

Environmental and anthropogenic driven transitions in the demersal ecosystem of Cantabrian Sea

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In the framework of global human-induced change, marine communities' often respond to changing conditions abruptly reorganizing into new equilibria. These shifts are difficult to predict and often imply irreversible adjustments due to hysteresis. Unraveling the role of the forces leading regime shifts is a major challenge. We explored the temporal evolution of 63 fish species representing the Cantabrian benthic-demersal community in response to environmental changes and fishing pressure in the period 1983–2018, using survey data. Via multivariate analysis and non-additive modeling of a community index and the system's main stressors, two decadal-scale regimes were revealed, suggesting a non-linear response of the community to its environment. The Integrated Resilience Assessment framework elucidated the response mechanism to the candidate stressors and allowed quantifying resilience dynamics. The decline in fishing pressure in the 1990s was associated with a gradual transition of the system, while further decline during the 2000s eroded the resilience of the system towards changes in its stressors, leading to a discontinuous response expressed as an abrupt, possibly irreversible shift in the 2010s. Given the teleconnected character of marine ecosystems, this regional study endorses the scientific effort for actions facing the dynamic impacts of climate change on exploited marine ecosystems.

Keywords: Cantabrian Sea, climate change, demersal community, fishing pressure, Integrated Resilience Assessment (IRA), multivariate analysis

Introduction

Natural systems often fluctuate around an average state dependent on the stability and/or variability of its external conditions. Such “stable states” refer to dynamic regimes with a defined range of deviations from an attractor over time (Scheffer and Carpenter, 2003; Vasilakopoulos and Marshall, 2015). Whether the system exhibits a smooth continuous reaction to changes in its stressors or if, at some point, abruptly shifts from its main tendency and basin of attraction, is a major management and conservation concern, as it determines the timing for the enforcement and extent of regulatory measures for preventing undesirable impacts in habitats and communities inhabiting them.

The development of a methodological framework for the study of abrupt shifts, also referred to as “critical transitions”, (Scheffer et al., 2009; Möllmann and Diekmann, 2012 and references therein; Vasilakopoulos et al., 2017) has been used to define the mechanisms of natural systems' response to their stressors, with an emphasis on detecting non-linear behaviours that may lead to the alternation of different ecological regimes once a critical threshold or tipping point is exceeded. A critical or utility threshold is the point in an ecological system at which small changes in environmental conditions produce substantial change (Samhuri et al., 2010, 2017). In recent years, many wide-scale sudden shifts in several biological and environmental systems of northeast (NE) Atlantic have been reported, attributed to a range of factors, both climatic and anthropogenic (Choi et al., 2005; Weijerman et al., 2005; Möllmann et al., 2009; Vasilakopoulos and Marshall, 2015). Hence, it comes as a relevant management issue to clarify whether a change of pattern in the structure

and function of an ecological community is due to a natural intrinsic variability or represents the non-linear amplification of stochastic physical forcing (Deyoung, 2008), often fostered by anthropogenic impact.

Until the mid-2000s, the upper layers of NE Atlantic acted as a main heat storage basin, but at that point, driven by extraordinary convective mixing events, the heat and salt gained slowly over the years, started being passed on to deeper levels and stored in the deeper ocean (Balmaseda et al., 2013; Somavilla et al., 2016). This trend went on until the mid-2010s, when salinity trends were reversed accompanied by above average temperatures (Lavín et al., 2020). As a general display of global warming in the area, Cantabrian Sea exhibited an increase in intermediate waters temperature and salinity during the period 1992–2003 (González-Pola et al., 2005). Over the periods 1978–1982 and 2003–2007, the temperature increase reached up to 0.8–1°C (Tasker, 2008). Cantabrian Sea corresponds to the subtropical boreal transition subprovince between the Atlantic boreal and the northern subtropical subprovinces, thus, life in this marine area may be highly sensitive and respond rapidly to small shifts in climate (Blanchard, 2005).

Furthermore, the temperate character of Cantabrian Sea has favoured the development of important mixed demersal fisheries mainly engaged on pair and otter trawling (Abad et al., 2010; Castro et al., 2010; Punzón et al., 2010). As a consequence of increasing effort and capacity, a generalized regime of stocks depletion was reached around the late-80s, which led to decreases in catches and yields of the traditionally exploited species, similar to those observed in other fishing grounds (Worm et al., 2009). However, due to the pro-

gressive implementation of fisheries management in the Atlantic Iberian waters within the framework of ICES (yearly TAC limits on landings and quotas (Castro et al., 2012), the 2002 reform of the EU's Common Fisheries Policy (Fernandes and Cook, 2013) and regional-specific management actions (Abad et al., 2010)), a rapid decline in landings reflected a recovery in species associated with demersal–benthic habitats (Fernandes and Cook, 2013; Modica et al., 2014; Fernandes et al., 2017; Hidalgo et al., 2017; Arroyo et al., 2019; Preciado et al., 2019).

Recent research has reported numerous alterations in the structure and function of Cantabrian Sea's ecosystem, some related to wide-scale climatic changes—mainly increasing temperatures (Perry et al., 2005; ICES, 2008; Tasker, 2008; Punzón and Villamor, 2009; Punzón et al., 2016; Punzón et al., 2020) and other to regional scaled anthropogenic stressors—such as the retirement of high levels of fishing pressure (Modica et al., 2014; Arroyo et al., 2017; Arroyo et al., 2019), as well as to their combined or synergistic effects. These studies hinted on the various scales at which either single or combined stressors have impacted Cantabrian Sea's ecosystem, but none has yet acknowledged the ecosystem's thresholds and resilience dynamics, which we stress as ecological features determinant when taking any management actions.

With the aim of contributing to the understanding of the concurrent effects of environmental and anthropogenic forces on complex natural systems, this study analyses a temperate demersal community's main tendencies and response to its main potential stressors. Through univariate and multivariate methods, as well as the application of an Integrated Resilience Assessment (IRA) (Vasilakopoulos and Marshall, 2015; Vasilakopoulos et al., 2017) on biomass estimates from a scientific survey, we argue that additive effects of anthropogenic pressures such as fishing and sea warming have eroded the resilience of this complex natural system, making it more vulnerable to abrupt shifts. In particular, a combination of continuous and discontinuous response mechanisms to fishing have been key to the evolution of the Cantabrian Sea's biological system in the last 40 years.

Material and methods

Study Area

Cantabrian Sea (NE Atlantic) is located between the Bay of Biscay and Atlantic Iberian waters (see Supplementary Figure S1 of Appendix 3 in Supporting Information). While it is often treated as a compact system in terms of geological, climatic, and ecological features, it can be understood as the union of two distinct subareas: on the eastern side, the southern Bay of Biscay, and on the western side, the Galician waters or Iberian Atlantic area. Given, it comprises a very heterogeneous environment and represents a subtropical/boreal transition zone, typical temperate-water species occur together with those of northern origin (Sánchez Olaso, 2004), including many species of commercial interest.

A weak circulation pattern in comparison with the main currents in the NE Atlantic basin (Blanchard and Vandermeersch, 2005) and east component winds in spring and summer, which favor the appearance of upwelling, stand out as the main environmental patterns in the Bay of Biscay. The most important upwelling phenomena are found in the western area, in the waters of Galicia, and they decrease in inten-

sity to the east. Upwelling events and the Iberian Poleward Current (IPC, also known as “Navidad” current) are the most common and important hydrographic events in Galicia and the Cantabrian Sea, both showing high seasonal and interannual variability (Koutsikopoulos and Le Cann, 1996), while NAO (North Atlantic Oscillation index) and EA (Eastern Atlantic pattern) act as the leading modes of variability for the whole eastern North Atlantic Central Waters and are known to affect marine populations of the European seas (Quinzán et al., 2020).

Data

To represent the biotic dimension of the ecosystem, a set of 63 fish species was selected from the Demersales survey data bank. This standardized bottom trawl survey (ICES International Bottom Trawl Survey Working Group, IBTSWG) provides data since 1983 and keeps sampling the area every autumn (September–October), except for 1987. It follows a stratified random sampling scheme, with five geographical sectors and five depth strata, in which sampling stations are selected randomly from 5×5 nautical miles rectangles, the number of hauls per stratum being proportional to the surface area available for trawling (ICES, 2017). The sampling unit consists on bottom trawls of 30 min at 3 knots, using a standard “baca” 44/60 otter trawl gear with 10 mm cod-end mesh size. The mean horizontal and vertical opening of the net for the whole series under study is 18.9 and 2.0 m, respectively. Catch processing and sorting are done following the IBTS procedures: species are sorted to species level, each species catch is weighed and a representative sample counted. Instead of using species abundance information (number of individuals), in our analyses we used biomass (in grams) per haul standardized by swept area (i.e. g km^{-2}), to avoid giving a disproportionate weight to small and abundant species compared to larger and less abundant species. To avoid misidentifications and possible misestimates, we selected those species that were at least identified in 30 hauls out of the average 126 hauls conducted yearly (Punzón et al., 2016).

