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Spatial-temporal variation of the Western Mediterranean Sea biodiversity along a latitudinal gradient

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ABSTRACT

The Mediterranean Sea is a large marine ecosystem with high heterogeneity in both environmental and ecological characteristics. It presents clear gradients from north to south and west to east. It is also an important area in terms of biodiversity and conservation of vulnerable species, and it suffers from several cumulative human impacts, such as fishing and climate change. Previous studies have characterized spatial and temporal patterns of species distributions and biodiversity indicators. However, a comprehensive analysis combining a wide representation of biodiversity indicators is still missing. In this study, we examined spatial and temporal changes of marine communities along a latitudinal gradient over the continental shelf ecosystems (25–500 m depth) of the Western Mediterranean Sea, from the Gulf of Lion in the north to the Gibraltar Strait in the south. We used information from the MEDITS trawl scientific surveys from 1994 to 2018, and we calculated relevant indicators to investigate spatial and temporal patterns in the region. We selected several indicators measuring alpha (species richness, Shannon diversity index and Pielou evenness index) and beta (decomposing both turnover and nestedness) diversity, as well as previously studied indicators identified to be sensitive to fishing and climate change impacts (biomass-based and trophic-level based metrics). We assessed differences in these indicators for the surveyed community as a whole and for fish, crustaceans and cephalopods, separately, over five regions. Our results show clear latitudinal gradients in some indicators: we observe a reversed pattern between richness (decreasing from south to north) and biomass trends (increasing from south to north) for the demersal community. We also found a generalized increase in β-diversity in most regions with time, and a decline in the trophic level of the surveyed community. In addition, we identify a remarkable increase in several indicators when only considering the cephalopods group, and a general low environmental status for the North Catalan Sea. We discuss our results considering the differences between regions and taxa related to the fishing activity and environmental dynamics that can act at different scales. This in-depth analysis illustrates how to use a selection of indicators that combine the capacity to detect ecological changes from regional to sub-regional scales.

1. Introduction

The Mediterranean Sea is an enclosed sea that was formed around 5 million years ago during the Pliocene when its only natural connection with oceanic waters, the strait of Gibraltar, opened allowing the influx of seawater into the system flooding, at the time, a mostly dried up basin

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(Coll et al., 2010). This event created a sea with particular features and gradients that have also shaped its own ecosystems and hosts several endemisms (Coll et al., 2010). One of the most characteristic traits of the Mediterranean basin is the northwest to southeast gradient of several physical variables such as higher temperature, and lower salinity and primary production towards the southeast. Biodiversity indicators (e.g., species richness) have also been described to decrease from the west to the east (e.g. Coll et al., 2010; Keller et al., 2016), despite the longitudinal gradient may not be so straightforward as shown in other studies (Gaertner et al., 2007).

Beyond the largely investigated west-east gradients over the whole basin, several regions in the Mediterranean display the combination of regional gradients and mesoscale features representing environmental and ecological spatial variation (Western Mediterranean, Liguria-Tyrrhenian Sea, Adriatic Sea and Aegean Sea among others). In the Western Mediterranean, the area from the Gulf of Lion (north) to the Alboran Sea (south) shows clear different hydrographic and productivity regions that have been used to define distinct environmental provinces (Rossi et al., 2014; Nieblas et al., 2014; d'Ortenzio and d'Alcalá, 2009). Also, in terms of biodiversity, the northwestern areas have been described as more diverse than the southeastern ones (Gaertner et al., 2007; Coll et al., 2010).

In addition to the influence of the environment in the distribution of species and the structure of marine communities (e.g. Navarro et al., 2016; Vilas et al., 2019; Lloret-Lloret et al., 2021), human activities can contribute to drive the changes in marine ecosystems. The fishing activity in the Mediterranean Sea has been historically very high (Lotze et al., 2006; Coll et al., 2010) and the region is still one of the FAOs fishing areas with the highest percentage of stocks fished at unsustainable or high levels besides the decreasing effort (Fao, 2020; FAO, 2020A). Due to the depletion of marine resources in most shelf fishing grounds and the improvement of technology, part of the fleet has bathymetrically shifted to higher depths (Coll et al., 2014; Farriols et al., 2017).

Other impacts threaten the stability and normal functioning of the ecosystems, such as habitat loss and invasive species, especially Lessepsian fauna migrating from the Suez Canal (Katsanevakis et al., 2016; Galil et al., 2017), pollution (Danovaro, 2003) and climate change (Ben Rais Lasram et al., 2010; Lejeusne et al., 2010; Hidalgo et al., 2018). In the case of the Western Mediterranean, their communities face other human related threats aside of overfishing (Fao, 2020; Fernandes et al., 2017; FAO, 2020A) such as eutrophication by discharges as well as accumulation of heavy metals (Danovaro, 2003) that exert most pressure in the coastal areas (Fiorenza et al., 2013). In general, human activities have cumulatively impacted living communities of the Mediterranean in numerous and synergistic ways. For example, marine predators (i.e. large species with a high trophic level) have notably declined from Mediterranean marine ecosystems (Ferretti et al., 2008) with important implications for marine food webs (Sala, 2004; Lotze et al., 2011), although few species have shown signs of recovery such as the Atlantic Bluefin tuna (Ifremer, 2019) or some vulnerable demersal elasmobranchs (Ramírez-Amaro et al., 2020, Hidalgo et al. 2021).

Previous studies in the Mediterranean Sea have described several spatiotemporal patterns of distribution of biodiversity, both at species, groups of species and the ecosystem level (e.g. Coll et al., 2010, 2012, Navarro et al., 2015; Keller et al. 2016, 2017a; Fernandez-Arcaya et al., 2019; Vilas et al., 2019). However, a community-based spatial integrative analysis with a wide range of ecological indicators selected based on their sensitivity to fishing or environmental impacts is still missing to compare patterns in important sub-regional areas in the Mediterranean Sea.

In this study, we fill this gap analyzing the spatiotemporal gradients of marine biodiversity from the Western Mediterranean Sea (from the Gulf of Lion to the Alboran Sea) with the aim to contribute to a better understanding of the changes of marine communities in this region following a continuous latitudinal gradient of environmental change. Using the intermediate scale of environmentally distinct regions over the continuous continental shelf gradient of the Western Mediterranean, we compare several areas according to a selection of indicators considering the multidimensional facets of biodiversity. The importance of such trait-based analysis can be seen in similar studies, such as the one performed in Atlantic waters (Pecuchet et al., 2017, Beukhof et al., 2019). In the latter, the study accounts for the distribution of certain life history traits showing that warmer waters favour opportunistic strategies (short lived and small species with low trophic levels), while colder waters with higher primary production and less variability have a bigger proportion of large long lived species.

Specifically, in our study we selected several indicators with the intention to cover different diversity components and community characteristics combining information of different groups (e.g. pelagic, demersal, predators). First, indicators of biodiversity were used, including beta diversity (hereafter β-diversity). The lack of data about this indicator and its components (turnover or change of identity and nestedness or subsampling) in the region needed to be addressed. This indicator can provide key information about the rates of change in the ecosystem as well as the identity of the change (Dornelas et al., 2014; Blowes et al., 2019). The differentiation in the components of β-diversity also helps to determine which are the underlying ecological processes driving biodiversity change through time, as both have been associated with different phenomena: limited space (Stegen et al., 2013) or high impacted areas (Shackell, et al., 2012) in the case of turnover, or orderly species loss in the case of pure nestedness (Baselga, 2010). Secondly, we added well studied indicators identified to be sensitive to fishing and climate change impacts: biomass-based and trophic-level based metrics (Shin et al., 2012; Bundy et al., 2012; Shannon et al., 2014; Coll et al., 2016; Fu et al., 2019).

Based on the literature available, we hypothesised that different ecological gradients and temporal changes according to different taxonomic groups may emerge, but also we expected to infer other ecological processes for specific taxonomic groups and sub-regions. Finally, our results could reflect as well the spatial–temporal heterogeneity of our study area, providing highly-resolved and novel information about the dynamic components of marine biodiversity in the Western Mediterranean Sea.

