

Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea

Jordi Grinyó, Andrea Gori, Michael Greenacre, Susana Requena, Antonio Canepa, Claudio Lo Iacono, Stefano Ambroso, Ariadna Purroy, Josep-Maria

Gili

▶ To cite this version:

Jordi Grinyó, Andrea Gori, Michael Greenacre, Susana Requena, Antonio Canepa, et al.. Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea. Progress in Oceanography, 2018, 162, pp.40-51. 10.1016/j.pocean.2018.02.002 . hal-04429765

HAL Id: hal-04429765 https://hal.science/hal-04429765v1

Submitted on 3 Mar 2024 $\,$

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1	Megabenthic assemblages in the continental shelf edge and upper
2	slope of the Menorca Channel, Western Mediterranean Sea
3	
4	Jordi Grinyó ^{a*} , Andrea Gori ^b , Michael Greenacre ^c , Susana Requena ^a , Antonio
5	Canepa ^d , Claudio Lo Iacono ^e , Stefano Ambroso ^a , Ariadna Purroy ^f , Josep-Maria
6	Gili ^a
7	
8	^a Institut de Ciències del Mar (ICM-CSIC), Pg. Marítim de la Barceloneta 37-49, 08003
9	Barcelona, Spain
10	^b Universitat de Barcelona, Facultat de Biologia, Departament de Biologia Evolutiva, Ecologia i
11	Cienciès Ambientals, Avda. Diagonal 645, 08028 Barcelona, Spain
12	°Universitat Pompeu Fabra, Departament d'Economia i Empresa, Ramon Trias Fargas 25–27,
13	08005 Barcelona, Spain
14	^d Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Avda. Altamirano
15	1480, Valparaiso, Chile.
16	^e National Oceanography Center-Southampton, European Way, Southampton SO14 3ZH,
17	United Kingdom
18	^f Institute of Oceanography and Fisheries, Šetalište I. Meštrovića 63, 21000 Split, Croatia
19	*Corresponding author at: aInstitut de Ciències del Mar (ICM-CSIC), Psg. Marítim de la
20	Barceloneta 37-49, 08003 Barcelona, Spain
21	E-mail address: grinyo@icm.csic.es, jordigrinyo85@gmail.com
22	
23	
24	Abstract
25	
26	Highly diverse megabenthic assemblages dominated by passive and active suspension
27	feeders have been recently reported in shelf edge environments of the Mediterranean

28 Sea. Due to their frequent association with species of commercial interest, these 29 assemblages have been heavily impacted by fishing practices. The vulnerability and 30 low resilience of these assemblages, composed mainly by long-living and slow-31 growing species, have motivated the implementation of management measures such 32 as the restriction of bottom trawling, and the establishment of large protected areas 33 including these environments. The Menorca Channel is one of the areas recently included in the protection frame of the European Union Natura 2000 network. 34 35 Quantitative analysis of video transects recorded at 95-360 m depth by manned 36 submersible and remotely operated vehicles were used to characterize megabenthic 37 assemblages, and assess their geographical and bathymetric distribution. Six different 38 assemblages were identified, mainly segregated by substrate and depth. Hard 39 substrates hosted coral gardens and sponge grounds, whereas soft sediments were 40 mainly characterized by large extensions of the crinoid Leptometra phalangium and 41 the brachiopod Gryphus vitreus. The good preservation of most of the observed 42 assemblages is probably related to a low bottom trawling pressure, which mainly 43 concentrates deeper on the continental slope. Because of their biological and 44 ecological value, management and conservation measures need to be established to 45 preserve these benthic assemblages.

46

47 Keywords

48 Mediterranean Sea; continental shelf edge; continental slope; benthic communities;

49 trawling; spatial and vertical distribution.

50

51

52 1. Introduction

54	Recent technological advances and increased availability of remotely operated
55	vehicles (ROVs), manned submersibles, and video-equipped towed gears have
56	significantly increased accessibility to mid and outer continental shelves, continental
57	slopes and seamounts, thus allowing the direct observation and quantitative study of
58	megabenthic assemblages (e.g. Etiope et al., 2010; Buhl-Mortensen et al., 2016). Rich
59	and highly diverse megabenthic assemblages mostly dominated by passive (e.g.
60	gorgonians, corals and black corals) and active (e.g. sponges) suspension feeders (e.g.
61	Emig, 1997; Bo et al., 2013; Bertolino et al., 2013), have been recently reported on
62	these environments in several locations of the Mediterranean Sea (Deidun et al., 2014;
63	Bo et al., 2009; 2012; 2015). These assemblages provide habitat (Mastrototaro et al.,
64	2010; Porteiro et al., 2013) and act as nurseries (Colloca et al., 2004; Bo et al., 2015)
65	for a wide variety of associated species, many of which are of commercial interest
66	(Abella et al., 2005; Maynou and Cartes, 2012).
67	These assemblages have been largely exposed to long-line and trammel net
68	fishing (Orejas et al., 2009; Sampaio et al., 2012; Mytilineou et al., 2014) as well as to
69	the impacts of bottom trawling, since they are distributed below 50 m depth where
70	bottom trawling is allowed (Council Regulation (EC) No 1967/2006) (Maynou and
71	Cartes, 2012; Fabri et al., 2014). Such fishing practices have dramatic effects on
72	megabenthic structuring species, which are often removed or severely damaged
73	(Fosså et al., 2002; Mytilineou et al., 2014), resulting in a decline in the biodiversity
74	and abundance of the associated fauna (Althaus et al., 2009; Clark et al., 2016). In the
75	Mediterranean Sea, bottom trawling has progressively increased in intensity since the
76	first half of the 20 th century and has steadily expanded toward greater depths (Sacchi,
77	2008). Consequently, decades of chronic trawling have widely impacted large areas of

78 the Mediterranean continental shelf and slope (e.g. Fabri et al., 2014), limiting 79 relatively well preserved megabenthic assemblages to remote (Díaz et al., 2015) or inaccessible rough, rocky floors (Bo et al., 2015). The ecological effects of bottom 80 81 trawling are extremely long lasting, since no recovery of deep megabenthic 82 assemblages dominated by anthozoans have been observed in areas closed to trawling 83 for more than ten years (Althaus et al., 2009; Williams et al., 2010). Due to the slow-84 growth and high longevity of most of the megabenthic species in these assemblages, it 85 has been suggested that their possible recovery could span from centuries to millennia 86 (Clark et al., 2016).

87 The vulnerability and low resilience of these communities (Althaus et al., 88 2009) have motivated the recent establishment of managed and protected areas on 89 continental shelves, continental slopes (Spalding et al., 2013; Bennecke and Metaxas, 90 2016) and seamounts (Sheppard et al., 2012; Huvenne et al., 2016) worldwide. In the 91 Mediterranean Sea, the protection of large areas of the continental shelf and slope has 92 been recently proposed as a part of an ecosystem-based management strategy of 93 marine resources and environments, which include the Menorca Channel (European 94 Union, Natura 2000 network, http://www.eea.europa.eu/data-and-maps/data/natura-95 2). Previous studies have investigated and characterized benthic assemblages in the 96 inner continental shelf (< 100 m) of the Menorca Channel (e.g. Joher et al., 2012; 97 Barberá et al., 2012; Grinyó et al., 2016), but the composition and distribution of 98 benthic assemblages on the outer continental shelf and upper slope still remain widely 99 unknown. Additional information is thus fundamental for the establishment of 100 effective management and conservation measures, as well as to monitor their 101 effectiveness.

102

Hence, the aims of this study were: (1) to characterize the composition of

103	megabenthic assemblages (defined here as assemblages constituted by sessile and low
104	motile invertebrates (i.e. echinoderms) larger than 2 cm (e.g. Seike et al., 2013)) on
105	the deep continental shelf and upper slope at 95-360 m depth in the Menorca
106	Channel; (2) to assess their geographical and bathymetric distribution; (3) to quantify
107	their biodiversity variation with depth; and (4) to compare their distribution with the
108	pressure of bottom trawling in the area.
109	
110	2. Materials and methods
111	
112	2.1 Study area
113	
114	The Menorca Channel is located in the Western Mediterranean Sea between Mallorca
115	and Menorca islands (39° 53' 0.73" N, 3° 29' 51.16" E) (Fig. 1a), as part of the
116	Balearic Promontory (Acosta et al., 2002). The study area covered the outermost
117	continental shelf (90–110 m), the shelf edge (110–180 m) and the upper slope (180–
118	350 m) of the channel. The continental shelf is characterized by smooth reliefs,
119	covered by maërl beds alternating with outcropping rocks of coralligenous, and
120	detritic coarse sediments (Barberá et al., 2012). Fine sands cover vast areas of the
121	northern part of the investigated section of the continental shelf at 100-110 m depth
122	(Grinyó et al., 2016). Smooth reliefs and large extensions of detritic sediments with
123	few isolated patches of outcropping rocks characterize most of the shelf edge and
124	continental slope (Grinyó et al., 2016). Vertical walls and sharp-edged rocky outcrops
125	are the dominant substrate near Cap Formentor (Fig. 1b) and in the Menorca Canyon
126	head (Fig. 1c) (Grinyó et al., 2016).

127 The northern shelf edge and continental slope of the Menorca Channel is 128 influenced by the Balearic Current (Balbín et al., 2012), which flows northward at 129 approximately 200 m depth (Ruiz et al., 2009). Conversely, the southern shelf edge 130 and upper slope are mostly influenced by the sporadic arrival of mesoscale structures 131 detached from the Algerian Current and the Almería Oran front (Millot, 1987; García 132 et al., 2005).



- 133
- 134

Fig. 1. The study area. (a) Bathymetry of the Menorca Channel: the map shows the location of the

video transects (1 to 45) and the location of the study area in the western Mediterranean. Frontal views

- of the continental slope of the north (b) and south (c) of the Menorca Channel with the continental shelf
 in the background. Black lines indicate the 100 and 500 m isobath and the red line indicates the shelf
 edge.
- 140

141 2.2 Sampling procedure

142

160

143 A total of 45 video transects (Fig. 1a, Supplementary material 1) were recorded 144 during four surveys conducted on board of the R/V "García del Cid" (September 145 2010, April 2011, October 2011, June 2012): 17 video transects were recorded with 146 the manned submersible JAGO (IFM-GEOMAR) during the first two surveys, and 28 147 video transects were recorded with the NEMO ROV (Gavin Newman) during the last 148 two surveys. Both instruments were equipped with a 1080 horizontal line resolution 149 camera, a manipulator arm and two parallel laser beams (0.5 m and 0.12 m for the 150 JAGO and the NEMO, respectively). Laser beams were used to determine a fixed 151 width of 0.5 m during video analysis and all transects were recorded with a close 152 zoom (\sim 0.5–1.5 m width). Both JAGO and NEMO moved at a constant speed of \sim 0.3 153 knots, and explored a depth range between 90 to 347 m. The positioning of JAGO and 154 NEMO was achieved with an underwater acoustic positioning system LinkQuest TrackLink 1500 HA. Transects were haphazardly located in order to cover the entire 155 156 study area, but areas showing morphological features possibly related to the presence 157 of rocky bottoms were explored more intensively (Fig. 1). Overall, a total seabed length of 37.7 km was video recorded. 158 159 In order to confirm the taxonomic identification of the megabenthic organisms

161 were collected by means of the JAGO and the NEMO manipulator arm, and

162 epibenthic sledges equipped with video cameras. Sampled organisms were fixed and

observed in the video transects, organisms of all 69 species considered in this study

163	preserved in 10% formalin as well as in absolute ethanol for posterior taxonomical
164	and genetic analyses. Organisms were identified to the lowest possible taxon, which
165	corresponded to species or genus.

