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Bottom trawl impacts on Mediterranean demersal fish diversity: not so obvious or are we too late?

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Abstract

Measures of biodiversity change may be useful as indicators if they are responsive to manageable drivers of biodiversity loss. However, there are many candidate indicators that are considered to be robust to survey artifacts and sensitive to manageable impacts. Using extensive survey data on demersal fish assemblages around the Balearic Islands (western Mediterranean) we analyze relationships among 'traditional', taxonomic and functional diversity indices, to identify a minimum set of indices that provide a good representation of the different aspects of diversity. Secondly we model the responses of the demersal fish community diversity to bottom trawl fishing pressure. To do so, we used two different approaches: i) considering fishing effort and depth as continuous explanatory variables; and ii) grouping samples according to bathymetric sampling strata and contrasting levels of fishing effort. The results show that diversity can be described using different complementary aspects such as species richness, evenness, and the taxonomic and functional breadth of the species present in a given community, displaying different responses to fishing pressure. However, the changes in diversity in response to fishing may only be detectable in those communities where the levels of fishing pressure have remained relatively low. When communities have been exposed to high levels of fishing pressure for a long period, the relevant changes in diversity may have happened long before the onset of monitoring of the fishery, and hence it may be too late to detect differences between levels of fishing effort. This seems to be the case on the middle slope of the Balearic Islands, where vulnerable species have disappeared or are very infrequent, and have been replaced by species better-adapted to fishing impacts.

Keywords: biodiversity; taxonomic diversity; functional diversity; fish; bottom trawling; fishing effort; Balearic Islands; western Mediterranean.

1. Introduction

Within the context of the Ecosystem Approach to Fisheries (EAF; Pikitch et al., 2004), indicators of biodiversity are used to assess fisheries and to monitor progress, in relation to management objectives, particularly those related to the integration of concerns about environmental and anthropogenic impacts (Balmford et al., 2005; Garcia and Cochrane, 2005; Rice and Rochet, 2005; Sutherland et al., 2006). However, there are many candidate indicators that are thought to be robust to survey artifacts such as sampling methods and measurement uncertainty, and yet sensitive to manageable impacts such as fishing or pollution (Rice, 2003; Fulton et al., 2005).

'Traditional' diversity measures, like Species richness (*S*), Shannon (*H'*) or Pielou's evenness (*J'*), measure the number of objects (species, taxa), reflect the relative abundances of objects within samples (dominance, evenness), or attempt to combine the two, and they assume that all species are equally important (Magurran, 2004; Mouchet et al., 2010). An alternative type of diversity index (N_{90}) was described by Farriols et al. (2015). It is based on SIMPER analysis (Clarke, 1993) and is defined as the mean number of species contributing up to 90% of within-group similarity in a group of samples. Farriols et al. (2015) considered it to be more sensitive to the synergistic effects of fishing impact and environmental variability than the 'traditional' diversity indices.

Considering that the relationships among species could provide additional information, taxonomic diversity indices were developed which reflect the relatedness among taxa in samples (Warwick and Clarke, 1995; Clarke and Warwick, 1998, 2001). These give complementary information to 'traditional' diversity indices (Warwick and Clarke, 2001; Leonard et al., 2006). More recently interest has grown in indices which reflect the functional composition of assemblages in some way. Although there is no standard methodology for their calculation, they generally use information about the biological and functional traits of species identified in samples to inform about how the overall assemblage may ecologically function (e.g. Tilman et al., 1997; Petchey and Gaston, 2002; Villéger et al., 2008; Laliberté and Legendre, 2010). Somerfield et al. (2008) describe how the relatedness indices of Warwick and Clarke may be adapted to give information about how the average functional breadth of a community may vary.

Several studies have addressed patterns in the diversity of fishes in the Mediterranean based on field surveys, the majority of them analyzing bathymetric patterns (Stefanescu et al., 1993; Moranta et al., 1998; Kallianiotis et al., 2000; Mérigot et al., 2007a, 2007b; Ordines et al., 2011), some analyzing spatial patterns (Gaertner et al., 2007, 2010, 2013; Granger et al., 2015; García-Ruiz et al., 2015; Navarro et al., 2015), but only a few studies analyzing temporal patterns (Gaertner et al., 2007, 2013; Granger et al., 2015). Although habitat loss and degradation, followed by exploitation, pollution, climate change, eutrophication and species invasions, maritime traffic and aquaculture, have all been identified as conspicuous threats to marine diversity in the Mediterranean

(Coll et al., 2010), trawl fishing has been identified as one of the most important factors that could impact the diversity of demersal fish assemblages (Coll et al., 2012). However, studies focused on this impact are scarce (Rochet et al., 2010; Navarro et al., 2015) and, as Granger et al. (2015) concluded, in the absence of knowledge based on data, specific modeling to analyze the effect of fishing effort on demersal fish diversity are necessary and need to be performed in forthcoming studies.

The high multispecificity of the bottom trawl fishery in the Mediterranean (Caddy, 1993; Lleonart and Maynou, 2003) highlights the importance of the use of diversity indices to study the effects of fishing on demersal communities. In this area, the Balearic Islands (western Mediterranean) represent a spot of maximum diversity (Granger et al., 2015). The marine ecosystems along the continental shelf and slope of this archipelago and their benthic and demersal communities have been subjected to regular trawl fishing since the middle of the 20th century (Oliver, 1983; Quetglas et al., 2013). Since the 1960s, when the deep-water trawl fishery started (Oliver, 1983), fishing effort has moved from the continental shelf to the slope to exploit the more-highly valued decapods crustaceans (Moranta et al., 2008; Hidalgo et al., 2009). Thus, the middle slope has been subjected to the highest level of fishing effort in the archipelago for at least four decades. Even so, the overall activity of the trawl fishery around the Balearic Islands has historically been lower than in adjacent areas, resulting in less impacted ecosystems and target resources off the archipelago, compared to those off the Iberian Peninsula (Quetglas et al., 2012).

Using extensive survey data from the Balearic Islands, in this study we analyze relationships among 'traditional', taxonomic and functional diversity indices to identify a minimum set of indicators that provide a good representation of changes in assemblages, taking into account the different aspects of diversity. We then model the responses of the demersal fish community diversity to bottom trawl fishing pressure using two different approaches: i) considering fishing effort and depth as continuous explanatory variables; and ii) considering bathymetric sampling strata and contrasting levels of fishing effort. The second approach allows us to analyze the performance of diversity indices in defined levels of fishing effort (low, medium, high and very high). The same indices were used for both approaches, except one (N_{90}) which could only be used in the second one as this index cannot be computed at sample level but needs a set of samples within a group.

2. Materials and Methods

2.1. Data sources

2.1.1. Fish assemblages

Data was collected during the International Bottom Trawl Survey in the Mediterranean (MEDITS). The characteristics of the sampling gear and protocols are explained in detail by Bertrand et al. (2002). This scientific survey has been conducted annually since 2001, during late spring in the Balearic Islands, covering the soft bottoms of the continental shelf and slope between 50 and 800 m depth. According to the MEDITS protocol, four depth strata were taken into account: (i) shallow shelf from 50 to 100 m; (ii) deep shelf from 101 to 200 m; (iii) upper slope from 201 to 500 m; and (iv) middle slope from 501 to 800 m. A total of 440 hauls (around 50 per year) carried out between 2006 and 2014 were analyzed (Table 1; Figure 1). In each haul, fish species were sorted and individuals were counted and weighed. Abundances of fish species were standardized to one square km, using the horizontal opening of the net and the distance covered in each haul, obtained using the SCANMAR system (Catch Control Systems, Scanmar AS, Åsgårdstrand, Norway) and Global Positioning System (GPS), respectively. Species with a markedly pelagic or mesopelagic habit were excluded from the analysis.

2.1.2. Fishing effort

Vessel Monitoring by satellite System (VMS) data consist of records which contain data on the geographic position, date, time and instantaneous velocity for each boat, approximately every two hours. For the bottom trawl fleet that operates in the Balearic Islands this information is available since 2006, the year in which this fleet was required to install VMS, and it was used to model the geographic distribution of fishing effort in the area and to estimate the fishing effort by fishing ground.

In the Balearic Islands trawlers are only allowed to work 12 hours per day (from 05:00 am to 05:00 pm) and 5 days per week (from Monday to Friday). In order to limit the VMS positions to when vessels were fishing, only the signals from this time period with an instantaneous velocity from 2 to 3.5 knots were selected to remove VMS signals from boats transiting to fishing grounds or ports. A total of 553526 signals were analyzed to define fishing grounds of the bottom trawl fishery in the Balearic Islands (Table 1). The VMS signals were assigned to a points net defined from a 0.01 degrees resolution grid using Matlab R2013a, and the different fishing grounds were inferred from VMS density contours assigned at each grid point (Figure 1). Finally, using expert knowledge of the bottom trawl fishery in the Balearic Islands, each fishing ground was checked in order to differentiate adjacent fishing grounds and delimit fishing grounds with low densities of VMS. Once the boundary of each fishing ground had been defined, the fishing effort was calculated as the number of boat fishing-trips to each fishing ground per year during the period 2006-2014. Each MEDITS sampling station was associated to a fishing ground and consequently to its fishing effort. Thus, within each fishing ground, all sampling stations were assigned the same fishing effort. The sampling stations that were not associated to a fishing ground (8, 10, 23 and 41; Figure 1) were matched to the lowest fishing effort value in each depth strata.

2.2. Data analysis

2.2.1. Diversity indices

Seventeen diversity indices were calculated (Table 2). They all were calculated at sample level, except N_{90} that it is calculated from groups of samples (see below). 'Traditional' diversity measures were Species richness (*S*), Margalef's richness (*d*), Pielou's evenness (*J'*), *Brillouin*, Fisher's α (*Fisher*), Rarefaction 10 (*ES(10)*), Rarefaction 20 (*ES(20)*), Shannon (*H'*), Simpson (*1-λ'*), and Hill's *N1*, *N2* and N_{∞} diversity indices (Magurran, 2004).

Taxonomic diversity (*Δ*) and taxonomic distinctness (*Δ**) require taxonomic information for the estimation of the path lengths between each pair of species (Warwick and Clarke, 1995). The indices were calculated using a taxonomic hierarchy (see Annex 1) derived from World Register of Marine Species (WoRMS Editorial Board, 2015) based on five levels: species, genera, families, orders and classes. The weights given to each level ω_{ij} were equidistant, being 20 for species belonging to different genera, 40 for species belonging to different family and same genera, 60 for species belonging to different order but same family, 80 for species belonging to different class and same order, and 100 for individuals belonging to same class.

Following Somerfield et al. (2008), functional versions of taxonomic diversity (*FΔ*) and taxonomic distinctness (*FΔ**) were also calculated. These indices are based on functional similarities between species instead of taxonomic ones. For their calculation a resemblance matrix among species derived from a functional traits matrix is used. A presence/absence traits matrix (see Annex 2) was constructed using; (i) data on fish shape, mean weight and maximum length from MEDITS bottom trawl surveys in the Balearic Islands; and (ii) data on reproduction from literature (Serena, 2005; Coll, 2006) and FishBase (Froese and Pauly, 2015). The measure used to define functional resemblance among species was the simple matching coefficient:

$$f_{ij} = 100 * (1 - \frac{a+d}{a+b+c+d});$$

where *a* is the number of traits common to species *i* and *j*, *b* the number possessed by *i* and not *j*, *c* the number possessed by *j* and not *i*, and *d* the number possessed by neither.

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 the 90% of within-group similarity calculated from abundance data for samples 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):

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

where y_{ij} is the abundance of the species *i* in the sample *j*, y_{ik} is the abundance of the species *i* in the sample *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 samples *j* and *k*, taking zero into account.

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

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

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 sample each time, producing lists of contribution to similarity by species for each. The N_{90} diversity index is the mean number of species which accumulates up to 90% of within-group similarity in all the re-samplings.

SIMPER analysis for each group of samples was also undertaken to see their species composition. The percentage of contribution of each species to within-group similarity was calculated as the mean value of species contributions to similarity taking all jack-knifes made by group of samples into account.

All diversity measures were calculated using PRIMER 7 (Clarke et al., 2014), except N_{90} which was calculated in R software, version 3.1.1 (R Core Team, 2014).

2.2.2. Relationships among diversity indices

The relationships among diversity indices calculated using sample data were quantified using the coefficient of determination (R^2) between the indices. This measure was preferred to correlation as it accounts for positive and negative relationships. Relationships among indices were visualized by hierarchical agglomerative clustering with group-average linkage. N_{90} was not included in this analysis, because it can not be calculated from single samples.

This analysis was used to select a subset of indices to study the impact of trawling on fish diversity. One index corresponding to each group detected in the cluster analysis was selected. When several indices gave similar information, the simplest and most meaningful index was chosen (Mérigot et al., 2007b).

