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The relative roles of the environment, human activities and spatial factors in the spatial distribution of marine biodiversity in the Western Mediterranean Sea

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Identifying the factors that affect the spatial distribution of marine biodiversity is a central issue to ecology. This knowledge is crucial to evaluate biodiversity patterns, to predict the impact of environmental change and anthropogenic activities, and to design accurate management programs. Here, we investigated the degree to which environmental features, human activities and spatial constraints interact and influence spatial gradients in marine biodiversity using the Western Mediterranean Sea as a model system. Our results revealed that a large fraction of the variability in biodiversity metrics of most marine groups analysed is accounted for by the joint effect of environment and human activities, environment and spatial variables or between all three groups of variables. In other words, major environmental variables and human activities have a collinear spatial structure, and thus an important part of the variation in biodiversity metrics can be attributed to these three groups of explanatory variables. Among pure effects, deviance partitioning results showed that the effect of environmental variables was more evident than the effect of human or spatial variables. The effect of single environmental and human variables considered in the analyses was different for different marine groups. This study contributes to the knowledge of the effects of ecological factors on the spatial distribution of marine biodiversity in the Mediterranean Sea, which is important in the development of more complex spatial analyses. Our results support the hypothesis that the joint effect of different predictor sets can be highly relevant in spatial patterns of biodiversity due to spatial collinearity. Thus, the simultaneous analysis of the relative effect of ecologically important predictor sets is important in preventing misinterpretations of the ecological mechanisms that explain spatial distribution of marine biodiversity.

Highlights

► We investigate how environment, human-stressors and space affect marine biodiversity. ► The effect of environment is more evident than human or spatial variables. ► Environmental and human variables have different effect for different marine groups. ► Joint effect is relevant in spatial patterns of marine biodiversity.

1. Introduction

As human activities develop and expand there is an increasing pressure on natural environments, which ultimately leads to the loss of biodiversity and ecosystem services (Millennium Ecosystem Assessment, 2005; Strategic Plan for Biodiversity 2011–2020). This is of great concern because biodiversity contributes to many aspects of marine ecosystems, including micro- and macro-biogeographic patterns, the evolution of marine communities and ecosystem functioning and resilience (Duffy, 2009; Armstrong et al., 2012). Biodiversity is also linked to ecosystem services and available economic and social resources for humans (Liquete et al., 2013).

The biodiversity of the marine environment is remarkable and is essential to human populations around the world in its support, provisioning and regulation of marine products and services, including cultural and societal benefits (Liquete et al., 2013; Worm et al., 2006). However, the marine environment is undergoing important and frequently deleterious changes, mostly induced by human activity (Worm et al., 2006). Climate change and anthropogenic activities are important threats to marine biodiversity, with the potential for serious and wide-scale ecological impacts on ocean ecosystems worldwide (Worm et al., 2006).

Due to the decline of biodiversity worldwide, countries and institutions have mobilized vast resources towards protecting and restoring species, communities and ecosystems (Brooks et al., 2006). At a global scale, for example, the Strategic Plan for the Convention on Biological Diversity (CBD) has established the Aichi Biodiversity Targets for signatory countries to achieve by 2020 (Secretariat of the Convention on Biological Diversity, 2010). At the European level, and in the marine realm, the Marine Strategy Framework Directive (MSFD) aims to achieve a Good Environmental Status (GES) in EU marine waters by 2020 (Directive 2008/56/EC).

Within this context, identifying and ultimately understanding the factors that currently affect the spatial distribution of marine biodiversity is a central issue (Albouy et al., 2012; Lasram et al., 2010; Morfin et al., 2012). This knowledge is crucial to the accurate evaluation of current biodiversity patterns, to predictions of the impact of climate change and anthropogenic activities, and to the designation of effective management programs through informing the selection, testing and monitoring of informative biodiversity indicators.

Until now, studies assessing the proximate factors explaining spatial variations in marine biodiversity and future projections have usually focused on the effect of environmental variables such as marine productivity, sea-surface temperature and bathymetry, among others (Albouy et al., 2012; Lasram et al., 2010; Morfin et al., 2012). However, in marine ecosystems it is well known that, beyond environmental variables, human activities also affect biodiversity, driving changes in species composition, abundance and distribution. Among human activities, fishing is one of the most important drivers of biodiversity in marine ecosystems (Worm et al., 2006). Other anthropogenic impacts are habitat degradation, pollution or the introduction of exotic species (Coll et al., 2012). Despite its importance, the relative contribution of human activities to the distribution of marine organisms has been only occasionally assessed and the number of studies that address this issue are scarce (Afán et al., 2014; Mackinson et al., 2009; Stelzenmüller et al., 2010), especially when compared to the terrestrial domain (Cardador et al., 2011; Llaneza et al., 2012). Moreover, the degree to which human stressors spatially interact amongst themselves and with other environmental variables and impact marine biodiversity is still a matter of debate (Claudet and Fraschetti, 2010; Coll et al., 2013b, 2010; Steenbeek et al., 2013). A more comprehensive understanding of these impacts and their interactions is thus needed for robust conservation planning (Crain et al., 2008; Folt et al., 1999).

Due to intrinsic biological differences among marine organisms, the response to the environment or human activities could differ substantially between marine groups. Indeed, changes in the environment and major anthropogenic stressors not only alter the number of species in most ecosystems, but also the relative abundance of biomass among species, leading to changes in the way species interact (Ward and Myers, 2005). Thus, in the current scenario of global change, in which environmental and human disturbances play a major role, understanding not only which factors affect biodiversity but also their relative effects on different taxonomic groups remains important. For example, species of high turnover rates such as jellyfish and cephalopods have increased their biomass and abundance in several ecosystems due to a reduction in predation pressure resulting from fisheries exploitation of their predators and a reduction in their competitors for their prey. They may have also benefited by an increase of seawater temperature caused by climate change (Coll et al., 2013a). On the contrary, elasmobranch abundance and biodiversity has been reduced in many areas as a consequence of overfishing and changes in environmental conditions related to climate change (Pennino et al., 2013; Worm et al., 2013). Similarly, human stressors and environmental factors can have different effects on different species, for example, can be involved in processes of trophic cascades and predation release (Ward and Myers, 2005).

The main objective of the present study is to examine the degree to which environmental features and human activities interact and influence spatial gradients of marine biodiversity using the Western Mediterranean Sea as a model system. The Western Mediterranean Sea is a highly impacted marine ecosystem where several human activities such as fishing, habitat use, aquaculture or tourism activities occur (Coll et al., 2012, 2010). Therefore, it provides an opportunity to identify some of the factors involved in spatially limiting species distributions and biodiversity.

