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## Ecological characterisation of a Mediterranean cold-water coral reef: Cabliers Coral Mound Province (Alboran Sea, western Mediterranean)

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### Abstract :

Scleractinian cold-water coral (CWC) reefs are key habitats for benthic fauna as they enhance spatial heterogeneity and biodiversity. Understanding their environmental and ecological dynamics has therefore important implications for biodiversity conservation. This is especially true for the Mediterranean Sea, where living cold-water coral reefs are rare. In this study, we present a quantitative analysis of the CWC assemblages from Cabliers Coral Mound Province, located in the Alboran Sea (westernmost Mediterranean). The province extends for 25 km, with some mounds rising up to 140 m from the surrounding seafloor and being partly topped by living CWC reefs. The observed megabenthic species were quantified through video analysis of three Remotely Operated Vehicle (ROV) dives (280 – 485 m water depth) and their distribution was related to mound geomorphic characteristics and seafloor terrain parameters, extracted from a high-resolution Autonomous Underwater Vehicle (AUV) multi-beam bathymetry. The pronounced abundance and size of scleractinian CWCs among the observed assemblages, makes Cabliers the only known coral mound province in the Mediterranean Sea with currently growing reefs. Within these reefs, several recruits and juveniles of the sebastid *Helicolenus dactylopterus* were observed, confirming the use of such habitats as nursery grounds by some commercially valuable fish species. The qualitative comparison between the fauna of Cabliers and Atlantic coral mounds suggest that the number of species associated with CWC mounds worldwide is even higher than previously thought. This finding has important implications for the conservation and management of CWC habitats in different geographic regions.

## Graphical abstract



## Highlights

► ROV footage unveiled thriving CWC reefs on the Cabliers Coral Mounds (W Mediterranean). ► Four benthic assemblages were identified, mainly driven by substratum type and depth. ► North and south Cabliers show different CWC reef stages from flourishing to decline ones. ► *H. dactylopterus* recruits and juveniles use CWC reefs as nursery grounds.

**Keywords** : Cold-water corals, Coral reefs, Benthic communities, AUV, ROV, Nursery grounds

**Regional terms** : Western Mediterranean Sea ; Alboran Sea ; Cabliers Coral Mound Province

## 60 1. INTRODUCTION

61

62 Over the last decade, the study of deep-sea benthic communities through Remotely Operated  
63 Vehicle (ROV) inspections has constantly expanded, largely due to ongoing technological  
64 improvements that have made ROV operating costs more affordable (Marsh et al., 2012; Neves  
65 et al., 2014; Gori et al., 2017; Khripounoff et al., 2017). Consequently, marine scientists have  
66 been able to describe a vast range of new deep-sea ecosystems and to characterise in more  
67 detail those that were already known to science (Roberts et al., 2006; Khripounoff et al., 2017;  
68 Bo et al., 2018). However, most of these studies are based on punctual observations, which  
69 inhibits to highlight the spatial distribution and ecological role of many benthic habitats and  
70 species at a regional scale. In parallel with ROV development, marine acoustics and  
71 Autonomous Underwater Vehicles (AUV) have also experienced significant technological  
72 advances and currently allow researchers to characterise the seafloor morphology at a metric  
73 scale (e.g. 1-2 m<sup>2</sup> pixel size; Huvenne et al., 2011; Wynn et al., 2014; Rona et al., 2015; Fabri  
74 et al., 2017). Therefore, combining ROV video-footage and AUV high-resolution multi-beam  
75 data allows for a detailed characterisation of benthic communities and helps to understand their  
76 spatial correlation with fine-scale seafloor geomorphology.

77 Among deep-sea benthic assemblages, cold-water corals are generally the focus of the research  
78 efforts from the scientific community, as they generate key habitats for benthic fauna (Freiwald  
79 et al., 2004; Roberts et al., 2006; Buhl-Mortensen et al., 2010). Several recent studies focused  
80 on the distribution of non-scleractinian cold-water corals, such as anthipatarians and octocorals  
81 (Fabri and Pedel 2012; Tong et al., 2012; Bullimore et al., 2013; Bo et al., 2014a, b; Grinyó et  
82 al., 2016, 2018; Pierdomenico et al., 2018). Nevertheless, stony (i.e. scleractinian) cold-water  
83 corals (hereafter mentioned as CWC) such as *Lophelia pertusa* and *Madrepora oculata* have  
84 become some of the most intensively studied species in the last decade (Freiwald et al., 2004;  
85 Roberts et al., 2009b; Huvenne et al., 2011; Mienis et al., 2014; Buhl-Mortensen et al., 2017;  
86 Lim et al., 2017; Lo Iacono et al., 2018a). CWC are solitary or colonial organisms that generally  
87 occur in areas characterised by hard substrata on which they can settle and that can form dense  
88 benthic assemblages across a depth range of 39 m (Norwegian fjords) to 2000 m (NW  
89 Mediterranean canyons) (Freiwald et al., 2004; Roberts et al., 2006; Lo Iacono et al., 2018b;  
90 Sartoretto and Zibrowius, 2018). Hard substrata are usually located on complex geomorphic  
91 features such as submarine canyons, seamounts, shelf edges and landslides, where enhanced  
92 food-rich bottom currents provide suitable environmental conditions for CWC settlement and  
93 growth (Orejas et al., 2009; Davies et al., 2009; Huvenne et al., 2011; Mienis et al., 2012; Lo

94 Iacono et al., 2012, 2014, 2018a). CWC have a worldwide distribution, but historically, their  
95 assemblages have been more extensively studied along the North Atlantic continental margins  
96 (Hovland and Risk, 2003; Kano et al., 2007; De Mol et al., 2011; Mazzini et al., 2012). Among  
97 the framework-building CWCs, *L. pertusa* is the most widespread and abundant species,  
98 followed by *M. oculata*, which is more abundant in warmer waters such as the Mediterranean  
99 Sea (Savini and Corselli 2010; Fabri et al., 2014; Taviani et al., 2017) and *Solenosmilia*  
100 *variabilis*, more common in the South Pacific Ocean (Koslow et al., 2001; Tresher et al., 2014).  
101 The spatial distribution of these species is not only controlled by the availability of suitable  
102 substrata but also by a complex interplay of many environmental factors such as temperature,  
103 salinity, pH, dissolved oxygen, sedimentation rates, current intensity and food supply (Dodds  
104 et al 2007; Davies et al., 2009; Maier et al., 2009; Duineveld et al., 2012; Naumann et al.,  
105 2014). Framework-building CWC generally grow in waters with temperatures between 3 and  
106 16 °C (Rogers, 1999, Davies and Guinotte, 2011) and salinity of 34-37 psu (Dullo et al., 2008).  
107 They are linked to high surface productivity and average bottom current speeds between 8 and  
108 15 cm s<sup>-1</sup> (Duineveld et al., 2012; Mienis et al., 2012).

109 Under persistent suitable environmental conditions, living framework-building CWCs can  
110 form dense reefs extending over hundreds of meters and rising up to a few meters above the  
111 surrounding seafloor (Mortensen et al., 2001; Lo Iacono et al., 2018b). Over longer timespans  
112 and by baffling sediments within the coral framework, these living reefs might develop into  
113 three-dimensional geomorphological features, known as coral mounds (Wienberg and  
114 Titschack, 2018). These mounds can vary in shape and reach heights of up to 380 m depending  
115 on their development stage (Kano et al., 2007; Mienis et al., 2007; Van Rooij et al., 2009; De  
116 Mol et al., 2011; Hebbeln et al., 2014; Buhl-Mortensen et al., 2017).

117 CWC reefs present a higher habitat complexity and heterogeneity than the surrounding  
118 seafloor, which allows for an increase in the number of available ecological niches (Jones et  
119 al., 1994; Buhl-Mortensen et al., 2010). These habitats may also act as shelter and nursery  
120 grounds for many benthic species that use the coral framework to hide from predators (Costello  
121 et al., 2005). Because of all the above mentioned ecological benefits provided, CWC reefs are  
122 considered biodiversity hotspots, with a biological richness comparable to that of shallow-  
123 water tropical reefs (Roberts et al., 2006; Buhl-Mortensen et al., 2010). Species richness in *L.*  
124 *pertusa* reefs is probably the highest within CWC, with more than 1300 associated species  
125 (Roberts et al., 2006). However, not all CWC reefs and mounds share the same fauna.  
126 Considerable differences in species composition have been observed between Norwegian and

127 African coral mound assemblages, which are dominated by *L. pertusa* (Buhl-Mortensen et al.,  
128 2017).

129 Due to their uniqueness, functional role and susceptibility to anthropogenic disturbances (Fosså  
130 et al., 2002; Althaus et al., 2009), framework-building CWC assemblages are considered  
131 vulnerable marine ecosystems (FAO, 2009). The OSPAR Commission and the General  
132 Fisheries Commission for the Mediterranean (GFCM) also count these assemblages within the  
133 lists of sensitive and threatened marine habitats that require protection (OSPAR, 2008; GFCM,  
134 2009). Therefore, understanding the environmental constraints and ecological interactions of  
135 these assemblages, has important implications for the determination of their spatial distribution  
136 and thus, diversity conservation. This is especially true for the Mediterranean Sea where living  
137 CWC reefs are very limited compared to the North Atlantic (Freiwald et al., 2004; Vertino et  
138 al., 2010; Lo Iacono et al., 2018b,c). Framework-building CWCs in the Mediterranean are  
139 generally represented by small populations or scattered colonies, mainly located in submarine  
140 canyons and on landslides (Orejas et al., 2009; Savini and Corselli, 2010; Vertino et al., 2010;  
141 Gori et al., 2013; Lastras et al., 2016; Fabri et al., 2014; Fanelli et al., 2017; Taviani et al.,  
142 2017).

143 Within the Mediterranean basin, coral mound clusters are mainly located in the Ionian Sea  
144 (Savini and Corselli, 2010), Tyrrhenian Sea (Remia and Taviani, 2005) and the Alboran Sea  
145 (Comas and Pinheiro, 2010; Lo Iacono et al., 2014). However, they are generally buried  
146 beneath meters of sediments or in a stage of decline (Hebbeln et al., 2009; Comas and Pinheiro,  
147 2010; Lo Iacono et al., 2012; Lo Iacono et al., 2014). An exception to this general observation  
148 are the coral-topped mounds located off Santa Maria di Leuca, Italy, where dense aggregations  
149 of *L. pertusa* and *M. oculata* have been observed growing on landslide blocks (Taviani et al.,  
150 2005; Vertino et al., 2010; Savini et al., 2016) and supporting a high biodiversity (Mastrototaro  
151 et al., 2010). Observations of living CWC have also been reported from two mound clusters in  
152 the Alboran Sea: the West Melilla Mounds (Lo Iacono et al., 2014) and the East Melilla  
153 Mounds (Comas and Pinheiro, 2010; Fink et al., 2013). Nevertheless, they only harbour small  
154 isolated colonies of *L. pertusa* or *M. oculata* and they are mostly covered by dense aggregations  
155 of non-scleractinian corals, sponges and echinoderms (Fink et al., 2013; Hebbeln and  
156 Wienberg, 2016; Lo Iacono et al., 2018b). Furthermore, none of these studies present a  
157 quantitative analysis of the megabenthic fauna inhabiting the coral mounds of the Alboran Sea.  
158 The same paucity of studies applies to the rest of the Mediterranean Sea, where only  
159 Mastrototaro et al. (2010) qualitatively characterised the fauna associated to Santa Maria di  
160 Leuca coral-topped mounds. Therefore, there is a knowledge gap regarding the relative

161 abundance of taxa associated to CWC reefs in the Mediterranean Sea. The absence of  
162 quantitative data is limiting the creation of solid baselines required to better understand these  
163 sensitive ecosystems, which would help towards a more appropriate conservation and  
164 management measures.

165 In the Alboran Sea, north-east of the East Melilla Mounds, the recently surveyed Cabliers Coral  
166 Mounds present thriving CWC assemblages growing on some of their crests (Lo Iacono et al.,  
167 2016; Corbera et al., 2017). Cabliers is a coral mound province extending NE-SW for 25 km  
168 (Fig. 1) and developing on a volcanic outcrop known as Cabliers Bank (Würtz et al., 2015) in  
169 a water depth range of 250-710 m. In order to contribute to increase the knowledge of CWC  
170 reefs in the Mediterranean Sea, this study aims to quantitatively describe for the first time the  
171 assemblages found on the Cabliers Coral Mounds. It also attempts to provide a detailed  
172 quantification of density and distribution of the main associated species, addressing a  
173 knowledge gap on a regional/basin scale. Specifically, we will:

174

175 - Determine the abundance, size and distribution of CWC and the most conspicuous  
176 associated taxa.

