Journal of Biogeography (J. Biogeogr.) (2017)

ORIGINAL ARTICLE

Size-spectra across geographical and bathymetric gradients reveal contrasting resilient mechanisms of recovery between Atlantic and Mediterranean fish communities

Manuel Hidalgo[1,*], Antoni Quetglas[1], Francesc Ordines[1], Lucía Rueda[1], Antonio Punzón[2], Marina Delgado[3], Luis Gil de Sola[4], Antonio Esteban[5] and Enric Massutí[1]

[1]Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, 07015 Palma, Spain, [2]Instituto Español de Oceanografía, Centro Oceanográfico de Santander, Promontorio San Martín, 39080 Santander, Spain, [3]Instituto Español de Oceanografía, Centro Oceanográfico de Cádiz, Muelle de Levante, 11006 Cádiz, Spain, [4]Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Puerto Pesquero, 29640 Fuengirola, Spain, [5]Instituto Español de Oceanografía, Centro Oceanográfico de Murcia, Varadero 1, 30740 San Pedro del Pinatar, Spain

*Correspondence: Manuel Hidalgo, Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, 07015 Palma, Spain.
E-mail: jm.hidalgo@ba.ieo.es

ABSTRACT

Aim Marine conservation often prioritizes measures based on ecosystem diversity, missing important information on the size and structure of communities such as that provided by body size-spectra (SS). While most studies have focussed on temporal or spatial patterns of SS, there is no research investigating their spatial heterogeneity, which is a key community trait revealing mechanisms of resilience. We aimed to comparatively determine the main patterns of variation of fish SS and their spatial heterogeneity across geographic and bathymetric gradients.

Location Shelf and slope Atlantic and Mediterranean demersal ecosystems.

Methods Using the information obtained from the experimental surveys, we calculated fish SS at four bathymetric strata and investigated the influence of the biomass of small-sized and large-sized fish on their temporal and spatial variation. We also assessed the functional relationship between the mean pattern and the spatial heterogeneity of SS as a characteristic structural trait of a community.

Results The variation in SS demonstrates that Atlantic communities were geographically and bathymetrically more connected, while those in the Mediterranean were more fragmented. The relationship between mean SS and its spatial heterogeneity was a community fingerprint differentiating two contrasting pathways of community recovery between Atlantic and Mediterranean ecosystems. Atlantic communities were recovering because of the temporal increasing contribution of large fish and a 'rescue effect' of neighbouring areas, which have spatially homogenized size structure. Mediterranean communities were, by contrast, spatially clustered and highly dependent on small-sized fish variability that hampers the capacity of ecosystems to recover after a chronic degradation.

Main conclusions Patterns of SS variation depend on the spatial complexity of communities, which contrasts between Atlantic and Mediterranean systems. Integrative analyses of size-based indicators (mean and variance) provide a complete assessment of the structural properties of communities and characterize the resilience mechanisms of recovery against perturbations under contrasting ecological contexts.

Keywords

Atlantic Ocean, community resilience, fish communities, Mediterranean Sea, rescue effect, size-spectra, spatial heterogeneity

Journal of Biogeography

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12976

INTRODUCTION

Several ecosystem and community indicators have been proposed to assess and monitor the health of marine ecosystems (e.g. Shin *et al.*, 2005; Greenstreet & Rogers, 2006 and references therein). Most indicators are generally defined as potentially sensitive to external stressors, particularly those of anthropogenic origin such as fishing impact (Trenkel & Rochet, 2003, 2010) or climate change (Levin *et al.*, 2010). They range from estimates of the properties of single species or multi-species group, such as size-based indicators, biomass ratios or biodiversity indices, to metrics at the ecosystem level often derived from modelling. While finding robust ecosystem and community metrics to test external effects has been proved difficult (Rice, 2000; Trenkel & Rochet, 2003), size-based indicators such as size-spectra (SS) are among the most currently used. This is because of their sensitivity to external stressors (Jennings & Dulvy, 2005; Sweeting *et al.*, 2009) while providing information about the structural properties of marine systems (Jennings *et al.*, 2001; Blanchard *et al.*, 2009).

The SS measure how the abundance or biomass of species decrease log-linearly with size as a result of the energy transfer among organisms of different size. Trophic positions of marine organisms often depend more on body size than on the taxonomic identity (Jennings *et al.*, 2001), and SS allow linking empirical observations with ecological and metabolic modelling (Blanchard *et al.*, 2009; Andersen & Beyer, 2015) or predator–prey theory (Kerr & Dickie, 2001; Law *et al.*, 2009). The slope of SS is often used to evaluate the size-selective impact of fishing activity (Jennings *et al.*, 2001; Sweeting *et al.*, 2009) (Fig. 1a), but it is also an indicator of the rate of energy transfer to upper trophic levels (Kolding & Zweiten, 2014). Altering the rate of energy transfer may affect the community resilience to perturbations (McCann, 2000). However, it is often difficult to evaluate the effects of fishing on the community structure, since they can be both direct by triggering disproportional mortality on larger individuals, or indirect by increasing the abundance of small prey species through predation release (increasing the slope; Shin *et al.*, 2005) (Fig. 1a). In addition, in communities highly dependent on recruitment and the productivity of small-sized fish, such as those in the Mediterranean Sea (Colloca *et al.*, 2013), slope variations might exclusively be a consequence of the changes in the intercept regardless of the impact of fishing on large fish.

Mounting research has focussed on the influence of anthropogenic and environmental drivers on the temporal (Blanchard *et al.*, 2005) and the spatial (Daan *et al.*, 2005; Sweeting *et al.*, 2009) variation of mean SS. However, few studies have investigated the spatial variance of the slope, rather than mean values, as an indicator of the spatial heterogeneity of a community in terms of individual size. Spatial variation of the slope can indeed be sensitive to external drivers, because of spatial selection of fishing pressure, clustering of the environmental drivers or fragmentation of the community dynamics (Hsieh *et al.*, 2010). In meta-population and community ecology, the relationship between the mean and the variance of species abundance has been largely used to investigate how system diversity reduces temporal variability, increasing the stabilizing capacities (e.g. portfolio effect, Anderson *et al.*, 2013). Thus, we hypothesize that combining mean and spatial variance of SS may contribute to characterize the stability and dynamics of marine communities in terms of their size-structure.

Here, we compare SS of continental shelf and slope fish communities of Atlantic and Mediterranean ecosystems with contrasting ecological, environmental and fishing impact characteristics (see Methods). Although several works have revealed the effects of fishing activity on those ecosystems

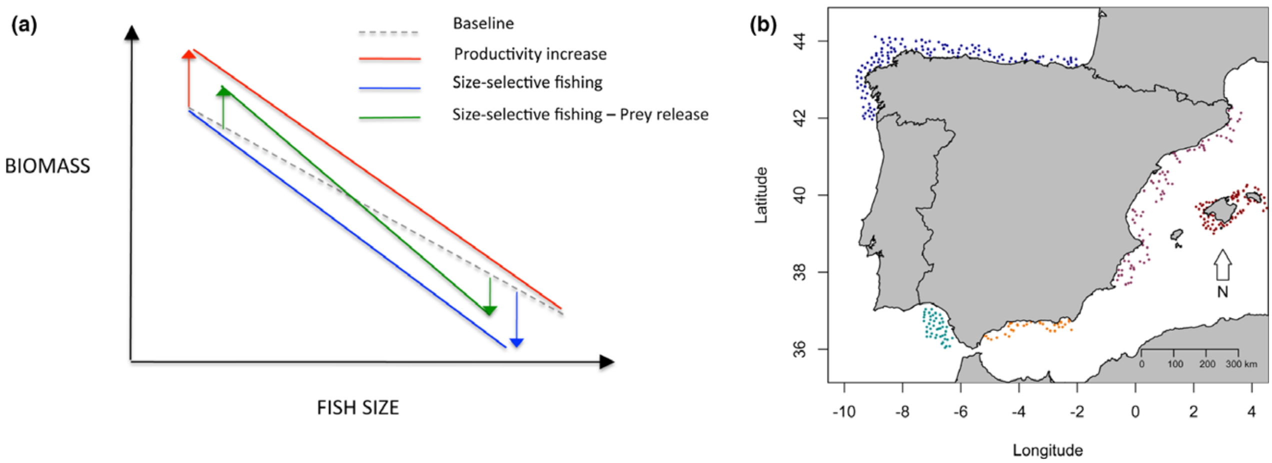

Figure 1 (a) Graphic representation of the potential drivers of variation of size-spectra over a baseline state. (b) Map representing the Iberian Peninsula and the Balearic Archipelago and the distribution of stations sampled in a given year in the five different geographic areas coded with different colours: Cantabric-Galician system (dark blue), Gulf of Cadiz (light blue), Mediterranean Iberian Peninsula (purple), Alboran Sea (yellow) and Balearic Archipelago (red).

