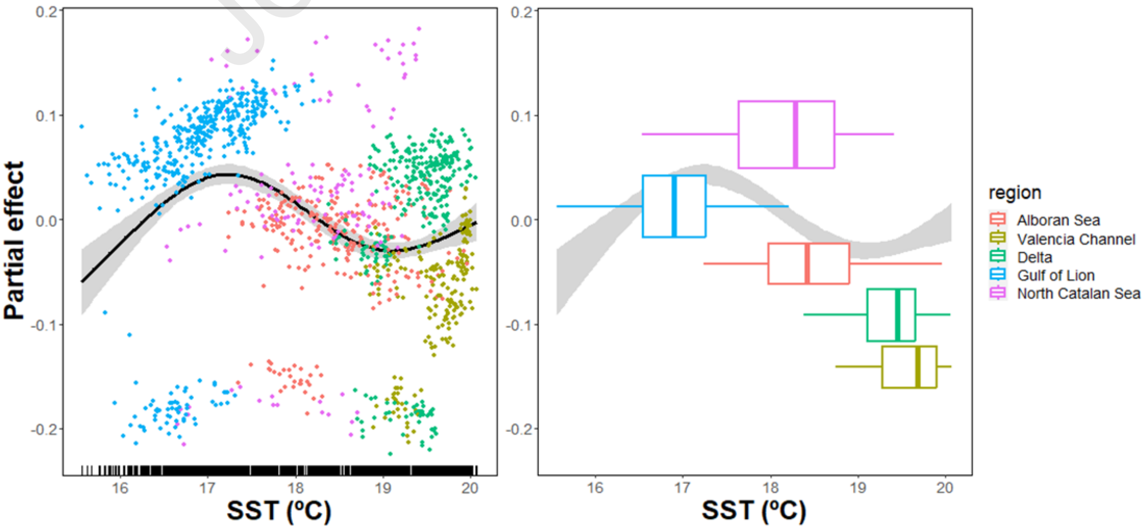

Figure 4: Residuals (left) and boxplots (right) of the partial effect of SST on the Jaccard index. The shaded areas of the partial plot indicate the 95% confidence interval.

Biomass and mean size

A decreasing trend was found between total cephalopods biomass and SST, reaching a minimum between 17 °C and 18 °C and a small increase at 19 °C (Fig. 5, Table 3). It also showed a non-linear increasing trend with biomass of crustaceans and with Fish B_{pred}, with a maximum value at ratios stabilized around 0.5 in the latter case. On the other hand, cephalopods biomass decreased with Chl-a and particularly with depth. The highest values were found in the shallow areas of the Gulf of Lion and the deep areas in central Northern Spain (i.e. Ebro Delta). The partial residuals of the effects of SST showed that the Catalan Coast and the Gulf of Lion areas were associated with the highest values of the indicator as well as the decrease on cephalopods biomass (Fig. 6).

SST had a negative effect on B_{pred} until 18.5 °C and of Chl-a until 0.3 mg/m3 (Fig. 5, Table 3). Residuals on the SST model showed a geographical pattern of this effect (Fig.6), where the Gulf of Lion and the Catalan Sea were associated to higher values of B_{pred} and the residuals of the rest of the independent variables were more homogenously distributed (Supplementary Material Figure S5). B_{pred} showed a nonlinear decreasing trend with depth and biomass of crustaceans, while fish B_{pred} had a positive linear relationship with this metric. Areas from the north had higher ratios of predators than southern areas such as the Alboran Sea (GSA1) showing a gradient between the former and the Gulf of Lion (Fig. 5).

Mean Size (Fig. 7, Table 3) had a negative nonlinear relationship with Chl-a and depth, and a dome-shaped relationship with SST with a maximum at 18 °C. It also had a clear positive relationship with fish B_{pred}. Highest mean sizes appeared in GSA6 areas, on grid cells where primary production was low and the ratio of predatory fishes was high.

