Megabenthic assemblages on bathyal escarpments off the west Corsican margin (Western Mediterranean)

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Abstract :

Deep-sea environments in the Mediterranean Sea have been widely degraded over the past decades and thus there is an urgent need to implement protection measures. Within European Union's Mediterranean waters vast extensions of the deep-sea ecologically relevant ecosystems have been protected by integrating them to the Natura 2000 network. Inside the French Exclusive Economic Zone, this network is currently expanding to off-shore areas, beyond 12 nautical miles. In this study, we characterized megabenthic biodiversity on target features located inside a designed site of the south west Corsican margin, particularly on a volcanic promontory on the south flank of the Ajaccio submarine canyon and a wall of the Valinco Canyon, between 1990 and 2250 m depth. By means of a fine scale three-dimensional photogrammetric analysis, four megabenthic assemblages segregated by substrate were identified. Hard substrate assemblages were characterized by the presence of sponges, polychaetes, gastropods and the squat lobster *Munida tenuimana* while soft sediment assemblages were characterized by the elpidiid holothurian *Penilpidia ludwigi* and an unidentified sabellid. Highest densities were registered on serpulid thanatocoenoses, which hosted widespread patches of an unidentified encrusting sponge. Lebensspuren had a diverse origin likely deriving from the activity of epibenthic, infaunal and bathypelagic organisms. In general, litter was not abundant at these offshore sites: in the Valinco site, it had both a marine and land-based origin while at the even more offshore Ajaccio site, it was mainly marine based. More extensive surveys would be advisable to confirm this trend. This study provides new insight on the ecology and diversity of Mediterranean deep-sea environments in the 2000 m bathymetric zone, highlighting the enduring knowledge gap surrounding orographically complex deep-sea escarpments in the basin.

Highlights

► Four benthic assemblages associated to different substrates were identified. ► On hard substrates sponges and polychaeta were the most abundant and diverse groups. ► Highest megabenthic organism densities were found on serpulid thanatocoenosis. ► Lebensspuren likely derived from epibenthic, infaunal and bathypelagic organisms. ► Litter items had both a marine and land-based origins.

Keywords : Benthic Biocoenoses, Bathyal, Lebensspuren, Marine Litter, Three-Dimensional Photogrammetry

Introduction

The deep sea (>200 m) is by far the most extensive biome on our planet, covering up to 66% of the Earth's surface (Bolgan and Parmentier, 2020). Great attention has been dedicated at improving the knowledge on the biodiversity and functioning of deep-sea ecosystems exposed to growing human impacts during the past decades (Ramirez-Llodra et al. 2010). Consequently, benthic ecological studies in bathyal (200-3000 m depth) and abyssal (3000-6000 m depth) environments have substantially increased (e.g. Amon et al., 2017, Fernández-Arcaya et al., 2017; Simón-Lledó et al., 2019a). Particularly, this research has mostly been focused on environments associated to high diversity, high biomass and productivity, or both, such as submarine canyons, cold-water coral (CWC) mounds, seamounts, mid-ocean ridges and diverse chemosynthetic environments (e.g. Ramires-Llodra et al. 2010; Buhl-Mortensen et al., 2010; Fernández-Arcaya et al., 2017; Levin et al., 2016; Rogers, 2018).

In the Mediterranean Sea, the discovery of several new CWC sites during the 1990's (e.g. Etiope et al., 2010) triggered an ongoing expansion of benthic ecological research on megabenthic assemblages beyond the shelf edge (> 200 m depth) using manned submersible and ROVs. This work has been largely focused on the study of three-dimensionally complex sessile suspension feeder assemblages (e.g. Orejas et al., 2009; Bo et al., 2014; Mastrototaro et al., 2017; Santín et al., 2018). In the Gulf of Lion,

Ligurian and Corsican shelves, the mapping and characterization of epibenthic assemblages of submarine canyons has mainly been conducted in 2008-2010 under the MEDSEACAN and CORSEACAN exploration programmes led by the French Agency of Marine Protected Areas (AAMP, now French Office for Biodiversity – OFB) in the upper bathyal zone, between 200 and 800 m depth (Fourt et al., 2014a, b, 2017, 2019). More generally, these explorations have been conducted from the lower circalittoral to the upper bathyal, with few studies venturing into the lower bathyal zone (Supplementary material 1).

Since the 1990s, most research conducted in lower bathyal Mediterranean environments have focused on the characterization of crustacean and fish assemblages (Cartes, 1993; Jones et al., 2003; Company et al., 2004; Sardà et al., 2004b; Sion et al., 2004), however other groups or multi-phyletic assemblages (Zibrowius, 1985; Olu et al. 2004; Cartes et al., 2009; Tecchio et al., 2011a; b; Mecho et al., 2014; Boury-Esnault et al., 2015; Sartoretto and Zibrowius, 2018) have received far less attention. Moreover, most benthic ecological studies in the lower bathyal have addressed megabenthic assemblages on soft sediment environments using bottom trawls and other bottom contact gears (Cartes et al., 2009; Ramírez-Llodra, 2008). Due to these gears' operational limitations on orographically complex hard bottoms, megabenthic assemblages on lower bathyal canyon walls and seamount flanks remain widely unknown (Zibrowius and Taviani, 2006). Only few underwater image-based studies have provided a minor glimpse on megabenthic diversity at lower bathyal assemblages of submarine canyons and seamounts (Sartoretto and Zibrowius, 2018; Bo et al., 2020). Although not dedicated to biological studies, geological surveys have contributed to these observations (Sosson and Guennoc, 1997), providing some clues to the occurrence of habitat structuring taxa on hard substrates, on which the need for protection measures is being considered.

