Large-scale spatio-temporal monitoring highlights hotspots of demersal fish diversity in the Mediterranean Sea

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ABSTRACT

Increasing human pressures and global environmental change may severely affect the diversity of species assemblages and associated ecosystem services. Despite the recent interest in phylogenetic and functional diversity, our knowledge on large spatio-temporal patterns of demersal fish diversity sampled by trawling remains still incomplete, notably in the Mediterranean Sea, one of the most threatened marine regions of the world. We investigated large spatio-temporal diversity patterns by analysing a dataset of 19,886 hauls from 10 to 800 m depth performed annually during the last two decades by standardised scientific bottom trawl field surveys across the Mediterranean Sea, within the MEDITS program. A multi-component (eight diversity indices) and multi-scale (local assemblages, biogeographic regions to basins) approach indicates that only the two most traditional components (species richness and evenness) were sufficient to reflect patterns in taxonomic, phylogenetic or functional richness and divergence. We also put into question the use of widely computed indices that allow comparing directly taxonomic, phylogenetic and functional diversity within a unique mathematical framework. In addition, demersal fish

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assemblages sampled by trawl do not follow a continuous decreasing longitudinal/latitudinal diversity gradients (spatial effects explained up to 70.6% of deviance in regression tree and generalised linear models), for any of the indices and spatial scales analysed. Indeed, at both local and regional scales species richness was relatively high in the Iberian region, Malta, the Eastern Ionian and Aegean seas, meanwhile the Adriatic Sea and Cyprus showed a relatively low level. In contrast, evenness as well as taxonomic, phylogenetic and functional divergences did not show regional hotspots. All studied diversity components remained stable over the last two decades. Overall, our results highlight the need to use complementary diversity indices through different spatial scales when developing conservation strategies and defining delimitations for protected areas.

Introduction

Both terrestrial and marine biodiversity suffer from multiple impacts by ever increasing direct human pressure and global environmental change (Coll et al., 2012; Halpern et al., 2008; Thuiller et al., 2011). Such disturbances may affect the diversity of species assemblages (Coll et al., 2012; D'agata et al., 2014). It can be monitored through the assessment of different components, or facets, such as species number, evenness and taxonomic, phylogenetic or functional diversity that take into account the degree of difference among species. These components enable the characterisation of species in terms of their evolutionary history (Webb et al., 2002) or their functional role on the basis of their traits (McGill et al., 2006). Recent proposals for measuring assemblage diversity have aimed to include these biological differences among species into complementary diversity indices (Cadotte et al., 2010; D'agata et al., 2014; Lefcheck et al., 2014; Schleuter et al., 2010; Stuart-Smith et al., 2013). Notably, it has been shown that phylogenetic and functional diversity can be complementary in assessing changes in the functioning of an ecosystem in response to external disturbances (Cadotte et al., 2009; D'agata et al., 2014), and even more sensitive to human pressure than species richness (D'agata et al., 2014). To date, studies at large spatio-temporal scales based on standardised field surveys remain scarce due to the associated logistical difficulties and costs related to the collection of species abundance data, creating phylogeny and/or measuring functional traits, particularly in the marine domain (D'agata et al., 2014; Gaertner et al., 2013; Stuart-Smith et al., 2013).

Due to its geological evolution and environmental conditions, the Mediterranean Sea is characterised by relatively high biodiversity (Coll et al., 2010). At the same time, it is one of the world's most threatened marine regions (Ben Rais Lasram et al., 2010; Coll et al., 2012, 2010). These threats result from a combination of various drivers such as pollution, habitat loss, introduction of new species, climate change and exploitation (Coll et al., 2012). They might have impacted the structure and composition of species assemblages, notably those of demersal fish targeted by intensive bottom trawling for commercial fishing (GFCM, 2012; Rochet et al., 2010). However, a study focused on demersal fish diversity sampled by trawling on the continental shelf and slope, based on species abundance data from standardised scientific surveys at large spatial and temporal scales in the Mediterranean Sea, is lacking. Previous studies exploring fish diversity at large scale in this area have provided insights based on gridded species presence–absence maps drawn on the basis of expert-based knowledge (e.g. Ben Rais Lasram et al., 2009; Coll et al., 2012; Mouillot et al., 2011) or on abundance data collected by visual census (e.g. Guidetti et al., 2014; Stuart-Smith et al., 2013). These works did not necessarily focus on demersal fish assemblages, or use the same sampling methodology (i.e. trawling), and could not investigate temporal trends. Elsewhere, species richness has been the focus of fish diversity assessments in the Mediterranean Sea (e.g. Ben Rais Lasram et al., 2009; Coll et al., 2012), as is usually the case worldwide. Very few works have considered phylogenetic and/or

functional fish diversity at large scale in this area (e.g. Mouillot et al., 2011; Stuart-Smith et al., 2013). Most of the available studies performed on coastal and continental shelf fish assemblages showed that the spatial pattern of fish diversity is not homogenous over the entire Mediterranean basin, with a decreasing north-west/south-east gradient of species richness and phylogenetic diversity (Coll et al., 2012; Mouillot et al., 2011), and north–south gradient of functional diversity (Mouillot et al., 2011) (see however Guidetti et al., 2014 for species richness sampled by visual census). The patterns, notably for species richness, are assumed to be related to a gradient in primary productivity (i.e. the rate at which energy is converted per unit area by photosynthetic and chemosynthetic autotrophs to organic substances (Begon et al., 2006)), which is inversely related to an increase in temperature and salinity (Coll et al., 2012). However, as highlighted by the these authors, sampling effort is known to be much lower in the southern and eastern regions and could thus bias the observed patterns of diversity (Coll et al., 2012). Studies dedicated to demersal fishes sampled by trawling within scientific surveys performed at large scale over the northern Mediterranean Sea did not find a west–east decreasing gradient for species richness, evenness and taxonomic diversity (Gaertner et al., 2007, 2013). Their analyses revealed no temporal patterns, but were restricted to a short temporal window (i.e. 4/3 years, 1996–1999/1998 respectively).