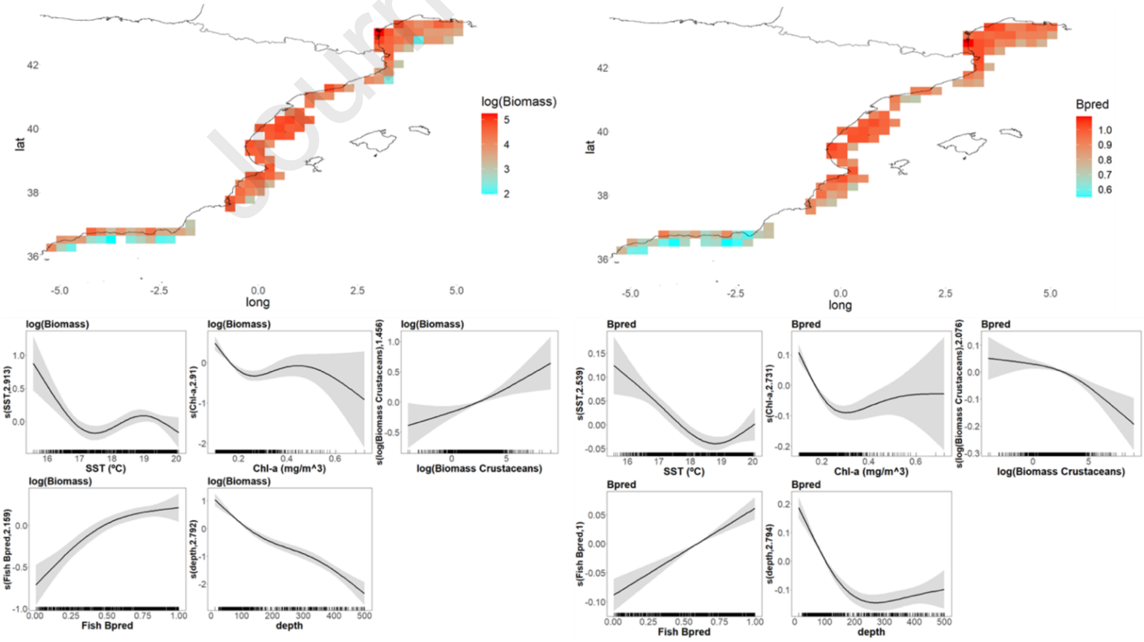

Figure 5: Spatial variation and smoothing effect of the of Biomass (log scale,left) and,B_{pred} (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