2. Methods

2.1. Study area and data set

The study area covers the continental shelf and upper slope of the Western Mediterranean of Spain and France, including depths from 25 m to 500 m (Fig. 1) as it is the stratum with most biodiversity and represents most of the main ecosystems within our region. The data used was collected from the international MEDITS trawl surveys between the years 1994 and 2019 (Spedicato et al., 2020) in 4041 sample stations over 25 years and integrated information of 586 species (Appendix table A1). The MEDITS program follows a standardized sampling protocol through the entire northern Mediterranean, from the duration of the trawling, the type and specifications of the gear used to the collection and analysis of the biological samples (Bertrand et al., 2002; Spedicato et al., 2020). MEDITS program uses the Geographical Statistical Areas (GSAs) as sampling areas, defined by the General Fisheries Commission for the Mediterranean (GFCM). The chosen area for this study covers the continuous north–south gradient of the Western Mediterranean area ranging from the Gulf of Lion (GSA7), through the Northern Spain (GSA6) to the Northern Alboran Sea (GSA1). The study area was divided in five regions (Fig. 1). The GSA6, Valencia Channel (CN), Ebro Delta (DE) and North Catalan Sea (CC), shares some similarities, with low chlorophyll levels, deep bathymetry and high sea surface temperature (SST) (Nieblas et al., 2014). CN and DE regions have a relatively wide continental shelf, and DE also receives intakes from several rivers such as the Ebro. The most northern area, the GSA7, Gulf of Lion (GL),

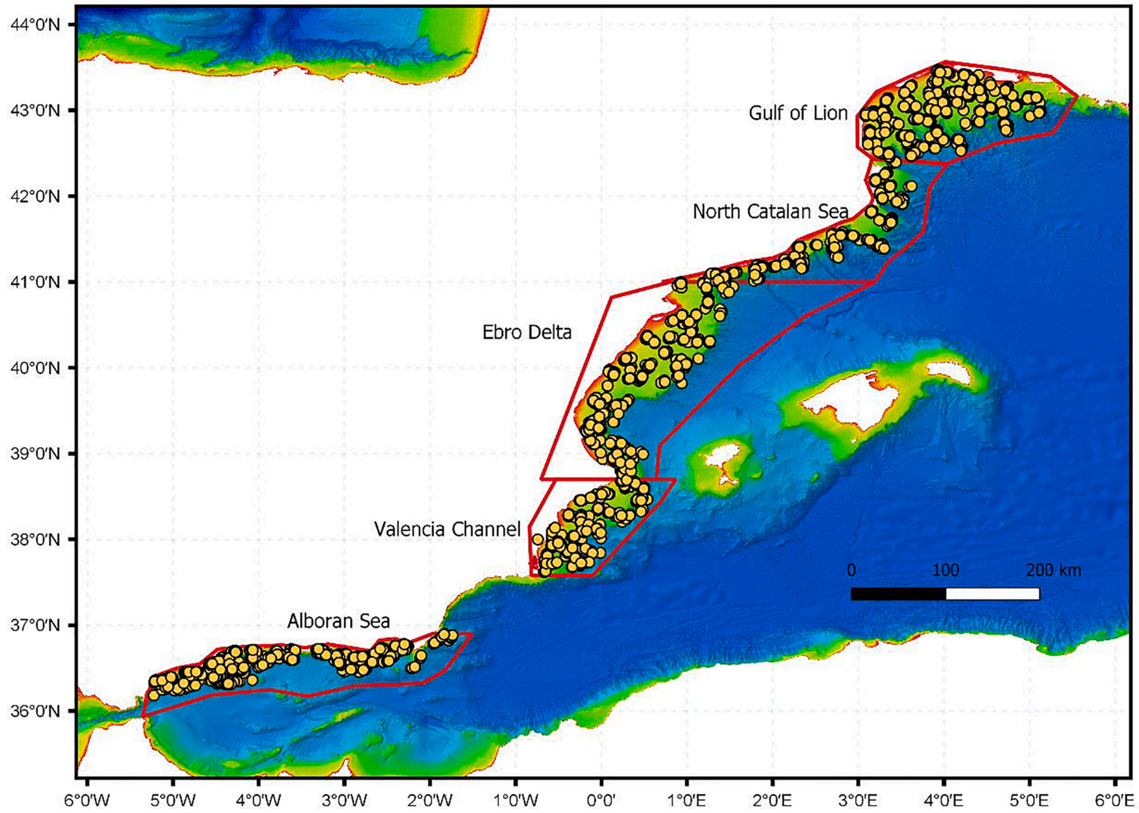


Fig. 1. Map of the study area and its subdivision in regions. Yellow dots represent the sampling stations of MEDITS campaigns used in the analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

features a low SST, shallow bathymetry, extended shelf and high and variable primary production driven by the peculiar oceanographic conditions and the Rhône River. The river generates a layer of high concentrations of nutrients up to a 100 m in depth, and even deeper during winter due to upwelling processes, that is spread through the area by the Ligurian current allowing fertilization of the whole Gulf (Nieblas et al., 2014)., while CC is characterized by a narrow continental shelf. Finally, the most southern area, GSA1, Northern Alboran Sea (AL), has a high and very variable primary production influenced by the inflow of waters from the Atlantic Ocean and highly dynamic mesoscale processes.

The data obtained from the surveys was firstly filtered for those registries that reported no individuals, following the protocol established by Dornelas et al. (2014). A second filter was applied to select only those species that appeared in 80% of the time in the temporal series considered. Lastly, for those indicators based on biomass or abundance indices, we also filtered out those species with low and heterogeneous catchability such as gregarious and small pelagic species (e.g., European sardine, *Sardina pilchardus* or boarfish, *Capros aper*). For the indicators based on absence-presence, this criterion was not applied.

For invertebrate species, we faced a challenge related to the heterogeneous sampling protocols among areas. While the surveys carried out in the Spanish Mediterranean areas performed a complete record of both the presence and the biomass of as many species as possible since 1994, in the Gulf of Lion only mandatory species under the MEDITS protocol were sampled until 2012. From this year onwards, the survey started a complete record of other species including crustaceans and cephalopods. To efficiently circumvent this limitation while ensuring the objectives of the study, we considered two separate invertebrate databases: i) first, to analyse the temporal variation, the entire sampling period (1994–2019) was considered but we selected for all the regions only those species sampled before 2012 in GL; ii) second, to perform the spatial analyses, all the species of the demersal community between 2012 and 2019 were used from every region.

2.2. Selection of ecological indicators

a) Biodiversity indicators

Different biodiversity metrics of both alpha and beta diversity were calculated (Table 1). For alpha diversity we focused on two main components of the alpha diversity: species richness (the amount of species present in the community of a region) was measured with the total number of species in the sample (McIntosh, 1967) and the Shannon index (H) (Shannon and Weaver, 1949). For the evenness, we used the Pielou evenness index (J) (Pielou, 1966) since it is constrained by values between 0 and 1, allowing for better comparison between different samples. The β-diversity was calculated with the Jaccard index to assess differences between communities separated with time using the first year of sampling. In the case of the temporal databases, the first year was 1994, while 2012 was used for the spatial database. The two components of β-diversity, turnover and nestedness, were also individually calculated.

b) Community and taxa-related indicators

Species were classified in three major taxonomic groups: fishes, crustaceans (only accounting for decapods, stomatopods and euphausiacids) and cephalopod mollusks (from now on referred as cephalopods). For the different species in each group a binary value for two traits (position in the water column, benthopelagic -hereafter referred as pelagic- or demersal species, and feeding type considering the species a predator or not) was also assigned, as well as a trophic level value using FishBase (Froese and Pauly, 2021) and SeaLifeBase (Palomares and Pauly, 2021). For the sake of data uniformity, the trophic level used was the one calculated based on consumed food items as it was the one available for most taxa. Following previous studies, we considered as "predator" those species that had a trophic level higher than 3.5 (Shin and Shannon, 2010). However, we also took into account if they had

Table 1
Definitions, equations, primary driver of influence (environment, fisheries or both) and references of indicators used in this study. N_i, B_i, W_i and TL_i corresponds to Number of individuals, Biomass, Weight and Trophic Level of *i* species, respectively.

Indicator	Definition	Equation	Primary driver	Reference
Biodiversity indicators				
Species richness (S)	Sum of species (*sp*) number	$\Sigma\ sp$	Both	McIntosh, 1967
Shannon index (H)	Measure of diversity and evenness. p_i is the proportion of individuals belonging to species *i* in the dataset	$-1*\Sigma((p_i)*ln(p_i))$	Both	Shannon and Weaver, 1949
Pielou evenness (J)	Measurement of frequency evenness on an ecosystem. *H*: Shannon index, *S*: Species richness	$H/ln(S)$	Both	Pielou, 1966
Jaccard index (β)	Measurement of community change over time. A & B: different sample setsComponents:-Nestedness or subsetting of the sample-Turnover or identity change.	$^{\lvert A\cap B\rvert}/_{\lvert A\cup B\rvert}$	Both	Dornelas et al., 2014; Blowes et al., 2019
Community and taxa-related indicators				
Biomass (B) and Abundance (N)	Biomass (B_i) and Abundance (N_i) of surveyed species *i.*	$\Sigma B_i\ \&\ \Sigma N_i$	Environment	Coll et al., 2016
Mean size (MS)	Mean weight (used as proxy of mean length indicator although less effective). *B*: biomass, *N*: abundance.	B/N	Fishing	Shin et al., 2018
Relative predatory Biomass (BPred)	Relationship between biomass of predator species (B_i) and the ecosystem or taxa group (*B*)	$\frac{\Sigma(Bi)}{B}$	Fishing	Coll et al., 2016
Relative pelagic Biomass (BPel)	Relationship between biomass of pelagic species and the ecosystem		Environment	Based on BPred
Relative fish Biomass (BFish)	Relationship between biomass of fish species and the ecosystem		Fishing	
Relative Cephalopod Biomass (BCeph)	Relationship between biomass of cephalopods and the ecosystem		Both	
Surveyed community trophic level (TLsc)	Mean trophic level of the surveyed species (TL_i). W_i: biomass of species i.	$\frac{\Sigma(TL_i*W_i)}{B}$	Environment	Shannon et al., 2014
Mean trophic level of species above 3.25 (TLs3.25)	Mean trophic level of species *i* above 3.25 ($TL_{i,3.25}$)	$\frac{\Sigma\left(TL_{i,3.25}*W_{i,3.25}\right)}{B_{3.25}}$	Fishing	
Mean trophic level of species above 4 (TLs4)	Mean trophic level of species *i* above 4 ($TL_{i,4.0}$, top predators)	$\frac{\Sigma\left(TL_{i,4.0}*W_{i,4.0}\right)}{B_{4.0}}$	Fishing	

reported maximum length greater than 20 cm and actively capture their food. The aim of this classification was to filter out small organisms like bobtail squids and species that are mostly scavengers such as shrimps.