In the recent decades, the number of human activities and pressures impacting bathyal environments (e.g. bottom trawling, marine litter, oil and gas exploration and exploitation, exploration for deep-sea mining) has increased and cumulated with large scale climate-driven ocean changes (Levin and Le Bris, 2015). In the deep Mediterranean, some anthropogenic pressures have substantially raised (e.g. bottom trawling, marine pollution, exploration for hydrocarbons), which combine with changes

in water properties and basin-scale circulation (Adloff et al. 2015). There is thus a pressing need for establishing a regional inventory that provides baselines for future management and conservation plans, which are currently lacking (Aguilar et al., 2017; Pierdomenico et al., 2019a). In the bathyal zone, canyons and seamounts are described as particular hotspots of biodiversity, fulfilling several of the ecological criteria of the Convention on Biological Diversity (CBD) for the identification of Ecologically or Biologically Significant Areas (EBSA), as well those of Vulnerable Marine Ecosystems (VMEs) from the FAO (Fernandez-Arcaya et al., 2017; Rogers, 2018; FAO 2019). Within the European Union's (EU) Mediterranean waters, the protection of large areas of the continental shelf and slopes, including numerous submarine canyon heads, have recently been achieved through their integration within the Natura 2000 network (EC 2020/96), which aims at preserving at least 10% of EU's territorial waters by 2020 and establish coherent protection networks, in line with the CBD and Nagoya recommendations (Aichi Target 11). In order to achieve this goal, the Natura 2000 network will expand to offshore areas, beyond the 12 nautical miles. Within the French exclusive economic zone five new offshore sites, expected to host particular biological features were considered fulfilling the Reef designation criteria under the Habitat directive (Fourt and Goujard, 2014). Among these new sites, several features including rocky outcrops and coral thanatocoenoses with associated submarine canyons of the south-western Corsican margin have been identified and an area named "Reefs of the Ajaccio Seamount and of the Valinco rocky outcrops" has been proposed to the European commission in 2017. It was integrated within the Natura 2000 network as a Site of Community Importance in 2018 (FR94022020). The main aim of the current study is to further document the largely unknown biodiversity patterns of this site. To achieve this goal, in this study we (1) assess megabenthic distribution along the explored bathymetric range, (2) address differences in standing stocks among different substrates, (3) characterize megabenthic assemblages, (4) characterize and quantify lebensspuren and (5) benthic litter, on two locations of this area corresponding to a volcanic promontory on the south flank of the deep branch of the Ajaccio submarine canyon and a steep wall in the Valinco Canyon (Fig. 1). We take advantage of recent, three-dimensional photogrammetry approaches, which have shown to be especially adequate to study megabenthic assemblages on steep bathyal environments (Robert et

al., 2017; Price et al., 2019). This method implemented from georeferenced still pictures acquired using the new hybrid-ROV Ariane has allowed to obtain key ecological information on habitat heterogeneity, fine-scale species habitat interaction and provided insight into organism abundance and assemblage diversity. Additionally, we discuss the significance of these results for the establishment of effective management tools and as baseline for monitoring changes in the diversity of these bathyal habitats in forthcoming years.

Materials and Methods:

Geographic setting

The study area is located in the south-western Corsica margin (Fig. 1a). This area is characterized by an extremely steep margin incised by the Valinco and Ajaccio submarine canyons, which extend from the continental shelf (~100 m depth) down to the foot of the island margin (2200 m depth) (Fig. 1b) where they merge into a major canyon system (Kenyon et al., 2002). On this area's continental slope, numerous volcanic promontories are found between 1200 m down to 2500 m depth (Rossi et al., 1998). These volcanic rocks originated during the Miocene and have a broad talc-alkaline character (Rossi et al., 1998; Rehault et al., 2012). These volcanic formations on the south-western Corsican margin have been reported to be cemented by manganese oxide coatings, as described for volcanic formations in the Ligurian, Sardinian and north Corsican margins (Rehault et al., 2012; Bo et al., 2020).

The intermediate and lower southwestern Corsican slope is influenced by three major water masses: the Levantine intermediate waters (LIW), which flow northward, between 200 – 800 m depth, the Tyrrhenian deep water found between 800 and 1500 m depth, and the western Mediterranean deep water which expands from 1500 down to the bottom (Millot, 1987; Send et al., 1999; Zuñiga et al., 2007).

Figure 1. a) Corsica Island, the black square indicates the section of the Corsican margin where Ajaccio and Valinco Canyons study sites are located. b) Close up of the south-western Corsican margin showing both sampling sites. Red stars indicate transect locations (bathymetric metadata and Digital Terrain Model data products have been derived from the EMODnet Bathymetry portal - <http://www.emodnet-bathymetry.eu> and projection from Bathy-morphologie régionale de la façade Méditerranée et Corse (édition 2014, résolution 100m) (Loubrieu et al., 2014).

This study's primary target was the summit and flank of a volcanic promontory located at 2060 - 2250 m depth range, 27 miles off Ajaccio (Fig. 1b, Table 1). Due to adverse meteorological conditions that affected access to this site, a second target in the same area but closer to the shore was visited and used for a comparative assessment. This second target is located on a steep wall of the Valinco canyon, between 1690 - 1990 m depth (Fig. 1b, Table 1).

Table 1. Transect location, depth range, on the seafloor and covered surface area. AP: Ajaccio promontory, VC: Valinco canyon, Lat.: latitude, Lon.: longitude, min.: minutes

Ariane Dive #	Location	Depth (start)	Depth (end)	Lat. (start)	Lon. (start)	Lat. (end)	Lon. (end)	Time (min.)	Covered surface (m ²)
104-02	AP	2256	2127	41.6349	8.2854	41.6352	8.2827	160	223
105-03	AP	2228	2050	41.6325	8.2886	41.6293	8.2902	122	3530
106-04	AP	2060	1994	41.6312	8.2889	41.6261	8.2841	230	2774
107-05	VC	1694	1950	41.6235	8.4182	41.6191	8.4257	215	1187

Image acquisition

A total of 4 ROV photographic transects (Table 1) were recorded during the Cylice-Eco oceanographic survey on board of the R/V “L’Europe” of the French Oceanographic Fleet (23 September 2018 to 6 October 2018). Three transects were recorded on the Ajaccio volcanic promontory and one on a wall of the Valinco Canyon (Fig. 1b, Table 1). Transects were performed with the Hybrid Remotely Operated Vehicle (H-ROV) Ariane (Ifremer), which has been designed to perform georeferenced photographic surveys of the seafloor to develop 2D-3D mosaics. The Ariane is equipped with a Nikon D5500 digital camera which allowed to acquire high-definition geo-referenced still images every 15 seconds (surveys at about 3 m above seabed). 1041 HD (6000 x 4000 pixels) still images were obtained covering a total area of 7714 m² (Table 1).