In the year 2013, the sampling vessel used in the survey was replaced, and despite the calibration operations between the new and the old vessel, the gear used in 2013 had a heavier footrope that entailed a more benthic catch (higher catchabilities for many benthic species). However, since 2014, the gear geometry was recalibrated, so from then on the survey data are coherent with the values reached previously (ICES, 2021). After testing for it, we found the results of our study were not majorly affected by 2013's data, so we present analyses based on the complete series. Species that are typically associated with the pelagic environment (e.g. anchovy, mackerel, etc.) were removed from the analyses to avoid possible biases caused by changes in catchability independent of sampling. In order to reduce the effect of outliers and homogenize the scale of the biological variables, each biomass value was standardized by subtracting the species mean and dividing it by the species standard deviation over the whole time series (Z-scores standardization).

With the aim of identifying the main stressors and mechanisms affecting the demersal ecosystem, 13 variables were explored (Supplementary Table S1 and Figure S2). The final set of variables was selected based on the following criteria: length of the covered period, representativeness for a specific ecosystem component or a specific driver, and low correlation

with other variables (Supplementary Figures S2 and S3). A Redundancy Analysis (RDA I in the following section) on the species and abiotic data sets also served the purpose of avoiding correlated and collinear variables (Möllmann et al., 2009). Since the abiotic variables showed different scales, they were standardized by means of function `decostand-standardize`, which standardizes values to zero mean and unit variance, in R package `vegan` (Oksanen et al., 2019). The final abiotic environment of the Cantabrian Sea is represented by four stressors: two regional hydroclimatic variables (annual mean sea surface temperature—SST—and salinity below the winter mixed layer—SBwML—), one global index (NAO index), and one variable that acts as proxy for fishing pressure (F_{com}), all of them are described below.

Weekly satellite-derived sea surface temperature data (OISST, <https://www.ncdc.noaa.gov/oisst>) from 1983 to 2018 have been used to obtain annual SST averaged values for the two main subareas (Galician margin and Bay of Biscay) i.e. mean SST was calculated for each $1^\circ \times 1^\circ$ grid in the subarea, and the averaged value for the whole are in the corresponding year calculated. SST was used as a proxy of the effect of surface temperature variability on demersal sources. Annual mean temperatures are increasing as a consequence of warming occurring especially during summer months (Borja et al., 2019).

To account for physical events that have taken place at mid-layers in the area (Balmaseda et al., 2013; Somavilla et al., 2016; Lavín et al., 2020), the annual average salinity at a depth between 300 and 600 m was calculated, excluding from this average the surface mixed layer depth affected by strong seasonality. The climatological maximum winter mixed layer in the area is within a depth of 250 m, and so we named this variable “SBwML”. Salinity data to calculate this index was obtained from salinity profiles from the ocean reanalysis (ECMWF Ocean Reanalysis System 4, ORAS4) (Balmaseda et al., 2013). The ORAS4 reanalysis provides monthly temperature, salinity, current, and sea level data at 42 pressure levels from 5 to 5000 m with higher vertical spacing towards the bottom and a spatial resolution of $1^\circ \times 1^\circ$.

Data for the main pattern of atmospheric variability in the Euro-Atlantic sector, NAO and winter NAO indexes, were provided by the Climate Analysis Section, National Center for Atmospheric Research (NCAR). The NAO has been previously considered to best explain variability in community composition and ecological regime shifts (Attrill and Power, 2002; Alheit et al., 2005), as have other large scale patterns of variability (e.g. the Atlantic Multidecadal Oscillation—AMO—, the Pacific Decadal Oscillation—PDO—, or El Niño-Southern Oscillation—ENSO—) (Newman et al., 2016; Bode et al., 2020). These global teleconnecting patterns are related by means of pantropical interactions and modulate one another (Cai et al., 2019; Zhang et al., 2019), so when discussing NAO's influence on the studied area, we are indirectly referring to the variability of other global climatic patterns.

As an approximation to the community removal rate, we used the assemblage-averaged fishing mortality (F_{com}). We followed Modica et al.'s (2014) approximation to obtain the region specific F_{com} , based on five commercial species data: *Lophius piscatorius*, *Lo. budegassa*, *Merluccius merluccius*, *Lepidorhombus boscii*, and *Le. whiffiagonis*. Therefore, to better inform target setting under the Marine Strategy Framework Directive (MSFD), we used the MSY reference points,

$F_{s,msy}$ for each species. F_{com} was calculated as

$$F_{com, Y} = \frac{\sum_{s=1}^5 F_{s,Y} / F_{s,msy}}{5},$$

where $F_{s,Y}$ is the fishing mortality estimates for each species in year Y, and $F_{s,msy}$ is each species maximum sustainable yield (MSY) reference point. The species reference points and annual stock assessment were downloaded from R package `ices-SAG` (Millar et al., 2019).

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

Data analysis

The biological time series had annual resolution and covered the periods 1983–1986 and 1988–2018. Data for the missing year, 1987, were filled with the average of 1986 and 1988 in order to have an even spacing between annual mean estimates (Moellman et al., 2009).

We applied multivariate analysis methods proposed in the Integrated Ecosystem Assessment (IEA) framework (Moellmann et al., 2009; Möllmann and Diekmann, 2012; Levin and Möllmann, 2015). The purpose of the first section of the study was to better understand the general trends of the demersal community, simplify it and look for potential regime shifts. A heatmap helped visualize the biotic system's temporal evolution, while Principal Components Analysis (PCA) was used to identify general trends on the time series and create a composite system variable, PCsys, the first principal component, which reduced the complexity of the species biomass data. Chronological clustering and sequential *t*-test analysis of regime shifts (STARS) were used to compare outcomes with the multivariate analyses results and contrast them with the previously detected patterns.

For a better understanding of the system's response to its main stressors, in the second section, we applied an RDA, and fitted additive and non-additive models on each system (PCsys)–stressor relationship following the approach of the IRA framework (Vasilakopoulos and Marshall, 2015; Vasilakopoulos et al., 2017). The IRA also allowed the estimation of the resilience dynamics of the studied community through the construction of a folded stability landscape.

Regime shift identification

We visualized the temporal biomass trends of each species in the data set reducing the data complexity into a heatmap. In it, species annual mean biomass data were categorized into quintiles and ordered according to their preferred temperature (as a proxy for the temperature affinity of the species). The preferred temperature index was estimated following the methodology described by Punzón et al. (2020) and trends were analysed using linear regression on R statistical language (R Core Team, 2021).

PCA (Zuur et al., 2007) allowed for a preliminary detection of system's shifting trends expressed as deviations from the mean values of the data. This simplification technique does not clarify any mechanisms of the system's response to changes in its environment. The main outputs of PCA are the principal components (PC scores or eigenvectors), which, plotted against time, show the underlying pattern of a specific component, and thus, if and when a sudden change occurred (Weijermann, 2005). Also, the PCA es-

timates the loadings of the species, i.e. the extent to which the original variables (in this case species) are related to the principal components. When performing this analysis, we focused on the variability between years and whether it was possible to establish different profiles or clusters. Two years would be close to each other if the relative contribution of the species' biomass were similar. It also allowed us to summarize the biomass data into an index or composite variable that could subsequently be analysed against the abiotic drivers.

We selected the environmental and anthropogenic stressors to be used in further analyses through an analysis of the covariates correlation jointly with a RDA. The RDA is a constrained version of PCA that models response variables as a function of explanatory variables and quantifies its associations (Zuur, 2007). It was selected as the proper constrained multivariate analysis after carrying a Detrended Correspondence Analysis (DCA), which produced the length of gradient of the ordination axis that hinted on the use of either a linear ordination technique (such as RDA and PCA), when the length was <3 , or unimodal (such as the Correspondence Analysis, CA) when it was higher (Hill and Gauch, 1980; Lepš and Šmilauer, 2003). The function for DCA is included in R package *vegan* (Oksanen et al., 2019). RDA was performed on the species data set and an initial abiotic dataset, consisting of 13 explanatory variables (Supplementary Table S1). The implementation of RDA for this purpose (RDA I) is described in Appendix 1 in Supporting Information.

As part of the effort to identify possible shifts of tendency in the survey data, instead of a typical clustering technique, which could ensemble non-successive years, we applied a chronological clustering to our biomass data (Legendre et al., 1985), a clustering variation that runs on ordered successive samples like time series. For this, after creating a similarity matrix combining samples into clusters, based on a permutation test and pre-defined significance and connectedness levels (Legendre et al., 1985), we used the Constrained Incremental Sums of Squares ("coniss" method, Grimm, 1987) as agglomeration method.