Thus, despite the recent interest in functional and phylogenetic diversity and previous studies dedicated to fish diversity in the Mediterranean Sea, our knowledge of large-scale spatial and temporal patterns of demersal fish diversity sampled by trawling in this area is still incomplete. The aim of this study is to analyse its diversity patterns using complementary indices on the basis of abundance data collected by trawling from 1994 to 2012 within a standardised scientific protocol over the northern Mediterranean but also Algeria and the eastern part of the Mediterranean Sea, which has hitherto been poorly sampled (Coll et al., 2012), and/or not included in standardised field surveys at large scale. The present study treats a data set of 19,886 sampled hauls performed on more than 20,000 km of coastline for a bathymetry of 10–800 m. More specifically, the main steps of our study are: (i) to quantify to what extent taxonomic, phylogenetic and functional components provide different information on demersal fish species, (ii) to investigate relationships (complementarity/redundancy) between indices of assemblages diversity, (iii) to analyse temporal trends of demersal fish diversity over the last two decades, and (iv) to identify, for different spatial scales over the Mediterranean Sea, groups of areas according to their diversity level (i.e. hotspots).

Materials and methods

Survey methods and data collection

The data was collected from annual bottom trawl surveys performed in May–July (except February, in Algeria) from 1994 to 2012 over the continental shelf (10–200 m depth) and the conti-

nental slope (200–800 m) of the Mediterranean Sea within the framework of the MEDITS scientific program (Bertrand et al., 2002). Our study area ranged from 34.5°N to 45.7°N and 5.3°W to 34.1°E and was divided into 18 operative Geographical Sub-Areas (GSAs), for which boundaries were established by the General Fisheries Commission for the Mediterranean Sea (www.gfcm.org, see Fig. 1 for the correspondence between GSA numbers and their names). The sampling procedures were standardised according to a common protocol over GSAs and years. The standard device was a bottom trawl GOC-73 with 20-mm cod-end mesh size. The average vertical opening of the gear was 2 m and its wing-span 18 m. All the tows were performed during daylight hours. Speed on the ground and duration of the tows were standardised to 3 knots and 30 min for shelf stations (10–200 m), and 60 min for upper slope, respectively (200–800 m) (see Bertrand et al., 2002 for full details). For each haul we collected raw fish abundance data, bathymetry, swept area (*i.e.* trawled surface) and haul coordinates. Information recorded by an underwater Scanmar system – to control the trawl geometry (horizontal and vertical openings, contact with the bottom) – as well as recorded swept area and trawling time, enabled us to select the tows that were properly carried out. The hauls in which only one or two fish species were caught and where their abundance was extremely low (total abundance below the first quartile, *i.e.* 133 individuals per haul) were excluded from analyses to remove potentially inoperative hauls. These hauls represented less than 3% of the total sampled hauls and were equally distributed over the study area. Overall, these selections of properly carried out hauls enabled us to perform accurate diversity comparisons over GSAs and years to avoid bias from different sampling effort among hauls. Among a total of 348 species sampled during surveys, we considered 186 species properly sampled by the bottom trawl system used, and properly identified by teams involved in this large scale program (Gaertner et al., 2013, 2010). This subset of 186 demersal fishes (*i.e.* benthic and bentho-pelagic fishes) was designed in such a way as to minimise potential bias caused by gear-selectivity (*e.g.* Lefcheck et al., 2014; Villéger et al., 2010), and to strictly limit the risk of a variability of accuracy in sampling identification between the different teams. The list of 186 species considered was set according to those used in (Gaertner et al., 2013, 2010) (see Appendix A for the list of species considered). Raw abundance data was normalised by the trawl surface, and the resulting species densities were used for indices computation. Some years for some GSAs were excluded when species identification during surveys was restricted to a specific spectrum of species and thus biased

assemblage diversity assessment. After cleaning up the data as described above, a total of 19,886 accurate sampled hauls were chosen from 1994 to 2012 (representing 97% of available hauls).

Diversity indices

We used eight species diversity indices to assess the main diversity components of demersal fish assemblages' diversity. Species richness (*S*), measuring the number of species in an assemblage (*i.e.* haul) and still the most widely used diversity index, was computed. We also used the Simpson evenness index $1 - D/(1 - 1/S)$ (Smith and Wilson, 1996), where $D = \sum_{i=1}^{S} p_i^2$ with p_i is the relative abundance of the *i*th species, Simpson *D* index being an heterogeneous index combining species richness and evenness (Simpson, 1949). Measures of taxonomic, phylogenetic and functional diversity were based on two versions of Rao's quadratic entropy index. First, on the basis of abundance data, Rao's quadratic entropy index (*Q*) provided a unifying calculation to investigate and compare from the same mathematical formula taxonomic, phylogenic, and functional divergences (*TD/PD/FD*) (Lefcheck et al., 2014; Mason et al., 2005; Pavoine, 2012; Rao, 1982). This has been successfully used in both terrestrial and marine analysis (Devictor et al., 2010; Lefcheck et al., 2014; Mouillot et al., 2011; Stuart-Smith et al., 2013). This index is defined as:

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} p_i p_j d_{ij}$$

where p_i and p_j are the relative abundance of the *i*th and *j*th species, d_{ij} the taxonomic, phylogenetic, or functional difference between two species *i* and *j* stored in a distance matrix. Note that in the case of all $d_{ij} = 1$ for every species pairs, this index is similar to the Simpson diversity index $1 - D$.

Next, we also computed Rao's quadratic entropy on the basis of presence/absence data to quantify taxonomic, phylogenetic and functional richness (*TR/PR/FR*). This index allowed the evenness component to be excluded. We employed a corrected version of this index, defined by Izsak and Papp (2000):