167 2.3 Video analysis

168

169 Quantitative video analysis was performed according to the methodology described 170 by Gori et al., (2011) and Grinyó et al., (2016), using Apple's Final Cut Pro software. 171 The length of each transect was estimated based on the records from the acoustic 172 positioning system (see details in Grinyó et al., 2016). Sequences with poor image 173 quality or too far away from the seafloor were considered unsuitable for analysis. The 174 remaining useful sequences comprised 93.3% of the total recorded material and 175 corresponded to a total distance of 35 km. The position of all megabenthic organisms 176 observed within a width of 0.5 m (estimated video coverage based on the laser beams) 177 was defined by the time elapsed since the beginning of the video transect to the 178 crossing of the laser beams by the organism (see details in Grinyó et al., 2016). 179 Seabed substrate type was classified (based on the Wentworth scale) into five 180 categories: fine sand, medium sand to gravel, cobbles and pebbles, maërl, and rock. 181 Seabed slope was classified into three categories: horizontal (0°-30°), sloping (30°-182 80°), or vertical (80°–90°); slope was estimated from the video by looking at the depth sensor (Gori et al., 2011; Ambroso et al., 2013; Grinyó et al., 2016). 183 184 185 2.4 Data treatment 186

187 2.4.1 Sampling unit characterization

189	Each transect was divided into a string of sampling units. Several sampling unit sizes
190	$(2, 5, 10, 15, 20, 30, 40 \text{ and } 50 \text{ m}^2)$ were used in the canonical correspondence
191	analysis (see below) in order to explore how sampling unit size may affect the
192	identification of the benthic assemblages, and their associated main environmental
193	features. Each sampling unit was characterized by the number of megabenthic
194	organisms of each identified species (density = number of individuals per m^2), as well
195	as by the average depth and coverage percentage for each substrate and slope
196	category.
197	
198	2.4.2 Canonical correspondence analysis
199	
200	Canonical correspondence analysis (CCA) is a multivariate constrained ordination
201	technique used to elucidate the relationships between species abundances (response
202	variables) and environmental variables (explanatory variables) (Ter Braak, 1986;
203	Greenacre and Primiceiro, 2013). CCA was used to define megabenthic assemblages
204	based on species composition, and to explore their relationship with the three
205	environmental factors obtained from the video transects: substrate, depth, and slope.
206	Since recording of video transects was restricted in time, other environmental
207	variables such us seawater temperature, turbidity or fluorescence could not be
208	considered in this study because they can show high seasonal variability
209	(consequently, any possible correlation between such variables and the observed
210	benthic assembles would have been highly fortuitous). Taxa that appeared with less
211	than three individuals were discarded from the analysis in order to avoid distortions.
212	Depth of sampling units was coded into four fuzzy categories that preserve all the

213	information in the variables while reducing it to a categorical scale (Aschan et al.,
214	2013). Such fuzzy-coding takes into account possible nonlinear relationships between
215	fauna abundance and depth (Greenacre and Primiceiro, 2013). The mean depth of
216	each of the four fuzzy categories are as follow: $dep1 = 106 \text{ m}$, $dep2 = 130 \text{ m}$, $dep3 = 100 \text{ m}$
217	188 m, and dep4 = 252 m. No transformation was applied to either environmental or
218	biological data. The CCA was performed with the function cca in the vegan package
219	(Oksanen et al., 2015) of the R software platform (R Core Team 2015). Additionally,
220	substrate, depth, and slope were tested to determine which was the best predictor by
221	means of the R function anova in the vegan package (Oksanen et al., 2015). Due to
222	the lack of previous information about sampling unit size for the characterization of
223	Mediterranean megabenthic assemblages in the outer continental shelf and upper
224	slope by means of quantitative video analysis, CCA was performed with different
225	sampling unit sizes (2, 5, 10, 15, 20, 30, 40 and 50 m ²).
226	
227	2.4.3 Megabenthic assemblages distribution and depth-related diversity
228	
229	The geographical distribution of each identified megabenthic assemblage in the study
230	area was reported by mapping its occurrence in the video transects on a
231	geographically referenced map using GIS (ESRI ArcGIS ArcInfo v10). The
232	bathymetric distribution of each assemblage was represented in 5 m depth intervals.
233	To compare species' turnover (or beta-diversity) among the outer continental shelf
234	(90–110 m depth), the shelf edge (110–180 m depth) and the upper slope (180–347 m $$
235	depth) randomized species accumulation curves were calculated (Vetter et al., 2010;
236	De Leo et al., 2014), using the statistical software R and the "vegan" package.
237	The method used finds the mean species accumulation curves and their standard

238 deviation from random permutations of data (n = 100), which avoids distortions in the 239 curves due to variations in species abundance and sampling effort (Gotelli and 240 Colwell, 2001).

241

242 2.4.4 Fishing activity in the study area

243

244 Fishing activity and location of fishing grounds (i.e. areas consistently fished through 245 time) in the study area were assessed by means of Vessel Monitoring System (VMS) 246 location data through the analysis of the number of fishing events per surface units. 247 VMS data were obtained in the framework of the LIFE+ INDEMARES project from 248 the General Directorate of Fisheries Management of the Spanish Ministry of 249 Agriculture, Food and Environment (MAGRAMA). Available VMS records from 250 January 2007 to July 2012 were included after examination to exclude erroneous 251 vessel identity, position or speed. To select the records referring to fishing activity, a 252 set of common criteria (Lee et al., 2010) was followed: duplicated records and records 253 close to ports were removed, and the interval between records was calculated in order 254 to only retain vessels moving at 2–3.5 knots, so that only vessel locations while 255 trawling are represented. The distribution of fishing activity in the study area was 256 assessed based on fishing events counts per cell unit based on a point summation method (Hintzen et al., 2010). A 250 m² cell was selected as the most suitable size 257 258 considering geographical factors and the available dataset (for further details, see Piet 259 and Quirijns, 2009). Only one record per vessel, day and cell was retained to avoid 260 overestimation of fishing activity (Hintzen et al., 2010). The centroids of each cell were extracted and weighted by the sum of fishing events for this cell. These 261 weighted centroids were used to identify statistically significant hot spots of fishing 262

263 activity in the study area using the Gi* statistic (Getis and Ord, 1996). 264 265 3. Results 266 267 A total of 69 megabenthic species belonging to seven phyla and twelve classes were 268 identified in the study area (Supplementary material 3). 269 270 3.1 Canonical Correspondence Analysis (CCA) 271 272 CCA analysis performed with different sampling unit sizes revealed a general 273 increase in the amount of inertia explained (i.e. explained variation of the data) by 274 environmental factors as sampling unit size increased (Table 1). However, as 275 sampling unit size increased, the resolution of the CCA output decreased (Table 1, 276 Supplementary material 2). This was due to: (1) a reduction in the total number of 277 sampling units, (2) an increase in the number of sampling units discarded from the analysis because affected by unsuitable sequences, and (3) an increased variability of 278 279 each sampling unit composition (due to the presence of several bottom types in large sampling units) (Table 1). A 5 m² sampling unit size was chosen as the best balance 280 281 between the inertia explained by environmental factors, and the number of 282 megabenthic assemblages identified (Table 1). This size exceeds those previously 283 used for shallow Mediterranean environments (e.g. Weinberg, 1978; Coppari et al., 284 2016), probably due to the wider range of environmental gradients and the much 285 larger number of species included in this study. 286

287 Table 1 Results of the CCA analysis performed at different sampling unit size (env. fact. = environmental factors).

Sampling	Species	Organism	Sampling units	Total inertia	Restricted	Unrestricted	% of inertia	Macrobenthic
unit size	number	number	number		inertia	inertia	explained by	assemblage
							env. fact.	number
2	69	39138	8639	28.36	3.03	25.32	10.69	6
5	69	38230	3372	20.96	3.28	17.68	15.6	6
10	69	32829	1537	18.5	3.39	15.11	18.3	5
15	69	31632	985	16.15	2.46	13.69	15.2	5
20	69	31358	713	15.17	3.44	11.73	22.6	5
30	69	27658	443	13.8	3.45	10.37	24.97	5
40	67	26023	316	13.25	3.57	9.67	13.25	5
50	67	20855	248	12.59	3.61	8.98	28.71	4

289

Using 5 m² sampling units, a total of 38230 organisms belonging to 69 megabenthic

species were considered in the analysis (Table 1). Crinoidea, exclusively represented

by the species *Leptometra phalangium*, was the most abundant and the third most

frequent class accounting for 31.8% of all observed organisms, occurring in 16.3% of

all sampling units (Table 2). Demospongiae, represented by 21 species

295 (Supplementary material 3), was the second most abundant and the second most

frequent class, accounting for 30.9% of all observed organisms, in 27.7% of all

sampling units (Table 2). The class Anthozoa, represented by 27 species

298 (Supplementary material 3), was the third most abundant and the first most frequent

class, accounting for 21% of observed organisms, in 29.8% of all sampling units

300 (Table 2). The remaining taxa were represented by 1–4 species (Supplementary

301 material 3), accounting for 0.02–8.2% of observed organisms, in 0.2–14.5% of all

302 sampling units (Table 2).

303

304 Table 2 Macrobenthic taxa occupancy and abundance in the study area. Occupancy (frequency of occurrence in the set of

305 sampling units); abundance (number of organisms). (subc. = subclass).