In particular, we investigated the relative importance of environmental variables (chlorophyll-a concentration, sea surface temperature, depth and dissolved -oxygen) and human activities (fishing activity and coastal-based impacts) on the spatial distribution of the richness, abundance, and biomass of the main marine demersal groups in the area (i.e., finfish, cephalopods, crustaceans and elasmobranchs) using deviance partitioning analyses (Bocard et al., 1992). Since spatial constraints can also affect species distribution and biodiversity (Cardador et al., 2014; Heikkinen et al., 2004; Pennino et al., 2013), we also included spatial variables in these analyses. To assess whether species of different commercial value respond differently to these factors, we also tested the differences between targeted and non-targeted species, i.e. commercial and non-commercial species in the Western Mediterranean. With these results, we contribute to the current knowledge on the spatial distribution of marine biodiversity in the Mediterranean Sea (Albouy et al., 2014, 2012; Coll et al., 2012, 2010; Lasram et al., 2010), and thus to establishing a baseline for predicting future changes and conservation challenges.

2. Material and Methods

2.2. Study area

The study area comprises the Iberian continental shelf and upper slope (down to 800 m depth) of the Western Mediterranean area, from the Cap de Creus in the north to the

Cabo de Palos in the south (Figure 1). The study area has a latitudinal gradient in both topographic and hydrographic features (Estrada, 1996). The continental shelf broadens in the south, and is widest around the Ebro Delta (up to 70 km; Figure 1). This area is particularly productive due to a combined effect of the Liguro- Provençal-Catalan current and the runoff of the Ebro River (Estrada, 1996). In the northern area the continental shelf is narrower, with the Liguro-Provençal-Catalan current flowing south-westwards along the continental slope (Figure 1).

The area is one of the most important fishing grounds of the Mediterranean Sea, particularly the area surrounding the Ebro Delta with a large fishing fleet operating in the region (Coll et al., 2012, Figure 2F). Similar to other coastal areas of the Mediterranean, other human threats related to human activities, such as marine pollution, aquaculture activities and the presence of invasive species, are also important (Coll et al., 2012).

2.3. Survey design and data used

The data used in the present study were obtained from the EU-funded Mediterranean Trawl Survey (MEDITS) developed between the years 2007-2011 in the Western Mediterranean (Figure 1). MEDITS surveys were carried out during the early summer period (May-July) and included standardized sampling with a bottom -trawl at predefined stations over the coastal and continental shelf areas and the upper slopes from 10 to 800 m depth (see MEDITS protocol for a detailled description; (Bertrand et al., 2002). MEDITS protocol uses a codend mesh size of 10 mm (stretched mesh) and the minimum size captured was 2.5 cm (*Aphia minuta*). For each trawling survey, richness (number of species), abundance (number of individuals) and biomass (weight in kg) of marine species collected was recorded, as well as information on the total area surveyed (km^2). In total, n=62, n=73, n=72, n=51 and n=74 trawling surveys were conducted in years 2007, 2008, 2009, 2010 and 2011, respectively. For modelling analyses, the location of trawling surveys was incorporated into a Geographic Information System (GIS) using the world projection WGS European 1984 in a grid of 0.1° of resolution (the same resolution of the environmental and human variables, see below). Duplicate samples (i.e. information on two or more trawling surveys within the same grid cell in a year) were averaged and handled as single observations. In total, 122 grids were surveyed over the course of the study period (2007-2011), with an average (±

standard deviation) of 66.4±9.86 grid cells per year. From the total trawling surveys accomplished in the study area 191 finfish species (44 target and 147 non-target species), 44 cephalopod species (14 target and 30 non-target species), 127 crustacean species (8 target and 119 non-target species) and 15 elasmobranch species were recorded (see Appendix S1 in Supporting Information).

2.4. Environmental, human and spatial variables

Environmental variables included (1) chlorophyll-a concentration (CHL, $mg \cdot C \cdot m^{-3}$), (2) sea surface temperature (SST, ºC), (3) depth (DEPTH, m), and (4) dissolved-oxygen (DO, $ml \cdot l^{-1}$) as a measure of spatial variation in oxygen availability (Figures 2B, 2C, 2D). Dynamic oceanographic variables such as SST and CHL were obtained from the Aqua MODIS sensor (http://oceancolor.gsfc.nasa.gov). Both SST and CHL were extracted as averaged estimates of spring monthly values (May-July) across years 2007 and 2011, to be consistent with the survey periods (see above). The depth variable (DEPTH) was downloaded from the ETOPO website (www.ngdc.noaa.gov/mgg/global/global.htm) (Figure 2A). DO was obtained from a combination of standard level data, ocean station data and high-resolution conductivity temperature-depth from annual estimates from 2007-2011 (Bio-Oracle Project; www.oracle.ugent.be; see Tyberghein et al., 2012 for more details).

As human variables, we used (1) coastal-based impacts and (2) fishing activity (Figures 2E and 2F). The coastal-based impact variable is a combined measure of inorganic and organic coastal pollution, nutrient runoff and hypoxia, aquaculture activities and the presence of invasive species in the study area (Coll et al., 2012). In Appendix S2 we provide further information regarding this layer.

The fishing activity variable is a proxy of the spatial distribution of the fisheries in the study area between 2007 and 2011. This variable describes the relative position of each grid cell of the study area within the spatial distribution of all fishing harbours, taking into account total fishing landings per harbour each year (Afán et al., 2014). It is assumed that fishing activity is likely to be higher in areas more connected to different harbours in the study area, taking into account their intensity (fishing landings). We considered 50 km as being the maximum distance reached for the fishing vessels from their harbour. Specifically, fishing activity in each grid cell i (F_i) was assessed using a modified version of an isolation function (Moilanen and Hanski, 1998), with F_i =

$\sum\exp(-\alpha\cdot d_{ij})\cdot P_j$, where d_{ij} is the Euclidian distance from grid cell i to each harbour j of the study area, P_j is the number of total fish landings (tons, 10^3 kg) in harbour j and α is a measure of the influence of fishing vessels, set so that the value of exp (–α • dij) were spread along a 0-1 gradient, becoming close to zero when distance is higher than 50 km and close to one when distance is close to 0 km (Figure 2 and see Appendix S3 in Supporting Information). Distribution of harbours in the study area and information on landings were obtained from different official sources (Appendix S3 in Supporting Information; fishing landing sources: www.agricultura.gva.es, http://www.carm.es; Fisheries department of the Catalonia Government catch statistics 1986–2011). All layers were obtained in the world projection WGS European 1984 with 0.1º of resolution.