$$Q^+ = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}$$

This corresponds to the sum of pair-wise taxonomic, phylogenetic or functional distances between species in an assemblage. As for any diversity index, it presents some limitations (Schmera
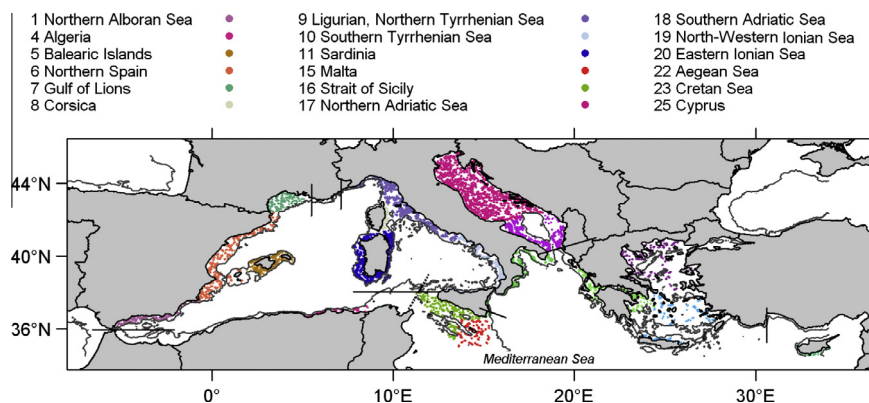
Fig. 1. Study area and sampling sites. Study area of trawl surveys based on the MEDITS program protocol with the position of 19,886 hauls sampled between 1994 and 2012 in 18 geographical sub-areas GSAs; each colour corresponds to one of the 18 Geographical Sub-Areas (GSA) defined by the General Fisheries Commission for the Mediterranean (www.gfcm.org). The grey line represents the sampling limit of 800 m depth. The spatial boundaries of the 7 biogeographical zones (Iberian-Lions, Tyrrhenian, Algerian-Maltese, Ionian, Adriatic, Aegean, and Cypriot) are delimited by thick black lines. The thick black dotted line represents the spatial boundary between eastern and western basins. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2007) but it has the advantage of being computed on the initial d_{ij}, *i.e.* without distortion of the initial information, in contrast to other existing functional diversity indices that are based on species distances from clustering methods computed on d_{ij} (*e.g.* Mérigot et al., 2010; Petchey and Gaston, 2002). In addition, if all species are strictly similar/redundant (from a phylogenetic or functional point of view), each d_{ij} and Q^+ equal 0. It results that d_{ij}, and in turn Q^+, increases with the complementarity between two species. Thus, this index will be naturally and logically positively correlated to species richness, to a greater or lesser extent depending on species redundancy. Functional diversity can also be investigated separately by specific indices (*e.g.* Villéger et al., 2008) that we also considered but which are not appropriate for taxonomic and phylogenetic diversity (see Appendix B, Part B1, Figs. B1 and B2). Otherwise, diversity indices can be computed within the recent framework of "effective species number" (Jost, 2006, see Appendix B, Part B2).

Because index values are scale-dependent, here we analysed spatial diversity patterns at different spatial scales: GSA ($m = 18$ modalities), biogeographical zones ($m = 7$) and basin ($m = 2$) (see Fig. 1). For each spatial unit (*e.g.* the 18 different GSAs) and for each year, we computed indices values by measuring (i) haul diversity (*i.e.* α-diversity) and (ii) total diversity over the hauls (*i.e.* γ-diversity) (Lande, 1996; Whittaker, 1972). Boundaries of GSAs correspond to those established by the General Fisheries Commission for the Mediterranean (www.gfcm.org, see above), while boundaries for basins or biogeographical zones are those defined in previous studies of species diversity patterns (Gaertner et al., 2007, 2013). In addition, species richness S per spatial unit is sensitive to the sampling effort, notably at GSA scale, and because the number of hauls performed was variable between GSAs-years (*i.e.* between 13 and 182 hauls), the comparison between S values per GSA was done on rarefied values to avoid bias, with S per GSA rarefied to 25 hauls (*i.e.* S deduced from the rarefaction curve of each GSA at 25 hauls) resulting in the exclusion of 19 GSAs-year. This number was an accurate compromise knowing that a lesser number of hauls led to a higher standard deviation associated with the mean rarefied species richness values, and a higher number of hauls would lead to the exclusion of years of GSA with a lower sampling effort. In addition, outcomes of statistical procedures with other rarefaction levels (15, 30, 35 hauls) underlined similar richness patterns (not shown). In contrast to S, Rao's quadratic entropy Q was not sensitive to sampling effort (no relation was observed between the γ-values and the number of sampled hauls per GSA). Consequently this index was not rarefied.

Taxonomic, phylogenetic and functional distances

Three distinct data sources were used to establish taxonomic, phylogenetic and functional distances, as is traditionally done for different species groups worldwide (*e.g.* D'agata et al., 2014; Devictor et al., 2010; Lefcheck et al., 2014; Mouillot et al., 2011).

For taxonomic richness and divergence (*TR* and *TD* respectively), distances between species were constructed using the Linnaean taxonomic classification (*e.g.* Lefcheck et al., 2014). The distance between two species from the same genus was set to 1, two species from the same family but different genus was 2, same order but different genus and family was 3, and so on. We considered a taxonomy including 5 levels (species, genus, family, order and class).

For functional richness and divergence (*FR* and *FD* respectively), pairwise distances between the 186 fish species were computed from 11 morphological traits measured in the field and on pictures, by mean of the ImageJ software (http://imagej.nih.gov/ij/), taken during 2011 and 2012 MEDITS surveys. For a given species, each continuous trait was computed from the mean values of about

ten individuals. Within demersal fish assemblages, some species are rare, preventing them from being caught several times during annual surveys. For these rare fish species that were not caught during these two surveys, we were constrained to consider one individual per species with pictures found at Fishbase (Froese and Pauly, 2011), selecting only those from the Mediterranean Sea. These morphological traits were related to food acquisition and locomotion, two main functions of fish closely related to feeding and habitat use (Albouy et al., 2011) (see Appendix C for the list of functional traits used in this study). We then selected complementary traits with low correlation (Pearson correlation coefficient $r < 0.5$), leading to exclusion of a single trait (*i.e.* the horizontal oral gap trait which was highly correlated to vertical oral gap trait, $r = 0.94$) from further analysis. Since functional traits were a set of mixed variable types, *i.e.* either quantitative (continuous) or qualitative (nominal and ordinal), Gower's coefficient was applied to compute functional distances between species (Gower, 1971).

For phylogenetic richness and divergence (*PR* and *PD* respectively), we used the phylogeny of 134 osteichthyes Mediterranean fish (representing 72% of the demersal species published in Meynard et al. (2012)). This phylogeny was based on mitochondrial and nuclear genes, and was calibrated using fossil records (see Meynard et al., 2012 for more details).

Statistical analyses below were thus focused on 134 demersal osteichthyes, among the initial 186 species, for which phylogeny is only available (not for 52 species, *i.e.* 39 elasmobranchs and 13 osteichthyes species).

