

Maerl beds inside and outside a 25-year-old no-take area

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ABSTRACT: Maerl beds, which harbour productive, diverse benthic communities, are threatened by human activities. Although some types of fishing activities can impact maerl beds, their effects are poorly studied due to the lack of appropriate un-fished control sites. In this study, we took advantage of the 25 yr old no-take Columbretes Islands Marine Protected Area (MPA) (NW Mediterranean) as the best available reference for pristine conditions and assessed (1) the conservation status of maerl beds in this MPA and (2) the impacts of fishing in nearby beds that are open to this activity. We compared macroalgal species richness (including both calcifying and non-calcifying species), maerl cover and the live proportion of maerl in 3 contiguous zones with different protection histories: inside the 25 yr old MPA (IN25), inside the adjacent 6 yr old MPA (IN6) and in the unprotected grounds surrounding the MPA where fishing continues (OUT). We also analysed differences between shallow (30 to 49 m) and deep (50 to 69 m) beds inside the IN25 area. As expected, all variables were higher in shallow than in deep beds within the IN25, likely because of greater irradiance and water motion in the shallow realm. Maerl cover and algal species richness were greater in deep beds within the IN25 than in the adjacent beds of the OUT region that was composed of similar bathymetric and sediment features, and thus protection from fishing activities in the MPA can best explain these differences. Nonetheless, the proportion of live maerl was similar in both areas. Factors such as differences in light exposure or fragmentation by fishing gear (thus generating new recruits) under a sufficiently intense hydrodynamic regime (thus avoiding burial) may mask fishing impacts on the fraction of live maerl. Similar maerl cover in long- and short-term protected contiguous beds suggests that recovery of such algal beds might occur within 6 yr after fishing cessation.

KEY WORDS: Maerl · Rhodolith cover · Live maerl · Fishing effects · Algal assemblages · Diversity · Marine protected areas · Northwestern Mediterranean

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INTRODUCTION

The Breton term 'maërl' refers to biogenic sediments comprised of living and dead unattached, non-geniculate coralline algae (i.e. un-segmented because they lack non-calcified joints). Attempts have been made to distinguish between maerl in the most frequently used sense (i.e. branched, twig-like struc-

tures) and rhodoliths, i.e. structures having nodules consisting principally or entirely of coralline algae that may or may not have a non-algal core (Bosence 1983a,b). Maerl or rhodolith beds occur as free-living algae that grow to form branched or spherical structures in successive layers, facilitated by their rotation on a substrate influenced by currents (e.g. Bosence 1976, Foster 2001).

Maerl beds are distributed worldwide in sedimentary infralittoral and circalittoral bottoms (Bosence 1983a,b, Foster 2001) and are common in European seas (Donnan & Moore 2003a,b). They can be found at depths ranging from 5 to 35 m in the Western Atlantic (Hall-Spencer 1998, BIOMAËRL team 1999, Foster 2001, Peña et al. 2014) and at greater depths in the Mediterranean (Jacquotte 1962, Ballesteros 1989, Soto 1990, Barberá et al. 2003, 2012a, Sciberras et al. 2009), although knowledge on their distribution and ecology is scarcer for the latter. Maerl beds play an important role in bioengineering marine ecosystems: the complex 3-dimensional structure built by maerl-forming algae provides a diverse biogenic substrate for a variety of organisms, predominantly red fleshy algae and associated fauna such as sponges, bryozoans, worms, bivalves, and urchins (e.g. Grall & Glémarec 1997, Hall-Spencer 1998, Steller et al. 2003, Hinojosa-Arango & Riosmena-Rodríguez 2004, Barberá et al. 2012a).

Maerl-forming algae are slow growing (average annual growth at the tip of approximately 1 mm yr^{-1} ; Adey & McKibbin 1970, Potin et al. 1990, Blake & Maggs, 2003) and long-lived (up to 30 yr; Birkett et al. 1998). Hence, renewal rates are low (e.g. 10 to 15 yr; Ballesteros 1989) and deposits can accumulate over 100s to 1000s of years. Thus, maerl beds are considered a non-renewable resource (Foster 2001, Blake & Maggs 2003). Because of their low resilience, threats to maerl habitats have received increased attention in recent decades (Bellan-Santini et al. 2002, Donnan & Moore 2003a,b), as reflected in legal instruments for their conservation as well as fishery regulations (i.e. Annex V of Habitats Directive 92/43/EEC, Barcelona Convention Decision 1999/800/EC, and Mediterranean Fisheries Regulation EC no. 1967/2006, Order AAA/2808/2012) forbidding fishing activities on seagrasses, maerl/rhodolith grounds and coralligenous formations.

Despite these protective measures, maerl beds continue to be threatened by human activities. Indeed, the most severe impacts—commercial extraction of rhodoliths (mainly as fertilizer) and habitat removal due to offshore construction activities—have resulted in irreversible changes to maerl beds over human-relevant timescales (Birkett et al. 1998, Donnan & Moore 2003a,b). Other severe threats include poor water or sediment quality (e.g. from aquaculture activities; Sanz-Lázaro et al. 2011) and towed fishing gear such as grabs and bottom trawls, as reported in the Atlantic (Hall-Spencer 1998, De Grave & Whitaker 1999, Hall-Spencer & Moore 2000a,b, Hauton et al. 2003). There are fewer studies investigating

fishing impacts on maerl in the Mediterranean (e.g. Ramos-Esplá & Sánchez-Lizaso 2002, Bordehore et al. 2003), even though fishing activities in this region are ubiquitous and have occurred since ancient times (e.g. Spanier et al. 2015). As a consequence, there are few un-fished maerl habitats that can be used as a reference.

The Columbretes Islands Marine Protected Area (MPA) is a Spanish Mediterranean marine reserve that was closed to fishing 25 yr ago (1990) and expanded 6 yr ago (2009). The MPA and surrounding area (in which traditional fishing activities occur) comprises rocky and coralligenous formations coexisting with sedimentary bottoms harbouring maerl beds. Based on the possibilities afforded by this scenario, we aimed to assess the effects of fishing on maerl beds by comparing algal species richness, maerl cover, and the proportion of live maerl in beds distributed at 3 sites with different histories of fishing restrictions: within the 25 yr old MPA (IN25), in the adjacent 6 yr old zone (IN6), and outside the MPA in the surrounding grounds offering no protection from fishing (OUT). Factors such as irradiance and water motion generate depth-related differences for the same variables between shallow (S) and deep beds (D). Therefore, the hypotheses of the current study were as follows: (1) depth affects maerl structure (comparison between D and S in IN25); (2) long-term protection affects maerl structure (comparison between IN25 and OUT in D); and (3) short-term protection affects maerl structure (comparison between IN25, IN6 and OUT in D). Finally, given the scarcity of records describing algal species in maerl beds in the region, and specifically in the Columbretes Islands, an additional objective of this study was to inventory the algal species present.