Photogrammetry reconstruction and analysis

The software Agisoft PhotoScan professional edition (v.1.2.5) was used to build 3D image reconstructions. Models were constructed following a sequential workflow (Fig. 2) specified by Agisoft Photoscan Professional software using a MacPro equipped with a 6 core Intel Xeon E5, with a processing speed of 3.5 GHz and an AMD FirePro D700 6144 MB image processor. The 3D reconstructions were employed to inspect fine-scale spatial positioning of all megafaunal species (here defined as organisms larger than 10 mm), lebensspuren formations defined as traces generated by epibenthic and infaunal organisms while feeding, moving or burrowing (Bell et al., 2013), and marine litter items. In Agisoft Photoscan, still images were examined and markers were placed to accurately georeference organisms, lebensspuren formation and marine litter items (Fig 2d). Once markers were placed, they were also visible in all other still images that cover the same position from a different angle, avoiding item duplication. Posteriorly, markers were exported as xyz text files for subsequent statistical analyses (Supplementary material 2).

Figure 2. a) Camera alignment (blue squares) and dense point cloud construction, b) mesh creation, c) textured mesh reconstruction, d) close up of 3D reconstruction (textured mesh) with marker flags showing the position of megabenthic organisms. (Scale bars: 1 m)

Megafaunal organisms were identified to the lowest possible taxonomic level. However, since organisms could not be sampled and identification to species level could not always be achieved, in some cases they were classified into morphospecies (visually distinct taxa) as it has been done in other image-based deep-sea studies (Robert et al., 2015; Simón-Lledó et al., 2019a). Lebensspuren formations were categorized based on their morphology and origin (Bell et al., 2013). Litter items were categorized based on the material they were made of and their origin. Marine litter is generally classified into two origin categories: land-based litter which originates from terrestrial sources and reaches the marine environment through wind or nearby waterways, and marine-based litter derived from discards generated in fisheries, aquaculture, marine traffic or military activities (Galgani et al., 2015). Substrates were classified into five different categories: soft sediments, bare rock, solitary coral thanatocoenosis, serpulid thanatocoenosis and compacted muds (Fig. 3). Bare rock and both types of thanatocoenoses were coated

with Mn-Fe oxides (Fig. 3b-d). Compacted muds occurred as vertical walls, occasionally displaying slabs at their base (Fig. 3e-3f).

Figure 3. Substrate types categories considered. a) Soft sediments, b) bare rock, c) solitary coral thanatocoenosis, d) serpulid thanatocoenosis, e) compacted muds vertical wall, f) compacted mud slabs at the base of a vertical wall. (Scale bar = 50 cm).

Statistical analysis

In each 3D photogrammetric reconstruction, megabenthic morphospecies and lebensspuren abundances were standardized by dividing the abundances registered in a certain substrate type by the surface covered by this particular substrate, thus obtaining density values. For all morphospecies and lebensspuren items, density was expressed as the number of individuals ($n \text{ ind m}^{-2}$) or items ($n \text{ items m}^{-2}$) per square meter, respectively. However, since encrusting sponge can undergo fission and fusion processes promoting clonality (Blanquer et al., 2009), for the encrusting unidentified sponge *Porifera* sp.1, density does not refer to individuals but individual patches.

Megabenthic assemblages were identified based on species composition by means of a non-metric multidimensional scaling ordination (nMDS) of the sampling units, with species abundances being square-root transformed, and ordination performed via a Bray-Curtis dissimilarity matrix. Adonis permutation multivariate analysis of variance and subsequent pairwise tests were used to test for significant differences amongst

assemblages. The nMDS and Adonis test were performed using the R-language function “metaMDS” and “Adonis”, available in the vegan library of the R software platform (Oksanen et al., 2016). Rare taxa, here defined as species occurring 3 times or less, were excluded from the nMDS analysis.

The Indicator value Indice (IndVal) was used to determine which taxa were representative from each assemblage. The IndVal method allows to identify combinations of species that permit to discriminate a group of samples from other samples in the analysis (Jordà Molina et al., 2019). IndVal measures were computed using the function *indval* included in the *labdsv* package (Roberts, 2013).

Results

Description of physical characteristics along ROV dives

In the Ajaccio Canyon, the volcanic promontory, was explored between 1994 and 2256 m depth. This area was characterized by high cliffs with complex geomorphological structures constituted by hard substrates and to a lesser extent gently sloping terraces covered by soft sediments (Fig. 3a), which represented 28.3% of explored surface. Bare rock was the most abundant substrate (Fig. 3b), covering 58% of the explored area. On overhangs and tilted walls protected from sediment deposition, solitary coral and serpulid thanatocoenosis (Fig. 3c and d) were found covering 6.7% and 7% of the explored surface, respectively.

The Valinco Canyon was explored between 1694 and 1950 m depth. The area was also characterized by the presence of vertical cliffs entirely constituted by compacted muds (Fig. 3e), which covered 76% of the explored area. Along the cliffs several terraces were observed being mostly covered by soft sediments (24% of explored surface) alternated by compacted mud slabs (Fig. 3f).