The three types of distances (taxonomic, functional and phylogenetic) were normalised between 0 and 1 by their respective maximum to be able to compare the three divergence and richness indices among them.

Statistical analysis

To compare and determine to what extent taxonomic, phylogenetic and functional components are complementary at the species level, we represented the plots of their pairwise distance matrices. We studied the dispersion of the species distances scatter plots (graphically and by mean of Pearson's correlation coefficient), and its lag from the first bisector representing the case for which the two matrices are identical.

To investigate the redundancy/complementarity of the different diversity indices computed for each haul (*i.e.* at the assemblage level), we used a Draftsman's plot and Pearson's correlation coefficients. This coefficient was preferred to non-parametric ones (*e.g.* Spearman) due to monotonic linear relationships between some indices. The Draftsman's plot, which represents the pairwise relationships among all indices in the same plot, allows selection of only non-correlated indices for further analyses, *i.e.* those which are complementary in their response at the assemblage level.

Finally, we investigated diversity patterns at different spatial scales (*i.e.* 18 GSAs, 7 biogeographical zones or 2 basins) through time (*i.e.* 19 years) by two complementary analyses: generalised linear models (GLM, McCullagh and Nelder, 1989) and regression trees (CART, Breiman et al., 1984). In both cases, the diversity indices were used as the response variable, while year and spatial variables (GSAs, biogeographical zones or basins) were used as explicative factors. In preliminary analysis, we also considered depth as a covariate in GLMs for α-diversity, and its effect was low (around 4.9%). In case of GLM for γ-diversity, bathymetry is not accurate enough to be included because an entire spatial unit is considered. GLM was implemented to quantify the global deviance explained by year and spatial factors, the part of this deviance attributed to each factor, as well as their potential interaction, while dealing with non-normal distributions. In complement, CART was applied to identify areas with similar levels of diversity

while selecting automatically relevant explicative factors (*i.e.* spatial and year factors).

Assumptions on Poisson conditional distributions and goodness of fit for GLMs were checked by complementary graphical diagnostics (normality of standardised residuals by using a quantile–quantile plot, homogeneity by plotting standardised residuals against fitted values, influence of values in the estimation of model parameters by Cook's distance and leverage effect).

Assessment of semi-variograms on residuals of mixed-effect GLMs for *S* and *FD* (values per haul) indicated that spatial autocorrelation was low at Mediterranean level, even if significant (due to the high number of observations). Residuals showed a spatial autocorrelation at small distances (within GSAs) for some GSAs, and varied according to the GSA considered. Thus different modelled (*i.e.* theoretical) variograms would have been needed for each GSA or groups of them. However, this implementation in a common model at the scale of the study, which aims to compare GSAs, is not yet possible with existing tools (Pinheiro and Bates, 2000).

All diversity indices and statistical analyses mentioned above were performed using R 3.0.1 software (R Core Team, 2013).

Results

### Relationships between taxonomy, phylogeny and functional diversity

Scatter plots between phylogenetic, taxonomic and functional distance matrices for the 134 osteichtyes fish species (not for the 186 species as phylogenetic information for 52 species is not available, see section 'Taxonomic, phylogenetic and functional distances' of the Material and Methods section) suggest that each diversity component provides different information on demersal fish species (Fig. 2). The overlap between functional information with phylogenetic/taxonomic information is very low, according to a high dispersion of the pairwise distance scatter plots and low Pearson's correlation values ($0.24 < r < 0.25$). A high dispersion of the scatter plot between taxonomic and phylogenetic components can also be observed, even if the overlap and the correlation is higher in that case ($r = 0.67$). These mismatches are also underlined by the lag of the scatter plots to the first bisector. Overall, these results show that all three components are complementary at the species level, *i.e.* that demersal species are not equally distant according to the information considered.

