

Community's ecological traits reflect spatio-temporal variability of climate change impacts

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ABSTRACT

Climate change is triggering shifts in species distribution eventually altering communities' biogeography. The composition of a community in terms of its species' ecological niche informs of a community's response to environmental conditions and impacts, which is central for a timely conservation. While the thermal niche has been widely explored, given it offers a direct link of warming effects on an assemblage, acknowledging the multivariate nature of a species niche can provide relevant insights of the reorganizations taking place at a community-level. We studied the mean and variance of 10 ecological traits at the community level in two regional ecosystems in the temperate East-Atlantic and the Mediterranean Sea, characterized by a distinct exposure to warming. Our findings revealed major temporal changes and spatial structuring in the traits and ranges explored over the last decades. Apart from confirming the expected general poleward, deep-ward shift, our results highlighted a widening of thermal and latitudinal ranges, possibly related to a 'flexibilization' of the communities in a context of global change. In addition, temporal patterns reflected how communities have adjusted around regime shifts known in both areas. Regional differences arose concerning the variance of depth ranges and area of distribution, as well as to the global evolution of the communities, which we argue are consequence of their different geographical features and ecological history. The comparison of two large multitaxon assemblages has disclosed a broad-scale motion of response to warming in the benthic-demersal domain. We expect this study will contribute to the understanding of the multivariate nature of global-change effects on marine fauna, which ultimately informs adaptive management.

1. Introduction

In the last decade, the ocean has kept on taking up a near-constant proportion of CO₂ emissions from human activities, resulting in profound, long-lasting changes in oceanographic features, among which increases in temperature are the most pervasive. As a consequence, most marine ecosystems in the globe have readjusted their structure and function to increasing temperatures, which for many NE Atlantic ecosystems has implied ecological regime shifts at various levels, from population (Goikoetxea and Irigoien, 2013; Cabrero et al., 2019) and community (Auber et al., 2015; Hidalgo et al., 2022a,b; Tsimara et al.,

2021) to ecosystem level (Möllmann and Diekmann, 2012; Alheit et al., 2019; Bode et al., 2020; IPCC et al., 2022). An important cue of climate change is the species tracking of their suitable temperature regimes which ultimately affects the width, depth and latitude of a community's coverage. Although it is generally expected that marine organisms will redistribute towards cooler (poleward and deeper) regions as a result of climate change, exceptions that result from local variations in temperature, trophic dynamics, species life history and interactions with other stressors are common (ICES, 2017; Molinos et al., 2018; Punzón et al., 2021; Sanz-Martin et al., 2023).

Climate change impacts display relevant spatial variability, which

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has been evidenced around the Iberian Peninsula even at the sub-regional scale (Aragão et al., 2022). On ecosystems associated to the Atlantic Ocean and the Mediterranean Sea this variability comes from contrasting exposure and sensitivity to climate change impacts, along with cumulative interaction with other stressors, such as fishing. On one side, the communities associated to the Atlantic shelf of Iberian Peninsula, while recovering from long term overfishing (Modica et al., 2014; Hidalgo et al., 2017; Arroyo et al., 2019; Punzón et al., 2021) are also experiencing the impacts of a sea surface warming rate of 0.23 °C per decade (Chust et al., 2022). Regional climate change projections for the southern Bay of Biscay also indicate decreases in surface salinity and a deepening of the winter mixing layer, two processes that have been going on so far and could be leading increases in nutrients and oxygen concentrations identified at sea surface (Erauskin-Extramiana et al., 2019; Chust et al., 2019, 2022). The effect of these impacts on populations and communities has been recognized in the area in several aspects, for example, in the niche tracking and earlier migration of the Northeast Atlantic albacore (Dufour et al., 2010; Chust et al., 2019), in changes in the spawning period of anchovy and mackerel in the Bay of Biscay (Punzón and Villamor, 2009; Erauskin-Extramiana et al., 2019; Rodríguez-Básalo et al., 2022) and as complex ecological regime shifts at various levels (Bode et al., 2020; Polo et al., 2022), to name a few. In general terms, deeper areas have experienced a much subtle and progressive increase of mean temperatures, but still show clear evidences of ‘meridionalization’, i.e. increase in the abundance of native fauna with southern affinities (Punzón et al., 2016 and references therein), reflected in the rising Community Weighted Mean Temperature of the Cantabrian benthic-demersal community (Punzón et al., 2021).

Compared with the Atlantic communities, fishing impacts on Mediterranean fish stocks and communities are large and ongoing (Arroyo et al., 2019; Fariols et al., 2019; FAO, 2022). Fishing pressure in combination with several additional anthropogenic drivers makes Mediterranean populations and communities highly responsive to natural environmental variability (e.g. Hidalgo et al., 2011, 2022; Quetglas et al., 2013). Mediterranean communities have shown to respond to global change heterogeneously in space, with a clear east to west gradient (Hidalgo et al., 2017; Fariols et al., 2019; D’Amen et al., 2022). Over the whole Mediterranean basin, the sea is warming at a rate of 0.35°C per decade (Pastor et al., 2020), fostering not only the ‘meridionalization’, but also the ‘tropicalization’ (increase in warm-affinity native and non-native species, respectively) of the communities and ecosystems (Bianchi, 2013; Fogarty et al., 2017 and references therein; Vasilakopoulos et al., 2017; Hidalgo et al., 2017; Hidalgo et al., 2022 a, b). The diversity of impacts related to climate change in this region also includes changes in the vertical mixing affecting primary production regimes (Macias et al., 2018), changes in the thermohaline circulation, the local hydrography (Ser-Giacomi et al., 2020), the strength of winter weather events (Gaertner et al., 2018) and an increasing frequency and intensity of marine heat waves (Darmaraki et al., 2019).

When it comes to assessing shifting niches at a community level, a straightforward approach is to investigate the community’s turnover regarding changes in its mean traits. Unlike taxonomic approaches, community weighted mean traits can better inform on a community response mechanism, by providing a more general understanding of species displacement due to their biogeographic affinities. The use of ecological traits (also found in literature as environmental or niche features, preferences, or spatial traits; De Bello et al., 2021) relies on marine organisms being constrained to a specific range of optimal environmental conditions, directly related to a sufficient access to the essential resources of either one of an organism’s life processes. An example of this mechanism is the supply of oxygen by ventilation and circulation that can only take place within a species’ specific thermal range (Pörtner, 2002; Drinkwater et al., 2010). The most studied environmental preference has undoubtedly been temperature, which comes as the most relevant environmental inductor of distributional changes at large scales (Collie et al., 2008; Cheung et al., 2010, 2013; Punzón et al.,

2016; Sanz-Martin et al., 2023). Yet, other stressors acting at a more local scale can have a large impact on the community’s composition and are too often ignored, whereas to get a more holistic understanding of ecological change it is crucial to study beyond the thermal realm of the niche (Lenoir and Svenning, 2015; Delgado et al., 2018).

In this research, we have aimed at a broad, more comprehensive look into the spatio-temporal dynamics of distribution shifts beyond the relative increase in thermophilic species. We have approached the shifting niches of two impacted benthic-demersal communities by analyzing simultaneously the mean and variance of the frequency distribution of various ecological traits, revealing the specific means in which ecosystems are experiencing climate change impacts (Fossheim et al., 2015; Pecuchet et al., 2016; Beukhof et al., 2019; Husson et al., 2022). Building on the recently published Community Weighted Mean Temperature (Punzón et al., 2021), we computed the Community Weighted Mean and Variance of sea bottom and surface temperatures, salinity, mean depth, latitude and species range size (i.e., area occupied) along with four descriptors of the communities’ distributional ranges, i.e., surface and bottom thermal tolerance ranges as well as latitudinal and depth ranges. Our expectation was that the spatio-temporal analyses of these indicators of communities’ weighted mean and variance of the ecological niche would provide additional evidence of the response mechanisms of demersal communities to human-induced environmental variability.

