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## Sponge assemblages in fishing grounds and seamounts of the Balearic Islands (western Mediterranean)

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## ABSTRACT

The Balearic Archipelago (western Mediterranean) is an area of great ecological interest due to the combination of complex geomorphology, highly oligotrophic waters and low fishing pressure. Sponges play a key role in benthic habitats, providing structural complexity and significantly contributing to their diversity and biomass. Here, we present an insight into the sponge communities of this archipelago from the analysis of samples collected during several scientific research surveys carried out on bottom trawl fishing grounds around the Balearic Islands and on sedimentary and rocky bottoms of the Mallorca Channel seamounts. Sampling was carried out with experimental bottom trawl, beam trawl, rock dredge and remotely operated vehicle (ROV). We analyzed species presence/absence data using multivariate methods in order to identify assemblages. Once identified, we characterized their biodiversity, biomass and taxonomic composition. A dbRDA analysis was conducted to test the influence of environmental variables and fishing pressure on the sponge communities. Up to 350 species are reported: 220 at bottom trawl fishing grounds and 189 at seamounts. Communities were structured by depth, temperature, currents, substrate and fishing pressure with sponge presence/absence, biomass and diversity also linked to the presence of deep algae beds. Taxonomic composition differed between bottom trawl fishing grounds and the seamounts, where this fishing activity is almost negligible, pointing to different sensitivity to this fishing impact among the different orders, particularly for Tetractinellida, which was much more diverse and abundant at seamounts.

## 1. Introduction

Sponges are key components of worldwide benthic biocenosis, usually being main contributors to biomass and biodiversity (Bell, 2008; and references therein). They also provide several important ecosystem services like the enhancement of bottom structural complexity, providing shelter and nursery areas to crustaceans, mollusks and fish, and contributing to nutrient recycling (Van Soest et al., 2012; Maldonado et al., 2017). The role of sponges in maintaining some ecosystems has proved to be important at oligotrophic areas, like tropical reefs and the deep sea, and it is probably critical in some areas of the Mediterranean (Maldonado et al., 2012; Rix et al., 2018; Bart et al., 2021). At those ecosystems, sponges optimize the nutrient fluxes by feeding on dissolved organic matter, which is recycled for the food web in a process involving particulate organic matter release in form of fecal pellets,

which are subsequently consumed by detritivores (de Goeij et al., 2013).

The Mediterranean is a highly studied area regarding sponge taxonomy (e.g. Topsent, 1928; Vacelet, 1969; Pulitzer-Finali, 1983; Boury-Esnault et al., 1994). It is considered a hotspot of sponge diversity (e.g. Xavier and van Soest, 2012; van Soest et al., 2012), with more than 700 reported species (de Voogd et al., 2023), a number that grows periodically with descriptions of new species and addition of new records (e.g. Sitja and Maldonado, 2014; Díaz et al., 2021). However, studies focusing on the factors shaping sponge distribution and their communities are scarce. Sarà (1962) and Boury-Esnault (1971) emphasized the importance of depth and substrate orientation on the distribution of infralittoral sponges. Uriz et al. (1992) pointed out the importance of light irradiation in structuring infralittoral sponge communities in the oligotrophic waters of Cabrera, in the Balearic Islands. According to these authors, because light had a direct effect on algae growth,

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competition for the substrate between algae and sponges was higher in oligotrophic areas with clear waters. A similar conclusion was reached by Kefalas et al. (2003), who studied the circalittoral sponge communities of the Aegean Sea, finding light irradiation as the factor causing a markedly different distribution than in other areas with less transparent waters. Due to sampling limitations, less and more fragmentary information is available for deeper strata. Some of the available studies highlight substrate, sedimentation rate and currents as main factors in absence of photosynthesis, also pointing out the similarity of some deep sea communities with those of dark caves (Vacelet, 1969; Vacelet et al., 1994). Pansini and Musso (1991) conducted a large study on bottom trawl fishing grounds of the Ligurian Sea, down to a depth of 700 m, identifying 66 species, not finding any significant environmental factor determining sponge assemblages, but indicating that trawling could have a major impact in structuring soft bottom communities. Other studies highlighted the differentiation between sponge communities associated with deep-sea coral banks and soft bottom communities (Longo et al., 2005; Calcinai et al., 2013).

More recently, the improvement of sampling technologies and knowledge of seafloor topography fostered a growing interest in studying less accessible deep-sea habitats, like seamounts or canyons (Morato et al., 2013; De la Torre et al., 2018; Grinyó et al., 2018;

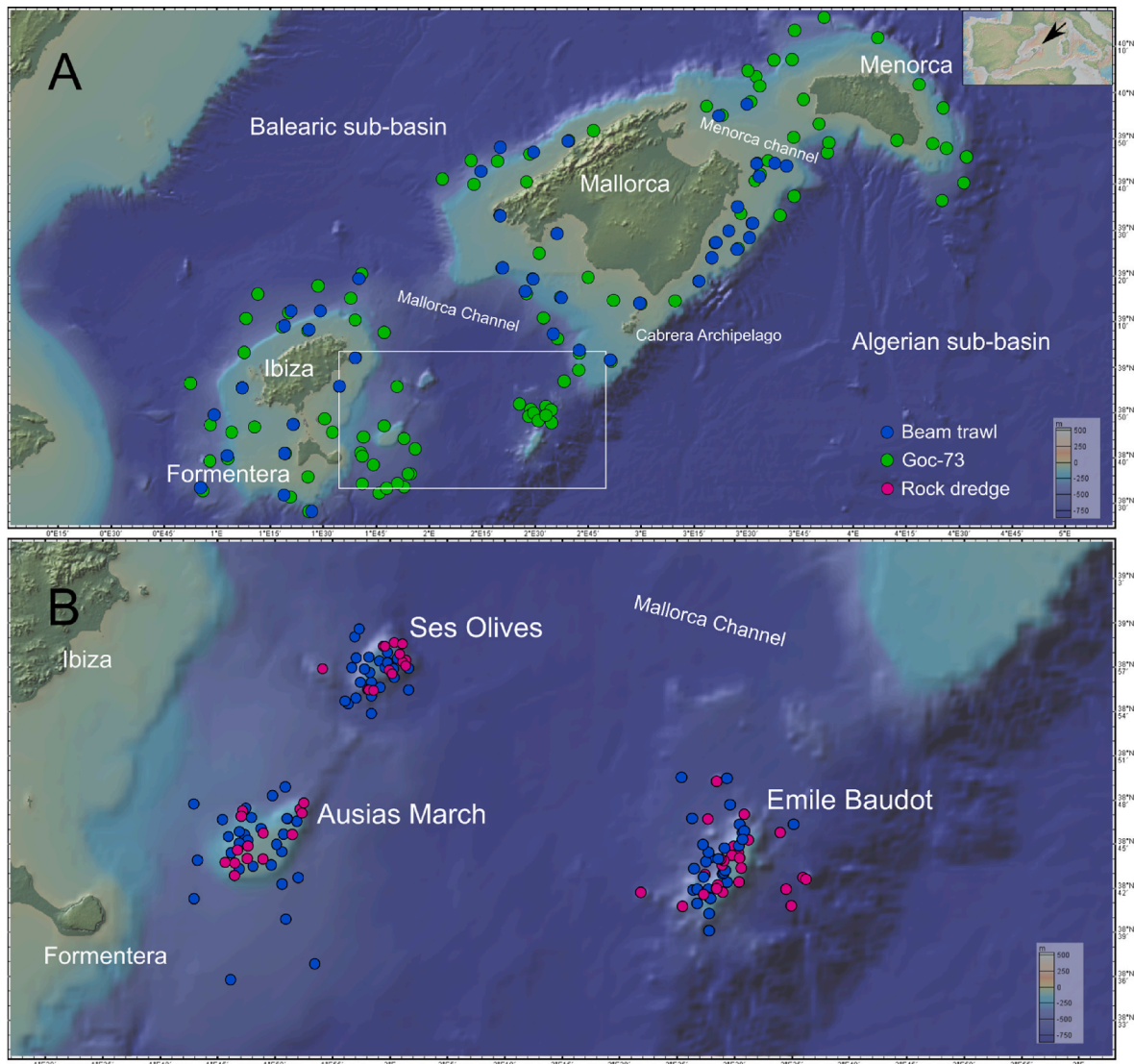
Corbera et al., 2019; Bo et al., 2021; Massutí et al., 2022), leading to the discovery of singular sponge communities, like keratose-dominated grounds in the Ligurian Sea (Enrichetti et al., 2020), diverse meso-photic grounds in the Levantine Sea (Idan et al., 2018, 2021) and a deep-sea lithistid reef in the Balearic Sea (Maldonado et al., 2015).

The aim of this work is to characterize the sponge communities of the Balearic Islands, including sedimentary and rocky bottoms of the circalittoral and bathyal domains in bottom trawl fishing grounds and seamounts. To do that, we have analyzed data and samples obtained with different sampling methods during several scientific research surveys.

## 2. Material and methods

### 2.1. Study area

The Balearic Promontory (western Mediterranean) is composed of four main islands and several islets, channels and seamounts (Acosta et al., 2003, Fig. 1). It is characterized by clear waters, as a consequence of lack of river runoff, the scarcity of rain and the high distance from the Iberian Peninsula, where terrigenous-muddy sediments from river discharges are widely distributed. By contrast, the sand and gravel



**Fig. 1.** Maps of the studied area showing the location of the sampling stations. A: Trawl fishing grounds at sedimentary bottoms on the continental shelf and slope around the Balearic Islands; B: Mallorca Channel with the seamounts Ses Olives, Ausias March and Emile Baudot.

calcareous biogenic sediments predominate in the Balearic Islands (Alonso et al., 1988). These oceanographic characteristics allow light intensity to reach 0.05% of surface values as deep as 110 m, enabling the growth of seaweeds in most of the continental shelf of the Archipelago (Canals and Ballesteros, 1997). As a consequence, benthic communities distribution and composition varies from that of the adjacent Iberian Peninsula and other Mediterranean areas (Pèrès and Picard, 1964; Ballesteros, 1994).

According to Ordines and Massutí (2009), seaweed communities including maërl, *Peysonellia* spp., *Osmundaria vulubilis* and *Laminaria rodriguezii* beds predominate in the coastal shelf of the Balearic Islands, while sedimentary bottoms of the deep shelf and upper slope show some other habitats of interest, like crinoids beds. Despite the pronounced oligotrophy of this Archipelago, the red algae beds show high diversity and benthic productivity (Ordines and Massutí, 2009), being the sponges one of the main benthic groups associated to these algal communities (Ordines et al., 2017).

Two main channels are present in the Balearic Archipelago: the Menorca Channel, between the islands of Mallorca and Menorca, and the Mallorca Channel, between the Pitiusas Islands (Ibiza and Formentera) and Mallorca. These channels are situated northern and southern of the Archipelago, being influenced by the oceanographic conditions of the Balearic and the Algerian sub-basins, respectively and playing an important role in the regional circulation, as passages for the exchange of water masses between them (Massutí et al., 2014; and references cited therein).

The Menorca Channel is characterized by having relatively shallow waters, a consequence of the continuity of the continental shelf between Mallorca and Menorca. It is influenced by atmospheric forcing (Monserrat et al., 2008; López-Jurado et al., 2008) and by the Balearic Current, which flows along the northern shelf margin and upper slope of the Balearic Promontory. This current, jointly with frontal meso-scale events between Mediterranean and Atlantic waters and input of old northern water into the channels, can act as external fertilization mechanism that enhance productivity off the Balearic Islands (Pinot et al., 1995; Fernández de Puellas et al., 2004). This channel harbors rich and diverse benthic habitats (Grinyó et al., 2018) and hence in 2014 it was declared a Site of Community Importance (SCI), under the Natura 2000 framework.

The Mallorca Channel is a seaway composed of diverse geomorphological features, with an bathyal plain descending to 1050 m depth that separate the continental shelves of Mallorca-Menorca and Ibiza-Formentera. It is mainly affected by density gradients and the warmer and less saline Atlantic waters (Monserrat et al., 2008; López-Jurado et al., 2008) and the trophic webs of the deep-water ecosystems are supported more by plankton biomass than by benthic productivity (Maynou and Cartes, 2000; Cartes et al., 2001). At the southern part of the Mallorca Channel there are three seamounts: Ses Olives and Ausias March of orogenic origin, and the Emile Baudot of volcanic origin. These seamounts have been recently studied, within the LIFE IP INTEMARES project (<https://intemares.es/en>) and the first results have mapped their geomorphological features showing a high diversity of species, especially benthic filter feeders like sponges, and habitats of special interest for conservation, including coralligenous outcrops and maërl beds at summits, deep-sea coral reefs at rocky escarpments and *Isidella elongata* and pockmarks fields on sedimentary bathyal bottoms (Massutí et al., 2022).

Historically, in the Balearic Islands the number of trawl fishing boats has remained very low compared to other areas of the Mediterranean coast of the Iberian Peninsula (Quetglas et al., 2012). According to these authors, the number of vessels per potential fishing ground surface, as a simple indicator of the fishing effort exerted, is one order of magnitude lower in the Balearic Islands than in the adjacent Peninsula coast. In the Archipelago bottom trawling is conducted on the shelf and slope (from 50 to about 750 m depth), with the upper bathymetric limit delimited by the end of *Posidonia oceanica* meadows. However, fishing grounds

between 50 and 100 m depth can overlap with red algae beds, which explains the high quantity of algae and benthic invertebrates in the discards of this fleet (Ordines et al., 2006). Some demersal fisheries are developed in the Mallorca Channel, mainly focused on the deep water decapod crustaceans shrimp (*Aristeus antennatus*) and the pandalid shrimp *Plesionika edwardsi* using bottom trawl in the adjacent bottoms of SO and AM and traps at the flanks and summits of the three seamounts, respectively (Massutí et al., 2022).

## 2.2. Sampling

Samples were collected during 12 oceanographic research surveys carried out from 2016 to 2021 in two main areas of the Balearic Islands: trawl fishing grounds on sedimentary bottoms of the continental shelf and upper and middle slope around the Balearic Islands, and the seamounts Emile Baudot (EB), Ausias March (AM) and Ses Olives (SO) at the Mallorca Channel (Fig. 1). These surveys were developed within the MEDITS (6 annual surveys from 2016 to 2021) and the Marine Strategy Framework (MSF; one survey in 2021) programs and the LIFE IP INTEMARES project (4 surveys in seamounts from 2018 to 2020 and one survey in Menorca Channel in 2019). The bathymetric ranges were 50–758 m depth at trawl fishing grounds and 89–1169 m depth at seamounts and surrounding areas.

Trawl fishing grounds were sampled by a Jennings type beam trawl (BT), designed to collect epi-benthos (Jennings et al., 1999) whose efficiency has been estimated by Reiss et al. (2006), and the experimental bottom trawl GOC-73 (GOC), a sampling device widely used in MEDITS surveys along the northern Mediterranean, to estimate the abundance and distribution of demersal resources and the impact of the fishing activity on benthic ecosystems (Spedicato et al., 2019). Sampling at the seamounts used the same BT for sedimentary bottoms and a rock dredge (RD) for rocky bottoms. The Remotely Operated Vehicle (ROV) *Liropus 2000* was also used to collect samples and images at the seamounts. More details of these surveys and sampling stations can be found in Table 1.

The BT has horizontal and vertical openings of 2 and 0.5 m, respectively, and a cod-end mesh size of 5 mm. Sampling was conducted at 2 knots, with an effective sampling duration between 5 and 15 min depending on depth. The GOC has horizontal and vertical net openings ranging 18–22 and 2.5–3 m, respectively, and a cod-end mesh size of 10 mm. Sampling was conducted at 2.8–3.0 knots, with an effective sampling duration between 20 and 60 min depending on depth. The RD is composed of a rectangular metallic frame with beveled edges, equipped with a 10 mm mesh cod-end, protected by another net of 20 mm meshes and leather covers on bottom and top sides. It was trawled in an upward direction over the seafloor at 0.5–1 knots, during 5–10 min.

There are significant differences in the catch efficiency and sampled surface between GOC, RD and BT devices. The BT is the most efficient one regarding benthic species, resulting in higher biomasses, while GOC is less efficient but sweeps much larger areas than the BT: 40,000–120,000 vs 370–1900 m<sup>2</sup>, respectively depending on depth. The surface sampled using the RD is difficult to estimate and it is specially misleading at rocky slopes, with high inclination such as those of the seamounts, whereas its efficiency largely depends on the nature of the rocky bottom and the capability of the dredge to pull off it.

Once samples were on deck, all the specimens were identified to the lowest taxonomic level by examining macroscopical and microscopical characters. Specimens that could not be identified on board were stored for further analyses in the laboratory, including the use of molecular markers (COI and 28S). Part of the taxonomic work has already been published (Díaz et al., 2020, 2021, Díaz et al.). After identification, wet biomass was weighted, and the number of individuals and/or fragments (for non-encrusting species) annotated.

**Table 1**

Summary of the sampling used in the present study, indicating the research survey, the sampling area (:trawl fishing grounds) and sampling device (RD: rock dredge; BT: beam trawl; GOC: the experimental bottom trawl GOC), as well as the stations analyzed in each survey and the number and percentages of samples with and without sponges by bathymetric range (50–90, 91–200 and 201–1000 m), corresponding to euphotic, mesophotic and aphotic Zones, respectively. During the INTEMARESA22B0720 survey, 37 stations with ROV were also developed along the whole bathymetric range. n.s.: bathymetric range not sampled.