177

178 - Determine which are the main megabenthic assemblages occurring on the Cabliers  
179 Coral Mounds

180

181 - Reveal which are the most important seafloor features driving the distribution of the  
182 species

183

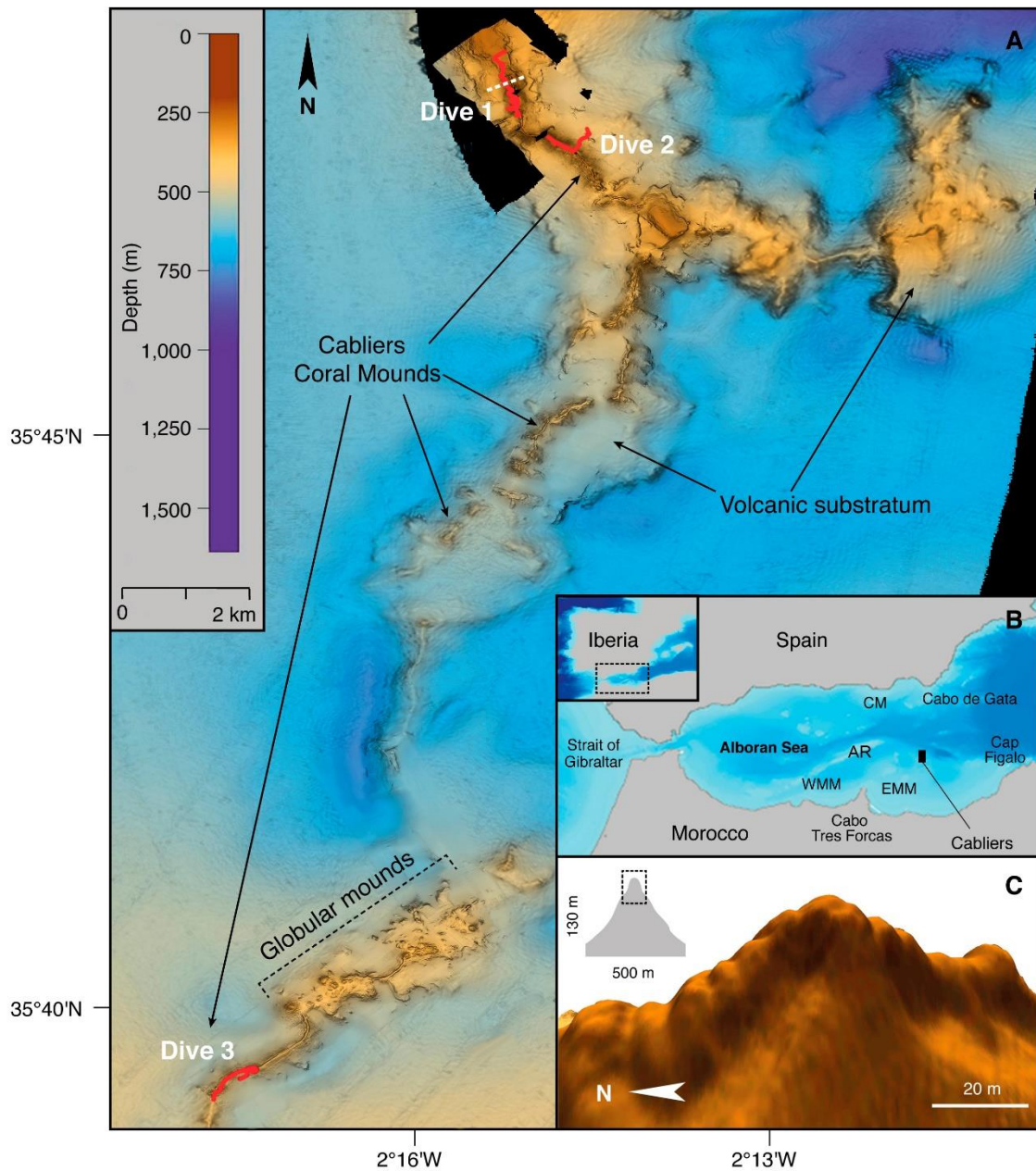
184 - Perform a qualitative comparison between the fauna found on these Mediterranean  
185 CWC mounds and the one observed on analogous structures of the Mediterranean Sea  
186 and the Atlantic.

187

## 188 **2. Geological and oceanographic characteristics of the Alboran Sea**

189

190 The Alboran Sea (AS) is a marginal sea located at the westernmost Mediterranean Sea,  
191 enclosed between the Iberian Peninsula (South Spain) and North Africa (North Morocco and  
192 Algeria) (Fig. 1B). This basin is bound by the Strait of Gibraltar to the west, by the Cabo de  
193 Gata to the northeast, and by Cap Figalo to the southeast (Fig. 1). The AS includes three main  
194 sub-basins (i.e. West, East and South Alboran Basins) separated by the Alboran Ridge (Fig. 1).



195

**Figure 1.** Bathymetric map of the IdefX AUV multi-beam bathymetry (2 m resolution) along the Cabliers Coral Mounds overlapped on shipboard bathymetry of the region (20 m resolution) (A). Inset of the Alboran Sea, the black rectangle indicates the location of the Cabliers Coral Mound Province (B). Three-dimensional representation of the mini-mounds occurring on the crest of the Cabliers Coral Mounds (C). The red lines on (A) indicate the path of the three Max-Rover ROV dives; the white dashed line indicates the location of the transversal mound section observed on (C). AR: Alboran Ridge, CM: Chella Mound, WMM: West Melilla Mounds, EMM: East Melilla Mounds.

196

197 The seafloor geomorphology of this basin is relatively complex, displaying long ridges and  
 198 several seamounts that have been carefully mapped in the frame of successive high-resolution  
 199 bathymetric cruises (e.g. Gràcia et al., 2006, 2012; Lo Iacono et al., 2008). These features are

200 intrinsically associated to the recent tectonic evolution of the basin and thus, related to the  
201 subducting slab located at the West Alboran Basin (Spakman et al., 2018).

202 The different tectonics domains are defined by large active strike-slip faults, such as the Al-  
203 Idrissi Fault System (FS) (Gràcia et al., 2006, 2012); Carboneras FS (Moreno et al., 2016),  
204 Averroes-Yusuf FS (Perea et al., 2017), as well as the prominent thrust-fault Alboran Ridge FS  
205 (Gómez de la Peña et al., 2018). In consequence, the Alboran Sea is a seismically active area,  
206 where moderate to large earthquakes have occurred in the past and recent times (Gràcia et al.,  
207 2012; Grevemeyer et al., 2015).

208 The water mass circulation in the AS is characterised by the interaction between Atlantic and  
209 Mediterranean water masses, which create a regional thermohaline circulation (Garcia  
210 Lafuente et al., 1998). Atlantic warmer and less saline waters ( $S \sim 36.2$  psu,  $T \sim 15$  °C) enter the  
211 AS through the Strait of Gibraltar and flow within the first 150-200 m of the water column at  
212 a velocity of  $\sim 50$ - $100$   $\text{cm} \cdot \text{s}^{-1}$  (Garcia Lafuente et al., 1998; Oguz et al., 2014). The denser,  
213 colder and slower Mediterranean waters ( $S \sim 38.4$  psu,  $T \sim 13.5$  °C) flow deeper and head out of  
214 the Mediterranean Sea at  $\sim 10$   $\text{cm} \cdot \text{s}^{-1}$  (Garcia Lafuente et al., 1998). The circulation of the  
215 Atlantic waters (AW) is mainly driven by two semi-permanent anticyclonic gyres (western and  
216 eastern Alboran Gyres) (Millot, 1999). After entering the Strait of Gibraltar, the AW is dragged  
217 towards the Spanish coast by the Western Alboran Gyre and then moves towards the African  
218 coast, where it meets the Eastern Alboran Gyre that brings the AW from Melilla to the Cabo  
219 de Gata (South Spain) (Millot, 1999). In contrast, the deeper Mediterranean Water, named  
220 Levantine Intermediate Water (LIW), flows in the opposite direction but without any effect  
221 from the surface gyres. The latter water mass forms in the Eastern Mediterranean basin and  
222 travels towards the AS, crossing the Western Mediterranean Basin.

223 Three coral mound clusters have been reported in the AS: the Chella Mound (Lo Iacono et al.,  
224 2018b), the West Melilla Mounds (Lo Iacono et al., 2014) and the East Melilla Mounds (Comas  
225 and Pinheiro, 2010; Fink et al., 2013). The Chella Mound is located off the Almeria coast, it  
226 presents a ridge-like mound that raises 15-70 m from the surrounding seafloor and extends for  
227 a maximum of 3.4 km (Lo Iacono et al., 2018b). The West and East Melilla Mounds are located  
228 off the coast of Cabo Tres Forcas, on the southern margin of the AS. The western mounds are  
229 smaller (1-48 m tall) and buried by fine sediments (Lo Iacono et al., 2014). On the other hand,  
230 the East Melilla Mounds are ridge-like features that can extend for up to 6 km and rise 20-60  
231 m from the seafloor (Comas and Pinheiro, 2010).

232 In this physiographic and oceanographic setting, the Cabliers Coral Mound Province is located  
233 northeast of the Cape Tres Forcas and the East Melilla Mounds.



234 **3. MATERIAL and METHODS**

235

236 **3.1. Data acquisition and processing**

237

238 Three ROV dives and a high-resolution AUV multi-beam bathymetric survey were performed  
239 on the Cabliers Coral Mounds during the SHAKE cruise, conducted on board the R/V  
240 Sarmiento de Gamboa in April-May 2015. Seafloor video transects were recorded by means of  
241 the ROV Max-Rover (Hellenic Centre of Marine Research - Greece), equipped with an HD  
242 video camera (1920x1080 pixels), a manipulator arm and two parallel laser beams, 10 cm apart.  
243 During the collection of the video transects, ROV positioning was estimated by means of an  
244 ultra-short baseline (USBL) transponder mounted on the vehicle, which gave a geographic  
245 position every 3 seconds approximately. The ROV tracks were projected to UTM using the  
246 Geographic Information System ArcGIS 10.3.1 (ArcGIS Development Team, 2015) and all  
247 outlier points of the navigation data were removed to obtain a smooth plot of the geo-referenced  
248 transect. Outliers were identified as points located at a distance away from the main path that  
249 the ROV could not have reached, even at its maximum speed ( $0.6 \text{ m s}^{-1}$ ). These outliers are  
250 usually the consequence of signal beam reflections on seafloor features. The total distance  
251 covered by the ROV dives across the mounds was 5.2 km. Dive 1 and 2 were recorded at the  
252 northern part of Cabliers, whereas Dive 3 was performed at the southernmost part. All transects  
253 covered sectors of both crest and flanks of the coral mounds (Fig. 1). The three dives were  
254 performed in water depths between 280 and 485 m and the length of the video-transects ranged  
255 from 1249 to 2516 m (Table 1). During the ROV dives, both biological and rock samples were  
256 acquired by means of the ROV mechanical arm. These samples were later used to help in faunal  
257 identification and bedrock characterisation.

258

259 **Table 1.** Geographical coordinates, depth and length for each of the ROV dives analysed in this study.

Dive	Date	Position		Depth range (m)	Length (m)
		Start	End		
1	21/05/2015	35°48'18" N, 2°15'17" W	35°47'55" N, 2°15'13" W	283-380	2516
2	22/05/2015	35°47'39" N, 2°14'35" W	35°47'34" N, 2°14'55" W	294-444	1250
3	21/05/2015	35°39'19" N, 2°17'47" W	35°39'29" N, 2°17'34" W	418-486	1401

260

261

262 High-resolution multi-beam bathymetric data were acquired by means of an EM2040  
263 Kongsberg Maritime multi-beam echo sounder (300 kHz), installed on the Autonomous  
264 Underwater Vehicle (AUV) IdefX (IFREMER - France). The AUV was programmed to  
265 acquire data 70 m above the seafloor, allowing for a metric-scale bathymetric resolution. The  
266 AUV collected the data with inertial navigation. Prior to the start of each survey, a calibration  
267 profile across the last 100 m of the water column was acquired on the flattest seafloor sectors.  
268 This calibration was used to calibrate the sound velocity during the multi-beam acquisition and  
269 in the post-processing phases.

270 All the multi-beam data obtained was processed on-board. The AUV navigation was corrected  
271 in Caraibes 4.3 by means of the RegBat module using both the bathymetric contours and the  
272 USBL as a reference for the correction of the inertial navigation. The data was then imported  
273 into CARIS HIPS and SIPS 9.1, where a constant zero value of tide was applied. Finally, spikes  
274 and noise were reduced through manual cleaning in areas of line overlap, and a bathymetric  
275 grid with a 2 m cell size was created as final outcome.

276

### 277 **3.2. Video analysis**

278

279 Video transects were analysed using the editing software Adobe Premiere Pro CS6, following  
280 the methodology described in Gori et al. (2011). Laser points projected by two parallel beams  
281 located on the ROV frame, separated 10 cm from each other, were used to estimate transect  
282 width and to measure species size. The field of view slightly varied in relation to the ROV  
283 distance from the seafloor, being reduced to 1 m when the vehicle was close to the seabed.

284 Due to intermittent malfunctioning of the USBL, the location of the organisms along the ROV  
285 track had to be acquired by means of the following procedure. Each video transect was divided  
286 into over 30 fragments determined by control points. From one control point to the following  
287 one, DVL data was used to determine the course and the track of the ROV. This was thoroughly  
288 checked combining ROV video images with AUV High-resolution bathymetry. For each  
289 fragment, ROV speed was calculated based on the vehicle's travelled distance and the time  
290 interval between the corresponding control points. Such velocities were then used to calculate  
291 the position of each observed organism by using the following formula:

292

$$x_t = x_i + v_i \cdot (t - t_i)$$

293 where  $x_t$  is the distance from the start of the track at which the organism was identified,  $i$  is the  
294 analysed fragment,  $x_i$  is the distance covered by the ROV until the start of the current fragment,

295  $v_i$  is velocity of the ROV in the current fragment,  $t$  is the time when the organism was identified  
296 in the video footage and  $t_i$  is the time at the start of the analysed fragment.

297 All tracks were edited to remove sections of footage where the ROV was stationary (i.e.  
298 collecting samples or recording close-up images). Non-valid sequences such as poor visibility  
299 footage, caused by sediment resuspension, or parts where organism identification was not  
300 possible due to inappropriate altitude of the ROV (i.e. > 4 m) were quantified, isolated and  
301 removed from the subsequent statistical analyses.

302 All megafaunal organisms visible along each transect, within a section of 1 m around the central  
303 point of the field of view, were counted and identified to the lowest, practicable taxonomic  
304 level (i.e. typically species). Organisms that were not possible to identify to the species level,  
305 were classified within higher taxonomic levels or designated as morphospecies (e.g. “white  
306 encrusting sponge”). For the species *Phanopathes rigida*, which commonly appeared forming  
307 dense aggregations, the quantification of single colonies was not always possible. Therefore,  
308 this species’ abundance was obtained through the quantification of such aggregations (hereafter  
309 named as living-patches). Density of CWC colonies (sensu Oliver, 1968) and associated  
310 megafauna were calculated by dividing each ROV transect into 2 m<sup>2</sup> sampling units (i.e. 2 m  
311 long x 1 m wide segments). This sampling unit size was chosen in order to quantify the species  
312 distribution along the transect at a high resolution. Moreover, the adopted sampling unit already  
313 resulted to be adequate for the analysis of deep-sea anthozoan assemblages in the western  
314 Mediterranean (Ambroso et al., 2013).

315 The size of each measurable living colony (sensu Oliver, 1968) of *M. oculata* and *L. pertusa*  
316 was calculated by means of still images, extracted from HD video footage when the parallel  
317 laser beams crossed the colony base. Still images were processed using the image software  
318 Macnification 1.8 (Orbicule, Inc.), which allows measurements of coral colonies by drawing a  
319 line along the largest diameter of the living coral. The same procedure was carried out to  
320 measure the total length of the most abundant fish species, the sebastid *Helicolenus*  
321 *dactylopterus*. Substratum type was the only environmental variable determined from the ROV  
322 footage and was classified into four classes: fine sands with coral rubble (CRFS), coral rubble  
323 (CR), dead coral framework with fine sands (CFFS) and dead coral framework (CF) (Fig. S1).