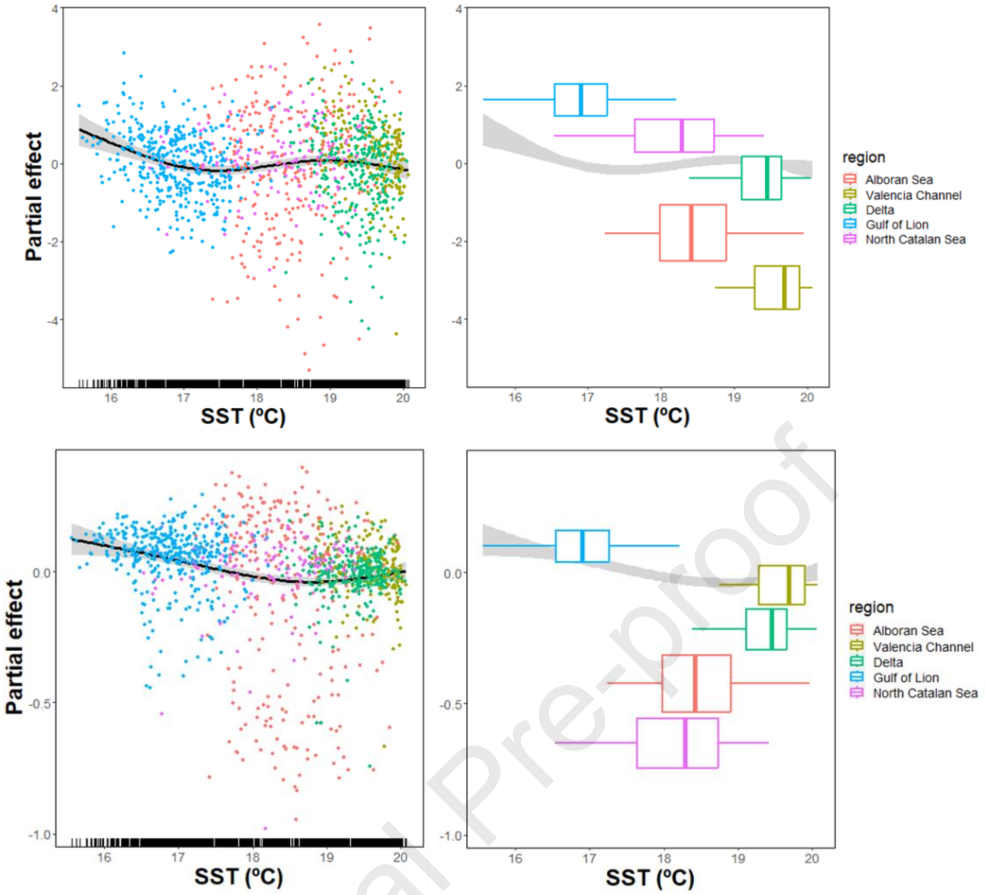

Figure 6: Residuals (left) and boxplots (right) for SST of the Biomass (log scale, upper row) and B_{pred} (lower row) models. The shaded areas of the partial plot indicate the 95% confidence interval.

Trophic level indicators

$TL_{3.25}$ presented a linear negative relationship with biomass of crustaceans (Fig. 8, Table 3). Meanwhile, for SST and depth, these relationships were positive but non-linear. The highest values of $TL_{3.25}$ were found within the cells of GSA6, an area with generally high SST and biomass of crustaceans (Fig. 8). Partial residuals seem to confirm this trend as the values of the residuals of the regions of the Valencia Channel and Ebro delta are higher than the other regions (Supplementary Material Figure S6).

For TL_4, Chl-a also showed a dome-shaped influence with a maximum near 0.4 mg/m^3. SST showed a positive relationship with TL_4, while the biomass of crustaceans and depth had a negative relationship. The highest values of TL_4 were found in the shallow waters and comparatively in the south, being associated with high productivity, intermediate values of SST and low values of biomass of crustaceans (Fig. 8). Some high values of TL_4 were also found on sparse cells corresponding to temperate shallow waters in the Gulf of Lion.

