Diversity, structure and spatial distribution of megabenthic communities in Cap de Creus continental shelf and submarine canyon (NW Mediterranean)

Carlos Dominguez-Carrió [a,b,*], Joan Lluís Riera [c], Katleen Robert [d,e], Mikel Zabala [c], Susana Requena [a,f], Andrea Gori [a,c], Covadonga Orejas [h,i], Claudio Lo Iacono [a,d], Claude Estournel [g], Guillem Corbera [a], Stefano Ambroso [a], Maria Jesús Uriz [j], Pablo J. López-González [k], Rafael Sardá [j], Josep-Maria Gili [a]

[a] Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003, Barcelona (Spain)
[b] Instituto de Investigação em Ciências do Mar - Okeanos, Departamento de Oceanografia e Pescas, Universidade dos Açores, Rua Prof. Doutor Frederico Machado 4, 9901-862, Horta (Portugal)
[c] Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 643, 08028, Barcelona (Spain)
[d] National Oceanography Centre, University of Southampton Waterfront Campus, European Way, SO14 3ZH, Southampton (UK)
[e] Fisheries and Marine Institute of Memorial University, 155 Ridge Rd, St. John's, NL A1C 5R3 (Canada)
[f] RSPB, Centre for Conservation Science, The Lodge, Sandy SG19 2DL, Bedfordshire (UK)
[g] Laboratoire d'Etudes en Géophysique et Océanographie Spatiales (LEGOS), CNRS/UPS/CNES/IRD, Avenue Edouard Belin 14, 31400, Toulouse (France)
[h] Instituto Español de Oceanografía, Centro Oceanográfico de Gijón (IEO-CSIC), Avenida Príncipe de Asturias 70 bis, 33212 Gijón (Spain)
[i] Hanse-Wissenschatfskolleg – Institute for Advanced Study (HWK), Lehmkuhlenbusch 4, 27753 Delmenhorst (Germany)
[j] Centre d'Estudis Avancats de Blanes, Consejo Superior de Investigaciones Científicas (CEAB-CSIC), Carrer d'acces a la Cala Sant Francesc 14, 17300, Blanes (Spain)
[k] Biodiversidad y Ecología Acuática, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Reina Mercedes 6, 41012, Sevilla (Spain)

ARTICLE INFO

ABSTRACT

The continental shelf and submarine canyon off Cap de Creus (NW Mediterranean) were declared a Site of Community Importance (SCI) within the Natura 2000 Network in 2014. Implementing an effective management plan to preserve its biological diversity and monitor its evolution through time requires a detailed characterization of its benthic ecosystem. Based on 60 underwater video transects performed between 2007 and 2013 (before the declaration of the SCI), we thoroughly describe the composition and structure of the main megabenthic communities dwelling from the shelf down to 400 m depth inside the submarine canyon. We then mapped the spatial distribution of the benthic communities using the Random Forest algorithm, which incorporated geomorphological and oceanographic layers as predictors, as well as the intensity of the bottom-trawling fishing fleet. Although the study area has historically been exposed to commercial fishing practices, it still holds a rich benthic ecosystem with over 165 different invertebrate (morpho)species of the megafauna identified in the video footage, which form up to 9 distinct megabenthic communities. The continental shelf is home to coral gardens of the sea fan *Eunicella cavolini*, sea pen and soft coral assemblages, dense beds of the crinoid *Leptometra phalangium*, diverse sponge grounds and massive aggregations of the brittle star *Ophiothrix fragilis*. The submarine canyon off Cap de Creus is characterized by a cold-water coral community dominated by the scleractinian coral *Madrepora oculata*, found in association with several invertebrate species including oysters, brachiopods and a variety of sponge species, as well as by a community dominated by cerianthids and sea urchins, mostly in sedimentary areas. The benthic communities identified in the area were then compared with habitats/biocenoses described in reference habitat classification systems that consider circalittoral and bathyal environments of the Mediterranean. The complex environmental setting characteristic of the marine area off Cap de Creus likely produces the optimal conditions for communities dominated by suspension- and filter-feeding species to develop. The uniqueness of this ecosystem and the anthropogenic pressures that it faces should prompt the development of effective management actions to ensure the long-term conservation of the benthic fauna representative of this marine area.

1. Introduction

The pressure exerted by human societies upon the world's oceans has increased significantly during the past decades and is expected to accelerate (Jouffray et al., 2020), having severe ecological consequences for the marine ecosystem. For many benthic habitats, human activities have led to biodiversity loss, depletion of key species, ecological changes in the structure of benthic communities and increased rates of species invasions, among other alterations to their normal functioning (Worm et al., 2006; Halpern et al., 2008). To overcome this situation, authorities worldwide have introduced maritime spatial planning actions and specific regulations to preserve marine biodiversity, where harmful activities such as waste disposal, commercial fishing or deep-sea mining are limited. In Europe, the first steps taken to protect the natural heritage at the scale of the continent consisted in the implementation of the Natura 2000 Network of protected areas (thereafter Natura 2000) following the Birds (EC, 1979) and Habitats Directives (EC, 1992). The Natura 2000 is a powerful tool designed to promote the maintenance of biodiversity in the European member states while considering economic, social, cultural and regional requirements (Evans, 2012). Although the initial efforts were mainly placed on terrestrial ecosystems, the number of Natura 2000 sites in the marine environment (Sites of Community Importance, Special Areas of Conservation and Special Protection Areas) has significantly increased in the past decades, and currently covers almost 9% of the European Union marine territory (Agnesi et al., 2020).

One of the recently declared Sites of Community Importance (SCI) in NW Mediterranean corresponds to the *South-West Gulf of Lions canyons system* (BOE, 2014), which includes the continental shelf and submarine canyon off Cap de Creus (NE Spain). This marine area is considered very complex in terms of geomorphology (Lo Iacono et al., 2012), water dynamics (Canals et al., 2006) and sediment transport (DeGeest et al., 2008), mostly due to the proximity of the submarine canyon to the shore. The funneling of large quantities of shelf waters through the canyon favors the export of suspended sediments and organic material from the shelf towards the deep (Palanques et al., 2006), promoting high rates of secondary productivity and hence the abundance of benthic species, especially suspension feeders (Gori et al., 2011; Orejas et al., 2009). The application of an ecosystem approach to efficiently manage this marine area must be based upon a thorough assessment of the different components that make up its benthic ecosystem, from the environmental characteristics to the biological communities, also considering the services they provide and the threats imposed by human activities (Curtin & Prellezo, 2010; Sardá et al., 2017). The first attempts to describe the composition and structure of the benthic communities found in the area date back to the 1970s, when Desbruyères et al. (1972) provided a detailed characterization of the macrofauna living on the continental shelf and Reyss (1971, 1972) defined the main species associations found inside the submarine canyon. Since then, the development of marine technology has allowed for more specific studies to evaluate the ecology of key benthic species, especially cold-water corals (CWCs) living in the submarine canyon (e.g. Orejas et al., 2009; Gori et al., 2013; Lo Iacono et al., 2018). However, a comprehensive analysis targeting the whole epibenthic diversity of the shelf and submarine canyon using non-intrusive techniques to update the work performed in the 70s was still lacking. The use of imaging technology (e.g. ROVs and manned submersibles) to generate *in-situ,* non-destructive, representative and potentially repeatable samples allows, not only for a thorough characterization of the benthic diversity, but could also to set the basis for a long-term monitoring program to assess the effects of the protection measures applied. The collection and analysis of underwater video images to characterize benthic communities in mesophotic and bathyal ecosystems in the Mediterranean has now become a common approach (e.g. De la Torriente et al., 2018; Enrichetti et al., 2019a; Grinyó et al., 2018). This methodology has already proven effective to identify long-term changes in the abundance of key or sensitive species in shallow-water MPAs worldwide (e.g. Sheehan et al., 2013; Haggarty et al., 2016), and could also be adopted to monitor shelf and deep-sea ecosystems if resources allow, especially with the increasing availability of cost-effective underwater video platforms (e.g. Phillips et al., 2019; Dominguez-Carrió et al., 2021a).

Besides the characterization of the biological diversity, a better understanding of the spatial distribution of the benthic fauna is critical to implement effective management measures, which would allow areas of conservation priority to be identified (Cogan et al., 2009; Gonzalez-Mirelis and Buhl-Mortensen, 2015). This is even more important if human activities (e.g. commercial bottom fishing, offshore wind farms) are to be made compatible with protection measures. Advances in mathematical modelling and the increased computational power available have significantly boosted our capacity to generate reliable maps displaying the spatial distribution of terrestrial and marine fauna (Guisan & Zimmermann, 2000; Brown et al., 2011). The use of modeling techniques (i.e. habitat suitability models, HSMs) that combine discrete information gathered from video images and the extent of different environmental parameters to predict the distribution of benthic species and assemblages is now common practice in shallow, but also deep-sea environments (e.g. Buhl-Mortensen et al., 2015a; Du Preez et al., 2016; Robert et al., 2016; De la Torriente et al., 2019). One of the standard approaches to model the spatial distribution of benthic communities corresponds to the 'assemble first, predict later' procedure (Ferrier & Guisan, 2006). First, biological data is classified into community-level entities using multivariate classification and/or ordination techniques and then their distribution is predicted based on modeled relationships with selected environmental parameters. Following this approach, we used the information collected in 60 underwater video-transects performed in Cap de Creus continental shelf and submarine canyon between 80 and 400 m depth prior to the implementation of the SCI (2007–2013) to (1) identify and characterize with as much detail as possible the composition and structure of the main megabenthic communities present in the area and (2) map their spatial distribution using HSMs. To predict the distribution of benthic communities, we used seafloor geomorphology (i.e. depth and terrain attributes derived from the multibeam bathymetry) and high-resolution oceanographic models (i.e. bottom current velocity) as environmental predictors together with an estimate of the bottom-trawling intensity, currently one of the main threats to the long-term conservation of the benthic fauna in the area.

2. Materials & methods

2.1. Study area

Cap de Creus shelf-canyon system is located in the southernmost part of the Gulf of Lions, in NW Mediterranean (Fig. 1). The continental margin of the gulf is incised by 12 submarine canyons that start at different distances from shore, with Cap de Creus being particularly close to land and producing a very marked narrowing of the shelf (Lastras et al., 2007). This particular geomorphological setting influences the general oceanographic circulation of the gulf (Millot, 1990), favoring the downwelling of cold shelf waters to the deep through the submarine canyon, particularly during winter and early spring (Canals et al., 2006). Downwelling events have a profound effect in bottom-current dynamics, leading to a marked supply of sediment and organic material from the shelf towards deeper areas of the canyon (Palanques et al., 2006; Ogston et al., 2008). Lo Iacono et al. (2012) provided a detailed description of the seabed geomorphology and substrate composition of the continental shelf and submarine canyon off Cap de Creus. The flat continental shelf (max. slope of 2.5°) displays a mixture of substrate types and bedforms that can be related to the bottom current regime of the area. Muddy and sandy bottoms are dominant, mainly from the inner shelf to depths of 90 m, where increasing amounts of coarser sediments and bioclastic gravels can be found, especially towards the shelf edge. Several areas of the shelf are characterized by a

dominance of rocky outcrops, particularly a belt parallel to the coastline north of the cape (90–100 m depth) and also on the deeper areas of the southern shelf (120–135 m depth). The flanks of the submarine canyon show contrasting seabed configurations, with the southern side characterized by steep rocky outcrops and overhanging walls and terraces, and the northern side with a generally smooth geomorphology, rounded gullies and scars, suggesting a higher depositional regime.

Cap de Creus peninsula was declared a maritime-terrestrial Natural Park in 1998 (Catalan Law 12/1985). Due to the high productivity of its waters and the diversity of the benthic habitats encountered along its coastline (e.g. Gori et al., 2011; Sardá et al., 2012), a shallow water peripheral belt along the cape was included inside the limits of the Natural Park, encompassing all littoral stages and the innermost part of the continental shelf (BOE, 1998). In 2014, the "South-West Gulf of Lions canyons system" was declared as a Site of Community Importance (SCI) of the Natura 2000 Network under the Habitats directive (BOE, 2014), encompassing a fully offshore surface area of 938 km^2.

2.2. Biological surveys

A total of 60 underwater video-transects were performed on the continental shelf and submarine canyon off Cap de Creus (Fig. 1) between 80 and 400 m depth, generating more than 47 hours of video footage and covering ~33 km of seafloor (Table 1). The images collected aimed to characterize the composition and structure of the megabenthic communities dwelling in the area with a high degree of detail. For this reason, dives were planned to cover as much area as possible while surveying all seabed substrates in each depth strata. Most dives were performed during 4 oceanographic cruises carried out between 2007 and 2012 on board of the R/V *García del Cid* (CSIC, Spain), and the remaining during two complementary surveys with smaller vessels. Underwater images were acquired using three different video platforms: (1) the ROV Nemo (Gavin Newman, freelance, UK), with a maximum operational depth of 300 m, equipped with an SD camera in 2009 (720 × 576 pixels) and an full HD camera in 2012 (1920x1080 pixels), an Easytrak USBL positioning system and a hydraulic grabber able to collect one sample per dive; (2) the JAGO submarine (GEOMAR,
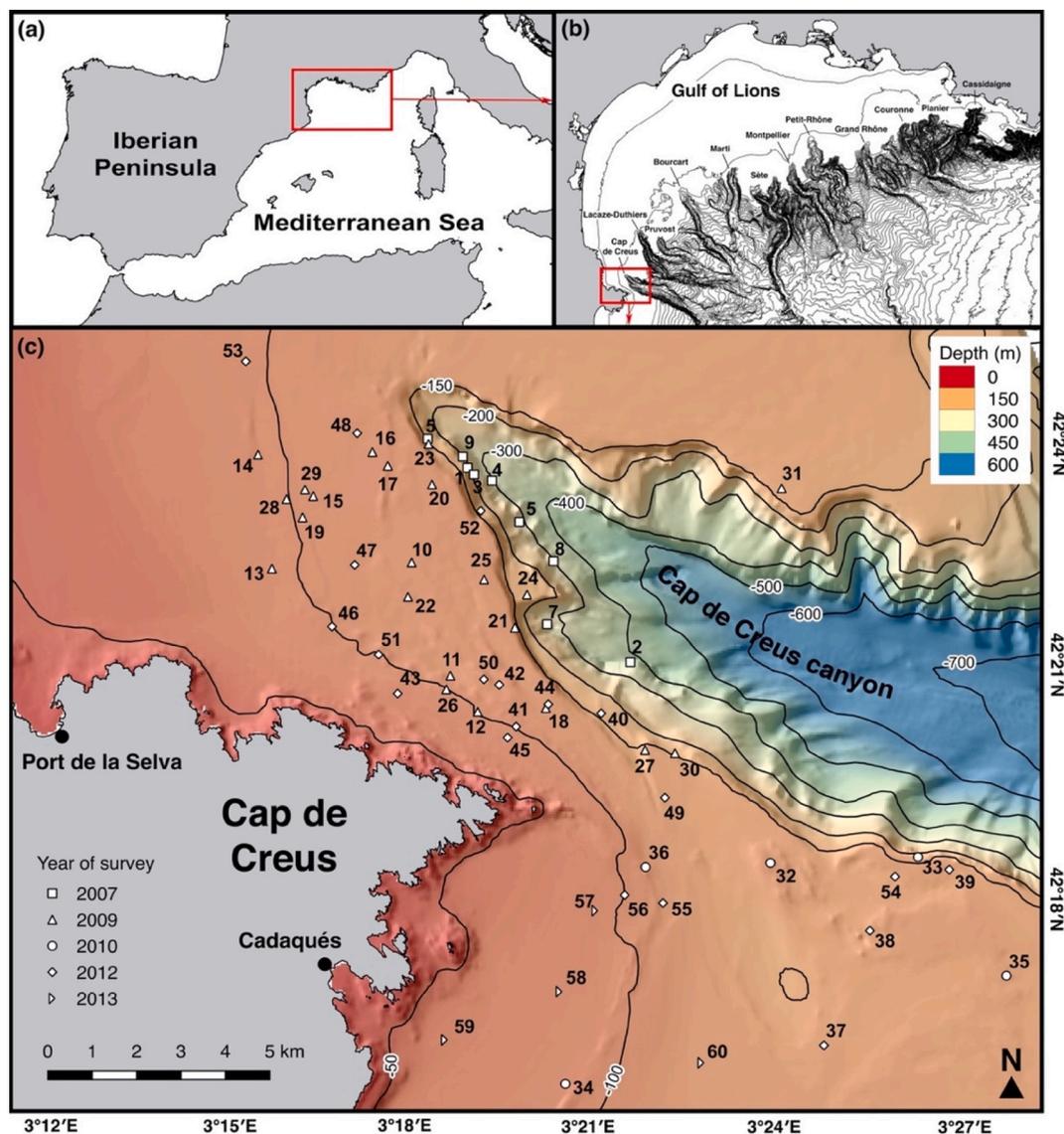
Fig. 1. (a-b) Location of Cap de Creus marine area in the southernmost part of the Gulf of Lions, NW Mediterranean. Names for the main submarine canyons that incise the continental shelf of the gulf are provided. (c) Map of the study area, which includes the continental shelf and submarine canyon off Cap de Creus. White symbols correspond to the mid-point of each of the 60 underwater dives analyzed for this study. Start-end geographical positions for each dive, as well as other associated metadata, can be found in Table 1. Depth isolines in meters.

Table 1
Metadata for the 60 underwater dives performed on the continental shelf and submarine canyon off Cap de Creus analyzed for this study. The location of the dives in the study area can be found in Fig. 1. Geographical positions, depths and dive lengths refer to the moment the underwater vehicle reached or left the seabed. Dive duration is given in hh:mm. Start-end latitudes and longitudes are given in decimal degrees in the World Geodetic System 1984 (WGS 84). SU: sampling unit.

Dive n°	Date (dd/mm/yy)	Vehicle	Start position Lon. E	Lat. N	End position Lon. E	Lat. N	Start-end depth (m)	Dive duration	Length (m)	n° SU
1	09/09/07	JAGO	3.314	42.390	3.314	42.390	215–186	00:29	83	6
2	09/09/07	JAGO	3.357	42.350	3.360	42.349	386–377	00:33	250	18
3	10/09/07	JAGO	3.316	42.387	3.314	42.389	199–173	01:39	675	50
4	12/09/07	JAGO	3.321	42.386	3.320	42.387	302–302	00:33	157	8
5	13/09/07	JAGO	3.329	42.378	3.329	42.380	316–302	01:27	386	23
6	13/09/07	JAGO	3.304	42.395	3.302	42.396	168–153	00:28	177	15
7	14/09/07	JAGO	3.334	42.357	3.334	42.356	234–236	01:41	597	41
8	15/09/07	JAGO	3.338	42.369	3.337	42.371	293–264	01:15	334	17
9	15/09/07	JAGO	3.315	42.393	3.313	42.390	282–165	01:40	544	44
10	25/08/09	Bleeper EVO	3.298	42.374	3.302	42.366	109–110	00:49	1027	56
11	26/08/09	Bleeper EVO	3.309	42.347	3.310	42.347	115–112	00:13	122	2
12	26/08/09	Bleeper EVO	3.313	42.342	3.318	42.337	98–95	01:18	718	33
13	26/08/09	Bleeper EVO	3.260	42.373	3.261	42.366	99–99	01:00	1347	46
14	27/08/09	Bleeper EVO	3.256	42.395	3.258	42.389	97–99	00:49	676	39
15	27/08/09	Bleeper EVO	3.271	42.386	3.272	42.382	102–103	00:45	476	28
16	27/08/09	Bleeper EVO	3.289	42.394	3.288	42.392	107–107	00:25	173	9
17	27/08/09	Bleeper EVO	3.293	42.391	3.297	42.389	106–107	00:20	438	26
18	27/08/09	Bleeper EVO	3.332	42.340	3.339	42.341	111–117	00:33	675	25
19	23/09/09	Nemo ROV	3.269	42.386	3.269	42.375	102–101	00:48	1463	77
20	23/09/09	Nemo ROV	3.306	42.388	3.303	42.384	111–111	00:29	504	30
21	23/09/09	Nemo ROV	3.327	42.358	3.327	42.355	151–118	00:32	436	21
22	24/09/09	Nemo ROV	3.299	42.364	3.297	42.362	111–108	00:45	291.5	17
23	26/09/09	Nemo ROV	3.304	42.394	3.303	42.394	148–142	00:23	83	4
24	27/09/09	Nemo ROV	3.333	42.363	3.328	42.363	166–160	01:00	475	22
25	27/09/09	Nemo ROV	3.322	42.367	3.315	42.365	121–115	00:58	625.4	37
26	27/09/09	Nemo ROV	3.309	42.347	3.307	42.342	111–94	00:57	587.1	32
27	28/09/09	Nemo ROV	3.364	42.332	3.361	42.331	130–148	00:18	321.1	13
28	28/09/09	Nemo ROV	3.267	42.382	3.259	42.384	100–99	01:08	533.5	26
29	28/09/09	Nemo ROV	3.272	42.385	3.268	42.385	102–101	00:44	405.9	24
30	29/09/09	Nemo ROV	3.371	42.331	3.370	42.331	160–150	00:18	91.3	2
31	29/09/09	Nemo ROV	3.400	42.385	3.400	42.385	137–137	00:19	90	5
32	13/06/10	JAGO	3.393	42.311	3.397	42.306	116–117	01:11	936.2	93
33	13/06/10	JAGO	3.434	42.310	3.439	42.309	132–128	01:05	636.3	55
34	14/06/10	JAGO	3.337	42.266	3.343	42.260	94–94	00:53	659.6	66
35	17/06/10	JAGO	3.460	42.289	3.463	42.282	127–125	01:33	1117.3	95
36	18/06/10	JAGO	3.363	42.307	3.364	42.308	108–114	01:25	892.64	85
37	06/07/12	Nemo ROV	3.409	42.270	3.412	42.273	126–126	00:29	505	30
38	06/07/12	Nemo ROV	3.424	42.293	3.423	42.296	127–126	00:44	348	20
39	06/07/12	Nemo ROV	3.444	42.310	3.449	42.305	147–129	01:17	760.3	43
40	07/07/12	Nemo ROV	3.450	42.304	3.347	42.337	128–125	01:17	830	49
41	07/07/12	Nemo ROV	3.329	42.336	3.326	42.336	99–96	00:30	347	20
42	07/07/12	Nemo ROV	3.323	42.343	3.322	42.347	108–109	00:28	432.5	21
43	07/07/12	Nemo ROV	3.296	42.343	3.294	42.343	90–88	00:14	178	10
44	07/07/12	Nemo ROV	3.336	42.340	3.336	42.342	115–116	00:11	178	10
45	08/07/12	Nemo ROV	3.325	42.337	3.327	42.331	98–91	00:39	784.7	44
46	08/07/12	Nemo ROV	3.277	42.361	3.277	42.353	103–97	00:39	865	51
47	08/07/12	Nemo ROV	3.286	42.371	3.280	42.369	109–105	00:29	574	34
48	09/07/12	Nemo ROV	3.286	42.398	3.281	42.397	108–104	00:32	583.1	30
49	09/07/12	Nemo ROV	3.368	42.325	3.366	42.319	127–123	01:08	872	52
50	09/07/12	Nemo ROV	3.321	42.351	3.316	42.343	107–102	00:50	949	56
51	09/07/12	Nemo ROV	3.290	42.352	3.289	42.350	96–98	00:29	284	17
52	09/07/12	Nemo ROV	3.324	42.377	3.312	42.384	210–115	01:42	1319	62
53	09/07/12	Nemo ROV	3.253	42.410	3.254	42.413	98–98	00:24	292	15
54	09/07/12	Nemo ROV	3.426	42.301	3.435	42.304	124–129	00:48	791	47
55	10/07/12	Nemo ROV	3.367	42.300	3.367	42.301	116–118	00:11	184.1	11
56	10/07/12	Nemo ROV	3.358	42.300	3.355	42.304	101–96	01:07	627	33
57	27/01/13	Bleeper EVO	3.345	42.298	3.353	42.299	90–96	00:29	639	38
58	06/06/13	Bleeper EVO	3.336	42.283	3.342	42.281	90–92	00:40	601	36
59	14/10/13	Bleeper EVO	3.308	42.267	3.308	42.276	83–79	00:30	704	19
60	04/12/13	Bleeper EVO	3.382	42.268	3.383	42.264	121–121	00:49	1235	53

Germany; Hissmann & Schauer, 2017), a two-person manned submersible with a maximum operational depth of 400 m, equipped with an HD camera (1440x1080 pixels), a LinkQuest Tracklink USBL positioning system and a hydraulic arm to collect multiple samples per dive and (3) the Bleeper EVO (ICM-CSIC, Spain), a small-sized ROV with a maximum operational depth of 150 m equipped with an SD camera (720 × 576 pixels) and no USBL positioning system (Gori et al., 2009). All three video platforms were equipped with parallel lasers that were used to scale the images recorded.

In order to identify the benthic invertebrate megafauna to the lowest possible taxonomic level from the video images, biological samples were also collected and examined by specialists. Live samples were collected from the same area surveyed by means of (1) a small epibenthic sledge, generally towed on soft-bottom areas of the continental shelf, and (2) the hydraulic arms of JAGO submarine and ROV Nemo, which allowed for a more selective collection of organisms in habitats not suited for epibenthic sleds or with a high ecological interest. All collected organisms were sorted, photographed and preserved prior to be taken to

specialists of different taxa for further identification. With all fauna identified to the lowest possible taxonomic level, the observations made from the video images were related to the species identifications. The photographic catalogue developed to assist in the annotation of the underwater images recorded for this study, which includes the invertebrate megafauna of the continental shelf and submarine canyon off Cap de Creus down to 400 m depth, can be found in Dominguez-Carrió et al. (2021b).

2.3. Video processing

The underwater video images recorded for this study were processed following the methodology described by Gori et al. (2011). To minimize errors in species identifications, the three video platforms moved close to the seabed at relatively low speeds (hardly ever exceeding 0.5 m·s^{-1}), producing an overall average speed of 0.21 ± 0.1 m·s^{-1}. The video footage was edited using the software Final Cut Pro 7 (Apple Inc.) to remove (1) initial sequences before the platform started to cruise at a constant speed over the seabed, (2) loops around the same location and (3) sequences where the platform stayed stationary over the seabed. Parts of the footage with low quality due to sediment re-suspension, excessive distance from the seabed and absence of laser beams were also identified, registered and excluded from all statistical analyses. Using the projection of the parallel laser beams over the seabed, all organisms larger than ~2–3 cm (excluding fish) that occurred within a fixed width of 30 cm (ROV) or 50 cm (manned submersible) along the path of the video transect were annotated by associating their occurrence to the time-code generated by the video-editing software. All organisms were identified to the lowest possible taxonomic level and manually annotated, with the exception of dense aggregations of *Ophiothrix fragilis*, which were recorded as an ordinal variable with five levels (Supplementary Fig. S1). Organisms that could not be identified to genus/species level due to lack of biological samples were classified as morphospecies and left at higher taxonomic levels (Order, Class, Phylum; see Dominguez-Carrió et al., 2021b).