As biodiversity metrics may be similar in neighbouring grid cells due to spatial autocorrelation, we added a third predictor set called “spatial factors” (Legendre and Legendre, 1998) to account for the effect of subjacent spatial structures that were not captured by the environmental and human factors considered. This spatial component was composed of the longitude and latitude of the central point of each grid cell and their interaction terms up to the third order (i.e., $x + y + x^2 + xy + y^2 + x^3 + x^2y + xy^2 + y^3$, Legendre & Legendre, 1998). Prior to the inclusion in the models, the spatial coordinates of each grid cell were centered on their respective means (i.e., they were divided by their average value in all grid cells of the study area).

2.5. Analytical procedures

We used deviance partitioning to analyse the importance of the different predictor sets considered (environment, human and spatial factors) for the richness, abundance and biomass of each marine group (Bocard et al., 1992). Deviance partitioning is a quantitative method that allows the pure effect of each predictor set to be separated from joint effects that cannot unambiguously be attributed to one predictor set or another due to spatial collinearity (Bocard et al., 1992; Cardador et al., 2011; Heikkinen et al., 2004; Llaneza et al., 2012). This analysis entails the calculation of incremental improvement in the model fit due to the inclusion of a predictor set in every possible model incorporating that predictor set. For these calculations, we constructed multivariate generalized linear models (GLMs) based on all potential combinations of the predictor sets considered, namely (1) environment, (2) human, (3) space, (4) environment + human, (5) environment + space, (6) human + space and (7) environment + human +

space (see conceptual diagram in Figure 3A). Both the linear and quadratic forms of environmental and human variables were included in the models to test for potential parabolic trends (i.e., higher and lower values of a variable imply an increase/decrease in biodiversity metrics compared with intermediate values). Note that testing the quadratic form of these variables implies the inclusion of both the variable and its squared term in a model.

We used biodiversity metrics of each marine group (i.e., richness, abundance and biomass) as response variables in the models (Table 1 for average values). Since we were interested in spatial patterns of biodiversity and because repeatability analyses showed high repeatability of biodiversity metrics in grid cells of the study area across years (0.6-0.9), we used averaged values of these variables across the five sampling years. We fitted a normal error distribution and identity-link functions for continuous data (abundance and biomass per surveyed area after log-transformation, i.e., number of individuals/km^2 and weight/km^2). For count data (richness) we used a Poisson error distribution and log-link function and included the natural logarithm of surveyed area as an offset in all models. We used multimodel inference based on Bayesian information criteria (BIC) and the 95% confidence model set within each model (Burnham, 2004; Whittingham et al., 2005). Variables with model-averaged weights of 0 in single environment or human models were not included in more complex models. Multimodel inference was implemented in R software by the functions ‘dredge’ and ‘model.avg’ from the ‘MuMIm’ library. Estimated contributions of different predictor sets were based on R^2 for abundance and biomass and pseudo-R^2 for richness (Heinzl and Mittlböck, 2003).

3. Results

3.1. Response to single environmental variables

When considering the single environmental models, the quadratic effect of depth received strong support on spatial biodiversity metrics of most of marine groups according to multimodel inference. That is the selection probabilities for both depth and its squared term, depth^2 , were high ($> 0{\cdot}67$), indicating that biodiversity metrics of most groups increased or decreased (positive or negative values of the squared term) in a curvilinear fashion with intermediate values of depth (Table 2). However, high support for linear effects of depth was also observed for some groups and biodiversity metrics (i.e., the selection probabilities are only high for depth, Table 2; Table S2 in Appendix S4 of Supporting Information). For example, the distribution of the richness, abundance and biomass of both target and non-target crustaceans showed high values in the deep waters (Figures 4E, 4F, 5E, 5F, 6E and 6F).

The other three environmental variables (SST, chlorophyll-a and dissolved -oxygen) where only selected with high to moderate probabilities (selection probabilities ranging between 1 and 0.42) on particular marine groups (Table 2; Table S2 in Appendix S4 of Supporting Information).

3.2. Response to single human variables

According to the single human models, both coastal-based impact and fishing activity had a wide effect on the richness, abundance and biomass of most marine groups (Table 2; Table S2 in Appendix S4 of Supporting Information). The selection probabilities of these variables according to multi-model inference were overall high, suggesting a high probability to be relevant explanatory variables. The main type of effect of the coastal-based factor were quadratic, with the abundance and biomass of non-target cephalopods, target crustaceans and elasmobranchs increasing at lower and upper values of coast-based impacts and the richness and abundance of target finfish and the richness, abundance and biomass of target cephalopods increasing at intermediate coastal-based impacts (Table 2; Table S2 in Appendix S4 of Supporting Information). In contrast, coastal-based impacts showed a negative lineal effect on the biodiversity metrics of non-target crustaceans and the richness of non-target cephalopods, and a positive lineal effect on the abundance of target/non-target finfish (Table 2; Table S2 in Appendix S4 of Supporting Information).

Fishing activity also showed a wide effect on the biodiversity indicators. In particular, fishing activity showed a negative quadratic effect on the richness, abundance and biomass of non-target crustaceans and elasmobranchs (biodiversity metrics increased with intermediate values of fishing activity; Table 2; Appendix S4 in Supporting Information).

For the richness, abundance and biomass of target finfish and cephalopods and the richness and abundance of non-target finfish, a quadratic response was found (they increased at lower and upper fishing activity values; Table 2; Table S2 in Appendix S4 of Supporting Information). The richness of target crustaceans and biomass of non-target finfish showed a positive and negative relationship with fishing activity, respectively (Table 2; Table S2 in Appendix S4 of Supporting Information).

3.3. Relative importance of environmental, human and spatial factors

According to deviance partitioning, the pure effect of environmental variables (fraction a in Figure 3A) accounted for the largest individual fractions of the variability in all biodiversity metrics of most marine groups (range: 7- 73%; but see exceptions for non-target crustaceans and elasmobranchs; Figure 3B-D). Joint effect of environmental and spatial variables was also important for most groups, suggesting that a large part of the environmental influence on biodiversity metrics was spatially structured. The pure effect of human factors was less important for most of the groups (range: 0.5-23%, see exceptions for the richness of elasmobranchs and non-target cephalopods; Figure 3B) as well as the joint effect of human and spatial factors (0.9-4.5%).

Interestingly, the joint effect (i.e., the effect that cannot be unambiguously attributed to one predictor set or another due to spatial autocorrelation) of environment + human activity or environment + human + space explained a high variability in the analyses (Figure 3B-D). Particularly, the joint effect of environmental, human and spatial factors (fraction g in Figure 3A) was especially important in accounting for the variability in the spatial patterns in abundance and biomass of elasmobranchs and target crustaceans and the richness of target/non-target finfish (Figure 3C, D). Interestingly, large fractions of the variability in the richness (Figure 3A) of target/non-target finfish, target/non-target crustaceans and elasmobranchs were accounted by the pure effect of spatial factors (fraction c in Figure 3B). The negative joint contribution of different set of predictors indicates that their relationship is mostly suppressive and not additive.

3.4. Predicted spatial biodiversity distributions

When considering their spatial distribution according to model predictions, the biodiversity indicators of target finfish showed higher values in the northern area of the study area (Figures 4A, 5A and 6A). In contrast, non-target fin-fish showed the highest values of richness in the southern area (Figure 4B), whereas abundance and biomass were high throughout the platform shelf of the study area (Figures 5B and 6B).

In regards to cephalopods, the predicted distribution showed that the abundance of target cephalopods was high in the central region of the study area, overlapping with high levels of fishing activity (Figures 5C and 6C). Non-target cephalopods showed higher biodiversity values outside the continental shelf (Figures 4D, 5D and 6D).

The distribution of the richness and abundance of both target and non-target crustaceans were similar, showing high values outside the continental shelf (Figures 4E, 4F, 5E and 5F). In contrast, the biomass of target crustaceans showed a spatial distribution opposite to that of non-target crustaceans (Figures 6E and 6F). Finally, the abundance and biomass of elasmobranches showed higher values in the northern regions of the study area (Figures 5H and 6H), and the richness of elasmobranchs was higher in the areas close to the coastal line throughout the study area and particularly in the southern area (Figure 4H).

4. Discussion

Distribution patterns of biodiversity are often the result of interacting factors that are difficult to disentangle and so, methods to identify joint effects and independent influences of such factors are valuable in both basic and applied ecology. Here, we investigated the relative influence of environmental variables, human activities and spatial factors to explain the spatial patterns of marine biodiversity in the Western Mediterranean using deviance partitioning analyses.

Our results revealed that a large fraction of variability of biodiversity metrics of most marine groups is accounted for by the joint effect of environment and human activities or spatial variables or between all three groups of variables. In other words, major environmental variables and human activities have a collinear spatial structure, and thus an important part of the variation in biodiversity metrics can be attributed to these three groups of explanatory variables.

In deviance partitioning results, the pure effect of environmental variables was more evident than the pure effect of human activities or spatial variables. Among the environmental variables, depth was important in describing the biodiversity patterns in the Western Mediterranean. This variable has already been widely used for investigating marine biodiversity (Macpherson, 2003; Kendall and Haedrich, 2006; Rex and Etter, 2010). In agreement with the most popular theory, one important response of biodiversity metrics of most marine groups to bathymetry in our study was a parabolic or hump-shaped response, so that peak biodiversity patterns occurred at an intermediate depth (Colwell and Lees, 2000; Kendall and Haedrich, 2006). However, some different responses were also observed for particular marine groups.

Although the other environmental factors included in our analyses have been described as important factors influencing the biodiversity gradients of marine biota (Albouy et al., 2012; Lasram et al., 2010; Morfin et al., 2012), here we found that their effect is more narrowly distributed than that of depth, with significant relationships found only for particular marine groups and biodiversity metrics. For example, dissolved-oxygen concentrations affected the biodiversity patterns of elasmobranchs, highlighting that although elasmobranchs are physiologically adapted to buffer hypoxia variations, they spatially respond in a strong way to variations in dissolved-oxygen concentrations (Speers-Roesch et al., 2012). Interestingly, the biomass of cephalopods responded positively to sea-surface temperature. This result was in line to that found in previous studies, which related the increase in the biomass of cephalopods to the increase in seawater temperatures due to climate change (Coll et al., 2013a).

Similarly, although we were expecting a positive response to chlorophyll-a, a proxy of marine productivity and biodiversity patterns (Chase and Leibold, 2004; Kendall and Haedrich, 2006), we found an opposite or non-effect response for most groups (see Table 2). This result could be explained by the fact that the data from the satellite-based sensors used in this analysis only assess chlorophyll-a within the top few metres of the water column, overlooking the chlorophyll-a concentrations in deeper waters (Barlow et al., 2002), where demersal species live. Alternatively, although we used chlorophyll-a values averaged over the spring period, the presence of time-lags between peaks of chlorophyll-a and resource availability for consumers may affect our results (Runge, 1998). We can neither discard the possibility that human activities are obscuring the effect of this variable due to spatial autocorrelation (as indicated by the relevant joint effect of environment and human activities in our study area). Indeed, more productive areas within the coastal shelf in our study area are highly impacted by human activities. Therefore, even if the coastal area is more productive, it is also more impacted and this could interact negatively with the species living in the continental shelf (Fig 2B,E).

In addition to the environment, the pure effect of human activities, i.e., fishing activity and coastal-based impacts, also influenced the spatial biodiversity patterns of different marine groups considered in the present study, although explained variation accounted for by these variables was low. In the case of fishing, the biodiversity metrics of non-target groups increased in a parabolic fashion with an intermediate level of fishing disturbance (Flöder and Sommer, 1999). The effect of an intermediate level of fishing activity could be allowing the coexistence of successful competitors and of competitively inferior species, resulting in maximal biodiversity (Flöder and Sommer, 1999; Savina et al., 2013). Contrary to these groups, the biodiversity metrics of target groups increased non-linearly with fishing activity, showing higher values in waters with higher fishing activity. In the case of finfish, this result may be the consequence of the fact that fisheries operate in areas with a high availability of target finfish and thus our results are highlighting those areas (Tittensor et al., 2010). Indeed, overall spatial overlap between environmental-human and between environment-human-space is higher for commercial species than for non-commercial ones according to deviance partitioning. For the cephalopods, although the former explanation is plausible, we could alternatively suggest that they may be favoured by the fishing activity per se. There are different studies indicating that some species of cephalopods are favoured by fishing activity due to a reduction in predation pressure resulting from fisheries exploitation of their predators and a reduction in their competitors for prey (Coll et al., 2013a). Coastal-based impacts also showed a negative effect on the richness of crustaceans, indicating that human activities on the coast are negatively affecting the marine biota as a consequence of pollution or aquaculture activities, among others (Coll et al., 2012; Worm et al., 2006).

Important, but less frequently considered in studies of distribution of marine populations, are spatial effects (Pennino et al., 2013). Due to spatial autocorrelation, values of particular variables in neighbouring sites can be more or less similar than in a random set of observations (Bocard et al., 1992). In our study, we found a significant latitudinal and longitudinal influence on patterns of spatial biodiversity. However, the pure effect of spatial variables on biodiversity metrics of most marine groups was small in deviance partitioning analyses, suggesting that a large fraction of their influence was related to the spatial structure of environmental and human variables considered. Although not conclusive, the remaining portion of their influence might reflect the role played by environmental or human variables not considered in the present study or past events (Legendre and Legendre, 1998), such as uneven historic human pressures, for example fishing activity in the coastal areas of the Mediterranean Sea (Azzurro et al., 2011; Coll et al., 2014).

