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Trait-Based Indicators of Marine Communities' Sensitivity to Climate Change and Fishing

Julia Polo[1] | Lucía López-López[2] | Georg H. Engelhard[3] | Antonio Punzón[2] | Manuel Hidalgo[4] | Louise A. Rutterford[3] | Marta Sainz Bariáin[2] | José Manuel González-Irusta[2] | Antonio Esteban[5] | Encarnación García[5] | Miguel Vivas[5] | Laurene Pecuchet[1]

[1]Norwegian College of Fishery Science, UiT, The Arctic University of Norway, Tromsø, Norway | [2]Centro Oceanográfico de Santander, Instituto Español de Oceanografía, Santander, Spain | [3]Centre for Environment Fisheries and Aquaculture Science (Cefas), Lowestoft Laboratory, Suffolk, UK | [4]Centro Oceanográfico de Baleares, Instituto Español de Oceanografía, Palma de Mallorca, Spain | [5]Centro Oceanográfico de Murcia, Instituto Español de Oceanografía, Murcia, Spain

Correspondence: Julia Polo (julia.polo@uit.no)

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ABSTRACT

Aim: Overexploitation of wildlife and anthropogenic climate change are key drivers of global biodiversity loss. Investigating how these stressors interact and affect ecosystems is critical for conservation efforts. Following trait-based vulnerability assessments, we propose two community-level sensitivity indicators: climate change (S_{CC}) and fishing pressure (S_{FP}).

Location: Cantabrian and Spanish Mediterranean Sea.

Methods: Both indicators were calculated for 246 fish and megabenthos species, sampled during 1994–2019 in two areas with contrasting levels of warming and fishing pressure. Indicator calculation was based on traits that, according to existing evidence, can be linked to (1) sensitivity to climate change (scored as S_{CC}) and (2) sensitivity to fishing pressure (S_{FP}). Using each species' sensitivity scores, and abundance data from the surveys, we explored whether these areas' community-level sensitivity has changed spatiotemporally in line with the expected functional responses to these predominant pressures.

Results: Although both regions have warmed, the Spanish Mediterranean is far more so. Its community-level S_{CC} has decreased, reflecting a shift in composition from warm-sensitive to warm-affinity species. In contrast, sensitivity dynamics in the Cantabrian Sea varied, with warm-sensitive species increasing in deeper areas and decreasing towards the inner Bay of Biscay. Decreasing fishing pressure in both regions paralleled an increase in sensitivity in the Cantabrian Sea, particularly among slow-reproducing, longer-lived species. The Spanish Mediterranean, however, showed a relative loss of fishing-sensitive, long-lived species and both cases showed spatial heterogeneity.

Main Conclusions: Associations are revealed between S_{CC} and S_{FP}, and climate change and fishing, respectively. We conclude that S_{CC} and S_{FP} are valuable indicators of the community-level sensitivities to these two pressures, and we discuss the limitations and assumptions that underly this and other trait-based approaches. We recommend wider usage of this kind of indicators, which could be applied globally to understand risks of marine communities to climate change and fishing.

1 | Introduction

Overexploitation of marine wildlife in combination with anthropogenic climate change are seen as key drivers of global biodiversity loss. Understanding the mechanisms by which climate change and fishing impact alter marine ecosystems is crucial for biodiversity conservation and sustainable resource management. To this aim, functional approaches, based on species' biological traits, are often used to characterise how vulnerable biological communities are to anthropogenic stressors. The overarching question in the present paper is whether a trait-based approach can be used to assess the sensitivity of marine communities to the impacts of climate change and fishing pressure—two of the most widespread pressures they are subject to.

Trait-based approaches use functional (i.e., nontaxonomic) information about ecological and biological features of each species in a community. These traits can be used to understand the vulnerability of communities to stress, providing a mechanistic basis for community assessments (De Juan et al. 2020). Trait-based assessments of the sensitivity of assemblages to single stressors have been widely applied (De Juan and Demestre 2012; Chessman 2013), as well as to examine their sensitivity to multiple stressors (Butt et al. 2022; Cao et al. 2023), or to address the potential interactions between stressors, which might even exacerbate or buffer their impacts as single stressors (Perry et al. 2010; Möllmann and Diekmann 2012). Here, we apply a trait-based approach to assess marine communities' sensitivities to their two main stressors, climate change and fishing.

Our study draws on the trait-based vulnerability assessment framework (Foden et al. 2013; Bueno-Pardo et al. 2021), which allows a straightforward assessment through three commonly recognised components of a system's vulnerability: exposure, sensitivity and adaptive capacity (IPCC 2007). Trait-based vulnerability assessments focus on the characteristics of the species related to their vulnerability and can be applied at various ecological levels, from populations to species to communities and ecosystems (De Lange et al. 2010; Hare et al. 2016). In an ecological setting, this framework typically starts by determining the sensitivity of species to a given pressure associated with the species' traits, through a predefined scoring system based on a combination of measurable data and/or expert judgement. Once all species' sensitivities to given pressures have been scored, a community-level sensitivity could be quantified by weighting trait scores by the abundance or biomass data for each species (Spencer et al. 2019; Allyn et al. 2020). Ultimately, the community's vulnerability would be understood as a function of its sensitivity, its adaptive capacity and its exposure to the given pressure. This approach has served to build community-level trait-based sensitivity indices to trawling disturbance (De Juan and Demestre 2012; González-Irusta et al. 2018) and to assess the vulnerability of entire ecosystems dependent on habitat-forming species, such as mangroves (Ellison 2015), or fishing communities to climate change (Pinnegar et al. 2019; Townhill et al. 2023).

In recent decades, the marine ecosystems to the northwest of the Iberian Peninsula (Cantabrian Sea) and its east (Spanish Mediterranean) have undergone contrasting levels of fishing pressure and anthropogenic warming. Sea temperatures in both regions have increased, but the Spanish Mediterranean more severely than the Cantabrian Sea, with increasing impacts at various ecological levels in the last two decades (Punzón et al. 2016, 2021; Bode et al. 2020; Chust et al. 2022; Polo et al. 2022). In fact, the Mediterranean's warming rate has been described as two to three times that of global oceans (Vargas-Yáñez et al. 2008; D'Amen et al. 2022). Concurrently, in the Cantabrian Sea, fishing pressure peaked in the 1980s and since then decreased substantially. Following the enforcement of strict fishing regulations in the 1990s, many stocks in this area recovered (Modica et al. 2014; Arroyo et al. 2017). The Spanish Mediterranean Sea has also experienced a decrease in fishing pressure, but it still endures overexploitation of many stocks (Farriols et al. 2019; FAO 2023). Given the different levels of exposure to warming and fishing pressure between the two regions (Aragão et al. 2022), different responses of their marine communities may be expected (cf. Hofstede, Hiddink, and Rijnsdorp 2010). This may also depend on the cumulative, possibly interactive effects of fishing pressure and warming (Punzón et al. 2016; Hidalgo et al. 2017), as well as on the ecological assemblages' structure and functioning (Hidalgo et al. 2022; Polo et al. 2022). Since these aspects ultimately define the communities' vulnerability to shifting conditions, approaches to fully acknowledge communities' response mechanisms are key for the design of effective adaptation and mitigation actions.

Here, we understand sensitivity as the susceptibility of a species' fitness to be negatively affected by a disturbance when exposed to it, as well as the incapacity of a species to avoid said negative effect or recover from it. This study aims to understand how marine communities differently exposed to climate change and fishing respond in terms of their community-level sensitivities. We have approached it by calculating and analysing two trait-based indicators of community sensitivity:

- One indicator describing *sensitivity to climate change*, hereafter referred to as S_{CC};
- and one indicator describing *sensitivity to fishing pressure*, hereafter S_{FP}.