Survey	Area	Device	Stations with sponges				Stations without sponges				TOTAL
			50–90	91–200	201–1000	Total	50–90	91–200	201–1000	Total	
<b>trawl fishing grounds</b>											
MEDITS 2016	Mallorca-Menorca	GOC	16	10	4	30	0	7	14	21	51
MEDITS 2017	Mallorca-Menorca	GOC	18	11	2	31	0	5	15	20	51
MEDITS 2018	Mallorca-Menorca	GOC	17	7	3	27	0	10	14	24	51
MEDITS 2019	Mallorca-Menorca	GOC	17	8	5	30	0	8	12	20	50
MEDITS 2020	Mallorca-Menorca	GOC	18	10	7	35	0	6	14	20	55
MEDITS 2021	Mallorca-Menorca	GOC	22	6	6	34	0	9	18	27	61
MEDITS 2021	Ibiza-Formentera	GOC	7	6	5	18	0	1	16	17	35
CIRCALEBA1121	Balearic Islands	BT	21	5	7	33	0	4	5	9	42
INTEMARES-A4	Menorca Channel	BT	43	n.s.	n.s.	43	0	n.s.	n.s.	n.s.	43
<b>Sub-Total</b>		<b>Sum</b>	179	63	39	281	0	50	108	158	439
		<b>%</b>	100	56	27	64	0	44	73	36	
<b>Seamounts</b>											
INTEMARES-A22B0718	Mallorca Channel	BT	n.s.	7	4	11	n.s.	0	6	6	17
		RD	n.s.	6	3	9	n.s.	0	0	0	9
INTEMARES-A22B1019	Mallorca Channel	BT	n.s.	13	29	42	n.s.	0	3	3	45
		RD	n.s.	5	9	14	n.s.	0	1	1	15
		GOC	n.s.	n.s.	10	10	n.s.	0	8	8	18
INTEMARES-A22B0720	Mallorca Channel	BT	n.s.	6	16	22	n.s.	0	1	1	23
		RD	n.s.	9	12	21	n.s.	0	3	3	24
<b>Sub-Total</b>		<b>Sum</b>	0	46	83	130	0	0	22	22	151
		<b>%</b>	n.s.	100	79	86	n.s.	0	21	15	
<b>Total</b>			179	109	122	410	0	50	130	180	590

### 2.3. Data analysis

The first three MEDITS surveys (2016–2018) and the first INTEMARES (2018) survey were used only for taxonomic purposes, while biomass and abundances were also annotated for the rest of surveys: MEDITS from 2019 to 2021, CIRCA-LEBA-1121 (MSF) and INTEMARES from 2019 to 2020 (Table 1).

In the case of GOC, biomass data was standardized to surface using the SCANMAR or MARPORT systems to determine the arrival and departure of the net to the bottom and its horizontal opening, and the distance covered in each haul. This method was also applied to standardize BT data, but using the width of the beam as horizontal opening. The data was then transformed to presence/absence for multivariate analyses purposes. RD data was also transformed to presence absence to be used in the multivariate analyses, but could not be standardized due to the difficulties to estimate the effective sampled surface. No ROV data was used in multivariate analyses. Faunistic lists were elaborated using the data collected from all surveys since 2016 and using all gears and ROV.

With the Primer 6 software (Primer, Plymouth, UK) we carried out independent multivariate analyses for GOC and BT samples collected from trawl fishing grounds, and BT and RD collected from seamounts. These analyses included a Cluster Analysis to detect assemblages and a Similarity Percentage Analysis (SIMPER; Clarke and Warwick, 1994), as well as number of species and biomass to describe them. To do so, the Sørensen-Dice coefficient was used to calculate a between-sample similarity matrix from biomass data previously transformed into presence/absence. Then samples were linked into clusters using the Unweighted Pair-Group Method with Arithmetic Mean. The resulting dendrogram was analyzed to detect significantly different groups using the Similarity Profile Routine test (SIMPROF; Clarke et al., 2008). These groups detected were considered assemblages. Then, SIMPER analysis was used to identify the most important species contributing to within group similarity. The total and mean species richness (S) and the mean standardized biomass of both sponges and algae (in terms of grams per 100 m<sup>2</sup>) were also estimated by each assemblage, except for those exclusively composed of samples from RD, in which it was not possible

to estimate the standardized biomass, due to the low efficiency of this gear and the impossibility to calculate the surface effectively sampled. The S was estimated for each seamount separately, as well as for all seamounts together and the trawl fishing grounds. Rarefaction species curves were calculated for seamounts and trawl fishing grounds, and in trawl fishing grounds also for each sampling method (GOC and BT).

We also investigated the taxonomic composition of the assemblages. To do that, we have calculated the number of orders and the number of species per order in seamounts and trawl fishing grounds, and for each of the assemblages detected.

#### 2.3.1. Environmental and fishing conditions

To characterize oceanographic variables, the outputs of the WMOP (Western Mediterranean Operational forecasting system) model, available in the Balearic Islands Coastal Observing and Forecasting System (SOCIB from its acronym in Spanish) have been considered (Tintoré et al., 2013); [https://www.socib.es/?seccion=modelling&facility=forecast\\_system\\_description](https://www.socib.es/?seccion=modelling&facility=forecast_system_description). WMOP is a high-resolution (2.6 km) 3D ROMS (Regional Ocean Modeling System) model, implemented in the western Mediterranean with a daily temporal resolution (Juza et al., 2016; Mourre et al., 2018). Values of water temperature and irradiance above the bottom, speed and direction of bottom currents and chlorophyll *a* concentration at the surface, as a proxy of primary production, were obtained by each of the sampling station during the period 2016–2021.

The EMODNET (European Marine Observation and Data Network) broad-scale seabed habitat map for Europe (EUSEaMap) has been used for benthic habitat characterization: <https://emodnet.ec.europa.eu/en/seabed-habitats>. The EUSEaMap includes several seafloor habitat classifications (Vasquez et al., 2021). For the present study, the kind of substrate included in this database has been used. In the Mallorca Channel seamounts, the habitat type of some sampling stations was checked according to the more accurate mapping of the seafloor recently obtained by the INTEMARES project (Massutí et al., 2022). Finally, due to the low concordance between the observations from scientific surveys and EMODNET data, samples from Mallorca Channel were also assigned to a nominal explanatory variable, but with only two categories: Rocky vs. Sedimentary bottoms.

In addition to the seafloor type, it has also been taken into account as an environmental variable, the density of rhodoliths-forming species and total algae, estimated during the same surveys as the sponge assemblages studied. The rhodoliths-forming species are considered as bioengineers (Foster, 2001; Nelson, 2009; Teichert, 2014). For each BT and GOC stations, the standardized rhodoliths and total algae biomass (g/100 m<sup>2</sup>) was estimated. For the seamounts this variable was not included in the analysis because at seamounts we included stations sampled with RD, a sampling device not appropriate for biomass estimations.

The fishing effort of the bottom trawl fleet was estimated from information collected by the Vessel Monitoring System (VMS). These data are available since 2006 and consist of position and instantaneous velocity that each fishing vessel sends automatically via satellite communications every 2 h. VMS signals generated during navigation were excluded from the analyses, by considering only those signals with instantaneous velocities ranging from 2 to 3.6 knots, which is the towing speed used by trawlers in the area. This information has been used to model the geographic distribution of bottom trawl fishing effort in the area and to estimate the fishing effort by fishing ground (Fariols et al., 2017; Guijarro et al., 2020). Each sampling station on the continental shelf and slope around the Balearic Islands was associated to a bottom trawl fishing ground and consequently to its fishing effort. The fishing effort represents the annual number of fishing trips that the fleet works in each fishing ground in the year in which each sampling station was surveyed.

There is no bottom trawling on the summits, flanks and nearby bottoms around the Mallorca Channel seamounts (Massutí et al., 2022), where the sampling effort was concentrated. In this area, bottom trawling is only carried out at three fishing grounds on adjacent sedimentary bottoms located at a certain distance from the seamounts, which show a similar fishing effort (Massutí et al., 2022). Therefore, in this area fishing effort has been considered as a quantitative explanatory variable, assigning sampling stations to two categories: Not Trawling vs. Trawling.

### 2.3.2. Relationships with environmental parameters

A distance-based-Redundancy Analysis (dbRDA), available in the CANOCO 5.1 package (ter Braak and Smilauer, 2018), was used to model the effect of environmental and fishing variables on the distribution of sponge species. Unlike multivariate indirect gradient analyses, canonical analyses such as RDA provide the means for conducting direct explanatory analyses in which the association among species can be studied with respect to their common and unique relationships with environmental variables (Peres-Neto et al., 2006). In dbRDA, case scores, obtained by a principal coordinate analysis (PCO) of a distance matrix, are further constrained by explanatory variables using RDA (Legendre and Anderson, 1999). Dependent variables were presence/absence of sponge species, while depth (m) and the environmental and fishing variables explained above (see Section Environmental and fishing conditions) were included in the RDA as continuous (temperature, irradiance, speed and direction of currents, chlorophyll *a* concentration, rhodoliths and total algae biomass and fishing effort on the Balearic Islands bottom fishing grounds) or nominal/categorical (seafloor type on the Balearic Islands bottom trawl fishing grounds, and rocky vs. sedimentary and trawling or not trawling in the Mallorca channel seamounts) explanatory variables. The distance matrix was conducted using the Bray-Curtis distance for presence/absence data.

The explanatory variables included in the db-RDA were selected by means of a protected forward selection (Blanchet et al., 2008; ter Braak and Smilauer, 2018) and the correlation between them was checked with the inflation factor, the Variance Inflation Factor of a variable in a multiple regression equation (Montgomery and Peck, 1982). The effect of each variable was tested using partial dbRDA models, which allow the effect of a particular explanatory variable to be analyzed after the rest of

the variables have been set as covariables (variables that are fitted to the species data before the ordination, which is carried out afterwards using only the residual variation). The significance of the models was assessed using the Monte Carlo permutation-based test (Manly, 1991).

## 3. Results

Sponges were found in 69% of the 590 stations sampled with GOC, BT and RD, in 85% of the 151 stations sampled in seamounts and in 64% of the 439 stations sampled in trawl fishing grounds (Table 1). Sponges appeared in all the 37 ROV transects carried out in seamounts. Species accumulation curves from both seamounts and trawl fishing ground showed similar tendencies, being close to plateau, which indicates that a large fraction of the sponge diversity has been sampled and documented (Fig. 2).

### 3.1. Sponge diversity

A total of 2800 samples were collected and kept in the authors collection in the Centre Oceanogràfic de les Balears, while some specimens have been deposited in the Marine Fauna Collection based at the Centro Oceanográfico de Málaga (Instituto Español de Oceanografía) and at the Museum of Evolution, Uppsala University (Uppsala, Sweden). So far, 350 species or taxa were identified: 189 at seamounts and 220 at trawl fishing grounds (Supplementary Table 1). Of those, only 61 were shared between both areas. The most diverse seamount was EB (*S* = 140 species or taxa), followed by AM (*S* = 111) and SO (*S* = 36) seamounts.

The species *Timea chondrilloides*, *Forcepia (Leptolabis) luciensis* and *Callyspongia septimaniensis* are new records for the Balearic Islands, although *C. septimaniensis* may have been reported by Bibiloni (1990) under the name of *Adocia simulans* (Johnston, 1842). Taxa not identified to the species level will be described on taxonomic articles elsewhere (Díaz et al.). At trawl fishing grounds, *Haliclona* sp3, *Suberites domuncula*, *Haliclona (Reniera) mediterranea* and *Lissodendoryx (Lissodendoryx) cavernosa* were the most frequent species, collected in 95 (33%), 88 (31%), 72 (25%) and 63 (22%) stations, respectively, while *Phorbastenia tenacior*, *Myxilla (Myxilla) iotrochotina*, *Haliclona (Reniera) mediterranea* and *Haliclona* sp3 were the species with more biomass. At seamounts, *Thenea muricata*, *Poecillastra compressa*, *Desmacella inornata* and *Foraminospongia balearica* were the most frequent species, being present in 41 (33%), 40 (32%), 36 (29%) and 28 (22%) stations, respectively, while *Hexadella* sp1, *Haliclona (Halichoelona)* sp. and *Geodia geodina* (Schmidt, 1868) were the species with more biomass.

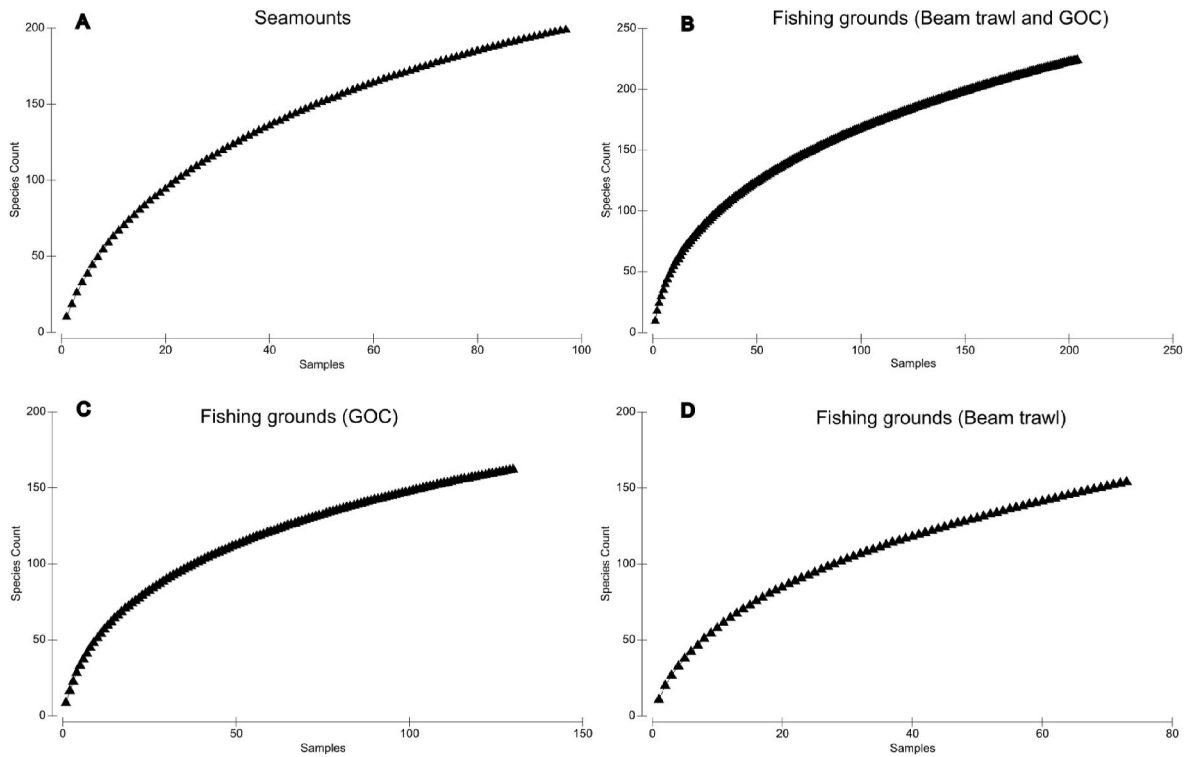
### 3.2. Sponge assemblages

We obtained three different dendrograms: one for the seamounts, resulting from the analyses of BT and RD samples (Fig. 3 and Table 2) and two for the trawl fishing grounds, one resulting from the analyses of GOC samples (Fig. 4 and Table 3) and other resulting from the analysis of BT samples (Fig. 5 and Table 4). The maps showing the distribution of assemblages in each dendrogram are shown in Fig. 6.

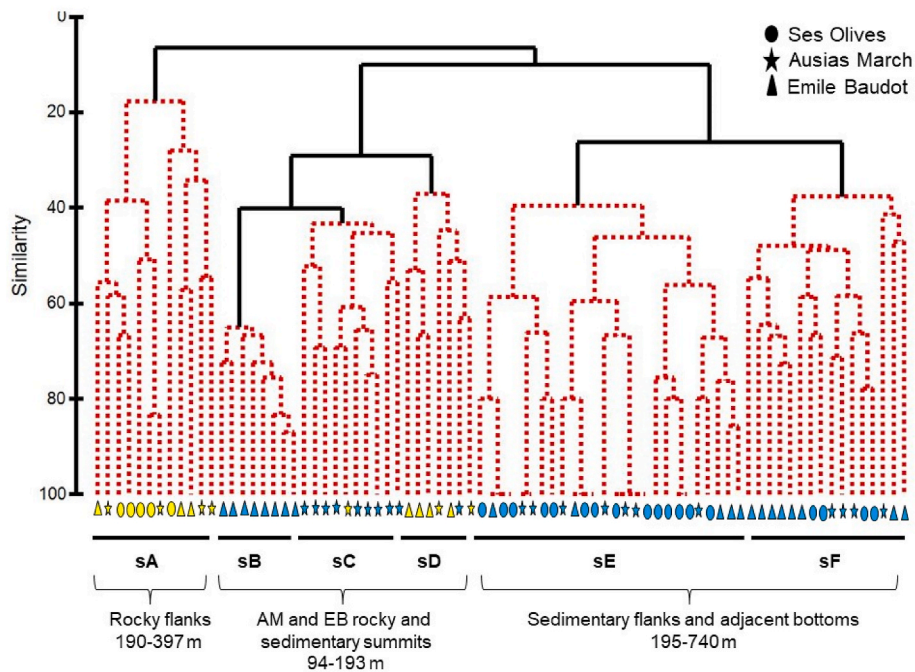
### 3.3. Seamounts

Dendrogram showed 6 different clusters (Fig. 3). Shallow summits of the AM and the EB seamounts (94–193 m) formed a main group that was subdivided in two groups corresponding to sedimentary assemblages (sB and sC), which clustered together, and a rocky group (sD). The other three groups were deeper (151–740 m), found in SO, AM and EB seamounts (assemblages sA, sE and sF).