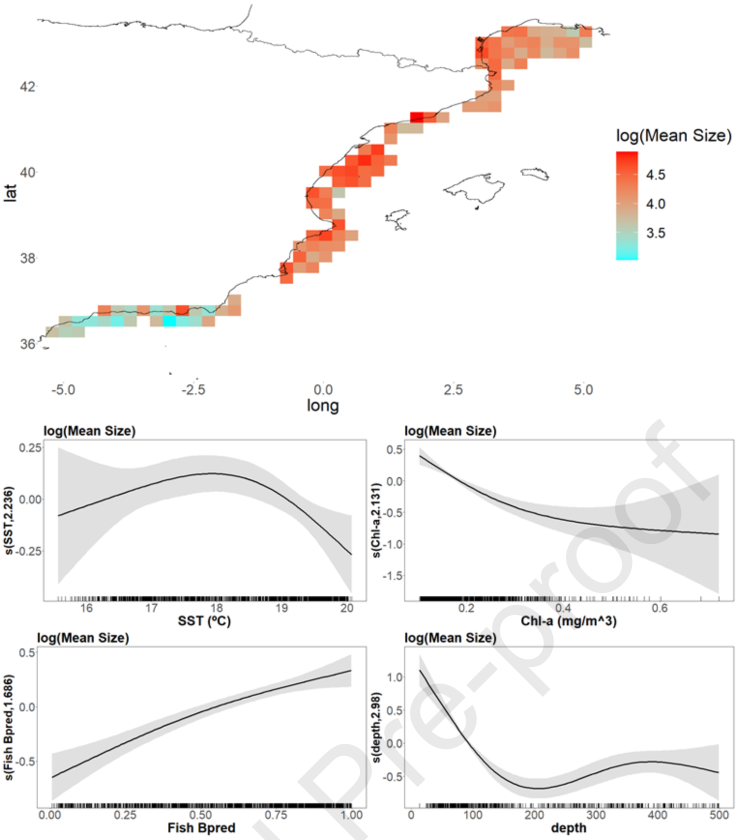

Figure 7: Spatial variation and smoothing effect of the Mean Size (log scale). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

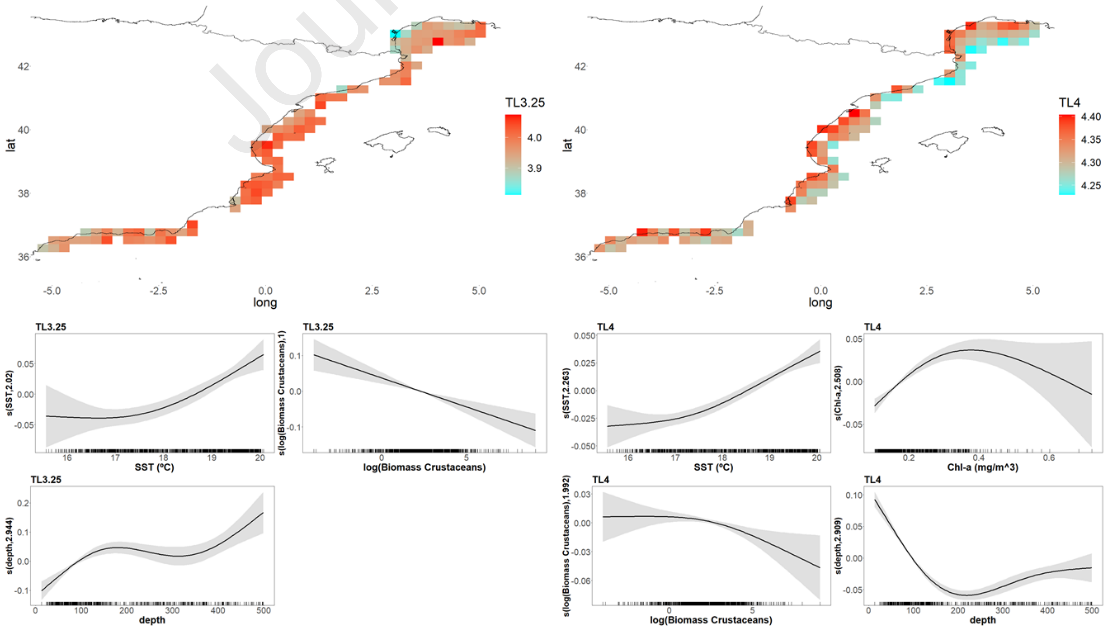

Figure 8: Spatial variation and smoothing effect of mean trophic level above 3.25 (left) and 4 (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

Table 3: GAM models summary for each ecological indicator. *** p<0.001, ** p<0.01, * p<0.05. edf = Estimated degrees of freedom of univariate smoothers; %DV = Deviance explained (percentage).