We also applied the STARS (Rodionov, 2005) to the biotic composite variable (PCsys), extracted from the biotic data PCA, as well as on the final selection stressors (see below). This method estimates a Regime Shift Index (RSI), i.e. a cumulative sum of normalized anomalies relative to each value of the time series analysed, and uses it to confirm or reject the null hypothesis of a regime shift at that year (Rodionov, 2006). Here, we set the cut-off length, the time scale in which shifts are detected, at 15 years and did the RSI estimation at a probability level p of 0.05, accounting for red noise through Ordinary Least Squares (OLS). The 3.2 version of this regime detection tool was downloaded from <http://www.beringclimate.noaa.gov/regimes>.

System–stressor relationship

Once the final environmental and anthropogenic stressors were singled out, a second RDA (RDA II) provided a preliminary visualization of the stressors connection to the evolution of the time series. To study the goodness of fit, RDA II adjusted R -squared (adj- R^2) fit was calculated. R -squared measures the amount of explained variation, but it tends to "reward" the inclusion of many explanatory variables, so the adjusted R -

squared served as an unbiased version of this regression statistic.

The IRA framework builds on the study of the multivariate development of natural systems proposed in the IEA by applying non-additive modeling on the system–stressor couple and quantifying ecological resilience to build stability landscapes (explained in detail in the section "Resilience assessment"). In the IRA framework, the relationship between PCsys and its drivers is assessed using PCsys as response variable in generalized additive models (GAMs) and threshold-GAMs (TGAMs) (Cianelli et al., 2004). Each of the four stressors with 0, 1, and 2 years of lag were used as explanatory variables in separate models. Testing potential lagged effect of the stressors was designed to detect a potential delayed response of the sampled biomass by species. GAMs are models that assume additive and stationary relationships between the response and explanatory variables while TGAMs are GAMs adjusted to account for abrupt changes in the response mechanism (Ciannelli et al., 2004). The basic GAM function used is included in R package *mgcv* (Wood, 2011). The "genuine" cross-validated squared prediction error (gCV), a modification of generalized cross validation proposed by Cianelli et al. (2004) that makes the goodness of fit of GAMs and TGAMs comparable, was computed for model selection and estimation of the threshold year. The optimal most explicative model was selected between every GAM and TGAM of PCsys' response to its stressors as well as the composite stressor variable with 0, 1, and 2 years of lag. When the biotic–abiotic system relationship was found to be non-stationary, the threshold year was identified by minimizing the gCV after running the model for every possible threshold years (Vasilakopoulos et al., 2017).

Following Jolliffe and Cadima (2016) and Weijerman (2005), the PCA and RDA were conducted based on the correlation matrix instead of the covariance coefficients. We used functions *PCA* and *rda* in R packages *FactoMineR* (Lê et al., 2008) and *vegan* (Oksanen et al., 2019), respectively.

Resilience assessment

The methodology for the resilience quantification and folded stability landscape estimation is based on the theory of critical transitions (Scheffer et al., 2001; Van Nes and Scheffer, 2007; Scheffer et al., 2009) and the related implementation within the IRA framework (Vasilakopoulos and Marshall, 2015; Vasilakopoulos et al., 2017). The fitted lines or branches of the optimal model (see the section "System–stressor relationship") in terms of both gCV and adjusted- R^2 were considered as the attractors of the system. Resilience for every year (t) was then estimated as the sum of two components: $vComp$, the vertical component, measured along the system axis as the negative distance from the attractor, and $hComp$, the horizontal component, measured along the stressor axis as the distance from the tipping point (Vasilakopoulos and Marshall, 2015). $vComp$ and $hComp$ are related to the resistance and precariousness of the system, respectively (Walker et al., 2004). Resilience at a given year was therefore estimated as $Res_t = vComp_t + hComp_t$.

The greater the Res_t estimate is, the further away from a "hilltop" the system lies, being less likely for it to shift to an alternate basin of attraction, conversely, at a tipping point, Res_t would be zero. The folded stability landscape was subsequently constructed through linear interpolation of all Res_t values onto a 100×100 grid.

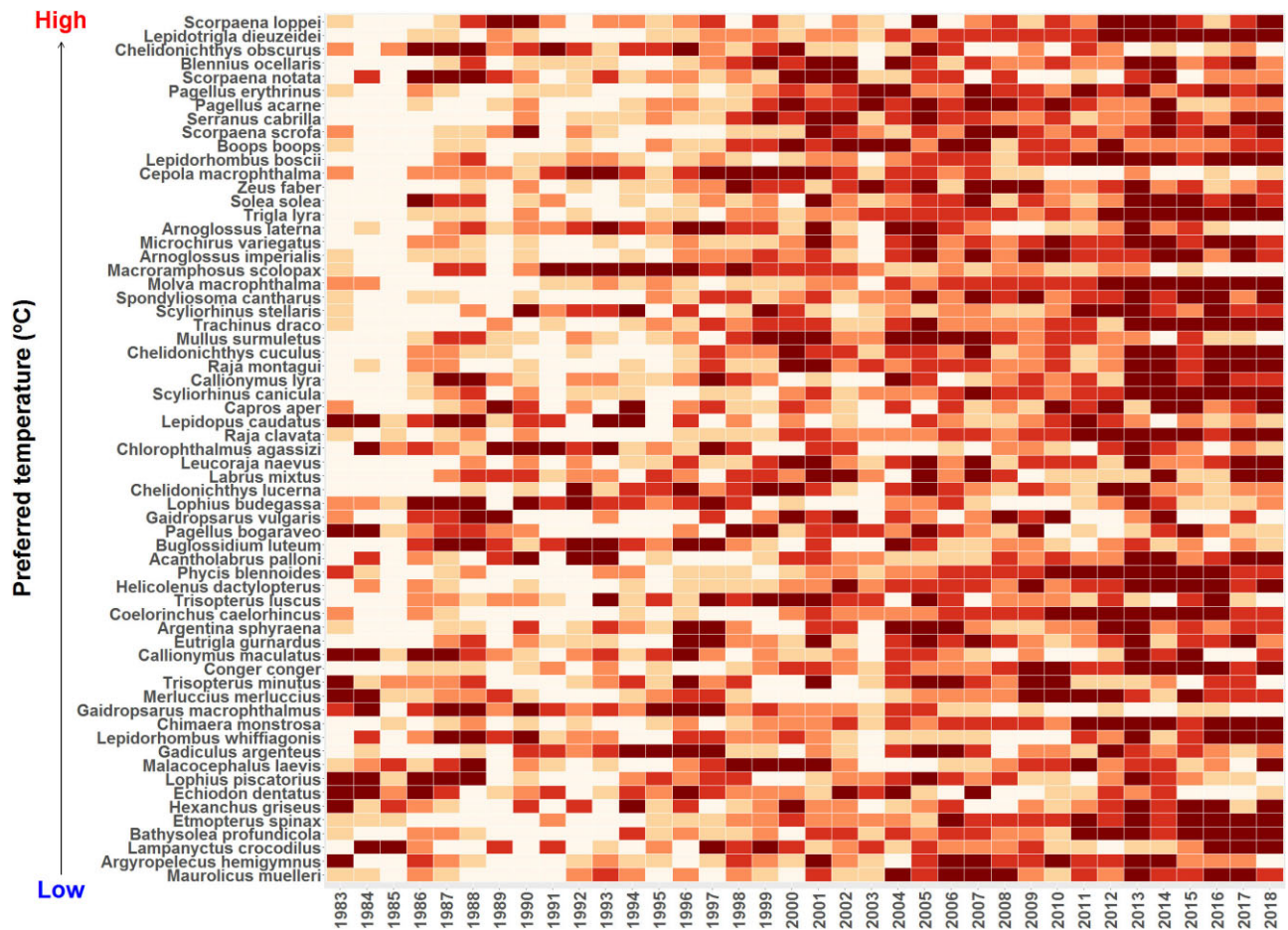


Figure 1 Heatmap of species annual mean biomass evolution. Time series were transformed into quintiles, and each quintile was given a specific tone of orange, highest quintiles symbolized by the darkest orange and white representing the lowest values of the variable. Arrow on the side informs that warmer affinity species are located in the upper side of the heatmap, and colder affinity species in the lower side.