Within the shallower assemblages, sC (97–135 m depth) was composed of samples from sedimentary bottoms (with the exception of one rocky station) at AM seamount. It showed high values of total and mean *S* (70 and  $16.9 \pm 1.9$  species, respectively) and the highest mean sponge and algae biomass ( $1342 \pm 840$  g/100 m<sup>2</sup> and  $4042 \pm 8178$  g/



**Fig. 2.** Species accumulation curves for the Seamounts (A) and fishing grounds (B-D). Graphs B-C shows the accumulation curves obtained with the different sampling methods on the fishing grounds (beam trawl and GOC), while graph D shows the accumulation curve for the total of species of the fishing grounds, including both sampling methods.



**Fig. 3.** Dendrogram of seamount assemblages identified from cluster analysis. Statistically significant groups are defined by the SIMPROF test and illustrated by discontinuous red lines. Samples are represented in circles (Ses Olives), triangles (Emile Baudot) and stars (Ausias March). Color represents the sampling device used in each station, with yellow indicating rock dredge and blue indicating beam trawl. Depth range, zone and bottom type are indicated by each cluster.

100 m<sup>2</sup>, respectively) of the seamounts (Table 2), with the second highest sponge biomass value on a single station of all the study (7685 g/100 m<sup>2</sup>). This group was characterized by *P. compressa*, *F. balearica*, *Calcarea* sp6 and *Hexadella* sp1 (Table 5; Fig. 7A and B). The group sB

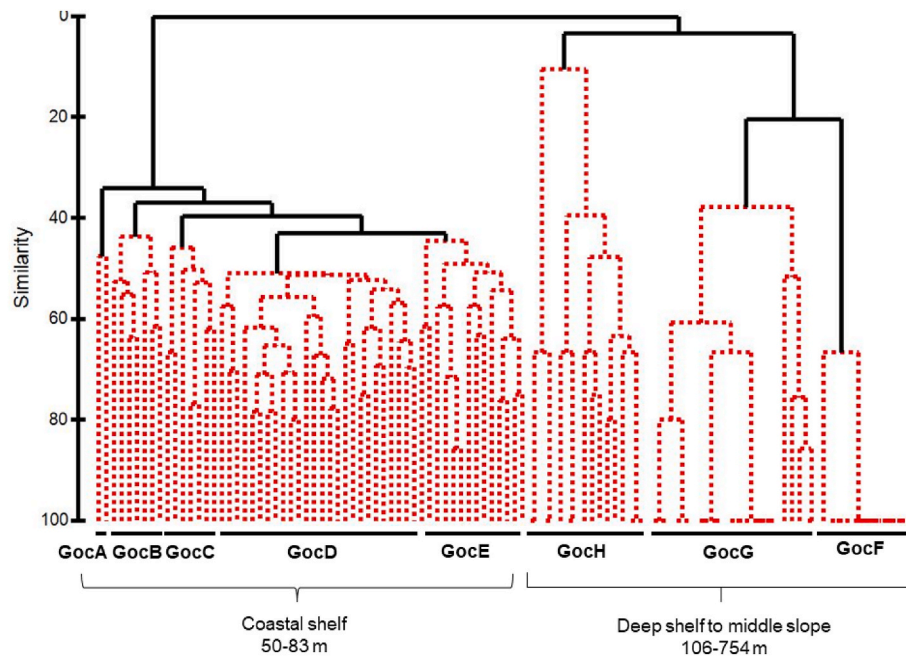
(141–154 m depth) was composed exclusively of sedimentary bottoms at EB seamount. This was the most diverse group of the seamounts, with total and mean *S* values of 71 and 30.6 ± 2.7 species, respectively, and it also showed high sponge biomass, with a mean value of 771 ± 189.8 g/

**Table 2**

Summary of results by each sponge assemblage detected at seamounts. Depth, mean and total species richness (S<sub>mean</sub> and S<sub>total</sub>), sponge biomass (B<sub>mean</sub>) and algae biomass (B<sub>amean</sub>) are expressed in terms of mean value (±standard error) and range values (minimum-maximum). Biomass values are only given for stations sampled with beam trawl and expressed in g/100 m<sup>2</sup>. The total values of S, as well as the sampling devices (BT: beam trawl; RD: rock dredge) are also shown.

Assemblage	N	Substrate	Device	Depth (m)	S <sub>mean</sub>	S <sub>total</sub>	B <sub>mean</sub>	B <sub>amean</sub>
sB	8	Sedimentary	BT	148 ± 1.2 (141–154)	30.6 ± 2.7 (20–42)	71	771.7 ± 189.8 (94–1843)	26 ± 43 (0–130)
sC	9	Mostly Sedimentary	BT/RD	115 ± 3.9 (97–135)	16.9 ± 1.9 (9–30)	70	1342.3 ± 839.8 (17–7684)	4042 ± 8178 (0–24151)
sD	7	Mostly rocky	BT/RD	117 ± 8.1 (94–193)	18.4 ± 2.7 (10–26)	69	19.77 <sup>a</sup>	2756 <sup>a</sup>
sE	26	Sedimentary	BT	513 ± 31.0 (278–740)	3.4 ± 0.4 (1–8)	20	8.3 ± 6.5 (0.01–169)	–
sF	16	Sedimentary	BT	338 ± 24.0 (195–511)	12.3 ± 1.3 (4–22)	55	25.9 ± 7.7 (1.8–90)	–
sA	12	Rocky	RD	277 ± 15.6 (191–397)	5.4 ± 0.5 (3–9)	31	–	–
Total	78	–	BT/RD	–	14.5 ± 1.1 (1–42)	185	433.6 ± 78.0 (0.01–7684)	2275 ± 483.3 (0–24151)

<sup>a</sup> The value corresponds to the only station sampled with beam trawl at that assemblage.



**Fig. 4.** Dendrogram of trawl fishing grounds assemblages identified from cluster analysis of the GOC samples. Statistically significant groups are defined by the SIMPROF test, and illustrated by discontinuous red lines. Depth range and zone are indicated by each cluster.

**Table 3**

Summary of results by each sponge assemblage detected at trawl fishing grounds with GOC. Depth, mean and total species richness (S<sub>mean</sub> and S<sub>total</sub>), sponge biomass (B<sub>mean</sub>) and algae biomass (B<sub>amean</sub>) are expressed in terms of mean value (±standard error) and range values (minimum-maximum). Biomass values are expressed in g/100 m<sup>2</sup>. The total values of S are also shown.

Assemblage	N	Substrate	Depth (m)	S <sub>mean</sub>	S <sub>total</sub>	B <sub>mean</sub>	B <sub>amean</sub>
GocE	14	Sedimentary	57 ± 1.1 (50–63)	13.1 ± 0.8 (8–19)	55	28.5 ± 8.0 (2.5–110.0)	572 ± 117 (157–1558)
GocB	7	Sedimentary	73 ± 4.1 (54–83)	11 ± 0.8 (7–13)	38	8 ± 4.7 (0.5–33.2)	658 ± 275 (19–1921)
GocD	26	Sedimentary	68 ± 1.5 (54–79)	20.8 ± 1.3 (12–36)	95	33.3 ± 11.3 (0.6–252.2)	788 ± 214 (45–4426)
GocC	7	Sedimentary	67 ± 3.4 (55–78)	13.1 ± 1.2 (7–16)	36	17.6 ± 12.3 (1.6–91.5)	407 ± 162 (111–1103)
GocA	2	Sedimentary	65 ± 3.5 (61–68)	13.5 ± 2.5 (11–16)	21	8.7 ± 3.7 (5.0–12.4)	527 ± 37 (490–564)
GocH	16	Sedimentary	195 ± 36.6 (106–625)	3.6 ± 0.8 (1–13)	27	0.6 ± 0.25 (2.7*10 <sup>-3</sup> –3.9)	–
GocG	22	Sedimentary	356 ± 46.1 (112–738)	2.6 ± 0.4 (1–8)	16	0.6 ± 0.4 (4.6*10 <sup>-4</sup> –8.2)	–
GocF	12	Sedimentary	459 ± 69 (111–754)	1.1 ± 0.1 (1–2)	2	0.02 ± 0.02 (8.4*10 <sup>-4</sup> –0.2)	–
Total	106	–	–	9.9 ± 0.7 (1–36)	158	12.2 ± 1.3 (8.4*10 <sup>-4</sup> –252.2)	590 ± 19.11 (19–4426)

100 m<sup>2</sup>, but low algae biomass (Table 2). This group contained the station with more species of all the study, with up to 42 species and a biomass of 1843 g/100 m<sup>2</sup>. It was characterized by *P. compressa*, *Hemiasiterella elongata*, *Penares helleri* and *Chelonaplyssilla* sp. (Table 5; Fig. 7C–E). The group sD (94–193 m depth) was composed of stations located in rocky bottoms (except one which was sedimentary) from AM and EB seamounts. Their total and mean S values were also high, up to 69 and 18.4 ± 2.7 species, respectively (Table 2), but biomass could not be estimated because all samples were collected using RD, except one

using BT with 19.8 g/100 m<sup>2</sup> of sponge biomass. This group was characterized by *Spongosorites* sp1, *Haliclona poecillastroides*, *F. balearica* and *Polymastia* sp3 (Table 5; Fig. 7F and G).

Within the deeper assemblages, sA (151–458 m depth) was composed by stations in rocky bottoms, showing total and mean S values of 31 and 5.4 ± 0.5 species, respectively. No biomass values were estimated for this group as it only contains samples collected with RD (Table 2). This group was characterized by *Jaspis* sp2, *Heteroxya* cf. *beauforti*, *Hamacantha* (*Hamacantha*) sp2 and *P. compressa* (Table 5;

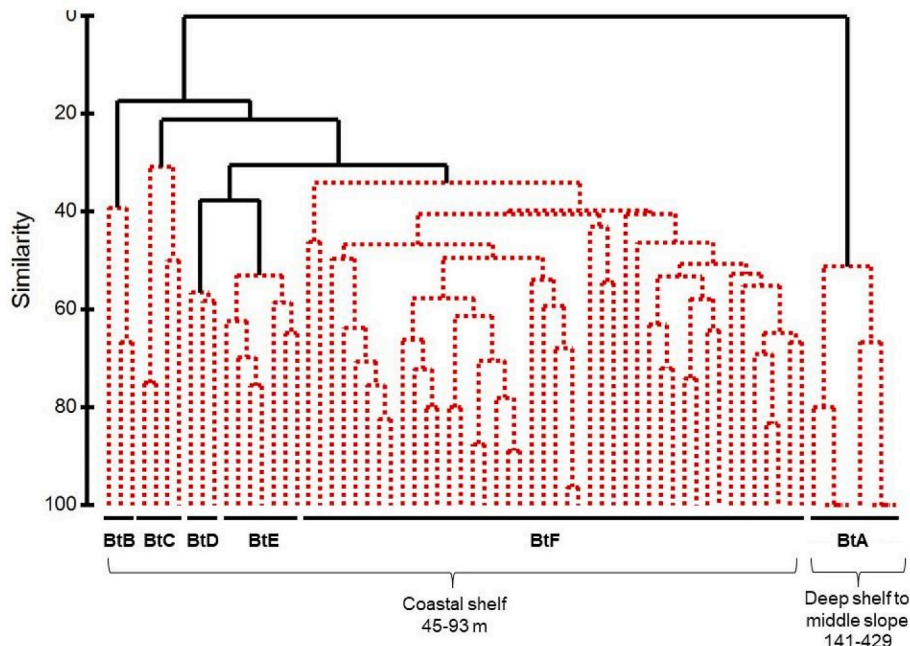


Fig. 5. Dendrogram of trawl fishing ground assemblages identified from cluster analysis of the beam trawl samples. Statistically significant groups are defined by the SIMPROF test, and illustrated by discontinuous red lines. Depth range and zone are indicated by each cluster.

Table 4

Summary of results by each sponge assemblage detected at trawl fishing grounds with beam trawl. Depth, mean and total species richness (S<sub>mean</sub> and S<sub>total</sub>), sponge biomass (B<sub>mean</sub>) and algae biomass (B<sub>amean</sub>) are expressed in terms of mean value (±standard error) and range values (minimum-maximum). Biomass values are expressed in g/100 m<sup>2</sup>. The total values of S are also shown.

Assemblage	N <sub>stations</sub>	Substrate	Depth (m)	S <sub>mean</sub>	S <sub>total</sub>	B <sub>mean</sub>	B <sub>amean</sub>
BtF	43	Sedimentary	64 ± 1.3 (45–93)	10.8 ± 0.7 (5–21)	83	364.2 ± 27.1 (2.0–7720.3)	23,981 ± 3441 (990–92493)
BtB	3	Sedimentary	59 ± 6.8 (50–72)	3.7 ± 1.7 (2–7)	8	18.1 ± 17.2 (0.6–52.5)	9326 ± 7946 (445–25179)
BtC	4	Sedimentary	71 ± 3.4 (67–71)	6.3 ± 1.1 (4–8)	16	16.8 ± 4 (6.1–24.2)	2056 ± 993 (9–3996)
BtD	3	Sedimentary	76 ± 4.3 (69–84)	18.3 ± 1.3 (17–21)	35	1478.6 ± 917.6 (121.6–3227.1)	36,773 ± 17,305 (4532–63,791)
BtE	7	Sedimentary	73 ± 2.7 (62–81)	26.3 ± 1.9 (22–36)	68	553.8 ± 125.8 (134.9–1136.4)	30,504 ± 12,991 (3513–85,607)
BtA	8	Sedimentary	248 ± 35.5 (141–429)	5.9 ± 2.2 (2–20)	26	15 ± 12.4 (0.05–101.3)	–
Total	68	–	–	11.9 ± 1.1 (2–36)	149	407.8 ± 69.2 (0.05–7720.3)	20,528 ± 1873 (445–92493)

Fig. 7H and I). The group sF (195–511 m depth) was composed of samples collected at the SO summit and sedimentary bottoms of the flanks of the three seamounts. It showed low total and mean S values (55 and 12.3±(1.3) species, respectively) and relatively low mean biomass (25.9 ± 7.7 g/100 m<sup>2</sup>; Table 2). It was characterized by *P. compressa*, *D. inornata*, *T. muricata*, *Hamacantha (Hamacantha) sp1*, *Dragmatella aberrans* and *Desmacella annexa* (Table 5). The group sE (278–740 m depth) was composed of samples collected at sedimentary bottoms of all seamounts. It showed low total and mean S values (20 and 3.4±(0.4) species, respectively) and a mean biomass of 8.26 ± 6.5 g/100 m<sup>2</sup> (Table 2). It was characterized by *T. muricata*, *D. innornata* and *D. annexa* (Table 5).