The geo-referenced positions of the underwater vehicle were processed to eliminate outlier points, generating a smoothed path over the seabed. The use of a fixed field of view along the video transect allowed for species annotations to be converted into estimated density values along a string of sampling units (SU). Being aware that the size of the SU could influence the results of the community analyses, species accumulations curves (including average and maximum number of species per SU) were created for SUs of different sizes, from 1 to 10 m^2 (Supplementary Fig. S2). A 5-m^2 SU was selected for this study since (1) it contained approximately 2/3 of the average number of species found in large SUs, (2) the maximum number of species observed was not much lower than that of large SUs, (3) the variability observed in the average number of species was low, (4) the number of SUs with no fauna identified was relatively small and (5) the density values obtained were large

enough to support any statistical treatment. After removing sequences with bad visibility or excessive distance from the seafloor, a total of 1991 5-m^2 SU were suitable for statistical analyses, which represented an area explored of nearly 10,000 m^2.

2.4. Environmental data

Several environmental parameters were considered to explore the role that both natural and anthropogenic drivers may have on the composition, structure and distribution of the megabenthic communities identified in Cap de Creus continental shelf and submarine canyon. The environmental variables used in this study are listed in Table 2, and summarized as follows:

Geomorphology. Substrate type was directly evaluated from the video footage based on 5 different categories, specifically defined according to the nature of the seabed in the study area: (a) Muddy fine to medium sands, (b) Medium sands to fine gravel, (c) Coarse gravels to pebbles, (d) Suboutcropping and (e) Outcropping rock, including boulders and slabs. Further descriptions of all substrate categories together with selected images are provided in Supplementary Fig. S3. The bathymetric (multibeam, MB) data collected for the shelf sector was provided by the Spanish Fisheries General Secretary and acquired in the frame of the ESPACE Project. To cover the entire study area, additional MB data were acquired within the DeepCoral and Life+ INDEMARES projects. MB data for the submarine canyon were acquired by the University of Barcelona, AOA Geophysics and the Institute of Marine Sciences (ICM-CSIC). After combining the different MB datasets, a 10x10 m cell-size bathymetric raster image of the area was produced between 20 and 850 m depth (Fig. 2a). Slope was calculated for each cell using the slope tool in the Spatial Analyst extension of ArcGIS (ESRI software), which calculates the maximum amount of change between contiguous cells, providing a value in degrees (Fig. 2b). The Topographic Position Index (TPI) for each cell using a radius of 30 m and 100 m was calculated with the Jenness Enterprises DEM Surface Tools of the ArcGIS software (Fig. 2e,f). TPI displays the difference between the focal cell depth and the mean depth of the surrounding cells in order to obtain information about the presence of pronounced or depressed geological features in the terrain, such as crests, mounds, canyons or gullies (Wilson et al., 2007). The Terrain Ruggedness Index (TRI) for each cell using a radius of 30 m and 100 m was computed in SAGA GIS using the tools provided by the Terrain Analysis | Morphometry library (Fig. 2g,h). TRI is a quantitative measure of the topographic heterogeneity since it is calculated as the square root of the sum of squared differences in depth between the central cell and its neighbouring cells (Riley et al., 1999).

Oceanography. The bottom current model used in this study was based on the free surface, generalized sigma vertical coordinate, 3D hydrodynamic model SYMPHONIE described by Marsaleix et al., (2008) and Marsaleix et al., (2012), and used in the Mediterranean for studies of coastal (e.g. Ulses et al., 2008) and offshore (Estournel et al., 2016)

Table 2
Explanatory variables included in the multivariate analyses to characterize the habitat in which the megabenthic communities develop in the study area (marked with a *) and used as raster layers in the predictive modelling (marked with ‡). Further information on how substrate type was categorized is provided in Supplementary Fig. S3. TPI: Topographic position index; TRI: Terrain Ruggedness Index; FI: Fishing Intensity. Further information for each explanatory variable can be found in Section 2.4. The main environmental characteristics for each of the 60 underwater dives analyzed for this study are provided in Supplementary Table S1.

Variable	Source	Original resolution	Type of variable
Substrate type*	Video footage	n.a.	Categorical (5 levels, described in the text)
Depth*‡	Multibeam bathymetry	10x10 m	Numerical, continuous
Slope*‡	Multibeam bathymetry	10x10 m	Numerical, continuous
TPI (30 & 100 m radius)*‡	Multibeam bathymetry	10x10 m	Numerical, continuous
TRI (30 & 100 m radius)‡	Multibeam bathymetry	10x10 m	Numerical, continuous
Northness‡	Multibeam bathymetry	10x10 m	Numerical, continuous
Eastness‡	Multibeam bathymetry	10x10 m	Numerical, continuous
Bottom current, avg. speed*‡	SYMPHONIE model	235x315 m	Numerical, continuous
Bottom currents, st. dev.*‡	SYMPHONIE model	235x315 m	Numerical, continuous
FI, n° of pings per unit area*‡	Vessel Monitoring System	250x250 m	Numerical, continuous
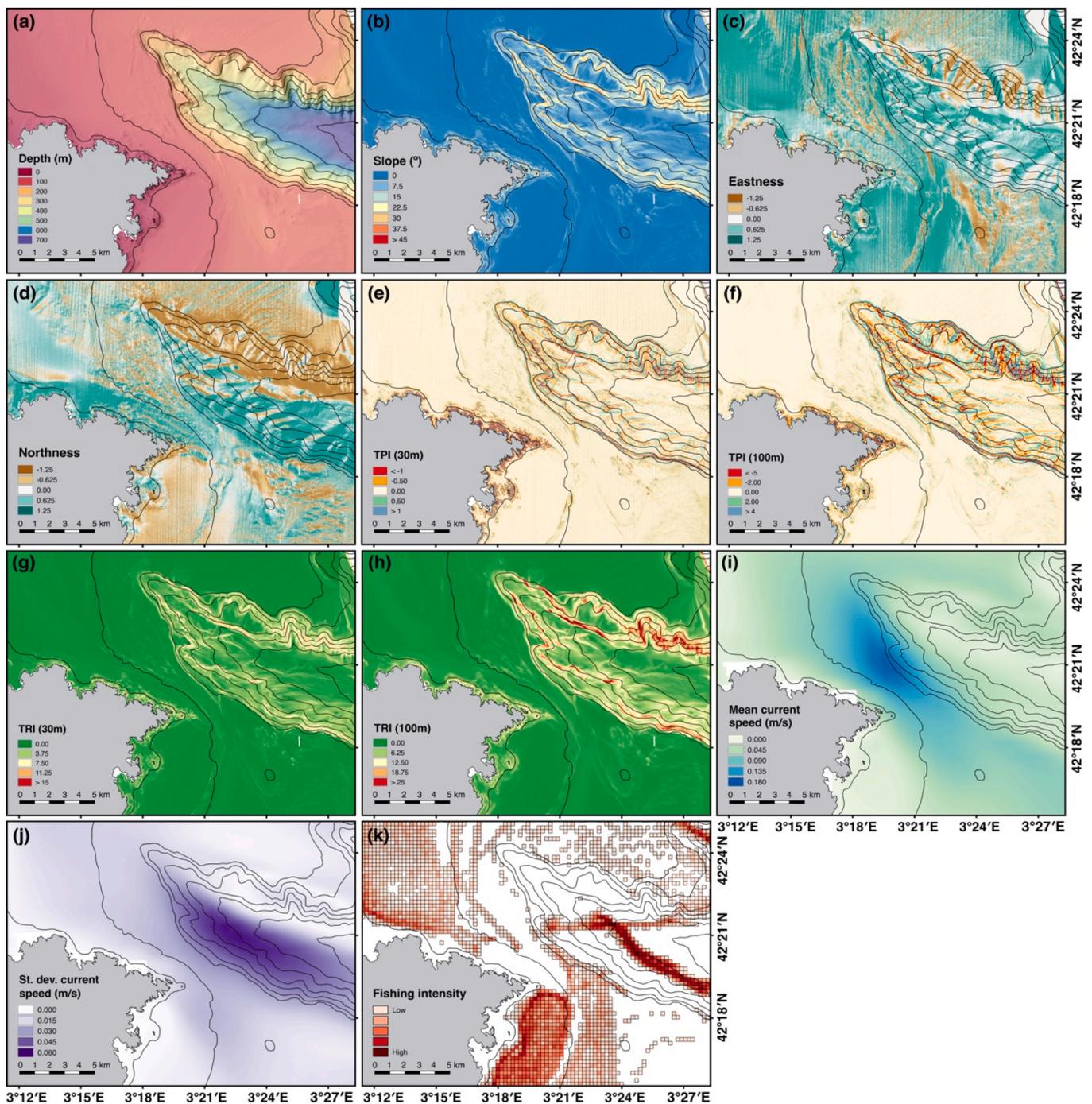
Fig. 2. Maps displaying the environmental raster layers included in the multivariate analyses and the predictive model. (a) Depth. (b) Slope, in degrees. (c) Eastness. (d) Northness. (e,f) Topographic Position Index (TPI) at 30 m and 100 m radius. (g,h) Terrain Ruggedness Index (TRI) at 30 m and 100 m radius. (i,j) Bottom current velocity averaged for the period 2000–2013, and standard deviation of monthly averages for the same period (values in m s^{-1}). Bottom current layers were upscaled from the original resolution by applying a bilinear interpolation. (k) Fishing intensity estimated from pings emitted by the bottom-trawling fleet during the period 2007–2012, calculated as a point summation method on a grid of 250x250 m based on "one fishing event per vessel and day per unit area". More information of how the raster layers were obtained is provided in Section 2.4.

processes. It classically solves the equations for temperature, salinity and the two components of horizontal current starting from initial conditions and using time-dependent forcing. The model was initialized and forced at its open boundaries by the NEMOMED8 model described in Herrmann et al., (2010). At the surface, the atmospheric forcing produced by the model ARPERA was used (Herrmann & Somot, 2008), which is a dynamic downscaling of the ERA40 climate model reanalysis (1976–2001) and the ECMWF (European Centre for Medium-Range Weather Forecasts) model reanalysis since 2001. This forcing consists

in daily averaged wind stress, solar flux, long wave net heat flux, sensible and latent heat flux and precipitation, leaving the diurnal cycle unresolved. The sea surface temperature is nudged toward the climatological one used in the NEMOMED8 model. This procedure is done to ensure consistency between the two models. The horizontal grid is curvilinear and covers a large part of the western Mediterranean. The grid pole was placed in the Pyrenees (2.02°E, 42.28°N) in order to optimize the resolution in the Cap de Creus region, with a pixel size of about ~300 m in the study area. The number of vertical levels was 40. In

the present application, a long run was performed, from January 2000 to December 2013. The application used the two components of the horizontal current at the first level above the bottom, which were extracted from the daily outputs of the model. As they are oriented along the axis of the model, they were first rotated to be along the WE and NS axis. The second step of the post-treatment was an interpolation on a regular grid to generate monthly averages for the years 2004 to 2008. From this large dataset, 2 maps were generated: the average current speed for the whole period (Fig. 2i) and the standard deviation of the monthly average current speeds (Fig. 2j). The oceanographic raster layers were resampled to a resolution of 10 m to match that of the bathymetric map by means of a bilinear interpolation process using the function *resample* of the *raster* package in the R environment.

Fishing intensity. Information about the commercial activity of bottom trawlers was obtained from the Vessel Monitoring System (VMS) provided by the General Directorate of Fisheries Management of the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA). The original raw dataset was subjected to a validation process to exclude errors in vessel identification, position and speed, as well as the removal of any duplicated positions. A second filtering selected those pings that corresponded to fishing activity inside the study area following a speed-rule approach (Lee et al., 2010). Pings with a vessel speed below 2 or above 3.5 knots were removed, as well as those points found less than 2 nautical miles from the neighbouring ports. The distribution and intensity of the fishing activity was then estimated considering only "one fishing event per vessel and day per unit area" and using a point summation method over a grid of squared cells, with data collected between January 2007 and July 2012. The size of the grid cell used was chosen after applying a minimum bounding rectangle (MBR) method (Chainey, 2013), which divides the shorter side of the study area's minimum bounding rectangle by 150, subsequently applying a fine-tuning process to match cell size to the needs of the study. After some trials, a 250x250 m cell grid provided the best fit (Fig. 2k), with the resulting raster layer resampled to a resolution of 10x10 m to match the resolution of the bathymetric map by means of a nearest neighbor interpolation process using the function *resample* of the *raster* package in R. All the processing of the VMS data was performed with geoprocessing techniques using the Marine Geospatial Ecology Tools library of the ArcGIS software.

2.5. Community analyses

After converting the annotations of the benthic fauna into a species-by-sites matrix of 5-m^2 sampling units (SUs), only sessile or low-mobility invertebrates were considered, removing all highly-mobile fauna such as cephalopods. All annotations belonging to the genus *Lanicides* (an extremely cryptic Terebellid Polychaete only identifiable when the video platform cruised very close to the seabed) were also removed from the analyses to avoid methodological biases (Supplementary Fig. S4). Two indices were used as proxies for alpha diversity (or intra-community diversity): species richness (S), understood as the number of megafauna species identified in any given SU, and the exponential of Shannon diversity index ($\exp[-\sum_{i=1}^{S} pi\ln(pi)]$), defined as the effective number of species since it displays a linear relationship with species richness when all species are equally common (Jost, 2007).

All SUs with no identifiable megafauna, those that were characterized by three types of substrate all of which below 50% coverage and those with massive aggregations of *O. fragilis* (densities above 20 ind·m^{-2}) were removed prior to classifying the SUs into discrete groups by means of hierarchical clustering. Density data were root-transformed, a common variance-stabilizing transformation for count-derived data. Then, Ward's minimum variance method was employed over a square root-transformed Bray-Curtis dissimilarity matrix using the *hclust* function in the *stats* package of the R software (R Core Team, 2016). The square root was selected because Bray-Curtis dissimilarity is non-metric, and the square root tends to euclidize distances, which is a desirable

property when using a clustering method based on Euclidean distances (Borcard et al., 2011). The same transformations and dissimilarity measures were used in all subsequent multivariate analyses (PERMANOVA, PCoA and dbRDA, see below). The optimal number of clusters (k) in which to split the dataset was chosen by selecting the highest overall average silhouette among all cluster solutions, where the silhouette provides an indication of how well samples lay within their clusters in comparison to their closest neighboring cluster (Rousseeuw, 1987). The average silhouette was calculated using the function *silhouette* in the *cluster* package (Maechler et al., 2017). A distance-based permutational multivariate analysis of variance (PERMANOVA) was employed to determine if the identified groups were significantly different from each other according to their species composition and density, and was calculated using the *adonis* function in the *vegan* package (Oksanen et al., 2016). The most representative species from each benthic community were identified using the indicator value index (IndVal), which gives higher values to those species that are found mostly in a single group and are also present in the majority of the samples belonging to that group (Dufrêne & Legendre, 1997). IndVal is calculated as the product of the relative frequency and relative average abundance in clusters, and its value is not affected by the abundance of other species (Legendre & Legendre, 2012). The 10 most representative species of each group were identified using the function *indval* in the *labdsv* package (Roberts, 2016).

All SUs were plotted on a bidimensional space by means of a Principal Coordinates Analysis (PCoA), which was computed over the Bray-Curtis dissimilarity matrix using the function *cmdscale* of the R package *stats*. A distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999) was then used as a constrained ordination method to estimate and visualize a model relating the response data (species information) with the explanatory variables (environmental features). After identifying those raster layers that showed a high degree of collinearity (Pearson greater than 0.8), the environmental variables selected to build the dbRDA were: substrate type (as a percentage in each sampling unit), depth, slope, TPI at 30 m and 100 m radius, bottom current velocity (average and standard deviation) and fishing intensity (Table 2). The variables depth, slope and fishing intensity were forth-root transformed before computing the dbRDA, which was calculated over the Bray-Curtis dissimilarity matrix applying the function *capscale* of the *vegan* package (Oksanen et al., 2016).

The groups derived from the cluster analyses were compared with existing biotopes/habitats described and included in reference lists that encompass the Mediterranean region: (1) the EUNIS Habitat classification system (European Union Nature Information System, https://eunis.eea.europa.eu/habitats.jsp), (2) the Updated Classification of Benthic Marine Habitat Types for the Mediterranean Region proposed by RAC/SPA as a tool to implement the agreements reached in the Barcelona Convention and its SPA/BD Protocol (SPA/RAC–UN Environment/MAP, 2019; Montefalcone et al., 2021) and (3) the reference list included in the Spanish inventory of Habitats and Marine Species (Inventario Español de Hábitats y Especies Marinos - IEHEM; Templado et al., 2013). Furthermore, each community identified was also assessed in order to consider its equivalence with (1) any of the habitat types listed in Annex I of the Habitats Directive (EC, 2013) and (2) any of the habitats potentially supporting VMEs in the Mediterranean defined by the Working Group on Vulnerable Marine Ecosystems (WGVME) of the General Fisheries Commission for the Mediterranean (GFCM, 2018).

2.6. Predictive mapping

The spatial distribution of the main benthic communities identified in the images was modeled using the Random Forest classification algorithm (RF; Breiman, 2001), a robust modelling algorithm when the response variable is of a categorical nature (Franklin, 2010). RF is a modelling approach commonly used to predict the distribution of shelf and deep-sea benthic communities or biotopes (e.g. Du Preez et al.,

2016; Cooper et al., 2019; Dolan et al., 2021; Goode et al., 2021; O'Brien et al., 2022), which has shown to perform as well as other predictive modelling techniques for benthic habitat mapping (Hasan et al., 2012; Robert et al., 2016). Random Forest builds a large number of trees using subsets of the data and the environmental variables, with each tree making a prediction and the final assignation being based on the majority (Breiman, 2001). Since RF is robust to larger number of predictor variables, the environmental layers used to build the model included water depth, slope, eastness, northness, TPI and TRI at 30 and 100 m radius, bottom current speed (average and standard deviation) and fishing intensity (Table 2, Fig. 2). The samples corresponding to the brittle star aggregation were not included in the predictive model due to its restricted distribution on the shelf and the mobility of its characteristic species, which would make predictions rather inaccurate. With the remaining samples, a total of 1500 trees were built in the model run with 8 variables randomly selected at each node. The model was constructed using 70% of the samples randomly selected and model accuracy and classification errors were assessed using the remaining 30% of the samples through a confusion matrix and kappa statistic. Variable importance based on the mean decrease in accuracy of the model and the mean decrease in Gini index were also computed. Full coverage maps were then created by predicting the response variable for each pixel of the bathymetry at a resolution of 10x10 m and limiting the output of the prediction to the depth range investigated (80–400 m). RF was run using the functions included in the *randomForest* package of the R software platform (Liaw & Wiener, 2002).

3. Results

3.1. Diversity of megabenthic fauna

Most of the areas surveyed belonged to the continental shelf (greater than 70 m) and were characterized by soft bottoms, ranging from muddy fine sands to fine gravels (66%). Areas with coarser particles (including coarse gravels and pebbles) represented ~20% of the area investigated, and rocky substrates accounted for around 14%. Over 100,000 organisms from 167 morphospecies were annotated from the video footage. Most taxa were assigned to species (55%) or genus (12%) level, with 27% of the species classified in higher taxonomic levels. The complete list of all morphospecies identified in Cap de Creus continental shelf and submarine canyon, organized by phylum and with information regarding their observed depth range and estimated density in the study area, is provided in Supplementary Table S2. Images for each morphospecies can be found in Dominguez-Carrió et al. (2021b).

Porifera. This was the most diverse phylum, with 55 morphospecies reported (33% of the total). Due to the limited number of samples collected from the submarine canyon, around 40% of the morphospecies were classified in high taxonomic levels. Porifera were very diverse on outcropping and suboutcropping rocks of the outer continental shelf, particularly on the southern sector, where a large variety of erect and encrusting sponges was reported. Some species were observed generating high-density patches that extended over several meters, including *Haliclona* cf. *elegans* (max. dens.: 14 ind·m²), *Stelligera stuposa* (7.4 ind·m²) and *Dysidea* spp. (5.2 ind·m²). Also relevant were the less frequent (but large in size) *Poecillastra compressa*, *Axinella polypoides* and *Desmacidon fruticosum*, generally in densities of 1–1.2 ind·m². Areas of the northern shelf, at around 100 m depth, hosted aggregations of the repent sponge *Suberites syringella* (14.4 ind·m⁻²). Inside the submarine canyon, large rocky outcrops were mostly dominated by a wide variety of encrusting sponges, most of which have not yet been identified to species level due to the lack of samples. The largest sponge reported in the canyon was the laminar-shaped *Pachastrella monilifera,* which reached densities of 0.6 ind·m⁻².

Cnidaria. A total of 40 morphospecies were assigned to the phylum Cnidaria. *Lytocarpia myriophyllum* was the only large hydroid observed, with colonies of impressive sizes generating small and very localized

patches on the shelf (~4 col·m⁻²). Anthozoa was a diverse and widely distributed group, with representatives in all areas explored. Pennatulaceans were common on the soft bottoms of the shelf, with up to 6 different species reported: *Pteroeides spinosum, Pennatula rubra, Cavernularia pusilla, Virgularia mirabilis, Veretillum cynomorium* and *Funiculina quadrangularis. Pteroeides spinosum* was the most widespread and abundant sea pen (3,861 records, 43% of SUs), reaching densities of 6.6 col·m⁻². The soft coral *Alcyonium palma*tum was also commonly observed on the shelf (3,905 records, 43% of SUs), with densities of up to 9 col·m⁻². The only gorgonian coral observed forming dense aggregations was the orange sea fan *Eunicella cavolini* (4,979 records, 19% of SUs)*,* mostly reported on the northern shelf (~100 m depth), with densities up to 25 col·m⁻². In deeper areas of the shelf and upper slope, where the substrate is composed by a mixture of coarse bioclastic gravels and sands, two cerianthid species were common: cf. *Cerianthus membranaceus,* which displayed a wider distribution but relatively low densities (1.8 ind·m⁻²), and *Arachnanthus oligopodus*, with a more restricted distribution but attaining densities above 20 ind·m⁻². Inside the submarine canyon, several scleractinian CWC species were observed, including *Madrepora oculata, Lophelia pertusa* (recently proposed to be transferred to the genus *Desmophyllum* as *D. pertusum*, see Addamo et al., 2016), *Dendrophyllia cornigera, Caryophyllia smithii* and *Desmophyllum dianthus*. Among all CWCs, *M. oculata* was by far the dominant species (291 records, 3% of SUs), with patches of more than 8 col·m⁻² and a total biomass larger than any other coral observed inside the submarine canyon.

Bryozoa. Ten morphospecies of Bryozoa were identified in the video images, all of them of a small size. The most abundant was the cheilostomate *Smittina cervicornis* (873 records, 12% of SUs), commonly observed on the mixed bottoms of the shelf (~100 m depth), where it reached densities of more than 4 col·m⁻². All remaining species had less than 100 records each for the whole area surveyed.

Annelida. Twelve morphospecies of polychaetes were identified in the video images. The most abundant was the widely distributed *Lanice conchilega* (5,908 records, 16% of SUs), found in shelf and shelf break areas with sands and small gravels. It was observed forming patches with densities of 10–20 ind·m⁻² along several hundreds of meters, reaching more than 25 ind·m⁻² in several locations. In areas characterized by the presence of coarser sediments and rocky outcrops, both in the deeper sector of the shelf and inside the submarine canyon, the serpulid *Protula tubularia* became very common (3,770 records, 33% of SUs), with maximum densities of almost 15 ind·m⁻². Less common was the sabellid *Sabella pavonina* (884 records, 16% of SUs), but observed both in the shelf and in the submarine canyon. It was generally reported as a solitary species on the soft bottoms of the continental shelf, but several high-density patches inside the submarine canyon were reported, some of which found on top of lost or abandoned fishing lines.

Mollusca. Ten morphospecies of mollusks were identified in the video images, most of them not yet identified to species level. The most abundant was the oyster *Neopycnodonte* cf. *zibrowii* (699 records, 3% of SUs), which appeared mostly on rocky outcrops and overhangs inside the submarine canyon, at depths of up to 300 m. Maximum recorded densities reached more than 9 ind·m⁻².

Brachiopoda. Although it is likely that the brachiopods observed belonged to the species *Gryphus vitreus* and/or *Terebratulina retusa,* the images recorded did not allow for conclusive identifications in all cases, and hence all records were left as "Unidentified Brachiopoda" (3,455 records, 8.5% of SUs). The presence of brachiopods was significant in rocky outcrops of the submarine canyon, at depths between 130 and 400 m depth. In those areas, maximum registered densities reached values of 45 ind·m⁻².

Arthropoda. At least twelve morphospecies of crustaceans were observed in the video images, most of them decapods. Due to difficulties in the determination of several individuals to species level because of the angle of the camera, hiding behavior or distance to the seabed, the species of the genus *Munida* (*M. intermedia* and *M. rugosa*) were grouped

as *Munida* spp. (632 records, 8% of SUs), and all hermit crabs (e.g. *Dardanus arrossor*, *Pagurus prideauxi*) were left as "Unidentified Hermit crab" (531 records, 16% of SUs). Although most galatheids were generally observed as solitary individuals hiding behind rocks or boulders, some areas hosted aggregations of *Munida* spp. of up to 4 ind·m^{-2}. Hermit crabs, on the contrary, were mostly observed on the soft sediments of the continental shelf.

Echinodermata. Up to 17 morphospecies of echinoderms were identified in the video images. Due to the large aggregations of the brittle star *Ophiothrix fragilis,* which accounted for more than 45% of the total number of records, almost one every two organisms identified in the video footage were echinoderms. The massive aggregations of *O. fragilis* (estimated densities above 600 ind·m^2; Supplementary Fig. S1) were only observed in one location on the continental shelf (105–110 m depth) just 3–4 km east of the cape (Dive 36). On the shelf, the crinoid *Leptometra phalangium* (3,155 records, 7.6% of SUs) was observed forming dense aggregations of more than 20 ind·m^{-2}, both on the northern and southern sectors. Several species of echinoderms were also observed on the shelf as solitary individuals or in low densities, such as sea stars (e.g. *Anseropoda placenta*, *Luidia ciliaris*), sea urchins (e.g. *Echinus acutus*, *Spatangus purpureus*) and sea cucumbers (e.g. *Holothuria* spp., *Cucumaria* sp., *Parastichopus regalis*). On the shelf break, where substrates were coarser and with a large bioclastic proportion, the cidarid cf. *Cidaris cidaris* (118 records, 4% of SUs) was frequent, generally appearing scattered along the seabed. Inside the submarine canyon, the sea urchins *E. melo* and *E. acutus* were often observed, the latter found forming aggregations of up to 3.6 ind·m^{-2} on top of rocky outcrops and cliff overhangs (287 records, 7% of SUs).