Results

Regime shift identification

In 1983–2018, there was a general increase in most species' biomass (Figure 1). The increasing trend was slightly more evident for species with a higher preferred temperature (top rows of the figure). When analysed via linear regression (Supplementary Figure S8 in the Supporting Information) the most “thermophilic” species trends showed almost twice the slope ($0.041 \text{ g km}^{-2} \text{ year}^{-1}$) than those associated with a lower preferred temperature ($0.022 \text{ g km}^{-2} \text{ year}^{-1}$). In the PCA applied to the species data matrix, PC1 and PC2 explained 32.6 and 9.5% of the variation, respectively (Figure 2). The output of the biotic system PCA was visualized by plotting PC yearly scores along the PC1 and PC2 axes on a two-dimensional figure (Figure 2a). These results suggested a gradual change: years 2011–2018 were grouped together while the rest of the series appeared to reflect a more progressive transition. Graphical representation of both principal components annual trends (Figure 2b) unveiled a directional transition of the PC1 during the whole series. As a composite biotic variable, we used the first principal component of the analysis (PC1, or PCsys when used as biomass composite variable), as it explained a high variance (32.6% of the information contained in the original biomass dataset) and captured the directional change in the system. When sorting the 63 species according

to their loadings in PC1 and PC2 (Supplementary Figure S7 of Appendix 3 in Supporting Information), the most contributive species to PC1 were *Raja clavata*, *Chelidonichthys cuculus*, *Lepidorhombus bosci*, *Scyliorhinus canicula*, *Chimaera monstrosa*, *Etmopterus spinax*, *Microchirus variegatus*, *Conger conger*, *Lepidotrigla dieuzeidei*, and *Bathysolea profundicola*. This group appears to have experienced a distinct increase of their biomass starting in the late 1990s that boosted after year 2011.

The results of the methods applied for the explanatory variable selection, the correlation calculation and RDA I, are presented in Appendix 4 in Supporting Information and in Supplementary Figures S2 and S4, respectively. The final dataset of possible drivers was set to 4 variables (F_{com} , SST, NAO, and SBwML), all of them considered representative of the main environmental and anthropogenic stressors (Figure 3a–d).

In the studied area, annual mean SST showed a fluctuating increase until year 2004, after which its rise stabilized (Figure 3a). Salinity below the winter mixed layer stratum remained stable until 2005, when it increased until reaching its peak in 2012, slowly after which it went back to its baseline. During the beginning of the time series (until year 1998) NAO and EA indexes presented equal phases, and in periods 1998–2002 and 2009–2012 they were opposite. The latter behaviour was associated with larger anomalies in the North Atlantic jet stream. Also, from year 1998 onwards, NAO's sig-

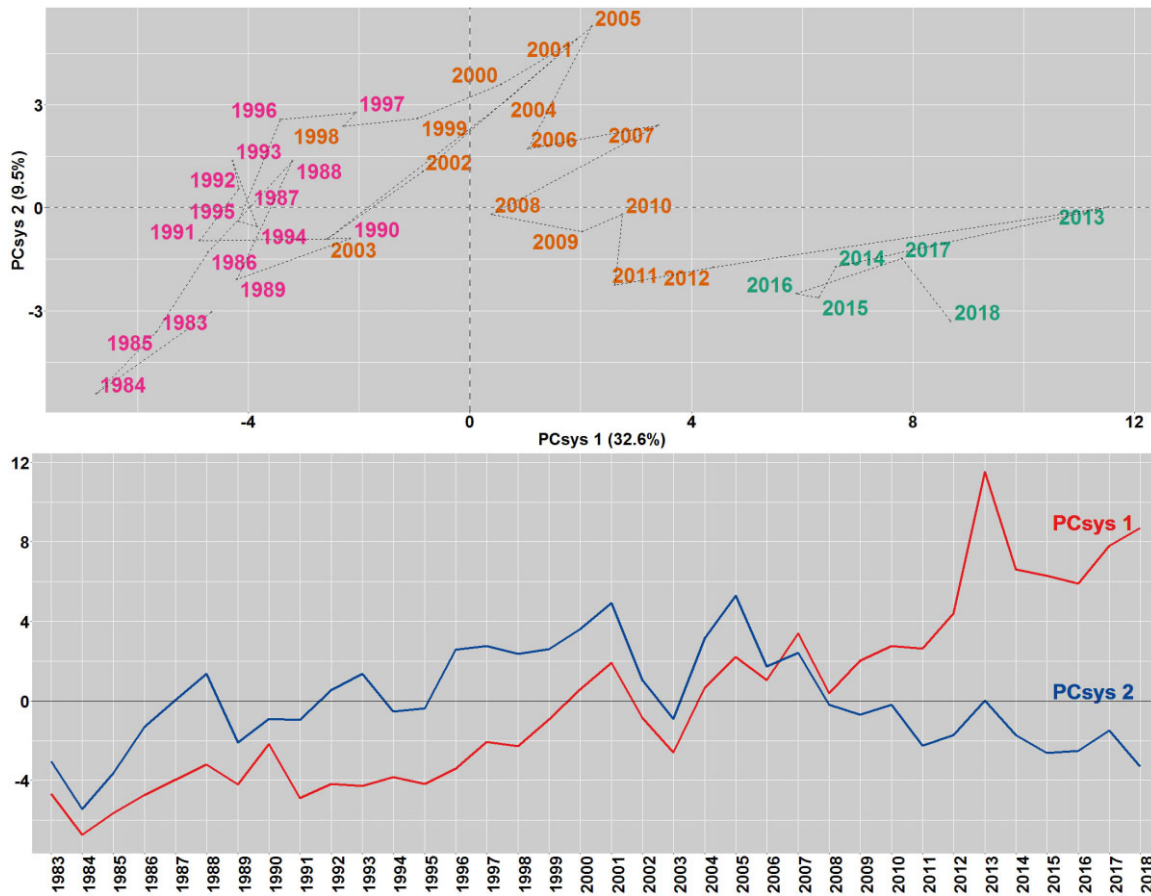


Figure 2 Biotic system's PCA. (a) Dashed line represents the time trajectory of PC1 vs PC2 of the PCA based on the correlation matrix. Years are coloured in accordance to the clusters produced by CONISS chronological clustering (see Figure 5). (b) Yearly PC-scores along the first two principal components of the PCA carried out for the Cantabrian Sea benthic-demersal system.

nal weakened, starting a period we will further refer to as a “non-NAO” period. This went on until an outstanding negative NAO episode in 2010 associated with extremely cold European climate events. As for F_{com} , its striking decrease (Figure 3d), started in 1988 and reached its lowest value in 2017. According to RDA I's results, neither upwelling, ENSO index nor mixed layer depth (winter minimum nor the annual mean) explained a significant amount of variance, so they weren't used in posterior analyses (STARS, GAM/TGAM fitting, and the resilience assessment). Since chlorophyll-A (ChlA) data started in year 1998, they were not incorporated to the main analyses so they would not compromise the length of the series.

The resulting triplot of the RDA fitted for the final set of stressors (RDA II) is presented in Figure 4 and its numerical output included as supporting information. The triplot summarizes the main patterns of variation in the species abundance data and visually relates them to the explanatory variables. The first and second constrained axes in RDA II (RDA 1 and RDA 2) explained, respectively, 24.6 and 4% of the total variance (inertia), which were more than the variance explained by the unconstrained axes (PC1 and PC2 of the RDA explain together 18%). This confirms that the biotic dataset is mainly structured by the covariates included in the analysis. F_{com} and SST exhibited opposite roles on the displaying of the years' scores in the RDA plot, and the same applies to NAO and SBwML. Warming trends in the area opposite to the F_{com} tendency (Figure 3a and d), with a correlation coefficient

of -0.3. SBwML also exhibited a slight correlation with the fishing pressure variable, with a correlation coefficient of -0.5 (Supplementary Figure S3 in Appendix 4 in Supporting Information).

In terms of years-environmental relations, it appears that F_{com} influence is major on the left side of the plot (years 1983–1999), its highest values associated with the start of the PCsys time series. The effect on the PCsys of SBwML and the SST parameter are mainly linked to the right side of the plot (years 2012–2018) (Figure 4). The triplot shows that NAO mildly related to intermediate years in the period 1998–2010, matching a “non-NAO” period (in which NAO index exhibited low absolute values).

The dendrogram (Figure 5) produced through a chronological clustering grouped together years 1983–1997 and 1998 until the end of the series. Apart from this main break in the time series, years 1998–2012 formed a secondary group inside the second period.