### 3.4. Trawl fishing grounds

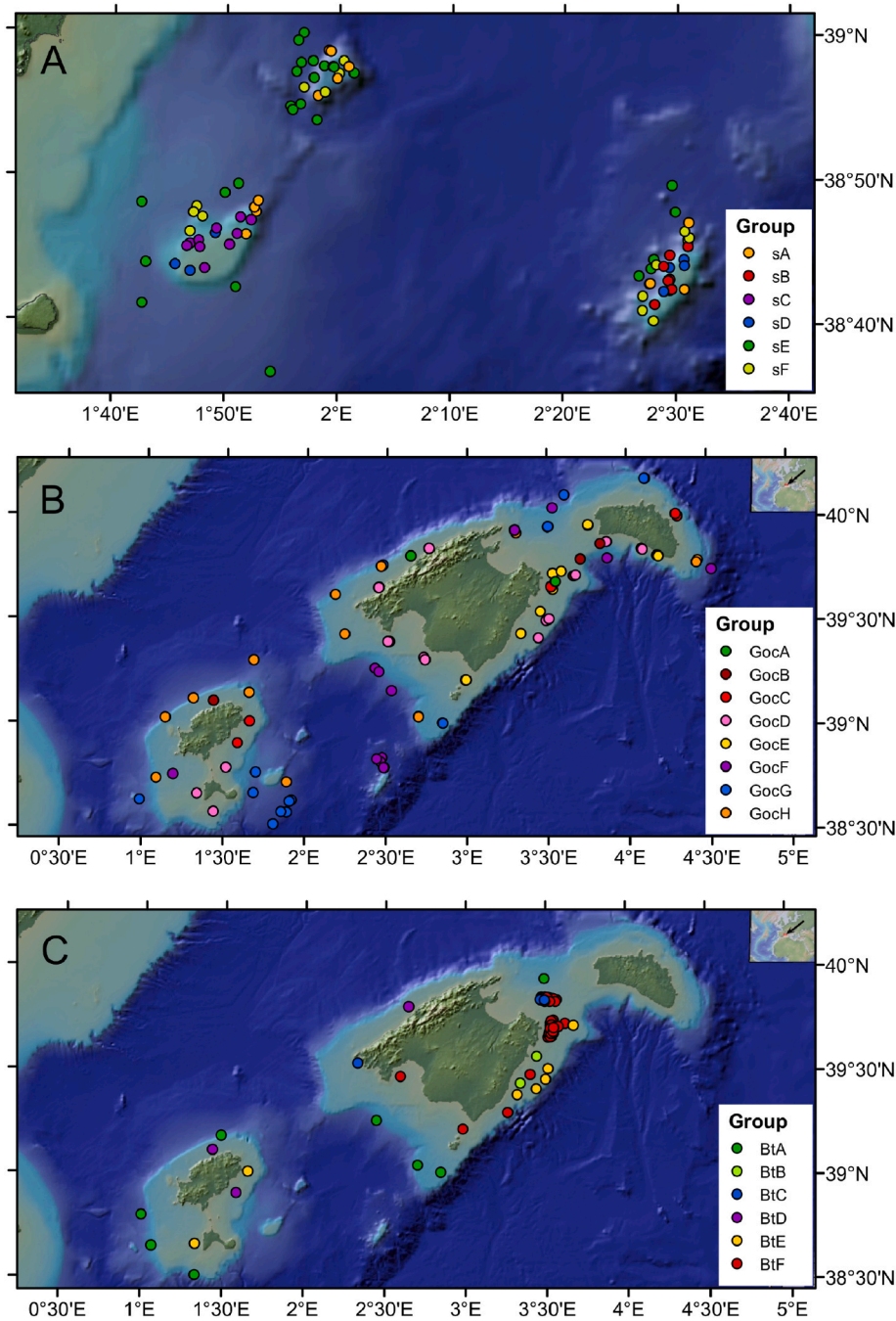
Both GOC (Fig. 4) and BT (Fig. 5) based dendrograms showed two main groups, one with coastal shelf groups (45–93 m) and the other with deep shelf to middle slope groups (106–750 m). Coastal shelf stations showed diverse types of algae assemblages, being dominated by red algae beds.

Regarding GOC dendrogram, coastal shelf group GocA was composed only of two samples at 61 and 70 m depth, with a total and mean S values of 21 and 13.5 ± 2.5 species, respectively and mean sponge and algae biomass of 8.7 ± 3.7 g/100 m<sup>2</sup> and 527 ± 37 g/100 m<sup>2</sup> (Table 3). It was characterized by *S. domuncula*, *Haliclona sp3*,

*C. septimaniensis*, *Baztella inops* and *Calcarea sp4* (Table 6). GocB (54–83 m depth) showed a value of total S (n = 38 species) higher than the previous group, but it had similar values of mean S (11 ± 0.8 species) and sponge and algae biomasses (8 ± 4.7 g/100 m<sup>2</sup> and 658 ± 275 g/100 m<sup>2</sup>) (Table 3). It was characterized by *S. domuncula*, *Axinella damicornis*, *Axinella verrucosa* and *Siphonochalina sp.* (Table 6). The group GocC (55–78 m depth), had a total S of 36 species and a mean S similar to previous groups (13.1 ± 1.2 species) and mean sponge and algae biomasses of 17.6 ± 12.3 g/100 m<sup>2</sup> and 407 ± 162 g/100 m<sup>2</sup> (Table 3). It was characterized by *S. domuncula*, *H. (R.) mediterranea*, *Siphonochalina balearica* and *Haliclona sp3* (Table 6). The other two clusters of the coastal shelf grouped most of the samples, and showed higher S and biomasses values. The group GocD (54–79 m depth) had a total and mean S values of 95 and 20.8 ± 1.3 species, respectively and a mean sponge and algae biomasses of 33.3 ± 11.3 g/100 m<sup>2</sup> and 788 ± 214 g/100 m<sup>2</sup> (Table 3). It was characterized by *Mycale (Aegogropila) syrinx*, *Haliclona sp3* and *S. domuncula* (Table 6). GocE (50–63 m depth) had total and mean S values of 55 and 13.1 ± 0.8, respectively and a mean sponge and algae biomasses of 28.5 ± 8.0 g/100 m<sup>2</sup> and 572 ± 117 g/100 m<sup>2</sup> (Table 3). It was characterized by *S. domuncula*, *Haliclona sp3*, *Dysidea sp1*, *M. (A.) syrinx* and *P. tenacior* (Table 6).

The clusters from the deep shelf to the middle slope showed very low values of S and biomass. The group GocF (111–754 m depth) had total and mean S values of 2 and 1.1 ± 0.1 species, respectively and a mean biomass of 0.024 ± 0.02 g/100 m<sup>2</sup> (Table 3). It was composed





**Fig. 6.** Maps showing the location of the sampling stations corresponding to each sponge assemblage obtained. A: Seamount groups. B-C: Fishing grounds groups obtained with GOC (B) and beam trawl (C).

exclusively by *D. annexa*, except for a single specimen of *Petrosia* (*Petrosia*) *raphida*. The group GocG (112–738 m depth) had a total and mean *S* of 16 and  $2.6 \pm 0.4$  species, respectively and a mean biomass of  $0.6 \pm 0.4$  g/100 m<sup>2</sup> (Table 3). It was characterized by *T. muricata*, with a much lower contribution of *D. annexa* (Table 6). The group GocH (106–625 m depth) had total and mean *S* values of 27 and  $3.6 \pm 0.8$  species, respectively and a mean biomass of  $0.6 \pm 0.25$  g/100 m<sup>2</sup> (Table 3). It was characterized by *P. compressa*, *H. poecillastroides*, *P. helleri* and *P. (P.) raphida* (Table 6).

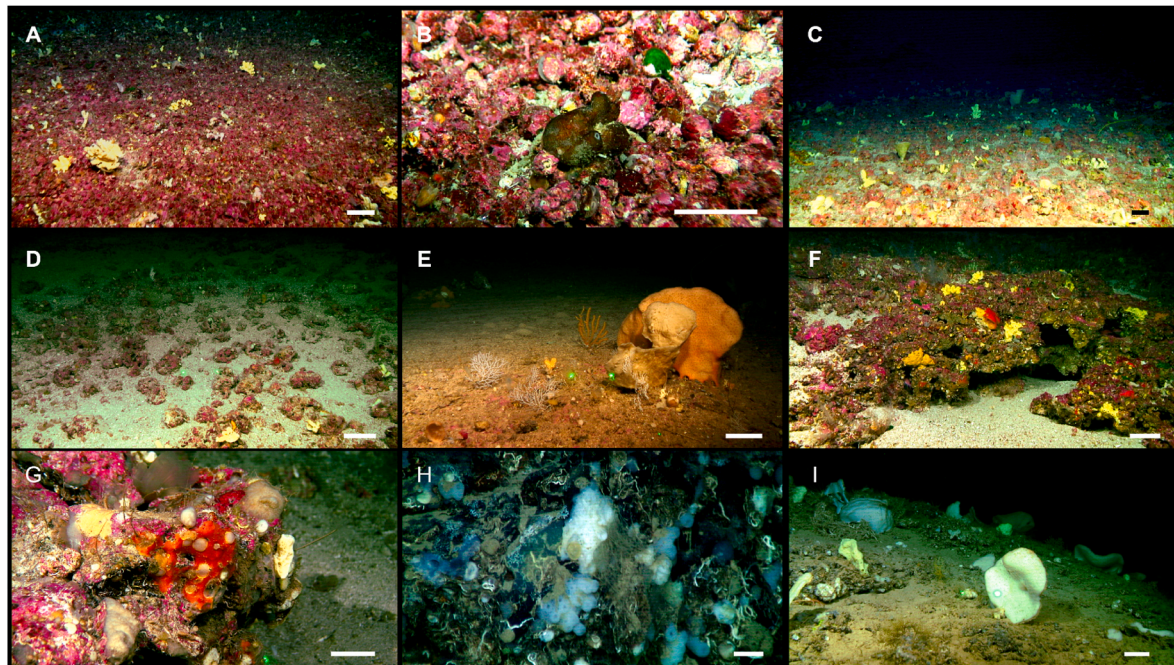
Regarding BT dendrogram, coastal shelf BtB (50–72 m depth) was the group with the lowest value of total *S* (8 species) and also had low values of mean *S* ( $3.7 \pm 1.7$  species) and sponge and algae biomasses with  $18 \pm 17.2$  g/100 m<sup>2</sup> and  $9326 \pm 7946$  g/100 m<sup>2</sup> (Table 4). It was

characterized by *S. domuncula* and *C. septimaniensis* (Fig. 8A and B, Table 7). The group BtC (67–71 m depth) had a total and mean *S* of 16 and  $6.3 \pm 1.1$  species, respectively and low mean sponge and algae biomasses, with  $17 \pm 4$  g/100 m<sup>2</sup> and  $2056 \pm 993$  g/100 m<sup>2</sup> (Table 4). It was characterized by *C. septimaniensis*, *Calcarea* sp1, *L. (L.) cavernosa*, *M. (A.) syrinx* and *Haliclona* sp4 (Table 7). The group BtD (69–84 m depth) had a total and mean *S* of 35 and  $18 \pm 1.3$  species, respectively and showed the highest mean biomasses values for both sponges and algae with  $1479 \pm 917.6$  g/100 m<sup>2</sup> and  $36,773 \pm 17,305$  g/100 m<sup>2</sup> (Table 4). It was characterized by *Raspaciona aculeata*, *A. damicornis*, *Tethya* sp2, *Phorbas* sp3 and *Paratimea* sp. (Fig. 8C, Table 7). The group BtE (62–81 m depth) had a total and mean *S* of 68 and  $26.3 \pm 1.9$  species, respectively and a mean sponge and algae biomasses of  $554 \pm 125.8$  g/100 m<sup>2</sup>

**Table 5**

SIMPER results for the seamounts assemblages identified from cluster analysis and SIMPROF test.  $S_i$ : average similarity; %  $S^*_i$ , percentage contribution to similarity.

Assemblages	Species	$S_i$	% $S^*_i$	Assemblages	Species	$S_i$	% $S^*_i$
<b>sA</b> $S_i$ : 29.92	<i>Jaspis</i> sp2	44.99	44.99	<b>sC</b> $S_i$ : 49.58	<i>Jaspis</i> sp1	5.62	74.1
	<i>Heteroxya</i> cf. <i>beauforti</i>	13.94	58.93		<i>Haliclona poecillastroides</i>	5.4	79.5
	<i>Hamacantha</i> ( <i>Hamacantha</i> ) sp2	13.27	72.2		<i>Discodermia polymorpha</i> Pisera & Vacelet, 2011	4.36	83.86
	<i>Poecillastra compressa</i>	8.98	81.18		<i>Chelonaplysilla</i> sp.	3.84	87.7
	<i>Tretodictyum reisiwigi</i>	7.15	88.33		<i>Penares helleri</i>	2.2	89.9
	<i>Phakellia robusta</i>	6.9	95.23		<i>Axinella</i> sp2	2.2	92.1
<b>sB</b> $S_i$ : 69.82	<i>Poecillastra compressa</i>	6.61	6.61	<b>sD</b> $S_i$ : 43.69	<i>Spongosorites</i> sp1	21.51	21.51
	<i>Hemiassterella elongata</i>	6.61	13.23		<i>Haliclona poecillastroides</i>	16.09	37.6
	<i>Penares helleri</i>	6.61	19.84		<i>Foraminospongia balearica</i>	9.94	47.54
	<i>Chelonaplysilla</i> sp.	6.61	26.45		<i>Polymastia</i> sp3	9.08	56.62
	<i>Haliclona</i> ( <i>Halichoelona</i> ) sp.	6.61	33.07		<i>Hamacantha</i> ( <i>Vomerula</i> ) <i>fulcula</i>	6.11	62.73
	<i>Phakellia robusta</i>	5	38.07		<i>Pachastrella monilifera</i>	5.8	68.53
	<i>Foraminospongia balearica</i>	5	43.07		<i>Jaspis</i> sp1	5.17	73.7
	<i>Jaspis</i> sp1	4.9	47.97		<i>Hexadella</i> sp1	5.17	78.87
	<i>Hexadella</i> sp1	4.83	52.8		<i>Axinella</i> sp7	3	81.87
	<i>Discodermia polymorpha</i>	4.83	57.63		<i>Hymedesmia</i> ( <i>Hymedesmia</i> ) sp2	3	84.87
	<i>Dragmatella aberrans</i>	4.71	62.34		<i>Scopaliniidae</i> sp1	3	87.88
	<i>Haliclona</i> sp13	4.71	67.06	<i>Timea</i> sp1	2.65	90.53	
	<i>Vulcanella gracilis</i> (Sollas, 1888)	3.61	70.67	<b>sE</b> $S_i$ : 50.10	<i>Thenea muricata</i>	71.77	71.77
	<i>Desmacella inornata</i>	3.61	74.27		<i>Desmacella inornata</i>	9.8	81.57
<i>Halichondriidae</i> sp2	3.32	77.59	<i>Desmacella annexa</i>		8.47	90.04	
<i>Tretodictyum reisiwigi</i>	3.24	80.83	<b>sF</b> $S_i$ : 47.37	<i>Poecillastra compressa</i>	20.09	20.09	
<i>Dendroceratida</i> sp3	2.37	83.21		<i>Desmacella inornata</i>	19.7	39.79	
<i>Petrosia raphida</i>	2.37	85.58		<i>Thenea muricata</i>	12.58	52.37	
<i>Petrosia</i> ( <i>Strongylophora</i> ) <i>vansoesti</i>	2.25	87.83		<i>Hamacantha</i> ( <i>Hamacantha</i> ) sp1	7.7	60.07	
<i>Haliclona poecillastroides</i>	2.19	90.02		<i>Dragmatella aberrans</i>	7.67	67.74	
<b>sC</b> $S_i$ : 49.58	<i>Poecillastra compressa</i>	18.18	18.18	<i>Desmacella annexa</i>	7.39	75.13	
	<i>Foraminospongia balearica</i>	14.52	32.7	<i>Hamacantha</i> ( <i>Vomerula</i> ) sp5	5.11	80.24	
	<i>Calcarea</i> sp6	10.96	43.66	<i>Tretodictyum reisiwigi</i>	3.85	84.09	
	<i>Hexadella</i> sp1	10.84	54.51	<i>Haliclona</i> ( <i>Rhizoniera</i> ) <i>rhizophora</i>	3.34	87.42	
	<i>Petrosia raphida</i>	8.22	62.72	<i>Hemiassterella elongata</i>	2	89.42	
	<i>Pennares euastrum</i>	5.75	68.47	<i>Jaspis</i> sp2	1.94	91.36	

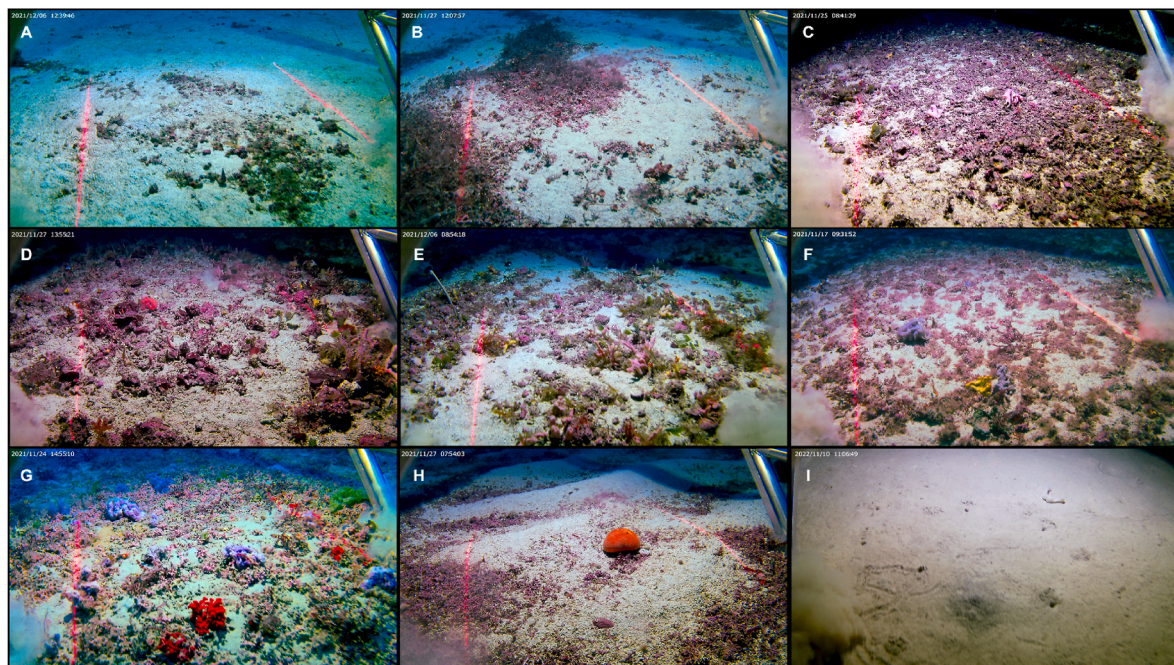


**Fig. 7.** ROV images of sponge communities identified in the seamounts of the Mallorca Channel (Balearic Islands, western Mediterranean). A: sponge gardens associated with rhodolith beds with high coverage in the AM seamount at 91 m depth; B: detail of a *Penares euastrum* individual at the AM seamount rhodolith beds, at 90 m depth; C-D: sponge gardens associated with rhodolith beds with middle coverage in the EB seamount at 132 m and 141 m depth; E: sponge garden at the deepest part of the mesophotic zone in the EB seamount at 149 m depth; F: sponges at rocky outcrops in the AM at 100 m depth; G: sponges at rocky outcrops in the EB seamount at 146 m depth; H-I: sponge gardens of the aphotic rocky bottoms in the EB (H) and the AM (I) seamounts at 326 m and 354 m depth, respectively. Scale bar 15 cm (A, C-F, I), 5 cm (B, G-H).