For this purpose, we first identified and compiled traits relevant to the species' sensitivity to each pressure for a wide range of representative species from both communities. Then, we converted trait values to sensitivity scores, indicating low to high or very high sensitivity to warming or fishing pressure (trawling). Finally, we calculated community-weighted mean (CWM) sensitivity indicators to warming and trawling by weighting species' sensitivity scores with species' abundance data from bottom trawl scientific surveys. We studied the annual time series of the communities' exposure to climate change and fishing and the CWM sensitivity for both regional seas, and their spatiotemporal patterns by calculating their temporal change at a fine spatial scale.

To assess if these trait-based indicators indeed reflect the communities' responses to changing sea temperatures and fishing pressure, we test the following hypotheses:

1. The indicator of community sensitivity to *climate change* will negatively respond to increases in sea temperature, given that warming would cause a reduced prevalence of warm-sensitive species, in favour of warm-affinity species;

2. The indicator of community sensitivity to *fishing* will negatively respond to an increase in fishing effort, given that high exploitation levels would lead to reduced prevalence of species with fishing-sensitive traits, in favour of those with fishing-resistant traits.

Finally, we discuss the wider usefulness of the two new multi-trait indicators for sensitivity to climate change and fishing, in these and other marine regions, to describe community-level responses and vulnerabilities to climate change and fishing, along with the limitations and assumptions of the approach.

2 | Methods

2.1 | Study Areas

This study is based on data collected in two demersal scientific surveys, DEMERSALES, in the southern Bay of Biscay (here Cantabrian Sea), and MEDITS, in the Spanish Mediterranean. Both apply a standardised methodology (ICES International Bottom Trawl Surveys; ICES 2017), consisting of a random sampling scheme stratified to the area, with various 'depth strata' and different geographical 'sectors'. The Cantabrian Sea is subdivided into five sectors—Miño River to Finisterre (MF), Finisterre-Estacas Cape (FE), Estacas cape-Peñas Cape (EP), Peñas Cape–Ajo Cape (PA) and Ajo Cape–Bidasoa River (AB)—and five depth strata (< 70 m, 70–120 m, 120–200 m, 200–500 m and > 500 m) (ICES 2017). The Spanish Mediterranean Sea is divided into three sectors—the Southeastern (Cape of Gata–Cape San Antonio; SE), the Gulf of Valencia (Cape San Antonio–Ebro Delta; GV) and the Northeastern (Ebro Delta–Cape of Creus; NE)—and five depth strata (< 50 m, 50–100 m, 100–200 m, 200–500 m and > 500 m) (Bertrand et al. 2002; Arroyo et al. 2019). These sectors are referred to in the map figures by their acronyms. The units of sampling in both regions are bottom trawl hauls of 30 min at 3 knots with standard 'baca' otter trawl gear. The net opening is 18.9 m horizontally and 2 m vertically in the DEMERSALES gear and 19.5 and 2.5 m, respectively, in the MEDITS survey. Species caught at each haul are identified taxonomically, weighed, counted and measured in length. In our analyses, we used density (number of individuals of a species) per haul standardised by the swept area, that is, number of individuals/km^2. While the Cantabrian demersal communities have been sampled every autumn in the DEMERSALES survey since 1983, the Western Mediterranean survey programme samples the benthic and demersal communities every spring since 1994, for comparison we thus restricted the study period to 1994–2019.

2.2 | Species Selection

The total number of species sampled over the study period was over 680 in the Cantabrian Sea and 620 in the Western Mediterranean. Among these, many species only occurred sporadically in the dataset, not allowing meaningful spatial or temporal analyses. Therefore, only a subset of species was retained; the criteria for species selection were three filters based on the visual inspection of accumulation curves outlined in Sáinz-Bariáin et al. (n.d.). The three filters applied to remove rare or low-abundance species within each survey were as follows: (i) The species had to be present in at least 12 years, then (ii) only species present in at least 12 hauls per year were included and finally, (iii) species with an abundance value under the first decile (of abundance data for the whole time series) were also excluded. The filtering resulted in a subset of 246 species that constituted the basis for subsequent analyses, 182 in the Cantabrian region and 197 in the Mediterranean (Table S1).

2.3 | Exposure—Stressors Dynamics

We analysed the communities' exposure to both climate- and fishing-related hazards by studying the spatiotemporal variation in warming and (bottom) trawling pressure. As a proxy for warming, we analysed temporal and spatial dynamics of sea surface temperature (SST), which we consider provides a broad, climate-relevant indicator, particularly for species with pelagic early life stages, and reflects changes that ultimately affect demersal communities (Rijnsdorp et al. 2009; Puerta, Quetglas, and Hidalgo 2016; Hidalgo et al. 2018). SST data came from the oceanic physics reanalysis product 'Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis', generated by CMEMS IBI-MFC (for a detailed description, see Sotillo et al. 2016). The model produced daily mean SST for the period 1994–2019 with a 0.05° spatial resolution, which we aggregated to 0.2° and then averaged to annual values per latitude/longitude of the 3294 sampling stations of the Cantabrian region and the 2177 of the Spanish Mediterranean region. As a proxy for trawling pressure, we used data on pair and otter trawling effort derived from vessel monitoring systems (VMS) and fishing vessel logbooks, provided by the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA). Data were aggregated to the total of annual hours of trawling activity per c-square per year (0.05°latitude × 0.05°longitude), in line with ICES VMS methodology (Hintzen et al. 2012), and covered the period 2009–2019 for the entire North Atlantic and 2010–2019 for the Mediterranean Iberian Coast. VMS is a satellite-based monitoring system that provides information related to the position of fishing vessels, which when combined with information from logbooks allows the estimation of the hours spent actively fishing in a given year at a given location, excluding time spent 'in route', 'searching' and 'drifting' (Punzón et al. 2016). To visually inspect the spatiotemporal trends of the communities' main stressors, we fitted linear regression models of SST and VMS data for each of the five depth strata in every geographical sector (five geographical sectors in the Cantabrian region and three in the Spanish Mediterranean). The slopes of the models were mapped with function stat_summary_hex in R package ggplot2 (Wickham 2016). The overall temporal dynamics of the stressors were explored using stat_smooth function in the same R package, with the display argument 'geom = smooth' (Wickham 2016).

2.4 | Traits Database

We selected (a priori) species traits to characterise the species according to their sensitivity to fishing and climate change based on previous studies (see Table S2 and first column of

TABLE 1 | Biological traits and ecological preferences used to characterise sensitivity to climate change (warming). The last six traits are numerical and were categorised by dividing the continuous variables into quantiles.

Sensitivity to climate change				
Trait	**Low sensitivity (Score = 1)**	**Moderate sensitivity (Score = 2)**	**High sensitivity (Score = 3)**	**Very high sensitivity (Score = 4)**
Spawning period	Nonseasonal (≥ 9)	Wide spawning season (3–8)	Narrow spawning season (≤ 3)	
Parental care	Guarder brooder, guarder bearer	Nonguarder planktonic lay	Nonguarder	Nonguarder benthic lay
Habitat	Pelagic, Bathypelagic	Demersal, Bathydemersal	Benthic, Suprabenthic	
Surface T^e affinity	> 20°C	15°C–20°C	≤ 15°C	
Bottom T^e affinity	> 13°C	10°C–13°C	≤ 10°C	
Surface T^e specificity (STS)	> 16°C	12°C–16°C	< 12°C	
Bottom T^e specificity (BTS)	> 23°C	19°C–23°C	< 19°C	
Mean depth affinity	> 200 m	95–200 m	< 95 m	
depth specificity	≤ 750 m	750–1300 m	≥ 1300 m	

Tables 1 and 2). We selected 12 life-history traits related to reproduction, growth and feeding to reflect species' sensitivity to fishing pressure, and 9 ecological and reproductive traits related to thermal, depth and habitat preferences and reproductive behaviour to reflect species' sensitivity to climatic changes. The traits were compiled for the most recurrent 246 species in the community at the lowest possible taxonomic level. The information was gathered from online databases, namely, WoRMS, BIOTIC (MarLIN 2006), FishBase (Froese and Pauly 2022), SeaLifeBase and PANGAEA (Beukhof, Dencker, and Palomares 2019), and diverse sources ranging from general handbooks to specialised papers. In total, more than 200 scientific publications were reviewed for this aim (see anonymised, *submitted for publication*).