Phylum	Class	Species	Occupancy		Abundance	
		number				
			Number	(%)	Number	(%)
Porifera	Demospongiae	21	936	27.76	11805	30.96
Cnidaria	Anthozoa	27	1004	29.8	8031	21
	Hydrozoa	3	14	0.42	16	0.04
Bryozoa	Gymnolaemata	1	31	0.92	47	0.12
Brachiopoda	Rhynchonellata	1	467	13.85	3219	8.20
Annellida	Polychaeta	4	491	14.56	2334	6.12
	Echiura	1	49	1.45	55	0.14
Echinodermata	Crinoidea	1	549	16.28	12126	31.8
	Ophiuroidea	1	64	1.90	416	1.09
	Echinoidea	4	127	3.77	144	0.38
	Holothuridae	2	15	0.44	15	0.04
	Astroidea	1	11	0.33	12	0.03
Chordata	Ascidiacea	2	4	0.18	10	0.02

³⁰⁷

In the CCA performed using 5 m² sampling units, environmental factors explained 308 309 15.6% of the variation in species abundance. The first axis (CCA1) explained 26.8% 310 of the variance, and the second axis (CCA2) explained 22.7% of the variance. 311 Substrate was the best predictor (inertia = 2.19) followed by depth (inertia = 1.30), and slope (inertia = 0.70). Six different megabenthic assemblages (Fig. 2a), 312 313 characterized by environmental factors (Fig. 2b) and most contributing species (Fig. 314 2c) were identified in the CCA analysis, for which illustrative in situ pictures (Fig. 3) and geographic (Fig. 4) and bathymetric distribution (Fig. 5) are also provided: 315

316

317 Assemblage A: occurring on shallow (95–110 m depth) maërl beds alternated with

318 small patches of coralligenous outcrops (Fig. 2b), is mostly characterized by the

319 sponges Haliclona cf. elegans and Aplysina cavernicola (Figs. 2c, 3a 3b and

320 Supplementary material 4).

2	n	1
З	L	T

322	Assemblage B: occurring on horizontal grounds covered by fine and coarse sands
323	throughout most of the explored depth range (110-280 m depth) (Fig. 2b), is mostly
324	characterized by the presence of the crinoid Leptometra phalangium (Figs. 2c, 3c and
325	Supplementary material 5).
326	
327	Assemblage C: occurring on horizontal grounds covered by medium sand to gravel
328	from shallow to deep (110-330 m depth) environments (Fig. 2b), is characterized by
329	the presence of the brachiopod Gryphus vitreus (Figs. 2c, 3d and Supplementary
330	material 6).
331	
332	Assemblage D: mostly found at shallow and intermediate depth (95–140 m depth) on
333	mixed cobbles and pebbles bottoms (Fig. 2b), is characterized by the polychaete
334	Salmacina dysteri and two unidentified sponge species belonging to the genus
335	Hamacantha and Haliclona (Figs. 2c, 3e, 3f and Supplementary material 7).
336	
337	Assemblage E: occurring in sloping rocky outcrops from shallow to deep
338	environments (95-337 m depth) (Fig. 2b), is characterized by the presence of the
339	gorgonians Eunicella cavolinii, Viminella flagellum, the soft coral Nidalia studeri, the
340	solitary coral Thalamophyllia gasti and the incrusting sponge Hamacantha falcula
341	(Figs. 2c, 3g, 3h, 3i, 3j, 3k and Supplementary material 8).
342	
343	Assemblage F: occurring on vertical rock outcropping mostly at shallow and
344	intermediate (95-210 m depth) environments (Fig. 2c), is characterized by an

- 345 incrusting sponge of the genus *Rhabderemia* (Figs. 2c, 31 and Supplementary material
- 346 9).
- 347



349 Fig. 2. Canonical correspondence analysis (CCA) ordination biplots of megabenthic species. In figure 350 2a the biplot shows the distribution of the sampling units (n = 3372), sampling units are colored 351 according to the dominant substrate: fine sands (yellow), medium sands to gravels (green), cobbles and 352 pebbles (orange), maërl (blue), outcropping rock (red). In figure 2b the biplot shows the substrate type 353 (FS = fine sands, MG = medium sands to gravels, PC= cobbles and pebbles, M = maërl, OR = 354 outcropping rock), seabed slope (Hor = horizontal, Slo = slopping, Ver = vertical) and depth, being 355 dep1 the shallowest and dep4 the deepest. In figure 2c the biplot shows the contribution of the different 356 species to the megabenthic assemblages, the scale of greys in the vectors indicate the degree of 357 correlation, being in black the highest correlation degree. Hal eleg = Haliclona cf. elegans, Ap cav = 358 Aplysina cavernicola, Ham sp2 = Hamacantha sp., Hal sp20 = Haliclona sp., Sal dys = Salmacina 359 dysteri, Lep pha = Leptometra phalangium, Gry vit = Gryphus vitreus, Tha gas = Thalamophyllia 360 gasti, Ham fal = Hamacantha falcula, Vim fla = Viminella flagellum, Eun cav = Eunicella cavolinii, 361 Nid stud =*Nidalia studeri*, Rhab sp2 = Rhabderemia sp.

362

363 3.2 Spatial and bathymetric distribution of megabenthic assemblages

364

365 Assemblage A was only observed in one single transect in the north eastern side of 366 the Menorca Channel (Fig. 4) and presented the narrowest bathymetric distribution (95–110 m depth) (Fig. 5). Assemblages B and C were widely distributed in both the 367 368 northern and southern areas of the channel occurring between 110 and 180 m depth 369 and between 110 and 240 m depth, respectively (Fig. 4). Assemblage D was observed 370 in only four locations in the channel, three in the northern side and one in the head of 371 the Menorca Canyon (Fig. 4), and partially coincided with assemblages A, E and F. 372 This assemblage was distributed between 95 and 140 m depth (Fig. 5). Finally, assemblages E and F mostly co-occurred in transects located in the proximity of Cap 373 374 Formentor and the Menorca Canyon's head (Fig. 4). However, assemblage E 375 presented a shallower distribution respect to assemblage F that reached the deepest 376 areas of the channel (340 m depth) (Fig. 5).



377

Fig. 4. Spatial distribution of megabenthic assemblages observed in the study area. Assemblages were
represented on the study area based on the transects where they occur, and following the colours as in
Figure 2a. Grey line represents the 100, 200 and 400 m isobath, red line represents the shelf edge.





383

384 Fig. 5. Bathymetric distribution of the megabenthic assemblages observed in the study area.

385 Assemblages were represented based on the colour as in Figure 2a.

387 3.3 Variation of megabenthic diversity with depth

388



by the outer continental shelf (90–110 m depth) and continental slope (180–347 m

- depth) (Fig. 6). Both shelf edge and continental slope species accumulation curves
- reach asymptote, highlighting that both depth ranges were representatively sampled.
- 393 Conversely, species accumulation curve for the outer continental shelf does not reach
- an asymptote as a consequence of limited sampling.



395



397 (blue) and the continental slope (orange).

398

399









Fig. 7. Bottom trawling effort in the Menorca Channel. Vessel speed has been filtered to the 2-3.5knots range so that only vessel locations while trawling are represented. Colors are proportional to

- trawling effort (see legend) and hot spot areas (identified using the Gi* statistic) are surrounded in
- 416 black lines and indicated by capital letters. Video transects are represented by black dots, and the area
- 417 included as Site of Community Interest in the Natura 2000 network is indicated by the green line. None
- 418 of the video transects considered in this study are located in the VMS hot spot areas.

420 **4. Discussion**

421

422 The six megabenthic assemblages identified in the study area are distributed

423 throughout the outermost continental shelf and upper slope of the Menorca Channel,

424 and are mainly segregated by substrate type and depth.

425 Sponge grounds composed by large demosponge species (>15 cm in height),

426 mostly characterized by the branched *Haliclona* cf. *elegans* and the tubular sponge

427 *Aplysina cavernicola* (Assemblage A), occur on a shoal located near the shelf edge

428 off Cap Formentor at 95–110 m depth (Fig. 4). This shoal presents a highly irregular

429 topography of vertical walls alternating with areas covered by maërl and

430 coralligenous outcrops. The close proximity of the shoal to the shelf edge (Fig. 4), and

431 its highly irregular topography, are in keeping with deep sponge grounds distribution

432 in the Mediterranean Sea (Bertolino et al., 2015) and in other areas of the world (e.g.

433 Klitgaard and Tendal, 2004; Maldonado et al., 2016). It has been suggested that the

434 irregular topography of these environments may cause the acceleration of local

435 currents (Rice et al., 1990) potentially favouring the presence of sponges (Beazley et

436 al., 2015). A. cavernicola and H. cf. elegans account for 73% of all observed

437 organisms, followed by other demosponge species such us *Poecillastra compressa*,

438 *Aaptos aaptos* and *Siphonochalina* sp., representing 21% of the observed organisms.

439 Species composition resembles that of other sponge grounds from flat rocky shoals

440	exposed to moderated currents, and high silting (derived from river discharge),
441	between 70 and 130 m depth in the Gulf of Santa Eufemia (southern Tyrrhenian Sea)
442	(Bertolino et al., 2013). Overall, sponge density (9.2 \pm 8.4 individuals m ⁻² (mean \pm
443	SD), max = 43 individuals m^{-2}) is similar to those observed in other Mediterranean
444	sponge grounds (Bo et al., 2011a), exceeding those observed in deep multispecific
445	sponge grounds in the North Atlantic (Kutti et al., 2013; Howell et al., 2016). The
446	lack of gorgonians (only represented by a few colonies of Paramuricea macrospina)
447	and antipatharians distinguishes this assemblage from Assemblage E, in which almost
448	all the same sponge species (except A. cavernicola) co-occur together with large
449	gorgonians and antipatharians (see below) (Supplementary material 3).
450	Leptometra phalangium beds (Fig. 3c) are widely distributed between 110 and
451	250 m depth in areas covered with both coarse and fine sands (Assemblage B),
452	agreeing with previous reports from detritic bottoms of the Western Mediterranean
453	shelf edge (e.g. Pérès, 1967; Michez et al., 2014). L. phalangium may reach very high
454	densities of more than 30 individuals m ⁻² (5.3 ± 3.2 individuals m ⁻² (mean \pm SD)), as
455	previously observed on detritic substrates at the foot of seamounts in the Tyrrhenian
456	Sea (Bo et al., 2010). In the Menorca Channel, this almost monospecific assemblage
457	(L. phalangium represents 95% of all observed organisms) mostly occurs on the shelf
458	edge (96% of occupied sampling units) (Fig. 4), in agreement with studies identifying
459	it as a typical shelf edge assemblage (e.g. Fredj, 1964; Kallianiotis et al., 2000;
460	Mangano et al., 2010). It has been suggested that Leptometra beds are mainly
461	constrained to shelf edge environments as they depend upon the exposure to bottom
462	currents that regularly carry high concentrations of suspended organic particles
463	(Lavaleye et al., 2002; Colloca et al., 2003). Absence of trawling activity is
464	fundamental for the persistence of high-density L. phalangium populations since the