Tunicata. A total of 16 morphospecies of tunicates were identified in the video images. Due to their size and lack of samples, almost 65% of the species had to be left in high taxonomic levels. The most abundant species was *Distomus variolosus* (213 records, 3% of SUs), generally observed growing on top of other organisms, such as the sea fan *E. cavolini*. The largest tunicate reported was a member of the Pyuridae/Styelidae family (80 records, 3% of SUs), always found as a solitary organism on the soft bottoms of the continental shelf.

3.2. Description of megabenthic communities

Considering the very dense aggregations of the brittle star *O. fragilis*

an independent assemblage (and hence not included in the community analysis), the optimal number of clusters into which split the data, based on the average silhouette criterion, was eight (Fig. 3a). The PERMANOVA test indicated significant differences among groups regarding their species composition and density (Supplementary Table S3), with all pair-wise differences between groups highly significant (p-perm < 0.001, post-hoc tests not shown). Clusters A and B were the most frequently observed in the video footage, present in 353 and 484 SUs, respectively. Conversely, clusters C and D were the least represented of all, with only 86 and 68 SU (Fig. 3b). The most characteristic species of each community, as identified by their Indicator Value index (IndVal greater than 0.1), are given in Table 3, together with average and maximum density values in their respective communities. Selected images that illustrate each of the megabenthic communities identified in Cap de Creus continental shelf and submarine canyon are provided in Fig. 4, and a short clip with video images recorded in each community is provided as Supplementary Video. Additionally, Supplementary Table S2 contains information regarding the average and maximum density recorded for each species within each community, as well as their depth range and prevalence in the study area.

The ordination of the SUs in a reduced space based on their species composition and density through a PCoA is given in Fig. 5. Groups A, B and E were clearly separated from each other, whilst groups C and D on one side, and F, G and H on the other, appeared to have some degree of overlap in the space defined by the first two principal coordinates. Groups C and D both appeared on the continental shelf, while F, G and H were typical from areas of the shelf edge and the submarine canyon. Dimensions 3 and 4 of the PCoA revealed that differences between these groups were larger than the first 2 principal coordinates suggested.

The following paragraphs contain a brief description of each benthic community based on their species composition, diversity and structure, the characteristics of their habitat as defined by the main environmental variables and their equivalence with the different habitat classification systems that consider the Mediterranean Sea.

(A) Mixed substrates of the continental shelf with *Eunicella cavolini*. Observed in 33% of the dives (353 SUs). A total of 126 invertebrate taxa were identified within this community, most of them Porifera or Cnidaria, but with representatives of all phyla (Fig. 6a). Most organisms were cnidarians (60%) and sponges (20%) (Fig. 6b), with the gorgonian *E. cavolini* as the most characteristic species (max. dens.: 25
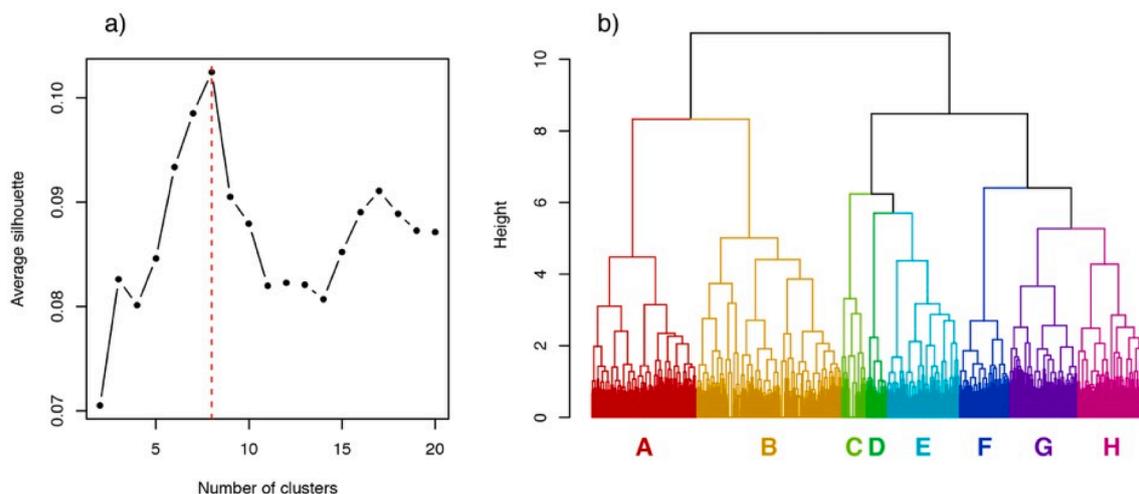
Fig. 3. (a) Overall average silhouette for each cluster solution. The optimal number of clusters in which the dataset can be split was 8, indicated by a red dashed line. (b) Ward's hierarchical dendrogram constructed using Bray-Curtis dissimilarities from square-root transformed density data. Clusters are indicated by the letters A to H. A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans. C: Shelf muds and sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*.

Table 3

List of indicator species for each benthic community determined by the Indicator Value (only IndVal values greater than 0.1 are shown, maximum of 10 species per community), with data on average and highest recorded density per sampling unit of 5 m². Com. = Community. A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans. C: Shelf muds and fine sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*.

Com.	Indicator species	IndVal	Density (ind·m⁻²) Avg. ± sd.	Max.
A	*Eunicella cavolini*	0.67	2.64 ± 3.93	25.6
	Smittina cervicornis	0.60	0.49 ± 0.65	4.2
	Suberites syringella	0.57	1.16 ± 2.03	14.4
	Epizoanthus sp.1	0.41	0.63 ± 1.15	8.0
	Alcyonium palmatum	0.34	1.25 ± 1.41	9.0
	Unidentified Polyclinidae sp.1	0.26	0.22 ± 0.60	6.8
	Alcyonium coralloides	0.25	0.18 ± 0.49	3.2
	Paralcyonium spinulosum	0.23	0.33 ± 0.74	6.4
	Pteroeides spinosum	0.19	0.81 ± 1.04	6.0
	Distomus variolosus	0.16	0.12 ± 0.39	3.2
B	*Pteroeides spinosum*	0.27	0.82 ± 0.99	6.6
	Cavernularia pusilla	0.20	0.25 ± 0.56	4.2
	Pennatula rubra	0.19	0.18 ± 0.30	2.0
	Alcyonium palmatum	0.17	0.53 ± 0.75	4.6
C	*Sabella pavonina*	0.35	0.33 ± 0.32	1.8
	Andresia partenopea	0.23	0.08 ± 0.16	0.8
D	*Leptometra phalangium*	0.88	6.81 ± 5.17	21.4
	Pteroeides spinosum	0.13	0.29 ± 0.30	1.4
	Pennatula rubra	0.17	0.10 ± 0.15	0.6
	Unidentified Decapoda sp.1	0.10	0.04 ± 0.11	0.6
E	*Lanice conchilega*	0.77	4.50 ± 4.73	28.2
	Arachnanthus oligopodus	0.31	1.26 ± 3.02	26.6
	Unidentified Sabellidae sp.2	0.11	0.05 ± 0.13	0.8
F	Unidentified Brachiopoda spp.	0.89	3.68 ± 5.37	48.0
	Galatheoidea spp.	0.72	0.64 ± 0.70	4.2
	Caryophyllia smithii	0.47	1.03 ± 1.51	11.4
	Unidentified encrusting Porifera sp.2	0.44	0.23 ± 0.38	2.8
	Unidentified encrusting Porifera sp.10	0.43	0.26 ± 0.44	2.2
	Protula tubularia	0.36	1.88 ± 2.31	14.8
	Madrepora oculata	0.36	0.31 ± 0.88	8.6
	Unidentified encrusting Porifera sp.4	0.34	0.32 ± 0.66	6.6
	Unidentified encrusting Porifera sp.6	0.32	0.13 ± 0.26	1.8
	Unidentified Polychaete sp.1	0.26	0.13 ± 0.35	3.6
G	*Dysidea* spp.	0.40	0.62 ± 0.88	4.4
	Haliclona cf. *elegans*	0.26	0.46 ± 1.40	14.0
	Hyrtios collectrix	0.24	0.14 ± 0.37	3.6
	Axinella damicornis	0.23	0.11 ± 0.25	2.0
	Stelligera stuposa	0.22	0.26 ± 0.68	7.4
	Iophon sp.1	0.22	0.16 ± 0.49	5.4
	Myxicola infundibulum	0.19	0.11 ± 0.17	1.0
	Poecillastra compressa	0.18	0.05 ± 0.13	1.0
	Salmacina dysteri	0.16	0.25 ± 0.67	7.2
	Haliclona sp.1	0.16	0.09 ± 0.21	1.2
H	*Protula tubularia*	0.23	0.91 ± 1.06	5.0
	Capnea sanguinea	0.21	0.16 ± 0.26	1.4
	cf. *Cerianthus membranaceus*	0.18	0.20 ± 0.32	1.6
	Unidentified Hermit crab	0.11	0.12 ± 0.19	1.0
	Mesacmaea mitchellii	0.11	0.19 ± 0.29	1.6

col·m⁻²), followed by the bryozoan *Smittina cervicornis* (max. dens.: 4.2 ind·m⁻²) and the yellow repent sponge *Suberites syringella* (max. dens.: 14 ind·m⁻²) (Table 3, Fig. 4a). This community had an average number of species per SU of 10 ± 5.1, with maximum values above 30, registering some of the highest values of exponential of Shannon diversity (Fig. 6c). Most SUs were observed on flat surfaces of the continental shelf, particularly on the northern side of the cape, at depths of 90–110 m (Fig. 7). Samples were found in a mixture of substrates, with sands, gravels, pebbles and outcropping rocks, mostly in areas of high bottom current speeds and low fishing activity. Based on its main indicator species, this community relates to the 'Circalittoral rock dominated by invertebrates with *Eunicella cavolini*' of the IEHEM list and the 'Offshore

circalittoral rock invertebrate-dominated covered by sediments | Facies with Alcyonacea (e.g. *Eunicella* spp)' of the Barcelona Convention (Table 4). There is currently no direct equivalent in the EUNIS Habitat classification system, where the closest biocenosis includes a wide range of littoral and shelf species ('Mediterranean offshore circalittoral rock'). This community could be considered part of the Habitat 1170 (Reefs) of the EU Habitats directive due to its substrate composition supporting a particular zonation over the continental shelf, which generates a sharp change in species composition, abundance and diversity compared to its surrounding areas. This community can also be considered an habitat potentially supporting VMEs in the Mediterranean, belonging to the category "Hard and soft-bottom coral gardens" as defined by the WGVME of the General Fisheries Commission for the Mediterranean.

(B) Shelf muds and sands with pennatulaceans and alcyonaceans. Observed in 42% of the dives (484 SUs). A total of 65 taxa were identified within this community, and although most phyla were represented (Fig. 6a), a large percentage of the organisms (93%) belonged to Cnidaria (Fig. 6b). *Pteroeides spinosum* was the most characteristic species, not only due to its size but because of its occurrence, present in 84% of the SUs. This pennatulacean achieved an average density of 0.82 ± 1 col·m⁻², with density peaks of 6.6 col·m⁻² (Table 3). Other characteristic species were the sea pens *Cavernularia pusilla* and *Pennatula rubra,* and the soft coral *Alcyonium palmatum* (Table 3; Fig. 4b), the latter found in densities of up to 9 col·m⁻². The average number of species per SU was 3.5 ± 1.7, with exponential of Shannon diversity values ranging between 2 and 4 (Fig. 6c). This community was mainly observed on subhorizontal and smooth areas of the continental shelf (90–130 m depth) dominated by soft substrates, primarily composed by sands and small gravels, and in some cases finer sediments, such as muds and fine sands (Fig. 7). Those areas displayed low average current velocities and had limited fishing activity. This community can be considered equivalent to the 'Facies with Pennatulacea' of the circalittoral bottoms included in the Barcelona Convention and EUNIS Habitat classification system, and can also be linked to several habitats of the IEHEM list, such as the 'Infralittoral and circalittoral detritic bottoms dominated by invertebrates with Pennatulacea (*Pennatula*, *Pteroides*, *Virgularia*)' (Table 4). Sea pen fields are currently considered species of conservation importance in the Atlantic Ocean by the OSPAR Convention, and are recognized as VME indicator habitats by the WGVME of the General Fisheries Commission for the Mediterranean.

(C) Shelf muds and fine sands with *Sabella pavonina*. One of the least observed communities (85 SUs). Only 24 taxa were identified in this community, with representatives of 5 phyla (Fig. 6a). More than 90% of the organisms belonged to Annelida (49%) and Cnidaria (45%), the remaining being mostly echinoderms (Fig. 6b). This community was primarily characterized by the Sabellid polychaete *S. pavonina* (Fig. 3c) and the anemone *Andresia parthenopea*, with average densities of 0.3 ± 0.3 and 0.08 ± 0.16 ind·m⁻² respectively (Table 3). The average number of species per SU was 2.2 ± 1.5, registering some of the lowest exponential of Shannon diversity values (Fig. 6c). Most samples were observed in flat areas of the shelf, at depths of 80–110 m, generally on muddy/sandy bottoms frequented by the bottom trawling fleet (Fig. 7). This community bears some resemblance with the 'Infralittoral and circalittoral detritic bottoms dominated by invertebrates with sabellid polychaetes' of the IEHEM list, although the latter likely refers to better structured and preserved habitats dominated by large numbers of sabellid polychates.

(D) Coarse sands of the shelf with *Leptometra phalangium*. Observed in 7% of the dives (68 SUs). A total of 51 species were identified, with representatives of 7 phyla (Fig. 6a). Most organisms were echinoderms (85%) due to the dominance of the sea lily *L. phalangium* (IndVal: 0.885, Table 3), with densities of up to 20 ind·m⁻² in patches extending for some hundreds of meters in length (Fig. 4d). The remaining organisms were mainly Cnidaria (Fig. 6b), such as the sea pens *P. spinosum* and *P. rubra* and the soft coral *A. palmatum* (Table 3). Also relevant was the presence of the polychaete *Lanice conchilega*,
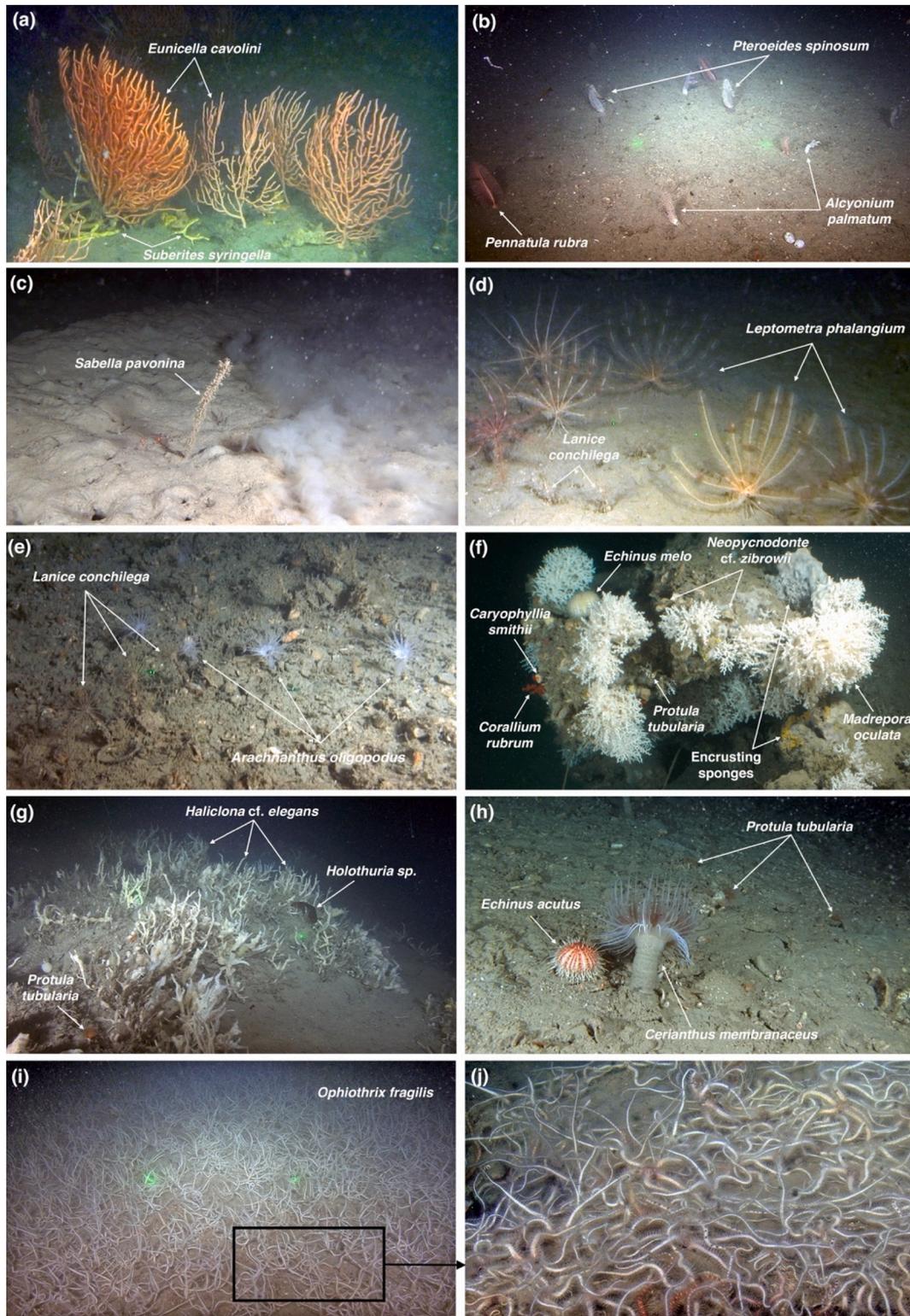
Fig. 4. Selected images showing the aspect of the megabenthic communities identified from the video footage recorded on the continental shelf and submarine canyon off Cap de Creus. Names of the most important species are given. A short clip with selected images recorded in each of the benthic communities identified is provided as Supplementary Video. Benthic communities: (a) Mixed substrates of the continental shelf with *Eunicella cavolini*. (b) Shelf muds and sands with pennatulaceans and alcyonaceans. (c) Shelf muds and sands with *Sabella pavonina*. (d) Coarse sands of the shelf with *Leptometra phalangium*. (e) Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. (f) Cold-water coral community with *Madrepora oculata*. (g) Sponges community in mixed substrates of the outer continental shelf. (h) Bathyal sands and gravels with cf. *Cerianthus membranaceus*. (i-j) Massive aggregation of the brittle star *Ophiothrix fragilis*. Image credits: (a,c,d,e) Nemo ROV, Gavin Newman / ICM-CSIC; (b,f,g,h,i,j) JAGO Team, GEOMAR, Kiel / ICM-CSIC.
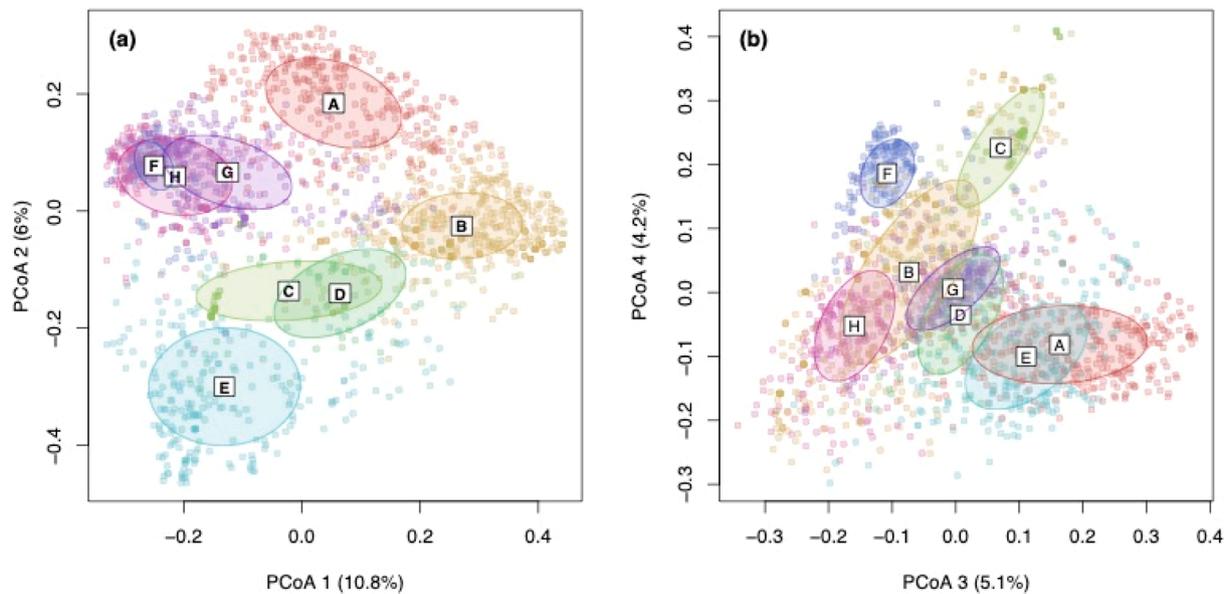
Fig. 5. Plot of axes 1–2 (a) and axes 3–4 (b) of the Principal Coordinates Analysis (PCoA) performed on the Bray-Curtis dissimilarity matrix after square-root data transformation. Ellipses represent standard deviations around each group centroid. Benthic communities: A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans and alcyonaceans. C: Shelf muds and fine sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*.

always in low densities. The average number of species per SU was 4.6 ± 1.4, with values of exponential of Shannon diversity generally low (Fig. 6c). This community was mainly found on flat areas of the continental shelf characterized by sands and a small proportion of gravels, mostly associated with low fishing intensities (Fig. 7). This community can be considered a specific facies of the offshore circalittoral bottoms included in the Barcelona Convention and the EUNIS habitat classification system, and also in the IEHEM list as part of the bathyal bottoms of the shelf and shelf edge (Table 4). Aggregations of *L. phalangium* have also been recognized as VME indicator habitats by the WGVME of the General Fisheries Commission for the Mediterranean.

(E) Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. Present in 25% of the dives (243 SUs). The total number of species identified was 30, belonging to 7 different phyla (Fig. 6a). Around 65% of the organisms were Polychaetes, 34% Cnidaria and 9% Echinodermata (Fig. 6b). This community was characterized by the presence of the polychaete *L. conchilega* (av. dens.: 4.5 ± 4.7 ind·m^{-2}) and the cerianthid *A. oligopodus* (av. dens.: 1.3 ± 3 ind·m^{-2}), both species with maximum local densities above 25 ind·m^{-2} (Table 3). The remaining species corresponded to small burrowing polychaetes and anthozoans, some of which have not yet been identified to species level due to lack of samples (Table 3). The average number of species per SU was 4.6 ± 2.3, with exponential of Shannon diversity values ranging between 2 and 3 (Fig. 6c). This community was primarily found in areas of the continental shelf and shelf edge, especially in front of the cape, where the hydrodynamic models displayed high temporal variability, indicating the likelihood of episodes of elevated bottom current intensities. This situation explains the large fraction of cobbles and pebbles observed (45%), which were mixed with muds (20%) and sands with small gravels (35%) (Fig. 7). Fishing activity was also highly variable, with samples located both in areas of low to medium intensities and also high intensities. The EUNIS list of habitats considers communities dominated by *L. conchilega* for sublittoral areas of the Atlantic, but there is no direct correspondence with Mediterranean shelf and slope aggregations, as it is also the case for the Barcelona Convention. To a certain extent, this community relates to the 'Mediterranean communities of shelf-edge detritic bottoms' purely based on the location where it was found (Table 4). Conversely, the IEHEM habitat list includes

communities dominated by *L. conchilega* both in circalittoral and bathyal detritic bottoms, which are likely equivalents of the benthic community identified in Cap de Creus.

(F) Cold-water coral community with *Madrepora oculata*. Observed in 13% of the dives (169 SUs). A total of 55 taxa belonging to 8 phyla were reported, with more than 60% classified as Porifera and Cnidaria (Fig. 6a). Some species could not be identified to species level due to the difficulties in collecting samples inside the canyon. The number of organisms from each phylum was the most balanced among all communities (Fig. 6b), displaying the highest average number of species per SU (11 ± 4.7; max.: 25) and the highest exponential of Shannon diversity values of the whole study area (Fig. 6c). Regarding its composition, this community was mainly characterized by the CWC *M. oculata*, with a biomass larger than any other species registered despite its overall low abundances (max. dens.: 8.6 col·m^{-2}; av. dens.: 0.31 ± 0.9 col·m^{-2}; Fig. 4f). Among the remaining species, the most common were brachiopods (dens.: ~50 ind·m^{-2}), galatheids hiding in between rocks, the cup coral *Caryophyllia smithii*, the polychaete *Protula tubularia*, the oyster *Neopycnodonte* cf. *zibrowii* and various encrusting sponges not yet identified to species level (Table 3; Fig. 4f). Some colonies of the CWCs *Dendrophyllia cornigera* and *Lophelia pertusa* were also observed, generally in low numbers and of a small size. This community showed the deepest distribution of all (165–388 m depth), with most samples found in areas of steep slopes characterized by the presence of large rocks, boulders and slabs (Fig. 7). Values of bottom current velocities were generally moderate, although the area registers high-intensity events in winter periods due to periodic storms that enhance sediment transport on the canyon head. The complex terrain also limits the activity of bottom trawlers, with very low values of bottom fishing intensity registered (Fig. 7). This community is currently included in the three habitat lists considered for this study (Table 4) and is part of Habitat 1170 (Reefs) of the EU Habitats directive. This community undoubtedly fits the FAO criteria of what constitutes a VME due to its structural complexity, high diversity of associated species and vulnerability to fishing activities and for this reason CWC reefs, oyster reefs and other large bivalves have been recognized as Mediterranean VME indicator habitats by the WGVME of the General Fisheries Commission for the Mediterranean.
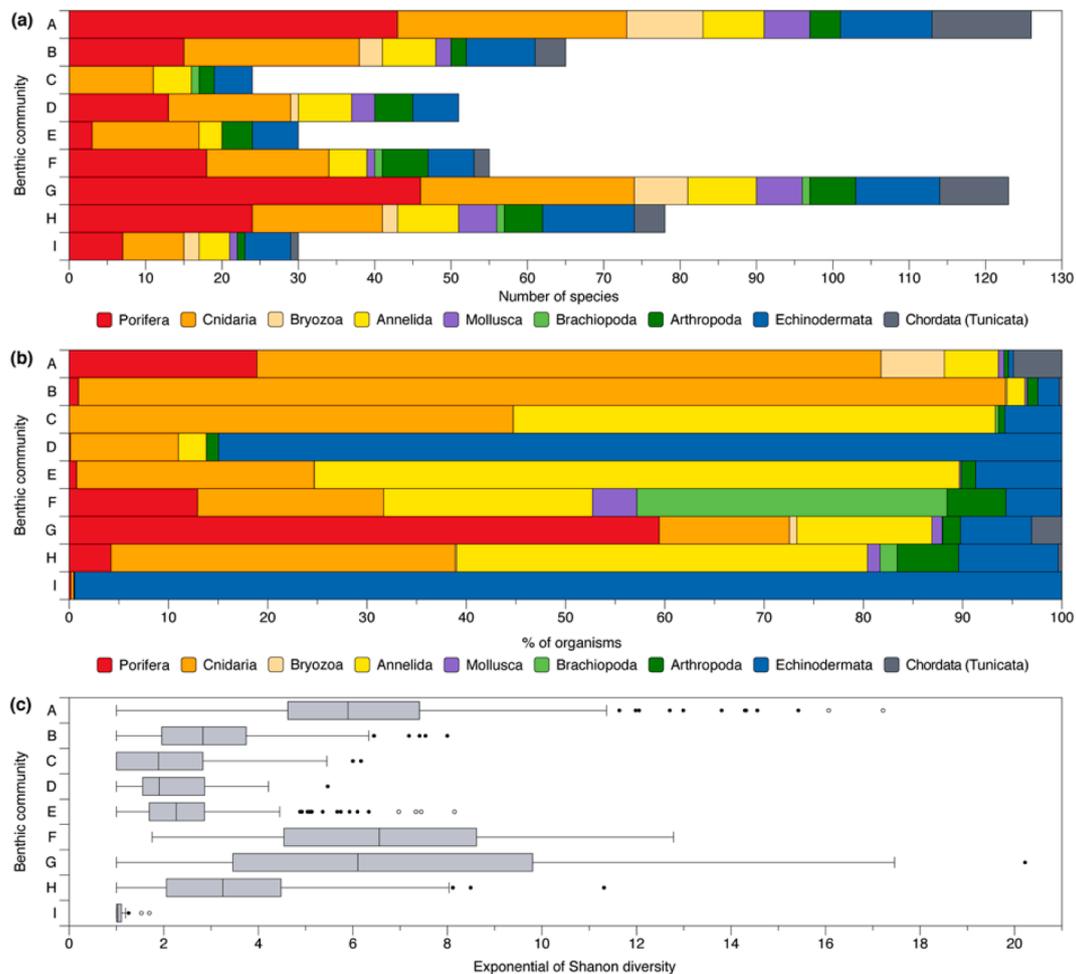
Fig. 6. Diversity of the 9 benthic communities identified on the continental shelf and submarine canyon off Cap de Creus. (a) Number of species reported in each benthic community, organized by phylum. (b) Percentage of organisms reported in each benthic community per phylum. (c) Box plot displaying the values of exponential of Shannon diversity (expH) in the different sampling units from each benthic community. Chordata in (a) and (b) only refers to tunicates, since no fishes were considered for this study. Benthic communities: A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans and alcyonaceans. C: Shelf muds and fine sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*. I: Massive aggregation of the brittle star *Ophiothrix fragilis*.

