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Effects of a fishing closure area on the structure and diversity of a continental shelf fish assemblage in the NW Mediterranean Sea

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ABSTRACT

Bottom trawling is the most extensive fishing activity affecting the continental shelf in Mediterranean waters. This gear has caused negative effects on the communities and topography of the seafloor. Temporal or spatial fishing closures have been proposed as strategies to reduce the disturbances caused by overfishing and for biodiversity recovery and restoration of ecosystems. The present study used various indicators to analyze and compare the differences between the demersal fish assemblages in a fishing closure area (FCA) established by the fishers of the Roses port (NW Mediterranean) and those on a fishing ground (FG) to assess the efficiency of this strategy two years after the cessation of fishing. Our findings demonstrated a noticeable increase in the abundance and biomass of all species in the FCA, especially species of small and medium size. Thus, our findings demonstrated that there were detectable shifts in the community (composition, rank abundance plots, ABC curves and diversity metrics) in a short time, evidencing slight disturbance effects on ecosystems. The present study also showed positive effects on the population structure, which had an increase in larger individuals, although the pattern varied between species. In particular, the European hake stock showed an increase in recruits, and the presence of large adults supported the suitability of this protection measure. Consequently, long time periods are not necessary to perceive noticeable benefits in terms of biodiversity recovery and ecosystem restoration in some deep marine ecosystems, and monitoring from the first year of fishing cessation is very important.

1. Introduction

Understanding the processes driving biological communities under multiple disturbances is an essential challenge in ecology and conservation science (Mouillot et al., 2013). The loss of biodiversity at the species (alpha diversity) or community level (beta diversity), habitat alteration, overexploitation of species or modification of the functional structure of ecosystems are some disturbances caused by current fishing practices (Worm et al., 2009; Wilson et al., 2010; Van Denderen et al., 2013; Osio et al., 2015). Among the most common types of fishing, bottom trawling is a worldwide fishing practice commonly conducted in the soft sediment of continental shelves and is especially important in European waters (Eigaard et al., 2017). At a global scale, it is estimated that approximately 22.36 million km^2 are subject to constant commercial trawling and to its chronic effects each year (Halpern et al., 2008). The direct effects of this fishing gear are mainly related to alteration, reduction or destruction of habitat and physical impacts on the seafloor, including a slight increase in surface roughness, the presence of berms and furrows, and the resuspension of sediments, which increases the turbidity of the water (Schwinghamer et al., 1998; Sparks-McConkey and Watling, 2001; Palanques et al., 2014; Consoli et al., 2017, 2018). These alterations may modify the functioning of benthic communities, creating problems for species that hunt by sight, filter feeders (Armstrong and Falk-Petersen, 2008) and especially burrowing organisms (Meysman et al., 2006; Herrel et al., 2011). Moreover, it can produce multiple shifts in food web relationships, the distribution of abundances and sizes within communities or selection towards certain strategies related to the life histories of species (Jones, 1992; Kaiser et al., 2002; Worm et al., 2009; Aburto-Oropeza et al., 2011). Even so, the altered communities have acquired some resilience against this continued exploitation over time (Jouffre and Inejih, 2005; Yemane et al., 2005).

The strategies to help mitigate overfishing disturbances have mainly focused on effort limitations and by-catch assessments (Stefansson and Rosenberg, 2005; Tsagarakis et al., 2014; Villasante et al., 2016) as well as on ecosystem approaches for maintaining and recovering biodiversity and integrity (Colloca et al., 2015; Trochta et al., 2018). In this context, the implementation of areas that are closed to fishing activities has become an

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increasingly useful tool within fisheries management strategies (Johannes, 1978; Kincaid et al., 2017; Khoukh and Maynou, 2018). These areas allow the recovery of biochemical characteristics and restructuration of the seafloor, favoring the recuperation of natural marine communities (Snelgrove and Butman, 1994; Van Hoey et al., 2004; Mumby et al., 2006; Lester et al., 2009; Hinz et al., 2017). The theory behind these areas establishes that a long period of time is necessary for recovery of the populations after the fishing activity ceases (McClanahan and Mangi, 2000; Russ and Alcala, 2004; Russ et al., 2005), although in some cases, the expected recovery does not take place at all (Hutchings, 2000). Besides, the increase of fish biomass and larger sizes of individuals within its boundaries should allow the emigration of adults and juveniles across the borders to adjacent areas ('spillover' phenomenon) (Williamson et al., 2004; Lester et al., 2009; Aburto-Oropeza et al., 2011; Hilborn and Ovando, 2014; Sala-Coromina et al., 2021).

The European hake (*Merluccius merluccius*) is one of the most important commercial species in the Mediterranean demersal ecosystem (Aldebert and Carries, 1988; Oliver and Massutí, 1995; Recasens et al., 1998; FAO, 2020). However, the annual landings of hake adults have been reducing in all Mediterranean ecoregions due to environmental changes, high fishing mortality among juveniles and the overexploitation of mature stocks (Aldebert et al., 1993; Lleonart et al., 2003; Hidalgo et al., 2011; STECF, 2015). However, the annual landings of hake adults have been reducing in all Mediterranean ecoregions due to environmental changes, high fishing mortality among juveniles and the overexploitation of mature stocks (Aldebert et al., 1993; Lleonart et al., 2003; Hidalgo et al., 2011; STECF, 2015). The improvement of fishing technology and nurseries' protection have been proposed as effective measures for avoiding the capture of juveniles and for preserving their stocks (Lleonart, 2001; Sardà et al., 2004; Khoukh and Maynou, 2018). But moreover, this species is primarily caught by bottom trawls, a fishing gear causing many ecosystem disturbances as above mentioned. In this context, a unilateral plan was undertaken by the fishers Association of Roses from the Roses harbor (Catalan coast, NW Mediterranean) to protect the hakes. In February 2014, they decided to close to all fishing activities (bottom trawl, longline and gillnet) an area of 51 km^2 on the continental shelf considered a nursery ground for juvenile hake (Colloca et al., 2015; Druon et al., 2015; Tugores et al., 2019), and well known by fishers. Subsequently, fisheries scientists were involved in the monitoring and assessment of the effects of this management measure on European hake's population as well as on benthic and fish communities. Although the first findings have already confirmed the suitability of this strategy for the whole of fish species (Recasens et al., 2016; Sala-Coromina et al., 2021), a next step is required from ecosystem approach to fisheries considering the structure and diversity of fish assemblages at the community and population levels. For that purpose, we studied two fish assemblages located in the closed area and in a neighboring fishing area at similar depths and substrates where the fishing activity was also focused on the capture of juvenile hake. Therefore, the main goals of the present study were to estimate, analyze and compare these indicators between the two areas: (i) by evaluating the changes in the composition and abundance (density and biomass), (ii) by displaying what species benefited and why, and (iii) by comparing the size structures of the populations of common species, especially the fishers' main target species, the European hake.

2. Material and methods

2.1. Study area and sampling

A monthly sampling method was developed from August 2015 to March 2016 in a fishing closure area (FCA) established by the local fishers in the Gulf of Roses (NW Mediterranean, Fig. 1). The FCA has a surface area of 51 km^2 and is located at depths from 120 to 150 m on a soft-bottom fishing ground (sandy-muddy mixture) with fully exploited by trawl fisheries until 2014. To analyze the hypothetical changes in the community structure and diversity inside the FCA, a similar fishing ground (FG) located near the FCA was also monitored, characterized by same depths and biological features (Fig. 1).

Samples were obtained onboard a Roses otter trawl fishing vessel using a commercial bottom trawl net with a cod-end with a square mesh size of 40 mm. Each month, four hauls of approximately one-hour duration were conducted during the same fishing day: two inside the FCA and two in the neighboring fishing ground (FG). After seven months of sampling, a total of 28 experimental hauls (14 in the FCA and 14 in the FG; Fig. 1 and Table 1) had been performed and analyzed. The swept area (km^2) was calculated based on the vessel speed (S, in knots), average horizontal opening of the net (BT, in m) and haul duration (H, in h) between the initial and final position of the gear on the bottom as follows: Swept area $= BT \text{ x } S \text{ x } H \text{ x } 1852/10^6$ (Sparre and Venema, 1998). All commercial fish species were identified at the species level, classified taxonomically (Nelson et al., 2016), counted, weighed and measured (total length TL, in cm). Finally, the species abundance (number of specimens n/km^2) and biomass (kg/km2) were calculated after standardization based on the swept area (Tables S1 and S2 in the Supplementary Material, SM).

2.2. Composition of fish assemblages

The composition similarity of fish assemblages from trawls of both areas was investigated using multivariate analyses performed with the software PRIMER v.6 (Clarke and Gorley, 2006). Abundance and biomass data from the trawls in the FCA and the nearby FG were square-root transformed to reduce the negative effect of the weighting of the most abundant species. A Bray-Curtis similarity matrix was calculated with these data, generating a nonmetric multidimensional scaling ordination (nMDS) to show the spatial grouping of the performed trawls.