In the database, each trait value was accompanied by the taxonomic rank for which it was retrieved, its reference and the available information on revised literature (anonymised, *submitted for publication*). Due to a lack of information on many traits for a large set of species (data do not exist or are not published), we assigned the mean value (or most frequent category for categorical traits) of that trait for the genus, if available, or else for the most immediate taxonomic category with information available for the trait in the trait database.

The set of six ecological traits was obtained from the bioclimatic envelope models developed by AQUAMAPS (Kaschner et al. 2019) and presence data from the Ocean Biogeographic Information System database (OBIS 2019). The mean depth and the depth range of species distribution were estimated based on the global species presence records (OBIS 2019) and the digital bathymetry provided by EMODNET (http://www.emodnet-bathymetry.eu). This approach was preferred over the depth data provided by AQUAMAPS, as EMODNET provided a better resolution, which is essential in regions with steep depth gradients such as our study regions. After the bibliographical review and the estimation of the missing features, a total of 3634 trait values were gathered with their corresponding taxonomic rank and only 71 taxa/species could not be assigned. Within the database, 73.5% of the traits were associated at the species level.

2.5 | Sensitivity Assessment

Based on previous literature, the trait categories were scored according to the sensitivity to each of the pressures they conferred on the species. The categories and their corresponding sensitivity scores to climate change (warming) and fishing (trawling) are summarised in Tables 1 and 2, respectively. We categorised the continuous variables by dividing them into quantiles to create groups with similar number of observations, a technique well supported by literature (Foden et al. 2013; Carr, Hughes, and Foden 2014; Böhm et al. 2016; González-Irusta et al. 2018).

While some vulnerability assessments separate the adaptive capacity attributes from those related to sensitivity, we considered both components together, following Hare et al. (2016). In general terms, due to the acceleration of metabolism (driven by increasing temperatures) and the selective extraction of the biggest organisms in the population (by fishing), scientific literature associates an increase in warming and/or fishing pressure, with decreases in longevity, body size, age at first maturity and trophic level and an increase in growth rates and fecundity, which correspond to faster life strategies (e.g., Beukhof, Frelat, and Pecuchet 2019; Wang et al. 2020).

TABLE 2 | Biological traits used to characterise sensitivity to fishing (trawling) pressure. The first seven traits are numerical and were categorised by dividing the continuous variables in quantiles.

Sensitivity to fishing pressure				
Trait	**Low sensitivity (Score = 1)**	**Moderate sensitivity (Score = 2)**	**High sensitivity (Score = 3)**	**Very high sensitivity (Score = 4)**
Longevity	< 5 years	5–10 years	> 11 years	
Body size	Small < 20 cm	Medium 20–50 cm	Large > 50 cm	
Fecundity	> 200,000 eggs	12,000–200,000 eggs	< 12,000 eggs	
Offspring size	> 1.5 mm	0.8–1.5 mm	< 0.8 mm	
Growth coefficient	$K > 0.60$	$K = 0.20–0.60$	$K < 0.20$	
Trophic level	Low trophic levels (< 3)	Intermediate trophic levels (3–4)	High trophic levels (> 4)	
Age at maturity	< 2 years	2–3 years	> 3 years	
Parental care	Nonguarder planktonic lay, Nonguarder	Nonguarder demersal lay	Guarder brooder (external care)	Guarder bearer (internal care)
Habitat	Pelagic, Bathypelagic	Demersal, Bathydemersal	Benthic, Suprabenthic	
Motility	Swimmer	Burrower, Crawler	Sessile	
Body shape	Fusiform	Eel-like, Elongated, Bullet-like	Flat, Lenticular	Globular, Compressiform, Hook shaped
Feeding mode	Scavenger, Generalist (including piscivorous), Detritivorous	Planktivorous	Surface deposit feeders, Benthivores, Suprabenthic feeders	Suspensivorous, Suspension feeders

Several traits that were first considered as contributing to the species' sensitivity to the pressure(s) were excluded from the final indicator, trait lists (Tables 1 and 2), due to inconsistent categorisations in the literature (e.g., body size and fecundity were excluded from the climate change sensitivity trait list; see references in Table S2).

We visually inspected the distribution of trait categories across levels of the two stressors categorised in levels of equal numbers of observations, using histograms (Figures S1 and S2). This enabled an overview of the structure of the response of the studied communities' traits to different degrees of intensity of the temperature and trawling effort.

Then, we computed the sensitivity of each species by calculating the mean sensitivity value across the different traits that characterised the species' functional niche. The mean sensitivities to trawling and climate change (separately) were computed for each species following the equation:

$$\text{Sensitivity}_s = \frac{\sum \text{Sensitivity}_{\text{TRAIT}n}}{N}$$

where *Sensitivity* would be the sensitivity score of the species *s* to either climate change or trawling, $\text{Sensitivity}_{\text{TRAIT}n}$ is the sensitivity value of each (*n*) trait responding to that stressor for a given species (s) and *N* is the total number of traits responding to the stressor.

To have a general overview of how species distribute in the 'sensitivity space' (S_{CC} as *x*-axis and S_{FP} as *y*-axis) and identify species particularly sensitive or resistant to climate change and fishing pressure according to our criteria, the species were plotted according to their sensitivity scores rescaled between 0 and 1.

After this, we calculated the sensitivity at the community level. To do so, the sensitivity obtained for each species was weighted by the abundance of each species in each sampling station, therefore estimating a sensitivity value for each sampling station, following the formula:

$$\text{Sensitivity}_{\text{Pressure}} = \frac{\sum \text{Sensitivity}_s \times \text{Density}_s}{\text{Density}_{\text{Total}}}$$

where $Sensitivity_{PRESSURE}$ to either 'Fishing Pressure', 'S_{FP}', or 'Climate Change', 'S_{CC}', is the community's weighted mean sensitivity at a given sampling station (located in a particular longitude/latitude and year), and $Density_s$ is a species density in number/km^2 at that sampling station. $Dens_{TOT}$ would be the sum of the individual densities of every species at that given sampling station. This way, each species' sensitivity would be weighted by its relative abundance, therefore making the final sensitivity values comparable in space and time.

To visually explore the temporal trends of the communities' sensitivities, we fitted, for each region, general additive models (GAMs; Hastie and Tibshirani 1990) to the sensitivity values (S_{CC} and S_{FP}) of every sampling station performed each year, using the stat_smooth function in R package ggplot2 (Wickham 2016) with the argument 'method = gam', limiting the degrees of freedom of the smoothers to 4 to avoid overfitting. Then, we analysed spatiotemporal patterns of the stressors (temperature and fishing) and the sensitivity indicators (S_{CC} and S_{FP}). To better capture finer-scale spatial variations in exposure and response, we aggregated the sampling stations' according to their depth strata and geographical sectors (including only aggregations with at least 10 sampling stations). For all groups of samples (23 in the Cantabrian region and 15 in the Mediterranean), linear regressions were performed to obtain the annual rates of change in the stressors and in the communities' sensitivity in each (i.e., the regressions' slopes).

3 | Results

3.1 | Climate and Fishing Pressure: Trends in the Exposure

Over the 1994–2019 study period, mean annual SST in the Spanish Mediterranean Sea increased significantly (linear regression, $p \leq 0.001$), on average by 0.04°C ± 0.006°C per year (mean change ± SE; Figure 1). By contrast, in the Cantabrian Sea, mean annual SST also varied (between 15.5°C and 16.4°C), but the trend was not significant over the study period (linear regression, $p = 0.26$; 0.006°C ± 0.005°C per year). At a finer spatial scale, the areas that warmed most are located along the Mediterranean (Figure 2), the Northeastern sector (NE in Figure 2), showing slightly higher warming; within the Cantabrian Sea, warming was highest towards the inner Bay of Biscay and least towards the outer Galician margin.