A similar pattern was identified when STARS was applied on the biomass composite variable (PCsys), which produced high Regime Shift Indices (RSI) for years 1997 (RSI = 0.967) and 2010 (RSI = 1.125) (Figure 6). The mean detected by STARS showed a stepwise trend containing two transitions, which seem to adjust consistently to the biotic index along the time series. There is a gradual leap around year 1997 and a second abrupt transition around year 2010 (Figure 6). F_{com} series produced a signal of two possible shift-

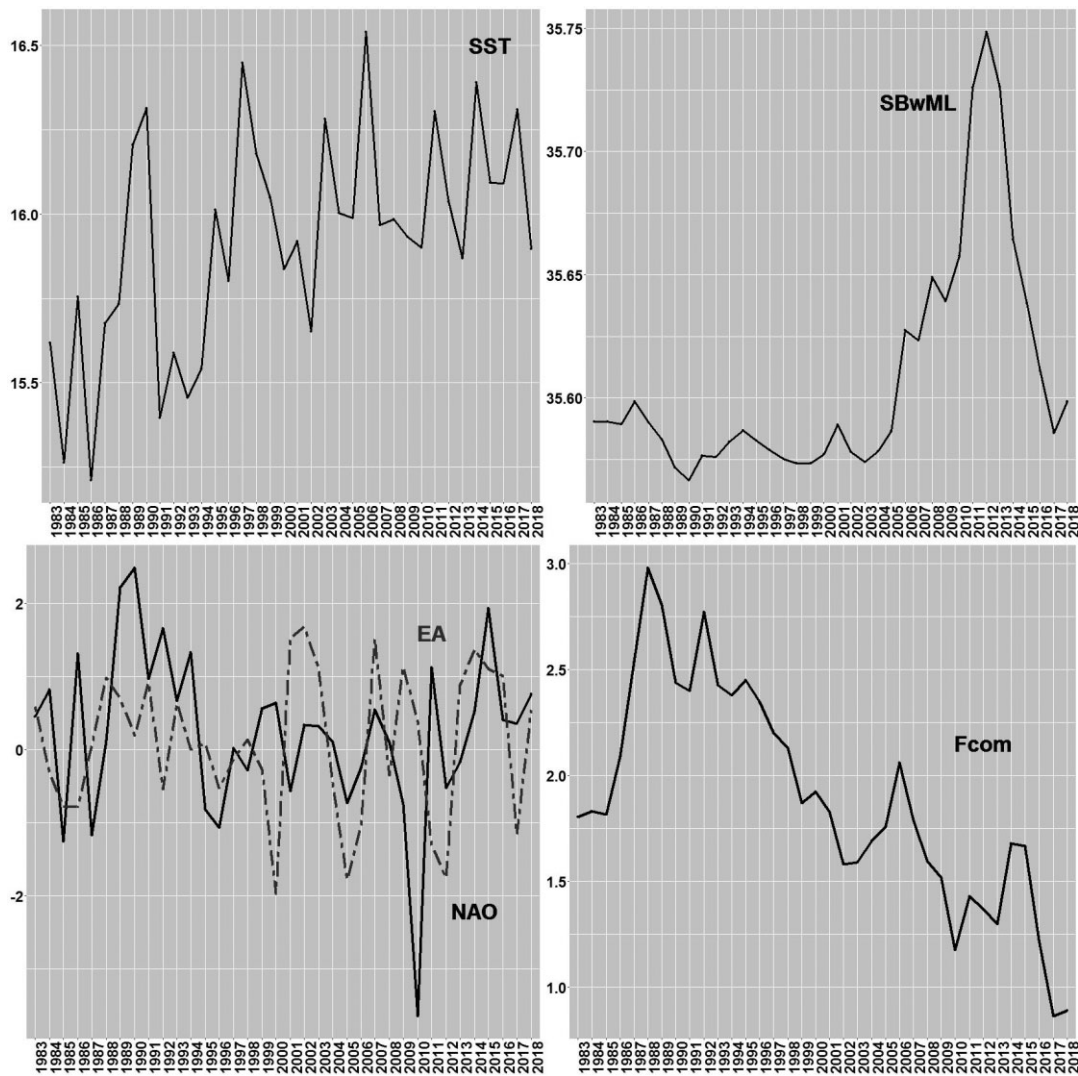


Figure 3 Abiotic variables evolution. (a) Annual mean SST. (b) Salinity below winter mixed layer. (c) Annual mean NAO index and winter average eastern Atlantic pattern indexes (wEA, dashed line). (d) Community averaged fishing mortality index (F_{com}) evolution along the time series.

ing tendencies in years 1999 and 2016, while SST had significant RSI values for year 1995. STARS applied on NAO did not produce any RSI, while SBwML showed a moderate RSI for year 2006 (Supplementary Figure S5 in Supporting Information).

System–stressor relationship

Through the comparison of the fits of additive (continuous) and non-additive (discontinuous) statistical models on the system–stressor relationship, this section of the analyses focused on assessing the type of system’s response. For the inclusion of PC_{sys} and the lagged and non-lagged stressors in models, we used the time series starting in year 1988. This was decided based on 1987 data being an estimation for both PC_{sys} and F_{com} as the average of adjacent years, and first and foremost, due to the perception in the model plots of the whole time series, of years 1983–1986 differing substantially from the subsequent ones in PC_{sys} values, which hinted they could be the tail of an older state.

The optimal fit for the system index (PC_{sys})–stressor relationship was a TGAM with 2-year lagged F_{com} and a utility

threshold in year 2012. The threshold year (2012) lied at a local minimum of F_{com} , as predicted by the theory of critical transitions. This model yielded an adjusted- R^2 of 87.6% and the lowest gCV among all models examined (a gCV value of 0.22) (Table 1). As shown in Figure 7, the model plot describes the first part of the series as a period in which the system had a smooth linear relationship with F_{com} ; the late 1990s gradual regime shift of the system revealed by STARS and chronological clustering being a continuous response to the change in F_{com} . Around year 2012, the system abruptly exited the previous system–stressor coupling and entered a new regime with a new, weaker, relationship with F_{com} .

Resilience assessment

Figure 8 represents the folded stability landscape of the benthodemersal community of the Cantabrian Sea in response to F_{com} . The PC_{sys}– F_{com} plot exhibits two basins of attraction around the TGAM branches identified earlier (Figure 7), which correspond to this complex natural system’s two regimes (system–stressor couplings), and two tipping points (F1 and F2). PC_{sys} values for years 1985–1987 have been

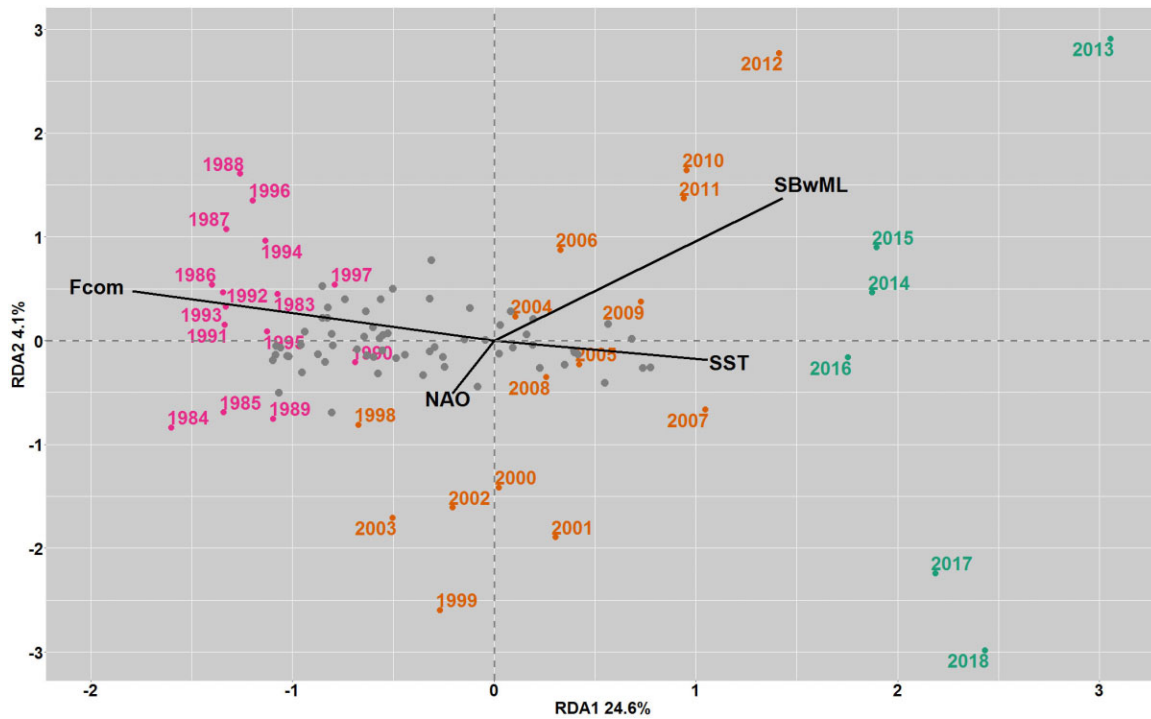


Figure 4 RDA II triplot. The explained variance of the first two axes of RDAII, i.e. the sum of all so-called canonical eigenvalues for the constrained axes divided by total variance (inertia) is 28.7% and the model adjusted- R^2 is 25.3%. The arrow length and direction corresponds to the variance explained by the variable. The angle between black lines reflects the correlations between explanatory variables. The narrower the angle, the stronger the correlation. Years are coloured in accordance to the clusters produced by CONISS chronological clustering (see Figure 5).

added to the graph without estimating their resilience, as they likely reflect the “tail” of an older state, as explained earlier.