A one-way permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008) with one fixed factor ('zone', with two levels) was computed from the Bray-Curtis similarity matrix to test the differences in abundance and biomass data between trawls from the FCA and FG. When significant differences ($p < 0.05$) were detected by the PERMANOVA analysis, a similarity percentage breakdown analysis (SIMPER) was conducted with the square-root transformed data to ascertain the species that most contributed to the observed dissimilarities between the two zones and to quantify their contributions and the differences in terms of average dissimilarity. Furthermore, a one-way analysis of similarity (ANOSIM) was also employed to determine the average rank of the similarities among the fish assemblages. This analysis compared the average rank similarities within and between the predefined groups of samples. Values of R close to 1 indicate strong separation between samples, while values close to 0 indicate no differences between them (Tuya et al., 2005; Johns et al., 2015).

2.3. Structure of fish assemblages

To determine the structure of fish assemblages and the numeric variability of the dominant and rare species, rank abundance plots (RADs, or Whittaker plots) (Magurran, 2004) were used. This plot is populated with all species of each sample, which are ranked from the most abundant to the least abundant (in number or biomass). Each species has a rank plotted on the x-axis

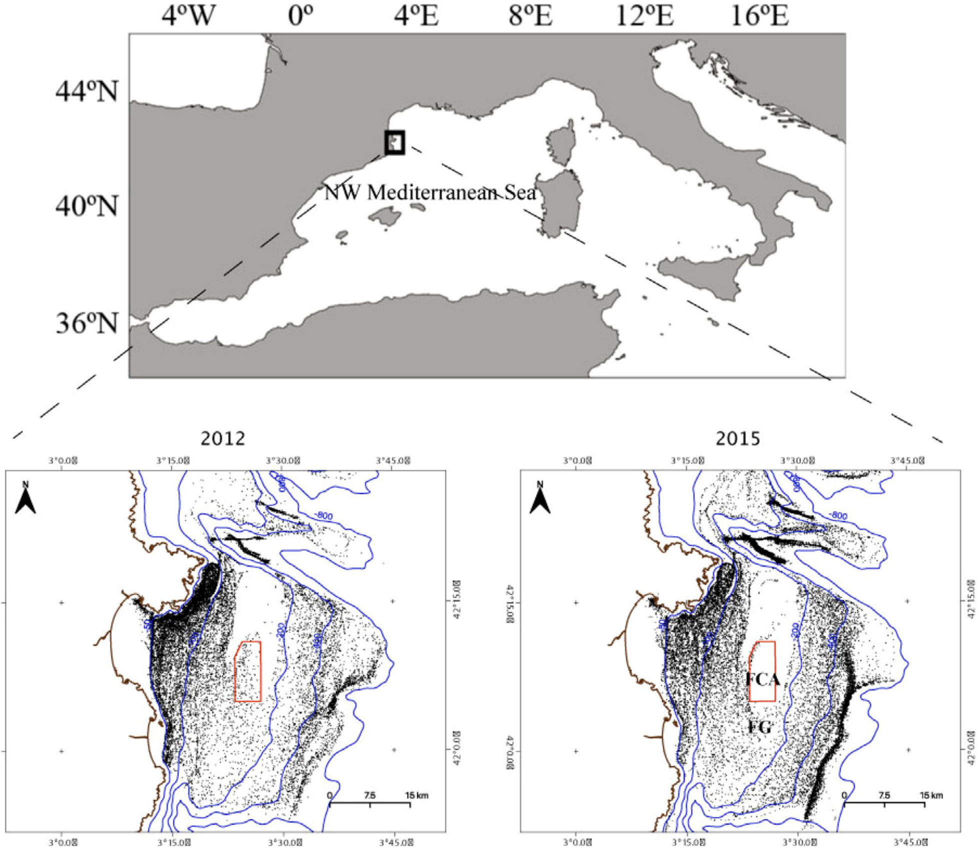

Fig. 1. Geographical map of the study zone: Bay of Roses (Catalonia, NW Mediterranean Sea). Fishing-trawl effort from Roses harbor fleet based on VMS (Vessel Monitoring System) data before (2012) and after (2015) area closure. FCA, fishing closure area; FG, fishing ground.

Table 1
Details of the hauls performed between August 2015–March 2016 inside the fishing closure area (FCA) and in the equivalent fishing ground (FG) in the Roses Bay (NW Mediterranean).

Fishing operation	Zone	Date	Initial (Lat, Lon)	Final (Lat, Lon)	Mean depth	Trawl duration (h)	Swept area (km^2)
D24	FCA	11/8/15	42°8.821’/3°25.132’	42°5.249’/3°24.581’	135.92	1.100	0.173
D27	FCA	11/8/15	42°5.525’/3°24.736’	42°10.053’/3°25.567’	133.98	1.167	0.184
D28	FCA	18/9/15	42°10.1802’/3°25.307’	42°5.482’/3°24.974’	136.97	1.000	0.157
D31	FCA	18/9/15	42°5.93’/3°24.235’	42°9.752’/3°24.979’	129.95	1.200	0.189
D32	FCA	19/10/15	42°9.088’/3°24.955’	42°5.211’/3°23.783’	131.08	1.133	0.178
D35	FCA	19/10/15	42°5.85’/3°24.89’	42°9.8’/3°25.71’	134.41	1.250	0.197
D36	FCA	11/11/15	42°9.913’/3°25.431’	42°5.694’/3°24.993’	134.65	1.217	0.192
D39	FCA	11/11/15	42°6.225’/3°24.65’	42°10.285’/3°25.21’	131.42	1.250	0.197
D40	FCA	1/12/15	42°9.51’/3°24.76’	42°6.23’/3°23.83’	127.58	1.000	0.157
D43	FCA	1/12/15	42°6.345’/3°24.845’	42°10.42’/3°25.887’	133.32	1.250	0.197
D44	FCA	20/1/16	42°9.415’/3°25.069’	42°5.221’/3°24.404’	132.74	1.250	0.197
D47	FCA	20/1/16	42°6.39’/3°24.375’	42°10.5’/3°25.17’	129.46	1.250	0.197
D48	FCA	7/3/16	42°9.18’/3°25.38’	42°5.85’/3°24.76’	136.06	1.000	0.157
D51	FCA	7/3/16	42°6.5’/3°24.7’	42°9.88’/3°25.25’	132.61	1.167	0.184
F25	FG	11/8/15	42°3.936’/3°23.081’	42°0.255/3°21.069’	134.71	1.267	0.199
F26	FG	11/8/15	42°1.589’/3°21.206’	42°4.509’/3°23.597’	130.89	1.083	0.171
F29	FG	18/9/15	42°3.26’/3°24’	42°0.817’/3°22.057’	139.99	1.083	0.171
F30	FG	18/9/15	42°1.569’/3°21.92’	42°4.569’/3°23.619’	132.41	1.017	0.160
F33	FG	19/10/15	42°3.36’/3°23.325’	42°0.35’/3°20.92’	133.59	1.000	0.157
F34	FG	19/10/15	42°1.004’/3°22’	42°4.45’/3°24.014’	135.92	1.167	0.184
F37	FG	11/11/15	42°3.375’/3°23.96’	42°0.3’/3°21.545’	137.66	1.000	0.157
F38	FG	11/11/15	42°1.2’/3°21.665’	42°3.86’/3°23.845’	134.06	1.000	0.157
F41	FG	1/12/15	42°3.565’/3°22.86’	42°0.76’/3°20.6’	129.95	1.000	0.157
F42	FG	1/12/15	42°1.37’/3°22.21’	42°4.37’/3°23.995’	135.04	1.000	0.157
F45	FG	20/1/16	42°3.463’/3°23.49’	42°0.068’/3°20.773’	135.98	1.167	0.184
F46	FG	20/1/16	42°1.48’/3°21.16’	42°4.33’/3°23.49’	130.46	1.000	0.157
F49	FG	7/3/16	42°3.43’/3°24.04’	42°0.63’/3°21.68’	137.45	1.000	0.157
F50	FG	7/3/16	42°1.67’/3°21.79’	42°4.0’/3°23.5’	132.13	1.000	0.157

and an abundance plotted on the *y*-axis. Thus, the abundance for the most abundant species is plotted at the highest position, followed by the next most common and so on (Fattorini et al., 2016).

