Spatio-temporal trends in diversity of demersal fish assemblages in the Mediterranean

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Summary: The high species richness, coupled with high proportion of endemism, makes the Mediterranean one of the world's 'biodiversity hotspots'. However, the continuous increase in fisheries in the last few decades has led to the overexploitation of their main commercial stocks. Using fishery-independent data collected under the framework of the MEDITS trawl surveys carried out over the last 20 years, we study the demersal fish diversity pattern in the Mediterranean at a large spatial and temporal scale to determine whether it is being affected by the general fishing overexploitation of the demersal resources. The detected diversity trends are compared with the spatio-temporal variation in bottom trawl fishing effort in the Mediterranean. Our results show a stability and even recovery of demersal fish diversity in the Mediterranean together with higher diversity values on the continental shelves of the Balearic Islands, Sardinia, Sicily and the Aegean Sea. At large temporal and spatial scales, the high diversity of demersal assemblages in the Mediterranean is associated with a reduction in bottom trawl fishing effort. The inclusion of species other than target ones through diversity indices is important in the implementation of an ecosystem-based fisheries management.

Keywords: biodiversity; fish assemblages; MEDITS; bottom trawling; fishing effort; Mediterranean Sea.

Tendencias espacio-temporales en la diversidad de peces demersales del Mediterráneo

Resumen: Debido a su alta riqueza específica y su gran proporción de organismos endémicos, el Mediterráneo es considerado un punto caliente de biodiversidad. No obstante el continuo crecimiento de las pesquerías en las últimas décadas ha

desembocado en una sobrexplotación de sus principales stocks comerciales. A través de datos independientes de las pesquerías recogidos en el marco de las campañas MEDITS desarrolladas durante las dos últimas décadas se ha estudiado el patrón de diversidad de peces demersales en el Mediterráneo a través de largas escalas temporales y espaciales para evaluar si este patrón se ve afectado por el estado general de sobrexplotación de sus recursos demersales. A continuación las tendencias detectadas en la diversidad han sido comparadas a la variación espacio-temporal del esfuerzo de la pesca de arrastre a través del Mediterráneo. Nuestros resultados muestran una estabilidad e incluso recuperación de la diversidad de peces demersales en el Mediterráneo junto a valores altos de diversidad en las plataformas continentales de las Islas Baleares, Cerdeña, Sicília y el mar Egeo. La alta diversidad de las asociaciones de peces demersales a escala tanto espacial como temporal está asociada a una reducción del esfuerzo pesquero. La inclusión de especies distintas a las objetivo a través de índices de diversidad es relevante en la implementación de la aproximación ecosistémica a la gestión de las pesquerías.

Palabras clave: biodiversidad; asociaciones de peces; MEDITS; arrastre de fondo; esfuerzo pesquero; mar Mediterráneo.

INTRODUCTION

The Mediterranean is considered one of the Large Marine Ecosystems of the world, owing to its bathymetry, hydrography, productivity and trophic webs (Duda and Sherman 2002). It is a semi-enclosed sea connected to the Atlantic Ocean through the Gibraltar Strait, to the Black Sea through the Dardanelles Strait and to the Red Sea through the artificial Suez Channel (Fig. 1). It acts as a concentration basin, and evaporation is higher in its eastern basin, causing the water level to decrease and salinity to increase from west to east (Coll et al. 2010). While temperature also increases eastwards (Coll et al. 2010), surface productivity, organic matter availability at the seafloor and the biomass of megabenthic fauna of deep ecosystems decrease eastwards (Bosc et al. 2004, Danovaro et al. 1999, Tecchio et al. 2011). The Mediterranean has narrow continental shelves and a large area of open sea. In fact, the continental shelf covers about 20% of the Mediterranean bottoms, whereas the slope covers about 60% (Sardà et al. 2004). Therefore, a large part of this basin can be classified as deep sea (Coll et al. 2010).

The high species richness, coupled with a high proportion of endemism, makes the Mediterranean one of the world's 'biodiversity hotspots' (Moranta et al. 2008, Coll et al. 2010, Lejeusne et al. 2010). Environmental variables such as temperature, productivity and distance from the Strait of Gibraltar have been shown to be causes of fish species richness distribution (Ben Rais Lasram et al. 2009, Meléndez et al. 2017). However, this high biodiversity is presently threatened by the combined action of anthropogenic impacts, introduction of alien species and climate change (Bianchi et al. 2012). Among human activities, fisheries are one of the most important factors affecting marine resources and ecosystems.

It is well known that fisheries have profoundly modified the structure of marine ecosystems (Dayton et al. 1995, Hall 1999, Kaiser and de Groot 2000). Effects of fishing on marine ecosystems include shifts in the food-web structure due to changes in predator-prey relationships (Kaiser et al. 2002); changes in size structure due to vulnerability and selection of fishing for large individuals (Gislason 2002, Jennings and Dulvy 2005, Daan et al. 2005); genetic selection of species with particular life-history traits, such as a higher growth rate and earlier age-at-maturity (Fromentin and Fonteneau 2001, Jørgensen et al. 2007); changes in the spatial distribution of target species (e.g. Ciannelli et al. 2013); effects on the population of non-target species (Pranovi et al. 2001, Ordines et al. 2014); and decrease of habitat complexity and changes on the benthic community structure (e.g. Callaway et al. 2002).

The natural resources of the Mediterranean have been subject to human exploitation since ancient times, when coastal communities started to use different fishing gears, some of which are still in use (Farrugio et al. 1993). Dramatic long-term changes in marine communities took place before the industrialization of fisheries that occurred in the 1950s, and have already been documented in some areas, such as the Adriatic Sea (Fortibuoni et al. 2010). Until 1950, the exploitation of Mediterranean resources was limited to fishing areas shallower than 200 m depth. In the last few decades, with the decline of stocks on the continental shelf, increasing market demand and the introduction of new technologies, trawl fisheries have expanded offshore and towards the deeper waters of the continental slope (Roberts 2002, Morato et al. 2006) to target valuable resources such as red shrimps (e.g. Demestre and Martín 1993, Guijarro et al. 2008, Masnadi et al. 2018).

In this area, fisheries are assessed within the framework of the General Fisheries Commission for the Mediterranean (GFCM), the regional fisheries management organization of the Mediterranean. Of the 27 Mediterranean stocks of fishing target species assessed by the GFCM in its last report, about 80% were considered overexploited (GFCM 2016). The presence of a high diversity of species and the absence of large monospecific stocks comparable to those inhabiting some wide areas of the open oceans are characteristic
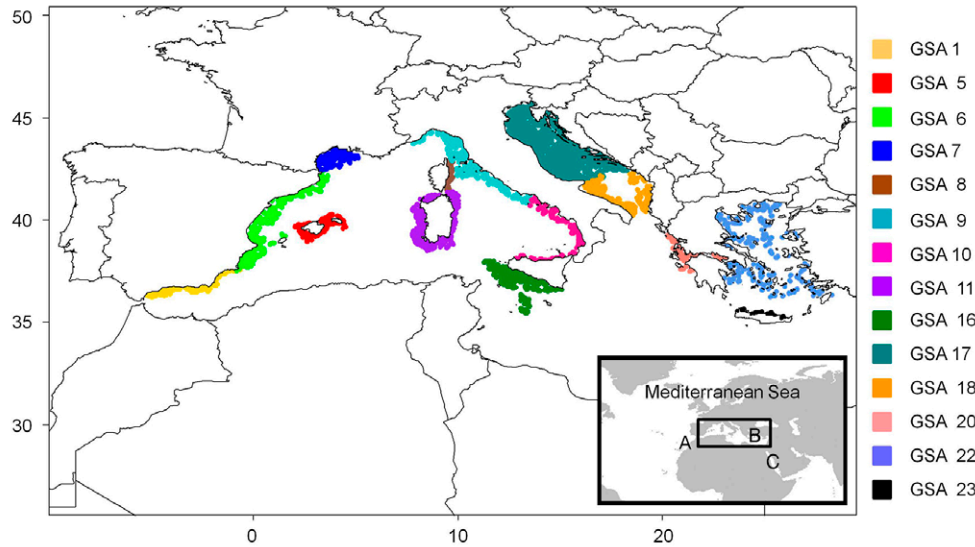
Fig. 1. – Map of the study area showing the 17540 hauls sampled between 1994 and 2015 in 15 geographical sub-areas (GSAs). Each colour corresponds to one of the GSAs defined by the GFCM (http://www.gfcm.org). The smaller map shows the location of the Mediterranean and its connections to the Atlantic Ocean through the Gibraltar Strait (A), the Black Sea through the Dardanelles Strait (B) and the Red Sea through the artificial Suez Channel (C).

of the Mediterranean demersal fisheries (Farrugio et al. 1993). Assessment at a community level is therefore crucial, particularly due to the multispecies nature of the bottom trawl fishery and also because a decline in the diversity of demersal assemblages has been reported due to fishing exploitation (e.g. Ungaro et al. 1998, Sabatini et al. 2013, Farriols et al. 2017). Assessment at a community level is also a requirement for the implementation of an ecosystem-based management of fisheries (Browman and Stergiou 2004).

The aim of this work is to study the demersal fish diversity pattern in the Mediterranean at a large spatial and temporal scale and to assess whether this pattern is being affected by the general fishing overexploitation of demersal resources in the area. To do so, we used fishery-independent data collected under the framework of the MEDITS trawl surveys carried out during the last 20 years. The detected trends were compared with the spatio-temporal variation in bottom trawl fishing effort in the Mediterranean Sea.

MATERIALS AND METHODS

Data

Demersal fish were collected during MEDITS bottom trawl surveys conducted from 1994 to 2015 in 14 geographical sub-areas (GSAs) along the European coasts of the Mediterranean Sea. Some GSAs have gaps in their sampling years: i) GSA 5 started sampling in 2001; ii) there are no data in 2002 for GSA 8 (technical problem of the boat); and iii) there are no data for 2002, 2007, 2009-2013 and 2015 for GSAs 20, 22 and 23. Sampling was performed during spring-summer in daylight hours using the GOC73 experimental gear, whose efficiency for catching demersal species has been tested by Fiorentini et al. (1999) and Dremière et al. (1999). For more details about the sampling strategy and protocol see Bertrand et al. (2002) and the MEDITS hand-

Table 1. – Name of the areas and number of samples analysed for each GSA.

GSA	Area	Samples
GSA 1	Northern Alboran Sea	743
GSA 5	Balearic Islands	650
GSA 6	Northern Spain	1459
GSA 7	Gulf of Lions	1143
GSA 8	Corsica	451
GSA 9	Ligurian, northern and central Tyrrhenian Sea	2468
GSA 10	Central and southern Tyrrhenian Sea	1333
GSA 11	Sardinia	1811
GSA 16	Strait of Sicily	1492
GSA 17	Northern Adriatic Sea	2296
GSA 18	Southern Adriatic Sea	1684
GSA 20	Eastern Ionian Sea	308
GSA 22	Aegean Sea	1427
GSA 23	Crete	175

book, instruction manual version 9 (MEDITS Working Group 2017).

A total of 17540 hauls performed between 46 and 866 m depth were analysed (Table 1, Fig. 1). Hauls shallower than 46 m depth were excluded from the analysis because they could not be found for all GSAs. The catch of each sample was sorted, identified to species level, counted, weighed and standardized to square km by using the horizontal opening of the net and the distance covered in each haul. Species with a pelagic or mesopelagic behaviour, like most species of the families Myctophydae (e.g. *Ceratoscopelus maderensis*) and Cupleidae (e.g. *Engraulis encrasicolus*), were excluded from the analysis. A species accumulation curve for each GSA was performed and we confirmed that differences in number of species were not due to differences in the number of hauls considered for each GSA (Table 1, Fig. S1).

Fish assemblages and diversity

Cluster analysis was used to analyse the structure of demersal fish assemblages and to identify different assemblages according to depth strata in each GSA. Rela-

tionships among samples were detected by hierarchical agglomerative clustering with group-average linkage after a forth root transformation of the data. The distance used to make groups was the Bray-Curtis similarity. These analyses were performed using PRIMER 7 (Clarke et al. 2014). The calculus of diversity indices explained below was made taking into account the groups of samples obtained from the cluster analysis.

The N_{90} diversity index was calculated following the procedure described by Farriols et al. (2015). It is the mean number of species contributing up to 90% of within-group similarity calculated from abundance data expressed as N km^{-2} and assigned a priori to groups. The calculation of N_{90} starts with the calculation of the contribution of each species to the within-group similarity using the Bray-Curtis similarity index (Bray and Curtis 1957), as proposed by Clarke (1993):

$$S_{jk}(i) = 100 \times \frac{2 \times \min(y_{ij}, y_{ik})}{\Sigma_{i=1}^{p}(y_{ij} + y_{ik})} ;$$

where y_{ij} is the abundance of the species i at the sampling site j, y_{ik} is the abundance of the species i at the sampling site k, p is the total number of species in j and k, and min (y_{ij}, y_{ik}) is the minimum value of the abundance of species i between the sampling sites j and k, also considering zeros.