2. Material and methods

The workflow followed for the study of the two benthic-demersal communities’ spatio-temporal evolution is summarized in Fig. 1 and depicted in the following sections.

2.1. Data and data treatment

2.1.1. Survey data

Species abundance data (number of individuals per km²) were gathered from two bottom-trawl surveys carried over the Atlantic and the Mediterranean shelves of Iberian Peninsula, over a geographical scale with substantial longitudinal, latitudinal and depth gradients. From the complete surveys datasets (consisting of over 680 species in the Cantabrian region and 620 in the Spanish Mediterranean) we settled on a set of 246 vertebrate and invertebrate species. This 246-species community was considered the most robust and representative set for both communities, and was reached after filtering each survey database through three criteria: (i) one that only kept species that occurred persistently along the time series (at least 12 years), (ii) one that kept species widely distributed in the study areas (which at least appeared in 12 hauls each year) and (iii) one that excluded the species that did not attain a minimum abundance per haul and thus did not contribute significantly to the total abundance of the community. Although rare species can have important impacts for the functioning of the ecosystem (e.g., keystone species), in this research we are interested in studying the overall changes in the communities’ composition in terms of abundance, thus rare species were excluded from the analyses by (iii) only keeping species with an abundance value over the first decile (within each haul).

The study areas encompass the Cantabrian Sea, extending from southern Bay of Biscay to north-west of the Spanish shelf, between the mouths of Miño and Bidasoa rivers, and the Mediterranean geographical subarea 6 (GSA6, for more information on this survey’s scheme, see Spedicato et al., 2019), the eastern Balearic Sea associated to the Iberian Peninsula coast. In the Bay of Biscay, bottom-trawl survey DEMERSALES has been conducted every autumn by the Spanish Oceanography Institute (IEO) since 1983 (with the exception of 1987). In the Spanish Mediterranean ecosystem, the MEDITS bottom trawl survey has sampled the benthic-demersal ecosystem every early summer since 1994. Both surveys use similar sampling protocols (DEMERSALES is standardized by the International Bottom Trawl Survey ICES Working Group, IBTS,

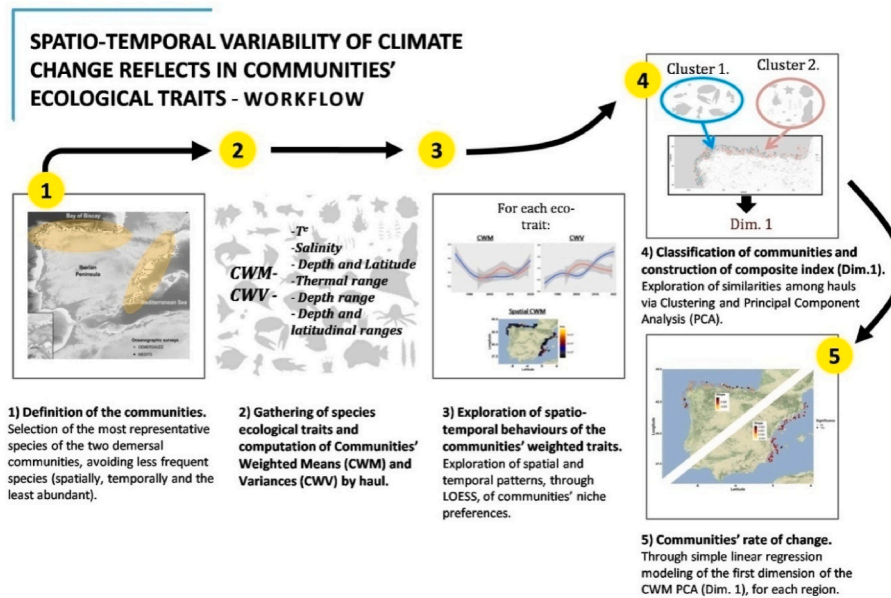


Fig. 1. Workflow of the present study, highlighting the different phases of the methodology applied to approach the spatio-temporal variability of the two communities studied, in terms of their ecological traits.

while MEDITS is standardized according to the recommendations of the Mediterranean Fisheries General Council, CGFM. Further reference for these organisms can be found in ICES, 2022; Spedicato et al., 2019, respectively for the Atlantic and the Mediterranean surveys) and present matching spatial coverage and resolution. To ensure consistency in the identification of invertebrates across the surveys in the Cantabrian region, we only analyzed hauls for the period 1994–2020. Therefore, the surveys cover the periods 1994–2020 (26 years) for DEMERSALES and 1994–2019 (25years) for MEDITS. Both surveys follow a stratified random sampling scheme with five depth strata (Spedicato et al., 2019; ICES, 2022). In our analyses we used density (in number of individuals of a species) per haul standardized by swept area (i.e., number of individuals/km²). The inclusion of both fish and invertebrate species in communities' studies can be challenging, as considering biomass instead of abundance data would tend to undervalue the contribution of invertebrates to the community but the use of abundance data could imply an over-influence of high density, small organisms. With this in mind we carried our analyses using abundance data in number of individuals, as we considered it would be a more balanced parameter, given the surveys use a sampling gear that ensures the exclusion of high-density, small pelagic and demersal organisms, which could have a big influence in the results.

2.1.2. Ecological traits (or preferences) data

As descriptors of each species niche preferences (ecological traits or eco-traits from now on) we collected an initial set of 22 ecological traits obtained from the bioclimatic envelope models developed by AQUAMAPS (Kaschner et al., 2019) and the Ocean Biogeographic Information System database (OBIS, 2019). They are listed in Table S1 in Supporting Information. We estimated the global distribution area of every species as those cells in which they had a probability of occurrence over 50%, extracting this information from the bioclimatic envelope models and therefore avoiding the bias of only considering the species' distribution and ecological preferences within the areas of study (Punzón et al., 2021 and references therein). Based on these distribution ranges we computed the mean value of each ecological variable (temperature, salinity, latitude, depth and extension of area occupied) as well as the 0.1 and 0.9 quantiles for each variable, which will be referred to as minimum and maximum values from now onwards. Ranges for some of the ecological traits were computed by subtracting the minimum (10th quantile) to the

maximum (90th quantile). We downloaded data on parameters commonly used to characterize the environmental preferences of demersal species such as sea surface (SST) and bottom (SBT) temperatures (mean, minimum (min.) and maximum (max.) values) and salinity (mean, min. and max. SSS), as well as data associated to the species distribution range, such as occupied area (expressed in km²), latitude (mean, min., max. and latitudinal range) and sea surface and bottom temperature tolerance ranges. Additionally, we calculated the depth (mean, min., max. and depth range) based on the species presence records (OBIS, 2019) and the digital bathymetry provided by EMODNET (<http://www.emodnet-bathymetry.eu>). For the species lacking a model in AQUAMAPS, we overlapped presence data with the AQUAMAPS environmental dataset, to obtain similar environmental data. We approached the species' environmental preferences following the procedure described by Punzón et al. (2021), considering the overall distribution range of each species, thus avoiding the bias of taking in consideration only parameters within the study area. Nevertheless, these environmental preferences should be considered as a proxy for the affinity of the species for specific environmental conditions, rather than the exact optimum niche preferences or ecological traits.