**Table 6**

SIMPER results for the trawl fishing grounds (GOC) assemblages identified from cluster analysis and SIMPROF test.  $S_i$ : average similarity; %  $S_i$ , percentage contribution to similarity.

Assemblages	Species	$S_i$	% $S_i$	Assemblages	Species	$S_i$	% $S_i$
<b>GocB</b> $S_i$ : 48.53	<i>Suberites domuncula</i>	25.09	25.09	<b>GocA</b> $S_i$ : 47.62	<i>Axinella damicornis</i>	7.08	69.88
	<i>Axinella damicornis</i>	25.09	50.18		<i>Callyspongia septimaniensis</i>	6.76	76.63
	<i>Axinella verrucosa</i>	18.52	68.7		<i>Hymedesmia (Stylopus) sp1</i>	3.99	80.63
	<i>Siphonochalina sp.</i>	10.81	79.51		<i>Lissodendoryx (Lissodendoryx) cavernosa</i>	2.74	83.37
	<i>Raspaciona aculeata</i>	6.46	85.97		<i>Siphonochalina sp.</i>	2.74	86.1
	<i>Callyspongia septimaniensis</i>	2.96	88.93		<i>Phorbas tenacior</i>	2.26	88.37
	<i>Antho (Antho) oxeifera</i>	2.96	91.89		<i>Axinella verrucosa</i>	2.15	90.51
	<b>GocD</b> $S_i$ : 54.35	<i>Mycale (Aegogropila) syrinx</i>	10.14		10.14	<b>GocE</b> $S_i$ : 51.26	<i>Suberites domuncula</i>
<i>Haliclona sp3</i>	9.27	19.41	<i>Haliclona sp3</i>	20	40		
<i>Suberites domuncula</i>	8.4	27.8	<i>Callyspongia septimaniensis</i>	20	60		
<i>Axinella damicornis</i>	6.88	34.68	<i>Bastella inops</i>	20	80		
<i>Haliclona mediterranea</i>	6.86	41.54	<i>Calcarea sp4</i>	20	100		
<i>Dictyonella incisa</i>	6.69	48.23	<b>GocF</b> $S_i$ : 59.81	<i>Suberites domuncula</i>	15.45	15.45	
<i>Antho (Antho) oxeifera</i>	4.76	52.99	<i>Haliclona sp3</i>	12.87	28.33		
<i>Tethya sp1</i>	4.02	57	<i>Dysidea sp1</i>	10.31	38.64		
<i>Dictyonella sp2</i>	3.89	60.9	<i>Mycale (Aegogropila) syrinx</i>	10.08	48.72		
<i>Dysidea sp1</i>	3.85	64.75	<i>Phorbas tenacior</i>	8.62	57.34		
<i>Phorbas tenacior</i>	3.75	68.5	<i>Lissodendoryx (Lissodendoryx) cavernosa</i>	7.52	64.85		
<i>Aqptos sp1</i>	3.71	72.21	<i>Acarus levii</i>	7.14	72		
<i>Axinella verrucosa</i>	3.51	75.71	<i>Siphonochalina sp.</i>	5.55	77.54		
<i>Callyspongia septimaniensis</i>	3.07	78.78	<i>Mycale (Aegogropila) contarenii</i>	4.64	82.18		
<i>Acarus levii</i>	3.03	81.81	<i>Myxilla (Myxilla) iotrochotina</i>	2.77	84.96		
<i>Raspaciona aculeata</i>	2.32	84.13	<i>Haliclona mediterranea</i>	2.75	87.71		
<i>Siphonochalina sp.</i>	2.28	86.41	<i>Raspaciona aculeata</i>	2.57	90.28		
<i>Chelonaplysilla sp.</i>	1.91	88.32	<b>GocH</b> $S_i$ : 36.89	<i>Poecillastra compressa</i>	42.43	42.43	
<i>Phorbas sp3</i>	1.84	90.16	<i>Haliclona poecillastroides</i>	30.7	73.13		
<b>GocC</b> $S_i$ : 51.22	<i>Suberites domuncula</i>	16.03	16.03	<i>Penares helleri</i>	15.01	88.14	
<i>Haliclona mediterranea</i>	16.03	32.06	<i>Petrosia (Petrosia) raphida</i>	10.58	98.72		
<i>Siphonochalina balearica</i>	11.56	43.62	<b>GocG</b> $S_i$ : 94.44	<i>Thenea muricata</i>	84	84	
<i>Haliclona sp3</i>	11.24	54.86	<i>Desmacella annexa</i>	7.95	91.96		
<i>Tethya sp1</i>	7.94	62.8	<i>Desmacella annexa</i>	100	100		



**Fig. 8.** Sponge communities identified in the Balearic Islands trawl fishing grounds. A-H: typical sponge assemblage from the euphotic zone associated with red algae beds. A-B: stations corresponding to the BtB assemblage, located at the east of Mallorca at 53 m (A) and 51 m (B), with low algae coverage. C: station corresponding to the BtD assemblage, located at north of Mallorca (73 m), with high algae cover and high sponge biomass. D-F: stations corresponding to the BtE assemblage, located at the east of Mallorca (D-E, 78 and 77 m, respectively) and west of Formentera (F, 69 m). G-H: station corresponding to the BtF assemblage, located west of Mallorca (G, 49 m), and east of Mallorca (H, 59 m) with high algae cover and high sponge biomass. I: station corresponding to the BtA assemblage, located east of Formentera, at 377 m. Distance between lasers: 75 cm. Images acquired through the HORUS photogrammetric sled.

**Table 7**

SIMPER results for the assemblages identified from cluster analysis and SIMPROF test. S<sub>i</sub>: average similarity; % S<sub>i</sub>, percentage contribution to similarity.

Assemblages	Species	S <sub>i</sub>	%S <sub>i</sub>	Assemblages	Species	S <sub>i</sub>	%S <sub>i</sub>		
<b>BtF</b> S <sub>i</sub> : 44.36	<i>Haliclona</i> sp3	20.9	20.9	<b>BtB</b> S <sub>i</sub> : 48.41	<i>Dysidea</i> sp1	2.66	76.66		
	<i>Lissodendoryx (Lissodendoryx) cavernosa</i>	16.47	37.37		<i>Suberites domuncula</i>	2.42	79.08		
	<i>Bubaris vermiculata</i>	10.39	47.76		<i>Siphonochalina</i> sp.	2.42	81.49		
	<i>Suberites domuncula</i>	8.21	55.97		<i>Dictyonella</i> sp2	2.42	83.91		
	<i>Calcarea</i> sp1	8.17	64.15		<i>Haliclona</i> sp9	2.42	86.33		
	<i>Haliclona mediterranea</i>	6.65	70.8		<i>Callyspongia septimaniensis</i>	2.38	88.71		
	<i>Baztella inops</i>	5.89	76.69		<i>Phorbas</i> sp3	2.38	91.09		
	<i>Myxilla (Myxilla) iotrochotina</i>	3.47	80.15		<b>BtA</b>	<i>Suberites domuncula</i>	82.79	82.79	
	<i>Dysidea</i> sp1	3.24	83.39		S <sub>i</sub> : 66.43	<i>Callyspongia septimaniensis</i>	17.21	100	
	<i>Mycale (Aegogropila) contareii</i>	3.24	86.63		<b>BtD</b>	<i>Thenea muricata</i>	77.42	77.42	
	<i>Callyspongia septimaniensis</i>	3.14	89.77		S <sub>i</sub> : 57.16	<i>Desmacella inornata</i>	14.52	91.94	
	<i>Siphonochalina</i> sp.	2.62	92.39		<b>BtC</b>	<i>Raspaciona aculeata</i>	15.08	15.08	
	<b>BtE</b>	<i>Haliclona</i> sp3	8.78		8.78	S <sub>i</sub> : 41.47	<i>Axinella damicornis</i>	15.08	30.16
	S <sub>i</sub> : 58.16	<i>Haliclona mediterranea</i>	8.78		17.56	<i>Tethya</i> sp2	15.08	45.24	
	<i>Axinella damicornis</i>	8.78	26.34	<i>Phorbas</i> sp3	15.08	60.32			
	<i>Phorbas tenacior</i>	6.24	32.58	<i>Paratimea</i> sp.	15.08	75.4			
	<i>Chelonaplysilla</i> sp.	6.24	38.82	<i>Raspailia viminalis</i>	5.55	80.95			
	<i>Baztella inops</i>	6.18	45.01	<i>Diplastrella bistellata</i>	4.86	85.81			
	<i>Microcionidae</i> sp1	4.36	49.36	<i>Dictyoceratida</i> sp3	4.86	90.67			
	<i>Antho (Antho) oxeifera</i>	4.13	53.49	<i>Callyspongia septimaniensis</i>	33.01	33.01			
	<i>Dictyonella incisa</i>	4.13	57.62	<i>Calcarea</i> sp1	27.91	60.93			
	<i>Haliclona</i> sp10	4.13	61.75	<i>Lissodendoryx (Lissodendoryx) cavernosa</i>	10.05	70.97			
	<i>Calcarea</i> sp1	4.08	65.83	<i>Mycale (Aegogropila) syrinx</i>	10.05	81.02			
	<i>Raspaciona aculeata</i>	4.08	69.92	<i>Haliclona</i> sp4	10.05	91.07			
	<i>Halichondria (Halichondria) sp1</i>	4.08	74						

and 30,504 ± 12,991 g/100 m<sup>2</sup> (Table 4). It was characterized by *Haliclona* sp3, *H. mediterranea*, *A. damicornis*, *P. tenacior*, *Chelonaplysilla* sp. and *B. inops* (Fig. 8D–F; Table 7). BtF group (45–93 m depth) showed the highest total S, with 83 species, and a mean S value of 10.8 ± 0.7 species, with a mean sponge and algae biomasses of 364 ± 27.1 g/100 m<sup>2</sup> and 23,981 ± 3441 g/100 m<sup>2</sup>, respectively (Table 4). This group included the sample with the highest sponge and algae biomasses of all the study (7720 g/100 m<sup>2</sup> and 92,493 g/100 m<sup>2</sup>). It was characterized by *Haliclona* sp3, *L. (L.) cavernosa*, *B. vermiculata*, *S. domuncula* and *Calcarea* sp1 (Fig. 8G and H, Table 7).

The cluster BtA (141–429 m depth), similarly to the deep samples obtained with GOC, showed low values of S and biomass. It had a total and mean S of 26 and 5.9 ± 2.2 species, respectively and a mean sponge biomass of 15 ± 12.4 g/100 m<sup>2</sup> (Table 4). It was characterized by *T. muricata* and *D. innornata* (Fig. 8I, Table 7).

### 3.5. Taxonomic composition

A total of 22 orders have been documented (Fig. 11), of which 19 belonging to the class Demospongiae. Of the total Demosponge orders, only Trachycladida and Sphaerocladina were not found at the present study. Twenty orders were found at seamounts, 21 at trawl fishing grounds and 18 were shared by both areas. Biemnida was exclusively found at seamounts and Chondrillida and Chondrosida were only found at trawl fishing grounds.

At seamounts, AM seamount had the highest number of orders (n = 20), followed by EB (n = 19) and SO (n = 12) seamounts. Clionaida was only found at AM seamount, while no orders were exclusive from neither the EB nor SO seamounts. In seamounts, the most diverse order was Tetractinellida with 28 species (Fig. 11A), followed by Haplosclerida, Axinellida, Suberitida, Poecilosclerida and Bubarida with 26, 21, 19, 18 and 15 species, respectively. Besides, Tetractinellida was the most diverse order in both EB, as in AM and SO seamounts, with 25, 19 and 7 species, respectively.

By assemblages, in groups sB, sC and sD, at the shallow summits of AM and EB seamounts, Tetractinellida was also the most diverse order, with 17, 16 and 11 species, respectively. Axinellida was the second most

diverse order in sD (12 species), while Haplosclerida was the second most diverse order in sB and sC (15 and 12 species, respectively). In the group sA, at rocky bottoms, Tetractinellida (7 species) and Axinellida (5 species) were the most diverse orders. At sedimentary bottoms, the group sE had Desmacellida as the most diverse order (4 species), followed by Bubarida, Merliida and Polymastida, each one with 3 species, while at group sF, Bubarida was the most diverse group (8 species), followed by Axinellida, Suberitida and Polymastida, with 7 species each one. Only one species of Tetractinellida in group sE and 6 in group sF were found.

At trawl fishing grounds (Fig. 11B), and considering both BT and GOC samples, the most diverse order was Poecilosclerida (47 species), followed by Axinellida, Haplosclerida, Dictyoceratida, Bubarida and Suberitida with 32, 27, 21, 19 and 16 species, respectively. Only Sceptulophora was exclusively found in GOC samples, while Lyssacinosa and Scopalinida were only found in BT samples. Contrarily to the seamounts, at trawl fishing grounds we found 21 Dictyoceratida species (against 5) and only 7 Tetractinellida (against 28).

Regarding GOC assemblages at trawl fishing grounds, coastal shelf groups (GocA–GocE) showed a similar composition, with Poecilosclerida, Haplosclerida, Axinellida and Dictyoceratida as the most diverse orders. At deep shelf and upper to middle slope, group GocF was exclusively composed of Desmacellida and Haplosclerida, while in groups GocG and GocH, Suberitida was the most diverse order with 4 species. In the group GocG, it was followed by Desmacellida and Axinellida with 3 and 2 species, respectively, while in group GocH the second most diverse orders were Axinellida and Haplosclerida, with 4 species each one.

For BT assemblages at trawl fishing grounds, coastal shelf groups (BtB–BtF) also showed a similar order composition, with Poecilosclerida as the most common and diverse order, followed by Haplosclerida and Axinellida. In group BtA, Bubarida, Desmacellida, Polymastida and Tetractinellida were the most diverse orders, each one with three species.

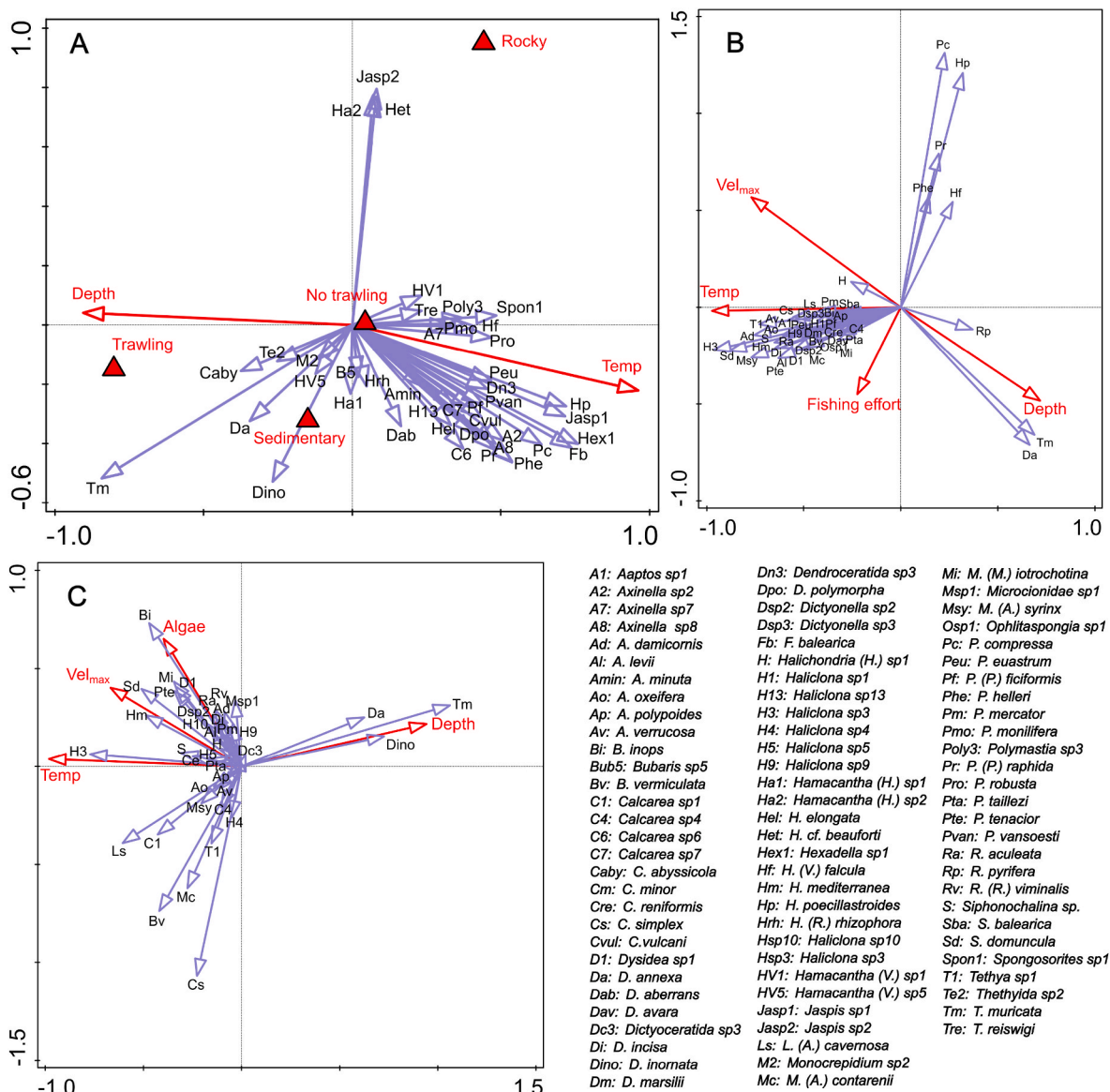


Fig. 9. Biplot for the dbrDA models with the species abbreviation correspondences. A: Seamounts data (beam trawl and rock dredge data); B: trawl fishing grounds (GOC data); C: trawl fishing grounds (beam trawl data).