465 fragility of this organism makes it extremely vulnerable to mechanical damage (Smith 466 et al., 2000). L. phalangium populations impacted by bottom trawling on the Cretan 467 continental shelf presented significantly lower densities five months after trawling 468 than non-impacted ones, suggesting a low recovering capacity (Smith et al., 2000). 469 Facies of L. phalangium have been associated with elevated densities of 470 benthopelagic fish, with high juvenile abundances, suggesting that this assemblage 471 may play a crucial role in the life cycle of numerous fish species, some of which are 472 of high commercial interest (e.g., Merlucius merlucius and Mullus barbatus) (Colloca 473 et al., 2004). The sea pen Funiculina quadrangularis, the polychaete Lanice 474 conchilega and the anemones Cerianthus membranaceus and Arachnanthus 475 oligopodus accompany L. phalangium on coarse sands. In submarine canyons of the 476 Western Mediterranean C. membranaceus and F. quadrangularis have also been 477 reported to occur alongside facies of L. phalangium (Würtz, 2012). F. quadrangularis presents a sparse distribution and occurs at low densities (0.6±0.3 colonies m⁻² (mean 478 479 \pm SD), max = 2.5 colonies m⁻²) contrasting with observations in bathyal 480 environments, where this species forms dense facies (Pérès and Picard, 1964). In fine 481 sand environments, L. phalangium generally occurs along with the sea pen Virgularia 482 mirabilis, the soft coral Alcyonium palmatum, and the sponge Thenea muricata on 483 fine sands. The presence of *T. muricata* and *V. mirabilis* on the shelf edge (~130 m 484 depth) is rather surprising, as both species have mostly been reported in deeper 485 settings (e.g. Michez et al., 2014). On fine sand floors, large hydrozoans have been 486 occasionally observed, such us Nemertesia antennina, Nemertesia ramosa or 487 Lytocarpia myriophyllum, which co-occurred alongside with L. phalangium in agreement with previous observations in the Tyrrhenian Sea (Massi, 2005). However, 488 489 these hydrozoans present very low abundances in the Menorca Channel

490 (Supplementary material 3), in contrast with dense facies observed in other areas of491 the Mediterranean Sea (Pérès and Picard, 1964).

492 The brachiopod Gryphus vitreus (Fig. 3d) constitutes 81% of all observed 493 organisms in Assemblage C. G. vitreus forms beds that sparsely cover (2 ± 3) individuals m^{-2} (mean \pm SD)) sandy grounds on and beyond the shelf edge, at 110– 494 495 330 m depth. This bathymetric distribution contrasts with observations from Corsica 496 and Provence where G. vitreus beds reach a maximum depth of 200 m and 250 m, 497 respectively (Emig, 1985; 1987). Conversely, communities dominated by G. vitreus 498 have been reported in deeper environments of 660-870 m depth in the Balearic Basin 499 (Cartes et al., 2009). In the upper slope, at 180–200 m depth, G. vitreus forms dense 500 aggregations with more than 25 individuals m⁻². However, these densities are rather 501 low if compared to those reported from continental slopes exposed to intense bottom 502 currents (600 individuals m⁻²) (Emig, 1987). In this regard, occurrences and 503 abundances of G. vitreus and other brachiopod appear to be directly related to 504 hydrodynamic conditions (Eshleman and Wilkens, 1979; Emig, 1987). 505 In the study area, G. vitreus beds (assemblage C) and L. phalangium facies 506 (assemblage B) present similar distributions, occasionally co-occurring for tens of 507 meters as previously shown in the Balearic Archipelago (Aguilar et al., 2014). 508 However, while facies of L. phalangium (Assemblage B) have been observed on both 509 fine and coarse sands, G. vitreus beds (Assemblage C) are basically restricted to 510 coarse sands (Figs. 2 and 4). This substrate segregation responds to the necessity of G. 511 vitreus to attach to small pebbles or shells on the surface of the sediment (Emig, 512 1987). The composition of accompanying species in coarse sands of assemblage B and C is very similar, with the sea pen F. quadrangularis, the polychaete L. 513 514 conchilega and the anemones C. membranaceus and A. oligopodus amongst the most

515 abundant. A. oligopodus and L. conchilega have often been reported in soft sediments 516 of the shelf edge and continental slope of the Mediterranean Sea (e.g. Pérès and 517 Picard, 1964; Emig, 1997), whereas, in the G. vitreus beds of the Menorca Channel, both species occasionally reach high densities (9.5 and 9 individuals m^{-2} , 518 519 respectively), agreeing with previous observations in the Western Mediterranean Sea 520 (Aguilar et al., 2014; Michez et al., 2014). The accompanying species reported in 521 assemblage C differ from those observed in deeper G. vitreus beds in the Balearic 522 Basin, which are accompanied by several sponge species and nemerteans (Cartes et 523 al., 2009). 524 The polychaete Salmacina dysteri (Fig. 3e) and two unidentified sponges 525 belonging to the genus Hamacantha and Haliclona (Fig. 3f) characterize the 526 Assemblage D, occurring on coarse sand with scattered cobbles and pebbles, at 95-527 140 m depth. These three species represent 63% of all observed organisms, and rarely 528 exceed densities of 1.5 individuals m². Despite the mixed substrate where this 529 assemblage has been observed, the vast majority of the organisms are associated with 530 hard substrates (e.g. the sponges P. compressa, A. aaptos and Pachastrella monilifera 531 (26% of observed organisms), and the gorgonians E. cavolinii and Swiftia pallida 532 (10% of observed organisms)). A similar situation has been identified in sandy 533 bottoms with Dendrophyllia cornigera coral rubble, which also present high 534 abundances of organisms associated to hard substrates (Michez et al., 2014). 535 Conversely, coarse sand patches are mainly occupied by echinoids, holothurians and 536 polychaetes (1% of observed organisms). Isolated L. phalangium has been 537 occasionally observed as well. The occurrence of Assemblage D in the same transects 538 than Assemblages A and E (Fig. 4) (mainly in the immediate proximities of 539 outcropping rocks and vertical walls on the shelf edge, and in areas of dead maërl

rhodolites in the proximities of shelf shoals) suggests that Assemblage D is a
transition between assemblages occurring on hard substrates and those located on
coarse sand ones.

543 The gorgonians E. cavolinii and Viminella flagellum, the soft coral Nidalia 544 studeri, the small solitary coral Thalamophyllia gasti and the incrusting sponge 545 Hamacantha falcula (Figs. 3g, 3h, 3i, 3j and 3k) characterize (43% of all observed 546 organisms) the sloping rocky substrates (Assemblage E) from the outer continental 547 shelf to the upper slope (95–340 m depth). Despite this wide bathymetric distribution, 548 this coral garden assemblage (sensu Stone, 2006; Buhl-Mortensen and Buhl-549 Mortensen, 2013) mostly occurs on the shelf edge and uppermost slope at 110-190 m 550 depth (72% of observed sampling units), on rocky outcrops and vertical walls near 551 Cap Formentor and at the Menorca canyon head (Fig. 4). Similarly, other coral 552 gardens have also been observed in the proximities of the shelf edge in several 553 locations of the Western Mediterranean Sea (e.g. Bo et al. 2012; Cau et al., 2017). 554 These environments are most likely exposed to regular currents, which may enhance 555 food availability for the large sized passive suspension feeders that characterize this 556 assemblage (Shepard et al., 1974; Balbín et al., 2012). Both the gorgonians E. 557 cavolinii and V. flagellum had previously been reported as dominant species of rocky 558 assemblages on the Mediterranean shelf edge (Bo et al., 2011b; Angiolillo et al., 559 2014). In the Menorca Channel, both species mostly form mixed assemblages along 560 with other species (Grinyó et al., 2016), but they can punctually form dense monospecific patches of more than 20 colonies m⁻², as also observed in other areas of 561 562 the Mediterranean Basin (Pedel and Fabri, 2011; Angiolillo et al., 2014). N. studeri and T. gasti form dense monospecific assemblages (30 colonies m⁻²). N. studeri 563 mostly occurs on gently sloping rocky outcrops, whereas *T. gasti* occurs on steeply 564

565 sloping rocky outcrops. The incrusting sponge H. falcula shows low maximum 566 densities of 5 individuals m^{-2} but of large size (> 20 cm diameter), covering large 567 areas of the rocky bottom, and perhaps excluding other species (Fig. 3k). Assemblage 568 E is the most diverse of the six megabenthic assemblages identified in the study area. 569 Eighteen species of demosponges have been observed as accompanying species (25% 570 of all observed organisms) mostly as scattered individuals spread throughout the transects $(2.4 \pm 4 \text{ individuals m}^2 \text{ (mean} \pm \text{SD}))$, only occasionally reaching high 571 densities (15 individuals m^{-2}). Some of these sponges reach large dimensions (> 20 572 573 cm height and width) such as the massive Haliclona magna or the fan shaped 574 Phakellia robusta, P. monilifera and P. compressa. Anthozoans account for 57% of 575 all observed organisms in Assemblage E, with 22 different species. Besides E. 576 cavolinii and V. flagellum, eight gorgonian species have been also observed in this 577 assemblage: Acanthogorgia hirsuta, Bebryce mollis, Callogorgia verticillata, 578 Corallium rubrum, Muriceides lepida, Paramuricea clavata, P. macrospina, and S. 579 *pallida*. Gorgonians formed multispecific high-density patches (~20 colonies m⁻²) 580 (Grinyó et al., 2016), which contrasts with the lower gorgonian diversity in coastal 581 and bathyal environments of the Mediterranean Sea (e.g. Gori et al., 2011; Cartes et 582 al., 2013). The antipatharians Antipathella subpinnata, Antipathes dichotoma and 583 Leiopathes glaberrima occur in low densities (1–4 colonies m⁻²) in mixed 584 assemblages with gorgonians, as also observed at similar depths in other areas of the 585 Mediterranean Sea (e.g. Bo et al., 2009, 2012; Deidun et al., 2014). Finally, the 586 recently described soft coral Chironephthya mediterranea (López-González et al., 587 2015) and *Paralcyonium spinulosum* are also largely represented in these rocky bottoms. Very similar anthozoan assemblages have also been described at similar 588 589 depths on rocky substrates in the southern Sardinian shelf edge (Cau et al., 2017). Due to the complex three-dimensional structure they form, and the slow growth of
gorgonian and antipatharian species (Sherwood and Edinger, 2009), deep coral
gardens are extremely vulnerable to physical damage by fishing, (Angiolillo et al.,
2015) and pollution (Silva et al., 2015), displaying extremely slow recovery (Althaus
et al., 2009).