2.2. Community-weighted mean ecological traits analyses

To characterize the benthic-demersal communities within each haul in terms of their ecological properties, we computed mean ecological values at the community level (CWM) as well as the community-weighted variance (CWV) of the niche traits. This approach consists in weighting the ecological trait for every species in a given haul (or 'community') by the relative abundance of said species in that given community. CWM and CWV for a given haul *i* are calculated following Gaüzère et al. (2019) as represented below.

$$CWM_i = \sum_{s=1}^R Eco - trait_s^* W_{Si} \quad CWV_i = \left(\sum_{s=1}^R Eco - trait_s^* W_{Si}^2 \right) - CWM_i^2$$

For a community with *R* species, with *W_{si}* the relative abundance of the species *s* at haul *i* and *Eco-trait_s* the species *s* mean trait value. The CWM described the average value of an ecological trait in a community, whereas the CWV describes the spread of the trait's values within the community. Note that a shifting CWV along a gradient would indicate an

increasing or decreasing variability in the species' ecological traits, but it would not reveal the direction of change. Changes in CWM along the same gradient would provide this insight. Both indexes were computed by weighting the ecological trait value of each single species by its abundance at a given sampling station, following the community-weighted mean trait value (CWM) approach (Grime, 1998).

As summarized in Fig. 1, after a first visual exploration of the dynamics of each ecological trait at community level in Generalized Additive Model (GAM) plots and testing each community weighted eco-trait for possible trends through a Mann-Kendall trend test for serially correlated data, we aimed at a multi-trait approach. For this purpose, the communities' ecological traits were studied simultaneously by classifying each sampling station by its ecological trait composition with a clustering technique and the construction of a composite index with Principal Component Analysis (PCA) (section 2.2.1). The study via linear regression of the first dimensions of the PCAs on the Mediterranean and Cantabrian datasets, which gathered most of the variation in the data, enabled the measurement of the magnitude and character of the distributional changes (section 2.2.2).

Prior to undertaking any statistical approach for the study of CWM and CWV dynamics, community weighted ecological trait data which were markedly right skewed were log-transformed to approach normally distributed variables (community weighted ecological traits). After that, every variable was standardized via function *decostand* in R package *vegan* (Oksanen et al., 2020). The final set of ecological traits analyzed in this work consisted often variables drawn from the initial set of 22 (Table S1), reached by excluding the most correlated and collinear ones. This selection was done by computing the Pearson coefficients for every variable combination and setting a threshold on a Pearson coefficient of 0.6 as well as choosing EMODNET's over AQUAMAPS' bathymetrical data, which were considered better quality data. To explore spatio-temporal patterns, we mapped the smoothed values of CWM and CWV and fitted General Additive Models (GAMs; Hastie and Tibshirani, 1990). GAMs were here used to visually explore the temporal dynamics of every community weighted ecological trait and were chosen over linear regression or other smoothing techniques so non-linear patterns emerging from the data could be visually observable. GAMs were fitted using the *gam* function in R package *mgcv* (Wood, 2011), assuming a Gaussian distribution of the error term and limiting the degrees of freedom of the smoothers to 4. The trends observed in the GAM plots were compared to the outputs of Mann-Kendall trend tests (carried for each community weighted eco-trait time series) modified to account for autocorrelation in time series data (Hamed and Rao, 1998).

2.2.1. Classification of the communities

Once the benthic-demersal communities at each haul were characterized by their community-weighted ecological traits, we studied every community eco-trait simultaneously, in the multi-trait approaches described in this and the next sections. First we looked for similarity patterns (in terms of the communities' eco-trait composition) across study areas (separately), to assess whether the response to climate change was spatially and/or temporally clustered. For this purpose, a non-hierarchical cluster technique, Partitioning around Medoids or PAM (Kaufman and Rousseeuw, 1986), was performed on the CWM composition of the hauls. We prioritized the identification of changes in the direction of the communities and focused this and the following analyses in the mean (CWM) over the variance (CWV) values of the traits. The cluster algorithm divided the datasets into *k* clusters, building each cluster around a median sample of the dataset (medoid). The integer *k* that endured well-separated clusters was identified by computing the Silhouette width (Rousseeuw, 1987; Pollard and van der Laan, 2005) and the minimum sum of square errors within clusters (SSE). Once sampling stations were identified as part of a cluster, in order to assess temporal changes in the communities' composition in terms of their eco-traits, we computed the yearly anomalies regarding the mean proportion of stations classified as Cluster 2 by subtracting from the number

of Cluster 2 hauls for a specific year the mean number of Cluster 2 hauls for the whole series.

We carried two Principal Component analyses (PCA) on the sampling stations and their CWM ecological trait composition, one for the Cantabrian and one for the Mediterranean time series. The two first principal dimensions (Dim.1 and Dim.2) of these PCAs provided information on the metrics of the communities' (understanding here each sampling station as a community) niche dimensions, the variance of their geographical range and the extent of the species tolerance to changes in physical conditions. To assess the communities' spatio-temporal variability, every CWM ecological trait was investigated simultaneously through the analysis of the first principal dimensions. The sampling stations' scores (coordinates) of the first and second principal dimensions were used to approach the extent or magnitude of the changes that have taken place in both studied communities, while the inspection of the CWM loadings (contribution of the weighted ecological traits to the principal dimensions) gave an idea on the nature of those changes. We used function *PCA* in R package *FactoMineR* (Lê et al., 2008) to conduct the PCA, which we based on the correlation matrix following Jolliffe and Cadima (2016).

2.2.2. Communities' rate of change in terms of their ecological traits

Each haul was assigned to its corresponding cell in a grid of 0.05° longitude and 0.05° latitude. C-squares were used for grid construction and as spatial indexing system (Rees, 2003). To unveil the spatio-temporal trends in CWM environmental preferences we constructed linear regression models for each time series of the first dimension of the CWM PCA (Dim. 1) in each C-square cell using year as a predictor. To build these models, we only kept C-square cells with a minimum of 5 sampling events along the time series. This meant that from the 592 grid cells sampled in the Cantabrian Sea (i.e., southern Bay of Biscay) (4464 sampling stations) only 219 remained (3628 sampling stations), and from the 375 C-squares sampled in Mediterranean Sea (2177 sampling stations in total), 142 cells (1670 sampling stations) were suited for the linear regression modeling. For a correct inference of the slope and p-value of each cell trend along the studied period, we accounted for the 'nestedness' of the data (the fact that hauls belonging to a single C-square could be spatially dependent) by explicitly including the model of the C-square nested effects in Generalized Linear Models constructed as follows:

$$\text{Dim 1} \sim \beta + \text{year/C-square} + \varepsilon$$

We assumed a normal distribution of residuals and 'identity' as the link function.

The slope of the models indicated if there was a directional positive or negative change in the studied parameter in the respective C-square cell. Finally, principal component analyses (PCAs) were applied to the temporal trends to identify similarities, spatial patterns and spatio-temporal trends between the CWMs.

All data handling and quantitative analyses were performed using R version 4.1.0.