The resilience of the system’s initial regime decreased along F_{com} ’s initial decline, which went from its highest values at the beginning of the series on to 2012, when the first tipping point was reached (Figure 8). Around 2012, a local minimum in F_{com} values matched a point in which the system’s recovery capacity was very weakened, leading to the abrupt change of the system state, also reflected by CONISS and STARS, as well as the change in the system–stressor relationship. Hereafter, the system entered a “shorter” regime, unfolding around a weaker attractor with lower resilience values. Nevertheless, there were clear signs of hysteresis after this regime shift: In years 2015–2016, the system experienced similar F_{com} values to those that had taken place in the second half of the 2000s without returning to its previous state (Figure 8).

Discussion

Through a combination of multivariate analysis and non-additive modeling, we interpreted the temporal development of a temperate demersal community. Main patterns were observed and associated with specific anthropogenic and environmental covariates. The analysis revealed a double shift of the biological system in the late 1990s and early 2010s, primarily resulting of a continuous and discontinuous responses, respectively, to fishing pressure and the effect of sea warming. We suggest the existence of an initial phase (during the 1988–2011 period), in which the benthic-demersal fish community was changing sharply but gradually in response to a declining fishing effort, and responded linearly to its impact. During that time, the mitigation of fishing pressure’s effects

overlapped with the emergence of a changing environment’s impacts, which drove the biological system to a point of low resilience at which the studied community, being presumably mostly climate-driven, exited its previous strong coupling with fishing (i.e. the change towards a less steep slope of the system– F_{com} ’s interaction). Our analyses provide evidence that the Cantabrian ecosystem still appears to be in a dynamic and directional progression. The resilience of the demersal community has been eroding over time and at its current state is prone to shift as conditions continue to change with a warming climate.

The analysis of demersal fish biomass trends showed a global increase in species abundances with two marked shifts, detected by STARS and the chronological clustering in the late 1990s decade and early 2010s. In a scenario characterized by the release of a historically severe fishing impact, we understand these shifts as responses to a combination of changes in forcing. On one side, in the late 1990s, fishing impact on the NE Atlantic ecosystems had softened, as progressive enforcement of fishing regulations notably decreased fishing pressure (Modica et al., 2014; Merillet et al., 2020). In our research, the study of this empirical natural system pointed to a gradual shift in years 1998–1999. Since the response to fishing pressure during those years is apparently linear, and concurs with a regime shift recently identified in NW Iberian coast plankton assemblages (Bode et al., 2020), a wider scale factor absent from this study’s analyses might also be contributing to this shift. On top of that, and parallel to the community’s complex process of recovery from a long history of high fishing effort (Modica et al., 2014; Arroyo et al., 2017; Punzón et al., 2020), global warming has provided a build-up in sea temperature, first limited to sea surface temperature, and later on

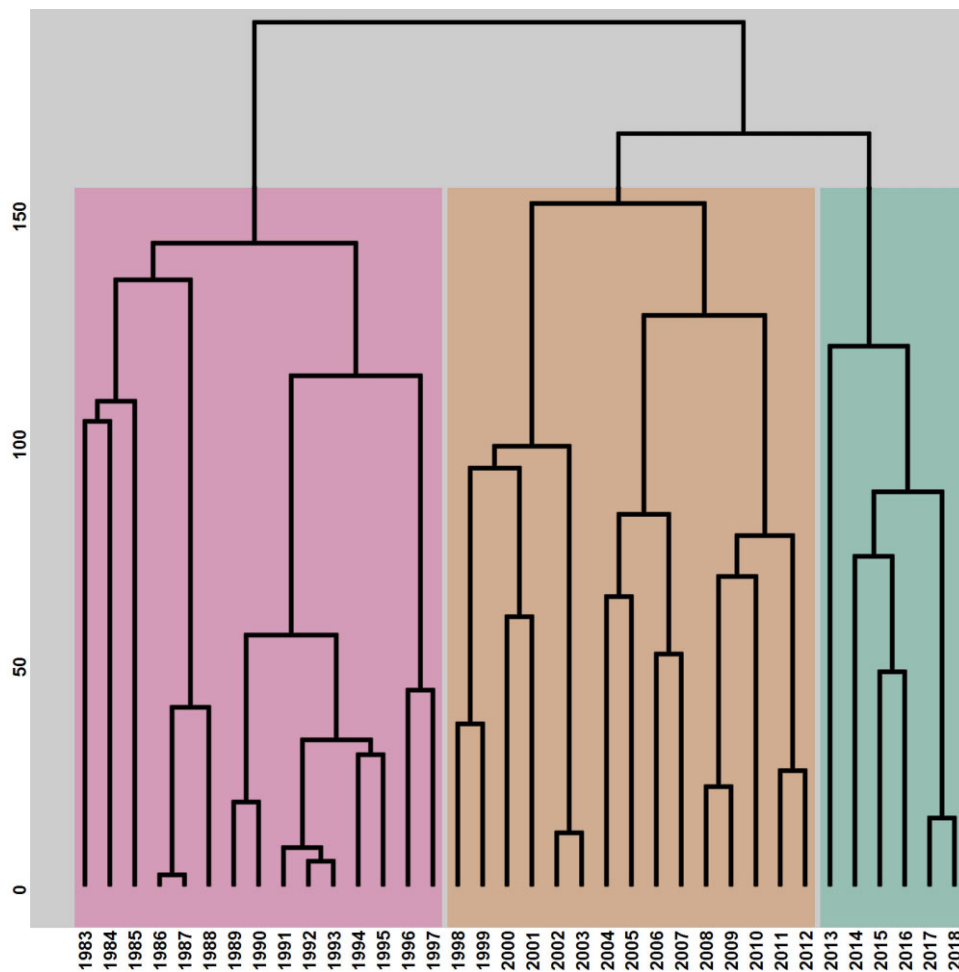


Figure 5 Dendrogram of the chronological clustering applied using the “coniss” method on the 63 demersal species time series. The three periods identified by the analysis are coloured differently and colours are used coherently in subsequent analyses.

also detectable at higher depths (González-Pola et al., 2005; Somavilla et al., 2016). These conditions have driven the demersal ecosystem into a process of meridionalization, i.e. a significant increase of abundance of temperate species with Lusitanian affinities, which accelerated around the late 1990s, when most species increased their abundance as a result of an increasing temperature (Punzón et al., 2016, 2020).

The late 1990s’ shift reflects the fast change of a system in response to concurrent changes in its drivers (i.e. continuous response); while the early 2010s’ shift emerges as the typical fold bifurcation regime shift (Scheffer et al., 2001, 2009), i.e. a discontinuous response taking place after a threshold in a stressor (or a combination of stressors) is exceeded. The Cantabrian Sea demersal ecosystem did not abruptly collapse after succumbing to an accumulation of stressors, but shifted towards a new stable state responding to the retirement of a historically severe fishing pressure parallel to a marked increase of water temperature.

On one side, RDA results pointed to F_{com} , the community averaged fishing mortality, having an important effect on the system for the 1983–1998 period. F_{com} presents its peak in year 1988 and starts a decline that reaches its lowest values in the last years of the studied series. It is in the last two years, 2017 and 2018, that for the first time in the whole series, an $F_{com} \leq 1$ is reached (0.86 and 0.89, respectively), which

corresponds to levels of exploitation consistent with MSY. In the period 1997–2003, improved management of fisheries achieved a 45% reduction in fishing pressure for the demersal Cantabrian community (Modica et al., 2014). This recovery is clearly reflected in our system variable, the PCsys. Initially, through the removal of biomass, fishing led to a near depletion of some targeted stocks, and had major impacts on the structure and functioning of the ecosystem (Arroyo et al., 2017, Hidalgo et al., 2017). Framed in the NE Atlantic rebuilding of previously overfished communities (Collie et al., 2013; Fernandes and Cook, 2013), management interventions achieved an increase in the biomass of the main predators and groups associated with demersal–benthic habitats. This was also observed as a homogenization of the Atlantic communities’ size structure, which very likely facilitated a broader (less regionalized) impact of climate variations (Shackell et al., 2012, Hidalgo et al., 2017). However, this increase in abundance does not necessarily imply the achievement of other community indicators “restoration end points”, which would carry the full recovery of the functionality of the ecosystem (Collie et al., 2013; Arroyo et al., 2019). At low levels of trawling, the system’s configuration abruptly changed, probably due to the effect of rapidly declining fishing in the previous period, followed by signs of hysteresis. The restoration trend of the benthic-demersal community regarding fishing im-