Megafaunal assessment

A total of 4508 megafaunal organisms were observed along the 7714 m² of seafloor explored during this study (Table. 2). In the Ajaccio volcanic promontory, a total of 20

morphospecies were identified (Table 2). Porifera and Polychaeta were the most diverse and abundant groups, being represented by 4 (Fig. 4 a-d) and 5 (Fig. 5 a-e) morphospecies and accounting 89% and 8.9% of all observed organisms, respectively (Table 2). The remaining phyla were represented by 11 morphospecies and accounted between 0.07% to 0.7% of all observed organisms (Table 2).

In the Valinco Canyon wall a total of 11 morphospecies were observed. Polychaeta, was the most diverse group, and along with Echinodermata were the most abundant phyla correspondingly representing 59.3% and 31.6% of observed morphospecies. The remaining phyla accounted for 1.3% and 3.9% of all observed organisms (Table 2). Rare taxa (≤ 3 records) represented 35% of the total morphospecies in the Ajaccio seamount and 73% in the Valinco canyon.

Table 2. Total abundance and taxonomic classification of megabenthic morphospecies quantified at the Ajaccio seamount and Valinco Canyon. (*) Observe that Group level has not been classified hierarchically, ranging from Phylum to species, to ease tabulation. n corresponds to the number of individuals except for Porifera sp.1 which corresponds to the number of patches.

Group (*)	Morphospecies	Canyon			
		Ajaccio		Valinco	
		n	%	n	%
Porifera	Porifera sp.1	3855	87.13	0	0
	Porifera sp.2	32	0.72	0	0
	Porifera sp.3	51	1.15	0	0
	Porifera sp.4	2	0.05	0	0
	cf. <i>Cladorhiza abyssicola</i>	0	0	1	1.3
Cnidaria	Hydrozoa	14	0.32	0	0
	<i>Desmophyllum dianthus</i>	3	0.07	0	0
	Actiniaria	0	0	1	1.3
Gastropoda	Gastropoda sp.1	24	0.54	0	0
	Gastropoda sp.2	2	0.05	0	0
Polychaeta	Polychaeta sp.1	295	6.67	27	35.5
	Amphinomid	11	0.25	0	0
	Sabellida	27	0.61	18	23.8
	Polynoid	3	0.07	0	0
	Serpulid	59	1.33	0	0
Decapoda	<i>Plesionika acanthonotus</i>	11	0.25	1	1.3
	<i>Aristeus antennatus</i>	1	0.36	0	0
	<i>Munida tenuimana</i>	11	0.09	1	1.3
Echinodermata	<i>Penilpidia ludwigi</i>	16	0.36	21	27.7
	<i>Ceramaster grenadensis</i>	4	0.09	2	2.6
	<i>Hymenodiscus coronata</i>	0	0	1	1.3
Chordata	Macrouridae	2	0.05	0	0

<i>Mora moro</i>	1	0.02	1	1.3
<i>Bathypterois dubius</i>	0	0	2	2.6

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302 Figure 4. a) Porifera sp.1, b) Porifera sp.2, c) Porifera sp.3, d) Porifera sp.4, e) Hydrozoa f) Unknown

303 actiniaria, g) *Desmophyllum dianthus*, h) Gastropoda sp.1 (Scale = 10 cm).

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307 Figure 5 a) Polychaeta sp.1, b) Amphinomid, c) Sabellid, d) Polynoid, e) Serpulid, f) *Munida tenuimana*,
 308 g) *Plesionika acanthonotus*, h) *Aristeus antennatus*, i) *Penilpidia ludwigi*, j) *Ceramaster grenadensis*, k)
 309 *Hymenodiscus coronata*, l) *Mora moro*, m) unknown macrourid, n) *Bathypterois dubius*. (Scale = 10 cm)

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311 **Bathymetric distribution**

Along the explored bathymetric range megabenthic morphospecies abundances generally ranged between 1 and 25 individuals (Fig. 6). However, at 2030 to 2070 m depth in an area that covered 155.6 m² (2% of the explored surface), Porifera registered an abrupt increment in abundance reaching values of 1400 individuals (here mostly Porifera sp.1 patches; Fig. 6b). This phylum presented the most restricted bathymetric distribution being constrained between 2000 and 2190 m depth (Fig. 6b). The remaining phyla presented a wider distribution, with Polychaeta and Echinodermata presenting the widest depth range (Fig. 6e-f).

Fig. 6. Bathymetric profile representation of the abundance of different faunal groups. Organisms total abundance (number of individuals) associated to each depth value has been plotted. a) All megabenthic, b) Porifera c) Gastropoda d) Polychaeta, e) Decapoda, f) Echinodermata. For Porifera, Porifera sp.1 individual patches have been added to the number of individuals for other species. Gray bands represent unexplored areas.

Standing stock variation among substrates

Overall morphospecies density was variable across the different substrates (Fig. 7a) with mean values ranging between 0.20 ± 0.07 ind. m⁻² (SD) on compacted muds to 47 ± 18 ind. m⁻² (SD) in serpulid thanatocoenosis (Fig. 7a). Porifera morphospecies (Fig.

4a-d) were restricted to hard substrate environments, with most individuals being found on coral and serpulid thanatocoenoses (Fig. 8), where highest densities were registered (Fig. 7b). Both Gastropoda (Fig. 4h) and Polychaeta (Fig. 5a-e) morphospecies were mostly found on bare rock environments (Fig. 8), where highest densities were recorded (Fig. 7c, d). However, it should be noted that an unidentified species of Sabellida (Fig. 5c) was exclusively found on soft sediment environments (Fig. 8), where it occurred at average densities of 0.08 ± 0.05 ind. m^{-2} (SD). Decapod species (Fig. 5f-g) were found on soft sediments, bare rocks and coral thanatocoenosis (Figs. 7e and 8), where highest densities were found. Finally, Echinoderms (Fig. 5i-k) were restricted to bare rock, coral thanatocoenosis and soft sediments (Fig. 7f and 8), where highest densities were registered (Fig. 7f).