595 Finally, vertical rocky substrates at 95–210 m depth are dominated by 596 incrusting sponges (Assemblage F), with an unidentified incrusting sponge of the 597 genus *Rhabderemia* (Fig. 31) accounting for 64% of all observed organisms (max = 23) individuals m⁻²), and other incrusting sponges representing 10% of all observed 598 599 organisms. Incrusting sponges seem to be the only organisms adapted to colonize this 600 environment, alternating with the conversely highly diverse coral gardens 601 (Assemblage E), depending on the substrate slope. 602 Unlike areas of the Gulf of Lion (Pérès and Picard, 1964; Orejas et al., 2009; 603 Gori et al., 2013; Fabri et al., 2014) and the Catalan margin (Lastras et al., 2016), only 604 a few colonies of the cold-water coral Madrepora oculata have been observed on 605 vertical rocky walls at 320 m depth in the Menorca Channel. This could suggest that 606 this species might be restricted to deeper environments in the study area (> 350 m

607 depth), as observed in other places of the Mediterranean Basin (e.g. Etiope et al.,

608 2010; Taviani et al., 2015).

Benthic communities in the shallow area of the Menorca Channel have been
also classified according to the European Nature Information System (EUNIS)
(Barberá et al., 2012). Amongst the deeper assemblages described in this study, *L. phalangium* beds (Assemblage B) correspond to the EUNIS facies "*L. phalangium* in
Mediterranean communities of the shelf-edge detritic bottom" (A5.472), whereas *G. vitreus* beds (Assemblage C) correspond to the EUNIS category "Communities of

615 bathyal detritic sands with G. vitreus" (A6.31). Conversely, the remaining 616 assemblages characterized in this study do not have a clear correspondence to EUNIS 617 categories. Sponge grounds (Assemblage A) can be only generically classified into 618 the EUNIS "Maërl bed" category (A5.51), whereas the transition assemblage 619 (Assemblage D) could fall within the EUNIS category of "Mosaics of mobile and 620 non-mobile substrata in the circalittoral zone" (X33). Classification into EUNIS 621 categories is more complex for the hard-bottom assemblages described in this study. 622 Coral gardens (Assemblage E) and vertical walls (Assemblage F) would both be 623 classified as EUNIS "Rocky substrates in circalittoral" (A4.2) and "Deep-sea bedrocks" (A6.11). These results highlight the limitations of EUNIS and the need to 624 625 improve this classification system for Mediterranean benthic environments occurring 626 below 100 m depth.

627 The highest megafaunal species richness and beta-diversity (i.e. species 628 turnover) is observed in the shelf edge (Fig. 6). This pattern probably results from the 629 synergy caused by habitat heterogeneity and hydrodynamic conditions along the shelf 630 edge. Indeed, rocky outcrops and vertical walls alternate with soft sedimented 631 grounds of varying grain sizes over the shelf edge. Moreover, both passive and active 632 suspension feeders may benefit from the stable environmental conditions and 633 hydrodynamic processes that enhance particle suspension in the near-bottom water 634 layers on the shelf edge (Thiem et al., 2006). It has also been suggested that the 635 observed increase in megafauna diversity at intermediate depths may result from the 636 merging of species with shallower and deeper distributions, causing a mid domain 637 effect (Colwell and Lees, 2000) as previously observed for deep coral communities in 638 the north Pacific (Stone, 2006; Matsumoto et al., 2007). 639 Benthic megafauna such as erect and massive sponges (Klitgaard and Tendal,

640 2004), gorgonians (Maynou and Cartes, 2012), antipatharians (Koslow et al., 2001) 641 and crinoids (Smith et al., 2000), are extremely sensitive to bottom trawling fishing. 642 Low trawling pressure at 100–500 m depth in the study area (Fig. 7) and the natural protection offered by rocky escarpments and vertical walls may explain the 643 644 preservation of the observed high-density and high-diverse megafauna assemblages 645 on the continental shelf edge. Protected bottom trawling on the continental shelf and 646 edge (Watling and Norse, 1998) has probably fragmented megabenthic assemblages 647 (Hall-Spencer et al., 2002), confining them to remote an inaccessible environments 648 (Díaz et al., 2015; Bo et al., 2015). The observed complexity and high-diversity of 649 benthic megafauna in the Menorca Channel, portrays how benthic community may 650 have been in several areas of the Mediterranean continental shelf and shelf edge 651 before the cumulative impact of decades of bottom trawling. Knowledge the 652 composition and distribution of deep benthic communities represent the 653 imprescindible baseline for the establishment of effective management measures for 654 the conservation and recovery of deep ecosystems in large marine protected areas 655 such as the Menorca Channel. Although the establishment of these large protection 656 zones may pose potentially challenging situations amongst stakeholders, economic 657 benefits may eventually materialize, including the recovery of degraded fisheries 658 (Pipitone et al., 2000) and the maintenance of ecosystem services (Balmford et al., 659 2002). 660

661 **5. Conclusions:**

662

663 - Six megabenthic assemblages are distributed throughout the outermost continental
664 shelf and upper slope of the Menorca Channel, being mainly segregated by substrate

665	type	and	depth.
-----	------	-----	--------

- Beds of the crinoid *Leptometra phalangium* and the brachiopod *Gryphus vitreus*dominate soft substrates.

669

- Sponges dominate hard substrates on the outer shelf, whereas gorgonians, corals and

671 incrusting sponges dominate hard substrates on the shelf edge and upper slope.

672

673 - The highest diversity of megabenthic species is found in the shelf edge, within the674 studied bathymetric range.

675

- Trawling pressure concentrates above 100 m depth and below 500 m depth;

677 consequently, low trawling pressure between 100 and 500 m depth probably

678 contributes to the preservation of the observed benthic assemblages.

679

680 Acknowledgements

681

682 The authors thank the crew of the R/V García del Cid, the JAGO team (J. Schauer

and K. Hissmann) from IFM-GEOMAR (Kiel, Germany), the NEMO ROV pilot

684 Gavin Newman. David Díaz, Andreu Santín, Maria Montseny, Anthi Oikonomou,

685 Artemis Atsalaki, Guillem Corbera for their advice and help during the oceanographic

686 surveys and the video analysis. We would like to thank Pablo J. López-González

687 (cnidarians), Maria Jesus Uriz (sponges), Rafael Sardà (polychaetes) and Mikel

688 Zabala (briozoans) for their help provided in the taxonomical identification. This

689 work was funded by the European project LIFE+ INDEMARES "Inventario y

690	designación de la red Natura 2000 en áreas marinas del estado español"
691	(LIFE07/NAT/E/000732).
692	
693	References
694	
695 696 697 698	Abella, A., Serena, F., Ria, M., 2005. Distributional response to variations in abundance over spatial and temporal scales for juveniles of European hake (<i>Merluccius merluccius</i>) in the Western Mediterranean Sea. Fisheries Research 71, 295–310. doi:10.1016/j.fishres.2004.08.036
700 701 702 703	 Acosta, J., Canals, M., López-Martínez, J., Muñoz, A., Herranz, P., Urgeles, R., Palomo, C., Casamor, J.L., 2002. The Balearic Promontory geomorphology (western Mediterranean): Morphostructure and active processes. Geomorphology 49, 177–204. doi:10.1016/S0169-555X(02)00168-X
704 705 706 707 708 709 710	Aguilar, R., Serrano, A., García, S., Alvarez, H., Blanco, J., López, J., Marín P., Pastor, X., 2014. Vulnerable habitats and species in the deep-sea Emile Baudot escarpment (South Balearic Islands) Surveyed by ROV. In Proceedings of the 1st Mediterranean symposium on the conservation of Dark Habitats. Pargent-Martini and M. Brichet, (Eds.), RAC/SPA Publ. Tunis. 2014
710 711 712 713 714 715	Althaus, F., Williams, A., Schlacher, T.A., Kloser, R.J., Green, M.A., Barker, B.A., Bax, N.J., Brodie, P., Schlacher-Hoenlinger, M.A., 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Marine Ecology Progress Series 397, 279–294. doi:10.3354/meps08248
713 716 717 718 719 720 721	Ambroso, S., Gori, A., Dominguez-Carrió, C., Gili, J.M., Berganzo, E., Teixidó, N., Greenacre, M., Rossi, S., 2013. Spatial distribution patterns of the soft corals <i>Alcyonium acaule</i> and <i>Alcyonium palmatum</i> in coastal bottoms (Cap de Creus, northwestern Mediterranean Sea). Marine Biology 160, 3059–3070. doi:10.1007/s00227-013-2295-4
722 723 724 725 726 727	 Angiolillo, M., Bavestrello, G., Bo, M., Cau, A, Cau, A., Giusti, M., Salvati, E., Tunesi, L., Canese, S., 2014. Distribution of the deep-dwelling gorgonian <i>Viminella flagellum</i> in the Italian Western Mediterranean Sea by means of multi- year ROV survey 2013-2014. In: 1st Mediterranean Symposium on the conservation of Dark Habitats, Portoroz, Slovenia 31 October 2014.
728 729 730 731 732 733	 Angiolillo, M., di Lorenzo, B., Farcomeni, A., Bo, M., Bavestrello, G., Santangelo, G., Cau, A., Mastascusa, V., Cau, A., Sacco, F., Canese, S., 2015. Distribution and assessment of marine debris in the deep Tyrrhenian Sea (NW Mediterranean Sea, Italy). Marine Pollution Bulletin 92, 149–159. doi:10.1016/j.marpolbul.2014.12.044
734	Aschan, M., Fossheim, M., Greenacre, M., Primicerio, R., 2013. Change in Fish