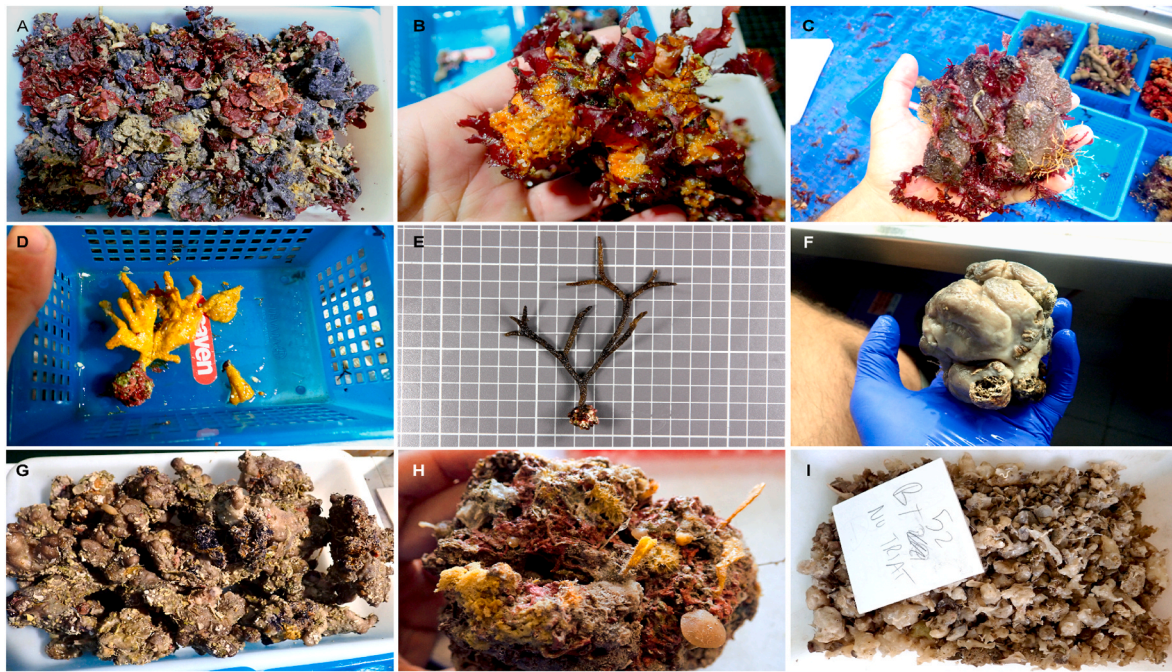
### 3.6. Relationship with environmental variables

We constructed three dbrDA models: one for seamounts (Fig. 9A), one for trawl fishing grounds using GOC data (Fig. 9B), and another the last one for trawl fishing grounds using BT data (Fig. 9C). The Seamount model explained the 36.8% of the sponge presence/absence variance while at fishing grounds, the BT model and the GOC model explained the 298.7% and the 33% of its variance, respectively. The significant variables of the seamount model were depth (variance explained: 7.25%; p-value = 0.001), substrate type (variance explained: 11.41%; p-value = 0.001), mean annual temperature at the bottom (variance explained: 10.71%; p-value = 0.001) and trawling activity (variance explained: 3.24%; p-value = 0.005). At trawl fishing grounds, the significant variables of the GOC model were depth (variance explained: 3.43%; p-value = 0.002), annual mean temperature (variance explained: 13.37%; p-value = 0.001), fishing effort (variance explained: 0.94%; p-value = 0.009) and maxim flow velocity (variance explained: 3.6%; p-value = 0.001) while the significant variables for the BT model were depth (variance explained: 5.11%; p-value = 0.001), total algae biomass (variance explained: 4.1%; p-value = 0.002), mean annual

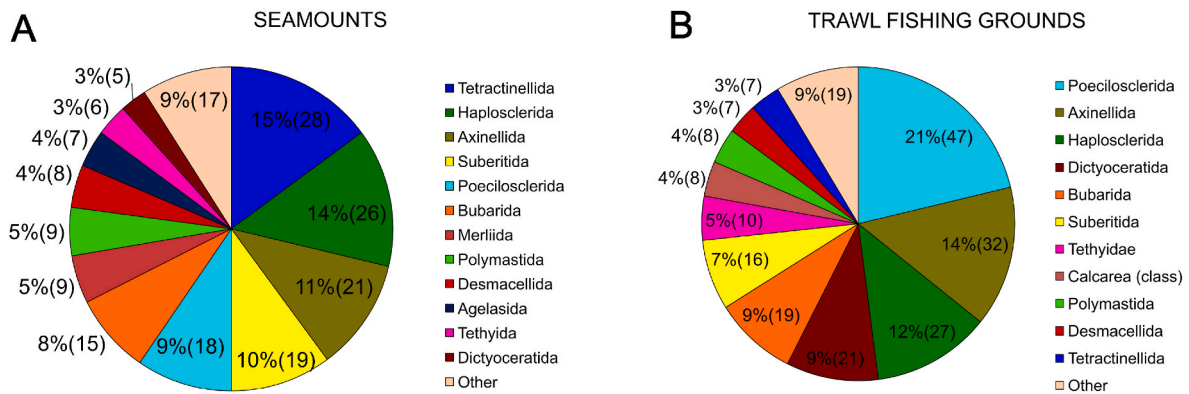
temperature (variance explained: 5.74%; p-value = 0.001) and maxim flow velocity (variance explained: 3.76%; p-value = 0.007).

At seamounts, most of the species were correlated with depth and mean temperature (Fig. 9A). Large mesophotic species like *H. poecillastroides*, *P. compressa*, *F. balearica*, *Hexadella* sp1 and *Spongosorites* sp1 were inversely related with depth and positively related with temperature. Those species characterize the assemblages sB, sC and sD, located at the shallow summits of the AM and the EB seamounts. Species more closely correlated to the substrate type were *D. inornata*, *D. annexa*, *C. abyssicola*, *T. muricata*, *Hamacantha* (H) sp1, *Hamacantha* (*Vomerula*) sp5, and *Monocrepidium* sp2 for sedimentary bottoms (found in assemblages sE and sF) and *Jaspis* sp2, *Hamacantha* (H) sp2, and *Heteroxya* cf. *beauforti* for rocky bottoms (assemblage sA). Fishing was only present on deep sedimentary bottoms where showed some negative correlation on small sedimentary species like *Hamacantha* (H) sp1, *Hamacantha* (*Vomerula*) sp5, *Monocrepidium* sp2 and *Bubaris* sp5.

The GOC model showed a strong correlation between sponge presence/absence with depth and mean annual temperature (Fig. 9B). Depth was positively related to the deep sea species *T. muricata* and *D. annexa* and *R. pyrifer* (found in assemblages GocF and GocG) and negatively



**Fig. 10.** Several examples of substrate used by sponges in the Balearic Islands trawl fishing grounds (A-G) and Seamounts (H-I). A: *Phorbastenacioid* sp using *Peyssonnelia* sp as substrate off west Mallorca, at 45 m depth; B: *Myxilla (Myxilla) itrochotina* using a soft red algae as substrate, at 69 m depth; C: Irciniidae sp3 using soft red algae as substrate, having incorporate most of the algae to its tissue, at 52 m depth; D-E: *Axinella damicornis* and *Raspailia (Raspailia) viminalis* using a rhodolith as substrate at 68 m and 72 m, respectively; F: *Penares helleri* using a dead rhodolith discarded by the trawling fleet as substrate, at 108 m depth; G: *Geodia geodina* using biogenic debris as substrate, with *Hexadella* sp. and other sponges growing in ephybiosis, at 108 m depth off AM seamount; H: encrusting sponges and small Axinellids growing on a partially dead rhodolith found at 102–138 m depth, off EB. I: Sample showing small encrusting species common at sF assemblage, using small organogenic sediments as substrate, at 320 m, off EB.



**Fig. 11.** Percentage of number of taxa in each order, in relation to the total species richness in seamounts and trawl fishing grounds samples. The number of species is also shown between brackets.

related to coastal shelf species like *P. tenacior*, *L (L) simplex*, *Haliclona* sp3 or *S. domuncula* (found in assemblages GocA-GocE). Also, *T. muricata*, *D. annexa* and *R. pyrifer* were negatively related to maxim flow velocity. Temperature showed a similar but inverse pattern with the same species. Fishing effort was negatively related to the presence of the large species *P. helleri*, *P. raphida*, *P. compressa*, *H. pocillastroides* and *H. (V.) falcula* (assemblage GocH).

As the previous models, the BT model showed a strong correlation with depth and mean annual temperature (Fig. 9A). Like in the previous GOC model, depth was positively related with *T. muricata* and *D. annexa*, but also with *D. innornata* (corresponding to BtA). Those species were negatively correlated with mean annual temperature, which was positively correlated with the presence of *Haliclona* sp3. Several species like the encrusting *B. innops* or the massive encrusting *M. (M.) itrochotina* and *P. tenacior* showed a positive correlation with the total benthic algae

biomass. Inversely, species like *C. simplex*, *M. (A.) contarenii*, *B. vermiculata* or *Tethya* sp1 showed a negative correlation with total benthic algae biomass. Finally, species like *S. domuncula* and *H. mediterranea* were highly correlated to maxim flow velocity and, to a lesser extent, to total benthic algae biomass.

#### 4. Discussion

##### 4.1. Sponge diversity

Our results, with 350 species, is one of the larger inventories of sponges published in the Mediterranean. Previous works reported 114 species from the Gulf of Lions, the Ligurian Sea and some areas of the Aegean Sea, between 90 and 765 m depth (Vacelet, 1969), 197 species from the Adriatic, Tyrrhenian, Ionian and Aegean seas between 0 and

700 m depth (Pulitzer-Finali, 1983), 173 species from the Balearic Islands (Bibiloni, 1990) and 96 species from a large region including the Gulf of Cadiz, the Strait of Gibraltar and the Alboran Sea, between 115 and 2110 m depth (Boury-Esnault et al., 1994).

Among the detected species, *Timea chondrilloides*, *Forcepia (Lep-tolabis) luciensis*, *Spinularia sarsii*, *Polymastia tissieri* and *Callyspongia septimaniensis* represent new records for the Balearic Islands, although *C. septimaniensis* may have been reported by Bibiloni (1990) under the name of *Adocia simulans* (Johnston, 1842). Taxa not identified to the species level will be published on taxonomic articles elsewhere.

The high sponge diversity reported in the present study can be explained by several factors. First, the higher intensity of sampling (590 stations, on which sponges were present in 439), than in the mentioned previous works: 53, 64 and 122 sampling stations in Vacelet (1969), Pulitzer-Finali (1983) and Boury-Esnault et al. (1994), respectively. This high number of sampling stations could allow us to find rare species or species that appear sporadically. For example, *Axinella vellerea*, *Lanuginella pupa*, *Melonanchora emphysema* and *Stryphnus ponderosus* were recorded only once. Second, the combination of sampling methodologies (BT, RD, GOC and ROV) allowed sampling of different habitats (in rocky and sedimentary bottoms, including different levels of fishing pressure, from trawl fishing grounds to the bottoms not exploited by bottom trawling in the flanks and summits of the seamounts).

The oceanographic characteristics of the Balearic islands must also play a role in the observed sponge diversity values. In fact, large faunistic lists were also documented in previous works performed in this area, even with fewer stations. Bibiloni (1990) reported 173 species from 83 sampling stations in caves and trawl fishing grounds between 0 and 200 m depth, Uriz et al. (1992) reported 98 species in only 13 sampling stations from 0 to 55 m depth at the Cabrera National Park southern Mallorca and, more recently, Santín et al. (2018) reported 109 species in the Menorca Channel between 50 and 350 m depth.

Waters around the Balearic Archipelago are much more oligotrophic than those of the adjacent Iberian Peninsula. The transparency of the waters could allow certain sponges to keep their photosynthetic symbionts deeper than in other areas, providing photosynthetic products, which can be a potential advantage on mesophotic depths (Keesing et al., 2012) and within an oligotrophic environment as the Mediterranean. For instance, we found some *Petrosia (P.) ficiformis* individuals with red cyanobacterial pigmentation down to 135–140 m depth, at the summit of EB seamount (SuppTable1).

The water transparency also allows algae to develop much deeper than in other areas. Total algae biomass was positively related to the presence of a majority of species on the BT dbRDA (Fig. 9C). Several types of red algae communities can be found down to 90 m depth at trawl fishing grounds, including soft (*Peysonnellia* spp., *Osmundaria volubilis*, *Phyllophora crispata* and *Halopteris filicina*) and calcareous (rhodoliths) species (Johér et al., 2012, 2015), while rhodoliths beds have been found down to 140 m depth in the Mallorca Channel seamounts (Massutí et al., 2022). Deep red algae beds can enhance sponge biodiversity and biomass in several ways. Sedimentary bottoms covered by red algae can act as rocky bottoms by providing substrate, a key limiting factor for aquatic sessile invertebrates (Maldonado et al., 2017). Although algae and sponges compete for the substrate, algae growing under low irradiances may show lower vitality (Bahia et al., 2010) and/or diminished allochemical production (Amade and Lemee, 1998; Pavia and Toth, 2000; Hellio et al., 2004) compared to mixotrophic and heterotrophic animals (Lesser et al., 2019) offering a more accessible substrate for sponges or other invertebrates to colonize (Gherardi, 2004).

Some authors have also suggested that the structural complexity provided by the red algae create shaded habitats, in which sciaphilous sponge species can develop (Santín et al., 2018), although at our study zone we did not find evidence of shading as an important process in the studied red algae beds. Most of the erect and massive sponge species as well as many of the epiphytic encrusting species grow next to the

pigmented areas of the algae (Fig. 10A–E) suggesting a sun-exposed growth.

In addition to structural complexity enhancement, red algae beds release dissolved organic matter (DOM) to the water column in form of exudates that can be consumed by sponges (de Goeij et al., 2013), hence boosting their presence and diversity.

## 4.2. Sponge assemblages

### 4.2.1. Seamounts

The shallow summit sedimentary groups sB and sC were exclusive from the EB and the AM seamounts, respectively. However, differing depths between both groups, with sC being slightly shallower (97–135 m) than sB (141–154 m), indicate that differences found in EB/AM were rather due to depth than to differences in the fauna composition in each seamount. This seems to be corroborated by the fact that the other group of the shallow summit (sD; 94–193 m), included both AM/EB seamounts, having a mixture of characterizing species. Interestingly the shallower sC has higher biomass values, which could be related to the growth of sponges with photosymbionts and by differences in DOM available in the environment released by red algae (Haas et al., 2010; Mueller et al., 2014; Lesser et al., 2019). This points out the importance of light penetration as a determining factor on the temperate mesophotic sponge communities (Uriz et al., 1992; Harris, 2022).

Assemblage sA shows some similarity with the “Hamacantha-Tretodictyum” assemblage described by Santín et al. (2018) at similar depths (250–350 m) in the Menorca channel, characterized by *Hamacantha (Vomerula) falcula*, *T. reiswigi*, *Haliclona mucosa* and *Hexadella cf. dedritifera*. However, no *Jaspis* species was reported in that work, and conversely, we recorded *Hamacantha (Hamacantha) sp2* instead of *Hamacantha (Vomerula) falcula* (Bowerbank, 1874), a thin blue-grayish species very similar in external morphology than the one indicated as *H. (v.) falcula* by those authors (see Fig. 8 h in Santín et al., 2018). In contrast, at Seamounts and trawl fishing grounds we always collected *H. (V) falcula* on sedimentary stations between 102 and 149 m. Besides, sA was also characterized by *Heteroxya cf. beauforti*, *P. compressa* and *P. robusta*. This discrepancy in taxa composition at ecologically similar assemblages of two close areas, suggest that equivalent sponge communities may present significant variations, even when separated by short distances. *T. reiswigi* is a hexactinellid reported in the western Mediterranean, mostly from vertical walls down to 632 m depth (Boury-Esnault et al., 2017). At the Cassidaigne canyon, it is known to occur together with other hexactinellids like *Farrea* sp. or *Oopsacas cf. minuta*, an association never observed in the present work (Fabri et al., 2017).

We detected two assemblages in deep sedimentary stations of the seamounts. The sF included the tetractinellids *P. compressa* and *T. muricata* and a very diverse group of small encrusting and vesicular species like *D. innornata*, *D. aberrans*, *Hamacantha (Hamacantha) sp1*, *Hamacantha (Vomerula) sp5*, small encrusting species of the genus *Bubaris* and *Eurypon*, and small species of the genus *Axinella* and *Polymastia*, among others. These are minute species grown on organogenic sediments like small pieces of shells, sea urchin spines and gravels (Fig. 10I and personal observation), which gave these groups a high diversity. This assemblage shows some similarity to those described at 639–1130 m by Longo et al. (2005) (Cape St. Maria di Leuca, southern Italy), associated to a deep-sea coral bank. Assemblage sE is similar to sF, but it shows much lower diversity and biomass values, probably because there were less organogenic sediments and higher proportion of muds of the area (Massutí et al., 2022). Besides, trawling occurs in a few stations of Se corresponding to the lower parts of the seamounts and the adjacent areas, a fact that could also explain the lower biodiversity in that assemblage, and the presence of resilient species like *T. muricata* and *D. annexa*, typically found at trawl fishing grounds (Pansini and Musso, 1991) (SuppTable 1).

#### 4.2.2. Trawl fishing grounds

At trawl fishing grounds coastal shelf sponge assemblages were always associated with red algae beds, used by many sponges as substrate (Fig. 10A–E), a correlation also reflected in the BT dBRDA model (Fig. 9C). Algae colonization by sponges seems to have a phylogenetic component, as according to our observations, boxwork to pralines rhodolith species like *Spongites fruticosus* seems to be more easily colonized than ramose species like *Lithothamnion corallioides* or *Phymatolithon calcareum*, perhaps because of its rugosity and/or deterrent metabolite production. Besides, massive rhodoliths create small crevices with no living algae that may induce sponge adherence, while ramose rhodoliths have smooth surfaces and are less cavernous (Basso, 1998). This pattern was also observed in a shallow rhodolith bed off the Pacific coast of Mexico (average depth of 3.5 m), Ávila et al. (2013) also reported a positive correlation between sponge abundance and diversity with rhodolith beds, finding highest levels of sponge diversity and abundance in areas dominated by spherical forms. On the other hand, soft algae like *Peysonnelia* spp. or *Osmundaria volubilis* seem to limit the growth of erect or arborescent sponges, maybe because they offer a less stable substrate than rhodoliths.

Assemblages BtB–BtC and GocA–GocB, with low diversity and sponge biomass values, were located at sandbanks with low algae biomass. Again, the correspondence with low sponge biomass and diversity and low algae is in consonance with the results by Ávila et al. (2013) off the Pacific coast of Mexico (Ávila et al., 2013) and highlighting the importance of algae for the development of sponge communities.

A striking difference between assemblages collected with BT and GOC was the dominance of *S. domuncula* for many GOC samples. It is the species that most contributes to similarity in all but one (GocD) coastal shelf assemblages, while its importance in BT assemblages is much lower. This may indicate a sparse distribution area yet GOC has a much higher effective sampling area than BT. *S. domuncula* is very abundant at trawl fishing grounds and probably resilient to trawling (Ordines et al., 2017). It quickly contracts when landed on board fishing vessels, a fact that may avoid air cavitation into the aquiferous system (Hamer et al., 2007). Contraction may also increase its density and favor the quick sinking after discard, and hence the survival to capture of this species, which could be related to its high abundances at trawl fishing grounds. This may also be the case of other massive free-living species like *Dictyonella incisa*, which is also very abundant in certain areas of the coastal shelf.

Below 90 m depth irradiance diminishes, red algae beds disappear and diversity and biomass of sponges drastically plummet. Some of the most abundant species in the deeper water assemblages were *T. muricata* and *D. annexa*. The first species has special root-like adaptations to anchor the substrate, a strategy that is also followed by other less common species like *R. pyrifer*, which also have distinct floor attaching modifications. Those species are also negatively correlated to maxim flow velocity, a fact that points its preference for areas with low hydrodynamic conditions, which generally have muddy bottoms and increased sedimentation rates (Rosenberg, 1995) (Fig. 9B and C). Some large massive species found at these assemblages (like *Penares helleri*), were mostly growing on dead coralligenous red algae, probably released by trawl fishing fleet from shallower hauls (Fig. 10F), indicating that substrate is an important factor in absence of photosynthesis. Besides, another issue is that species inhabiting this group must face its aquiferous system obstruction by sedimentation. Mud resuspension can be caused by currents or by trawling (Arjona-Camas et al., 2022) and is potentially harmful for sponges. It is known that certain species develop strategies to face sedimentation, like mucus production to avoid pore obstruction (McGrath et al., 2017; Kornder et al., 2022). This may be the case of *D. annexa*, which expels mucus on deck and is very abundant in the deep shelf and shelf break, and can be found in great biomasses in several stations north off the Menorca channel (personal observation).

#### 4.2.3. Seamounts vs trawl fishing grounds

A striking difference between seamounts and trawl fishing grounds is the low number of shared species between the two areas ( $S = 61$ , 17% of the total here reported). Part of this is explained by bathymetric differences (the shallowest station at trawl fishing grounds was at 45 m while the shallowest station at seamounts was at 93 m), meaning that at trawl fishing grounds there are shallow water communities not expected to be present at seamounts. However, the difference is also patent at deeper, overlapping bathymetric ranges (below 90–100 m), where only 28 species are shared. Interestingly, those 28 species represent 61% of the total ( $S = 46$ ) number of species at that depth range on the trawl fishing grounds, but only 15% at seamounts (of a total  $S$  of 190, or 135 if we stick to sedimentary bottoms). This indicates that at trawl fishing grounds the sponge diversity is concentrated on the coastal shelf and it suffers a dramatic decrease below, by contrast to seamounts, which are very diverse at deep waters. As shown in the dBRDA GOC model (Fig. 9B), fishing pressure seem to affect more intensively lower mesophotic species, like *P. compressa*, *H. poecillastroides*, *P. (P.) raphida* *H. (V.) falcula* and *P. helleri*. In this regard, sponge assemblages found at the lower mesophotic AM and the EB seamounts summits probably represent ancestral, undisturbed stages of the same communities.

In both trawl fishing grounds and seamounts, depth was the main factor determining sponge assemblages, separating shallow and deep groups. As discussed before, separation between shallow and deep assemblages was probably caused by the levels of light irradiance at the bottom, yet the boundaries determined by SIMPER tests match well with the disappearance of red algae beds. However, those limits differ between the two areas, being found at 90–100 m depth at trawl fishing grounds and at ~135–140 m depth at seamounts. This large difference can be explained by several factors, like the higher water transparency at the seamounts (Massutí et al., 2022) and by the effect of bottom trawling, which may create nepheloid layers that reduce the light penetration at trawl fishing grounds (restricting the red algae beds development below 90–100 m) (Minnery, 1990).

This difference in light penetration and fishing pressure may explain why some shallow species that are very common at coastal shelf trawl fishing grounds are found on greater depths at the seamount summits. Some examples are: *A. vaceleti* (84 vs. 116 m, respectively), *A. verrucosa* (83 vs. 127 m), *A. polypoides* (80 vs. 99 m), *P. (P.) ficiformis* (81 vs. 151 m), *Penares euastrum* (79 vs. 127 m), *B. vermiculata* (93 vs. 98 m) and *D. incisa* (82 vs. 98 m). Conversely, the shallower presence of *T. muricata* (112 vs. 122 m) and *R. pyrifer* (110 vs. 225 m), at trawl fishing grounds may be related to an increased presence of fine sediments and mud in the seafloor near the islands, in comparison with the prevalence of coarser sediments in the seamount summits (Massutí et al., 2022).

Taxonomic composition also changes between both areas, at least for some groups like Tetractinellida or Dictyoceratida. In part, these differences can be attributed to bathymetric differences, especially in orders typical of shallow waters, like Dictyoceratida, more represented in trawl fishing grounds than in Seamounts (21 vs 5 spp, respectively). These sponges have no spicules, a fact that has been interpreted as a consequence of evolutionary adaptation to shallow habitats with high temperature and lower Si concentrations (Alvarez et al., 2017).

More surprising is the different number of Tetractinellida between trawl fishing grounds and Seamounts (7 vs. 28 species, respectively). This could indicate a special sensitivity of Tetractinellids to bottom trawling, as has been suggested by Colaço et al. (2022) in grounds of *Geodia* species in the Barents Sea. In fact, we didn't observe mucus production in any of the tetractinellids collected. This is a typical physiological response associated with mechanical damage, air exposure or high sedimentation rates, which is widespread in trawl fishing grounds species like *L. (L.) cavernosa*, *M. (M.) iotrochota*, *H. mediterranea*, *Haliclona* sp3, *H. poecillastroides*, *D. annexa* and *Ophlitaspongia* sp. Besides, low growing rates can also make the group more susceptible to anthropogenic impacts. Recently, Morganti et al. (2022) estimated the age and annual growth of several specimens of *Geodia parva* and



*Geodia hentscheli*, two species constituting a dense sponge ground at Langseth Ridge (Central Arctic Ocean), to be hundreds of years (with a community average age of 300 years) and having growths of 0.55 mm/year. At trawl fishing grounds we have observed many species having soft algae embedded in its tissue, which suggest a fast growth (Fig. 10B and C). It is plausible that trawling selected the fast growing and more resilient sponges to the detriment of slow growing (and probably long lived) species or groups of sponges. In fact, two *Geodia* species (*Geodia geodina* and *Geodia matrix* Díaz & Cárdenas, in press) as well as other tetractinellids like *Pachastrella monilifera* are very common at the summits of AM and EB seamounts (Fig. 10G), but absent at trawl fishing grounds. Those large species are habitat builders that probably contribute to the overall maintenance of the ecosystem.

The present work confirms the Balearic Islands as an area of great diversity of sponges within the Mediterranean, which can be explained by its particular oceanographic features. This is notable at the trawl fishing grounds of the coastal continental shelf around the Archipelago and at the shallow summits of the Mallorca Channel seamounts AM and EB. The development of deep red algae beds seems to be one of the main reasons, because they offer a suitable habitat, substrate and potential source of food in the form of DOM. The distribution of deep algae beds determines the sponge communities in both trawl fishing grounds and seamounts. Below the limit of presence of those beds, sponges are conditioned by substrate type and probably by the effects of bottom trawling. Further works must include those areas that have been neglected in this work: the rocky bottoms of the continental shelf and slope. Its study will also show if the differences that we detect between the seamounts and the trawl fishing grounds are caused by fishing impacts or can be explained by the different nature of trawl fishing grounds and the Mallorca channel seamounts. Overall, our results highlight the importance and complexity of the relationship with red algae for the sponge communities of the Balearic Islands and points those ecosystems as sponge biodiversity reservoirs.

#### 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.

#### Data availability

The authors do not have permission to share data.

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#### Appendix A. Supplementary data

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#### References

- Acosta, J., Canals, M., López-Martínez, J., Muñoz, A., Herranz, P., Urgeles, R., et al., 2003. The Balearic Promontory geomorphology (western Mediterranean): morphostructure and active processes. *Geomorphology* 49 (3–4), 177–204.
- Alonso, B., Guillén, J., Canals, M., Serra-Kiel, J., Acosta, J., Herranz, P., Sanz-Alonso, J. L., Calaf, A., Catafau, E., 1988. Los sedimentos de la plataforma continental balear.
- Alvarez, B., Frings, P.J., Clymans, W., Fontorbe, G., Conley, D.J., 2017. Assessing the potential of sponges (Porifera) as indicators of ocean dissolved Si concentrations. *Front. Mar. Sci.* 4, 373.
- Amade, P., Leme, R., 1998. Chemical defence of the Mediterranean alga *Caulerpa taxifolia*: variations in caulerpenyne production. *Aquatic toxicology* 43 (4), 287–300.
- Arjona-Camas, M., Puig, P., De Leo, F.C., Garner, G., Paradis, S., Durán, R., Palanques, A., 2022. Influence of natural processes and bottom trawling in the nepheloid layer structure off Vancouver Island (British Columbia, Canada, NE Pacific). *Front. Mar. Sci.* 8, 2111.
- Ávila, E., Riosmena-Rodríguez, R., Hinojosa-Arango, G., 2013. Sponge–rhodolith interactions in a subtropical estuarine system. *Helgol. Mar. Res.* 67 (2), 349–357.
- Bahia, R.G., Abrantes, D.P., Brasileiro, P.S., Pereira Filho, G.H., Amado Filho, G.M., 2010. Rhodolith bed structure along a depth gradient on the northern coast of Bahia State, Brazil. *Braz. J. Oceanogr.* 58, 323–337.
- Ballesteros, E., 1994. The deep-water *Peyssonnelia* beds from the Balearic Islands (western Mediterranean). *Mar. Ecol. Prog. Ser.* 105, 233–253.
- Bart, M.C., Hudspeth, M., Rapp, H.T., Verdonschot, P.F., De Goeij, J.M., 2021. A deep-sea sponge loop? Sponges transfer dissolved and particulate organic carbon and nitrogen to associated fauna. *Front. Mar. Sci.* 8, 604879.
- Basso, D., 1998. Deep rhodolith distribution in the Pontian Islands, Italy: a model for the paleoecology of a temperate sea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 137 (1–2), 173–187.
- Bell, J.J., 2008. The functional roles of marine sponges. *Estuar. Coast Shelf Sci.* 79, 341–353.
- Bibiloni, M.A., 1990. Fauna de Esponjas de las Islas Baleares. Variación cualitativa y cuantitativa de la población de esponjas en un gradiente batimétrico. comparación Balears-Costa Catalana. Doctoral dissertation. Universitat de Barcelona.
- Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. *Ecology* 89, 2623–2632.
- Bo, M., Coppari, M., Betti, F., Enrichetti, F., Bertolino, M., Massa, F., et al., 2021. The high biodiversity and vulnerability of two Mediterranean bathyal seamounts support the need for creating offshore protected areas. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 31 (3), 543–566.
- Boury-Esnault, N., 1971. Spongiaires de la zone rocheuse littorale de Banyuls-sur-mer I. Écologie et répartition. *Vie Milieu* 159–191.
- Boury-Esnault, N., Pansini, M., Uriz, M.J., 1994. Spongiaires bathyaux de la mer d'Alboran et du golfe ibéro-marocain. *Mémoires du Muséum national d'histoire naturelle*, p. 160, 1993.
- Boury-Esnault, N., Vacelet, J., Dubois, M., Goujard, A., Fourt, M., Perez, T., Chevaldonne, P., 2017. New hexactinellid sponges from deep Mediterranean canyons. *Zootaxa* 4236 (1), 118–134.
- Braak, C.J.F., Smlauer, P., 2018. *Canoco Reference Manual and User's Guide: Software for Ordination* (version 5.10). Microcomputer Power, Ithaca, NY, USA, p. 536.
- Calcinai, B., Moratti, V., Martinelli, M., Bavestrello, G., Taviani, M., 2013. Uncommon sponges associated with deep coral bank and maerl habitats in the Strait of Sicily (Mediterranean Sea). *Ital. J. Zool.* 80 (3), 412–423.
- Canals, M., Ballesteros, E., 1997. Production of carbonate particles by phyto-benthic communities on the Mallorca-Menorca shelf, northwestern Mediterranean Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 44 (3–4), 611–629.
- Cartes, J.E., Maynou, F., Morales-Nin, B., Massutí, E., Moranta, J., 2001. Trophic structure of a bathyal benthopelagic boundary layer community south of the Balearic Islands (southwestern Mediterranean). *Mar. Ecol. Prog. Ser.* 215, 23–35.
- Clarke, K.R., Warwick, R.M., 1994. Similarity-based testing for community pattern: the two-way layout with no replication. *Marine biology* 118, 167–176.
- Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *J. Exp. Mar. Biol. Ecol.* 366, 56–69.
- Colaco, A., Rapp, H.T., Companyà-Llovet, N., Pham, C.K., 2022. Bottom trawling in sponge grounds of the Barents Sea (Arctic Ocean): a functional diversity approach. *Deep Sea Res. Oceanogr. Res. Pap.* 183, 103742.
- Corbera, G., Iacono, C.L., Gràcia, E., Grinyó, J., Pierdomenico, M., Huvenne, V.A., et al., 2019. Ecological characterisation of a Mediterranean cold-water coral reef: cabliers coral mound province (Alboran Sea, western Mediterranean). *Prog. Oceanogr.* 175, 245–262.
- De Goeij, J.M., Van Oevelen, D., Vermeij, M.J., Osinga, R., Middelburg, J.J., De Goeij, A. F., Admiraal, W., 2013. Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342 (6154), 108–110.
- De la Torre, 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 Res. Oceanogr. Res. Pap.* 135, 9–22.