Pair and otter trawling efforts have overall decreased in both areas during 2009/2010–2019 (linear regression, Cantabrian Sea: $p = 0.0009$; mean change ± SE = −7.86 ± 1.62 h per c-square per year; Spanish Mediterranean Sea: $p = 0.04$; mean change −15.6 ± SE 6.21 h per c-square per year). At a finer spatial scale, the only exceptions were two areas where fishing pressure remained at similar levels for the whole period: the inner Bay of Biscay (Figure 2) and the Gulf of Valencia towards the south of the Western Mediterranean region. In general, fishing showed higher spatial heterogeneity than warming.

3.2 | Species' Sensitivities to Climate Change and Fishing Pressure

An assessment of the 246 species' sensitivities to climate change (S_{CC}) and their sensitivities to fishing pressure (S_{FP}) revealed a slight statistically significant correlation between the two indicators (Figure 3) (Pearson's $r = 0.22$, df = 243, $p = 0.0007$). Species of different phyla were mixed across the 'climate and fishing pressure sensitivity space'. Based on our sensitivity scores, certain species emerged as particularly sensitive or resistant to climate change, fishing pressure or both. Atlantic electric ray *Tetronarce nobiliana* and marbled electric ray *Torpedo marmorata* emerged as having the highest sensitivity to fishing ($S_{FP} = 1$), although not to climate change ($S_{CC} < 0.5$). Forty-five species were categorised as 'resistant' to both

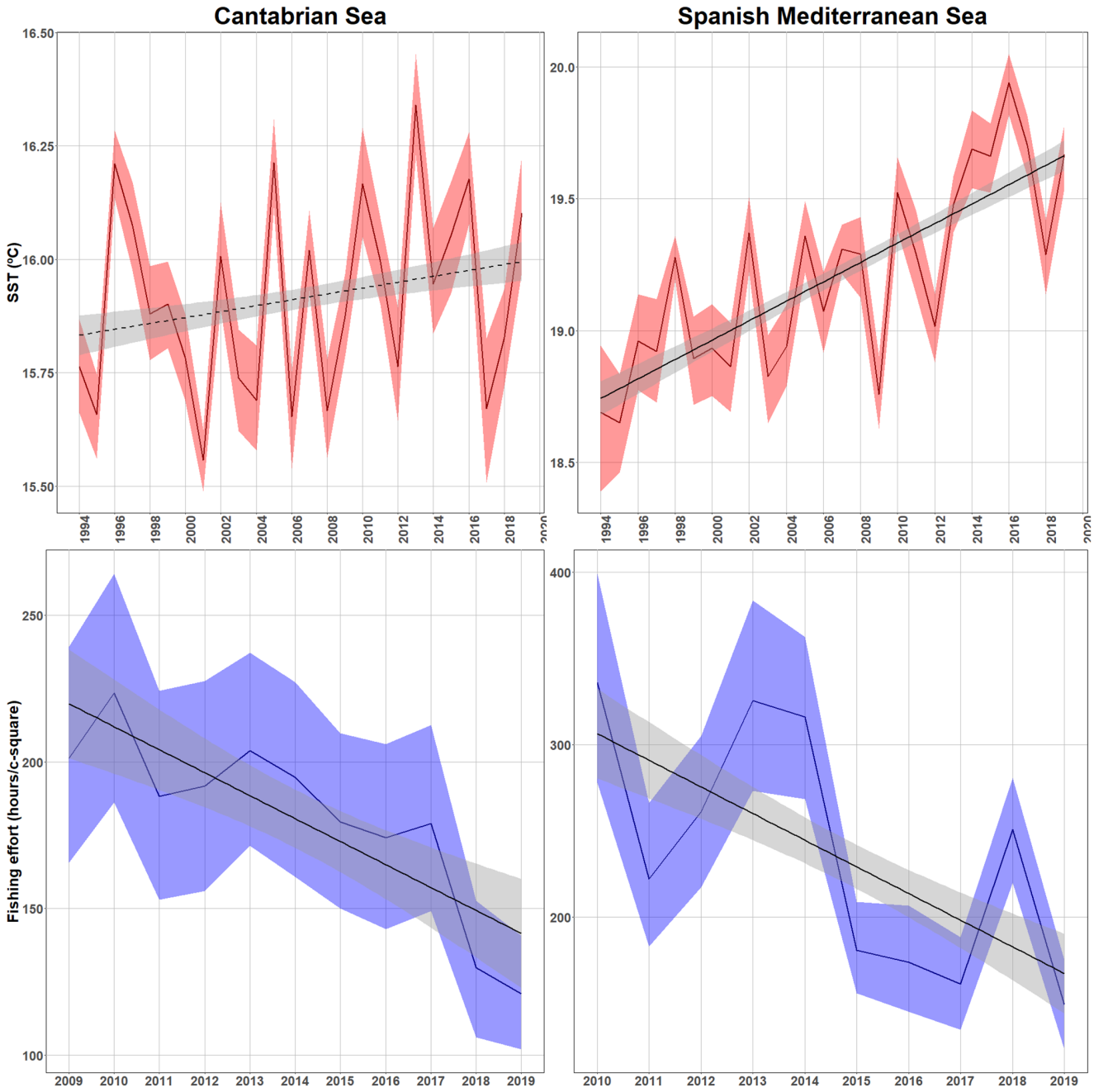

FIGURE 1 | Temporal variability of the two main system stressors, temperature (SST) (top) and fishing pressure (based on VMS data of the period 2009/2010–2019) (bottom). The dark-red line and dark-blue line represent the mean annual SST and fishing effort (expressed as hours fished per grid cell of c-square, 0.05°×0.05°), respectively, for all sampling stations for each region. Shaded envelopes represent the 95% confidence intervals across all stations in a given year. Continuous black lines were added to visualise general significant linear trends with grey-shaded confidence intervals, while the dashed line represents a nonsignificant linear tendency. A summary of the results of the linear regressions can be found in Table S3.

pressures (i.e., $S_{CC} < 0.5$ *and* $S_{FP} < 0.5$); assessed as most resistant among these were two fish species (anchovy *Engraulis encrasicolus* and pearlsides *Maurolicus muelleri*) and two squid species (*Illex coindetii* and *Abralia veranyi*) with both $S_{CC} < 0.3$ and $S_{FP} < 0.3$. The species assessed as most 'sensitive' to both pressures was the tunicate *Corella parallelogramma* (with $S_{CC} = 1$). Two species of pelican's foot snail (*Aporrhais pespelecani* and *Aporrhais serresiana*), rabbit fish *Chimaera monstrosa* and megrim *Lepidorhombus whiffiagonis,* had also high values of sensitivity to climate change.

3.3 | Community-Level Sensitivity to Climate Change and Fishing Pressure

At the community level, the two indicators, S_{CC} and S_{FP}, displayed high interdecadal variability in both areas (Figure 4). In the Cantabrian Sea, communities' sensitivity to climate change, S_{CC}, and fishing pressure, S_{FP}, showed contrasting patterns, almost opposite. S_{CC} declined during 1994–2002, whereas S_{FP} increased, peaking around 2005. Then, S_{CC} increased, reaching a peak at the beginning of the 2010s, with the trend reversely