Figure 7. Average densities of megabenthic organisms across the different substrate types. R: bare rock, CT: coral thanatocoenosis, ST: serpulid thanatocoenosis, CM: compacted muds, SS: soft sediments (mean $\pm$ SD). For Porifera, densities refer to both Porifera sp.1's individual patches and individuals for the other species. Rare taxa are not included.

Figure 8. Relative morphospecies abundance (%) across the five substrate types. n = number of individuals (for Porifera sp.1, n represents the number of patches). Numbers within the bars: relative % within a substrate category. Rare taxa are not included.

Assemblage composition

In the nMDS analysis the first axis clearly segregated assemblages occurring on soft sediments from those occurring on hard substrates (Fig. 9). Permutation multivariate analysis and subsequent pair wise test revealed that for all substrate categories megabenthic assemblages significantly differed from one another ($p < 0.001$), except for rock and compacted muds, where no significant differences were found. Therefore, four megabenthic assemblages could be identified (Fig. 9):

Bare rock assemblage: this assemblage was mainly observed on rock substrates coated by oxides and to a lesser extent on compacted muds (Fig. 3b, 3e). A total of 12 different species constituted this assemblage (Figs. 8 and 9). Both Gastropod sp.1 and the amphinomid Polychaeta characterized this assemblage (Table 3 and Figs. 4h and 5b).

Coral thanatocoenosis assemblage: this assemblage was constituted by 8 different species, six of which were sessile (Figs. 8 and 9). Its characteristic species was the decapod *Munida tenuimana* (Table 3 and Fig. 5f).

Serpulid thanatocoenosis assemblage: this assemblage was constituted by 5 different species and was characterized by the sponge *Porifera* sp.1 (Table 3 and Fig. 4a). This encrusting sponge represented 98% of all observed organisms reaching densities of up to 180 patches. m^{-2} .

Soft sediment assemblages: this assemblage was constituted by 5 different species amongst which, an unidentified sabellid and the holothurian *P. ludwigi* (Figs. 5c and 5h) were the dominant ones, respectively representing 48% and 37% of all observed organisms.

Fig. 9 Non-metric multidimensional scaling (nMDS) ordination plot. R= bare rock, CT=coral thanatocoenosis, ST = serpulid thanatocoenosis, CM= compacted muds and SS= Soft sediments. Amphi = Amphinomid, Bat_med: *Bathypterois dubius*, Cer_gre = *Ceramaster grenadensis*, Des_dia = *Desmophyllum dianthus*, Gas_sp1= Gastropoda sp1, Hydr = Hydrozoa, Hym_cor: *Hymenodiscus coronata*, Mun_teu = *Munida tenuimana*, Pen_lud = *Penilpidia ludwigi*, Ple_aca = *Plesionika acanthonotus*, Por_sp1 = Porifera sp.1, Por_sp2 = Porifera sp.2, Por_sp3 = Porifera sp.3, Por_sp4 = Porifera sp.4, Pol_sp1 = Polychaeta sp.1, Sabel = Sabellid, Serpu= Serpulid

Table 3. Taxa characterizing each megabenthic assemblage based on their IndVal values. R: bare rock, CT: solitary coral thanatocoenosis, ST = serpulid thanatocoenosis, SS: soft sediments.

Assemblage	Species	IndVal
R	Gastropoda sp.1	0.2
	Amphinomid	0.2
CT	<i>Munida tenuimana</i>	0.4
ST	Porifera sp.1	0.6
SS	<i>Penilpidia ludwigi</i>	0.5
	Sabellida	0.4

Lebensspuren

Lebensspuren formations were categorized based on their morphology and origin (Bell et al., 2013). Consequently, five distinct categories were identified: crawl marks, decapod tracks, depressions, mounds and pocks (small holes) (Fig. 10). In the Ajaccio promontory a total of 226 lebensspuren formations were observed, pocks and mounds (Fig. 10d-e) being the most abundant formations representing 48% and 23% (Fig. 17) of all lebensspuren formations, respectively. In the Valinco canyon a total of 282 lebensspuren formations were found, mounds and crawl marks (Fig. 16a and d) were the most abundant formations with respectively 67% and 18% of all lebensspuren formations (Fig. 17). Except for pocks and decapod tracks, lebensspuren densities were significantly higher in the Valinco canyon.

Figure 10. Categories of Lebensspuren formations a) crawl marks, b) decapod tracks, c) depression, d) mounds, e) pocks (scale bar = 10 cm).

Figure 11. Average Density of lebensspuren categories found in the Ajaccio seamount and the Valinco canyon. * represents significant differences ($p < 0.001$, uni-variate Adonis test using density as response variable). Error bars (SD).

Marine litter

Litter items were categorized into five different categories: single use plastics (plastic wrappers, bags, small fragments), glass bottles, cans, textile (shoes and cloth fragments) and military debris (Fig. 12).

Figure 12. Marine litter debris categories Single use plastic debris: a) plastic fragment, b) plastic bag. Textile debris: c) cloth fragment, d) broken shoe. Glass bottles and cans: e) can and glass bottle, f) paint can, g) can. Military debris: h) ammunition casing. (scale = 10 cm).

In the Ajaccio promontory twelve marine litter items belonging to 5 different categories were observed (Fig. 13). Clothes, glass bottles and military debris were the most

abundant categories, accounting each for 25% of all litter items (Fig. 13). In the Valinco canyon six marine litter items belonging three categories were observed, plastic debris was the most abundant category (Fig. 13). Marine litter in Ajaccio and Valinco reached densities of 0.001 items m^{-2} and 0.006 items m^{-2} , respectively.

Figure 13. Frequency of occurrence of marine litter items.