Considering the relative abundance, the dominant species were the most numerically abundant (Moyes and Magurran, 2019). To reduce the maximum number of dominant species and to

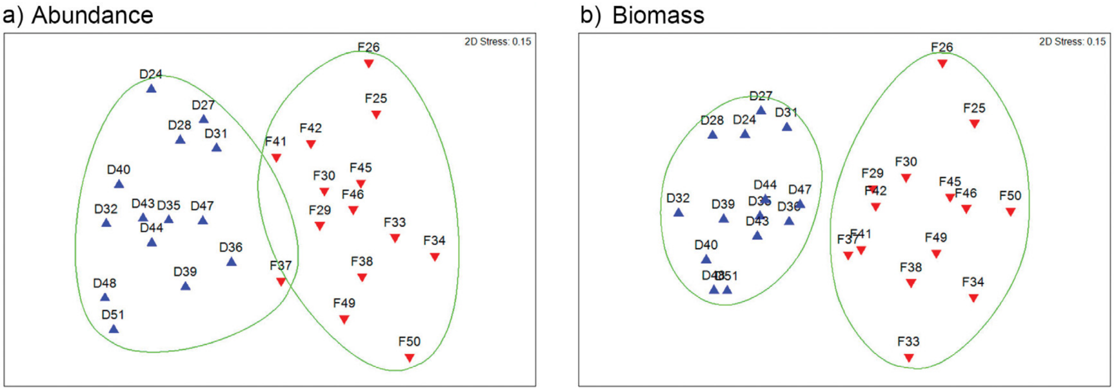

Fig. 2. Ordination plot (nMDS) for abundance (a) and biomass (b) of the sampling hauls from the fishing closure area (FCA, in blue) and fishing ground (FG, in red) in the NW Mediterranean Sea. Dashed lines indicate the similarity level of 65%. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

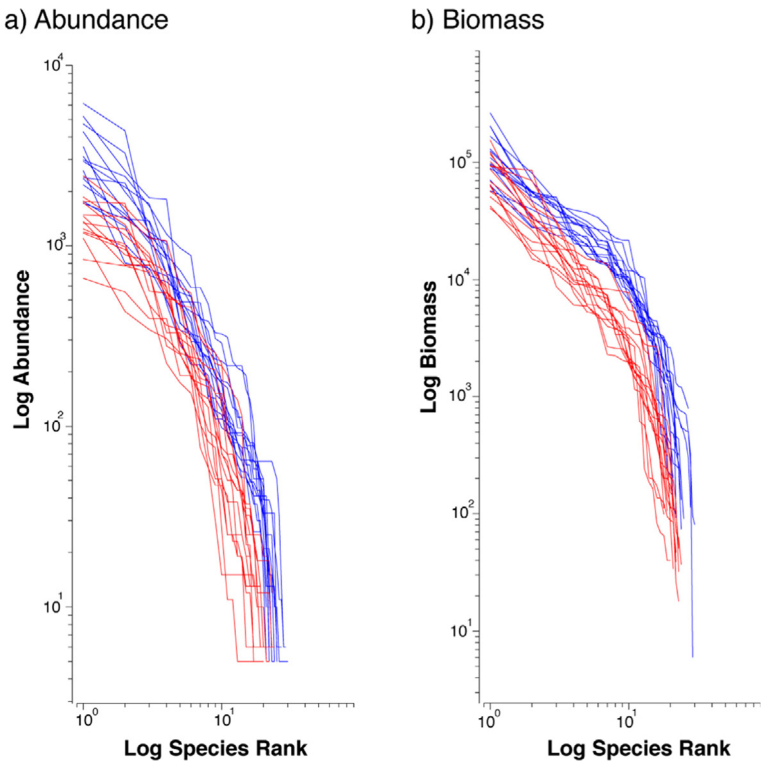

Fig. 3. Rank order $\log_2$-abundance plots of the species sampled from the fishing closure area (FCA, in blue) and fishing ground (FG, in red) in the NW Mediterranean Sea using abundance (a) and biomass (b) data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

establish a general criterion for all hauls, we only considered a species dominant when it exceeded 20% relative abundance, and rare species were defined as having less than 0.01% relative abundance (Matias et al., 2012; Hercos et al., 2013). The RAD plots were graphed using the package 'vegan' (Oksanen et al., 2019) in the R environment (R. Development Core Team, 2017).

The changes in the dominance patterns of the fish assemblages based on the abundance and biomass were assessed using the abundance–biomass comparison (ABC) curves and the W-statistic (Warwick, 1986). These plots can have three patterns: equilibrium, moderate disequilibrium and strong disequilibrium (Warwick, 1986; Warwick et al., 1987). Ecological equilibrium is expected when the abundance curve is below the biomass curve (W-statistic $>$ ater 0), which indicated that the assembly is dominated by one or more species represented by a few *K*-selected individuals (e.g., large size, moderate abundance, long life and slow growth). Moderate disequilibrium appears when the abundance and biomass curves are close ($W = 0$), showing an inequality between the numerically dominant species and the species with high biomass values. A community is strongly in disequilibrium when the curve of abundance is above that of biomass ($W < 0$), which indicates that the assembly is dominated by one or a few *r*-selected species (e.g., small size, large abundance, short lifetime, quick sexual maturity and year-round larval dispersal) (Blanchard et al., 2004; Sambou et al., 2016). A nonparametric Mann–Whitney *U* test was used to detect significant differences in the W-statistic between areas. The abundance and biomass comparison curves and the W-statistic (Clarke, 1990) were obtained using the package 'forams' (Aluizio, 2015) in R.

2.4. Length–frequency distribution analyses

The length analysis was performed on the dominant (*L. dieuzeidei*, *M. merluccius*, *T. capelanus* and *T. trachurus*) and most common (*E. gurnardus*, *L. boscii*, *M. barbatus*, *P. blennoides* and *T. lyra*) species of commercial interest and that had > ater 100 sampled specimens in each area (see results). Given that the main target of the closure area was the recovery of *M. merluccius*, we considered that a convenient complete sampling for this species would cover an annual period. For each species, the mean length between the fishing and closure areas was compared using a Mann–Whitney *U* test, and the length–frequency distributions were examined using a two-sample Kolmogorov–Smirnov test. Monte Carlo simulations were used to overcome uncertainty regarding the asymptotic distributions of KS test statistics under the null hypothesis (Abadie, 2002) by using the 'ks.boot' function (100,000 simulations) in the package *Matching* (Sekhon, 2020) in R. Finally, the effect of the fishery closure on stocks was also analyzed comparing the lengths at the 95th percentile ($L_{0.95}$) (Dimarchopoulou et al., 2018). The comparisons were performed using the quant.test function in the package 'snpar' (Qiu, 2014) in R.

2.5. Diversity measurements

The following six commonly used functional traits describing the ecological niches of species with their corresponding categories (Table S3 in the SM) were used to functionally define all species (Cartes et al., 2002; Halpern and Floeter, 2008; Somerfield et al., 2008; Farré et al., 2013, 2016); body shape, swimming type, motility, diet, maximum size and vertical distribution in the water column (Table S4 in the SM). Maximum size was considered a numeric variable, motility and vertical distribution were categorized as ordered factors, and the remaining traits were coded as unordered factors. From this functional categorization of species, several indices jointly considering the abundance and biomass data (square-root transformed) of species were quantified in each haul to explore different facets of the functional diversity of each community:

(a) Functional evenness (*FEve*), functional divergence (*FDiv*) and functional dispersion (*FDis*) were obtained based on functional space theory (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010; Schleuter et al., 2010). They were calculated as a convex hull volume generated from traits returned following the principal coordinates analysis (PCoA) on a square-root-corrected species-by-species Gower distance matrix for negative eigenvalues (Legendre and Legendre, 1998) (the R^2, which indicates the quality of the reduced spatial representation of the traits, was 0.670 with four PCoA axes; for the position of the species in the functional space, see Fig. S1 in the SM). *FEve* measures whether mean species traits are distributed regularly within an occupied trait space; *FDiv* is an index that determines how the abundance of species is spread within the volume of the functional space occupied by species; and FDis evaluates the average distance to the centroid of the functional space.

(b) Rao's quadratic entropy (FD_Q) (Rao, 1982) measures the average distance between two randomly selected individuals in the community and considers both the functional traits and the abundance (distribution) of these traits within the assemblage (Botta-Dukát, 2005; Loiseau et al., 2016).

(c) Functional group richness (*FGR*) represents the number of functional units found in each assemblage, which are obtained from a functional dendrogram. A similarity cut-off of 0.43 was used for FGR based on the maximum length of basal branches in the functional dendrogram using the McQuitty method (Stuart-Smith et al., 2013). In this case, only the abundance data were used.

In addition, two ecological indices were also computed, namely, species richness (S) and Shannon's diversity index (H') (Shannon and Weaver, 1949). The Shapiro–Wilk W test was used to determine the normality of all indices by area. Since the null hypothesis was rejected in some cases ($p < 0.05$), the pairwise differences were tested with nonparametric tests (Mann–Whitney tests). Bartlett's test for establishing the homogeneity of variance and Student's t-test were applied to compare the differences in the average values of all diversity metrics between areas using a Monte Carlo procedure with 10,000 permutations. In addition, a dendrogram of the cluster analysis based on Manhattan distance was utilized to find similar functional groups of fish. All indices were calculated using the function *FDindexes* from the package 'fundiv' (Bartomeus, 2016) in R.