324

### 325 **3.3. Statistical analyses**

326

327 The differences in taxonomic composition and diversity amongst the ROV dives were explored  
328 via species relative abundance, species richness (S) and Shannon diversity index (H') values.

329 The distribution of the most relevant and abundant taxa observed in the video transects was  
330 then plotted, displaying species density against the bathymetric profile and along the transect  
331 length of each dive. All 2582 sampling units were used in density plots, 1253 of them  
332 corresponding to Dive 1, 626 to Dive 2 and 703 sampling units to Dive 3.

333 Regarding CWC size structure, descriptive statistical parameters such as skewness and kurtosis  
334 were calculated to determine if the population was dominated by small or large colonies. Both  
335 *M. oculata* and *L. pertusa* populations, with more than 1000 and 100 colonies respectively,  
336 were large enough to perform robust skewness and kurtosis tests. Both tests assume normality  
337 as a null hypothesis. Skewness is a measure that gives information about the symmetry of a  
338 distribution. A population has an asymmetrical distribution when the skewness is statistically  
339 significant ( $p < 0.05$ ). If skewness is positive, it indicates a higher percentage of small colonies,  
340 whereas negative values of skewness relate to a higher proportion of large ones. If skewness  
341 values are close to 0 it indicates that the size structure of the colonies is close to a normal  
342 distribution. On the other hand, if the kurtosis test is statistically significant ( $p < 0.05$ ) it means  
343 that data distribution has shorter or longer tails than expected for a normal distribution.

344 Skewness and kurtosis were calculated using the functions *agostino.test* (Komsta and  
345 Novomestky, 2012) and *anscombe.test* (Anscombe and Glynn, 1983) from the *moments*  
346 package of the R software (Komsta and Novomestky, 2012; R core team, 2017). Colony size  
347 of *M. oculata* and *L. pertusa* was plotted using 10 cm size classes. *M. oculata* average size was  
348 also plotted against the bathymetric profile and along the transect length in Dive 1, which was  
349 the only dive with an abundance high enough to observe size patterns along geomorphologic  
350 features. The colony size data from this dive was log-transformed to achieve normality and  
351 differences between average size of CWC growing on the flanks and the crest of the mound  
352 were assessed by means of a Student's *t*-test. The determination of crest and flank areas was  
353 performed through a combination of visual assessment of the footage and the ROV location.

354 A Spearman rank correlation was used to verify that CWC density increases towards the  
355 summit of ridge-like features (hereafter mentioned as mini-mounds) occurring at the crest of  
356 the coral mounds. A moving average of period 5 was applied to the CWC density data to  
357 exclude small scale variability. This data was then correlated to the values of a fine scale  
358 bathymetric position index (BPI) (inner radius: 5 m, outer radius: 10 m), which detected most  
359 of the mini-mound features on the AUV multi-beam along the Cabliers mounds crest. The BPI  
360 is a measure consisting on a second order derivative of the seafloor surface that determines the  
361 elevation of each grid cell in relation to the surrounding landscape of the bathymetry. This

362 derivative produces a new raster where geomorphological features such as crests, slopes,  
363 depressions and flat areas are indicated.

364 To evaluate the relationships between megafaunal abundance and seafloor features (see below)  
365 a canonical correspondence analysis (CCA) was performed. CCA is a multivariate constrained  
366 ordination test that attempts to explain the effect of each environmental variable on species  
367 distribution (Greenacre and Primiceiro, 2013). Taxa that had an abundance lower than five  
368 individuals were not considered in the analysis to avoid noise in the final outputs. Furthermore,  
369 off-mound areas (i.e. regions of fine sands and outcropping rock), occurring at the beginning  
370 of Dive 1 and 2 were not considered for the assemblage analyses. The CCA was carried out for  
371 the three Dives, to identify the composition of the main assemblages occurring on the mound  
372 and the seafloor physical characteristics influencing their distribution. The CCA was executed  
373 using the *cca* function from the *vegan* package (Oksanen et al., 2013) of the R software (R core  
374 team, 2017). This was performed together with the function *anova.cca*, which runs an  
375 ANOVA-like permutation test. This test was used to assess the significance of each seafloor  
376 feature and to determine which was the variable that had a greater effect on the distribution of  
377 megafaunal species (Chambers and Hastie, 1992). The CCA was performed for sampling unit  
378 sizes of 2, 4, 10 and 20 m<sup>2</sup> in order to assess how spatial scale affects the determination of  
379 benthic assemblages and their corresponding environmental setting.

380 The environmental variables used in the CCA statistical analysis, included depth and seafloor  
381 terrain parameters (i.e. slope, terrain roughness, aspect and bathymetric position index) that  
382 were derived from the high-resolution bathymetry using the Add-on RSOBIA (Le Bas, 2016)  
383 and Benthic Terrain Modeller (Walbridge et al., 2018) within the Geographic Information  
384 System software, ArcGIS 10.3.1 (ArcGIS Development Team, 2015). The roughness raster  
385 was obtained using the VRM algorithm (Sappington et al., 2007). In this analysis, the BPI was  
386 computed at a broad scale (inner radius: 10 m, outer radius: 20 m) to account for large-scale  
387 features that can have a greater effect on species distribution. Values of all these seafloor  
388 features were obtained from the central point of each sampling unit of the video transects, using  
389 the *extract* function from the *raster* package within the R software v 3.4.0 (R core team, 2017).  
390 Substratum type was also included in the CCA analysis, as four different variables coded for  
391 presence absence. The substratum type with the higher cover was assigned to each sampling  
392 unit.

393

394

395

396 **4. RESULTS**

397

398 **4.1. Physiography of the Cabliers Coral Mounds**

399

400 The Cabliers Coral Mounds developed over a rocky outcrop, witnessed in the ROV footage  
401 and interpreted in the AUV bathymetry. Collected rock samples during Dives one and two  
402 helped to determine the substratum as being of volcanic origin. The mounds generally present  
403 a ridge-like morphology with an average height of ~77 m and a maximum of 140 m. Flanks  
404 are 35° steep on average. Overall, the sections of the mounds with a greater relief exhibited  
405 wider bases. The high-resolution AUV multi-beam bathymetry revealed that the crests of the  
406 mounds consist of a series of consecutive mini-mounds (Fig. 1C). These smaller features,  
407 whose internal structure consists of dead coral framework and baffled sediments, can rise up  
408 to 7 m on top of the mound's crest and extend for 23 m in width. Towards the southern part of  
409 the Cabliers, a field of complex globular mounds developed (Fig. 1A); these mounds have an  
410 average diameter of 121 m and rise up to ~40 m from the surrounding seafloor. This field of  
411 globular mounds occupies an area of about 3 x 1 km. South of this region, Cabliers is again  
412 exclusively formed by aligned ridge-like mounds.

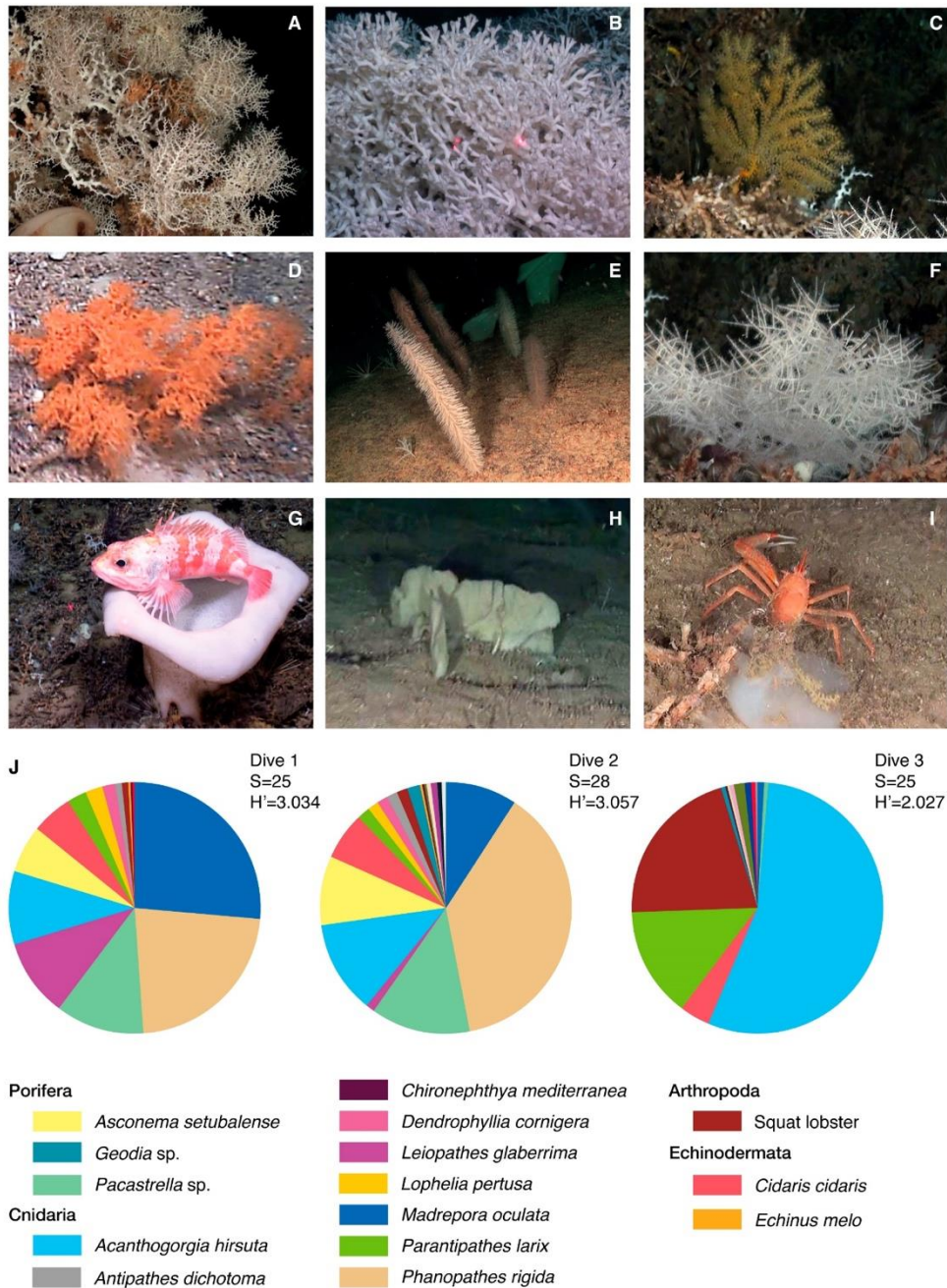
413

414 **4.2. General Megafaunal Characteristics**

415

416 A total of 2582 sampling units (2 m<sup>2</sup>) were obtained from the ROV dives, in which 7737  
417 organisms representing 49 different taxonomic groups were identified (Table S1). 64.1% of  
418 these organisms, could be identified to species or genus level, whereas 13.1% were included in  
419 broader taxonomic categories, and 22.8% were considered as morphospecies. The most  
420 abundant species was the antipatharian *Phanopathes rigida* with 1532 colonies, followed by  
421 the gorgonian *Acanthogorgia hirsuta* (n = 1491), and *M. oculata* (n = 1160). These species  
422 represented respectively the 19.6%, 18.9% and 15.5% of all identified organisms. Other  
423 commonly observed species were the sponge *Asconema setubalense* (12% of the total) and the  
424 antipatharian *Parantipathes larix* (5%).

425



**Figure 2.** Most abundant fauna observed in the ROV footage (A-I), and (J) species relative abundance, richness (S) and diversity (H') of each dive. *Madrepora oculata* (A), *Lophelia pertusa* (B), *Acanthogorgia hirsuta* (C), *Leiopathes glaberrima* (D), *Parantipathes larix* (E), *Phanopathes rigida* (F), *Asconema setubalense* (sponge) and *Heliconelus dactylopterus* (fish) (G), *Pacastrella* sp. (H), Squat lobster (I). Still images A, C, E, F and H, © OCEANA.

426

427  
428 *4.2.1. Northern sector - Dives 1 and 2*

429 The seafloor observed on the two northern dives, which were 490 m apart (Fig. 1), was  
430 characterised by areas of fine sediments mixed with coral rubble at the base of the mounds that

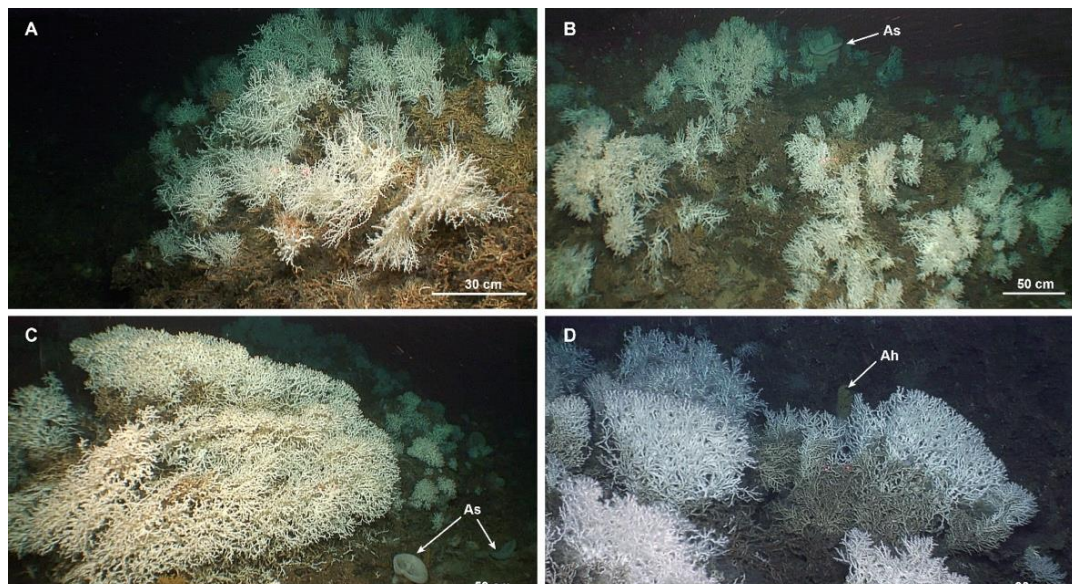


431 changed to coral rubble when approaching the crests. Dives 1 and 2 showed a rather similar  
 432 taxonomic composition with only a change in the dominant taxa (Fig. 2).  
 433 Dive 1 was dominated by dense populations of *M. oculata* accompanied by *L. pertusa* (Fig. 3),  
 434 which represents the main constructor building the mini-mound like features located at the crest  
 435 of the coral mounds. The two species were observed closely cohabiting and even in some cases  
 436 fusing colony branches (Fig. 4). *P. rigida* was the second most abundant species in this dive  
 437 followed by other megafaunal species such as *L. glaberrima*, *Pachastrella* sp. and *A. hirsuta*.  
 438 Megafauna in Dive 2 was dominated by *P. rigida* and *Pachastrella* sp., accompanied by other  
 439 abundant taxa, like *A. hirsuta*, *M. oculata* and *A. setubalense*. Even though there was not a  
 440 substantial difference in species richness between dives, Dive 2 presented the highest value for  
 441 this parameter, with 28 taxa compared to the 25 from Dive 1. In regards to species diversity  
 442 ( $H'$ ), both dives presented very similar values (Dive 1:  $H'=3.0$ / Dive 2:  $H'=3.1$ ), regardless of  
 443 the dramatic decrease in living CWC abundance from Dive 1 to Dive 2 (from 967 colonies in  
 444 Dive 1 to 178 in Dive 2) (Fig. 2).