3. Results

3.1. Community-weighted ecological traits

The temporal and spatial patterns of the community-weighted mean and variance of the studied ecological traits revealed major similarities between study areas, although some traits did show regional divergence (Fig. 2 and Table S1). Regarding temporal trends, the Cantabrian benthic-demersal community showed a rising CWM surface thermal affinity (SST), although at bottom (SBT), the rise only takes place after year 2000. The Spanish Mediterranean CWM SST and SBT showed an initial apparent decrease that lifted after mid-2000s. The community's salinity (CWM SSS) affinity values in Cantabrian Sea have decreased,

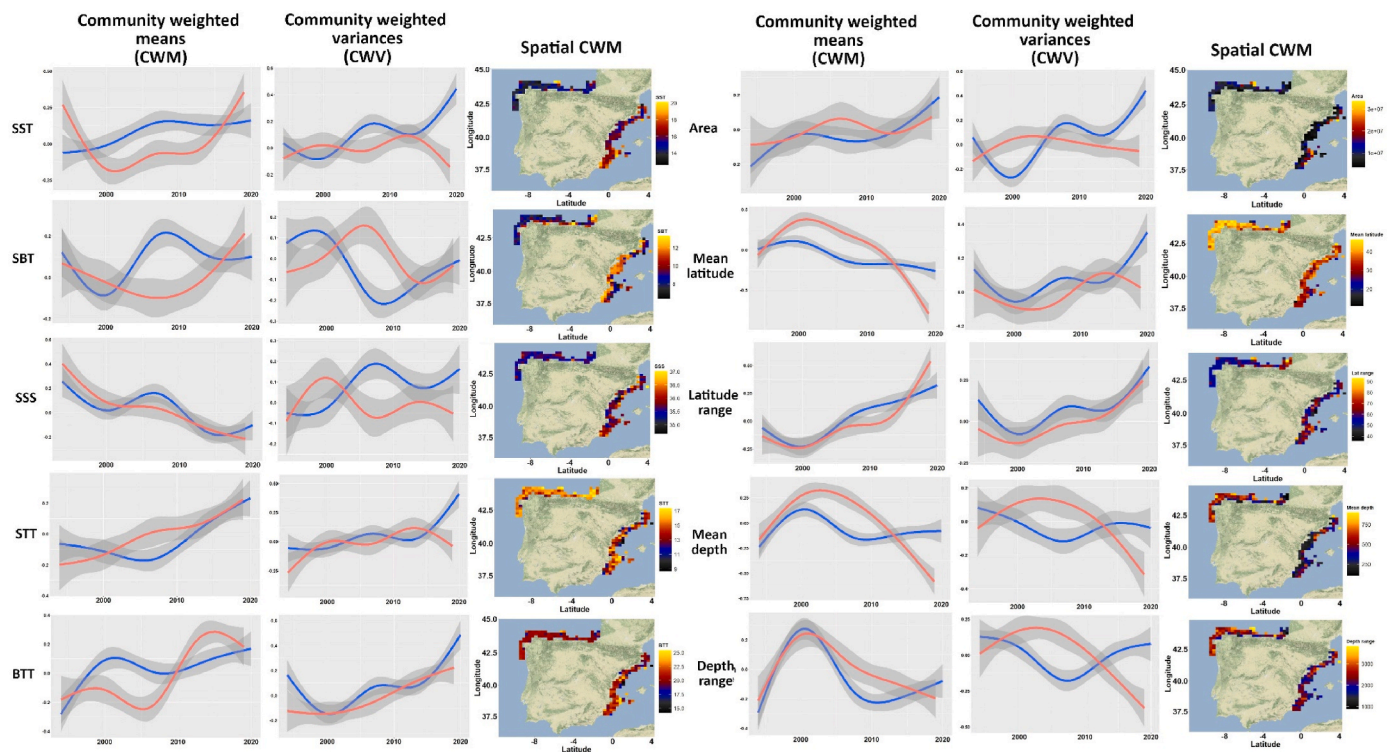


Fig. 2. Community-weighted mean values (CWM) and community-weighted variance (CWV) of sea surface and bottom temperature (SST and SBT, respectively), sea surface salinity (SSS), surface and bottom temperatures tolerance ranges (STT and BTT, respectively) and area occupied (Area), latitude (Mean latitude) and latitudinal range, depth (Mean depth) and depth range. Blue line and red line represent the observed changes in community-weighted means (left column) and variances (right column) in the Cantabrian and Mediterranean seas, respectively, and the grey area represents the 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

while the Mediterranean’s CWM SSS declined across the time series. As for the thermal ranges inhabited by the Cantabrian community, the range of tolerance to surface temperatures (CWM STT) increased while bottom thermal range (CWM BTT) showed an upward trend. The range of surface temperature tolerated by the Mediterranean community widened steadily along the series, having last decade’s increase been sharper for these communities’ bottom temperature tolerance range.

The mean area occupied by the species structuring the Cantabrian community (CWM area) showed an increasing trend. The Spanish Mediterranean CWM area showed a moderate increasing trend. CWM latitude of both Cantabrian and Spanish Mediterranean communities have generally decreased along the study periods, with a short increasing phase in the Mediterranean region that reversed by year 2000 and is mirrored by CWM depth. In the Cantabrian region, CWM depth has no clear trend. The latitudinal layout, i.e., the distributional range in latitude, of the species forming the Cantabrian communities shifted from a relatively smooth negative trend around low values to an increase towards a wider latitudinal range right after year 2000, tendency mirrored by the Spanish Mediterranean communities. In parallel, at Cantabrian Sea the depth range of the community (CWM depth range) has fluctuated, similarly to the Mediterranean communities. In both regions CWM depth ranges widened initially and contracted after year 2000.

Variances of certain community traits (mid-column of Fig. 2 and Table S1) showed similar temporal patterns between areas. In the Cantabrian community the CWV of every trait has experienced fluctuating but apparent increases, except for thermal affinity at bottom (CWV SBT), that has decreased from the beginning of the series, showing, however, a recent upward trend that started around 2010, and the range of distribution in depth (CWV depth range), which has fluctuated but at present shows values that do not differ from its initial ones. Spanish Mediterranean communities’ eco-traits’ CWV displayed

generalized rising trends, except for CWV salinity, SBT, mean depth and depth range, which had fluctuating trends, but were identified as decreasing by the adapted Mann-Kendall trend test.

Every trend described above matches those identified in the outputs of the Mann-Kendall trend tests for serially correlated data (Fig. S3 in Supporting Information). Not every community weighted eco-trait showed temporal autocorrelation, and only CWM BTT, CWM mean latitude, CWM latitudinal range, CWV SST, CWV STT and BTT trends were significant in the Cantabrian region. The Mediterranean communities showed significant trends for every CWM eco-trait excepting CWM SSS and SBT. As for Mediterranean CWV trends, only CWV STT and BTT, CWV mean depth and depth range trends were significant. Significance and autocorrelation of the trends detected by the modified Mann-Kendall tests are included in Fig. S2 and Fig. S3 in Supporting Information.

The CWM traits values varied spatially (right column of Fig. 2). The lowest values of CWM temperatures (SST and SBT) are observed in the community associated to the Cantabrian Sea, with lower values at the western part of the study area, the Galician margin, and increasing towards the eastern part, the inner Bay of Biscay. CWM SBT reflects the bathymetry of both areas for its most part, except for the areas of the Galician margin influenced by upwelling, and the mid latitudes of the Spanish Mediterranean coast, where species feature affinity to warmer waters even at higher depths. CWM salinity showed higher values at lower depths in both areas and its lowest values in the Mediterranean communities, which showed considerable spatial heterogeneity. The thermal ranges inhabited by the species are narrower and more spatially variable in the Mediterranean area.