(G) Sponge community in mixed substrates of the outer continental shelf. Observed in 38% of the dives (214 SUs). This community was one of the richest and most diverse, with 123 taxa from 8 different phyla registered (Fig. 6a), with almost 60% of the organisms reported as Porifera (Fig. 6b). The 6 most representative taxa were the sponges *Dysidea* spp. (both *D. tupha* and *D. avara,* difficult to tell apart from the images and considered together), *Haliclona* cf. *elegans*, *Hyrtios collectrix*, *Axinella damicornis*, *Stelligera stuposa* and *Iophon* sp. (Table 3). These sponges were found in variable densities, with several of those species observed forming dense aggregations, such as *Haliclona* cf. *elegans* (10–15 ind·m^{-2}; Fig. 4g). Other species of interest were the Polychaetes *Myxicola infundibulum* and *Salmacina dysteri* (Table 3). The average number of species per SU was 9.1 ± 6.3, one of the highest reported, and displaying some of the highest exponential od Shannon diversity values among all communities (Fig. 6c). The sponge grounds were primarily observed on the outer shelf, especially on the southern side of the submarine canyon, but also extending into the upper slope. Dominant substrates were sands with a fraction of gravels (in some areas possibly corresponding to suboutcropping rocks that could not be determined from the video images) and rocky outcrops (Fig. 7). Low current velocities and very low fishing activity were registered in the samples that belonged to this community. Based on its most representative species, this community could be included in the 'Biocenosis of Mediterranean

shelf-edge rock' (MD151) of the EUNIS habitat classification system, under the category 'Facies with small sponges (sponge ground)' of the 'Shelf-edge rock' category (MC1.521) of the Barcelona Convention and in the 'Bathyal rock covered by sediments with dominance of sponges' of the IEHEM list (Table 4). It could also be considered part of the Habitat 1170 (Reefs) of the EU Habitats Directive due to its phisiographic and sedimentary characteristics, which generates a sharp change in species composition, abundance and diversity compared to its surrounding areas. This community undoubtedly fits the FAO criteria of what constitutes a VME due to its structural complexity, high diversity of associated species and vulnerability to bottom fishing activities. For this reason, deep-sea sponge aggregations on hard and soft bottoms have already been included as habitats potentially supporting VMEs in the Mediterranean by the WGVME of the General Fisheries Commission for the Mediterranean.

(H) Bathyal sands and gravels with cf. *Cerianthus membranaceus*. Observed in 32% of the dives (235 SUs). A total of 78 taxa were identified within this community (Fig. 6a), most organisms reported as Polychaetes (41%) and Cnidarians (35%) (Fig. 6b). The most characteristic species were the Polychaete *Protula tubularia* and the anthozoans *Capnea sanguinea*, cf. *Cerianthus membranaceus* and *Mesacmaea mitchellii* (Table 3), with sea urchins of the species *Echinus acutus* also commonly observed (Fig. 4). The abundances of all species were relatively low in
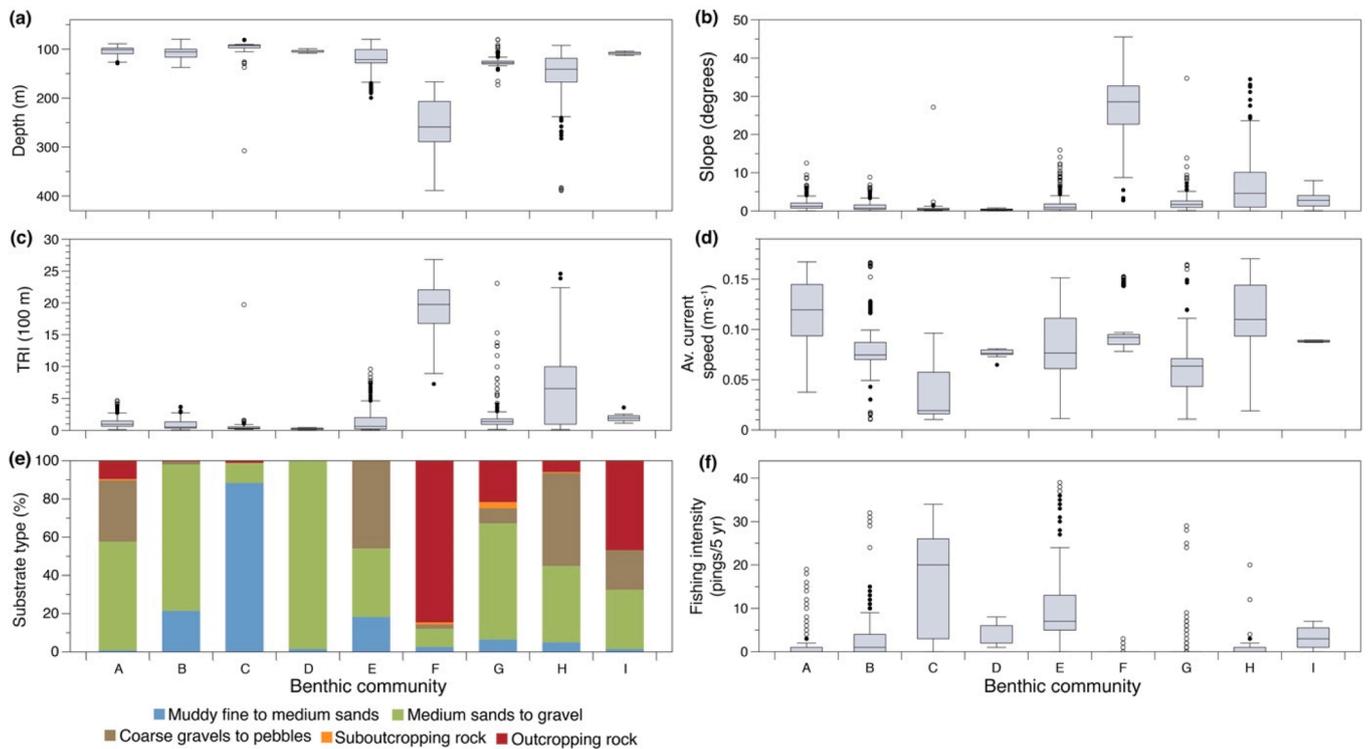
Fig. 7. Main environmental characteristics registered in the sampling units where each megabenthic community was observed. (a) Depth, in meters. (b) Slope derived from the multibeam bathymetry, in degrees. (c) Terrain ruggedness Index (TRI) calculated at 100 m radius. (d) Average bottom current speed for the period 2000–2013. (e) Substrate type derived from the video images. (f) Fishing intensity estimated from the Vessel Monitoring System, in pings/5 yr per surface area. Benthic communities on the X axis labelled from A to I correspond to: A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans and alcyonaceans. C: Shelf muds and fine sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*. I: Massive aggregation of the brittle star *Ophiothrix fragilis*.

most cases (Table 3), and the organisms were generally observed sparsely distributed along the surveyed area. The average number of species per SU was 4.4 ± 2.3, with values of exponential of Shannon diversity generally between 2 and 4 (Fig. 6c). This community was mainly located on the slopes of the shelf break and inside the submarine canyon, in depths of 110–250 m. It was found in areas characterized by very strong bottom currents, with a very coarse substrate composition, mainly with gravels and pebbles mixed with coarse sands (Fig. 7). Not much bottom trawling activity was registered in areas where this community was observed. Based on the species composition, there does not seem to exist a direct correspondence between this community and the EUNIS habitat classification system besides its Atlantic counterpart: '[*Cerianthus lloydii*] and other burrowing anemones in circalittoral muddy mixed sediment', and hence it should be included in the broader category of 'Biocenosis of Mediterranean open-sea detritic bottoms on shelf-edge' (Table 4). Regarding the Barcelona Convention, it could be included under the 'Facies with Ceriantharia (e.g. *Cerianthus* spp., *Arachnanthus* spp.)' of the 'Upper bathyal muds' based on its dominant species and depth distribution, although the sediment composition in Cap de Creus has a much coarser fraction. The IEHEM habitat list includes 'Bathyal detritic bottoms with cerianthids (*Arachnanthus*, *Cerianthus*, *Pachycerianthus*)', which corresponds to the community composition observed in Cap de Creus. Tube-dwelling anemone patches are included as habitats potentially supporting VMEs in the Mediterranean by the WGVME of the General Fisheries Commission for the Mediterranean, and the observed accumulations of large bivalve shells in the areas where this community was present (Supplementary Fig. S6) could favour its consideration as Habitat 1170 (Reefs) of the Habitats Directive.

(I) Brittle star aggregation with *Ophiothrix fragilis*. The massive aggregations of *O. fragilis* were only observed in one single dive,

appearing in a relatively small area of the continental shelf in front of the easternmost sector of the cape, at 105–110 m depth (35 SUs). This assemblage was characterized by the presence of high numbers of the brittle star *O. fragilis* (estimated densities above 600 ind·m^{-2}), observed forming patches extending over tens of meters in length. The number of brittle stars was so high that in some areas the whole underlaying substrate was fully covered by this species (Fig. 4i), be it sands, gravels, pebbles or outcropping rocks. The number of associated species identified was 30, belonging to 8 phyla (Fig. 6a), with low exponential of Shannon diversity values due to the large dominance of the brittle stars over the remaining species (Fig. 6c). This community is included in all 3 habitat lists considered (Table 4), always under mixed or detritic sedimentary bottoms. It is equivalent to the 'Facies with *Ophiothrix quinquemaculata*' of the 'Biocenosis of Mediterranean muddy detritic bottoms' in the EUNIS habitat classification system, and to the 'Facies with Ophiuroidea (e.g. *Ophiothrix* spp.)' of the 'Circalittoral mixed sediment' in the Barcelona Convention. The IEHEM habitat list also includes aggregations of brittle stars within infralittoral and circalittoral muddy detritic bottoms.

3.3. Influence of environmental parameters

The triplot resulting from the dbRDA analysis, including all SUs, the explanatory variables and the most important species is shown in Fig. 8. The model explained 15.2% of the variability, with the first 2 axes explaining almost 60% of the constrained inertia of the biological dataset (39% and 21%, respectively). The overall test of significance showed that the canonical relationship between the biological data and the explanatory variables was highly significant ($p < 0.001$; 999 permutations), as most of the variables included in the model when tested independently, except the soft substrates (marginal tests, $p < 0.05$; 999

Table 4

Equivalence of the 9 invertebrate communities (Com.) identified in this study with different biocenosis/habitats included in the 3 main reference lists of marine habitat types that include Mediterranean circalittoral and bathyal ecosystems (further details and bibliographical references are provided in Section 2.5). The code of the habitat is given before the habitat name. Communities that could be included under the Habitat 1170 (Reefs) of the Annex II of the Habitats Directive are marked with a (*). Habitat names corresponding to the IEHEM list have been translated to English from its original form in Spanish for an easier understanding. Depth range corresponds to the depths at which each community was observed in the study area. A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans. C: Shelf muds and sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*. I: Brittle star aggregation with *Ophiothrix fragilis*. n.c.: no correspondence.

Com.	Indicator species	Depth range (m)	EUNIS (2019)	Barcelona Convention (2019)	IEHEM (2013)
A*	*Eunicella cavolini, Smittina cervicornis, Suberites syringella, Epizoanthus* sp.	89–129	MD15 | Mediterranean offshore circalittoral rock	MD1.523 | Offshore circalittoral rock invertebrate-dominated covered by sediments | Facies with Alcyonacea (e.g. *Eunicella* spp)	0302022307 | Circalittoral rock dominated by invertebrates with *E. cavolini*
B	*Pteroeides spinosum, Cavernularia pusilla, Pennatula rubra, Alcyonium palmatum*	80–137	MD55 | Mediterranean offshore circalittoral sand	MC6.512 | Coastal terrigenous muds | Facies with Pennatulacea	0304051401 | Infralittoral and circalittoral detritic bottoms dominated by invertebrates with Pennatulacea (*Pennatula, Pteroides, Virgularia*)
C	*Sabella pavonina, Andresia partenopea*	81–137	MD65 | Mediterranean offshore circalittoral mud	n.c.	0304051404 | Infralittoral and circalittoral detritic bottoms dominated by invertebrates with sabellid polychaetes (*Megalomma vesiculosum, Sabella* sp., *Bispira volutacornis*)
D	*Leptometra phalangium, Pteroeides spinosum, Pennatula rubra*	99–108	MD4512 | Biocenosis of Mediterranean open-sea detritic bottoms on shelf-edge | Facies with *Leptometra phalangium*	MD5.514 | Offshore circalittoral sand | Facies with Crinoidea (e.g. *Leptometra* spp.)	0402031106 | Bathyal detritic bottoms with fields of *Leptometra phalangium* 04020403 | Fields of *Leptometra phalangium* in bathyal bottoms of the shelf edge
E	*Lanice conchilega, Arachnanthus oligopodus*	80–200	MD451 | Biocenosis of Mediterranean open-sea detritic bottoms on shelf-edge	n.c.	0304051405 | Infralittoral and circalittoral detritic bottoms dominated by invertebrates with *Lanice conchilega* 0402031103 | Bathyal detritic bottoms with *Lanice conchilega*
F*	Brachiopoda, *Galathea* spp., *Caryophyllia smithii*, encrusting sponges, *Madrepora oculata*	166–388	MF1512 | Mediterranean lower bathyal *Madrepora oculata* reefs	ME1.515 | Upper bathyal rock invertebrate-dominated | Facies with Scleractinia	04010112 | Bathyal rock with white corals (*Lophelia-Madrepora-Desmophyllum*)
G*	*Dysidea* spp., *Haliclona elegans, Hyrtios collectrix, Axinella damicornis, Stelligera stuposa*	80–172	MD151 | Biocenosis of Mediterranean shelf-edge rock	MC1.521b | Shelf edge rock | Coralligenous outcrops covered by sediment | Facies with small sponges (sponge ground)	04010208 | Bathyal rock covered by sediments with dominance of sponges
H	*Protula tubularia, Capnea sanguinea,* cf. *Cerianthus membranaceus*, Hermit crabs, *Mesacmaea mitchellii*	92–388	MD451 | Biocenosis of Mediterranean open-sea detritic bottoms on shelf-edge	ME6.51A Upper bathyal muds | Facies with Ceriantharia (e.g. *Cerianthus* spp., *Arachnanthus* spp.)	0402031104 | Bathyal detritic bottoms with ceriantharians (*Arachnantus, Cerianthus, Pachycerianthus*)
I	*Ophiothrix fragilis*	104–112	MC4511 | Biocenosis of Mediterranean muddy detritic bottoms | Facies with *Ophiothrix quinquemaculata*	MC4.515 | Circalittoral mixed sediment | Facies with Ophiuroidea (e.g. *Ophiothrix* spp.)	0304051504 | Infralittoral and circalittoral muddy detritic bottoms with aggregations of brittle stars (*Ophiothrix fragilis*)

permutations).

The ordination in a reduced space separated well the samples belonging to the different communities, although a certain overlap in species composition occured on the edges of the groupings, possibly due to transition areas. Pennatulaceans and alcyonaceans were representative taxa in samples located in shallow areas, which were characterized by soft substrates, mainly sands with a percentage of fine gravels. Soft-bottom areas where fishing intensity was low were dominated by Cnidaria species such as *P. spinosum, A. palmatum, C. pusilla* and *P. rubra*, which mainly belonged to communities B and D. The tube-forming polychaete *Lanice conchilega* was well represented in samples with a moderate level of fishing activity, in areas of low current speed and finer sediments, such as muds and fine sands. Areas exposed to strong bottom currents were characterized by the presence of the gorgonian *E. cavolini*, the sponge *S. syringella*, the bryozoan *Smittina cervicornis* and the zoantharid *Epizoanthus* sp.1, as well as the brittle star *O. fragilis*, which seemed to be confined to the northern sectors of the cape. Areas of steep slopes and high variability in bottom current speeds favored the presence of rocky outcrops, which were associated with the tube-building polychaete *P. tubularia*, different species of brachiopods and the solitary cup coral *Caryophyllia smithii*, the oyster *Neopycnodonte* cf. *zibrowii* and at least two species of Galathoidea. At such depths, the cerianthid cf. *Cerianthus membranaceus* and the actinia *Mesacmaea mitchellii* dominated areas with coarse sediments, where bioclastic shells represented a large fraction of the gravels and pebbles observed.

3.4. Spatial distribution

The spatial distribution of the diversity of benthic megafauna and the different communities identified in Cap de Creus is given in Fig. 9. The species richness (Fig. 9a) and the values of the exponential of Shannon (Fig. 9b) for each sampling unit suggests the existence of 3 areas of high ecological value, which correspond to the community of mixed substrates dominated by the gorgonian *E. cavolini*, the sponge grounds and the cold-water coral community with *M. oculata*. These high diversity areas are found, respectively, on the northern side of the cape at around 100 m depth, on the deepest sector of the southern continental shelf and on the canyon head, between 200 and 300 m depth. The spatial distribution of the benthic communities in the study area, as determined from the clustering analysis, is shown in Fig. 9c, and the predicted distribution obtained from the RF algorithm is shown in Fig. 9d. The RF model had an overall accuracy of 83.9% (95% CI: 0.8057, 0.8687) and a Kappa statistic of 0.806. According to the evaluation, the communities that were better classified by the model were the cold-water coral community (F), with a precision (percentage of predictions that are correctly classified) of 94%, followed by the shelf-dwelling communities dominated by the crinoid *L. phalangium* (Community D, precision: 89%) and the sea fan *E. cavolini* (Community A, precision: 88%), and the soft-

bottom community with the polychaete *L. conchilega* (Community E, precision: 86%). These four communities also presented the highest values (greater than 92%) for balanced accuracy (the mean of sensitivity and specificity). Lower precision and accuracy values occurred in benthic communities that occupied similar habitats. This was the case of the community of shelf muds with Sabellids (Community C, precision: 68%), confounded in several cases with the shelf-dwelling community with sea pens (Community B), the latter also confounded with the sponges community found on the outer shelf (Community G). Precision values and the confusion matrix can be found in Supplementary Table S4, while full classification metrics for each community are provided in Supplementary Table S5.

According to the distribution predicted by the model (Fig. 9d), the soft-bottom community with sea pens and alcyonaceans (Community B) occupied a large area on the shelf, mainly where fishing intensity is low. At similar depths but with higher trawling intensities, the community of fine sediments with *S. pavonina* (Community C) was generally dominant. The community characterized by the sea fan *E. cavolini* (Community A) was predicted on the northern side of the cape, mostly following the 100 m depth isoline. Its distribution seems to be restricted to areas of the shelf where bottom currents are moderate to high. The community characterized by a high diversity of sponge species (Community G) was predicted on the deepest part of the shelf, in areas relatively far from shore and where fishing intensity is low. The model predicted the shelf edge and a large part of the submarine canyon to be occupied by the community of coarse sediments with cf. *Cerianthus membranaceus* (Community H), which develops in areas of high slopes and relatively high bottom current velocities. A fine strip between 200 and 300 m depth (and in some points reaching down to 400 m) was predicted to be colonized by the community of CWC with *M. oculata* (Community F), which develops on hard substrates, a relatively common feature in areas of steep slopes on the southern flank of the submarine canyon. According to the mean decrease in accuracy and Gini index, depth and average bottom current velocity were the most important factors determining the spatial distribution of the benthic communities in the study area (Supplementary Fig. S5). The standard deviation of the bottom current velocity and terrain ruddgeness index at large scales also appeared as important factors, although their contribution was substantially lower. The intensity of bottom trawling partly explained the observed patterns, but overall it was less relevant than the environmental parameters listed above when considering the study area as a whole.

4. Discussion

This study represents the most detailed characterization ever made to the megabenthic communities of the continental shelf and submarine canyon off Cap de Creus, an area included in 2014 as a Site of Community Importance (SCI) of the Natura 2000 Network (*South-West Gulf of Lions canyons system*). With over 33 km of seabed explored and a total of 47 hours of video footage evaluated, this study updates the results provided in the pioneering work developed by Desbruyères et al. (1972) and Reyss (1971, 1972) on the continental shelf and submarine canyon off Cap de Creus, later complemented with new environmental and ecological information in the works of Orejas et al. (2009), Lo Iacono et al. (2012), Madurell et al. (2012) and Gori et al. (2013). Furthermore, the results presented in this study will expand our knowledge on the composition and distribution of shelf and slope communities of the western Mediterranean, whose study has seen an increase in recent years with several works that characterize mesophotic and deep-sea benthic diversity using underwater video images (e.g. Taviani et al., 2017, 2019; Grinyó et al., 2018; De la Torriente et al., 2018; Pierdomenico et al., 2019; Enrichetti et al., 2019a; Moccia et al., 2021).

4.1. Diversity of benthic megafauna

The footage recorded on the continental shelf and submarine canyon off Cap de Creus revealed the existence of a very diverse benthic ecosystem, with 167 morphospecies of the megafauna identified from the video images (that is, excluding fishes and other highly mobile organisms such as cephalopods; images of the megafauna identified provided in Dominguez-Carrió et al., 2021b). Although the fauna observed represents only a small fraction of all macrobenthic species reported for the area (1,041 invertebrate species identified to date; Lo Iacono et al., 2012), our results are on the upper band when compared to other video-based studies performed in similar habitats of the western and central Mediterranean Sea, which reported a similar or lower number of megabenthic species (e.g. Grinyó et al., 2018; Pierdomenico et al., 2019; Enrichetti et al., 2019a; Moccia et al., 2021). Although it is possible that the large sampling effort of our study could partly explain the high diversity of epibenthic species reported, the complex environmental setting that characterizes the marine area off Cap de Creus should not be disregarded. The positive effect that submarine canyons have on the abundance and diversity of benthic fauna compared to adjacent open slopes has long been recognised (e.g. Canals et al., 2019; Fernandez-Arcaya et al., 2017; Levin and Sibuet, 2012), most possibly playing a key role in the maintenance of high rates of biodiversity in the Cap de Creus marine area. Indeed, the narrow continental shelf and the closeness of the submarine canyon to the coastline generates a highly heterogenous environment (Lo Iacono et al., 2012), which increases the number of potential ecological niches in a relatively small area. This situation could favor the richness of epibenthic species observed, especially if compared to similar environments found in other areas of the Gulf of Lions (Fabri et al., 2014). In Cap de Creus, shelf waters, which are much richer in nutrients and phytoplankton than the open sea thanks to the discharge of the Rhone river (Cruzado & Velasquez, 1990), flow from the shelf towards the deep through the canyon, reaching its deepest parts during events of dense-shelf water cascading (Canals et al., 2006). This large water flux provokes strong near-bottom currents that mobilize large amounts of suspended particles rich in organic matter (Palanques et al., 2006), likely favoring the development of suspension- and filter-feeding organisms. In fact, sponges and cnidarians were the two most diverse phyla observed in the images, both representing more than 50% of the total invertebrate diversity reported. Furthermore, several large species of suspension feeders were observed generating high-density patches, which are known to further promote species richness at the local scale by providing habitat to a set of other associated species (Buhl-Mortensen et al., 2010; D'Onghia et al., 2010; D'Onghia, 2019; Rossi et al., 2017), some of which with commercial value (e.g. lobsters and demersal fishes).

4.2. Structure and representativeness of benthic communities

Ackowledging the caveats of the methodology employed (i.e. identifying species from video images, differences in underwater vehicles and camera resolutions), the benthic megafauna observed on the continental shelf and submarine canyon off Cap de Creus displayed a very discernible community structure, with 9 contrasting species associations identified from the video footage. Similar to the rest of the Mediterranean Sea, the images showed the existence of a clear transition area at 150–170 m depth, which coincides with the boundary between the continental shelf and the beginning of the upper slope (Lastras et al., 2007). In Cap de Creus, the mid and outer continental shelf is characterized by a variety of habitats that range from high-depositional fine-grained areas to rocky outcrops (Lo Iacono et al., 2012), a situation that generates enough environmental variability to support up to 7 different benthic communities. As expected, soft-bottom areas of the shelf hosted less diverse epibenthic communities than those found on harder substrates, the latter mostly characterized by coral gardens and sponge aggregations. Differences in species diversity and composition due to

habitat heterogeneity and substrate charateristics have long been reported for circalittoral and bathyal habitats (Levin & Dayton, 2009; Lacharité & Metaxas, 2017), with highly-depositional landscapes commonly providing less-favourable conditions for the development of epibenthic fauna due to the lack of consolidated substrates for the attachment of sessile species. Furthermore, soft-bottom habitats are generally more exposed to impacting bottom-contact fishing activities (Eigaard et al., 2016), which can further reduce the abundance and diversity of epibenthic fauna (Buhl-Mortensen et al., 2016; Sciberras et al., 2018). Below the shelf break, only two major benthic communities were identified, one of which corresponds to the emblematic community of CWCs characterized by the scleractinian coral *Madrepora oculata*. This community was mostly observed on large boulders, rocky outcrops and steep walls in the canyon head, as previously reported for the area (Orejas et al., 2009; Gori et al., 2013).

The ecological interest of the communities identified in the video footage and their importance for the management and conservation of the benthic diversity within the limits of the SCI are discussed in the following sections.

4.2.1. Mixed substrates of the continental shelf with Eunicella cavolini.

This community should be regarded as one of the most diverse, not only for the continental shelf, but for the study area as a whole. Its main structuring species, the octocoral *Eunicella cavolini*, reached maximum densities of 25 col·m^{-2}, similar values to those reported in close-by areas such as the Balearics (Grinyó et al., 2016) or the Ligurian basin (Enrichetti et al., 2019a). In Cap de Creus, this community seems to be mostly distributed along a narrow strip that stretches for almost 10 km on the northern side of the cape, following the 100 m isobath (Community A in Fig. 9d). Other octocorals, such as *Eunicella singularis* and *Paramuricea clavata*, which are known to form dense aggregations at shallower depths (Gori et al., 2011), were rarely observed in the video images, suggesting a severe change in gorgonian dominance below 70–80 m depth. The presence of rocky outcrops along the 100 m isobath (Lo Iacono et al., 2012), together with year-round bottom currents that remove fine-grained sediments (DeGeest et al., 2008), likely provide the optimal conditions for a population *E. cavolini* to fully develop, where a constant supply of food particles can lead to high octocoral abundances (Weinbauer & Velimirov, 1995). Further, the increased tridimensionality produced by the colonies of *E. cavolini* might also be fostering higher rates of associated benthic diversity, as suggested by the 126 species identified within this community so far (and with likely more species not identifiable from video images), a pattern also reported for other octocorals in shallow (Ponti et al., 2016) and deep-sea ecosystems (Buhl-Mortensen et al., 2010; De Clippele et al., 2015). In fact, several of the associated species were observed living on top or attached to the sea fans, most likely in the search of better feeding conditions due to the capacity of coral aggregations to alter near-bottom water flow patterns and local sedimentation rates (Valisano et al., 2016). The presence of large octocorals is also known to favor the presence of mobile organisms, such as demersal fishes and cephalopods, which may use coral gardens to breed and as refuge (D'Onghia, 2019). In Cap de Creus, up to 16 demersal fish species were identified within this community (C. Dominguez-Carrió, in prep.), providing evidence of the nursery and refuge effect that this community might have in promoting life on the otherwise less structurally complex continental shelf. One of the most abundant species of this community was the bryozoan *Smittina cervicornis*, which appeared as the second highest ranked species according to the indicator value (IndVal). This species was very commonly found in samples collected from soft-bottom areas of Cap de Creus continental shelf using a small benthic sled (Madurell et al., 2013). The authors reported that collected colonies were always found dead, hypothesizing that bryozoans were probably swept away from shallower areas by the predominant bottom currents. The results of our study suggest that a portion of the samples that were collected in close-by areas were likely exported from this community. Also abundant was the reptant sponge *Suberites*

syringella (max. dens.: 14.4 org. m^{-2}), historically documented as very common on shelf environments in parts of the western (Bertolino et al. 2013; Pansini & Musso, 1991) and eastern Mediterranean Sea (Voultsiadou-Koukoura & Van Soest, 1993). In those areas, this species generally appears as solitary or gathering in close groups, but always with lower density values than those reported for Cap de Creus.

In the Atlantic region, aggregations of gorgonians are not subject to directed national or international protection regimes, but they are now classified under the category of "coral gardens", which are considered 'Threatened and/or declining' due to their sensitivity to demersal trawling and longlining, temperature change and acidification in the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR). In the Mediterranean, there are no specific regulations for the protection of octocoral-dominated communities besides those afforded by the Habitats Directive to the red coral *Corallium rubrum*, the designation of *Isidella elongata* beds as Sensitive Habitats (UNEP/MAP-RAC/SPA, 2010) and the species included in the Annex II of the Barcelona Convention. For this reason, specific actions should be taken to promote the conservation of shelf-dwelling gorgonian populations, which can be of key importance in promoting local diversity in low complexity habitats, and whose long-term viability could be severely affected by the effect of fishing practices. Besides improving their protection, restoration measures could also be considered an effective approach to improve the conservation of these populations, such as the cost-effective actions already implemented in Cap de Creus in collaboration with local fishers to reintroduce by-catch colonies back into their habitat (Montseny et al., 2021).

4.2.2. Shelf muds and sands with pennatulaceans and alcyonaceans.

Sea pens are characteristic species of the Mediterranean and Atlantic continental shelf, both in muddy and sandy substrates (Gili & Pagès, 1987; Greathead et al., 2007; Ruiz-Pico et al., 2017). In Cap de Creus, soft-bottom areas of the shelf were colonized by (at least) 6 different species of sea pens, representing most of the known sea pen diversity of the Mediterranean Sea (Bastari et al., 2018; Altuna & Poliseno, 2019). *Pteroeides spinosum* was the most widespread species, present in more than 80% of the samples, and with density values (max.: 6.6 col·m^{-2}) similar to those reported for other areas of the Mediterranean (e.g. Porporato et al., 2014). Less abundant sea pens, such as *Pennatula rubra, Cavernularia pusilla* and *Virgularia mirabilis,* may actually display higher densities that those reported here due to their capacity to withdraw inside the sediment (Ambroso et al., 2013b; Chimienti et al., 2018). In fact, some colonies of *P. rubra* and *C. pusilla* were observed half buried inside the sediment, providing an indication of the prevalence of this phenomenon. The whip-like sea pen *Funiculina quadrangularis,* reported as the most common pennatulacean species in areas of the Cantabrian (Ruiz-Pico et al., 2017) and central Mediterranean (Terribile et al., 2015), appeared only in two locations of the study area, always in the form of isolated colonies. It is difficult to determine the reason for this low number of records, but it could be hypothesized that this species might require more stable conditions (Greathead et al., 2007) than those found in Cap de Creus to fully develop, or it might present a different sensitivity to bottom fishing practices than other smaller-sized pennatulaceans, more resilient to the passing of the trawl nets. The sea pen species observed in Cap de Creus were mostly found in association with the soft coral *Alcyonium palmatum*, which displayed densities of up to 9 col·m^{-2}. The littoral distribution of *A. palmatum* in Cap de Creus (30–60 m depth) was recently assessed by imaging tools (Ambroso et al., 2013a), with reported densities much lower than those obtained in this work, indicating that the preferred habitat of this species likely corresponds to the soft-bottom substrates of the continental shelf, which generally have a much finer sediment composition than shallower coastal areas.

Just like large octocorals, pennatulaceans are also known to foster species richness in homogeneous landscapes (such as continental shelves) due to the increase in the tridimensionality of the habitat they

provide (De Clippele et al., 2015). In this regard, sea pens not only play a fundamental role in the maintenance of the biological diversity (Buhl-Mortensen et al., 2010), but they can also act as nurseries for free-living species (e.g. crustaceans and fishes), which can use them as shelter during their larval and early-life stages (Baillon et al., 2014; D'Onghia, 2019). In Cap de Creus, a large number of invertebrate and fish species were observed in the images recorded within this community, some of which with high commercial value, including the European hake, the forkbeard, the red mullet and the monkfish (C. Dominguez-Carrió, in prep.). Pennatulaceans have long been recognized as key components of soft-bottom circalittoral and bathyal habitats of the Mediterranean, and the species identified within this community were already regarded as relevant in the sub-community of shelf detritic (Detritic du Large, DL) described by Desbruyères et al. (1972) for this same area. The high sensitivity of pennatulaceans to bottom trawling activities and their role in diversity maintenance has favored their inclusion in the List of threatened and/or declining species and habitats in the Northeastern Atlantic by OSPAR (Curd, 2010), which aims to provide a general framework to improve their conservation in the Atlantic. Sea pen fields are also considered VME indicator habitats by ICES and the GFCM, although no specific protection measures currently exist for the Mediterranean. Their key ecological role in soft-bottom habitats of the continental shelf and their sensitivity to bottom fishing practices should encourage policy makers to develop effective management measures to ensure their long-term conservation.

4.2.3. Shelf muds and fine sands with Sabella pavonina.

It corresponds to the most impoverished community of all, both in terms of species richness (24 spp.) and abundances ($\sim$0.75 org·m^{-2}). Most organisms were polychaetes (90%), mainly tube-forming sabellids such as *Sabella pavonina*. It is very likely that the species association observed within this cluster does not actually correspond to a natural community *per se*, but responds to the long-term exposure of the soft-bottom areas of the continental shelf to bottom-trawling activities. The negative effects of commercial bottom fishing on the composition and structure of benthic communities have long been recognized (e.g. Hiddink et al., 2017), and increasing fishing intensities can lead to changes in the dominance of the benthic taxa, favoring the most resilient, opportunistic or robust species and promoting a decrease (or disappearance) of long-lived, structuring or most vulnerable species (Buhl-Mortensen et al., 2016). In fact, the burrowing capacity of sabellid species could be the underlying reason behind their dominance in trawled areas of Cap de Creus, since hiding into the sediment as nets swipe the seafloor likely increases their survival capacity. Once fishing intensity surpasses a certain threshold, however, it is possible that even those more resilient species cannot cope with the disturbance, and are fully removed. This seemed to be the case for several sampling units found in the same area, where no species of the megafauna were reported at all from the images. Due to methodological constraints, those samples had to be excluded from the community analyses. It is possible that a more specific study targeting the effects of bottom trawling on the abundance and diversity of benthic species (such as that of Buhl-Mortensen & Buhl-Mortensen, 2018 in Norwegian waters) could provide a better indication of the effects of botton-fishing activities on the soft-bottom communities of the continental shelf off Cap de Creus.

4.2.4. Coarse sands of the shelf with Leptometra phalangium

Aggregations of the crinoid *L. phalangium* have long been regarded as characteristic of circalittoral and bathyal habitats of the Mediterranean Sea (Pérès & Picard, 1964), generally associated to flat areas of the shelf and shelf edge with muds, sands and gravels, where mid to strong bottom currents are common (Pérès, 1967). Dense patches of these crinoids have been reported from shelf and shelf break areas of the western (Grinyó et al., 2018), central (Colloca et al., 2003; Leonard et al., 2020) and eastern Mediterranean (Kallianiotis et al., 2000), where they can reach local densities of 15–30 ind·m^{-2}. In Cap de Creus, *L. phalangium*

had already been identified by Desbruyères et al. (1972) as part of the sub-community of shelf detritic of the mid and outer continental shelf, which also includes the community of pennatulaceans and alcyonaceans and the brittle star aggregation identified in this work. Based on our results, *L. phalangium* displays a shallower distribution in Cap de Creus than that reported in other shelf environments of the Mediterranean (Community D in Fig. 9d), with surprisingly no records from the actual shelf break (130–150 m depth). Such differences may be related to the high current speeds that recurrently hit the shelf break area off Cap de Creus, reaching velocities up to 50 cm·s^{-1} during strong downwelling events (Puig et al., 2008). These conditions likely provide a less suitable habitat than that found in similar depths elsewhere in the Mediterranean, moving the preferential habitat of the species towards shallower areas of the continental shelf. In the Mediterranean Sea, bottoms with *L. phalangium* have historically been included in the shelf-edge detritic community (Biocenose des fonds detritiques du large, DL; Pérès & Picard, 1964; Pérès, 1967), which is generally distributed along bathyal habitats of the shelf break and the upper slope. High densities of *L. phalangium* are known to increase habitat heterogeneity, further enhancing secondary production. They play a key role as nursery grounds for fish recruits and juveniles (Colloca et al., 2004), being associated with several fish species, including the European hake and the red mullet (Reale et al., 2005). Since crinoid aggregations are highly sensitive to bottom fishing practices (e.g. Mallol, 2005), they are currently considered Sensitive Habitats (SH) relevant for fisheries in the Mediterranean Sea by the Mediterranean Action Plan (UNEP/MAP-RAC/SPA, 2010), and their presence should be highly considered when defining new protected areas and elaborating management plans. In fact, any area with high abundances of this species could become a candidate site for Specially Protected Areas of Mediterranean Importance (SPAMI).

4.2.5. Sands and gravels of the outer shelf with Lanice conchilega and Arachnanthus oligopodus.

The most abundant species of this community corresponds to the polychaete *L. conchilega*, a ubiquitous terebellid of shelf and slope habitats of the western Mediterranean, with records in the Alboran sea (Rueda et al., 2021), the Iberian Peninsula (Ramirez-Llodra et al., 2009; Martín et al., 2011) and the Balearic Islands (Grinyó et al., 2018; Aguilar et al., 2014). *Lanice conchilega* forms extensive aggregations in areas of the outer shelf and the shelf break off Cap de Creus (Community E in Fig. 9d), with densities of 10–20 ind·m^{-2}. Such aggregations were already reported in the 1960s, mainly in the southern flank of the submarine canyon (180–200 m depth) after several dives performed with the manned submersible SP300 (Reyss & Soyer, 1965). The authors reported that these polychaetes represented, in some dives, a large percentage of the observed biomass (up to 15 ind·m^{-2}), being very abundant in detritic substrates of a biogenic origin (bivalve shells), a situation still observed nowadays. Although no reported densities are provided for other areas of the Mediterranean, several authors have documented high abundances of these ploychates in shelf and shelf break environments (Marín et al., 2011; Aguilar et al., 2014; Gomez-Ballestero et al., 2015; Lastras et al., 2016). Nonetheless, the densities of *L. conchilega* in the Mediterranean basin are always some orders of magnitude lower than those reported in intertidal flats of the North Sea, the Waden Sea and the English Channel, where aggregations of these terebellids can reach thousands of individuals per square meter (Heuers et al., 1997; Ropert & Dauvin, 2000). Positive effects on macrofaunal density, species richness and community composition have been reported in those areas (Rabaut et al., 2007) due to the increase in habitat quality provided by the tubes formed by the polychaetes in uniformed environments, resulting in a higher survival rate of the associated benthic species (Van Hoey et al., 2008). In Cap de Creus, a total of 50 megafauna species were observed within this community, most of them in low abundances. It is very likely that the structuring capacity of *L. conchilega* to generate a positive effect on the associated benthic

community (species richness and biomass) requires a minimum density threshold possibly not reached in Cap de Creus. In fact, as suggested by Simboura et al. (1998), this species might behave as opportunistic in trawled areas that have intermediate fishing intensities. Specific studies performed on the resistance of this species to bottom trawling have shown the great survivorship capacity of *L. conchilega* to the passing of the beam trawl, with similar densities in trawled and untrawled areas (Rabaut et al., 2008). The polychaetes generate an external structure made of sand grains and bioclastic components (e.g. bivalve shells and foraminifers) a few centimeters in height, which is likely removed by the trawl net while the animal hides inside the sediment, surviving the fishing event. These observations are supported by the high number of *L. conchilega* tubes that were collected with a small sled used to sample areas of the continental shelf (data not provided), where no live parts of the annelids were collected. In several sectors of the southern shelf, the Mediterranean endemic species of ceriantharian *A. oligopodus* was observed in association to *L. conchilega*, reaching densities above 20 ind·m^{-2}. Fields of this ceriantharian have seldom been documented in other areas of the Mediterranean (Michez et al., 2014; Forero Mejia et al., 2015), and it would seem interesting to further investigate aspects of its ecology and distribution, and whether its association with the polychaetes is observed elsewhere in the Mediterranean.

4.2.6. Cold-water coral community with Madrepora oculata.

This iconic community observed in the submarine canyon off Cap de Creus includes 3 of the most important scleractinian CWC species of the Mediterranean deep sea: *Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera*. The ecology of CWC species in the Mediterranean has been extensively studied in the past decades, with observations reported across a wide range of areas, including the Alboran Sea (Corbera et al., 2019), the Catalan margin (Lastras et al., 2016), the Gulf of Lions (Orejas et al., 2009; Gori et al., 2013; Fabri et al., 2014), the Adriatic Sea (Freiwald et al., 2009), the Ionian Sea (Mastrototaro et al., 2010; Taviani et al., 2017) and the Aegean Sea (Vafidis et al., 1997). In Cap de Creus, the presence of deep-sea scleractinian corals has been known for more than 100 years thanks to the pioneering work of Pruvot (1895), who deployed several grabs and dredges to better understand the benthic diversity of the area. A description of the CWC community in the Mediterranean Sea ('Biocenose des coraux blancs') was already provided several decades ago by Pérès & Picard (1964), and complemented some years later by the work of Reyss (1971), who gave a very detailed characterization of the components that make up this community in Cap de Creus and Lacaze-Duthiers canyons based on the observations made from a manned submersible. Recent studies have further evaluated the ecology of CWC species inside Cap de Creus canyon by means of visual methods, providing new clues on their distribution, abundance and population size structure in the area (Orejas et al., 2009; Gori et al., 2013; Lo Iacono et al., 2018). The present study complements the works performed until now, providing new quantitative data on the structure of the community as a whole. As previously reported (Orejas et al., 2009), the community was mainly characterized by the presence of the scleractinian coral *Madrepora oculata*, with patches that reached densities of more than 8 col·m^{-2} and a total biomass much larger than any other invertebrate species, a pattern observed in other deep-sea areas of the Mediterranean (Chimienti et al., 2019). This situation contrasts with the general trend of the northeast Atlantic, where *Lophelia pertusa* is generally reported with similar (Arnaud-Haond et al., 2017) or higher abundances (Buhl-Mortensen et al., 2015b) than *M. oculata* at depths of 200–400 m, with increasing densities towards higher latitudes. In Cap de Creus, *L. pertusa* was observed in low numbers (densities of less than 1 col·m^{-2}), with colonies sparsely distributed on rocky outcrops. This was also the case for the yellow coral *D. cornigera*, with few colonies reported in the video footage, most of them of small size and scattered along the seabed, as already described by Orejas et al. (2009).

Cold-water corals are known to play a key role in promoting benthic diversity at the local scale, favoring the presence of other species when

compared to adjacent non-coral areas, not only for invertebrate species (Henry & Roberts, 2007; Mastrototaro et al., 2010; Lessard-Pilon et al., 2010; Rueda et al., 2019) but also for demersal fishes (D'Onghia et al., 2010; Linley et al., 2017; D'Onghia, 2019). In Cap de Creus, more than 50 invertebrate species were identified in association to this CWC community, most of which Cnidaria or Porifera. In terms of abundance, brachiopods were the most relevant group, with some high-density patches observed in rocky outcrops (up to 45 ind·m^{-2}). It is likely that these values include more than one species of brachiopod, but the definition of the video recordings and the distance kept with respect to the seabed made it impossible to identify each individual down to species level, more especially knowing that different brachiopod species co-occur at bathyal depths in the area (Reyss, 1971), sharing the same habitat (Fourt et al., 2017). Within those rocky outcrops, especially in overhangs or vertical cliffs, dense aggregations of the oyster *Neopycnodonte* cf. *zibrowii* were also recorded. This giant deep-sea oyster has been widely documented in other areas of the Atlantic and the Mediterranean Sea (Beuck et al., 2016), and its association with CWCs in the Mediterranean has only recently been reported (Taviani et al., 2019), suggesting the need to implement specific protection measures to preserve this unique biotope. Besides the large number of brachiopods and oysters, the CWC community also hosted other invertebrate species of interest, including the red coral *Corallium rubrum*. With just 40 colonies annotated, most of which only a few centimeters in height, this species had a less structured population than that found on the littoral zone (Tsounis et al., 2006) and the continental shelf (Rossi et al., 2008). It is possible that the colonies of the submarine canyon are somehow isolated from the genetic pool of the population due to the downwelling current regime common in the area, which might generate a one-way connection between colonies located at different depths. The large rocky outcrops within the southern flank of the submarine canyon were also home to a wide variety of sponge species, most of which of an encrusting nature. Due to the complexity of collecting samples in the canyon, several of those species still remain unidentified, and further surveys will be required to unveil the whole Porifera diversity that was observed in the images. Besides encrusting species, the most conspicuous sponge was the fan-shaped *Pachastrella monilifera*, a common species of bathyal habitats of the western Mediterranean (Angeletti et al., 2013; Bo et al., 2015; Santín et al., 2019) known to play a key structuring role in deep ecosystems, attracting numerous invertebrate and fish species, as well providing a secondary substrate for other associated fauna (Bo et al., 2011). Cold-water coral reefs of *L. pertusa* and *M. oculata* have long been regarded as SH by the Mediterranean Action Plan of the United Nations Environment Programme (UNEP/MAP-RAC/SPA, 2010), and their presence should be highly considered when designing MPAs. The reported high densities of *Neopycnodonte* oysters within this community further highlights the ecological relevance of this deep-sea benthic community, which fits the FAO criteria of what consitutes a VME (FAO, 2009) due to the high structural complexity provided by its main components, its high associated species diversity, its vulnerability to commercial longline fishing (Orejas et al., 2009; Dominguez-Carrió et al., 2020) and its slow recovery after disturbance (Rooper et al., 2011; Huvenne et al., 2016).

4.2.7. Sponge community in mixed substrates of the outer continental shelf.

The sponge-dominated community observed on the outer part of the southern continental shelf (Community G in Fig. 9d) was remarkably diverse, with more than 120 invertebrate species of the megafauna identified in the images. A large variety of erect and encrusting sponges was reported, adding up to at least 50 different sponge species, some of which already given for the area over 100 years ago (Pruvot, 1895). More specifically, the sparse rocky outcrops found at the end of the shelf were predominantly colonized by the sponge *Haliclona* cf. *elegans*, with local densities of 15 ind·m^{-2}. Mixed substrates with a higher percentage of soft sediments displayed a more complex species composition, with several other sponges observed in high abundances (e.g. *Dysidea* spp.,

Stelligera stuposa) and/or high sizes (e.g. *Poecillastra compressa, Axinella polypoides, Desmacidon fruticosum*). Sponges represented more than 60% of the total number of organisms annotated within this community, a pattern not observed elsewhere in the study area and that reinforces its singularity. This dominance of sponges at the end of the southern shelf might be explained by the presence of suitable substrates for attachment and the availability of food and nutrients in the form of suspended particles provided by the recurrent bottom currents, which possibly provide appropriate conditions for the growth of filter-feeding species (Genin et al., 1992; Hanz et al., 2021). Although generally observed in low densities, large Porifera are considered key components of Mediterranean mesophotic and deep-sea benthic ecosystems, with several studies now reporting diverse sponge-dominated communites across its basin (e.g. Santín et al., 2018; Enrichetti et al., 2020; Canessa et al., 2021). In fact, the association of sponges found in deep Mediterranean continental shelves was already described several decades ago by Pérès & Picard (1964), who used the term 'biocoenosis of offshore rocky bottoms' (originally named 'Roche du large', RL) to include all its associated epibenthic diversity. The species listed by the authors hold a high degree of affinity with the sponges reported for this study, although some characteristic species were not identified in the images evaluated, not even as rare or solitary individuals (e.g. *Rhizaxinella pyrifera, Phakellia ventilabrum* and *Petrosia ficiformis*).

Due to their capacity to increase the structural complexity of the habitat, sponge fields can favor higher rates of species diversity and abundance in comparison to non-sponge grounds (Beazley et al., 2013; McIntyre et al., 2016; Maldonado et al., 2017). The increased tridimensionality generated by erect sponges is known to provide shelter for several fish species, to the extent that sponge fields should be regarded as important nursery areas (Hogg et al., 2010). In Cap de Creus, 19 different species of fish were reported within the sponge fields (C. Dominguez-Carrió, in prep.), some of them with high commercial value, including *Conger conger, Phycis blennoides, Trisopterus* sp. and *Lepidorhombus boscii*. Sponge-mediated facilitation processes have only recently started to be examined in Mediterranean and Atlantic sponge-dominated communities, (Bo et al., 2011; Cathalot et al., 2015), and further studies will be needed to better determine the role played by sponge grounds in enhancing local diversity and ecosystem functioning in bathyal environments. The capacity of sponge grounds to enhance biodiversity, together with their sensitivity to commercial fishing, has favored their consideration as SH relevant for fisheries in the Mediterranean high seas by the Mediterranean Action Plan (UNEP/MAP-RAC/SPA, 2010), as well as VMEs by FAO in the International Guidelines for the Management of Deep-sea Fisheries in the High Seas (FAO, 2009). Hence, effective actions should be taken to protect the well-preserved and highly-diverse sponge grounds found on the deepest part of the southern continental shelf off Cap de Creus, especially since they develop in areas of the outer shelf that have not yet been targeted by the bottom-trawling fleet. Furthermore, it is likely that these diverse and fragile sponge grounds extend further south beyond the limits of the SCI, in an area historically not affected by the activity of bottom trawlers (Ribó et al., 2018) but currently considered for the implementation of offshore wind farms (Lloret et al., 2022).

4.2.8. Bathyal sands and gravels with cf. Cerianthus membranaceus.

The soft-bottom areas of the shelf break and upper slope with a large fraction of gravels and pebbles (mostly of a biogenic origin) were characterized by a low number of epibenthic species, with the tube anemone cf. *Cerianthus membranaceus* as the most conspicuous, generally with densities below 0.5 ind·m^{-2}. This cosmopolitan species is widely distributed across the western Mediterranean, with individuals generally scattered across large areas. It is currently reported along a wide bathymetric range, from littoral habitats (Cebrián & Ballesteros, 2004; Sardá et al., 2012) and shelf environments (Bo et al., 2012; Forero Mejia et al., 2015; Enrichetti et al., 2019b) all the way down to bathyal depths inside submarine canyons (Lastras et al., 2016; Fiala-Medioni

et al., 2012). Although not shown in the IndVal results due to their scattered distribution, the tube anemone appeared alongside the sea urchins *Echinus acutus* and cf. *Cidaris cidaris,* an association already reported in the same area by Reyss & Soyer (1965) after several dives performed with a manned submersible on the shelf break and canyon head (180–300 m depth). As reported by the authors, those species were more commonly observed on the southern flank, an area more influenced by bottom currents and with a much coarser sediment composition, which likely generates less suitable conditions for other burrowing species, such as sea pens and soft corals. Interestingly, the authors reported several accompanying species in high densities that were only seldom observed within this community during our study (e.g. *L. conchilega* and *L. phalangium*), while three indicator species determined by the IndVal analysis (*Protula tubularia, Capnea sanguinea* and *Mesacmaea mitchelli*) were not mentioned in their work. In the latter case, such differences could be attributed to the small size of the species, which could have gone unnoticed to the authors due to the distance kept between the manned submersible and the seabed.