445

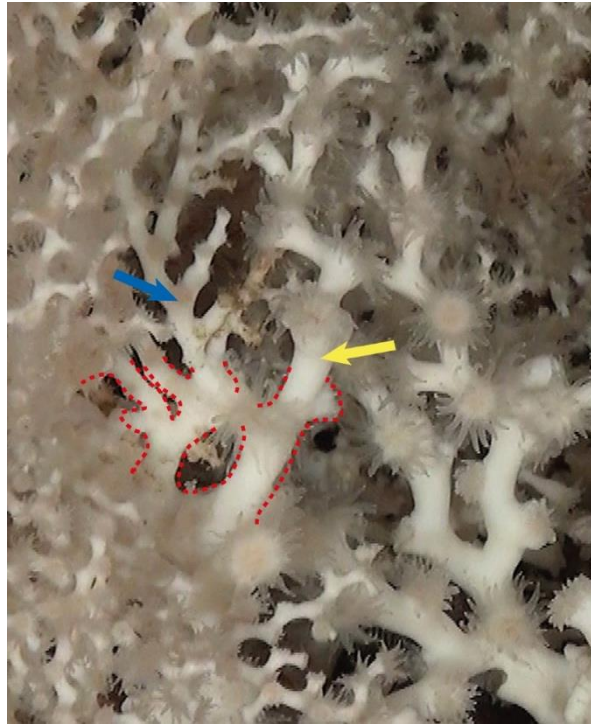
446 *4.2.2. Southern sector - Dive 3*

447 In this dive, 15.1 km south of the northern dives (Fig. 1), video footage showed that the type  
 448 of substratum along the mound's flanks was similar to the one observed in the northern region  
 449 (coral rubble mixed with fine sediments) although with a higher abundance of fine sediments.



**Figure 3.** Living reefs of *M. oculata* (A, B) and *L. pertusa* (C, D) forming the mini-mounds observed on top of the northern Cabliers Province. The largest *L. pertusa* colony measured in the area is 306 cm wide (C). Arrows indicate some of the accompanying megabenthic species living within and around the reefs. Ah: *A. hirsuta*, As: *A. setubalense*





**Figure 4.** *L. pertusa* (yellow arrow) and *M. oculata* (blue arrow) chimaera-like colony. Silhouette of the fusing branches is highlighted by a red dashed line.

451 The same increase in deposited sediment was observed at the crest, where the dead coral  
 452 framework was draped by a larger amount of fine sediments than in northern Cabliers. Video  
 453 data collected during Dive 3 also showed a different combination of dominant species in  
 454 comparison to the northern sector (Fig. 2). This dive was essentially dominated by the  
 455 gorgonian species *A. hirsuta* (55%) and characterised by very a few colonies of *M. oculata*.  
 456 Furthermore, squat lobsters and *P. larix* were also more abundant in this dive in comparison to  
 457 the northern ones, where they just occurred as accompanying species of *M. oculata* and *L.*  
 458 *pertusa* assemblages. Although the number of species observed in Dive 3 was the same as in  
 459 Dive 1, the diversity of the former was much lower (Dive 3  $H'=2.027$ ), probably due to the  
 460 dominance of three species that represented over 80% of the observed organisms (Fig. 2).

461

### 462 **4.3. Scleractinian cold-water corals**

463

#### 464 *4.3.1 Density and distribution*

465 *M. oculata* was the most abundant scleractinian species growing on Cabliers, representing 85%  
 466 of the total (scleractinian) abundance in contrast with the 8% of *L. pertusa* and 6% of  
 467 *Dendrophyllia cornigera*. As shown in Figure 5 and Table 2, living CWC density in the

468 northern sector of the province decreases from Dive 1 to Dive 2, with almost a total absence of  
 469 these species occurring in Dive 3 (i.e. southernmost mound sector). The maximum density  
 470 values for *M. oculata* and *L. pertusa* were 6 and 5 col·m<sup>-2</sup>, both of them observed in Dive 1  
 471 (Fig. 5). White and orange chromatic morphotypes were found for both species, with the first  
 472 being the most abundant (>95%). *M. oculata* and *L. pertusa* showed greater densities at the  
 473 crest of the mounds, especially towards the northernmost part of the province (290-320 m water  
 474 depth) (Figs. 3, 5). Conversely, the mounds' flanks, which were mainly covered by coral  
 475 rubble, were almost completely depleted of CWC (Fig. 5). This is particularly evident in Dive  
 476 1, where there were no corals growing on the flanks or the densities were comparatively rather  
 477 low (Fig. 5). Dive 2 and 3 presented lower densities of both coral species regardless of the  
 478 location and thus, for these dives, density differences between mound's crest and flanks were  
 479 less apparent. Furthermore, in Dive 1, coral density on the mound's crest was found to be  
 480 significantly and positively correlated to the presence of mini-mounds ( $p < 0.001$ ,  $\rho = 0.4$ ),  
 481 identified by high BPI values (Fig. S2). This CWC distribution pattern was apparent in the  
 482 detailed section of the Dive 1 density plot (Fig. 5B), in which the density peaks for both *M.*  
 483 *oculata* and *L. pertusa* match with the summits of the mini-mound features observed on the  
 484 crest of the mound.

485

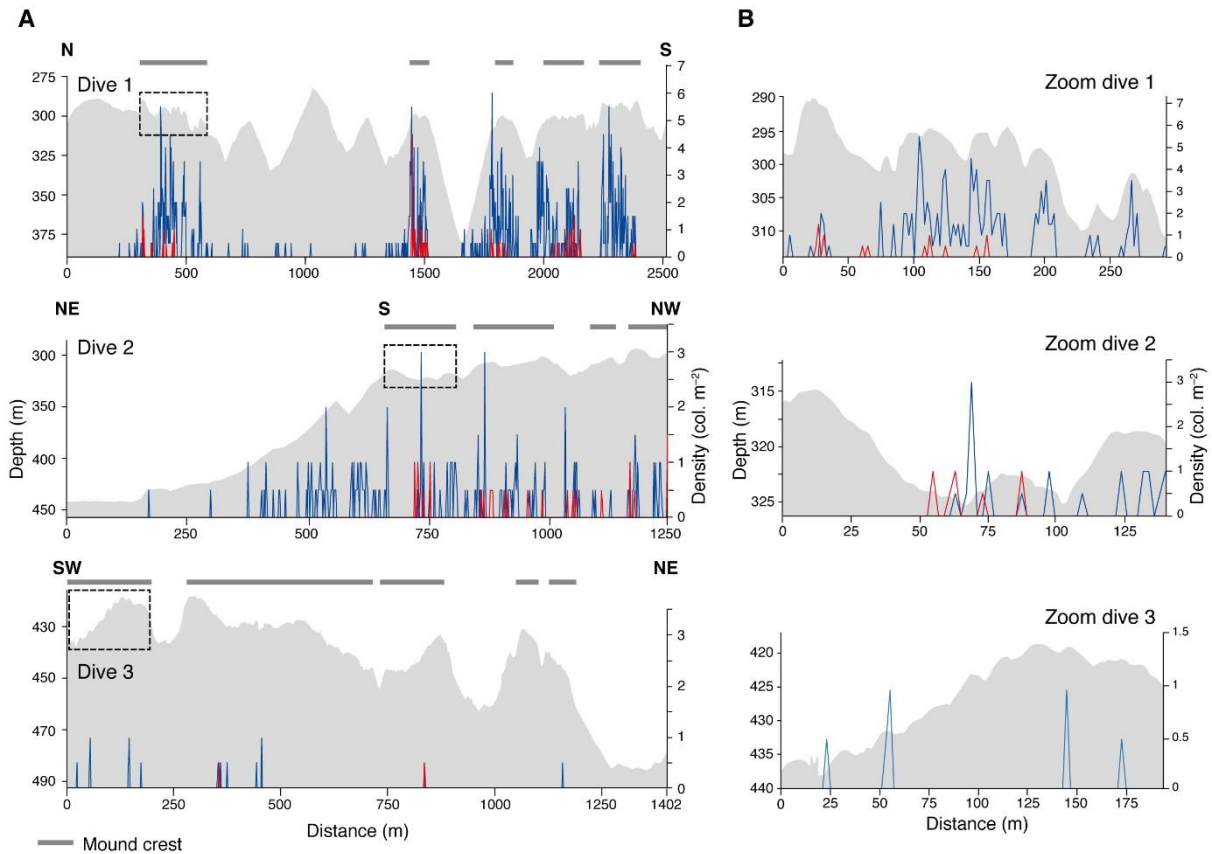
486 **Table 2.** Average density of the most abundant and relevant species in each ROV dive performed on the  
 487 Cabliers Coral Mounds, with scleractinian CWCs also displaying average colony size.

	<i>Madrepora oculata</i>		<i>Lophelia pertusa</i>		<i>Acanthogorgia</i>	<i>Parantipathes</i>	<i>Phanopathes</i>	<i>Leiopathes</i>	<i>Asconema</i>
	Density (patch m <sup>-2</sup> )	Size (cm)	Density (patch m <sup>-2</sup> )	Size (cm)	<i>hirsuta</i>	<i>larix</i>	<i>rigida</i>	<i>glaberrima</i>	<i>setubalense</i>
Dive 1	0.81±1.87	21.6±11.5	0.14±0.53	49.3±38.3	0.27±0.72	0.08±0.3	0.65±1.6	0.29±0.98	0.17±0.51
Dive 2	0.28±0.7	11.34±6.4	0.04±0.25	31.8±20.6	0.36±0.82	0.05±0.24	1.14±1.89	0.03±0.29	0.27±0.37
Dive 3	0.02±0.17	9.25±2.6	0.002±0.05	-	1.31±2.25	0.33±0.71	-	-	-

488

#### 489 4.3.2. Size structure

490 In total, 1178 and 139 colonies of *M. oculata* and *L. pertusa* were measured, some of them  
 491 being out of the video analysis range (1 m) for species density quantification. Similarly to the  
 492 observed density pattern, the average size of these corals decreased from Dive 1 to Dive 2  
 493 (Table 2), with *L. pertusa* being almost absent in Dive 3, where only one colony was observed  
 494 and measured. Colony size ranged from 4 to 130 cm for *M. oculata* and from 7 to 306 cm for  
 495 *L. pertusa* (Fig. 3). The high abundance of *M. oculata* in Dive 1 allowed to observe that  
 496 colonies found on the flanks of the mound had significantly smaller ( $p < 0.001$ ) average sizes  
 497 ( $12 \pm 4.6$  cm) than the ones at the crest ( $22.1 \pm 8.9$  cm) (Fig. 6C). Considering the colonies  
 498 from the whole study area, both *M. oculata* and *L. pertusa* had a higher percentage of smaller



**Figure 5.** Bathymetric profile (grey shading) and density plots of *Madrepora oculata* (blue) and *Lophelia pertusa* (red) for each ROV dive (A). Zooms from the black-dotted boxes in graph A, which allow to appreciate the correlation between coral density and mini-mound summits (B). Dark grey lines on top of the graphs indicate the fragments of each dive where the ROV was travelling over the crest of the mounds. Transect orientation is noted at the top of each graph.