The correlation between diversity components at the assemblage/haul level was studied by mean of correlations between all pairs of indices computed for each haul (Fig. 3). First, Simpson evenness and divergence indices *TD*, *PD* and *FD* (computed by Rao's quadratic entropy *Q*) display similar density distributions and are highly correlated to each other (Pearson's index: $0.72 < r < 0.96$, Fig. 3). In other words, there was very little difference in patterns between these indices, all linked to the evenness component. Indeed, *TR/FR/PR* computed by Rao's quadratic entropy Q^+ (based on presence/absence data to remove the contribution of evenness) were not correlated to *TD/PD/FD* ($0.11 \leqslant r \leqslant 0.2$), but strongly correlated to each other ($r \geqslant 0.98$) and to *S* ($r \geqslant 0.99$). Finally, Simpson evenness (as well as *TD*, *PD*, *FD*) and *S* provide complementary information on the response of demersal fish diversity at the assemblage/haul level ($0.16 < r < 0.2$). Considering these results, subsequent analyses will focus on *S* and *FD*, which provided different responses in patterns of demersal fish assemblage diversity. Between Simpson evenness and the different divergence indices *TD*, *PD*, *FD*, we choose *FD* because no study for the Mediterranean has to date provided a large-scale spatio-temporal analysis of functional diversity based on abundance and on species traits measured on demersal fish individuals sampled by trawling during scientific surveys.
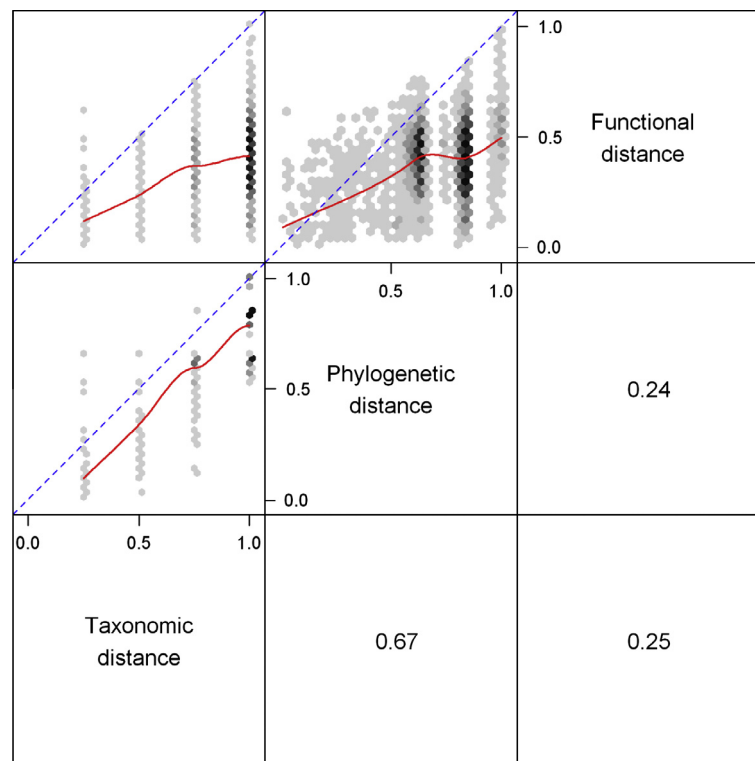
Fig. 2. Matrix plots between phylogenetic, taxonomic and functional species distance matrices of 134 osteichtyes fish species. In the upper panel, each point represents a species' pairwise distances according to two diversity components. If a species is considered equally distant for both components, then the point is placed on the first bisector (*i.e.* $y = x$) representing the situation for which both matrices are identical (*i.e.* have the same values). The continuous line represents a local weighted regression ("loess"). The Pearson correlation coefficient is represented in the lower panel.
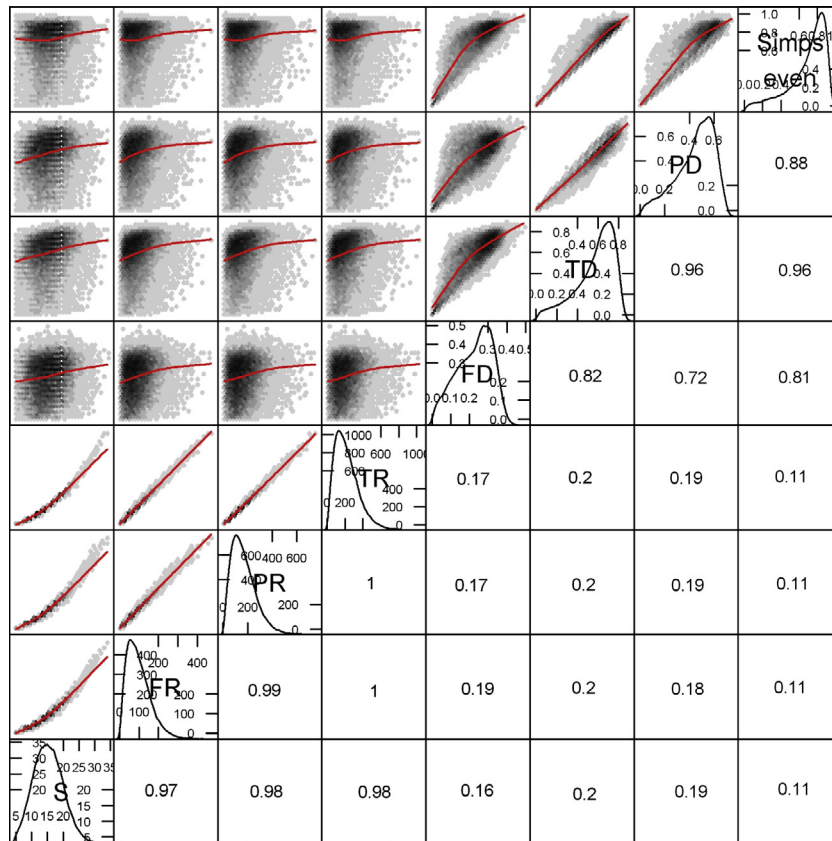
Fig. 3. Draftsman's plot of diversity indices computed on 19,886 hauls. In the upper panel, the pairwise relationship, the continuous line representing a local weighted regression ("loess"). The Pearson correlation coefficient is represented in the lower panel, and the marginal distribution for each index in the diagonal. S is species richness; $TD/PD/FD$ are taxonomic, phylogenetic, functional divergences respectively, computed by Rao's quadratic entropy Q on fish abundance data; $Simps$ $even$ is Simpson evenness; $TR/PR/FR$ are taxonomic, phylogenetic and functional richness, computed by the modified Rao's quadratic entropy Q^+ on fish presence/absence data.

Note that pairwise relationships between indices per haul were also computed on the list of 186 species (*i.e.* both osteichthyes and chondrichthyes for which a common phylogeny is not yet available, see section 'Taxonomic, phylogenetic and functional distances' of the Material and Methods section). Similar results were obtained (Appendix D, Fig. D1), suggesting that the above analyses and results focusing only on osteichthyes were representative for taxonomic and functional diversity patterns.

Spatio-temporal patterns of demersal fish diversity

We analysed spatial diversity patterns at different spatial scales, *i.e.* GSA, biogeographical zone and basin, using two levels of diversity, *i.e.* α-diversity (the diversity measured in each haul) and γ-diversity (the total diversity of the spatial unit of interest), rarefied for species richness values. Hereafter, we focused on the analyses made at the scale of the GSAs because corresponding models displayed the highest values of explained deviance for both species richness S and functional divergence FD (see Appendix E for analyses performed at the scales of the biogeographical zone and basin).

Species richness S

Our results indicate a spatial differentiation both at local and regional scales and a temporal stability of S. Firstly, the GLM regressing S per haul (α-diversity) against the GSAs/years explained 18.9% of the deviance (Table 1). A significant regional differentiation by S was observed in the Mediterranean area (~10.5% of deviance, $p < 0.001$). The effect of year, even if significant, was very weak (<2% of deviance, $p < 0.001$). Nonetheless, interaction between spatial and temporal factors explained 6.7%

Table 1
Generalized linear model (GLM) investigating spatio-temporal variability of species richness S and functional divergence FD.
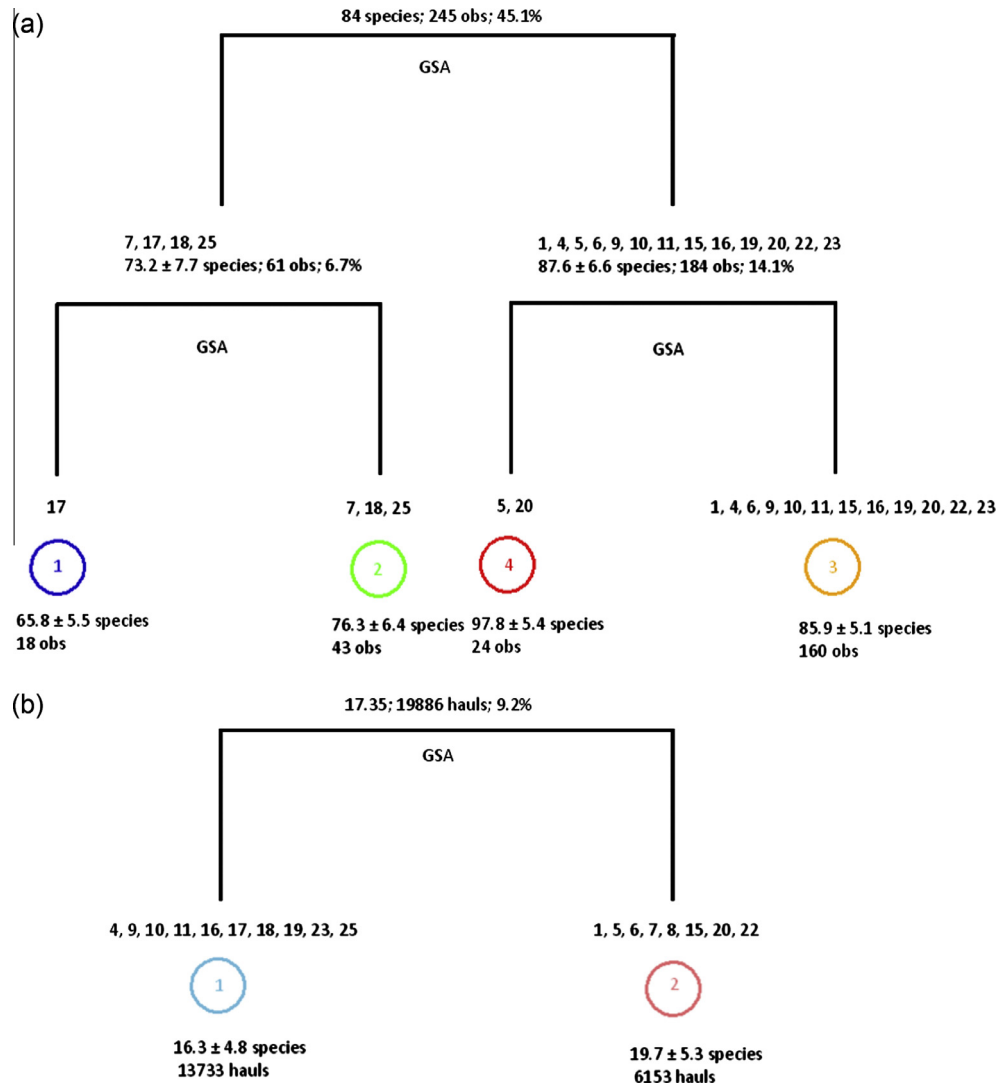
	Total (%)	GSA	Year	GSA:Year
S				
α-diversity	18.85	10.52% (17)	1.76% (18)	6.65% (229)
γ-diversity	76.81	70.61% (16)[a]	6.2% (18)	[b]
$1 - FD$				
α-diversity	7	2.4% (17)	<1% (18)	4%
γ-diversity	10.47	4.72% (17)	5.75% (18)	[b]

Indices measured per haul (*i.e.* α-diversity) and per GSA (*i.e.* γ-diversity) on 19,886 hauls for 19 years in 18 geographical sub-areas (GSA) of the Mediterranean Sea. GLM including both Year and GSA as explicative factors, with a Normal and Gamma error distributions were considered for S and $1 - FD$ respectively, with an identity link in both cases. Percentages represent the part of deviance explained by each variable in the same model, with degrees of freedom in brackets. All effects are significant ($p < 0.05$). Note that S computed per GSA was rarefied to 25 hauls (see Materials and Methods section).

[a] Due to the rarefaction method, GSA 8 is excluded from the analysis, the total number of hauls being below 25 for each year in this GSA.

[b] Models for S and $1 - FD$ per GSA do not include interaction, as one value per GSA and per year is available.

of the model deviance ($p < 0.001$), being significant for some GSAs. Regression tree based on S per haul explained 9.2% of the total variance, with a single split of two groups of GSAs based on spatial partitioning: (i) Iberian – Gulf of Lions area, eastern Ionian Sea, Aegean Sea and Malta (mean of 19.7 ± 5.3 species per haul, standard deviation) and (ii) central Mediterranean GSAs (Adriatic Sea and western Italian areas), Algeria and Cyprus (mean of 16.3 ± 4.8 species per haul, Figs. 4a and 5a).

(a)

84 species; 245 obs; 45.1%

GSA

7, 17, 18, 25
73.2 ± 7.7 species; 61 obs; 6.7%

1, 4, 5, 6, 9, 10, 11, 15, 16, 19, 20, 22, 23
87.6 ± 6.6 species; 184 obs; 14.1%

GSA

GSA

17

7, 18, 25

5, 20

1, 4, 6, 9, 10, 11, 15, 16, 19, 20, 22, 23

1

2

4

3

65.8 ± 5.5 species
18 obs

76.3 ± 6.4 species
43 obs

97.8 ± 5.4 species
24 obs

85.9 ± 5.1 species
160 obs

(b)

17.35; 19886 hauls; 9.2%

GSA

4, 9, 10, 11, 16, 17, 18, 19, 23, 25

1, 5, 6, 7, 8, 15, 20, 22

1

2

16.3 ± 4.8 species
13733 hauls

19.7 ± 5.3 species
6153 hauls

Fig. 4. Regression tree models for fish species richness S. Values computed (a) per haul (*i.e.* α-diversity), and (b) per GSA (*i.e.* γ-diversity) across the Mediterranean Sea. The splitting variable (Geographical Sub Area GSA and Year) and its modalities value (see Fig. 1) are shown on each branch (horizontal lines). The terminal nodes show the S mean values and associated standard deviations, number of observations (*obs*, *i.e.* rarefied S values) per node and hauls from which the mean values have been computed for γ and α-diversity, respectively. Note that due to the rarefaction method, GSA8 is excluded from the per GSA analysis (*i.e.* γ-diversity), the total number of hauls of being below 25 for each in this GSA.

Secondly, the GLM regressing rarefied S per GSA (γ-diversity) against the same co-variables explained a much greater part of the variability (about 76.8% of the deviance). Spatial differentiation still explained the bulk of the deviance (70.6%, $p < 0.001$), while the contribution of temporal variability is still weak even if significant (6.2%, $p < 0.05$). Interaction could not be quantified because there was only one value of S per GSA and per year. Similarly, the regression tree model based on γ-diversity explained 65.9% of the total variance (Fig. 5b), with temporal stability and spatial partitioning. Overall, this model identified 4 main areas based on rarefied S (Figs. 4b and 5b): (i) northern Adriatic Sea (mean of 65.8 ± 5.5 species), (ii) Cyprus, southern Adriatic Sea and Gulf of Lions (76.3 ± 6.4 species), (iii) Algeria, Iberian area, western and southern Italian areas, Malta, Aegean and Cretan seas (85.9 + 5.1 species), and (iv) Baleares and eastern Ionian Sea (97.9 ± 5.4 species).

To sum up, statistical analysis (regression tree models and GLMs) showed that species richness S is mostly spatially structured; however it does not display a longitudinal gradient for any of the investigated scales (see also Appendix E, Fig. E1, Table E1). At both scales, we also underlined the temporal stability of S patterns during the last two decades.

Functional divergence FD

FD values computed per haul (α-diversity) and total regional diversity (γ-diversity) for each GSA followed both asymmetric left skewed distributions (Fig. 3). Thus, a simple value transformation $(1 - FD)$ allowed an exponential family distribution to be achieved to implement a GLM. In both cases, according to the residual analysis, gamma distribution was found to be the most appropriate among this distribution family.

In contrast to the results we obtained on S, GLM showed that functional divergence was temporal and spatially stable, for both values by haul or by GSA, explaining only ∼7% and ∼10.5% of the deviance, respectively (Table 1). Similarly, in both cases, regression trees computed on $1 - FD$ did not provide strong and specific groups of GSAs/years (not shown), highlighting a stability of FD over all GSAs and years studied, with absence of longitudinal gradients in functional divergence. However, FD was highly heterogeneous within each GSA (see Appendix E, Fig. E2).

In short, our results underlined hotspots for species richness at both local and regional scales. In contrast, functional divergence did not show regional hotspots. For both indices, there was an absence of an eastwards/southwards decreasing diversity gradient,
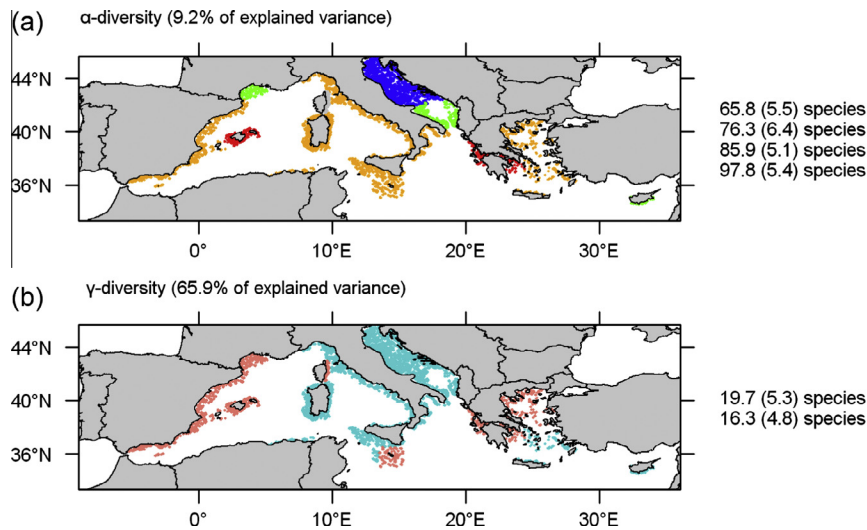
Fig. 5. Map of spatial partitioning of fish species richness *S* resulting from regression tree models. Values computed (a) per haul (*i.e.* α-diversity), and (b) per GSA (*i.e.* γ-diversity) according the regression tree models (see Fig. 4) implemented for 19 years and 18 Geographical Sub Areas (GSAs) in the Mediterranean Sea. Note that due to the rarefaction method, GSA8 is excluded from the per GSA analysis (*i.e.* γ-diversity), the total number of hauls of being below 25 for each in this GSA. Values represent *S* mean values and associated standard deviation.

and high temporal stability during the last two decades (and by extension for the 6 other indices considered in this study, each of them being strongly correlated with *S* or *FD*, see above).

Discussion

Complementarity between diversity components and indices

For demersal Mediterranean fishes, our analyses at species level support the idea that information provided by taxonomic, phylogenetic and functional diversity components are different and complementary. While several studies have suggested the use of existing Linnaean taxonomy as a proxy for phylogeny (see references in Lefcheck et al. (2014)), our study suggests that taxonomic distances may not fully reflect evolutionary relationships drawn by molecular phylogeny (Crozier et al., 2005). Indeed, discrete taxonomic levels (*i.e.* genus, family, etc.) limit the resolution of species differences compared to those derived from continuous DNA sequence variation. Furthermore, the stronger mismatch between species function and phylogeny is in agreement with a recent meta-analysis demonstrating that phylogenetic differences between species (*i.e.* evolutionary history) does not necessarily capture functional differences (Kelly et al., 2014). Overall, the assumption that traits are correlated or predicted by phylogeny, in part stems from the widely held thought that Linnaean taxonomy is predictive of features of organisms (see references in Kelly et al. (2014)), and might not hold for the demersal Mediterranean fishes. Therefore, considering taxonomic, phylogenetic and functional data might be an accurate way to describe species differences of demersal Mediterranean fishes.

At the haul scale, we found that the use of two indices is sufficient for evaluating patterns in phylogenetic, functional or taxonomic richness and divergence, and that species richness and evenness can provide good proxies for demersal fish assemblages sampled by trawling in the Mediterranean Sea. Strong correlations between the divergence indices corroborate a recent proposal to use only one of them as a suitable proxy (Lefcheck et al., 2014). Taxonomical divergence has been suggested by some authors, because species taxonomy is generally fully available and does not require more intensive collection of functional traits and phylogenetic data (Lefcheck et al., 2014), knowing that phylogenetic and functional data require intensive experimentation and

computation, and are thus costly and time-consuming. Its use as a proxy is thought to be suitable when the evolutionary relationships between species are well delineated by taxonomy (Lefcheck et al., 2014; Ricotta et al., 2012), especially when using detailed taxonomy to translate evolutionary distances (Lefcheck et al., 2014). In a counter-intuitive way, even if taxonomy does not capture the phylogenetic or functional signals, divergence indices can be highly correlated because they are mostly driven by species relative abundance (*i.e.* Simpson evenness index (Smith and Wilson, 1996)). This is confirmed by the decomposition of *Q* proposed by Pavoine et al. (2013) to identify the main driving forces of this index (see Appendix F). Thus, in our case, species evenness describes the trends of divergences indices.

The correlation between divergence indices has been also studied in other previous studies (Devictor et al., 2010; Lefcheck et al., 2014; Mouillot et al., 2011); however, their results are not directly comparable with our findings being based on different data (*e.g.* presence/absence data at resolution of $0.1° \times 0.1°$ established by expert knowledge, and not necessarily targeting the same groups of fishes and/or with the same sampling methodology), different spatial scales as well as different mathematical versions of the quadratic entropy index (γ, β levels in the context of diversity decomposition paradigm, *e.g.* Devictor et al., 2010; Meynard et al., 2011).

To sum up, the correlation analysis between the different diversity indices led us to select only two diversity indices for the demersal fish assemblages studied, confirming the need to use several indices for fish diversity assessment, as previously advocated (*e.g.* D'agata et al., 2014; Gaertner et al., 2013, 2010; Mérigot et al., 2007; Stuart-Smith et al., 2013). However, the implementation of widely used richness and divergence indices that would allow comparison of taxonomic, phylogenetic and functional diversity within a single mathematical framework is not supported. Finally, our results support the framework of a shortlist of diversity indices proposed by Gaertner et al. (2010) for investigating the multi-component aspect of demersal diversity to facilitate large scale studies and their comparison (Gaertner et al., 2013; Lefcheck et al., 2014).

Spatio-temporal patterns of demersal fish diversity

Species richness *S* showed relatively low levels of diversity in the Adriatic Sea and Cyprus, and relatively high levels in the east-

ern Ionian and Aegean seas, Iberian region and Malta at both local and regional scales. In contrast to *S*, divergence indices, and therefore evenness, remained spatially stable between spatial areas (GSAs). Thus, whatever the diversity index used and the spatial scales considered, diversity patterns of demersal fish assemblages sampled by trawling in the continental shelf and slope differ from studies dedicated to the Mediterranean coastal and continental fishes that were based on different sampling methodologies and fish groups (see references above), and which generally argued for a longitudinal decreasing western/eastern gradient of phylogenetic diversity and species richness, and for a decreasing north–south gradient of functional diversity (Ben Rais Lasram et al., 2009; Coll et al., 2010; Mouillot et al., 2011) (see however Guidetti et al., 2014 for species richness sampled by visual census). The absence of a west/east decreasing trend we observed further suggests that primary production (or more generally food availability) is possibly not the major factor explaining large scale patterns of species richness *S* and evenness of demersal fish assemblages sampled by trawling, as previously suggested for *S* (Gaertner et al., 2007). Effects of cumulative human activities, such as exploitation (notably trawling), but also pollution and habitat degradation, could also impact the diversity of these demersal fish assemblages (Coll et al., 2012). However, the large temporal scale of our analysis highlighted that the diversity of Mediterranean demersal fish assemblages has remained stable over the last two decades for all indices considered. This suggests that human pressure had probably already impacted the fish diversity prior to the start of the present survey (*i.e.* 1994). Furthermore, a loss in species richness can occur only if species "disappear" (or became rare and are not sampled anymore) without species gain (*e.g.* resulting from availability in niche space). Such situations imply unusually strong anthropogenic pressure that would involve more than fishing alone (overfishing can indeed lead to the collapse of fish populations, but hardly to their disappearance).

The remarkable species diversity in the Mediterranean basin needs effective management. We have pointed out that the scale of diversity analysis (*i.e.* GSA, Biogeographical zone, Basin) and measurement (α- and γ-diversity) can change our perception of hotspot locations. Spatial patterns of *S* at regional scale (γ-diversity) generally overlapped with those observed at haul scale (α-diversity), but there were some exceptions. The Gulf of Lions had one of the lowest regional *S* values while *S* per haul was one of the highest (suggesting a lower species turnover in this area, *i.e.* β-diversity). Conversely, the Strait of Sicily, Algeria and the Tyrrhenian Sea presented relatively low species richness at the haul scale (α-diversity), but relatively high rarefied species richness at the regional scale (γ-diversity). This underlines the importance of the choice of scales for practical delimitation of priority zones for protection when dealing with assemblage diversity (Devictor et al., 2010).

In conclusion, our study provides a snapshot of the state of the spatio-temporal patterns of demersal fish diversity assessed by complementary diversity components and based on a large standardised data set from scientific trawl samplings. It confirms the importance of considering complementary indices in species diversity assessment, showing that the location of diversity hotspots differs according to species richness or evenness components, and the spatial scale of investigation. We also show that the widely computed Rao's quadratic entropy is not always useful for directly comparing taxonomic, phylogenetic and functional diversity, their patterns being linked to the evenness component (Pavoine et al., 2013). This points to research perspectives to develop original diversity indices. Finally, our analysis represents a preliminary step towards studies focused on the drivers of demersal fish diversity in the Mediterranean Sea by revealing a high spatial differentiation of species richness, and stability of evenness and divergence indices across this area. Identifying more explicitly the biotic factors (such as species aggregation, competition or dispersal limitations, *e.g.* Boulangeat et al., 2012; Cavieres et al., 2014; Loreau and Mouquet, 1999), and abiotic factors (such as environmental variables as well as anthropogenic pressure, *e.g.* Coll et al., 2012), in species diversity habitat models would extend our findings within the frame of complementary work dedicated to this aspect. However, a more precise investigation of the effects of these factors requires data availability (*e.g.* species interactions, fishing effort from Vessel Monitoring System (VMS) data) as well as specific modelling analyses that will need to be performed in forthcoming studies.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2014.10.002.

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