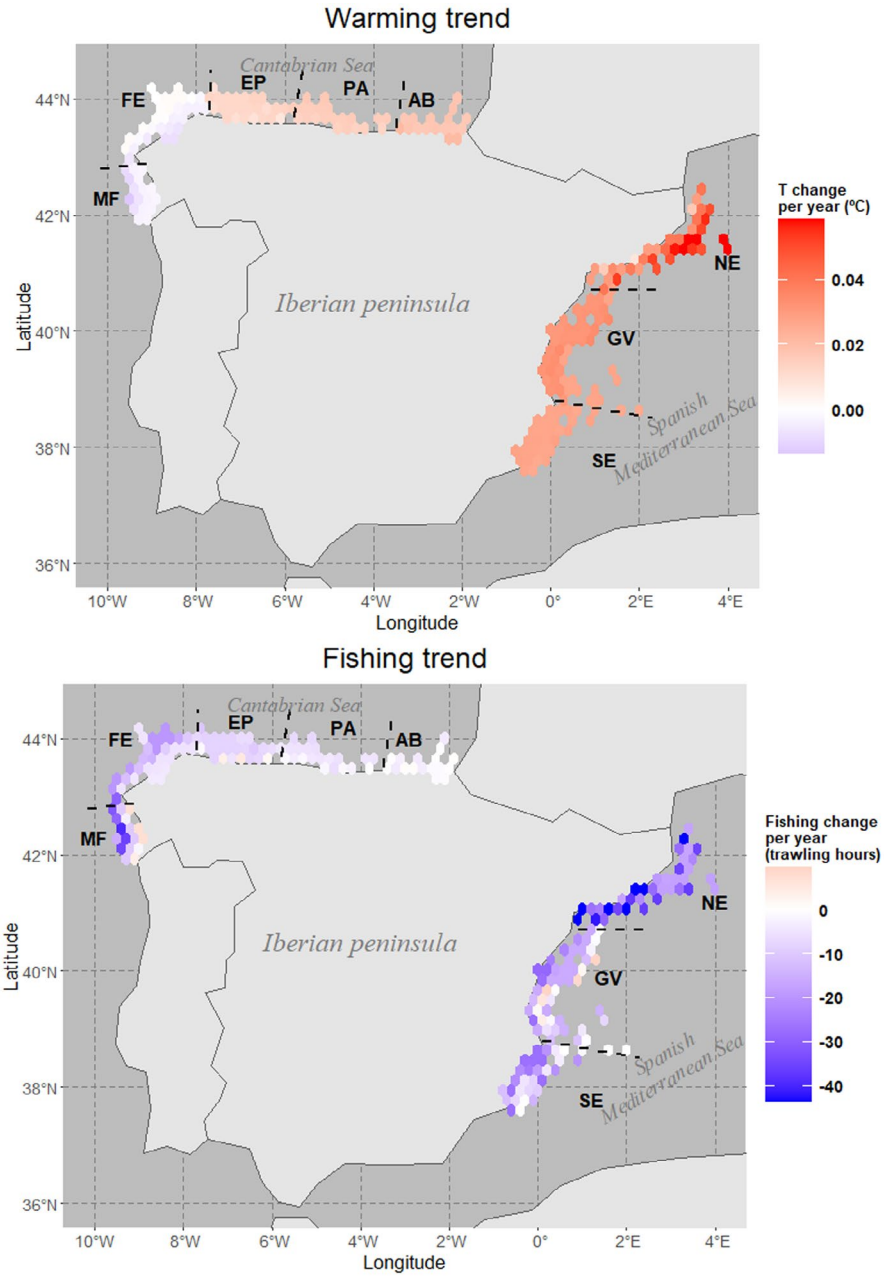

FIGURE 2 | Spatial patterns of change in mean annual SST (top) and fishing pressure (lower panel). In general, the Spanish Mediterranean region has undergone higher warming (dark red areas) than the Cantabrian region (light red, blue and white). In the spatiotemporal representation of fishing pressure, darker grid cells correspond to areas with pronounced decreases of otter and pair trawling effort, and light blue, white and light red areas are subregions in which tendencies are close to 0 or even slightly positive. The geographical sectors' initials are explained in the Material and Methods section of the text.

mirrored by S_{FP}. In the Spanish Mediterranean Sea, the communities' sensitivity to both stressors declined similarly until the beginning of 2000s. After 2000, S_{CC} stabilised and S_{FP} continued to decline albeit at a lower rate.

When assessing spatial variation in rates of change in communities' sensitivity, we found that the sites where community-level sensitivities decreased most, in terms of both warming and fishing, were along the Spanish Mediterranean coast (Figure 5). Within this region, S_{CC} decreased most steeply in the central area (Gulf of Valencia, Sector GV in Figure 5). Highest increases in S_{CC} were further south (Sector SE). Within the Cantabrian Sea, the deepest regions (> 500 m depth) experienced clear increases in S_{CC}. The sector with higher S_{CC} slope values for every of its depth strata is the northernmost sector (EP in Figure 5). By contrast, towards the inner Bay of Biscay (Sector AB), S_{CC} generally decreased.

Rates of change in S_{FP} in the Mediterranean region were more spatially homogeneous in terms of latitude than those of S_{CC}, with steeper decreases in S_{FP} in the shallowest strata. The two easternmost Cantabrian subregions (PA and AB sectors) showed decreases in S_{FP} in their shallowest strata, and towards the east and south, communities showed increases in S_{FP}.

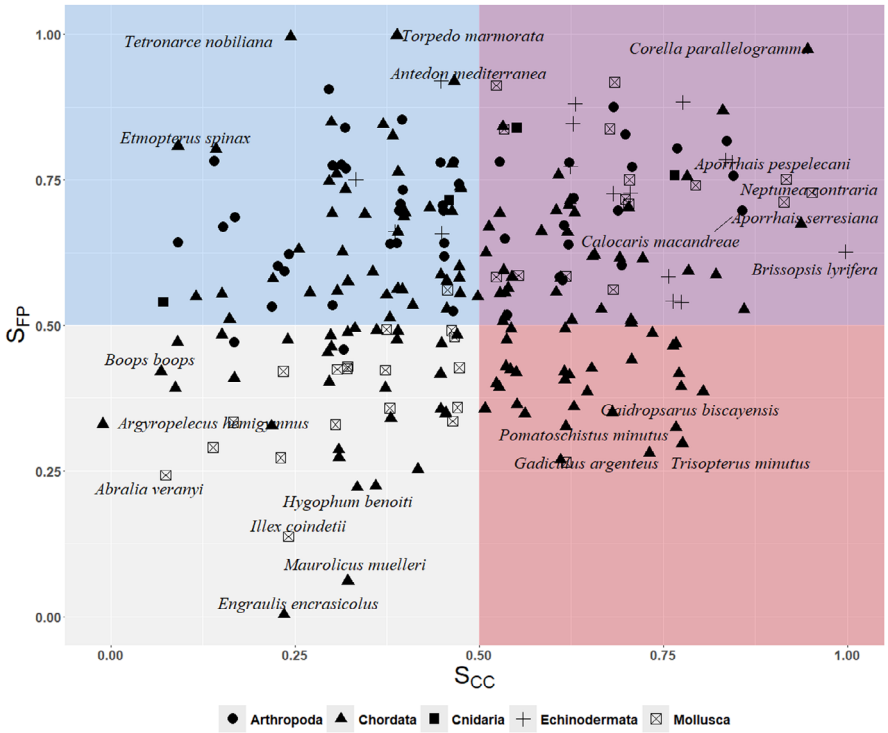

FIGURE 3 | Species position in the 'sensitivity space', where the *x*-axis and *y*-axis represent sensitivity to climate change (S_{CC}) and to fishing pressure (S_{FP}), respectively. Species belonging to different phyla are represented by different symbols following the bottom legend, and the background colours (or quadrat positions) correspond to the different levels of sensitivity: White (lower left quadrant) containing species 'resistant' to both pressures (i.e., $S_{CC} < 0.5$ and $S_{FP} < 0.5$); red (lower right quadrant), species 'resistant' to fishing pressure but 'sensitive' to warming; blue (upper left quadrant), species 'sensitive' to fishing but 'resistant' to warming; and purple (upper right quadrant), species 'sensitive' to both pressures (i.e., $S_{CC} > 0.5$ and $S_{FP} > 0.5$).

In the Spanish Mediterranean, where SST increased and S_{CC} decreased, there was a strong negative correlation between the two variables' trends across all locations (Spearman's correlation: $r_s = -0.77$, $p < 0.01$). In the Cantabrian Sea where neither the trend in S_{CC} nor in SST was significant, changes in these two variables were not correlated (Spearman's correlation: $r_s = -0.1$, $p = 0.63$). Neither region showed a significant correlation between the time trends of fishing pressure and those of S_{FP} (Spearman's correlation: Cantabrian Sea: $r_s = 0.21$, $p = 0.35$; Spanish Mediterranean: $r_s = 0.24$, $p = 0.39$). However, average fishing pressure was significantly, negatively correlated with S_{FP} in both areas (Cantabrian Sea: $r_s = -0.08$, $p = 0.002$; Spanish Mediterranean: $r_s = -0.32$, $p < 0.001$). Average fishing pressure was also negatively correlated with change in S_{FP} in the Spanish Mediterranean ($r_s = -0.63$, $p < 0.013$) although not in the Cantabrian Sea ($r_s = -0.33$, $p = 0.12$). The correlation coefficients and p-values are also summarised in Table S4.

4 | Discussion

In two regions to the northwest and east coastal shelves of the Iberian Peninsula, two trait-based indicators of sensitivity (S_{CC} and S_{FP}) revealed contrasting responses of the marine communities in terms of their sensitivities to climate change and fishing exploitation. This study also evidenced geographic gradients in the system's exposure to these stressors. By contrast, S_{CC} and S_{FP} showed how both communities have undergone a clear turnover in terms of the prevalence of sensitive species, closely following the systems' two main stressors dynamics. Not only do these results illustrate how communities changed with regard to the abundances of species sensitivity to warming and trawling pressure but they also revealed particular 'inflection points' in the early 2000s that appear to coincide with ecological regime shifts previously detected in both areas related to environmental changes and shifts in fishing effort (Hidalgo et al. 2022; Polo et al. 2022, 2024).

In line with the two hypotheses raised by this research, the trends and patterns of the communities' sensitivity appeared to respond to changes in temperature and fishing efforts in both regions. The prevalence of species classified as sensitive to warming and fishing pressure has changed since the 1990s. For example, in the Cantabrian Sea, the indicators of sensitivity to climate change and fishing showed contrasting patterns with maxima and minima that matched in time. Between 1994 and the early 2000s, these communities experienced an increase in prevalence of species sensitive to fishing, paralleled by a decrease in those sensitive to warming. During this period, various fish stocks in the Cantabrian Sea were in a recovery phase, following overexploitation during the 1980s (Guénette and Gascuel 2012; Arroyo et al. 2017). The effects of fishing on marine communities tend to exhibit certain delays (Modica et al. 2014), but since we expected S_{FP} to be able to capture this recovery, if not showing immediate responsiveness to it, the spatiotemporal dynamics of S_{FP} should mirror those of fishing effort. Also, although it impacts

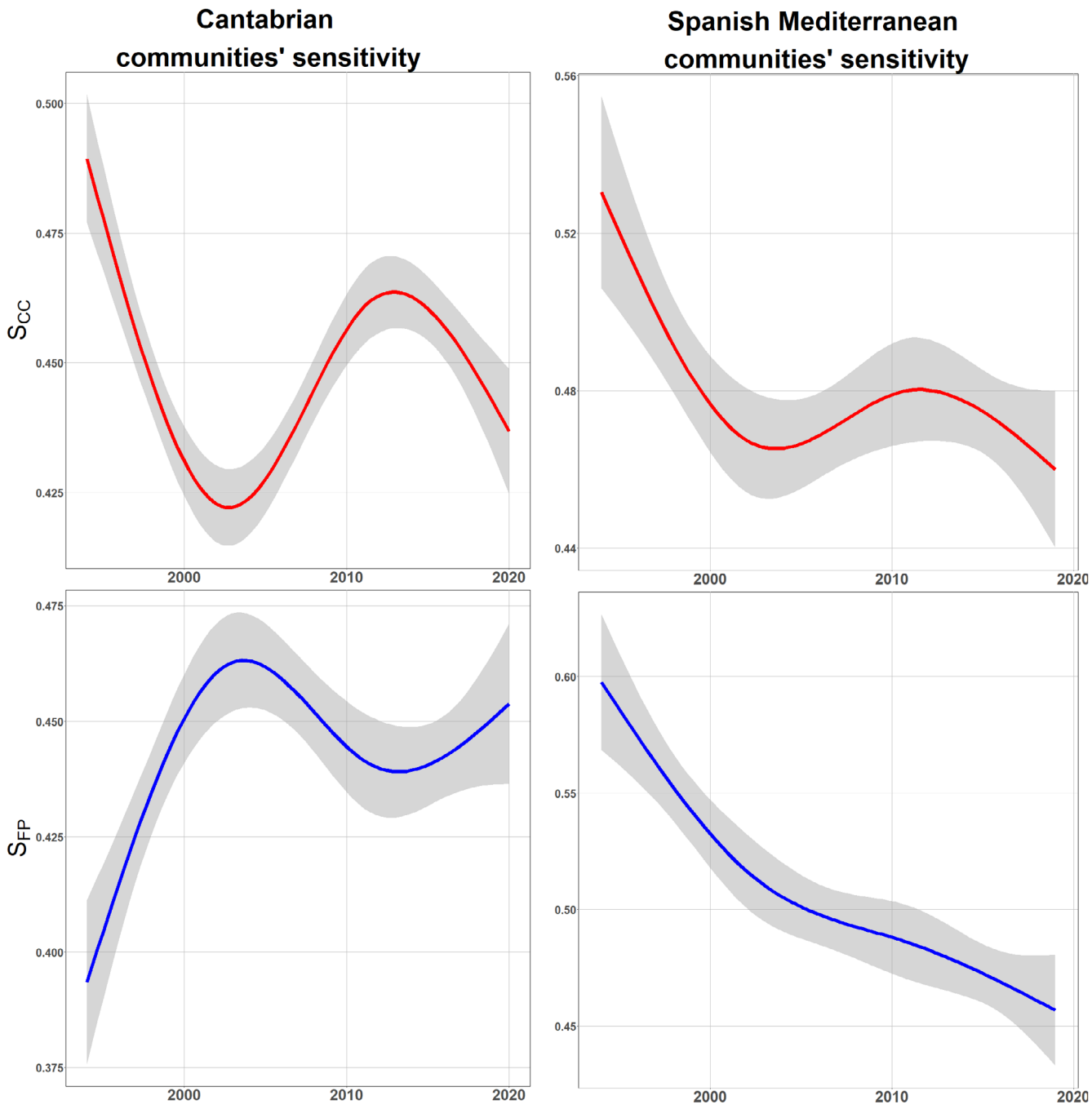

FIGURE 4 | Changes in community-level sensitivity to climate change, S_{CC} (top plots, red line), and community-level sensitivity to fishing pressure, S_{FP} (bottom plots, blue line), in the Cantabrian Sea (left column) and Spanish Mediterranean Sea (right column). Shaded areas represent 95% confidence intervals.

bentho-demersal communities as a whole, high fishing pressure usually implies selective removal of species with slower life histories (e.g., larger, long-lived and higher age at maturity; De Juan, Thrush, and Demestre 2007; Planque et al. 2010; Pecuchet et al. 2017), and this has been demonstrated for the Cantabrian Sea (Modica et al. 2014; Hidalgo et al. 2017). On these points, our study shows that following the implementation of stricter fisheries regulations in the Cantabrian Sea (Modica et al. 2014; Arroyo et al. 2017; González-Irusta et al. 2018; Serrano et al. 2022), communities indeed experienced a large recovery in sensitivity towards fishing pressure, as demonstrated by increased S_{FP}. This was followed by fluctuations in S_{FP} around 2010, but the region generally maintained high sensitivity values until 2019.