- de Voogd, N.J., Alvarez, B., Boury-Esnault, N., Cárdenas, P., Díaz, M.-C., Dohrmann, M., Downey, R., Goodwin, C., Hajdu, E., Hooper, J.N.A., Kelly, M., Klautau, M., Lim, S. C., Manconi, R., Morrow, C., Pinheiro, U., Pisera, A.B., Ríos, P., Rützler, K., Schönberg, C., Turner, T., Vacelet, J., van Soest, R.W.M., Xavier, J., 2023. World Porifera Database.
- Díaz, J.A., Ramírez-Amaro, S., Ordines, F., Cárdenas, P., Ferriol, P., Terrasa, B., Massutí, E., 2020. Poorly known sponges in the Mediterranean with the detection of some taxonomic inconsistencies. *J. Mar. Biol. Assoc. U. K.* 100 (8), 1247–1260.
- Díaz, J.A., Ordines, F., Massutí, E., Cárdenas, P., in press. From caves to seamounts: the hidden diversity of tetractinellid sponges from the Balearic Islands, with the description of eight new species. *PeerJ*. doi:10.7717/peerj.16584.
- Díaz, J.A., Ramírez-Amaro, S., Ordines, F., 2021. Sponges of Western Mediterranean seamounts: new genera, new species and new records. *PeerJ* 9, e11879.
- Enrichetti, F., Bavestrello, G., Betti, F., Coppari, M., Toma, M., Pronzato, R., et al., 2020. Keratose-dominated sponge grounds from temperate mesophotic ecosystems (NW Mediterranean Sea). *Mar. Ecol. 41* (6), e12620.
- Fabri, M.C., Bargain, A., Paireud, I., Pedel, L., Taupier-Letage, I., 2017. Cold-water coral ecosystems in Cassidaigne Canyon: an assessment of their environmental living conditions. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 137, 436–453.
- Farriols, M.T., Ordines, F., Somerfield, P.J., Pasqual, C., Hidalgo, M., Guijarro, B., Massutí, E., 2017. Bottom trawl impacts on Mediterranean demersal fish diversity: not so obvious or are we too late? *Contin. Shelf Res.* 137, 84–102.
- Fernández de Puellas, M.L., Valencia, J., Jansá, J., Morillas, A., 2004. Hydrographical characteristics and zooplankton distribution in the Mallorca channel (Western Mediterranean): spring 2001. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 61 (4), 654–666.
- Foster, M.S., 2001. Rhodoliths: between rocks and soft places. *J. Phycol.* 37, 659–667.
- Gherardi, D.F., 2004. Community structure and carbonate production of a temperate rhodolith bank from Arvoredo Island, southern Brazil. *Braz. J. Oceanogr.* 52, 207–224.
- Grinyó, J., Gori, A., Greenacre, M., Requena, S., Canepa, A., Iacono, C.L., et al., 2018. Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea. *Prog. Oceanogr.* 162, 40–51.
- Guijarro, B., Ordines, F., Pasqual, C., Valls, M., Quetglas, A., Massutí, E., 2020. La pesca de ròssec al voltant de l'arxipèlag de Cabrera. In: Grau, A.M., Fornós, J.J., Mateu, G., Oliver, P.A., Terrasa, B. (Eds.), *Arxipèlag de Cabrera: Història Natural, Monografies de la Societat d'Història Natural de les Balears*, vol. 30, pp. 375–391.
- Haas, A.F., Naumann, M.S., Struck, U., Mayr, C., el-Zibdah, M., Wild, C., 2010. Organic matter release by coral reef associated benthic algae in the Northern Red Sea. *J. Exp. Mar. Biol. Ecol.* 389 (1–2), 53–60.
- Hamer, B., Jaklin, A., Pavicic-Hamer, D., Brummer, F., Muller, W.E.G., Zahn, R.K., Batel, R., 2007. Contribution to the ecology of the sponge *Suberites domuncula* (olivi, 1792) (Porifera, Demospongiae, hadromerida): sponge contraction. *Presenius Environ. Bull.* 16 (8), 980.
- Harris, B., 2022. The Distribution and Feeding Ecology of Temperate Marine Sponges through Shallow and Mesophotic Habitats (Doctoral Dissertation. Open Access Te Herenga Waka-Victoria University of Wellington).
- Hellio, C., Marechal, J.P., Véron, B., et al., 2004. Seasonal variation of antifouling activities of marine algae from the brittany coast (France). *Mar. Biotechnol.* 6, 67–82. <https://doi.org/10.1007/s10126-003-0020-x>.
- Idan, T., Shefer, S., Feldstein, T., Yahel, R., Huchon, D., Ilan, M., 2018. Shedding light on an East-Mediterranean mesophotic sponge ground community and the regional sponge fauna. *Mediterr. Mar. Sci.* 19 (1), 84–106.
- Idan, T., Shefer, S., Feldstein, T., Ilan, M., 2021. New discoveries in Eastern Mediterranean mesophotic sponge grounds: updated checklist and description of three novel sponge species. *Mediterr. Mar. Sci.* 22 (2), 270–284.
- Jennings, S., Alvsåvg, J., Cotter, A.J.R., Ehrlich, S., Greenstreet, S.P.R., Jarre-Teichmann, A., et al., 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. *Fish. Res.* 40 (2), 125–134.
- Joher, S., Ballesteros, E., Cebrian, E., Sánchez, N., Rodríguez-Prieto, C., 2012. Deep-water macroalgal-dominated coastal detritic assemblages on the continental shelf off Mallorca and Menorca (balearic islands, western mediterranean). *Bot. Mar.* 55 (5), 485–497.
- Joher, S., Ballesteros, E., Rodríguez-Prieto, C., 2015. Contribution to the study of deep coastal detritic bottoms: the algal communities of the continental shelf off the Balearic Islands, Western Mediterranean. *Mediterr. Mar. Sci.* 163, 573–590.
- Juza, M., Moure, B., Renault, L., Gómar, S., Sebastián, K., Lora, S., Beltran, J.P., Frontera, B., Garau, B., Troupin, C., Torner, M., Heslop, E., Casas, B., Escudier, R., Vizoso, G., Tintoré, J., 2016. SOCIB operational ocean forecasting system and multi-platform validation in the Western Mediterranean Sea. *Journal of Operational Oceanography* 9, s155–s166.
- Keasing, J.K., Usher, K.M., Fromont, J., 2012. First record of photosynthetic cyanobacterial symbionts from mesophotic temperate sponges. *Mar. Freshw. Res.* 63 (5), 403–408.
- Kefalas, E., Tsiirtsis, G., Castritsi-Catharios, J., 2003. Distribution and ecology of Demospongiae from the circalittoral of the islands of the Aegean Sea (eastern mediterranean). *Hydrobiologia* 499, 125–134.
- Kornder, N.A., Esser, Y., Stoupin, D., Leys, S.P., Mueller, B., Vermeij, M.J., Huisman, J., de Goeij, J.M., 2022. Sponges sneeze mucus to shed particulate waste from their seawater inlet pores. *Curr. Biol.* 32 (17), 3855–3861.
- Lesser, M.P., Slattery, M., Laverick, J.H., Macartney, K.J., Bridge, T.C., 2019. Global community breaks at 60 m on mesophotic coral reefs. *Global Ecol. Biogeogr.* 28 (10), 1403–1416.
- Longo, C., Mastrototaro, F., Corriero, G., 2005. Sponge fauna associated with a Mediterranean deep-sea coral bank. *J. Mar. Biol. Assoc. U. K.* 85 (6), 1341–1352.
- López-Jurado, J.L., Marcos, M., Monserrat, S., 2008. Hydrographic conditions affecting two fishing grounds of Mallorca island (Western Mediterranean): during the IDEA Project (2003–2004). *J. Mar. Syst.* 71 (3–4), 303–315.
- Maldonado, M., Ribes, M., van Duyl, F.C., 2012. Nutrient fluxes through sponges: biology, budgets, and ecological implications. *Adv. Mar. Biol.* 62, 113–182.
- Maldonado, M., Aguilar, R., Blanco, J., García, S., Serrano, A., Punzón, A., 2015. Aggregated clumps of lithistid sponges: a singular, reef-like bathyal habitat with relevant paleontological connections. *PLoS One* 10 (5), e0125378.
- Maldonado, M., Aguilar, R., Bannister, R., Bell, J., Conway, J., Dayton, P., et al., 2017. Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. *Marine animal forests: The ecology of benthic biodiversity hotspots*.
- Manly, B.F.J., 1991. *Randomization and Monte Carlo Methods in Biology*. Chapman and Hall, London, UK.
- Massutí, E., Olivar, M.P., Monserrat, S., Rueda, L., Oliver, P., 2014. Towards understanding the influence of environmental conditions on demersal resources and ecosystems in the western Mediterranean: motivations, aims and methods of the IDEADOS project. *J. Mar. Syst.* 138, 3–19.
- Massutí, E., Sánchez-Guillamón, O., Farriols, M.T., Palomino, D., Frank, A., Bárcenas, P., et al., 2022. Improving scientific knowledge of Mallorca Channel Seamounts (western mediterranean) within the framework of Natura 2000 Network. *Diversity* 14 (1), 4.
- Maynou, F., Cartes, J.E., 2000. Community structure of bathyal decapod crustaceans off south-west Balearic Islands (western Mediterranean): seasonality and regional patterns in zonation. *J. Mar. Biol. Assoc. U. K.* 80 (5), 789–798.
- McGrath, E.C., Smith, D.J., Jompa, J., Bell, J.J., 2017. Adaptive mechanisms and physiological effects of suspended and settled sediment on barrel sponges. *J. Exp. Mar. Biol. Ecol.* 496, 74–83.
- Minnery, G.A., 1990. Crustose coralline algae from the Flower Garden Banks, Northwestern Gulf of Mexico; controls on distribution and growth morphology. *J. Sediment. Res.* 60 (6), 992–1007.
- Monserrat, S., López-Jurado, J.L., Marcos, M., 2008. A mesoscale index to describe the regional circulation around the Balearic Islands. *J. Mar. Syst.* 71 (3–4), 413–420.
- Montgomery, D.C., Peck, E.A., 1982. *Introduction to Linear Regression Analysis*. Wiley, New York, p. 504.
- Morato, T., Kvale, K.Ø., Taranto, G.H., Tempera, F., Narayanaswamy, B.E., Hebbeln, D., et al., 2013. Seamount physiography and biology in the north-east atlantic and mediterranean sea. *Biogeosciences* 10 (5), 3039–3054.
- Morganti, T.M., Slaby, B.M., de Kluijver, A., et al., 2022. Giant sponge grounds of Central Arctic seamounts are associated with extinct deep life. *Nat. Commun.* 13, 638. <https://doi.org/10.1038/s41467-022-28129-7>.
- Moure, B., Aguiar, E., Juza, M., Hernandez-Lasheras, J., Reyes, E., Heslop, E., Escudier, R., Cutolo, E., Ruiz, S., Mason, E., Pascual, A., Tintoré, J., 2018. Assessment of high-resolution regional ocean prediction systems using multi-platform observations: illustrations in the Western Mediterranean Sea. In: Chassignet, E., Pascual, A., Tintoré, J., Verron, J. (Eds.), *New Frontiers in Operational Oceanography, GODAE Ocean View*, pp. 663–694.
- Mueller, B., Van Der Zande, R.M., Van Leent, P.J.M., Meesters, E.H., Vermeij, M.J., Van Duyl, F.C., 2014. Effect of light availability on dissolved organic carbon release by Caribbean reef algae and corals. *Bull. Mar. Sci.* 90 (3), 875–893.
- Nelson, W.A., 2009. Calcified macroalgae: critical to coastal ecosystems and vulnerable to change. *Mar. Freshw. Res.* 60, 787–801.
- Ordines, F., Massutí, E., 2009. Relationships between macro-epibenthic communities and fish on the shelf grounds of the western Mediterranean. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 19 (4), 370–383.
- Ordines, F., Massutí, E., Guijarro, B., Mas, R., 2006. Diamond vs. square mesh codend in a multi-species trawl fishery of the western Mediterranean: effects on catch composition, yield, size selectivity and discards. *Aquat. Living Resour.* 19 (4), 329–338.
- Ordines, F., Ramón, M., Rivera, J., Rodríguez-Prieto, C., Farriols, M.T., Guijarro, B., et al., 2017. Why long term trawled red algae beds off Balearic Islands (western Mediterranean) still persist? Regional studies in marine science 15, 39–49.
- Pansini, M., Musso, B., 1991. Sponges from trawl-exploitable bottoms of ligurian and tyrrhenian seas: distribution and ecology. *Mar. Ecol. 12* (4), 317–329.
- Pavia, H., Toth, G.B., 2000. Influence of light and nitrogen on the phlorotannin content of the brown seaweeds *Aspophyllum nodosum* and *Fucus vesiculosus*. *Hydrobiologia* 440 (1–3), 299–305.
- Péres, J.M., Picard, J., 1964. *Nouveau manuel de bionomie benthique de la mer Méditerranée*. Station Marine d'Endoume.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87 (10), 2614–2625.
- Pinot, J.M., Tintoré, J., Gomis, D., 1995. Multivariate analysis of the surface circulation in the Balearic Sea. *Prog. Oceanogr.* 36 (4), 343–376.
- Pulitzer-Finali, G., 1983. A Collection of Mediterranean Demospongiae (Porifera) with, in Appendix, a List of the Demospongiae Hitherto Recorded from the Mediterranean Sea, vol. 84. *Annali del Museo civico di storia naturale Giacomo Doria*, pp. 445–621.
- Quetglas, A., Guijarro, B., Ordines, F., Massutí, E., 2012. Stock Boundaries for Fisheries Assessment and Management in the Mediterranean: the Balearic Islands as a Case Study. *Centro Oceanográfico de Baleares*.
- Reiss, H., Kröncke, I., Ehrlich, S., 2006. Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 63 (8), 1453–1464.

- Rix, L., de Goeij, J.M., van Oevelen, D., Struck, U., Al-Horani, F.A., Wild, C., Naumann, M.S., 2018. Reef sponges facilitate the transfer of coral-derived organic matter to their associated fauna via the sponge loop. *Mar. Ecol. Prog. Ser.* 589, 85–96.
- Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands Journal of Sea Research* 34 (4), 303–317.
- 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 Res. Oceanogr. Res. Pap.* 131, 75–86.
- Sarà, M., 1962. Distribuzione ed ecologia dei Poriferi in acque superficiali del Golfo di Policastro (Mar Tirreno). *Annali del Pontificio Istituto Superiore di Scienze e Lettere S. Chiara* 12, 191–215.
- Sitja, C., Maldonado, M., 2014. New and rare sponges from the deep shelf of the alboran island (Alboran Sea, western mediterranean). *Zootaxa* 3760 (2), 141–179.
- Spedicato, M.T., Massutí, E., Mérigot, B., Tserpes, G., Jadaud, A., Relini, G., 2019. The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Sci. Mar.* 83, 9–20.
- Teichert, S., 2014. Hollow rhodoliths increase Svalbard' shelf biodiversity. *Sci. Rep.* 4, 6972.
- Tintoré, J., Vizoso, G., Casas, B., Heslop, E., Pascual, A., Orfila, A., Ruiz, S., Martínez-Ledesma, M., Torner, M., Cusi, S., Diedrich, A., Balaguer-Huguet, P., Gómez-Pujol, L., Álvarez-Ellacuría, A., Gómara, S., Sebastian, K., Lora, S., Beltrán, J.P., Renault, L., Melanie, J., Alvarez-Berastegui, D., March, D., Garau, B., Castilla, C., Cañellas, T., Roque, D., Lizarán, I., Pitarch, S., Carrasco, M.A., Lana, A., Mason, E., Escudier, R., Conti-Sampol, D., Sayol, J.M., Barceló-Llull, B., Alemany, F., Reglero, P., Massutí, E., Velez-Belchi, P., Ruiz, J., Oguz, T., Gómez, M., Alvarez, E., Ansorena, L., Manriquez, M., 2013. SOCIB: the balearic islands coastal ocean observing and forecasting system responding to science, technology and society needs. *Mar. Technol. Soc. J.* 47 (1), 101–117.
- Topsent, E., 1928. Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert Ier de Monaco: résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco 74, 1–376 pls I–XI.
- Uriz, M.J., Rosell, D., Martín, D., 1992. The sponge population of the Cabrera Archipelago (Balearic Islands): characteristics, distribution, and abundance of the most representative species. *Mar. Ecol.* 13 (2), 101–117.
- Vacelet, J., 1969. Eponges de la roche du large et de l'étage bathyal de Méditerranée: Récoltes de la soucoupe plongeante Cousteau et dragages. *Éditions du Muséum* 59 (No. 2).
- Vacelet, J., Boury-Esnault, N., Harmelin, J.G., 1994. Hexactinellid cave, a unique deepsea habitat in the scuba zone. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 41 (7), 965–973.
- Van Soest, R.W.M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N.J., Santodomingo, N., Vanhoorne, B., Kelly, M., Hooper, J.N.A., 2012. Global diversity of sponges (Porifera). *PLoS One* 7 (4), e35105. <https://doi.org/10.1371/journal.pone.0035105>.
- Vasquez, M., Allen, H., Manca, E., Castle, L., Lillis, H., Agnesi, S., et al., 2021. EUSeaMap 2021. A European Broad-Scale Seabed Habitat Map.
- Xavier, J.R., van Soest, R.W.M., 2012. Diversity patterns and zoogeography of the Northeast Atlantic and Mediterranean shallow-water sponge fauna. *Hydrobiologia* 687, 107–125. <https://doi.org/10.1007/s10750-011-0880-4>.