Discussion

Diversity considerations

In the study area a total of 24 epibenthic morphospecies were identified (Table 1) agreeing with previous species richness values from lower bathyal environments in other areas of the Mediterranean Sea (Ramírez-Llodra et al., 2008; Tecchio et al., 2011a). In bathyal and abyssal environments in other oceanographic basins, image-based studies with lower or similar sampling efforts (830 – 11000 m^2) reported higher megabenthic species richness values, ranging between 55 to 118 species (Jones et al., 2007; Soltwedel et al., 2009; Henry et al., 2014; Simón-Lledó et al., 2019a; 2019b). These moderately low species richness values found in deep-sea Mediterranean

environments have been proposed to derive from the synergy of hydrodynamic conditions and recent geologic history (Danovaro et al., 2010; Sartoretto and Zibrowius, 2018). Deep Mediterranean waters are homeothermic at relatively high temperatures (ca. 13-14°C from 300 m depth to the bottom) and present high salinity from about 38 to 39.5, and are generally oligotrophic (Turchetto et al., 2007; Grinyó et al., 2017). These environmental conditions have been suggested to prevent the colonization of deep-sea Atlantic species (Danovaro et al., 2010). Consequently, it has been theorized that deep-sea Mediterranean fauna comprises a fraction of deep-sea Atlantic species that have been able to adapt to the warm, saltier and oligotrophic conditions of the deep Mediterranean Sea (Bouchet and Taviani, 1992). Moreover, abrupt hydrological oscillations that occurred during the last glaciation (70000 to 18000 years BP) are thought to have harshened environmental conditions in bathyal and abyssal Mediterranean environments further obstructing the entrance and establishment of deep-sea Atlantic species (Zibrowius, 1980; Emig and Geistdoerfer, 2004).

Among the different morphospecies porifera and polychaeta were the most diverse and abundant groups respectively, representing 87.4% and 9.7% of all observed organisms (Table 3). This contrasts with previous knowledge on Mediterranean megabenthic assemblages occurring below 1200 m and 2200 m depth, where these groups are deemed to be rather scarce (Cartes et al., 2009; Tecchio et al., 2011a; 2011b). However, it should be noted that most studies conducted within this bathymetric range have addressed megabenthic assemblages on soft sedimentary environments (Cartes et al., 2009; Tecchio et al., 2011a;b; Mecho et al., 2014) and just a handful have focused on benthic assemblages on steep hard bottom environments (Sartoretto and Zibrowius, 2018). Thus, steep escarpments in deep bathyal environments of the Mediterranean, still remain widely unknown.

Among the different sessile taxa, anthozoans were rather scarce being restricted to two species and four observations (Table 3). This anthozoan paucity contrasts with Mediterranean bathyal environments above 1500 m depth where anthozoans can make up for a large proportion of megabenthic assemblages (De la Torriente et al., 2018; Aymà et al., 2019; Corbera et al., 2019; Bo et al., 2020; Bilan et al., 2020). Additionally, in bathyal and abyssal environments in other oceanographic basins anthozoan diversity and abundance tend to be higher (Thresher et al., 2014; Durden et

al., 2015; Simon-Lledó et al., 2019b) than those reported in lower bathyal Mediterranean environments (Sartoretto and Zibrowius, 2018). This might indicate that the environmental conditions below 1500 m depth in the Mediterranean Sea limit anthozoan diversity and abundance.

Furthermore, rare morphospecies (≤ 3 records) greatly contributed to species richness, representing 33.3% and 66.6% of all morphospecies in the Ajaccio volcanic promontory and the Valinco canyon, respectively (Table 3). This appears to be a common feature of megabenthic assemblages on bathyal and abyssal environments where rare taxa can make up for a large proportion of megabenthic assemblages (Durden et al., 2015; Simón-Lledó et al., 2019a; Delavenne et al., 2019). Though, it is unclear if this high representation of rare taxa derives from insufficient sampling effort or if in fact reflects natural patterns in deep-sea megabenthic assemblage's species richness (Simón-Lledó et al., 2019a).

Standing stock and assemblage composition

Megabenthic species abundance varied across the explored bathymetric range, experiencing an abrupt increment between 2030 and 2075 m depth (Fig. 3) where highest densities were registered (180 encrusting sponge patches m^{-2}). Although it is entirely due to the occurrence of the numerous patches of the peculiar Porifera sp.1, this pattern contrasts with the common conception that megabenthic organisms' density decreases with depth (Rex et al., 2006). However, in seamounts and canyons in other areas of the world similar situations have been observed (Santín et al., 2018; Thresher et al., 2014). Megabenthic organism's depth distribution is conditioned by the joined effect of several factors such as water temperature, hydrodynamic processes and the availability of both food and suitable substrates (Orejas et al., 2009; Robert et al., 2017; Vad et al., 2019). In the study area, 89% of the organisms that formed this peak of abundance occurred on serpulid thanatocoenosis, which represented 34% of all substrate within this depth range, indicating that this substrate positively influenced organism's abundance.

In this regard, megabenthic assemblages were segregated by different substrate types (Fig. 6). On hard substrate three different megabenthic assemblages were found.

Bare rock assemblages occurred on both Fe-Mn oxide-coated rocks (95.6%) and compacted muds (4.4%) covering a surface of 3817 m². This contrasts with previous research on seamounts, which clearly differentiated between assemblages occurring on polymetallic crusts from those occurring on other hard substrates (Schlacher et al., 2014). Furthermore, assemblages occurring on polymetallic crusts on Pacific seamounts presented lower densities than those occurring on other adjacent hard substrates (Grigg et al., 1987; Schlacher et al., 2014). This differs from the present study as overall organism density (Fig. 4a) on Fe-Mn coated rocks and compacted muds did not significantly differed (PERMANOVA, *Pseudo-F* = 0.584, *P* = 0.485). This assemblage was characterized by the presence of gastropods and polychaetes (Fig. 4 and Table 3) and several sponge species (Fig. 5), but other groups characteristic of shallower Mediterranean Fe-Mn oxide coated environments such as bryozoans and bivalves were completely absent (Toscano and Raspini, 2005).