735 736 727	Community Structure in the Barents Sea. PLoS One 8, 1–12. doi:10.1371/journal.pone.0062748
738 739 740 741 742	Balbín, R., Flexas, M.M., López-Jurado, J.L., Peña, M., Amores, A., Alemany, F., 2012. Vertical velocities and biological consequences at a front detected at the balearic sea. Continental Shelf Research 47, 28–41. doi:10.1016/j.csr.2012.06.008
742 743 744 745 746 747 748	 Balmford A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Matthew, R., Rosendo, S., Roughgarden, J., Trumper, K., Turner, R.K., 2002. Economic Reasons for Conserving Wild Nature. Science 297, 950–953. doi:10.1126/science.1073947
749 750 751 752 753	Barberá, C., Moranta, J., Ordines, F., Ramón, M., Mesa, A., Díaz-Valdés, M., Grau, A.M., Massutí, E., 2012. Biodiversity and habitat mapping of Menorca Channel (western Mediterranean): implications for conservation. Biodiversity and Conservation 21, 701–728. doi:10.1007/s10531-011-0210-1
754 755 756 757 758	Beazley, L., Kenchington, E., Yashayaev, I., Murillo, F.J., 2015. Drivers of epibenthic megafaunal composition in the sponge grounds of the Sackville Spur, northwest Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 98, 102– 114. doi:10.1016/j.dsr.2014.11.016
759 760 761 762 763	Bennecke, S., Metaxas, A., 2016. Effectiveness of a deep-water coral conservation area: evaluation of its boundaries and changes in octocoral communities over 13 years. Deep Sea Research Part II: Topical Studies in Oceanography In press. doi:10.1016/j.dsr2.2016.06.005
764 765 766 767 768	Bertolino, M., Bo, M., Canese, S., Bavestrello, G., Pansini, M., 2015. Deep sponge communities of the Gulf of St Eufemia (Calabria, southern Tyrrhenian Sea), with description of two new species. Journal of the Marine Biologica Association of the United Kingdom 95, 1371–1387.
769 770 771 772 773	Bertolino, M., Bo, M., Canese, S., Bavestrello, G., Pansini, M., 2013. Deep sponge communities of the Gulf of St Eufemia (Calabria, southern Tyrrhenian Sea), with description of two new species. Journal of the Marine Biological Association fo the United Kingdom 95, 1371–1387. doi:10.1017/S0025315413001380
774 775 776 777 778	 Bo, M., Bavestrello, G., Angiolillo, M., Calcagnile, L., Canese, S., Cannas, R., Cau, A., Elia, M.D., Oriano, F.D., Follesa, M.C., Quarta, G., Cau, A., 2015. Persistence of Pristine Deep-Sea Coral Gardens in the Mediterranean Sea (SW Sardinia). PLoS One 1–21. doi:10.1371/journal.pone.0119393
779 780 781 782 782	Bo, M., Canese, S., Bavestrello, G., 2013. Discovering Mediterranean black coral forests: <i>Parantipathes larix</i> (Anthozoa: Hexacorallia) in the Tuscan Archipelago, Italy. Italian Journal of Zoology 81, 112–125. doi:10.1080/11250003.2013.859750
784	Bo, M., Canese, S., Spaggiari, C., Pusceddu, A., Bertolino, M., Angiolillo, M., Giusti,

785 786 787	M., Loreto, M.F., Salvati, E., Greco, S., Bavestrello, G., 2012. Deep Coral Oases in the South Tyrrhenian Sea. PLoS One 7. doi:10.1371/journal.pone.0049870
788 789 790 791 792	Bo, M., Bertolino, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., Pansini, M., Taviani, M., 2011a. Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. Hydrobiologia 687, 163–177. doi:10.1007/s10750- 011-0964-1
793 794 795 796 797	 Bo, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., Cerrano, C., Salvati, E., Greco, S., 2011b. Coral assemblage off the Calabrian Coast (South Italy) with new observations on living colonies of <i>Antipathes dichotoma</i>. Italian Journal of Zoology 78, 231–242. doi:10.1080/11250001003652619
798 799 800 801 802	 Bo, M., Di CaMillo, C.G., Bertolino, M., Povero, P., Misic, C., Castellano, M., Covazzi Harriague, A., Gasparini, G.P., Borghini, M., Schroeder, K., Bavestrello, G., 2010. The megabenthic assemblages of the Verdelli Seamount (North Tyrrhenian Sea). Biologia Marina Mediterranea 17, 94-97.
803 804 805 806 807	Bo, M., Bavestrello, G., Canese, S., Giusti, M., Salvati, E., Angiolillo, M., Greco, S., 2009. Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. Marine Ecology Progress Series 397, 53–61. doi:10.3354/meps08185
808 809 810 811 812 813	 Buhl-Mortensen, L., Serigstad, B., Buhl-Mortensen, P., Olsen, M.N., Ostrowski, M., Błażewicz-Paszkowycz, M., Appoh, E., 2016. First observations of the structure and megafaunal community of a large Lophelia reef on the Ivorian-Ghanaian margin (the Gulf of Guinea). Deep Sea Res. Part II: Topical Studies in Oceanography In press, doi:10.1016/j.dsr2.2016.06.007
814 815 816 817	Buhl-Mortensen, P., Buhl-Mortensen, L., 2013. Diverse and vulnerable deep-water biotopes in the Hardangerfjord. Marine Biology Research 10, 253–267. doi:10.1080/17451000.2013.810759
817 818 819 820 821 822 823	Cartes, J.E., Lo Iacono, C., Mamouridis, V., López-Pérez, C., Rodríguez, P., 2013. Geomorphological, trophic and human influences on the bamboo coral <i>Isidella</i> <i>elongata</i> assemblages in the deep Mediterranean: To what extent does Isidella form habitat for fish and invertebrates? Deep Sea Research Part I: Oceanography Research Paper 76, 52–65. doi:10.1016/j.dsr.2013.01.006
823 824 825 826 827 828 828	Cartes, J.E., Maynou, F., Fanelli, E., Romano, C., Mamouridis, V., Papiol, V., 2009. The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: Environmental gradients influencing assemblges composition and biomass trends. Journal of Sea Research 61, 244–257.
830 831 832 833 834	 Cau, A., Moccia, D., Follesa, M.C., Alvito, A., Canese, S., Angiolillo, M., Cuccu, D., Bo, M., Cannas, R., 2017. Coral forests diversity in the outer shelf of the south Sardinian continental margin. Deep Sea Research Part I, <i>in press</i>

835 836 837	Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A., Rowden, A.A., 2016. The impacts of deep-sea fisheries on benthic communities: A review ICES Journal of Marine Science 73, 51–69, doi:10.1093/icesims/fsv123
838	
839 840 841 842	Colloca, F., Cardinale, M., Belluscio, A., Ardizzone, G., 2003. Pattern of distribution and diversity of demersal assemblages in the central Mediterranean sea. Estuarine Coastal Shelf Science 56, 469–480. doi:10.1016/S0272- 7714(02)00196-8
843	
844 845 846 847 848	Colloca, F., Carpentieri, P., Balestri, E., Ardizzone, G.D., 2004. A critical habitat for Mediterranean fish resources: shelf-break areas with <i>Leptometra phalangium</i> (Echinodermata: Crinoidea). Marine Biology 145, 1129–1142. doi:10.1007/s00227-004-1405-8
849 850 851 852	Colwell, R.K., Lees, D.C., 2000. The mid-domain effect: Geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15, 70–76. doi:10.1016/S0169-5347(99)01767-X
853 854 855 856 857	Coppari, M., Gori, A., Viladrich, N., Saponari, L., Canepa, A., Grinyó, J., Olariaga, A., Rossi, S., 2016. The role of Mediterranean sponges in benthic-pelagic coupling processes: Aplysina aerophoba and Axinella polypoides case studies. Journal of Experimental Marine Biology and Ecology 477, 57-68.
858 859 860 861 862	 Deidun, A, Andaloro, F., Bavestrello, G., Canese, S., Consoli, P., Micallef, A., Romeo, T., Bo, M., 2014. First characterisation of a <i>Leiopathes glaberrima</i> (Cnidaria: Anthozoa: Antipatharia) forest in Maltese exploited fishing grounds. Italian Journal of Zoology 82, 37–41. doi:10.1080/11250003.2014.986544
863 864 865 866	De Leo, F.C., Vetter, E.W., Smith, C.R., Rowden, A.A., McGranaghan, M., 2014. Spatial scale-dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and diversity off the Main and Northwest Hawaiian Islands. Deep Sea Res. Part II 104, 267–290.
867 868 869 870 871 872 873 874 875 876	 Díaz, D., Bo, M., Gaamour, A., Ambroso, S., Bavestrello, G., Bed Abdallah, L., Ben Salem, S., Benmassaoued, R., Canese, S., Cerasi, S., Cherif, M., Djabou, H., Dominguez-Carrió, C., Goñi, R., Grinyó, J., Gutiérrez, V., Jaziri, S., Khemiri, S., Koched, W., Nurus, P., Mallol, S., Misaoui, H., Ben Amor, M.M., Muñoz, A., Palomeque, R., Profeta, A., Rjeibi, O., Santín, A., Gili, J.M., 2015. Towards Ecosystem Conservation and sustainable artisanal fisheries in the Mediterranean basin. In: ICES Annual Science Conference 2015. Copenhagen, Denmark. ICES CM 2015/F:23.
877 878 879	Emig, C.C., 1997. Bathyal zones of the Mediterranean continental slope: an attempt. Publicación Espececial Instituto Español Oceanografia 23, 23–33.
880 881 882	Emig, C.C., 1987. Offshore brachiopods investigated by submersible. Journal of Experimental Marine Biology and Ecology 108, 261–273.
883 884	Emig, C.C., 1985. Distribution et synécologie des fonds à Gryphus vitreus (Brachiopoda) en Corse. Marine Biology 90, 139–146 (1985).

885	
886	Eshleman, W.P., Wilkens, J.L., 1979. Brachiopod orientation to current direction and
887	substrate position (Terebratalia transversa). Canadian Journal of Zoology 57,
888	2079–2082. doi:10.1139/z79-274
889	
890	Etiope, G., Savini, A., Lo Bue, N., Favali, P., Corselli, C., 2010. Deep-sea survey for
891	the detection of methane at the "Santa Maria di Leuca" cold-water coral mounds
892	(Ionian Sea, South Italy). Deep Research Part II: Topical Studies in
893	Oceanography 57, 431–440. doi:10.1016/j.dsr2.2009.08.020
894	
895	Fabri, M., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D., Freiwald, A., 2014.
896	Megafauna of vulnerable marine ecosystems in French mediterranean submarine
897	canyons: Spatial distribution and anthropogenic impacts. Deep Sea Research Part
898	II: Topical Studies in Oceanography 104, 184–207.
899	doi:10.1016/j.dsr2.2013.06.016
900	
901	Fosså, Jan Helge, Mortensen, P.B, Furevik, D.M., 2002. The deep-water coral
902	Lophelia pertusa in Norwegian waters: distribution and fishery impacts.
903	Hydrobiologia $4/1$, 1–12. doi:10.1023/A:1016504430684
904	
905	Fredj, G., 1964. Contributions a l'etude bionomique de la Mediterranee occidentale
906	(Cole du Var et des Alpes marilimes-cole occidentale de Corse). Fascicule 2: La
907	Pulletin Institut Ossensoratio de Manaco 62 1 55 62
900	Bunetin Institut Oceanografic de Monaco, 05 1-55. 05.
909	Carcía A Alemany F. Valaz Balchí P. Lónaz Jurado I.I. Cortás D. de la Sarna
910 911	I M González Pola C Rodrauez I M Inasá I Ramírez T 2005
912	Characterization of the bluefin tuna snawning habitat off the Balearic
913	Archinelago in relation to key hydrographic features and associated
914	environmental conditions. Collectted Volume of Scientific Papers ICCAT 58
915	535-549
916	
917	Getis, A., Keith Ord, J.K., 1996. Local spatial statistics: an overview. Spatial analysis:
918	modelling in a GIS environment 374.
919	
920	Gori, A., Rossi, S., Berganzo, E., Pretus, J.L., Dale, M.R.T., Gili, J.M., 2011. Spatial
921	distribution patterns of the gorgonians Eunicella singularis, Paramuricea clavata
922	and Leptogorgia sarmentosa (Cap of Creus, Northwestern Mediterranean Sea).
923	Marine Biology 158, 143–158.
924	
925	Gori, A., Orejas, C., Madurell, T., Bramanti, L., Martins, M., Quintanilla, E., Marti-
926	Puig, P., Lo Iacono, C., Puig, P., Requena, S., Greenacre, M., Gili, J.M., 2013.
927	Bathymetrical distribution and size structure of cold-water coral populations in
928	the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean).
929	Biogeosciences 10, 2049–2060. doi:10.5194/bg-10-2049-2013
930	
931	Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in
932	the measurement and comparison of species richness. Ecology Letters 4, 379-
933	391.
934	