3. Results

3.1. Composition of fish assemblages

A total of 50 fish species that belonged to 18 orders and 29 families were collected (Tables S1 and S2). A similar number of species was found in both areas, with 44 in FCA *vs* 46 in FG. Most landings were mainly represented, both in abundance as biomass, by the same species (*Merluccius merluccius*, *Lepidotrigla dieuzeidei, Trisopterus capelanus, Trachurus trachurus* and *Lepidorhombus boscii*). Some species were numerically (abundance) relevant but had low biomass, due to their very small size (e.g., *Capros aper*), while other, heavier species (*Conger conger*, *Phycis blennoides*, *Scorpaena elongata*, *Mullus* spp.) stood out in terms of biomass. Despite this similarity in proportions, a clear segregation was observed between the hauls from the FCA and those from the nearby FG (Fig. 2a and b), which was caused by composition differences in the less common remaining species.

The PERMANOVA results confirmed that the trawls from the FCA and FG differed significantly in both abundance (*Pseudo-F* test = 11.735, $p = 0.0001$, permutations = 9937) and biomass data (*Pseudo-F* test = 14.027, $p = 0.0001$, permutations = 9931). Similarly, ANOSIM also suggested dissimilarity in the species compositions of the landings from the two areas ($R = 0.740$ and 0.754 in abundance and biomass comparison, respectively; level of significance: 0.01%). In the abundance analysis, the SIMPER results revealed an average dissimilarity of 37.8% between the FCA and FG samples. *L. dieuzeidei* was the species that most contributed to the observed differences between zones (15.4%) (Table 2). Regarding the biomass comparison, the differences between zones (39.5%) were also mostly attributed to *L. dieuzeidei* (10.1%), although they were closely followed by *S. elongata* (7.7%), *Mullus surmuletus* (7.4%), *T. trachurus* (6.9%), *M. merluccius* (6.1%) and *C. conger* (5.3%), all of which were more abundant in mean in FCA (Table 2).

3.2. Rank abundance plots

The RAD plots of abundance provided intra- and inter-area variability, which showed notable differences related to the number of dominant and rare species (Figs. 3 and S2). *L. dieuzeidei* or *M. merluccius* was the dominant species in 67% of the total hauls, and they were jointly dominant in 29% of the total hauls in the FCA, while *C. aper* and *T. capelanus* were only dominant in two hauls in the FCA (Table 3). The number of rare species according to the abundance data varied from 8 to 19 and 4 to 15 in the FCA and FG, respectively (Table 3). Although the range was similar in both areas, approximately 29% of the hauls in

Table 2
SIMPER analysis showing the percentage of dissimilarity between closed fishing closure area (FCA) and fishing ground (FG) samples from the Roses Bay (NW Mediterranean), and the species that most contribute to this dissimilarity for both abundance and biomass data. For each species, the average values of abundance and biomass in each ground, the average dissimilarity and the percentage of dissimilarity contribution are provided. Species contributing up to 50% of cumulative dissimilarity are listed.

Abundance data (n/km^2)	Average dissimilarity = 37.8%				
	FCA	FG			
Species	Av. Abundance	Av. Abundance	Av. Diss	Contrib. %	Cum. Contrib. %
Lepidotrigla dieuzeidei	51.9	15.9	5.8	15.4	15.4
Trachurus trachurus	20.9	23.4	2.3	6.0	21.4
Merluccius merluccius	44.5	35.2	2.1	5.6	27.1
Argentina sphyraena	15.7	4.1	2.1	5.6	32.7
Engraulis encrasicolus	8.7	7.1	1.8	4.6	37.3
Capros aper	27.2	20.2	1.7	4.5	41.8
Helycolenus dactylopterus	10.5	0.5	1.6	4.3	46.1
Trisopterus capelanus	31.4	31.0	1.4	3.6	49.7
Mullus surmuletus	10.8	3.4	1.3	3.4	53.0

Biomass data (kg/km^2)	Average dissimilarity = 39.5%				
	FCA	FG			
Species	Av. Biomass	Av . Biomass	Av. Diss	Contrib. %	Cum. Contrib. %
Lepidotrigla dieuzeidei	210.9	60.6	4.0	10.1	10.1
Scorpaena elongata	115.9	2.6	3.0	7.7	17.8
Mullus surmuletus	145.5	35.5	2.9	7.4	25.2
Trachurus trachurus	147.8	135.6	2.7	6.9	32.1
Merluccius merluccius	328.8	278.1	2.4	6.1	38.2
Conger conger	133.3	69.0	2.1	5.3	43.5
Argentina sphyraena	68.8	17.8	1.6	3.9	47.4
Phycis blennoides	124.3	70.0	1.5	3.8	51.3

Table 3
Number of dominant and rare species by stations in the fishing closure area (FCA) and fishing ground (FG) from the Roses Bay (NW Mediterranean). Data are given for abundance and biomass.

Ground	Station	Abundance			Biomass		
		Dominant	Dominant species	Rare	Dominant	Dominant species	Rare
FCA	D24	2	*L. dieuzeidei*/*M. merluccius*	8	1	*M. merluccius*	6
	D27	1	*M. merluccius*	12	1	*M. merluccius*	10
	D28	1	*C. aper*	9	1	*T. trachurus*	9
	D31	1	*L. dieuzeidei*	12	1	*T. trachurus*	10
	D32	1	*L. dieuzeidei*	17	1	*M. merluccius*	16
	D35	1	*L. dieuzeidei*	9	1	*M. merluccius*	6
	D36	2	*L. dieuzeidei*/*M. merluccius*	9	1	*M. merluccius*	6
	D39	2	*L. dieuzeidei*/*T. capelanus*	19	1	*M. merluccius*	15
	D40	1	*M. merluccius*	11	1	*M. merluccius*	16
	D43	1	*L. dieuzeidei*	9	1	*M. merluccius*	8
	D44	1	*L. dieuzeidei*	10	1	*L. dieuzeidei*	9
	D47	1	*L. dieuzeidei*	10	1	*M. merluccius*	9
	D48	2	*M. merluccius*/*L. dieuzeidei*	13	1	*M. merluccius*	15
	D51	2	*M. merluccius*/*L. dieuzeidei*	12	1	*M. merluccius*	12
FG	F25	1	*M. merluccius*	14	1	*M. merluccius*	8
	F26	1	*M. merluccius*	11	1	*M. merluccius*	8
	F29	2	*T. trachurus*/*T. capelanus*	11	2	*T. trachurus*/*M. merluccius*	10
	F30	2	*M. merluccius*/*T. trachurus*	14	2	*T. trachurus*/*M. merluccius*	15
	F33	2	*M. merluccius*/*T. capelanus*	15	1	*M. merluccius*	12
	F34	2	*T. capelanus*/*M. merluccius*	11	2	*M. merluccius*/*T. capelanus*	10
	F37	2	*T. capelanus*/*M. merluccius*	9	1	*M. merluccius*	9
	F38	2	*T. capelanus*/*M. merluccius*	11	2	*M. merluccius*/*T. capelanus*	11
	F41	0	–	7	1	*M. merluccius*	9
	F42	2	*T. trachurus*/*M. merluccius*	7	1	*M. merluccius*	4
	F45	2	*T. trachurus*/*M. merluccius*	4	2	*M. merluccius*/*T. trachurus*	8
	F46	2	*M. merluccius*/*T. capelanus*	8	1	*M. merluccius*	6
	F49	1	*M. merluccius*	7	1	*M. merluccius*	10
	F50	1	*M. merluccius*	13	1	*M. merluccius*	11

the FG presented values smaller than those in the FCA. When biomass was used to build the plots, the major difference in the patterns was found between areas at the level of common species (Fig. 3). In the FCA, *M. merluccius* was clearly the dominant species, and only two hauls were replaced by *T. trachurus* and one haul was replaced by *L. dieuzeidei* (Table 3). In contrast, two species acquired were dominant in most FG hauls (c.a. 64%): *M. merluccius* and *T. trachurus* or *T. capelanus*, which attained higher values than *M. merluccius* in 43% of hauls (Table 3). In the remaining cases, *M. merluccius* was the only dominant species. The number of rare species was very similar in both areas, with 6–16 in FCA and 4–15 in FG (Table 3).

3.3. Abundance–biomass comparison curves

The ABC curves obtained for each haul during the study period for each type of ground are given in Fig. 4. In most hauls in the FCA, the cumulative percentage dominance of the abundance

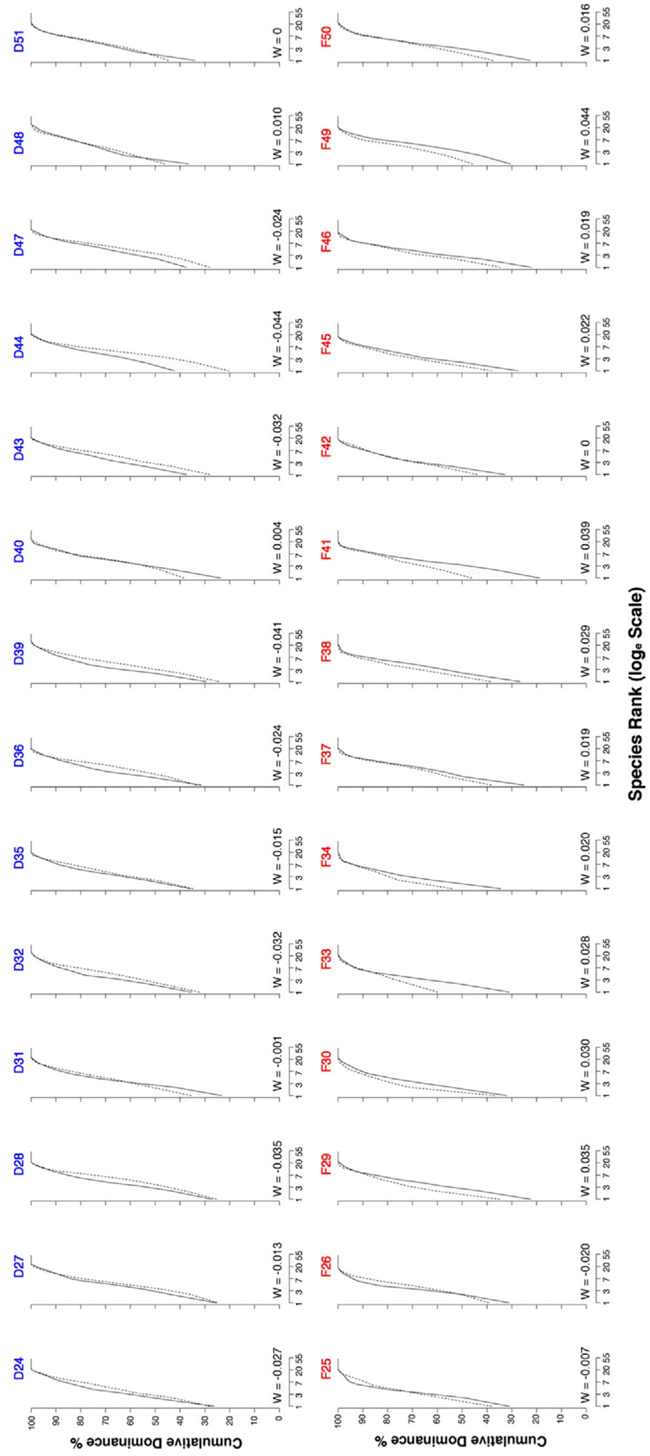

Fig. 4. ABC curves and W-values of the sampling hauls from the fishing closure area (FCA, in blue) and fishing ground (FG, in red) in the NW Mediterranean Sea. The dashed line indicates biomass; the solid line shows abundance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

curves was located above the biomass curves, indicating disequilibrium, which was represented W statistics with negative values. Only hauls #31, #40, #48 and #51 showed an overlap between curves (W $\approx$ 0), denoting partially unbalanced environmental conditions (Fig. 4). In contrast, the patterns of the curves in FG were characterized by a higher cumulative percentage dominance of biomass and thus W statistics with positive values, revealing that the majority of sites were ecologically in equilibrium. Haul #25 and #42 presented overlapping curves, and haul #26 also showed strong disturbance conditions (Fig. 4). Significant differences were detected between areas (Mann–Whitney test, U = 14.5, p = 0.001).

3.4. Length–frequency distribution analyses

The mean length was significantly higher in the FCA for all species except *M. merluccius* (Mann–Whitney test, $U = 2\,797\,863$, p = 0.320) and *L. dieuzeidei* (U = 154 566, p = 0.320) (Table 4). The comparative analysis of $L_{0.95}$ also revealed significantly higher values in most species in the FCA and was only similar between areas for *E. gurnardus* and *T. lyra* (Table 4, Figs. 5 and 6). Additionally, significant variations were found in the length–frequency distribution between areas in all species (Kolmogorov–Smirnov test, $p < 0.001$) (Table 4). In *M. merluccius*, the population structure was characterized by an increment of recruits (10–13 cm, Demestre and Sánchez, 1998) and larger adults in the FCA (Fig. 5). Other major changes were evident in *T. trachurus* and *T. capelanus*, with a clear variation in the shape of distribution and a numeric increase in the last mode. However, the patterns were much more similar between areas for *L. dieuzeidei*, although with a slight right-skewed distribution in the FCA (Fig. 5). For common species, the structural variability found in *L. boscii*, *P. blennoides* and *E. gurnardus* was similar to that described for *T. trachurus* and *T. capelanus*, with a noticeable increase in large fishes (Fig. 6). Only the population structures of *T. lyra* and *M. barbatus* were not benefited, except for a slight increase in large specimens (Fig. 6).

3.5. Diversity changes

The values of the diversity metrics of each haul are given in Table S5 (in the SM). The mean values of *FDis*, FD_Q, *H'* and *S* showed significant differences between areas (t-test = 5.083, df = 26, $p < 0.001$ for *FDis*; t-test = 3.801, df = 26, $p < 0.001$ for FD_Q; t-test = 4.806, df = 26, $p < 0.001$ for *H'*; t-test = 3.596, df = 26, p = 0.001 for *S*), reaching higher values in the FCA (Fig. 7). In contrast, *FEve* (Mann–Whitney test, U = 116, p = 0.427) and *FDiv* (U = 72, p = 0.256) did not show significant changes between areas (Fig. 7).

A total of seven functional groups (*FGR*) were identified from the cluster dendrogram constructed on the basis of functional trait dissimilarity (Fig. 8a): *FGR*-1 represented small-medium species with carangiform locomotion (e.g., *T. trachurus* and *M. surmuletus*); *FGR*-2 included all asymmetrical flatfishes (e.g., *L. boscii*, *A. laterna* and *C. linguatula*); *FGR*-3 was composed by species with sedentary oblong shapes and epibenthic habits (e.g., *B. ocellaris*, *C. maculatus*, *L. budegassa*, *L. dieuzeidei* and *H. dactylopterus*); *FGR*-4 was formed by species with benthopelagic oval shapes and balistiform locomotion (*C. aper*, *M. scolopax* and *Z. faber*); *FGR*-5 grouped species with large-sized anguilliform shapes inhabiting benthopelagic habitats (*C. conger* and *C. macrophthalma*); *FGR*-6 encompassed by roving species with subcarangiform locomotion (e.g., *M. merluccius*, *T. capelanus* and *P. blennoides*); and *FGR*-7 was composed by endobenthic species with anguilliform shapes and balistiform locomotion (*A. anguiformis* and *O. rufus*). Considering the sum of the relative abundances of these functional groups (Table S6 in the SM), the greater abundance in the FCA was linked to *FGR*-3 (Fig. 8b).

Table 4
Summarizing the fish length descriptives for the dominant and most common species captured in the fishing closure area (FCA) and fishing ground (FG) from the Roses Bay (NW Mediterranean). n, number of specimens sampled; KS test, Kolmogorov–Smirnov test, $L_{0.95}$, the fish length at 95th percentile; Q-test, quantile test; *U* test, Mann–Whitney test. In bold, significant comparisons.

Species	Area	n	Length (mm)				*U* test	KS test	Percentile	
			mean	sd	min	max			$L_{0.95}$	Q-test
E. gurnardus	FCA	95	211.1	36.1	113.0	294.0	6927	0.571	263.0	12
	FG	116	192.7	41.1	100.0	287.0	**$p = 0.001$**	**$p < 0.001$**	251.0	$p = 0.336$
L. boscii	FCA	545	196.7	40.6	54.0	336.0	112915.5	0.500	279.8	0.951
	FG	367	184.4	23.2	116.0	294.0	**$p < 0.001$**	**$p < 0.001$**	223.7	**$p< 0.001$**
L. dieuzeidei	FCA	946	112.4	17.4	61.0	154.0	154566	0.643	137.0	10
	FG	315	111.4	18.1	67.0	159.0	$p = 0.320$	**$p < 0.001$**	137.0	**$p = 0.003$**
M. merluccius	FCA	2598	202.9	71.4	54.0	590.0	2797863	0.634	333.0	21.3
	FG	2106	198.2	66.7	45.0	590.0	$p = 0.180$	**$p < 0.001$**	311.8	**$p< 0.001$**
M. barbatus	FCA	385	179.6	34.7	105.0	290.0	74962	0.643	234.0	14
	FG	341	171.2	32.7	90.0	290.0	**$p = 0.001$**	**$p < 0.001$**	220.0	**$p = 0.003$**
P. blennoides	FCA	254	238.9	67.7	126.0	396.0	32584	0.583	377.4	0.951
	FG	193	199.7	35.4	112.0	342.0	**$p < 0.001$**	**$p < 0.001$**	264.4	**$p< 0.001$**
T. trachurus	FCA	332	188.1	39.0	105.0	272.0	136563	0.500	240.0	22
	FG	531	148.3	38.2	87.0	278.0	**$p < 0.001$**	**$p < 0.001$**	222.5	**$p< 0.001$**
T. lyra	FCA	129	149.7	25.9	95.0	237.0	19052.5	0.556	197.4	14.4
	FG	251	143.8	24.9	99.0	260.0	**$p = 0.005$**	**$p < 0.001$**	183.0	$p = 0.084$
T. capelanus	FCA	587	151.9	29.8	82.0	294.0	273916.5	0.625	212.0	17.5
	FG	747	139.6	24.7	80.0	237.0	**$p < 0.001$**	**$p < 0.001$**	190.0	**p <0.001**

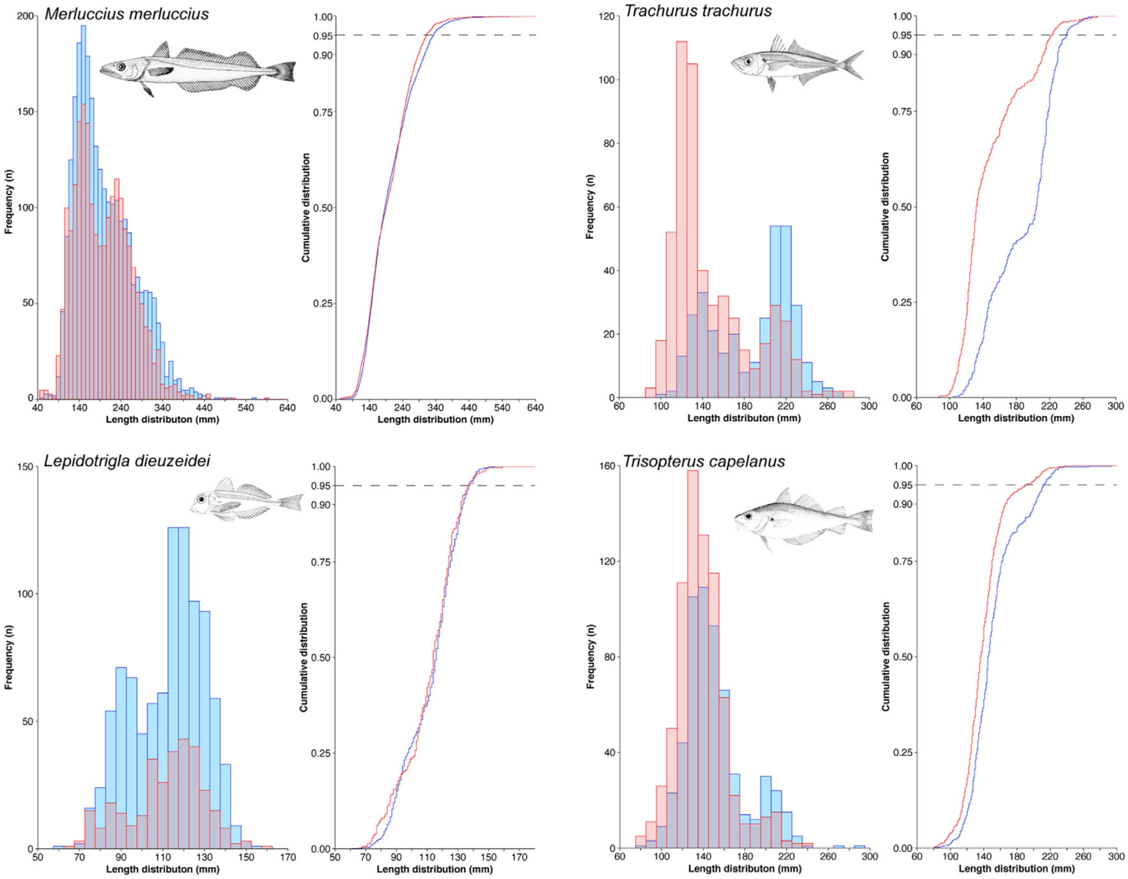

Fig. 5. Length–frequency distributions and cumulative distributions of the catch of the more relevant ecological species sampled from the fishing closure area (FCA, in blue) and fishing ground (FG, in red) in the NW Mediterranean Sea. The dashed line indicates the lengths at the 95th percentile ($L_{0.95}$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Source: Images were taken from FAO catalogs.

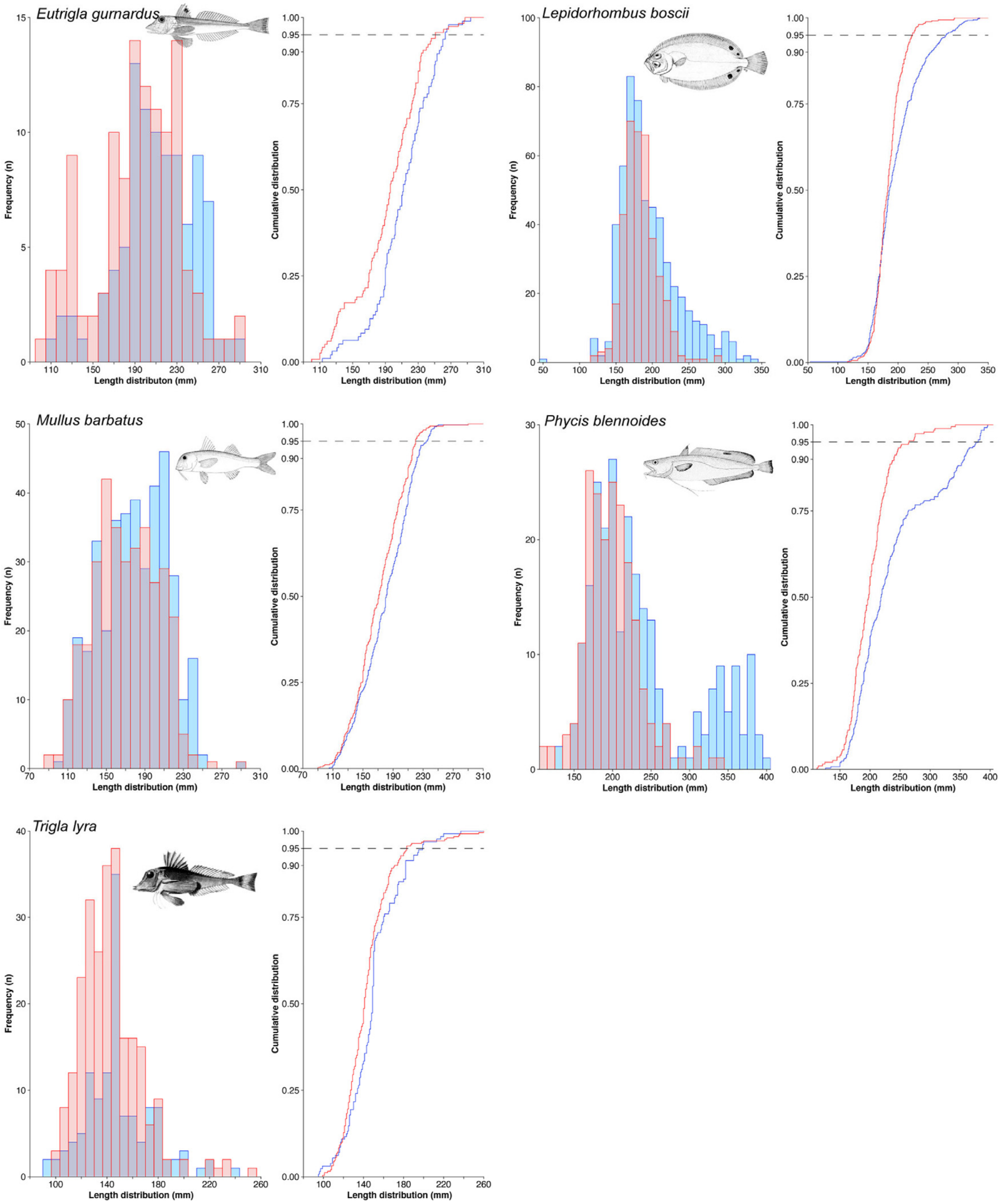

Fig. 6. Length–frequency distributions and cumulative distributions of the catch of some species of economic importance from the fishing closure area (FCA, in blue) and fishing ground (FG, in red) in the NW Mediterranean Sea. The dashed line indicates the lengths at the 95th percentile ($L_{0.95}$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Source: Images were taken from FAO catalogs

4. Discussion

This study seems to reveal changes at the community and population levels in demersal fish assemblages a short time after the cessation of fishing activity on the continental shelf in the NW Mediterranean Sea. Considering the commercial importance of *M. merluccius* throughout this geographical subarea area of (named 'northern GSA-06') (Recasens et al., 1998; Lleonart et al., 2003), the increase in recruits in the FCA can be considered great news for the population dynamics of fisheries stock enhancement. From an ecological approach, the noticeable increase in many species was the key factor explaining the evolution of the structure and composition of the fish assemblage inside the FCA. Interestingly, the initial recovery of the community entailed a drastic disturbance, although the remaining indicators analyzed in the present study (i.e., species distribution, length–frequency and diversity metrics) showed a clear benefit on the fish assemblage from the cessation of fishing. These findings reinforce the need for the implementation of new management scenarios at the regional scale in the NW Mediterranean, including networks of closed (spatially and/or temporally) areas that are essential as nurseries and spawning areas (Khoukh and Maynou, 2018; Russo et al., 2019) following the policy of directorate-general for Maritime Affairs and Fisheries of the European Union. Indeed,

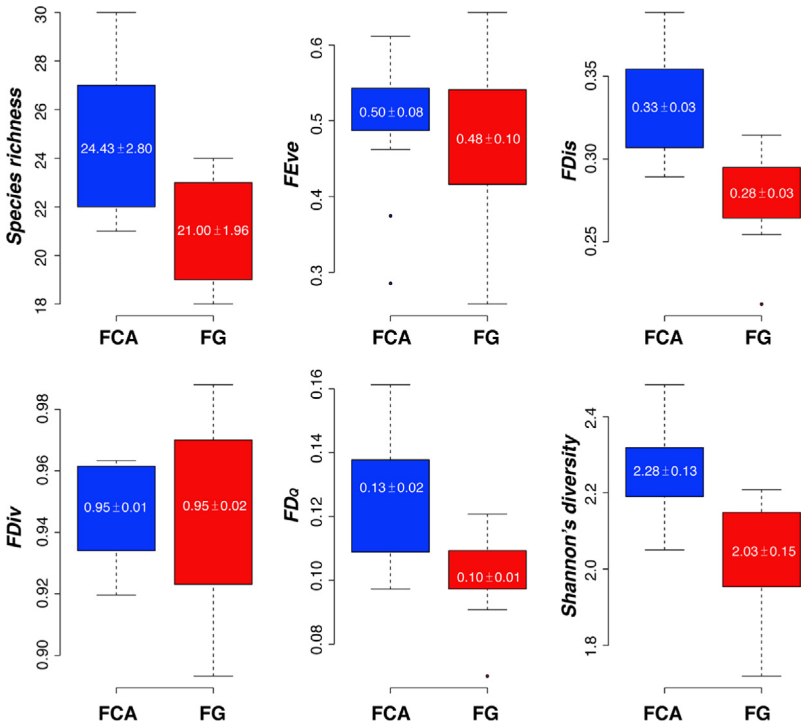

Fig. 7. Boxplots of diversity metrics from the fishing closure area (FCA, in blue) and fishing ground (FG, in red) in the NW Mediterranean Sea. *FEve*, functional evenness; *FDiv*, functional divergence; *FDis*, functional dispersion; and FD_Q, Rao's quadratic entropy. The mean and standard deviation by metric and area are given inside the boxes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

it is worth emphasizing that the success of this project was mainly due to the effective self-enforcement by local stakeholders and the general support of the broader community, which are essential in the protection and regulation of marine areas (Aburto-Oropeza et al., 2011; Jentoft et al., 2012; de Oliveira, 2013).

Nonetheless, these results must be interpreted with caution and a number of limitations should be borne in mind. The primary limitation to the generalization of these results is that statistic design based on before-after-control impact (BACI, Underwood, 1991 was not possible to be applied since it was not an advice scientific before the creation of FCA. For that reason, an alternative strategy was to evaluate a nearby fishing area with similar oceanographic characteristics. Certainly, the major problem of this decision was the closeness between areas and the likelihood a shelter effect for many species with migratory behavior. Assuming this circumstance, the fact is that FCA favored the recruitment of hake's juveniles (main task of project) and the biomass increase of other species. The second limitation concerns to number and period of hauls performed, however that was due to absence of specific economic planning for the exhaustive monitoring of areas studied. Despite these limitations, the findings are enough interesting within the regional fishing policy.

4.1. Effects at the community level

Numerous studies have demonstrated that reserves and fishing closure areas benefit the protection, restoration and functioning of marine ecosystems (Gell and Roberts, 2003; Costello and Ballantine, 2015; Sala and Giakoumi, 2018). Although the recovery of these ecosystems requires a large period of time (McClanahan and Mangi, 2000; Russ and Alcala, 2004; Russ et al., 2005), shifts do occur in the first years. Although only some species underwent important changes in terms of relative abundance and biomass, most species were benefited from fishing closures, especially those species characterized by sedentary behavior (e.g., *C. cuculus*, *H. dactylopterus*, *S. elongata* and *L. dieuzeidei*). Other species with greater motility, such as *M. surmuletus*, which are negatively affected by the water turbidity produced by trawling (Aguirre and Lombarte, 1999; Lombarte et al., 2000) were also favored by the closure. In fact, small, opportunistic and short-lived species are generally the first to recolonize the habitat (Warwick, 1986; Blanchard et al., 2004; Yemane et al., 2005; Claudet et al., 2010). The closure had a great impact on the community structure through (a) alterations in dominance or codominance. In particular, the presence of *L. dieuzeidei* increased noticeably, which may be due to the strong biogeographic affinity of this species with the studied ecoregion (NW Mediterranean Sea) (Colloca et al., 2019). (b) There were also small fluctuations in the species abundance distributions (RAD plots), which were higher considering the biomass. Overall, the RAD plots were not greatly influenced by the number of dominant and rare species since they were similar in the studied areas (FCA *vs* FG). However, the distribution of biomass within the FCA favored the presence of opportunistic species, generating a more homogeneous pattern that was clearly different. (c) There were shifts in the tendency of ABC curves and the W-statistic; the equilibrium condition was lost in the assemblage, and the community was transformed into a moderate disturbance state. In this sense, a heavy disturbance in the exploited fish assemblage could have been expected (Yemane et al., 2005; Kantoussan et al., 2007), but the lack of evidence of stress in the FG suggests some resilience of the assemblage against continued exploitation, as has been described in other communities (Jouffre and Inejih, 2005). Finally, (d) there was a positive effect on biodiversity, especially in functional diversity, with an increase in *FDis* and FD_Q since these species were distributed in the periphery of functional space and presented particular functional traits concerning trophic guild, swimming and body shape.

The recovery of ecosystems after the cessation of fishing allows the allocation of biomass inside fish assemblages, which is

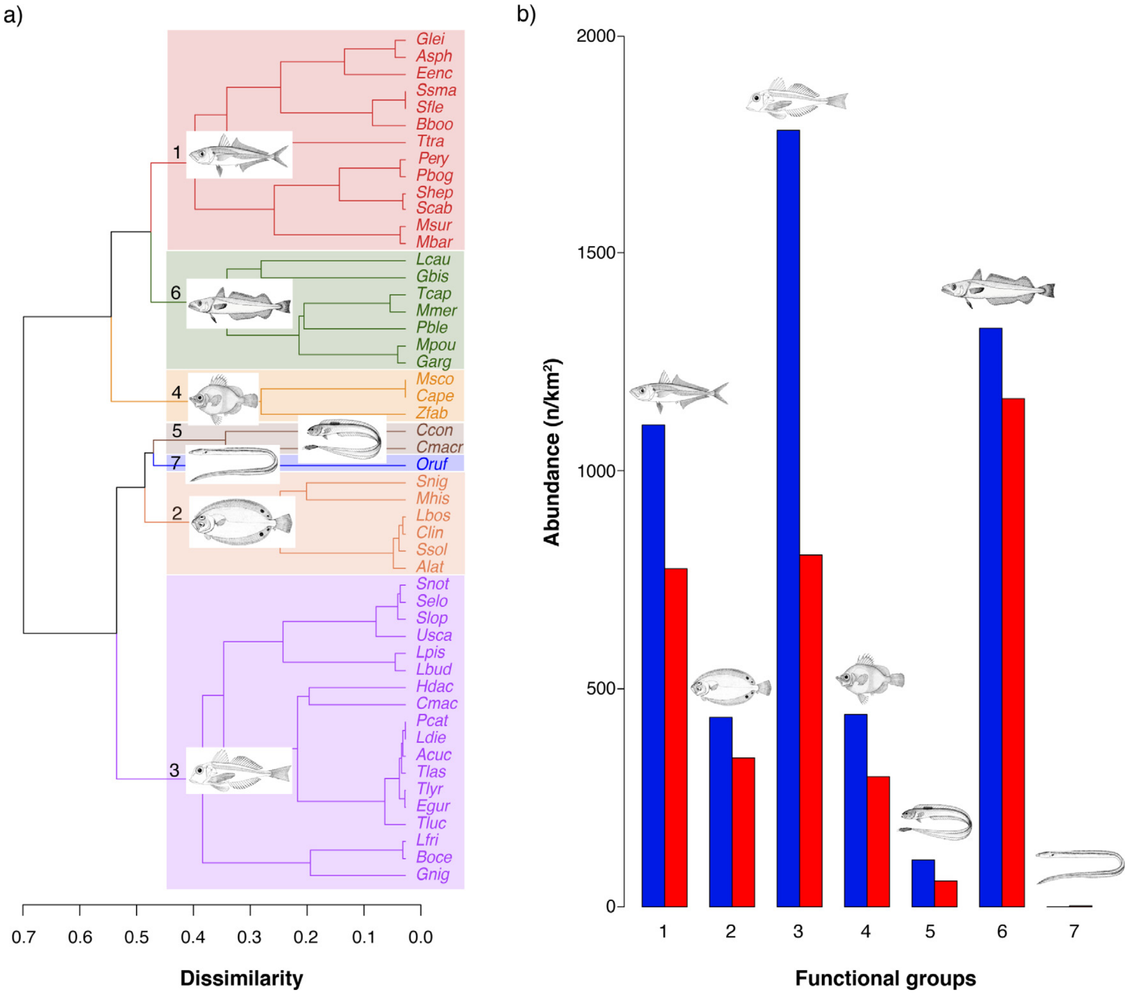

Fig. 8. (a) Dendrogram of dissimilarity (Manhattan) between species based on the functional trait matrix. Functional groups are given with numbers and color boxes. The acronym of each species is provided in Table S1. (b) Cumulative abundance bar chart (n/km^2) of the seven identified functional groups in the fishing closure area (FCA, in blue) and fishing grounds (FG, in red) in the NW Mediterranean Sea. Images of the representative species in each functional group are provided (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Source: Images were taken from FAO catalogs.

dependent on resource use, spatial domain and the habitat structure (Tokeshi, 1993; Southwood, 1996; Magurran and Henderson, 2003). It is known that trawling activities produce dramatic physical effects on the seafloor (e.g., plowing, near-bottom turbidity or substrate degradation) that damage the meiofaunal, infaunal and epibenthic communities (Smith et al., 2000; de Juan and Demestre, 2012; Puig et al., 2012; Eigaard et al., 2017). In this context, studies have demonstrated that the recovery period is shorter in soft-bottom than hard-bottom habitats (Kaiser et al., 2006; Kenchington et al., 2006; Foden et al., 2010). Although information concerning this factor was not obtained during the present study, it is highlighted that opportunistic species prey on a wide variety of infaunal and epibenthic invertebrates as well as on plankton (Montanini et al., 2017). The present study suggested a partial recovery of these communities after the cessation of fishing activity, which may be due to a higher availability of prey and/or a better detection of prey/predator via visual, acoustic, mechanical or chemical mechanisms (Nevitt, 2008). In fact, many species with a wider niche breadth can use the camouflage sit-and-wait method and their prominent eyes (visual mechanism) to detect prey (e.g., *H. dactylopterus* and *S. elongata*) (Hobson, 2006; Santon et al., 2018), and other species are particularly well adapted for locating potential prey at or just beneath the sediment surface via mechanical and chemical reception associated with pectoral fin rays (e.g., *L. dieuzeidei* and *C. cuculus*) or barbels (e.g., *Mullus* spp.) (Bardach and Case, 1965; Lombarte and Aguirre, 1997; Montanini et al., 2017). In both cases, species with particular sensory abilities seem to be favored after cessation of fishing.

4.2. Effects at the population level

The adverse impacts of bottom trawling include reductions in the population fraction of large and intermediate individuals, which affects the size structure and life history traits (e.g., maximum length, size at maturity and growth rate) (Daan et al., 2005; Speirs et al., 2016). In the case of Mediterranean trawl fisheries, the fishing effort is concentrated mainly in the juvenile fraction of commercial species (Lleonart et al., 2003), which is key to the delimitation of MPAs (marine protected areas) or FRAs (fishery restricted areas) for the protection of nursery grounds (Russo et al., 2019). Given the dominant role of size in marine ecosystems, different size-based indicators have been developed to describe changes in the structure of communities or populations (more detail in (Shin et al., 2005). Generalizing a response of all species considered in this study is inappropriate, among other reasons, because the population size structure is intrinsically linked to the biology of species, intraspecific competition for resources (e.g., food availability or habitat) and trophic interactions

(Jennings et al., 2001; Olsen et al., 2004; Audzijonyte et al., 2014). Overall, the recovery of larger adults is a common response of many species to the cessation of fishing pressure (Daan et al., 2005; Molloy et al., 2009; Kuparinen et al., 2009).

The increase reported in the FCA in the $L_{0.95}$ of some species reinforces this theory and demonstrates the recovery of some stocks at the local scale, especially in largest fish species. For instance, larger specimens of *L. boscii* suggest a noticeable migration to shallower waters, which it is characteristic of this fish species (Sánchez et al., 1988). The individuals of *P. blennoides* reach larger sizes in deeper waters (Cohen et al., 1990; Rotllant et al., 2002), but the existence of larger adults may be interpreted as an adaptive strategy to a higher availability of food in shallower waters (Alioua et al., 2018). By contrast, the juveniles and adults of *T. capelanus* were captured in similar proportion, why the presence of larger specimens was simply a direct effect of the FCA. The population size structure of *M. merluccius* showed a greater proportion of juveniles (L_{50}, female length at first maturity, approximately 36 cm TL, (Recasens et al., 1998, 2016; Colloca et al., 2002) in both areas. However, higher recruitment (especially from 14–24 cm in TL) and larger specimens (30–44 cm in TL) were detected in the FCA. In this sense, complementary studies have indicated that the temporal and spatial protection of hake spawning and recruitment areas on the Catalan coast could have an effect comparable to a reduction of fishing effort of up to 20% (Khoukh and Maynou, 2018), resulting in a significant increase in the catches, biomass and spawning stock biomass (Martín et al., 2019). Conversely, small- and medium species, such as *L. dieuzeidei*, *E. gurnardus*, *M. barbatus*, *T. lyra* and *T. trachurus,* showed less variability in the number of large specimens between areas. The smallest species, *L. dieuzeidei*, presented similar sizes (minimum, maximum, average, $L_{0.95}$), and the population was clearly differentiated between juveniles and adults in the two compared areas. However, medium species, such as *E. gurnardus*, *T. lyra* and *T. trachurus*, showed lower recruitment. This may be due to the presence of a higher number of large (ichthyophagous) predators in the community (e.g., *M. merluccius*, *C. conger* and *L. piscatorius*). Besides, the slow–medium growth rates (ca. 0.1-0-25 year^{-1}) may also influence in a fast recovery of larger specimens in the populations gurnards (i.e., *L. dieuzeidei*, *E. gurnardus* and *T. lyra*) (Papaconstantinou, 1981, 1982; Başusta et al., 2017, strongly affected by the excess fishing pressure (Colloca et al., 2019). In contrast, *M. barbatus* did not show a strong increment in size in the FCA, likely because it is favored by the water turbidity generated by fishing activity in the nearby fishing grounds (Lombarte and Aguirre, 1997; Palanques et al., 2014). The low mobility of this species, pelagic life of their eggs and larvae, and similar environmental conditions between areas can explain the absence of differences observed in the current study, which it already described in another spatial context (Tserpes et al., 2019).

5. Conclusions

Within European waters, bottom trawling is, due to its economic, environmental and social footprints, one of the more important fishing activities (Eigaard et al., 2017). Studies on the effects of temporal and spatial closures in the continental shelf have demonstrated the suitability of this strategy for the recovery of hake stocks (Khoukh and Maynou, 2018; Russo et al., 2019), but the knowledge obtained in the present study also reinforces the positive benefit at the community level. Thus, our results and the progressive decrease in terms of landings observed along the Catalan coast (NW Mediterranean) during recent years (Catalan Government Database, 2018) should be critical for European marine policy within the Marine Strategy Framework Directive (MSFD, 2008/56/EC). The present study has shown the usefulness of some indicators for describing the general dynamics of populations and communities (Nogueira et al., 2018), especially when the closure period is short. This initial knowledge about the impacts on the closure area will allow a better understanding of ecosystem evolution and its implications in the fishing management of the region. However, more conclusive results about the efficiency of the FCA regarding biodiversity and community structure restoration and conservation will require longer protection times and probably an expansion of the spatial coverage, including the protection of a wider variety of different bottoms and habitats.

CRediT authorship contribution statement

V.M. Tuset: Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **M. Farré:** Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **U. Fernández-Arcaya:** Data curation, Writing - review & editing. **M. Balcells:** Data curation, Writing - review & editing. **A. Lombarte:** Conceptualization, Data curation, Writing - review & editing. **L. Recasens:** Conceptualization, Methodology, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2021.101700.

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