To assess the state of the ecosystem and of different taxonomic and species groupings, several additional indicators were selected based on the IndiSeas initiative (Shin et al., 2012; Bundy et al., 2012; Coll et al., 2016; Fu et al., 2019; Indiseas, 2020) (Table 1). IndiSeas indicators were initially chosen to track fishing effects on marine ecosystems. Some IndiSeas indicators were also identified as being especially sensitive to changes in primary productivity due to climate variability. Examples of the first type are the relative biomass of predators (BPred), the mean size of the community (MS) and trophic-based indicators such as the trophic levels in the community (TLsc), the mean trophic level of the community for species with trophic levels above 3.25 (TLs3.25) and the trophic level of the community considering predators above 4 (TLs4). Some indicators sensitive to environmental change, such as the total community biomass (B) and the mean trophic level of the entire surveyed community (TLsc), were also included (Shannon et al., 2014; Coll et al., 2016).

2.3. *Data analyses*

The heterogeneity of the database did not allow us to develop a complete spatiotemporal analysis (i.e. ANCOVA). Therefore, spatial and temporal analyses were developed separately in two different subsets of the database. To analyse spatial differences among sub-regions, we applied an analysis of variance (ANOVA) to compare the indicator mean values of the different regions across the study area (Fig. 1). Afterwards, linear regressions were applied to assess the long-term temporal variation of each indicator. In each region, the different indicators were considered as the dependent variable, and the region was the independent categorical variable for the ANOVA analysis. Before the analyses, we tested that indicators followed the conditions of normality and homogeneity of variances applying the Shapiro and Levene tests, respectively. In the linear regressions, we considered time as the explanatory continuous variable per region. For this purpose, the indicator-time relationship was adjusted assuming a linear relationship between the two variables to compare the rates of increase or decrease (i.e. regression parameter) of the temporal trends. We then compared these trends between different regions for each indicator.

To further test and examine the differences between regions in the ANOVA, we used a Tukey pairwise comparison with 95% confidence intervals. Spatial patterns were summarized by grouping the statistically significant different regions. Two criteria were taken for grouping regions by their mean value: if the region was significantly distinct to the boundary areas or if regions showed significant differences in two pairwise comparisons.

All the indicators were calculated using R version 3.6.3 (R Core Team, 2021). The Jaccard index and its components were calculated using the R package betapart (Baselga and Orme, 2012).

3. Results

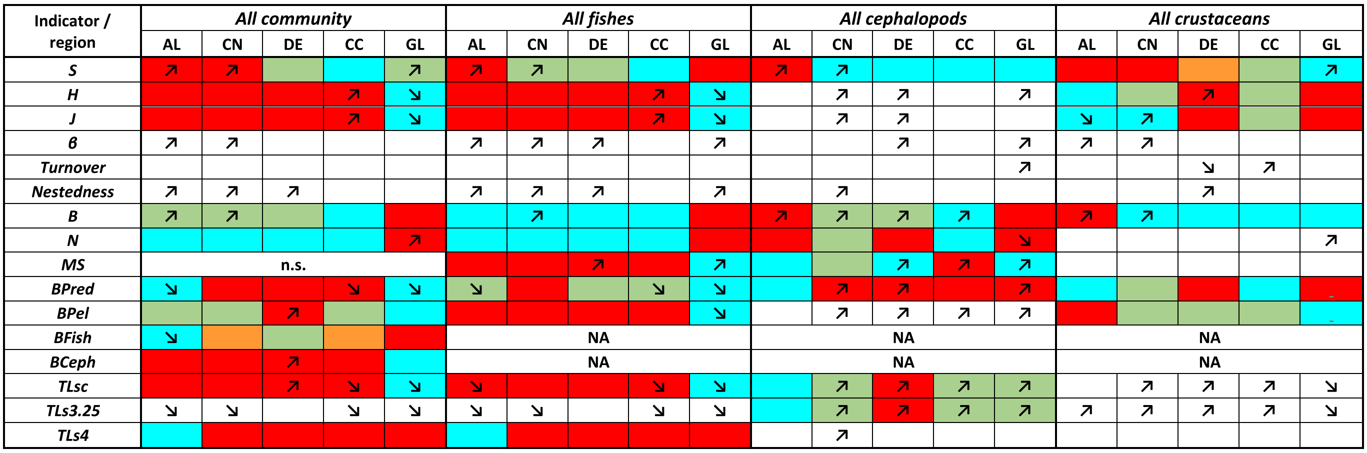
We present the summary of spatial and temporal trends for all surveyed species, demersal species and pelagic species using the biodiversity indicators first, and followed by the community and taxa-related indicators, as in Table 1. For each indicator, a general spatial description is first given followed by the main temporal pattern in the different subregions. All statistical results are shown in Appendix Tables A3 to A6.

3.1. *Biodiversity indicators*

Overall, the highest species richness (S) mean values were recorded in the southern areas of the study, the Alboran Sea and in the Channel, where significant differences were found in comparison with the rest of the regions (Table 2). The surveyed community and fish species richness were also highest in the south (with the exception for all fish and demersal fish richness in the Gulf of Lion), and they presented the lowest values in the North Catalan Sea when considering all and demersal fishes as well as the entire and demersal community ($F_{4,35} = 7.05$; $p < 0.001$) (Tables 2 and 3; Fig. 2a and 2b). The species richness showed general and significant increasing temporal trends in almost all areas and with the lowest significant slope values in the Gulf of Lion (slope, $sl = 0.44$, p

Table 2

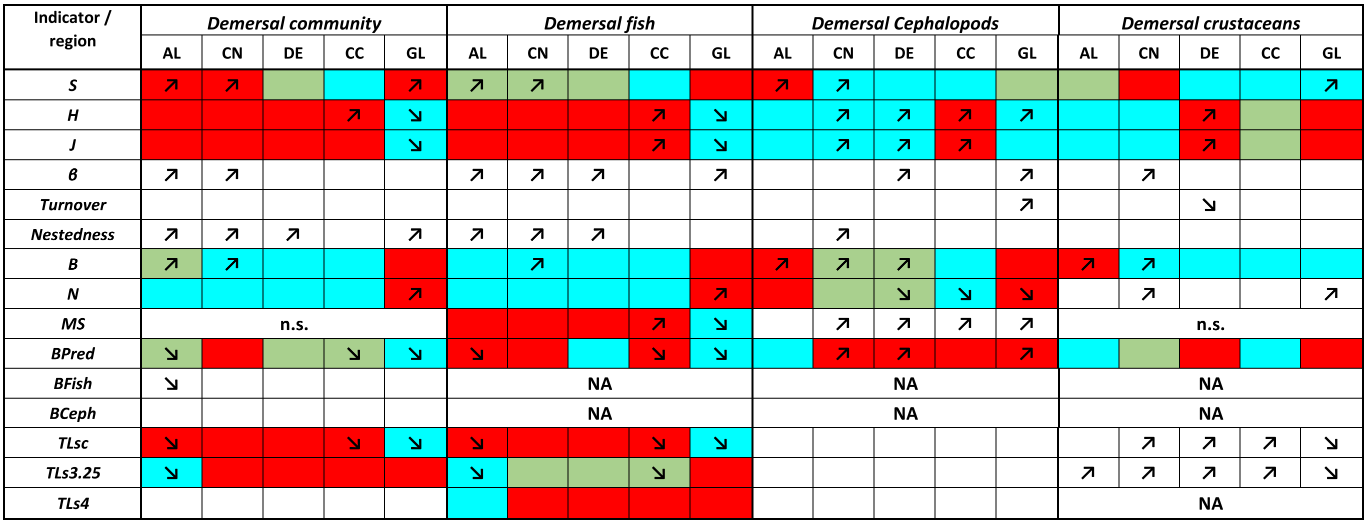
Summary of the spatial and temporal trends of the taxa (considering all species), in color the regional significant differences (red being the highest mean value, orange and green middle values, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the direction of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. Colors in regional differences are only depicted when there are significant differences by region.



Indicator / region	*All community*					*All fishes*					*All cephalopods*					*All crustaceans*				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
S	🟥 ↗	🟥 ↗	🟩	🟦	🟩 ↗	🟥 ↗	🟩 ↗	🟩	🟦	🟥	🟥 ↗	🟦 ↗	🟦	🟦	🟦	🟥	🟥	🟧	🟩	🟦 ↗
H	🟥	🟥	🟥	🟥 ↗	🟦 ↘	🟥	🟥	🟥	🟥 ↗	🟦 ↘		↗	↗		↗	🟦	🟩	🟥 ↗	🟩	🟥
J	🟥	🟥	🟥	🟥 ↗	🟦 ↘	🟥	🟥	🟥	🟥 ↗	🟦 ↘		↗	↗			🟦 ↘	🟦 ↗	🟥	🟩	🟥
β	↗	↗				↗	↗	↗		↗			↗		↗	↗	↗			
Turnover															↗			↘	↗	
Nestedness	↗	↗	↗			↗	↗	↗		↗		↗						↗		
B	🟩 ↗	🟩 ↗	🟩	🟦	🟥	🟦	🟦 ↗	🟦	🟦	🟥	🟥 ↗	🟩 ↗	🟩 ↗	🟦 ↗	🟥	🟥 ↗	🟦 ↗	🟦	🟦	🟦
N	🟦	🟦	🟦	🟦	🟥 ↗	🟦	🟦	🟦	🟦	🟥	🟥	🟩	🟥	🟦	🟥 ↘					↗
MS	n.s.					🟥	🟥	🟥 ↗	🟥	🟦 ↗	🟦	🟩	🟦 ↗	🟥 ↗	🟦 ↗					
BPred	🟦 ↘	🟥	🟥	🟥 ↘	🟦 ↘	🟩 ↘	🟥	🟩	🟩 ↘	🟦 ↘	🟦	🟥 ↗	🟥 ↗	🟥	🟥 ↗	🟦	🟩	🟥	🟦	🟥
BPel	🟩	🟩	🟥 ↗	🟩	🟦	🟥	🟥	🟥	🟥	🟦 ↘		↗	↗	↗	↗	🟥	🟩	🟩	🟩	🟦
BFish	🟦 ↘	🟧	🟩	🟧	🟥	NA					NA					NA				
BCeph	🟥	🟥	🟥 ↗	🟥	🟦	NA					NA					NA				
TLsc	🟥	🟥	🟥 ↗	🟥 ↘	🟦 ↘	🟥 ↘	🟥	🟥	🟥 ↘	🟦 ↘	🟦	🟩 ↗	🟥 ↗	🟩 ↗	🟩 ↗		↗	↗	↗	↘
TLs3.25	↘	↘		↘	↘	↘	↘		↘	↘	🟦	🟩 ↗	🟥 ↗	🟩 ↗	🟩 ↗	↗	↗	↗	↗	↘
TLs4	🟦	🟥	🟥	🟥	🟥	🟦	🟥	🟥	🟥	🟥		↗								

Table 3

Summary of the spatial temporal trends of the different demersal taxa, in color the regional significant differences (red being the highest mean value, orange and green middle, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the directions of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. Colors in regional differences are only depicted when there are significant differences by region.



Indicator / region	*Demersal community*					*Demersal fish*					*Demersal Cephalopods*					*Demersal crustaceans*				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
S	🟥 ↗	🟥 ↗	🟩	🟦	🟥 ↗	🟩 ↗	🟩 ↗	🟩	🟦	🟥	🟥 ↗	🟦 ↗	🟦	🟦	🟩	🟩	🟥	🟦	🟦	🟦 ↗
H	🟥	🟥	🟥	🟥 ↗	🟦 ↘	🟥	🟥	🟥	🟥 ↗	🟦 ↘	🟦	🟦 ↗	🟦 ↗	🟥 ↗	🟦 ↗	🟦	🟦	🟥 ↗	🟩	🟥
J	🟥	🟥	🟥	🟥	🟦 ↘	🟥	🟥	🟥	🟥 ↗	🟦 ↘	🟦	🟦 ↗	🟦 ↗	🟥 ↗	🟦	🟦	🟦	🟥 ↗	🟩	🟥
β	↗	↗				↗	↗	↗		↗			↗		↗		↗			
Turnover															↗			↘		
Nestedness	↗	↗	↗		↗	↗	↗	↗				↗								
B	🟩 ↗	🟦 ↗	🟦	🟦	🟥	🟦	🟦 ↗	🟦	🟦	🟥	🟥 ↗	🟩 ↗	🟩 ↗	🟦	🟥	🟥 ↗	🟦 ↗	🟦	🟦	🟦
N	🟦	🟦	🟦	🟦	🟥 ↗	🟦	🟦	🟦	🟦	🟥 ↗	🟥	🟩	🟩 ↘	🟦 ↘	🟥 ↘		↗			↗
MS	n.s.					🟥	🟥	🟥	🟥 ↗	🟦 ↘		↗	↗	↗	↗	n.s.				
BPred	🟩 ↘	🟥	🟩	🟩 ↘	🟦 ↘	🟥 ↘	🟥	🟦	🟥 ↘	🟦 ↘	🟦	🟥 ↗	🟥 ↗	🟥	🟥 ↗	🟦	🟩	🟥	🟦	🟥
BFish	↘					NA					NA					NA				
BCeph						NA					NA					NA				
TLsc	🟥 ↘	🟥	🟥	🟥 ↘	🟦 ↘	🟥 ↘	🟥	🟥	🟥 ↘	🟦 ↘							↗	↗	↗	↘
TLs3.25	🟦 ↘	🟥	🟥	🟥	🟥	🟦 ↘	🟩	🟩	🟩 ↘	🟥						↗	↗	↗	↗	↘
TLs4						🟦	🟥	🟥	🟥	🟥						NA				

< 0.05, in the surveyed community and sl $= 0.37$, $p < 0.05$, in the demersal community; Fig. 2c, Table 2). A spatial gradient from north (lower values) to south (higher values) was also observed for cephalopods and crustaceans (Table 2; Fig. 2e and f), with increasing temporal trends, too.

Both Pielou evenness (Tables 2 and 3, Fig. 3) and Shannon index showed roughly similar spatial patterns, with the lowest values in the Gulf of Lion. On the contrary, we observed an inverse gradient for cephalopods, where the North Catalan Sea featured the highest values and the Alboran Sea the lowest ($F_{4,35} = 3.741$; $p < 0.05$). Pielou index showed contrasting temporal trends depending on the region with decreasing trend with time in the Gulf of Lions (slope, sl $= -0.02$, $p < 0.001$), while an increase with time was observed for demersal cephalopods in most regions, where significant relationships were reported (slope, sl $= 0.02$, $p < 0.001$; Fig. 3f).

Results evidenced that there were no significant spatial differences in β-diversity or its components between different regions (Tables 2, 3 and 4). However, β-diversity increased with time showing an upwards trend in many of the regions and groups (Fig. 4). Regarding the β-diversity components, turnover was found to have a significant increase mostly on the North Catalan Sea in many of the considered groups (Tables 2–4, Fig. 4e) in contrast, nestedness showed a general significant increase in most regions within all taxa and taxonomic groups, especially in fish (Table 2, Fig. 4c).

3.2. Community and taxa-related indicators

The Biomass (B) indices showed a general gradient with a negative south-north pattern, with larger biomass values in the Gulf of Lion (Tables 1, 2 and 3). Cephalopods (both all and demersal) showed higher values as well in the Alboran Sea. In contrast, crustaceans showed highest values in the Alboran Sea, while in the other regions values were low. Temporal changes in biomass showed increasing trends specially in cephalopods group and in the Alboran Sea (Tables 2, 3, 4, Appendix Table A3, A4 and A5), with few exceptions such as pelagic fishes of the Gulf of Lion that show a clear decreasing trend (sl $= -20.82$, $p < 0.05$)

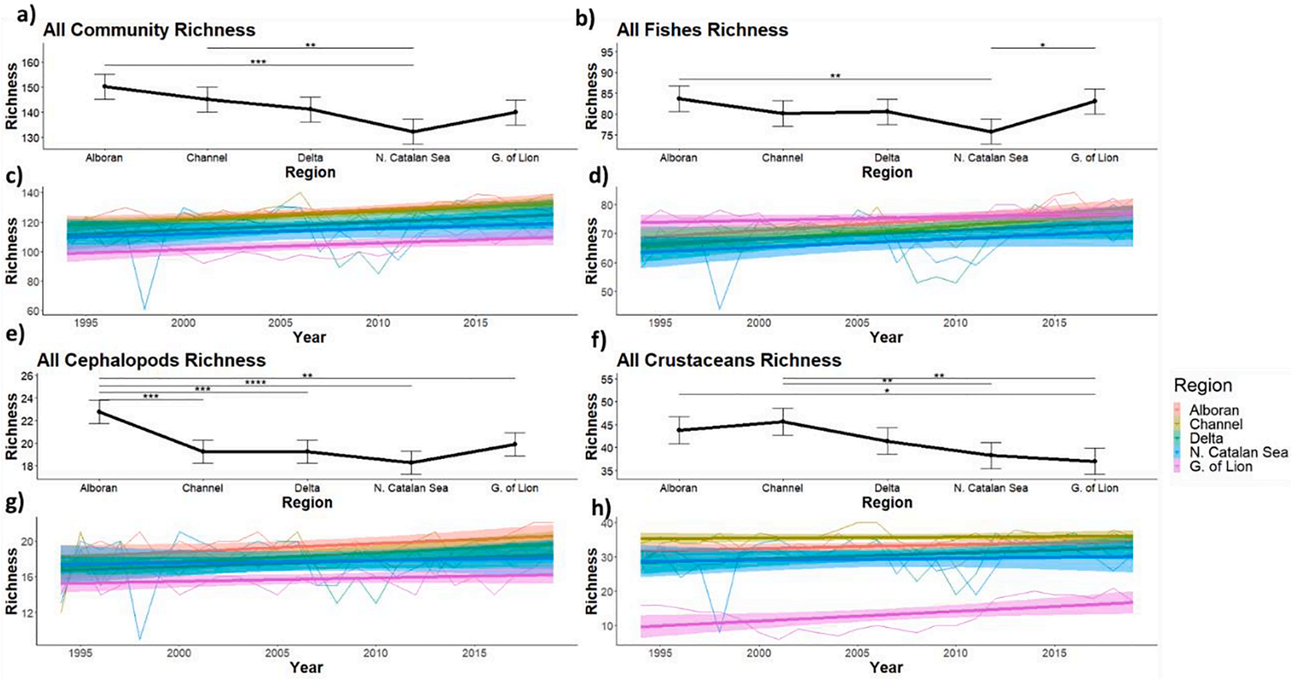


Fig. 2. Temporal trends, pairwise contrast and mean values of species richness (S) for the surveyed community, and for fishes, cephalopods and crustaceans. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate the standard error over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

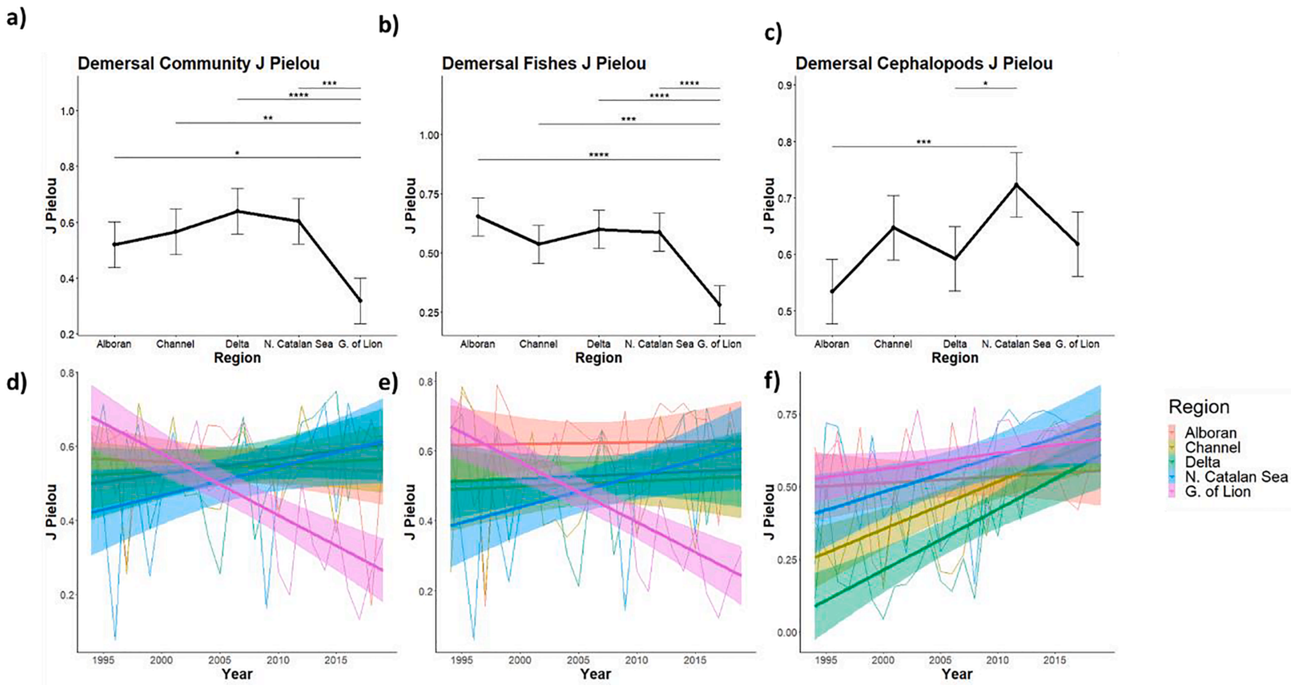


Fig. 3. Temporal trends, pairwise contrast and mean values of Pielou evenness J index for the demersal surveyed community, and for fish and cephalopods. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

(Table 4).

A gradient similar to that of biomass appeared in the surveyed community abundance (N) trends for all regions (Tables 2, 3, 4 and Appendix Table A6), where the Gulf of Lion presented the highest mean values well above those reported for the other regions, while pelagic taxa showed highest values in the south (Table 4). A temporal pattern of increase was observed (Tables 2 and 3), with the exception of demersal cephalopods showing declines.

The mean size indicator (MS) was found to have non-significant spatial differences for the majority of groups except for all and demersal fishes and cephalopods (Tables 2 and 3), which showed significant spatial differences with low values in the Gulf of Lion. However,

Table 4

Summary of the spatial temporal trends of the different bentho-pelagic taxa, in color the significant regional differences (red being the highest mean value, orange and green middle, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the direction of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. * Beta diversity and its components were disregarded for pelagic invertebrates because of the small number of species. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	*Pelagic community*					*Pelagic fish*					*Pelagic Cephalopods*					*Pelagic crustaceans*				
	AL	*CN*	*DE*	*CC*	*GL*	*AL*	*CN*	*DE*	*CC*	*GL*	*AL*	*CN*	*DE*	*CC*	*GL*	*AL*	*CN*	*DE*	*CC*	*GL*
S	🟥	🟥	🟧	🟩	🟦	🟥	🟥	🟦	🟦	🟦	🟥	🟥	🟥 ↗	🟥 ↗	🟦	🟥	🟥	🟩	🟩 ↘	🟦
H	🟥	🟩	🟩	🟦	🟦 ↗	🟥 ↗	🟩	🟩	🟩	🟦 ↗	🟥	🟥	🟩	🟩	🟦	🟥 ↘	🟥	🟥	🟥 ↘	🟦 NA
J					↗	🟥 ↗	🟩	🟩	🟩	🟦 ↗	🟥	🟥	🟩	🟩	🟦	🟥 ↘	🟥	🟥	🟥	🟦 NA
β					↗					↗	*					*				
Turnover				↗																
Nestedness	↗		↗		↗	↗		↗		↗										
B		↗	↗		↗					↘		↗	↗	↗	↗	🟥	🟦	🟦	🟦	🟦
N	🟥	🟩	🟩	🟩 ↘	🟦 ↘					↘		↗	↗	↗	↗					
MS	↗	↗	↗		↗									↘	↘					
BPred	🟦	🟩	🟥	🟥 ↗	🟥 ↗			↗			🟦 ↘	🟥	🟥	🟥	🟥	NA				
BFish	🟥	🟩	🟦	🟩 ↘	🟩 ↘	NA					NA					NA				
BCeph	🟦	🟩	🟥	🟩 ↗	🟥 ↗	NA					NA					NA				
TLsc	🟦	🟩	🟥	🟩 ↗	🟦 ↗						NA									
TLs3.25	🟥	🟥	🟥 ↗	🟥	🟦	↘			↘	↘	NA					🟥	🟥	🟥	🟥	🟦
TLs4	🟦	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟦	🟩	NA					NA				

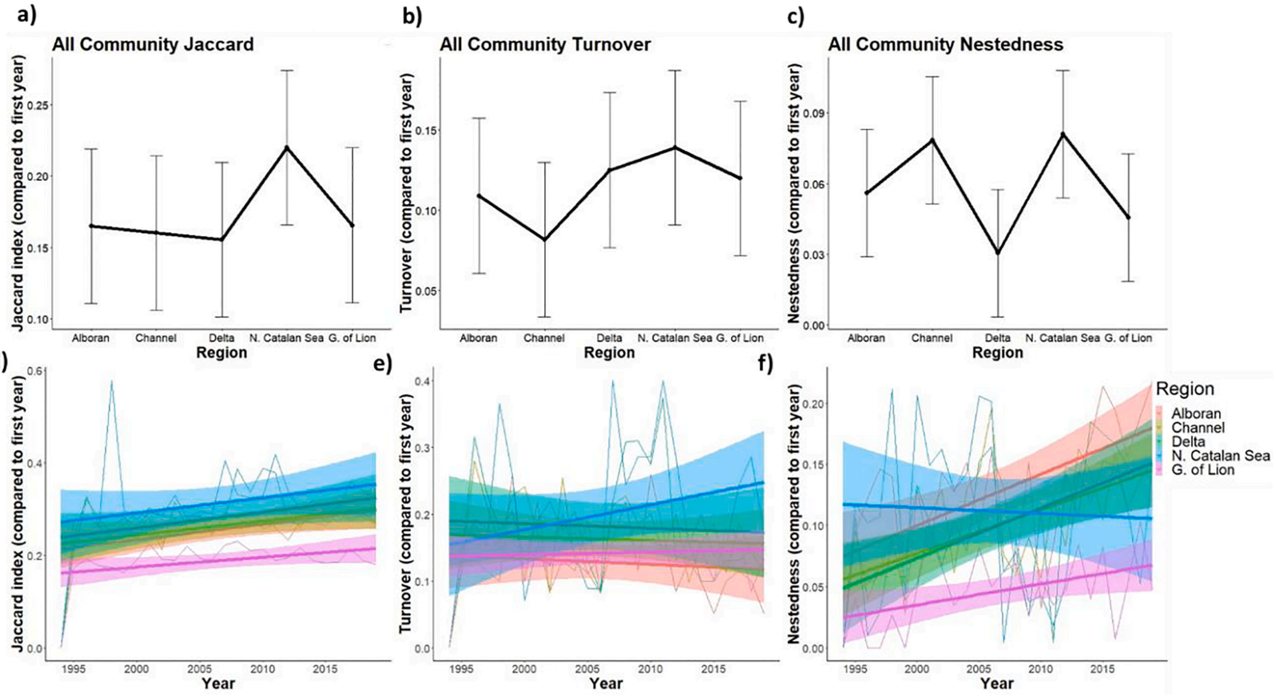


Fig. 4. Temporal trends, pairwise contrast and mean values of β-diversity, turnover and nestedness for the surveyed community. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

cephalopods ($F_{4,35} = 6.11$, p-value < 0.001) did not display a clear gradient, while in the case of fishes all the regions up until the Gulf of Lion showed higher means. Mean size increased with time in various regions with some exceptions such as demersal fishes in the Gulf of Lion and pelagic cephalopods in the Catalan Coast and the Gulf of Lion (Table 4).

Relative biomass of predators (Bpred) did not display clear gradients for the surveyed community and the fishes (with the exception of the pelagic community), but rather showed low values in both extremes of the study area and higher values in the central regions (Table 2, Fig. 5a). The pelagic species ($F_{4,35} = 4.77$, $p < 0.01$) as well as the cephalopods groups (Tables 2, 3 and 4) showed south-north gradients with highest biomass values in northern areas. Significant temporal decreasing trends were reported for fishes and the surveyed community, only showing an increasing trend in the pelagic community of the North Catalan Sea and the Gulf of Lion regions (slope, $sl = 0.02$, $p < 0.001$).

Results showed how the Relative Fish Biomass (BFish) for the surveyed community was lower in the southern sub-regions than in the northern ones, showing a positive gradient to the north in the study area only interrupted by a decrease in the mean value of the Delta region ($F_{4,35} = 7.623$, $p < 0.01$) (Appendix Table A5, Table 2, Fig. 6a). For the pelagic community, the highest values were found in the Alboran Sea,

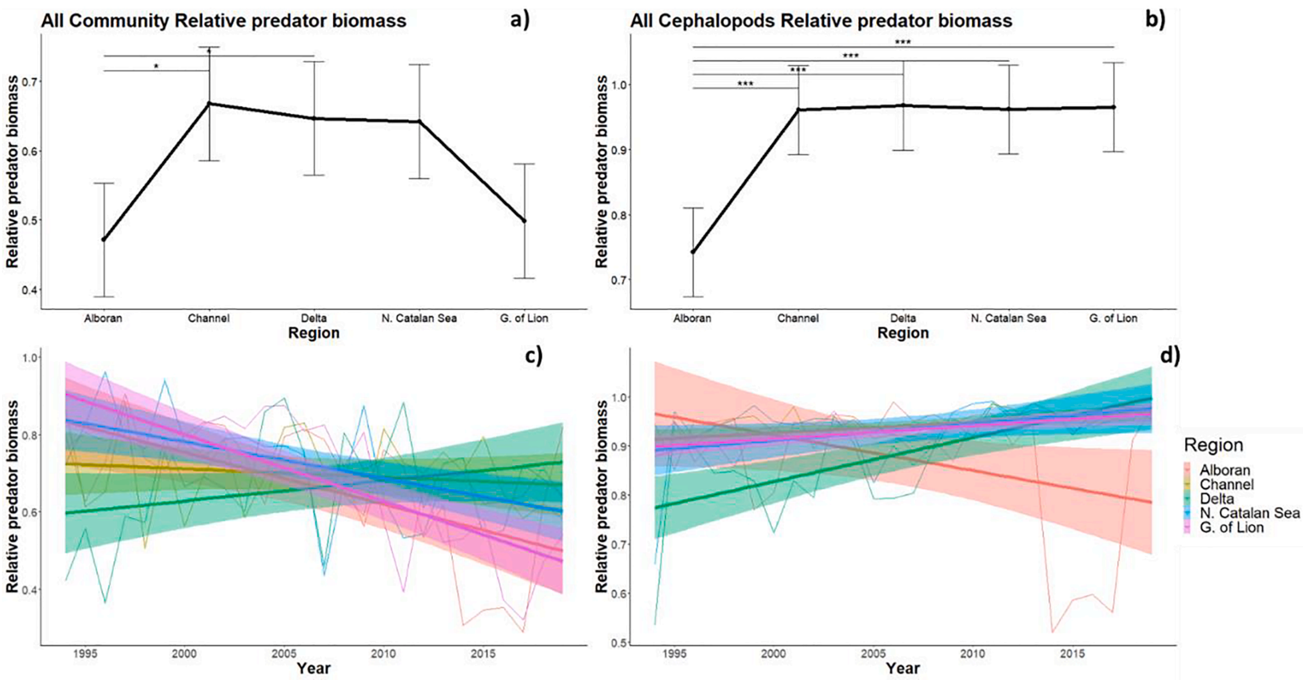


Fig. 5. Temporal trends, pairwise contrast and mean values of Bpred for the surveyed community (left) and cephalopods (right). Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

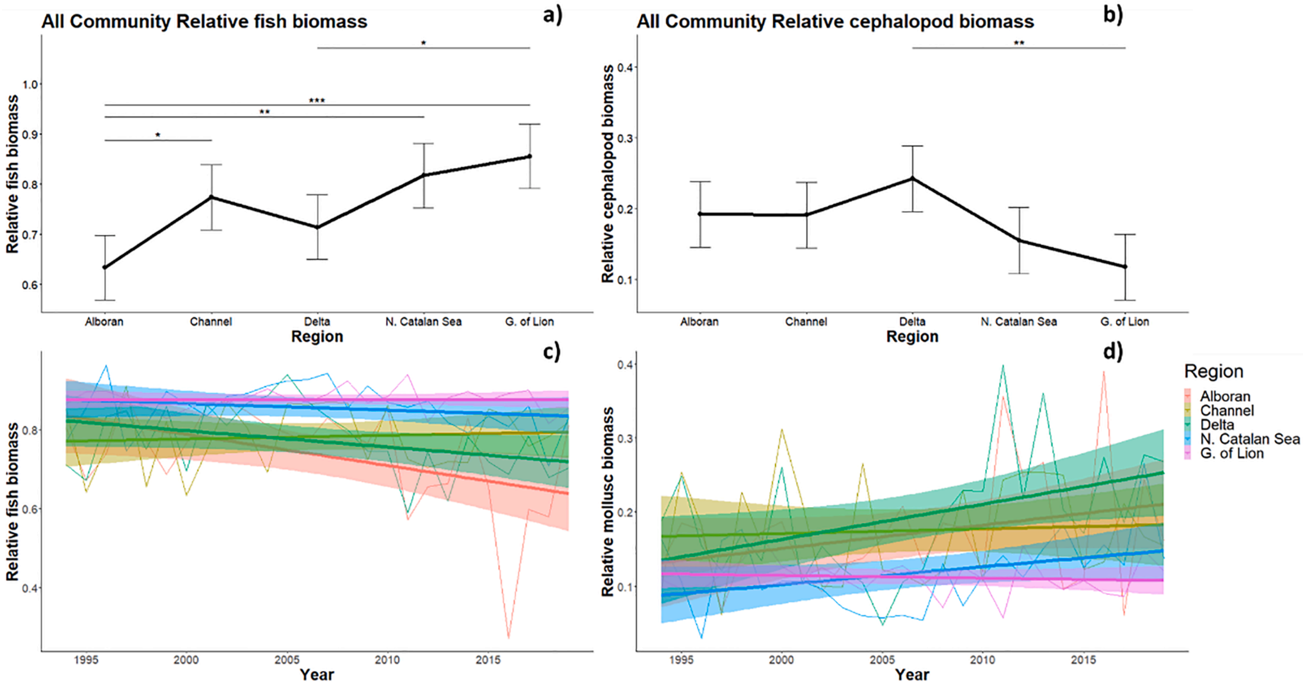


Fig. 6. Temporal trends, pairwise contrast and mean values of BFish (left) and BCeph (right) for the surveyed community. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

while the Delta showed the lowest (Table 4). In the case of the Relative Cephalopods Biomass (BCeph), there was no discernible pattern although the surveyed community the Gulf of Lion showed the lowest mean value ($F_{4,35} = 4.112$, $p < 0.01$). Regarding the temporal trends, the biomass of fishes showed a negative trend in the Alboran Sea when considering the surveyed community and demersal species (Tables 2 and 3), and a negative temporal trend was registered for the pelagic community in the northernmost sub-regions, the Northern Catalan Sea and the Gulf of Lions (Table 4, Fig. 6c). On the contrary, the Relative Biomass of Cephalopods (BCeph) showed a significant positive relationship with time in the Delta region ($sl = -0.004$, $p < 0.05$) when looking at the demersal species, and a positive increase in the North Catalan Sea (sl =

0.02, $p < 0.01$) and the Gulf of Lion (sl = 0.02, $p < 0.001$) when looking at the pelagic community (Table 4, Fig. 4d).

Both all surveyed community and the fish community showed lower levels of the TLsc and higher levels of TL3.25 in the north (Table 2, Fig. 7a). TLs4 showed a clear increasing south-north gradient. Cephalopods did not show clear spatial gradients but their maximum values of trophic level indicators were observed in the Delta region. The TLsc presented decreasing temporal trends in several regions for all the surveyed community and the fish community, more pronounced in the Gulf of Lions (Tables 2, 3 and 4; Fig. 7c). Cephalopods and crustaceans, on the contrary, displayed an increasing trend in both TLs3.25 and TLsc indicators (Tables 2 and 3).

3.3. *General patterns*

Regarding the spatial analyses, four types of gradients were identified in the study area: (i) a clear increase on indicator values from south to north gradient (such as the case of trophic level indicators and the biomass), (ii) a clear decrease from south to north gradients (such as richness and the Shannon Index in some demersal taxa), (iii) gradients interrupted by extreme mean values in one of the regions (such as fish biomass), and (iv) unclear patterns with one or two regions that showed significant differences from the rest (such as TLs4 of all and demersal cephalopods and the relative predator biomass of demersal fishes). In addition, our study illustrated that the β-diversity indicators were similar between regions.

Regarding temporal changes, species richness tended to increase with time, while in some cases the Pielou evenness index decreased, less when looking at cephalopods and crustaceans compared to fishes. On the other hand, β-diversity showed an increase with time in most regions, regardless of taxa and species groupings. Nestedness was the component that reported most positive slopes at the expense of turnover, although the North Catalan Sea and the Gulf of Lion regions reported statistically significant increases in turnover in cephalopods and crustaceans.

Biomass indicators showed some declines with time for all surveyed communities and fish communities, including the pelagic species from the northern areas, and increases for cephalopod communities. In fact, cephalopods experienced positive temporal trends in most indicators, species groupings and regions, especially in richness and biomass, where we observed very pronounced slopes in some regions. Trophic level indicators showed declines when looking at the surveyed community and the fish community in several regions, while they showed increases for cephalopods and crustaceans.

4. Discussion

In this study, we quantified marine biodiversity and community changes in the Western Mediterranean Sea, and documented contrasting temporal trends and relevant geographic gradients and spatial differences across five sub-regions and taxonomic groups. Our results enabled us to identify which indicators followed continuous geographic gradients, likely influenced by biogeographic features and long-term environmental drivers, and which were more specific to given regions, likely influenced by local fishing impacts and other sub-regional scale processes. The main patterns emerging from our results were associated to taxonomic diversity, β-diversity and its components, relative abundances and biomasses, and tropic level. Our study also reveals emerging characteristic patterns in specific sub-regions and specific taxonomic groups beyond fish (i.e. in the North Catalan Sea and for cephalopods and crustaceans).

Some of our results show similarities to those featured in previous studies (Navarro et al., 2016; Fernandez-Arcaya et al. 2019; Farriols et al., 2020), but we additionally used taxonomic and species groupings (i.e. demersal and pelagic) for our approach and established a regionalization of the gradients. We also computed a wide range of complementary indicators, from classic ones such as species richness and the Shannon index, to more integrative ones such as β-diversity and trophic level-based indicators. As such, our study complements previous studies providing novel results.

According to our results, the richness indicator follows the expected pattern of diversity, decreasing from southern to northern regions. This

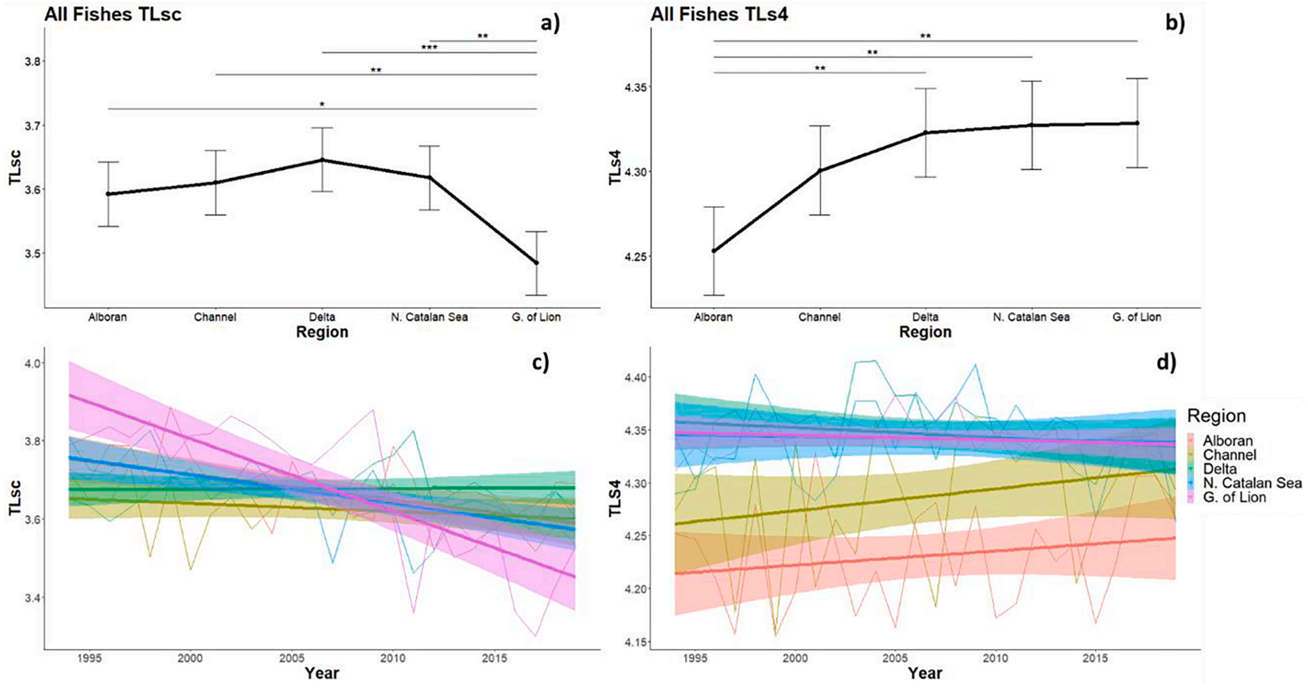


Fig. 7. Temporal trends, pairwise contrast and mean values of TLsc (above) and TLs4 (below) of all fishes. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

is a well-described pattern in ecology where warmer areas tend to show larger number of species (Worm and Tittensor 2018). This can be explained by environmental gradients such as an increase in temperature or decrease in primary production from the northern to the south most area (Estrada, 1996; Bosc et al., 2004). It is important to notice as well the biogeographical complexity of the Alboran Sea, which represents a confluence of Mediterranean species with the species runoff received from the Atlantic side that can expand northwards along the Iberian Mediterranean cast (Real et al., 2021). When looking at the whole surveyed community and the community of fish (both with all species and the demersal species) this gradient was interrupted by the lowest values appearing in the North Catalan Sea, which matches results found in other studies for non-target finfish as well as analysis of the whole ecosystem (Navarro et al., 2015, Gaertner et al., 2007). In both cases, the region reported less species both at spatial grid level and for a regional mean. This pattern could be due to an intense and cumulative human activity in the Catalan Sea area (Taconet et al., 2019), or the reduced area of the continental shelf in this sub-region that increases niche and habitat competition.

We also document how the number of species increases in almost all regions with time, although the decrease in richness is rarely documented in the literature and it is usually a sign of the synergy of several human impacts aside from overfishing (Granger et al., 2015). The increase in our study could be attributed to a decrease in fishing effort, especially of bottom trawlers in some areas (Farriols et al., 2017), or other factors like climate change, which has been linked in temperate systems with an increase in sea temperature and the tropicalization of Mediterranean ecosystems (Antão et al., 2020; Gordó-Vilaseca et al., 2021). Indeed, Hidalgo et al. (2021) have recently reported increases of the thermal affinity of these communities, observed for fish, crustacean and cephalopods. However, the causal relationship between richness and any or a combination of these drivers need to be further investigated. It is important to highlight that the number of sampling points per year remained constant with time and results from previous rarefaction curves using the same data show that our sampling effort was sufficient, thus differential sampling effort per year can be ruled out as a possible reason for this trend (Gaertner et al., 2013; Keller et al. 2016).

The lack of statistical significance of the spatial effects for β-diversity could be attributed to the reduced time period analysed in this study (2012–2019), which was applied to compensate for the sampling comparative challenges. It is thus likely that the composition of species has been kept relatively stable over the period used for the spatial analyses. The β-diversity did show, however, temporal significant changes from 1994, with increases over the studied period in most regions, alongside the previously described trends of richness. These increases indicate a lower level of similarity within communities with time, and illustrates the already described pattern of overall change in species but not loss of diversity in natural ecosystems (Dornelas et al., 2014). In all our cases where there were significant temporal relationships in β-diversity, they were mainly associated with a generalized increase of nestedness and a consequent decrease in turnover in most regions. Therefore, in most sectors, nestedness was the main component of biodiversity change, caused by species changes making species-poor sites to resemble a subset of species-rich sites (Baselga, 2010). The region with the highest rate of increase in nestedness over the study period was the Alboran Sea. These results suggest that our studied communities over the different regions became subsets of the original communities by losing or gaining species. This process can be associated with a long term temporal change such as climate change (Vale et al., 2021) and the associated warming of temperate waters as reported for the Mediterranean (Bianchi and Morri, 2003; Salat et al. 2019), or a higher Atlantic-Mediterranean flux of species through the Gibraltar strait in the case of Alboran (Real et al., 2021).

Changes in primary production dynamics have been recently shown as a potential additional driver because temporal changes in species composition mediated by productivity-driven regime shifts have been reported in the study systems in 2001 and 2009 for the Alboran Sea and the Northern Spain, respectively (Hidalgo et al. 2021). While the Mediterranean region could not experience much change in the identity or replacement of species, it could be subjected to losses of different ecosystem functions as β-diversity changes occur in an orderly and non-random manner (Baselga, 2010). Spatial erosion of marine communities due to anthropogenic impacts and a consequent increase in β-diversity has also been observed in other highly impacted areas (Shackell et al., 2012). This process has been previously suggested for the Mediterranean Sea, with higher spatial heterogeneity in its communities due to the long-lasting anthropogenic impact (Hidalgo et al., 2017).

On the contrary, in the North Catalan Sea and the Gulf of Lion, it was the turnover component that dominated the temporal change in β-diversity, consistent with the highest values of beta diversity observed and indicating the replacement of species between sites. In these regions, species replacement seemed to be the most influential driver of biodiversity change and so the change in identity of their communities. The strong dependence of Mediterranean species upon the primary production dynamics (Fu et al., 2018; Hidalgo et al. 2021), and the dynamism of contrasting trophic pathways (Puerta et al. 2015), might trigger strong turnover of species over the North Catalan Sea. In addition, a greater competition in this sub-region is expected as species have to share a smaller ecological space over a narrow continental shelf (Stegen et al., 2013), which could be the reason of this difference of turnover influence. These factors, especially the available space and potential decrease of habitat competition would favour species replacement. The increasing β-diversity is an expected result considering that marine ecosystems usually have high values due to the very mobile species that live within their communities (McGill et al., 2015), including potential biological invaders that could explain the turnover values in areas such as the North Catalan Sea. Meridionalization (or the increase of southern thermophile species due to warming waters) of northern regions such as the North Catalan cost and Gulf of Lion can have an influence as well (Bianchi and Morri, 1993; Boero et al., 2008; Coll et al., 2010; Lloret et al., 2015). However, this process may have a reduced impact in our results since infrequent species were filtered out before analyses. Overall, studies on the β-diversity in the marine environments in general, and in the western Mediterranean in particular, are scarce and our study contributes to fill the gap in the region.

Another of the most relevant patterns observed in this study was the overall high values of abundance and biomass in the Gulf of Lion in contrast to lower ones in the rest of the regions. These spatial patterns are similar to those previously described by Navarro et al. (2015) and partially match those of Fernandez-Arcaya et al. (2019). They also match the macroecological patterns observed in marine ecosystems, where temperate communities tend to show lower rates of biodiversity values and higher biomasses (Worm and Tittensor 2018). This spatial difference can be attributed to the higher primary production in the northern area compared to southern regions (Estrada 1996; Bosc et al. 2004). Interestingly, the lowest levels of biomass and abundance in GSA06 (i.e. Valencia Channel, Ebro Delta and North Catalan Sea) for megafauna in deeper areas (500–800 m) reported in 2012–2015 by Fernandez-Arcaya et al. (2019) match with the identification of lower levels of some of our indicators in the same sub-regions, but at shallower habitats, which can be related with comparatively higher levels of fishing exploitation reported for GSA06 (Fernandez-Arcaya et al. 2019; Taconet et al. 2019).

Our study also showed extreme values in several indicators in the Gulf of Lion and the Alboran Sea. This pattern was not recurrent and consistently observed, with different spatial variation observed across the type of indicator or the taxonomic species group. These deviations causing some discontinuous trends may be linked to the heterogeneity in both the north and south most areas seen in environmental drivers or human impacts. A similar case can be seen in the Aegean Sea (Gaertner et al., 2007), where diversity is higher than in nearby western seas despite being in the eastern Mediterranean due to an increased amount of nutrients from anthropogenic origin. Both, the Gulf of Lion and the Alboran Sea are the two areas where the environmental gradients suffer more clear discontinuities, particularly from the primary production and hydrographic perspective (Bosc et al., 2004), which could explain those spatial patterns. In addition, the Alboran Sea has biogeographic singularities in terms of biodiversity as it represents an ecological transition ecosystem between the Atlantic and the Mediterranean (Real et al., 2021). Conversely, these higher values in the extremes could be also a consequence of the lower values in the central area of GA06 related to higher human impacts, as previously discussed.

Regarding results by taxonomic groups, cephalopods and crustaceans showed the most consistent spatial patterns with a north–south gradient in many of their indicators. These patterns correspond to the higher proportion of relative fish biomass in northern bioregions for the surveyed community, and with higher temperatures and lowest primary production in the south (Bosc et al., 2004; Colella et al, 2016). In the case of cephalopods, the increases in most of the study area with time suggest that they may become the "winners" in the region. This increase is consistent with other studies in the Western Mediterranean (Coll et al., 2013; Keller et al., 2016, Hidalgo et al. 2021), and at a global scale (Doubleday et al., 2016; Coll et al., 2021), indicating positive changes of short life-cycle species such as cephalopods under cumulative anthropogenic effects. Cephalopods are fast growing species and are positively affected by increasing temperatures that synergistically interact with the removal of both predators and competitors by fishing, thus allowing boosting production of a few cephalopod species (Keller et al., 2017b; Coll et al., 2021). Besides cephalopods, our study also reveals similar patterns in crustaceans, which are generally short life-cycle species compared to most fish, consistent with recent studies in the area (Hidalgo et al. 2021).

Taking into account the different trends in the trophic level-based indicators and their equivalence to the different fishing scenarios proposed by Shannon et al. (2014), the changes in trophic levels observed in our study hint towards a fishing down scenario, especially in the North Catalan Sea. This is in line with previous results investigating trends in specific regions (Coll et al., 2009). In the North Catalan Sea specifically, there has been an increase in species with low trophic level (TLsc) and a negative relationship between time and the mean surveyed trophic level above 4. This is probably signalling the intense exploitation reported in the area (Coll et al., 2008; Pennino et al., 2017; Coll et al., 2021). In fact, the indicators analysed in this study picture the North Catalan Sea region as an area with high rates of diversity change, a fishing down process especially notable considering fish, low mean values of richness, abundance and biomass, and decreases in overall biomass and relative biomass of predators. All these values and changes can been associated with overfishing (Shannon et al., 2014) and pollution (Johnston and Roberts, 2009) intensified by the smaller extension of the continental shelf. In southern areas like the Alboran Sea and the Channel, in contrast, some indicators show positive temporal trends (such as the relative biomass of predators and mean surveyed trophic level above 3.25 of crustaceans) and could be related to recoveries of certain species after the decline of fishing effort, as seen for species of chondrichthyans (Ramírez-Amaro et al., 2020, Hidalgo et al. 2021).

Considering our outcomes and the potential limitations of our study, we highlight that some indicators can be prioritized to measure changes in community diversity due to their statistical significance, consistency and responsiveness. Overall, general indicators, such as species richness, abundance and biomass, were more informative to track long-term spatial and temporal changes in our study area, as they showed more statistically significant relationships and clearer patterns. Others were more complex to interpret, such as evenness and dominance indicators, β-diversity and its components and trophic levels. A reason behind this difficulty of interpretation could be their higher sensitivity to differences between areas and thus their influence by local environmental and human drivers distributed heterogeneously in space.

Our study also highlights that further studies are needed to investigate the dominant mechanistic drivers behind the patterns observed, as well as to elucidate the spatial scale (regional or local) at which these drivers act. Further studies should analyse the effect of cumulative human drivers like fisheries exploitation and/or pollution and environmental factors, such as temperature and primary production, as these are most likely the drivers influencing change. A finer analysis exploring the indicators by depth could also offer more insights as the shelf and slope areas do have different natural communities because of oceanographic conditions and environmental factors, but also face different human impacts (Farriols et al., 2017; Fernandez-Arcaya et al. 2019). In this context, a more detailed spatial analysis is also recommended to confirm those areas with high biodiversity change as well as the most vulnerable areas or those that are most impacted (such as the North Catalan Sea) or may be recovering (such as the Alboran Sea o the Channel). This can be a useful information to be considered for the design and the establishment of marine protected areas (MPAs) and other effective area-based conservation measures (OECMs) for the protection of biodiversity and the sustainable use of marine resources (e.g., Coll et al. 2015; Giménez et al., 2020).

Our study, however, presented some limitations as some traits like the trophic level or the mean size may not capture real changes in the traits but the relative change in biomasses. This is so because the values were taken from available online databases representing information from the entire population. Values from online databases may not be the most suitable due to the oligotrophic and warm environment of the Mediterranean Sea compared to other areas, showing quicker maturation and smaller sizes at maturity for many species due to the temperature size rule (Atkinson, 1995; Silva et al., 2006; van Rijn et al., 2017). Another issue is that certain ecosystem functions (e.g. productivity, energy transfer, nutrient cycling) as well as functional groups of ecological importance (such as elasmobranchs, mesopelagic species, or small pelagic fish) are not well captured by our indicators. Lastly, the use of linear effects for the identification of characteristic or recurrent patterns and effects may have masked some non-linear trends that were not considered in favour of analysing long-term effects (Blanchard et al., 2010).

In summary, we have detected spatial gradients and temporal changes in biodiversity indicators through the study area, both at community level and at taxa group level with clear winners (cephalopods) and losers (the North Catalan Sea sub-region) in a context of change. Despite some limitations, this in-depth analysis of the Western Mediterranean ecosystem illustrates the use of a selection of traditional and integrative biodiversity indicators that combine the capacity to detect ecological changes both at a regional and a sub-regional scale.

CRediT authorship contribution statement

Carlos Veloy: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization. **Manuel Hidalgo:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization. **Maria Grazia Pennino:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Encarnación Garcia:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Antonio Esteban:** Resources. **Cristina García-Ruiz:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Gregoire Certain:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Sandrine Vaz:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Angélique Jadaud:** Investigation, Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Marta Coll:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization.

Declaration of Competing Interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108674.

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