In terms of traits related to the species distributional ranges, the communities are composed of species with wider ranges of distribution the further from the coastline in both areas, with distinct higher values in the southern regions of the Mediterranean Sea. CWM depth appeared

to be generally shallower in the Mediterranean community and inner Bay of Biscay and Cantabrian coast communities. Both CWM Depth and Depth range mostly reproduce the bathymetry and geographic gradients in both areas. Spanish Mediterranean communities show much lower CWM latitudes. While on average these communities are only 5° of latitude apart, their CWM latitude varied by as much as 15° in many cases. Communities in the westernmost edge of Cantabrian Sea are those with distribution ranges wider in depth but more limited distributions in latitude. The Mediterranean communities had generally higher CWM latitudinal ranges and lower CWM depth ranges than the Atlantic communities, with a strong heterogeneous gradient.

3.2. Classification of sampling stations

The most reasonable grouping patterns for both Cantabrian and Mediterranean seas CWM datasets were identified as a $k = 2$ (Fig. S3 and Fig. S4). The Silhouette width value was equally high for a $k = 2$ and a $k = 5$ in the Mediterranean dataset, and we opted for the $k = 2$ grouping as there were fewer fluctuations in the size of the $k = 2$ silhouette plots. The environmental preferences typifying each cluster group were determined and are listed in Fig. 3 and plotted in Fig. S5 in the Supporting Information. In the Cantabrian region stations with higher community bottom and surface thermal affinities, narrower depth range and smaller area occupied are grouped together in Cluster 1. The second cluster comprises stations characterized by much lower community-weighted mean bottom temperatures and stations with higher relative abundance of species with extensive distribution areas and able to tolerate wider depth ranges. Thermal ranges (STT and BTT), mean salinity, latitude and depth slightly differ between groups, but differences are not decisive. The two differentiated communities seem to coexist in time (top Fig. 3) and space (Fig. S6 in Supporting Information). As for Mediterranean benthic-demersal communities they were also clustered in two main community types (bottom Fig. 3). Firstly, PAM grouped together sampling stations with higher mean bottom thermal affinity and salinity, smaller area of distribution and narrower latitude range as well as thermal tolerance ranges (STT and BTT). Stations of the second group, mostly found in the second half of the studied time series, have lower mean preferred bottom temperature, wider latitude range and lower values of mean depth and latitude, meaning they display higher relative abundance of species inhabiting more southern, shallower waters. At this community, the two groups are more distinctively distributed in time and space.

The first dimension (Dim. 1) of the Principal Components Analysis on the CWM ecological traits accounted for 34.1 % of variation in the

Cantabrian data and 40.5 % of variation in Mediterranean data. Cantabrian Sea communities are distributed along a gradient defined by their preferred bottom temperature, the surface temperature range of tolerance and the area occupied by the species (Figs. 4 and 5). Thus, this dimension defined by the PCA marks, on the positive side of the x-axis, sampling stations defined by species with wider distributions, broad temperature ranges of tolerance (surface and bottom) and spread across

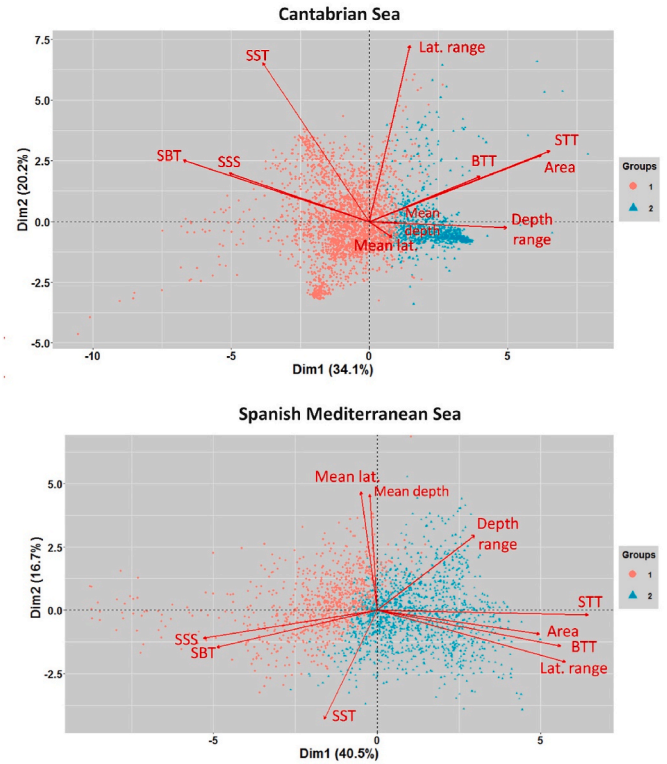


Fig. 4. Principal Component Analysis (PCA) of Cantabrian (top) and Spanish Mediterranean (bottom) sampling stations. The clustering results were also plotted over these PCA biplots. Stations are colored according to the cluster groups described in the legend and in Fig. 3, and the red arrows correspond to the community weighted mean ecological traits. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

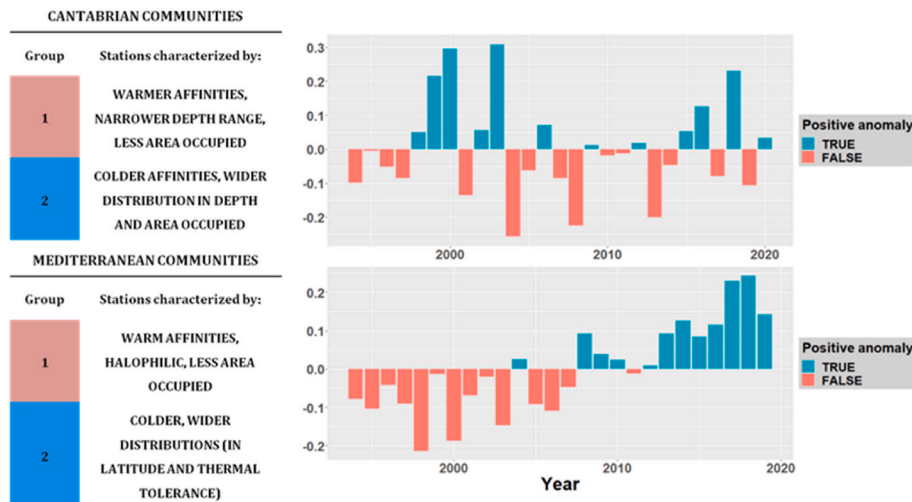
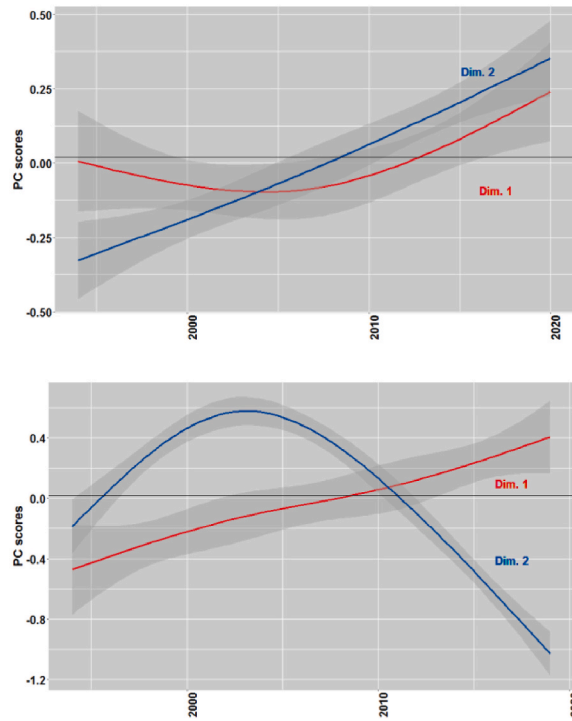
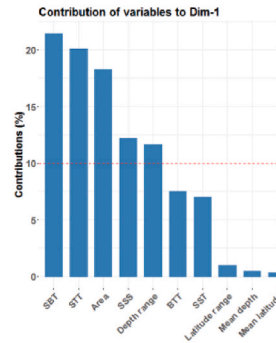


Fig. 3. Annual anomalies regarding the mean proportion of stations classified as Cluster 2 for the whole series, and environmental properties characterizing Cantabrian and Mediterranean cluster groups.