In the Mediterranean Sea, thanatocoenoses are ubiquitous on hard substrate environments between 200 and 3500 m depth (Zibrowius, 1985; Aghib et al., 1991; Galil and Zibrowius, 1998; Toscano and Raspini, 2005). As it has been observed in the study area (Figs. 2c and 2d), thanatocoenoses are generally black, resulting from a Fe-Mn oxide coating (Zibrowius, 1985; Sartoretto and Zibrowius, 2018; Bo et al., 2020). Thanatocoenosis constitute complex three-dimensional structures that provide habitat and substrate to numerous species (Aguilar et al., 2017) being able to host diverse and complex benthic assemblages (Corbera et al., 2019). However, depending on the subfossil remains that constitute each thanatocoenosis benthic assemblages can differ both in terms of abundance and species composition (Rosso et al., 2010). This was the case of both benthic assemblages occurring on thanatocoenoses in the study area (Figs. 7-9 and Table 3).

Assemblages on solitary coral thanatocoenosis presented higher species richness than those occurring on serpulid thanatocoenosis (Fig. 8) and where characterized by *Munida tenuimana* (Fig. 5f; Table 3). This squat lobster is a common inhabitant of bathyal environments in the western Mediterranean (Cartes, 1993) where it has been observed to occur on both live and dead coral assemblages (Mastrototaro et al., 2010). It is likely that the three-dimensional structure formed by the dead coral framework provides refuge to this species (Taviani et al., 2017). Furthermore, it should be noted that 85% of

the observed organisms were sponges contrasting with previous reports on solitary coral thanatocoenosis where this group was quite scarce (Sartoretto and Zibrowius, 2018). Similarly, on serpulid thanatocoenosis, sponges were the most abundant group (Figs. 7, 8). This assemblage was dominated by Porifera sp.1 (Fig. 4a and Table 3), which represented 98% of all observed organisms forming dense aggregates that reached densities of 180 encrusting sponge patches m^{-2} (62 ± 58 MEAN $\pm$ SD). This density value is amongst the highest ever registered for encrusting sponges in Mediterranean bathyal environments (Santín et al., 2018; Bo et al., 2020). This could indicate that serpulid thanatocoenosis in deep bathyal environments provide a rather suitable substrate for this particular encrusting sponge. It should be noted, that encrusting sponges can undergo fission and fusion processes which could alter sponge patch surface area and density over time (Blanquer et al., 2009). Although we do not know if Porifera sp.1 experiences fission or fusion it would be advisable that future studies also considered this species' patch surface area as done in other deep-sea studies addressing community dynamics (Boolukos et al., 2019).

On soft sediment environments assemblages were constituted by typical inhabitants of Mediterranean bathyal muds such as *Hymenodius coronata* (Fig. 5k), *Bathypterois dubius* (Fig. 5n) and *Plesionika acanthonotus* (Fig. 5g), which have been commonly encountered on experimental trawls below 1000 m depth (Cartes et al., 2009; Mecho et al., 2014). This assemblage was characterized by an unidentified species of sabellid and the elpidiid holothurian *Penilpidia ludwigi* (Fig. 5c, 5i), which were the most abundant species. This unknown sabellid was sparsely distributed, reaching maximum densities of 0.4 ind. m^{-2} , resembling previous observations on bathyal sediments in submarine canyons of the Catalan margin, where sabellid reached densities of 0.5 ind. m^{-2} (Mamouridis et al., 2011). Lastly, *P. ludwigi* has been recently described to occur across the entire Mediterranean covering a wide bathymetric range (480 – 4760 m depth) (Chimienti et al., 2019). Although, this species can form dense aggregates reaching densities of 300 ind. m^{-2} (Chimienti et al., 2019), in the study area it was quite scarce, reaching maximum densities of 2 ind m^{-2} .

Lebensspuren

In both sampling locations lebensspuren presented a similar composition but densities in Valinco were generally higher (Fig. 11). Lebensspuren density is considered to result from a combined effect of both the bioturbation capacity of a benthic community and physical processes that regulate lebensspuren residence time (Bell et al., 2013). Megabenthic assemblage composition and density have been suggested to influence lebensspuren residence time and consequently its density (Bell et al., 2013). Nevertheless, no significant differences in soft sediment assemblage composition (Fig. 9) nor organism density (PERMANOVA, Pseudo-F: 0.867; p-value: 0.489) were found between both sampling locations. Moreover, among the different environmental factors influencing lebensspuren density surface productivity and organic matter flux to the deep-sea are thought to strongly relate to lebensspuren formation (Kitchell et al., 1978; Anderson et al., 2011; Bell et al., 2013). Based on general organic carbon flux patterns in submarine canyons it is possible that the Valinco sampling location, which covered a shallower bathymetric range and is closer to the canyon head (Table 1 and Fig 1b), receive higher organic carbon fluxes thus promoting lebensspuren formation (Smith et al., 2008; Rumín-Caparrós et al., 2013). Yet, this hypothesis should be carefully considered as organic carbon fluxes at these depths, in both sampling locations on the oligotrophic Corsica south-west margin, are still unknown.

Determining the origin of lebensspuren formation can contribute to increase knowledge on local deep-sea biodiversity (Przeslawski et al., 2012). Crawl marks (Fig. 10a) were observed to derive from *P. ludwigi* locomotion. The other lebensspuren formations could not be related with any of the other megabenthic organisms observed in the study area. However, in bathyal sediment grounds in the Toulon Canyon, hole aggregations such as the once encountered in this study area (Fig. 10e) were associated with the decapod crustacean *Calcoecaris macandreae*, which forms semi-permanent burrow complexes with multiple entrances (Anderson et al., 1991; Gerino et al., 1995).

Mounds with an apical vent (Fig. 10d) have been identified as echiuran burrows (Gerino et al., 1995). In the study area, most mound slopes were covered by radial bands (Fig. 10d), being consistent with proboscis imprints left by echiurans while deposit-feeding (Bett and Rice, 1993).

On the other hand, narrow depressions (Fig. 10c) have been considered to result from the interaction of bathypelagic vertebrates with the seafloor (Marsh et al., 2018).