4.2.9. Brittle star aggregation with Ophiothrix fragilis.

Five dense patches of the brittle star *O. fragilis*, some extending over several tens of meters, were filmed in front of the easternmost part of Cap de Creus during one single dive at 105–110 m depth. Based on the images recorded, maximum densities in those patches were estimated to be above 600 ind·m^{-2}, which may seem very high but are still much lower than the 7,000 ind·m^{-2} previously reported for the Bay of Seine (Dauvin et al., 2013). Massive aggregations of brittle stars in littoral areas of the northeast Atlantic have been known for decades (Holme, 1984; Aronson, 1989), and this aggregative behavior seems to respond to improved feeding and reproductive conditions for this species, also reducing the likelihood of being swept away by bottom currents (Warner, 1971). Aggregations of bittle stars are not a rare phenomenon in the Mediterranean Sea, and Pérès (1967) considered those high-density patches as common in muddy detritic bottoms, as observed in Cap de Creus. In fact, dense patches of *O. fragilis* (previously identified as *O. quinquemaculata;* Perez-Portela et al., 2012) were already documented in the same area several decades ago by Guille (1965), as well as in other areas of the continental shelf along the Rousillon coast (Guille, 1964) and the Adriatic Sea (Fedra et al., 1976). Behavioral studies have demonstrated that the optimal suspension-feeding activity of this species is achieved when bottom current speeds are kept below 20 cm·s^{-1} (Davoult & Gounin, 1995). In these conditions, brittle stars rise two or three arms towards the oncoming current to catch suspended particles that serve as food source. This feeding behavior was observed in a large number of the brittle stars filmed in the massive aggregations detected in Cap de Creus, which were found in an area that registered average bottom current speeds of around 10 cm·s^{-1}. It is likely that the highly productive waters that reach the southern part of the Gulf of Lions, together with the sustained bottom current regime of the area, provide optimal conditions for dense aggregations of these suspension feeders to be formed. Several studies have shown that massive aggregations of *O. fragilis* are generally stable through time (Holme, 1984; Blanchet-Aurigny et al., 2012), and it would seem interesting to monitor the evolution of this population in the forthcoming years.

4.3. Environmental-vs-fishing effects on community distribution

At the scale of the study area, the spatial distribution of the invertebrate megafauna mainly responds to a combination of depth, substrate type and bottom current speed. Although depth cannot be considered a factor as such but an axis along which other environmental parameters change (e.g. temperature, water pressure, light availability, etc.), it emerged as the main environmental driver determining the distribution of the benthic communities in the study area. Historically, depth has been regarded as a main structuring force at local scales for littoral (e.g. Chappuis et al., 2014), sublittoral (e.g. Garrabou et al., 2002) and deep

Mediterranean ecosystems (e.g. Cartes et al., 2009). In Cap de Creus, a clear zonation pattern could be detected at the level of the shelf break, with six communities found almost exclusively on the continental shelf, two found between the outer shelf and the upper slope and one with a deeper distribution, located exclusively inside the submarine canyon. This depth-related pattern has already been identified in other canyon incised continental margins of the Mediterranean Sea (Pierdomenico et al., 2019; Moccia et al., 2021) and the Atlantic Ocean (Bernardino et al., 2019). Substrate type, which was not completely independent from the dominant bottom current regime, also played an important role in the structuring of the benthic fauna. In fact, certain benthic communities showed a clear preference for specific substrate types. For instance, the communities dominated by pennatulaceans or crinoids were mostly found in sedimentary areas characterized by mud, sand and small gravels, always with a high percentage of sand. In contrast, the CWC community was primarily observed on large rocky outcrops and cliff overhangs inside the submarine canyon, as previously reported for the area (Orejas et al., 2009; Gori et al., 2013). In this case, suspension and filter feeders that live attached to hard surfaces (corals, sponges, brachiopods and oysters) likely benefit from the high availability of food particles resulting from the funneling of shelf waters towards the deep through the canyon (Pasqual et al., 2010; Lo Iacono et al., 2018). The assembly and maintenance of epifauna diversity in benthic communities has historically been linked to water flow dynamics, with communities exposed to high current speeds generally displaying more species and higher abundances (Palardy & Witman, 2014). Increased water flows are related to sediment removal and generate a greater flux of food particles (Genin et al., 1992) that favor the growth of suspension feeders due to increases in their capture rates (Best, 1988). This seems to be the case not only for the CWC community, but also for the community associated to the octocoral *E. cavolini*, which fully develops in areas of the shelf exposed to mid-to-strong bottom currents. Nonetheless, our results suggest that the diversity of the epibenthic communities does not

increase linearly with bottom current speeds. Very strong currents could overcome the threshold for their mechanical stability and reduce particle deposition, favouring the accumulation of coarser sediments, such as gravels and pebbles, therefore limiting the potential settlement of long-lived sessile species due to the dynamic nature of the substrate. In fact, areas of the shelf break with observed accumulations of large shells due to strong currents seemed to result in an impoverished community, dominated by mobile detritivores (sea urchins and holothurians) and burrowing anthozoans (small actiniarians and cerianthavians), with a lack of arborescent corals and sponges.

Considering the survey area as a whole, fishing intensity was not identified as a key factor determining the spatial distribution of benthic communities, and certainly had less overall influence than depth, substrate type and bottom current speed. This result possibly responds to the restrictive set of conditions required by the fishing fleet to develop their activities, mostly centered on soft-sediment areas of the flat continental shelf. At a regional scale, the commercial fleet tends to concentrate its activity producing areas of very high fishing intensities, generally leaving unsuitable areas unfished (Stelzenmüller & Rogers, 2008). This pattern seems clear in Cap de Creus, where the complex geological setting limits the activity of commercial trawlers to specific sedimentary areas of the shelf and the deep part of the submarine canyon. Although the effects of fishing practices on the distribution of epibenthic species and communities in Cap de Creus appeared to be low, we can expect fishing intensity to be an important factor in areas suitable for the activity of trawlers, where fishing occurs at very high frequencies. Such specific analyses should be evaluated further based on a well-defined experimental design in order to draw more robust conclusions.

4.4. Predicted spatial distribution

The Random Forest algorithm performed well to predict the
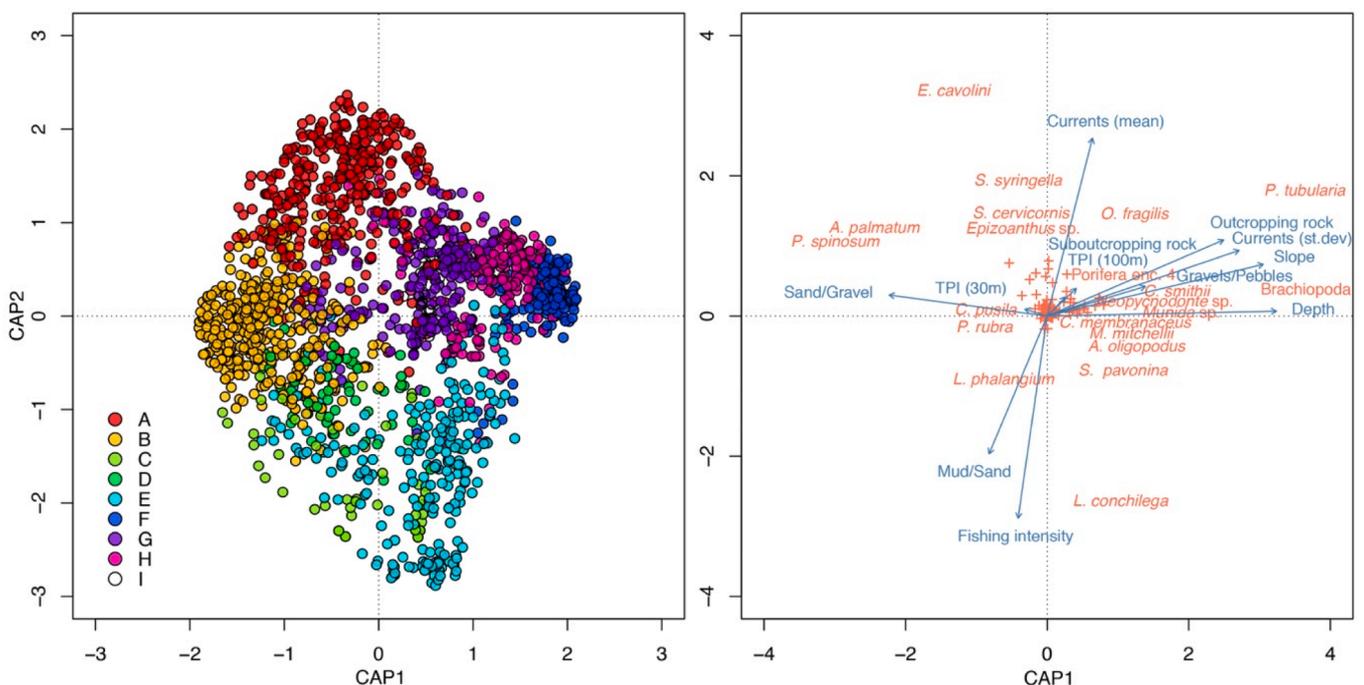
Fig. 8. Distance-based Redundancy Analysis (dbRDA) computed on Bray-Curtis dissimilarity distance over square-root density data and transformed environmental data. (a) Sampling units, colored according to the benthic community. (b) Species scores (red) and environmental variables (blue vectors). Only the species with highest scores are labeled. Crosses represent the centroids of the remaining species. TPI: Topographic Position Index. Benthic communities: A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans and alcyonaceans. C: Shelf muds and fine sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*. I: Massive aggregation of the brittle star *Ophiothrix fragilis*.
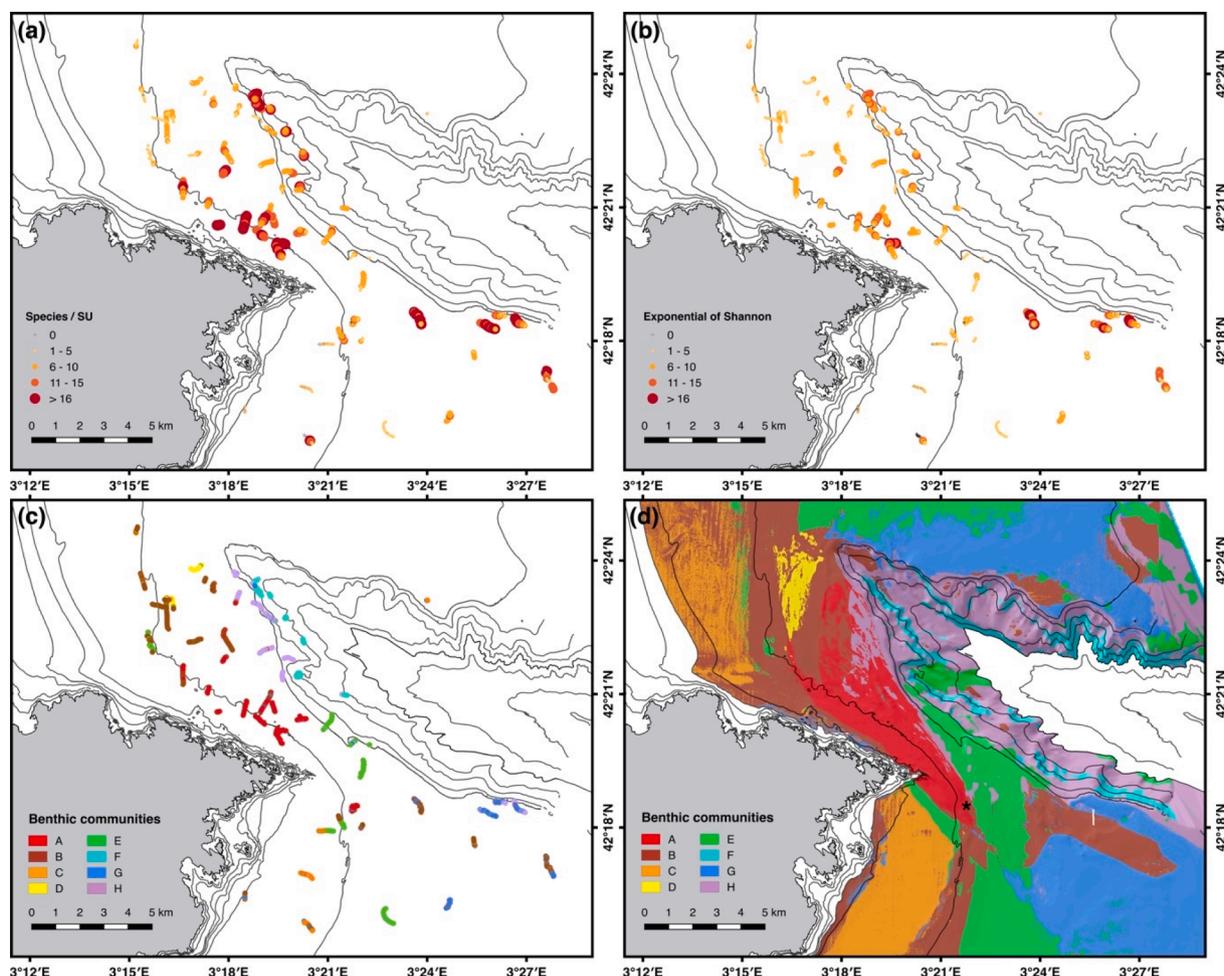
Fig. 9. Spatial distribution of the diversity of the megabenthic fauna in Cap de Creus continental shelf and submarine canyon as determined by the (a) number of species observed in each samping unit and (b) exponential of Shannon index calculated for each sampling unit. (c) Spatial distribution of the benthic communities derived from the Ward's clustering algorithm per sampling unit. (d) Predicted distribution of the identified benthic communities as derived from the Random Forest model output. Benthic communities: A: Mixed substrates of the continental shelf with *Eunicella cavolini*. B: Shelf muds and sands with pennatulaceans and alcyonaceans. C: Shelf muds and fine sands with *Sabella pavonina*. D: Coarse sands of the shelf with *Leptometra phalangium*. E: Sands and gravels of the outer shelf with *Lanice conchilega* and *Arachnanthus oligopodus*. F: Cold-water coral community with *Madrepora oculata*. G: Sponges community in mixed substrates of the outer continental shelf. H: Bathyal sands and gravels with cf. *Cerianthus membranaceus*. The location where the aggregation of the brittle star *Ophiothrix fragilis* was found is indicated with a * in (d).

distribution of benthic communities in the study area, with an overall accuracy of 83.3%. The resulting map (Fig. 9d) shows a clear zonation pattern along the depth gradient, as observed in other continental margins worldwide, with benthic communities occupying restricted depth bands (Carney, 2005). The communities dominated by octocorals and CWCs were classified with high accuracy, most possibly due to the restricted environmental conditions required by both communities to fully develop. *E. cavolini* was primarily found on shelf areas on the northern side of the cape (~100 m depth) in a characteristic mixture of substrates (Lo Iacono et al., 2012) and a mid-to-strong bottom current regime, while CWCs were mostly found at depths of 200–300 m inside the submarine canyon, in areas with steep slopes and rocky outcrops (Orejas et al., 2009; Lo Iacono et al., 2018). The communities found on the soft-bottoms of the shelf had higher rates of misclassification, particularly those found in areas exposed to intermediate and high fishing intensities. This situation possibly relates to the capacity of bottom trawling to alter the structure of the benthic community (Clark et al., 2016; Yesson et al., 2016), leading to less clear patterns to emerge and limiting the predictive capacity of the model. Also, it is worth considering that predictions made for less sampled areas, such as the north-eastern continental shelf and the northern flank of the submarine canyon, should be taken with caution, and further exploratory surveys

would surely improve the predicting capacity of the model in data-poor areas.

This work does not represent the first attempt to map the distribution of benthic communities along the marine area off Cap de Creus, and benthic cartographies for the littoral area (Sardá et al., 2012), the continental shelf (Desbruyères et al., 1972) and the submarine canyon (whole community by Reyss, 1971; CWCs by Lo Iacono et al., 2018) were already developed several years ago. Although the new map generated in this study could provide clues on how the benthic ecosystem has evolved during the past decades, differences between maps could not only originate from actual ecological changes occurred through time, but also from differences in the resolution and accuracy of the methods used to survey the fauna and produce the maps. The fraction of the biota detected using video images will inherently be different to that of samples collected using Van Veen grabs. This is mainly the case of the continental shelf (Desbruyères et al., 1972), where dissimilarities in the distribution of benthic communities are somewhat evident, although the depth-related zonation pattern identified in the 1970s still remains visible in present times. The previous work of Desbruyères et al. (1972) used a top-down approach to delimit the different habitats/communities, with distinct sediment types first identified and then related to the dominant faunistic composition. Three different benthic

communities were reported by the authors on the continental shelf, with their spatial limits coincident with changes in the sediment composition still detectable today. The bottom-up approach employed in this study, where species associations were first identified and then related to the dominant substrate types prior to modelling, generated a slightly different picture, both in terms of species associations and consequently in their spatial distribution. A similar situation occurs with the submarine canyon, where limited overlap exists between the communities mapped by Reyss (1971) and the current representation obtained in this study. More similarities exist between the predicted distribution of the CWC community from this study and the distribution of the main scleractinian corals predicted in the work of Lo Iacono et al. (2018). In this case, the spatial extent of the corals mainly follows a narrow bathymetric band (~200–350 m depth) along the southern flank of the submarine canyon, with higher occurrences in areas of higher slopes, a proxy for hard substrates. Areas with a more sub-horizontal physiography and exposed to low-to-medium hydrodynamic energy, generally coinciding with depositional environments, display a higher component of muds and sands, where burrowing and scavenger fauna become dominant. This is the case for the cerianthin community, found in areas located around the high slopes where CWCs and associated species tend to thrive.

4.5. Need for sustainable management

Several of the invertebrate species observed in the images recorded in Cap de Creus are currently considered under threat in the Mediterranean Sea, and special measures should be implemented to ensure human activities in the area are in commitment with their long-term conservation. This is the case of the CWCs *Lophelia pertusa, Madrepora oculata, Desmophyllum dianthus* and *Dendrophyllia* cornigera, all of which are assessed as 'Endangered (EN)' in the IUCN Red List of Threatened Species (Otero et al., 2017) and also included in the List of endangered or threatened species (Annex II) of the 'Protocol concerning Specially Protected areas and Biological Diversity in the Mediterranean' (UNEP/MAP-SPA/RAC, 2018), the latter also including the reported sponges *Axinella polypoides, Sarcotragus foetidus* and *Tethya* sp. The IUCN has also assessed the octocoral *Paramuricea clavata and* the sea pens *Pennatula rubra, Pteroeides spinosum* and *Funiculina quadrangularis* as 'Vulnerable (VU)' and the octocorals *Eunicella cavolini and E. singularis* as 'Near threatened (NT)' (Otero et al., 2017), all of those present in the study area and some with a high prevalence. The red coral *Corallium rubrum,* considered 'Endangered (EN)' in the IUCN Red List of Threatened Species (Otero et al., 2017), is the only species observed in the images that appears in the Habitats Directive (Annex V), which enforces specific regulations regarding its sustainable exploitation. However, since this species is not of commercial interest in the study area given the depths at which it was observed, such regulations do not apply.

Besides the flagged species listed above, several of the benthic communities observed in the images should be regarded as natural habitats for conservation listed in Annex I of the Habitats Directive. Up to three communities could be regarded as Habitat 1170 (Reefs) due to the presence of hard substrata arising from the seafloor and producing a clear zonation of benthic communities, which at the same time has a positive effect on the species richness and the diversity of the area. These communities correspond to the coral gardens of the continental shelf dominated by *E. cavolini,* the diverse sponge grounds of the outer shelf and the CWC community inside the submarine canyon. It is also likely that several areas of the community of bathyal sands and gravels with cf. *Cerianthus membranaceus* could be included under Habitat 1170 (Reefs) due to the observed accumulations of large bivalve shells in areas where this community was present (see Supplementary Fig. S6). Such biogenic hard bottoms can be important due to the increased habitat for attachement they supply to epibiotic species, fostering species richness at the local scale. Finally, and although the concept of VME was first embraced to define fragile habitats of the high seas that could be

threatened by human activities, several of the benthic communities observed in Cap de Creus may fit the definition provided by FAO of what constitutes a VME (FAO, 2009). These communities are not only biologically diverse and structurally complex contributing to increase the functional significance of the habitat (e.g. providing shelter and refuge for a large number of invertebrate and fish species), but also their conservation depends on how human activities are managed, since they may have a very slow path to recovery after disturbance. In fact, several of the benthic species and communities observed in the images are considered as habitats potentially supporting VMEs in the Mediterranean by the WGVME of the General Fisheries Commission for the Mediterranean (GFCM, 2018) (further details in Section 3.2), and their presence should be highly considered when designing management measures to ensure their long-term conservation.

The marine area surrounding Cap de Creus peninsula is currently under the umbrella of several conservation designations part of national and European regulations. The focal area of this study is found within the limits of a Site of Community Importance (SCI) of the Natura 2000 Network, designated under the Habitats Directive in 2014 (BOE, 2014). However, there are other Special Protection Areas (SPAs) and Special Areas of Conservation (SACs) in nearby areas along the coastline, as well as the Mediterranean Cetacean Migration Corridor further offshore (complete maritime spatial planning of the area in Lloret et al., 2022). This concentration of regulated areas under different regimes responds to the richness of species and habitats that can be found along this marine area, whose outstanding diversity has been recognized for decades. The Habitats Directive states that SCIs should become Special Areas of Conservation (SAC) as soon as possible, within six years at most after the declaration. This regulatory change, which has not yet been effective for this SCI, should lead to the establishment of management priorities based on the ecological importance of the site, aiming to maintain (or restore) in a good conservation status the natural habitats listed in Annex I of the directive, especially against potential threats that could lead to habitat degradation. With the increasing pressure of offshore activities potentially inducing state changes in the marine ecosystem, the implications of human activities should adequately be assessed in view of the site's conservation objectives. In this regard, the composition and spatial distribution of benthic communities provided in this study should be considered a valuable resource for managers and stakeholders when defining management actions to ensure the long-term conservation of the benthic diversity of the area, also serving as baseline data to detect changes that may occur in the future.

Declaration of Competing Interest

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

Cadaqués) for their valuable help during the littoral surveys with the min-ROV Bleeper EVO, and to Xavier Turon for his assistance in the identification of Tunicates. We are also grateful to the General Directorate of Fisheries Management of the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA) for providing of the VMS data and to Dan Orange (AOA Geophysics Inc.) for the bathymetric data of the submarine canyon. This work acknowledges the AEI 'Severo Ochoa Centre of Excellence' accreditation (CEX2019-000928-S). CD-C acknowledges the financial support received by the EU funded projects Life+ INDEMARES (LIFE07/NAT/E/000732) and ENPI ECOSAFIMED (ENPI CBC MED 2007-2013) and by the FCT-IP Project UIDP/05634/2020. CO is deeply grateful to the Hansewissenschaftskolleg – Institute for Advanced Study (HWK) for a fellowship she obtained from October 2021 to July 2022. The final version of the manuscript improved thanks to the valuable comments of anonymous reviewers.

Data availability

The georeferenced layers containing the spatial distribution of the benthic communities and its associated diversity (as shown in Fig. 9) can be downloaded from the SEANOE scientific data portal using the following link: https://www.seanoe.org/data/00784/89630/.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2022.102877.

References

Addamo, A.M., Vertino, A., Stolarski, J., García-Jiménez, R., Taviani, M., Machordom, A., 2016. Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. BMC Evolutionary Biology 16, 108. https://doi.org/10.1186/s12862-016-0654-8.

Agnesi, S., Annunziatellis, A., Chaniotis, P., Mo, G., Korpinen, S., Snoj, L., Tunesi, L., Reker, J., 2020. Spatial Analysis of Marine Protected Area Networks in Europe's Seas III. In: ETC/ ICM Technical Report 3/2020: European Topic Centre on Inland, Coastal and Marine waters, p. 40 pp..

Aguilar, R., Serrano, A., García, S., Alvarez, H., Blanco, J., Lopez, J., Marín, P., Pastor, X., 2014. Vulnerable habitats and species in the deep-sea Emile Baudot escarpment (South Balearic Islands) surveyed by ROV. In: 1st Mediterranean Symposium on the conservation of Dark Habitats, pp. 15–20.

Altuna, A., Poliseno, A., 2019. Taxonomy, Genetics and Biodiversity of Mediterranean Deep-Sea Corals and Cold-Water Corals. In: Orejas, C., Jiménez, C. (Eds.), Mediterranean cold-water corals: past, present and future. Springer, pp. 121–156. https://doi.org/10.1007/978-3-319-91608-8_14.

Ambroso, S., Gori, A., Dominguez-Carrió, C., Gili, J.M., Berganzo, E., Teixidó, N., Greenacre, M., Rossi, S., 2013a. Spatial distribution patterns of the soft corals *Alcyonium acaule* and *Alcyonium palmatum* in coastal bottoms (Cap de Creus, northwestern Mediterranean Sea). Marine Biology 160, 3059–3070. https://doi.org/10.1007/s00227-013-2295-4.

Ambroso, S., Dominguez-Carrió, C., Grinyó, J., López-González, P.J., Gili, J.M., Purroy, A., Requena, S., Madurell, T., 2013b. In situ observations on withdrawal behaviour of the sea pen *Virgularia mirabilis*. Marine Biodiversity 43, 257–258. https://doi.org/10.1007/s12526-013-0172-5.

Angeletti, L., Taviani, M., Canese, S., Foglini, F., Mastrototaro, F., Argnani, A., Trincardi, F., Bakran-Petricioli, T., Ceregato, A., Chimenti, G., Macic, V., Poliseno, A., 2013. New deep-water cnidarian sites in the southern Adriatic Sea. Mediterranean Marine Science 15, 263–273. https://doi.org/10.12681/mms.558.

Arnaud-Haond, S., van den Beld, I.M.J., Becheler, R., Orejas, C., Menot, L., Frank, N., Grehan, A.J., Bourillet, J.-F., 2017. Two "pillars" of cold-water coral reefs along Atlantic European margins: Prevalent association of *Madrepora oculata* with *Lophelia pertusa*, from reef to colony scale. Deep-Sea Research Part II 145, 110–119. https://doi.org/10.1016/j.dsr2.2015.07.013.

Aronson, R.B. (1989) Brittlestar Beds: Low-Predation Anachronisms in the British Isles. *Ecology*, **70**, 856–11. https://doi.org/10.2307/1941354.

Baillon, S., Hamel, J.F., Mercier, A., 2014. Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. Plos One 9, e111519. https://doi.org/10.1371/journal.pone.0111519.