Changes in the community composition



First axis PCA



Second axis PCA

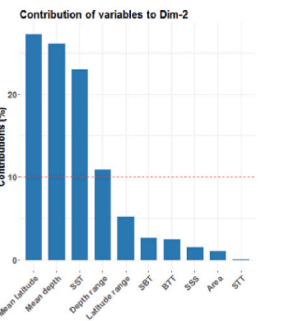
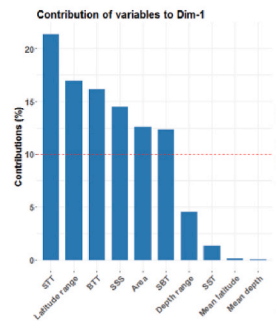
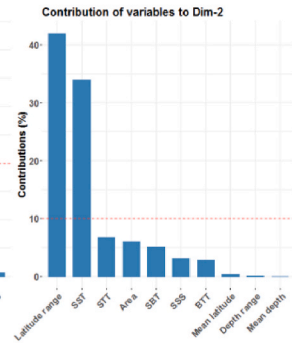


Fig. 5. Cantabrian (top) and Spanish Mediterranean (bottom) observed changes in community composition across the time series (left plots). Red line shows the evolution of the first principal component of the PCA, and blue line represents the temporal changes of the second dimension of the PCA. Main contributing ecological traits to first and second axis of the PCA are represented in the four right plots. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

larger areas and depth ranges; and on the negative side, stations with higher mean thermal affinity and higher community mean salinity. After year 2005, the community shifted towards wider distribution ranges in extension as well as in thermal, depth and latitudinal range (top Fig. 5). Also, the Cantabrian community has undergone an increase in mean surface thermal affinity.

In the Spanish Mediterranean Sea, the communities have a strictly monotonic increasing trend in their first dimension, transitioning from stations with a higher CWM SBT, CWM SSS, and narrow CWM distributional ranges (in depth, latitude and area occupied), towards stations characterized by larger CWM temperature ranges of tolerance and wider latitudinal expansion. The ecological properties that most contribute to the first axis of variation of Mediterranean data refer to the thermal range of tolerance and the latitudinal range, while the second axis mostly segregates stations with higher CWM latitude and depth and low surface temperature (more dominant at the beginning of the time series) from stations with higher surface thermal affinity and lowest CWM depths and latitudes (ecological traits or preferences whose dominance increased throughout the study period, bottom Fig. 5).

The integrity of the groups identified by the clustering technique in both studied datasets was corroborated in the PCA, as shown in top and bottom.

3.3. Spatio-temporal changes of the communities in terms of their ecological preferences

The temporal changes of benthic-demersal community' niche traits (summarized in Dim. 1, the first dimension of the CWM traits PCA) varied spatially (Fig. 6). This figure only displays the coefficients of the significant temporal models (to visualize also non-significant models see Supporting Information Fig. S6). The communities inhabiting the Cantabrian Sea presented a negative trend in 33% of the surveyed C-squares.

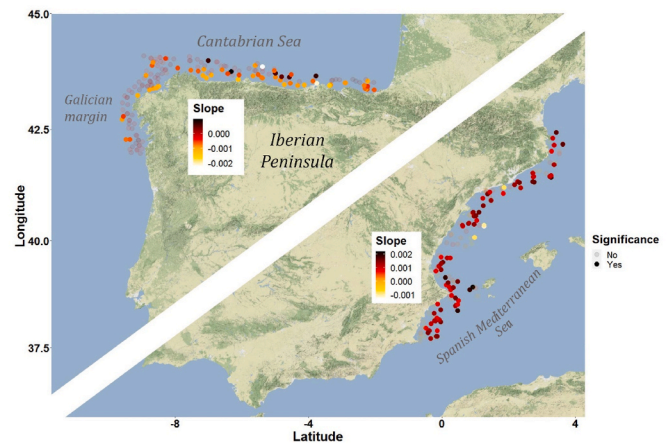


Fig. 6. Spatial distribution of community change in terms of its species ecological traits or preferences. Colored points indicate the direction of change across the time series, the dominant environmental preferences towards which communities have shifted, as obtained from the coefficients of the first dimensions (Dim. 1) models for Cantabrian Sea and Mediterranean Sea communities. Non-significant models are indicated with a semi-transparent point. Darker dots correspond to C-squares with a positive trend, i.e. towards higher values in the first axis of the PCA, and yellow and white cells are those in which the GLM models had a negative trend, which in both areas reflects an evolution towards stations dominated by warm-affinity, more restrictively distributed species. Note that the scales in the Cantabrian Sea and the Spanish Mediterranean are independent and directly comparable. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

In these cells, mostly allocated in the shallower part of the southern Bay of Biscay coast, there has been a shift towards more thermophilic communities, with a species composition more limited in their ranges of distribution. Only 5% of the cells showed the opposite trend, i.e., towards wider ranges of distribution in depth, wider thermal niches and affinity for colder waters. These communities are located in deeper waters of the inner Bay of Biscay. Most of the Mediterranean C-squares analyzed, approximately a 70%, showed a displacement towards a species composition with wider distributions in latitude, wider thermal ranges and area occupied, and affinity for colder temperatures. This trend has been more pronounced in communities inhabiting deeper areas.

4. Discussion

Global change is driving major changes in the location of suitable habitat for many species worldwide, and Iberian marine ecosystems are no exception. Our findings have revealed that shifts in species distributions of benthic-demersal communities around Iberian Peninsula are ubiquitous and prevalent. We have studied two communities known to be closely tracking changes in sea surface temperature and have found their ‘tropicalization’ processes resemble in many respects and are not limited to the increasing contribution of warm-affinity species, but also affect their distributional ranges, with regional differences that regard not only mean values but also the variance of community’s ecological preferences (eco-traits). In the last four decades, the composition of the Cantabrian Sea benthic-demersal communities, in the North-East Atlantic, has vastly changed its mean thermal affinity in the process of accommodating higher abundances of species from lower latitudes and shallower areas. In parallel, it stands out how the Spanish Mediterranean communities ‘tropicalization’ process features a general widening of the community’s ecological ranges. Both regions have also experienced a high variation in most of the studied niche related preferences. Differences in communities’ response arise from the biotic systems’ different adaptive capacity, which we argue are mostly a result of their climatic and physical environment and their demographic structure, which imply different coping mechanisms to external disturbances.

4.1. Evolution of single community-weighted ecological traits

Temperature is one of the main axes of the ecological niche space, as it serves as proxy for distributional features such as latitude and depth and it is a determinant factor of the distribution of species (Kleisner et al., 2017). The temperature of preference of a biotic assemblage is expected to show a direct response to warming; therefore, it has been the species ecological trait most commonly used to assess range shifts and turnover of species in warming environments at the community level (e.g. Cheung et al., 2013; Vasilakopoulos et al., 2017; Morley et al., 2018). In this respect, as can be appreciated in Fig. 2 as well as in the Mann-Kendall outputs (Tables S2 and S3 in Supporting Information) we identified an increase in Cantabrian Sea CWM temperatures and bottom thermal ranges, indicating not only that this community is increasing its preferred temperatures, but also increasing and diversifying its thermal tolerance. In addition, CWM Latitude and Depth are decreasing, reflecting the community’s hosting of species from lower mean latitudes and shallower depths, a known process in the area and the expected response as some populations progressively meet the limits of their thermal niche (Ter Hofstede et al., 2010; Le Marchand et al., 2020; Chaudhary et al., 2021). It is also in line with Punzón et al. (2021), who documented a decrease in boreal cold-favoring species in the Cantabrian community parallel to a thriving of Lusitanian warm-favoring species. In contrast, our results showed temporal fluctuations in the Spanish Mediterranean benthic-demersal CWM SST and SBT. This is differing to the results of Hidalgo et al. (2022a,b), who found the community had undergone a widespread rise in the relative contribution of thermophilic fish and invertebrate species. This increase, which would be expected at

an area with significantly higher warming trends (D’Amen and Azzurro, 2020), is only discernible in our results after the mid-2000s, at a time in which the widening of Spanish Mediterranean’s CWM sea surface thermal range also took off for the thermal range at bottom. Around this period, between the late 90s and mid-2000s, a regime shift across various trophic levels has been observed (Tsimara et al., 2021; Hidalgo et al., 2022 a, b). Hidalgo et al. (2022b) associated it mostly to primary production dynamics facilitated by a long-term continuous anthropogenic degradation. We can infer the pervasiveness of this shift from the change in tendency of many of the Mediterranean’s community ecological traits studied here. CWM and variance of mean depth and latitude of Mediterranean communities, for example, started reflecting a relative increase in shallower species from lower latitudes, which also implied more variability in preferred latitudes but narrower depth ranges (CWM Depth Range) as well as fewer variability in terms of mean depth (Depth’s CWV).

In this same line, a shifting point also arose during the first decade of 2000 for most of the ecological traits (e.g., CWM SST, SBT, SSS, STT, BTT, Area and Lat. range) in the Cantabrian Sea community. This change matches a regime shift that has been interpreted as a response to the combination of a changing environment and the release from a historically severe fishing pressure (Polo et al., 2022) as well as a cue of a more global ecological regime shift in NE Atlantic (Hemery et al., 2008; Luczak et al., 2011; Auber et al., 2015; Bode et al., 2020). In our study, it translates as minor changes in the system’s trends, which is driven towards lower CWM salinity, a period with no consistent trends in thermal affinities and a rise of the range of tolerance to surface temperatures as well as the community’s distribution in latitude. This period is characterized by a decrease in fishing efforts, and thus the relieve of large effects of fishing in the community, but also by a sharper emergence of warming effects (Punzón et al., 2016; Punzón et al., 2021; Polo et al., 2022). The expansion appreciated in the thermal and latitudinal communities’ ranges in this second period complements the most straightforward expectation, which would be a response mostly characterized by a steeper rise of thermal affinities. The increase of mean and variance of temperature tolerances within the community is observed in both study areas, and it reflects the increasing relative contribution of species with eurythermal niches. These species would be favored at the expense of more stenothermal organisms, as a tolerance to wide temperature ranges would allow them to settle and succeed more easily in rapidly warming environments than species heavily constrained in their thermal tolerances (Dahlke et al., 2020). In the Mediterranean community, these sharp increases in mean thermal ranges could be due to the increasing abundances of ‘flexible’ species, with larger niche breadths, which would allow communities to better cope with environmental extremes and environmental instability (Sexton et al., 2017).

We might find more on this ‘flexibilization’ of niche breadths at other community features, such as CWM Depth and Depth ranges, Salinity and distribution in latitude. It is noteworthy that Spanish Mediterranean species pool’s preferred depths are generally shallower than the Cantabrian Sea’s (along with narrower depth ranges). In the Galician margin of Cantabrian Sea CWM depth values typical from upper-slope communities (500–750 m) extend to coastal areas, while in the most southern communities of Spanish Mediterranean show CWM depths of continental shelves (250 m) that extend to the upper slope. The increase of shallow water species at depth in this area of Mediterranean Sea might relate to the increase in the relative contribution of species of Atlantic origin (Navarro-Barranco et al., 2019; Real et al., 2021). Atlantic species entering the Mediterranean through the Strait of Gibraltar are generally species with preference for shallow depths, given the barrier effect of this shallow corridor for deep biota, and show narrow bathymetric ranges but broad in latitude, which makes them more easily adapted to new environments (Real et al., 2021). This turnover is indeed one of the characteristics of the previously mentioned regime shift described by Tsimara et al. (2021) and has also been observed by Sanz-Martin et al. (2023), whom associated it to a

displacement in the centers of gravity of key species in the community towards higher depths and linked this configuration of the community, mainly composed of species with shallower distributions, to higher sensitivity to natural environmental variability (e.g. changes in primary production). In their study, Sanz-Martin et al. (2023) also identified key demersal species shifting their abundance distributions in accordance to sub-regional patterns of warming. They studied climate velocity and climate trajectories in the Western Mediterranean ecosystem and described a local maximum of warming in the Gulf of Valencia, in the middle of the study area, where climate trajectories originated and diverged to the North and the South. In our results the Gulf of Valencia came out as the area with higher CWM SBT, suggesting a sub-regional adaptation of the community to higher warming rates.

Among the key ecological niche axes for marine species, salinity is also considered to have an important role in structuring benthic communities and has been previously related to shifts in biomass (Neumann et al., 2016; Weinert et al., 2016). As seen in Fig. 2, around year 2000, within the Cantabrian Sea benthic-demersal community, CWM salinity abruptly shifted from a positive to a negative trend and sharply increased its variance, an ecological variation apparently disconnected from fluctuations in environmental salinity, which has not substantially changed in the area during the studied period (Chust et al., 2022). In the Spanish Mediterranean, on the other hand, there was a steep decrease in CWM salinity over time, which contrasts with the increase in environmental salinity described in the area from surface to deep waters (Vargas-Yáñez et al., 2017). Given the decoupling of the ecological indicator of CWM salinity from actual in-situ salinity values, the appreciated decreases are probably another sign of a higher dominance in the community of flexible species with mainly Atlantic distributions, and thus lower mean salinities, with respect to more stenotic, endemic Mediterranean species, with higher mean salinity affinities. The climate-driven range contraction for a large number of native species in the western Mediterranean Sea was predicted by Albouy et al. (2013) and might be also reflected in the decreases of certain community traits' variance, i.e. thermal affinity at bottom, mean depth and depth range. This means that while better adapted species are increasing in abundance, abundance of other non-adaptive species is lost.

Regarding the ecological traits directly related to geographical distribution, processes driving both Cantabrian Sea and Spanish Mediterranean communities are alike once more. Community Weighted Mean (CWM) area did not show any consistent pattern and latitudinal and depth ranges showed opposing responses. Latitudinal ranges within the community are generally increasing and diversifying (i.e., increasing in variance), while depth ranges are generally decreasing and homogenizing (i.e., decreasing in variance). These contrasting patterns suggest that species with wide latitudinal distributions have had an adaptive advantage under changing conditions, unlike species with wider depth distributions, which could be related to the fact that adaptability along the depth gradient has a physiological limit that demersal species might have already exhausted (Rutterford et al., 2015). In fact, large latitudinal distributions are commonly related to some sort of structuring at the meta-population level, providing species with increased phenotypic plasticity and thus a higher capacity to adapt to changing conditions at the regional scale (Sultan and Spencer, 2002). High phenotypic plasticity to adapt to novel environments, i.e. environmental generalists, is a common characteristic of species moving into new environments or experiencing strong environmental change, with large, generalist, motile species assumed to have the greatest advantage (Fraimer et al., 2017). While only pertaining to ecological traits, our results also suggest that having a wide latitudinal distribution could have indirectly conferred species an adaptive advantage under changing environments.