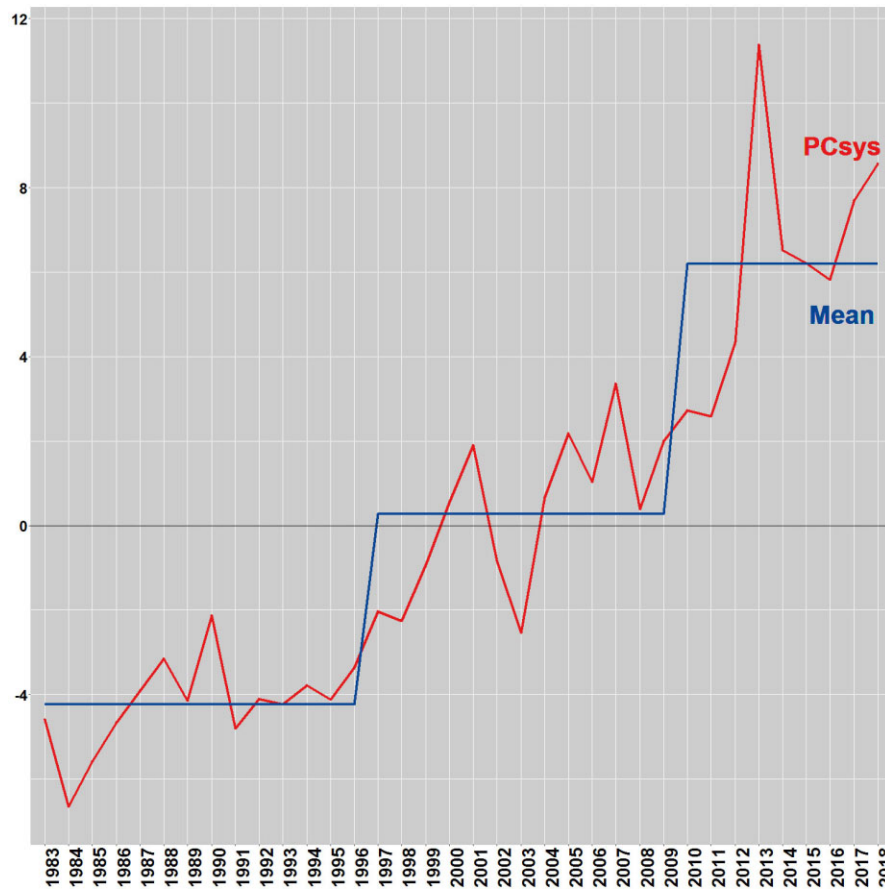


Figure 6 Plot of STARS applied on the PCsys. Blue line shows the stepwise trend containing the regime shift in the mean detected by STARS method. Red line represents the first principal component of the PCA of the biotic system.

pacts is undoubted and noticeable in the change of configuration of the community presented here. In fact, species that were favoured in the recent period are mainly cartilaginous fish (rays and sharks), known to have a high sensitivity to trawling due to their equilibrium (K) life-history strategies (de Juan et al., 2020), and commercial species (such as hake, four spot megrim, and conger eel), which corroborates our finding that fishing is indeed the key factor shaping the system. If global ecosystem stability is to be expected, however, the heavy decline in fishing needs to be interpreted along with an ongoing dynamic process of change captured by the decreasing values of resilience (see below). The probable shift of fishing activity to deeper grounds, an increasing pressure on pelagic species (Abad et al., 2010; Arroyo et al., 2019) and a systemic resilience breach enabled by climate conditions never experienced before (Punzón et al., 2016; Somavilla et al., 2016) are also an important part of the present's state of affairs.

During the second period of the time series, late 1990s–2018, while moving towards an area of low resilience, an important change in tendency took place, located around years 2010 and 2012. A sharp increase in several fish species biomass around those years boosted the system into a new configuration. STARS and chronological clustering applied to our data detect it as a second shift, which would initiate a 6-year period until the end of the series. Over those 6 years, the system was positively affected by temperature and salinity,

and somehow detached from the influence of fishing (apparent as a smoothing of the slope in the PCsys– F_{com} relationship), while for the intermediate phase, years 1998–2012, the community's dynamics are apparently less subject to the interannual variation of SST and the impact of overfishing. We suggest wider environmental drivers, other than those included in our analyses, might have been at play over this period. The regional hydroclimatic conditions then, coincide with a period of La Niña-like conditions in the tropical Pacific (cold phase of ENSO), a positive phase of AMO and low absolute values of the NAO index in the North Atlantic (a “non-NAO” period). Independently of the index used to approach climatic forcing, this period between 1997 and 2012 is marked by a reorganization of heat budget and circulation in all ocean basins. In particular, in the North Atlantic these years were characterized by cooling conditions at the ocean surface which favoured a large transfer of heat and salt from upper to deeper ocean layers (Somavilla et al., 2016). Community Weighted Mean Temperature (CWMT) calculated for the area reflects this warming and salting of mid-layers, which could have affected recruitment processes and bathymetric and geographical displacement of species (Auber et al., 2015; Punzón et al., 2016, 2020). In 2011, months after an extreme NAO annual mean value, the system experienced a striking intake of fresher waters, which reversed the previous salting trend that had been going on since the 2005 strong winter mixing. From year 2012 onwards, the increasing trend of abundances in the

Table 1 Numerical output of GAM and TGAM fits for every stressor relationship to the biotic index.

Stressor	Lag	Fits	gCV	Threshold year
SST	0	TGAM ($R^2_{adj.} = 78.1\%$)	0.383	2010
		GAM ($R^2_{adj.} = 19.1\%$)	0.865	
	1 year	TGAM ($R^2_{adj.} = 73\%$)	0.562	2011
		GAM ($R^2_{adj.} = 20.4\%$)	0.865	
	2 years	TGAM ($R^2_{adj.} = 74.4\%$)	0.681	2011
		GAM ($R^2_{adj.} = 20.7\%$)	0.859	
F_{com}	0	TGAM ($R^2_{adj.} = 86.3\%$)	0.223	2012
		GAM ($R^2_{adj.} = 68.5\%$)	0.330	
	1 year	TGAM ($R^2_{adj.} = 84.8\%$)	0.257	2012
		GAM ($R^2_{adj.} = 66.6\%$)	0.372	
	2 years	TGAM ($R^2_{adj.} = 87.6\%$)	0.220	2012
		GAM ($R^2_{adj.} = 71.2\%$)	0.354	
Salinity below ML	0	TGAM ($R^2_{adj.} = 84.1\%$)	0.375	2012
		GAM ($R^2_{adj.} = 39.6\%$)	0.710	
	1 year	TGAM ($R^2_{adj.} = 81.9\%$)	0.292	2012
		GAM ($R^2_{adj.} = 50.5\%$)	0.572	
	2 years	TGAM ($R^2_{adj.} = 78.8\%$)	0.366	2013
		GAM ($R^2_{adj.} = 61.9\%$)	0.459	
NAO	0	TGAM ($R^2_{adj.} = 67.8\%$)	0.883	2010
		GAM ($R^2_{adj.} < 0\%$)	1.079	
	1 year	TGAM ($R^2_{adj.} = 70.8\%$)	0.569	2011
		GAM ($R^2_{adj.} < 0\%$)	1.051	
	2 years	TGAM ($R^2_{adj.} = 72.1\%$)	0.478	2011
		GAM ($R^2_{adj.} < 0\%$)	1.086	

The model with minimum gCV is highlighted in red and corresponds to that of a 2-year lagged F_{com} discontinuous response of PCsys with a utility threshold in the year 2012.

studied community continues, while CWMT coherently decreases along the drop-off in temperature and salinity at mid-depths (Punzón et al., 2020).

Of all these expressions of external forcing, fishing pressure stands out in our statistical analyses as the most critical feature for the system. Nevertheless, by taking account of previous research in which climate has been associated with the general boost in biomass, frequency of occurrence, and CWMT (Punzón et al., 2016, 2020) altogether with the opposed trends warming and fishing display at long-term scale (Ter Hofstede et al., 2010; Ter Hofstede and Rijnsdorp, 2011; Hidalgo et al., 2017), we consider the definite inducer of both state shifts on the benthic-demersal realm was a combination of environmental and anthropogenic factors. It has thoroughly been discussed how surface oceanic features are strong drivers for demersal resources (e.g. Alemany et al., 2013; Druon et al., 2015; Sion et al., 2019). For instance, changes in air–sea heat exchanges linked to the water column vertical structure and occurrence of ecological hotspots are often primary drivers of marine resources (e.g. Behrenfeld and Boss, 2014; Somavilla et al., 2020; Druon et al., 2021), becoming also triggers of re-

gional scale shifts in highly impacted ecosystems (Hidalgo et al., 2022). In terms of the system's response to warming, the inertia driving the main system trends at the present moment is also uncertain and it is fair to assume the system finds itself inside an ongoing process of change. Its resilience in response to fishing has been eroding in reference to the 1990s decade, and at present, Cantabrian demersal ecosystem moves along a faint attractor, fluctuating even without clear stochasticity driving it. In this transition scenario, further studies at smaller spatial (i.e. local) and ecological (i.e. food web or species-level) scales need to be conducted to suggest appropriate management strategies aimed at foreseeing anomalies in response to warming as well as regulating fisheries expansions (Arroyo et al., 2019). Even when systemic changes have not yet been observed, many marine ecosystems whose resilience was slowly compromised got to a situation of collapse that could have been predicted and reversed (Choi et al., 2005; Hamazaki et al., 2005; Carpenter et al., 2011). In the case of the Cantabrian Sea, current values of resilience are also associated with a pronounced sensitivity to environmental variability and low predictability of the type and direction of it response. This calls

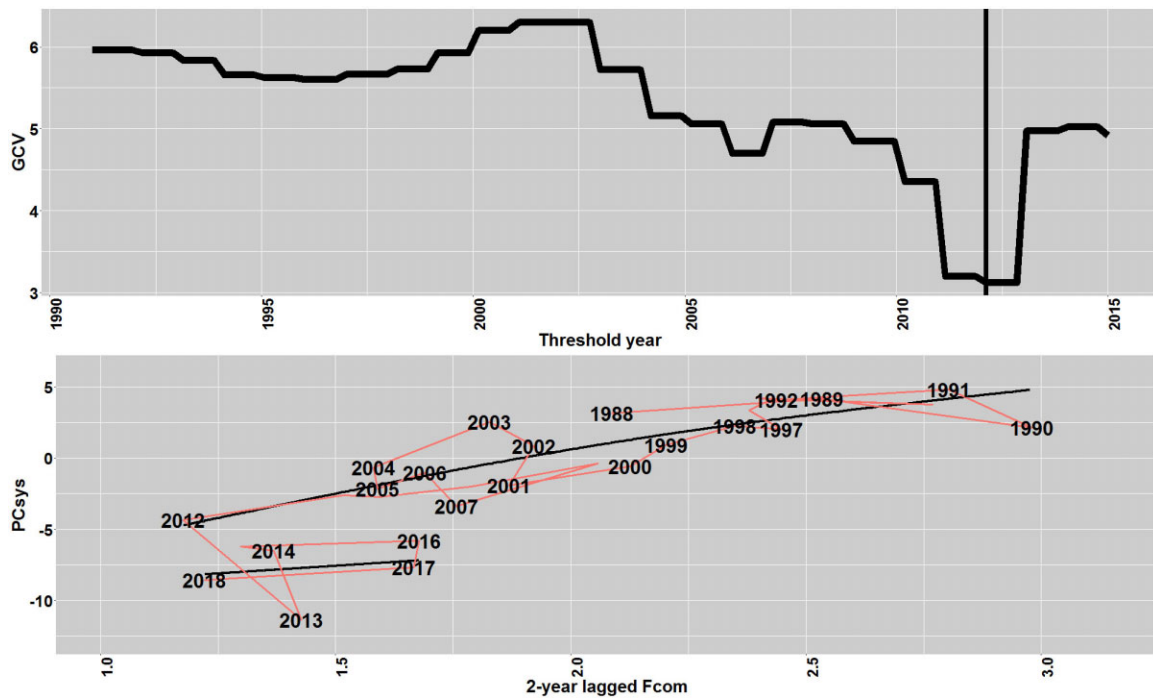


Figure 7 (a) Fitting of TGAM on PCsys and 2-year lagged F_{com} relationship. Black lines indicate the fitted TGAMs and red line the chronological path of the series. (b) gCV values of TGAM with threshold year fitted on the relationship between system state indicator (Pcsys) and 2-year lagged F_{com} .

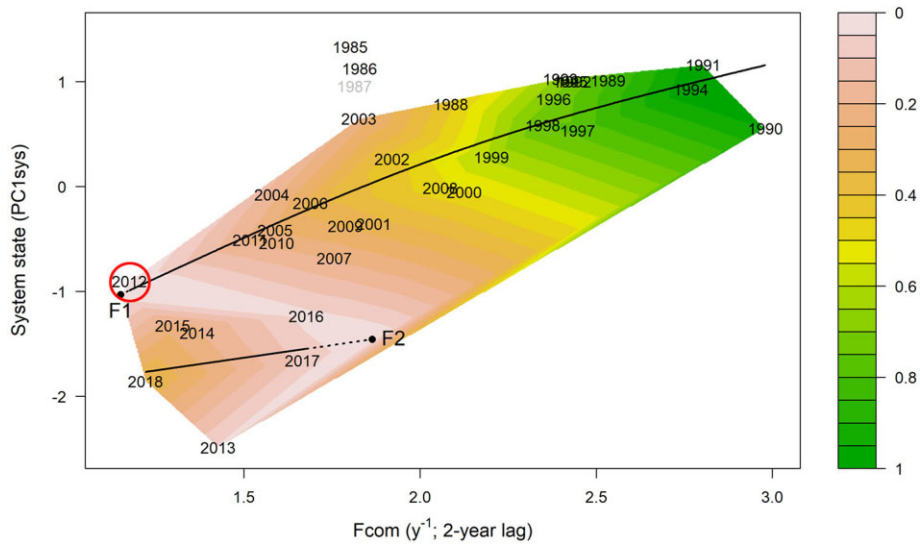


Figure 8 Folded stability landscape and relative resilience estimates. The system’s change has a horizontal component in which conditions (2-year lagged F_{com}) change, and a vertical component which represents system’s state changes. Dotted black line indicates the possible extensions of the linear attractors (mean numerical properties of the system for a given period). F1 and F2 are indicating the tipping points assumed locations. Threshold year 2012 is highlighted by a red circle.

for implementation of adaptive management (Hidalgo et al., 2022).

This is the first application of an IRA in a marine community of the NE Atlantic. There are two main novelties in this study compared to previous IRA applications on empirical marine communities (Vasilakopoulos et al., 2017; Damalas et al., 2011; Ma et al., 2021; Tsimara et al., 2021; Hidalgo et al., 2022). First, the system dynamics in 1988–2018 form a stability landscape with three system states but two system–stressor

couplings (basins of attraction), due to the regime shift of the late 1990s taking place at a point of rapidly declining fishing. This scheme is theoretically possible (Scheffer et al., 2001), but has not been previously observed in an empirical setting. Second, the inclusion of F_{com} as a stressor and its eventual manifestation as the key stressor shaping a system are unique, in the sense that previous studies had not examined any proxy of fishing as candidate stressor, but environmental variables alone.

The shifts we report here lie within a history of mostly climate-driven shifts identified in NE Atlantic and Mediterranean Sea at different ecological levels. Particularly, the late 1990s' transition taking place in Cantabrian Sea benthodemersal community coincides with the late 1990s shift detected by other authors in the area (Hemery et al., 2008; Luczak et al., 2011; Auber et al., 2015; Bode et al., 2020, to name a few). In the Mediterranean Sea, where climate change and fishing have also been defined to act as a tandem in deteriorating the ecosystem structure and function (Albouy et al., 2015), multiple climate-induced regime shifts were associated with the global acceleration in the rise of SST after the 1997/1998 El Niño event (Vasilakopoulos et al., 2017). Climate variability in the Northern Hemisphere has been postulated as the dominant factor inducing regime shifts in North Atlantic ecosystems (Möllmann and Diekmann, 2012), but in many studies fishing pressure was accounted responsible for debilitating resilience and triggering trophic cascades, both significant contributors to the occurrence of regime shifts (Alheit et al., 2005; Choi et al., 2005; Auber et al., 2015).

The disentangling of the opposed long term trends of past fishing impacts and present warming is still a critical challenge. The identification of the driver/s to which a natural system responds to at a given time is a cornerstone of the design of plausible adaptive measures to cope with climate change impacts (Hidalgo et al., 2022b). Our results provide new insights to face this challenge, by looking into a process associated with these interacting drivers over time, and the way they have shaped the system in the most recent period. Either abrupt or smoothly, Cantabrian Sea ecosystem is currently reflecting the consequences of its vulnerability to fishing and climate change. We corroborate that marine communities have complex, distinctive adaptation mechanisms to changes in their environment, inextricably dependent on their resilience dynamics. When aiming for environmental sustainability and human welfare, it is imperative to carry a careful monitoring of the ecosystem's resilience dynamics, with a specific study of their implications on the configuration of the ecosystem, so as to enable an integrative assessment of current and future marine ecosystems.

Supplementary material

Supplementary material is available at the *ICES/JMS* online version of the manuscript.

Author contributions

AP conceived the research idea, coordinated the project in which it was conducted, compiled data, wrote code, and analysed data; PV wrote code and analysed data, including the visualization of IRA's framework results; RS collated environmental data; MH conceived the research idea and coordinated all analyses; JP wrote code, carried analyses, curated data, including visualization, and wrote the original draft of the manuscript. All authors contributed to writing and editing of the manuscript.

Conflict of interest

The authors declare no competing conflict of interest.

Data availability statement

Data supporting the findings of this study are openly available in OSF at <http://doi.org/10.17605/OSF.IO/W4EH3>, reference number DOI 10.17605/OSF.IO/W4EH3.

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