While understanding the response of organism to multiple environmental factors is interesting from an ecological point of view, quantifying the way these multiple variables interact and combine in space to determine species distributions may be even more informative from a management point of view, but little is known about these interactions. Deviance partitioning allows the separation of the pure effect of each predictor set from the joint effects that cannot unambiguously be attributed to one predictor set or another due to spatial collinearity (Bocard et al., 1992; Cardador et al., 2011; Heikkinen et al., 2004; Llaneza et al., 2012). These results would allow ranking conservation priorities using objective criteria such as the independent contribution of each variable in explaining variability in biodiversity distributions patterns. However, although this approach has been extensively used in terrestrial ecosystems, to our knowledge this is the first study that applies this approach in marine ecosystems. The results presented here show that the joint effect of different predictor sets can be very relevant in the marine realm as well. Thus, the simultaneous analysis of the relative effects of ecologically important predictor sets is essential to preventing misinterpretations of the ecological mechanisms that explain spatial distribution of marine biodiversity. With these results, we contribute to the current knowledge on the spatial distribution of marine biodiversity in the Mediterranean Sea (i.e. Albouy et al., 2012; Coll et al., 2010, 2012; Lasram et al., 2010), advancing progress toward the development of more complex spatial analyses (Pennino et al., 2013; Steenbeek et al., 2013).

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Table 1

Descriptive statistics (mean and standard deviation) of environmental variables, human variables, and biodiversity metrics of finfish, cephalopods, crustaceans and elasmobranchs in the Western Mediterranean during the years 2007-2011.

Variable		Units	Mean	SD
Habitat				
Depth	Depth	m	-160	200
Chl-*a*	Spring chlorophyll-*a*	mg·m^{-3}	0.44	0.22
SST	Spring sea surface temperature	ºC	17.64	0.77
Oxygen	Dissolved oxygen concentration	ml·l^{-1}	-0.46	0.05
Human stressors				
Coastal impact	Long-term coastal-based impacts	impact unit	0.19	0.13
Fishing intensity	Cumulative fishing intensity	tonnes landed	142261	87177
Biodiversity descriptors				
RICHNESS				
Target fish	Total number of species	species	7.6	2.7
Non-target fish	Total number of species	species	9.4	2.7
Target cephalopods	Total number of species	species	3.5	1.5
Non-target cephalopods	Total number of species	species	1.1	0.9
Target crustaceans	Total number of species	species	0.7	0.7
Non-target crustaceans	Total number of species	species	6.3	4.1
Elasmobranchs	Total number of species	species	1.1	0.9
ABUNDANCE				
Target fish	Total number of individuals	ind·km^{-2}	16167	34457
Non-target fish	Total number of individuals	ind·km^{-2}	14413	18945
Target cephalopods	Total number of individuals	ind·km^{-2}	1734	1982
Non-target cephalopods	Total number of individuals	ind·km^{-2}	84.5	175.2
Target crustaceans	Total number of individuals	ind·km^{-2}	312	634
Non-target crustaceans	Total number of individuals	ind·km^{-2}	2645	4393
Elasmobranchs	Total number of individuals	ind·km^{-2}	341	880
BIOMASS				
Target fish	Total biomass	kg·km^{-2}	340	443
Non-target fish	Total biomass	kg·km^{-2}	189	256
Target cephalopods	Total biomass	kg·km^{-2}	106	168
Non-target cephalopods	Total biomass	kg·km^{-2}	3.5	7.3
Target crustaceans	Total biomass	kg·km^{-2}	7.4	16.4
Non-target crustaceans	Total biomass	kg·km^{-2}	12.5	15.9
Elasmobranchs	Total biomass	kg·km^{-2}	47	100

Table 2

Model-averaged results for the biodiversity metrics of different marine groups according to single environmental and human models in the Western Mediterranean Sea. The acronyms are: SST=sea-surface temperature, CHL=Chlorophyll-*a*, DO=Dissolved-oxygen, Fishing=fishing activity, and Coastal=coastal-based impacts. The table indicates the relative importance (i.e., selection probability in the 95% confidence set of models) of each variable for each marine group and the type of response ("+"= positive; "-"= negative). Relative importance and response are not provided for variables with selection probability lower than 0.4, since these probabilities are similar to that obtained using null predictors (Whittingham et al. 2005).

	ENVIRONMENTAL MODEL								HUMAN MODEL			
	Depth	Depth^2	SST	SST^2	CHL	CHL^2	DO	DO^2	Fishing	Fishing^2	Coastal	Coastal^2
RICHNESS												
Target finfish	1(-)	1(+)							1(-)	1(+)	1(+)	1(-)
Non-target finfish	1(-)	1(+)							0.95(-)	0.95(+)	1(+)	0.43(-)
Target cephalopods	1(-)	1(+)							1(-)	1(+)	1(+)	1(-)
Non-target cephalopods					0.88(-)						0.43(-)	
Target crustaceans									0.46(+)		0.40(-)	
Non-target crustaceans	0.65(+)						0.58(+)	0.42(+)	0.97(+)	0.97(-)	0.57(-)	
Elasmobranchs			0.86(-)	0.69(+)			0.50(+)		0.78(+)	0.73(-)	0.43(+)	
ABUNDANCE												
Target finfish	1(-)								1(-)	0.67(+)	1(+)	0.61(-)
Non-target finfish	1(-)	0.69(+)							0.64(-)	0.47(+)	1(+)	
Target cephalopods	1(-)	1(+)					0.66(+)		1(-)	1(+)	1(+)	1(-)
Non-target cephalopods					0.78(-)		0.52(-)		0.64(+)	0.51(-)	0.92(-)	0.73(+)
Target crustaceans	1 (+)	1(-)							1(+)	1(-)	1(-)	1(+)
Non-target crustaceans	0.99(+)	0.95(-)	0.96(-)						0.81(+)	0.81(-)	0.56(-)	
Elasmobranchs					0.48(-)		1(+)	0.95(+)	1(+)	1(-)	1(-)	0.68(+)
BIOMASS												
Target finfish	1(-)								0.90(-)	0.38(+)	1(+)	
Non-target finfish	1(-)	0.69(+)							0.4(-)		1(+)	
Target cephalopods	1(-)		0.85(+)						0.73(-)	0.73(+)	1(+)	1(-)
Non-target cephalopods	1(-)	1(-)							0.79(+)	0.68(-)	1(-)	1(+)
Target crustaceans	1 (+)	1(-)							1(+)	1(-)	1(-)	1(+)
Non-target crustaceans	0.97 (+)	0.67(-)	1(-)				0.66(+)		1(+)	1(-)	0.46(-)	
Elasmobranchs					0.48(-)		1(+)	0.95(+)	1(+)	1(-)	1(-)	0.63(+)

Fig. 1. (A) Distribution of the sampled fishing grids in the Western Mediterranean Sea, the main topographic locations and marine currents (LPC Current; Liguro- Provençal-Catalan Current). (B) The geographic position of the studied area in the Mediterranean Basin.