4.2. Communities' niche spatio-temporal changes

When combining the CWM traits into a multi-eco-trait indicator

(through the study of the first dimension of the PCAs, Dim. 1) (Fig. 6), contrasting temporal dynamic patterns between Cantabrian and Spanish Mediterranean communities emerged. Cantabrian stations confirmed a generalized 'tropicalization', trending towards an increased predominance of warmer affinities, narrower ranges and distribution areas. Conversely, Mediterranean stations showed an increasing predominance of wider distributions (both in latitudinal and thermal values) hinting for a complex mechanism of temperate communities at accommodating climate change, in which environmentally constrained species are replaced by more cosmopolitan ones. These tendencies are not spatially even in neither area. In Cantabrian Sea, communities along the depth gradient have followed opposite directions. Shallower stations have shifted towards a more thermophilic composition whilst the community associated to the outer continental margin (in the inner Bay of Biscay as well as the Galician margin) was driven towards wider thermal and depth ranges and higher predominance of species with wide distributional range areas. This comes up as expected, since assemblages inhabiting the coastal areas are generally more exposed to climate change impacts than those in the open ocean, either by the quicker exchange of heat from and to the atmosphere or by the increased frequency of exceptional storm events and freshwater runoff from terrestrial flooding (Whiteley et al., 2018; Simões et al., 2021). The community associated to the westernmost area of the Cantabrian Sea (Galician margin) is somehow protected from the loss of its most sensitive species (those less tolerant to environmental changes or already inhabiting their thermal limits), due to not only a more direct contact to a larger water mass, but also to spring and summer upwelling, an oceanographic phenomenon known to soothe the annual warmest extremes in the area (Lavin et al., 2006; Santos et al., 2012). In the Mediterranean region, CWM traits follow a more consistent trend at the local scale, with most sampling stations displaying positive trends and thus undergoing the described change towards species with larger latitudinal ranges and colder temperature affinities. This generalized widening of most distributional ranges in Mediterranean benthic-demersal communities might be yet another sign of the projected reductions in abundances of endemic and native species (Albouy et al., 2013). Despite it being a generalized progression, it also shows some bathymetrical segregation, deep stations in the Catalanian margin and Ibiza Channel show the highest rates of change while at the central Gulf of Valencia there is a cluster of sampling stations where trends are not significant, which pinpoints once again the singularity of this area, where the highest climate warming velocities in the study area take place (Sanz-Martin et al., 2023).

As part of our effort to analyze general patterns of the communities' niche, we have studied large temporal trends in two areas known to have certain heterogeneity in their exposure to external perturbations as well as in their ecosystem structure. Studies that analyze marine communities' niche reorganizations at a more local scale and integrating regional dynamics are still needed and could probably help achieve a more accurate picture of ecosystems' responses to anthropogenic impacts, which is of central importance for adaptive approaches to ecosystem management (Aragão et al., 2022). Our approach attempted at a wide, multivariate look of how environment determines communities' distribution, but our analysis did not directly explore cause-effect relations neither considered fishing pressure as a possible driver of these complex community changes.

In an additional note, we must account for the possible over-interpretation of the results of the PCA, as this is a method in which possible temporal structures of time series (such as non-stationarity or autocorrelation) are not accounted for (Planque and Arneberg, 2018). Also, the studied CWM ecological preferences have proved to be a good indicator of the community dynamics, but they are calculated based only on the most frequent and abundant organisms in the communities, thus not reflecting immediate immigration-extinction dynamics or the entry or leakage of non-indigenous species (NIS), a rare phenomenon in the Cantabrian Sea (Punzón et al., 2016) but quite common in the

Mediterranean region, where the rate of detection of NIS has accelerated after the year 2000 (Coll et al., 2010; Arndt and Schembri, 2015; Marbà et al., 2015).

The ecological indicators studied here might be useful for ecological forecasting. Since climatic predictions for these two areas highly differ, we would expect most indicators to follow different temporal trajectories. On one side, warming in Cantabrian Sea is projected in various RCP/SSP scenarios to slow down due to a debilitating Atlantic meridional overturning circulation (Gierz et al., 2015). Also, the spatial continuity of Atlantic communities might make them more adaptive to changing conditions, i.e., they could sustain a more pervasive effect of global impacts (Shackell et al., 2012; Hidalgo et al., 2017; Polo et al., 2022). Mediterranean Sea perspectives are more severe; it is one of the most responsive regions to climate change and is expected to be affected by many climatic risks along with a warming average of 2.8 °C by 2080–2099 (Albouy et al., 2013; Hidalgo et al., 2022). Mediterranean's marine fauna highly contributes to the world's marine biodiversity through, among others, many endemic species. We encourage further studies that elaborate on the specific effects of this biogeography shifts on taxonomy and biomass dynamics at a species level, and to properly assess the extent of the transition into a 'tropicalized', cosmopolitan community effects, which might already be affecting the ecosystems' functionalities. At a time in which marine ecosystems are increasingly affected by anthropogenic-driven pressures, notably climate change, it is primordial to understand marine community responses to these pressures to better anticipate and mitigate ecosystem changes.

CRediT authorship contribution statement

Julia Polo: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Antonio Punzón:** Conceptualization, Investigation, Methodology, Supervision, Writing – original draft. **Manuel Hidalgo:** Conceptualization, Funding acquisition, Resources, Supervision. **Laurene Pecuchet:** Investigation, Writing – original draft. **Marta Sainz-Bariáin:** Formal analysis, Methodology. **José Manuel González-Irusta:** Investigation, Methodology. **Antonio Esteban:** Data curation. **Encarnación García:** Data curation, Investigation. **Miguel Vivas:** Data curation, Investigation. **Luis Gil de Sola:** Data curation. **Lucía López-López:** Conceptualization, Formal analysis, Funding acquisition, Project administration, Validation, Writing – original draft.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.indic.2024.100421>.

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Julia Polo is a postdoctoral researcher in Quantitative Ecology in the University of Tromsø, Norway. She finished a doctoral thesis on climate change impacts on marine ecosystems at Spanish Oceanography Institute, in a region of northern Spain that looks out into Cantabrian Sea. Before that she dedicated some years to working at sea, learning from fishers in Mediterranean and North-East Atlantic seas and participating in every scientific survey she could embark on in North Atlantic Ocean. Along with the Human Impacts research team at Spanish Oceanography Institute, she became involved in the study of shifting demersal communities in response to diverse fishing pressures and environmental variability. After a period acquiring experience at sampling marine communities, she experienced the complexities of data processing and analysis, and nowadays is a bit further in the path to study the synergistic impacts of climate change and fishing on exploited communities. At present she is very interested in the entry of new species and rearrangement of functional traits in temperate ecosystems, and how they are affecting and will affect the fisheries associated with them. Within her postdoctoral position she keeps on acquiring tools to identify the impacts of climate change in areas as temperate as the Bay of Biscay and as extreme as North Pole. She is also training on the best ways to communicate useful, fair science to the general public, as well as to the rest of the scientific community.