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Bottom trawling and environmental variables drive the biodiversity of mediterranean demersal assemblages

Davide Agnetta[1]✉, Ivano Vascotto[1], Diego Panzeri[1], Igor Celić[1], Cosimo Solidoro[1], Tomaso Fortibuoni[2], Saša Raicevich[2] & Simone Libralato[1]

Marine ecosystems are healthy with a high degree of biodiversity. Assessing how factors affect spatial and temporal patterns of biodiversity is an essential task for the Ecosystem Based Management approach. In this work, we investigated the effect of fisheries disturbance and ocean variables in determining α- and β-diversity of Mediterranean demersal assemblages. Generalized additive mixed models were used to explain the spatio-temporal variability of diversity indices from 2014 to 2020 in three Mediterranean subregions as a function of covariates. An in-depth analysis also made it possible to decouple the effects of bottom trawling from the other covariates. The results show that several fishing activities and environmental variables influence biodiversity, but the direction of change depends on the subregion considered. Bottom trawling instead has a quasi-linear erosion effect on α- and β-diversity in all areas. Valuable commercial species and threatened rays and sharks importantly characterized the sites with low fishing impact. Results are a step towards the development of conservation and management strategies, particularly in the context of the Marine Strategy.

Keywords Biodiversity, Demersal assemblage, Fishing, Ocean variables, Marine strategy

Marine biodiversity traditionally refers to all the different kinds of living organisms within a given area. It includes organisms from large animals such as mammals to tiny, single-cell algae and underpins species interconnection, stability of ecosystem and evolutive complexity[1–4]. With less biodiversity, these connections weaken and sometimes even break down, harming species and impacting ecosystem functioning[5]. Ecosystems with high biodiversity are generally stronger and more resilient to regime shifts than those with fewer species. Higher biodiversity increases the capacity of an ecosystem to absorb disturbances and reorganize while maintaining essential functions and services[6,7].

Marine biodiversity is important to humans in many ways. Phytoplankton, algae, and plants, for example, are essential to life by largely contributing to oxygen production and the carbon cycle[8,9]. Marine species also provide food, bioproducts, medicines, and aesthetic benefits[10]. If biodiversity declines, these services could decrease, and with them human health and income[10–12]. Although the Earth's biodiversity is so rich that many species have yet to be discovered, many marine species are threatened with local extinction due to human impacts such as habitat destruction, overexploitation, effects of climate change, introduction and spread of invasive species, and pollution[13]. Assessing the role of human impact and environmental factors in determining the spatial and temporal effects on biodiversity is an essential task for the Ecosystem Based Management (EBM) approach[14]which allows for understanding the complex patterns and processes in the ecosystem and potentially protecting the largest number of species that are simultaneously under multiple threats[15]. A better understanding of this complexity and the multidimensionality of diversity operating at different spatial and temporal scales is, therefore, an important step towards an integrative ecosystem assessment[16].

Overfishing is one of the most worrisome disturbances on marine ecosystems across short temporal scales[14,17,18]. It affects fish populations and benthic assemblages by leading to changes in their size, abundance, and composition[19–21]. In intensely fished areas, especially where bottom trawling is practiced, the loss of demersal predatory biomass[19,22,23] and a severe decrease of long-lived species abundance[24] determines a reshuffle of trophic processes through direct and indirect effects[25–28] with a consequent alteration of biodiversity[19]. Despite the importance of biodiversity, its quantification through classical indices such as α- and β-diversity and direction

[1]National Institute of Oceanography and Applied Geophysics - OGS, Trieste, Italy. [2]Italian Institute for Environmental Protection and Research - ISPRA, Rome, Italy. ✉email: dagnetta@ogs.it

of changes in relation to human impacts, especially at large scales are quite limited all around the world[19,29]. This kind of assessment could be particularly useful for the Mediterranean Sea, where hotspots of biodiversity[30] could be loomed with high fishing pressure and climate changes[31–33].

Previous works on Mediterranean biodiversity generally focused on single habitats or local communities close to the coast. They were mainly based on abundance ranked counts by visual census[34,35]. At a large scale, the diversity of the Mediterranean has been investigated by using presence–absence maps of fish built on expert-based knowledge[36–38]reviewed through online databases of taxa diversity[39] or modelled by considering trophic relationships of functional groups and anthropogenic stressors[40].

An assessment based on standardized scientific monitoring at large temporal and spatial scales was rarely carried out due to the associated logistical difficulties and costs related to the collection of data at the species level. In one case, the biodiversity of demersal communities of continental shelf and slope has been explored by using datasets coming from the International Bottom Trawl Survey in the Mediterranean (MEDITS) program[41] until to the year 2012[42]. More recently, a similar evaluation, but at a smaller spatial scale, has been proposed in the Ionian Sea[43] and in the Balearic Sea[44] by examining β-diversity across the years 1994–2012 and 1994–2015, respectively. This kind of biodiversity evaluation at a regional scale along environmental gradients and impacting human activities, for the Mediterranean Sea, is lacking.

Studying how multiple factors may influence biodiversity can provide insights into marine conservation and spatial management and, particularly, can contribute to the implementation of the EU Marine Strategy Framework Directive (Directive 2008/56/EC, MSFD hereafter) process. The quantification of biodiversity changes in relation to covariates can help explain potential causes of declining biodiversity. Disentangling the effects of fishing from other sources of biodiversity variability, such as environmental variables, might support future management actions.

This work examined the spatial patterns of demersal assemblage biodiversity over seven years (from 2014 to 2020) in large areas of three Mediterranean subregions defined by the MSFD. Generalized additive mixed models were used to explain the spatio-temporal variability of biodiversity in relation to environmental covariates and fishing pressure. Based on data collected by the MEDITS program, we calculated α-diversity, measured as the Effective Number of Species[45] and the non-directional β-diversity following the approach by Legendre and De Cáceres[46]. Β-diversity is in direct correspondence with the variance of community structure[47,48]and its decomposition also allows for expressing the degree of uniqueness of a site (haul) with respect to a subregional average community. Moreover, to disentangle the effect of bottom trawling at the community and species level connected with changes in biodiversity, we focused on differences between two groups of hauls markedly different in terms of the fishing pressure.

Materials and methods

Area of study

In this study, we focused on the three Mediterranean subregions bordering Italy as identified by the MSFD: the Adriatic Sea (MAD), the Ionian Sea and the Central Mediterranean Sea (MIC), and the Western Mediterranean Sea (MWE) (Fig. 1).

MAD is very shallow and under the influence of intense lateral (river runoff and southward transport) and surface (wind and air temperature) stresses, and the northern basin represents the largest shelf area in the Mediterranean Sea[49]. The shelf floor is of sedimentary origin, and further from the shore, the mud gradually takes over, favoring the establishment of a community of muddy sands. From a fishery perspective, the Adriatic Sea is one of the areas in the Mediterranean with the highest number of operating trawlers and landings of demersal fish[50].

MIC subregion is an oligotrophic basin deeper than the Adriatic Sea and acts as an intersection for major Mediterranean currents[51]. The Ionian basin shows a complex geomorphology and biocenotic structure, especially along the Calabrian-Sicilian coasts, crossed by active canyons that transport materials from the break of the platform to the bathyal depth[52]. The Sicilian Channel is characterized by a two-layer exchange current system with an east-west gradient of inflows and outflows[53]. The shallowest offshore seabed, the Adventure Plateau, which is considered a biodiversity hotspot[54]is in the north-western sector and is stippled by several rocky banks[55]. The bottom trawling fleet is one of the most commercially important in the Mediterranean Sea and targets mixed assemblages of fish and cephalopods on the outer shelf and deep-water shrimps on the upper and middle slope[54].

MWE subregion is characterized by the presence of three main water masses and circulation structures[56]. The Tyrrhenian shores are characterized by the presence of a dense network of submarine canyons[57]while in the open sea submerged marine terraces and seamounts[58] contribute to the structural complexity of the regional marine system. The relatively small extension of the shelf makes this area denser in terms of trawlers among the Italian seas[50]; in addition to common target species (fish, cephalopods and crustaceans), the main target of bottom trawling is the red shrimp localized in canyons and accessible bathyal plains[59].

Data and analysis

Exploring patterns of diversity

To explore the pattern of diversity, we first calculated α and β-diversity indices from the data collected by the MEDITS program[41] across Geographical Sub-Areas (GSAs, Fig. 1). For each subregion, the analysis was performed on the biomass (bij) (Kg Km^{-2}) of the demersal species j per haul i (that is a single trawl operation, where a fishing net (trawl) is towed along the seafloor to collect samples of marine life), over the years 2014–2020 (Fig. 2). Species were retained based on the list used by Granger et al. (2015) and if they were present in more than 1% of hauls (cut-off) in each subregion.

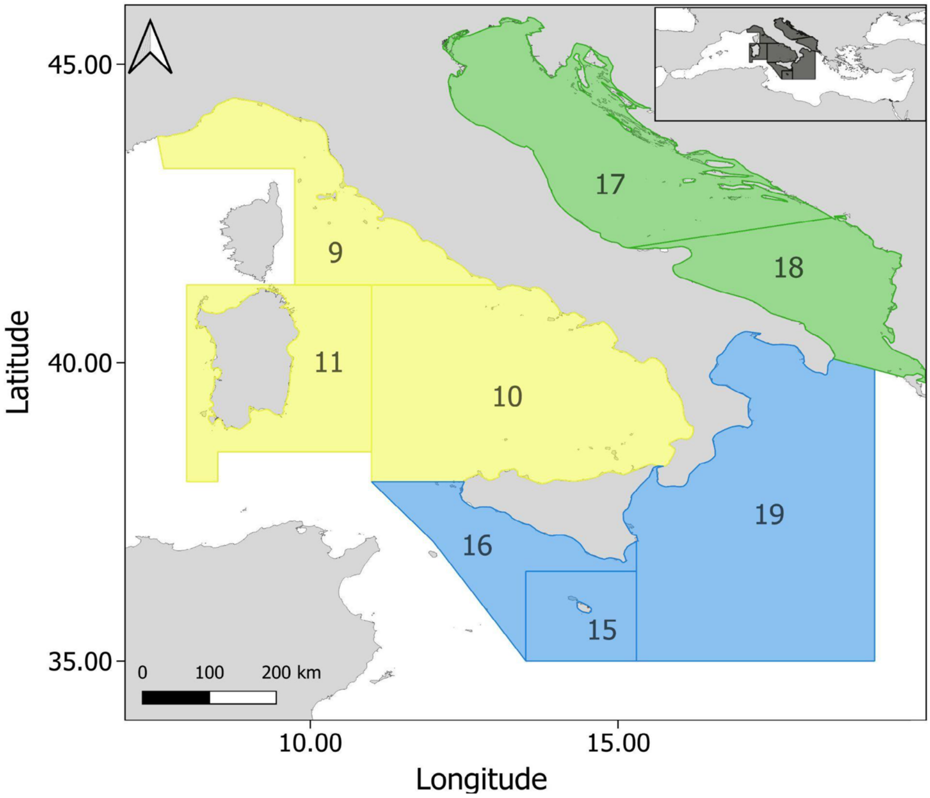

Fig. 1. Spatial domain of large portions of the three MSFD subregions. Data from GSAs 17 and 18 were used to represent the Adriatic Sea subregion (MAD). Data from GSAs 15, 16, and 19 were used to represent the Ionian Sea and Central Mediterranean Sea subregion (MIC). Data from GSAs 9, 10, and 11 were used to represent the Western Mediterranean Sea subregion (MWE). GSAs are the geographical subareas defined by the GFCM (General Fisheries Commission for the Mediterranean Sea).

For each haul, i the composition (proportion p) of the j species was calculated using the biomass data following Eq. 1:

$$p_{ij} = b_{ij} / \sum\nolimits_{j=1}^{n} b_{ij} \tag{1}$$

The choice to work with biomass rather than abundance has been guided by the fact that the MEDITS samples cover a wide range of sizes. Because of the power-law distribution of marine organisms[60]we expected to find a great number of small organisms. Thus, using biomass the community would have appeared more balanced in proportion between large (top predators) and small species (small pelagic fish).

Alpha diversity index

For each haul, we calculated the Hill number of order 1 (also known as Shannon entropy, H') on community composition as an index of α-diversity. Later, we transformed H' into the Effective Number of Species (ENS) as a more intuitive measure of diversity. Particularly, ENS is the number of species with even biomass that generate the same H' calculated (Jost et al. 2006). H' and the ENS α- diversity index were calculated following Eq. 2a and 2b using the < diversity > function of the R package < vegan.R>:

$$H_i' = -\sum\nolimits_{j=1}^{n} p_{ij} ln\, p_{ij} \qquad (2a) \qquad\qquad ENS_i = exp\left(H_i'\right) \qquad (2b)$$

Beta diversity index

To compute the total β-diversity (BD) of each subregion, we followed the method proposed by Legendre and De Cáceres (2013) that isthe biomass data were transformed using the square root of their proportions (Hellinger transformation). Then, the BD contributions were obtained by calculating the Euclidean distance from the average community profile $\sqrt{p_j}$ (Eq. 3a) and divided by the total variance $\sum\nolimits_{i}^{n}\sum\nolimits_{j}^{m} bd_{ij}$.

$$bd_{ij} = \left(\sqrt{p_{ij}} - \overline{\sqrt{p_j}}\right)^2 \quad (3a)$$

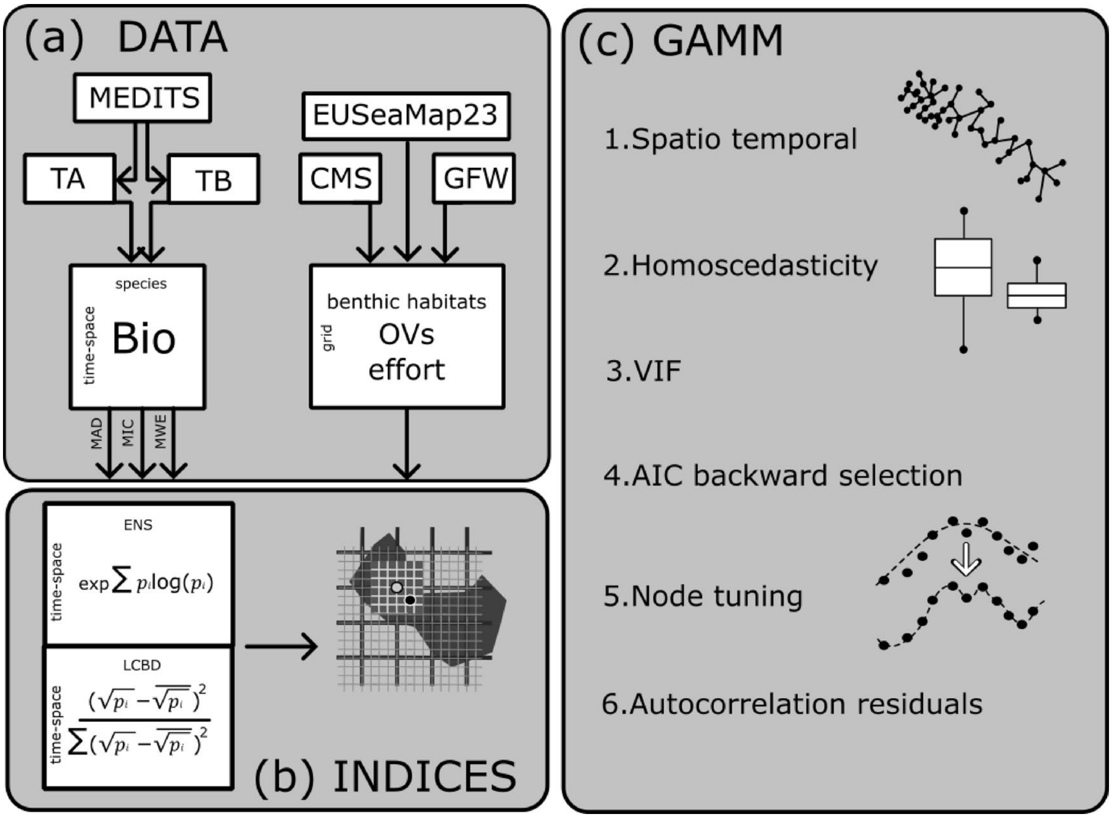

Fig. 2. Flowchart of **a**) data preparation, **b**) indices of α- and β-diversity used and **c**) steps of GAMM analysis.

For every haul i, the Local Contribution to β-diversity $(LCBD_i)$ can be calculated by summing the contribution of all species *m* for each haul, following Eq. 3b

$$LCBD_i = \sum_{j=0}^{m} \frac{bd_{ij}}{\sum \sum bd_{ij}} \qquad (3b)$$

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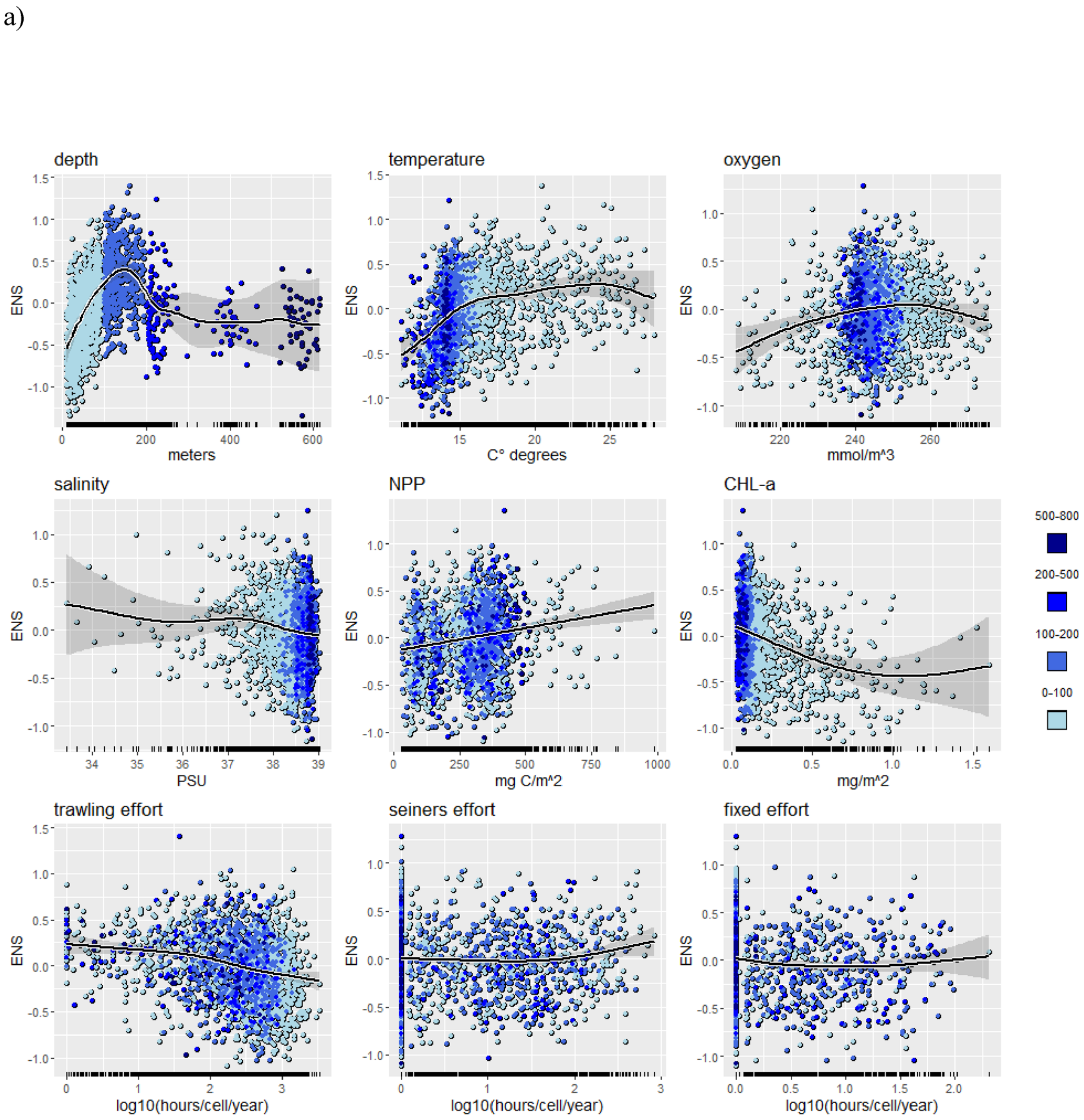
Generalized additive mixed model (GAMM)
To analyze the spatial and temporal patterns of diversity at the local scale (individual haul, ENS values, Supplementary Fig. 1, 2, 3) and understand why specific sites (hauls) exhibit greater uniqueness in species composition (LCBD values, Supplementary Fig. 4, 5, 6), we gathered data on habitats, environmental variables, and fishing activities (Fig. 2a).

Habitats
The benthic habitat data was obtained by a marine biotope classification map (EUSeaMap 2023 Broad-Scale Predictive Habitat Map for Europe) provided by EMODnet service (https://emodnet.ec.europa.eu/en; Montefalcone et al.[61]). The table of benthic habitats used in this study is reported in Supplementary Tables 1 and showed in Supplementary Fig. 7.

Ocean variables
Additionally, a series of relevant ocean variables for the marine environment were used (OVs - Fig. 2a Data panel and Supplementary Fig. 7). The OVs considered in this work are bottom temperature (tmp_bot in °C), bottom dissolved oxygen (oxy in mmol m^{-3}), bottom salinity (sal_bottom in PSU), integrated chlorophyll-a 0–200 m (chl in mg m^{-2}), bottom particulate organic carbon (poc_bot in mg m^{-3}), and integrated net primary production in the water column 0–200 m (npp in mg m^{-2}). OVs were extracted from the Copernicus Marine Service (CMS, https://data.marine.copernicus.eu/products*)* as estimated by the 3D coupled physical and biogeochemical model for the Mediterranean Sea with a horizontal resolution of 1/24°[62].

Fishing effort
Finally, several fishing effort activities (Supplementary Fig. 7) were added as covariates because of their well-recognized impact on demersal assemblages. Yearly fishing effort was obtained from the Global Fishing Watch service (GFW, https://globalfishingwatch.org/*)* in the form of hours of apparent fishing effort calculated from



b)

Fig. 3. GAMM analysis for the MAD subregion shows partial contribution of covariates (a) to α-diversity (ENS) and (b) to β-diversity (LCBD). The colors identify a depth stratum (0–100 m light blue, 100–200 m blue, 200–500 m shade blue, 500–800 m dark blue). Only significant covariates are shown.

the automatic identification system (AIS) with a horizontal resolution of 1/100°. The fishing activities considered were: trawling, seiners, fixed gears, and others (squid jaggers, dredges, trollers, drifting longlines, and pole and line). Each MEDITS haul point (black point Fig. 2b Indices panel) was then associated with the corresponding benthic habitats (dark gray shape Fig. 2b Indices panel) and the closest OV detection point (light gray point Fig. 2b Indices panel). Additionally, local fishing effort was associated with each MEDITS haul point. Since the two datasets did not match spatially, a square of 6/100° (cell = 36 km^2) centered on the OV detection point (dark gray square Fig. 2b Indices panel) was used to sum fishing effort.

The spatial and temporal distribution of diversity indices and their relationship with the variables gathered was studied through the application of a Generalized Additive Mixed Model (GAMM)[63] per subregion, considering a total of 1947, 1501 and 1997 hauls for MAD, MIC and MWE, respectively. Hauls covered a depth

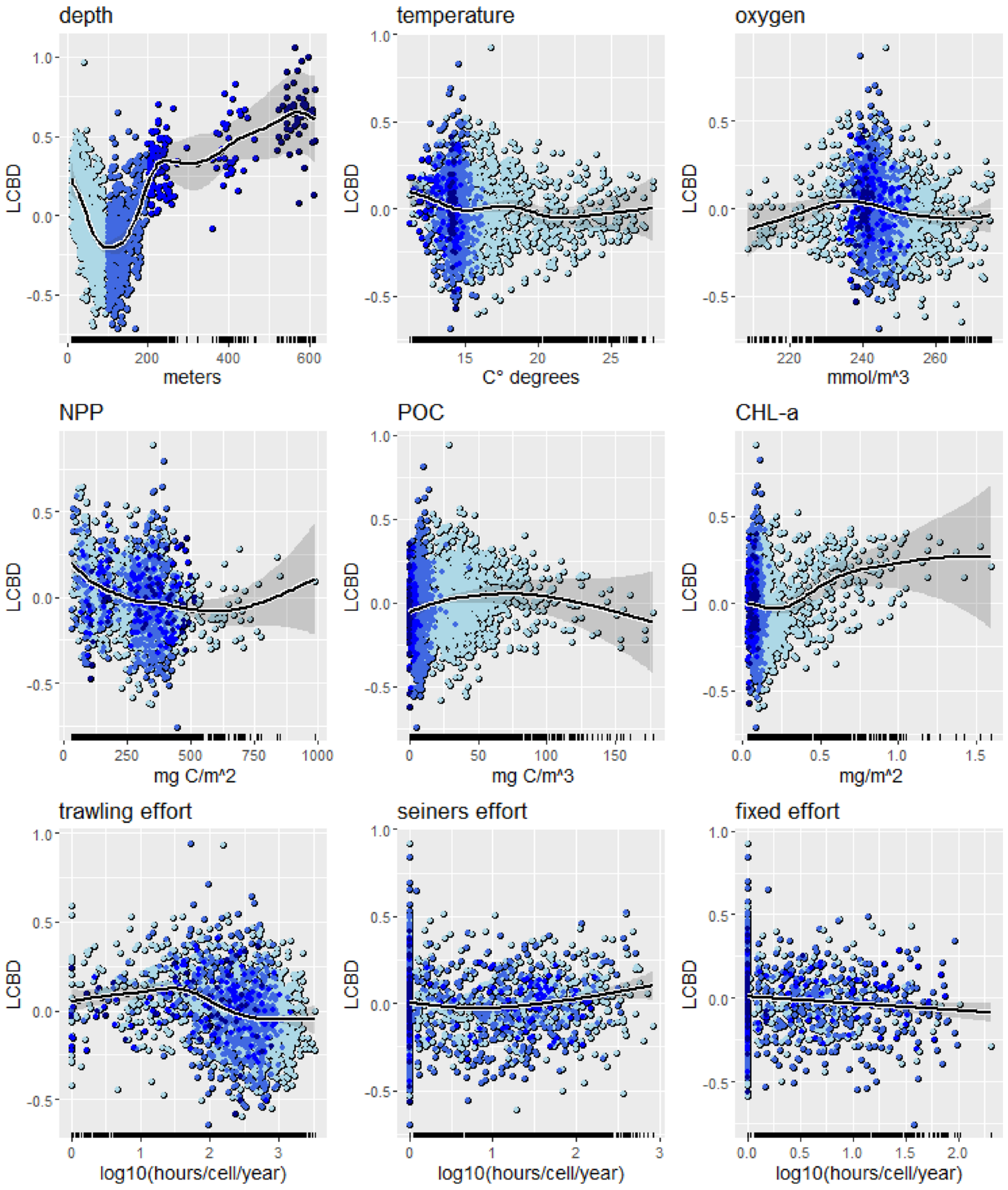


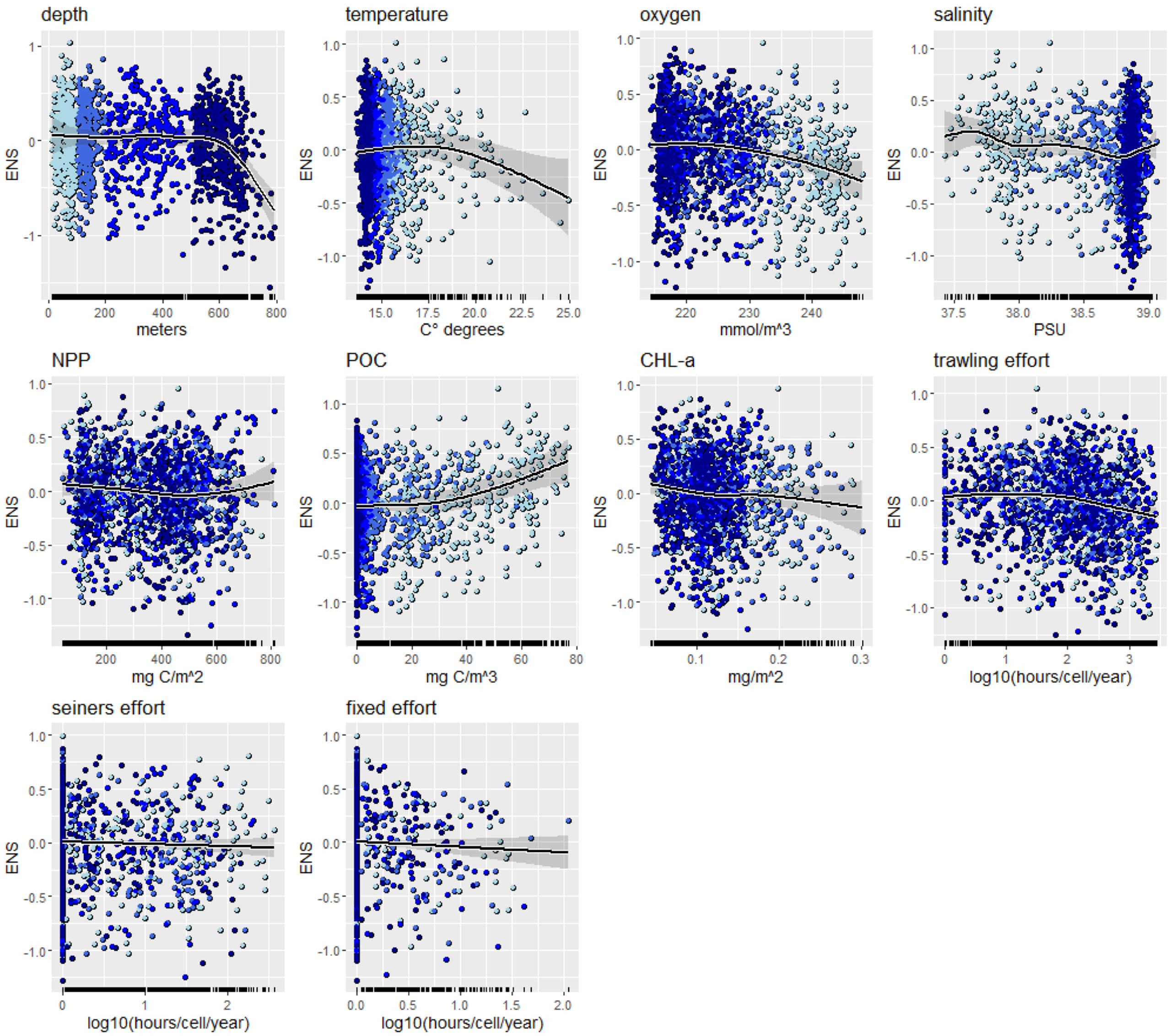
Fig. 3. (continued)

range between 10 and 800 m in all subregions. After preliminary analyses (Supplementary Fig. 8), the full model included a temporal factor (year), a spatial factor (benthic habitats), a set of covariates (depth, OVs, and the log effort of four fishing activities). Moreover, where the condition of homogeneity of variance (homoscedasticity - LeveneTest) of fixed factor was not respected, we added a random spatial factor (such as in the case of benthic habitats).

For each subregional model, the covariates (OVs + fishing effort) were checked for collinearity using their variance inflation factor (VIF) and definitively eliminated if no increase in the Akaike Information Criterion (AIC) was detected (Fig. 2c). Once any further simplification was possible, we determined the adequate number of nodes per covariate with the help of the gam.check function of the < mgcv.R > package. Finally, we checked for possible residuals' autocorrelation patterns by adding to the model a spatially defined Gaussian autocorrelation term and by visual inspection of the semi-variograms (Supplementary Final models section with Supplementary Figs. 9–11).

Given the continuous and strictly positive nature of the α- and β-diversity values, the distribution family used in the model was Gamma. Assuming a multiplicative effect of the covariates on the response variable, the link function chosen was the logarithm.

a)



b)

Fig. 4. GAMM analysis for the MIC subregion shows partial contribution of covariates (a) to α-diversity (ENS) and (b) to β-diversity (LCBD). The colors identify the assigned stratum. (0–100 m light blue, 100–200 m blue, 200–500 m shade blue, 500–800 m dark blue). Only significant covariates are shown.

Effects of bottom trawling on biodiversity

To assess the effects of bottom trawling we calculated biodiversity indices at the community and species level. We selected two groups of hauls that are largely different in the fishing pressure for each subregion and analyzed for differences in the biodiversity indices. The two groups were: low, the hauls impacted by less than 10 h of trawling during the year (effort < 10 h×cell^{-1}×year^{-1}) which is also corresponded approximately to the 10° percentile in the distribution of trawling effort and high, the hauls being trawled for more than 1000 h in a year (effort > 1000 h×cell^{-1}×year^{-1}), corresponding to about the 90° percentile.

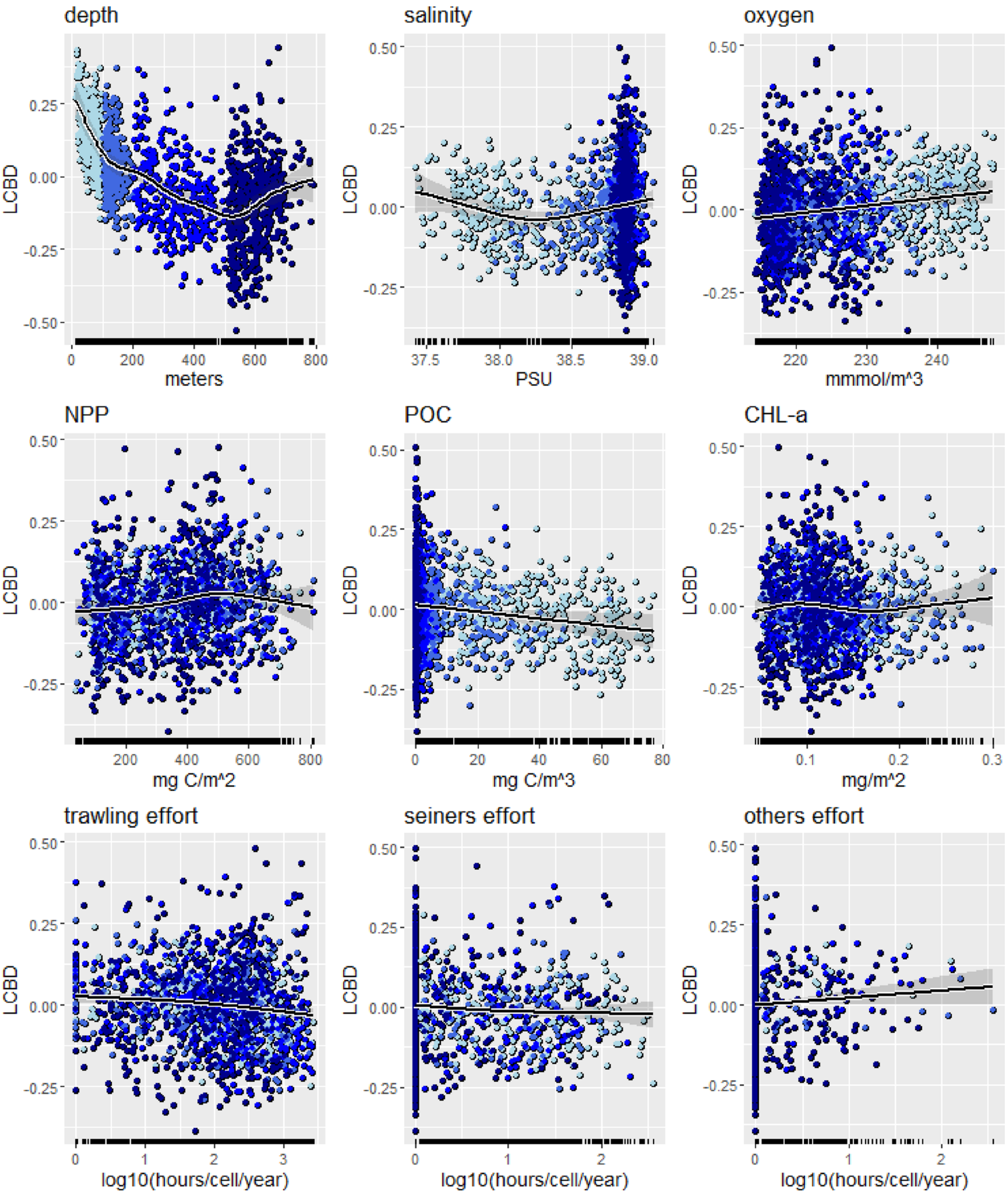


Fig. 4. (continued)

Community level
Differences between the two groups were first investigated at the community level by performing the analysis on the residuals of the GAMM model once the trawling was removed from the covariates pool. Pairwise tests on residual ENS (α index) and LCBD (β index), respectively, were conducted to test median differences between the two groups by the application of the non-parametric quantile test (QT)[64]. The QT was carried out using the quantileTest function of < EnvStats > package.

Species level
Differences between the two groups at species level were evaluated by using the IndVal index[65]which was calculated for each species using the untransformed biomass table (Fig. 2a). The index is given by the multiplication of two independent components: the fidelity and the specificity of species t in the group of hauls and has a range between 0 and 1 (package < indicspecies.R>). Finally, the statistical significance of the relationship between the species and each site group is tested using a permutation test with $p < 0.05$ for significance. In addition, we checked if among indicative species there were vulnerable and threatened species (https://www.iucnredlist.org/)

		Factors		**Ocean Variables**							**Fishing effort**			
		Year	**Benthic habitats**	**Depth**	**Temp**	**Oxy**	**Salinity**	**NPP**	**POC**	**CHL-a**	**Trawling**	**Seiners**	**Fixed gear**	**Others**
ENS	MAD	**2.61**	**4.55**	**4.26**	**2.10↑**	**0.63**	0.36↓	**0.50↑**		**0.84↓**	**2.25↓**	0.27	*0.33*	
	MIC	*1.55*	**3.64**	**4.03**	*0.52*	*0.71↓*	*0.30↓*	0.28↓	**1.15↑**	0.35	**1.45↓**	0.04↓	0.07↓	
	MWE	*1.21*	*1.01*	*1.00*	*0.10↓*	**1.55↑**			*0.21↓*		**1.04**			
LCBD	MAD	**5.84**	**8.49**	**27.76**	*1.34*	*1.45*		**5.26↓**	0.59	**1.87↑**	**7.61↓**	*1.13↑*	*0.66↓*	
	MIC	*0.89*	**3.80**	**12.44**		*0.69↑*	*1.25*	*0.98↑*	0.48↓	0.77	**1.32↓**	*0.47↓*		0.27↑
	MWE	*0.53*	**3.93**	**14.54**		**1.92↓**		*1.45↑*	**2.24**	*0.60↓*	**1.20↓**	*1.00*	*1.21*	

Table 1. Summary of the contributions of the covariates. The values represent the proportion of deviance explained for α- and β-diversity patterns for the three subregions. The arrows represent relationships that are: predominantly negative (down), predominantly positive (up), or non-linear. Missing values stand for covariates eliminated during the backward selection and not relevant for the final GAMM. The values are in italics and bold if the covariates were highly significant (p-value < 0.001), are instead in italics if they were significant (0.001<p-value<0.05), otherwise they are in roman if they were not significant (p-value > 0.05).

and their consistent difference between the two groups. Handling of data and all the statistical analyses were performed with R computing environment[66] and R Studio[67].

Results

Explaining patterns of biodiversity

After applying the cut-off, more than 100 species for each of the three sub-regions were retained. The complete list of species used in this study is presented in Supplementary Tables 2, and the position of the hauls is presented in Supplementary Figs. 1–6.

The MAD subregion was characterized by the lowest BD (0.67), while the MIC and MWE subregions had a higher degree of diversity (MIC = 0.79, MWE = 0.78). When considering the temporal distribution, both diversity indices did not show any clear trends in the three subregions, but some years were characterized by higher-than-average values (Supplementary Fig. 12).

The proportion of deviance explained depended on the subregion. For α-diversity, the model explained 39.8% of the total deviance for MAD, 21.3% for MIC, and 7.36% for MWE. When considering β-diversity, the models explained a greater portion of deviance. For the MAD, the proportion of deviance explained was the greatest (62.1%), followed by the MIC (53.3%) and the MWE (43.5%). The relations between ENS and LCBD and the covariates depended on which subregion is taken into consideration and a summary of the unique contributions of each covariate in explaining the total deviance is shown in Table 1.

For ENS, depth, trawling effort, and benthic habitats uniquely explain more deviance than other covariates. The effect of trawling on ENS was negative, while the effect on depth and benthic habitats was nonlinear. Among the OVs, only temperature and oxygen were always significant in explaining the α-diversity patterns. However, among the three subregions, there was no common pattern in the shape of the smoothing curves (Figs. 3a, 4a and 5a). Similarly, when considering LCBD, depth, benthic habitats, and trawling effort showed the most important and consistent pattern across the three systems, and again, the impact of trawling effort was mainly negative (Figs. 3b, 4b and 5b). The effect of depth on ENS and LCBD was always significant, but when compared inside the subregion, it appeared to show opposite trends between the two. This is not immediately evident from Table 1 since the patterns were non-linear. Yet observing the splines we can see for MAD that ENS peaked when LCBD was the lowest between 100 and 200 m (Fig. 3a and b). Similarly, in MWE the ENS was the lowest when the LCBD was the highest in the shallowest hauls (Fig. 5a and b). Among the OVs, four covariates were always significant in their contribution to the LCBD model (Chlorophyll-a, POC, NPP, and oxygen); also in this case, it was not possible to identify a common pattern for the OVs across the three subregions (Figs. 3b, 4b and 5b).

Bottom trawling effects on biodiversity

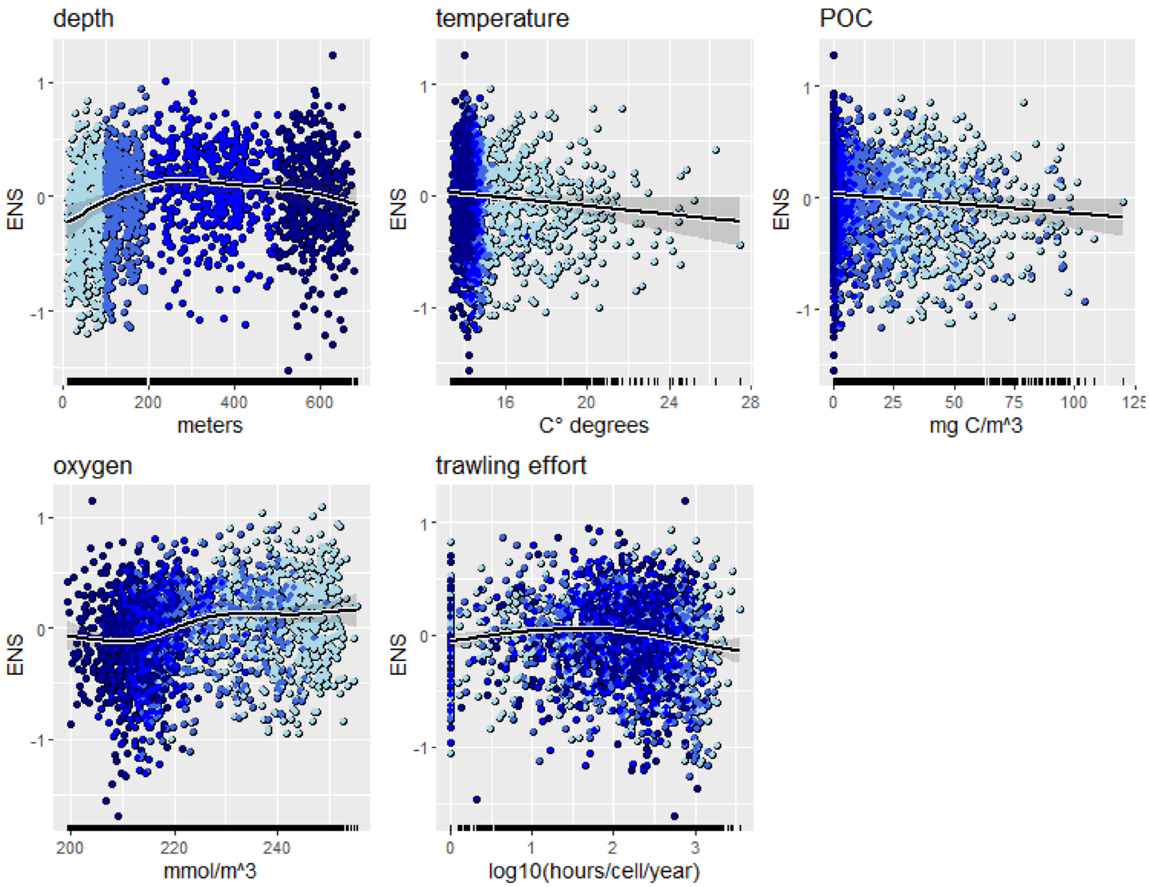
Considering hauls grouped by effort (high and low), quantile test shows that in each subregion, the median of both ENS and LCBD diversity at community level was always significantly higher in the low group, except for residual ENS in MWE (Supplementary Fig. 13).

In all the three subregions, the high group had a lower number of indicative species resulting from the INDVAL analysis with the permutation test (15 in MAD, 10 in MIC, and 21 in MWE, Fig. 6 and Supplementary Table 3) than the low group (44 in MAD, 39 in MIC, and 40 in MWE, Fig. 6 and Supplementary Table 3) and was generally composed of small fish and common cephalopods. Indicative species of the low group included several commercial species, species of higher body mass and rare species as well. Although vulnerable or endangered rays and sharks contributed little in biomass to the total community, they were almost exclusively and significantly higher in INDVAL, in the low group (Supplementary Table 3).

Discussion

Our results show that bottom trawling and environmental variables significantly affect biodiversity patterns in each of the three subregions studied. These effects are in addition to the expected effects of factors such as benthic habitat and natural variability that commonly characterize ecosystems over time (e.g., Pérès and Picard[68], Montefalcone et al.[61]).

a)



b)

Fig. 5. GAMM analysis for the MWE subregion shows partial contribution of covariates (a) to α-diversity (ENS) and (b) to β-diversity (LCBD). The colors identify the assigned stratum (0–100 m light blue, 100–200 m blue, 200–500 m shade blue, 500–800 m dark blue). Only significant covariates are shown.

Exploring patterns of biodiversity

We found that several environmental variables, specific for each subregion considered, play a role in explaining the variance of the diversity indices. Depth and oxygen always affect the variance of α-diversity (ENS) and β-diversity (LCBD) in all subregions, with depth making the largest contribution in terms of deviance. The role of depth as a structuring factor of abundance, biomass, and diversity has been demonstrated for many different taxa[43,69,70]. However, the relationship of biodiversity with depth does not always meet expectations[70]and it can appear in opposite directions depending on the taxonomic group studied and the diversity index used. For example, species richness derived from the total count of many taxonomic groups was overall higher in shallow waters than in deep waters in a previous work[71]. On the contrary, the β-diversity of fish and invertebrates in the Balearic was higher in deeper waters than in coastal waters[44].

Although we confirm that depth is a major factor for diversity, a smoothed, hump-shaped curve was observed, especially in the Adriatic subregion (MAD). In addition, the ENS and LCBD functions in each subregion showed an opposite concavity with a maximum near 150–200 m depth when viewed visually. Higher values of α-diversity (ENS) corresponding to hauls at the end of the continental shelf can be explained by a concentration of fish biomass of several species in this zone. A similar pattern of fish biomass was found by Katsanevakis et al. (2009) in a study on the distribution of demersal fish species in the Mediterranean Sea as a function of depth. The same ecological phenomenon may also explain why we found lower β-diversity values (LCBD) at higher ENS. Indeed, at 150–200 m depth, the hauls were more similar to the typical community taken as reference (i.e.

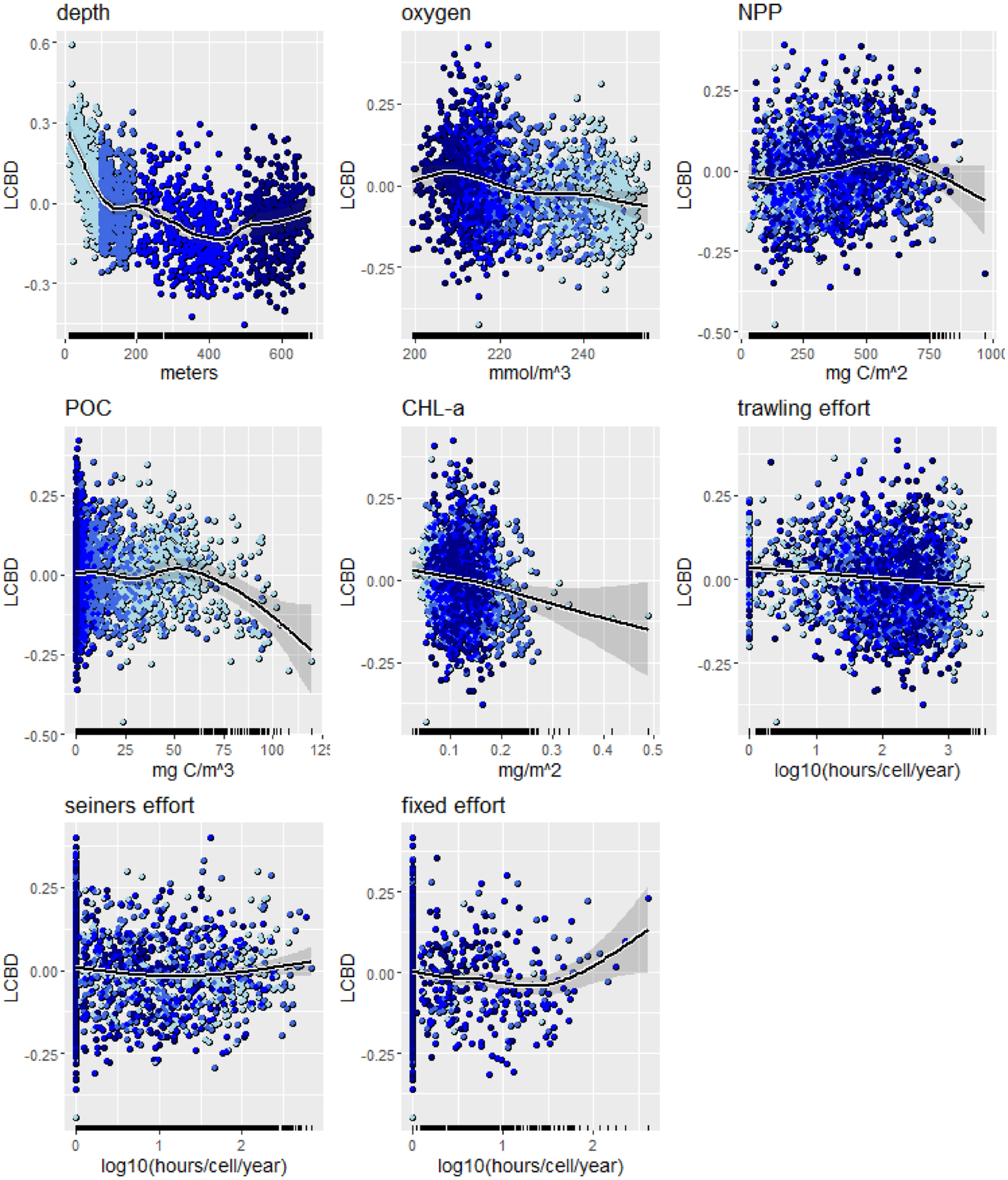


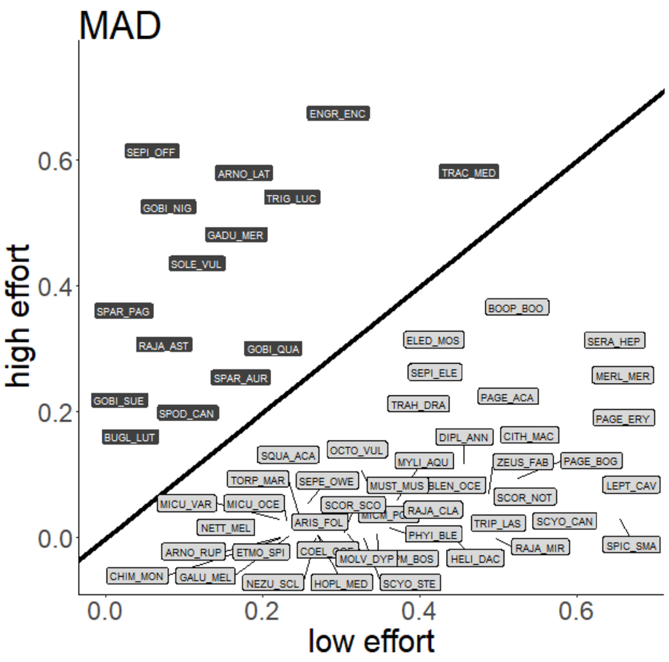
Fig. 5. (continued)

common species with an average biomass), making the species composition in the hauls more homogeneous (lower LCBD values).

The relationships between all the other environmental variables and biodiversity indices are mainly described by nonlinear functions with unclear directions between indices and specific patterns for each subregion. The variability of these environmental variables is generally high, but even if species can respond quickly, their specific behavior may not be reflected in the α- and β community indicators or may be masked in some way by the main variation at different scales, which is determined by more structuring environmental factors such as depth and benthic habitats or a combination of several variables. Further studies focusing on areas with different prevailing environmental conditions may help in assessing the effect of environmental variables on diversity indices.

Although fishing activities, such as seiners and fixed gear, significantly explain the variance in ENS and LCBD, only bottom trawling consistently has a negative quasi-linear impact on biodiversity indices in all subregions. For this reason, we focused further analysis on the relationships between bottom trawling and biodiversity.

a)



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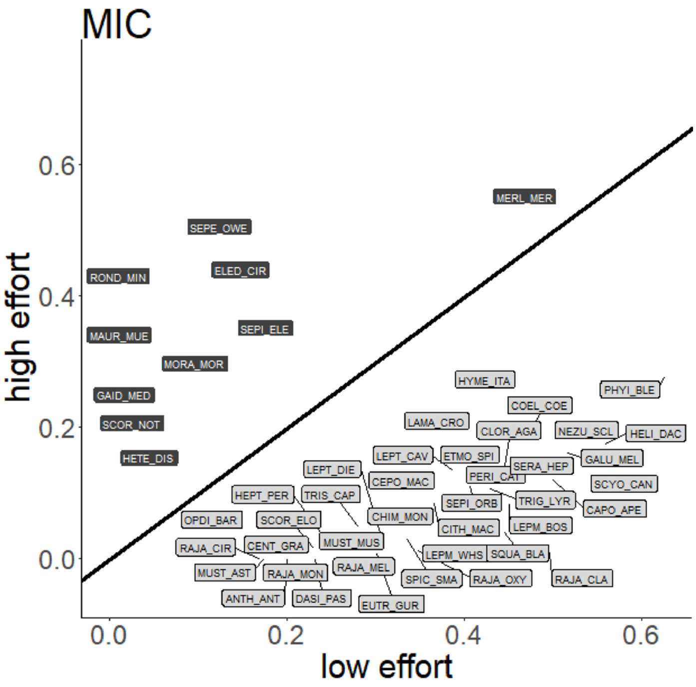

c)

Fig. 6. For each subregion (**a**) MAD, (**b**) MIC and (**c**) MWE, the displacement of the indicative species resulting significantly different in INDVAL (x, y axis) in the group with high (dark grey) and low (light grey) fishing effort, respectively. The full name of the species is in Supplementary Table 3.

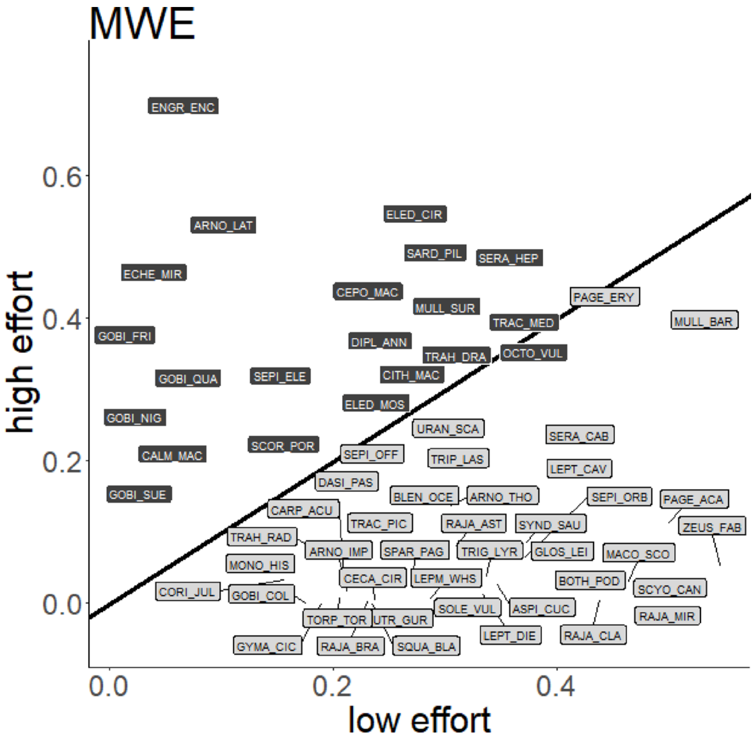

Fig. 6. (continued)

Bottom trawling effects on biodiversity

Although the importance of ecosystem-based management is increasingly recognized[15,33,72,73]there is little scientific evidence of the actual impact of fisheries on biodiversity indices for large oceanic systems and the Mediterranean Sea in particular. This is likely due to the impossibility of controlled experimental ecosystem manipulations and the lack of suitable time series or spatial replicates that allow experimental approaches[74]. However, some indirect evidence comes from visual fish counts in coastal marine protected areas[24,75].

By focusing on two groups of hauls that differ greatly in terms of fishing pressure and separating the effects of bottom trawling from the other variables, we were able to show that this fishing activity has a consistent negative effect at the level of individual hauls (ENS) and across hauls (LCBD) in each subregion. Although not always statistically significant, median α and β index values were lower in more heavily trawled hauls than in less heavily fished hauls. Similar results have been reported from the North Sea, where the direct and indirect effects of fishing were negative on biomass, species richness[76,77]and Rényi entropy[78]. In addition, K dominance curves used in other studies have shown that intensively fished areas are dominated by fewer species[79] and suggest analogy with our findings.

To date, the behavior of β-diversity indices in relation to anthropogenic stressors such as fishing and at the scales studied here has been little investigated. Only recently have authors demonstrated higher values of a directional β-diversity index between groups associated with site heterogeneity, particularly invertebrate composition, due to the high cumulative human impacts near the Spanish coast[44].

We found that hauls with a lower influence of bottom trawling have higher values of β-diversity (higher LCBD), i.e., these hauls are more unique and heterogeneous. Although high heterogeneity has been linked to low diversity in other systems[44]in our case, the heterogeneity characterizing the group of hauls less affected by bottom trawling is not ecologically negative. In fact, the indicative species (INDVAL) analysis shows a higher biomass of important commercial species such as hake, pandora, and red mullet in less impacted haul group.

It is widely recognized that bottom trawling reduces the biomass of demersal species by negatively affecting the abundance and size of species[19,33,77] and could promote a prey release[80]. Small pelagic fish and cephalopods may have surged in abundance due to a reduction in predation pressure by resulting as indicative species in the higher trawled hauls.

Our results indicate that sensitive species such as rays and sharks, although with low absolute biomass, are more likely to occur in less trawled hauls. In the North Sea, the impact of fishing was limited to inducing decreases in the abundance of species that have slow life histories and are particularly vulnerable to exploitation[81]. This suggests that also changes in the biomass of vulnerable indicator species may also provide a measure of the impact of fishing.

Several studies carried out in the Mediterranean Sea have investigated the distribution of α-diversity measures to determine spatial variation of biodiversity[82]. In this study we found that α-diversity is significantly affected by environmental variables and fisheries although it was difficult to define common relationships between α-diversity and OVs across subregions. In particular, the ENS as a measure of α-diversity has shown relationship with temperature and oxygen in all subregions analyzed. However, the explained deviance of models relating ENS to OVs and effort was very low in some cases thus suggesting very low predictive capacities.

Conversely, models relating β-diversity and covariates were performing better in terms of explained deviance (around 50%). The β-diversity index here used reflects community composition relative to a sub-regional average and resulted very useful in identifying how unique places are related to covariates especially to bottom trawling.

Overall, both α- and β-diversity resulted higher in less disturbed areas, possibly indicating where communities are more stable and resilient[83]. Our findings evidence the prominent negative role of bottom trawling with respect to other fishing activities in driving biodiversity of demersal communities. Pollution[84]nutrient enrichment[85] and invasive species[86] have been shown to have detrimental effects on species richness and biodiversity, especially near the coasts. Although further studies need to explore the potential role of these factors and other stressors once large dataset became available and more investigations must be done to develop a clear reference value, the characterization of α- and β-diversity in relation to covariates at the large scales here used represents a step towards the development of conservation and management strategies, particularly in the context of the Marine Strategy.

Data availability

The datasets supporting this article are within the paper or have been uploaded as part of the Supplementary Material. Raw MEDITS data can be found at the Joint Research Centre Data Catalogue (https://data.jrc.ec.europa.eu/dataset/f25092c4-3f0f-449f-ba60-5fbfe385defc).

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Author contributions

DA, SR and SL conceptualization, DA wrote the original draft, DA and IV fromal analysis, all authors revised and edited the paper.

Declarations

Competing interests

The authors declare no competing interests.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethics statement

The authors were responsible for correct and appropriate use of the data with regard to scientific ethics.

Additional information

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Correspondence and requests for materials should be addressed to D.A.