(e.g. Trenkel & Rochet, 2010; Modica *et al.*, 2014), few studies have investigated SS variation and none by means of an Atlantic-Mediterranean comparative approach. In this study, we first investigate the spatial and temporal variation of the SS mean slope and its coefficient of variation (CV) as putative indicators of the spatial heterogeneity across bathymetric gradients (from shallow shelf to middle slope) and contrasting ecosystems in the Atlantic and the Mediterranean. For each system, we investigate the functional relationship between the SS mean and the spatial heterogeneity, and we expect to characterize the resilient capabilities of a given community attending to the functional form of this relationship. To understand the spatial and temporal variation of these SS indicators, we determine the influence of the small-sized and large-sized components of fish community.

MATERIALS AND METHODS

Study areas

Five areas have been analysed separately given the contrasting geographic and oceanographic scenarios for analytical and comparative purposes: Cantabric-Galician system and Gulf of Cadiz in the Atlantic Ocean, and Mediterranean Iberian Peninsula, Balearic Archipelago and Alboran Sea in the western Mediterranean (Fig. 1b).

The Cantabric-Galician system is dominated by wind driven oceanographic processes and summer coastal upwelling in the western area, while it is more dependent on the variability of the central water masses and on mesoscale structures in the eastern area (Álvarez *et al.*, 2010). In the Gulf of Cadiz, the circulation is dominated by Mediterranean Outflow Water, which forms a strong bottom current flowing towards the west and north-west. The interaction of this outflow water with topography and the entrainment process induces significant circulation in the surface layer (Peliz *et al.*, 2009). In the Mediterranean, the environment is highly clustered at local scale (Rossi *et al.*, 2014), which makes the spatiotemporal dynamics of the organisms highly adapted to local conditions (Puerta *et al.*, 2015). In the Mediterranean Iberian Peninsula, winter processes such as the vertical mixing and the amount of intermediate waters formed by deep convection dominate the hydrography that ultimately affects the marine ecosystems in the Balearic Archipelago in spring and early summer (Balbín *et al.*, 2014). The Alboran Sea is the most heterogeneous environment of our study systems and it is characterized by a turbulent mixing because of exchanges of Mediterranean and Atlantic waters and persistent anticyclonic gyres that create oligotrophic conditions. However, the incoming Atlantic jet strongly enhances primary and secondary production in surface waters around the gyres in comparison to other Mediterranean regions (Oguz *et al.*, 2014).

In terms of fishing impact, the state of north-east Atlantic populations has shown evident signs of recovery (Fernandes & Cook, 2013; Modica *et al.*, 2014) and change (Punzón *et al.*, 2016). However, it is still unclear how this improvement has affected the dynamics and the structure of the Atlantic communities and ecosystems. By contrast, Mediterranean stocks are in an alarming decline, which calls for new measures to promote fisheries sustainability (Vasilakopoulos *et al.*, 2014).

Data

This study uses the information of four different fishery-independent bottom trawl surveys carried out to evaluate the status of demersal and megaepibenthic ecosystems of the Spanish continental shelf and slope. In the Atlantic, surveys have been conducted in autumn (September–October) since 1983 along the Cantabric and Galician coast (Sánchez & Serrano, 2003) and since 1994 in the Gulf of Cadiz (Silva *et al.*, 2011). In the Mediterranean, surveys are conducted in spring (May–June) and started in 1994 off the Iberian Peninsula (Bertrand *et al.*, 2002) and in 2001 off the Balearic Archipelago (Massutí & Reñones, 2005). See ICES (2010) and Bertrand *et al.* (2002) for technical details of the surveys in the Atlantic and Mediterranean respectively. To apply a comparative platform among all study areas, which show sharp bathymetric gradients delineating different fish communities (e.g. Sánchez & Serrano, 2003; Massutí & Reñones, 2005), sampling stations were analysed separately in four depth strata: shallow shelf (50–100 m), deep shelf (100–200 m), upper slope (200–500 m) and middle slope (below 500 m).

Data used included the number of individuals caught by species and length category per swept area on a given footprint (distance towed × wingspread) in a sampling station. Catch at length (L) were converted to weight (W) at length using length–weight relationships ($W = aL^b$), where a and b parameters were obtained from each specific survey or, when not available, from FishBase (www.fishbase.org). Catch weight at length for species and length class in each sampling was standardized to density (g km^{-2}). To calculate the biomass spectra, standardized catch weight at length was allocated to body weight classes, each of length 0.5 on a $\log_2$ scale from 0 (1 g) to 17 (131,072 g), encompassing a total of 34 body classes. The biomass spectra analyses are only applicable to individuals over the size ranges that are effectively sampled by the gear (Jennings & Dulvy, 2005), excluding individuals below the size that were not effectively sampled. The threshold applied was 32 g (body class 10).

Linear models were used to regress $\log_2$ normalized biomass (i.e. total biomass per body weight class divided by weight span of the weight class) against the midpoint of each $\log_2$ weight class, with sampling station as a grouping factor. This grouping factor specifies the partitioning of the data according to which linear models are fitted to provide sampling station-specific estimates (Pinheiro & Bates, 2000). To perform the analyses, we applied the 'lmList' function of the *nlme* R library. These station-specific estimates were used to calculate the mean annual values of the slope and the annual CV (standard deviation/mean) considering the mean and the variation of slopes across sampling stations in a year. They were calculated for each area and bathymetric strata. We also assessed the mean versus CV relationships as a potential community fingerprint to be compared among areas and bathymetric strata.

To analyse the temporal variation of the mean and CV of the slope, we assessed the influence of the small-sized and large-sized components of SS. This approach also facilitates geographic and bathymetric comparisons. Estimates of standardized biomass of small-sized and large-sized components of SS per sampling station and year were calculated. From all increments of body weight classes finally selected for each spectrum, fish individuals in the smallest 15% of size classes were considered 'small-size', while fish individuals in the largest 25% of size classes were considered 'large-size'. Preliminary analyses were performed with different threshold values, having yielded similar results (not shown). In addition, species richness was also measured at each sampling station to evaluate the potential influence of fish diversity on the variability of mean slope and CV of SS.

Analyses

For each area and bathymetric stratum, linear models were applied to analyse the influence of the biomass of the small-sized and large-sized fraction, the species richness and their interactions on the temporal variation of the mean slopes and their CV. The influence of small-sized fish on SS is an indication of variation in the mean productivity of the system, which is mainly affected by the environmental influence on the high turnover component of the spectra (Kolding & Zweiten, 2014; Fig. 1a) while it can be also influenced by the indirect effects of fishing in the community (Daan *et al.*, 2005), or even direct effects in poorly size-selective (e.g. Mediterranean, Sweeting *et al.*, 2009; Colloca *et al.*, 2013) or indiscriminate fisheries (McCann *et al.*, 2016). An influence of the large-sized fish is, by contrast, a likely indication of increase or release of fishing impact. Once all the model combinations were tested, the final model showing the highest goodness-of-fit for each area and stratum was selected based on the minimization of the Akaike information criterion (AIC). Before analysis, we calculated the variance inflation factor (VIF) to assess the potential collinearity among the three covariates. A conservative cut-off VIF value of three was applied (Zuur *et al.*, 2009), and we found no evidence of collinearity. Residuals were checked for the absence of temporal autocorrelation applying the autocorrelation function (*acf*) on the residuals of each linear model. Normality of the residuals was checked using Lilliefors and Shapiro-Wilk tests. Although slopes of SS are always negative, we modelled them as absolute values for an easier interpretation of linear model coefficients. That is, the slope value is positively proportional to the steepness in the linear models.