Indicator	Drivers	Intercept	edf	%DV
Richness	SST	1.697 ± 0.012	1.988***	23.6
	Log(Biomass Crustaceans)		1***	
	Depth		2.864***	
B-diversity (Jaccard index)	SST	0.183 ± 0.002	2.988***	10.9
	Chl-a		2.855***	
	Log(Fishing effort)		2.020***	
	Fish B_{pred}		1**	
	Depth		1 *	
Log(Biomass)	SST	3.988 ± 0.312	2.913***	25
	Chl-a		2.910***	
	Log(Biomass crustaeans)		1456 **	
	Fish B_{pred}		2.159***	
	Depth		2.792 ***	
B_{pred}	SST	0.878 ± 0.005	2. 539***	27.5
	Chl-a		2.731***	
	Log(Biomass crustaeans)		2.076***	
	Fish B_{pred}		1***	
	Depth		2.794 ***	
Log(Mean Size)	SST	4.079 ± 0.031	2.236*	10.02
	Chl-a		2.131***	
	Log(Fishing effort)		1.442	
	Fish B_{pred}		1.686***	
	Depth		2.980***	
$TL_{3.25}$	SST	3.977 ± 0.005	2.020***	8.82
	Log(Biomass crustaceans)		1***	
	Depth		2.944***	
TL_4	SST	4.328 ± 0.002	2.263***	34.5
	Chl-a		2.508***	
	Log(Fishing effort)		2.706	
	Log(Biomass crustaceans)		1.992 **	
	Depth		2.909***	

Overall trends

In most of the dependent variables, SST showed a change of trend between 17 °C and 19 °C, corresponding mostly with the transition area of the Catalan coast between the Gulf of Lion and the Ebro delta broad shelf (Fig. 1). Values on the indicators switched from a descending curve to an ascending one and were associated with the spatial gradient of this variable, corresponding to three thermal areas. Chl-a showed a similar pattern, with an inflection point that indicated a change in response between 0.3 and 0.4 mg/m^3, which is mainly associated to the extreme areas in the Gulf of Lion and the Alboran Sea (Supplementary Material Figures S3 and S4). The effects on cephalopods' indicators were mainly associated with the geographic pattern of these two covariates, although in the case of Chl-a it seems to show a reduced geographical component in some indicators unlike SST, where a large geographic effect is apparent. These shifts in trends experienced between the Alboran Sea must be taken with caution, since the effects and the mechanisms behind them are not the same as those found in the Gulf of Lion-Catalan Coast area. This is due to its particularities as a transitional zone between the Atlantic and the Western Mediterranean and the influence of the ocean in its oceanography and the high turnover of species in this ecosystem. Those indicators showing a larger influence by environmental variables were β-diversity and B_{pred}, which revealed gradients alongside the Western Mediterranean coast. When looking at the partial residuals of β-diversity and B_{pred}, the spatial effect responsible for these gradients was visible and associated to SST, as values from each region are structured in differentiated clusters along the termal gradient (Supplementary Material Figures S1 to S5).

Those indicators most influenced by other types of variables, both biotic and human, showed less clear spatial patterns in the effects, likely indicating regional impacts. This was revealed by the partial residuals of all the regions, which were distributed in a more homogenous way along the curve of the smoothing effect with no differences between the regions. This would correspond to more heterogeneous effects on the indicators selected going beyond regional environmental gradients. Examples of these effects are fishing effort on ß-diversity or Biomass of crustaceans on Richness.

Overall, GSA1 had lower values in most indicators than the ones in the rest of the study area, except for TL_4. GSA6 area presented intermediate or high values for the different indicators, with the exception of the areas adjacent to the Ebro delta (e.g. Biomass, B_{pred}) and Valencia channel (e.g. ß-diversity). Grid cells within the Valencia channel area tended to have lower values than those in the rest of the GSA6 region. GSA7 showed high values for many indicators compared to the rest of the Western Mediterranean, like Biomass or B_{pred}.