935 936	Greenacre, M., Primicerio, R., 2013. Chapter 13. Correspondence Analysis, in: Multivariate Analysis of Ecological Data. p. 177.
937	doi:10.1177/0049124106290316
938	
939	Grinyó, J., Gori, A., Ambroso, S., Purroy, A., Calatayud, C., Dominguez-Carrió, C.,
940	Coppari, M., Lo Iacono, C., López-González, P.J., Gili, J.M., 2016. Diversity,
941	distribution and population size structure of deep Mediterranean gorgonian
942	assemblages (Menorca Channel, Western Mediterranean Sea). Progress in
943	Oceanography 145, 42–56. doi:10.1016/j.pocean.2016.05.001
944	
945	Hall-Spencer, J., Allain, V., Fosså, J.H., Copernic, P.N., 2002. Trawling damage to
946	Northeast Atlantic ancient coral reefs. Proceedings of the Royal Society of
947	London B: Biological Sciences 269, 507–511. doi:10.1098/rspb.2001.1910
948	
949	Hintzen, N.T., Piet, G.J., Brunel, T., 2010. Improved estimation of trawling tracks
950	using cubic Hermite spline interpolation of position registration data. Fisheries
951	Research 101, 108–115. doi:10.1016/j.fishres.2009.09.014
952	
953	Howell, KL., Piechaud, N., Downie, AL., Kenny, A., 2016. The distribution of
954	deep-sea sponge aggregations in the North Atlantic and implications for their
955	effective spatial management. Deep Sea Research Part I: Oceanographic
956	Research Paper 115, 309–320. doi:10.1016/j.dsr.2016.07.005
957	
958	Huvenne, V.A.I., Bett, B.J., Masson, D.G., Le Bas, T.P., Wheeler, A.J., 2016.
959	Effectiveness of a deep-sea cold-water coral Marine Protected Area, following
960	eight years of fisheries closure. Biological Conservation 200, 60-69.
961	doi:10.1016/j.biocon.2016.05.030
962	
963	Joher, S., Ballesteros, E., Cebrian, E., Sánchez, N., Rodríguez-Prieto, C., 2012. Deep-
964	water macroalgal-dominated coastal detritic assemblages on the continental shelf
965	off Mallorca and Menorca (Balearic Islands, Western Mediterranean). Botanica
966	Marina 55, 485–497. doi:10.1515/bot-2012-0113
967	
968	Kallianiotis, A., Sophronidis, K., Vidoris, P., Tselepides, A., 2000. Demersal fish and
969	megafaunal assemblages on the Cretan continental shelf and slope (NE
970	Mediterranean): Seasonal variation in species density, biomass and diversity.
971	Progress in Oceanography 46, 429–455. doi:10.1016/S0079-6611(00)00028-8
972	
973	Klitgaard, A.B., Tendal, O.S., 2004. Distribution and species composition of mass
974	occurrences of large-sized sponges in the northeast Atlantic. Progress in
975	Oceanography 61, 57–98. doi:10.1016/j.pocean.2004.06.002
976	
977	Koslow, J.A., Gowlett-Holmes, K., Lowry, J.A., O'Hara, T., Poore, G.C.B., Williams,
978	A., 2001. Seamount Benthic Macrofauna off Southern Tasmania: Community
979	Structure and Impacts of Trawling. Marine Ecology Progress Series 213, 111-
980	125. doi:10.3354/meps213111
981	
982	Kutti, T., Bannister, R.J., Fosså, J.H., 2013. Community structure and ecological
983	function of deep-water sponge grounds in the Traenadypet MPA-Northern
984	Norwegian continental shelf. Continental Shelf Research 69, 21–30.

985	doi:10.1016/j.csr.2013.09.011
986	
987	Lastras, G., Canals, M., Ballesteros, E., Gili, JM., Sanchez-Vidal, A., 2016. Cold-
988	Water Corals and Anthropogenic Impacts in La Fonera Submarine Canyon Head,
989	Northwestern Mediterranean Sea. PLoS One 11, e0155729.
990	doi:10.13/1/journal.pone.0155/29
991	
992	Lavaleye, M.S.S., Duineveld, G.C.A., Berghuis, E.M., Kok, A., Witbaard, R., 2002.
993	A comparison between the megafauna communities on the N. W. Iberian and
994	Celtic continental margins—effects of coastal upwelling? Progress in
995	Oceanography 52, 459–476.
996	
997	Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and
998	accessible methods to provide high-resolution estimates of fishing-effort
999	distributions from vessel monitoring system (VMS) data. ICES Journal of
1000	Marine Science 67 , $1260-1271$. doi:10.1093/icesjms/isq010
1001	L'and Canada D. L. Crimer's L. Cili L.M. 2015 Chinese Holes and discussion of
1002	Lopez-Gonzalez, P.J., Grinyo, J., Gili, J.M., 2015. Chironephthya meaiterranea n. sp.
1003	(Octocoralita, Alcyonacea, Nidaliidae), the first species of the genus discovered
1004	In the Mediterranean Sea. Marine Biodiversersity 45, $667-688$.
1005	do1:10.100//\$12526-014-0269-5
1000	Maldanada M. Aquilar D. Donnistar D. L. Jamos, J. Convey, K.W. Davitar, D.K.
1007	Cristing D. Cutt. I. Kelly, M. Kenshington E.I. D. Love, S.D. Shirley, A.
1000	Cristina, D., Guit, J., Keny, M., Kenchington, E.L.K., Leys, S.P., Shirley, A., Tandal, O.S., Dann, H.T., Klava, D., Vavna, C.M. 2016, Spange Chaving as
1009	Very Marine Hebitate: A Synthetic Deview of Types Structure Functional rela
1010	and Conservation Concerns, in: Animal Forest, np. 2, 20, doi:10.1007/078.2
1011	210 17001 5
1012	519-17001-5
1013	Mangano M.C. Porporato F. De Domenico F. Profeta A. Busalacchi B. 2010
1014	Lantometra nhalangium (I Müller 1841) Fields from the Southern Tyrrhenian
1015	Sea: Preliminary Data on the Associated Fauna Biologia Marina Mediterranea
1010	17 304_305
1018	17, 504 505.
1019	Massi, D., 2005, Composizione dello" sporco"(macrobenthos non commerciale) della
1020	pesca a strascico Campagna GRUND 2004-Stretto di Sicilia.
1021	
1022	Mastrototaro, F., D'Onghia, G., Corriero, G., Matarrese, A., Maiorano, P., Panetta, P.,
1023	Gherardi, M., Longo, C., Rosso, A., Sciuto, F., Sanfilippo, R., Gravili, C.,
1024	Boero, F., Taviani, M., Tursi, A., 2010. Biodiversity of the white coral bank off
1025	Cape Santa Maria di Leuca (Mediterranean Sea): An update. Deep Sea Research
1026	Part II: Topical Studies in Oceanography 57, 412–430.
1027	doi:10.1016/j.dsr2.2009.08.021
1028	
1029	Matsumoto, A.K., Iwase, F., Imahara, Y., Namikawa, H., 2007. Bathymetric
1030	distribution and biodiversity of cold-water octocorals (Coelenterata:
1031	Octocorallia) in Sagami Bay and adjacent waters of Japanese Bulletin of Marine
1032	Science 81, 231–251.
1033	
1034	Maynou, F., Cartes, J.E., 2012. Effects of trawling on fish and invertebrates from

1035 1036 1037	deep-sea coral facies of <i>Isidella elongata</i> in the western Mediterranean. Journal of the Marine Biological Association of the United Kingdom 92, 1501–1507. doi:10.1017/S0025315411001603
1038	doi.10.101//.50020515/111001005
1039	Michez N., Fourt M., Aish A., Bellan G., Bellan-Santini D., Chevaldonné P., Fabri
1040	MC., Goujard A., Harmelin JG., Labrune C., Pergent G., Sartoretto S.,
1041	Vacelet J., Verlague M., 2014, Typologie des biocénoses benthiques de
1042	Méditerranée Version 2, Rapport SPN 2014 - 33, MNHN, Paris, 26 pages.
1043	
1044	Millot C 1987 Circulation in the western Mediterranean-sea. Oceanological Acta
1045	10 143-149 doi:10 1016/S0924-7963(98)00078-5
1046	10, 115 115. doi:10.1010/00/21 7505(50)00070 5
1047	Mytilineou C. Smith C.I. Anastasopoulou A. Papadopoulou K.N. Christidis G
1048	Bekas P Kavadas S Dokos I 2014 New cold-water coral occurrences in the
1049	Fastern Ionian Sea: Results from experimental long line fishing. Deen Sea
1050	Research Part II: Tonical Studies in Oceanography 99, 146–157
1051	doi:10.1016/i.dsr2.2013.07.007
1051	doi.10.1010/j.doi2.2015.07.007
1052	Oksanen I Blanchet F.G. Friendly M. Kindt R. Legendre P. McGlinn D
1054	Minchin P.R. O'Hara R.B. Simpson G.L. Solvmos P. Stevens H.H. Szoecs
1055	F Wagner H 2015 Vegan: community ecology package R-package version
1055	E., Wagner, H., 2015. Vegan. community ecology package. R-package version.
1057	Oreias C. Gori A. Lo Jacono C. Puig P. Gili I. Dale M. 2009 Cold-water
1058	corals in the Can de Creus canvon, northwestern Mediterranean: snatial
1050	distribution density and anthronogenic impact. Marine Ecology Progress Series
1055	397 37_51 doi:10.3354/mens08314
1061	<i>377, 37–31.</i> doi:10.3334/incp300314
1062	Pedel L. Fabri M.C. 2011 Description et cartographie des biocénoses benthiques
1063	rencontrées au cours de la campagne MEDSEACAN (Aamp/Comex)
1064	rencontrees au cours de la campagne mildolli renni (mampi contex).
1065	Pérès, J.M., Picard, J., 1964, Nouveau Manuel de Bionomie benthique dela Mer
1066	Mediterranee. Station Marine d'Endoume.
1067	
1068	Pérès, J., 1967. The Mediterranean benthos. Oceanography and Marine Biology: an
1069	Annual Review 5, 449–533.
1070	
1071	Piet, G.J., Ouiriins, F.J., 2009. The importance of scale for fishing impact estimations.
1072	Canadian Journal of Fisheries and Aquatic Sciences 66, 829–835.
1073	doi:10.1139/F09-042
1074	
1075	Pipitone, C., Badalamenti, F., D'Anna, G., Patti, B., 2000. Fish biomass increase after
1076	a four-year trawl ban in the Gulf of Castellammare (NW Sicily, Mediterranean
1077	Sea). Fisheries Research 48, 23–30, doi:10.1016/S0165-7836(00)00114-4
1078)
1079	Porteiro, F.M., Gomes-Pereira, J.N., Pham, C.K., Tempera, F., Santos, R.S., 2013.
1080	Distribution and habitat association of benthic fish on the Condor seamount (NE
1081	Atlantic, Azores) from in situ observations. Deep Sea Research Part II: Topical
1082	Studies in Oceanography 98, 114–128. doi:10.1016/i.dsr2.2013.09.015
1083	6 1 <i>J</i> -
1084	R Core Team, 2014. R: A language and environment for statistical computing. R

1090

1094

1098

1103

1107

1111

- Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.
- 1087 Rice, A.L.; Turston, M.H.; New, A.L., 1990. Dense aggregations of a hexactinellid
 1088 sponge, in the Porcupine Seabight (northeast Atlantic Ocean) and possible
 1089 causes. Progress in Oceanography 24, 179–196.
- Ruiz, S., Pascual, A., Garau, B., Faugère, Y., Alvarez, A., Tintoré, J., 2009.
 Mesoscale dynamics of the Balearic Front, integrating glider, ship and satellite
 data. Journal of Marine Systems 78, S3–S16. doi:10.1016/j.jmarsys.2009.01.007
- Sacchi, J., 2008. The use of trawling nets in the Mediterranean. Problems and
 selectivity options. Options Mediterraneennes. Série b: Etudes et Recherches 62,
 87–96.
- Sampaio, Í., Braga-Henriques, A., Pham, C., Ocaña, O., de Matos, V., Morato, T.,
 Porteiro, F.M., 2012. Cold-water corals landed by bottom longline fisheries in
 the Azores (north-eastern Atlantic). Journal of the Marine Biological Association
 of the United Kingdom 92, 1547–1555. doi:10.1017/S0025315412000045
- Seike, K., Shirai, K., Kogure, Y., 2013. Disturbance of Shallow Marine Soft-Bottom
 Environments and Megabenthos Assemblages by a Huge Tsunami Induced by
 the 2011 M9.0 Tohoku-Oki Earthquake. PLoS One e65417.
- Shepard, F.P., Marshall, N.F., McLoughlin, P.A., 1974. Currents in submarine
 canyons. Deep Sea Research and Oceanogrphic Abstracts 21, 691–706.
 doi:10.1016/0011-7471(74)90077-1
- 1112 Sheppard, C.R.C., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe, C., Craig, M.T., Ebinghaus, R., Eble, J., Fitzsimmons, N., Gaither, M.R., Gan, C.H., 1113 1114 Gollock, M., Guzman, N., Graham, N.A.J., Harris, A., Jones, R., Keshavmurthy, 1115 S., Koldewey, H., Lundin, C.G., Mortimer, J.A., Obura, D., Pfeiffer, M., Price, 1116 A.R.G., Purkis, S., Raines, P., Readman, J.W., Riegl, B., Rogers, A., Schleyer, M., Seaward, M.R.D., Sheppard, A.L.S., Tamelander, J., Turner, J.R., Visram, 1117 1118 S., Vogler, C., Vogt, S., Wolschke, H., Yang, J.M.C., Yang, S.Y., Yesson, C., 1119 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: Why it is the 1120 world's largest no-take marine protected area. Aquatic Conservation: Marine and Freshwater Ecosystems 22, 232–261. doi:10.1002/aqc.1248 1121
- Sherwood, O.A., Edinger, E.N., 2009. Ages and growth rates of some deep-sea
 gorgonian and antipatharian corals of Newfoundland and Labrador. Canadian
 Journal of Fisheries and Aquatic Science 66, 142–152. doi:10.1139/F08-195
- Silva, M., Etnoyer, P.J., MacDonald, I.R., 2015. Coral injuries observed at mesophotic Reefs after the Deepwater Horizon oil discharge. Deep Sea Research Part II Topical Studies in Oceanography 129, 96–107. doi:10.1016/j.dsr2.2015.05.013
- 1131
- Smith, C.J., Papadopoulou, K.N., Diliberto, S., 2000. Impact of otter trawling on an
 eastern Mediterranean commercial trawl fishing ground. ICES Journal of Marine

1134 1125	Sciences 57, 1340–1351. doi:10.1006/jmsc.2000.0927
1135	Snalding M.D. Maliana I. Milam A. Eitzgerald F. Hala I. 7, 2012 Protecting
1127	maring spaces: global targets and changing approaches. Occar Veerback 27
1137	112 249
1130	215-248.
1140	Stone, R.P., 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution,
1141	fine-scale species associations, and fisheries interactions. Coral Reefs 25, 229-
1142	238. doi:10.1007/s00338-006-0091-z
1143	
1144	Taviani, M., Angeletti, L., Canese, S., Cannas, R., Cardone, F., Cau, A., Cau, A.B.,
1145	Follesa, M.C., Marchese, F., Montagna, P., Tessarolo, C., 2015. The "Sardinian
1146	cold-water coral province" in the context of the Mediterranean coral ecosystems.
1147	Deep Sea Research Part II: Topical Studies in Oceanography In press.
1148	doi:10.1016/j.dsr2.2015.12.008
1149	
1150	Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector-
1151	technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.
1152	
1153	Thiem, Ø., Ravagnan, E., Fosså, J.H., Berntsen, J., 2006. Food supply mechanisms
1154	for cold-water corals along a continental shelf edge. Journal of Marine Systems
1155	60, 207–219. doi:10.1016/j.jmarsys.2005.12.004
1156	
1157	Vetter, E.W., Smith, C.R., De Leo, F.C., 2010. Hawaiian hotspots: enhanced
1158	megafaunal abundance and diversity in submarine canyons on the oceanic
1159	islands of Hawaii. Marine Ecology 31, 183–199.
1160	
1161	Watling, L., Norse, E.A., 1998. Disturbance of the Seabed by Mobile Fishing Gear: A
1162	Comparison to Forest Clearcutting. Conservation Biology 12, 1180–1197.
1163	doi:10.1046/j.1523-1739.1998.0120061180.x
1164	
1165	Weinberg, S., 1978. Mediterranean octocorallian communities and the abiotic
1166	environment. Marine Biology 49, 41–57.
1167	
1168	Williams, A., Schlacher, T.A., Rowden, A.A., Althaus, F., Clark, M.R., Bowden,
1169	D.A., Stewart, R., Bax, N.J., Consalvey, M., Kloser, R.J., 2010. Seamount
1170	megabenthic assemblages fail to recover from trawling impacts. Marine Ecology
1171	31, 183–199. doi:10.1111/j.1439-0485.2010.00385.x
1172	
11/3	Wurtz, M., 2012. Mediterranean Submarine Canyons: Ecology and Governance.
11/4	International Union for the Conservation of Nature, Gland, Switzerland and
11/5	iviaiaga, Spain.
11/0	
1177	
1178	
1179	Figure Legends of Figures larger than 10 M:

1180	
1181	Fig. 3 Most contributing species to the CCA a) Haliclona cf. elegans, b) Aplysina cavernicola, c)
1182	Leptometra phalangium, d) Gryphus vitreus, e) Salmacina dysteri, f) Hamacantha sp. 2 (white circle)
1183	and Haliclona sp. 1 (black circle), g) Eunicella cavolinii, h) Viminella flagellum i) Nidalia studeri, j)
1184	Thalamophyllia gasti, k) Hamacantha falcula, l) Rhabderemia sp. Scale Bar: 5 cm.
1185	
1186	Supplementary material captions:
1187	
1188	Supplementary material 1: Transect location, length, depth (minimum and maximum depth), main
1189	substrate (> 50% coverage of sampling units) (M: maërl, CBP: cobbles and pebbles, MS: medium
1190	sands, FS: fine sands, R: rocky substrates), main slope (> 50% coverage of sampling units)(H:
1191	horizontal, S: slopping, V: vertical).
1192	
1193	Supplementary material 2: Variation in the resolution of the canonical correspondence analysis (CCA)
1194	ordination biplots when using different sampling unit sizes. Sampling units are colored according to the
1195	dominant substrate: fine sands (yellow), medium sands to gravels (green), cobbles and pebbles
1196	(orange), maërl (blue), outcropping rock (red).
1197	
1198	Supplementary material 3: Megabenthic species abundance, mean and maximum density, bathymetric
1199	distribution, and assemblage occurrence.
1200	
1201	Supplementary material 4: Multispecific demosponge assemblage (pink sponge = Haliclona cf.
1202	<i>elegans</i> , bright yellow sponges = <i>Aplysina cavernicola</i>) on maërl beds located on the continental shelf
1203	at 99 m depth (transect 22 on Fig. 1).
1204	
1205	Supplementary material 5: Leptometra phalangium bed at the shelf edge at 130 m depth (transect 44 on
1206	Fig. 1).
1207	
1208	Supplementary material 6: Gryphus vitreus bed at the upper slope at 200 m depth (transect 27 on Fig.
1209	1).

1210	
1211	Supplementary material 7: Cobble grounds with few large demosponges at 130 m depth (transect 30 on
1212	Fig. 1).
1213	
1214	Supplementary material 8: Multispecific coral garden (white gorgonian = Eunicella cavolinii, yellow
1215	gorgonian = Acanthogorgia hirsuta, white tubular sponge = Haliclona magna) at the shelf edge 150 m
1216	depth (transect 3 on Fig. 1).
1217	
1218	Supplementary material 9: Vertical wall densely colonized by the incrusting sponge Rhabderemia sp.

1219 at 130 m depth (transect 45 on Fig. 1).