MATERIALS AND METHODS

Study area

Sampling for the study was conducted in the Columbretes Islands Marine Reserve (hereafter referred to as the MPA) and surrounding fishing grounds (Fig. 1) between 2 and 10 August 2014. The Columbretes Islands is an archipelago situated in the northwestern Mediterranean, 50 km from the coast of the Iberian Peninsula at the edge of the continental shelf. The MPA was designated in 1990 with a surface area of 44 km^2 , and was expanded to the north and south in 2009 to encompass a total area of 55 km^2 . The enlarged 6 yr old protected area consti-

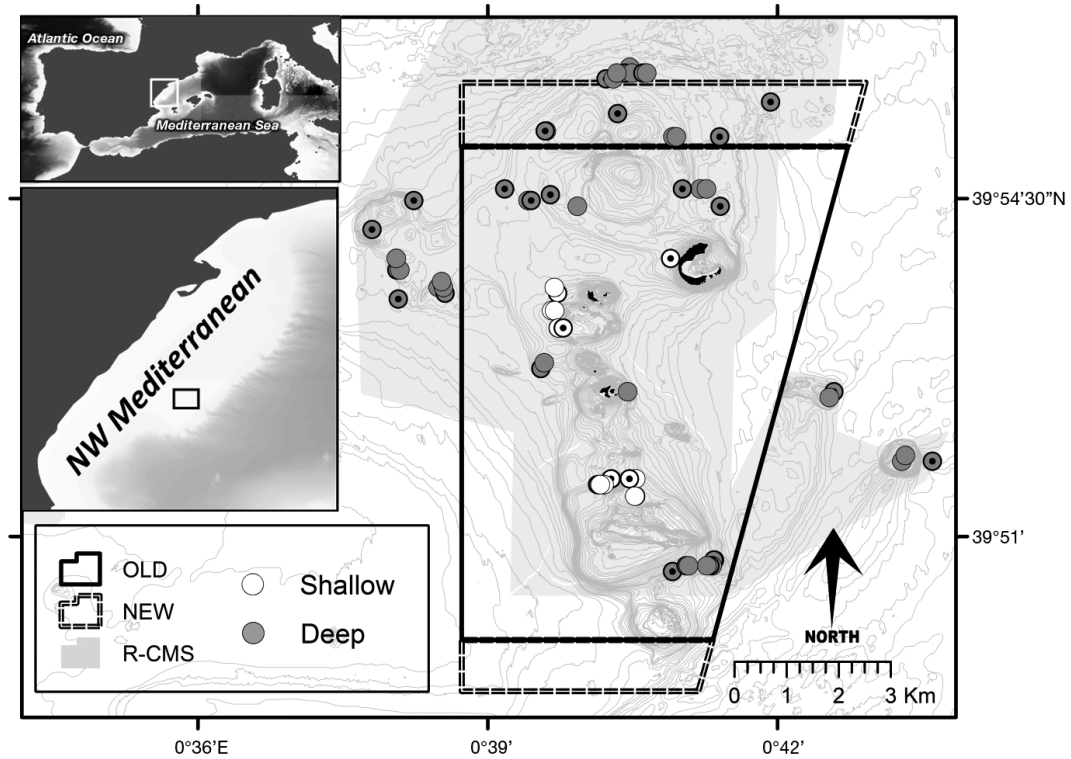


Fig. 1. Study area and sampling locations. R-CMS substrata (rock - coarse and mixed sediment) are delimited by grey shading. Continuous-line polygon: 25 yr old MPA (IN25); dashed-line polygon: newly expanded MPA (IN6). White and grey circles: shallow and deep valid grabs, respectively (circles with a black dot inside indicate the grabs where sediment samples were collected)

tutes a transition zone from the long-term protected area and fully fished, adjacent fishing grounds. The MPA extends from the intertidal to 80 m and harbours volcanic rock, coralligenous habitats and sedimentary habitats where the maerl beds begin at 30 m. The fishing grounds around the MPA consist of bottoms at depths ranging from 60 to 100 m, with patches of rock and maerl distributed over expanses of gravel, sand and mud. The MPA legislation prohibits all commercial fishing within its borders, and this regulation is well enforced. After designation of the MPA, bottom trawl and artisanal fishing efforts were relocated to open fishing grounds (Masip 1998, Goñi et al. 1999), later coalescing towards the boundaries of the MPA to harvest spillover (Fig. 1) (Goñi et al. 2006).

Sampling design

The factor 'protection history' (i.e. protection from fishing activities) was defined with 3 levels: IN25 (inside the MPA, 25 yr of protection), IN6 (inside the MPA, 6 yr of protection) and OUT (outside the MPA, no protection). Depth was defined with 2 levels: shal-

low (S; 30 to 49 m) and deep (D; 50 to 69 m). Shallow maerl beds are only present inside the IN25, and fishing activities are only performed in deep regions.

The following effects were tested by 1-way analysis: (1) effect of depth, comparing S and D maerl beds at the IN25 protection history level; (2) effect of long-term protection, comparing IN25 and OUT protection history levels within the D depth factor; (3) effects of short-term protection, comparing IN25, IN6 and OUT protection history levels within the D depth factor in the north sector of the study area (grey box in Fig. 1). Intense fishing activity along the boundary of the MPA has previously been described in this sector (Goñi et al. 2006).

For effects (1) and (2), 19 to 25 valid random grab samples were collected for each factor–level combination. To test effect (3), 9 random grab samples per protection level were collected in the northern sector. In total, 72 maerl grab samples were processed and analysed.

Sample collection and processing

Maerl and sediment samples were collected using a van Veen grab with a surface area of 0.09 m² (0.3 ×

0.3 m) and a 20 cm substrate penetration depth. A broad-scale predictive bionomic distribution of substrata obtained from the EUSeaMap project (www.emodnet-seabedhabitats.eu/) was used, as this is the only available information on seabed habitat distribution in the study area. We focussed our sampling randomly on the 'rock - coarse and mixed sediment' substrate category (R-CMS; grey shading in Fig. 1). Due to the lack of detailed bionomic information, prior to sampling, visual real-time observations were conducted using a submarine sled-mounted 360° TV camera. Grab stations were randomly assigned to areas showing continuous maerl cover.

Sediment (200 g) from a subset of grab samples was removed and stored frozen for later granulometric analysis according to the procedures established by Buchanan (1984). Sediment textural characteristics were established by dry sieving using a series of sieves ranging in mesh size (2 mm, 1 mm, 500 µm, 250 µm, 125 µm, 63 µm and <63 µm). Granulometric parameters (% gravel, % sand, % mud, and ϕ [mean particle diameter]) were obtained using Gradistat® software (Blott & Pye 2001) following the estimation methods of Folk & Ward (1957).

Rhodoliths and fleshy algae were extracted using superposed sieves of 4 and 1 mm mesh, sorted and identified to the lowest possible taxonomic level (Peña & Bárbara 2004, Braga & Aguirre 2009, Harvey & Woelkerling 2007, Rodríguez-Prieto et al. 2013). Algal cover (total and by species) was measured as the area (cm²) occupied by all algal thalli horizontally extended on a 250 cm² methacrylate sheet with a 25 cm² grid. Cover was expressed as the percentage of area occupied in terms of the grab sample unit area (30 × 30 cm). Because maerl occurs in layers, this percentage can exceed 100%.