4. Discussion

This study provides a multidimensional perspective of the cephalopod community to further comprehend their ecology and role in marine ecosystems. Previous studies examined the interactions between this taxon and drivers at a species level (Miyahara et al., 2005; Moreno et al., 2014; Otero et al., 2009; Xavier et al., 2016; among others) or considered different types of cephalopods such as squids and octopus represented by a single species (e.g. Puerta et al., 2015) (see Supplementary Material Table S1 for further details in a summarized review performed for the present study). While others studies have focused on the community analysing the variation of species composition (Keller et al., 2017a), we here investigated the cephalopod community from a different perspective: using a set of complementary ecological indicators that offer a wider picture about this diverse group along with their response to both environmental drivers and anthropogenic pressures. Our study brings novel elements to the spatial nature of the impacts of both environmental and human drivers, whether they present regionally heterogeneous or geographically effects structured in gradients. In fact, while spatial patterns of the indicators were already hinted in a recent study (Veloy et al., 2022), we here identify the main responsible drivers of the known regional patterns including those observed at a finer scale. For instance, values of the biomass of predatory cephalopods display a positive south-north gradient (mainly due to the effect of SST), while $TL_{3.5}$ displays maximum values on the southern parts of GSA6 and intermediate ones on the northern areas. On the other hand, ß-diversity, which was not showing any significant spatial effects when looking at a regional scale in past studies, revealed a positive south-north gradient in our study, mainly driven by the SST gradient.

Species richness has been suggested to follow large geographical gradients, with particular latitudinal variation along the Mediterranean Sea (Coll et al., 2010; Navarro et al., 2015; Veloy et al., 2022). However, at a regional scale, our study did not show marked geographical trends, highlighting maximum values around the Valencia Channel. This is consistent with recent unpublished studies evidencing a regional southern displacement of the demersal community in the Iberian Peninsula following sub-regional pathways of climate velocity (Sanz-Martín et al., 2024). These could increase local responses of diversity in southern regions of GSA6 associated to local displecents to avoid sub-optimal thermal habitats. In fact, richness and ß-diversity appear to have complementary patterns, with cells showing high values of ß-diversity generally having low species richness and vice versa (Pennino et al., 2024). This is especially apparent in GSA6 and GSA7. Some areas with the lowest values of richness tended to be associated with low biomass of crustaceans and low SST, similarly to what was found in recent studies (Keller et al., 2016; Oesterwind et al., 2022; Vilas et al., 2019), which are likely related to lower food availability .

Fishing impact was only observed to have a significant effect on ß-diversity, which is consistent with previous studies suggesting the erosion of the spatial structure of communities with a consequent decreases in connectivity between putative meta-communities (Hidalgo et al., 2017; Shackell et al., 2012). The exploitation pressure, especially in large species with more fecundity and mobility, could trigger the destabilization of northern ecosystems and also explain a smaller number of species at a local and regional level. This mechanism has been particularly observed in the GSA6 (Hidalgo et al., 2022b; Pennino et al., 2024; Veloy et al., 2022).

The biomass of the cephalopod community was found to be very influenced by environmental drivers, which had a marked geographical effect likely driven by SST. Our results show that SST displays a generally negative relationship with cephalopod biomass, with the colder areas of the Western Mediterranean having more biomass than warmer ones consistent with recent studies (Schickele et al., 2021). Interestingly, in areas such as the Portugal shelf the trend is inverse to our observations, yet it shares a similar threshold of change at 17 °C in surface waters for *L. vulgaris* (Moreno et al., 2014). In the Mediterranean area, differences in responses between cephalopod taxa were also noted with some species associated to cooler waters, while others thrive on warmer environments (Keller et al., 2017b; Puerta et al., 2014). These variations in the non-stationary environmental effects among species could affect the response of the overall group related with the variation of species composition of cephalopods community in different areas, and ultimately limiting a regional global response of the cephalopods community to warming.

Cephalopod biomass appears to be positively influenced by crustacean biomass, showing a close link between cephalopods population and prey availability. It is consistent with species-specific relationships of cephalopods in our study area (Puerta et al., 2015), being notable that prey and predators have similar spatial patterns as it can be seen as well in GSA7. Biomass of predators (fishes) also result in higher biomass of cephalopods, reaching an optimum at intermediate values, which could suggest that higher values could keep stable cephalopod biomass likely due to high pressure from predators (Bakun and Csirke, 1998). Although we here considered crustaceans as the prey item of cephalopods, larger species (specially squids) may also tend to prey more on fishes in oceanic ecosystems (Lordan et al., 1998). However, at a Mediterranean scale, previous studies supports that even on relatively large species, crustaceans are present to some degree on their diet (Puerta et al., 2015). Previous research and the smaller sizes of the cephalopod species found in the study area may support that the proportion of piscivory might not the high enough to alter the results and their interpretation in the present study.