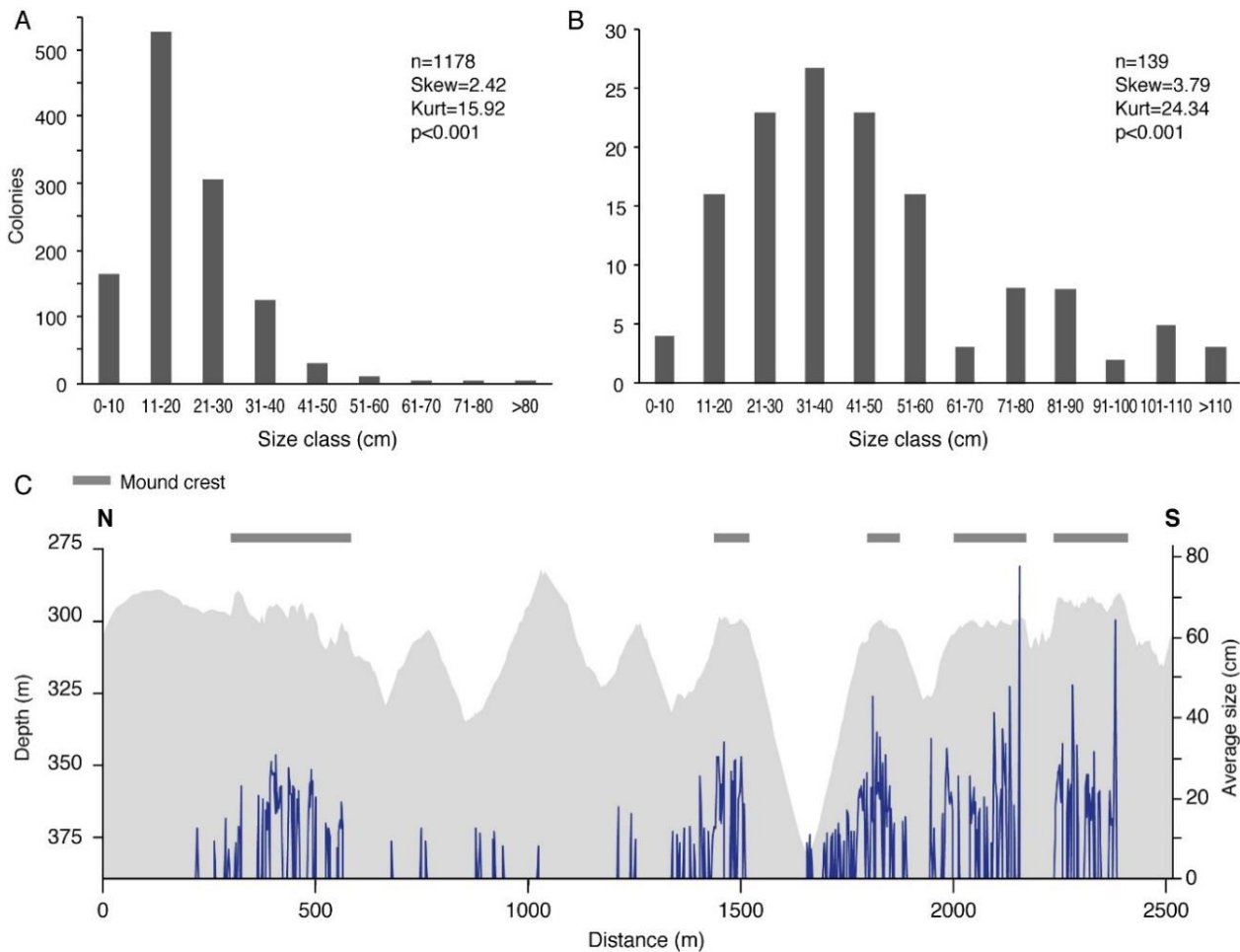
499 size classes than expected in a normal distribution, with significantly positive values of  
 500 skewness ( $p < 0.001$ ,  $skew_M = 2.42$  and  $skew_L = 3.79$  respectively) and presented a long-tailed  
 501 distribution ( $p < 0.001$ ,  $kurt_M = 15.92$  and  $kurt_L = 24.34$ ) with some large colonies (Fig. 6).

502

#### 503 **4.4. Main Associated Species**

504

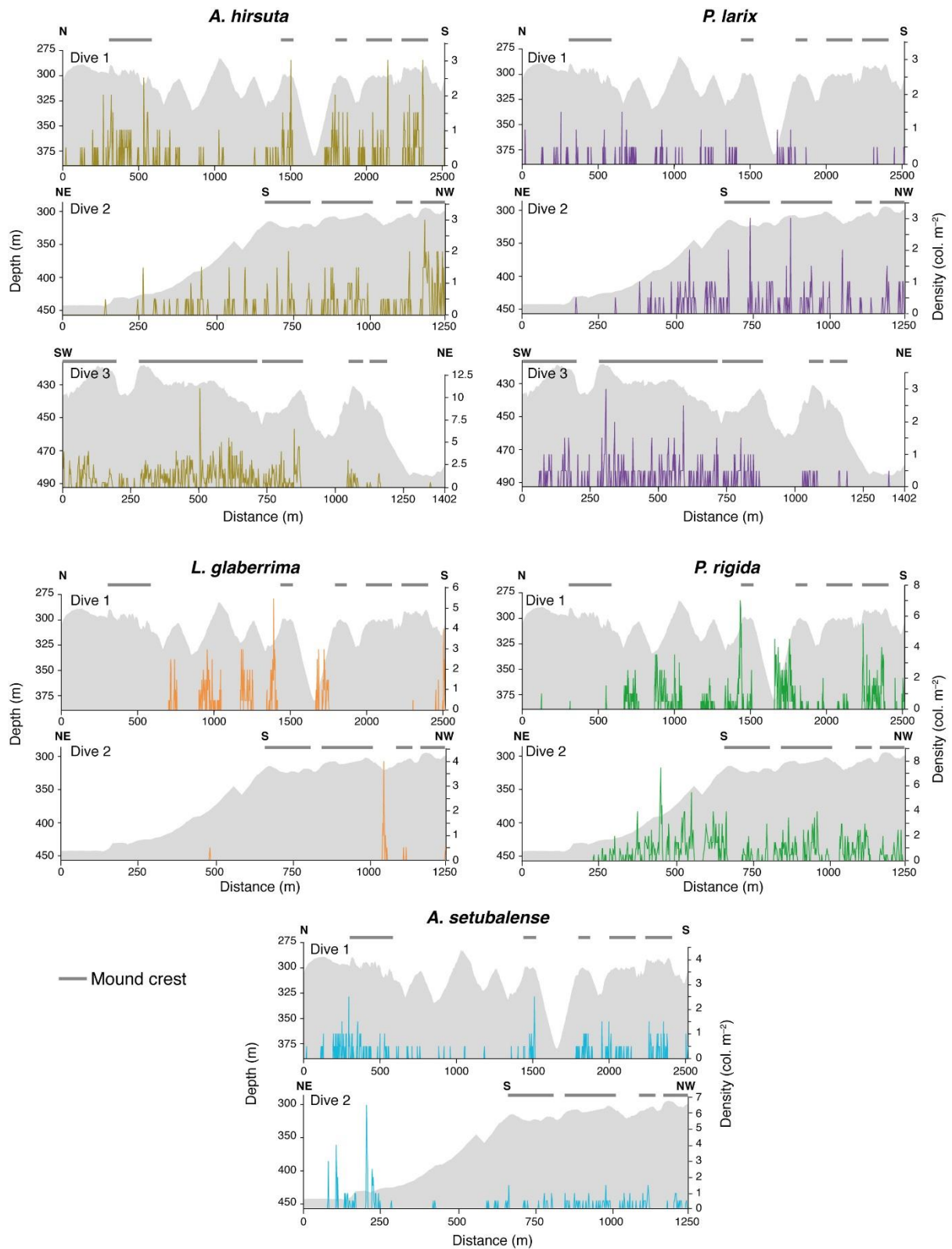
505 Amongst the most abundant species observed on Cabliers, only the gorgonian *A. hirsuta* and  
 506 the black coral *P. larix* occurred in all dives, with their density increasing towards the south of  
 507 the mound province (Table 2, Fig. 7). The maximum density values of *A. hirsuta* and *P. larix*  
 508 were 11.5 and 3  $\text{col} \cdot \text{m}^{-2}$  respectively (Fig. 7). The distribution of *A. hirsuta* and *P. larix* was  
 509 widespread across the mounds, although they both presented their highest abundances at the  
 510 crest (Fig. 7). Both *A. hirsuta* and *P. larix* showed greater abundances in Dive 3 (southern  
 511 Cabliers), where living framework-building CWCs were absent and these two species could



**Figure 6.** Colony size structure of *Madrepora oculata* (A) and *Lophelia pertusa* (B), together with the average size of *M. oculata* every 2 m<sup>2</sup> along Dive 1 (C). Grey shading indicates the bathymetric profile of the dive. Dark grey lines denote the fragments of the dive where the ROV operated along the mound’s crest. Transect orientation is noted at the top of graph C. n: number of colonies; Skew: skewness; Kurt: kurtosis.

512 thrive on the exposed dead coral framework that constitutes the mound’s crest (Fig. 7, see also  
513 Fig. 9).

514 The black corals *P. rigida*, *L. glaberrima* and the sponge *A. setubalense* were only found in  
515 Dive 1 and 2, where living CWCs were abundant. Both *P. rigida* and *A. setubalense* presented  
516 a higher average density in Dive 2. The highest density value observed for *P. rigida* and *A.*  
517 *setubalense* was 7.5 living-patches·m<sup>-2</sup> and 6.5 col·m<sup>-2</sup> respectively (Fig. 7). *L. glaberrima* had  
518 a maximum density of 5.5 col·m<sup>-2</sup> (Fig. 7). *P. rigida* and *L. glaberrima* showed a high density  
519 on the coral rubble from the mound’s flanks of Dive 1, for water depths ranging from 300 m to  
520 375 m (Fig. 7). However, in Dive 2 *L. glaberrima* was nearly absent and the flanks were  
521 dominated by *P. rigida*. The latter species was also observed growing on the mounds’ crest at  
522 the end of Dive 1 and throughout the entire Dive 2. The sponge *A. setubalense* was observed  
523 with a greater density on the mound’s crest, with up to 2.5 ind·m<sup>-2</sup>, using the coral framework



524

**Figure 7.** Bathymetric profile (grey shading) and density plots of *Acanthogorgia hirsuta*, *Parantipathes larix*, *Leiopathes glaberrima*, *Phanopathes rigida* and *Asconema setubalense*. Dark grey lines denote the fragments of the dive where the ROV operated along the mounds' crest. Transect orientation is noted at the top of each dive.

525 as substratum to colonise. However, there was one exception at the beginning of Dive 2, where  
526 this species was observed growing on top of a volcanic outcrop at ~425 m water depth, reaching  
527 its highest density (6.5 ind·m<sup>-2</sup>).

528 Throughout the three ROV dives a total of 519 fish individuals were observed, from which 184  
529 were identified in Dive 1, 195 in Dive 2 and 138 in Dive 3. The most abundant species was  
530 *Helicolenus dactylopterus* with 181 individuals, followed by *Hoplostethus mediterraneus* (n =  
531 175) and *Nezumia aequalis* (n = 60). Other species, some of them considered as commercially  
532 valuable, such as *Pagellus bogaraveo*, *Conger conger*, *Scorpaena scrofa* and some  
533 pleuronectids were also observed along Cabliers Coral Mounds. 111 individuals of *H.*  
534 *dactylopterus* were measured, showing sizes ranging from 5.1 to 35.6 cm and an average total  
535 length of 16.8 ± 7.4 cm. The 20% percent of these individuals have a length under 10 cm, which  
536 corresponds to the size of recruit and juvenile stages.

537

#### 538 **4.5. Environmental drivers and assemblages**

539

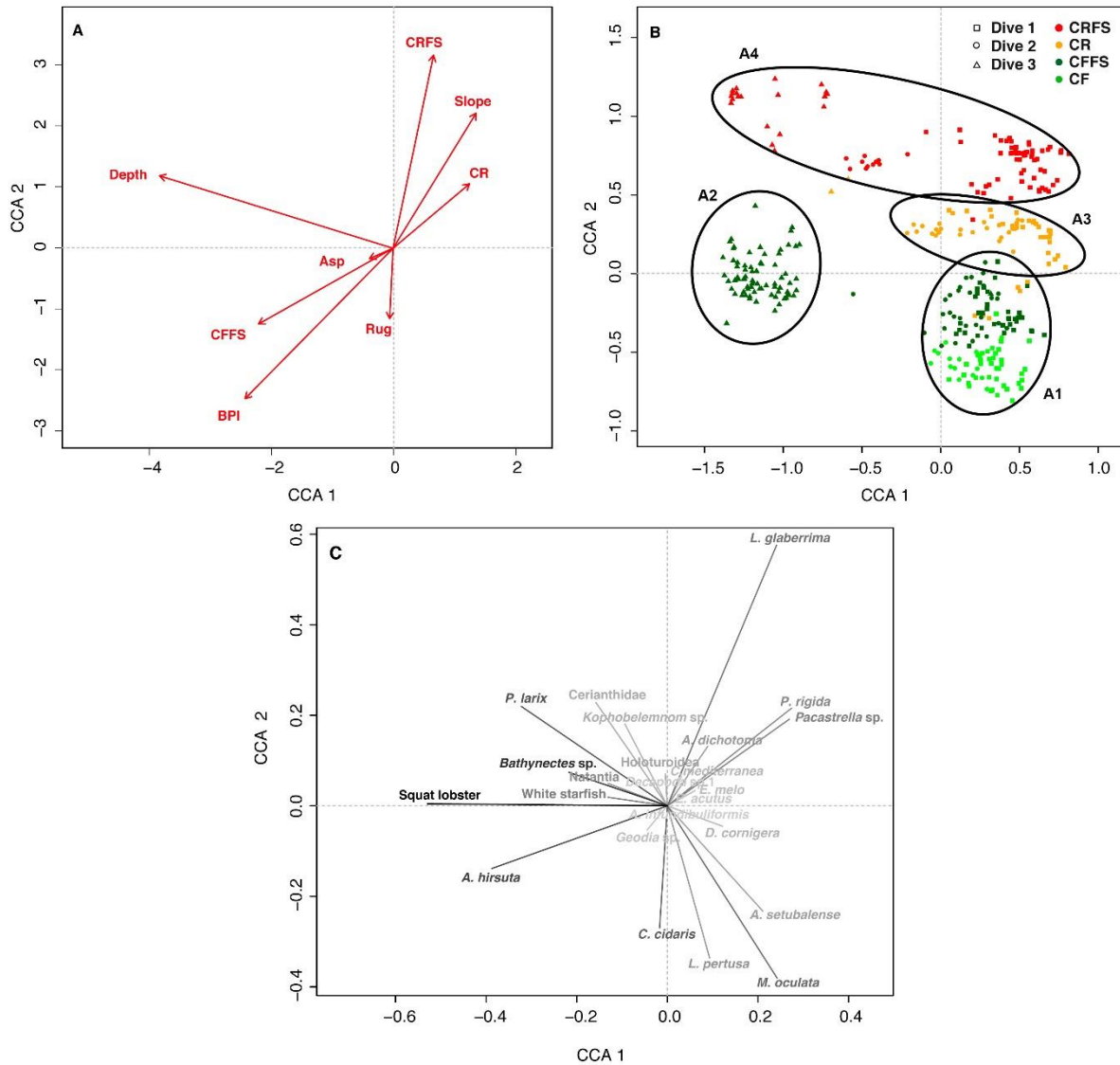
540 The set of CCA analyses performed adopting sampling units with different sizes (2, 4, 10 and  
541 20 m<sup>2</sup>) showed an increase in the inertia explained by seafloor features with larger sampling  
542 units (Table S2). However, with increasing sampling unit size, CCA faunal and environmental  
543 resolution were reduced due to a decrease in the number of sampling units and a higher  
544 variability of environmental factors within each sampling unit. Therefore, the optimal sampling  
545 unit size for the CCA analysis was set at 10 m<sup>2</sup>, which had the best equilibrium between  
546 percentage of inertia explained by seafloor features and CCA resolution.

547 The ANOVA-like permutation analysis demonstrated that all environmental factors (depth,  
548 slope, aspect, substratum type and BPI), apart from terrain roughness, were statistically  
549 significant predictors (p<0.01) and together explained 19.7% of the variation in species  
550 abundance. The first two CCA axes represented 10.3 and 5.6% of the total variance. Regarding  
551 predictor performance, the combined explanatory power of the four substratum types was the  
552 most relevant in determining species distribution, explaining 9.9% of the variation, followed  
553 by depth, which explained a further 7.4% (Fig. 8). The CCA ordination together with the  
554 ANOVA-like permutation tests, allowed identifying four megabenthic assemblages  
555 characterised by different dominant species and controlled by different seafloor features (Fig.  
556 8).

557 Assemblage 1 was mainly characterised by the scleractinians *M. oculata* and *L. pertusa*  
558 together with the echinoderm *Cidaris cidaris* and the sponge *A. setubalense* (Fig. 3). These



559 species mainly occurred on the northern and shallower parts of the mounds' crests (Dive 1, 2),  
 560 growing on dead coral framework (CF) (Fig. 8).  
 561 Assemblage 2 occurred on the deeper and southern parts of the mounds' crests (Dive 3), where  
 562 dead coral framework with fine sediments (CFFS) was the main substratum type. These areas



**Figure 8.** Canonical correspondence analysis (CCA) results. The first bi-plot (A) shows all significant seafloor variables considered in the analysis in relation to the axes CCA1 and CCA2. The second bi-plot (B) displays the 10 m<sup>2</sup> sampling units ordination based on species abundance and composition, constrained by the seafloor variables and coloured according to their substratum type. The third bi-plot (C) shows the contribution of each species to the megabenthic assemblages. The grey scale of each species indicates the degree of correlation to the seafloor variables, being black the highest correlation. The length and position of the vectors gives information about their relationship to the axes. Vectors parallel to an axis denote a correlation and their length defines the strength of such correlation. CRFS: coral rubble and fine sediments, CR: coral rubble, CFFS: dead coral framework and fine sediments

563 were covered by aggregations of the gorgonian *A. hirsuta*, squat lobsters and the anthipatharian  
564 *P. larix* (Fig. 8).

565 Assemblage 3 occurred on the northern and shallowest parts of the mounds' flanks (Dive 1, 2),  
566 where the seafloor is steep and coral rubble (CR) is the most common substratum type. This  
567 assemblage is characterised by the presence of *P. rigida*, together with the incrusting sponge  
568 *Pachastrella* sp (Fig. 8).

569 Finally, Assemblage 4 comprehended sampling units from all ROV dives and presented a  
570 varying taxonomic composition. It was mainly characterised by the presence of *L. glaberrima*  
571 and other antozoans such as the pennatulacean *Kophobelemnem* sp., cerianthids and some  
572 colonies of *P. larix*. These taxa generally occurred on coral rubble with fine sediments (CRFS)  
573 on the deeper parts of the flanks of the mounds (i.e. steep slopes) (Fig. 8).

574

575

## 576 **5. DISCUSSION**

577

### 578 **5.1. Cabliers Coral Mound**

579

580 The Cabliers Coral Mounds are among the most extensive coral mound features in the Alboran  
581 Sea (Comas and Pinheiro, 2010; Fink et al., 2013; Lo Iacono et al., 2014; Lo Iacono et al.,  
582 2018b). As other mounds (Hovland and Risk, 2003; Buhl-Mortensen et al., 2010), they  
583 developed on a volcanic basement that can be observed at the start of Dive 2 and is well  
584 recognisable in the high-resolution AUV bathymetry. This outcrop probably functioned as a  
585 substratum for CWC colonization and subsequent mound development. As described in  
586 Duggen et al. (2004) the outcrop on which the Cabliers Coral Mounds developed, known as  
587 Cabliers Bank, probably consists of an andesite basement, dated Middle to Late Miocene.

588 As with some other giant coral mounds (Buhl-Mortensen et al., 2017), Cabliers ridge-like  
589 mounds could be the product of smaller mounds coalescing to form giant elongated coral  
590 mounds. This is suggested by the occurrence of numerous mini-mounds aligned along the crest  
591 of the northern Cabliers Mounds, where the most thriving CWC assemblages were observed.  
592 However, an extensive and more detailed geomorphological study of Cabliers Mounds is  
593 required to prove this hypothesis.

594

### 595 **5.2. Scleractinian cold-water corals**

596



597 The incidence of higher density of living CWC at the crest of the mounds agrees with previous  
598 observations from other coral mounds and is probably caused by the presence of more  
599 favourable environmental conditions (Freiwald et al., 2004; Huvenne et al., 2005; Davies et  
600 al., 2009; Lo Iacono et al., 2018). Furthermore, the dive segments that crossed the crest of the  
601 mounds, showed that the peaks in *M. oculata* and *L. pertusa* density generally matched with  
602 the presence of the mini-mound like features (Figs. 3, 5). Considering that the highest CWC  
603 density values are observed at the top of these mini-mounds, it could be hypothesised that these  
604 features are the engine that drives CWC mound growth (Lo Iacono et al., 2018b). These mini-  
605 mound features are comparatively elevated to the rest of the mound's crest, thus their summit  
606 is probably exposed to higher current speeds, which might prevent sedimentation on the corals  
607 growing there. Additionally, such current speeds might cause a higher amount of food to be  
608 advected towards the mini-mounds' summit, providing the most suitable conditions for CWC  
609 growth.

610 Framework-building CWC densities are highly variable in the Mediterranean Sea. The Cap de  
611 Creus Canyon, in the NW Mediterranean, presents average densities of both species oscillating  
612 between 0.1-0.4 col·m<sup>-2</sup> for *M. oculata* and 0.004-0.01 col·m<sup>-2</sup> for *L. pertusa* (Orejas et al.,  
613 2009; Gori et al., 2013). In the Lacaze-Duthiers Canyon, Gori et al. (2013) explored with an  
614 ROV a distance of 8362 m, where 555 and 97 colonies of *M. oculata* and *L. pertusa* were  
615 counted. This would relate to an average density of 0.044 col·m<sup>-2</sup> and 0.012 col·m<sup>-2</sup> for each  
616 species, comparable to the values observed in other regions of the Mediterranean, where *M.*  
617 *oculata* and especially *L. pertusa* generally occur as small populations or sparse colonies on  
618 complex geomorphic features (Savini and Corselli, 2010; Lastras et al., 2016; Fabri et al., 2017;  
619 Taviani et al., 2017). Therefore, average densities of *M. oculata* and *L. pertusa* on northern  
620 Cabliers (0.81 and 0.14 col·m<sup>-2</sup> respectively) are considerably greater than the ones observed  
621 for most of the other CWC assemblages described in the Mediterranean Sea. Only the coral-  
622 topped mounds from Santa Maria di Leuca province seem to present an abundance comparable  
623 to the Cabliers assemblages, however no quantitative data are yet available for this area (Savini  
624 and Corselli, 2010; Vertino et al 2010; Savini et al., 2016; Bargain et al., 2017). In terms of  
625 coral mounds, almost the totality of these geomorphologic features discovered to date in the  
626 Mediterranean Sea are in a complete stage of decline, with only some sparse living colonies of  
627 *M. oculata* and *L. pertusa* (Hebbeln and Wienberg, 2016). The absence of anthropogenic  
628 footprint in the ROV footage suggests that the Cabliers living reefs are in a likely pristine  
629 status, which is remarkable considering its proximity to both the coasts of Spain and Morocco,  
630 where industrial fishing practices are intense (Aguilar et al., 2017).

631 The northern mounds of the Cabliers Coral Mound Province resemble the characteristics of  
632 their thriving Atlantic counterparts, on which a mixture of abundant living coral and exposed  
633 dead coral framework is commonly observed (Buhl-Mortensen et al., 2010). The megabenthic  
634 assemblages observed in Dive 1 matches with the typical spatial patterns of living CWC reefs,  
635 in which the area occupied by dead coral framework is greater than the coverage of living  
636 corals (Mortensen et al., 1995; Buhl-Mortensen et al., 2017). The average density of *M. oculata*  
637 in northern Cabliers (Dive 1: 0.81 col·m<sup>-2</sup>) presents similar values to those observed in the  
638 prolific Atlantic regions such as the Logachev Mounds (1.04 col·m<sup>-2</sup>) (Arnaud-Haond et al.,  
639 2017). In contrast, *L. pertusa* density is much higher in the Logachev Mounds (1.41 col·m<sup>-2</sup>)  
640 in comparison to Cabliers (0.14 col·m<sup>-2</sup>). This makes sense, since Atlantic coral mounds  
641 generally present a higher relative abundance of *L. pertusa* contributing to form CWC reefs  
642 (Buhl-Mortensen et al., 2017). The reason for this discrepancy could be due to the higher water  
643 temperatures of the Mediterranean Sea compared to the north Atlantic. Warmer temperatures  
644 in the Mediterranean, which cause a higher oxygen demand by the corals (Dodds et al., 2007),  
645 are combined with a lower availability of dissolved oxygen (i.e. from 6-6.2 ml l<sup>-1</sup> in the North  
646 Atlantic to 3.75 ml l<sup>-1</sup> in the Mediterranean) (Davies et al., 2008; Freiwald et al., 2009). In this  
647 setting, *L. pertusa* might be closer to its ecological boundary, which could explain its lower  
648 abundances compared to *M. oculata* (Dodds et al., 2007; Freiwald et al., 2009; Davies and  
649 Guinotte, 2011). However, this assumption would require further investigation.

650 Besides the high coral density observed on the northern region of Cabliers, 2% of *M. oculata*  
651 and 32% of *L. pertusa* coral colonies from these mounds reached sizes over 50 cm in diameter  
652 (Figs. 3, 6). This suggests that CWC have been thriving on northern Cabliers during the recent  
653 past. On the other hand, there is also an important percentage (58%) of small colonies (<20  
654 cm) of *M. oculata*, which suggests either a high recruitment rate or frequent fragmentation of  
655 larger colonies into smaller ones. According to the skewness results, the *L. pertusa* population  
656 on Cabliers is characterised by medium-sized colonies (20-40 cm = 36%) (Fig. 6). This trend  
657 could be a consequence of a lower recruitment rate and/or a lower fragmentation of *L. pertusa*,  
658 due to its thicker and less fragile skeleton in comparison to *M. oculata*. Gori et al. (2013)  
659 observed a similar trend in the Gulf of Lions, where *L. pertusa* also presented larger colony  
660 sizes than *M. oculata*. However, in that region, both species generally showed smaller coral  
661 colony sizes than the ones observed on Cabliers.

662 Along with CWC density, colony size also increased towards the crest of the Cabliers Coral  
663 Mounds. This is probably caused by a higher substratum stability that allows corals on the sub-  
664 horizontal crest to grow larger than the ones on the sloping flanks. Simultaneously a greater

665 food supply might occur across the crest of the mounds, where bottom currents are generally  
666 expected to be stronger (Mienis et al., 2012; Cyr et al., 2016; Lo Iacono et al., 2018).  
667 Similarly to what has been reported in other studies (Mastrototaro et al., 2010; Mienis et al.,  
668 2012; Duineveld et al., 2012; Oguz et al., 2014), the presence of flourishing CWC assemblages  
669 on Cabliers is probably linked to suitable oceanographic conditions. In this regard, the Cabliers  
670 Coral Mounds are located within the Levantine Intermediate Water, a water mass regarded by  
671 Taviani et al. (2017) as hosting most of the living CWC assemblages occurring in the  
672 Mediterranean Sea. Nevertheless, the CWCs present in Cabliers showed a dramatic decrease  
673 in abundance towards the southern region of the province (Figs. 2, 5). This pattern could be  
674 caused by the presence of slower current speeds in the southern region, which could explain  
675 the greater amount of fine sediments observed at the mound's crest. Weaker currents would  
676 also bring less amount of food to the corals and generate lower resuspension of organic material  
677 from the seafloor, preventing corals from a sufficient food intake (Duineveld et al., 2004).  
678 Furthermore, the crest of the coral mounds from southern Cabliers is found at a greater water  
679 depth (Dive 3: ~420-445 m) than the crest of the northern ones (Dive 1 and 2: ~280-325 m).  
680 This fits the results from the CCA analysis, where depth was found to be one of the main  
681 environmental drivers affecting species distribution (Fig. 8). In this sense, the southern, less  
682 prolific part of Cabliers would be considerably further away from the AW-LIW interface (150-  
683 200 m water depth) (Millot, 2009). The global coral mound distribution generally matches with  
684 the presence of close sharp thermo- and haloclines, indicating that such water mass interfaces  
685 might be relevant for the proliferation of CWC reefs (Dullo et al., 2008; Matos et al., 2017; Lo  
686 Iacono et al. 2018). However, the considerable differences in CWC abundance within the  
687 northern sector of Cabliers (Dive 1 and Dive 2), suggests that at a local-scale, other variables  
688 than depth contribute towards the creation of suitable conditions for the development of such  
689 thriving CWC assemblages.

690

### 691 **5.3. Megabenthic species distribution and environmental variables**

692

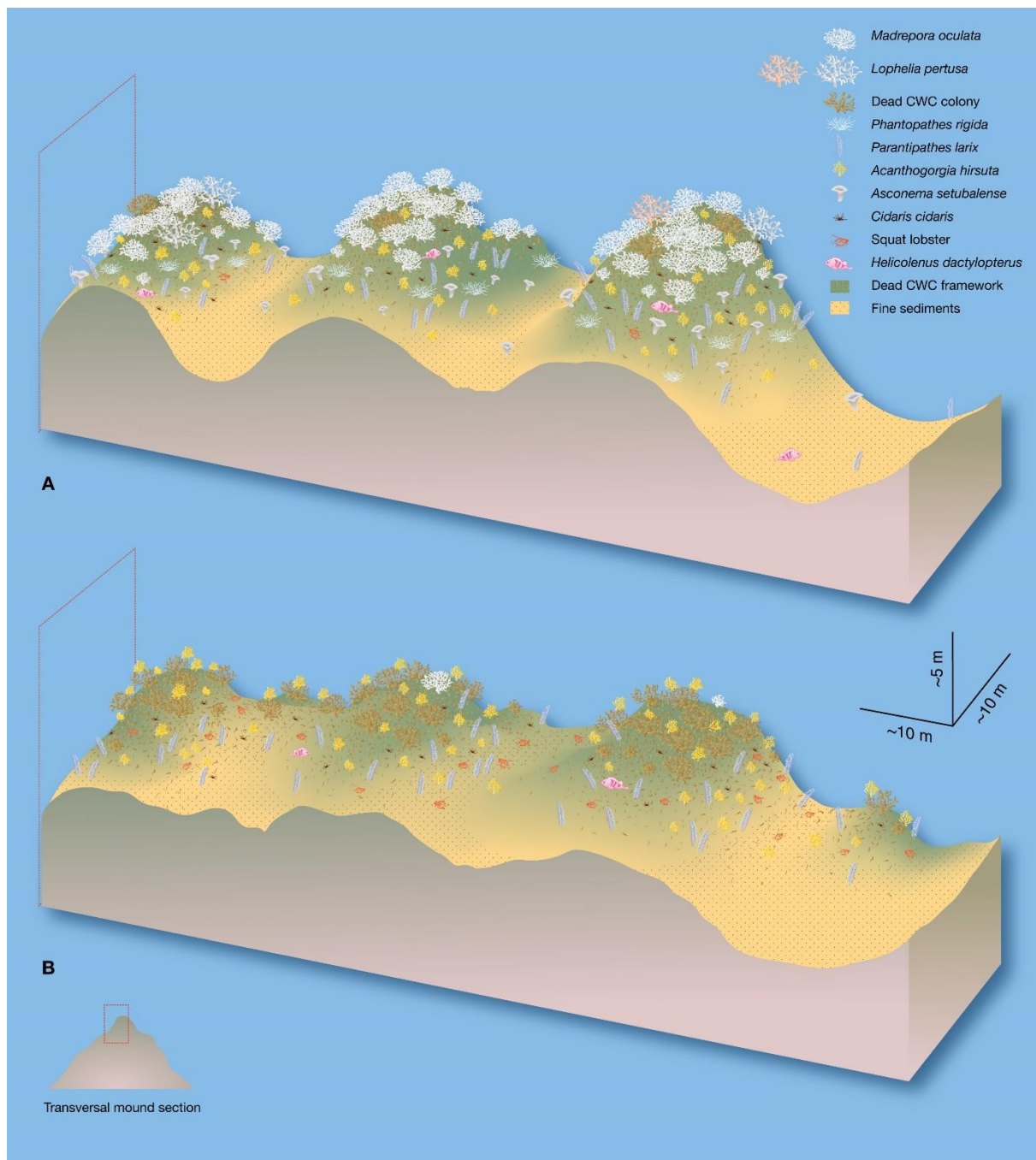
693 The CCA analysis divided the Cabliers fauna into four main assemblages, which were mainly  
694 determined by substratum type and water depth, two environmental variables that have been  
695 long regarded as important factors determining species distribution in benthic habitats (Zajac  
696 et al., 2000; Santín et al., 2017, 2019). The most common substratum types on a coral mound  
697 derive from dead CWCs, which suggests that as some other ecosystem engineers, framework-

698 building corals affect the distribution of the rest of species in the habitat even after they die  
699 (Jones et al., 1994).

700 The megabenthic fauna observed on the Cabliers Coral Mounds mostly features sessile benthic  
701 suspension feeders (e.g. octocorals, antipatharians, sponges) that generally grow on the hard  
702 substrata provided by dead coral framework and off-mound outcropping volcanic rocks. This  
703 is the typical type of fauna found worldwide on coral mounds (Roberts et al., 2006;  
704 Mastrototaro et al., 2010; Buhl-Mortensen et al., 2010, 2017). Such geomorphological features  
705 are indeed areas with a high hard substrata availability for larval settlement and generally  
706 exposed to strong bottom currents, which provide a suitable environment for suspension  
707 feeding (Mortensen and Fosså, 2006; Mienis et al., 2012).

708 Most of the species associated with stony CWCs in Cabliers are also conspicuous in other areas  
709 of the Mediterranean Sea. For instance, *A. hirsuta* has also been observed in other regions of  
710 the Alboran Sea (i.e. Al Idrissi Bank and Chella Mound) (Coiras et al., 2011; De la Torriente  
711 et al., 2018), as well as on shelf edge and slope settings of the western and central  
712 Mediterranean Sea (Bo et al., 2015; Cau et al., 2015; Oceana, 2015; Grinyó et al., 2016). Within  
713 the antipatharians, *L. glaberrima* is a very abundant species in areas of the upper slope of the  
714 Mediterranean Sea (>130 m water depth) (Vertino et al., 2010; Angeletti et al., 2014; Bo et al.,  
715 2015; Ingrassia et al., 2016). The same is true for *P. larix*, which is widespread across the  
716 Mediterranean, mostly growing on the upper continental slope (Bo et al., 2014a). On the  
717 contrary, the high abundance of *P. rigida* is remarkable, considering this species is Atlantic  
718 (Opresko, 2009) and has been observed for the first time in the Mediterranean Sea on the  
719 Cabliers Coral Mounds (Bo et al., 2018). The fishes found on Cabliers have also been observed  
720 in other bathyal regions of the Mediterranean Sea (Fabri et al., 2014; Taviani et al., 2017; Deval  
721 et al., 2018). Furthermore, *H. dactylopterus* presented individuals covering all the size classes  
722 previously described for this species (Deval et al., 2018), which means that these fishes inhabit  
723 CWC reefs during most of their life stages. It is especially important to point out the 20% of  
724 juveniles and recruits (<10 cm) of this species observed on the Cabliers Coral Mounds, which  
725 confirms the use of CWC assemblages as nursery grounds by a commercially valuable species.

726 In terms of spatial distribution, some of the sessile species mentioned have been observed to  
727 occur on the mini-mounds located at the crest of Cabliers Coral Mounds. However, when dense  
728 aggregations of living CWC cover the summit of these mini-mounds, the associated species  
729 are displaced to areas with a higher percentage of exposed dead coral framework (Fig. 9). The  
730 availability of this substratum increases towards the mini-mound flanks and there, organisms  
731 such as *A. setubalense* and *P. larix* increase in abundance (Fig. 9). Nevertheless, smaller



**Figure 9.** Schematic representation of the megabenthic species distribution on the mini-mounds located on the crest of northern (A) and southern (B) Cabliers Coral Mound.

732 species, such as *A. hirsuta* and *C. cidaris*, manage to grow amongst dense *M. oculata* and *L.*  
 733 *pertusa* colonies (Figs. 7, 9). The regions between mini-mounds, where fine sediments drape  
 734 the dead coral framework or are interspersed with it, seem to have a lower megabenthic  
 735 abundance (Fig. 9). This is probably due to the lack of hard substratum on which benthic sessile  
 736 organisms could settle.

737 Although all the mentioned species were observed in northern Cabliers, they do not present a  
 738 homogeneous distribution along the mounds. Similarly to framework-building CWC, some

739 species such as *P. rigida*, *A. setubalense* and *L. glaberrima* decrease in abundance or are  
740 completely absent at the southern region of Cabliers (Dive 3; Fig. 2, 9). This suggests that a  
741 marked change in the environmental conditions (e.g. greater depth, weaker current regime or  
742 lower food supply) occurs towards the southern part of the mound, which far from only  
743 affecting scleractinian corals is also detrimental for the proliferation of the latter taxa.  
744 Some other species, such as *A. hirsuta* and *P. larix* show an increase in abundance towards  
745 south Cabliers. This pattern could be related to the absence of living CWCs in that region,  
746 which allows other organisms to thrive and dominate the areas of dead coral framework and  
747 fine sediments (Fig. 7, 9). We hypothesise that when environmental conditions are suitable,  
748 framework-building corals outcompete these species, which are therefore confined to less  
749 suitable sectors of the reef, where dead CWC framework dominates as substratum.  
750 In conclusion, Cabliers megabenthic assemblages change from thriving CWC reefs at the north  
751 (Dive 1), to dead coral framework mixed with fine sediments and colonised by octocorals,  
752 antipatharians and squat lobsters, at the south (Dive 3) (Fig. 2, 9). The changes in taxonomic  
753 composition, abundance and diversity from north to south Cabliers could be a representation  
754 of the different ecological succession stages that can occur in a coral mound throughout  
755 flourishing and decline periods (Mortensen and Fosså, 2006). However, in order to get a more  
756 comprehensive overview of Cabliers and confirm these observations, more images or video-  
757 transects should be acquired along and across the mounds, and a more detailed study of the  
758 environmental conditions should be performed.

759

#### 760 **5.4. Faunal comparison with Mediterranean and Atlantic Mounds**

761

762 The characterisation of biogeographic provinces has essential implications for understanding  
763 the evolutionary and ecological processes that caused the existing large-scale biodiversity  
764 patterns (Whittaker et al., 2005; Lomolino et al., 2006). In this sense, they can be of use to  
765 predict the areas where certain habitats or species can occur and to foresee the response of such  
766 ecosystems to cumulative disturbances (Rice et al., 2010). Biogeographic provinces might also  
767 help to detect potentially vulnerable marine ecosystems (VMEs) and to create representative  
768 marine protected area networks (Rice et al., 2010). Therefore, comparing the taxonomic  
769 composition of the Cabliers Coral Mound megafauna with the one observed on analogous  
770 Mediterranean and Atlantic geomorphologic features might help towards a better  
771 understanding of the taxonomic linkages amongst the known CWC mound provinces, which

772 would improve the baseline needed for the designation of sensible marine protected area  
773 networks.

774 The type of megafaunal taxa observed on Cabliers showed several similarities with what has  
775 been previously described on the thriving Atlantic CWC mounds (Mortensen and Fossa, 2006;  
776 Henry and Roberts, 2007; Buhl-Mortensen et al., 2017). Some organisms such as gorgonians,  
777 hexactinellid sponges, demosponges, squat lobsters, and sebastid fishes are within the shared  
778 fauna between Cabliers Coral Mounds and its Mediterranean and Atlantic analogues (Roberts  
779 et al., 2008, 2009a; Vertino et al., 2010; Purser et al., 2013; Ross et al., 2017). However, as  
780 observed in Buhl-Mortensen et al. (2017), the fauna associated to CWC mounds can present  
781 considerable taxonomic differences amongst provinces, even though such species belong to the  
782 same functional groups.

783 Within the Mediterranean Basin, the coral mound clusters are in a general stage of decline.  
784 Some of them have been reported to be mostly covered by aggregations of gorgonians, sponges  
785 and echinoderms (Hebbeln, 2009; Hebbeln and Wienberg, 2016). Probably the coral reefs  
786 observed in Santa Maria di Leuca (Central Mediterranean Sea) are the closest ones to Cabliers  
787 in terms of reef-building coral abundance and megafaunal composition. Both of them present  
788 demosponges, antipatharians and gorgonians as the main species accompanying *M. oculata*  
789 and *L. pertusa* reefs (Mastrototaro et al., 2010; Vertino et al., 2010). Within these taxonomic  
790 groups, *Pachastrella* sp., *A. hirsuta* and *L. glaberrima* dominate the accompanying fauna in  
791 both regions (Mastrototaro et al., 2010; Vertino et al., 2010). However, the hexactinellid sponge  
792 *A. setubalense* and the antipatharian *P. rigida* are only observed in abundance on Cabliers.

793 Norwegian CWC mounds exhibit gorgonians, demosponges and anemones, within the most  
794 conspicuous reef associated fauna. The bivalve *Acesta excavata* is also a common species on  
795 these mounds. Although both Norwegian coral mounds and Cabliers contain gorgonians, the  
796 former are populated by *Paragorgia arborea* and *Primnoa resedaeformis* (Purser et al., 2013;  
797 Buhl-Mortensen et al., 2017), while the latter is covered by dense aggregations of *A. hirsuta*.  
798 The same occurs with demosponges, which are an important component of Cabliers (i.e.  
799 *Pachastrella* sp.), yet the dominant species are different from those observed on Norwegian  
800 mounds (i.e. *Geodia* sp. and *Mycale lingua*) (Purser et al., 2013; De Clippele et al., 2018).  
801 Furthermore, bivalves and anemones are not within the dominant associated fauna observed on  
802 Cabliers.

803 The Mingulay Reef Complex, located on the Scottish continental shelf, presents a taxonomic  
804 composition similar to the Norwegian mounds, with no hexactinellid sponges and the  
805 demosponges *Geodia* sp. and *M. lingua* occurring among the *L. pertusa* colonies (Roberts et

806 al., 2009a; De Clippele et al., 2018). However, dense gorgonian aggregations were not  
807 observed on the Mingulay Reef Complex (Roberts et al., 2009a).

808 Irish and African Atlantic CWC mounds are generally populated by large assemblages of  
809 hexactinellid sponges, whose silicic skeleton contributes to the structural formation of the  
810 mounds (van Soest et al., 2007; Henry and Roberts, 2007; Buhl-Mortensen et al., 2017).  
811 Although this taxonomic group is also present on Mediterranean coral mounds (i.e. Cabliers),  
812 the species do not coincide. *Rosella nodastrella*, *Aphrocallistes bocagei* and *A. beatrix*  
813 dominate the associated fauna of Irish and African coral mounds (van Soest et al., 2007; Henry  
814 and Roberts, 2007; Buhl-Mortensen et al., 2017), whereas *A. setubalense* is the dominant  
815 hexactinellid sponge on Cabliers. Such as in Norwegian Mounds, anemones (i.e. *Phelliactis*  
816 sp.), and bivalves (i.e. *Acesta* sp.) thrive on the Irish and the African mounds respectively  
817 (Roberts et al., 2008; Buhl-Mortensen et al., 2017).

818 On the western Atlantic, in the Gulf of Mexico and off North Carolina and Florida's coast,  
819 several coral mounds arise (Ross, 2006; Ross and Nizinski, 2007; Hebbeln et al., 2014; Mienis  
820 et al., 2014; Ross et al., 2017). In accordance to the African mounds, the hexactinellid sponge  
821 *A. Beatrix* is observed forming aggregations on these American mounds (Ross and Nizinski,  
822 2007). Other suspension feeders such as gorgonians (*Keratoisis* spp.), antipatharians (*L.*  
823 *glaberrima* and *Bathypathes alternata*) and stylasterid corals are also amongst the main  
824 associated species to the *L. pertusa* reefs of these mounds.

825 As already stated, Atlantic coral mounds mostly present *L. pertusa* as the main reef-building  
826 species, sometimes accompanied by *M. oculata*, *Enallopsamia profunda* and *Solenosmillia*  
827 *variabilis* (Roberts et al., 2008; Buhl-Mortensen et al., 2017; Ross et al., 2017). On the other  
828 hand, Cabliers shows a considerably higher proportion of *M. oculata*, accompanied by *L.*  
829 *pertusa* and *D. cornigera*.

830 This faunistic comparison among coral mound provinces suggests that although most  
831 taxonomical groups of organisms observed on Cabliers are common to those witnessed on  
832 Atlantic coral mounds (Henry and Roberts, 2007; Ross and Nizinski, 2007; Purser et al., 2013;  
833 Buhl-Mortensen et al., 2017; Ross et al., 2017), there are considerable differences at the species  
834 level. These variations in the megafaunal composition are probably determined by  
835 biogeographic factors. Although in most regions the species associated to CWC mounds are  
836 probably subjected to similar conditions in terms of current speed and food supply, other  
837 environmental variables, such as water temperature and dissolved oxygen might influence their  
838 distribution. Another factor that limits species distribution is larval dispersal, which depends  
839 on water mass circulation, larval longevity and motility. Therefore, changes in environmental



840 variables due to the incidence of contrasting oceanographic conditions, together with the  
841 presence of biogeographical barriers (e.g. Strait of Gibraltar) might prevent some of these  
842 species from being found in different CWC mound provinces.

843 Even though CWCs were already known to host a large diversity of organisms, the taxonomic  
844 differences observed between mound provinces suggest that the number of species associated  
845 to these habitats is even higher than previously thought (Roberts et al., 2006). As a consequence  
846 of the high biodiversity of these ecosystems and their high vulnerability to anthropogenic  
847 disturbances (Althaus et al., 2009; Armstrong et al., 2014), many measures have been taken by  
848 the United Nations and the Food and Agriculture Organisation (FAO) to protect CWC habitats  
849 (Davies et al., 2017). Several international legislations have defined CWC assemblages as  
850 vulnerable marine ecosystems (VMEs) and have included them in the list of endangered  
851 habitats (EU Habitats Directive, OSPAR, 2008). However, in order to efficiently implement  
852 such conservation measures, more detailed information about the distribution, taxonomic  
853 composition and ecological state of CWC mounds needs to be provided. This is especially true  
854 for the Mediterranean Sea, where to the moment, the Cabliers Coral Mounds are the only giant  
855 CWC mounds hosting living CWC reefs. Therefore, further exploring and research efforts are  
856 required in this field to unveil and study new coral mound provinces in order to better constrain  
857 the environmental conditions that allow the formation and endurance of these  
858 geomorphologically complex bioconstructions.

859

## 860 **6. CONCLUSIONS**

861

862 - ROV footage integrated with high-resolution AUV bathymetry unveiled thriving CWC reefs  
863 with uncommonly high coral densities occurring on the top of some of the Cabliers Coral  
864 Mounds, western Mediterranean Sea.

865 - Similarly to the Atlantic CWC mounds, coral density and size increase towards the top of the  
866 Cabliers Coral Mounds, probably due to higher food supply and structural stability.

867 - Statistical analyses showed the presence of four megabenthic assemblages, whose distribution  
868 was mainly determined by substratum type and depth.

869 - The presence of several *H. dactylopterus* individuals under 10 cm confirms that CWC  
870 assemblages are used by commercially valuable species as nursery grounds.

871 - The changes in CWC abundance, taxonomic composition and diversity between north and  
872 south Cabliers could be a representation of the different succession stages that can occur in a  
873 coral mound throughout flourishing and decline stages.

874 - The taxonomic differences observed between Atlantic and Mediterranean coral mounds, in  
875 terms of megabenthic assemblages, indicate that the amount of species associated to CWC reefs  
876 is probably higher than previously thought.

877 - The present study helped to gain insight into the structure of Mediterranean CWC reefs and  
878 their associated species. However, a broader quantitative baseline would be required to better  
879 understand the environmental constraints of these ecosystems in the Mediterranean Sea and to  
880 contribute towards an improved management of CWC assemblages.

881

## 882 **ACKNOWLEDGEMENTS**

883

884 Guillem Corbera is funded by the Graduate School of the National Oceanography Centre  
885 Southampton (GSNOCS), with the collaboration of the NGO OCEANA. The data for this study  
886 was collected during the Spanish national project SHAKE (CGL2011-30005-C02-02, PI:  
887 Eulàlia Gràcia). We acknowledge the European Ocean facilities Exchange Group (OPEG) who  
888 facilitated the use of the AUV IdefX from IFREMER (France) and the EU Eurofleets-2 Project,  
889 which provided the ROV Max Rover from HCMR (Greece) during the SHAKE Cruise. We  
890 are indebted with the technical teams of UTM-CSIC, IFREMER and HCMR, for their support  
891 provided during the SHAKE cruise. We gratefully acknowledge all the participants on the  
892 SHAKE cruise and the crew on board of the R/V Sarmiento de Gamboa for their professional  
893 work during the expedition. Finally, we would like to thank the scientific illustrator Jordi  
894 Corbera for the design of the schematic representation of the assemblages found on Cabliers.

895

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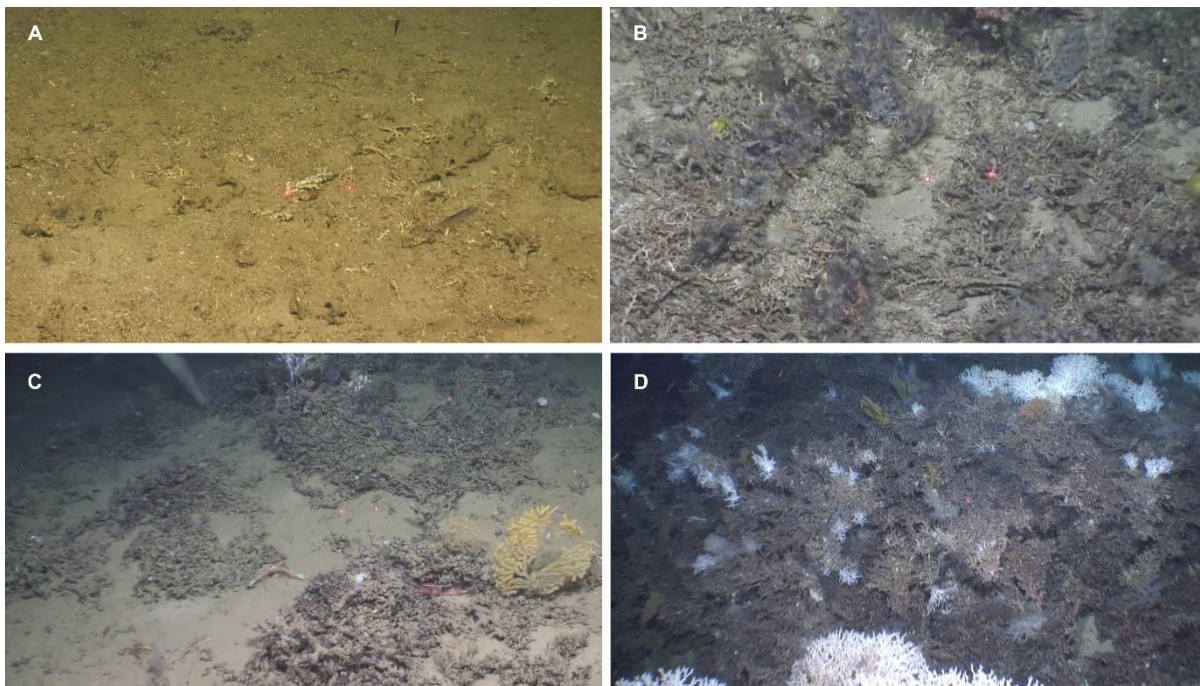
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1405 **Supplementary Material**

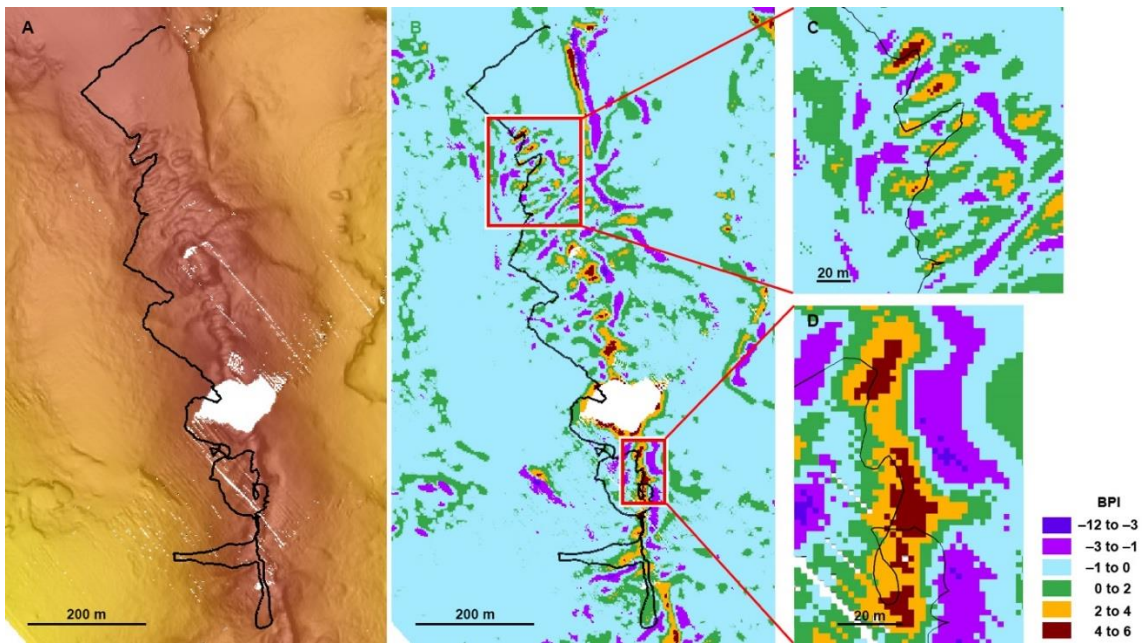
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1408 **Figure S1.** Substrate types observed on the Cabliers Coral Mound. Fine sands with coral rubble (A), coral rubble  
1409 (B), coral framework with fine sands (C) and coral framework (D).

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1412 **Figure S2.** Map showing the Dive 1 ROV path (black line) on the AUV bathymetry (A) and the fine scale  
1413 bathymetric position index (BPI; inner radius: 5 m, outer radius: 10 m) (B) used to identify the mini-mound like  
1414 features located on the crest of the mound. Zooms from the red dashed boxes (C, D) show the areas where the  
1415 ROV travelled over the crest of the mound. Dark and light purple represent negative elevation features (i.e. valleys,  
1416 troughs); light blue and green indicate flat and gentle slopes; orange and brown denote positive elevation features  
1417 (i.e. mini-mounds). Here the spearman rank correlation was used to assess the correlation between coral density  
1418 and mini-mound occurrence.

**Table S1.** Abundance of the species identified in each ROV Dive and total abundance for the whole study area.

		Northern Cabliers		Southern Cabliers	Total
		Dive 1	Dive 2	Dive 3	
Cnidaria	<i>Phanopathes rigida</i>	816	716	0	1532
	<i>Acanthogorgia hirsuta</i>	345	228	918	1491
	<i>Madrepora oculata</i>	967	178	15	1160
	<i>Leiopathes glaberrima</i>	368	21	0	389
	<i>Parantipathes larix</i>	97	31	234	362
	<i>Lophelia pertusa</i>	84	27	2	113
	<i>Dendrophyllia cornigera</i>	59	25	2	86
	<i>Antipathes dichotoma</i>	30	29	0	59
	<i>Cerianthus</i> sp.	0	0	13	13
	<i>Chyronephthia mediterranea</i>	5	2	2	9
	<i>Kophobelemnem</i> sp.	1	1	6	8
	<i>Callogorgia verticillata</i>	1	0	0	1
Porifera	<i>Pacastrella</i> sp.	413	244	10	667
	<i>Asconema setubalense</i>	219	171	0	390
	<i>Geodia</i> sp.	0	30	8	38
	<i>Axinella infundibulum</i>	1	12	1	14
	<i>Hamacantha falcata</i>	0	13	0	13
	White encrusting sponge	0	8	0	8
	Yellow encrusting sponge	0	2	0	2
Echinodermata	<i>Cidaris cidaris</i>	186	116	68	370
	<i>Echinus melo</i>	7	5	0	12
	Asteroidea 1	1	1	9	11
	<i>Echinus acutus</i>	5	1	0	6
	Holothuroidea 1	3	2	1	6
	Asteroidea 2	0	0	4	4
	Holothuroidea 2	0	0	2	2
Arthropoda	Galattheoidea	25	27	348	400
	<i>Bathynectes</i> sp.	0	4	22	26
	Decapoda	5	0	9	14
Mollusca	Ostreida	0	12	0	12
Chordata	<i>Helicolenus dactylopterus</i>	93	46	42	181
	<i>Hoplostetus mediterraneus</i>	27	110	38	175
	<i>Nezumia aequalis</i>	24	15	21	60
	<i>Pagellus bogaraveo</i>	21	1	20	42
	<i>Capros aper</i>	7	0	0	7
	<i>Anthias anthias</i>	5	0	0	5
	<i>Scorpaena scrofa</i>	3	2	0	5
	Pleuronectidae	2	0	0	2
	<i>Physcis blennoides</i>	2	0	0	2
	<i>Conger conger</i>	0	0	1	1
	<i>Scyliorhinus canicula</i>	0	1	1	2
	Unidentified fish	1	21	15	37

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1421

**Table S2.** Results of the CCA analysis implemented at different sampling unit sizes.

<b>SU size</b>	<b>SU N°</b>	<b>Total inertia</b>	<b>Constrained inertia</b>	<b>Unconstrained inertia</b>	<b>% Inertia explained by env. fact.</b>	<b>N° of assemblages</b>
2	2159	8.6164	0.9363	7.6801	10.87	5
4	739	6.3787	0.8853	5.4934	13.88	5
10	349	4.0646	0.7633	3.3013	18.78	4
20	215	2.9713	0.6927	2.2786	23.31	3

1422