Due to the patchy distribution of maerl beds, to maximize the comparability of maerl samples, valid grabs were considered those with maerl cover ≥100% (or the grab sample unit area, 30 × 30 cm). The percentage of live and dead maerl was recorded for both the total sample and individual species. The arbitrary criterion used to deem maerl as being alive was 'rhodoliths with a coloured surface ≥10%' (Bordehore et al. 2003, Steller et al. 2003). The following variables were measured for each maerl sample: macroalgal species richness (*S*; including both calcifying and non-calcifying algae), maerl cover (%; total and main species), and proportion of live maerl main species. Main species were those with a frequency of occurrence and a percent cover ≥75%. Sediment samples were collected from 37 valid grab maerl samples (circles with black dots in Fig. 1).

Data analysis

Draftsman plots and principal component analysis (PCA) by means of normalized Euclidean distances (Clarke & Warwick 2001) were used for an exploratory analysis of environmental variables. The matrix of environmental variables for each station included depth, % gravel, % mud and mean grain diameter (% sand was highly correlated with % gravel [$r = 0.983$, $p < 0.001$] and was not included in the analysis). With the exception of depth, all variables were $\log(x + 1)$ transformed.

Multidimensional scaling (MDS) ordination and cluster analysis were used to identify groups of samples based on algal composition. The Bray-Curtis similarity index was chosen as the similarity coefficient, and group average as the clustering algorithm. Similarity profile (SIMPROF) permutation tests were used to identify clusters in the data, and analysis of similarity (ANOSIM) was used to test for differences in algal assemblage composition among treatments (Clarke & Warwick 2001, Clarke et al. 2008). The matrix of variables included the cover (%) of algal species contributing to more than ≥5% of the total cover. Multivariate analyses were performed with the software PRIMER v6 (Clarke & Gorley 2006).

One-way ANOVA was used to test for differences at the univariate level for the 3 effects described above (see 'Sampling design' above). Our hypotheses were as follows: (1) depth affects maerl structure (comparison between D and S within IN25); (2) long-term protection affects maerl structure (comparison IN25/OUT in D); and (3) short-term protection affects maerl structure (comparison IN25/IN6/OUT in D). The variables of maerl structure we tested were macroalgal species richness, maerl cover (%; total and main species), and proportion of live maerl (% main species). Prior to analysis, Cochran's test was used to check for homogeneity of variances in the treatment data, which is especially important in unbalanced designs. When Cochran's test showed significant differences for all possible data transformations, the significance level was lowered from $p < 0.05$ to $p < 0.01$ to reduce the likelihood of a Type I error. When ANOVA detected significant differences, a Student-Newman-Keuls (SNK) post hoc test was applied to define differences among the treatments (Underwood 1981). Univariate analyses were performed with SPSS v.12, which allows for ANOVA analysis in the case of unbalanced sampling design.

Table 1. Mean (\pm SE) environmental variables in maerl beds according to depth and fishing history factor combinations. IN25: inside the 25 yr old MPA; IN6: inside the 6 yr old MPA; OUT: outside the MPA; S: shallow strata; D: deep strata

Zone	IN25 (S)	IN25 (D)	IN6 (D)	OUT (D)	Total
No. of stations	19	20	9	25	73
Depth	41.8 \pm 1.1	55.8 \pm 0.8	57.1 \pm 1.3	59.0 \pm 0.9	53.5 \pm 1.0
Depth range (m)	34–49	50–63	54–65	52–67	34–67
% Gravel	21.8 \pm 2.6	24.6 \pm 4.7	18.6 \pm 4.1	20.5 \pm 2.7	22.0 \pm 1.9
% Sand	77.4 \pm 2.6	74.1 \pm 4.6	80.9 \pm 4.4	78.8 \pm 2.6	77.1 \pm 1.9
% Mud	0.8 \pm 0.4	1.3 \pm 0.3	0.5 \pm 0.4	0.7 \pm 0.2	0.9 \pm 0.2
Mean particle diameter (ϕ ; μm)	1049.1 \pm 110.2	1112.9 \pm 136.9	1137.9 \pm 38.2	1037.2 \pm 85.7	1074.8 \pm 58.0

RESULTS

Sediment characteristics

PCA did not segregate the sediment samples by depth or protection history, a result that was confirmed by ANOVA ($p > 0.05$). The sediments sampled corresponded to the 'gravelly sand' or 'sandy gravel' categories defined by Shepard (1954). Overall, the grain type composition was found to be 22.0% gravel, 77.1% sand and 0.9% mud. The mean (\pm SE) particle diameter was 1074.8 \pm 58 μm (Table 1), ranging from 500 to 2700 μm .

Algal community in maerl beds of the Columbretes Islands

A total of 72 species of algae were identified in the study area. These included 7 species of maerl-forming rhodophytes: *Lithophyllum racemus* (Lamarck) Heydrich, *Lithothamnion corallioides* (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan, *Mesophyllum lichenoides* (J. Ellis) Me. Lemoine, *Mesophyllum expansum* (Philippi) Cabioch & M.L. Mendoza, *Phymatolithon calcareum* (Pallas) W. H. Adey & D. L. McKibbin, *Spongites fruticosus* Kützinger and 1 unidentified *Mesophyllum* species (see Appendix).

The maerl-associated fleshy algae included 65 species: 8 ochrophytes, 50 rhodophytes and 7 chlorophytes (Appendix). Six additional taxa did not correspond to any species reported to date from the Mediterranean; these taxa will be identified using molecular tools. The fleshy algae found in rhodolith beds ranged from crustose forms to large brown algae such as *Laminaria rodriguezii* Bornet. Rhodophytes with erect thalli were dominant, representing nearly 77% of the algal cover, whereas the order Peyssonneliales, with 11 species, accounted for 16% of the algal cover. The mean (\pm SE) values per sample were as follows: algal species richness: 9.4 \pm 0.4;

maerl cover: 362.5 \pm 36.2%; and proportion of live maerl: 48.8 \pm 3.5%. The most abundant species were *L. corallioides* and *S. fruticosus*, both with 100% occurrence and 221.0 and 97.1% cover, respectively (Appendix). Other common seaweeds included the Ochrophyta *Halopteris filicina* (59.5% occurrence, 14.6% cover), the Rhodophyta *Peyssonnelia rubra* (60.8% occurrence, 11.8% cover), and the Chlorophyta *Valonia macrophysa* (50.0% occurrence, 0.4% cover) (Appendix).

Maerl algal communities in shallow and deep beds inside IN25

Cluster and SIMPROF analyses of algal species cover within the IN25 region revealed 2 assemblages (45.3% similarity level) associated with the 2 depths (Fig. 2). ANOSIM confirmed this difference ($R = 0.634$, $p < 0.001$), which was mainly characterized by a higher maerl cover in the shallow than in the deep stratum (618 vs. 359%; ANOVA, $F_{1,37} = 5.356$, $p < 0.05$) (Fig. 3). Algal species richness was similar at the 2 depths, with 11.2 \pm 0.6 and 10.3 \pm 0.8 mean (\pm SE) species sample⁻¹ and a total of 45 and 46 species (19 and 20 samples each) at the shallow and deep strata, respectively. Of the main maerl-forming species, *L. corallioides*, prevailed in shallow beds (ANOVA, $F_{1,37} = 16.069$, $p < 0.001$) while *S. fruticosus* dominated in deep beds (ANOVA, $F_{1,37} = 8.390$, $p < 0.01$). The fraction of live maerl was higher in shallow beds for both *L. corallioides* (ANOVA, $F_{1,37} = 8.201$, $p < 0.001$) and *S. fruticosus* (ANOVA, $F_{1,37} = 7.658$, $p < 0.001$). Algae present only in the deep stratum were the brown algae *H. filicina* and *L. rodriguezii* (Table 2). Less-abundant species such as *P. calcareum*, *Amphiroa rubra*, *M. expansum* and *M. lichenoides* were more prevalent in shallow beds (Table 2); *Peyssonnelia rosa-marina*, *P. rubra* and *Peyssonnelia crispa* were also more abundant in the shallow stratum, although not significantly (Table 2).