The biological and environmental drivers on mean size, meaning the high biomass of crustaceans, high B_{pred} of fishes and low primary productions, are similar to those observed in the Eastern Mediterranean (Arvanitidis et al., 2002). However, it is possible that the negative relationship between mean size and Chl-a could be due to an indirect effect of fishes over cephalopods. As observed at species level, it could be a consequence of the competition with other fishes during paralarval phases (Keller et al., 2017b; Puerta et al., 2015), decreasing food availability and therefore limiting survival and growth. This would also be especially notable in areas with high SST, which increases growth rates on hatchlings at the cost of shortening maturation and lifespan (Hatfield, 2000; Pecl and Jackson, 2008). On such systems and with reduced food availability, paralarvae do not benefit from the faster metabolic rates resulting in a smaller size at adulthood (Pecl and Jackson, 2008; Pierce et al., 2008; Xavier et al., 2016). At a community level, lower mean size seems to suggest that there are more small-sized species in those areas, where fish B_{pred} is lower. Small cephalopods, such as sepiolids or the genus *Allotheutis*, are present on the diet of more fish species than larger cephalopods, thus fish predation or its reduction would play a bigger role in their dynamics (Daly et al., 2001; Velasco et al., 2001). We can also remark the possible contribution that recruits may have on our selected indicators. As seasonal recruitment peaks of some species occur during the sampling season, between May and June (Pierce et al., 2010; Tursf et al., 1995) and also has shown spatial variability between areas due to regional environmental conditions (Puerta et al., 2016b).

$TL_{3.25}$ was found to be associated to low biomass of crustaceans as well as areas with low ratios of predator fishes. The trophic level of TL_4 was also related to low biomass of crustaceans. The reason behind could be the competition with fishes as well as their possible predation pressure. The observed decline of fishes due to high exploitation levels would indirectly favour higher trophic levels in cephalopods, especially as seen with $TL_{3.25}$ (Caddy and Rodhouse, 1998; Coll et al., 2010; Hastie et al., 2009; Pennino et al., 2017). This may support the hypothesis of the cephalopod replacement in response to the removal of fishes, especially at high trophic levels.

Out of all drivers, fishing effort was the least influential driver as it only showed significant effects on the β-diversity. In general, cephalopods seem to be less sensitive to direct human local impacts than to environmental ones, which may be linked to their short life strategy that also make them less susceptible to be affected by the continuous pressure of fishing (Quetglas et al., 2016). The biology of this group becomes both an advantage and a hindrance, as this greater dependence on environmental factors can make them more susceptible to climate variations. One example could be warming, which has been shown to affect cephalopods at species level (Forsythe, 2004; Georgakarakos et al., 2002; Xavier et al., 2016), and at a community level in this study. The response observed to an increasing SST is either negative for some of the key indicators, such as the total biomass of cephalopods or the biomass of predatory cephalopods, or becomes negative after reaching certain temperature threshold like in mean size. It is worth to acknowledge, however, that in the case of this last indicator it could be also caused by peaks in recruitment of species like *Eledone cirrhosa* (Tursf et al., 1995), which are also fairly abundant in our data. This is especially relevant in our study area, as northward migrations and expansions in response to increasing SST (i.e. meridionalization) are limited by landmass on the Gulf of Lion region.