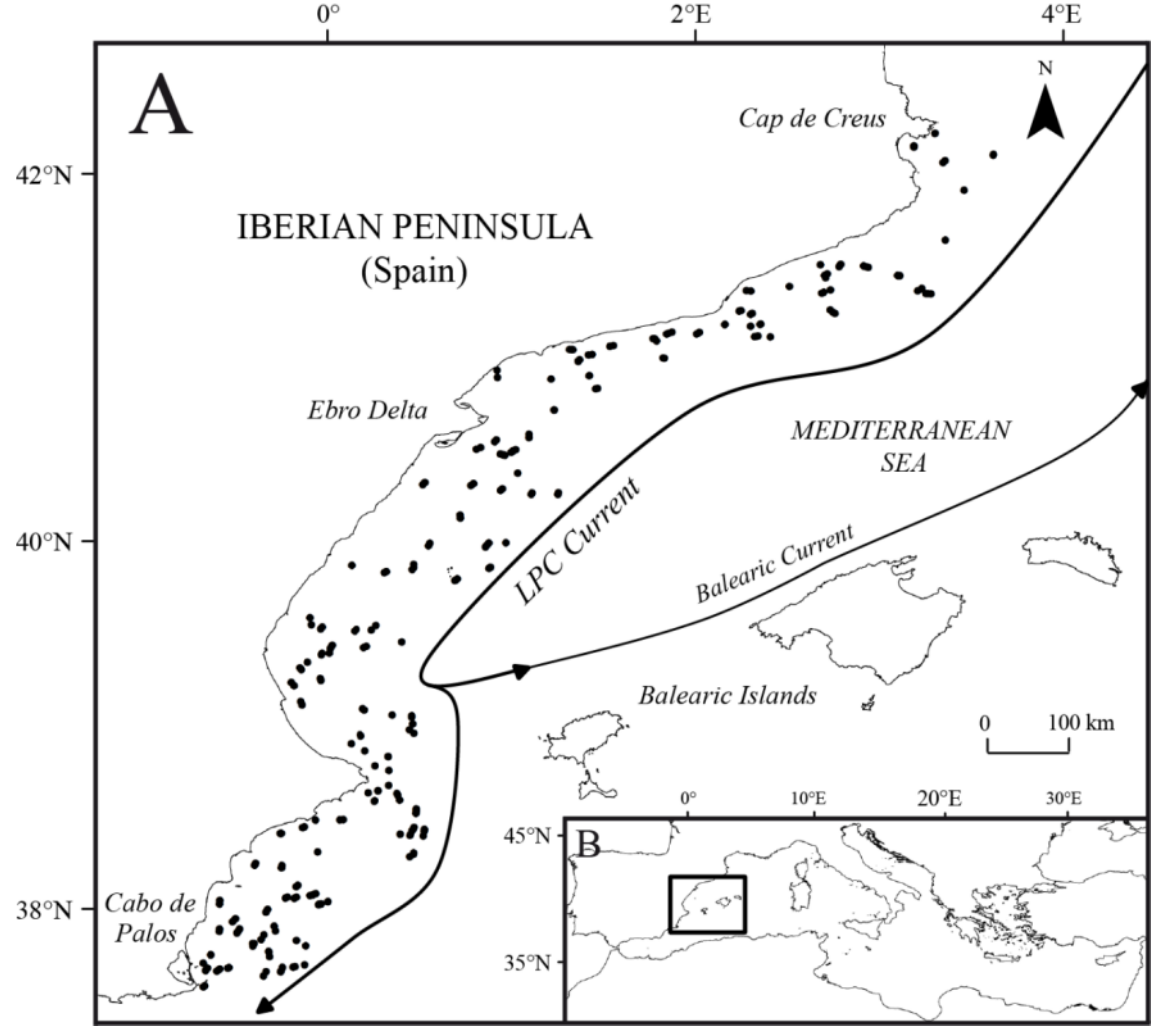

Fig. 2. (A) Depth gradients, (B) spring chlorophyll-*a* concentrations, (C) spring sea surface temperature SST values, (D) annual dissolved oxygen, (E) coastal-based impacts, and (F) fishing activity in the Western Mediterranean.

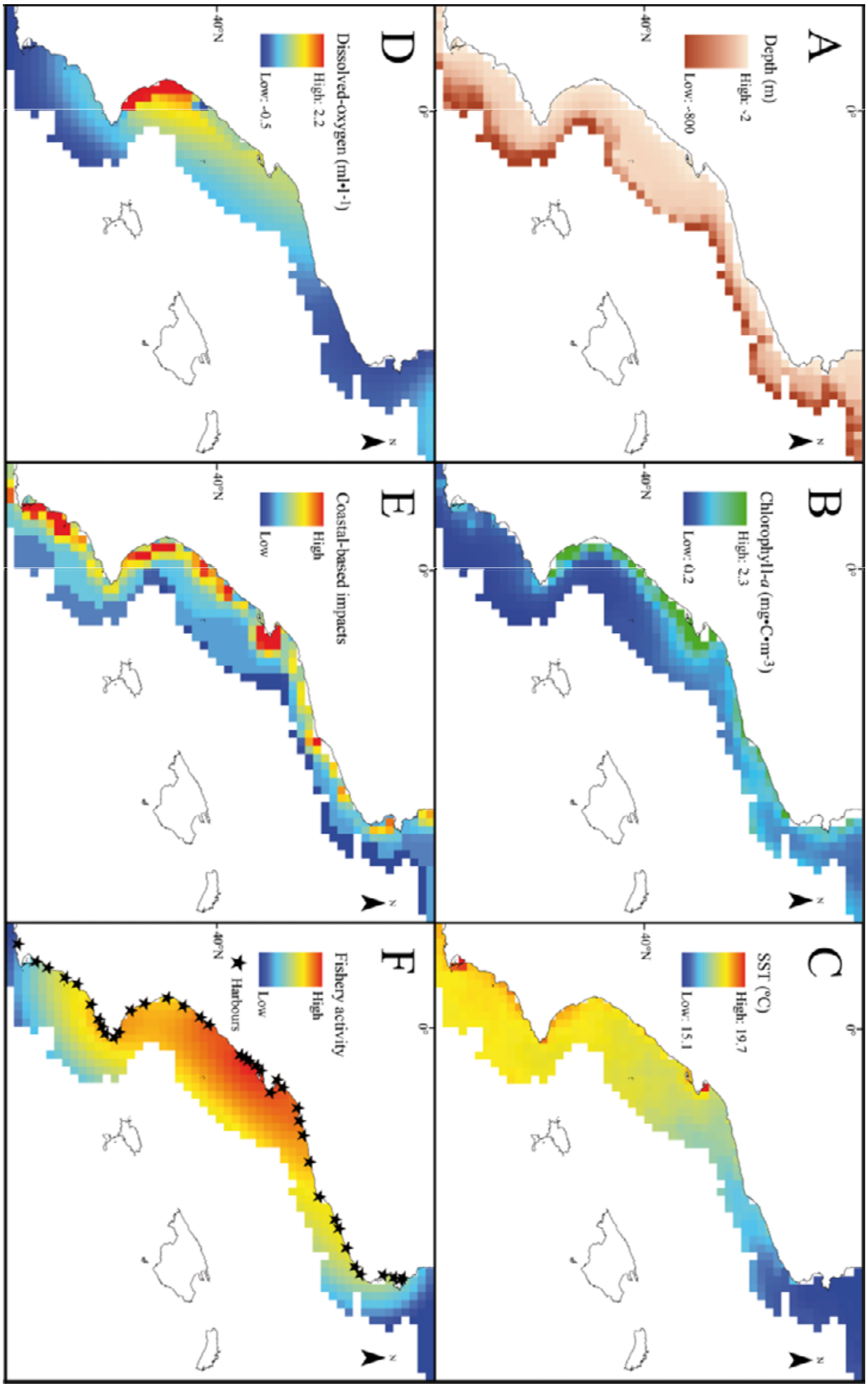

Fig. 3. (A) Conceptual diagram showing the variation in the dependent variable (richness, abundance or biomass) due to three groups of explanatory variables: environment, human and space, and *U* is the unexplained variation and the results of the pure and joint contribution of habitat, human and spatial variables on (B) richness (total number of species), (C) abundance (ind·km^{-2}) and (D) biomass (kg·km^{-2}) for each marine group (TFF= target finfish; NTFF=non-target finfish; TCEP=target cephalopods; N-TCEP=non-target cephalopods; TCRUS=target crustaceans; N-TCRUS=non-target crustaceans; ELAS=elasmobranchs).

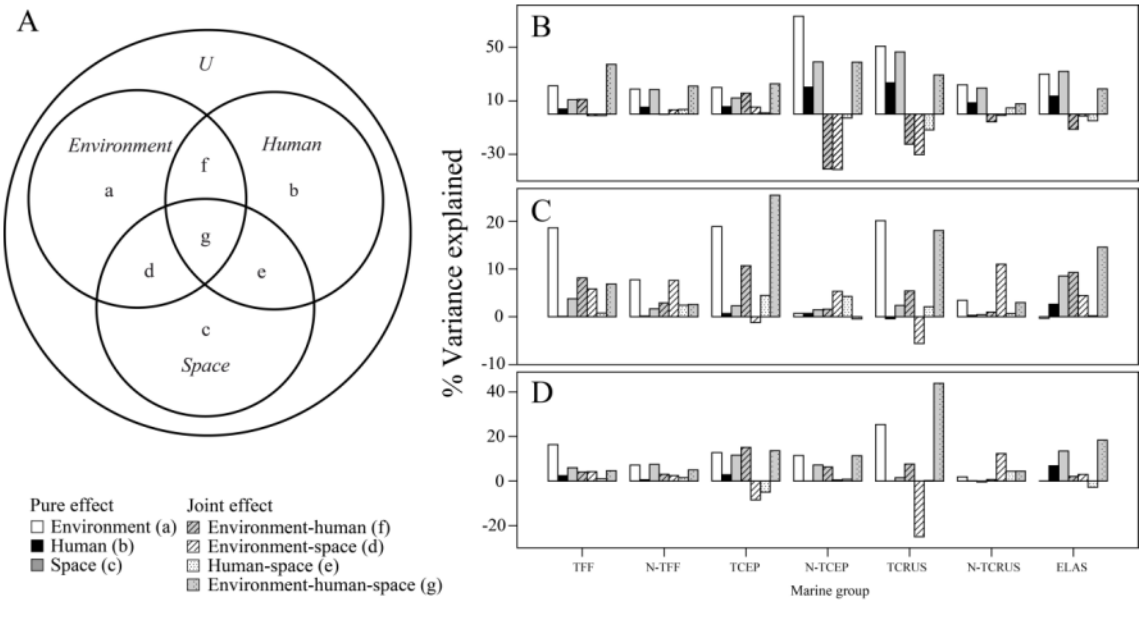

Fig. 4. Predicted distribution of the richness (number of species) in the Western Mediterranean of (A) target finfish, (B) non-target finfish, (C) target cephalopods, (D) non-target cephalopods, (E) target crustaceans, (F) non-target crustaceans and (G) elasmobranchs.

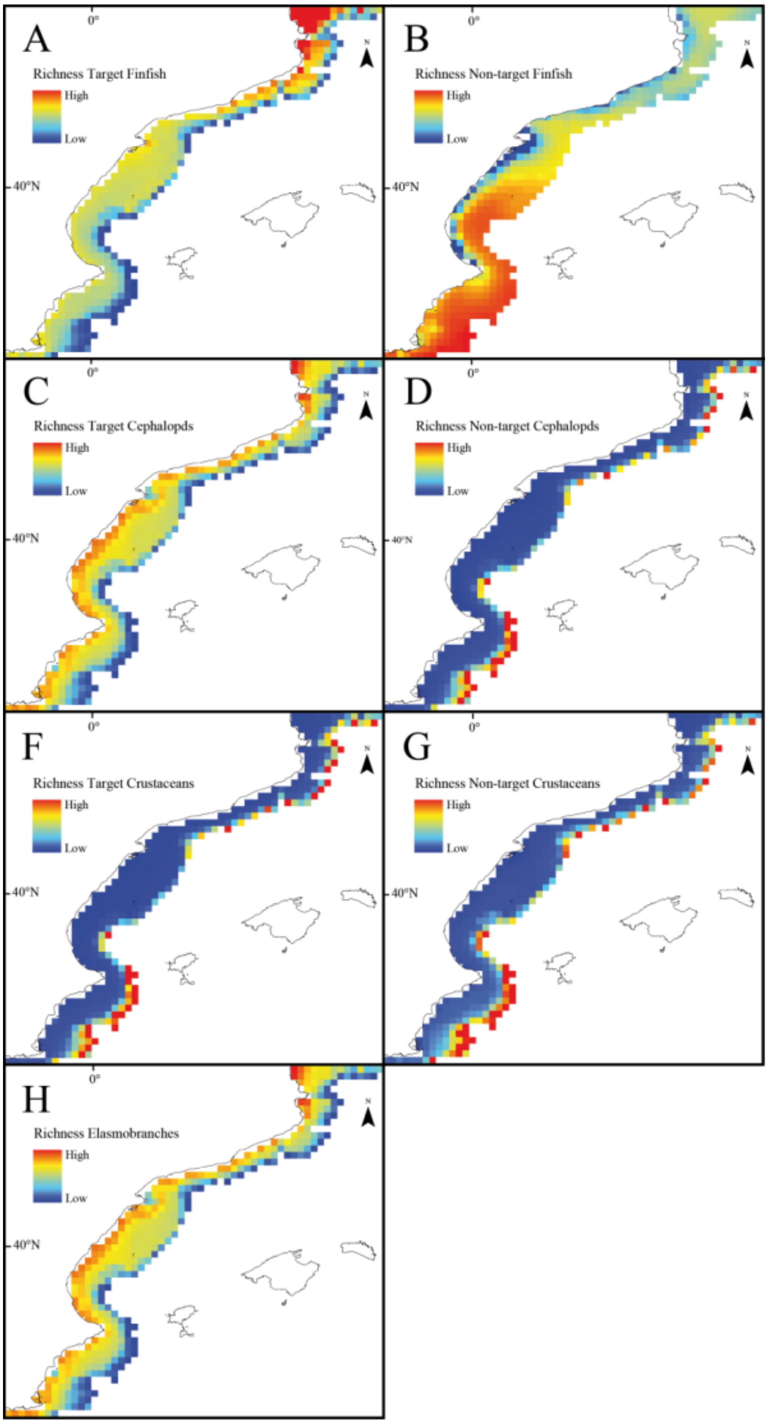
A
Richness Target Finfish
High
Low
B
Richness Non-target Finfish
High
Low
C
Richness Target Cephalopds
High
Low
D
Richness Non-target Cephalopds
High
Low
F
Richness Target Crustaceans
High
Low
G
Richness Non-target Crustaceans
High
Low
H
Richness Elasmobranches
High
Low
0°
40°N
N

Fig. 5. Predicted distribution of the abundance (ind·km^{-2}, in log) in the Western Mediterranean of (A) target finfish, (B) non-target finfish, (C) target cephalopods, (D) non-target cephalopods, (E) target crustaceans, (F) non-target crustaceans and (G) elasmobranchs.

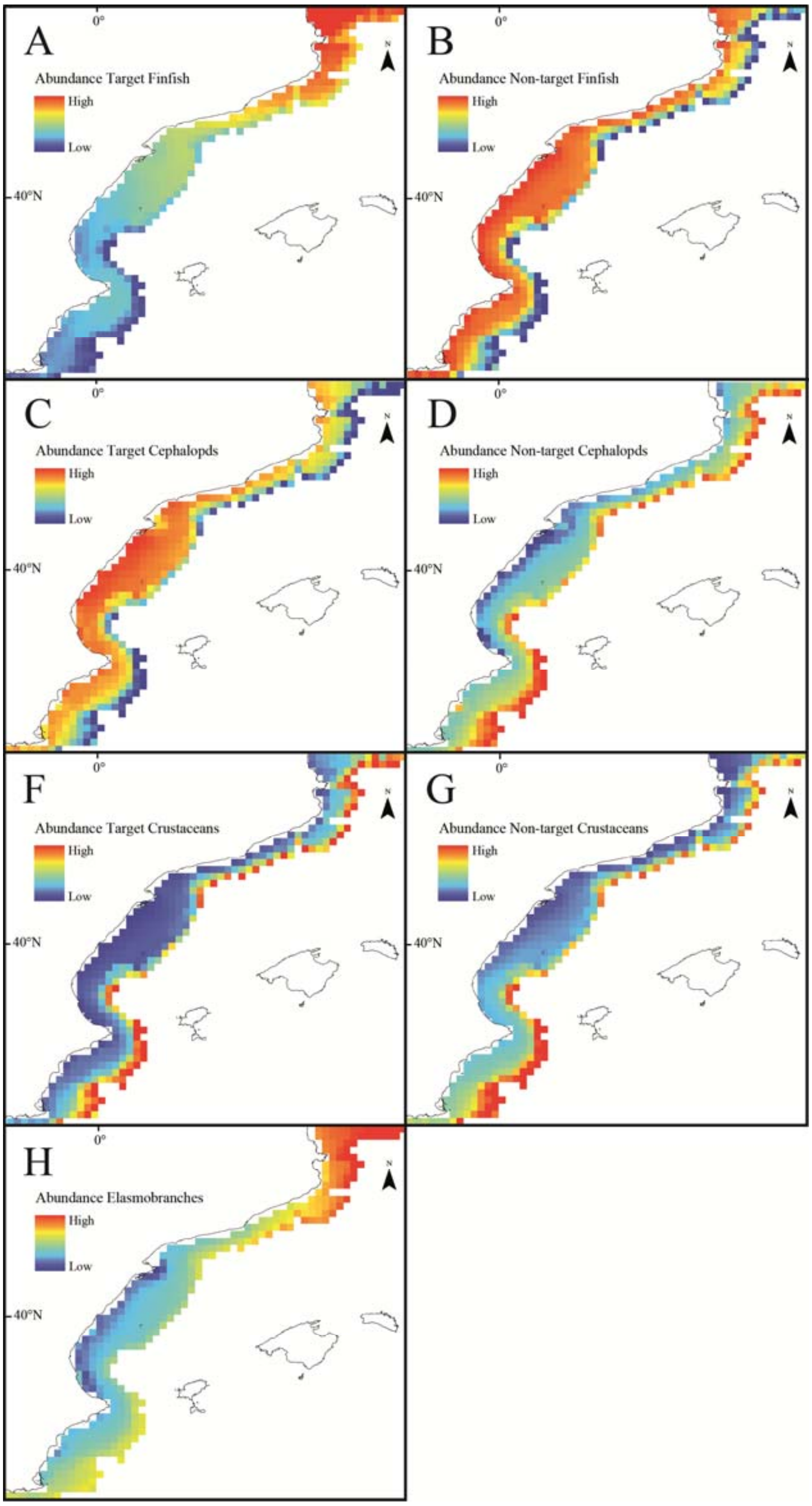

Fig. 6. Predicted distribution of the biomass (kg·km^{-2}, in log) richness (number of species·km^{-2}) in the Western Mediterranean of (A) target finfish, (B) non-target finfish, (C) target cephalopods, (D) non-target cephalopods, (E) target crustaceans, (F) non-target crustaceans and (G) elasmobranchs.