2.2.3. Trawling impacts on fish diversity

Two different approaches were applied. The first approach considered fishing effort as a continuous variable (number of fishing trips), while in the second it was treated as a discrete variable, taking levels of fishing effort (LFE) into account. This second approach allows us to analyze the performance of indicators in extreme values of fishing effort:

a) *Continuous approach*

Generalized Additive Modeling (GAM; Hastie and Tibshirani, 1986) was applied to analyze the effect of fishing effort and depth, included in the models as continuous variables, on the selected demersal fish diversity indices. Sampling year was included as a factor in the models to take into account the inter-annual variability. This technique is a nonparametric regression, used to inspect the nonlinear relationships between dependent (response variable: diversity indices) and explanatory (covariates: depth and fishing effort) variables. The GAM models were formulated as follows:

$$Y_i = s(Depth) + s(FE) + year;$$

where Y_i are diversity indices selected from Section 2.2.2, and *FE* is the fishing effort as number of fishing trips. Minimization of both the Generalized Cross-Validation (GCV) and the Akaike Information Criterion (AIC) were used to select the best model. For all models, the assumptions of variance homogeneity and normal distribution of residuals were checked and confirmed from residual plots (see Annex 3). All GAM analyzes were carried out with R using the mgcv library (Wood, 2004).

b) Stratified approach

The diversity indices selected were the same as those used in the continuous approach plus N_{90}. For this approach each sampling station was classified according to a four LFE scale established from the range of fishing effort detected in the study area. Sampling stations located in fishing grounds subjected to <75, 76-375, 376-675 and >676 fishing trips per year were assigned to the low, medium, high and very high LFE, respectively. Analyses were done within each bathymetric strata considered in the sampling scheme (see Section 2.1.1), because they are coincident with the main bathymetric communities of demersal species and resources on the continental shelf and slope of the western and central Mediterranean (e.g. Massutí and Reñones, 2005; Biagi et al., 2002; Colloca et al., 2003). Sampling station 14, originally assigned to the medium LFE, was re-assigned to the high LFE because, particularly in the shallow shelf it showed a larger difference with the rest of sampling stations belonging to the medium LFE than to those in the high LFE (Figure 2).

A two way ANOVA was applied to test for significant effects of LFE and year on the diversity indices. In the case of the N_{90}, the values used in the two-way ANOVA were the number of species contributing up to the 90% of within-group similarity in each jack-knife done in the calculation routine of the N_{90} within each year, depth stratum and LFE. In the middle slope the calculation of N_{90} was not possible, because the number of samples per year in the very high LFE group (2 samples) was insufficient to calculate mean and standard deviation from a jack-knife routine, so the number of species which accumulates up to 90% of within-group similarity in the SIMPER analysis was used. For all indices that showed a significant interaction between year and LFE, LFE within each year were compared using Student's *t* test. SIMPER was used to compare the composition of communities in samples from different LFE within each depth stratum.

3. Results

3.1. Relationships among diversity indices

Cluster analysis separated four groups of diversity measures at a level of R^2= 0.45, corresponding to a correlation of 0.55 (Figure 3): (i) indices that are mainly influenced by the number of species (*S*, *d* and *Fisher)*; (ii) indices that are influenced by the relative abundance distribution of species (*N1*, *N2*, *H'*, *Brillouin*, *ES(10)*, *ES(20)*, *1-λ'*, *J'*, *Δ*, N_∞ and *FΔ)*; (iii) indices that are mainly influenced by taxonomic information about the species (*Δ*)*; and (iv) indices that are mainly influenced by functional information about the species (*FΔ*)*. Some indices showed high within-group correlations. This was the case of *Fisher* and *d* (R^2 ≥ 0.98) in the (i) group, and *ES(10), ES(20), Brillouin*, *H'*, *N1* and *N2* (R^2 ≥ 0.89), and *J'*, 1-*λ'* and *Δ* (R^2 ≥ 0.89) in the (ii) group.

In order to simplify the analysis and considering the high correlation showed by some of the indices, only one index from each group with R^2 ≥ 0.85 in the cluster analysis was selected. These indices were *S*, *d*, *J'*, *H'*, N_∞, *Δ*, FΔ* and *FΔ**, plus the N_{90} diversity index in the case of the stratified approach.

3.2. Trawling impacts on fish diversity

3.2.1 Continuous approach

The final models for each diversity index were the most complete ones where all the covariates were significant. GCV and AIC values for final models are presented in Table 3.

GAM modeling showed that some years had significant effect on *S*, *d*, *J'*, N_∞, *Δ** and *FΔ* during the period under consideration (Table 4; Figure 4). All the indices were significantly influenced by the bathymetry (Table 4; Figure 4). *S* and *d* increased from 50 to around 200 m, and then decreased to around 600 m, remaining constant to 800 m. Both *J'* and *H'* showed a similar pattern, as expected from their high correlation ($R^2 \geq 0.83$; Figure 3), and their values decreased from 50 to a minimum around 300 m, from where they increased to around 600 m and remained constant between 600 and 800 m. Both Δ^* and $F\Delta^*$ showed a continuous increase with depth. Fishing effort only showed a significant effect on *J'*, Δ^* and $F\Delta^*$ (Table 4; Figure 4). *J'* was positively and linearly influenced by fishing effort, whereas Δ^* and $F\Delta^*$ were negatively influenced.

3.2.2 Stratified approach

The two-way ANOVA showed significant inter-annual differences for *S*, *d* and N_{90} on the shallow and deep shelf, $F\Delta$ and N_{90} on the upper slope and *S* and *d* on the middle slope (Table 5). The LFE had a significant effect on *J'* and N_{90} on the shallow shelf, *S, d,* and N_{90} on the deep shelf, *S, J', H'* and $F\Delta$ on the upper slope and *J'* and *H'* on the middle slope (Table 5). When significant differences appeared, *S*, *d* and N_{90} showed higher values in the lower LFE of each particular bathymetric stratum, whereas contrary, *J'*, *H'* and $F\Delta$ showed higher values in the higher LFE of each particular bathymetric stratum (Figure 5). N_{90} was the only index showing a significant interaction between year and LFE (Table 5), indicating that inter-annual fluctuations do not follow the same pattern in the areas with different LFE. Despite this interaction on both the shallow and the deep shelf the values of N_{90} in the lower LFE were significantly higher than values in the higher LFE for most years (Figure 6; Table 6).

The species contributing to N_{90} varied markedly between LFE (Table 7). Some species contributed to N_{90} in one LFE but not in the other. On the shallow shelf *Lepidotrigla cavillone* only contributed to N_{90} in the low LFE, whereas *Pagellus acarne* and *Mullus barbatus barbatus* only contributed in the medium LFE. On the deep shelf *Deltentosteus quadrimaculatus*, *Mullus surmuletus*, *M. barbatus barbatus* and *Raja clavata* only contributed to N_{90} in the low LFE, whereas *Trisopterus minutus* only contributed in the medium LFE. On the upper slope, *Glossanodon leioglossus, Scyliorhinus canicula, Trigla lyra, Synchiropus phaeton, Helicolenus dactylopterus* and *Merluccius merluccius* only contributed to N_{90} in the low LFE whereas *Galeus melastomus*, *Coelorinchus caelorhinchus* and *Phycis blennoides* only contributed in the medium LFE. On the middle slope *Hymenocephalus italicus* and *Etmopterus spinax* only contributed to N_{90} in the high LFE whereas *Notacanthus bonaparte*, *Polyacanthonotus rissoanus*, *Lepidion lepidion* and *Mora moro* only contributed in the very high LFE.

The contribution to similarity and the abundance of the elasmobranch *S. canicula* were higher in the low and medium LFE on the shallow shelf and in the low LFE on the deep shelf (Table 7). The contribution to similarity of the teleost *M. surmuletus* was higher in the low and medium LFE on the shallow shelf.

Serranus hepatus, *L. cavillone* and *M. merluccius* showed low contributions in the low LFE on the deep shelf but they were the most highly contributing species in the medium LFE. On the upper slope the most highly contributing species were also different between LFE, with *G. leiglossus* accounting for 29% of the similarity in the low LFE but not appearing in the medium LFE, in which *Gadiculus argenteus* accounted for 70% of the similarity. On the middle slope, *P. blennoides* and *G. melastomus* showed the highest contributions and abundances in the high LFE whereas in the very high LFE the highest contribution was given by *Nezumia aequalis*, also followed by *G. melastomus*.

4. Discussion

This work studies biodiversity from a comprehensive and integrated point of view and highlights the importance of detecting the effects of fishing on diversity when monitoring and managing bottom trawl fisheries. Although it is well known that biodiversity is a multidimensional concept (Purvis and Hector, 2000; Mérigot et al., 2007a, 2007b), the comparison of sixteen diversity indices developed in the present study shows that some of them are highly correlated. However, there is a clear differentiation between the indices related to species counts, including their relative abundance or not, and those incorporating information about taxonomy or functionality of the species. Four groups of indices measuring complementary aspects of diversity are identified: (i) species richness, represented by indices highly influenced by the number of species; (ii) evenness, represented by indices that take into account the relative abundance of the species; (iii) taxonomy, represented by indices mainly influenced by taxonomic information; and (iv) functionality, represented by indices mainly influenced by functional information about species.

As expected, taxonomic diversity (Δ) groups with Simpson (and therefore other evenness measures) as there is a strong mechanistic relationship between these measures (Clarke and Warwick, 1998). What is more, if all species are in one genus all those indices collapse to the same measure. The index Δ can be highly influenced by the relative abundances of species, leading to situations in which the evenness component may mask the taxonomic or functional aspects of interest. This was the motivation for the development of Δ^*, which can be seen as a measure of pure taxonomic relatedness. Our results demonstrate a similar performance for the functional versions of these measures, $F\Delta$ and $F\Delta^*$. A recent study on the diversity of demersal fish in the Mediterranean (Granger et al., 2015) has shown that both functional and taxonomic diversity indices were highly correlated with Simpson's diversity index. In that sense, it is important that general statements, such as the finding by Granger et al. (2015), are understood in the context of the exact measures used and how they are related to each other mathematically, not just ecologically.

A clear relationship between demersal fish diversity and depth is shown, but with different, and even opposite, trends for some groups of indices. Although the relationships between depth and diversity of demersal fish assemblages have not always a straightforward interpretation (Gaertner et al., 2013), our results are in agreement with those found both in western (Mérigot et al., 2007a, 2007b) and eastern (Labropoulou and Papaconstantinou, 2004) Mediterranean. In this area species abundance is higher on the continental shelf, coinciding with lower evenness (higher dominance). These bathymetric differences in fish diversity also coincide with changes in the composition of demersal assemblages with depth (e.g. Massutí and Reñones, 2005; Biagi et al., 2002; Colloca et al., 2003).

A clear effect of fishing effort on evenness (*J'*) is detected in both the continuous and the stratified approaches. This index increases with increasing fishing effort and its mean value is higher at the higher level of fishing effort than at the lower levels in all bathymetric strata, except for the deep shelf. In the second approach, the indices *H'* and *FΔ*, which are highly correlated with *J'*, also show similar results as might be expected. While this may suggest that fishing exploitation works as a factor that increases the evenness of the communities and decreases the dominance of species (Zhou et al., 2010), it is also worth noticing that fishing pressure is not an independent process. Fishers choose where to go, and differences in diversity among fishing grounds may not be a result of fishing effort, but a cause. Fishermen choose grounds to fish on the basis of their knowledge of the species that inhabit them, and it is possible that grounds with more diverse assemblages are more attractive for fishing. However, the decrease on indices like *Δ*, FΔ*, S* and N_{90} with the increasing fishing effort points to the removal of dominant species of the community as the most likely explanation.

The continuous decreasing trend of *Δ** with increasing fishing effort, i.e. in heavily fished areas the members of assemblages tend to be more closely related to each other taxonomically, supports the hypothesis that taxonomic indices may be more sensitive to community changes than ‘traditional’ ones (Hall and Greenstreet, 1998; Rogers et al., 1999; Leonard et al., 2006). In our case, the increased sensitivity of *Δ** could detect the small differences in fish diversity due to trawling during the relatively short study period (2006-2014). The reduction of *FΔ** with respect to the increasing fishing effort, i.e. in heavily fished assemblages the fish are more similar functionally, implies that one effect of fishing is to remove functional variety. Further research would be necessary to determine whether changes in the functional components of the communities represent the organisms’ adaptations to the environment or their response to stress (de Juan et al., 2007). These results are not fully confirmed from the stratified approach, in which significant differences between levels of fishing effort for *FΔ** and *Δ** are not detected. However, it should be recognized that in such situations it is to be expected that correlational statistical approaches will have more power to detect change than categorical ones, and the lack of significance in a test should not be interpreted as the absence of an effect (Somerfield et al., 2002).

Although there is an increasing general concern about the importance of the role played by species in the ecosystems, there is no consensus about how functions (or 'functioning') should be quantified (Tilman et al., 1997; Petchey and Gaston, 2002; Villéger et al., 2008; Laliberté and Legendre, 2010). Functional diversity indices do not always have a straightforward interpretation. Leaving aside the important differences in the ways in which indices may be formulated (Somerfield et al., 2008), the values of functional diversity indices are highly dependent on the functional traits chosen to calculate the functional similarities between species, the weights given to each trait and the quality of the data that traits rely on (Petchey and Gaston, 2006; Somerfield et al., 2008). Although we have selected a few relevant functional traits based on reliable data, mainly from bottom trawl surveys conducted in the area, several variations in these factors could influence the results. In the present work, the similarity between the definition of $F\Delta^*$ and Δ^* leads to a similar interpretation, with $F\Delta^*$ seen as 'the expected (weighted) functional distance between any two randomly chosen individuals of the sample, considering that they belong to different species'. Hence, lower values of $F\Delta^*$ with high levels of fishing effort correspond to shorter average functional distance among species living in the most impacted areas. However, we found higher values of $F\Delta^*$ on the middle slope, where levels of fishing pressure are the highest. This stratum has the lowest number of species, but they display large functional differences. Thus, the increase in functional diversity could be due to the absence of species with intermediate functional distances in the community (that would decrease $F\Delta^*$) or to disappearance of this species due to fishing. Nevertheless the role of some functions in ecosystems, along with the importance of functional redundancy, still remains unclear (Tilman et al., 1997; Levin and Lubchenco, 2008). For a given number of species, assemblages with higher functional trait dispersion are expected to result in greater ecosystem adaptability, but they may also show greater vulnerability since any species loss will result in the loss of more functions (Wiedmann et al., 2014).

Although the continuous approach does not show a significant effect of fishing effort on *S*, the stratified approach shows significantly lower values of *S* at medium levels of fishing effort compared to low ones on the deep shelf and the upper slope. While it is true that a loss in species richness can occur only if species 'disappear', they may appear to do so if they become rare and are not sampled. The decrease of *S* observed in this study apparently relate primarily to changes in the frequency of occurrence of some species.