The selection of indicators shown in this manuscript also responds to the need of the EU's Marine Strategies Framework Directive (MSFD) to assess the state of marine communities. These ecological metrics were complementary to some of the proposed descriptors within the framework, specifically for D1 and D4 related to both biodiversity as well as trophic ecology (IEO and MAGRAMA, 2012a, 2012b). This study takes into account some indicators not considered in the current MSFD work, such as the ß-diversity, that can be useful to better understand the different components of biodiversity from local to regional scales. Other chosen indicators correspond to already established metrics and objectives. For instance, B_{pred} is equivalent to the descriptor 4.2 (proportion of species on high levels of the trophic chain). Meanwhile, trophic level indicators help to assess the state of the trophic chain of the taxa of study. Overall, the use of various indicators highlights the relevance of our study to inform future policy recomendations.

Our results also call for caution when referring to cephalopods as general winners to expected warming. While they have been thriving compared to other taxa such as fishes, and in spite of their opportunistic lifestyle, the observed responses of indicators to SST suggest that detrimental effects could be expected, particularly in geographically localized areas with higher warming. Based on our results lower values of biomass, mean size and ratio of predator species could be observed in the aforementioned areas. It is also important to consider that this study reflects the mean response for the entire Cephalopoda class, therefore differences between species sometimes turn into opposite responses to the same environmental pressures attending to their life history characteristics (e.g. benthopelagic o benthic habitat), as it is the case of *Illex coindetii* and *Eledone cirrhosa* (Puerta et al., 2014). On the Western Mediterranean basin, the squid was associated with colder waters while the aforementioned octopod was seen to displace towards warmer environments. This is also relevant in terms of fisheries management as the increase in fishing effort might affect cephalopod communities by changing their relative species composition with a differential effect of those inhabiting in the benthic or the pelagic realm.

It is worth noticing that our results may represent a snapshot of the community since the MEDITS data samples are only from one season (in the summer, between May and June). Some of the considered factors have shown different effects during summer and winter on some cephalopod species. For example, significant effects of primary production were reported on warmer seasons for two cephalopod species while fisheries played a significant role in their winter distribution (Lloret-Lloret et al., 2021). Thus the spatial distribution of the indicators could vary along the year showing seasonal patterns of migration due to some species tend to move towards northern regions during summer (Lloret-Lloret et al., 2021; Vilas et al., 2019), while it is also possible that the seasonal turnover of species may maintain the community properties and indicators stable (Moranta et al., 2008). Changes in community composition have not been studied as this work only aimed to analyze the cephalopod community as a whole. Despite this, the results might still hint at some changes in the composition of this subset of the Western Mediterranean community. Forecasts of future scenarios would be difficult as other possibly influential drivers (such as stratification of the water column), as well as the potential adaptive processes of the different species have not been taken into account (Hidalgo et al. 2018).

In summary, we have been able to describe relationships between key aspects of the cephalopod ecology with environmental, human and biotic drivers of change. Our results highlight that the cephalopod community of the Western Mediterranean will likely continue to change, mainly due to changes in environmental conditions related to climate change, such as an increase in sea warming or changes in primary production. However, these changes will not necessary result in boosted cephalopod populations. Drivers related to the structure of the biotic community, such as prey availability and the concurrence of competitors, can also influence cephalopods future dynamics, illustrating that this taxon is highly dependent to different ecosystems compartments and the whole ecosystem structure and functioning. We conclude that to ensure a sustainable fisheries management of the cephalopods community within the study area an ecosystem-based approach is needed, considering the subregional differences within larger regions.

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Data Availability statement

The data underlying this article were provided by IEO under licence / by permission. Data can be shared on request to the IEO.

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Highlights

- Effects of environmental, biotic and human drivers were investigated for ecological indicators of cephalopods
- Dynamics of this taxon are mainly influenced by sea temperature, explaining geographical gradients in several metrics
- Relationships with biotic variables could hint at the decrease of high trophic fishes.
- Fishing has little effect on cephalopods with β-diversity being the only indicator influenced by this variable
- Potential negative effects of warming on indicators challenge the idea of cephalopods as a climate change winners.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: