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A functional trait-based approach to disentangle trawling disturbance on bentho-demersal assemblage composition: Evidence from a heavily exploited fishing ground (South-central Mediterranean Sea)

Gabriele Di BONA[1], Manuel BERLINO[2,3], Gianluca SARÀ[1,3], and M. Cristina MANGANO[2,3]

[1] Laboratory of Ecology, Department of Earth and Marine Science (DiSTeM), University of Palermo, Palermo, Italy
[2] Stazione Zoologica Anton Dohrn, Dipartimento di Ecologia Marina Integrata, Sicily Marine Center, Lungomare Cristoforo Colombo (complesso Roosevelt), 90142 Palermo, Italy
[3] NBFC, National Biodiversity Future Center, Piazza Marina 61, 90133 Palermo, Italy

Corresponding author: Gabriele Di Bona; gabriele.di.bona16@gmail.com

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Abstract

Trawling along continental shelves causes severe disruptions to benthic communities by altering sedimentary compositions and increasing species mortality, thus favoring opportunistic species over long-living, ecologically important ones. This study was carried out in the southern Strait of Sicily, a highly exploited fishing ground, using a trait-based ecosystem approach to assess the impacts of trawling in sandy and muddy sediments. The intensity of fishing here, measured by the swept area ratio (0.36-37.37), has exhibited a gradient from coastline to offshore, peaking along the eastern continental shelf. Surveys, being part of studies, captured 8191 individuals from 103 species (70% demersal). Demersal species' density decreased with fishing intensity but increased with temperature, while benthic species density correlated positively with temperature and chlorophyll concentration. Taxonomic diversity was unaffected by fishing intensity but driven by chlorophyll, negatively for demersal species and positively for benthic diversity. Functional diversity showed no significant variation. Multivariate analysis explained limited variance in taxonomic and functional composition, highlighting the homogenization of benthic communities due to chronic trawling and bathymetric variation. Assemblages in this study reflected long-term exploitation, favoring opportunistic species and masking functional adaptations to fishing and environmental gradients. These findings emphasize the subtle yet significant impacts of chronic disturbances on benthic ecosystems, underscoring the value of trait-based analyses for assessing ecological responses in highly exploited zones.

Keywords: trait-based approach; traits; functional diversity; taxonomic diversity; bottom trawling; Mediterranean Sea.

Introduction

Trawling is a highly scattered fishing activity, predominantly concentrated along continental shelves worldwide (Amoroso *et al.*, 2018), causing various direct and indirect effects on benthic communities. The nets used in trawling alter sedimentary composition (Collie *et al.*, 2000; Puig *et al.*, 2012) and increase mortality rates of numerous species, reducing biomass and abundance compared with undisturbed conditions (Hiddink *et al.*, 2006). Chronic trawling can significantly alter community composition and structure (de Juan *et al.*, 2007; Howarth *et al.*, 2018), favoring opportunistic and scavenger species, while negatively impacting long-living species with crucial ecosystem roles, such as suspension-feeders and structuring species (Tillin *et al.*, 2006; Mangano *et al.*, 2013; Hiddink *et al.*, 2019).

Estimating variations among the abundance of target species is vital for characterizing trawling impacts. However, an ecosystem-based approach is increasingly necessary in order to understand the broader influences of this disturbance on all community components, focusing on their roles within the ecosystem. By examining what organisms do within their ecosystem rather than just their taxonomic identity, Trait-Based Approaches (TBA), for example, offers significant insights into benthic assemblage functioning (de Juan *et al.*, 2007; de Juan *et al.*, 2022). TBA applied to marine benthic data have enhanced our understanding of changes in benthic functioning along environmental gradients (Tillin *et al.*, 2006; Bolam *et al.*, 2014; Howarth *et al.*, 2018). These approaches are based on the theory that species coexist by shaping their niche according to adaptations to environmental conditions, which can be described by individual measurable characteristics (functional traits) linked by definition to their performance, survival, and ecological role (Violle *et* *al.*, 2007). Therefore, some of those characteristics could be used as response traits to determine species sensitivity or resilience to environmental changes and anthropogenic disturbances.

Understanding the effects brought about by trawling on the great variety of bentho-demersal communities is essential to design and inform effective fisheries management and sustainable resource exploitation plans (Eayrs *et al.*, 2020; McConnaughey *et al.*, 2020). Community responses to trawling can vary and are based on gear type, habitat, and fishing behavior/history (Sciberras *et al.*, 2018), necessitating a clear definition of relationships between disturbance, species, and environmental conditions. Many studies compare frequently trawled areas with less trawled ones (Hiddink *et al.*, 2017), revealing a clear negative impact of fishing disturbance. However, many fishing grounds exhibit highly heterogenous and patchily distributed disturbance gradients, influenced by time and spatial scales of observation (Mangano *et al.*, 2017; Amoroso *et al.*, 2018; Ferrà *et al.*, 2018).

In the Mediterranean Sea, trawling predominantly affects the continental shelf up to about 200 meters and decreases offshore (Mangano *et al.*, 2014; Mangano *et al.*, 2015; Eigaard *et al.*, 2017; Ferrà *et al.*, 2018). Bottom trawlers, and their main operating gear, are poorly selective. They cause a hugely negative impact on a wide range of species, including those prioritized for conservation (FAO, 2020). The Strait of Sicily, a zone of high biodiversity (Coll *et al.*, 2012), hosts one of the largest fishing fleets in the Mediterranean, including the Mazara del Vallo fleet and fleets from Libya, Malta, and Tunisia (Farrugio & Soldo, 2014). This region has suffered from a long history of exploitation, making multi-year management plans crucial for safeguarding demersal stocks, especially for key species like deep-water rose shrimp (*Parapenaeus longirostris*) and European hake (*Merluccius merluccius*). These plans are promoted by international organizations, such as the General Fisheries Commission for the Mediterranean (GFCM), and implemented at the national level (GSA 16 Management Plan 2018-2020).

Several studies have assessed the effects of disturbances that fishing caused on bentho-demersal assemblages in the Strait of Sicily (Gristina *et al.*, 2006; Dimech *et al.*, 2012; Milisenda *et al.*, 2017; Agnetta *et al.*, 2019). Nevertheless, there is limited information from the easternmost area, the Malta bank, which has an extensive continental shelf. This study aims to explore the impact that fishing disturbances have on bentho-demersal assemblage composition by utilizing data from fishing surveys conducted along the continental shelf between Portopalo di Capo Passero (Sicily) and Malta.

Specifically, this study employs a numerical approach to analyze the composition relating to the abundance of sampled benthic assemblages, using it as a proxy for community composition along environmental and fishing intensity gradients. By considering a coast-to-offshore gradient, the study captures the full range of variability in these potential covariates.

In addition to examining community compositions, the study assesses the effects brought about by trawling as also natural disturbances on the functional structure of the assemblage, using biological traits that reflect community responses to fishing pressure. To gain a more comprehensive understanding of how these gradients influence the condition of communities, community composition was complemented by the estimation of key community metrics, such as diversity indices. Thus, this contributes toward providing additional insights of ecosystem changes along the investigated gradients. Combining taxonomic and trait analysis provides a comprehensive understanding of the interaction between anthropogenic and natural disturbances in shaping community structure, especially in intensely trawled areas like the one under investigation. Our outcomes provide insights into an ecosystem approach to fisheries for a central area into the Mediterranean basin.

Methods

Study area

The study area encompasses the continental shelf extending between Malta and the southernmost area of Sicily. This includes Portopalo di Capo Passero (36.68611° N, 15.13611° E), as a part of the Malta bank (Fig. 1). This shelf is characterized by sand and muddy sediments, and moderate to a strong current with kinetic energy [EMODnet data; (Martin Miguez *et al.*, 2019)]. This plays host mainly to Mediterranean biocenosis of coastal and shelf-edge detritic bottoms (A5.46, A5.47 of EUNIS classification). A small area on the northeast of Malta is characterized by Coralligenous habitat [A3 of EUNIS classification; (Bialik *et al.*, 2022)]. As a part of the Sicilian-Tunisian platform, the seafloor bathymetry of the area varies very little ranging from 50 m to 150-200 m, approximately.

This area is bountiful for trawling due to its high productivity and biodiversity (Coll *et al.*, 2012). Bottom trawlers show a high variability in the exploited fishing areas, which may change during the same day from the continental shelf to the middle slope, up to 700 m depth. Trawler hauls are characterized by a vast number of species of fish, crustaceans, and molluscs in various commercial categories. The area hosts Portopalo di Capo Passero fishing fleets which account for 4% of the gross tonnage at Sicilian ports (Popescu, 2010), which are mainly focused on deep-water rose shrimp (*Parapeneus longirostris*) catches. These trawlers operate mainly on short-distance fishing trips, which range from 1 to 2 days out at sea, with fishing taking place on the outer shelf and upper slope (Farrugio & Soldo, 2014). Moreover, this area, being located between the General Fisheries Commission for the Mediterranean Geographical Subarea (GSA) 15 and 16, is often overshadowed by information coming from the fleets operating in the Adventure Bank area (GSA 16), and from the fleets associated with the island of Malta (GSA 15). However, it is located near potential spawning and nursery grounds of *P. longirostris*

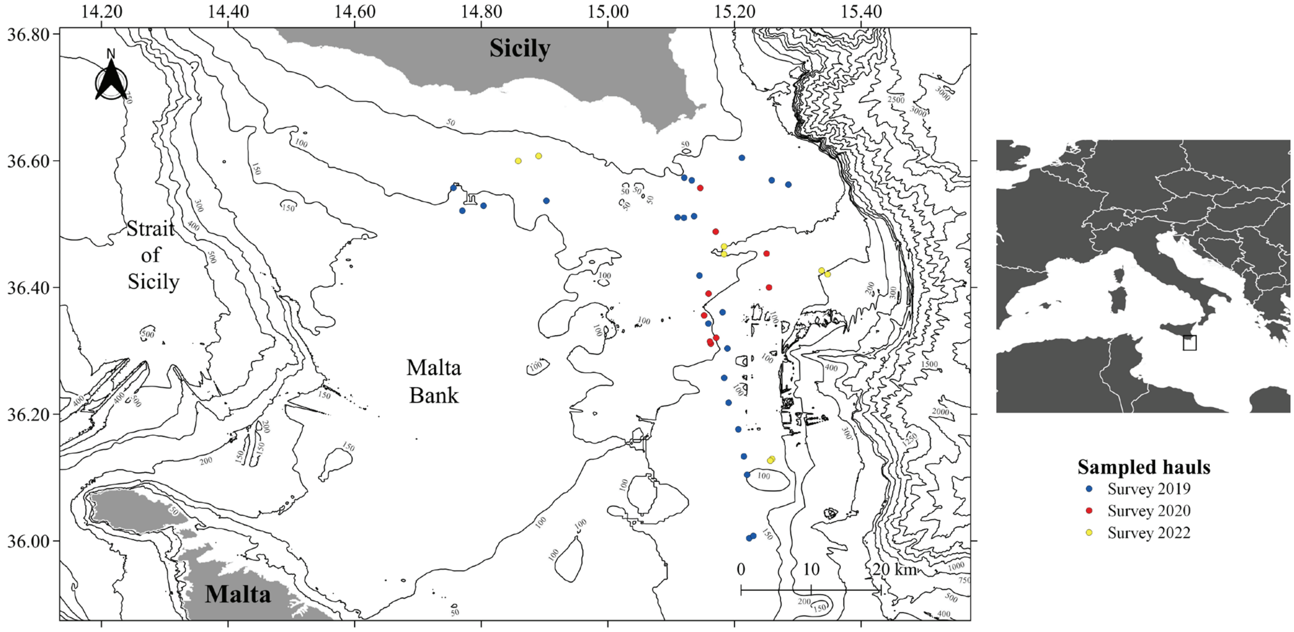

Fig. 1: Study area with main isobaths and sampling hauls done during the three fishing surveys. The dots shown are the average between the starting point and the ending point coordinates of each haul.

and *M. merluccius*, and high-density distribution of demersal species of high economic interest locally, such as *Mullus barbatus* (Linnaeus, 1758), as well as being characterized by intense trawling near the coast (Farrugio & Soldo, 2014; Fiorentino *et al.*, 2017), further proving the importance of increasing ecological knowledge of the inhabiting benthic-demersal community.

Fishing intensity and fishing surveys

Fishing activity undertaken by the trawling fleet around the area was estimated using the open-source fishing effort Automatic Identification System (AIS) data at 100th degree resolution available from (Global Fishing Watch, 2022) for the period 2016-2020. The study area was divided into a raster grid of 1 km^2 cell size. Based on this, Swept Area Ratio (SAR) was calculated and used as the indicator of fishing intensity (Amoroso *et al.*, 2018) which represented the total area swept by trawl gear over a defined time period (usually 1 year) divided by the total seabed area at a defined spatial scale (the grid cell). First, aggregated satellite daily data was filtered to consider only signals linked to trawling activity and assigned to the corresponding cell. Owing to the absence of information regarding vessel size and engine of each vessel signal, an average Mediterranean otter door width of 89.89 m and trawling speed of 2.9 knots was extracted from (Sala *et al.*, 2019) and (Eigaard *et al.*, 2016), respectively, and used in accordance with the number of signals per cell to calculate the swept areas per cell. Swept areas belonging to the same cell were summed and then divided by the area of the cell to obtain the ratio. An annual average raster of the period 2016-2020 was used to extract SAR information to link to the sampling hauls. Although SAR data span from 2016 to 2020 and do not perfectly match the sampled period, spatial patterns of trawling effort have been shown to be relatively stable over time (Jennings *et al.*, 2012), therefore, it is reasonable to assume that, despite differences in absolute values, the observed fishing intensity gradient in the available dataset is also reflected in the later years.

Catches and bycatch data analyzed in this study were collected from three fishing surveys conducted along the study area. These samples were collected in May 2019, July 2020, and July 2022 (hereafter referred as HCP1, HCP2, and HCP3), falling within the actions conducted in the framework of two INTERREG Italy-Malta projects (respectively “HARMONY” Operational Program call n. 01/2017 and “SenHAR” Operational Program call n. 02/2019) co-funded by the European Regional Development Fund. A 17.9 m long and 27 ton commercial otter trawler (distance across the mouth of the net 40 m, headline height 1.7 m, and legal codend mesh size) was deployed for the sampling activity. For every trawl, a standard vessel speed of 5.56 km/h (3 knts) was selected. A total of 40 trawls were carried out during the three surveys along the bathymetry and fishing intensity gradients that proceed orthogonally from the coastline (following the local fishing behavior). Each trawl was assigned to a fishing intensity value through overlapping fishing routes to the average fishing intensity raster; then, the total distance for each single trawl was measured. For each of them, the distances of trawl passing through each raster cell were taken and converted into relative frequencies, dividing their value by the total distance of the corresponding trawl. Each relative frequency was then multiplied by the intensity value of each corresponding cell in order to obtain a weighted average, representing overall, the average value of the area involved in each catch. The bathymetry and coordinates of all the trawls were recorded on board through the vessel’s GPS and echo sounder, and validated through QGIS and EMODnet DTM rasters. For each trawl, a subsample of the total catch was collected including commercial and by-catch species and considered as a proxy of the composition of the community. Due to the well-known reported high presence of the deep-water rose shrimp (*Parapenaeus longirostris*) in all the catches specifically more abundant in Sicilian trawled fishing grounds; (Milisenda *et al.*, 2017), the species was removed from the analysis in order to avoid that occurrence dominance of this species masked and flattened the response of the remaining fraction of the assemblage. Once landed, the samples were frozen and transported to the Laboratory of Ecology (University of Palermo, Italy) for taxonomic identification and measurement. The total wet weight and number of individuals of each species of the hauls were estimated. To reduce possible bias that may be linked to the different durations, and therefore, different lengths of the hauls, and to reduce the effect of rare and dominant species in the dataset, abundances were transformed with Hellinger transformation (Legendre & Legendre, 2012) prior to analysis. To discern what domain of the targeted assemblage is more affected by trawling, each species was assigned to the "demersal" or "benthic" category. The demersal category accounted for all fish species and mobile invertebrates (e.g., shrimps and cephalopods) that interact with the seabed. These were often considered the primary targets of fishing activities in the study area and, more in general, by otter trawls in the Mediterranean Sea. In contrast, the benthic category encompasses most invertebrates inhabiting the seabed with lower mobility, which are frequently treated as nontarget bycatch by fishermen as accidentally caught in the net.

Diversity indices assessment and statistical analysis

After taxonomic identification of catches, four different diversity indices species richness, Shannon-Wiener's Index, Simpson's Index (1-D), and Pielou's evenness Index; (Magurran, 20130] were computed using R package vegan (Oksnaen *et al.,* 2019) for each sample (haul), to assess assemblage taxonomic biodiversity of the benthic and demersal domains. Species richness gives a count of species, but Shannon-Wiener and Simpson's indices consider both richness (number of taxonomic units) and evenness (distribution of individuals among units), helping to assess community structure more comprehensively. Pielou's evenness Index further refines this understanding by highlighting how evenly individuals are distributed among species.

A collection of five biological traits describing species characteristics related to life history and behavior were selected as response traits to account for the possible effects of fishing activity and environmental variables on functional response of benthic-demersal assemblages (Table 1). Even though there are no objective criteria on selecting which are the most suitable response traits (*sensu* Violle *et al.*, 2007) linked to fishing disturbance, the aforementioned traits are commonly used in literature to assess effects on marine benthic community (van Denderen *et al.*, 2015; Bolam *et al.*, 2017; Foveau *et al.*, 2017; Ocaña *et al.*, 2019; de Juan *et al.*, 2020), and their information is easier to obtain in open-source online databases. Each trait was divided into fuzzy coded modalities, spanning from 0 to a maximum sum of 1, according to

Table 1. Biological traits and their modalities selected for the study.

Trait	Modalities
Maximum size	● <1 cm (L_1) ● 1-2 cm (L_1_2) ● 2-10 cm (L_2_10) ● 10-20 cm (L_10_20) ● 20-50 cm (L_20_50) ● >50 cm (L_50)
Longevity	● < 1 year (T_1) ● 1-3 years (T_1_3) ● 3-10 years (T_3_10) ● >10 years (T_10)
Egg development location	● Asexual/budding (edAsex) ● Sexual – pelagic eggs (edPel) ● Sexual – benthic eggs (edBen) ● Sexual – brood eggs (edBrood)
Mobility	● Sessile (mSess) ● Swim (mSwim) ● Crawl/creep/climb (mCrawl) ● Burrowers (mBurrow)
Feeding mode	● Suspension (fSusp) ● Surface deposit (fSurf) ● Sub-surface deposit (fSubsurf) ● Scavenger/opportunist (fScav) ● Predator (fPred)

the information found on the source databases to obtain a taxon-by-trait matrix (Supplementary material M2). According to this, each modality represents the proportion expressed by a species for that specific trait. The obtained matrix was combined with Hellinger-transformed species abundance-by-sites matrix in order to calculate the community-weighted means (CWM) of each trait and a set of five functional diversity indices: Functional richness (F.Rich), Functional evenness (F.Eve), Functional divergence (F.Div), Functional dispersion (F.Dis) and Rao's index (Rao). Similarly to taxonomic diversity indices, these are the ones that provide information about the range of trait expression (aspect of richness) and the distribution of such traits in the community (aspect of evenness). F.Rich measures the range of functional traits within a community by assessing the volume occupied by a species in its trait space; F.Eve measures how evenly species and their traits are distributed in functional space; F.Div assesses how species traits are distributed around the mean trait value, indicating niche differentiation, while F.Dis measures the spread of species in its trait space, considering both richness and abundance. Finally Rao integrates both species abundance and pairwise functional trait differences, offering a comprehensive view of functional diversity. CWMs for categorical traits data, as they are accounted in this study, represent the percentages of a given modality of the trait in a community, while the indices encompass three different components of functional diversity: richness, evenness, and divergence (De Bello *et al.*, 2021).

Multivariate tests were used to test for differences in measured species abundances (as number of individuals and biomass) and CWM values between hauls of different fishing intensity values. To test and eventually disentangle the influence of other natural variables, bathymetry (m), bottom temperature (°C), bottom dissolved oxygen (mmol/L), chlorophyll concentration at the sea bottom (mg/m3), seabed shear stress due to the currents (N/m^2), and seabed slope (°) assigned to each trawl were considered (Table S1; environmental variables were downloaded from Copernicus and EMODnet databases and assigned to each trawl with the same method applied for SAR).

Before the analysis, the correlation of the aforementioned variables was checked in combination with the spatial autocorrelation of hauls through Moran's I index (Moran, 1984). Furthermore, to highlight if hauls changed with the environmental variables, a k-means clusterization (number of clusters = 2) and a Principal Component Analysis (PCA) were applied. The distribution of total and single taxa abundances, CWMs, taxonomic diversity and functional diversity indices along the variables and in space, was visually inspected as well for both the domains. To investigate whether survey year and sampling month had a significant effect on abundance composition, a PERMANOVA was performed, followed by a PERMDISP analysis (using year and month as explanatory factors) to assess the assumption of homogeneity of variances within groups. Finally, the dominant species for each domain was individuated through Berger-Parker's dominance Index (Magurran, 2013). These preliminary assessments were done to help to visualize similarities between samples and assist statistical result interpretation underlying which were covarying variables the most with assemblage structure.

We needed to see if fishing intensity and the other variables affected catch assemblage (benthic and demersal) taxonomic composition. For this purpose, a redundancy analysis (RDA) was performed with Hellinger-transformed data and standardized [mean equal to zero and s.d. (standard deviation) equal to 1] environmental variables associated with the sampled hauls. Following the first RDA, a forward stepwise approach was applied to select the main variables leading to the variability of the assemblage, and to reduce collinearity issues among them. The latter variables were then included in a partial RDA with latitude and longitude coordinates of the hauls as a conditioning factor. This was done in order to isolate the effect of the variables from the effect accounted by the spatial distance of the samples. The same approach was also applied on computed benthic and demersal CWMs to check the effects on functional composition. The effects of variables on taxonomic and functional diversity indices and on total densities were explored with a linear regression model. This was performed after checking the assumptions of normality of the residuals and homoscedasticity through Shapiro-Wilk normality and Breusch-Pagan tests, respectively. When normality was violated, a linear model with permutation was applied, while in the case relating to heteroscedasticity, the regression models were performed using heteroscedasticity-consistent standard errors through R package sandwich (Zeileis, 2004; Zeileis *et al.*, 2020). Statistical analyses were conducted using the R package, Version R-4.2.0 (R Core Team, 2022).

Results

Fishing intensity around the study area showed a gradient from coastline to the offshore zone with higher concentration along the eastern margin of the continental shelf (Fig. 2). SAR values spanned from 0.36 to 37.37 with an average ± s.d. value of 9.86 (±7.60). Owing to the topographical structure of the area and to the sampling design reflecting the local fishing behavior, all considered variables showed a significant correlation with latitude variation, especially depth and fishing intensity (Fig. S1). Specifically, it was found that, proceeding to lower latitudes (south direction), depth tends to increase ($r = -0.76$), while fishing intensity decreases ($r = 0.76$). Fishing intensity ($r = -0.67$), as well as the main environmental variables such as temperature ($r = -0.76$), dissolved oxygen ($r = -0.59$) and chlorophyll concentration ($r = -0.72$) were negatively correlated with depth. Those relations reflect the clusterization of sampled hauls obtained from k-means and PCA biplot (Fig. 3), highlighting a cluster more in proximity of the coast with higher and more dispersed value of the above-mentioned variables, and a deeper cluster with an opposite trend.

A total of 8191 individuals (HCP1: 3776; HCP2:

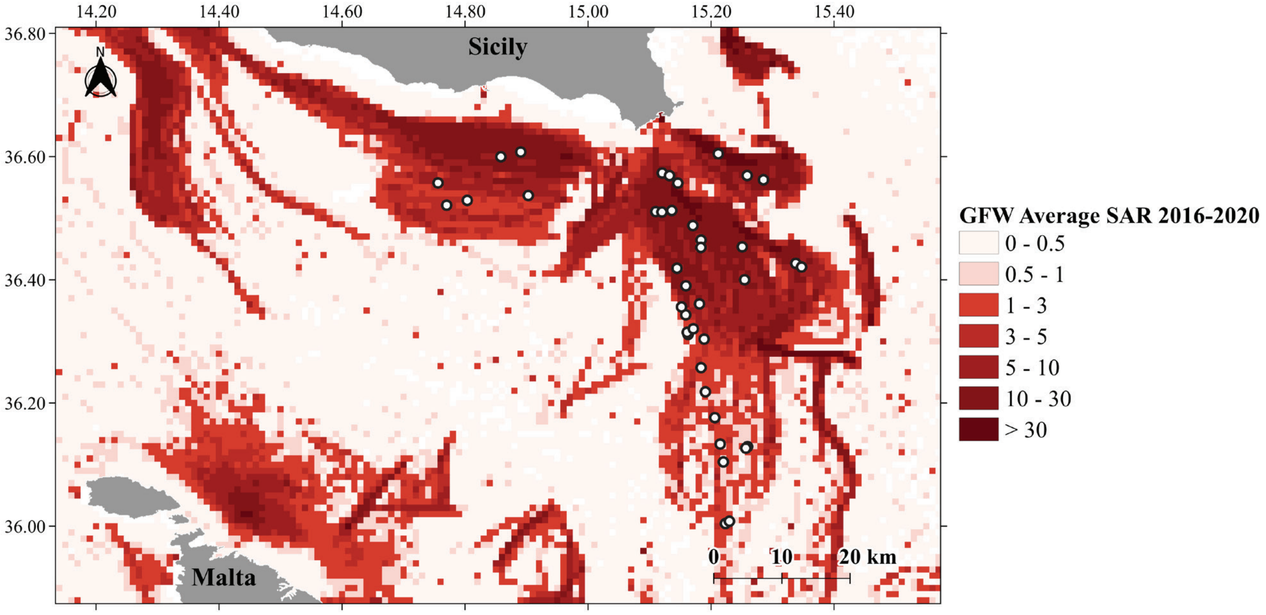

Fig. 2: Fishing intensity raster map expressed as Swept Area Ratio (SAR) of the study area obtained from analysis of Global Fishing Watch AIS data. Dots represent hauls sampled during the surveys.

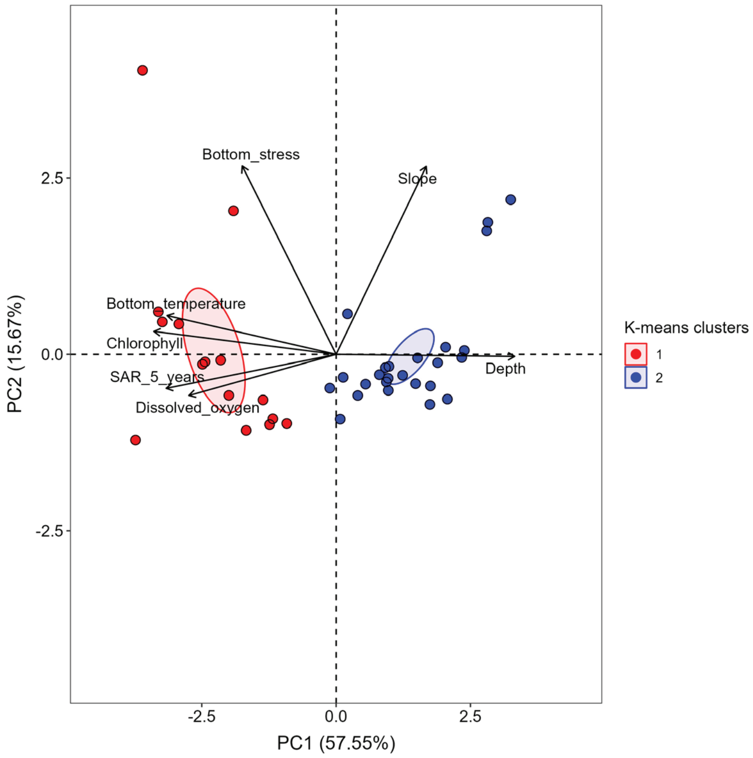

Fig. 3: PCA ordination plot of sampled hauls based on associated environmental variables and fishing intensity. Variables axes direction displays environmental dependency while their length shows their relative importance. It can be seen as a clustering tendency along PC1 axes mostly attributed to depth that is negatively correlated with bottom temperature, chlorophyll concentration, dissolved oxygen and fishing intensity. Color of the points represent the clusters obtained by k-means cluster algorithm with 2 groups that further underlines the tendency described in the ordination plot.

2286; HCP3: 2129) for a total of 115.98 kg (HCP1: 60.76; HCP2: 35.70; HCP3: 19.52), were caught during the three surveys. These specimens belonged to 103 species of which 51 were demersal and 52 benthic species (Table S2). Demersal domain accounted for 70% (62% for biomass) of all individuals with an average total density per haul of 354 (±296 s.d.) individuals/km^2 and 4.87 (±3.39 s.d.) kg/km^2. Average ± s.d. benthic total density per haul were, respectively, 158 ±144 individuals/km^2 and 2.84 ±3.37 kg/km^2.

Excluding *Parapenaeus longirostris* from the dataset, dominance scores were relatively low. The most dominant demersal species on average was *Trachurus trachurus* (15.3%) followed by *Arnoglossus laterna* (9.7%)

and *Merluccius merluccius* (8.12%) (Fig. S2). Benthic domain was mainly dominated by the genera *Alcyonium* (27.63%) and *Munida rugosa* (16.83%) followed by two species of Pennatulidae: *Pennatula phosphorea* (4.30%) and *Pteroeides griseum* (4.08%) (Fig. S3). Demersal domain diversity tends to be higher than that of benthic for all the considered taxonomic indices (Table 2).

CWMs calculation highlighted an assemblage dominated by demersal organisms with maximum size between 10 and 20 cm (46.6%), a lifespan between 3 and 10 years (71.2%), pelagic eggs (80.3%), swimming through water (95.4%), and showing a predatory behavior (91.6%). Benthic domain was mainly characterized by organisms with maximum size between 2 and 10 cm (51.4%), a lifespan between 3 and 10 years (53.7%), releasing eggs in the water column or brooding (36.1% and 39.4%), crawling on the seabed, (54.5%) or staying attached to it (28.7%) and feeding on suspended organic matter (40.7%) or upon dead animals (24.0%). Mirroring those responses, the benthic domain showed a slightly higher functional evenness and functional divergence than the demersal domain (Table 2).

Linear regression models on total densities of demersal species, accounting for biomass values, revealed a negative effect of fishing intensity, instead a positive effect of sea bottom temperature was observed if the total number of individuals was considered. Similarly, total counts of benthic domain were positively influenced by temperature, while fishing intensity showed only a weak negative effect. Benthic biomass densities were positively related only to chlorophyll concentration (Table 3). Despite the trends shown on graphs (Fig. S4, Fig. S5) no significant effects of bathymetry were observed.

Assemblage taxonomic diversity seemed to not be influenced by fishing intensity. Chlorophyll concentration proved to be the main driver negatively affecting all indices associated with the demersal domain and positively influencing benthic species richness and Shannon-Wiener's Index. Secondarily, bottom shear stress had a significant positive effect on demersal Shannon-Wiener, Simpson and Pielou's Indices, while with a negative effect on Simpson (Table 3).

Similarly, functional diversity indices did not show effects led by fishing intensity variation. F.Rich of the demersal domain was positively related to bottom temperature variation while changes in chlorophyll concentration significantly reduced F.Dis and Rao. For the benthic domain only a positive effect of bottom shear stress to F.Rich was detected (Table 4).

Multivariate RDA analysis revealed that only a small portion of the variance (not higher than 29%) observed in taxonomic (species abundance) and functional (CWMs) composition was explained by the variables included in this study. Neither of the PERMANOVA nor PERMDISP analyses provide evidence of a significant effect of sampling year or season on the abundance composition of species (Table S3, Table S4). Variables accounted for approximately 10% variance more for the demersal domain than the benthic one and, in both cases, models applied to species count data showed a slightly better fit than those applied to CWMs (Table 5). Most variation, in the demersal domain, was attributed to bathymetry, followed by bottom temperature, fishing intensity and –to a lesser extent– to seabed shear stress and slope if taxonomic composition is considered. Fishing intensity and slope showed a stronger effect when accounting for functional composition. For the benthic domain fishing intensity, bottom temperature and bathymetry led the constrained variation explained by the RDA model with taxonomic data, while temperature was removed when functional data were considered. Introducing spatial coordinates as a condition factor decreased, as expected, the variation explained by the model and by the variables, indicating not only an effect caused by the spatial proximity of the hauls but also by the combination of environmental, anthropogenic and spatial source of variability (Table S5). This aspect is amplified especially for the benthic domain, where the proportion of variance explained by latitude and longitude variation is similar if not higher than the portion accounted for by fishing intensity and bathymetry (Table 5). Despite the analysis being applied both for biomass and count data, only the latter was reported on account of having turned out better results.

As proof of these results, the ordination plots of the RDA models displayed a clustered data close to the center with only a few species or trait modalities determining differences among the hauls (longer vectors; Figs. 4, 5, Fig. S6, Fig. S7). In the ordination plot of CWMs, some pattern of correlation of certain trait modalities with explanatory variables could be seen. For the demersal domain, trait modalities like the feeding mode scavenger/opportunist (fScav) and benthic egg development mode

Table 2. Summary (mean ±s.d.) of taxonomic (Sp.Rich = species richness, H = Shannon's Index, 1-D = Simpson's Index, J = Pielou's evenness) and functional (F.Rich = functional richness, F.Eve = functional evenness, F.Div= functional divergence, F.Dis = functional dispersion, Rao = Rao's Index)l diversity indices computed for demersal and benthic domains.

Domain	**Taxonomic**				**Functional**				
	Sp.Rich	**H**	**1-D**	**J**	**F.rich**	**F.Eve**	**F.Div**	**F.Dis**	**Rao**
Demersal	15.47	2.10	0.82	0.78	0.41	0.63	0.87	0.18	0.04
	±4.31	±0.38	±0.10	±0.11	±0.22	±0.08	±0.03	±0.03	±0.01
Benthic	9.15	1.46	0.64	0.70	0.54	0.72	0.81	0.26	0.07
	±4.02	±0.46	±0.17	±0.17	±0.26	±0.11	±0.07	±0.06	±0.02

Table 3. Results of linear regression models applied to demersal and benthic densities and to the four selected taxonomic diversity indices (Sp.Rich = species richness, H = Shannon's Index, 1-D = Simpson's Index, J = Pielou's evenness) in relation to fishing intensity and other environmental variables. Significant results are underlined, while empty spaces indicate that the corresponding variable was removed during the stepwise selection. SAR = fishing intensity expressed as swept area ratio, Depth = bathymetry expressed in meters, BTemp = sea bottom temperature in Celsius, DO = dissolved oxygen concentration at the sea bottom in mmol/L, Chl= chlorophyll concentration at the sea bottom in mg/L, Stress = seabed shear stress expressed in N/m^2, Slope = slope of the sea bottom in degrees.

Variables		Demersal						Benthic					
		D.count	D.biomass	Sp.Rich	H	1-D	J	D.count	D.biomass	Sp.Rich	H	1-D	J
SAR	Slope	-17.21	-0.35					-6.49	-0.18	-0.181		0.007	0.008
	p	0.090	0.002					0.007	0.087	0.141		0.044	0.008
Depth	Slope				0.009	0.003	0.002			-0.064			
	p				0.009	0.002	0.019			0.029			
Btemp.	Slope	96.24	0.82	2.376	0.236	0.063	0.033	65.05			-1.256		
	p	0.023	0.120	0.003	0.001	0.001	0.110	0.009			0.162		
DO	Slope	17.62	0.20						0.29			-0.014	-0.025
	p	0.181	0.104						0.079			0.191	0.001
Chl	Slope			-94.834	-10.714	-2.728	-2.143		72.86	78.414	6.109		
	p			0.029	0.004	0.004	0.050		0.023	0.051	0.058		
Stress	Slope	-1018.21		-12.801	1.465	0.546	0.773					-0.701	-0.792
	p	0.130		0.079	0.043	0.004	0.001					0.007	0.003
Slope	Slope	97.21			-0.137	-0.028	-0.038				-0.137	-0.056	-0.039
	p	0.071			0.005	0.019	0.011				0.047	0.258	0.424
Adj R2		0.18	0.14	0.16	0.39	0.43	0.34	0.28	0.21	0.38	0.25	0.24	0.34

Table 4. Results of linear regression models applied to the five selected functional diversity indices (F.Rich = functional richness, F.Eve = functional evenness, F.Div= functional divergence, F.Dis = functional dispersion, Rao = Rao's Index) in relation to fishing intensity and other environmental variables. Significant results are underlined, while empty spaces indicate that the corresponding variable was removed during the stepwise selection. SAR = fishing intensity expressed as swept area ratio, Depth = bathymetry expressed in meters, BTemp = sea bottom temperature in Celsius, DO = dissolved oxygen concentration at the sea bottom in mmol/L, Chl= chlorophyll concentration at the sea bottom in mg/L, Stress = seabed shear stress expressed in N/m^2, Slope = slope of the sea bottom in degrees.

Variables		Demersal					Benthic				
		F.Rich	F.Eve	F.Div	F.Dis	Rao	F.Rich	F.Eve	F.Div	F.Dis	Rao
SAR	Slope	-0.012						0.006			-0.001
	p	0.101						0.221			0.156
Depth	Slope						0.005				
	p						0.056				
Btemp.	Slope	0.100			0.015	0.005	0.081			0.016	0.007
	p	0.001			0.001	0.001	0.048			0.009	0.036
DO	Slope						0.021		0.015		
	p						0.130		0.028		
Chl	Slope				-0.682	-0.190					
	p				0.015	0.019					
Stress	Slope	-0.793		-0.123			1.044				
	p	0.074		0.072			0.055				
Slope	Slope	-0.058	-0.019		-0.009	-0.002	-0.091				-0.007
	p	0.043	0.383		0.198	0.232	0.038				0.070
Adj R2		0.32	0.05	0.06	0.28	0.24	0.33	0.04	0.11	0.10	0.16

Table 5. Summary table of the results obtained from Redundancy Analysis (RDA) applied to species count data (Taxonomic) and to CWMs (Functional) for both demersal and benthic domain (values between brackets represent the *p*-value obtained after permutations). Full RDA reports the results obtained from the model including stepwise selected variables while Partial RDA refers to the model including the selected variables but removing the variance explained by spatial coordinates of the sampled hauls (expressed by Latitude and Longitude). Adj.R2 = adjusted R squared representing the variance explained by the RDA models.

% of intertia explained by	Demersal				Benthic			
	Taxonomic		Functional		Taxonomic		Functional	
	Full RDA	Partial RDA	Full RDA	Partial RDA	Full RDA	Partial RDA	Full RDA	Partial RDA
Constraining factors	40.26% (0.001)		31.85% (0.001)	26.93% (0.001)	24.91% (0.001)	19.36% (0.001)	19.61% (0.008)	12.50% (0.044)
Condition factors (Lat,Lon)		11.26%		8.21%		12.61%		16.92%
SAR	6.23% (0.001)	5.61% (0.003)	9.92% (0.003)	5.41% (0.037)	11.83% (0.001)	6.97% (0.002)	4.01% (0.185)	8.85% (0.027)
Depth	14.12% (0.001)	7.66% (0.001)	6.35% (0.032)	6.05% (0.027)	5.10% (0.026)	7.12% (0.002)	15.60% (0.008)	3.65% (0.191)
BTemp	7.04% (0.002)	7.09% (0.002)	6.92% (0.013)	7.68% (0.011)	7.99% (0.004)	5.27% (0.013)		
DO	4.58% (0.014)	4.14% (0.017)						
Chl								
Stress	3.48% (0.066)	3.51% (0.043)						
Slope	4.79% (0.008)	4.55% (0.009)	8.66% (0.006)	7.80% (0.013)				
Adj.R2	0.29	0.22	0.24	0.19	0.18	0.13	0.15	0.08

(edBen) appeared to be more correlated to fishing intensity vector while egg development mode like pelagic (edPel) and feeding mode predator (fPred) were correlated more with bathymetry in an opposite direction to the previous ones (Fig. 4). Clusterizations of trait modalities is more evident for the benthic domain where modes like maximum size (20-50 cm), longevity (>10 yrs), egg development mode asexual/budding (edAsex) and pelagic (edPel), the sessile mobility (mSess), suspension feeding mode (fSusp) were correlated and in the opposite direction from traits like maximum size (2-10 cm), longevity (3-10 yrs), brood eggs development mode (edBrood), crawling mobility (mCrawl), feeding modes surface deposit (fSurf), and scavengers (fScav), even if correlation with constraining variables (bathymetry and fishing intensity) is less strong than the one with unconstrained axes (vectors oriented more along the PC1 than RDA1; see Fig. 5).

Discussion

Our results highlighted minimal differences in the bentho-demersal assemblage composition along the measured fishing intensity gradient across the continental shelf in the easternmost area of the Strait of Sicily. The assemblage appears to result from both intense bottom trawling –as indicated by the consistently high SAR values– and bathymetric variation. SAR values exceeding 0.1 years^{-1} indicate that a community is trawled at least once every ten years, a critical threshold for distinguishing unfished from fished assemblages. This distinction is particularly relevant in sedimentary habitats, where a higher threshold of SAR values of 3 years^{-1} can effectively differentiate trawled from untrawled areas (Bolam *et al.*, 2017). In our study area, the observed SAR values significantly exceed this threshold, indicating intense fishing pressure, with the area being trawled approximately every 40 days. This intense and frequent disturbance greatly reduces the likelihood of recovery for several species, particularly long-lived ones. Those patterns are characteristics of other fishing grounds across the Strait of Sicily, where trawling has been conducted for decades (Consoli *et al.*, 2016; Terribile *et al.*, 2016; Milisenda *et al.*, 2017). In these contexts, bathymetry is a key factor characterizing the community for two main reasons. First, bathymetry is strongly correlated with the spatial distribution of fishing activity (Eigaard *et al.*, 2017; Amoroso *et al.*, 2018; Metcalfe *et al.*, 2018), the annual intensity gradient showed a patchy spatial distri-

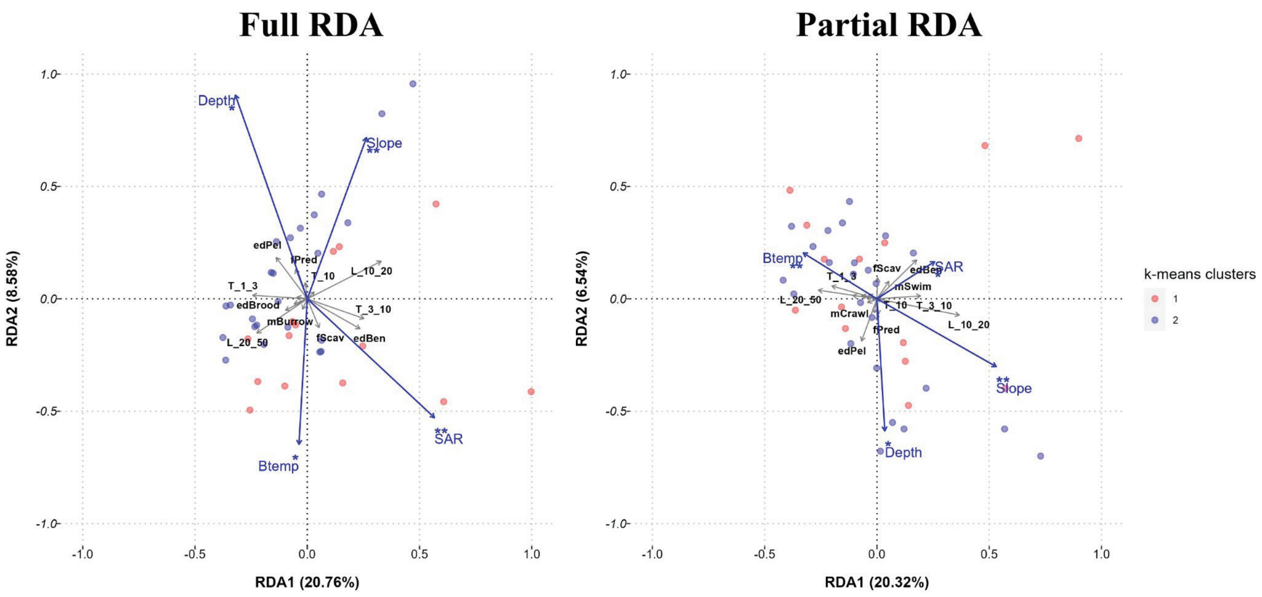

Fig. 4: Ordination of the all demersal CWMs of each trait modalities along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left, is the RDA triplot of the model accounting for stepwise selected variables, while on the right is displayed the partial RDA accounting for spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represent the clusters obtained from a k-means classification according to the variables associated with the hauls (SM1- Table S1). Stars represent the significance level of the *p*-value for each term: * for $p<0.05$, ** for $p<0.01$, *** for $p<0.001$.

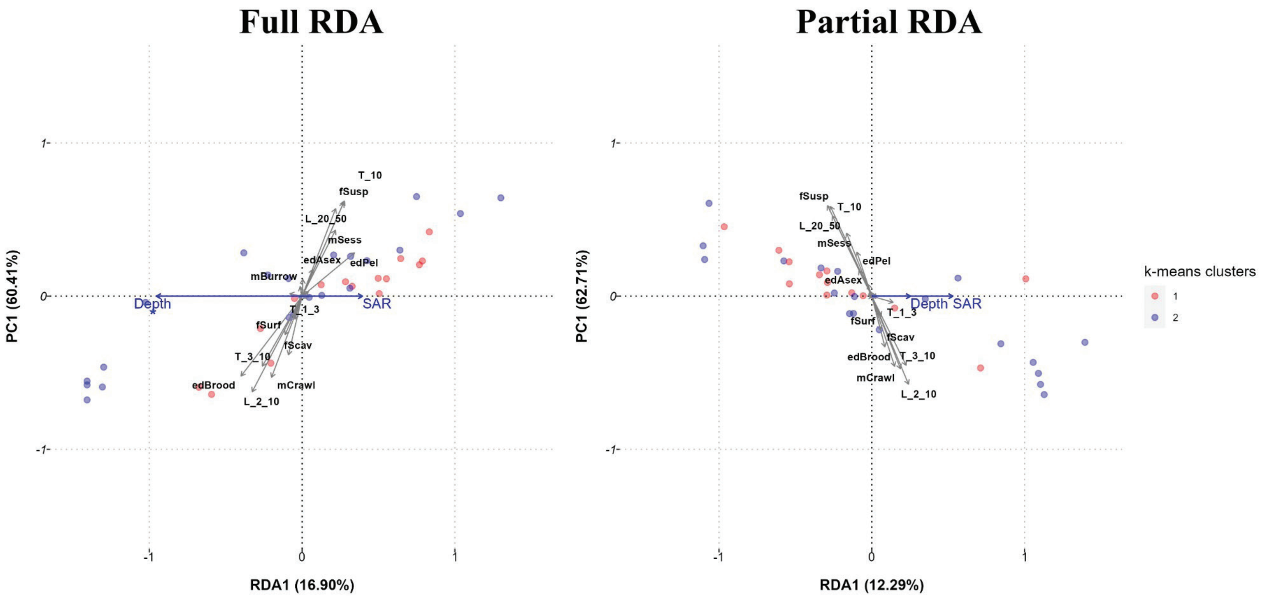

Fig. 5: Ordination of the all benthic CWMs of each traits modalities along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left, is the RDA triplot of the model accounting for stepwise selected variables, while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represent the clusters obtained from a k-means classification according to the variables associated with the hauls (SM1-Table S1). Stars represent the significance level of the *p*-value for each term: * for $p<0.05$, ** for $p<0.01$, *** for $p<0.001$.

bution, decreasing offshore. Fishermen, constrained by policies (Regulation (EU) 2019/1241), tend to fish closer to the coast to maximize revenue (Dimech *et al.*, 2012). Continuous trawling creates a "cultivation effect" (Mangano *et al.*, 2013), favoring species with rapid reproductive cycles and short lifespans, making them dominant in trawled areas; a well-known effect in Mediterranean fishing grounds where communities are dominated by opportunistic and resilient species such as *Parapenaeus longirostris* and *Aristeomorpha foliacea* (Dimech *et al.*, 2012), as we observed in the dominance of *Parapenaeus longirostris* in our data. Second, the spatial variation of key environmental characteristics, such as temperature and sediment composition, follows a bathymetric gradient which was mirrored in the clustering of the sampled hauls in association with the investigated covariates and the strong correlation of many of them with depth. A shallow seabed exhibits strong habitat heterogeneity and different ecotonal transitions, becoming more homogenous at greater depths. This gradient further differentiates the community composition (Cartes *et al.*, 2002; Cosentino & Giacobbe, 2008; Dimech *et al.*, 2008; Papiol *et al.*, 2012). However, in the study area, characterized by the gradually sloping seabed, there is no clear change in community composition, but rather a less pronounced transition as we have observed in the low variance explained by the investigated variables and the centrality of data in the ordination plots. Additionally, the long history of trawling may have diminished small-scale habitat heterogeneity, as observed by (Terribile *et al.*, 2016).

Despite only minor variations in assemblage composition being evident in RDAs, bathymetry and fishing intensity consistently account for a significant portion of the explained variation across both domains. As depth increases, the community appears to become less influenced by environmental variations that could mask the impacts of fishing disturbance. Consequently, it becomes more sensitive to such disturbances, as highlighted by studies such as (Bolam *et al.*, 2017) and (Sciberras *et al.*, 2018). Furthermore, the likelihood that the area is involved by frequent trawling events decreases. In fact, in the study, the average fishing intensity values of the observed hauls belonging to the deeper cluster was half of the one reported for the shallower cluster. Comparative studies, such as those by (Tillin *et al.*, 2006) and (van Denderen *et al.*, 2015), show that fishing disturbance has a greater effect in areas less prone to high levels of natural disturbance.

The greatest effects on diversity indices and total densities led by bottom temperature and chlorophyll concentration in the linear models can be considered indirectly linked to depth variation. In shallower areas, increased primary production from nutrient runoff and higher temperatures shape species niches, favoring those with higher thermal tolerance and benefiting from increased productivity. Seabed chlorophyll concentration positively affects benthic biomass and diversity, as also reported by (Hiddink *et al.*, 2006), who found that infaunal biomass in the North Sea increases with sediment chlorophyll content until reaching a plateau.

Some dominant demersal species, such as *Trachurus trachurus* and *Arnoglossus laterna*, are closely linked to temperature changes and chlorophyll concentration (as a proxy for food availability) (Paulo-Martins *et al.*, 2011; Leitão, 2015; Punzòn *et al.*, 2021), correlating with these variables in ordination plots and showing positive trends in scatter plots of their abundances. Bathymetry and sediment characteristics could explain a portion of trait variability, with deeper hauls belonging to muddy and coarse sediments favoring sessile suspension feeders and burrowing surface-deposit feeders, while shallower ones associated with coarse sediments are dominated by smaller scavenging and predator species. This pattern, reflected in the partial RDA of the benthic community, differentiates small crawling scavengers with fast lifecycles from sessile long-lived suspension feeders. However, this pattern was mostly explained by residuals of the model, likely due to the low resolution of habitat maps or environmental variation and species interaction not accounted for in the covariates of the model.

Sediment homogeneity increases with stress from towed fishing gear, which remove shell debris and coarser sediments that support more complex communities (Handley *et al.*, 2014). Opportunistic and scavenger species, such as *Spicara maena* and *Stylocidaris affinis*, show positive correlations with increased fishing intensity in the RDA ordination plots comparable with data observed in other studies (Demestre *et al.*, 2000, Strain *et al.,* 2012, Mangano *et al.,* 2013). These organisms, which feed on carrion and organic remains, benefit from the organic contributions from sediment resuspension caused by nets and discarded bycatch. Their rapid recovery times and motility make them less vulnerable to fishing disturbances than more sessile species like suspension feeders and grazers (de Juan *et al.*, 2009; Mangano *et al.*, 2014; Mangano *et al.*, 2015).

Despite observing an increase in the relative abundance of small benthic species, trawling is generally associated with an overall negative trend in benthic communities. This is consistent with findings from other studies in frequently disturbed shallow areas, where the increase in opportunistic species is accompanied by a decline in overall community health (Hinz *et al.*, 2009; Kaiser *et al.*, 2006).

The reported presence of dominant sessile suspension feeders in the benthic domain, even if apparently contradictory, was probably linked to two factors. First, despite that experimental design followed a pressure gradient, it is reasonable that the frequent trawling activity occurring in the study area had already acquired an influence on community adaptation, involving in a long term also the areas in which low-pressure values were observed. These would mask abrupt changes in the response of species with longer recovery times, such as Alcyonidae and Pennatulidae*,* over the gradient, as there would be no comparison with a pristine condition, while less vulnerable species with short recovery times more easily show a response as a function of the gradient (Sciberras *et al.*, 2018). In fact, although it is clearly demonstrated that trawling alters the structure and composition of the benthic-demersal communities, this response pattern is often found only by comparing areas in which this activity is exercised in a negligible manner with areas subject to a frequent disturbing activity (Hiddink *et al.*, 2017). The other reason could be linked instead to the distribution of those species along the environmental gradients. A moderate increase of hydrodynamic conditions and organic matter flows benefits those species, and often their optimum could be found at relatively moderate depths of between 40 and 60 m (Ambroso *et al.,* 2013). So even though fishing intensity should drive a reduction of abundances of this vulnerable species, the distribution could be more influenced locally from the positive effects induced by the increase of shear stress, chlorophyll concentration, and bottom temperatures of shallower areas, as can be seen in the scatter plot of the abundance of *Alcyonium sp.* and *Pteroides griseum* (Fig. S3). This is also in line with the lack of effect of fishing intensity in diversity indices, and the low variance explained by this pressure in the models, as other variables or biotic interaction could shape the current state of the community.

Furthermore, the absence of a general influence of variables in the functional response of the two investigated domains highlights the homogenization processes possibly exerted by intense trawling pressure on the community (Tillin *et al.*, 2006; De Juan *et al.*, 2007; Handley *et al.*, 2014) that has selected species with traits more compliant with this type of impact in the long term. Even if those species respond differently to the stress by sharing similar traits' expressions, the community shows to be resilient to change in its structure due to the impact of fishing (Muntadas *et al.*, 2016). This concept could be redirected to the low functional divergence measured by the analyzed assemblage and its relatively high functional evenness. It can also be noted that functional responses of community could often show nonlinearity both to environmental variables and fishing impact (Lundquist *et al.*, 2018), therefore, smallscale areas such as our fishing ground, could not be sufficient to examine the relationship through different habitat responses across fishing gradients in order to show a clear pattern of trait variation.

Despite the robustness of our approach in assessing community responses to chronic trawling disturbances, some limitations must be acknowledged. The study provides a snapshot of the bentho-demersal community without access to historical data (or time-series analyses) that could help differentiate between natural fluctuations and long-term shifts induced by fishing pressures. This limitation makes it challenging to establish whether the current assemblage structure is the result of recent environmental and anthropogenic influences or reflects a longer trajectory of gradual change. Additionally, the absence of pristine, undisturbed, reference sites restricts our ability to fully isolate the effects of trawling from other environmental drivers. It must be considered that identifying pristine areas unaffected by bottom trawling in the Mediterranean Sea is increasingly challenging due to the extensive and long-standing nature of this fishing practice (de Juan *et al.*, 2009; Colloca *et al.*, 2017). While the study effectively incorporates key environmental variables and evaluates their contributions to community variability, the relatively small portion of variance explained by the models suggests that other unmeasured biotic and abiotic factors may also play a role. Moreover, our analysis primarily considers species-level biological traits without accounting for intraspecific variability or ontogenetic shifts, which could further refine our understanding of functional diversity and species interactions. Nevertheless, despite these limitations, the observed patterns align themselves with findings from similar studies, reinforcing the validity of our conclusions regarding the effects of chronic trawling. These considerations highlight the complexity of assessing community responses in persistently disturbed ecosystems, and suggest that future research incorporating long-term data, broader environmental gradients, and finer-scale trait variability could further enhance our understanding of fishing-induced impacts.

In conclusion, coupling taxonomic analysis with functional ones through Biological Trait Analysis and diversity indices, proved to be a useful approach to increase the understanding and interpretation of community responses in chronically disturbed areas. As a matter of fact, the sole usage of normal indices of diversity applied to the taxonomic composition of assemblages may not correctly reflect the influence of the fishing disturbance compared with functional changes that last longer over time and allow one to observe differences even in communities already adapted to such a condition (de Juan *et al.*, 2007; Farriols *et al.*, 2017; Sciberras *et al.*, 2018). Here, we have highlighted the influence of fishing around the southern seabed of the coasts of Cape Passero, an area that has been poorly studied compared with the neighboring fishing grounds of the Strait of Sicily, but that has an important economic value for the Sicilian fishing fleets (Popescu *et al.*, 2010; Farrugio & Soldo, 2014). Despite the relatively narrow investigation time window, the selected approach allowed the identification of exploitation trends comparable to those observed in other similar studies, confirming that heavily trawled fishing grounds are less prone to show clear trends of response in benthic and demersal communities where the scattered source of variation is most likely attributed to the different tolerances within the environmental gradients.

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collation. G.D.B. analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors have no conflicts of interest to declare.

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Supplementary Data

The following supplementary information is available online for the article:

Fig. S1: Correlation charts of the variables considered in the study (values are expressed as Pearson’s correlation coefficient while the symbols represent the significance level of the p-value: ‘ for $p<0.1$, * for $p<0.05$, ** for $p<0.01$, *** for $p<0.001$)

Fig. S2:Distribution of the most dominant demersal species densities (total number of individual/km^2 after Hellinger transformation) along the selected variables (as can be seen in the scatter plots with linear trends). Arn_lat = *Arnoglossus laterna*; Mer_mer = *Merluccius merluccius*; Tra_tra = *Trachurus trachurus*.

Fig. S3: Distribution of the most dominant benthic species densities (total number of individual/km^2 after Hellinger transformation) along the selected variables (as can be seen in the scatter plots with linear trends). Alc_sp = *Alcyonium sp.*; Mun_rug = *Munida rugosa*; Pte_gri = *Pteroides griseum*.

Fig. S4: Distribution of demersal densities (total number of individual/km^2) along the study area (as can be seen in the bubble plot where bigger points represent higher density values) and along the selected variables (as can be seen in the scatter plots with linear trends). For each haul, densities were obtained by dividing total individuals/biomasses by the corresponding swept area.

Fig. S5: Distribution of benthic densities (total number of individual and biomasses/km^2) along the study area (as can be seen in the bubble plots where bigger points represent higher density values) and along the selected variables (as can be seen in the scatter plots with linear trends). For each haul, densities were obtained by dividing total individuals/biomasses by the corresponding swept area.

Fig. S6:Ordination of the all demersal species along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left the RDA triplot of the model accounting stewpwise selected variables while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represent the clusters obtained from a k-means classification according to the variables associated to the hauls (SM1-S1). Stars represent the significance level of the p-value for each term: * for p<0.05, ** for p<0.01, *** for p<0.001.

Fig. S7: Ordination of the all benthic species along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left the RDA triplot of the model accounting stewpwise selected variables while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represent the clusters obtained from a k-means classification according to the variables associated to the hauls (SM1-S1). Stars represent the significance level of the p-value for each term: * for p<0.05, ** for p<0.01, *** for p<0.001.

Table S1. Variables associated with the sampled hauls and summary of the two clusters obtained from the k-mean classification.

Table S2. List of species collected and identified during the fishing surveys in the study area.

Table S3. PERMANOVA table with results of the analysis on community abundance composition between the three sampling year and months. DF: degree of freedom, SumSq: sum of squares, R2: coefficient of determination, F = F-statistic value.

Table S4. ANOVA table representing significant test of results obtained from PERMIDISP analysis on community abundance composition between the sampling years and months. DF: degree of freedom, SumSq: sum of squares, MeanSq = mean squares, F = F-statistic value.

Table S5. Variation partitioning between environmental (Env), anthropogenic (Ant) and spatial variables (Spat) accounted in RDA models for demersal and benthic domains. Combinations (Env+Ant, Env+Spat, Ant+Spat, All) constitute the proportion of variation explained by the coo occurence of both the variables in the model while Tot and Res represent the total variation explained by the model and by the residuals, respectively. See Table 5 for the environmental variables considered in each RDA model.