By contrast, the S_{CC} of communities in the Cantabrian Sea fluctuated, initially decreasing between 1994 and the early 2000s, then rising until the early 2010s, after which it dropped again. This could be reflecting how rising temperatures challenge the sustainability of climate-sensitive species (e.g., cold-affinity species with short spawning seasons, no parental care and narrower, more specific depth and temperature preferences). While at the scale of our study, we did not find a strong warming signal in the Cantabrian Sea, other studies have revealed a warming

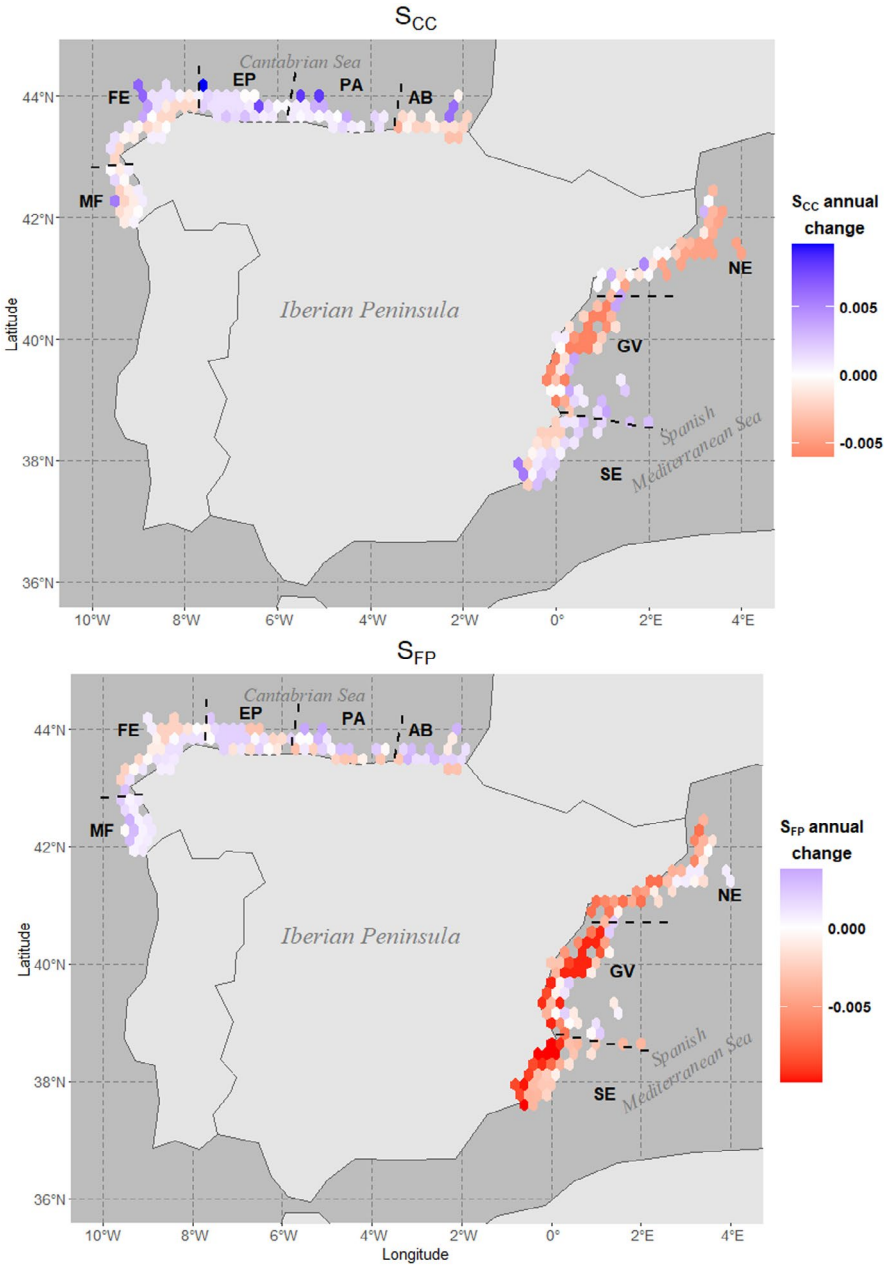

FIGURE 5 | Spatiotemporal variation of sensitivity to warming (upper map) and sensitivity to trawling (lower map). The communities with negative trends of sensitivity scores, in red, have undergone a decrease in the relative abundance of sensitive traits, while in communities with positive trends, represented as blue hexagons, sensitive traits' contribution has increased.

trend in the last decades (at a rate of 0.10°C–0.25°C per decade; Chust et al. 2022). The relative loss of climate-sensitive species in the area is less evident than in Mediterranean communities, likely associated with these and other differences in the regions' stressors dynamics. A sound interpretation of these community-level sensitivity patterns needs to account for possible trade-offs in the traits' responses to warming and fishing, at species (Rademaker, van Leeuwen, and Smallegange 2024) and community level. Such trade-offs might explain that, across all species, S_{CC} and S_{FP} were not fully independent, but showed some degree of correlation (Figure 3), despite the considerable variation within the 'sensitivity space'. Although the final selection of traits structuring each indicator ultimately resulted in a limited overlap between them, a partial correlation would still be expected in a natural context, where change in one stressor (e.g., reduced fishing pressure, affecting S_{FP}) might indirectly affect the sensitivity indicator for the other stressor (e.g., S_{CC}). Also, fishing's selectivity has a very direct impact on community composition (Planque et al. 2010; Guénette and Gascuel 2012) and thus on community-weighted traits, but some properties of the communities such as inertia, hysteresis or lagged responses can mask the extent of other stressors' impacts (Friberg et al. 2011). Temperature often interacts with other pressures (Hewitt, Lundquist, and Ellis 2019) and its effects are often nonlinear (Hsieh et al. 2005; Burkett et al. 2005; Vasilakopoulos et al. 2017) due to cumulative nonlinear species-specific responses to warming (Lindmark, Karlsson, and Gårdmark 2023). Changes in the prevalence of sensitive species may be better understood if both

stressors were considered together (in an additive manner or accounting for possible synergistic or antagonistic interactions).

In Spanish Mediterranean waters, communities showed clear decreases in both S_{FP} and S_{CC}, indicating reduced prevalence of species sensitive to either fishing or warming, reflecting the generalised shift in community composition in the region (Hidalgo et al. 2022). S_{FP} generally decreased while S_{CC} initially decreased and plateaued after the early 2000s. The stabilisation of S_{CC} in the later part of the time series in this region may indicate a community that progressively responded to warming through increased domination of warm-affinity species, at the expense of the more specialist, stenotherm and/or having narrower niche widths. Such relative loss of sensitive species, or 'flexibilitation' of the communities, has been described as a coping mechanism in situations of environmental instability (Sexton et al. 2017) and has been previously associated with communities in this region (Farriols et al. 2017; Polo et al. 2024). The decline in S_{FP} documented here aligns with studies that raised awareness of a still heavy fishing impact on assemblages in the Western Mediterranean Sea (Farriols et al. 2017; FAO 2018).

Within each region, finer-scale spatial distributions of community-level sensitivity to climate change were coherent with local hotspots of warming: within the Cantabrian Sea, towards the inner Bay of Biscay (Chust et al. 2022); and within the Spanish Mediterranean Sea, located centrally in the Gulf of Valencia and towards the Northeast. The Gulf of Valencia, in particular, is seen as a 'local maximum of warming', where climate trajectories tend to originate and diverge to the North and South (Sanz-Martin et al. 2024); accordingly, this subregion appears to be inhabited by communities with particularly high bottom thermal affinities (Polo et al. 2024). The subregion to the north of the Spanish Mediterranean (i.e., the Gulf of Lion), however, was depicted in our study as a subregion occupied by communities with a moderate level of sensitivity to climate change and fishing, despite this area having been defined as a 'cul de sac' for climate migrants (Ben Rais Lasram et al. 2010; Burrows et al. 2014). This unexpected outcome might be due to the Gulf of Lion acting as a climatic refuge for cold-water species (Sabatés et al. 2006). On another note, the spatiotemporal heterogeneity in the indicator of sensitivity to warming in the Cantabrian region, contrasting with the more homogeneous process of warming, could be related to a methodological issue if the selection of traits used for S_{CC} were in fact responsive to both fishing and climate or other stressors or ecological processes not accounted for in this study, such as upwelling, which is known to highly influence this subregion's communities (Bode et al. 2009; Santos et al. 2012). Moreover, communities in the Galician margin and westernmost Cantabrian Sea have experienced significant increases in the relative contribution of species sensitive to fishing, which is consistent with the generalised recovery of the communities from fishing (Modica et al. 2014; Arroyo et al. 2017).

In the studied communities, our scoring system identified species highly sensitive to both warming and fishing the tunicate *Corella parallelogramma*, the sea snails *Aporrhais pespelicani* and *A. serresiana* (the latter specially sensitive to climate change) and the chondrichthyan *Chimaera monstrosa*, a species inhabiting deep and cold waters and considered highly vulnerable (De Juan et al. 2020) and classified 'Near Threatened' on the IUCN Red List (Dulvy et al. 2021). The flatfish *Lepidorhombus whiffiagonis* (megrim) also had high values of sensitivity to climate change. This cold-affinity species is expected to decrease in abundance in future warming scenarios (Maltby et al. 2020) and has already decreased in biomass in the Cantabrian region (Punzón et al. 2016). Highest scoring in sensitivity to fishing pressure ($S_{FP}=1$) were *Tetronarce nobiliana*, a top predator and largest species in the electric ray family Torpedinidae (Mulas et al. 2021), and the greater weeverfish *Trachinus draco*, which, however, had S_{CC} values below 0.5 (the latter corroborating low vulnerability to climate change as found by Bueno-Pardo et al. 2021). At the other end of the sensitivity spectrum, various widely distributed squid species including *Abralia veranyi*, *Illex coindetii* and *Histioteuthis reversa* scored low in sensitivity and hence may be considered resistant species; so did *Octopus vulgaris*, a species previously assessed as relatively tolerant to fishing and environmental impacts (González-Irusta et al. 2018; Bueno-Pardo et al. 2021), and two small pelagic fishes, *Maurolicus muelleri* (cold affinity) and *Engraulis encrasicolus* (previously identified as having low vulnerability to climate change, related to high adaptive capacity: Bueno-Pardo et al. 2021).

The traits selected for the computation of our indicators were intended to capture different features of species directly related to their vulnerabilities to climate change and fishing. Within this selection, approximately half of the trait categories responded to the different levels of pressure as expected (Figures S1 and S2). For example, most life-history traits responded as expected to changes in fishing pressure, such as 'Feeding mode' and 'Motility'; or the 'Body shape' category 'sessile, compressiform, globular or hook shaped', which was less abundant in areas with high trawling effort. However, the other half of the trait categories did not follow our literature-based expectations, mainly those of the ecological traits (e.g., species with narrower thermal ranges were more abundant in warm areas or species with higher mean SST of affinity appeared more in low-temperature hauls). Some of these responses can be related to concrete ecological dynamics that may not fully support the general assumptions on which we based our scoring system. One example of this could be the lower sensitivity to warming of warm-affinity species, which has proven not to be universal, suggesting that low-latitude species could be most vulnerable to warming since they live closer to their thermal optima (Rummer et al. 2014; Payne et al. 2016). Another plausible explanation for the apparently contradictory direction in the response of some of these traits is that we might not be anticipating (or identifying) nonlinearities in the response to the stressor. Previous studies have sometimes revealed dome-shaped relationships between a pressure and one or more traits, where trait values peaked at intermediate levels of the pressure. This was the case with the trait 'Recruitment' in response to wind turbulence (Ottersen et al. 2010), and with the traits 'Growth', 'Body length' and 'Lifespan' in response to temperature (Beukhof, Dencker, and Pecuchet 2019). In addition, if a threshold in the trait–stressor relationship has not been reached or (in case of already degraded ecosystems) if the threshold is located at much lower levels of pressure than the ones we are studying in our time series, with the methods applied here we will not observe the expected direction of the pressure's effect

on the trait categories. Following previous trait-based species and community assessments (Hare et al. 2016; González-Irusta et al. 2018; Bueno-Pardo et al. 2021), this degree of variability in the trait–stressor relationship did not halt us from including these traits to calculate indicators of sensitivity.

Furthermore, we applied a rigorous categorisation (or ranking) of continuous traits, such that sensitivity categories contained a similar number of observations. However, accounting for intrinsic ecological thresholds in the categorisation of some traits could be more adequate, or even exploring continuous sensitivity values, thus accommodating the continuous nature of some trait data. In this study, for example, we categorised the trait 'Depth Range' in <750 m, 750–1300 m and >1300 m, but attributing different sensitivity levels to species inhabiting the coastal zone from those of the wider continental shelf, continental slope and the deep ocean could be also done (Sanz-Martin et al. 2024). Another alternative approach could be to classify communities according to the species' ecological affinities through clustering techniques (Punzón et al. 2021). In this respect, we suggest that depending on the study region and communities being investigated, different thresholds may be appropriate for categorising individual traits. For example, in the 'Fecundity' trait as categorised here, the level most sensitive to fishing included species with relatively low fecundity, producing $<12{,}000$ eggs annually; however, this differs from other studies: Pecl et al. (2014), in their 'rapid assessment of fisheries species sensitivity to climate change', set a threshold for their most sensitive category at species producing <100 eggs annually; while Bueno-Pardo et al. (2021) applied a threshold of <1000 eggs. These differences could affect the final output of an assessment, but its reliance on multiple traits and considering context-dependent trait responses can reduce the risk of inaccurate results.

Further efforts in understanding traits' responses to their environment may help resolve cases where contradictory scorings were found in literature. For example, species' 'Habitat position' within the water column has been inconsistently regarded in terms of climate change sensitivity; some authors considered pelagic species more sensitive than benthic species, which have access to thermal refugia (Burrows et al. 2019; Chaudhary et al. 2021), while others considered high mobility in pelagic species to be advantageous, with the ability to exploit the entire water column and avoid extreme events (Pinnegar et al. 2019; Le Marchand et al. 2020; Bueno-Pardo et al. 2021). Preliminary studies on the direction of the trait response as well as on the different influence (i.e., weight) traits may have on a communities' eventual response, specific to the community under study, could provide additional confidence in the scoring system.

This trait-based assessment of the sensitivities of two communities with different exposure to climate change and fishing was a first attempt to study these biological communities' responses to their two most important external drivers. While it is known that exploitation may interact with warming in influencing populations' vulnerability (Möllmann and Diekmann 2012; Free et al. 2019), in our approach we did not examine any interacting effects on traits' responses. Ignoring potential interactive effects of warming and fishing pressure on exploited ecosystems may be inaccurate, ultimately leading to inefficient conservation strategies (Kath et al. 2018). However, together with vulnerability assessments at different ecological levels (species, functional group, stock level, etc.), this study complements existing information on the challenges raised by climate change and human exploitation of marine ecosystems. The indicators proposed in our study can potentially be applied as monitoring metrics to assess marine communities' response to pressures, and even allow the detection of early-warning signals, supporting the consolidation of the trait-based vulnerability framework to ultimately inform regional actions of ecosystem-based management.

5 | Conclusion

We conclude that the two indicators proposed here—describing community-level sensitivity to climate change (S_{CC}) and fishing pressure (S_{FP})—are appropriate to describe how marine communities respond to these two pressures. The study evidenced associations between trends and patterns in S_{CC} and S_{FP}, and climate change and fishing, respectively. We outline the limitations and assumptions that underlie this and other trait-based approaches. Given that climate change and overexploitation of marine communities are among the most pervasive threats to marine wildlife globally, we recommend wider exploration of this methodology and indicators. In principle, the framework could be applied to any marine community with available traits data, to understand the sensitivities and risks of marine life to climate change and fishing.

Author Contributions

J.P., L.L.L., A.P., M.H. conceptualized the study, analyzed the data and interpreted the results; L.L.L., A.P. and M.H. conducted the funding acquisition and L.L.L. lead the project in which the study was originally designed; J.P., G.H.E., L.A.R., M.S.B. and J.M.G.I. contributed to the methodological approach, formal analyses and revision of results; A.E., E.G. and M.V. carried the data curation; L.P. coordinated and supervised the study; J.P. wrote the first draft of the manuscript and lead its revision; all authors were part of the writing and validation of the last version of the revised manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in OSF repository at https://osf.io/72vhk/?view_only=e2be7e9acb0d48dbba5dc367078d4ff5.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13959.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.