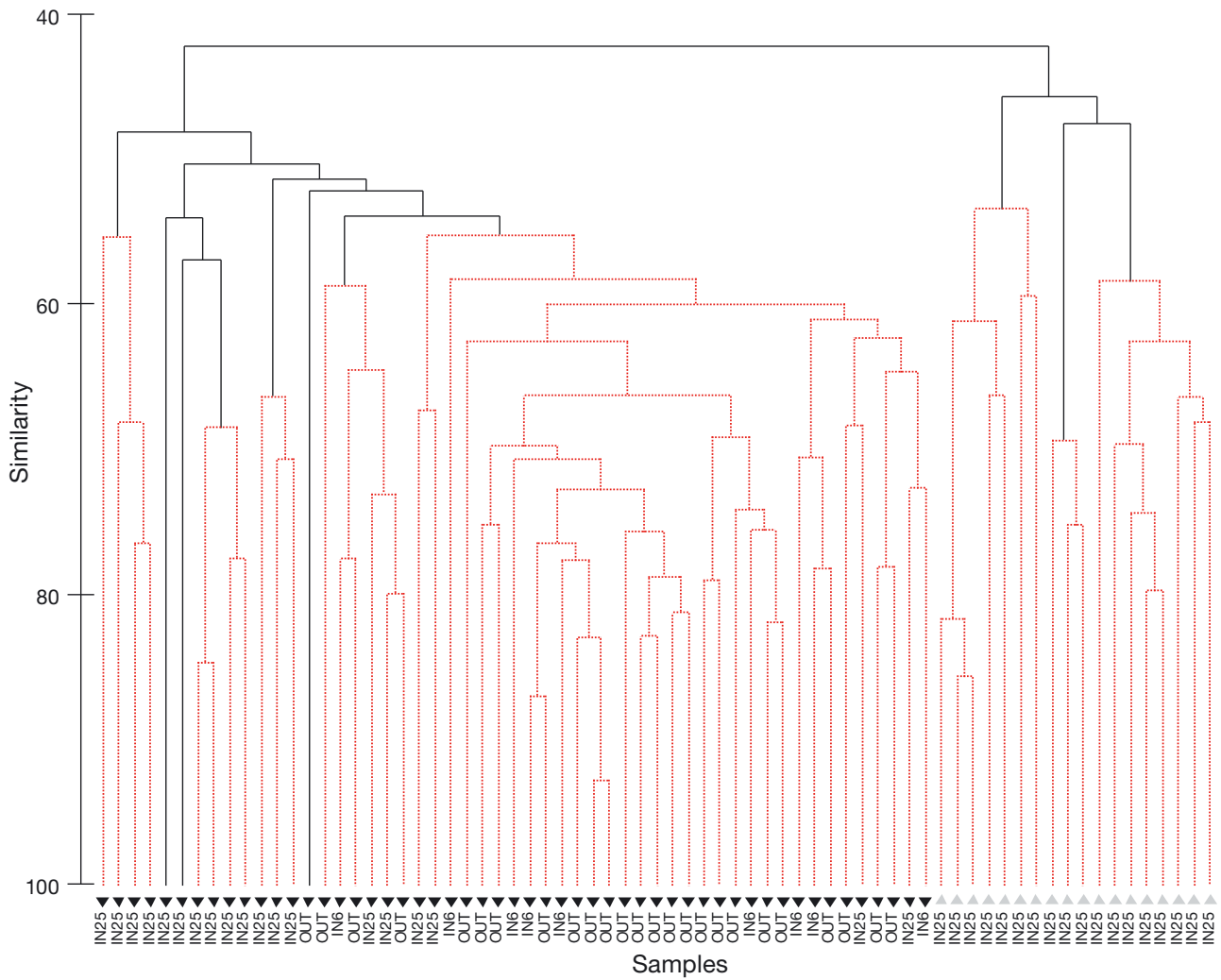


Fig. 2. Clustering (CLUSTER) ordination of samples based on the matrix of algae (% cover) in stations inside the 25 yr old MPA (IN25), inside the 6 yr old MPA (IN6) and outside the MPA (OUT). Shallow samples (▲) and deep samples (▼). Continuous black lines indicate segregation of groups of samples with significant dissimilarity (SIMPROF)

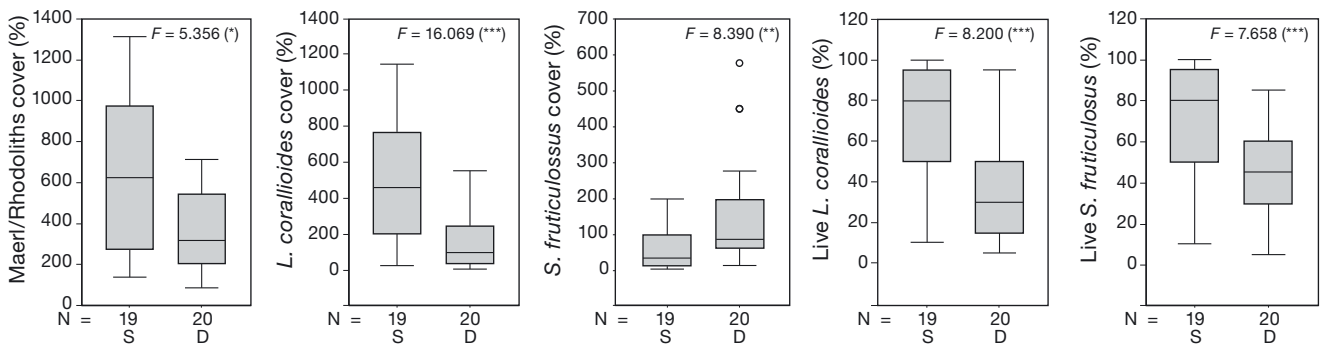


Fig. 3. Total maerl cover (%) and cover and live fraction (%) of the main species (*Lithothamnion corallioides* and *Spongites fruticosus*) in shallow (S) and deep (D) beds of the 25 yr old MPA (IN25). The horizontal line within the box indicates the median, box indicates the interquartile range, whiskers indicate the minimum and maximum values, and dots indicate outliers. ANOVA results are indicated: $F = F$ -ratio; $p =$ level of significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Table 2. Mean (\pm SE) percent cover of main maerl-forming algae in beds of shallow (S) and deep (D) bottoms of the long-term marine protected area (IN25) and the live percentage for the 2 main species. The results of 1-way ANOVA are specified. F = F -ratio; p = level of significance (ns: not significant; ** p < 0.01; *** p < 0.001)

	IN25 (S) (n = 19)	IN25 (D) (n = 20)	$F_{1,37}$ (p)
Rhodophyta			
Maerl/rhodoliths			
<i>Lithothamnion racemosum</i>	1.0 \pm 0.3	0.2 \pm 0.1	5.421 (ns)
<i>Lithothamnion corallioides</i>	501.1 \pm 76.1	160.0 \pm 38.8	16.069 (***)
<i>Phymatolithon calcareum</i>	6.0 \pm 2.0	0.1 \pm 0.1	51.625 (***)
<i>Spongites fruticosus</i>	62.8 \pm 14.7	158.1 \pm 37.8	8.389 (**)
<i>Mesophyllum expansum</i>	4.5 \pm 1.9	0.0 \pm 0.0	16.820 (***)
<i>Mesophyllum lichenoides</i>	1.9 \pm 0.8	0.2 \pm 0.2	8.948 (***)
Non-maerl species			
<i>Amphiroa rubra</i>	5.8 \pm 2.8	0.0 \pm 0.0	16.682 (***)
<i>Peyssonnelia rosa-marina</i>	3.1 \pm 1.8	0.9 \pm 0.6	1.245 (ns)
<i>Peyssonnelia rubra</i>	36.5 \pm 11.8	6.5 \pm 2.6	1.590 (ns)
<i>Phyllophora crispa</i>	5.1 \pm 3.4	1.0 \pm 0.5	0.014 (ns)
Ochrorophyta			
<i>Halopteris filicina</i>	0.0 \pm 0.0	15.4 \pm 4.8	
<i>Laminaria rodriguezii</i>	0.0 \pm 0.0	7.4 \pm 6.6	
% Live <i>Lithothamnion corallioides</i>	68.0 \pm 7.4	35.7 \pm 6.0	8.200 (***)
% Live <i>Spongites fruticosus</i>	72.6 \pm 5.8	45.5 \pm 5.0	7.658 (***)

Maerl algal communities in beds with different protection histories (deep stratum only)

Long-term protection

Mean species richness per sample was slightly higher in the long-term protected area IN25 (10.3 ± 0.8) than in the fished area OUT (7.8 ± 0.5) (ANOVA,

$F_{1,43} = 6.756$, $p < 0.05$). However, the total number of algal species identified was notably larger within IN25 (46 species) than in OUT (35 species) (20 and 25 samples each).

A number of rare species (e.g. *Nemastoma dumontioides*, *Chryssomenia ventricosa* and *L. rodriguezii*) and more common red algae (e.g. *Tricleocarpa fragilis*, *Gloiocladia repens*, and *Peyssonnelia coriacea*, *P. duby* and *P. harveyana*) were only recorded within IN25. Moreover, interspecific differences by genus were found. For example, *Kallymenia requienii* was recorded in the OUT region, but *K. feldmannii* and *K. patens*, 2 rarer species, were only found within IN25. Similarly, for the genus *Gloiocladia*, *G. furcata* was ubiquitous, whereas *G. repens* and *G. microspora* were present only inside IN25.

Maerl cover and cover of the main species of maerl-forming algae were higher inside IN25 than in the OUT region (ANOVA, maerl cover $F_{1,43} = 28.331$, $p < 0.001$; *L. corallioides* cover $F_{1,43} = 4.199$, $p < 0.05$; *S. fruticosus* cover $F_{1,43} = 4.319$, $p < 0.05$) (Fig. 4). Although Fig. 4 suggests a higher fraction of dead *L. corallioides* inside the IN25 than the OUT region, and a higher fraction of dead *S. fruticosus* within OUT than IN25, these differences were not significant (ANOVA, *L. corallioides* $F_{1,43} = 1.189$ $p > 0.05$; *S. fruticosus* $F_{1,43} = 0.390$ $p > 0.05$).

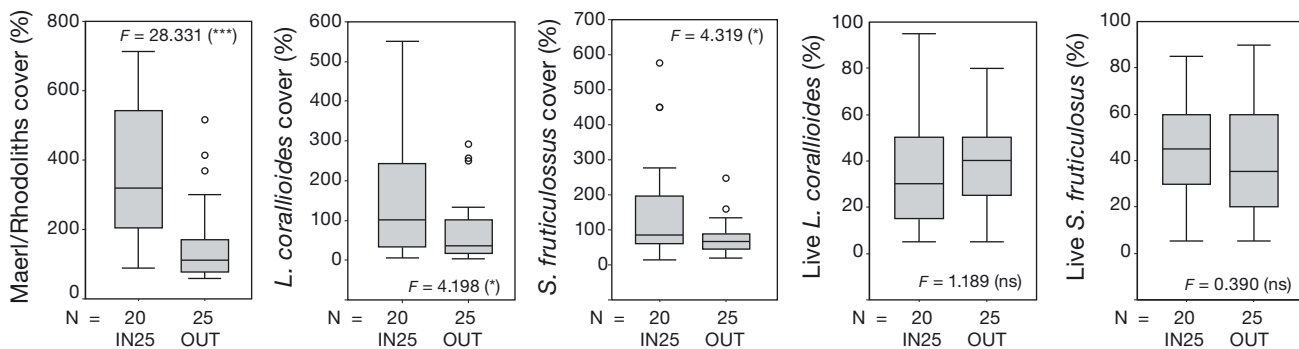


Fig. 4. Long-term protection: total maerl cover (%) and cover and live fraction (%) of the main species (*L. corallioides* and *S. fruticosus*) in deep beds (D) in the 25 yr old MPA (IN25) and in the fished area (OUT). The horizontal line within the box indicates the median, box indicates the interquartile range, whiskers indicate the minimum and maximum values, and dots indicate outliers. ANOVA results are indicated: F = F -ratio; p = level of significance (ns: not significant; * p < 0.05; *** p < 0.001)

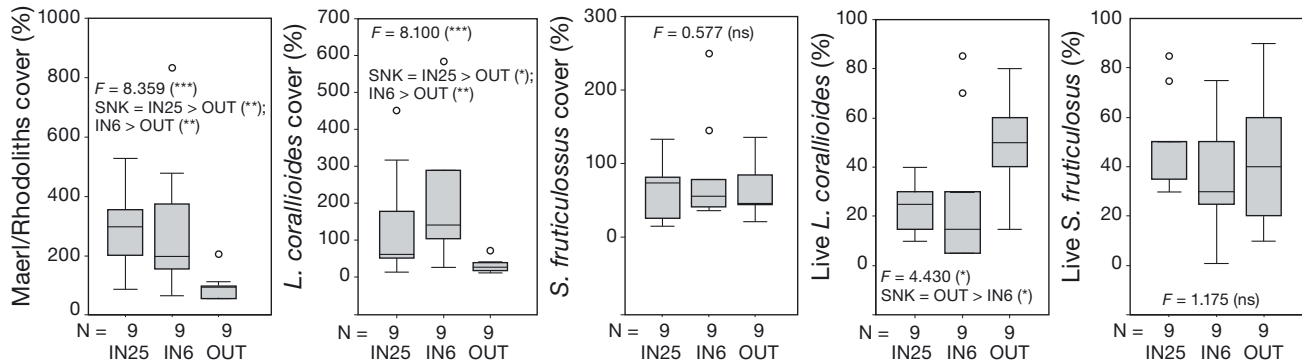


Fig. 5. Short-term protection: total maerl cover (%) and cover and live fraction (%) of the main species (*L. corallioides* and *S. fruticulosus*) in deep (D) beds inside the 25 yr old MPA (IN25), the 6 yr old MPA (IN6) and the fished area outside (OUT) (grey-line box in Fig. 1). The horizontal line within the box indicates the median, box indicates the interquartile range, whiskers indicate the minimum and maximum values, and dots indicate outliers. ANOVA and Student-Newman-Keuls (SNK) results are indicated. F = F -ratio; p = level of significance (ns: not significant; * p < 0.05; ** p < 0.01; *** p < 0.001)

Short-term protection (northern zone)

In the northern section (grey line box in Fig. 1), both the number of species and mean species per sample were higher within the IN25 area (32 species, 10.4 ± 0.7 species sample⁻¹) than in both the IN6 (23 species, 8.2 ± 1.0 species sample⁻¹) and OUT areas (26 species, 7.2 ± 0.3 species sample⁻¹) (9 samples each), but without statistical differences (ANOVA, $F_{2,24} = 2.02$, $p > 0.05$). The values of overall maerl cover (ANOVA, $F_{2,24} = 8.359$, $p < 0.001$) and *L. corallioides* cover (ANOVA, $F_{2,24} = 8.100$, $p < 0.05$) were lower in the OUT area than IN25 and IN6 (Fig. 5). In contrast, the fraction of live *L. corallioides* was highest in the OUT area (ANOVA, $F_{2,24} = 4.430$, $p < 0.05$; Fig. 5). However, *S. fruticulosus* cover and the live fraction did not differ among beds with different histories of protection, i.e. IN25, IN6 and OUT (ANOVA, $p > 0.05$) (Fig. 5).

DISCUSSION

This is the first study to focus on the effects of fishing on maerl beds in the Mediterranean Sea using a long-term protected area as a reference for unfished conditions. The existence of the 25 yr old no-take MPA, which contained maerl beds that extended into the short-term protected grounds as well as to fished beds outside the MPA offered a rare opportunity to study fishing impacts on maerl beds. The fished beds exhibited lower maerl cover than both the long- and short-term protected beds at a similar depth. Unexpectedly, the proportion of live maerl was similar or higher (depending on the species) in the fished area compared to the protected beds. Factors such as exposure to light or currents and/or rhodolith fragmenta-

tion (natural or induced by disturbance) could explain these observed differences in live maerl proportions. Moreover, this study highlights the diversity and effective conservation of maerl beds in the Columbretes Islands, and it contributes to our limited knowledge of the ecology and distribution of maerl bottoms in the Mediterranean. Our work also provides the first inventory of the maerl bed algal community in the region, with records of species as yet unidentified in the Mediterranean, and it highlights the depth-related characteristics of maerl-associated algal communities.

Algal community of maerl beds of the Columbretes Islands

The studied maerl beds of the Columbretes Islands exhibited the typical maerl arrangement (i.e. in patches or bands). Despite the restriction in our study that maerl cover had to be $\geq 100\%$ for a grab sample to be considered valid, extremely high maerl cover values were found in comparison with other reports (e.g. Ballesteros 1989, Hall-Spencer & Moore 2000b). Indeed, maerl cover exceeded 1000% in the shallow bottoms of the IN25 area, where the overall average was 360%, of which 50% was alive. These high values of maerl cover indicate the thickness of the maerl layers inside the long-term MPA, an indicator of the complexity of maerl beds (Birkett et al. 1998, Foster 2001). Nonetheless, because maerl beds were not surveyed beyond 67 m depth, further studies should be conducted to evaluate the structure of deeper maerl beds, as maerl communities can reach depths of 100 m in the oligotrophic and transparent waters of the Mediterranean (e.g. Malta Island, Sciberras et al. 2009; Menorca Channel, Barberá et al. 2012a).

Maerl beds in the study area were dominated by 2 species: *Lithothamnion corallioides* and *Spongites fruticosus*. The former prevailed in shallow beds (30 to 49 m), in association with a diverse community of erect seaweeds. Maerl beds with *L. corallioides* and *Peyssonnelia* spp. dominance have been reported in Mediterranean muddy sedimentary bottoms protected from currents (Benidorm Island, Bordehore et al. 2003; south of Menorca Island, Barberá et al. 2012a), although the mud fraction of sediments in the present study was very low. In contrast, maerl with *S. fruticosus* dominance has been reported in areas of the Menorca Channel exposed to strong currents (Barberá et al. 2012a). The dominance of both species in our study suggests that a complex set of environmental factors interact in the area of the Columbretes Islands (e.g. turbidity resulting from Ebro discharges), requiring further studies to elucidate the drivers that favour such assemblages.

Although our study was conducted in a single season (summer), algal species richness was found to be considerably high, amounting to 72 species at bottom depths between 34 and 67 m. Over a 2 yr sampling period, Ballesteros (1989) catalogued 80 species of algae in beds dominated by the maerl-forming alga *Phymatolithon calcareum* at 40 to 51 m depth in Girona (NW Mediterranean). In addition to seasonal fluctuations in light and water temperature as well as sampling effort, substrate and sediment features are essential factors that influence the diversity and abundance of algal species observed in association with maerl beds (Ballesteros 1989, Hily et al. 1992, De Grave 1999). Our inventory also contained species not previously reported in the Mediterranean; these taxa will be identified using molecular tools. Moreover, a number of rare species were only recorded in the long-term protected area, e.g. *Nemastoma dumontioides*, *Chrysomenia ventricosa*, *Kallymenia feldmannii* and *K. patens*.

Maerl algal communities in shallow and deep beds inside IN25

In spite of the influence of irradiance on the diversity of associated algal species in maerl beds (Ballesteros 1989, Hily et al. 1992, Grall & Glémarec 1997, Foster 2001), we recorded similar numbers of algal species for the 2 bathymetric strata within IN25. However, multivariate and univariate analyses revealed bathymetric differences in algal cover and species composition. In particular, lower cover in deep stations was observed for species such as *L. coral-*

lioides, *P. calcareum*, *Mesophyllum lichenoides*, and *Peyssonnelia* spp., whereas *Mesophyllum expansum* and *Amphiroa rubra* were absent from deep samples but present in shallow samples. Given the absence of fishing impacts, the higher mean maerl cover in shallow relative to deeper beds inside IN25 can only be attributed to light attenuation with increasing depth, among the most important factors that directly affect maerl growth and survival (Foster 2001).

In addition to irradiance, other factors such as nutrient availability and temperature can affect algal diversity and growth (Steller & Foster 1995, Foster 2001). Furthermore, water motion is a key factor determining the growth and distribution of maerl species that require moderate-to-strong seabed currents to facilitate thallus movement and growth and to prevent burial and silt smothering (Hall-Spencer 1998, Marrack 1999, Wilson et al. 2004). Although none of these environmental factors were directly assessed in this study, the relatively small scale of the study area and its location at the edge of the continental shelf leads us to assume that all bottoms are subject to a similar current regime. Sediment (type and grain size) also affects the biological characteristics of maerl (e.g. species composition, coverage; Foster 2001, Bordehore et al. 2003), and it is well known that sediment can be related to depth and fishing impacts (Gray & Elliott 2009). In this study, no differences in sediment granulometric features were observed between bathymetric strata or among zones with different protection histories. However this is, to some extent, an artefact of our sampling strategy, as the criterion for defining valid grabs enforced similar substrate features with an adequate composition for development of maerl beds.

Effects of protection from fishing activities

Long-term protection

The number of algal species identified in the long-term protected areas was markedly higher than that in the fished area at a similar depth. This result concurs with previous studies indicating that fishing causes a reduction in algal species richness in maerl communities (Coleman & Williams 2002, Barberá et al. 2003, Bordehore et al. 2003).

Moreover, maerl cover and cover of the 2 prevalent maerl-forming species, *L. corallioides* and *S. fruticosus*, were higher in the long-term unfished areas than in the nearby fished beds at similar depths. A century before the creation of the MPA, bottom

trawlers and artisanal boats frequented the Columbretes Islands from the mainland (the Iberian Peninsula) and the Balearic Islands (Masip 1998, Goñi et al. 1999). It is well known that bottom fishing with mobile gear affects habitat structure via extraction of benthic organisms and their burial by the physical impact of fishing gear. These perturbations have the immediate effects of reducing algal cover, one of the best indicators of bottom fishing (e.g. Watling & Norse 1998, Jennings & Kaiser 1998). Extraction of maerl during fishing activities as by-catch may also cause burial, fragmentation and dispersion (De Grave & Whitaker 1999, Hall-Spencer & Moore 2000a,b, Barberá et al. 2003). Rhodoliths taken on-board in fishing gear may be returned to the water in or near the fishing site or may be somewhat displaced as gear is cleaned while sailing to the next fishing location. Moreover, re-suspension and settlement of fine sediment over rhodoliths causes anoxia and death (Wilson et al. 2004). Therefore, the ratio of living to non-living maerl is also a good indicator of fishing perturbation in maerl beds (Hall-Spencer 1999, Hall-Spencer & Moore 2000a,b, Grall & Hall-Spencer 2003). For this reason, a similar or smaller fraction of live maerl in beds within the IN25 area compared to that of the fished grounds may seem unexpected. However, where maerl cover increases to a level that impedes light penetration, the fraction of live maerl is likely to decline as deeper layers of dead rhodoliths accumulate (Foster 2001).

Water motion may be another factor affecting the fraction of live maerl, with moderate water motion inhibiting settlement of fine sediments or reducing their accumulation via re-suspension while promoting rhodolith growth (Marrack 1999, Wilson et al. 2004). Although data on water currents are not available, it is known that the bottoms in the Columbretes Islands are affected by the southwest-flowing Catalan Current, which is controlled by wind energy, with velocity fluctuations that are catalogued as moderate to strong (with median speed between 2 and 20 cm s⁻¹ and a maximum speed of 60 cm s⁻¹) (Muñoz et al. 2005, Grifoll et al. 2012). Such a factor may explain the lack of maerl burial through the study area. Moreover, Foster (2001) suggested that the intense mechanical impact of fishing gear liberates living fragments broken from larger thalli, and that this is a significant source of new recruits in established beds, thereby increasing the density of living rhodoliths. Hence, high quantities of living fragments in rhodolith beds can be an indicator of physical disturbance (Foster 2001), albeit a high level of fragmentation was not detected in the present study.

Bottom trawling may also contribute to modification of the morphology and size structure of rhodoliths (De Grave & Whitaker 1999, Hall-Spencer & Moore 2000b). Ongoing work on maerl beds in the Columbretes area has revealed larger sizes of this species in the older area of the MPA but smaller sizes of *L. corallioides* in the 6 yr old region. This finding can help to explain the observations for this species in IN6, where higher cover but a lower live fraction was found in comparison with OUT. Barberá et al. (2012b) (Menorca Channel, Balearic Islands) also found higher cover and smaller sizes of *L. corallioides* in an area with higher trawling intensity. These results suggest that the mechanical impacts of fishing can affect rhodolith shape and size structure differently depending on the different morphologies and structure of the rhodoliths (ramified *L. corallioides* and nucleated *S. fruticulosus*) (M. Cabanellas-Reboredo et al. unpubl. data). In addition, *L. corallioides* may be more vulnerable to fragmentation due to the mechanical impacts of fishing gear (Foster 2001). For example, in the case of continuous trammel net perturbation, fragmentation generates new recruits, increasing the cover of smaller rhodoliths that are continually being removed and therefore resulting in higher quantities of live rhodoliths. Moreover, these changes are detectable on a short temporal scale.

In this study area, trammel-netting for spiny lobster (the main target of artisanal fishing; Goñi et al. 2006) could impact maerl beds, largely by entangling rhodoliths when bad weather forces the nets to remain in the water for several days and during net-cleaning with maces (S. Mallol pers. obs.). However, as burial is not expected to be caused by trammel-netting, this activity is not likely to reduce the proportion of live maerl. To date, no published study has addressed the impacts of trammel nets on maerl, and perhaps for that reason, the observation of Borg et al. (1998), which was based on a single gillnet fishing set, has been repeatedly cited in articles and reports as documenting trammel-net impacts on maerl beds. Data from on-board sampling of >1000 spiny lobster trammel-net fishing sets in the Menorca Channel (Balearic Islands) indicate that 70% of fishing sets are free of maerl; in these cases, entangled maerl was most often freed by shaking the rhodoliths off the net, causing exceptional breakage (S. Mallol et al. unpubl. data).

Short-term protection

In the northern section of the study area, which encompassed contiguous grounds with maerl beds

within IN25, IN6 and OUT, the number of algal species and maerl cover was lowest in OUT; an expected result. This was due mainly to loss of the dominant, more fragile ramified *L. corallioides*. In contrast, the cover of *S. fruticosus*, a robust nucleated species, was similar in the 3 zones with different protection histories.

The similarity of *S. fruticosus* cover in beds under short- and long-term protection may suggest that the maerl beds in the short-term MPA (before being protected from the concentrated lobster trammel effort along the northern boundary of IN25) have recovered only after 6 yr of no fishing. At a similar temporal scale, Hall-Spencer (1999) described immediate physical impacts of towed demersal fishing gear on the reduction of live maerl (>25%), which remained discernible for 5 yr. Alternatively, as mentioned earlier, such a finding may indicate that trammel-netting impacts (even if concentrated spatially) are not likely to cause the type of physical impacts described for bottom mobile fishing gear. However, cover was lower when comparing the long-term protected area and the fished area. The physical impacts of trammel nets would be notable at a short temporal scale.

Although the live fraction of *L. corallioides* did not differ between the long-term protected and fished beds when assessed globally and with a larger sample (see previous section), a significantly greater fraction of live *L. corallioides* was found in the north sector and with fewer samples. This may be an artefact of sampling because all valid grabs in the north OUT zone were collected very close to one another (see Fig. 1), indicating that maerl beds were more discontinuous in that area. Moreover, local conditions such as muddy features, bottom orientation to currents and illumination as well as fragmentation of thalli to provide living fragments may also influence the proportion of live maerl (e.g. Birkett et al. 1998, Foster 2001). The observation that the fraction of live *S. fruticosus* did not differ among areas with different protection histories is in line with its reduced sensitivity to fragmentation because this species does not have a branched morphology (M. Cabanellas-Reboredo et al. unpubl. data).

Limitations of approach

Although in the present study control samples originated from 2 distinct areas located on the 2 sides of the MPA, establishing multiple control sites for the analysis was not possible due to the limited number of samples. The low number of valid samples ob-

tained at the end of the survey forced us to pool all samples together. However, the analysis may not adequately partition the effect of protection from other sources of variation (Benedetti-Cecchi et al. 2003). The appropriate approach to assess effects of MPAs (as well as environmental impacts) should include sampling design with multiple control sites (Benedetti-Cecchi et al. 2003, Underwood & Chapman 2003, Claudet & Guidetti 2010).

CONCLUSIONS

This study provides baseline information on the diversity and composition of algal species and characteristics of the maerl beds of the Columbretes Islands. This information will be of use in future ecological assessments and for implementing current EU directives (i.e. Habitat Directive, Water Directive and Marine Strategy) and Council Regulations (EC/1967/2006) in the Mediterranean Sea. Given the slow growth rates of rhodoliths and slow renewal rates of maerl beds, the results also provide evidence that protection of small areas, such as the Columbretes Islands, helps to conserve and safeguard this non-renewable resource.

Bathymetry was found to influence important community changes in terms of diversity, cover and proportion of live maerl. In particular, the most important species showed higher cover in shallow strata. Some species were specific to shallow waters and others at greater depths. Nevertheless, the total number of algal species recorded in the 2 bathymetric ranges was similar, despite the importance of irradiance on algal diversity. Protection from fishing appears to have favoured higher diversity of algal species in maerl communities. In addition, maerl cover was higher in the long-term protected and recently protected MPAs than in nearby fished beds at similar depths. Moreover, cover appears to be the most important indicator for these differences, whereas the live proportion of maerl was similar among the areas with different protection histories. However, the conclusions of this study should be viewed with caution because of the limitations of the approach used in the analysis of data.

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Appendix. List of algal species recorded in maerl beds of the Columbretes Islands, in the shallow stratum (S; 30 to 49 m) or in the deep stratum (D; 50 to 69 m), or in both strata. F: frequency of occurrence; C: cover

Species	Stratum	F (%)	C (%)	Species	Stratum	F (%)	C (%)
Phylum Ochrophyta				Phylum Rhodophyta			
<i>Asperococcus bullosus</i>	S	1.4	0.0	<i>Leptofauchea coralligena</i>	D	16.2	0.2
<i>Dictyopteris polipodioides</i>	S,D	21.6	0.5	<i>Lithophyllum racemus</i>	S,D	17.6	0.4
<i>Dictyota</i> sp.	S,D	27.0	1.3	<i>Lithothamnion corallioides</i>	S,D	100.0	221.0
<i>Dictyotal indeterminada</i>	S	2.7	0.0	<i>Lomentaria subdichotoma</i>	D	2.7	0.0
<i>Halopteris filicina</i>	D	59.5	14.6	<i>Meredithia microphylla</i>	S,D	5.4	0.0
<i>Laminaria rodriguezii</i>	D	4.1	2.9	<i>Mesophyllum expansum</i>	S,D	14.9	1.3
<i>Spermatochnus paradoxus</i>	S	4.1	0.1	<i>Mesophyllum lichenoides</i>	S,D	16.2	0.6
<i>Zanardinia typus</i>	D	2.7	0.1	<i>Mesophyllum</i> sp.	S,D	8.1	0.2
Phylum Rhodophyta				<i>Nemastoma dumontioides</i>	S	2.7	0.0
<i>Aeodes marginata</i>	D	12.2	0.3	<i>Neurocaulon foliosum</i>	D	5.4	0.1
<i>Amphiroa rigida</i>	S	2.7	0.0	<i>Osmundaria volubilis</i>	S	1.4	0.0
<i>Amphiroa rubra</i>	S	13.5	1.5	<i>Peyssonnelia coriacea</i>	D	1.4	0.0
<i>Bonnemaisonia asparagoides</i>	S	1.4	0.0	<i>Peyssonnelia crispata</i>	S,D	13.5	0.3
<i>Botryocladia botryoides</i>	D	4.1	0.0	<i>Peyssonnelia duby</i>	D	1.4	0.0
<i>Botryocladia chiajeana</i>	S	2.7	0.0	<i>Peyssonnelia harveyana</i>	D	1.4	0.0
<i>Calliblepharis jubata</i>	D	10.8	0.4	<i>Peyssonnelia rosa-marina</i>	S,D	20.3	1.1
<i>Chondria</i> sp.	S,D	4.1	0.1	<i>Peyssonnelia rubra</i>	S,D	60.8	11.8
<i>Chrysimenia ventricosa</i>	S	1.4	0.0	<i>Peyssonnelia squamaria</i>	S,D	9.5	1.0
<i>Chylocladia verticillata</i>	S	1.4	0.0	<i>Peyssonnelia stoechas</i>	S,D	2.7	1.2
<i>Cryptonemia tuniformis</i>	S,D	59.5	1.0	<i>Peyssonnelia</i> sp.	D	1.4	0.0
<i>Cryptonemia lomation</i>	S,D	10.8	0.1	<i>Peyssonnelia</i> sp. 2	D	1.4	0.0
<i>Dasyopsis plana</i>	D	1.4	0.0	<i>Peyssonnelia</i> sp. 3	D	1.4	0.0
Delesseriaceae indet.	D	13.5	0.2	<i>Phyllophora crispa</i>	S,D	31.1	1.8
<i>Erythrogllossum sandrianum</i>	D	21.6	0.3	<i>Phymatolithon calcareum</i>	S,D	25.7	1.6
<i>Gelidium spinosum</i>	S	1.4	0.0	<i>Rhodymenia ardissoni</i>	S	1.4	0.0
Gigartinales indet. sp. 1	D	2.7	0.0	Rhodophyta indet.	D	4.1	0.2
Gigartinales indet. sp. 2	D	1.4	0.0	<i>Sphaerococcus coronopifolius</i>	S	10.8	0.1
Gigartinales indet. sp. 3	D	1.4	0.0	<i>Spongites fruticosus</i>	S,D	100.0	97.1
<i>Gloiocladia furcata</i>	D	8.1	0.1	<i>Tricleocarpa fragilis</i>	S	4.1	0.3
<i>Gloiocladia microspora</i>	S,D	9.5	0.2	Phylum Chlorophyta			
<i>Gloiocladia repens</i>	S,D	2.7	0.1	<i>Acetabularia acetabulum</i>	S	1.4	0.0
Halymeniales indet.	D	1.4	0.0	<i>Fabellia petiolata</i>	S	1.4	0.1
<i>Haraldia lenormandii</i>	D	24.3	0.4	<i>Microdictyon tenuous</i>	S	1.4	0.0
<i>Kallymenia feldmannii</i>	D	1.4	0.0	<i>Palmophyllum crassum</i>	S	2.7	0.0
<i>Kallymenia patens</i>	S	1.4	0.0	<i>Ulva olivascens</i>	D	2.7	0.0
<i>Kallymenia requienii</i>	S,D	23.0	0.3	<i>Valonia macrophysa</i>	S,D	50.0	0.4
<i>Laurencia pelagossae</i>	S	2.7	0.0	<i>Valonia utricularis</i>	S,D	4.1	0.2

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