Bastari, A., Pica, D., Ferretti, F., Micheli, F., Cerrano, C., 2018. Sea pens in the Mediterranean Sea: habitat suitability and opportunities for ecosystem recovery. ICES Journal of Marine Science 40, 261. https://doi.org/10.1093/icesjms/fsy162.

Beazley, L., Kenchington, E., Murillo, F.J., Sacau, M., 2013. Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. ICES Journal of Marine Science 70, 1471–1490. https://doi.org/10.1093/icesjms/fst124.

Bernardino, A.F., Gama, R.N., Mazzuco, A.C.A., Omena, E.P., Lavrado, H.P., 2019. Submarine canyons support distinct macrofaunal assemblages on the deep SE Brazil margin. Deep-Sea Research Part I 149, 103052. https://doi.org/10.1016/j.dsr.2019.05.012.

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 of the UK 95, 1–17. https://doi.org/10.1017/S0025315413001380.

Best, B.A., 1988. Passive suspension feeding in a sea pen: effects of ambient flow on volume flow rate and filtering efficiency. Biological Bulletin 175, 332. https://doi.org/10.2307/1541723.

Beuck, L., Aguilar, R., Fabri, M.C., Freiwald, A., Gofas, S., Hebbeln, D., Lopez Correa, M., Ramos Martos, A., Ramil, F., Sanchez Delgado, F., Taviani, M., Wienberg, C., Wisshak, M., Zibrowius, H., 2016. Biotope characterisation and compiled geographical distribution of the deep-water oyster *Neopycnodonte zibrowii* in the Atlantic Ocean and Mediterranean Sea. Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee 41, 462.

Blanchet-Aurigny, A., Dubois, S.F., Hily, C., Rochette, S., Le Goaster, E., Guillou, M., 2012. Multi-decadal changes in two co-occurring ophiuroid populations. Marine Ecology Progress Series 460, 79–90. https://doi.org/10.3354/meps09784.

Bo, M., Bertolino, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., Pansini, M., Taviani, M., 2011. Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. Hydrobiologia 687, 163–177. https://doi.org/10.1007/s10750-011-0964-1.

Bo, M., Canese, S., Spaggiari, C., Pusceddu, A., Bertolino, M., Angiolillo, M., Giusti, M., Loreto, M.F., Salvati, E., Greco, S., Bavestrello, G., 2012. Deep coral oases in the South Tyrrhenian Sea. PlosOne 7, e49870–14. https://doi.org/10.1371/journal.pone.0049870.

Bo, M., Bavestrello, G., Angiolillo, M., Calcagnile, L., Canese, S., Cannas, R., Cau, A., D'Elia, M., D'Oriano, F., Follesa, M.C., Quarta, G., Cau, A., 2015. Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PlosOne 10, e0119393–21. https://doi.org/10.1371/journal.pone.0119393.

BOE, 1998. Ley 4/1998, de 12 de marzo. de Protección de Cap de Creus, Boletín Oficial del Estado, Madrid.

BOE, 2014. Orden AAA/1299/2014, de 9 de julio, por la que se aprueba la propuesta de inclusión en la lista de lugares de importancia comunitaria de la Red Natura 2000 de los espacios marinos ESZZ16001 Sistema de cañones submarinos occidentales del Golfo de León, ESZZ16002 Canal de Menorca, ESZZ12002 Volcanes de fango del Golfo de Cádiz y ESZZ12001 Banco de Galicia. Boletín Oficial del Estado, Madrid.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer Science & Business Media. https://doi.org/10.1007/978-1-4419-7976-6.

Breiman, L., 2001. Random Forests. Machine Learning 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Brown, C.J., Smith, S.J., Lawton, P., Anderson, J.T., 2011. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuarine, Coastal and Shelf Science 92, 502–520. https://doi.org/10.1016/j.ecss.2011.02.007.

Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., Raes, M., 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31, 21–50. https://doi.org/10.1111/j.1439-0485.2010.00359.x.

Buhl-Mortensen, L., Mortensen, P.B., Dolan, M.J.F., Gonzalez-Mirelis, G., 2015a. Habitat mapping as a tool for conservation and sustainable use of marine resources: Some perspectives from the MAREANO Programme, Norway. Journal of Sea Research 100, 46–61. https://doi.org/10.1016/j.seares.2014.10.014.

Buhl-Mortensen, L., Olafsdottir, S.H., Buhl-Mortensen, P., Burgos, J.M., Ragnarsson, S.A., 2015b. Distribution of nine cold-water coral species (Scleractinia and Gorgonacea) in the cold temperate North Atlantic: effects of bathymetry and hydrography. Hydrobiologia 759, 39–61. https://doi.org/10.1007/s10750-014-2116-x.

Buhl-Mortensen, L., Ellingsen, K.E., Buhl-Mortensen, P., Skaar, K.L., Gonzalez-Mirelis, G., 2016. Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition. ICES Journal of Marine Science 73, i98–i114. https://doi.org/10.1093/icesjms/fsv200.

Buhl-Mortensen, P., Buhl-Mortensen, L., 2018. Impacts of Bottom Trawling and Litter on the Seabed in Norwegian Waters. Frontiers in Marine Science 5, 42. https://doi.org/10.3389/fmars.2018.00042.

Canals, M., Puig, P., Durrieu de Madron, X., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. Nature 444, 354–357. https://doi.org/10.1038/nature05271.

Canals, M., Danovaro, R., Marco Luna, G., 2019. Recent advances in understanding the ecology and functioning of submarine canyons in the Mediterranean Sea. Progress in Oceanography 179, 102171. https://doi.org/10.1016/j.pocean.2019.102171.

Canessa, M., Bavestrello, G., Trainito, E., Bianchi, C.N., Morri, C., Navone, A., Cattaneo-Vietti, R., 2021. A large and erected sponge assemblage on granite outcrops in a Mediterranean Marine Protected Area (NE Sardinia). Regional Studies in Marine Science 44, 101734. https://doi.org/10.1016/j.rsma.2021.101734.

Carney, R., 2005. Zonation of deep biota on continental margins. Oceanography and Marine Biology: An Annual Review 43, 211–278.

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 assemblages composition and biomass trends. Journal of Sea Research 61, 244–257. https://doi.org/10.1016/j.seares.2009.01.005.

Cathalot, C., van Oevelen, D., Cox, T.J.S., Kutti, T., Lavaleye, M., Duineveld, G.C.A., Meysman, F.J.R., 2015. Cold-water coral reefs and adjacent sponge grounds:

hotspots of benthic respiration and organic carbon cycling in the deep sea. Front. Mar. Sci. 2, 37. https://doi.org/10.3389/fmars.2015.00037.

Cebrian, E., Ballesteros, E., 2004. Zonation patterns of benthic communities in an upwelling area from the western Mediterranean (La Herradura, Alboran Sea). Scientia Marina 68, 69–84. https://doi.org/10.3989/scimar.2004.68n169.

Chainey, S.P., 2013. Examining the influence of cell size and bandwidth size on kernel density estimation crime hotspot maps for predicting spatial patterns of crime. Bulletin of the Geographical Society of Liege 60, 7–19.

Chappuis, E., Terradas, M., Cefalì, M.E., Mariani, S., Ballesteros, E., 2014. Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. Estuarine, Coastal and Shelf Science 147, 113–122. https://doi.org/10.1016/j.ecss.2014.05.031.

Chimenti, G., Angeletti, L., Mastrototaro, F., 2018. Withdrawal behaviour of the red sea pen *Pennatula rubra* (Cnidaria: Pennatulacea). The European Zoological Journal 85, 64–70. https://doi.org/10.1080/24750263.2018.1438530.

Chimienti, G, Bo, M., Taviani, M., Mastrototaro, F., 2019. Occurrence and biogeography of Mediterranean cold-water corals. In: Orejas, C., Jiménez, C. (Eds.), Mediterranean cold-water corals: past, present and future. Springer, pp. 213–244. https://doi.org/10.1007/978-3-319-91608-8_19.

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, i51–i69. https://doi.org/10.1093/icesjms/fsv123.

Cogan, C.B., Todd, B.J., Lawton, P., Noji, T.T., 2009. The role of marine habitat mapping in ecosystem-based management. ICES Journal of Marine Science 66, 2033–2042. https://doi.org/10.1093/icesjms/fsp214.

Colloca, F., Cardinale, M., Belluscio, A., Ardizzone, G.D., 2003. Pattern of distribution and diversity of demersal assemblages in the central Mediterranean Sea. Estuarine, Coastal and Shelf Science 56, 469–480. https://doi.org/10.1016/S0272-7714(02)00196-8.

Colloca, F., Carpentieri, P., Balestri, E., Ardizzone, G.D., 2004. A critical habitat for Mediterranean fish resources: shelf-break areas with *Leptometra phalangium* (Echinodermata: Crinoidea). Marine Biology 145, 1129–1142. https://doi.org/10.1007/s00227-004-1405-8.

Cooper, K.M., Bolam, S.G., Downie, A.L., Barry, J., 2019. Biological-based habitat classification approaches promote cost-efficient monitoring: an example using seabed assemblages. Journal of Applied Ecology 56, 1085–1098. https://doi.org/10.1111/1365-2664.13381.

Corbera, G.L., Iacono, C., Gràcia, E., Grinyó, J., Pierdomenico, M., Huvenne, V.A.I., Aguilar, A., Gili, J.M., 2019. Ecological characterisation of a Mediterranean cold-water coral reef: Cabliers Coral Mound Province (Alboran Sea, western Mediterranean). Progress in Oceanography 175, 245–262. https://doi.org/10.1016/j.pocean.2019.04.010.

Cruzado, A., Velasquez, Z.R., 1990. Nutrients and phytoplankton in the Gulf of Lions, northwestern Mediterranean. Continental Shelf Research 10, 931–942. https://doi.org/10.1016/0278-4343(90)90068-W.

Curd, A. (2010) Background Document for Seapen and Burrowing Megafauna Communities. OSPAR Commission.

Curtin, R., Prellezo, R., 2010. Understanding marine ecosystem-based management: A literature review. Marine Policy 34, 821–830. https://doi.org/10.1016/j.marpol.2010.01.003.

D'Onghia, G., Maiorano, P., Sion, L., Giove, A., Capezzuto, F., Carlucci, R., Tursi, A., 2010. Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep Sea Research Part II: Topical Studies in Oceanography 57, 397–411. https://doi.org/10.1016/j.dsr2.2009.08.022.

D'Onghia, G. (2019) Cold-water corals as shelter, feeding and life-history critical habitats for fish species: Ecological interactions and fishing impact. In: Orejas, C. & Jiménez, C. (eds.) Mediterranean cold-water corals: past, present and future. Springer. pp. 335-356. https://doi.org/10.1007/978-3-319-91608-8_30.

Dauvin, J.C., Méar, Y., Murat, A., Poizot, E., Lozach, S., Beryouni, K., 2013. Interactions between aggregations and environmental factors explain spatio-temporal patterns of the brittle-star *Ophiothrix fragilis* in the eastern Bay of Seine. Estuarine, Coastal and Shelf Science 131, 171–181. https://doi.org/10.1016/j.ecss.2013.07.005.

Davoult, D., Gounin, F., 1995. Suspension-feeding activity of a dense *Ophiothrix fragilis* (Abildgaard) population at the water-sediment interface: Time coupling of food availability and feeding behaviour of the species. Estuarine, Coastal and Shelf Science 41, 567–577. https://doi.org/10.1016/0272-7714(95)90027-6.

De Clippele, L.H., Mortensen, P.B., Buhl-Mortensen, L., 2015. Fauna associated with cold water gorgonians and sea pens. Continental Shelf Research 105, 67–78. https://doi.org/10.1016/j.csr.2015.06.007.

De la Torriente, A., Serrano, A., Fernández-Salas, L.M., García, M., Aguilar, R., 2018. Identifying epibenthic habitats on the Seco de los Olivos Seamount: Species assemblages and environmental characteristics. Deep-Sea Research Part I 135, 9–22. https://doi.org/10.1016/j.dsr.2018.03.015.

De la Torriente, A., González-Irusta, J.M., Aguilar, R., Fernández Salas, L.M., Punzón, A., Serrano, A., 2019. Benthic habitat modelling and mapping as a conservation tool for marine protected areas: A seamount in the western Mediterranean. Aquatic Conservation: Marine & Freshwater Ecosystems 29, 732–750. https://doi.org/10.1002/aqc.3075.

DeGeest, A.L., Mullenbach, B.L., Puig, P., Nittrouer, C.A., Drexler, T.M., Durrieu de Madron, X., Orange, D.L., 2008. Sediment accumulation in the western Gulf of Lions, France: The role of Cap de Creus Canyon in linking shelf and slope sediment dispersal systems. Continental Shelf Research 28, 2031–2047. https://doi.org/10.1016/j.csr.2008.02.008.

Desbruyères, D., Guille, A., Ramos, J., 1972. Bionomie benthique du plateau continental de la côte catalane espagnole. Vie et Milieu 23, 335–363.

Dolan, M.F.J., Ross, R.E., Albretsen, J., Skarðhamar, J., Gonzalez-Mirelis, G., Bellec, V.K., Buhl-Mortensen, P., Bjarnadóttir, L.R., 2021. Using Spatial Validity and Uncertainty Metrics to Determine the Relative Suitability of Alternative Suites of Oceanographic Data for Seabed Biotope Prediction. A Case Study from the Barents Sea, Norway. Geosciences 11, 48. https://doi.org/10.3390/geosciences11020048.

Dominguez-Carrió, C., Sanchez-Vidal, A., Estournel, C., Corbera, G., Riera, J.L., Orejas, C., Canals, M., Gili, J.M., 2020. Seafloor litter sorting in different domains of Cap de Creus continental shelf and submarine canyon (NW Mediterranean Sea). Marine Pollution Bulletin 161, 111744. https://doi.org/10.1016/j.marpolbul.2020.111744.

Dominguez-Carrió, C., Fontes, J., Morato, T., 2021a. A cost-effective video system for a rapid appraisal of deep-sea benthic habitats: The Azor drift-cam. Methods in Ecology and Evolution 12, 1379–1388. https://doi.org/10.1111/2041-210X.

Dominguez-Carrió, C., Lopez-González, P.J., Uriz, M.J., Zabala, M., Sardá, R., Turon, X., Orejas, C., Gori, A., Gili, J.M., 2021b. Photographic catalogue of the invertebrate megafauna identified in the video footage recorded on the continental shelf and submarine canyon off Cap de Creus (NW Mediterranean) as part of the Life+ INDEMARES project. 52, pp. Zenodo. https://doi.org/10.5281/zenodo.5794759.

Du Preez, C., Curtis, J.M.R., Clarke, M.E., 2016. The structure and distribution of benthic communities on a shallow seamount (Cobb Seamount, Northeast Pacific Ocean). PlosOne 11, e0165513. https://doi.org/10.1371/journal.pone.0165513.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Ec,, 1979. Council Directive 79/409/EEC of 2 April 1979 on the conservation of wild birds. Official Journal L 103.

EC (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.

EC (2013) Interpretation Manual of European Union Habitats. In: EUR28. European Commision DG Environment, 144 pp.

Enrichetti, F., Dominguez-Carrió, C., Toma, M., Bavestrello, G., Betti, F., Canese, S., Bo, M., 2019a. Megabenthic communities of the Ligurian deep continental shelf and shelf break (NW Mediterranean Sea). PlosOne 14, e0223949. https://doi.org/10.1371/journal.pone.0223949.

Enrichetti, F., Bava, S., Bavestrello, G., Betti, F., Lanteri, L., Bo, M., 2019b. Artisanal fishing impact on deep coralligenous animal forests: A Mediterranean case study of marine vulnerability. Ocean and Coastal Management 177, 112–126. https://doi.org/10.1016/j.ocecoaman.2019.04.021.

Enrichetti, F., Bavestrello, G., Betti, F., Coppari, M., Toma, M., Pronzato, R., Canese, S., Bertolino, M., Costa, G., Pansini, M., Bo, M., 2020. Keratose-dominated sponge grounds from temperate mesophotic ecosystems (NW Mediterranean Sea). Marine Ecology 41, e12620. https://doi.org/10.1111/maec.12620.

Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G.E., Egekvist, J., Fock, H.O., Geitner, K., Gerritsen, H.D., González, M.M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J.R., Papadopoulou, N., Posen, P.E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C.J., Vanelslander, B., Rijnsdorp, A.D., 2016. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES Journal of Marine Science 74, 847–865. https://doi.org/10.1093/icesjms/fsw194.

Estournel, C., Testor, P., Damien, P., D'Ortenzio, F., Marsaleix, P., Conan, P., Kessouri, F., Durrieu de Madron, X., Coppola, L., Lellouche, J.M., Belamari, S., Mortier, L., Ulses, C., Bouin, M.N., Prieur, L., 2016. High resolution modeling of dense water formation in the north-western Mediterranean during winter 2012–2013: Processes and budget. *Journal of Geophysical Research* –. Oceans 121, 5367–5392. https://doi.org/10.1002/2016JC011935.

Evans, D., 2012. Building the European Union's Natura 2000 network. Nature Conservation 1, 11–16. https://doi.org/10.3897/natureconservation.1.1808.

Fao, 2009. International guidelines for the management of deep-sea fisheries in the High Seas 73, pp..

Fabri, M.C., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D., Freiwald, A., 2014. Megafauna of vulnerable marine ecosystems in French mediterranean submarine canyons. Spatial distribution and anthropogenic impacts. Deep-Sea Research Part II 104, 184–207. https://doi.org/10.1016/j.dsr2.2013.06.016.

Fiala-Medioni, A., Madurell, T., Romans, P., Reyss, D., Pibot, A., Watremez, P., Ghiglione, M., Ferrari, B., Vuillemin, R., Lebaron, P., 2012. ROV and submersible surveys on faunal assemblages in a deep-sea canyon (Rech Lacaze-Duthiers, Western Mediterranean Sea). Vie et Milieu 62 (4), 173–190.

Fedra, K., Ölscher, E.M., Scherübel, C., Stachowitsch, M., Wurzian, R.S., 1976. On the ecology of a North Adriatic benthic community: Distribution, standing crop and composition of the macrobenthos. Marine Biology 38, 129–145. https://doi.org/10.1007/BF00390766.

Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A.L., Davies, J.S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V., Macmillan-Lawler, M., Martín, J., Menot, L., Nizinski, M., Puig, P., Rowden, A.A., Sanchez, F., van den Beld, I., 2017. Ecological Role of Submarine Canyons and Need for Canyon Conservation: A Review. Frontiers in Marine Science 4, 5. https://doi.org/10.3389/fmars.2017.00005.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. Journal of Applied Ecology 43, 393–404. https://doi.org/10.1111/j.1365-2664.2006.01149.x.

Forero Mejia, A., Bo, M., Canese, S., Bavestrello (2015) I ceriantari del circalitorale profondo Mediterraneo. 46° Congresso della Società Italiana di Biologia Marina, Roma.

Fourt, M., Goujard, A., Perez, T., Chevaldonné, P. (2017) Guide de la faune profonde de la mer Méditerranée. Exploration des roches et canyons sous-marins des côtes françaises. Muséum National d'Histoire Naturelle, Paris. 184 pp.

Franklin, J. (2010) Mapping Species Distributions. Cambridge University Press (UK). 340 pp.

Freiwald, A., Beuck, L., Rüggeberg, A., Taviani, M., Hebbeln, D., 2009. The White Coral Community in the Central Mediterranean Sea Revealed by ROV Surveys. Oceanography 22, 58–74. https://doi.org/10.5670/oceanog.2009.06.

Garrabou, J., Ballesteros, E., Zabala, M., 2002. Structure and dynamics of north-western mediterranean rocky benthic communities along a depth gradient. Estuarine, Coastal and Shelf Science 55, 493–508. https://doi.org/10.1006/ecss.2001.0920.

Genin, A., Paull, C.K., Dillon, W.P., 1992. Anomalous abundances of deep-sea fauna on a rocky bottom exposed to strong currents. *Deep Sea Research Part I*. Oceanographic Research Papers 39, 293–302. https://doi.org/10.1016/0198-0149(92)90110-F.

Gili, J.M., Pagès, F., 1987. Pennatulaceos (Cnidaria, Anthozoa) recolectados en la plataforma continental catalana (Mediterráneo occidental). Miscellania Zoologica 11, 25–39.

Gomez-Ballestero, M., Vazquez, J.-T., Palomino, D., Rovere, M., Bo, M., Alessi, J., Fiori, C., Würtz, M., 2015. Seamounts and Seamount-like Structures of the Western Mediterranean. In: Atlas of the Mediterranean Seamounts and Seamount-Like Structures. IUCN, Gland, Switzerland and Málaga, Spain, pp. 59–109.

Gonzalez-Mirelis, G., Buhl-Mortensen, P., 2015. Modelling benthic habitats and biotopes off the coast of Norway to support spatial management. Ecological Informatics 30, 284–292. https://doi.org/10.1016/j.ecoinf.2015.06.005.

Goode, S.L., Rowden, A.A., Bowden, D.A., Clark, M.R., Stephenson, F., 2021. Fine-Scale Mapping of Mega-Epibenthic Communities and Their Patch Characteristics on Two New Zealand Seamounts. Frontiers in Marine Science 8, 765407. https://doi.org/10.3389/fmars.2021.765407.

Gori, A., Olariaga, A., Orejas, C., Rossi, S., Quesada, S., Valentin, A., Bosch, I., Turró, J., Mestre, M., Sanz, J.L., Teixidó, J., Gili, J.-M., 2009. Bleeper-EVO: An Easy-to-Handle ROV for Benthic Study. Oceanography 22, 75. https://doi.org/10.5670/oceanog.2009.07.

Gori, A., Rossi, S., Berganzo, E., Pretus, J.L., Dale, M.R.T., Gili, J.M., 2011. Spatial distribution patterns of the gorgonians *Eunicella singularis*, *Paramuricea clavata*, and *Leptogorgia sarmentosa* (Cape of Creus, Northwestern Mediterranean Sea). Marine Biology 158, 143–158. https://doi.org/10.1007/s00227-010-1548-8.

Gori, A., Orejas, C., Madurell, T., Bramanti, L., Martins, M., Quintanilla, E., Marti-Puig, P., Lo Iacono, C., Puig, P., Requena, S., Greenacre, M., Gili, J.M., 2013. Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). Biogeosciences 10, 2049–2060. https://doi.org/10.5194/bg-10-2049-2013.

Greathead, C.F., Donnan, D.W., Mair, J.M., Saunders, G.R., 2007. The sea pens *Virgularia mirabilis*, *Pennatula phosphorea* and *Funiculina quadrangularis*: distribution and conservation issues in Scottish waters. Journal of the Marine Biological Association of the UK 87, 1–10. https://doi.org/10.1017/S0025315407056238.

Grinyó, J., Gori, A., Ambroso, S., Purroy, A., Calatayud, C., Dominguez-Carrió, C., Coppari, M., Lo Iacono, C., López-González, P.J., Gili, J.M., 2016. Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Progress in Oceanography 145, 42–56. https://doi.org/10.1016/j.pocean.2016.05.001.

Grinyó, J., Gori, A., Greenacre, M., Requena, S., Canepa, A., Lo Iacono, C., Ambroso, S., Purroy, A., Gili, J.M., 2018. Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea. Progress in Oceanography 162, 40–51. https://doi.org/10.1016/j.pocean.2018.02.002.

Guille, A. (1964) Observations faites en soucoupe plongeante a la limite inférieure d'un fond a *Ophiothrix quinquemaculata* d. ch. a au large de la côte du Roussillon. *Rapports de la Commission Internationale pour lExploration Scientifique de la Mer Mediterranee*, **18 (2)**, 115–118.

Guille, A., 1965. Exploration en soucoupe plongeante Cousteau de l'entrée nord-est de la baie de Rosas (Espagne). Bulletin de l'Institut océanographique de Monaco 65, 1–13.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9.

Haggarty, D.R., Shurin, J.B., Yamanaka, K.L., 2016. Assessing population recovery inside British Columbia's Rockfish Conservation Areas with a remotely operated vehicle. Fisheries Research 183, 165–179. https://doi.org/10.1016/j.fishres.2016.06.001.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952. https://doi.org/10.1126/science.1149345.

Hanz, U., Roberts, E.M., Duineveld, G.C.A., Davies, J.S., van Haren, H., Rapp, H.T., Reichart, G.-J., Mienis, F. (2021) Long-term Observations Reveal Environmental Conditions and Food Supply Mechanisms at an Arctic Deep-Sea Sponge Ground. *Journal of Geophysical Research - Oceans*, **126**, e2020JC016776. https://doi.org/10.1029/2020JC016776.

Henry, L.A., Roberts, J.M., 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Research Part I*. Oceanographic Research Papers 54, 654–672. https://doi.org/10.1016/j.dsr.2007.01.005.

Herrmann, M.J., Somot, S., 2008. Relevance of ERA40 dynamical downscaling for modeling deep convection in the Mediterranean Sea. Geophysical Research Letters 35, L04607–5. https://doi.org/10.1029/2007GL032442.

Herrmann, M.J., Sevault, F., Beuvier, J., Somot, S., 2010. What induced the exceptional 2005 convection event in the northwestern Mediterranean basin? Answers from a modeling study. Journal of Geophysical Research 115, C12051–19. https://doi.org/10.1029/2010JC006162.

Hasan, R.C., Ierodiaconou, D., Monk, J., 2012. Evaluation of Four Supervised Learning Methods for Benthic Habitat Mapping Using Backscatter from Multi-Beam Sonar. Remote Sensing 4, 3427–3443. https://doi.org/10.3390/rs4113427.

Heuers, J., Jaklin, S., Zuhlke, R., Dittmann, S., Gunther, C.P., Hildenbrandt, H., Grimm, H., 1997. A model on the distribution and abundance of the tube-building polychaete *Lanice conchilega* (Pallas, 1766) in the intertidal of the Wadden Sea. Verhandlungen der Gesellschaft fur Okologie 28, 207–215.

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, C. R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proceedings of the National Academy of Sciences of the United States of America 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114.

Hissmann, K., Schauer, J., 2017. Manned submersible "JAGO". Journal of large-scale research facilities 3, A110. https://doi.org/10.17815/jlsrf-3-157.

Hogg, M.M., Tendal, O.S., Conway, K.W., Pomponi, S.A., Van Soest, R.W.M., Gutt, J., Krautter, M., Roberts, J.M., 2010. Deep-Sea Sponge Grounds: Reservoirs of Biodiversity. UNEP/WCMC, Cambridge, UK.

Holme, N.A., 1984. Fluctuations of Ophiothrix fragilis in the western English Channel. Journal of the Marine Biological Association of the United Kingdom 64, 351–378. https://doi.org/10.1017/s0025315400030058.

Huvenne, V.A.I., Bett, B.J., Masson, D.G., Le Bas, T.P., Wheeler, A.J., 2016. Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. Biological Conservation 200, 60–69. https://doi.org/10.1016/j.biocon.2016.05.030.

Jouffray, J.-B., Blasiak, R., Norström, A.V., Österblom, H., Nyström, M., 2020. The Blue Acceleration: The Trajectory of Human Expansion into the Ocean. One Earth 2, 43–54. https://doi.org/10.1016/j.oneear.2019.12.016.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439. https://doi.org/10.1890/06-1736.1.

Kallianiotis, A., Sophronidis, K., Vidoris, P., Tselepides, A., 2000. Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): seasonal variation in species density, biomass and diversity. Progress in Oceanography 46, 429–455. https://doi.org/10.1016/S0079-6611(00)00028-8.

Lacharité, M., Metaxas, A., 2017. Hard substrate in the deep ocean: How sediment features influence epibenthic megafauna on the eastern Canadian margin. Deep-Sea Research Part I 126, 50–61. https://doi.org/10.1016/j.dsr.2017.05.013.

Lastras, G., Canals, M., Urgeles, R., Amblas, D., Ivanov, M., Droz, L., Dennielou, B., Fabrés, J., Schoolmeester, T., Akhmetzhanov, A., Orange, D., García-García, A., 2007. A walk down the Cap de Creus canyon, Northwestern Mediterranean Sea: Recent processes inferred from morphology and sediment bedforms. Marine Geology 246, 176–192. https://doi.org/10.1016/j.margeo.2007.09.002.

Lastras, G., Canals, M., Ballesteros, E., Gili, J.M., Sanchez-Vidal, A., 2016. Cold-water corals and anthropogenic impacts in la Fonera submarine canyon head, northwestern Mediterranean Sea. Plos One 11, e0155729. https://doi.org/10.1371/journal.pone.0155729.

Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. ICES Journal of Marine Science 67, 1260–1271. https://doi.org/10.1093/icesjms/fsq010.

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69, 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.

Legendre, P., Legendre, L., 2012. Numerical Ecology, 3rd English Edition. Elsevier, Amsterdam.

Leonard, C., Evans, J., Knittweis, L., Aguilar, R., Alvarez, H., Borg, J.A., García, S., Schembri, P.J., 2020. Diversity, distribution, and habitat associations of deep-water echinoderms in the Central Mediterranean. Marine Biodiversity 50, 1–15. https://doi.org/10.1007/s12526-020-01095-3.

Lessard-Pilon, S.A., Podowski, E.L., Cordes, E., Fisher, C.R., 2010. Megafauna community composition associated with *Lophelia pertusa* colonies in the Gulf of Mexico. An update. Deep Sea Research Part II 57, 1882–1890. https://doi.org/10.1016/j.dsr2.2010.05.013.

Levin, L.A., Dayton, P.K., 2009. Ecological theory and continental margins: where shallow meets deep. Trends in Ecology and Evolution 24, 606–617. https://doi.org/10.1016/j.tree.2009.04.012.

Levin, L.A., Sibuet, M., 2012. Understanding continental margin biodiversity: a new imperative. Annual Review of Marine Science 4, 79–112. https://doi.org/10.1146/annurev-marine-120709-142714.

Liaw, A., Wiener, M., 2002. Classification and Regression by *randomForest*. R News 2 (3), 18–22.

Linley, T.D., Lavaleye, M., Maiorano, P., Bergman, M., Capezzuto, F., Cousins, N.J., D'Onghia, G., Duineveld, G.C.A., Shields, M.A., Sion, L., Tursi, A., Priede, I.G., 2017. Effects of cold-water corals on fish diversity and density (European continental margin: Arctic, NE Atlantic and Mediterranean Sea): Data from three baited lander systems. Deep Sea Research Part II 145, 8–21. https://doi.org/10.1016/j.dsr2.2015.12.003.

Lloret, J., Turiel, A., Sole, J., Berdalet, E., Sabatés, A., Olivares, A., Gili, J.-M., Vila-Subirós, J., Sardá, R., 2022. Unravelling the ecological impacts of large-scale offshore wind farms in the Mediterranean Sea. Science of the Total Environment 824, 153803. https://doi.org/10.1016/j.scitotenv.2022.153803.

Lo Iacono, C., Orejas, C., Gori, A., Gili, J.M., Requena, S., Puig, P., Ribó, M., 2012. Habitats of the Cap de Creus Continental Shelf and Cap de Creus Canyon, Northwestern Mediterranean. In: Harris, P., Baker, E. (Eds.), Seafloor geomorphology as benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, Amsterdam, pp. 457–469. https://doi.org/10.1016/B978-0-12-385140-6.00032-3.

Lo Iacono, C., Robert, K., Gonzalez-Villanueva, R., Gori, A., Gili, J.M., Orejas, C., 2018. Predicting cold-water coral distribution in the Cap de Creus Canyon (NW Mediterranean): Implications for marine conservation planning. Progress in Oceanography 169, 169–180. https://doi.org/10.1016/j.pocean.2018.02.012.

Madurell, T., Orejas, C., Requena, S, Gori, A., Purroy, A., Lo Iacono, C., Sabatés, A., Dominguez-Carrió, C., Gili, J.-M. (2012) The benthic communities of the Cap de Creus canyon. In Würts (Ed.) Mediterranean Submarine Canyons: Ecology and Governance. Gland, Switzerland and Málaga, Spain: IUCN. 216 pages.

Madurell, T., Zabala, M., Dominguez-Carrió, C., Gili, J.-M., 2013. Bryozoan faunal composition and community structure from the continental shelf off Cap de Creus (Northwestern Mediterranean). Journal of Sea Research 83, 123–136. https://doi.org/10.1016/j.seares.2013.04.013.

Maechler, M., Rousseeuw, P., Struyf, A., Hornik, K., Studer, M., Roudier, P., Gonzalez, J. (2017) Package cluster: "Finding groups in data": Cluster analysis extended.

Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E.L.R., Leys, S.P., Pomponi, S.A., Rapp, H.T., Rützler, K., Tendal, O.S., Vacelet, J., Young, C.M. (2017) Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns. In: Rossi S., Bramanti L., Gori A., Orejas C. (eds) Marine Animal Forests. Springer, Cham. pp. 145-183. https://doi.org/10.1007/978-3-319-17001-5_24-1.

Mallol, S. (2005) Anàlisi dels descartaments efectuats per la flota d'arrossegament en el Golf de Lleó. PhD thesis, Universitat de Girona.

Marín, P., Pastor, X., Aguilar, R., Garcia, S., Pardo, E., Ubero, J. (2011) Montañas submarinas de las Islas Baleares: Canal de Mallorca 2011. Propuesta de protección para Ausias March, Emile Baudot y Ses Olives. Oceana.

Marsaleix, P., Auclair, F., Floor, J.W., Herrmann, M.J., Estournel, C., Pairaud, I., Ulses, C., 2008. Energy conservation issues in sigma-coordinate free-surface ocean models. Ocean Modelling 20, 61–89. https://doi.org/10.1016/j.ocemod.2007.07.005.

Marsaleix, P., Auclair, F., Duhaut, T., Estournel, C., Nguyen, C., Ulses, C., 2012. Alternatives to the Robert-Asselin filter. Ocean Modelling 41, 53–66. https://doi.org/10.1016/j.ocemod.2011.11.002.

Martín, P., Aguilar, R., García, S., Pardo, E., 2011. Montes Submarinos del Mediterráneo: Seco de Palos. Propuesta de protección, Oceana, p. 44.

Mastrototaro, F., D'Onghia, G., Corriero, G., Matarrese, A., Maiorano, P., Panetta, P., Gherardi, M., Longo, C., Rosso, A., Sciuto, F., Sanfilippo, R., Gravili, C., Boero, F., Taviani, M., Tursi, A., 2010. Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea) An update. Deep Sea Research Part II 57, 412–430. https://doi.org/10.1016/j.dsr2.2009.08.021.

McIntyre, F.D., Drewery, J., Eerkes-Medrano, D., Neat, F.C., 2016. Distribution and diversity of deep-sea sponge grounds on the Rosemary Bank Seamount. NE Atlantic. *Marine Biology* 163, 603. https://doi.org/10.1007/s00227-016-2913-z.

Michez, N., Fourt, M., Aish, A., Bellan, G., Bellan-Santini, D., Chevaldonné, P., Fabri, M.C., Goujard, A., Harmelin, J.G., Labrune, C., Pergent, G., Sartoretto, S., Vacelet, J., Velarque, M. (2014) Typologie des biocénoses benthiques de Méditerranée. Rapport SPN 2014 - 33, MNHN, Paris. 26 pp.

Millot, C., 1990. The Gulf of Lions' hydrodynamics. Continental Shelf Research 10, 885–894. https://doi.org/10.1016/0278-4343(90)90065-T.

Moccia, D., Cau, A., Bramanti, L., Carugati, L., Canese, S., Follesa, M.C., Cannas, R., 2021. Spatial distribution and habitat characterization of marine animal forest assemblages along nine submarine canyons of Eastern Sardinia (central Mediterranean Sea). Deep-Sea Research Part I 167, 103422. https://doi.org/10.1016/j.dsr.2020.103422.

Montefalcone, M., Tunesi, L., Ouerghi, A., 2021. A review of the classification systems for marine benthic habitats and the new updated Barcelona Convention classification for the Mediterranean. Marine Environmental Research 169, 105387. https://doi.org/10.1016/j.marenvres.2021.105387.

Montseny, M., Linares, C., Viladrich, N., Biel, M., Gracias, N., Baena, P., Quintanilla, E., Ambroso, S., Grinyó, J., Santín, A., Salazar, J., Carreras, M., Palomeras, N., Magí, L., Vallicrosa, G., Gili, J.-M., Gori, A., 2021. Involving fishers in scaling up the restoration of cold-water coral gardens on the Mediterranean continental shelf. Biological Conservation 262, 109301. https://doi.org/10.1016/j.biocon.2021.109301.

O'Brien, J.M., Stanley, R.R.E., Jeffery, N.W., Heaslip, S.G., DiBacco, C., Wang, Z., 2022. Modeling demersal fish and benthic invertebrate assemblages in support of marine conservation planning. Ecological Applications 32, e2546. https://doi.org/10.1002/eap.2546.

Ogston, A.S., Drexler, T.M., Puig, P., 2008. Sediment delivery, resuspension, and transport in two contrasting canyon environments in the southwest Gulf of Lions. Continental Shelf Research 28, 2000–2016. https://doi.org/10.1016/j.csr.2008.02.012.

Otero, M.M., Numa, C., Bo, M., Orejas, C., Garrabou, J., Cerrano, C., Kružic, P., Antoniadou, C., Aguilar, R., Kipson, S., Linares, C., Terrón-Sigler, A., Brossard, J., Kersting, D., Casado-Amezúa, P., García, S., Goffredo, S., Ocaña, O., Caroselli, E., Maldonado, M., Bavestrello, G., Cattaneo-Vietti, R. Özalp, B. (2017). Overview of the conservation status of Mediterranean anthozoans. IUCN, Malaga, Spain. x + 73 pp.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., OHara, R.B., Simpson, G.L., Sólymos, P., Stevens, M.H.H., Wagner, H.H. (2016) Package "vegan" version 2.3-5. 285 pp.

Orejas, C., Gori, A., Lo Iacono, C., Puig, P., Gili, J.M., Dale, M.R.T., 2009. Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. Marine Ecology Progress Series 397, 37–51. https://doi.org/10.3354/meps08314.

Palanques, A., Durrieu de Madron, X., Puig, P., Fabres, J., Guillén, J., Calafat, A.M., Canals, M., Heussner, S., Bonnin, J., 2006. Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. Marine Geology 234, 43–61. https://doi.org/10.1016/j.margeo.2006.09.002.

Palardy, J.E., Witman, J.D., 2014. Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities. Ecology 95, 286–297. https://doi.org/10.1890/12-1612.1.

Pansini, M., Musso, B., 1991. Sponges from Trawl-Exploitable Bottoms of Ligurian and Tyrrhenian Seas: Distribution and Ecology. Marine Ecology 12, 317–329. https://doi.org/10.1890/12-1612.1.

Pasqual, C., Sanchez-Vidal, A., Zúñiga, D., Calafat, A.M., Canals, M., Durrieu de Madron, X., Puig, P., Heussner, S., Palanques, A., Delsaut, N., 2010. Flux and composition of settling particles across the continental margin of the Gulf of Lion: the role of dense water cascading. Biogeosciences 7, 217–231. https://doi.org/10.5194/bg-7-217-2010.

Pérès, J.M., Picard, J., 1964. Nouveau manuel de binomie benthique de la Mer Mediterranee. Recueil des Travaux de la Station marine d'Endoume 31, 5–137.

Pérès, J.M., 1967. The Mediterranean benthos. Oceanography and Marine Biology: An Annual Review 5, 449–553.

Pérez-Portela, R., Almada, V., Turon, X., 2012. Cryptic speciation and genetic structure of widely distributed brittle stars (Ophiuroidea) in Europe. Zoologica Scripta 42, 151–169. https://doi.org/10.1111/j.1463-6409.2012.00573.x.

Phillips, B.T., Licht, S., Haiat, K.S., Bonney, J., Allder, J., Chaloux, N., Shomberg, R., Noyes, T.J., 2019. DEEPi: A miniaturized, ro- bust, and economical camera and computer system for deep-sea exploration. Deep-Sea Research Part I 153, 103136. https://doi.org/10.1016/j.dsr.2019.103136.

Pierdomenico, M., Cardone, F., Carluccio, A., Casalbore, D., Chiocci, F., Maiorano, P., D'Onghia, G., 2019. Megafauna distribution along active submarine canyons of the central Mediterranean: Relationships with environmental variables. Progress in Oceanography 171, 49–69. https://doi.org/10.1016/j.pocean.2018.12.015.

Ponti, M., Grech, D., Mori, M., Perlini, R.A., Ventra, V., Panzalis, P.A., Cerrano, C., 2016. The role of gorgonians on the diversity of vagile benthic fauna in Mediterranean rocky habitats. Marine Biology 163, 120. https://doi.org/10.1007/s00227-016-2897-8.

Porporato, E.M.D., Mangano, M.C., De Domenico, F., Giacobbe, S., Spanò, N., 2014. First observation of *Pteroeides spinosum* (Anthozoa: Octocorallia) fields in a Sicilian coastal zone (Central Mediterranean Sea). Marine Biodiversity 44, 589–592. https://doi.org/10.1007/s12526-014-0212-9.

Pruvot, G., 1895. Coup d'oeil sur la distribution générale des invertébrés dans la région de Banyuls (Golfe du Lion). Archives de zoologie expérimentale et générale 3, 629–658.

Puig, P., Palanques, A., Orange, D.L., Lastras, G., Canals, M., 2008. Dense shelf water cascades and sedimentary furrow formation in the Cap de Creus Canyon, northwestern Mediterranean Sea. Continental Shelf Research 28, 2017–2030. https://doi.org/10.1016/j.csr.2008.05.002.

R Core Team, 2016. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M., Degraer, S., 2007. A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. Estuarine, Coastal and Shelf Science 75, 525–536. https://doi.org/10.1016/j.ecss.2007.05.041.

Rabaut, M., Braeckman, U., Hendrickx, F., Vincx, M., Degraer, S., 2008. Experimental beam-trawling in *Lanice conchilega* reefs: Impact on the associated fauna. Fisheries Research 90, 209–216. https://doi.org/10.1016/j.fishres.2007.10.009.

Ramirez-Llodra, E., Company, J.B., Sardà, F., Rotllant, G., 2009. Megabenthic diversity patterns and community structure of the Blanes submarine canyon and adjacent slope in the Northwestern Mediterranean: a human overprint? Marine Ecology 31, 167–182. https://doi.org/10.1111/j.1439-0485.2009.00336.x.

Reale, B., Sartor, P., Ligas, A., Viva, C., Bertolini, D., De Ranieri, S., Belcari, P. (2005) Demersal species assemblage on the *Leptometra phalangium* (J. Müller, 1841) (Echinodermata; Crinoidea) bottoms of the northern Tyrrhenian Sea. *Biologia Marina Mediterranea*, **12** (1), 571–574.

Reyss, D., Soyer, J., 1965. Etude de deux valees sous-marines de la mer Catalane (Compte rendu de plongées en soucoupe plongeante S P 300). Bulletin de l'Institut océanographique de Monaco 65, 1356.

Reyss, D., 1971. Les canyons sous-marins de la mer Catalane le rech du Cap et le rech Lacaze-Duthiers. III - Les peuplements de macrofaune benthique. Vie et Milieu 22, 529–613.

Reyss, D., 1972. Les canyons sous-marins de la mer catalane. Le rech du Cap et le rech Lacaze-Duthiers. IV - Étude synécologique des peuplements de macrofaune benthique. Vie et Milieu 23, 101–142.

Ribó, M., Durán, R., Puig, P., Van Rooij, D., Guillén, J., Masqué, P., 2018. Large sediment waves over the Gulf of Roses upper continental slope (NW Mediterranean). Marine Geology 399, 84–96. https://doi.org/10.1016/j.margeo.2018.02.006.

Riley, S.J., DeGloria, S.D., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5, 23–27.

Robert, K., Jones, D.O.B., Roberts, J.M., Huvenne, V.A.I., 2016. Improving predictive mapping of deep-water habitats: Considering multiple model outputs and ensemble techniques. Deep-Sea Research Part I 113, 80–89. https://doi.org/10.1016/j.dsr.2016.04.008.

Roberts, D.W., 2016. Labdsv: Ordination and Multivariate Analysis for Ecology. R Package Version 1.8-0.

Rooper, C.N., Wilkins, M.E., Rose, C.S., Coon, C., 2011. Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Continental Shelf Research 31, 1827–1834. https://doi.org/10.1016/j.csr.2011.08.003.

Ropert, M., Dauvin, J.C., 2000. Renewal and accumulation of a *Lanice conchilega* (Pallas) population in the baie des Veys, western Bay of Seine. Oceanologica Acta 23, 529–546. https://doi.org/10.1016/S0399-1784(00)00143-2.

Rossi, S., Tsounis, G., Orejas, C., Padrón, T., Gili, J.M., Teixidó, N., Gutt, J., 2008. Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). Marine Biololgy 154, 533–545. https://doi.org/10.1007/s00227-008-0947-6.

Rossi S., Bramanti L., Gori A., Orejas C. (2017) Animal Forests of the World: An Overview. In: Rossi S., Bramanti L., Gori A., Orejas C. (eds) Marine Animal Forests. Springer, Cham. pp. 1-28. https://doi.org/10.1007/978-3-319-21012-4_1.

Rousseeuw, P.J., 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. Journal of computational and applied mathematics 20, 53–65. https://doi.org/10.1016/0377-0427(87)90125-7.

Rueda, J.L., Urra, J., Aguilar, R., Angeletti, L., Bo, M., García-Ruiz, C., González-Duarte, M.M., López, E., Madurell, T., Maldonado, M., Mateo- Ramírez, A., Megina, C., Moreira, J., Moya, F., Ramalho, L.V., Rosso, A., Sitjà, C., Taviani, M. (2019) Cold-Water Coral Associated Fauna in the Mediterranean Sea and Adjacent Areas. In: Orejas, C. & Jiménez, C. (eds.) Mediterranean cold-water corals: past, present and future. Springer. pp. 295-333. https://doi.org/10.1007/978-3-319-91608-8_29.

Rueda, J.L., Gofas, S., Aguilar, R., la Torriente, de, A., García Raso, J.E., Iacono, Lo, C., Luque, Á.A., Marina, P., Mateo-Ramírez, Á., Moya-Urbano, E., Moreno, D., Navarro-Barranco, C., Salas, C., Sánchez-Tocino, L., Templado, J., Urra, J. (2021) Benthic Fauna of Littoral and Deep-Sea Habitats of the Alboran Sea: A Hotspot of Biodiversity. In: Alboran Sea - Ecosystems and Marine Resources. Springer Nature, pp. 285–358. https://doi.org/10.1007/978-3-030-65516-7_9.

Ruiz-Pico, S., Serrano, A., Punzón, A., Altuna, A., Fernández-Zapico, O., Velasco, F., 2017. Sea pen (Pennatulacea) aggregations on the northern Spanish shelf: distribution and faunal assemblages. Scientia Marina 81, 413. https://doi.org/10.3989/scimar.04359.06A.

Santín, A., Grinyó, J., Ambroso, S., Uriz, M.J., Gori, A., Dominguez-Carrió, C., Gili, J.M., 2018. Sponge assemblages on the deep Mediterranean continental shelf and slope (Menorca Channel, Western Mediterranean Sea). Deep-Sea Research Part I 131, 75–86. https://doi.org/10.1016/j.dsr.2017.11.003.

Santín, A., Grinyó, J., Ambroso, S., Uriz, M.J., Dominguez-Carrió, C., Gili, J.M., 2019. Distribution patterns and demographic trends of demosponges at the Menorca Channel (Northwestern Mediterranean Sea). Progress in Oceanography 173, 9–25. https://doi.org/10.1016/j.pocean.2019.02.002.

Sardá, R., Rossi, S., Martí, X., Gili, J.M., 2012. Marine benthic cartography of the Cap de Creus (NE Catalan Coast, Mediterranean Sea). Scientia Marina 76, 159–171. https://doi.org/10.3989/scimar.03101.18D.

Sardá, R., Requena, S., Dominguez-Carrió, C., Gili, J.-M., 2017. Ecosystem-Based Management for Marine Protected Areas: A Systematic Approach. In: Goriup, P. (Ed.), Management of Marine Protected Areas: a Network Perspective. John Wiley & Sons Ltd, pp. 145–162. https://doi.org/10.1002/9781119075806.ch8.

Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish and Fisheries 106, 438. https://doi.org/10.1111/faf.12283.

Sheehan, E.V., Stevens, T.F., Gall, S.C., Cousens, S.L., Attrill, M.J., 2013. Recovery of a temperate reef assemblage in a marine protected area following the exclusion of towed demersal fishing. Plos One 8, e83883. https://doi.org/10.1371/journal.pone.0083883.

Simboura, N., Zenetos, A., Pancucci Papadopoulou, M.A., Thessalou Legaki, M., Papaspyrou, S., 1998. A baseline study on benthic species distribution in two neighbouring gulfs, with and without access to bottom trawling. Marine Ecology 19, 293–309. https://doi.org/10.1111/j.1439-0485.1998.tb00469.x.

SPA/RAC–UN Environment/MAP, 2019. Updated Classification of Benthic Marine Habitat Types for the Mediterranean Region. Tunis (Tunisia). 15 pp.

Stelzenmüller, V., Rogers, S.I., 2008. Spatio-temporal patterns of fishing pressure on UK marine landscapes, and their implications for spatial planning and management.

ICES Journal of Marine Science 65, 1081–1091. https://doi.org/10.1093/icesjms/fsn073.

Taviani, M., Angeletti, L., Canese, S., Cannas, R., Cardone, F., Cau, A., Cau, A.B., Follesa, M.C., Marchese, F., Montagna, P., Tessarolo, C., 2017. The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep Sea Research Part II 145, 61–78. https://doi.org/10.1016/j.dsr2.2015.12.008.

Taviani, M., Angeletti, L., Cardone, F., Montagna, P., Danovaro, R., 2019. A unique and threatened deep water coral-bivalve biotope new to the Mediterranean Sea offshore the Naples megalopolis. Scientific Reports 9, 3411. https://doi.org/10.1038/s41598-019-39655-8.

Templado, J., Ballesteros, E., Galparsoro, I., Borja, Á., Serrano, A., Martín, L., Brito, A., 2013. Guia Interpretativa. Inventario Español De Hábitats Marinos, Ministerio de Agricultura, Alimentación y Medio Ambiente, p. 230.

Terribile, K., Evans, J., Knittweis, L., Schembri, P.J., 2015. Maximising MEDITS: Using data collected from trawl surveys to characterise the benthic and demersal assemblages of the circalittoral and deeper waters around the Maltese Islands (Central Mediterranean). Regional Studies in Marine Science 3, 163–175. https://doi.org/10.1016/j.rsma.2015.07.006.

Tsounis, G., Rossi, S., Gili, J.M., Arntz, W.E., 2006. Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). Marine Biology 149, 1059–1070. https://doi.org/10.1007/s00227-006-0302-8.

Ulses, C., Estournel, C., Bonnin, J.D., de Madron, X., Marsaleix, P., 2008. Impact of storms and dense water cascading on shelf-slope exchanges in the Gulf of Lion (NW Mediterranean). Journal of Geophysical Research 113, C02010. https://doi.org/10.1029/2006JC003795.

UNEP/MAP-SPA/RAC, 2018. Protocol concerning specially protected areas and biological diversity in the Mediterranean - Annex II: List of endangered or threatened species. RAC/SPA, Tunis, p. 10.

Vafidis, D., Koukouras, A., Voultsiadou-Koukoura, E., 1997. Actiniaria, Corallimorpharia, and Scleractinia (Hexacorallia, Anthozoa) of the Aegean Sea, with a checklist of the Eastern Mediterranean and Black Sea species. Israel Journal of Zoology 43, 55–70.

Valisano, L., Notari, F., Mori, M., Cerrano, C., 2016. Temporal variability of sedimentation rates and mobile fauna inside and outside a gorgonian garden. Marine Ecology 37, 1303–1314. https://doi.org/10.1111/maec.12328.

Van Hoey, G., Guilini, K., Rabaut, M., Vincx, M., Degraer, S., 2008. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems. Marine Biology 154, 1009–1019. https://doi.org/10.1007/s00227-008-0992-1.

Voultsiadou-Koukoura, E., Van Soest, R.W.M., 1993. Suberitidae (Demospongiae, Hadromerida) from the North Aegean Sea. Beaufortia 43, 176–186.

Warner, G.F., 1971. On the ecology of a dense bed of the brittle-star *Ophiothrix fragilis*. Journal of the Marine Biological Association of the UK 51, 267–282. https://doi.org/10.1017/S0025315400031775.

Weinbauer, M.G., Velimirov, B., 1995. Morphological variations in the Mediterranean sea fan *Eunicella cavolini* (Coelenterata: Gorgonacea) in relation to exposure, colony size and colony region. Bulletin of Marine Science 56 (1), 283–295.

GFCM (2018) Report of the second meeting of the Working Group on Vulnerable Marine Ecosystems (WGVME) from the General Fisheries Commission for the Mediterranean. FAO headquarters, Italy, 26-28 February 2018.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy 30, 3–35. https://doi.org/10.1080/01490410701295962.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790. https://doi.org/10.1126/science.1132294.

Yesson, C., Fisher, J., Gorham, T., Turner, C.J., Hammeken Arboe, N., Blicher, M.E., Kemp, K.M., 2016. The impact of trawling on the epibenthic megafauna of the west Greenland shelf. ICES Journal of Marine Science 74 (3), 866–876. https://doi.org/10.1093/icesjms/fsw206.

UNEP/MAP-SPA/RAC, 2010. Fisheries conservation and vulnerable ecosystems in the Mediterranean open seas, including the deep seas. By de Juan, S. and Lleonart, J. Ed. RAC/SPA, Tunis: 103 pp.