The index N_{90} also shows significant lower values at the high level of fishing effort compared to the low one on the shallow shelf and at the medium level of fishing effort compared to the low one on the deep shelf. This result is in accordance with those from a recent study conducted in the same area, where the only index that showed a significant response of diversity to fishing effort was N_{90} (Farriols et al., 2015). Like mean *S*, N_{90} is also sensitive to the frequencies of occurrence of species in samples. The sensitivity of N_{90} to fishing effort is due to reductions in the frequency of occurrence and in the evenness of species among samples in communities affected by fishing impacts. The significant interaction detected between fishing effort and year for N_{90} indicates that there is a different response of the index depending on the level of fishing effort. As suggested in Farriols et al. (2015), this effect could be related to a different response of the communities to environmental changes, with higher sensitivity to these changes in communities more impacted by fishing (Perry et al., 2010, Planque et al., 2010, Navarro et al., 2015).

The contrasting results obtained in the shelf and the slope of the Balearic Islands give relevant information about the current state of the demersal fish communities inhabiting these depths and habitats. Except for differences in evenness, in the middle slope there are no clear differences in fish diversity between different levels of fishing effort. Trawl fishing effort is the highest in this depth stratum, showing areas subject to high and very high levels of fishing effort, due to the displacement of the bottom trawl fishery from the shelf to the slope (Moranta et al., 2008; Hidalgo et al., 2009) that started in the middle of the 20th century (Oliver, 1983). Even the lowest fishing effort level associated to this stratum may have been too high for the most vulnerable components of the fish community. These species may have experienced the effects of trawl fishing (i.e. removing or decreasing frequency of occurrence of the most vulnerable species) long before the period analyzed in the present work.

Early descriptions of these trawl fishing grounds by Maurin (1968) from bottom trawl surveys showed the regular presence of vulnerable species, such as the deep water corals *Funiculina quadrangularis* and *Isidella elongata*, which now have almost disappeared in the area. Works on the ichthyofauna of the Balearic Islands repeatedly recorded the presence of demersal elasmobranchs such as *Scyliorhinus stellaris, Galeorhinus galeus*, *Rhinobathos* spp. and *Squatina* spp. (Ferrer, 1930; de Buen, 1935; Oliver, 1944; Maurin, 1968), that are no longer present in survey catches (see Annex 1). In fact these, and other vulnerable species such as *Squalus acanthias* and *Torpedo torpedo*, which do not appear in survey catches either, have been catalogued as extinct, critically endangered or endangered in the red lists of fishes of the Balearic Islands (Mayol et al., 2000; Grau et al., 2015). The disappearance of these top predators indicates that major changes in the fish communities studied may have happened long before the period of the present study (2006-2014), during which there have been no clear changes in the fishing effort of the bottom trawl fleet.

On the other hand, the benthic communities of the fishing grounds on the Balearic shelf do not seem to be as transformed as those on the slope, probably due to their greater extent and the lower fishing effort received. In fact, some of these fishing grounds overlap with sensitive habitats such as maërl and crinoids beds (Ordines and Massutí, 2009). This lower fishing impact still allows the presence on the shelf of some vulnerable fish species, not only those adapted to the highest levels of fishing pressure. On the slope, fish species are few and scarce and represent only a small percentage of the abundance of the demersal fauna, which is clearly dominated by decapods crustaceans (Guijarro et al., 2011). However, on the shelf the vulnerable fish species should be even more abundant in the areas subjected to low fishing pressure, leading to detectable differences of fish diversity between the higher and the lower levels of fishing effort in this stratum. In the strata showing significant differences in fish diversity using N_{90}, the SIMPER results show differences in species contribution of demersal fish species between levels of fishing effort. Some elasmobranchs, considered highly vulnerable to fishing impacts (Stevens et al., 2000; Quetglas et al., 2016), are more abundant and contribute more to within-group similarity in the areas with low levels of fishing effort. Examples include *Scyliorhinus canicula* on the shallow shelf, deep shelf and upper slope, and *Raja clavata* on the deep shelf. *Galeus melastomus* shows the opposite pattern in the upper slope, but this could be due to the distinct mean depth of the groups of samples associated to medium (408 m) and low (286 m) levels of fishing effort, and the bathymetric distribution of this species in the area, which only starts to be abundant below 350-400 m depth (Ramírez-Amaro et al., 2015).

On the middle slope, differences in N_{90} could not be tested due to the low number of sampling stations in the very high level of fishing effort. However SIMPER results show that the vulnerable species *Etmopterus spinax,* is only present in the high level of fishing effort. By contrast, whereas the abundance of the elasmobranch *G. melastomus* is higher in the high level of fishing effort, differences in contributions to similarity from the very high and high levels of fishing effort are less evident. The scavenging and opportunistic behaviour of *G. melastomus* (Fanelli et al., 2009; Anastasopoulou et al., 2013) could counteract its vulnerability to fishing exploitation through its feeding on animals damaged by the trawl or on other scavengers (Kaiser and Spencer, 1994). There is also a high contribution to within-group similarity of opportunistic species like *Nezumia aequalis* and *Nothacanthus bonaparte* (Iwamoto, 2015; Mauchline and Gordon, 1986), in the very high level of fishing effort. *N. aequalis* exhibits a benthopelagic behaviour, searching in the sediment with a diet consisting largely of epibenthic and infaunal invertebrates (e.g. polychaetes and amphipods; Macpherson, 1979), whose availability could be favoured by trawl fishing. *N. bonaparte* has also been considered to be a benthic scavenger (Tecchio, 2012).

Our results have shown changes in fish diversity due to the effect of fishing effort on demersal fish communities, but not for all depth strata and diversity indices analyzed. That could be due to the continuous exploitation of the studied area for a long period of time which may have prevented to detect those changes during the relatively short time period analyzed (2006-2014). To assess the whole potential of those diversity indices to monitor the effects of fishing on fish communities, a longer time-series preferably closer to the start of the fishing activity in the area, would be needed. However, achieving such a time series may be difficult and an alternative could be the study of time-series collected following a decline in fishing effort, perhaps through the closure of a fishery. The comparison of results obtained from other Mediterranean areas with different ranges of fishing effort would also achieve this purpose. Although in the present study we have distinguished four levels of trawl fishing effort, low, medium, high and very high, we must be aware that the effort in the Balearic Islands is lower than that exerted on adjacent areas off Iberian coast (Quetglas et al., 2012). Thus higher differences in fish diversity would be expected from the comparison of these more contrasting areas, which would be highly valuable for the assessment of the effects of fishing on fish communities.

The study of demersal fish diversity from a comprehensive and integrated point of view shows that diversity can be described using different complementary aspects such as species richness, evenness, and taxonomic and functional breadth of the species present in a given community. Each one of them may have a different response to fishing impact. However, changes in diversity may only be detectable in those communities where the levels of fishing pressure have remained relatively low. When they have been exposed for a long period to high levels of fishing pressure, the changes in diversity attributable to fishing may have happened long before the start of monitoring of the fishery and therefore it is too late to detect differences between different levels of fishing effort. This seems to be the case on the middle slope of the Balearic Islands, where vulnerable species have disappeared or are very infrequent, and have been replaced by species more adapted to the impacts of fishing.

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Annex 1. Taxonomic classification of the demersal fish species in the International Bottom Trawl Survey in the Mediterranean (MEDITS) based on the World Register of Marine Species' (WoRMS Editorial Board, 2015) classification.

Class	Order	Family	Genus	Scientific name
Actinopterygii	Anguilliformes	Chlopsidae	Chlopsis	*Chlopsis bicolor*
		Congridae	Conger	*Conger conger*
			Gnathophis	*Gnathophis mystax*
		Nemichthyidae	Nemichthys	*Nemichthys scolopaceus*
		Nettastomatidae	Facciolella	*Facciolella oxyrhyncha*
			Nettastoma	*Nettastoma melanurum*
		Ophichthidae	Echelus	*Echelus myrus*
			Ophichthus	*Ophichthus rufus*
			Ophisurus	*Ophisurus serpens*
	Aulopiformes	Aulopidae	Aulopus	*Aulopus filamentosus*
		Chlorophthalmidae	Chlorophthalmus	*Chlorophthalmus agassizi*
		Evermannellidae	Evermannella	*Evermannella balbo*
		Ipnopidae	Bathypterois	*Bathypterois mediterraneus*
		Synodontidae	Synodus	*Synodus saurus*
	Beryciformes	Trachichthyidae	Hoplostethus	*Hoplostethus mediterraneus mediterraneus*
	Gadiformes	Gadidae	Gadiculus	*Gadiculus argenteus*
			Micromesistius	*Micromesistius poutassou*
			Trisopterus	*Trisopterus minutus*
		Lotidae	Gaidropsarus	*Gaidropsarus biscayensis*
			Molva	*Molva dypterygia*
		Macrouridae	Coelorinchus	*Coelorinchus caelorhincus*
			Hymenocephalus	*Hymenocephalus italicus*
			Nezumia	*Nezumia aequalis*
			Trachyrincus	*Trachyrincus scabrus*
		Merlucciidae	Merluccius	*Merluccius merluccius*

	Moridae	Gadella	*Gadela maraldi*
		Lepidion	*Lepidion lepidion*
		Mora	*Mora moro*
	Phycidae	Phycis	*Phycis blennoides*
		Phycis	*Phycis phycis*
Lophiiformes	Lophiidae	Lophius	*Lophius budegassa*
		Lophius	*Lophius piscatorius*
Notacanthiformes	Notacanthidae	Notacanthus	*Notacanthus bonaparte*
		Polyacanthonotus	*Polyacanthonotus rissoanus*

Annex 1. Continued.

Class	Order	Family	Genus	Scientific name
Actinopterygii	Ophidiiformes	Bythitidae	Cataetyx	*Cataetyx alleni*
		Ophidiidae	Benthocometes	*Benthocometes robustus*
			Ophidion	*Ophidion barbatum*
			Ophidion	*Ophidion rochei*
		Alepocephalidae	Alepocephalus	*Alepocephalus rostratus*
		Argentinidae	Argentina	*Argentina sphyraena*
			Glossanodon	*Glossanodon leioglossus*
		Microstomatidae	Nansenia	*Nansenia oblita*
	Perciformes	Ammodytidae	Gymnammodytes	*Gymnammodytes cicerelus*
		Blenniidae	Blennius	*Blennius ocellaris*
			Parablennius	*Parablennius tentacularis*
		Callanthiidae	Callanthias	*Callanthias ruber*
		Callionymidae	Callionymus	*Callionymus maculatus*
			Synchiropus	*Synchiropus phaeton*
		Centrolophidae	Centrolophus	*Centrolophus niger*
			Schedophilus	*Schedophilus medusophagus*
		Cepolidae	Cepola	*Cepola macrophthalma*
		Epigonidae	Epigonus	*Epigonus constanciae*
			Epigonus	*Epigonus denticulatus*
			Epigonus	*Epigonus telescopus*
		Gobiidae	Deltentosteus	*Deltentosteus collonianus*
			Deltentosteus	*Deltentosteus quadrimaculatus*
			Lesueurigobius	*Lesueurigobius friesii*
			Lesueurigobius	*Lesueurigobius sanzi*
		Labridae	Coris	*Coris julis*
		Mullidae	Mullus	*Mullus barbatus barbatus*
			Mullus	*Mullus surmuletus*

	Polyprionidae	Polyprion	*Polyprion americanum*
	Serranidae	Anthias	*Anthias anthias*
		Serranus	*Serranus cabrilla*
		Serranus	*Serranus hepatus*
	Sparidae	Dentex	*Dentex dentex*
		Diplodus	*Diplodus annularis*
		Diplodus	*Diplodus vulgaris*
		Pagellus	*Pagellus acarne*
		Pagellus	*Pagellus bogaraveo*
		Pagellus	*Pagellus erythrinus*
		Pagrus	*Pagrus pagrus*
		Spondyliosoma	*Spondyliosoma cantharus*
	Trachinidae	Trachinus	*Trachinus draco*
		Trachinus	*Trachinus radiatus*

Annex 1. Continued.

Class	Order	Family	Genus	Scientific name
Actinopterygii	Perciformes	Trichiuridae	Lepidopus	*Lepidopus caudatus*
		Uranoscopidae	Uranoscopus	*Uranoscopus scaber*
		Zoarcidae	Melanostigma	*Melanostigma atlanticum*
	Pleuronectiformes	Bothidae	Arnoglossus	*Arnoglossus imperialis*
			Arnoglossus	*Arnoglossus laterna*
			Arnoglossus	*Arnoglossus rueppelii*
			Arnoglossus	*Arnoglossus thori*
			Bothus	*Bothus podas*
		Citharidae	Citharus	*Citharus linguatula*
		Cynoglossidae	Symphurus	*Symphurus ligulatus*
			Symphurus	*Symphurus nigrescens*
		Scophthalmidae	Lepidorhombus	*Lepidorhombus boscii*
			Lepidorhombus	*Lepidorhombus whiffiagonis*
			Zeugopterus	*Zeugopterus regius*
		Soleidae	Microchirus	*Microchirus ocellatus*
			Microchirus	*Microchirus variegatus*
			Monochirus	*Monochirus hispidus*
			Pegusa	*Pegusa lascaris*
			Solea	*Solea vulgaris*
	Scorpaeniformes	Dactylopteridae	Dactylopterus	*Dactylopterus volitans*
		Peristediidae	Peristedion	*Peristedion cataphractum*
		Scorpaenidae	Scorpaena	*Scorpaena elongata*
			Scorpaena	*Scorpaena loppei*
			Scorpaena	*Scorpaena notata*
			Scorpaena	*Scorpaena porcus*
			Scorpaena	*Scorpaena scrofa*
		Sebastidae	Helicolenus	*Helicolenus dactylopterus*

	Triglidae	Chelidonichthys	*Chelidonichthys cuculus*
		Chelidonichthys	*Chelidonichthys lucerna*
		Chelidonichthys	*Chelidonichthys obscurus*
		Eutrigla	*Eutrigla gurnardus*
		Lepidotrigla	*Lepidotrigla cavillone*
		Lepidotrigla	*Lepidotrigla dieuzeidei*
		Trigla	*Trigla lyra*
		Trigloporus	*Trigloporus lastoviza*
Syngnathiformes	Syngnathidae	Syngnathus	*Syngnathus acus*
Zeiformes	Zeidae	Zeus	*Zeus faber*

Annex 1. Continued.

Class	Order	Family	Genus	Scientific name
Elasmobranchii	Carcharhiniformes	Pentanchidae	Galeus	*Galeus melastomus*
		Scyliorhinidae	Scyliorhinus	*Scyliorhinus canicula*
		Triakidae	Mustelus	*Mustelus asterias*
			Mustelus	*Mustelus mustelus*
	Rajiformes	Dasyatidae	Dasyatis	*Dasyatis centroura*
			Dasyatis	*Dasyatis pastinaca*
		Myliobatidae	Myliobatis	*Myliobatis aquila*
		Rajidae	Dipturus	*Dipturus oxyrinchus*
			Leucoraja	*Leucoraja circularis*
			Leucoraja	*Leucoraja naevus*
			Raja	*Raja brachyura*
			Raja	*Raja clavata*
			Raja	*Raja miraletus*
			Raja	*Raja polystigma*
			Raja	*Raja radula*
			Rostroraja	*Rostroraja alba*
	Squaliformes	Centrophoridae	Centrophorus	*Centrophorus granulosus*
		Dalatiidae	Dalatias	*Dalatias licha*
		Etmopteridae	Etmopterus	*Etmopterus spinax*
		Oxynotidae	Oxynotus	*Oxynotus centrina*
		Squalidae	Squalus	*Squalus blainville*
	Torpediniformes	Torpedinidae	Torpedo	*Torpedo marmorata*
Holocephali	Chimaeriformes	Chimaeridae	Chimaera	*Chimaera monstrosa*

Annex 2. Functional traits for the fish species used to calculate functional diversity (*FΔ)* and functional distinctness (*FΔ**) indices. Species are grouped according to; (i) their reproductive characteristics as: external fertilization (EF1); external fertilization forming a mucilage (EF2); internal fertilization, egg layers

(IF1); internal fertilization, viviparous or ovoviviparous (IF2); (ii) shape: Flat (F); Elongate (E); Laterally flat (LF); Rounded (R); (iii) Mean weight: > 10 g (MW1); > 100 g (MW2); > 500 g (MW3); > 1000 g (MW1): and (iv) Maximum length: > 15 cm (MxL1); > 30 cm (MxL2); > 60 cm (MxL3); > 120 cm (MxL4). Information of shape, mean weight and maximum length from International Bottom Trawl Survey in the Mediterranean (MEDITS). Information on reproduction from literature (Serena, 2005; Coll, 2006) and FishBase (Froese and Pauly, 2015).

	Reproduction				Shape				Mean Weig		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW
Chlopsis bicolor	1	0	0	0	0	1	0	0	1	0	0
Conger conger	1	0	0	0	0	1	0	0	1	1	0
Gnathophis mystax	1	0	0	0	0	1	0	0	1	0	0
Nemichthys scolopaceus	1	0	0	0	0	1	0	0	1	0	0
Facciolella oxyrhyncha	1	0	0	0	0	1	0	0	1	1	0
Nettastoma melanurum	1	0	0	0	0	1	0	0	1	0	0
Echelus myrus	1	0	0	0	0	1	0	0	1	1	0
Ophichthus rufus	1	0	0	0	0	1	0	0	1	0	0
Ophisurus serpens	1	0	0	0	0	1	0	0	1	1	0
Aulopus filamentosus	1	0	0	0	0	0	0	1	1	1	0
Chlorophthalmus agassizi	1	0	0	0	0	0	0	1	1	0	0
Evermannella balbo	1	0	0	0	0	0	1	0	0	0	0
Bathypterois mediterraneus	1	0	0	0	0	0	0	1	0	0	0
Synodus saurus	1	0	0	0	0	0	0	1	1	1	0
Hoplostethus mediterraneus mediterraneus	1	0	0	0	0	0	1	0	1	0	0

Annex 2. Continued.

	Reproduction				Shape				Mean Weigh		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW3
Gadiculus argenteus	1	0	0	0	0	0	0	1	0	0	0
Micromesistius poutassou	1	0	0	0	0	0	0	1	1	0	0
Trisopterus minutus	1	0	0	0	0	0	0	1	1	0	0
Gaidropsarus biscayensis	1	0	0	0	0	0	0	1	0	0	0
Molva dypterygia	1	0	0	0	0	1	0	0	1	0	0
Coelorinchus caelorhincus	1	0	0	0	0	0	0	1	1	0	0
Hymenocephalus italicus	1	0	0	0	0	0	0	1	0	0	0
Nezumia aequalis	1	0	0	0	0	0	0	1	1	0	0
Trachyrincus scabrus	1	0	0	0	0	0	0	1	1	1	0
Merluccius merluccius	1	0	0	0	0	0	0	1	1	0	0
Gadela maraldi	1	0	0	0	0	1	0	0	0	0	0
Lepidion lepidion	1	0	0	0	0	1	0	0	1	0	0
Mora moro	1	0	0	0	0	0	0	1	1	0	0
Phycis blennoides	1	0	0	0	0	0	0	1	1	0	0
Phycis phycis	1	0	0	0	0	0	0	1	1	1	0
Lophius budegassa	1	0	0	0	1	0	0	0	1	1	0
Lophius piscatorius	1	0	0	0	1	0	0	0	1	1	1
Notacanthus bonaparte	1	0	0	0	0	1	0	0	1	0	0
Polyacanthonotus rissoanus	1	0	0	0	0	0	0	1	0	0	0

Annex 2. Continued.

	Reproduction				Shape				Mean Weig		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW3
Cataetyx alleni	0	0	0	1	0	0	0	1	0	0	0
Benthocometes robustus	1	0	0	0	0	0	0	1	0	0	0
Ophidion barbatum	1	0	0	0	0	1	0	0	1	0	0
Ophidion rochei	1	0	0	0	0	1	0	0	1	0	0
Alepocephalus rostratus	1	0	0	0	0	0	0	1	1	0	0
Argentina sphyraena	1	0	0	0	0	0	0	1	0	0	0
Glossanodon leioglossus	1	0	0	0	0	0	0	1	0	0	0
Nansenia oblita	1	0	0	0	0	0	0	1	1	0	0
Gymnammodytes cicerelus	1	0	0	0	0	1	0	0	0	0	0
Blennius ocellaris	1	0	0	0	0	0	0	1	1	0	0
Parablennius tentacularis	1	0	0	0	0	0	0	1	0	0	0
Callanthias ruber	1	0	0	0	0	0	0	1	1	0	0
Callionymus maculatus	1	0	0	0	0	0	0	1	0	0	0
Synchiropus phaeton	1	0	0	0	0	0	0	1	1	0	0
Centrolophus niger	1	0	0	0	0	0	0	1	1	1	1
Schedophilus medusophagus	1	0	0	0	0	0	0	1	1	1	1
Cepola macrophthalma	1	0	0	0	0	1	0	0	1	0	0
Epigonus constanciae	1	0	0	0	0	0	0	1	0	0	0
Epigonus denticulatus	1	0	0	0	0	0	0	1	0	0	0
Epigonus telescopus	1	0	0	0	0	0	0	1	1	0	0

Annex 2. Continued.

	Reproduction						Shape		Mean Weigh		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW3
Deltentosteus collonianus	1	0	0	0	0	0	0	1	0	0	0
Deltentosteus quadrimaculatus	1	0	0	0	0	0	0	1	0	0	0
Lesueurigobius friesii	1	0	0	0	0	0	0	1	0	0	0
Lesueurigobius sanzi	1	0	0	0	0	0	0	1	0	0	0
Coris julis	1	0	0	0	0	0	0	1	1	0	0
Mullus barbatus barbatus	1	0	0	0	0	0	0	1	1	0	0
Mullus surmuletus	1	0	0	0	0	0	0	1	1	0	0
Polyprion americanum	1	0	0	0	0	0	0	1	1	1	1
Anthias anthias	1	0	0	0	0	0	0	1	1	0	0
Serranus cabrilla	1	0	0	0	0	0	0	1	1	0	0
Serranus hepatus	1	0	0	0	0	0	0	1	1	0	0
Dentex dentex	1	0	0	0	0	0	0	1	1	1	1
Diplodus annularis	1	0	0	0	0	0	1	0	1	0	0
Diplodus vulgaris	1	0	0	0	0	0	1	0	1	1	0
Pagellus acarne	1	0	0	0	0	0	0	1	1	0	0
Pagellus bogaraveo	1	0	0	0	0	0	0	1	1	1	0
Pagellus erythrinus	1	0	0	0	0	0	0	1	1	0	0
Pagrus pagrus	1	0	0	0	0	0	0	1	1	1	0
Spondyliosoma cantharus	1	0	0	0	0	0	0	1	1	1	0

Annex 2. Continued.

	Reproduction				Shape				Mean Weig		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW3
Trachinus draco	1	0	0	0	0	0	0	1	1	0	0
Trachinus radiatus	1	0	0	0	0	0	0	1	1	1	0
Lepidopus caudatus	1	0	0	0	0	1	0	0	1	0	0
Uranoscopus scaber	1	0	0	0	0	0	0	1	1	1	0
Melanostigma atlanticum	1	0	0	0	0	0	0	1	0	0	0
Arnoglossus imperialis	1	0	0	0	1	0	0	0	1	0	0
Arnoglossus laterna	1	0	0	0	1	0	0	0	0	0	0
Arnoglossus rueppelii	1	0	0	0	1	0	0	0	0	0	0
Arnoglossus thori	1	0	0	0	1	0	0	0	0	0	0
Bothus podas	1	0	0	0	1	0	0	0	1	0	0
Citharus linguatula	1	0	0	0	1	0	0	0	1	0	0
Symphurus ligulatus	1	0	0	0	1	0	0	0	0	0	0
Symphurus nigrescens	1	0	0	0	1	0	0	0	0	0	0
Lepidorhombus boscii	1	0	0	0	1	0	0	0	1	0	0
Lepidorhombus whiffiagonis	1	0	0	0	1	0	0	0	1	1	0
Zeugopterus regius	1	0	0	0	1	0	0	0	1	0	0
Microchirus ocellatus	1	0	0	0	1	0	0	0	1	0	0
Microchirus variegatus	1	0	0	0	1	0	0	0	1	0	0
Monochirus hispidus	1	0	0	0	1	0	0	0	1	0	0
Pegusa lascaris	1	0	0	0	1	0	0	0	1	1	0
Solea vulgaris	1	0	0	0	1	0	0	0	1	1	0

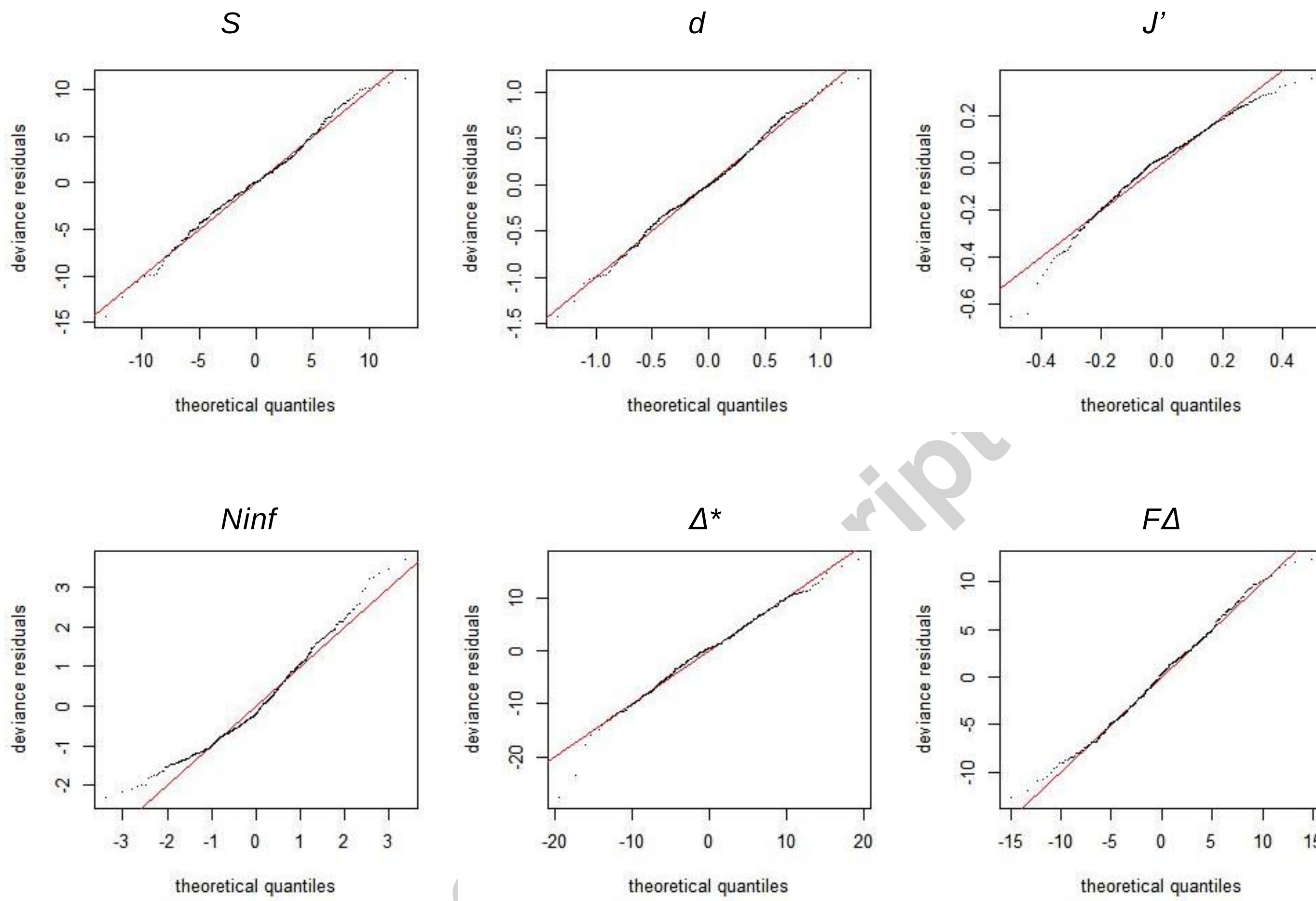
Annex 2. Continued.

	Reproduction						Shape		Mean Weig		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW3
Dactylopterus volitans	1	0	0	0	0	0	0	1	1	1	1
Peristedion cataphractum	1	0	0	0	0	0	0	1	1	0	0
Scorpaena elongata	0	1	0	0	0	0	0	1	1	1	0
Scorpaena loppei	0	1	0	0	0	0	0	1	1	0	0
Scorpaena notata	0	1	0	0	0	0	0	1	1	0	0
Scorpaena porcus	0	1	0	0	0	0	0	1	1	1	0
Scorpaena scrofa	0	1	0	0	0	0	0	1	1	1	0
Helicolenus dactylopterus	0	0	1	0	0	0	0	1	1	0	0
Chelidonichthys cuculus	1	0	0	0	0	0	0	1	1	0	0
Chelidonichthys lucerna	1	0	0	0	0	0	0	1	1	1	0
Chelidonichthys obscurus	1	0	0	0	0	0	0	1	1	0	0
Eutrigla gurnardus	1	0	0	0	0	0	0	1	1	0	0
Lepidotrigla cavillone	1	0	0	0	0	0	0	1	1	0	0
Lepidotrigla dieuzeidei	1	0	0	0	0	0	0	1	1	0	0
Trigla lyra	1	0	0	0	0	0	0	1	1	0	0
Trigloporus lastoviza	1	0	0	0	0	0	0	1	1	0	0
Syngnathus acus	0	0	0	1	0	1	0	0	1	0	0
Zeus faber	1	0	0	0	0	0	1	0	1	1	0

Annex 2. Continued.

	Reproduction				Shape				Mean Weig		
Species	EF1	EF2	IF1	IF2	F	E	LF	R	MW1	MW2	MW3
Galeus melastomus	0	0	1	0	0	0	0	1	1	1	0
Scyliorhinus canicula	0	0	1	0	0	0	0	1	1	1	0
Mustelus asterias	0	0	0	1	0	0	0	1	1	1	1
Mustelus mustelus	0	0	0	1	0	0	0	1	1	1	1
Dasyatis centroura	0	0	0	1	1	0	0	0	1	1	1
Dasyatis pastinaca	0	0	0	1	1	0	0	0	1	1	1
Myliobatis aquila	0	0	0	1	1	0	0	0	1	1	1
Dipturus oxyrinchus	0	0	1	0	1	0	0	0	1	1	1
Leucoraja circularis	0	0	1	0	1	0	0	0	1	1	1
Leucoraja naevus	0	0	1	0	1	0	0	0	1	1	0
Raja brachyura	0	0	1	0	1	0	0	0	1	1	1
Raja clavata	0	0	1	0	1	0	0	0	1	1	1
Raja miraletus	0	0	1	0	1	0	0	0	1	1	0
Raja polystigma	0	0	1	0	1	0	0	0	1	1	0
Raja radula	0	0	1	0	1	0	0	0	1	1	1
Rostroraja alba	0	0	1	0	1	0	0	0	1	1	1
Centrophorus granulosus	0	0	0	1	0	0	0	1	1	0	0
Dalatias licha	0	0	0	1	0	0	0	1	1	1	1
Etmopterus spinax	0	0	0	1	0	0	0	1	1	0	0
Oxynotus centrina	0	0	0	1	0	0	0	1	1	1	1
Squalus blainville	0	0	0	1	0	0	0	1	1	1	1
Torpedo marmorata	0	0	0	1	1	0	0	0	1	1	0
Chimaera monstrosa	0	0	1	0	0	0	0	1	1	1	1

Annex 3. Residual plots from GAM modeling showing the residuals deviation from normality for each diversity index selected from the cluster analysis (*S*, *d*, *J'*, *H'*, N_∞*(Ninf)*, *Δ*, FΔ* and *FΔ**).



References

Anastasopoulou, A., Mytilineou, C., Lefkaditou, E., Dokos, J., Smith, C. J., Siapatis, A., Bekas, P., and Papadopoulou, K. N. 2013. Diet and feeding strategy of blackmouth catshark *Galeus melastomus*. Journal of Fish Biology, 83: 1637–1655.

Balmford, A., Crane, P., Dobson, A., Green, R. E., and Mace, G. M. 2005. The 2010 challenge: data availability, information needs and extraterrestrial insights. Philosophical Transactions of the Royal Society of London, Biological Sciences, 360: 221–228.

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

Biagi, F., Sartor, P., Ardizzone, G. D., Belcari, P., Belluscio, A., and Serena, F. 2002. Análisis of demersal assemblages off Tuscany and Latium coasts (north-western Mediterranean). Scientia Marina, 66: 233–242.

Bray, J. R., and Curtis, J. T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs, 27: 325–349.

Caddy, J. F. 1993. Some future perspectives for assessment and management of Mediterranean fisheries. Scientia Marina, 57: 121–130.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18: 117–143.

Clarke, K. R., Gorley, R. N., Somerfield, P. J., and Warwick, R. M. 2014. Change in marine communities: an approach to statistical analysis and interpretation. 3rd edition. PRIMER-E, Plymouth. 260 pp.

Clarke, K. R., and Warwick, R. M. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology, 35: 523–531.

Clarke, K. R., and Warwick, R. M. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology Progress Series, 216: 265–278.

Coll, M. 2006. Modelización de flujos y uso de indicadores ecológicos como aproximación al estudio de las pesquerías mediterráneas. PhD Thesis. Universitat de Barcelona, 538 pp.

Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W. W. L., Christensen, V., Karpouzi, V. S., *et al*. 2012. The Mediterranean Sea under siege: Spatial overlap between marine biodiversity, cumulative threats and marine reserves. Global Ecology and Biogeography, 21: 465–480.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., *et al*. 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PloS One, 5: e11842.

Colloca, F., Cardinale, M., Belluscio, A., and Ardizzone, G. D. 2003. Structure and diversity of demersal assemblages in the central Mediterranean Sea. Estuarine, Coastal and Shelf Science, 56: 469–480.

de Buen, F. 1935. Fauna ictiológica. Catálogo de los peces ibéricos: de la planicie continental, aguas dulces, pelágicos y de los abismos próximos. 1ª Parte: Notas y Resúmenes. Instituto Español de Oceanografía, Ser. II, 88: 1–90.

de Juan, D., Thrush, S., and Demestre, M. 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Marine Ecology Progress Series, 334: 117–129.

Fanelli, E., Rey, J., Torres, P., and Gil de Sola, L. 2009. Feeding habits of blackmouth catshark *Galeus melastomus* Rafinesque, 1810 and velvet belly lantern shark *Etmopterus spinax* (Linnaeus, 1758) in the western Mediterranean. Journal of Applied Ichthyology, 25 (Suppl. 1): 83–93.

Farriols, M. T., Ordines, F., Hidalgo, M., Guijarro, B., and Massutí, E. 2015. N_{90} index: A new approach to biodiversity based on similarity and sensitive to direct and indirect fishing impact. Ecological Indicators, 52: 245–255.

Ferrer, J. 1930. Catálogo de los peces de Menorca. 2ª ed. Tipografía Mahonesa, Maò. 39 pp.

Fisher, R. A., Corbet, A. S., and Williams, C. B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology, 12: 42–58.

Froese, R., and Pauly, D. 2015. Fishbase. Available from www.fishbase.org.

Fulton, E. A., Smith, A. D. M., and Punt, A. E. 2005. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science, 62: 540–551.

Gaertner, J. C., Bertrand, J. A., Relini, G., Papaconstantinou, C., Mazouni, N., De Sola, L. G., Dourbet, J.-P., *et al*. 2007. Spatial pattern in species richness of demersal fish assemblages on the continental shelf of the northern Mediterranean Sea: A multiscale analysis. Marine Ecology Progress Series, 341: 191–203.

Gaertner, J.-C., Maiorano, P., Mérigot, B., Colloca, F., Politou, C.-Y., Gil De Sola, L., Bertrand, J. A., *et al*. 2013. Large-scale diversity of slope fishes: pattern inconsistency between multiple diversity indices. PloS One, 8: e66753.

Gaertner, J.-C., Mérigot, B., Rélini, G., Bertrand, J. A., Mazouni, N., Politou, C.-Y., Gil de Sola, L., *et al.* 2010. Reproducibility of the multi-component aspect of species diversity across different areas and scales: towards the constitution of a shortlist of complementary indices for monitoring fish diversity? Ecography, 33: 1123–1135.

Garcia, S. M., and Cochrane, K. L. 2005. Ecosystem approach to fisheries: a review of implementation guidelines. ICES Journal of Marine Science, 62: 311–318.

García-Ruiz, C., Lloris, D., Rueda, J. L., García-Martínez, M. C., and Gil de Sola, L. 2015. Spatial distribution of ichthyofauna in the northern Alboran Sea (western Mediterranean). Journal of Natural History, 49: 1191–1224.

Granger, V., Fromentin, J.-M., Bez, N., Relini, G., Meynard, C. N., Gaertner, J.-C., Maiorano, P., *et al*. 2015. Large-scale spatio-temporal monitoring highlights hotspots of demersal fish diversity in the Mediterranean Sea. Progress in Oceanography, 130: 65–74.

Grau, A.M., Mayol, J., Oliver, J., Riera, F., and Riera, I. 2015. Llibre vermell dels peixos de les Illes Balears. Conselleria de Medi Ambient, Agricultura i Pesca, 150 pp.

Guijarro, B., Tserpes, G., Moranta, J., and Massutí, E. 2011. Assessment of the deep water trawl fishery off the Balearic Islands (western Mediterranean): from single to multi-species approach. Hydrobiologia, 670: 67–85.

Hall, S. J., and Greenstreet, S. P. 1998. Taxonomic distinctness and diversity measures: responses in marine fish communities. Marine Ecology Progress Series, 166: 227–229.

Hastie, T. J., and Tibshirani, R. 1986. Generalized additive models. Statistical Science, 1: 297–318.

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

Hill, M. O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology, 54: 427.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology, 54: 187–211.

Iwamoto, T. 2015. *Nezumia aequalis*. The IUCN Red List of Threatened Species 2015: e.T198597A15575063. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T198597A15575063.en.

Kaiser, M. J., and Spencer, B. E. 1994. Fish scavenging behaviour in recently trawled areas. Marine Ecology Progress Series, 112: 41–50.

Kallianiotis, A., Sophronidis, K., Vidoris, P., and Tselepides, A. 2000. Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): Seasonal variation in species density, biomass and diversity. Progress in Oceanography, 46: 429–455.

Labropoulou, M., and Papaconstantinou, C. 2004. Community structure and diversity of demersal fish assemblages : the role of fishery. Scientia Marina, 68(Suppl. 1): 215–226.

Laliberté, E., and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91: 299–305.

Leonard, D. R. P., Clarke, K. R., Somerfield, P. J., and Warwick, R. M. 2006. The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. Journal of Environmental Management, 78:52–62.

Levin, S. A., and Lubchenco, J. 2008. Resilience, Robustness, and Marine Ecosystem-based Management. BioScience, 58: 27–32.

Lleonart, J., and Maynou, F. 2003. Fish stock assessments in the Mediterranean: state of the art. Scientia Marina, 67: 37–49.

Macpherson, E. 1979. Ecological overlap between macrourids in the Western Mediterranean Sea. Marine Biology, 53: 149–159.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science, Malden. 256 pp.

Margalef, R. 1958. Information theory in ecology. General Systems, 3: 36–71.

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

Mauchline, J., and Gordon, J. D. M. 1986. Foraging strategies of deep-sea fish. Marine Ecology Progress Series, 27: 227–238.

Maurin, C. 1968. Ecologie ichthyologique des fonds chalutables atlantiques (de la Baie Ibero-Marocaine a la Mauritanie) et de la Mediterranee occidentale. Revue des travaux de l'Institut des pêches maritimes, 32(1): 1–144.

Mayol, J., Grau, A.M., Riera, F., and Oliver, J. 2000. Llista vermella dels peixos de les Balears. Documents Tècnics de Conservació, II(7): 1-126.

Mérigot, B., Bertrand, J. A., Gaertner, J.-C., Durbec, J.-P., Mazouni, N., and Manté, C. 2007a. The multi-component structuration of the species diversity of groundfish assemblages of the east coast of Corsica (Mediterranean Sea): Variation according to the bathymetric strata. Fisheries Research, 88: 120–132.

Mérigot, B., Bertrand, J. A., Mazouni, N., Manté, C., Durbec, J.-P., and Gaertner, J.-C. 2007b. A multi-component analysis of species diversity of groundfish assemblages on the continental shelf of the Gulf of Lions (north-western Mediterranean Sea). Estuarine, Coastal and Shelf Science, 73: 123–136.

Moranta, J., Stefanescu, C., Massutí, E., Morales-Nin, B., and Lloris, D. 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin , western Mediterranean). Marine Ecology Progress Series, 171: 247–259.

Moranta, J., Quetglas, A., Massutí, E., Guijarro, B., Hidalgo, M., and Diaz, P. 2008. Spatio-temporal variations in deep-sea demersal communities off the Balearic Islands (western Mediterranean). Journal of Marine Systems, 71: 346–366.

Mouchet, M. A., Villéger, S., Mason, N. W. H., and Mouillot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24: 867–876.

Navarro, J., Coll, M., Cardador, L., Fernández, Ángel M., and Bellido, J. M. 2015. The relative roles of the environment, human activities and spatial factors in the spatial distribution of marine biodiversity in the Western Mediterranean Sea. Progress in Oceanography, 131: 126–137.

Oliver, F. 1944. Catálogo de la Fauna Marítima de Mallorca. Publicaciones del Instituto Social de la Marina.

Oliver, P. 1983. Les resources halieautiques de la Méditerranée, Premiere Partie: Méditerranée occidentale. Studies and Reviews. General Fisheries Council of the Mediterranean, 59: 1-135.

Ordines, F. and Massutí, E. 2009. Relationships between macro-epibenthic communities and fish on the shelf grounds of the western Mediterranean. Aquatic Conservation: Marine and Freshwater Ecosystems, 19: 370-383.

Ordines, F., Massutí, E., Moranta, J., Quetglas, A., Guijarro, B., and Fliti, K. 2011. Balearic Islands vs Algeria: two nearby western Mediterranean elasmobranch assemblages with different oceanographic scenarios and fishing histories. Scientia Marina, 75: 707–717.

Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and man- agement responses. Journal of Marine Systems, 79: 427–435.

Petchey, O. L., and Gaston, K. J. 2002. Functional diversity (FD), species richness and community composition. Ecology Letters, 5: 402−411.

Petchey, O. L., and Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. Ecology Letters, 9: 741–758.

Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. Journal of Theoretical Biology, 10: 370–383.

Pielou, E. C. 1975. Ecological diversity. Wiley, New York. 165 pp.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., *et al*. 2004. Ecosystem-based fishery management. Science, 305: 356–347.

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I., Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensi- tivity to climate? Journal of Marine Systems, 79: 403–417.

Purvis, A., and Hector, A. 2000. Getting the measure of biodiversity. Nature, 405: 212–219.

Quetglas, A., Guijarro, B., Ordines, F., and Massutí, E. 2012. Stock boundaries for fisheries assessment and management in the Mediterranean: the Balearic Islands as a case study. Scientia Marina, 76: 17–28.

Quetglas, A., Ordines, F., Hidalgo, M., Monserrat, S., Ruiz, S., Amores, Á., Moranta, J. *et al*. 2013. Synchronous combined effects of fishing and climate within a demersal community. ICES Journal of Marine Science, 70: 319–328.

Quetglas, A., Rueda, L., Álvarez-Berastegui, D., and Massutí, E. 2016. Contrasting responses to harvesting and environmental drivers of fast and slow life history species. PLoS One 11: e0148770.

R Core Team. 2014. R: A language and environment for statistical computing. Available: http://www.r- project.org/.

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

Rice, J. 2003. Environmental health indicators. Ocean & Coastal Management, 46: 235–259.

Rice, J., and Rochet, M.-J. 2005. A framework for selecting a suite of indicators for fisheries management. ICES Journal of Marine Science, 62: 516–527.

Rochet, M. J., Trenkel, V. M., Carpentier, A., Coppin, F., de Sola, L. G., Léauté, J. P., Mahé, J.-C., *et al*. 2010. Do changes in environmental and fishing pressures impact marine communities? An empirical assessment. Journal of Applied Ecology, 47: 741–750.

Rogers, S. I., Clarke, K. R., and Reynolds, J. D. 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-East Atlantic. Journal of Animal Ecology, 68: 769–782.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. American Natulalist, 102: 243–282.

Serena, F. 2005. Field identification guide to the sharks and rays of Mediterranean and Black Sea. FAO species identification guide for fishery purposes. FAO, Rome.

Shannon, C. E., and Weaver, W. 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana.

Simpson, E. H. 1949. Measurement of diversity. Nature, 163: 688.

Somerfield, P. J., Clarke, K. R., Olsgard, F. 2002. A comparison of the power of categorical and correlational tests applied to community ecology data from gradient studies. Journal of Animal Ecology, 71: 581–593.

Somerfield, P. J., Clarke, K. R., Warwick, R. M., and Dulvy, N. K. 2008. Average functional distinctness as a measure of the composition of assemblages. ICES Journal of Marine Science, 65: 1462–1468.

Stefanescu, C., Lloris, D., and Rucabado, J. 1993. Deep sea fish assemblages in the Catalan Sea (western Mediterranean) below a depth of 1000 m. Deep-Sea Research Part I, 40: 695–707.

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494.

Sutherland, W.J., Armstrong-Brown, S., Armsworth, P.R., Brereton, T., Brickland, J., Campbell, C.D., Chamberlain, D.E., *et al*. 2006. The hundred ecological questions of highest UK policy relevance. Journal of Applied Ecology, 43: 617-627.

Tecchio, S. 2012. Mediterranean deep-sea ecosystems: biodiversity, functioning and vulnerability. PhD Thesis. Universitat de Barcelona, 147 pp.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. Science, 277: 1300−1302.Tsimenides, N., Tserpes, G., Machias, A., and Kallianiotis, A. 1991. Distribution of fishes on the Cretan shelf. Journal of Fish Biology, 39: 661–672.

Villéger, S., Mason, N. W. H., and Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89: 2290–2301.

Warwick, R. M., and Clarke, K. R. 1995. New "biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Marine Ecology Progress Series, 129: 301–305.

Warwick, R. M., and Clarke, K. R. 2001. Pratical measures of marine biodiversity based on relateness of species. Oceanography and Marine Biology Annual Review, 39: 207-231.

Wiedmann, M., Aschan, M., Certain, G., Dolgov, A, Greenacre, M., Johannesen, E., Planque, B. *et al*. 2014. Functional diversity of the Barents Sea fish community. Marine Ecology Progress Series, 495: 205–218.

Wood, S.N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association. 99:673-686.

WoRMS Editorial Board. 2015. World Register of Marine Species. Available from www.marinespecies.org at VLIZ.

Zhou, S., Smith, A. D. M., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S. *et al*. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proceedings of the National Academy of Sciences, 107: 9485–9489.

Figure 1. Map of the Balearic Islands, showing the International Bottom Trawl Survey in the Mediterranean (MEDITS) sampling stations (black dots) and the fisheries grounds identified (black contours). The points represent the 0.01 resolution grid used to assign the Vessel Monitoring by satellite System (VMS) signals. The color bar represents the intensity of VMS signals during the period 2006–2014.

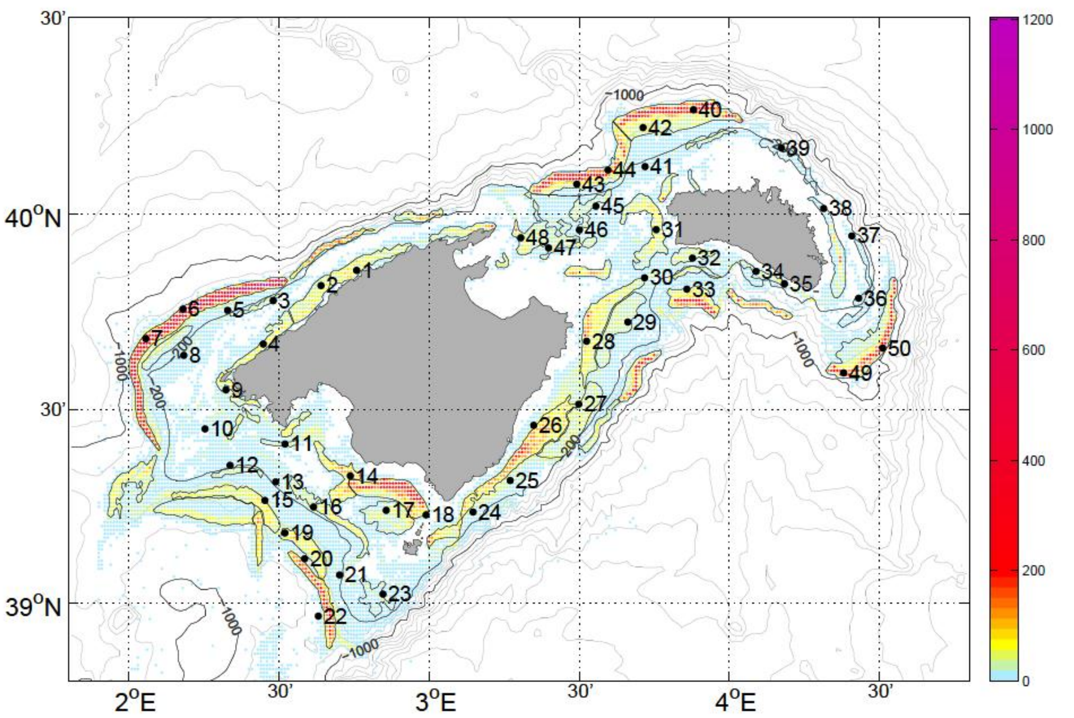


Figure 2. Mean annual fishing effort at each sampling station by depth strata used to the classification of each sampling station into levels of fishing effort (LFE). Blue bar: low LFE; yellow bar: medium LFE; red bar: high LFE; and purple bar: very high LFE.

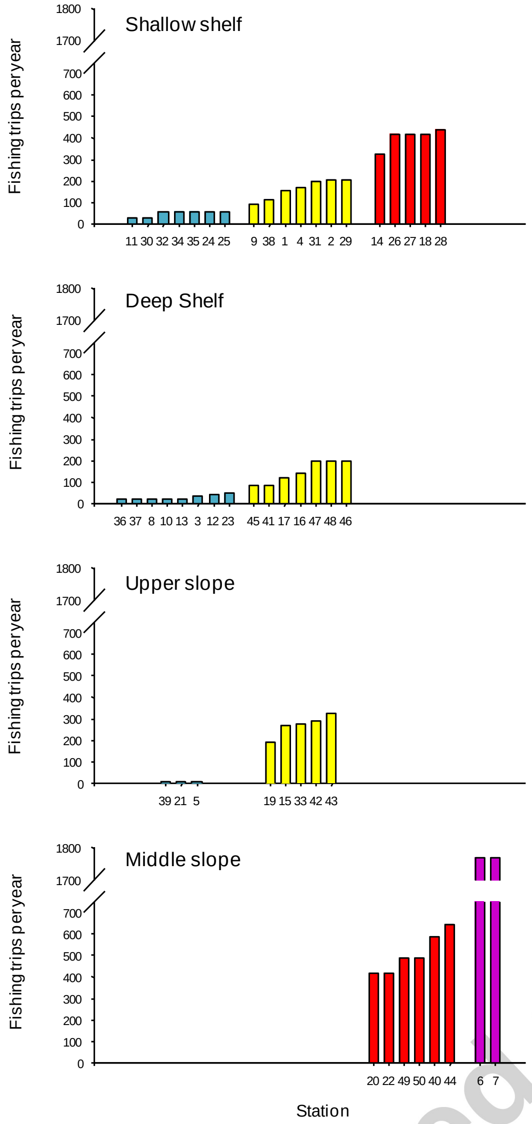


Figure 3. Relationships between the sixteen diversity indices analyzed based on the coefficient of determination R^2. The data used for the cluster analysis were the values of the indices for each sample during the sampling period (2006-2014). The legend shows the groups that represent complementary aspects of diversity: (i) species richness, (ii) evenness; (iii) taxonomy; and (iv) functionality. The dashed line shows the correlation level (R^2=0.85) used to select the diversity indices used in the analysis: *S*, *d*, *J'*, *H'*, N_∞*(Ninf)*, *Δ*, FΔ* and *FΔ**.

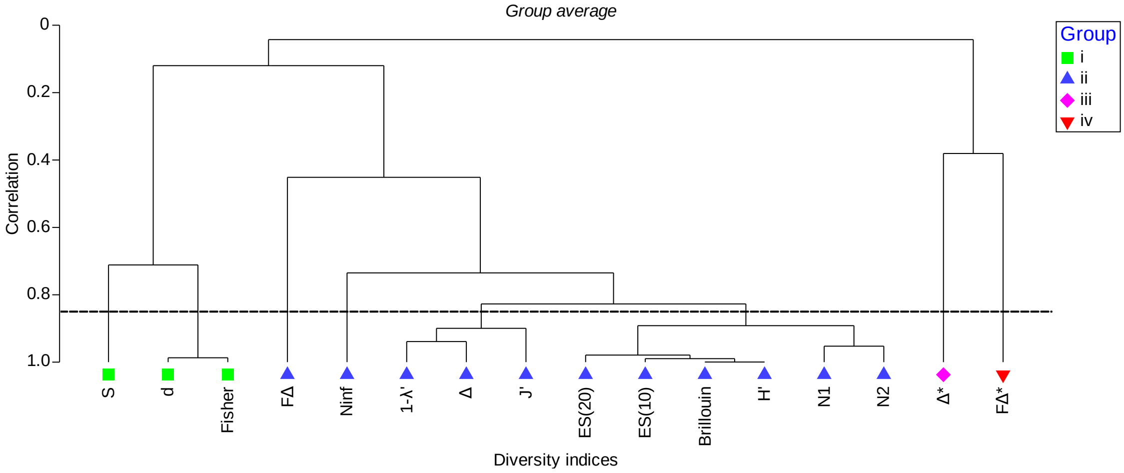
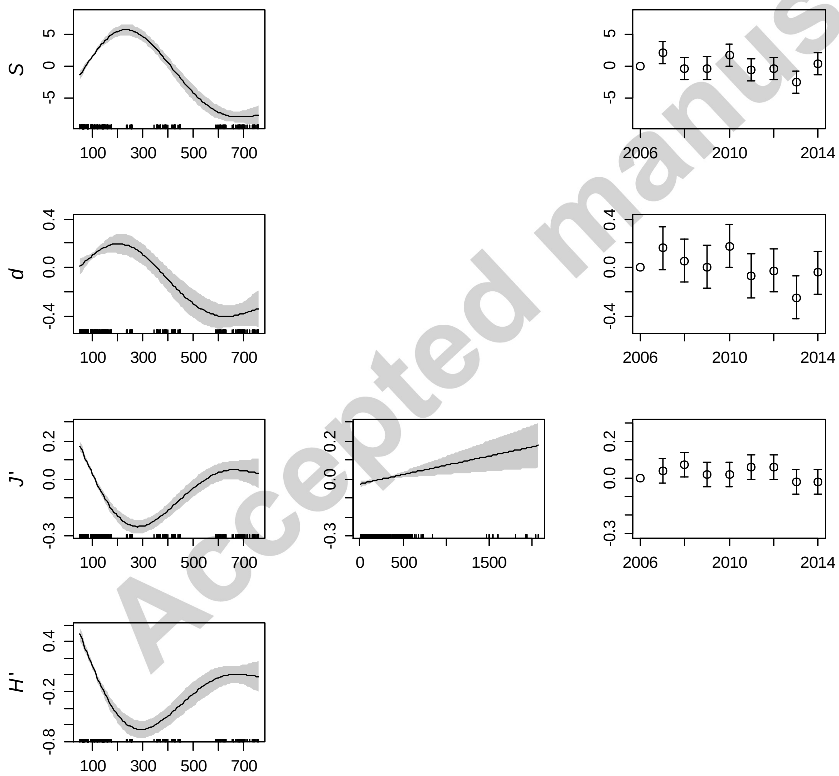


Figure 4. Results of GAM analysis showing the responses of the diversity indices selected from the cluster analysis (*S*, *d*, *J'*, *H'*, N_{∞}*(Ninf)*, *Δ**, *FΔ* and *FΔ**) to depth and fishing effort. Responses for year factor are also presented. Shaded areas and dispersion values represent 95% confidence intervals.



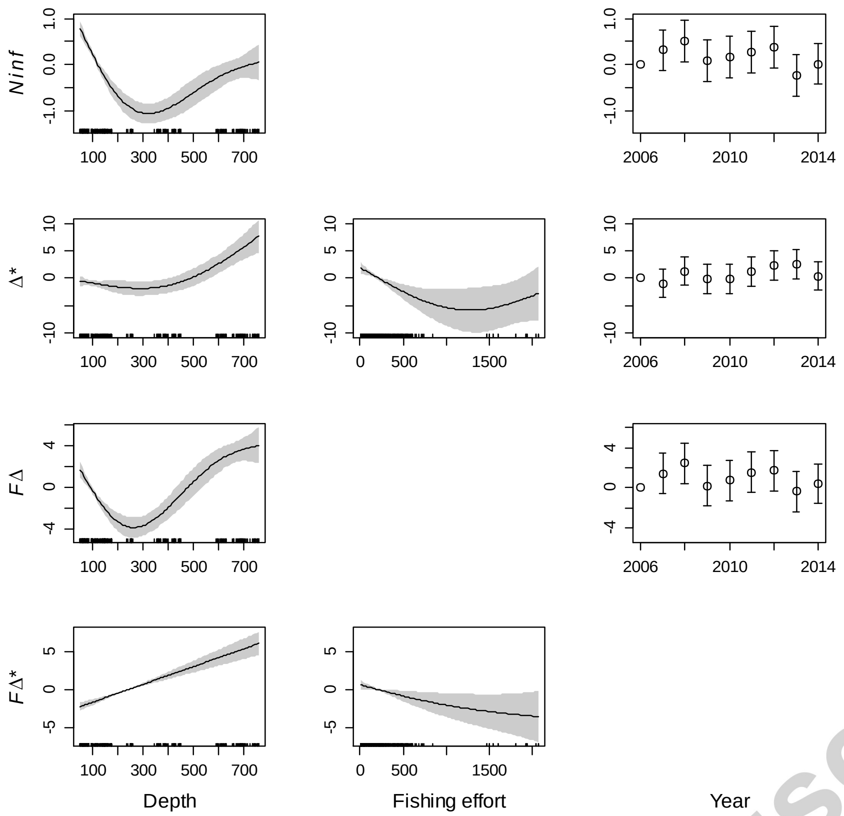


Figure 5. Mean values and standard deviation of the diversity indices selected from the cluster analysis (*S*, *d*, *J'*, *H'*, N_{∞} *(Ninf)*, *Δ*, FΔ* and *FΔ**) and N_{90}. Blue square: low level of fishing effort; yellow square: medium level of fishing effort; red square: high level of fishing effort; and purple square: very high level of fishing effort. The levels of significance obtained from the ANOVA for the fishing effort factor are also represented. *: p<0.05, **: p<0.01, ***: p<0.001.

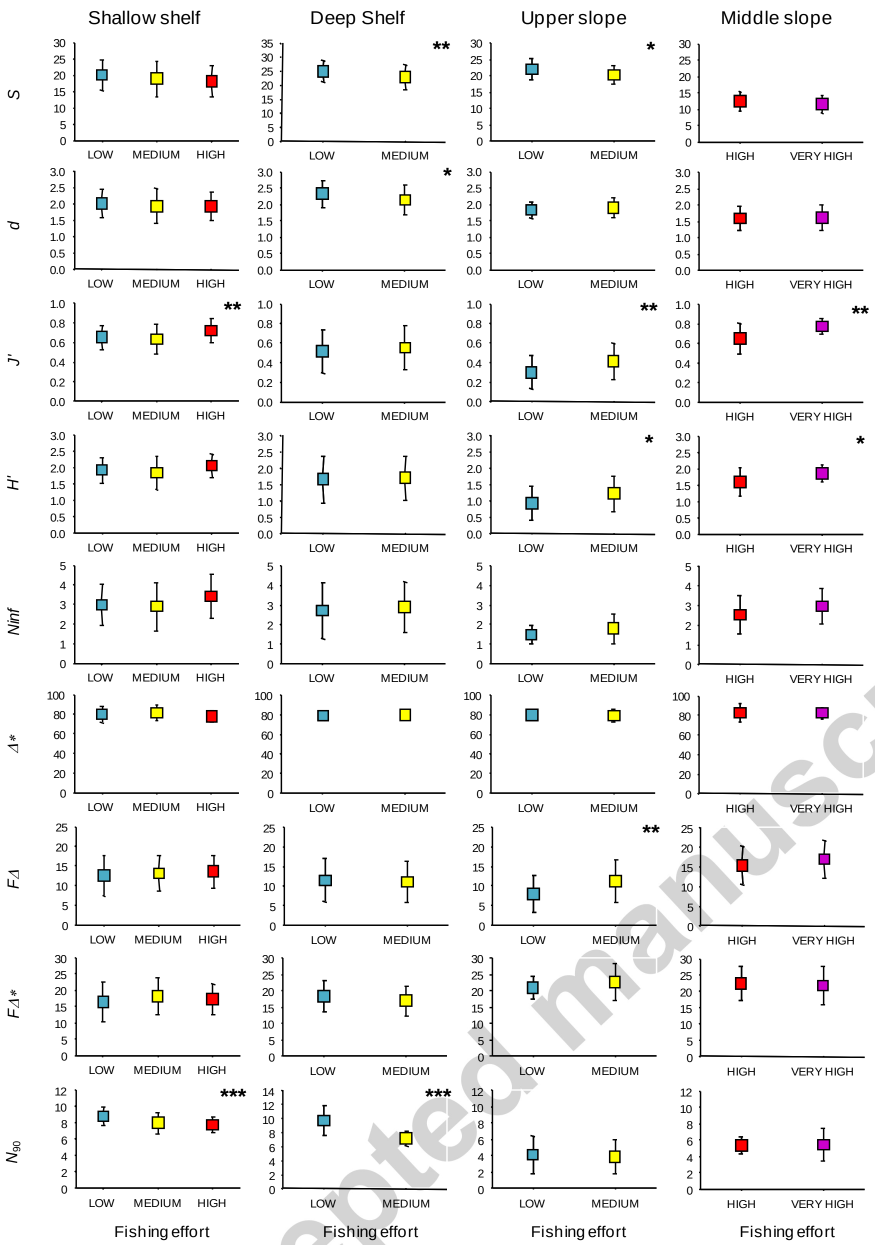


Figure 6. Mean values and standard deviation of the N_{90} diversity index during the period 2006-2014. Blue dots: low level of fishing effort; yellow dots: medium level of fishing effort; red dots: high level of fishing effort; and purple dots: very high level of fishing effort.

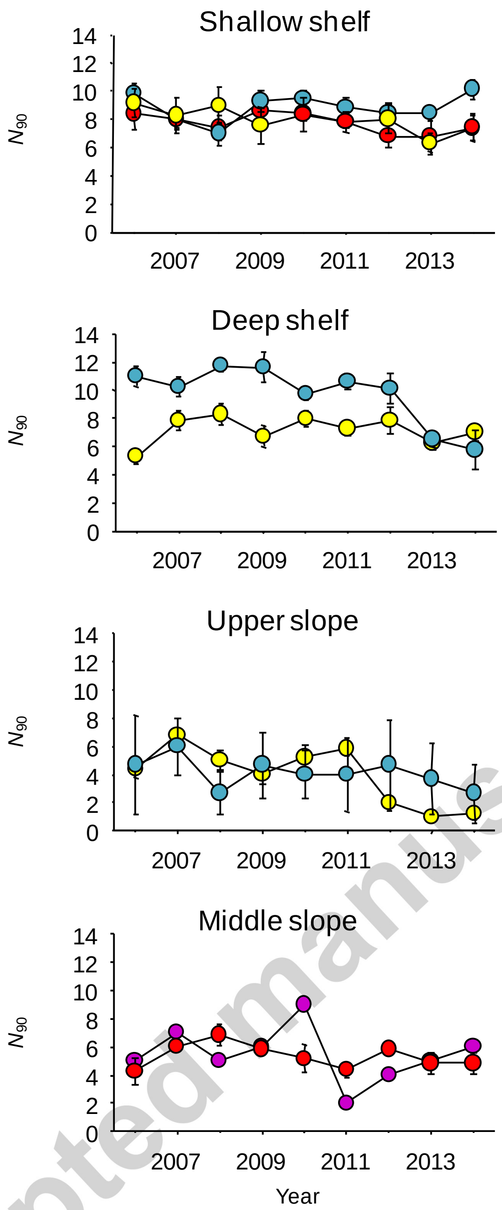


Table 1. Number of samples analyzed to calculate diversity indices from International Bottom Trawl Survey in the Mediterranean (MEDITS) and number of signals of Vessel Monitoring by Satellite System (VMS) analyzed to associate fishing effort to each sampling station by year from the Spanish Ministry of Agriculture, Food and Environment.

	2006	2007	2008	2009	2010	2011	2012	2013	2014
Samples	44	50	50	50	48	48	49	50	50
VMS	59234	57828	61649	58589	59413	62150	69744	59779	65140

Table 2. Diversity indices analyzed. $x_i(i = 1, \dots, S)$ denotes the number of individuals of the ith species, $N(= \sum_{i=1}^{S} x_i)$ is the total number of individuals in the sample, $p_i(= x_i/N)$ is the proportion of all individuals belonging to species *i*, N_{max} is the abundance of the species that are most representative in the sample, ω_{ij} is the taxonomic path length between species *i* and *j*, f_{ij} is the functional dissimilarity between species *i* and *j*.

Diversity index	**Formula**	**Symbol**	**Description**	**References**
Species richness	Number of species	*S*	Total number of species	-
Fisher's α	$S = \alpha Ln(1 + \frac{N}{\alpha})$	*Fisher*	Shape parameter under the assumption that species abundance distribution follows a log series distribution	Fisher et al. (1943)
Simpson	$1 - \lambda' = 1 - \frac{\sum_{i=1}^{S} x_i(x_i - 1)}{N(N-1)}$	*1-λ'*	Probability that two individuals drawn at random from an infinite community belong to the same species	Simpson (1949)
Shannon	$H' = \sum_{i=1}^{S} p_i \text{ Ln } p_i$	*H'*	Measure of the uncertainty about the	Shannon and Weaver (1949)

			species of the nearest neighbour of an individual from the community	
Margalef's richness	$d = \frac{S-1}{\operatorname{Ln} N}$	*d*	Number of species adjusted to the number of individuals	Margalef (1958)
Pielou's evenness	$J' = H'/\operatorname{Ln} S$	*J'*	Equitability in the distribution of abundances of species in a community	Pielou (1966)
Rarefaction 10	$ES_{10} = \sum_{i=1}^{S}[1 - \frac{(N-x_i)!\,(N-10)!}{(N-x_i-10)!\,N!}]$	*ES(10)*	Expected number of species in 10 individuals	Sanders (1968) and Hurlbert (1971)
Rarefaction 20	$ES_{20} = \sum_{i=1}^{S}[1 - \frac{(N-x_i)!\,(N-20)!}{(N-x_i-20)!\,N!}]$	*ES(20)*	Expected number of species in 20 individuals	Sanders (1968) and Hurlbert (1971)
Reciprocal Berger-Parker	$N\infty = \frac{N}{N_{max}}$	N_∞	Inverse of the dominance of species	Hill (1973)

Table 2. Continued.

Diversity	**Formula**	**Symb**	**Descripti**	**References**

index		ol	on	
Hill's N1	$N1 = \exp H'$	*N1*	Exponential of Shannon	Hill (1973)
Hill's N2	$N2 = \frac{1}{\sum_{i=1}^{S} p_i{}^2}$	*N2*	Reciprocal of Simpson	Hill (1973)
Brillouin	$\text{Brillouin} = \frac{\text{Ln}\{\frac{\text{N!}}{x_1!\ x_2! \dots x_S!}\}}{N}$	*Brillouin*	Finite population size version of Shannon	Pielou (1975)
Taxonomic diversity	$\Delta = 2\frac{\sum\sum_{i<j}(\omega_{ij}x_i x_j)}{N(N-1)}$	*Δ*	Taxonomic distance expected between two individuals randomly selected	Warwick and Clarke (1995)
Taxonomic distinctness	$\Delta^* = \frac{\sum\sum_{i<j}(\omega_{ij}x_i x_j)}{\sum\sum_{i<j}(x_i x_j)}$	*Δ**	Taxonomic distance expected between two individuals randomly selected, considering that they belong to different species	Warwick and Clarke (1995)
Functional diversity	$F\Delta = 2\frac{\sum\sum_{i<j}(f_{ij}x_i x_j)}{N(N-1)}$	*FΔ*	Functional distance expected between two individuals randomly selected	Modified from Somerfield et al. (2008)
Functional distinctness	$F\,\Delta^* = \frac{\sum\ \sum_{i<j}(f_{ij}x_i x_j)}{\sum\ \sum_{i<j}(x_i x_j)}$	*FΔ**	Functional distance expected between two individuals randomly selected, considering that they belong to different	Modified from Somerfield et al. (2008)

			species	
N_{90}	See section 2.2.1	N_{90}	Number of species contributing up to the 90% of within-group similarity in terms of abundance	Farriols et al. (2015)

Table 3. Results of the Generalized Cross-Validation (GCV) and the Akaike Information Criterion (AIC) of the final GAMs for the diversity indices selected from the cluster analysis: *S*, *d*, *J'*, *H'*, N_∞, *Δ*, FΔ* and *FΔ**. Covariates are Depth and Fishing Effort (FE). Year is included as a factor in the model. All variables shown in the model formulations were significant.

	GCV	AIC
S= s(Depth)+ year	17.71	2516.94
d= s(Depth)+ year	0.18	508.36
J'=s(Depth)+ s(FE)+ year	0.03	-343.04
H'= s(Depth)	0.27	671.32
Ninf= s(Depth)+ year	1.23	1342.25
Δ= s(Depth)+ s(FE)+ year*	41.21	2888.46
FΔ= s(Depth)+ year	24.06	2651.80
FΔ= s(Depth)+ s(FE)*	26.98	2702.54

Table 4. Results of the GAMs for the diversity indices selected from the cluster analysis: *S*, *d*, *J'*, *H'*, N_∞, *Δ*, FΔ* and *FΔ**. Covariates are Depth and Fishing Effort. Years showing a significant effect on each variable are also included. The deviance explained for the final model is also included. *: p<0.05, **: p<0.01, ***: p<0.001, ns: non-significant effect.

Variables	Definitive model

	Depth	Fishing effort	Year	Deviance
S	***	ns	2007*, 2010*, 2013**	49.50%
d	***	ns	2010*, 2013**	21.80%
J'	***	**	2008*	41.90%
H'	***	ns	ns	28.30%
N_∞	***	ns	2008*	22.80%
*Δ**	***	**	2013*	9.71%
FΔ	***	ns	2008*	19.10%
*FΔ**	***	*	ns	14.90%

Table 5. Results of two-way ANOVA testing the effects of year and level of fishing effort (LFE) and the interaction of both factors in the variation of each of the diversity indices analyzed (*S, d, J', H',* N_∞*, Δ*, FΔ, FΔ* and* N_{90}). df and MS are the degrees of freedom and mean square values, respectively. *: p<0.05, **: p<0.01, ***: p<0.001.

		Shallow shelf				Deep shelf				Upper slope				Middle slope			
		df	MS	F	p	df	MS	F	p	df	MS	F	p	df	MS	F	p
S	Year	8	84.55	3.57	***	8	48.30	3.22	**	8	12.97	1.45	0.20	8	17.12	2.42	*
	LFE	2	53.86	2.27	0.11	1	161.78	10.78	**	1	51.46	5.75	*	1	8.44	1.19	0.28
	Year*LFE	16	11.64	0.49	0.95	8	15.51	1.03	0.42	8	5.86	0.65	0.73	8	9.62	1.36	0.24
	Error	139	23.68			116	15.01			51	8.96			52	7.08		
d	Year	8	0.59	2.73	**	8	0.35	2.07	*	8	0.16	2.13	0.05	8	0.34	3.11	**
	LFE	2	0.15	0.71	0.50	1	1.17	6.82	*	1	0.12	1.60	0.21	1	0.02	0.14	0.71
	Year*LFE	16	0.13	0.61	0.88	8	0.16	0.95	0.48	8	0.01	0.18	0.99	8	0.21	1.87	0.09
	Error	139	0.22			116	0.17			51	0.07			52	0.11		
J'	Year	8	0.02	0.89	0.53	8	0.06	1.13	0.35	8	0.04	1.45	0.20	8	0.01	0.39	0.92
	LFE	2	0.11	5.74	**	1	0.04	0.80	0.37	1	0.21	7.44	**	1	0.23	11.15	**
	Year*LFE	16	0.01	0.63	0.86	8	0.02	0.36	0.94	8	0.03	0.89	0.54	8	0.01	0.63	0.75
	Error	139	0.02			116	0.05			51	0.03			52	0.02		

H'	Year	8	0.12	0.63	0.75	8	0.61	1.23	0.29	8	0.42	1.65	0.14	8	0.16	1.08	0.39
	LFE	2	0.59	3.07	0.05	1	0.05	0.10	0.75	1	1.61	6.33	*	1	0.99	6.68	*
	Year*LFE	16	0.14	0.75	0.74	8	0.20	0.41	0.91	8	0.21	0.82	0.59	8	0.13	0.84	0.57
	Error	139	0.19			116	0.50			51	0.25			52	0.15		
N_∞	Year	8	0.88	0.66	0.72	8	2.70	1.41	0.20	8	0.59	1.37	0.23	8	0.76	0.87	0.55
	LFE	2	3.58	2.70	0.07	1	0.82	0.43	0.51	1	1.61	3.73	0.06	1	3.05	3.50	0.07
	Year*LFE	16	1.19	0.89	0.58	8	0.43	0.22	0.99	8	0.27	0.63	0.75	8	1.06	1.22	0.31
	Error	139	1.33			116	1.91			51	0.43			52	0.87		
*Δ**	Year	8	95	1.62	0.12	8	18.10	1.41	0.20	8	35.12	1.08	0.39	8	29.87	0.36	0.94
	LFE	2	166	2.83	0.06	1	30.20	2.34	0.13	1	12.66	0.39	0.54	1	0.07	0.00	0.98
	Year*LFE	16	7	0.11	1.00	8	2.80	0.21	0.99	8	36.96	1.13	0.36	8	39.18	0.47	0.87
	Error	139	59			116	12.90			51	32.65			52	83.84		
FΔ	Year	8	24.43	1.09	0.37	8	50.06	1.80	0.08	8	52.68	2.61	*	8	29.89	1.39	0.22
	LFE	2	14.49	0.65	0.53	1	4.94	0.18	0.67	1	168.47	8.33	**	1	39.91	1.85	0.18
	Year*LFE	16	10.66	0.47	0.96	8	21.02	0.75	0.64	8	24.27	1.20	0.32	8	28.85	1.34	0.25
	Error	139	22.45			116	27.86			51	20.22			52	21.57		
*FΔ**	Year	8	37.64	1.19	0.31	8	20.22	0.93	0.50	8	30.42	1.34	0.25	8	33.32	1.13	0.36
	LFE	2	48.64	1.53	0.22	1	64.91	2.98	0.09	1	40.24	1.77	0.19	1	6.01	0.20	0.65
	Year*LFE	16	19.83	0.62	0.86	8	14.96	0.69	0.70	8	15.88	0.70	0.69	8	33.96	1.15	0.34
	Error	139	31.75			116	21.77			51	22.75			52	29.43		
N_{90}	Year	8	6.00	7.68	***	8	23.69	41.98	***	8	13.84	6.00	***				
	LFE	2	18.24	23.34	***	1	214.45	380.00	***	1	0.56	0.24	0.62				
	Year*LFE	16	3.94	5.05	***	8	17.58	31.15	***	8	6.42	2.78	*				
	Error	139	0.78			116	0.56			51	2.31						

Table 6. t-Test values comparing levels of fishing effort (LFE) of the N_{90}, diversity index for each depth strata. L, M, H and VH are low, medium, high and very high LFE, respectively. SS, DS, US and MS are shallow shelf, deep shelf, upper slope and middle slope, respectively. The levels of significance obtained from the student-t for the fishing effort factor for each year are also represented. *: p<0.05, **: p<0.01, ***: p<0.001.

		2006	2007	2008	2009	2010	2011	2012	2013	2014
SS	L-M	1.32	-0.55	-3.46**	3.06**	2.15	2.56*	0.89	6.12***	6.01***
	H-M	-1.20	-0.46	-2.38*	1.68	0.11	-0.09	-2.18	0.97	-0.05
	H-L	-2.51*	0	0.81	-1.72	-3.32**	-2.99*	-3.45**	-3.45**	-6.02***
DS	L-M	17.09***	6.61***	10.87***	10.18***	6.52***	12.80***	4.33***	0.81	-2.21*
US	L-M	-0.16	0.90	3.03*	-0.63	1.36	1.57	-1.97	-2.51*	-1.60
MS	H-VH	-	-	-	-	-	-	-	-	-

Table 7. 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 %contr. is the mean value of the percentage contribution of each species to within group similarity, taking into account all the jack-knifes made by group of depth strata, level of fishing effort (LFE) and year. *Sim* is the within-group similarity by depth strata subjected to different LFE. L, M, H and VH are low, medium, high and very high LFE, respectively. SS, DS, US and MS are shallow shelf, deep shelf, upper slope and middle slope, respectively.

	A	%contr.		*A*	%contr.		*A*	%contr.
SS L; mean *Sim*=30.38%			SS M; mean *Sim*=26.38%			SS H; mean *Sim*=34.82%		
Scyliorhinus canicula	1768	25	*Scyliorhinus canicula*	1787	32	*Serranus cabrilla*	1504	31
Serranus cabrilla	1620	19	*Serranus cabrilla*	1252	15	*Scyliorhinus canicula*	692	16
Trachinus draco	1257	12	*Mullus surmuletus*	2793	14	*Trigloporus lastoviza*	1168	14
Mullus surmuletus	2152	8	*Trigloporus lastoviza*	823	10	*Trachinus draco*	707	14
Trigloporus lastoviza	1012	7	*Trachinus draco*	527	8	*Scorpaena notata*	418	4
Serranus hepatus	1800	6	*Serranus hepatus*	1518	3	*Serranus hepatus*	683	4
Chelidonichthys	48	4	*Scorpaena notata*	17	2	*Arnoglossus thori*	30	3

cuculus	9			4			9	
Lepidotrigla cavillone	570	3	*Pagellus acarne*	737	2	*Pagellus erythrinus*	363	3
Scorpaena notata	390	3	*Chelidonichthys cuculus*	267	2	*Mullus surmuletus*	482	2
Arnoglossus thori	280	3	*Pagellus erythrinus*	377	2	*Scorpaena scrofa*	99	2
Scorpaena scrofa	235	2	*Mullus barbatus barbatus*	472	1			

Table 7. Continued.

	A	%contr.		*A*	%contr.
DS L; mean *Sim*=20.80%			DS M; mean *Sim*=28.17%		
Chelidonichthys cuculus	2887	22	*Merluccius merluccius*	4213	26
Glossanodon leioglossus	48175	18	*Serranus hepatus*	2467	26
Scyliorhinus canicula	1291	11	*Lepidotrigla cavillone*	1496	11
Serranus hepatus	1115	8	*Scyliorhinus canicula*	1115	8
Lepidotrigla cavillone	1135	8	*Glossanodon leioglossus*	61339	6
Merluccius merluccius	782	7	*Trisopterus minutus*	802	5
Deltentosteus quadrimaculatus	1002	5	*Trachinus draco*	686	5
Mullus surmuletus	1163	4	*Chelidonichthys cuculus*	1018	3
Trachinus draco	433	4			
Mullus barbatus barbatus	289	2			
Raja clavata	205	2			
US L; mean *Sim*=20.40%			US M; mean *Sim*=40.20%		
Glossanodon leioglossus	147998	29	*Gadiculus argenteus*	30376	70
Scyliorhinus canicula	1646	16	*Galeus melastomus*	2322	11
Micromesistius poutassou	8619	10	*Coelorinchus caelorhincus*	1203	4
Gadiculus argenteus	11201	10	*Micromesistius poutassou*	847	3
Trigla lyra	603	8	*Phycis blennoides*	429	3

Synchiropus phaeton	654	7			
Helicolenus dactylopterus	332	7			
Merluccius merluccius	2169	5			
MS H; mean *Sim*= 35.62%			MS VH; mean *Sim*= 40.27%		
Phycis blennoides	369	33	*Nezumia aequalis*	112	25
Galeus melastomus	408	25	*Galeus melastomus*	163	23
Nezumia aequalis	170	16	*Phycis blennoides*	116	12
Hymenocephalus italicus	134	9	*Notacanthus bonaparte*	84	11
Symphurus ligulatus	35	4	*Polyacanthonotus rissoanus*	24	8
Etmopterus spinax	33	3	*Lepidion lepidion*	59	6
			Symphurus ligulatus	57	5
			Mora moro	25	5

Highlights: We identify a minimum set of indices that represent different aspects of diversity; We model the responses of demersal fish diversity to bottom trawl fishing pressure; Poor selective fishing exploitation, as the bottom trawl, increases evenness; Detectable changes in diversity in areas where fishing pressure have remained low.