The contribution of each species i to the total similarity of the group S_i is the mean value of $S_{jk}(i)$ for the assigned group, and the total similarity in a group (Sim) is the addition of S_i for all the species in the group:

$$Sim = \Sigma_{i=1}^{p} S_i .$$

Then, the contribution of S_i is calculated as a percentage of Sim. Species contributions are calculated for each re-sampling in a jack-knife routine, which removes a number of samples each time, producing lists of contribution to similarity by species in each re-sampling. Because the groups of samples for each GSA, strata and year were large, we removed 10% of the samples in each re-sampling with a 50% replacement. That is, 50% of samples removed in a re-sampling must be different from previous ones. In this way, we obtain values of deviation for N_{90} other than 0 for groups with a large number of observations. The N_{90} diversity index is the mean number of species which accumulate up to 90% of within-group similarity in all the re-samplings. N_{90} was calculated using R scripts, version 3.1.1 (R Core Team 2014). Similarity percentage analysis (SIMPER) for each group of samples was also undertaken to see their species composition.

Diversity indices, such as species richness (S) and Pielou evenness (J'), which have shown some kind of response to fishing impact for demersal fish assemblages in the Mediterranean (Farriols et al. 2017), were also included in this work. These traditional indices are also helpful for comparison with previous works. S is the raw number of species in each haul and J' was calculated as follows:

$$J' = \frac{\Sigma_{i=1}^{S} p_i \ln p_i}{\ln S} ;$$

where p_i is the proportion of all individuals belonging to species i and S is the total number of species in the sample.

Fishing effort

Information on annual fishing effort was collected from the working group reports of the GFCM (http://www.fao.org/gfcm/data/safs/en/) and the Scientific, Technical and Economic Committee for Fisheries (STECF, https://stecf.jrc.ec.europa.eu/reports/medbs). Fishing effort data were compiled by trawl fleet targeting different species. The units vary between the different reports, being mainly provided in terms of number of vessels, kilowatts per days at sea and gross tonnage per days at sea (see Table S1).

To estimate fishing effort in each depth stratum obtained from cluster analysis, the strata were associated with the main target species of the fleets. Because target species varied between GSAs, we considered i) *Mullus barbatus* or *Mullus surmuletus* for the continental shelf; ii) *Nephrops norvegicus* or *Parapenaeus longirostris* for the shelf break/upper slope; and iii) *Aristeus antennatus* or *Aristaeomorpha foliacea* for the lower slope.

To compare temporal trends in fishing effort and demersal fish diversity, the longest series of fishing effort available for each GSA and depth stratum regardless of the kind of units were selected. When we found no values of fishing effort for a certain GSA, experts were contacted to obtain a trend in number of vessels in that area.

Temporal and spatial analysis

In order to analyse temporal trends in diversity, linear regressions were fitted to the mean values of S, J' and N_{90} for each year, GSA and depth stratum. Linear regression analyses with the annual values of fishing effort in each GSA (see Fishing effort section in Materials and Methods) and depth stratum were also performed. The exploration of the scatter plots of the time series together with the comparison of Pearson (assuming linear pattern) and Spearman (suitable also for other monotonic patterns than the linear) correlation coefficients were done. The values of both correlation coefficients were similar, indicating that the detected trends could be fitted using a simple linear model. Thus, the linear regression and the Pearson coefficient of correlation were presented along with the coefficient of determination (i.e. variance explained). These analyses were carried out with R, version 3.1.1 (R Core Team 2014).

In order to observe spatial differences in diversity by GSA, time series of mean values and standard deviation of each diversity index (see Data section for years included in each GSA) were plotted. For those series with a significant temporal trend, the diversity values at the beginning and the end of the time series were plotted instead of mean values and standard deviation.

SIMPER analysis for each group of samples from N_{90} was also performed to see differences in species
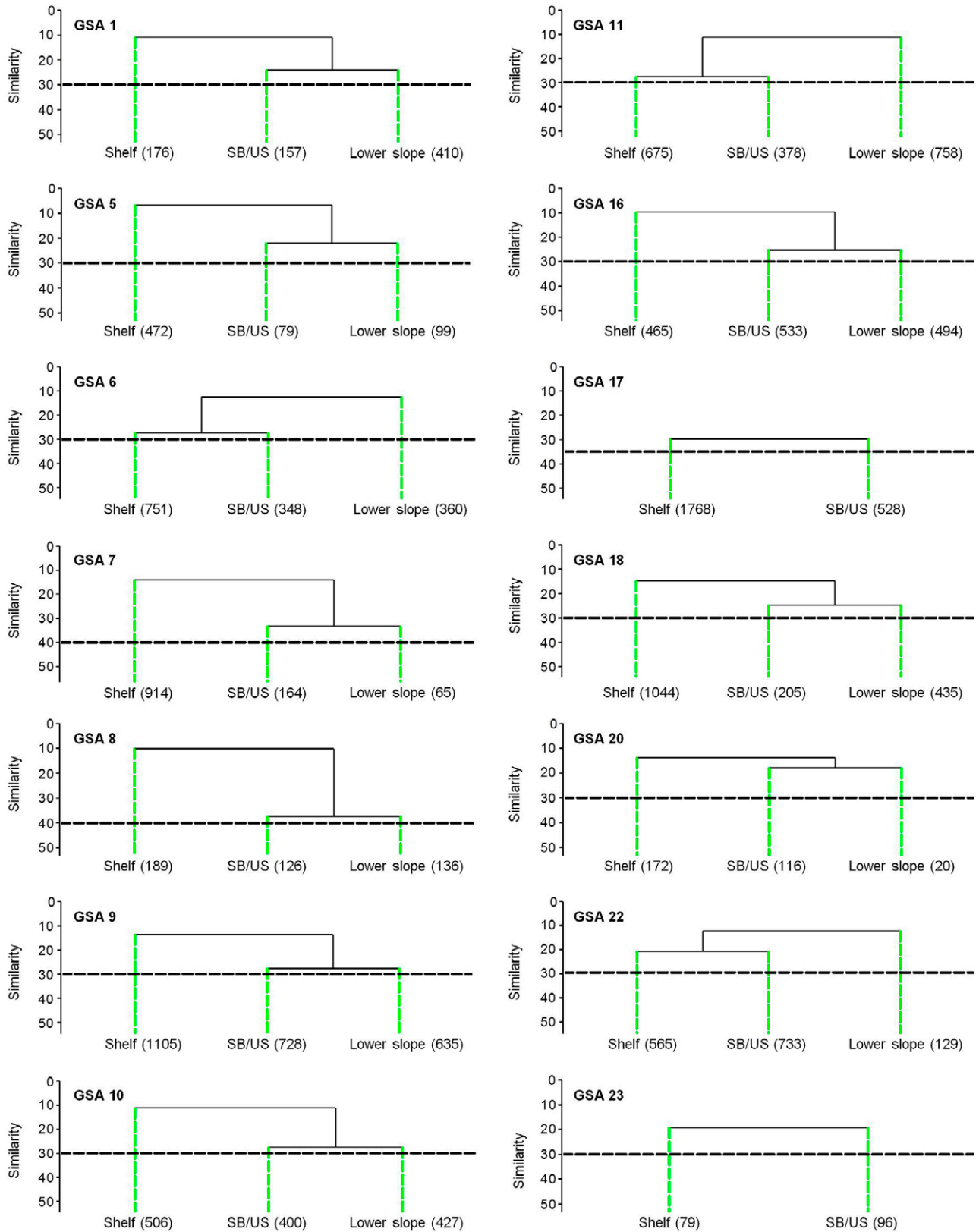
Fig. 2. – Cluster of samples obtained from MEDITS surveys. The data used for the cluster analysis were the double root transformation of abundances of demersal fish species for each sample during the sampling period of each GSA. The dashed line shows the similarity level used to classify the depth strata: shelf, shelf break/upper slope (SB/US) and lower slope. The number in brackets represents the number of samples in each depth stratum.

composition in each GSA. The percentage of contribution of each species to within-group similarity was calculated as the mean value of species contributions to similarity, taking all groups of observations by year and stratum for each GSA into account.

RESULTS

Community structure

Results from cluster analysis detecting main fish assemblages for each GSA are shown in Figure 2. Three groups of samples were selected from most GSAs, corresponding to a level of similarity of between 30% and 40%. Maximum, minimum and mean depths of each cluster group per GSA were obtained. According to these depth values, samples were grouped in three different depth strata: shelf, shelf break/upper slope and lower slope (Table 2, Fig. 2). For GSAs 17 and 23 only two groups were selected. GSA 17 has no samples below 350 m, and GSA 23 has a negligible sample number over 496 m (Table 2). For GSAs 7 and 20 samples in the lower slope group were not enough to calculate the N_{90} throughout the time series, so both lower slope groups were omitted from the temporal and spatial analysis.

In 9 out of the 12 GSAs showing lower slope samples, samples from the shelf break/upper slope clustered with samples from the lower slope. The exceptions were GSAs 6, 11 and 22, where samples from the shelf break/upper slope clustered with those from the continental shelf. Minimum, maximum and mean depths for each group of samples from cluster analysis are shown in Table 2. Mean depth of continental shelf samples ranged from 76 m in GSA 1 to 125 m in GSA 10, while for the shelf break/upper slope they ranged from 180 m in GSA 17 to 421 m in GSA 7, and for the lower slope between 496 m in GSA 11 and 699 m in GSA 7.

Temporal trends

Although the analysis of temporal evolution for N_{90}, S and J' showed no significance in most GSAs and depth strata (Table 3, Fig. 3 and Figs S2-S4), some trends were detected. N_{90} increased on the continental shelf of GSAs 1, 8 and 20, the shelf break/upper slope of GSAs 7, 11 and 18 and the lower slope of GSA 11 and only decreased on the shelf break/upper slope of GSA 5 (Table 3, Fig. 3 and Fig. S2). S increased on the continental shelf of GSAs 8 and 10, the shelf break/upper slope of GSAs 7, 8, 10 and 22 and the lower slope of GSAs 8, 10, 11, 16 and 18 and decreased on the shelf break/upper slope of GSA 17 and the lower slope of GSA 9 (Table 3, Fig. 3 and Fig. S3). J' increased on the continental shelf of GSA 7, the shelf break/upper slope of GSAs 7 and 8 and the lower slope of GSA 11 and decreased on the continental shelf of GSAs 10 and 16, the shelf break/upper slope of GSAs 5 and 22 and the lower slope of GSAs 1 and 8 (Table 3, Fig. 3 and Fig. S4). These trends were confirmed when the last year of the time series (2014) for GSAs 20, 22 and 23 was excluded (Table 3).

Table 2. – Minimum, maximum and mean depth of samples grouped in each depth stratum (shelf, shelf break/upper slope and lower slope) from cluster analysis for each GSA.

GSA	Strata	Minimum depth	Maximum depth	Mean depth
GSA 1	Shelf	50	168	76
	Shelf break/upper slope	118	373	203
	Lower slope	219	807	519
GSA 5	Shelf	46	258	108
	Shelf break/upper slope	316	698	402
	Lower slope	581	756	678
GSA 6	Shelf	50	147	84
	Shelf break/upper slope	82	392	183
	Lower slope	257	798	505
GSA 7	Shelf	55	155	93
	Shelf break/upper slope	214	705	421
	Lower slope	414	866	699
GSA 8	Shelf	56	158	94
	Shelf break/upper slope	261	510	350
	Lower slope	405	583	510
GSA 9	Shelf	50	399	118
	Shelf break/upper slope	141	640	340
	Lower slope	364	757	559
GSA 10	Shelf	50	350	125
	Shelf break/upper slope	170	616	365
	Lower slope	339	693	594
GSA 11	Shelf	50	292	97
	Shelf break/upper slope	109	357	198
	Lower slope	219	725	496
GSA 16	Shelf	51	220	94
	Shelf break/upper slope	108	654	333
	Lower slope	436	794	630
GSA 17	Shelf	50	235	91
	Shelf break/upper slope	62	332	180
GSA 18	Shelf	50	349	104
	Shelf break/upper slope	111	397	270
	Lower slope	247	732	501
GSA 20	Shelf	55	189	94
	Shelf break/upper slope	149	664	379
	Lower slope	483	800	654
GSA 22	Shelf	50	340	109
	Shelf break/upper slope	107	708	336
	Lower slope	337	791	579
GSA 23	Shelf	57	155	91
	Shelf break/upper slope	115	496	245

When quantitative analysis in temporal evolution of fishing effort could be made, the detected significance mainly showed a decreasing trend (Table 4, Fig. 3). This is the case of the continental shelf in GSAs 1, 5, 6 and 7, the shelf break/upper slope in GSAs 1, 11, 17 and 18 and the lower slope in GSAs 5 and 11. It increased only on the continental shelf and the lower slope of GSA 18. Expert knowledge suggested increasing trends in fishing effort for the lower slope in GSAs 20, 22 and 23 and decreasing trends on the continental shelf of GSAs 8, 9, 16, 20, 22 and 23 and on the lower slope of GSAs 1, 7 and 8 (Table 4, Fig. 3).

In 6 of the 7 cases in which an increment of N_{90} was detected, it coincided with a decrease in fishing effort (Tables 3-4, Fig. 3). Of the 11 cases showing increases in species richness, S, only in 3 cases was the increase in S coupled with a decrease in fishing effort. In 5 cases there was no trend in fishing effort, while in only one case the increase in S was coupled with an increase in fishing effort. In 2 cases, no information on the temporal evolution of fishing effort was available (Tables 3-4, Fig. 3). 10 GSAs showed significant trends in Pielou eveness, J'; in 2 of them J' increased and fishing effort decreased, while 3 GSAs showed a decrease in both J' and fishing

Table 3. – Results of linear regression analysis of the time series for N_{90}, species richness (S) and Pielou evenness (J') for each GSA and depth stratum (shelf, shelf break/upper slope and lower slope). Slope values of the adjusted linear regressions (b), adjusted R-squared values and p-values (p) are presented. *, p <0.05; **, p <0.01; ***, p <0.001. For GSAs 20, 22 and 23: [a] results for time series 1994-2006; and [b] results for time series 1994-2014.

Index	GSA	Shelf b	Shelf Adjusted R^2	Shelf p	Shelf break/upper slope b	Shelf break/upper slope Adjusted R^2	Shelf break/upper slope p	Lower slope b	Lower slope Adjusted R^2	Lower slope p
N_{90}	GSA 1	0.209	0.051	*	0.047	–0.050	0.383	0.001	0.430	0.955
	GSA 5	–0.090	–0.010	0.287	–0.286	0.473	**	0.037	–0.052	0.565
	GSA 6	–0.027	–0.029	0.683	0.063	–0.034	0.321	–0.112	0.031	0.059
	GSA 7	0.041	0.200	0.462	0.079	0.391	*			
	GSA 8	0.195	–0.052	**	0.089	0.294	0.070	0.041	0.376	0.175
	GSA 9	–0.005	–0.044	0.923	–0.027	0.105	0.483	–0.013	–0.049	0.493
	GSA 10	–0.101	0.463	0.128	0.068	0.005	0.121	–0.014	0.025	0.523
	GSA 11	0.084	–0.031	0.136	0.090	0.119	*	0.083	0.338	*
	GSA 16	–0.066	0.455	0.398	0.019	0.025	0.593	0.012	–0.044	0.540
	GSA 17	0.012	0.088	0.540	0.013	0.083	0.798			
	GSA 18	–0.036	0.004	0.647	0.141	–0.046	*	–0.036	0.031	0.111
	GSA 20[a]	0.487	0.503	**	0.115	–0.066	0.553			
	GSA 20[b]	0.315	–0.066	**	0.225	0.007	0.069			
	GSA 22[a]	0.054	–0.065	0.577	–0.110	0.023	0.289	–0.053	–0.003	0.351
	GSA 22[b]	0.064	–0.070	0.279	0.044	0.344	0.579	0.015	0.045	0.706
	GSA 23[a]	0.075	0.061	0.231	–0.156	–0.007	0.360			
	GSA 23[b]	0.099	–0.090	0.098	0.038	0.152	0.740			
S	GSA 1	–0.044	–0.040	0.658	0.010	–0.049	0.898	0.036	0.005	0.305
	GSA 5	0.013	–0.082	0.914	–0.136	0.092	0.154	–0.089	–0.005	0.351
	GSA 6	–0.030	–0.044	0.728	0.090	0.018	0.254	–0.017	–0.041	0.674
	GSA 7	–0.055	–0.017	0.427	0.142	0.331	**			
	GSA 8	0.161	0.169	*	0.149	0.180	*	0.134	0.203	*
	GSA 9	–0.027	–0.026	0.504	–0.023	–0.026	0.505	–0.061	0.151	*
	GSA 10	0.122	0.138	*	0.197	0.411	***	0.165	0.336	**
	GSA 11	0.064	0.026	0.226	0.041	–0.017	0.433	0.080	0.227	*
	GSA 16	0.026	–0.035	0.600	0.112	0.101	0.082	0.105	0.145	*
	GSA 17	0.010	–0.048	0.861	–0.130	0.196	*			
	GSA 18	0.041	–0.031	0.550	0.109	0.055	0.152	0.142	0.278	**
	GSA 20[a]	0.297	0.149	0.118	0.582	0.492	**			
	GSA 20[b]	0.166	0.072	0.182	0.230	0.117	0.136			
	GSA 22[a]	0.099	–0.042	0.471	0.359	0.410	*	–0.251	0.465	*
	GSA 22[b]	0.089	0.019	0.286	0.304	0.546	**	–0.031	–0.077	0.712
	GSA 23[a]	–0.021	–0.111	0.957	–0.095	–0.088	0.742			
	GSA 23[b]	0.274	0.035	0.257	0.134	–0.034	0.466			
J'	GSA 1	0.003	0.051	0.160	0.000	–0.050	0.988	–0.004	0.430	***
	GSA 5	–0.003	–0.010	0.370	–0.020	0.473	**	0.002	–0.052	0.562
	GSA 6	0.001	–0.029	0.533	0.001	–0.034	0.589	–0.002	0.031	0.210
	GSA 7	0.004	0.200	*	0.007	0.391	**			
	GSA 8	0.000	–0.052	0.937	0.004	0.294	**	–0.004	0.376	**
	GSA 9	0.001	–0.044	0.745	0.002	0.105	0.077	0.000	–0.049	0.874
	GSA 10	–0.008	0.463	***	0.002	0.005	0.304	–0.002	0.025	0.229
	GSA 11	–0.001	–0.031	0.554	0.004	0.119	0.064	0.004	0.338	**
	GSA 16	–0.005	0.455	***	0.002	0.025	0.230	0.000	–0.044	0.729
	GSA 17	–0.002	0.088	0.098	–0.004	0.083	0.104			
	GSA 18	0.002	0.004	0.312	–0.001	–0.046	0.790	–0.001	0.031	0.211
	GSA 20[a]	–0.003	–0.023	0.406	–0.003	–0.090	0.688			
	GSA 20[b]	–0.001	–0.066	0.663	0.004	0.007	0.320			
	GSA 22[a]	–0.002	–0.059	0.549	–0.013	0.673	***	–0.003	–0.042	0.461
	GSA 22[b]	0.001	–0.070	0.710	–0.007	0.344	*	–0.004	0.045	0.237
	GSA 23[a]	–0.004	–0.065	0.548	–0.018	0.329	*			
	GSA 23[b]	0.000	–0.090	0.937	–0.009	0.152	0.093			

Table 4. – Results of linear regression analysis of the time series of fishing effort of the longest series available for each GSA and depth stratum (shelf, shelf break/upper slope and lower slope). Slope values of the adjusted linear regressions (b), adjusted R-squared values and p-values (p) are presented. Qualitative values of slopes are obtained from expert knowledge. *, p <0.05; **, p <0.01; ***, p <0.001; ns, non-significant.

GSA	Shelf b	Shelf Adjusted R^2	Shelf p	Shelf break/upper slope b	Shelf break/upper slope Adjusted R^2	Shelf break/upper slope p	Lower slope b	Lower slope Adjusted R^2	Lower slope p
GSA 1	–8.800	0.717	*	–10.890	0.865	***	Decreasing		
GSA 5	–5.118	0.898	***	7.500	0.163	0.175	–7.530	0.526	**
GSA 6	–11.659	0.808	***	3.248	0.071	0.204	0.000	0.510	0.117
GSA 7	–13.821	0.765	**				Decreasing		
GSA 8	Decreasing						Decreasing		
GSA 9	Decreasing			1.820	–0.081	0.874	8.109	–0.088	0.669
GSA 10	Increasing		ns	–7.385	0.197	0.063	Decreasing		ns
GSA 11	63.572	0.390	0.058	–13.226	0.372	*	–25.227	0.867	***
GSA 16	Decreasing						–4.700	0.167	0.272
GSA 17	9.617	–0.054	0.467	–6.822	0.360	*	Decreasing		ns
GSA 18	75.448	0.644	**	–14.548	0.581	*	29.516	0.301	*
GSA 20	Decreasing						Increasing		
GSA 22	Decreasing						Increasing		
GSA 23	Decreasing						Increasing		

Fig. 3. – Trends obtained from linear regression of N_{90}, species richness (S), Pielou evenness (J') and fishing effort (FE) per GSA and depth stratum (shelf, shelf break/upper slope and lower slope). Trends obtained from the analysis are in continuous lines and trends from expert knowledge in discontinuous line and grey background. n.s., non-significant trends; -, no data available. For GSAs 20, 22 and 23 trends of time series 1994-2006 and 1994-2014 are presented. When results of trends differ, trends from 1994-2006 are presented on the left and trends from 1994 to 2014 on the right of the cell.
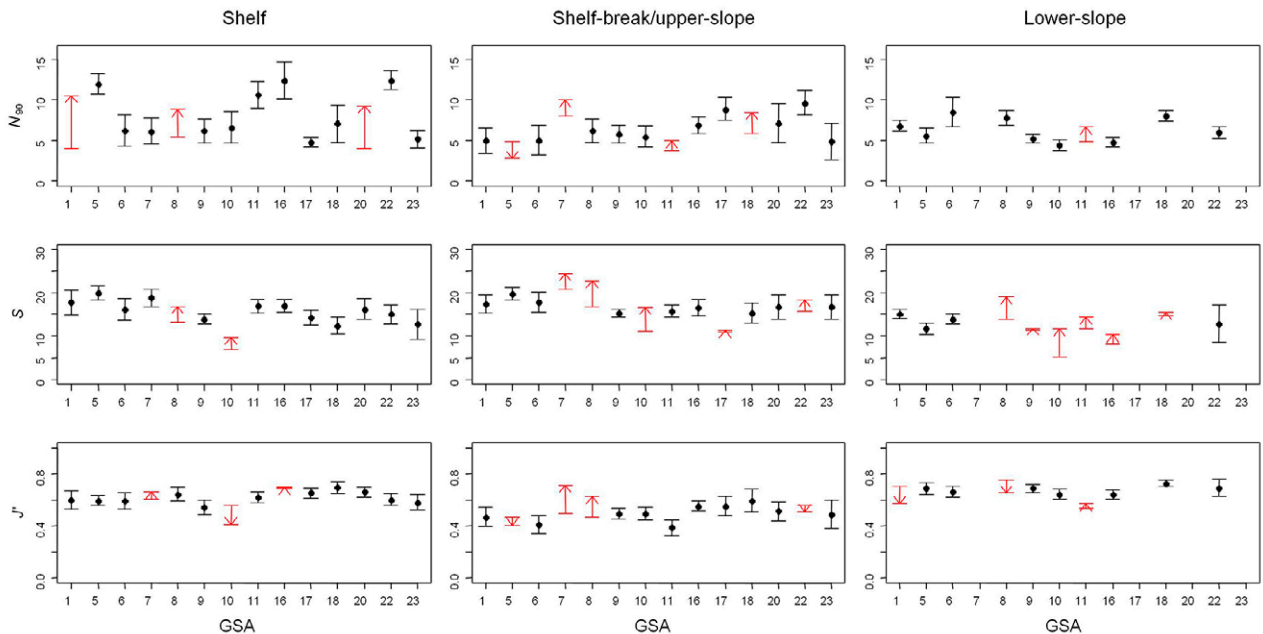

Fig. 4. – Mean values and standard deviations of N_{90}, species richness (S) and Pielou evenness (J') during the whole time series considered for each GSA and depth strata (shelf, shelf break/upper slope and lower slope). In series with a significant temporal trend, values at the beginning and end of the time series are presented in red. Red arrows point to the last value of the time series. For GSAs 20, 22 and 23 the whole time series were taken into account (1994-2014). Note that in some cases the trend of time series does not match the arrow's direction (see Table 2).

effort. Two GSAs showed a decrease in J' coupled with no trend in fishing effort, while no information on fishing effort trend was available in 3 cases (Tables 3-4, Fig. 3).

Spatial patterns

Mean values of N_{90}, S and J' showed differences between GSAs and depth strata (Fig. 4). Regarding

N_{90}, the continental shelf of GSAs 5, 11, 16 and 22 showed higher values than the rest of the GSAs in this depth stratum and even than the shelf break/upper slope and lower slope values. Within the shelf break/upper slope, the highest values of N_{90} were estimated in GSAs 7, 16, 17, 18, 20 and 22, while on the lower slope the highest values were for GSAs 6, 8 and 18. S showed similar values on the continental shelf of all GSAs, with the exception of GSA 10, which showed a lower value. A similar situation was observed on the shelf break/upper slope, with similar values of S in all GSAs, except for GSA 17 with a lower value, and GSAs 7 and 8, which showed the highest values. On the lower slope, the values of S were similar in all GSAs, with the exception of GSAs 9, 10 and 16, which showed lower values. J' showed similar values on the continental shelf in all GSAs, except GSAs 9 and 10, which showed lower values. The same scenario was observed on the shelf break/upper slope, with similar values of J' in all GSAs with the exception of GSAs 1, 5, 6 and 11, which showed lower values. On the lower slope, GSA 11 showed the lowest value of J', while similar values were obtained in the rest of the GSAs.

The similarity percentage (SIMPER) analysis also showed differences in the species contribution between GSAs and depth strata (Tables 5 and 6). The species with the highest percentage contribution to within-group similarity on the continental shelf, shelf break/upper slope and lower slope, respectively, were the following: *Serranus hepatus, Gadiculus argenteus* and *Galeus melastomus* in GSA 1; *Scyliorhinus canicula, G. argenteus* and *Phycis blennoides* in GSA 5; *Merluccius merluccius, Micromesistius poutassou* and *P. blennoides* in GSA 6; *Mullus barbatus, G. argenteus* and *G. melastomus* in GSA 8; *M. merluccius, G. argenteus* and *P. blennoides* in GSA 9; *Glossanodon leioglossus, Chlorophthalmus agassizi* and *Hymenocephalus italicus* in GSA 10; *S. hepatus, G. leioglossus* and *P. blennoides* in GSA 11; *M. merluccius, G. argenteus* and *Nezumia sclerorhynchus* in GSA 16; *M. merluccius, Helicolenus dactylopterus* and *P. blennoides* in GSA 18; and *S. hepatus, Argentina sphyraena* and *N. sclerorhynchus* in GSA 22 (Table 5). The species with the highest percentage contribution to within-group similarity were *T. minutus* on the continental shelf and *G. argenteus* on the shelf break/upper slope in GSA 7; *Lepidotrigla cavillone* on the continental shelf and *C. agassizi* on the shelf break/upper slope in GSA 20; and *L. cavillone* on the continental shelf and *A. sphyraena* on the shelf break/upper slope in GSA 23. In GSA 17, *M. merluccius* was the species with the highest contribution on both the continental shelf and the shelf break/upper slope (Table 5).

Some species showed a high percentage contribution to within-group similarity in most years of the time series and for most of the GSAs (Table 6). On the continental shelf, these species were *S. hepatus, L. cavillone, M. barbatus* and *M. merluccius*. On the shelf break/upper slope, only *G. argenteus* was present in all GSAs, while on the lower slope those species were *P. blennoides, G. melastomus* and *Etmopterus spinax*.

DISCUSSION

The results have confirmed that demersal fish assemblages are highly structured in the Mediterranean. In fact, we were able to identify three common assemblages in most GSAs corresponding to the continental shelf, shelf break/upper slope and lower slope strata of each area. There were only two GSAs, the northern Adriatic Sea and Crete, that did not present lower slope assemblages, due to the shallower depth surveyed in these areas compared with the rest of GSAs. Although the number of samples was not enough to follow their temporal series, the Gulf of Lions and the eastern Ionian Sea also followed this depth structure. The results confirm the findings of previous works on the structure of demersal assemblages in the Mediterranean, showing that for fishes (Ungaro et al. 1999, Labropoulou and Papaconstantinou 2004, García-Ruiz et al. 2015) and other taxonomic groups (Tserpes et al. 1999, Colloca et al. 2003, Massutí and Reñones 2005) they are strongly organized along a depth gradient.

Despite the similar bathymetric gradient along the Mediterranean, the results showed differences in the bathymetric limitations and composition of demersal fish assemblages between GSAs. This is not surprising considering that oceanographic conditions vary between GSAs, and bathymetric distributions of communities respond according to these variations. In fact, we incorporated cluster analysis to escape from the assumption that communities are structured according to MEDITS strata, and we made an analysis based on real assemblages for each GSA. Therefore, the analysis of demersal fish diversity based on cluster analysis for each particular area of the Mediterranean is more accurate than the assignation of a depth stratum to the samples analysed for the whole Mediterranean, the method that has been generally used up to now.

Our results show a stability and even recovery of demersal fish diversity in the Mediterranean. Of the 114 temporal series analysed, only 27% showed a significant trend, with an increasing pattern in 71% of the cases showing significant trends. N_{90} and species richness (S) showed increasing trends in most cases (87.5% and 84.6%, respectively), while Pielou evenness (J') was the indicator that showed the highest proportion of decreasing trends (60%). This stability was also shown in the only study analysing long temporal series from bottom trawl survey data (1994-2012) for the whole Mediterranean (Granger et al. 2015). These authors took into account three scales of analysis corresponding to 18 GSAs, 7 biogeographical zones and 2 basins at a depth ranging from 10 to 800 m. The assemblages by depth were not considered, which could explain why they did not detect any recovery.

The continuous increase in fisheries in the last few decades has led to the overexploitation of the main commercial stocks in most Mediterranean areas (Colloca et al. 2013, Sartor et al. 2014). However, bottom trawl fisheries in the Mediterranean have decreased recently, due to the economic losses of this activity (Quetglas et al. 2017; Table 4) and the implementation of additional management measures, such as the prohibition of bot-

Table 5. – Similarity Percentage analysis (SIMPER) summary table of species appearing in the 90% cut-off of within-group similarity. A is the mean abundance (individuals km⁻²) of each species, and %C is the mean value of the percentage contribution of each species to within-group similarity, taking into account each SIMPER made by group of GSA, depth strata and year. Depth strata are shelf, shelf break/upper slope (SB/US) and lower slope.

GSA 1 Shelf	A	%C	GSA 1 SB/US	A	%C	GSA 1 Lower slope	A	%C
Serranus hepatus	1629	31	*Gadiculus argenteus*	7829	37	*Galeus melastomus*	2533	26
Pagellus acarne	4684	24	*Helicolenus dactylopterus*	2509	16	*Nezumia aequalis*	2046	22
Merluccius merluccius	418	8	*Micromesistius poutassou*	7519	12	*Hoplostethus mediterraneus*	1460	15
Cepola macrophthalma	687	6	*Lepidopus caudatus*	6280	9	*Coelorinchus caelorhincus*	1315	13
Mullus barbatus	1237	6	*Merluccius merluccius*	1217	8	*Phycis blennoides*	364	8
Callionymus maculatus	514	3	*Phycis blennoides*	706	5	*Etmopterus spinax*	245	3
Arnoglossus laterna	237	3	*Scyliorhinus canicula*	491	3	*Trachyrincus scabrus*	744	2
Serranus cabrilla	338	2	*Coelorinchus caelorhincus*	873	2	*Micromesistius poutassou*	299	2
Arnoglossus thori	544	2						
Scyliorhinus canicula	158	2						
Lesueurigobius sanzi	255	1						
Trachinus draco	103	1						
GSA 5 Shelf			**GSA 5 SB/US**			**GSA 5 Lower slope**		
Scyliorhinus canicula	1348	25	*Gadiculus argenteus*	24060	68	*Phycis blennoides*	425	30
Serranus hepatus	1464	12	*Galeus melastomus*	2222	9	*Galeus melastomus*	440	24
Serranus cabrilla	743	11	*Coelorinchus caelorhincus*	1592	5	*Nezumia aequalis*	226	19
Trachinus draco	548	9	*Chlorophthalmus agassizi*	2906	5	*Hymenocephalus italicus*	174	7
Mullus surmuletus	1163	6	*Phycis blennoides*	461	3	*Notacanthus bonaparte*	55	4
Lepidotrigla cavillone	741	5	*Helicolenus dactylopterus*	506	3	*Lepidion lepidion*	93	4
Merluccius merluccius	1007	5				*Symphurus ligulatus*	45	3
Glossanodon leioglossus	28236	5						
Chelidonichthys cuculus	893	5						
Trigloporus lastoviza	448	4						
Scorpaena notata	163	1						
Pagellus erythrinus	179	1						
Mullus barbatus	312	1						
GSA 6 Shelf			**GSA 6 SB/US**			**GSA 6 Lower slope**		
Merluccius merluccius	2955	45	*Micromesistius poutassou*	57532	40	*Phycis blennoides*	698	43
Trisopterus minutus	2248	19	*Gadiculus argenteus*	9766	20	*Galeus melastomus*	381	22
Cepola macrophthalma	514	7	*Merluccius merluccius*	4285	19	*Micromesistius poutassou*	300	4
Mullus barbatus	487	7	*Trisopterus minutus*	1754	6	*Nezumia aequalis*	79	4
Serranus hepatus	408	7	*Helicolenus dactylopterus*	914	3	*Trachyrincus scabrus*	166	4
Lepidotrigla cavillone	250	3	*Scyliorhinus canicula*	811	3	*Hymenocephalus italicus*	55	3
Pagellus erythrinus	98	1				*Gadiculus argenteus*	422	3
Lophius budegassa	56	1				*Symphurus nigrescens*	67	2
						Scyliorhinus canicula	130	2
						Coelorinchus caelorhincus	128	2
						Gaidropsarus biscayensis	58	2
GSA 7 Shelf			**GSA 7 SB/US**			**GSA 7 Lower slope**		
Trisopterus minutus	6435	47	*Gadiculus argenteus*	6804	39			
Merluccius merluccius	3239	19	*Galeus melastomus*	1470	11			
Eutrigla gurnardus	1651	12	*Micromesistius poutassou*	7815	10			
Serranus hepatus	896	5	*Phycis blennoides*	561	8			
Lepidotrigla cavillone	1297	4	*Coelorinchus caelorhincus*	1068	7			
Cepola macrophthalma	561	2	*Helicolenus dactylopterus*	719	7			
Lesueurigobius friesii	513	2	*Lepidorhombus boscii*	417	6			
			Trigla lyra	565	5			
GSA 8 Shelf			**GSA 8 SB/US**			**GSA 8 Lower slope**		
Mullus barbatus	4127	20	*Gadiculus argenteus*	17009	47	*Galeus melastomus*	1246	29
Lepidotrigla cavillone	1287	19	*Galeus melastomus*	2979	11	*Hymenocephalus italicus*	535	19
Scyliorhinus canicula	941	15	*Chlorophthalmus agassizi*	4386	9	*Coelorinchus caelorhincus*	405	12
Serranus hepatus	1157	14	*Micromesistius poutassou*	2373	8	*Phycis blennoides*	248	8
Pagellus erythrinus	538	10	*Scyliorhinus canicula*	1119	7	*Helicolenus dactylopterus*	169	6
Chelidonichthys cuculus	352	5	*Lepidotrigla dieuzeidei*	1147	4	*Nezumia sclerorhynchus*	223	6
Serranus cabrilla	283	3	*Argentina sphyraena*	842	3	*Hoplostethus mediterraneus*	254	6
Mullus surmuletus	373	2				*Etmopterus spinax*	196	4
Trigloporus lastoviza	162	1				*Chlorophthalmus agassizi*	280	4
Lepidotrigla dieuzeidei	432	1						
GSA 9 Shelf			**GSA 9 SB/US**			**GSA 9 Lower slope**		
Merluccius merluccius	4334	55	*Gadiculus argenteus*	5253	52	*Phycis blennoides*	490	27
Trisopterus minutus	1076	16	*Merluccius merluccius*	4894	13	*Hymenocephalus italicus*	527	27
Mullus barbatus	551	8	*Phycis blennoides*	564	12	*Galeus melastomus*	439	22
Serranus hepatus	274	4	*Chlorophthalmus agassizi*	896	6	*Nezumia sclerorhynchus*	239	9
Lepidotrigla cavillone	271	4	*Galeus melastomus*	289	4	*Etmopterus spinax*	105	7
Arnoglossus laterna	110	3	*Micromesistius poutassou*	1322	4			
Glossanodon leioglossus	4801	2						

Table 5 (Cont.). – Similarity Percentage analysis (SIMPER) summary table of species appearing in the 90% cut-off of within-group similarity. A is the mean abundance (individuals km^{-2}) of each species, and %C is the mean value of the percentage contribution of each species to within-group similarity, taking into account each SIMPER made by group of GSA, depth strata and year. Depth strata are shelf, shelf break/upper slope (SB/US) and lower slope.

GSA 10 Shelf	A	%C	GSA 10 SB/US	A	%C	GSA 10 Lower slope	A	%C
Glossanodon leioglossus	16087	12	*Chlorophthalmus agassizi*	11376	61	*Hymenocephalus italicus*	1152	49
Merluccius merluccius	2725	57	*Phycis blennoides*	479	8	*Nezumia sclerorhynchus*	351	19
Lepidotrigla cavillone	598	3	*Hymenocephalus italicus*	1128	7	*Phycis blennoides*	199	11
Mullus barbatus	502	7	*Gadiculus argenteus*	1290	7	*Galeus melastomus*	255	10
Serranus hepatus	490	4	*Merluccius merluccius*	1039	6	*Etmopterus spinax*	70	4
Lepidopus caudatus	463	2	*Helicolenus dactylopterus*	226	2			
Trisopterus minutus	236	2						
Cepola macrophthalma	91	3						
Arnoglossus laterna	80	2						

GSA 11 Shelf	A	%C	GSA 11 SB/US	A	%C	GSA 11 Lower slope	A	%C
Serranus hepatus	1751	26	*Glossanodon leioglossus*	77021	51	*Phycis blennoides*	879	31
Merluccius merluccius	2903	22	*Merluccius merluccius*	6301	13	*Hymenocephalus italicus*	818	20
Lepidotrigla cavillone	1131	9	*Trisopterus minutus*	5084	11	*Gadiculus argenteus*	8361	18
Trisopterus minutus	2474	9	*Argentina sphyraena*	4673	9	*Galeus melastomus*	987	12
Mullus barbatus	840	7	*Lepidotrigla dieuzeidei*	1590	5	*Chlorophthalmus agassizi*	3734	5
Serranus cabrilla	344	4	*Scyliorhinus canicula*	1175	4	*Etmopterus spinax*	122	3
Chelidonichthys cuculus	368	3				*Merluccius merluccius*	848	2
Scyliorhinus canicula	335	3						
Mullus surmuletus	200	2						
Trigloporus lastoviza	191	2						
Trachinus draco	105	2						
Argentina sphyraena	2800	2						
Citharus linguatula	227	1						

GSA 16 Shelf	A	%C	GSA 16 SB/US	A	%C	GSA 16 Lower slope	A	%C
Merluccius merluccius	970	25	*Gadiculus argenteus*	5100	26	*Nezumia sclerorhynchus*	982	40
Serranus hepatus	785	11	*Merluccius merluccius*	1622	20	*Hymenocephalus italicus*	573	19
Lepidotrigla cavillone	1327	10	*Chlorophthalmus agassizi*	3368	14	*Galeus melastomus*	318	17
Chelidonichthys cuculus	548	7	*Coelorinchus caelorhincus*	1231	10	*Nezumia aequalis*	383	7
Mullus barbatus	580	7	*Hymenocephalus italicus*	768	8	*Hoplostethus mediterraneus*	134	5
Mullus surmuletus	261	5	*Phycis blennoides*	314	7	*Phycis blennoides*	79	3
Raja miraletus	302	5	*Lepidopus caudatus*	2220	6			
Serranus cabrilla	181	4						
Citharus linguatula	234	3						
Argentina sphyraena	912	2						
Trisopterus minutus	280	2						
Trigloporus lastoviza	131	2						
Arnoglossus laterna	116	2						
Lepidotrigla dieuzeidei	588	2						
Scyliorhinus canicula	102	2						
Zeus faber	52	2						
Trachinus draco	77	1						

GSA 17 Shelf	A	%C	GSA 17 SB/US	A	%C	GSA 17 Lower slope	A	%C
Merluccius merluccius	931	28	*Merluccius merluccius*	2155	43			
Mullus barbatus	1344	20	*Micromesistius poutassou*	3434	33			
Trisopterus minutus	861	18	*Trisopterus minutus*	312	5			
Serranus hepatus	1150	13	*Lepidopus caudatus*	489	5			
Cepola macrophthalma	327	6	*Gadiculus argenteus*	379	3			
Lepidotrigla cavillone	359	2	*Lesueurigobius friesii*	201	2			
Merlangius merlangus	161	2						
Eutrigla gurnardus	108	2						

GSA 18 Shelf	A	%C	GSA 18 SB/US	A	%C	GSA 18 Lower slope	A	%C
Merluccius merluccius	939	43	*Helicolenus dactylopterus*	466	11	*Phycis blennoides*	405	20
Trisopterus minutus	424	20	*Chlorophthalmus agassizi*	663	10	*Nezumia sclerorhynchus*	305	14
Mullus barbatus	317	7	*Micromesistius poutassou*	823	8	*Galeus melastomus*	282	13
Serranus hepatus	175	6	*Glossanodon leioglossus*	2993	7	*Hoplostethus mediterraneus*	319	11
Lepidotrigla cavillone	376	4	*Argentina sphyraena*	1378	6	*Coelorinchus caelorhincus*	318	10
Chelidonichthys cuculus	232	4	*Lepidopus caudatus*	338	4	*Hymenocephalus italicus*	254	10
Arnoglossus laterna	106	3	*Gadiculus argenteus*	587	4	*Etmopterus spinax*	167	9
Cepola macrophthalma	81	2	*Phycis blennoides*	109	4	*Helicolenus dactylopterus*	117	4
Lesueurigobius friesii	74	2	*Chelidonichthys cuculus*	470	4			
			Scyliorhinus canicula	146	3			
			Lepidorhombus boscii	65	2			
			Arnoglossus rueppelii	153	2			
			Lepidotrigla cavillone	238	2			
			Merluccius merluccius	895	25			

Table 5 (Cont.). – Similarity Percentage analysis (SIMPER) summary table of species appearing in the 90% cut-off of within-group similarity. A is the mean abundance (individuals km^{-2}) of each species, and %C is the mean value of the percentage contribution of each species to within-group similarity, taking into account each SIMPER made by group of GSA, depth strata and year. Depth strata are shelf, shelf break/upper slope (SB/US) and lower slope.

GSA 20 Shelf	A	%C	GSA 20 SB/US	A	%C	GSA 20 Lower slope	A	%C
Lepidotrigla cavillone	1299	26	*Chlorophthalmus agassizi*	6565	28			
Serranus hepatus	1416	24	*Gadiculus argenteus*	9073	24			
Mullus barbatus	1145	15	*Argentina sphyraena*	3257	14			
Merluccius merluccius	527	11	*Merluccius merluccius*	860	6			
Arnoglossus laterna	329	5	*Lepidopus caudatus*	444	4			
Trisopterus minutus	359	3	*Helicolenus dactylopterus*	361	4			
Pagellus erythrinus	272	2	*Scyliorhinus canicula*	187	3			
Argentina sphyraena	2318	2	*Peristedion cataphractum*	714	2			
Citharus linguatula	142	2	*Coelorinchus caelorhincus*	588	2			
			Hymenocephalus italicus	677	2			
			Phycis blennoides	129	2			
GSA 22 Shelf			**GSA 22 SB/US**			**GSA 22 Lower slope**		
Serranus hepatus	1774	19	*Argentina sphyraena*	12691	27	*Nezumia sclerorhynchus*	626	43
Trisopterus minutus	1666	13	*Gadiculus argenteus*	5823	18	*Hymenocephalus italicus*	575	14
Merluccius merluccius	1890	11	*Merluccius merluccius*	505	10	*Trachyrincus scabrus*	251	9
Citharus linguatula	569	11	*Micromesistius poutassou*	2037	7	*Phycis blennoides*	119	8
Lepidotrigla cavillone	887	10	*Chlorophthalmus agassizi*	5423	6	*Coelorinchus caelorhincus*	317	8
Mullus barbatus	785	5	*Phycis blennoides*	169	5	*Hoplostethus mediterraneus*	105	6
Chelidonichthys cuculus	968	4	*Scyliorhinus canicula*	372	5	*Etmopterus spinax*	66	4
Lophius budegassa	178	4	*Lepidorhombus boscii*	151	4			
Argentina sphyraena	3244	4	*Coelorinchus caelorhincus*	1395	4			
Serranus cabrilla	221	3	*Hymenocephalus italicus*	801	3			
Scyliorhinus canicula	195	3	*Helicolenus dactylopterus*	148	2			
Arnoglossus laterna	164	2	*Lepidopus caudatus*	431	2			
Dentex maroccanus	458	2						
Mullus surmuletus	246	1						
GSA 23 Shelf			**GSA 23 SB/US**			**GSA 23 Lower slope**		
Lepidotrigla cavillone	2773	38	*Argentina sphyraena*	16100	49			
Mullus barbatus	3330	21	*Chlorophthalmus agassizi*	9753	10			
Serranus hepatus	2784	12	*Merluccius merluccius*	1305	9			
Citharus linguatula	262	7	*Chelidonichthys cuculus*	758	6			
Pagellus erythrinus	627	6	*Coelorinchus caelorhincus*	657	6			
Arnoglossus laterna	855	4	*Helicolenus dactylopterus*	330	5			
Serranus cabrilla	263	3	*Lepidotrigla cavillone*	400	2			
			Phycis blennoides	109	2			
			Gadiculus argenteus	3003	2			

tom trawling within 1.5 nautical miles of the coast (EC Regulation 1967/2006). However, this recent measure has possibly displaced part of the trawl fishing effort from the shelf to deeper bathymetric zones (Tserpes et al. 2011). Our results show that increasing trends in N_{90} and S and decreasing trends in J' coincide in some cases with decreasing trends in bottom trawl fishing effort. There could therefore be a cause and effect relation, because it is in accordance with the expected effect of fishing on biodiversity. The increasing trend in N_{90} with decreasing fishing effort reinforces the previous results that confirm the usefulness of this index for detecting the effects of fishing on demersal fish diversity. The increase of evenness with increasing fishing effort has been suggested by some authors (Murawski 2000, Zhou et al. 2010) due to the reduction of dominant species by fishing (Cury et al. 2000, Rice 2000) and has been confirmed by the study of the effects of fishing on evenness indices (D'Onghia et al. 2003, Farriols et al. 2017). However, the expected increase in S and decrease in J' with decreasing fishing effort are not always observed in our results. There are some differences in the aspects of diversity that each of these indices capture. Increasing N_{90} values with decreasing fishing effort indicate an increase in the frequency of occurrence and the evenness of the distribution of species abundances due to expan-

sion to areas with the most favourable environmental conditions. On the other hand, an increase in S and a decrease in J' with decreasing fishing effort implies an increase in the number of species and an increase in the dominance of some species, respectively. Although both number of species and evenness are also affecting N_{90}, the calculation of each of these indices is extremely different. N_{90} takes into account the homogeneity or heterogeneity of all the samples of a stratum and year for each GSA in its calculation and involves the most frequent and abundant species in the group without losing species identity through the comparison among all the samples in the group. In contrast, S and J' in a group are calculated from their mean values and consequently species identity is lost. This may explain why extreme values of fishing effort were needed to detect the effects of fishing in S and J' in previous works (Farriols et al. 2017). In some cases, N_{90} showed no trend when there was a trend in fishing effort and viceversa. This finding could be due to several causes. It is either too early to detect the effects of decreasing fishing effort on demersal fish diversity or the decrease is not sufficiently important to change the diversity trend. Similarly, increasing trends in fishing effort could not result in a decrease in fish diversity due to the adaptation of demersal fish communities to fishing exploitation.

Table 6. – Number of years that each species contributed to the 90% cut-off of within-group similarity, taking into account each similarity percentage analysis (SIMPER) by GSA, depth stratum and year during the time series. Depth strata are shelf, shelf break/upper slope (SB/US) and lower slope.

Stratum	Species	GSA													
		1	5	6	7	8	9	10	11	16	17	18	20	22	23
Shelf	*Argentina sphyraena*	-	-	-	-	3	4	1	9	13	-	2	9	6	-
	Arnoglossus imperialis	-	-	-	-	-	-	-	-	4	-	-	-	-	-
	Arnoglossus laterna	8	-	3	6	-	12	10	-	10	4	12	11	8	4
	Arnoglossus rueppelii	-	2	-	-	-	-	-	-	-	-	-	-	-	-
	Arnoglossus thori	7	3	-	-	5	-	-	6	4	-	-	-	-	-
	Callionymus maculatus	12	-	1	2	-	-	-	-	-	2	3	-	-	-
	Cepola macrophthalma	16	-	18	11	-	4	13	4	1	18	11	-	3	-
	Chelidonichthys cuculus	-	14	-	-	17	-	1	15	19	3	13	7	12	-
	Chelidonichthys obscurus	-	-	-	-	-	-	-	-	7	-	-	-	-	-
	Citharus linguatula	-	-	2	1	-	1	-	6	18	1	-	4	14	12
	Deltentosteus collonianus	-	-	-	-	-	-	-	1	-	-	-	-	-	-
	Deltentosteus quadrimaculatus	1	3	1	-	4	-	1	5	-	-	-	-	-	2
	Dentex maroccanus	-	-	-	-	-	-	-	-	-	-	-	1	6	-
	Diplodus annularis	-	-	-	-	-	-	-	1	-	-	-	2	1	-
	Eutrigla gurnardus	-	-	1	22	-	-	-	-	-	5	3	1	3	-
	Glossanodon leioglossus	-	12	-	-	-	8	17	-	-	-	-	-	-	-
	Gymnammodytes cicerelus	-	-	-	-	-	-	-	1	-	-	-	-	-	-
	Helicolenus dactylopterus	-	-	-	-	-	-	2	-	-	-	-	-	-	-
	Lepidopus caudatus	1	-	-	-	-	1	8	-	1	-	2	-	-	-
	Lepidotrigla cavillone	4	14	12	18	20	15	16	22	22	9	15	14	14	13
	Lepidotrigla dieuzeidei	1	-	-	-	4	-	-	1	6	-	-	3	2	-
	Lesueurigobius friesii	-	-	1	7	-	4	1	-	-	2	6	-	3	-
	Lesueurigobius sanzi	6	-	1	-	-	-	-	-	-	-	-	-	-	-
	Lesueurigobius suerii	-	-	-	-	-	-	4	-	-	-	-	-	-	-
	Lophius budegassa	-	-	6	2	-	-	-	-	-	2	6	-	14	1
	Merlangius merlangus	-	-	-	-	-	-	-	-	-	10	-	-	-	-
	Merluccius merluccius	21	14	22	22	2	22	22	22	22	22	22	13	14	1
	Microchirus boscanion	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Micromesistius poutassou	-	-	-	1	-	-	-	-	-	-	3	-	-	-
	Mullus barbatus	17	4	20	2	20	21	20	22	19	22	17	14	14	13
	Mullus surmuletus	-	14	-	-	7	-	-	10	17	-	-	-	4	1
	Ophichthus rufus	2	-	2	-	-	-	-	-	-	-	-	-	-	-
	Pagellus acarne	21	-	2	-	2	-	-	-	1	-	-	-	-	4
	Pagellus bogaraveo	5	-	-	-	-	-	-	-	-	-	-	-	-	-
	Pagellus erythrinus	3	5	3	-	21	-	5	3	4	2	-	8	-	12
	Phycis blennoides	-	-	-	-	-	-	3	-	-	-	1	-	-	-
	Pomatoschistus marmoratus	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Pomatoschistus microps	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Raja clavata	-	2	-	-	-	-	-	-	-	-	-	-	2	-
	Raja miraletus	-	-	-	-	4	-	-	2	22	-	-	-	-	-
	Scorpaena notata	1	4	-	-	-	-	-	2	-	-	-	-	-	-
	Scorpaena scrofa	-	3	-	-	-	-	-	-	-	-	-	-	-	-
	Scyliorhinus canicula	5	14	-	-	21	-	-	15	12	-	-	-	12	-
	Serranus cabrilla	10	14	-	-	13	-	-	20	21	-	-	2	14	4
	Serranus hepatus	22	14	20	20	20	22	18	22	21	22	18	13	14	5
	Symphurus nigrescens	2	-	1	-	-	-	-	-	-	-	1	-	2	-
	Trachinus draco	6	14	-	-	-	-	-	12	8	-	-	-	-	-
	Trigloporus lastoviza	-	14	-	-	2	-	-	11	11	-	-	-	-	-
	Trisopterus luscus	-	-	1	-	-	-	-	-	-	-	-	-	-	-
	Trisopterus minutus	-	2	20	22	-	22	6	22	5	22	22	7	14	-
	Uranoscopus scaber	-	-	-	-	-	-	-	-	3	-	-	-	-	-
	Zeus faber	-	3	-	-	1	-	-	1	10	-	-	1	-	-
SB/US	*Argentina sphyraena*	-	-	6	3	10	3	-	19	5	-	6	12	14	14
	Arnoglossus rueppelii	1	-	2	-	-	-	-	-	-	-	10	-	-	1
	Callionymus maculatus	2	-	-	-	-	-	-	-	-	-	-	-	-	-
	Cepola macrophthalma	-	-	1	2	-	-	-	-	-	3	-	-	-	-
	Chelidonichthys cuculus	-	-	-	-	1	-	-	1	-	1	11	-	1	10
	Chlorophthalmus agassizi	-	12	-	3	18	18	22	-	20	-	15	11	8	6
	Coelorinchus caelorhincus	5	8	-	20	4	3	5	-	20	-	-	3	12	2
	Epigonus denticulatus	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Epigonus telescopus	-	-	-	-	-	-	-	-	1	-	-	-	-	-
	Gadiculus argenteus	21	14	20	22	21	22	19	1	21	8	6	12	13	5
	Galeorhinus galeus	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	Galeus melastomus	-	10	-	22	20	15	2	-	-	-	-	1	1	-
	Glossanodon leioglossus	-	-	-	-	2	-	-	22	-	-	7	-	-	-
	Helicolenus dactylopterus	17	4	11	21	1	7	5	-	7	1	22	8	9	5
	Hoplostethus mediterraneus	-	-	-	-	-	-	-	-	-	-	-	1	-	1
	Hymenocephalus italicus	-	2	-	-	-	1	19	-	20	-	-	5	11	2
	Lepidopus caudatus	10	-	1	-	-	1	5	-	15	10	5	5	2	-
	Lepidorhombus boscii	-	2	-	19	5	1	-	-	-	-	7	3	9	2
	Lepidorhombus whiffiagonis	-	-	-	-	-	-	-	-	-	1	1	-	-	-
	Lepidotrigla cavillone	-	-	-	-	-	-	-	-	-	-	2	-	-	3
	Lepidotrigla dieuzeidei	-	-	-	-	9	-	-	9	-	-	3	3	1	1

Table 6 (Cont.). – Number of years that each species contributed to the 90% cut-off of within-group similarity, taking into account each similarity percentage analysis (SIMPER) by GSA, depth stratum and year during the time series. Depth strata are shelf, shelf break/upper slope (SB/US) and lower slope.

Stratum	Species	GSA													
		1	5	6	7	8	9	10	11	16	17	18	20	22	23
	Lesueurigobius friesii	-	-	-	-	-	-	-	-	-	7	2	-	-	1
	Lophius budegassa	-	-	1	-	-	-	-	-	-	2	-	-	2	1
	Merluccius merluccius	15	-	22	2	4	22	18	21	22	22	22	10	14	10
	Micromesistius poutassou	10	4	22	21	18	11	3	2	-	22	16	-	10	2
	Mullus barbatus	-	-	3	-	-	-	-	-	-	2	7	-	-	-
	Mullus surmuletus	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	Nezumia sclerorhynchus	-	-	-	-	-	-	-	-	-	-	-	2	1	-
	Pagellus bogaraveo	5	-	-	1	-	-	-	-	-	-	1	-	2	-
	Peristedion cataphractum	-	-	-	-	-	-	-	-	-	-	4	8	-	1
	Phycis blennoides	9	7	4	22	1	21	22	-	21	5	13	4	9	4
	Scorpaena elongata	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Scyliorhinus canicula	10	-	8	1	20	-	-	8	-	-	10	4	13	-
	Serranus hepatus	3	-	-	-	-	-	-	-	-	-	-	-	-	-
	Symphurus nigrescens	1	-	-	-	-	-	1	-	-	-	1	-	-	-
	Synchiropus phaeton	-	1	-	1	-	-	-	-	-	-	-	-	-	-
	Trachyrincus scabrus	-	-	-	1	-	-	-	-	-	-	-	-	-	-
	Trigla lyra	-	-	-	14	1	-	-	-	-	-	2	-	-	-
	Trisopterus minutus	-	-	12	-	-	1	-	19	-	14	-	3	4	-
	Zeus faber	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Lower slope	*Alepocephalus rostratus*	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Argentina sphyraena	-	-	-	-	-	-	-	1	-	-	-	-	-	-
	Chimaera monstrosa	-	-	-	-	-	-	-	-	1	-	3	-	2	-
	Chlorophthalmus agassizi	-	-	-	-	10	-	-	16	-	-	6	-	-	-
	Coelorinchus caelorhincus	22	-	9	-	21	-	1	-	7	-	21	-	10	-
	Epigonus denticulatus	5	-	5	-	-	-	-	-	-	-	-	-	-	-
	Etmopterus spinax	13	7	2	-	13	21	7	16	1	-	20	-	5	-
	Gadiculus argenteus	2	-	15	-	4	-	-	22	-	-	-	-	-	-
	Gaidropsarus biscayensis	-	-	6	-	-	-	-	-	-	-	-	-	-	-
	Galeus melastomus	22	14	22	-	21	22	21	22	22	-	22	-	2	-
	Glossanodon leioglossus	-	-	-	-	-	-	-	1	-	-	-	-	-	-
	Helicolenus dactylopterus	5	-	9	-	19	-	-	7	1	-	16	-	-	-
	Hoplostethus mediterraneus	22	-	1	-	15	2	4	-	17	-	21	-	7	-
	Hymenocephalus italicus	-	11	13	-	21	22	21	22	21	-	20	-	13	-
	Lepidion lepidion	-	6	3	-	-	-	-	-	-	-	-	-	-	-
	Lepidopus caudatus	1	-	1	-	-	-	-	-	-	-	-	-	-	-
	Lepidorhombus boscii	-	-	3	-	1	-	-	1	-	-	-	-	1	-
	Lophius budegassa	-	-	-	-	-	-	-	-	-	-	-	-	1	-
	Merluccius merluccius	-	-	-	-	-	-	-	8	-	-	3	-	1	-
	Micromesistius poutassou	6	-	20	-	-	-	-	-	-	-	1	-	-	-
	Mora moro	-	3	-	-	-	-	-	1	-	-	-	-	-	-
	Nettastoma melanurum	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	Nezumia aequalis	22	14	18	-	-	1	-	-	3	-	-	-	-	-
	Nezumia sclerorhynchus	-	-	-	-	16	21	21	4	19	-	22	-	13	-
	Notacanthus bonaparte	-	5	5	-	-	-	-	-	-	-	-	-	-	-
	Pagellus bogaraveo	-	-	1	-	1	-	-	-	-	-	-	-	-	-
	Phycis blennoides	21	14	22	-	19	22	22	22	13	-	21	-	13	-
	Polyacanthonotus rissoanus	-	1	-	-	-	-	-	-	-	-	-	-	-	-
	Scyliorhinus canicula	-	-	12	-	-	-	-	-	-	-	-	-	-	-
	Symphurus ligulatus	-	3	2	-	-	1	-	-	-	-	-	-	-	-
	Symphurus nigrescens	-	-	8	-	-	-	-	2	-	-	-	-	1	-
	Trachyrincus scabrus	11	-	13	-	2	3	-	-	-	-	1	-	9	-

It must also be considered that there is a high complexity in the evaluation of fishing effort in the whole area. Available temporal series used to analyse fishing effort do not cover the whole time series of demersal fish diversity in all cases (see Table S1), and the inclusion of more years of the temporal series to the analysis could lead to different trends of fishing effort. In addition, as the nominal spatio-temporal pattern of fishing effort on a Mediterranean-wide level is not available, the use of different effort estimates in the areas may increase the uncertainty of the model. Moreover, number of fishing vessels is a poor proxy for effort, because does not account for other capacity changes (e.g. length overall, or kilowatts), because it does not account for technological creep and or temporal and spatial changes of fishing operations (Anticamara et al. 2011). For instance, though the regulation decreasing fishing capacity has been in place since 1991, the gross tonnage of the fleets may be increasing because boats are decreasing in number (decommissioning) but increasing in size over time (e.g. Fortibuoni et al. 2017) or because vessels have increased trawling time. This issue is enormously relevant for the Mediterranean Sea, where fisheries are managed by effort control and technical measures in contrast to quotas (northern EU seas; see Cardinale and Scarcella 2017) and should be considered when the results are interpreted. However, in the Spanish and French Mediterranean, restrictions on hours of trawling would not permit an unlimited increase in fishing effort with a decreasing number of vessels (REAL DECRETO 1440/1999, de 10 de septiembre; Arrêté n° 99-162 du 10 juin 1999).

In any case, a more appropriate indicator than number of vessels should be used for fishing effort whenever possible.

Regarding spatial patterns, we did not find the expected longitudinal decreasing west-east pattern in species richness observed in previous works on fish communities (Quignard and Tomasini 2000, Coll et al. 2010). Nor was this trend observed for N_{90} and J' in any depth stratum. The absence of a western/eastern decreasing trend further suggests that primary production or temperature regime are possibly not the major factor explaining large-scale patterns of diversity in demersal fish assemblages, as suggested by Gaertner et al. (2007). However, it is difficult to compare our results with diversity values obtained with non-standardized data mainly collected from fish inventories from other works. Moreover, due to the limited sampling approach (i.e. data concerning only one guild of fishes or limited to specific depths, gear or habitat), some of regional inventories are useless for comparative studies (Psomadakis et al. 2012). Recent studies based mainly on standardized time series data also question the previously considered west-east decreasing diversity trend in the Mediterranean (Gaertner et al. 2013, Granger et al. 2015, Peristeraki et al. 2017).

The highest diversity values were found on the continental shelf of insular areas, such as the Balearic Islands, Sardinia, Sicily and the Aegean Sea. This higher diversity can be explained by taking into account the peculiarities of the distinct biogeographic sectors within the Mediterranean (Lejeusne et al. 2010), which can be characterized by the shallow water biota (Bianchi et al. 2012). In the Strait of Sicily, for example, the meeting of western and eastern Mediterranean species produces a peak in fish species richness in the central Mediterranean (Ben Rais Lasram et al. 2009, Garofalo et al. 2007). The greater sampling effort of the present work compared with previous ones (Morri et al. 1999, Koukouras et al. 2001) could affect the unexpectedly high diversity values found in the Aegean Sea. The presence of algae facies deeper than 50 m around the Balearic Islands is likely to enhance demersal fish diversity in this area. Coralligenous and maerl communities are very characteristic of the Mallorca-Menorca continental shelf up to 85-90 m depth (Canals and Ballesteros 1997, Ordines and Massutí 2009), and this has been pointed out as a plausible reason for the differences observed between the coastal demersal resources of the Balearic Islands and the adjacent Iberian Peninsula (Massutí and Reñones 2005). In fact, habitat type has been shown to affect the distribution of demersal species, most of them being more abundant and showing a better condition in maerl and *Peyssonnelia* beds (Ordines and Massutí 2009, Ordines et al. 2009, 2015), which have also shown high diversity of fish.

The results of SIMPER analyses reinforce the idea of maerl and *Peyssonnelia* beds causing high diversity values also on the continental shelves of Sicily, Sardinia and the Aegean Sea. The species *Serranus cabrilla, Scyliorhinus canicula* and *Mullus surmuletus*, which in the Balearic Islands have shown to be more abundant in these habitats (Ordines and Massutí 2009) contribute

to N_{90} mainly in this archipelago, Sardinia, Sicily and the Aegean Sea. Similar habitats to those found on the Balearic shelf have been reported in some of these areas, like the Aegean Sea (Georgiadis et al. 2009). The presence of a higher number of vulnerable species like demersal chondrichthyans in the Balearic Islands, Sardinia, Sicily and the Aegean Sea (Bertrand et al. 2000, Damalas and Vassilopoulou 2011, Ramírez-Amaro et al. 2015) compared with adjacent areas could also contribute to the higher fish diversity values found there.

The spatial distribution of the bottom trawl fishing effort by GSA shows that the number of vessels per km² is low on the continental shelf of the Balearic Islands, Sardinia and the Aegean Sea (Colloca et al. 2017). The coincidence of areas with a low fishing effort with areas with a high diversity is in accordance with previous works, in which higher values of N_{90} and S and lower values of J' were associated with areas with a low fishing effort (Farriols et al. 2017). The lower fishing effort exerted by the relatively smaller bottom trawl fleets in these areas could have preserved, at least to some extent, their fish diversity along with a better conservation of their sensitive and essential habitats, such as maerl and *Peyssonnelia* beds. These habitats are precisely those most affected by the low selectivity and damaging collateral effects of bottom trawling on seabed communities, which decrease the presence of biogenic habitats, leading to a reduction in the biodiversity on exploited bottoms (e.g. Norse and Watling 1999, Smith et al. 2000, Hiddink et al. 2006).

Spatial patterns of demersal fish diversity on the shelf-break/upper slope and lower slope of the Mediterranean are different to those detected on the continental shelf. Areas with the highest diversity values on the continental shelf do not coincide with areas with the highest diversity values on the shelf break/ upper slope and lower slope. Although the assignment of depth strata was different in previous works and the comparison is not straightforward, a different pattern on shelf and slope areas was also observed for species richness (Gaertner et al. 2007, 2013). This is likely due to differences in the distribution of cumulative threats to marine biodiversity, which are mainly concentrated in coastal areas and on the continental shelf of the Mediterranean (Coll et al. 2012), and to the presence of particular habitats on the shelf break and slope bottoms, which may represent potential hot spots of biodiversity (Danovaro et al. 2010). Although the distribution of deep-sea diversity is different to that on the continental shelf, it is affected by similar factors: changes in spatial distribution of fishing effort together with habitat type. For example, higher N_{90} values on the slope of northern Spain could be related to the presence of submarine canyons in the area where high values of biodiversity have been reported (see Fernández-Arcaya et al. 2017 for a review). However, the description of deep-sea habitats has just been implemented for some particular areas of the Mediterranean, and this information is not exhaustive at all (Danovaro et al. 2010). Moreover, an intensive habitat mapping based on MEDITS samples

would be useful to relate demersal fish assemblages to their corresponding habitats, as has been done in some continental shelf areas (e.g. Ordines and Massutí 2009).

The outcomes of the present study show that at large temporal and spatial scales bottom trawl fisheries have reduced the diversity of demersal assemblages in the Mediterranean. However, in recent decades a generally stable scenario or even a slight recovery trend have been highlighted. This result would have not been expected if the alarming overexploitation status of Mediterranean stocks were taken into account, which underlines the importance of using diversity indices to study the effects of fishing on demersal assemblages. Therefore, a change from the assessment of demersal resources based on exploited monospecfic stocks to one based on the study of whole demersal fish assemblages is needed due to the high multispecificity of the bottom trawl fishery in the Mediterranean (Caddy 1993, Lleonart and Maynou 2003). The inclusion of species other than target ones made in this work through diversity indices is therefore important for the implementation of an ecosystem-based fisheries management (Browman and Stergiou 2004).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link:
http://scimar.icm.csic.es/scimar/supplm/sm04977esm.pdf

Table S1. – Temporal series of fishing effort measures in number of vessels, kilowatt per day at sea (kW*days at sea) and gross tonnage per days at sea (GT*days at sea) for each GSA and species. Species considered in each depth stratum are i) *Mullus barbatus* or *Mullus surmuletus* for the continental shelf; ii) *Nephrops norvegicus* or *Parapenaeus longirostris* for the shelf break/ upper slope; and iii) *Aristeus antennatus* or *Aristaeomorpha foliacea* for the lower slope. Effort measures used to calculate trends in fishing effort for each GSA and stratum are marked with (*). References are listed below the table.

Fig. S1. – Species accumulation curves for each GSA. Note that for all GSAs asymptotic values of species counts are reached.

Fig. S2. – Mean values of N_{90} diversity index during the period 1994–2015 for each GSA and depth strata. Black dots, shelf; blue dots, shelf break/upper slope; red dots, lower slope.

Fig. S3. – Mean values of species richness (*S*) during the period 1994–2015 for each GSA and depth strata. Black dots, shelf; blue dots, shelf break/upper slope; red dots, lower slope.

Fig. S4. – Mean values of Pielou evenness (*J'*) during the period 1994–2015 for each GSA and depth strata. Black dots, shelf; blue dots, shelf break/upper slope; red dots, lower slope.

Spatio-temporal trends in diversity of demersal fish assemblages in the Mediterranean

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Supplementary material

Table S1. – Temporal series of fishing effort measures in number of vessels, kilowatt per days at sea (kW*days at sea) and gross tonnage per days at sea (GT*days at sea) for each GSA and species. Species considered in each depth stratum are i) *Mullus barbatus* or *Mullus surmuletus* for the continental shelf; ii) *Nephrops norvegicus* or *Parapenaeus longirostris* for the shelf break/upper slope; and iii) *Aristeus antennatus* or *Aristaeomorpha foliacea* for the lower slope. Effort measures used to calculate trends in fishing effort for each GSA and stratum are marked with (*). References are listed below the table.

GSA	Species	Effort measure	Years	Reference
GSA 1	*M. barbatus*	Number of vessels	2005-2007	SAC GFCM 2008a
	M. barbatus	kW*days at sea (*), GT*days at sea	2009-2013	STECF 2015a
	P. longirostris	kW*days at sea (*)	2003-2015	STECF 2016b
GSA 5	*A. antennatus*	Number of vessels (*)	2011	SAC GFCM 2012a
	A. antennatus	Number of vessels (*)	1998-2009	SAC GFCM 2010a
	A. antennatus	Number of vessels (*)	1999-2010	SAC GFCM 2011a
	M. barbatus	Number of vessels	2000-2009	SAC GFCM 2010b
	M. barbatus	kW*days at sea, GT*days at sea	2009-2012	STECF 2013b
	M. surmuletus	Number of vessels	2000-2009	SAC GFCM 2010c
	M. surmuletus	Number of vessels (*)	2000-2010	SAC GFCM 2011b
	N. norvegicus	Number of vessels (*)	2002-2009	SAC GFCM 2010d
	N. norvegicus	kW*days at sea, GT*days at sea	2009-2013	STECF 2015a
	P. longirostris	kW*days at sea, GT*days at sea	2009-2012	STECF 2013a
GSA 6	*A. antennatus*	Number of vessels	1996-2006	SAC GFCM 2007
	A. antennatus	kW*days at sea, GT*days at sea	2009-2014	STECF 2015b
	M. barbatus	Number of vessels (*)	1999-2010	SAC GFCM 2011c
	M. barbatus	Number of vessels, kW*days at sea, GT*days at sea	2009-2012	STECF 2013b
	M. surmuletus	Number of vessels (*)	1998-2009	SAC GFCM 2010e
	N. norvegicus	Number of vessels (*), kW*days at sea, GT*days at sea	2004-2015	STECF 2016b
	P. longirostris	Number of vessels	2001-2010	SAC GFCM 2011d
	P. longirostris	Number of vessels	2001-2011	SAC GFCM 2012b
	P. longirostris	Number of vessels	2001-2012	SAC GFCM 2013
	P. longirostris	Number of vessels, kW*days at sea, GT*days at sea	2009-2012	STECF 2013a
GSA 7	*M. barbatus*	Number of vessels	2002-2013	STECF 2014a
	M. barbatus	Days at sea, kW*days at sea, GT*days at sea	2004-2006	STECF 2008a
	M. barbatus	Number of vessels	2004-2008	SAC GFCM 2009a
	M. barbatus	Number of vessels	2004-2009	SAC GFCM 2010f
	M. barbatus	Number of vessels (*)	2004-2011	SAC GFCM 2012c
	M. surmuletus	Number of vessels	2004-2010	SAC GFCM 2011e
GSA 9	*A. foliacea*	kW*days at sea	2004-2012	STECF 2013a
	A. foliacea	kW*days at sea (*)	2004-2014	STECF 2015b
	N. norvegicus	kW*days at sea	2004-2013	STECF 2014a
	N. norvegicus	Number of vessels, kW*days at sea, GT*days at sea	2004-2015	STECF 2016b
	P. longirostris	kW*days at sea (*)	2002-2015	STECF 2016b
	P. longirostris	kW*days at sea	2004-2013	STECF 2015a
	P. longirostris	Number of vessels	2006-2008	SAC GFCM 2009b
GSA 10	*A. foliacea*	kW*days at sea	2004-2014	STECF 2015b
	P. longirostris	kW*days at sea (*)	2002-2015	STECF 2016b
	P. longirostris	kW*days at sea	2004-2012	STECF 2013a
GSA 11	*A. foliacea*	Number of vessels, kW*days at sea (*), GT*days at sea	2004-2014	STECF 2015b
	M. surmuletus	GT*days at sea (*)	2004-2012	STECF 2013b
	N. norvegicus	Number of vessels, kW*days at sea, GT*days at sea	2004-2015	STECF 2016b
	P. longirostris	kW*days at sea (*)	2002-2015	STECF 2016b
GSA 15-16	*A. foliacea*	GT*days at sea	2004-2008	SAC GFCM 2009c
GSA 16	*P. longirostris*	Number of vessels	2006-2007	SAC GFCM 2008b
GSA 17	*M. barbatus*	kW*days at sea (*), GT*days at sea	2004-2012	STECF 2013b
	N. norvegicus	kW*days at sea (*)	2002-2015	STECF 2016b
GSA 17-18	*M. barbatus*	kW*days at sea, GT*days at sea	2004-2014	STECF 2016a
	N. norvegicus	kW*days at sea, GT*days at sea	2006-2014	STECF 2016a
GSA 18	*A. foliacea*	kW*days at sea (*), GT*days at sea	2002-2014	STECF 2016a
	M. barbatus	kW*days at sea (*)	2004-2013	STECF 2015a
	P. longirostris	kW*days at sea, GT*days at sea (*)	2007-2014	STECF 2016a
GSA 22-23	*P. longirostris*	Days at sea, kW*days at sea, GT*days at sea	2003-2006	STECF 2008a

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SAC GFCM. 2008b. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - *Parapenaeus longirostris* - GSA 16. FAO.

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SAC GFCM. 2009b. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - *Parapenaeus longirostris* - GSA 9. FAO.

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SAC GFCM. 2010b. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - Mullus barbatus - GSA 5. FAO.

SAC GFCM. 2010c. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - Mullus surmuletus - GSA 5. FAO.

SAC GFCM. 2010d. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) -

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SAC GFCM. 2010f. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - Mullus barbatus - GSA 7. FAO.

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SAC GFCM. 2011d. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - Parapenaeus longirostris - GSA 6. FAO.

SAC GFCM. 2011e. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - Mullus barbatus - GSA 7. FAO.

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SAC GFCM. 2012b. Scientific Advisory Committee on Fisheries of the General Fisheries Comission of the Mediterranean (SAC GFCM) - Stock assessment forms of the Sub-Committee on Stock Assessment - Parapenaeus longirostris - GSA 6. FAO.

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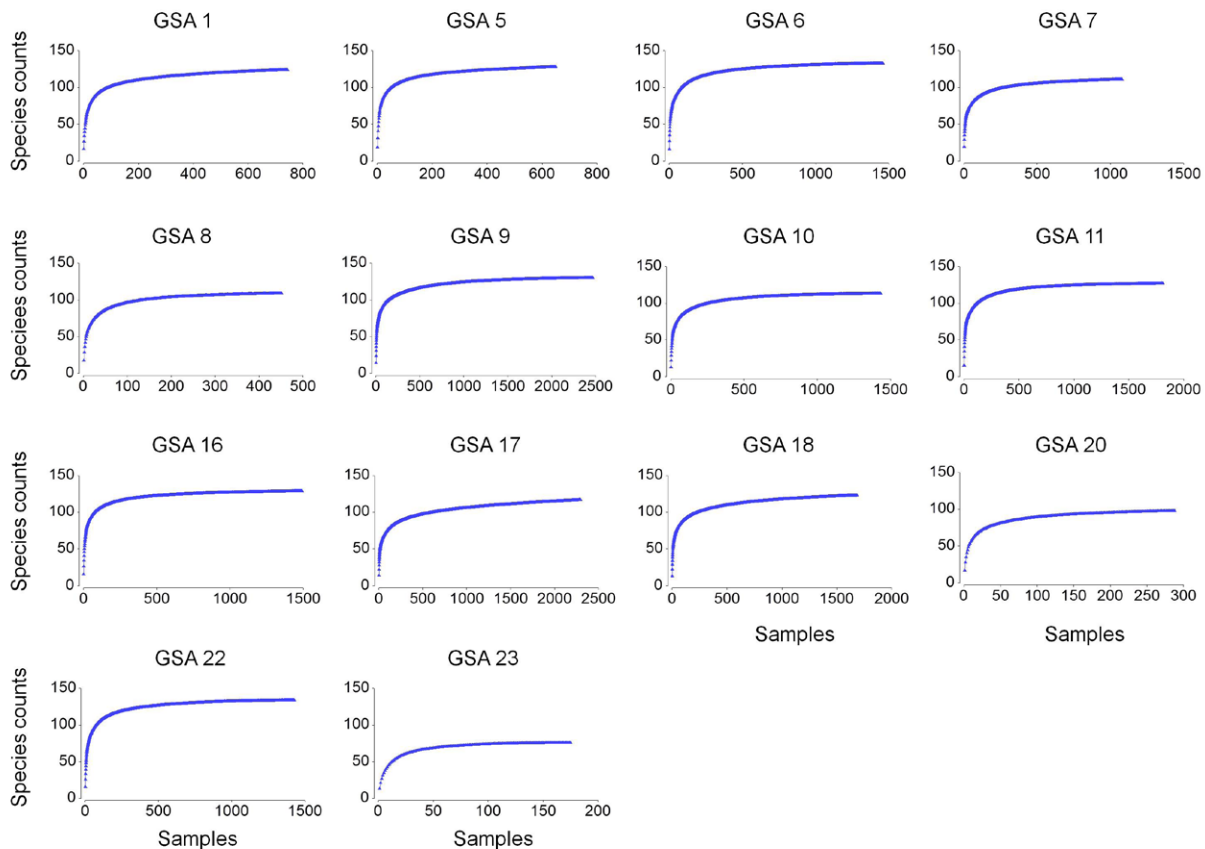

Fig. S1. – Species accumulation curves for each GSA. Note that for all GSAs asymptotic values of species counts are reached.
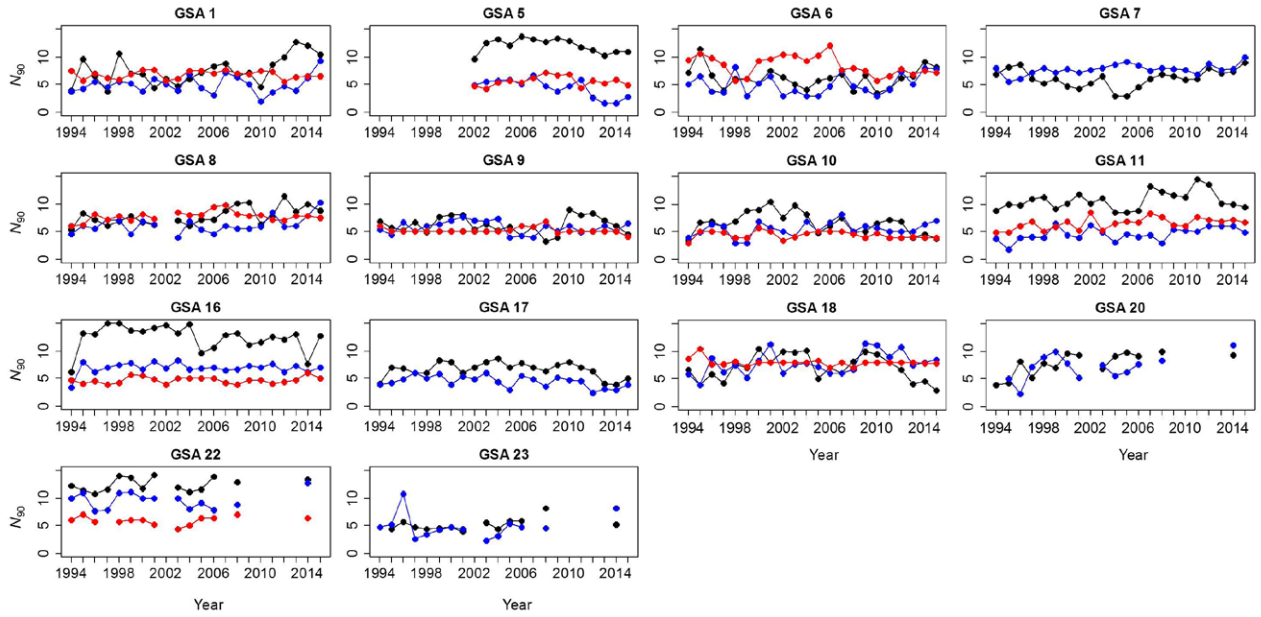
Fig. S2. – Mean values of N_{90} diversity index during the period 1994–2015 for each GSA and depth strata. Black dots, shelf; blue dots, shelf break/upper slope; red dots, lower slope.
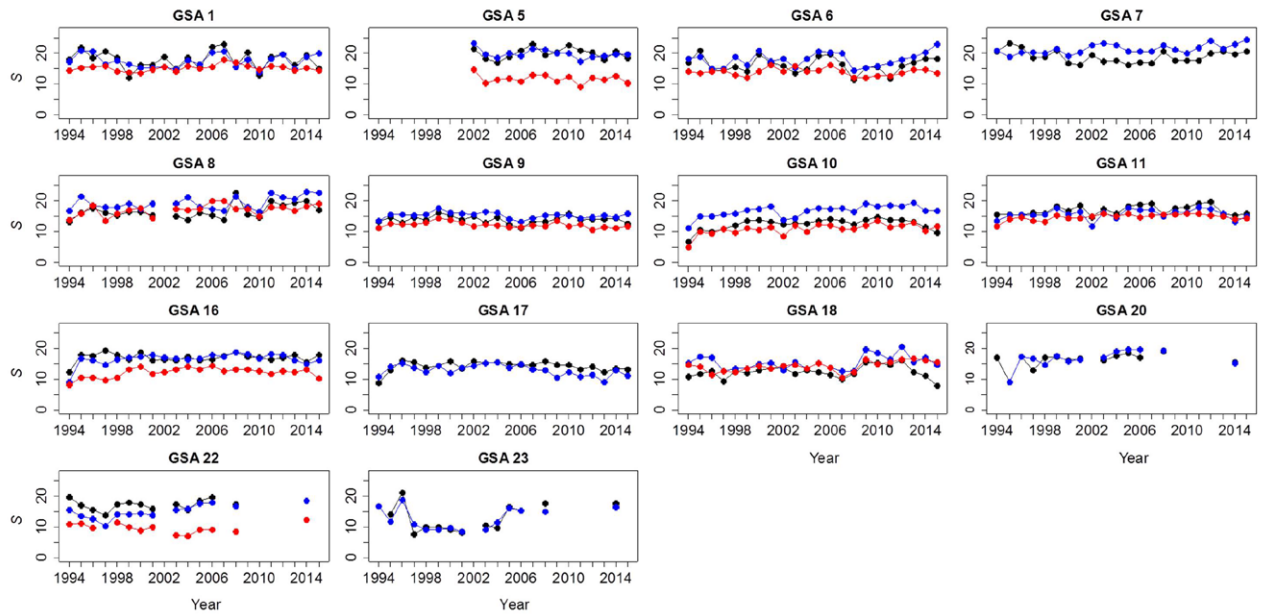

Fig. S3. – Mean values of species richness (S) during the period 1994–2015 for each GSA and depth strata. Black dots, shelf; blue dots, shelf break/upper slope; red dots, lower slope.
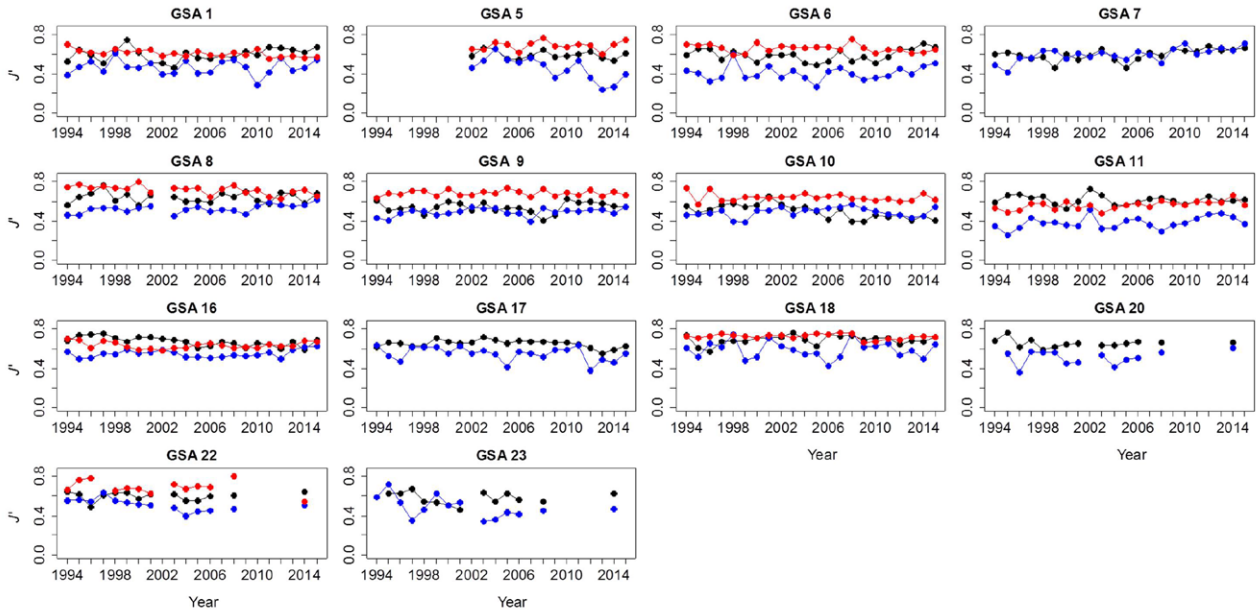
Fig. S4. – Mean values of Pielou evennes (*J'*) during the period 1994–2015 for each GSA and depth strata. Black dots, shelf; blue dots, shelf break/upper slope; red dots, lower slope