To assess which areas were more sensitive to the influence of small-sized and large-sized fish, and to the community diversity, we performed Spearman rank correlations at each sampling station between each of the drivers and the slope values, assuming potential monotonic relationships. To counteract the problem of multiple comparisons of Spearman's rank correlations performed over space, we used a Bonferroni correction for the significance values. Only those sampling stations that could be followed in time for more than 11 years (the shortest time series in the Balearic Archipelago) were considered for the correlations.

RESULTS

Mean size-spectra per area and stratum

Mean SS per bathymetric stratum and area are presented in Fig. 2, with the statistics of all the linear regressions in Appendix S1 in Supporting Information. They show, on average, a smaller slope on the Cantabric-Galician shallow shelf (ShS) (Fig. 2a), with higher mean density in the Balearic Archipelago. In the deep shelf (DeS, Fig. 2b) and the upper slope (UpS, Fig. 2c), the Cantabric-Galician and Balearic Archipelago displayed very similar mean SS. In these three bathymetric strata, Mediterranean Iberian Peninsula, Alboran Sea and Gulf of Cadiz showed similar and intermediate patterns. In the deepest stratum, the middle slope (MiS), the slope of all the areas was generally less steep, with the exception of the Cantabric-Galician and Gulf of Cadiz that displayed slopes similar to other bathymetric strata. Mean SS of MiS showed higher geographic variability in the mean value (Fig. 2d), with the most productive fish spectrum observed in the Alboran Sea and the lowest in the Balearic Archipelago and the Mediterranean Iberian Peninsula.

Time series of the size-spectra's mean slope and coefficient of variation

Time series of the mean annual slope of SS showed non-linear temporal trends in all areas and bathymetric strata (see Appendix S2). Time series of SS slopes in the DeS and UpS in the Atlantic areas showed correlated temporal patterns both in the Cantabric-Galician shelf (Cor = 0.61, $P < 0.05$, Fig. 3a) and the Gulf of Cadiz (Cor = 0.60, $P < 0.05$, Fig. 3b). By contrast, DeS and UpS displayed uncorrelated temporal patterns within each region in the Mediterranean (Fig. 3c–e, all $P > 0.05$). No temporal correlation was found in any of the regions with ShS or MiS strata.

The inter-annual pattern of the CV was generally highly variable with no evidence of non-linear trends (see Appendix S2). Significant and negative temporal trends (i.e. $P < 0.05$ in the slope of this relationship) were tested and only observed for the DeS (Fig. 4a) and the UpS (Fig. 4b) of the Cantabric-Galician system, and the MiS of the Alboran Sea (Fig. 4c), with slopes of the SS spatially more homogeneous towards recent years. Conversely, the MiS of the Balearic Islands showed a positive and significant temporal trend with more spatially heterogeneous slopes in recent years (Fig. 4d). The rest of the time series did not show any significant temporal pattern (see Appendix S2).

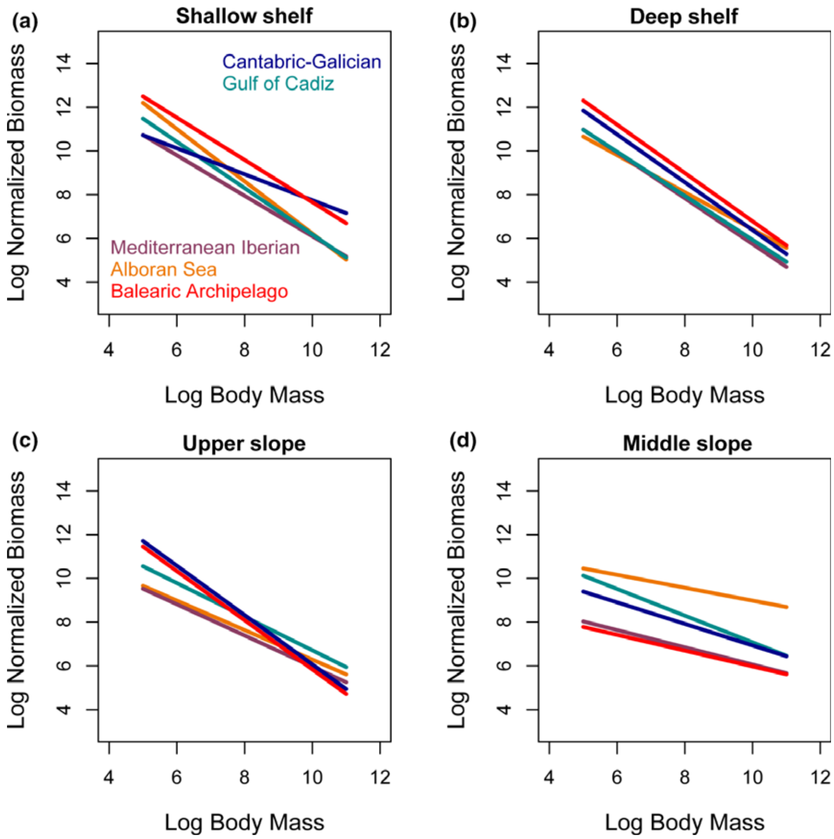

Figure 2 Mean biomass spectra for the shallow shelf (a), deep shelf (b), upper slope (c) and middle slope (d). Colour coding for the different geographic areas as in Fig. 1: Cantabric-Galician system (dark blue), Gulf of Cádiz (light blue), Mediterranean Iberian Peninsula (purple), Balearic Archipelago (red) and Alboran Sea (yellow). See Appendix S1 for the statistics of all the linear regressions of the mean biomass spectra.

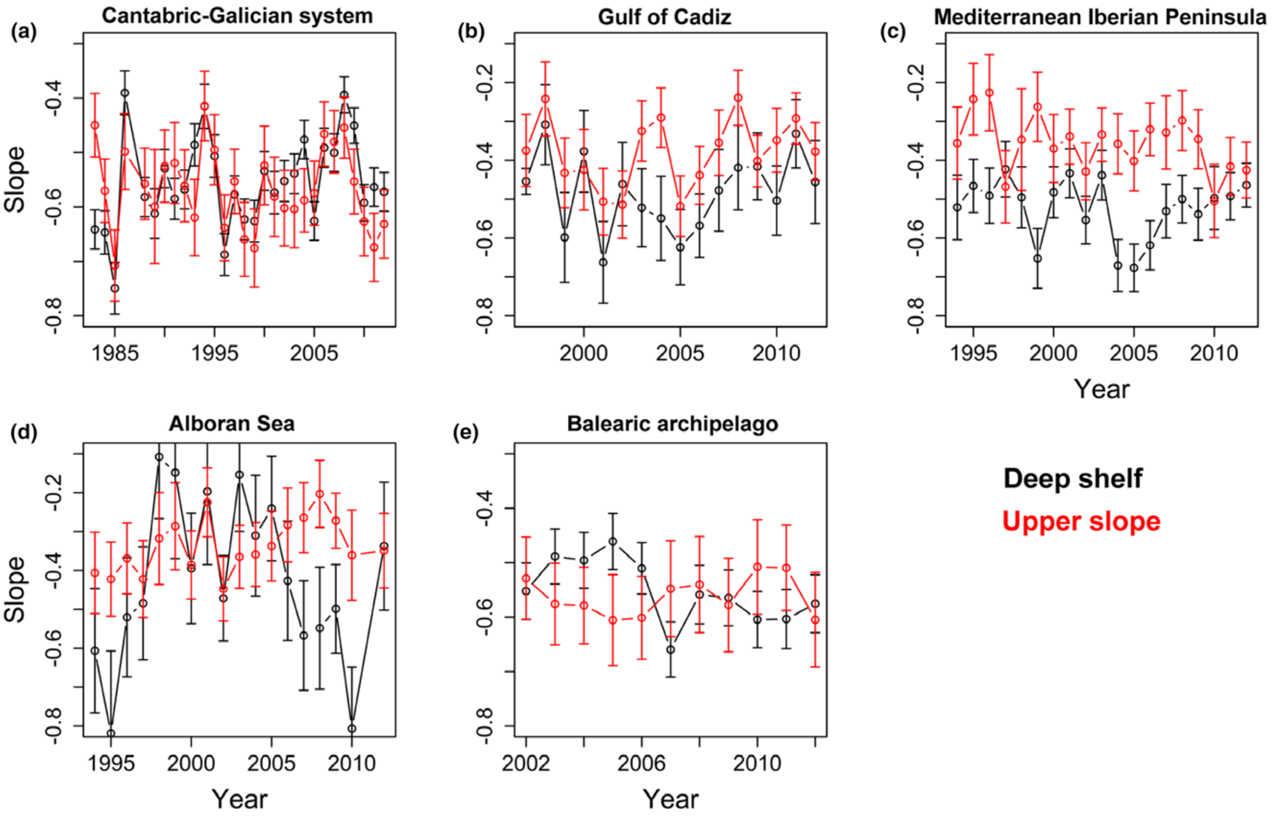

Figure 3 Time series of size-spectra slope for the deep shelf (black) and the upper slope (red) of the different geographic areas: Cantabric-Galician system (a), Gulf of Cadiz (b), Mediterranean Iberian Peninsula (c), Alboran Sea (d) and Balearic Archipelago (e). See Appendix S2 for time series of all the bathymetric strata and geographic areas.

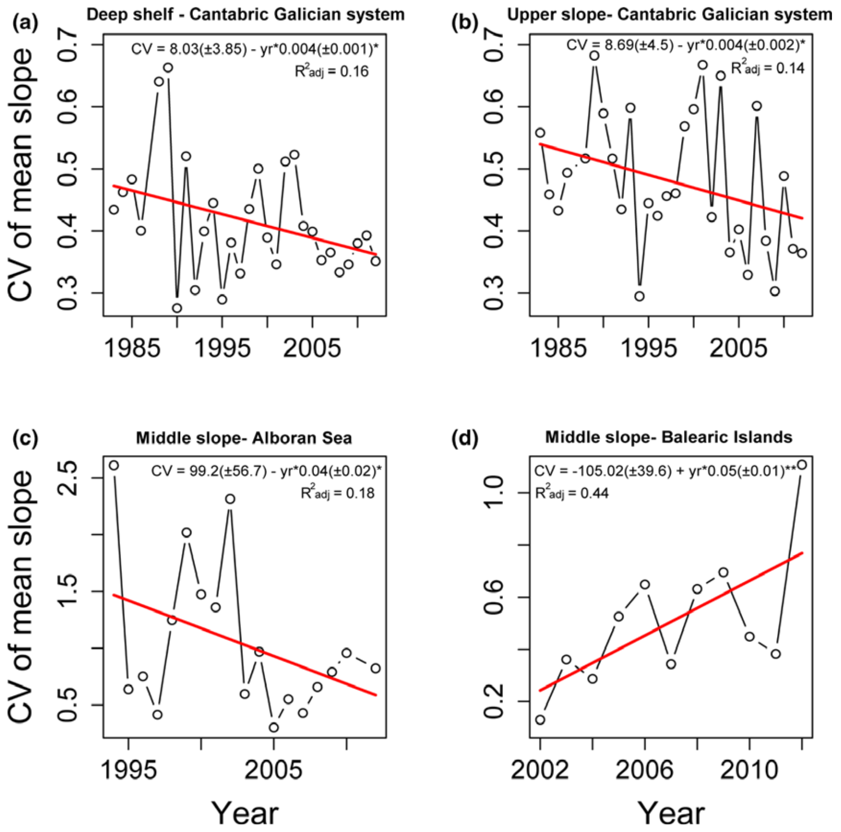

Figure 4 Time series of the coefficient of variation (CV) of the mean annual slope of the size-spectra for the deep shelf (a) and the upper slope (b) of the Cantabric-Galician system and, middle slope of the Alboran Sea (c) and Balearic Archipelago (d). Red line represents the linear regression adjustment to temporal trend (significant slope in all the relationships: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$). See Appendix S2 for time series of all the bathymetric strata and geographic areas.

Mean slope versus CV relationships

The relationship between the mean annual values of the slope and their CV defined a system-specific fingerprint of the community, while it displays two contrasting patterns (illustrative examples in Fig. 5 and all the relationships in Appendix S3). The first pattern represented high heterogeneity (high CVs) in years with steeper slopes (more negative values). The ShS, DeS and UpS of the Cantabric-Galician system followed this pattern (see Appendix S3). From a comparative perspective, SS are spatially more heterogeneous in the UpS than the DeS of the Cantabric-Galician system for a given value of the mean slope (Fig. 5a,b), with a similar decreasing rate of CV in the two bathymetric strata. The second pattern was the opposite, showing more spatial homogeneity in years with steeper slopes (i.e. low CVs). This pattern was followed by the rest of geographic areas and bathymetric strata with the exception of ShS and DeS of the Balearic Archipelago, which did not display any clear relationship (see Appendix S3). As an illustrative example, the UpS and MiS in the Alboran Sea showed this pattern with low variable and steeper slopes in the UpS compared to MiS (Fig. 5c,d), and a higher rate of CV increase in the later.

Influence on the temporal variation

Table 1 summarizes the results of the best linear models on the annual values of both the mean slope and the CVs. Almost all models analysing the temporal variation of the mean slope evidenced a primary positive effect of the biomass of the small-sized individuals, indicating steeper slopes in years with higher production of small fish. A secondary and opposed effect of large-sized fish was observed in half of the systems with steeper slopes in years with depleted biomass of large fish. In the two systems where the best model did not show a significant effect of small-sized fish (UpS in the Balearic Archipelago and MiS in the Cantabric-Galician system) species richness showed a positive effect on the steepness of the slope.

In the models analysing the temporal variation of CV, a negative effect of the biomass of large-sized fish was observed in almost half of the models evidencing an increase of the spatial heterogeneity in years with depleted abundance of large fish (Table 1). A positive effect of the abundance of small fish and a negative effect of species richness appeared to be more residual. Interacting terms were not significant ($P > 0.05$) in any of the models investigated for the two response variables: mean slope and CV. The residuals of all the models followed a normal structure ($P > 0.05$, Lilliefors

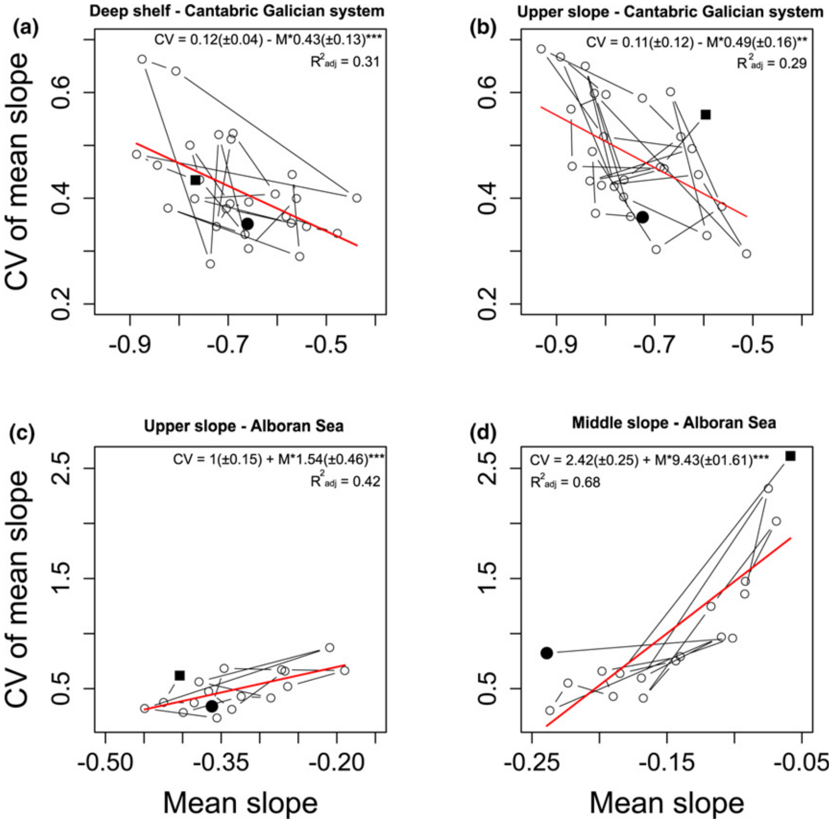

Figure 5 Relationship between coefficient of variation (CV) and the mean slope of the size-spectra for the deep shelf (a) and the upper slope (b) of the Cantabric-Galician system in the Atlantic that illustrate an inverse correlated pattern of this relationship. The upper slope (c) and the middle slope (d) of the Alboran Sea in the Mediterranean are examples of the positive correlated pattern in this relationship. See Appendix S3 for these relationships for all the bathymetric strata and geographic areas. Red line represents the significant linear adjusted relationship (significant slope in all the relationships: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$). Black squares represent the beginning of the time series and black circle the end.

test and Shapiro-Wilk test) and were not temporally correlated ($P > 0.05$, *acf*).

Influence on the spatial variation

At a spatial scale, the variation of the slope was generally associated with the variation of the biomass of small fish. This is particularly evident in the two shallower strata (ShS, Fig. 6a, and DeS, Fig. 6b). For the ShS, this influence was much more scattered in the Atlantic when compared with the Mediterranean, while for the DeS this influence is widespread in the Cantabric-Galician system with some small-scale spots of influence of large fish (Fig. 6b). However, the UpS of the Cantabric-Galician system displayed an important geographic segregation of the small-fish effect located in the Cantabric area (north of the Iberian Peninsula), while the effect of the large fish was observed on the Galician area (north-west of the Iberian Peninsula) (Fig. 6c). In the Gulf of Cadiz, there was a largely distributed effect of small fish from the ShS to the UpS (Fig. 6a–c), while this effect was only observed on the ShS and DeS in the Balearic Islands (Fig. 6a,b). Few and scattered spatial effects were observed on the MiS (Fig. 6d). No significant effect of richness was observed in any area and bathymetric strata.

DISCUSSION

Along with functional complementarities of different fish groups (Rice *et al.*, 2013), the spatiotemporal variation of SS are essential fingerprints of marine communities. In the same way that fish populations depend on its demographic structure to cope with external disturbances, communities rely on their structural properties, being the SS one of the main pillars of resistance and resilience. The dynamics of benthic–pelagic coupling (Trueman *et al.*, 2014), the net influence of sub-surface primary production and pelagic subsidies (Stasko *et al.*, 2016), and how this ultimately affects the transfer efficiency along the trophic chain highly differ across bathymetric and geographic gradients, and those are primary important drivers of SS. Because of the difficulty of investigating regionally specific processes that take into account the aforementioned drivers, in this study, we focus on the main commonalities and differences emerged from a cross-system comparison to shed new light on key mechanisms underlying the biogeography of fish communities. Our study shows both common properties, which are independent of the variability at local scale, but also contrasting regional dynamics between Atlantic and Mediterranean communities. Mean SS per area reveal some relevant differences between these two large regions. For instance, Atlantic communities do not always show less steep spectra as it would be expected from systems having higher biomass of large fish compared with the Mediterranean (Colloca *et al.*, 2013), which generally has stronger contribution of small-sized species displaying high turnover rates (Sweeting *et al.*, 2009).

One of the main contrasting patterns observed between the Atlantic and Mediterranean systems is the different degree of connectivity of fish communities between

Table 1 Linear models with the highest goodness-of-fit (see Methods) for all areas (Cantabric-Galician system, Gulf of Cadiz, Mediterranean Iberian Peninsula, Alboran Sea and Balearic Islands) and bathymetric strata (shallow shelf, deep shelf, upper slope and middle slope). Intercept (Int.) and slope (± standard error) of statistically significant covariates (small-sized, S-sized; large-sized, L-sized; richness, Rich.) are presented for models fitted on mean annual values of slope and on the coefficient of variation (CV). Number of observations (N) and adjusted R^2 (R^2_{adj}) are also included. Note that to facilitate the interpretation of the results, the slope was modelled as absolute value – that is, the slope value is positively proportional to the steepness.

	Mean annual slope						CV annual slope					
Bathymetric strata/Area	Int.	S-sized	L-sized	Rich.	N	R^2_{adj}	Int.	S-sized	L-sized	Rich.	N	R^2_{adj}
Shallow shelf												
Cantabric-Galician system	−0.14	0.04 ± 0.01**	–	–	29	0.33	–	–	–	–		
Gulf of Cadiz	−0.02	0.1 ± 0.01***	−0.05 ± 0.009***	–	18	0.82	–	–	–	–	–	–
Mediterranean Iberian Peninsula	−0.33	0.14 ± 0.01***	−0.08 ± 0.02***	–	19	0.86	0.10	–	−0.006 ± 0.003*	–	19	0.21
Alboran Sea	−0.97	0.12 ± 0.01***	–	–	19	0.58	–	–	–	–		
Balearic Islands	−0.56	0.07 ± 0.01**	–	–	11	0.61	1.2	–	−0.06 ± 0.03*	–	11	0.25
Deep shelf												
Cantabric-Galician system	0.1	0.1 ± 0.01***	−0.07 ± 0.01***	–	29	0.87	1.14	–	−0.06 ± 0.03*	–	29	0.23
Gulf of Cadiz	0.03	0.1 ± 0.01***	−0.07 ± 0.01**	–	18	0.73	–	–	–	–	–	–
Mediterranean Iberian Peninsula	−0.13	0.05 ± 0.02*	–	–	19	0.32	–	–	–	–	–	–
Alboran Sea	−0.01	0.1 ± 0.01***	−0.07 ± 0.03*	–	19	0.78	0.44	–	–	−0.015 ± 0.004*	19	0.43
Balearic Islands	−0.48	0.08 ± 0.01***	–	–	11	0.85	2.46	0.03 ± 0.03*	−0.22 ± 0.06**	–	11	0.57
Upper slope												
Cantabric-Galician system	0.11	0.1 ± 0.01***	−0.08 ± 0.01***	–	29	0.75	1.16	–	−0.05 ± 0.03*	–	29	0.21
Gulf of Cadiz	0.41	0.05 ± 0.01***	−0.05 ± 0.02*	–	18	0.65	–	–	–	–	–	–
Mediterranean Iberian Peninsula	−0.23	0.05 ± 0.01**	–	–	19	0.44	0.08	0.005 ± 0.002*	–	−0.004 ± 0.001*	19	0.34
Alboran Sea	0.11	0.04 ± 0.01**	–	–	19	0.43	0.22	–	−0.01 ± 0.005*	–	19	0.31
Balearic Islands	0.57	–	−0.03 ± 0.01*	0.01 ± 0.003**	11	0.76	−1.23	0.11 ± 0.04*	–	–	11	0.39
Middle slope												
Cantabric-Galician system	0.007	–	–	0.02 ± 0.005**	25	0.27	–	–	–	–	–	–
Gulf of Cadiz	−0.12	0.13 ± 0.02***	−0.09 ± 0.03*	–	18	0.64	–	–	–	–	–	
Mediterranean Iberian Peninsula	0.28	0.09 ± 0.01***	−0.08 ± 0.01***	–	19	0.91	0.5	–	−0.04 ± 0.01**	–	19	0.41
Alboran Sea	−0.19	0.03 ± 0.01*	–	–	19	0.31	–	–	–	–	–	–
Balearic Islands	−0.42	0.07 ± 0.02**	–	–	11	0.54	1.29	–	−0.07 ± 0.01*	–	11	0.29

***, $P < 0.001$; **, $P < 0.01$; *$P < 0.05$.

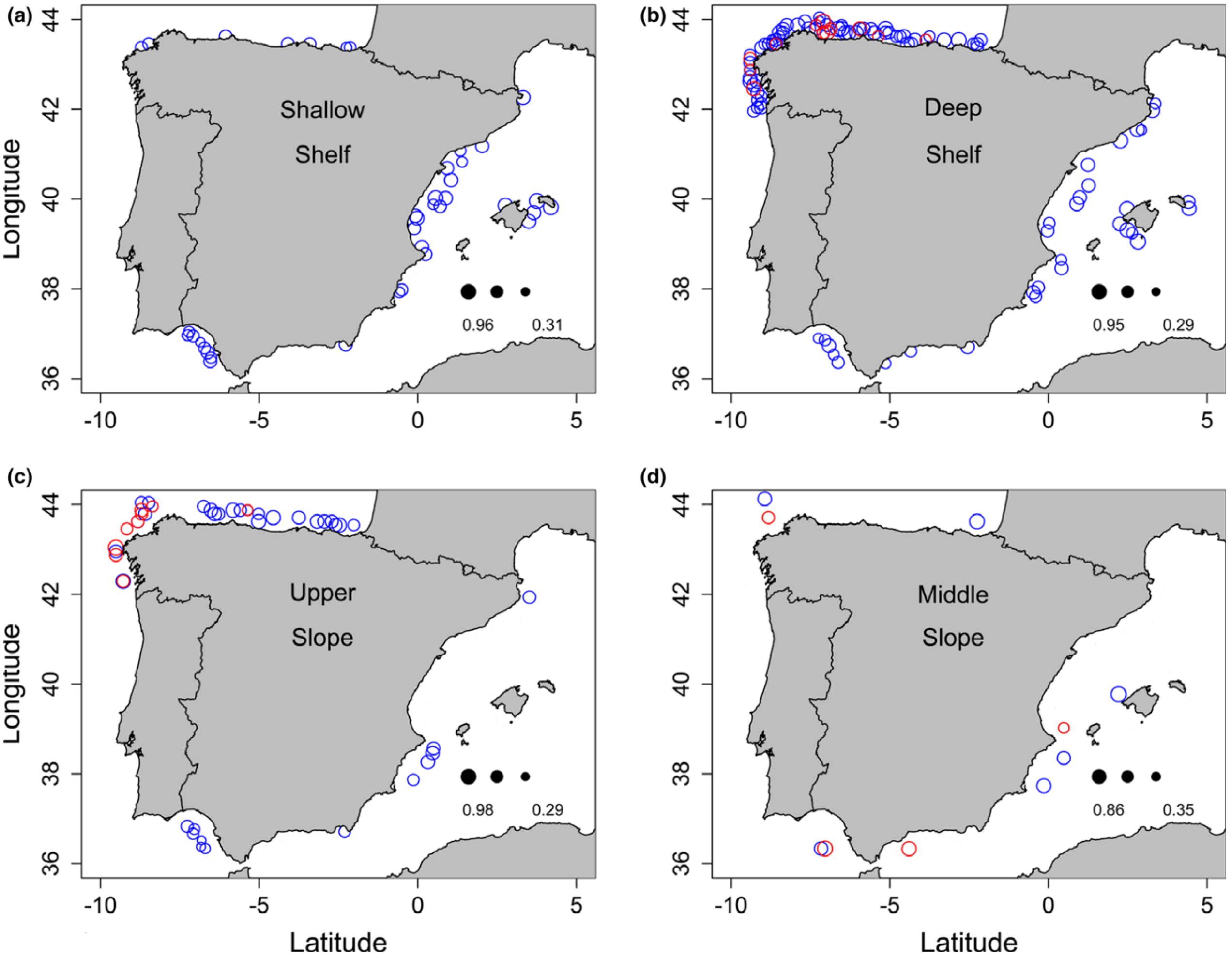

Figure 6 Spearman rank correlation coefficients calculated at a given sampling station between the mean annual slope and the small-sized component (blue bubbles), and the large-size component (red bubbles) of the fish community for the shallow shelf (a), deep shelf (b), upper slope (c) and middle slope (d). Note that for graphical representation of the correlations and comparison of values in all areas, correlations have been standardized and represented as absolute values (see Table 1 for direction of the effects). Significance of correlation coefficients has been adjusted by Bonferroni correction.

bathymetric strata. While the Atlantic deep-shelf and upper-slope communities display correlative inter-annual patterns, those in the Mediterranean show independent temporal patterns between bathymetric strata. This evidences that communities in the Mediterranean are bathymetrically (and also geographically, see below) more segregated than those in the Atlantic Ocean. This indicates that similar biotic and abiotic drivers would influence SS in the Atlantic at a larger spatial scale, while different drivers may be discordant at each stratum in the Mediterranean. For instance, fishing has a homogeneous impact across strata in the Atlantic (Punzón *et al.*, 2010), whereas fishing effort displays spatial heterogeneity in some areas of the Western Mediterranean (e.g. Farriols *et al.*, 2015).

Our study reveals temporal variation in the spatial heterogeneity of SS of certain Atlantic communities with lower values of CV towards recent years, particularly in the Cantabric-Galician region. It evidences structural changes in the Atlantic with communities spatially more homogeneous in terms of fish size in the recent years. This would indicate spatial recovery of the community because of lower fishing impact while maintaining similar mean SS. Such interpretation is consistent with Modica *et al.* (2014), who found two contrasting periods in terms of fishing mortality of the most harvested species that shifted to lower impact from the early 90s.

Deep-sea ecosystems (i.e. middle slope) showed the most contrasting SS among regions. They displayed larger variation of fish production, with higher values (i.e. spectra intercept) in the Atlantic than in the Mediterranean, except the Alboran Sea likely due to the high abundance of large deep-sea elasmobranches in this area (Ramírez-Amaro *et al.*, 2015). Owing to its low turnover and long life cycles of its main species, deep-sea ecosystems are highly vulnerable (Clarke *et al.*, 2015). Our work also evidences a high level of spatial heterogeneity (e.g. higher spatial dissimilarity in terms of size) towards recent years in several systems. For instance, a generalized steepness of mean spectra in Cantabric-Galician middle slope during the last two decades, which contrasts with the pattern observed in the shelf and the upper slope, is in accordance with the general current degradation of Atlantic deep-sea ecosystems (Clarke *et al.*, 2015). In the Mediterranean Sea, the observed fast increase in the heterogeneity of SS in the middle slope off the Balearic Islands suggests a potential increase of the fishing impact on deep-sea communities. This result is consistent with a documented bathymetric displacement of fishing activity towards deep-sea waters to harvest crustaceans with a consequent impact on fish communities (Hidalgo *et al.*, 2009).

As a general pattern, mean biomass of small-sized individuals drives short-term temporal variation of the mean slope in almost all systems analysed, while mean biomass of large-sized fish shapes the long-term pattern of SS as well as the CV. This suggests that inter-annual variability of productivity of small-sized fish mainly of short-lived species and the recruitment of medium- and large-sized fish are the main causes that shape short-term fluctuations of size-spectra. This may be caused by the effect of regional and local environmental variability, but also by direct fishing impacts on poorly size-selective systems such as the Mediterranean Sea (Sweeting *et al.*, 2009; Colloca *et al.*, 2013) or indirect effects related to the potential increase of prey abundance in response to predator declines (Daan *et al.*, 2005). However, long-term trends of SS are especially dependent on drivers affecting the abundance of large-sized fish, basically a curtailment or increase in fishing impact. Fishing activity on demersal ecosystems generally shows size selection towards the large fish. This not only reduces their abundance, affecting the mean slope of the SS, but also erodes the species distribution by local depletions of large individuals that can affect the spatial heterogeneity in terms of fish size (Ciannelli *et al.*, 2013). In addition, the impact of regional-scale environmental changes such as the progressive increase in the bottom temperature in the Atlantic cannot be disregarded. Recent studies in the Cantabric-Galician shelf show warming-induced changes in the distribution of demersal fish that triggered a northward shift of the species distribution limits and changes in richness (Punzón *et al.*, 2016), which has also been observed in closed Atlantic regions (e.g. North Sea, Hiddink & Hofstede, 2008). This may decrease the species differentiation among habitats and contribute to the spatial homogeneity of the community in terms of size as observed in our results.

One of the most novel outcomes of our study is that the relationship between the mean slope of the SS and its CV is a recurrent fingerprint revealing structural properties of a given community. Our results reveal two contrasting patterns of this relationship related to different spatial structure of fish communities. First, an inverse relationship between the mean size-spectrum and its CV reveals communities spatially more even and homogenous when the SS slope is less steep. This was primarily observed in the Cantabric-Galician system. We argue that this pattern is a consequence of a regional-scale dynamics affecting this community with large geographic and bathymetric continuity of the fish communities, in which the increase of biomass of large fish occurs homogenously in space as a clear sign of ecosystems recovery (Modica *et al.*, 2014). This is also consistent with the competition theory (Pimm & Hyman, 1987) and previous studies (e.g. North Sea, Daan *et al.*, 2005) that suggest a compensatory redistribution of individuals after a size-dependent mortality (e.g. fishing). Fish take advantage of the less competitive environment where fishing has occurred, resulting in less spatial variation in the spectra. We expected observing this pattern in most systems. Conversely, the most recurrently observed pattern was the opposite – a direct relationship between the mean SS and its CV, revealing more heterogeneous communities as the slopes of the SS decrease. We suggest that this functional relationship is restricted to communities covering a small area (e.g. Gulf of Cadiz) or communities geographically and bathymetrically clustered, which is the case of deep-sea and Mediterranean Sea communities. In this case, the increase of community biomass of large fish occurs at small scales and most likely in asynchrony with other community patches that, in essence, increases the spatial complexity of the community in terms of fish size. This is consistent with the recent research that evidences that population and communities in the Mediterranean are adapted to environmental conditions at local scale, triggering contrasting dynamics at short distances (Puerta *et al.*, 2015). However, further research on mechanistic ecological modelling would be required to provide complementary evidences to this interpretation.

At local scale (i.e. sampling stations), the influence of small-sized fish was recurrent. In the shallow Atlantic and Mediterranean communities, the effects of small-sized fish are generally widespread. Besides a generally scattered effect of large fish observed in sporadic locations from deep shelf to middle slope, our results reveal an underlying pattern in the Cantabric-Galician upper slope with a clear geographic segregation of the large fish effects restricted to the Galician area (north-west of the Iberian Peninsula). Because this is the Atlantic area with the historically highest fishing impact within the study systems (MAGRAMA, 2012), a temporal decrease in the fishing impact in the Galician area reported in recent studies (Modica *et al.*, 2014) allowed increasing the abundance of large fish. This observation echoes the regional trend in CV in the Cantabric-Galician systems and suggests that a recovery of the Atlantic community might have started because of the decrease of fishing in this area and bathymetric strata. As evidenced in our study, this would allow the recovery of the large-sized component of the fish communities that ultimately triggered a progressive homogenization of the whole Cantabric-Galician Sea likely favoured by the bathymetric continuity of communities and a 'rescued' neighbouring effect (Shackell *et al.*, 2012).

In a meta-community context, communities with larger spatial continuity and spatial scale of similarity have an advantage in heavily exploited systems, because locally depleted populations are more likely to be 'rescued' by neighbouring areas (Shackell *et al.*, 2012). This is consistent with the pattern observed in the Atlantic shelf-slope ecosystems at the Cantabric-Galician Sea and its history of recovery (see above). By contrast, communities with a small spatial scale of similarity display higher complexity in the fish metacommunity structure (Shackell *et al.*, 2012). This might have the advantage of an 'ecological insurance' against local perturbations that are not easily transmitted to neighbouring areas. However, it has also the disadvantage of hampering the capacity of ecosystems to recover after long-term and established fishing impacts in a region because of the lack of the 'rescued' effect. This may be the case in the Mediterranean Sea with a documented long-term impact of fishing (Vasilakopoulos *et al.*, 2014).

CONCLUSIONS, BROAD SCALE IMPLICATIONS AND FUTURE CHALLENGES

Our study provides evidence of two contrasting pathways of both degradation and recovery of fish size-structure between the Atlantic and Mediterranean ecosystems. Atlantic communities, particularly those in the north of the Iberian Peninsula, have benefited from a broad geographic and bathymetric continuity of communities that provide them higher capabilities in terms of resilient mechanisms as observed in the recovery over the last decades. Such recovery mainly emerged from a reduction of fishing impact in the Galician waters (NW Iberian peninsula) that allowed an increase of biomass of large fish and consequent change in the size-structure of the whole region. By contrast, Mediterranean communities are much more fragmented and highly dependent on the variation of small fish. This isolation may hamper a potential recovery once anthropogenic pressures decrease in the region because all ecological processes will operate mainly at local scale.

Our study may have large implications for other Mediterranean and Atlantic areas. Current marine science calls for a better understanding of the consequences of the depletion of fish stocks in the structure of communities and ecosystems, but even more importantly for their future recovery capacity (Worm *et al.*, 2009). Although Atlantic fish populations have successfully recovered (Fernandes & Cook, 2013), no study investigated how this improvement has affected the dynamics and the structure of the Atlantic communities and ecosystems. This is of high relevance knowing that the 'rescue effect' has been an important mechanism of recovery observed in certain Atlantic ecosystems (Shackell *et al.*, 2012). Our study demonstrates that the mean and the spatial variability of size-structure are important elements to understand these mechanisms.

By contrast, Mediterranean stocks are in an alarming decline (Vasilakopoulos *et al.*, 2014) and large-scale research on the communities' size-structure is needed to understand to what extent the observed fragmented patterns are replicated in other Mediterranean areas. Given the relevance of fish size on marine food webs (Blanchard *et al.*, 2009), it is essential to understand whether the spatial and temporal patterns of variation of SS are a consequence of the chronic degradation of the Mediterranean systems or a natural fragmentation of the meta-communities. Our results provide the basis to frame further research on the spatiotemporal dynamics of fish size that will also benefit from taking into account the ecological function of different fish groups (Blanchard *et al.*, 2009; Rice *et al.*, 2013), to assess the health of marine ecosystems combining information of both structural properties and ecological functions.

ACKNOWLEDGEMENTS

We thank all the dedicated people, who have worked on the research vessel surveys of the Spanish Institute of Oceanography (IEO) included in the study. M.H. was funded by MYFISH project (EU contract number 289257) and a post-doctoral contract from the regional government of the Balearic Islands co-funded by the European Social Fund 2014-2020. This research is also framed in the project 'ECLIPSAME' (Synergistics effects of Climate and Fishing on the demersal ecosystems of the North Atlantic and western Mediterranean, CTM2012-37701) co-funded by the Spanish Ministry of Economy and Competitiveness (http://www.mineco.gob.es/) and the European Commission.

REFERENCES

Álvarez, M., Gomez-Gesteira, M., deCastro, M., Gomez-Gesteira, J.L. & Dias, J.M. (2010) Summer upwelling frequency along the western Cantabrian coast from 1967 to 2007. *Journal of Marine Systems*, **79**, 218–226.

Andersen, K.H. & Beyer, J. (2015) Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish and Fisheries*, **16**, 1–22.

Anderson, S.C., Cooper, A. & Dulvy, N.K. (2013) Ecological prophets: quantifying meta population portfolio effects. *Methods in Ecology and Evolution*, **4**, 971–981.

Balbín, R., López-Jurado, J.L., Flexas, M.M., Reglero, P., Vélez-Velchí, P., González-Pola, C., Rodríguez, J.M., García, A. & Alemany, F. (2014) Interannual variability of the early summer circulation around the Balearic Islands: driving factors and potential effects on the marine ecosystem. *Journal of Marine Systems*, **138**, 70–81.

Bertrand, J.A., Gil de Sola, L., Papaconstantinou, C., Relini, G. & Souplet, A. (2002) The general specifications of the MEDITS surveys. *Scientia Marina*, **66**, 9–17.

Blanchard, J.L., Dulvy, N.K., Jennings, S., Ellis, J.R., Pinnegar, J.K., Tidd, A. & Kell, L.T. (2005) Do climate and fishing influence size based indicators of Celtic Sea fish community structure. *ICES Journal of Marine Science*, **62**, 405–411.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.-J. & Benoît, E. (2009) How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*, **78**, 270–280.

Ciannelli, L., Fisher, J., Skern-Mauritzen, M., Hunsiker, M., Hidalgo, M., Frank, K. & Bailey, K. (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes. *Marine Ecology Progress Series*, **480**, 227–243.

Clarke, J., Milligan, R.J., Bailey, D.M. & Neat, F.C. (2015) A scientific basis for regulating deep-sea fishing by depth. *Current Biology*, **25**, 2425–2429.

Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Klavdija, J., Bellido, J.M. & Fiorentino, F. (2013) Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish and Fisheries*, **14**, 89–109.

Daan, N., Gislasson, H., Pope, J.C. & Rice, J.C. (2005) Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science*, **62**, 177–188.

Farriols, M.T., Ordines, F., Hidalgo, M., Guijarro, B. & Massutí, E. (2015) N90 index: a new approach to biodiversity based on similarity and sensitive to direct and indirect fishing impact. *Ecological Indicators*, **52**, 245–255.

Fernandes, P.G. & Cook, R.M. (2013) Reversal of fish stock decline in the Northeast Atlantic. *Current Biology*, **23**, 1432–1437.

Greenstreet, S.P.R. & Rogers, S.I. (2006) Indicators of the health of the fish community of the North Sea: identifying reference levels for an Ecosystem Approach to Management. *ICES Journal of Marine Science*, **63**, 573–593.

Hidalgo, M., Massutí, E., Guijarro, B., Moranta, J., Ciannelli, J., Lloret, J., Oliver, P. & Stenseth, N.C. (2009) Population effects and changes in life-history traits in relation to phase transitions induced by long-term fishery harvesting: European hake off the Balearic Islands. *Canadian Journal of Fisheries and Aquatic Science*, **66**, 1355–1370.

Hiddink, J.G. & Hofstede, R.T. (2008) Climate induced increases in species richness of marine fishes. *Global Change Biology*, **14**, 453–460.

Hsieh, C.H., Yamauchi, A., Nakazawa, T. & Wang, W.F. (2010) Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Science*, **72**, 165–178.

ICES (2010) *Manual for the international bottom trawl surveys*. Revision VIII. Addendum to ICES CM 2010 SSGESST/06. ICES, Lisbon, Portugal.

Jennings, S. & Dulvy, N.K. (2005) Reference points and reference directions for size-based indicators of community structure. *ICES Journal of Marine Science*, **62**, 397–404.

Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Boon, T. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934–944.

Kerr, S.R. & Dickie, L.M. (2001) *The biomass spectrum. A predator-prey theory of aquatic production*. Columbia University Press, New York, 320 pp.

Kolding, J. & Zweiten, A.M. (2014) Sustainable fishing of inland waters. *Journal of Limnology*, **73**, 132–148.

Law, R., Plank, M.J., James, A. & Blanchard, J.L. (2009) Size-spectra dynamics from stochastic predation and growth of individuals. *Ecology*, **90**, 802–811.

Levin, P.S., Damon, M. & Samhouri, J.F. (2010) Developing meaningful marine ecosystem indicators in the face of a changing climate. *Stanford Journal of Law, Science, and Policy*, **1**, 36–48.

MAGRAMA (2012) Estrategia marina para la demarcación noratlántica. Parte II. *Análisis de presiones e impactos*, 176 pp. Available at: http://www.mapama.gob.es/es/costas/temas/proteccion-medio-marino/II_Analisis_Presiones_Noratlantica_tcm7-203225.pdf. (In Spanish)

Massutí, E. & Reñones, O. (2005) Demersal resource assemblages in the trawl fishing grounds off the Balearic Islands (western Mediterranean). *Scientia Marina*, **69**, 167–181.

McCann, K.S. (2000) The diversity–stability debate. *Nature*, **405**, 228–233.

McCann, K.S., Gellner, G., McMeans, B.C., Deenik, T., Holtgrieve, G., Rooney, N., Hannah, L., Cooperman, M. & Nam, S. (2016) Food webs and the sustainability of indiscriminate fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, **73**, 656–665.

Modica, L., Velasco, F., Preciado, I., Soto, M. & Greenstreet, S.P.R. (2014) Development of the large fish indicator and associated target for a North-East Atlantic fish community. *ICES Journal of Marine Science*, **71**, 2403–2415.

Oguz, T., Macias, D., Garcia-Lafuente, J., Pascual, A. & Tintore, J. (2014) Fueling plankton production by a meandering frontal jet: a case study for the Alboran sea (Western Mediterranean). *PLoS ONE*, **9**, e111482.

Peliz, A., Marchesiello, P., Santos, A.M.P., Dubert, J., Teles-Machado, A., Marta-Almeida, M. & Le Cann, B. (2009) Surface circulation in the Gulf of Cadiz: inflow-outflow coupling and the Gulf of Cadiz slope current. *Journal of Geophysical Research*, **114**, C03011.

Pimm, S.L. & Hyman, J.B. (1987) Ecological stability in the context of multispecies fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**(S2), s84–s94.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effects models in S and S-PLUS*. Springer, New York.

Puerta, P., Hunsiker, M., Quetglas, A., Alvarez-Berastegui, D., Esteban, A., Gonzalez, M. & Hidalgo, M. (2015) Spatially explicit modeling reveals cephalopod distributions match contrasting trophic pathways in the western Mediterranean Sea. *PLoS ONE*, **10**, e0133439.

Punzón, A., Hernández, C., Abad, E., Castro, J., Pérez, N. & Trujillo, V. (2010) Spanish otter trawl fisheries in the Cantabrian Sea. *ICES Journal of Marine Science*, **67**, 1604–1616.

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J.M. & López-López, L. (2016) Response of a temperate demersal fish community to global warming. *Journal of Marine Systems*, **161**, 1–10.

Ramírez-Amaro, S., Ordines, F., Terrasa, B., Esteban, A., García, C., Guijarro, B. & Massutí, E. (2015) Demersal chondrichthyans in the western Mediterranean: assemblages and biological parameters of their main species. *Marine and Freshwater Research*, **67**, 636–652.

Rice, J. (2000) Evaluating fishery impacts using metrics of community structure. *ICES Journal of Marine Science*, **57**, 682–688.

Rice, J., Daan, N., Gislason, H. & Pope, J. (2013) Does functional redundancy stabilize fish communities? *ICES Journal of Marine Science*, **70**, 734–742.

Rossi, V., Ser-Giacomi, E., López, C. & Hernández-García, E. (2014) Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. *Geophysical Research Letters*, **60**, 86–99.

Sánchez, F. & Serrano, A. (2003) Variability of demersal fish communities of the Cantabrian Sea during the decade of the 1990s. *ICES Marine Science Symposia*, **219**, 249–260.

Shackell, N.L., Fisher, J.A.D., Frank, K.T. & Lawton, P. (2012) Spatial scale of similarity as an indicator of metacommunity stability in exploited marine systems. *Ecological Applications*, **22**, 336–348.

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J.G. & Gislason, H. (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science*, **62**, 384–396.

Silva, L., Vila, Y., Torres, M.A., Sobrino, I. & Acosta, J.J. (2011) Cephalopod assemblages, abundance and species distribution in the Gulf of Cadiz (SW Spain). *Aquatic Living Resources*, **24**, 13–26.

Stasko, A.D., Swanson, H., Majewski, A., Atchison, S., Reist, L. & Power, M. (2016) Influences of depth and pelagic subsidies on the size-based trophic structure of Beaufort Sea fish communities. *Marine Ecology Progress Series*, **549**, 153–166.

Sweeting, C.J., Badalamenti, F., D'Anna, G., Pipitone, C. & Polunin, N.V.C. (2009) Steeper biomass spectra of demersal fish communities after trawler exclusion in Sicily. *ICES Journal of Marine Science*, **66**, 195–202.

Trenkel, V. & Rochet, M.J. (2003) Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community. *Canadian Journal of Fisheries and Aquatic Science*, **60**, 67–85.

Trenkel, V. & Rochet, M.J. (2010) Combining time trends in multiple metrics for identifying persistent changes in population processes or environmental stressors. *Journal of Applied Ecology*, **47**, 751–758.

Trueman, C.N., Johnston, G., O'Hea, B. & MacKenzie, K.M. (2014) Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140669.

Vasilakopoulos, P., Maravelias, C.D. & Tserpes, G. (2014) Alarming decline of Mediterranean fish stocks. *Current Biology*, **24**, 1–6.

Worm, B., Hilborn, R., Baum, J.K. *et al.* (2009) Rebuilding global fisheries. *Science*, **325**, 578–585.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G. (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, NY.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Biomass spectra statistics of all the systems.
Appendix S2 Annul slope and CV of all biomass spectra.
Appendix S3 Relationship between mean slope and CV for all biomass spectra.

BIOSKETCH

Manuel Hidalgo is a post-doctoral researcher based at Spanish Institute of Oceanography. He is interested in regional and large-scale patterns in ecology, particularly in relation to the structure and function of marine populations, communities and ecosystems.

Author contributions: M.H. conceived the study and designed the analysis; A.Q., F.O., L.R., A.P., M.D., L.G.D., A.E. and E.M. participated in the long-term fieldwork; M.H. carried out the statistical modelling with input from F.O. and L.R. All authors contributed to the manuscript text.

Editor: Jani Heino