Woodside et al. (2006) reported narrow oblique depressions between 1700 – 2100 m depth in the eastern Mediterranean attributing their formation to Cuvier's beaked whale (*Ziphius cavirostris*) foraging on the seafloor. Although the depressions in the study area morphologically resembled those reported by Woodside et al. (2006), their dimension were slightly smaller reaching maximum lengths and widths of 0.7 cm and 0.4 cm, respectively (Fig. 10c) and thus the origin of this depressions remains unclear.

Marine litter

Marine litter was observed in all dives but in small quantities compared to previous studies in the Mediterranean Sea. Unlike other canyon systems of the western Mediterranean close to shore and urbanized areas, no massive aggregations were observed (Pierdomenico et al., 2019a). Marine litter in the study area was scatteredly distributed and densities reached values of 0.001 items m⁻² in Ajaccio and 0.006 items m⁻² in Valinco. These density values were consistent with previous observations on deep bathyal environments (>1000 m depth) in other oceanographic basins (Mordecai et al., 2011; Pham et al., 2014) and the Mediterranean (Galgani et al., 1995; Tubau et al., 2015).

Litter composition in both sampling stations differed (Fig. 13). In Ajaccio glass, textile (mainly shoes and jeans) and military debris (ammunition casings) were the most abundant components (Fig. 13). Conversely, Valinco presented a more homogeneous composition with single use plastic items (plastic bags) and glass bottles (beer bottles) as the most abundant component (Fig. 13), being in line with previous observations in Mediterranean bathyal environments (Cau et al., 2019). Metal, glass and textile debris in deep-sea environments are thought to originate from marine based anthropogenic activities as they rapidly sink and do not travel long distances (Koutsodendris et al., 2008). Conversely, the vast majority of single use plastics has a land-based origin (Cau et al., 2019). Thus, it would be reasonable to hypothesize that in Ajaccio litter mostly originated from marine-based sources, while in Valinco it has both a marine and land-based origin. However, more extensive studies would be required to confirm this pattern and support the hypothesis. Finally, no interactions between marine litter and motile or

sessile fauna were observed, in contrast with what has been observed in regions with higher litter densities (Pierdomenico et al., 2019a; 2019b).

Conservation remarks

The broad consensus on the biological and ecological relevance of deep-sea topographic structures, such as seamounts and submarine canyons, subjected to increasing levels of anthropogenic impacts, reinforces the need for more exhaustive biodiversity assessments, crucial for the development of conservation policies (Clark and Dunn, 2012; Fernández-Aracaya et al., 2017). Henceforth, the present study represents the first in-depth study on benthic assemblages in deep bathyal environments (> 1000 m depth) of the Corsican margin. This study has allowed to identify distinct megabenthic assemblages associated to particular substrates. In this regard, it is worth remarking the ecological relevance of the encountered thanatocoenoses, which hosted very extended patches of unidentified encrusting sponges (Fig. 5). This result is consistent with the identification of the Ajaccio site under the “reef” habitat typology (1170) of the Natura 2000 network and the relevance of thanatocoenoses for conservation of bathyal Mediterranean habitats (SPA/RAC UN Environment/MAP 2019). This novel finding contrasts with the common conception that megabenthic assemblages on deep bathyal Mediterranean environments are sparsely populated and constitutes a remarkable feature for conservation purposes. Although we don’t know anything about the striking Porifera sp.1 encountered here, deep-sea sponge aggregations elsewhere are currently listed as vulnerable marine ecosystems (VMEs) by the FAO (2009).

As part of future surveys of this offshore Natura 2000 site (beyond 12 nautical miles from shore), the use of 3D georeferenced models of benthic assemblages will provide a reliable baseline for future monitoring.

Conclusions

- 24 morphospecies were identified, agreeing with species richness values in other areas of the Mediterranean. But as observed in other deep-sea environments rare taxa (≤ 3 records) made up for a large proportion of all observed species.

- Four megabenthic assemblages were identified in the study area being segregated by substrate type. Assemblages on hard substrates were characterized by the presence of sponges, polychaetes, and squat lobsters while soft substrates were characterized by the presence of an unidentified sabellid and the elpidid holothurian *Penilpidia ludwigi*.
- Highest densities were found on serpulid thanatocoenosis, which hosted extended encrusting sponge patch aggregations.
- In the study area, lebensspuren likely derived from biogenic processes exerted by epibenthic (crawl marks), infaunal (pocks and mounds) and bathypelagic (depressions) organisms.
- Litter occurrence was low in the studied area, with litter items in Ajaccio promontory mostly being of likely marine-based origin as they were mainly (91.7%) represented by fast-sinking items (glass, metal, military debris). Conversely, in Valinco canyon, litter had a more mixed origin, as half of all items were single use plastics and the rest were fast sinking items.

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Supplementary material caption

Supplementary material 1: Bibliographic compilation of benthic research in Mediterranean bathyal environments. Depth categorization is based on Emig and Geistoerfer, 2004. CS: continental shelf, SE: Shelf edge, S: slope, C: canyon, M: seamount.

Supplementary material 2: Marker xyz txt file.

Author contribution

Jordi Grinyó: Conceptualization, methodology, data acquisition, data curation, formal analysis, data curation, Writing - original draft; Writing - review & editing.

Nadine Le Bris: Funding acquisition, conceptualization, methodology, data acquisition, data curation, Writing - original draft; Writing - review & editing.

Pierre Chevaldonné: Funding acquisition, data acquisition, writing-review & editing

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1565 Thomas Schohn: methodology, writing-review & editing

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Journal Pre-proof

Highlights

- Four benthic assemblages associated to different substrates were identified
- On hard substrates sponges and polychaeta were the most abundant and diverse groups
- Highest megabenthic organism densities were found on serpulid thanatocoenosis
- Lebensspuren likely derived from epibenthic, infaunal and bathypelagic organisms
- Litter items had both a marine and land-based origins.

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: