Megafauna distribution along active submarine canyons of the central Mediterranean: Relationships with environmental variables

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A B S T R A C T

The tectonically-controlled margins off Southern Italy are carved by several shelf-indenting submarine canyons that are periodically flushed by sedimentary gravity flows. In this study, the distribution of benthic and demersal megafauna within the thalweg of some of these canyons (i.e. the Gioia-Petrace and Caulonia Marina canyons in the Tyrrhenian and the Ionian Calabrian margins, respectively, and the Sant'Agata, San Gregorio, Tremestieri and Messina canyons in the Messina Strait) was studied using Remotely Operated Vehicle video transects. The relationships between fauna distribution and environmental conditions (i.e. seafloor type, depth, slope, aspect and canyon system) extracted from video footage and bathymetric data were assessed to identify the main physical drivers influencing the megafaunal assemblages within active submarine canyons. These latter have their heads in shallow water, so representing highly dynamic environments affected by present-day sediment transport. Hierarchical Cluster Analysis allowed to distinguish seven different assemblages occurring in the study areas. PERMANOVA analysis showed significant differences among species groups associated to different sea-floor types, depth ranges and canyon systems. Distance-based linear modeling (DistLM) identified the canyon system as the main factor explaining the variability of the megafaunal assemblages across the study areas. In the Gioia and Petrace canyons, both characterized by homogenous fine-grained sediment, the assemblages were mainly dominated by Polychaeta Sabellidae and Ceriantharia. The almost total absence of sessile fauna at the canyons' head was interpreted as an effect of a strong physical disturbance due to the impact of sedimentary flows. In the canyons of the Messina Strait, the presence of more varied seafloor encompassing fine and coarse sediment along with an higher spatial heterogeneity of physical disturbance, determined more diversified faunal assemblages, featuring species associated with hard and soft substrates. More in detail, in the Sant'Agata, San Gregorio and Messina canyons the colonization of cobbles and boulders by slow-growing species vulnerable to physical disturbance such as the gorgonians *Acanthogorgia hirsuta* and *Swiftia dubia* was recorded. For the Tremestieri canyons a stronger impact by sedimentary flows was reflected both by a very high abundance of land-based litter and the lowest values of species richness. Interactions between megafauna and marine litter, whose widespread occurrence was recorded on the floor of all these canyons, have been also presented and discussed. Although in several cases litter caused entanglement of benthic species, the anthropogenic debris was also used as growing substrate or shelter by some invertebrates and fishes, suggesting complex fauna-litter interactions that should be better explored. Overall, the large variability in morphology and seafloor characteristics across the studied canyons is reflected on the variability of megafauna assemblages, suggesting a strong influence of the physical conditions specific of each canyon in controlling fauna distribution.

1. Introduction

Submarine canyons are geomorphic features of the continental margins that provide a direct pathway for sediment transport and dense water cascading from coastal to deep waters, enhancing the availability of particles, organic matter and phytodetritus (Vetter and Dayton, 1998, 1999; Turchetto et al., 2007; Canals et al., 2009), thus playing a paramount role in the functioning of the deep-sea ecosystems

(Danovaro et al. 2010; Ramirez-Llodra et al., 2010a; Fernandez-Arcaya et al., 2017). The increased food resources availability related to the sedimentary inputs and the water mass circulation, along with the complex distribution of physical habitats, may represent favourable conditions for benthic fauna dwelling in canyons (Vetter and Dayton, 1998, 1999; De Leo et al., 2010). Specifically, shelf-indenting canyons characterized by very active sedimentary and oceanographic processes during high-stand period are those commonly recognized as hot-spot of biomass and biodiversity in the deep sea (Danovaro et al., 2010; De Leo et al., 2010; Ramirez-Llodra et al., 2010a; Würtz, 2012; Fernandez-Arcaya et al., 2017). On the other hand, shelf-indenting canyons affected by enhanced advection of shelf resuspended sediments or fluvial input can be periodically flushed by sedimentary gravity flows (Puig et al., 2014 and references therein). Benthic fauna, especially slow-growing and fragile species, affected by these processes may struggle to survive due to the physical disturbance of the seafloor associated with sedimentary fluxes (Okey, 1997; Paull et al., 2010; Harris, 2014).

It is common knowledge that distribution patterns of communities are induced by spatial gradients in the environmental conditions (Levin et al., 2001). Depth, seafloor morphology, sediment grain size, hydrodynamic regime and food supply are all recognized as important factors driving the distribution of megafauna in deep-sea environment (Kostylev et al., 2001; Beaman and Harris, 2007; Buhl-Mortensen et al., 2009; Cartes et al., 2009; Serrano et al., 2011; Baker et al., 2012). However, understanding how these factors influence species distribution and assemblages composition in highly dynamic environments such as submarine canyons can be very challenging, especially considering that physical processes interact and operate over a range of scales. Indeed, previous studies showed that faunal distribution and biodiversity within canyons are regulated by a complex interplay of multiple factors, including depth, habitat heterogeneity, seafloor disturbance and food supply (Okey, 2003; McClain and Barry, 2010; van Oevelen et al., 2011; Baker et al., 2012; Miller et al., 2012; Quattrini et al., 2015; Ross et al., 2015; Smith and Lindholm, 2016), which in turn depends on a large number of physical factors such as shelf and canyon morphology, proximity to river systems, substrate lithology, prevailing oceanographic conditions, sediment transport processes, sedimentation rates, nutrient input and depth (Harris and Whiteway, 2011; Puig et al., 2014).

The complex topography of submarine canyons, that prevented the use of traditional sampling gears, has been successfully surveyed by Remotely Operated Vehicles (ROV), manned submersibles, towed cameras or benthic lander (King et al., 2008; Freiwald et al., 2009; Orejas et al., 2009; Miller et al., 2012; Angeletti et al., 2014; Bo et al., 2014; D'Onghia et al., 2015a, 2015b; Ross et al., 2015; Pierdomenico et al., 2016; Cau et al. 2017). Video inspections are also generally less invasive on fragile deep-sea ecosystems, thus providing information on the species small-scale distribution, activity and behaviour (e.g. Costello et al. 2005 and references therein; King et al., 2008 and references therein; D'Onghia et al., 2011; Baker et al., 2012; Ross et al., 2015). However, the noise and light of underwater vehicles may either scare away or attract fish causing under or over estimations of the true abundances (Costello et al., 2005; Jamieson et al., 2006; Stoner et al., 2008; Ryer et al., 2009).

In the Mediterranean Sea more than 500 submarine canyons have been identified based on low-resolution bathymetric dataset (Harris and Whiteway, 2011). The increasing interest in the bio-ecology of the Mediterranean canyons is strongly related to the high rates of endemism and the presence of CWC (e.g. Gili et al., 2000; Freiwald et al., 2009; Orejas et al., 2009; Gori et al., 2013; Angeletti et al., 2014; Pierdomenico et al., 2016; Taviani et al., 2017). Most of the canyons explored are located in the western Mediterranean, in relation both to their geological and sedimentary processes (e.g. Berné and Loubrieu, 1999; Canals et al., 2004, 2009; Puig et al., 2008) as well as to their biodiversity and fishery resources (e.g. Cartes et al., 1994; Stefanescu et al., 1994; Gili et al., 2000; Palanques et al., 2005; Sabatini et al.,

2007; Sardà et al., 2009; Ramirez-Llodra et al., 2010b; Farrugio, 2012; Gori et al., 2013; Fabri et al., 2014). Differently, in the central Mediterranean only the Bari Canyon in the southern Adriatic Sea (e.g. Ridente et al., 2007; Trincardi et al., 2007; Canals et al. 2009; Rubino et al., 2010; Carniel et al., 2012; Bo et al. 2012; Angeletti et al. 2014; D'Onghia et al., 2015a, 2015b, 2016) and the Gioia Canyon in the southern Tyrrhenian sea (Gamberi and Marani, 2007, 2008; Pierdomenico et al., 2016, 2018; Casalbore et al., 2014, 2018) have been studied in relation to their morpho-sedimentary and ecological characterization.

Moreover, it is necessary to consider that shelf-indenting canyons can also represent a main pathway for the transport of anthropogenic debris from coastal to deeper areas, thus becoming hot-spots of marine litter (Galgani et al., 1996; Ramirez-Llodra et al., 2013; Pham et al., 2014; Tubau et al., 2015). In the Mediterranean regions, where the coastlines are strongly anthropized and the narrow continental shelves are carved by numerous submarine canyons, the transport of marine litter and their interaction with the local biota are of main concern (UNEP, 2015). Once litter debris gets into the marine environment it may provide additional habitat for benthic and benthopelagic organisms (Tubau et al., 2015), potentially influencing the relative abundance of certain organisms within assemblages, even through the introduction of alien species (Barnes, 2002; Galil, 2007; Barnes et al., 2009).

This study will contribute to the understanding of the relationships between megabenthic fauna distribution and physical habitat characteristics (depth, slope gradients, seafloor type) along the thalweg of different shelf-indenting canyons of the central Mediterranean (southern Italy). Noteworthy, these canyons are characterized by active sediment transport processes and by a large variability in morphology, sediment supply, and hydrodynamic regime, that may be used to test the influence of the different environmental conditions on the faunal distribution. The intensity of seafloor disturbance related to sedimentary processes along the different canyons was estimated by the trace of the current/flow effects on the seafloor, i.e. sediment grain size and geomorphological features (i.e. bedforms, comet marks….), as well as by previous studies (Ridente et al., 2014; Bosman et al., 2017). Furthermore, due to the widespread occurrence of anthropogenic debris on the floor of these canyons, several examples of interactions between megafauna and marine litter are presented and discussed.

2. Materials and methods

2.1. Study area

The study was carried out on different submarine canyons affecting tectonically-controlled margins located in the Southern Italy, such as the Gioia-Petrace and Caulonia Marina canyons in the Tyrrhenian and the Ionian Calabrian margins, respectively, as well as the Sant'Agata, San Gregorio, Tremestieri and Messina canyons in the Messina Strait. The choice of these canyons was motivated by the fact that their head is located at shallow depths (< 50 m), very close to the coast and above all off the mouth of short and steep river courses (locally named *fiumara*) characterized by a torrential regime (Sabato and Tropeano, 2004). These river courses are dry most of the year, except for short intervals of intense water supply, when flash-floods occur. During these events, large amount of sediment is released at the river mouth and possibly evolves into hyperpycnal flows moving on the seafloor (e.g., Chiocci and Casalbore, 2011; Casalbore et al., 2011, 2017).

This peculiar setting is due to the interplay between the Mediterranean meteo-marine conditions and the complex orographic setting of the study area, being related to the formation of the Apennine-Maghrebide thrust belt due to the westward subduction of the Ionian oceanic slab beneath the Calabrian Arc (e.g., Malinverno and Ryan, 1986). Specifically, these coastal areas are characterized by regional uplift rates in the order of 1 mm/y since the Middle Pleistocene

and up to 2 mm/y if averaged to the Holocene (Antonioli et al., 2006). Largely due to this tectonic evolution, the facing continental margins are characterized by a very narrow to nearly absent continental shelf, abruptly passing to steep slopes largely carved by mass-wasting features, such as landslides, gullies and canyons (Chiocci and Casalbore, 2017 and reference therein).

A last consideration regards the strong urbanization of these coastal sectors, often associated with the lack of proper solid waste management. Therefore, flash-flood hyperpycnal flows generated at the mouth of the river courses can result in the transport and deposition of a large amount of litter in the deep sea via the submarine canyons.

2.2. Previous knowledges of the canyons studied

2.2.1. Gioia and Petrace canyons

The Gioia Canyon together with the Petrace and Mesima canyons is a 60 km-long canyon system, draining the entire continental margin of the southern Tyrrhenian Calabria, down to its connection with the Stromboli Valley at 1700 m water depth (Gamberi and Marani, 2007). The canyon system consists of two main courses (i.e. the Gioia and the Mesima canyons) that run parallel, changing from rectilinear to meandering courses, before merging in a single lower reach at 1000 m depth. The Petrace Canyon is a small tributary of the Gioia Canyon that develops for about 12 km and converges into the Gioia Canyon at about 540 m water depth (Fig. 1a).

The upper reach of the Gioia Canyon is characterized by a width of 600–1500 m and V-shaped cross-section, with an axial incision from some tens of meters up to few hundreds of meters deep (Pierdomenico et al., 2016). The canyon head is formed by two branches that surround the main entrance of the Gioia Tauro harbor (Fig. 1a). The Petrace Canyon has a width of about 500 m, and shows an overall lower height of canyon flanks (20–50 m) and higher sinuosity with respect to the Gioia Canyon. The head of the Petrace Canyon is located at about 10 m water depth, just off the Petrace *fiumara* that along with the Mesima *fiumara* represent the main water courses draining the Gioia Tauro coastal plain.

Littoral sedimentary dynamic in this area is characterized by longshore currents converging into the Gioia Canyon from the northern and southern direction, and funneling coastal sediment into the canyon head (D'Alessandro et al., 2002). A recent sediment transport activity within the thalweg is witnessed both by the occurrence of coaxial crescent-shaped bedforms (Casalbore et al., 2014; Pierdomenico et al., 2016) and morphological variations recognized through repeated multibeam surveys performed in the last decade (Bosman et al., 2017). Similarly, the flat-bottomed thalweg of the Petrace Canyon is also characterized by coaxial trains of crescent-shaped bedforms, with wavelength of 30–150 m and height of 3–6 m, which can be interpreted as a proxy of recent sedimentary dynamics (Pierdomenico et al., 2016).

Characterization of the benthic habitats and associated fauna along the upper reach of the Gioia Canyon showed the presence along the canyon margins of *Funiculina quadrangularis* and *Isidella elongata*, indicator taxa of sensitive habitat (GFCM, 2009) and vulnerable marine ecosystems (Pierdomenico et al., 2016). However, these species were severely impacted by fishing activities as shown by Pierdomenico et al. (2018).

2.2.2. Channelized features in the Messina Strait

The overall physiography of the Messina Strait is characterized by a main axial canyon (the Messina Canyon), running for about 25 km along a NNE-SSW direction between 350 m and 1350 m water depth (Ridente et al., 2014). The Messina Canyon divides the Sicilian (to the west) from the Calabrian (to the east) continental margins. Both margins are characterized by a very narrow or totally absent continental shelf, passing abruptly to a steep and largely incised continental slope. Several channelized features were recognized, debouching downslope into the Messina Canyon. Most of these erosive features do not form

well defined and individual canyon systems in the upper slope, as in the case of the Gioia and Petrace canyons. On the contrary, they can display flat-bottomed heads originating from large embayment on the coastline (i.e. the San Gregorio Canyon in Fig. 1b) or form headless canyons at water depths of 300–400 m, at the base of a steep slope apron formed by unconfined sedimentary gravity flows (Ridente et al., 2014), such as offshore Sant'Agata or Tremestieri (Fig. 1b). By integrating subaerial and submarine topography, it is evident the relationship between the mouth of *fiumara* and the submarine channelized features, so indicating a strong feedback in their evolution (Casalbore et al., 2011; Goswami et al., 2017).

2.2.3. Caulonia Marina Canyon

The Caulonia Marina Canyon (Fig. 1c) is located on the Ionian margin of the Calabria off the mouth of three short and steep rivers, i.e. the Allaro, Amusa and Precariti *fiumara*. The canyon has been surveyed through multibeam system and its morphology has been firstly described by Tessarolo et al. (2008). The upper part of the canyon is defined by a single and straight trunk down to 750 m water depth, where it turns westward. The canyon head is located at depths shallower than 20 m (limit of the bathymetric survey), about 500 m far from the coastline. The canyon is V-shaped in cross-section, showing a width variable from 2.5 km in the coastal sector up to 3.5 km at 1150 m water depth (lower limit of the bathymetric survey). A paper of Morelli et al. (2011) shows that the Caulonia Marina Canyon merges downslope with the close Siderno Canyon at about 1800 m water depth. Moreover, the authors also highlight the tectonic control of the NW–SE trending regional fault systems on the development of these canyons.

2.3. Data collection

Data were collected in the framework of the National Project RITMARE, during the oceanographic cruise RITMARE 2016, carried out from 11 to 24 February 2016 on-board the R/V MINERVA UNO. The main purpose of the cruise was the assessment of marine litter distribution along several submarine canyons of the southern Italy, in order to evaluate the influence of sedimentary and hydrodynamic processes on the emplacement of marine litter in the deep sea. Multibeam bathymetry of the canyons studied (10 m horizontal resolution), collected between 2009 and 2012 in the framework of the Magic project (Marine Geohazard Along the Italian Coasts, Chiocci and Ridente, 2011), was available and used as reference to plan the ROV surveys. Only for Caulonia Marina Canyon, low resolution bathymetric data from GEBCO (www.gebco.net) was used.

During the 2016 cruise, 15 ROV dives were performed along the upper reach of 7 submarine canyons of the southern Italy, at depths ranging from 120 to 575 m (Table 1; Fig. 1). About two dives per canyon system were performed and ROV inspections explored only the thalweg area, since large concentrations of litter are found in this sector of submarine canyons with respect to canyon walls and margins (Tubau et al., 2015). The length of the transects ranged from 470 to 2165 m, for a total of ~13.4 km of ROV track and 25 h of acquired videos.

The video transects were conducted using the remotely operated vehicle POLLUX III (Global Electric Italiana, maximum operative depth 600 m) equipped with a Sony CCD 1/3″ navigation camera, a Sony HD-RCX115E high-definition camera, ultra-short baseline positioning system (USBL), that provided detailed records of the ROV tracks along the seabed, and two parallel laser beams spaced 20 cm, to estimate the visual field of the camera and the area inspected during the dives.

2.4. Video analysis

The quantitative analyses of the video sequences included the identification and enumeration of benthic and demersal megafauna, the description of the seafloor texture and the identification and enumeration of marine litter.
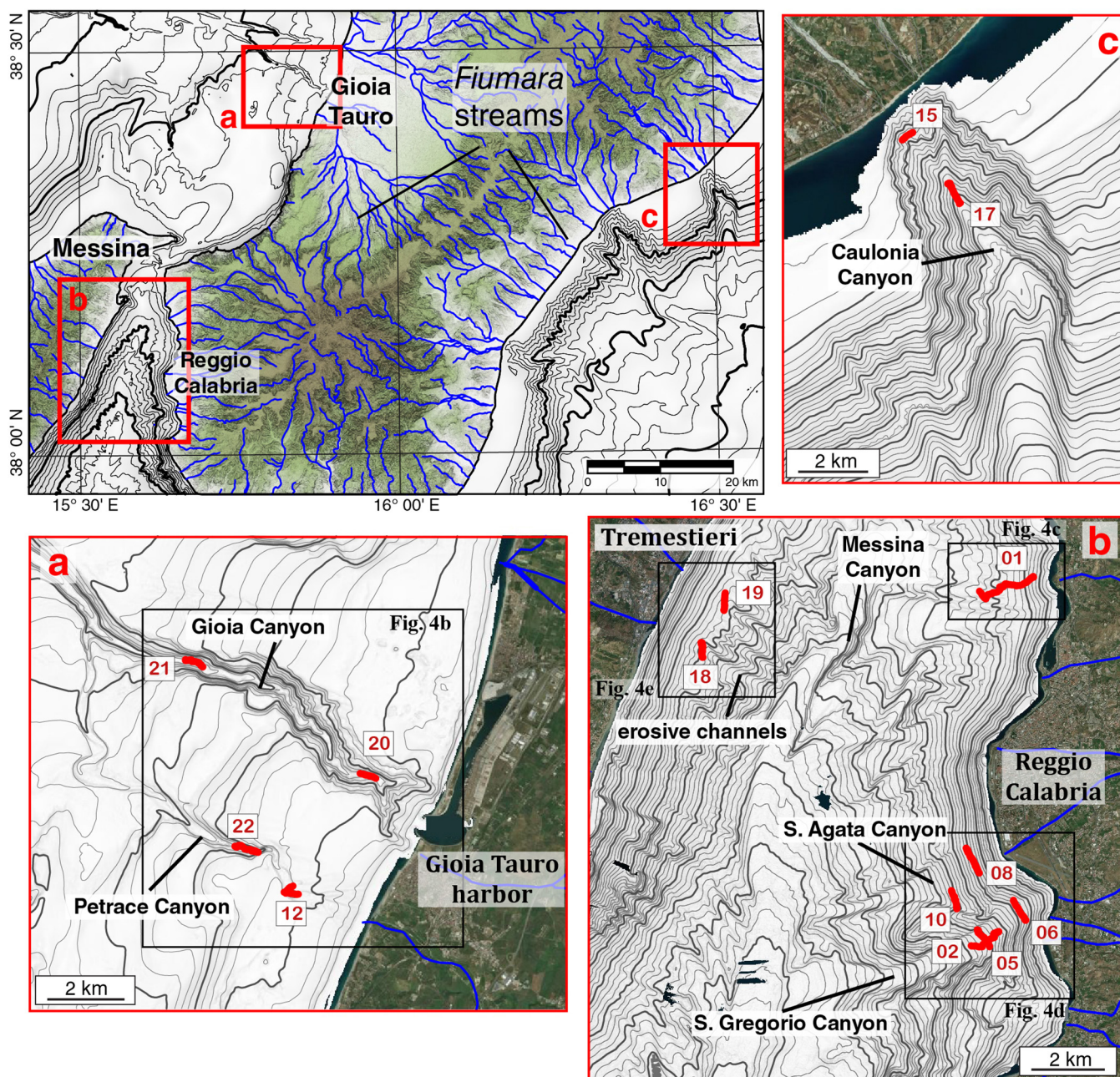
Fig. 1. Bathymetric map and shaded relief map of the onland sector (data downloaded from Aster GDEM, https://lpdaac.usgs.gov/) showing the three study areas (denoted by red boxes) along the Tyrrhenian (a) and Ionian (c) calabrian margins, and in the Messina Strait (b). The fluvial drainage is indicated by the blue lines. Contour interval 100 m; bold contours every 500 m. The insets show the location of the video transects (indicated by red lines) perfomed during the oceanographic cruise Ritmare 2016. Contour interval 25 m; bold contours every 100 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

All organisms larger than 2 cm were identified to the lowest possible taxonomic level and georeferenced along the ROV track, based on their timing of occurrence in the video footage and the USBL navigation data. The difficulty of sampling all the observed fauna prevented the accurate taxonomic determination to species level. This issue mostly occurred for certain taxonomic categories, such as Porifera, Scleractina and Annelida, for which samples availability is essential to analyze particular diagnostic features. Classification was accomplished by the use of current taxonomic guides for the Mediterranean (Carpine and Grasshoff, 1975; Tortonese, 1980; Zibrowius, 1980; Whitehead et al., 1986; Fisher et al., 1987; Falciai and Minervini, 1992; Guerra, 1992; Ardovini and Cossignani, 1999; d'Udekem d'Acoz, 1999; Cossignani and Ardovini, 2011). The nomenclature adopted for the different

taxonomic groups is that reported in the relevant update check-list: World Register of Marine Species: WoRMS available online at http://www.marinespecies.org/.

The characterization of physical habitats was based on video observation, allowing to identify four classes of seafloor texture that were mapped along the transects: silty sediment, sandy sediment, coarse sediment (corresponding to a heterogeneous seabed formed by accumulations of gravel, pebbles, cobbles and occasionally large boulders) and sub-outcropping/outcropping rock. Marine litter larger than 2 cm, lying on the seafloor or transported by bottom currents, was also identified and counted.

Starting from the beginning of each transect, all video sequences were then split into successive fragments 100 m long, which are

Table 1

List of ROV dives performed during the oceanographic cruise Ritmare 2016. Location, water depth and transect length are indicated.

Location	Track	Coordinates				Depth Range min − max (m)		Length (m)
		Start		End				
		Latitude	Longitude	Latitude	Longitude			
Messina Canyon head	ROV-01	38°08′40.8″ N	15°38′42.9″E	38°08′28.0″N	15°37′41.6″E	148	333	2165
San Gregorio Canyon	ROV-02	38°03′10.0″N	15°37′29.1″E	38°03′22.7″N	15°38′00.6″E	433	575	1253
San Gregorio Canyon	ROV-05	38°03′26.3″N	15°37′31.9″E	38°03′08.9″N	15°37′50.0″E	478	518	1051
San Gregorio Canyon	ROV-06	38°03′32.6″N	15°38′31.4″E	38°03′50.7″N	15°38′17.5″E	243	276	818
Sant'Agata Canyon	ROV-08	38°04′37.8″N	15°37′24.1″E	38°04′15.3″N	15°37′38.9″E	275	314	1215
Sant'Agata Canyon	ROV-10	38°03′44.2″N	15°37′13.2″E	38°03′59.5″N	15°37′07.1″E	508	524	701
Tremestieri	ROV-18	38°07′30.6″N	15°32′26.2″E	38°07′43.9″N	15°32′23.9″E	384	424	723
Tremestieri	ROV-19	38°08′13.0″N	15°32′50.4″E	38°08′28.4″N	15°32′51.9″E	337	381	722
Gioia Canyon	ROV-20	38°27′21.7″N	15°52′24.1″E	38°27′17.4″N	15°52′40.8″E	239	263	504
Gioia Canyon	ROV-21	38°28′58.5″N	15°49′19.0″E	38°28′52.1″N	15°49′37.6″E	464	486	903
Petrace Canyon	ROV-12	38°25′47.8″N	15°51′11.5″E	38°25′41.0″N	15°51′17.2″E	123	138	825
Petrace Canyon	ROV-22	38°26′21.6″N	15°50′10.1″E	38°26′16.3″N	15°50′34.7″E	217	260	1131
Caulonia Canyon	ROV-15	38°20′20.6″N	16°28′59.9″E	38°20′13.5″N	16°28′47.1″E	145	158	470
Caulonia Canyon	ROV-17	38°19′12.1″N	16°29′54.8″E	38°19′31.0″N	16°29′43.8″E	450	526	891

hereafter designated as sampling units. Counts of megafauna observed within a width of 1 m (estimated video coverage based on the laser beams) were reported for each sampling unit and converted to individuals/m², as well as count of marine litter, which was converted to items/m². Five classes of litter abundance were defined and assigned to each sampling unit: no litter, low (1–5 items/m²), medium (5–10 items/m²), high (10–25 items/m²) and very high (> 25 items/m²). Each sampling unit was also associated to the corresponding seafloor class and submarine canyon system. Additional seafloor descriptors used for the statistical analyses, specifically depth, slope and aspect, were extracted from the available bathymetric data using the terrain analysis tool included in the open source software QGIS Version 2.18 (https://www.qgis.org/it/site) and associated to each sampling unit. These terrain attributes are commonly used as abiotic surrogates to understand fauna distribution and have proven their value in a broad range of ecological studies (Brown et al., 2011 and references therein). Seafloor characteristic such as depth and sediment composition, as well as slope (that controls the stability of sediments) and aspect (that influences exposure to dominant and/or local currents) are known to be important environmental variables controlling benthic species distribution (McArthur et al., 2010).

Sequences where sediment suspension obscured the images or when the height of the ROV above the seafloor was too high (> 2 m) to properly identify megafauna organisms were quantified and removed from the subsequent analyses. 11 sampling units, corresponding to ~7% of the total ROV transects length, were thus removed from the analyses. Due to the possible avoidance of ROV vehicle by some mobile organisms, fish species were also removed from the dataset prior to statistical analyses. Finally, to avoid distortions that could be produced by rare data, sampling units containing only one or two taxa were removed prior to the analyses. This procedure excluded all the sampling units from the Caulonia Marina Canyon, where fauna abundance and diversity were extremely low. Therefore, the quantitative relationships between patterns in multivariate community structure and seafloor terrain variables were assessed only for the Gioia and Petrace canyons and for the submarine canyons of the Messina Strait.

2.5. Statistical analyses

To identify the megabenthic assemblages occurring along the canyons investigated, a hierarchical cluster analysis with group-averaged linkage was performed, using a Bray–Curtis similarity matrix derived from the square root transformation of the data, and applying a similarity profile analysis (SIMPROF) to the resemblance matrix to identify significantly different clusters. Key taxa that characterized the clusters

were identified using the similarity percentage (SIMPER) routine of the PRIMER v6 software (Clarke and Gorley, 2006). Characterizing taxa were defined as those taxa that contributed > 5% to cluster similarity. Non-metric multidimensional scaling plot (nMDS) was generated using the Bray–Curtis similarity matrix to represent the relative distance between sampling units and to visually assess their relationships with environmental variables.

One-way permutational multivariate analysis of variance (PERMANOVA) was used to test the significance of differences in assemblages composition between different seafloor classes, different canyons and depth ranges. Nested design for PERMANOVA was not possible due to the unbalanced sampling during the ROV surveys; not only ROV dives explored different depth ranges along different canyons, but these last are in turn often associated to distinct seafloor types, making the dataset unsuitable for multifactor nested design. A PERMDISP test (a distance-based test for multivariate dispersion, Anderson et al., 2008) was also carried out to assess the homogeneity of multivariate dispersion among groups associated with different seafloor classes, canyons and depth ranges.

To explore the influence of seafloor parameters on the variability of megabenthic fauna a distance-based linear modelling (DistLM) was performed, using the PRIMER PERMANOVA + add-on package (Anderson et al., 2008). Environmental data (seafloor class, depth, canyon system, slope and aspect) were log-transformed (log (x + 1)) and normalised and a step-wise procedure was adopted to test their importance, using Akaike's information criterion (AIC) to rank the resulting model. Prior to DistLM, the categorical variables "seafloor class" and "canyon system" were transformed into as many binary variables as the categories of the two nominal variables and then grouped into two "*indicator sets*", following the procedure illustrated in the PRIMER PERMANOVA + add-on manual (Anderson et al., 2008). Each "*indicator set*" includes all the binary variables belonging to the corresponding categorical variable and is treated as a single predictor variable by the DistLM analysis. Draftsman plots and correlation matrices were also produced to exclude potential multicollinearity of predictor variables. Distance-based redundancy analysis (dbRDA) was then applied to visualize the influence of the predictor variables identified as significant by DistLM.

Finally, to compare species richness among different canyons, randomized species accumulation curves were calculated (De Leo et al., 2014; Pierdomenico et al., 2017), using the statistical software R and the "vegan" package. Species accumulation curves were calculated for each canyon system and for each seafloor class, by pooling all the sampling units from all transects within each canyon or seafloor typology, respectively. The method used finds the mean species
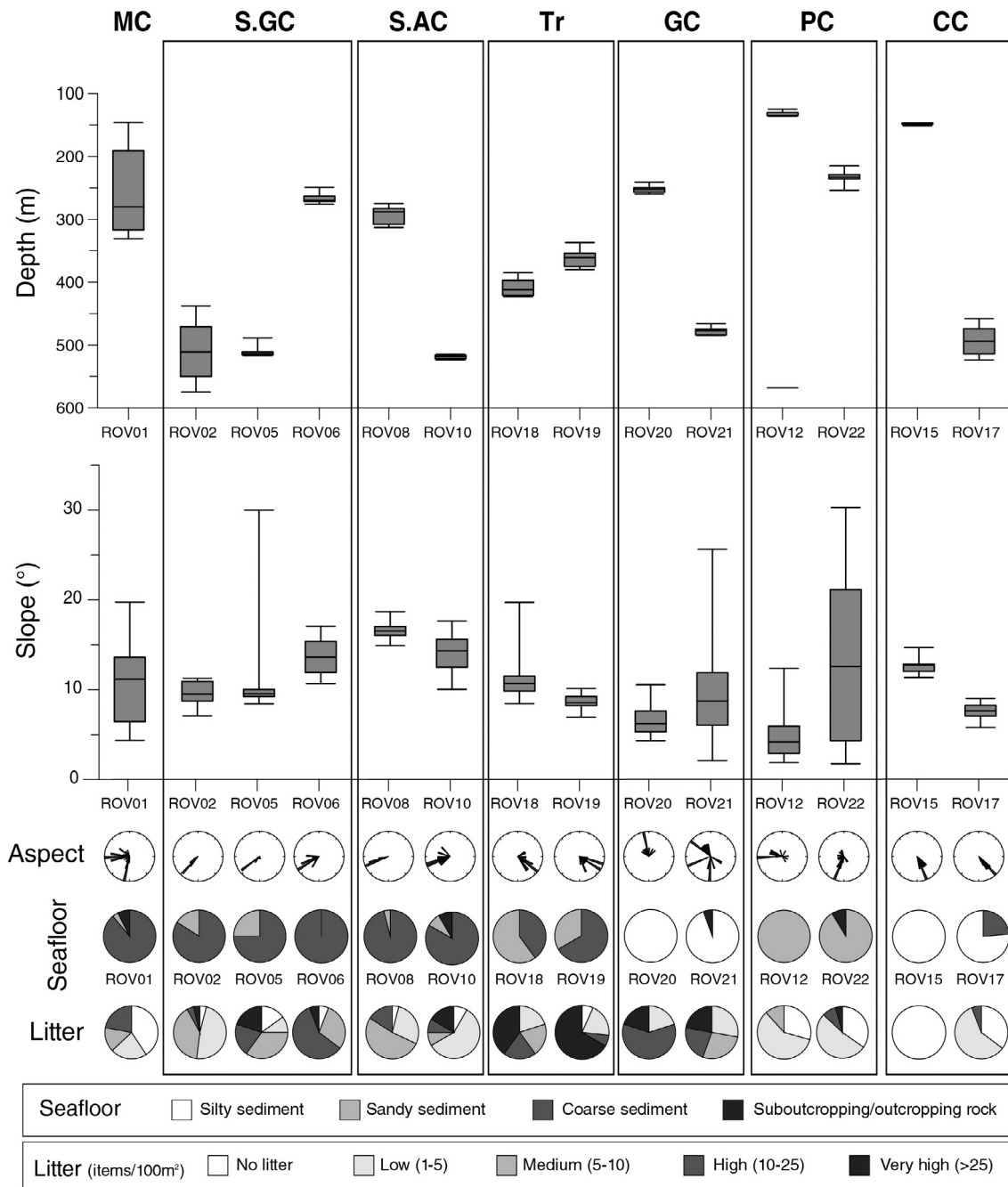
Fig. 2. Pie charts, box plots and rose diagrams illustrating the variability of environmental factors, including litter abundance, associated with each ROV dive along different canyons. MC-Messina Canyon, S.GC-San Gregorio Canyon, S.AC-Sant'Agata Canyon, Tr-canyons off Tremestieri, GC-Gioia Canyon, PC-Petrace Canyon, CC-Caulonia Marina Canyon.

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

3. Results

3.1. Physical habitat characteristics of the canyons investigated

The integrated analysis of ROV videos and multibeam data allowed to define the physical characteristics of the benthic habitats of the canyons studied, revealing a large variability in seafloor composition and geomorphological features, along with variable abundance of

marine litter (Fig. 2).

As a whole, the canyons of the Messina Strait were characterized by coarser and steeper seafloor compared to the canyons of the Tyrrhenian (Gioia and Petrace canyons) and Ionian (Caulonia Marina Canyon) areas and by higher abundances of marine litter (Fig. 2).

On the Calabrian side of the Messina Strait, the dives at the head of the Messina Canyon (ROV-01) and those along the thalweg of San Gregorio (ROV-02, ROV-05 and ROV-06) and Sant'Agata canyons (ROV-08 and ROV-10) showed the occurrence of a highly heterogeneous seafloor, composed by sandy sediment with interspersed pebbles, cobbles and boulders (Fig. 3a–d). Bedform fields occurred in areas dominated by fine sediment, whereas comet marks were observed at the foot of large cobbles and boulders, consistent with the action of bottom
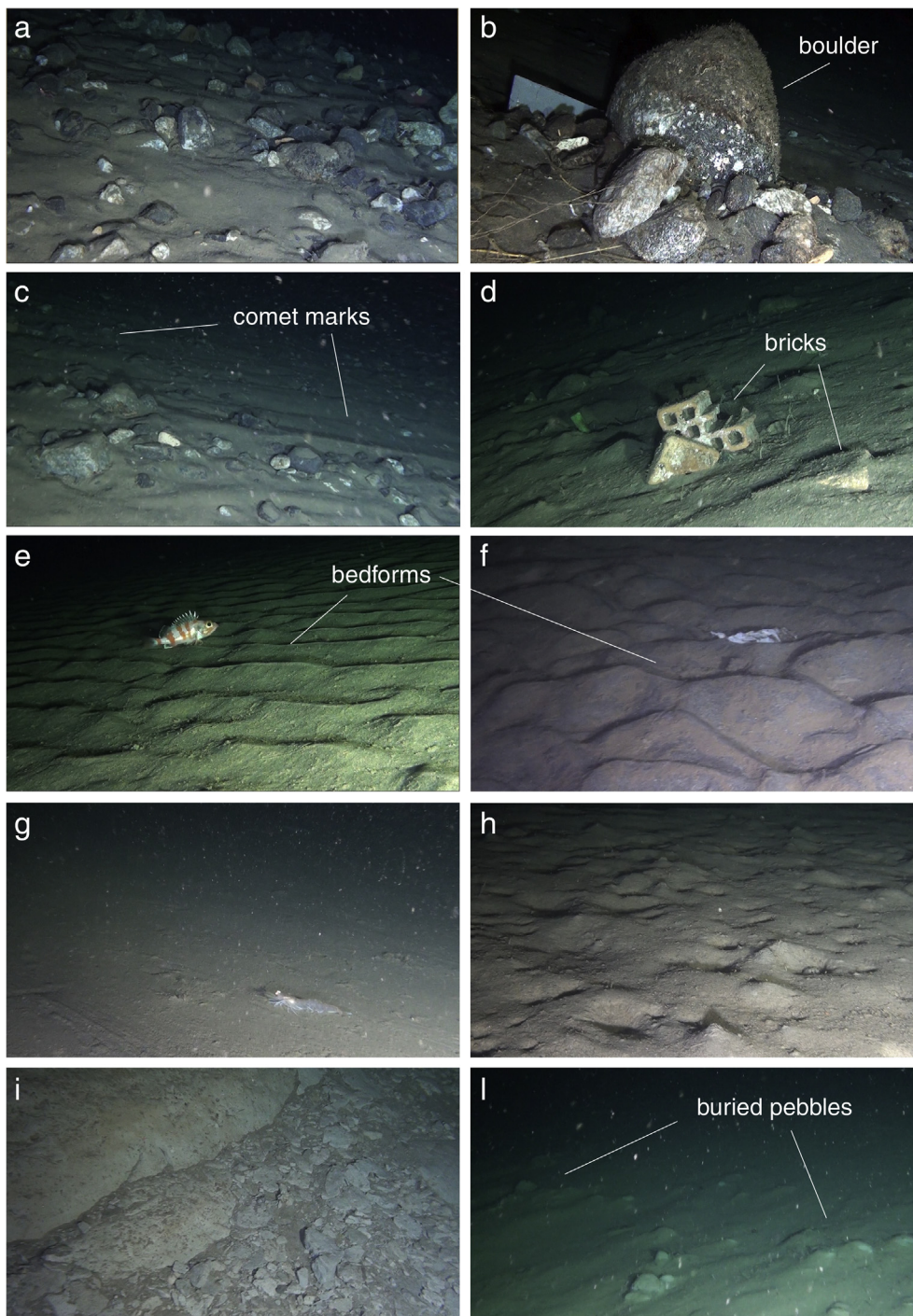
Fig. 3. ROV images showing the seafloor classes derived from the video analysis and the main seafloor features observed along the different canyons. (a) Coarse sediment, Messina Canyon head, −170 m; (b) Coarse sediment, Sant'Agata Canyon, −300 m; (c) Coarse sediment, San Gregorio Canyon, −490 m; (d) Coarse sediment, San Gregorio Canyon, −250 m; (e) Sandy sediment, Tremestieri, −400 m; (f) Silty sediment, Gioia Canyon, −260 m; (g) Silty sediment, Gioia Canyon, −240 m; (h) Sandy sediment, Petrace Canyon, −130 m; (i) suboutcropping/outcropping rock, Petrace Canyon, −220 m; (l) Coarse sediment, Caulonia Marina Canyon, −500 m.

currents flowing downcanyon (Fig. 3c). Seafloor gradients along the thalweg were on average ≥10° and higher slope values were observed in the shallower sectors of the canyons (Fig. 2, ROV-06 and ROV-08, in San Gregorio and Sant'Agata canyons, respectively), where abundant vegetal material and *Posidonia oceanica* detritus were also observed.

On the Sicilian side of the Messina Strait, at the head of the canyons off Tremestieri (ROV18, ROV-19) the seafloor had mean gradients of ∼10° and was characterized by large areas of sandy sediment with bedforms (Fig. 3e), alternated with gravel and cobbles accumulations, often distributed in patches of limited extent (few squares meters). Compared to the canyons of the Calabrian side of the Messina Strait, the percentage of coarse seafloor, as well as the frequency of large boulders, were lower (Fig. 2).

Differently from the Messina Strait, the ROV dives along the thalweg of the Gioia (ROV-20 and ROV-21) and Petrace (ROV-12 and ROV-22) canyons showed a less steep seafloor dominated by fine-grained sediment, of silty and sandy composition respectively (Figs. 2 and 3g–h). Bedform fields were locally observed in both canyons at all surveyed depths, from 120 to 500 m depth (Fig. 3f). Sub-outcropping and outcropping mudstones occurred at the base of the flanks of both canyons, associated with steep escarpments (Fig. 3i). In the Petrace Canyon abundant terrestrial vegetal detritus, including large wood pieces, was observed.

The thalweg of Caulonia Marina Canyon, in the Ionian Calabrian margin, was characterized by silty seafloor. In the deeper dive (ROV-17 at 500 m, Fig. 2) small patches of cobbles and pebbles were locally

observed; in most cases cobbles and pebbles were partially buried by a silty veneer (Fig. 3l).

Litter abundance showed a large variability across the different canyons and within the same canyon, where seafloor areas without litter or with few sparse items alternated with sectors characterized by larger litter abundances (Fig. 2). As a whole, the highest abundances of marine litter were observed at the head of the erosive channels off Tremestieri, while the lowest abundances were recorded in Caulonia Marina Canyon (Fig. 2). Gioia and San Gregorio canyons were characterized by medium-high abundances, whereas Sant'Agata Canyon showed slightly lower abundances of marine litter (Fig. 2). Petrace Canyon was on average characterized by low abundances of litter. About 75% of the observed litter was represented by plastic. In the canyons of the Messina Strait a large variability of litter composition was observed, including glass, paper, clothes, fishing debris and heavy litter items such as metal object and building material (Fig. 3d).

3.2. Distribution and abundance of megafauna

The video sequences used for the quantitative analyses of megafauna covered a linear distance of more than 10 km across a wide range of substrates, depths and slopes. The benthic and benthopelagic assemblage recorded from the overall study area counted a total of 106 taxa, 1 algal taxon, 64 invertebrates and 41 fish taxa (including all taxonomic levels) respectively (Table 2). San Gregorio Canyon, with 52 taxa (36 invertebrates and 16 fishes), includes a little less than 50% of the fauna corporation recorded. High values of taxa richness were also logged in the Petrace and Sant'Agata canyons, with 37 (18 invertebrates and 19 fish) and 32 (1 alga, 20 invertebrates and 11 fish) taxa respectively. In the Tremestieri area only 19 taxa (14 invertebrates and 5 fish taxa) were recorded (Table 2).

Seven different megabenthic assemblages, with a mean within-assemblage similarity between 27% and 76%, were identified from the cluster and SIMPROF analyses, whose distribution is shown in Fig. 4.

Assemblage A was mostly characterized by high abundances (up to > 100 ind/m^2) of a Polychaeta Sabellidae, whose identification is currently under analysis, that co-occurred with dense population of Ceriantharia (up to 1.3 ind/m^2). Another species observed frequently in this assemblage was the Holothuroidea *Parastichopus regalis*. Assemblage A occurred exclusively on silty bottoms of the Gioia Canyon, between 470 and 490 m depth (Fig. 4).

Assemblage B was quite similar to the previous one, being mostly characterized by the widespread occurrence of the Polychaeta Sabellidae (max density 6 ind/m^2) observed in Assemblage A, and Ceriantharia (Fig. 5de), together with the Crustacea *Plesionika* spp., including *Plesionika antigai* (Fig. 6a) and *P. heterocarpus* (up to 0.46 ind/m^2). Other less frequent taxa that characterized this assemblage include different species of Pennatulacea (*Pennatula rubra*, *Pteroides spinosum* (Fig. 5c), *Virgularia mirabilis*) and *P. regalis*. Assemblage B was mainly distributed in the Petrace Canyon at 220–235 m depth, where other cnidarian species such as the Actiniaria *Andresia partenopea* were frequently reported, but it was also locally observed in the San Gregorio Canyon, at the base of the flanks at 510 m depth.

Assemblage C was mainly characterized by benthic sessile taxa including solitary Scleractinia (cf. *Caryophyllia (C.) calveri*, up to 0.78 col/m^2) and Polychaeta Serpulidae (mainly attributable to the species *Serpula vermicularis*, up to 1.95 ind/m^2) that colonized hard substrates such as boulders and large cobbles, and by mobile taxa including the Echinoidea *Cidaris cidaris* (Fig. 5f) and the Crustacea *Plesionika* spp., including *Plesionika heterocarpus* and *P. antigai* (Fig. 6a), that were also present on fine sediments. Assemblage C mostly occurred at the head of the erosive channels off Tremestieri between 340 and 420 m, although it was also observed at the summit of a small ridge at the Messina Canyon head and in the shallower transect in the San Gregorio Canyon at 250–270 m depth.

Assemblage D is mostly characterized by the occurrence of the

Alcyonacea *Acanthogorgia hirsuta* (Fig. 5a) (up to 0.6 col/m^2), accompanied by *Swiftia dubia* (Fig. 5b), although with significantly lower frequency (max abundance 0.07 col/m^2), and by Polychaeta Serpulidae. Other common species also observed in Assemblage D included the Echinoidea *C. cidaris*, the Annelida Polychaeta cf. *Praxillura maculata,* several species of Ceriantharia (Fig. 5d) and solitary Scleractinia. This assemblage was only observed on coarse seafloor at the head of the Messina Canyon, between 150 and 190 m depth.

Assemblage E was characterized by the widespread occurrence of the Alcyonacea *S. dubia* (up to 0.4 col/m^2) and of Polychaeta Serpulidae on hard substrates constituted by boulders and cobbles, whereas the Annelida Polychaeta cf. *P. maculata* (max abundance 0.27 col/m^2) was commonly observed, widespread over fine sediments. Another common species of this assemblage was the Crustacea *Plesionika* spp. (partially attributable to the species *P. martia and P. gigliolii*) (Fig. 6b). Assemblage E occurred on coarse seafloor at the head of the Sant'Agata erosive channel, in a depth range of 280–310 m.

Assemblage F is largely dominated by Polychaeta Serpulidae that represent the most common taxa (up to 0.95 ind/m^2) colonizing cobbles and boulders, along with the Crustacea *Plesionika* spp and Polychaeta Sabellidae. Other taxa, including solitary Scleractinia, Ceriantharia and Pennatulacea were not frequent and were observed with overall low densities. Assemblage F occurred along San Gregorio and Sant'Agata canyons, mostly in their deepest sectors between 500 and 580 m depth, but was also locally present in shallower areas at 270–280 m depth.

Assemblage G was the most heterogeneous in terms of faunal composition among the groups recognized by the cluster and SIMPROF analyses, having the lowest within-assemblage similarity percentage. The most frequent taxon was represented by the Crustacea *Plesionika* spp. (max abundance 0.35 ind/m^2), that was accompanied by different species depending on the canyon. This assemblage was in fact distributed in all the canyons on different seafloor types and different depths, with the exception of the erosive channels off Tremestieri. In the Gioia Canyon, the most common species were the Crustacea *Parapeneus longirostris* (up to 0.1 ind/m^2) and *Parastichopus regalis*, while in the Petrace Canyon, accompanying taxa were Polychaeta Sabellidae. Conversely Assemblage G in the Messina Strait's canyons features as common taxa the Echinoidea *C. cidaris* and Ceriantharia.

Regarding the fish species, *Chlorophthalmus agassizi* and *Helicolenus dactylopterus* were recorded in all areas investigated, but also *Coelorinchus caelorhincus* was frequently observed in most of the canyons explored (Table 2; Fig. 6c–e). *C. agassizi* resulted also the most abundant fish, particularly in the canyons off Tremestieri and in the Petrace Canyon where different specimens were often observed resting together on seabed throughout the ROV transects (Fig. 6c). *H. dactylopterus* was always seen as solitary individual on different seafloor types, with a resulting lower density in all areas (Fig. 6e). *Macroramphosus scolopax* and *Capros aper* (Fig. 6f) were also recorded in most areas but with low density. Although identified only in one area, the fish *Trachurus* spp. showed a higher density mostly due to the presence of many individuals schooling near the seafloor of the Gioia Canyon. All the other fish were occasionally observed with very low densities (Table 2).

3.2.1. Caulonia Marina Canyon

The ROV transects carried out in the Caulonia Marina Canyon showed low abundance of megabenthic fauna and the lowest taxa richness values recorded in the whole study area, that determined exclusion of sampling units pertaining to this canyon from the statistical analyses. The benthic sessile megafauna in this canyon was almost exclusively represented by Ceriantharia and, to a lesser extent, by Polychaeta Sabellidae both present however with low density values (max abundances of 0.07 ind/m^2 and 0.03 ind/m^2, respectively). The highest density values were recorded for the Crustacea *Plesionika* spp. (up to 0.25 ind/m^2) and few individuals of the crustacean *Paromola cuvieri* were observed in the deeper transect at 495–520 m depth.

Table 2

List of the benthic and bentho-pelagic taxa recorded by ROV in the different canyons of the Central Mediterranean investigated, with relative mean density (ind/m^2) estimated per unit area and total number (N) of taxa identified in each area. n.e.: not estimated density.

PHYLUM Taxa	Caulonia Canyon	Gioia Canyon	Messina Canyon	Petrace Canyon	San Gregorio Canyon	Sant'Agata Canyon	Tremestieri
RHODOPHYTA							
Corallinales			n.e.			n.e.	
FORAMINIFERA							
cf. *Pelosina* sp.				0.013			
PORIFERA							
Encrusting Demospongiae					n.e.	n.e.	
CNIDARIA							
Anthozoa							
Alcyonacea							
Acanthogorgia armata Verrill, 1878			0.001				
Acanthogorgia hirsuta Gray, 1857			0.149				
Swiftia dubia (Thomson, 1929)			0.019			0.107	
Pennatulacea							
Funiculina quadrangularis (Pallas, 1766)					0.001		
Kophobelemnon stelliferum (Müller, 1776)		0.005					
Pennatula phosphorea Linnaeus, 1758					0.003		
Pennatula rubra (Ellis, 1761)				0.010	0.064		
Pteroeides spinosum Ellis, 1764		0.002		0.009	0.006		
Veretillum cynomorium (Pallas, 1766)				0.001			
Virgularia mirabilis (Müller, 1776)				0.001			
Ceriantharia	0.033	0.285	0.027	0.012	0.022	0.005	0.010
Actiniaria							
Calliactis parasitica (Couch, 1842)					0.003		
Actinauge richardi (Marion, 1882)		0.004					
Amphianthus dohrnii (Koch, 1878)							0.021
Andresia partenopea (Andrès, 1883)				0.007	0.003		
Scleractinia							
colonial Scleractinia					0.001		
solitary Scleractinia			0.145	0.050		0.003	0.254
Zoantharia							0.012
Epizoanthus sp.	0.001				0.055		
Hydrozoa		0.518				0.002	0.088
Lytocarpia myriophyllum (Linnaeus, 1758)				0.002			
MOLLUSCA							
Gastropoda							
Calliostoma sp.					0.001	0.001	
Coralliophila panormitana (Monterosato, 1869)					0.001		
Fusinus sp.			0.001				
Galeodea echinophora (Linnaeus, 1758)					0.001		
Thylacodes arenarius (Linnaeus, 1758)						0.004	
Vermetus sp.					0.001		
Bivalvia							
Teredinidae					0.003		
Cephalopoda							
Sepia spp.		0.002					
Sepia orbignyana Férussac [in d'Orbigny], 1826				0.002			
Callistoctopus macropus (Risso, 1826)		0.001				0.002	
Octopus spp.		0.002					
ANNELIDA							
Polychaeta							
Bonellia viridis Rolando, 1822				0.002			
Polychaeta Sabellidae spp.	0.011		0.003	0.035	0.303	0.038	
Polychaeta Sabellidae sp.		109.452		2.102	0.256		
Polychaeta Serpulidae spp.		0.110	0.124	0.006	0.712	0.684	1.426
Polychaeta Terebellida					0.001		
cf. *Praxillura maculata* Moore, 1923			0.163		0.091	0.091	0.019
ARTHROPODA							
Malacostraca							
Parapenaeus longirostris (Lucas, 1846)	0.011	0.058			0.001		
Plesionika spp.	0.036	0.030	0.005	0.242	0.095	0.058	0.217
Plesionika antigai Zariquiey Álvarez. 1955		0.006		0.003	0.002	0.002	
Plesionika edwardsii (Brandt, 1851)	0.001						
Plesionika gigliolii (Senna, 1902)						0.004	0.008
Plesionika heterocarpus (A. Costa, 1871)				0.002	0.013		0.003
Plesionika martia (A. Milne-Edwards, 1883)					0.010	0.003	
Plesionika narval (Fabricius. 1787)					0.002		
Palinurus elephas (Fabricius, 1787)				0.001			
Dardanus calidus (Risso, 1827)					0.006	0.001	
cf. *Dromia personata* (Linnaeus, 1758)							0.002
Paromola cuvieri (Risso, 1816)	0.004				0.001		
Calappa granulata (Linnaeus, 1758)						0.001	

(*continued on next page*)

Table 2 (*continued*)

PHYLUM Taxa	Caulonia Canyon	Gioia Canyon	Messina Canyon	Petrace Canyon	San Gregorio Canyon	Sant'Agata Canyon	Tremestieri
Spinolambrus macrochelos (Herbst, 1790)					0.001		
Bathynectes maravigna (Prestandrea, 1839		0.001				0.001	
BRYOZOA							
Gymnolaemata							0.015
BRACHIOPODA							
Rhynchonellata							
Gryphus vitreus (Born, 1778)						0.004	
ECHINODERMATA							
Ophiuroidea		0.002			0.006		
Asteroidea						0.001	
Peltaster placenta (Müller & Troschel, 1842)					0.002		
Tethyaster subinermis (Philippi, 1837)	0.006				0.001		
Echinoidea							
Cidaris cidaris (Linnaeus, 1758)			0.124		0.081		30.814
Echinus melo Lamarck, 1816					0.001		
Holothuroidea							
Parastichopus regalis (Cuvier, 1817)	0.012	0.033		0.010	0.001		0.002
CHORDATA							
Actinopterygii			0.001	0.007			
Echelus myrus (Linnaeus, 1758)				0.002			
Ophisurus serpens (Linnaeus, 1758)				0.001			
Conger conger (Linnaeus, 1758)					0.002		
Gnathophis mystax (Delaroche, 1809)					0.001		
Argentinidae Bonaparte, 1846					0.001		
Chlorophthalmus agassizi Bonaparte, 1840	0.009	0.006	0.009	0.206	0.016	0.008	0.319
Myctophidae Gill, 1893	0.059	0.001		0.002	0.002	0.009	
Gadiformes			0.001	0.001			
Moridae		0.001					
Gadidae				0.001			
Micromesistius poutassou (Risso, 1827)				0.001			
Phycis blennoides (Brünnich, 1768)		0.001			0.002		
Merluccius merluccius (Linnaeus, 1758)			0.000	0.003			
Macrouridae	0.001	0.006				0.001	
Coelorinchus caelorhincus (Risso, 1810)	0.002	0.005	0.001		0.004		0.008
Hymenocephalus italicus Giglioli, 1884	0.001	0.003			0.002		
Benthocometes robustus (Goode & Bean, 1886)		0.001					
Hoplostetus mediterraneus mediterraneus Cuvier, 1829	0.003				0.006	0.009	
Macroramphosus scolopax (Linnaeus, 1758)			0.005	0.072	0.005	0.003	
Scorpaena spp.					0.001		
Scorpaena notata Rafinesque, 1810						0.001	
Helicolenus dactylopterus (Delaroche, 1809)	0.002	0.001	0.001	0.016	0.025	0.006	0.014
Triglidae		0.002					
Chelidonichthys cuculus (Linnaeus, 1758)				0.001		0.001	
Trigla lyra Linnaeus, 1758					0.001		
Capros aper (Linnaeus, 1758)			0.016	0.021	0.004	0.002	
Serranidae					0.001		
Serranus cabrilla (Linnaeus, 1758)				0.001			
Trachurus spp. Rafinesque, 1810		0.218					
Sparidae	0.002						
Pagellus bogaraveo (Brünnich, 1768)							0.030
Mullus barbatus barbatus Linnaeus, 1758	0.002			0.001			
Mullus surmuletus Linnaeus, 1758			0.001	0.002			
Gobiidae				0.002			
Deltentosteus quadrimaculatus (Valenciennes, 1837)				0.002			
Lepidopus caudatus (Euphrasen, 1788)	0.002				0.001		
Bothus podas (Delaroche, 1809)						0.002	
Symphurus spp.	0.004						
Lepidorhombus boscii (Risso, 1810)						0.001	0.003
Soleidae				0.001			
N taxa	**20**	**27**	**21**	**37**	**52**	**32**	**19**

3.3. Relationships between megafaunal distribution and seafloor variables

PERMANOVA results indicated a significant influence of seafloor composition (Pseudo-F = 9.8, ρ[perm] < 0.01, df = 2) on faunal distribution. Results from PERMANOVA analysis also showed significant differences among assemblages of different canyons (Pseudo-F = 8.8, ρ[perm] < 0.01 df = 5) and a significant influence of depth (Pseudo-F = 4.7, ρ[perm] < 0.01, df = 4) on the observed fauna. The results of the PERMDISP test did not reveal differences in assemblage dispersion between groups associated to different seafloor (F = 0.26, ρ[perm] = 0.8), although significant variations in the homogeneity of multivariate dispersions within groups associated to different canyons and depth ranges (F = 6.8, ρ[perm] < 0.01 and F = 7.7, ρ[perm] < 0.01, respectively) were detected.
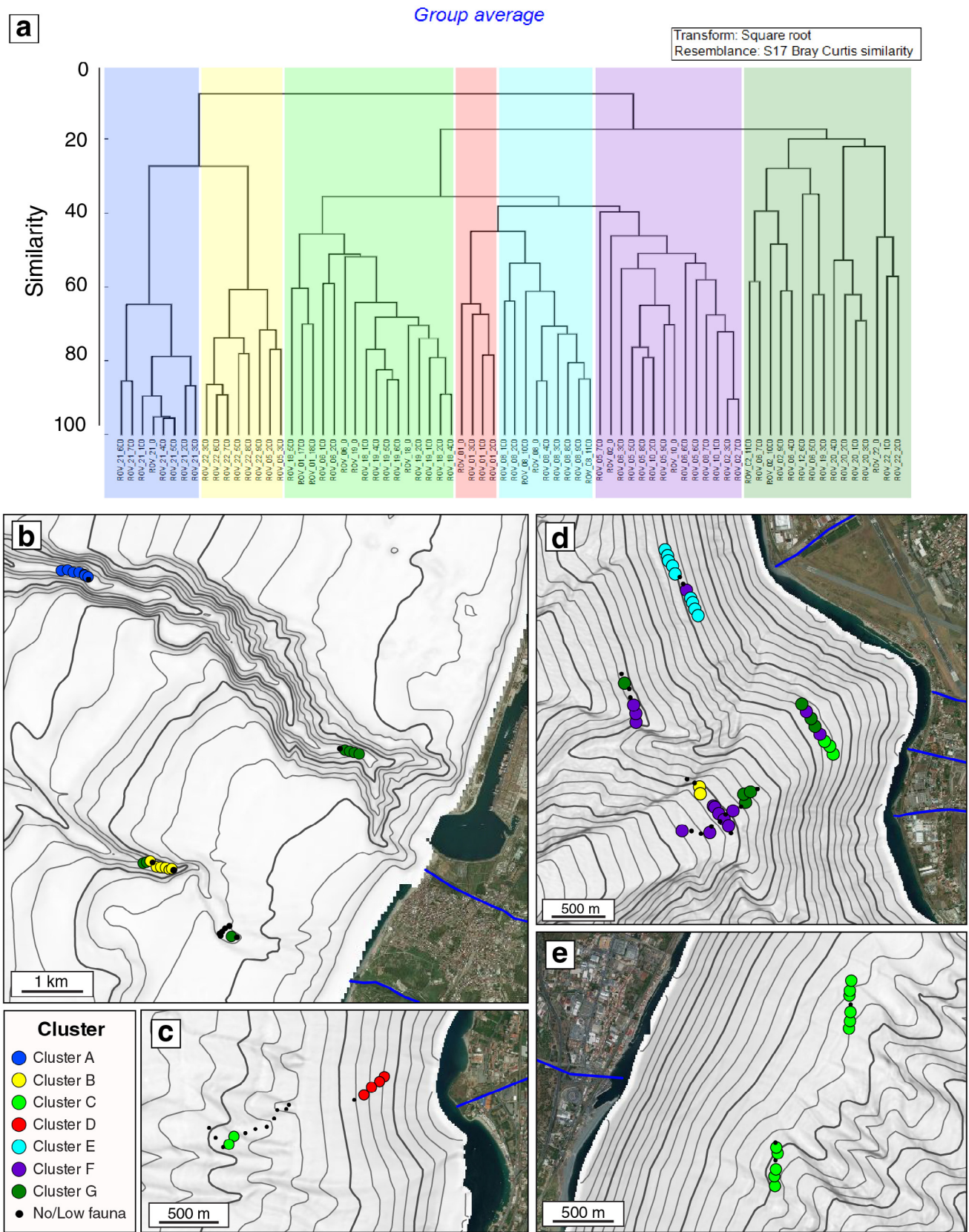
Fig. 4. a: Dendrogram of hierarchical cluster analysis of species data conducted on the 100 m-long sampling units. The colored boxes indicate the megafaunal assemblages and colors refer to the legend in (b). b–d: Bathymetric maps showing the spatial distribution of the assemblages identified from the cluster analysis. Sampling units with no or low fauna, that were excluded from the analysis, are also shown. Contour lines every 25 m; bold contour lines every 100 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
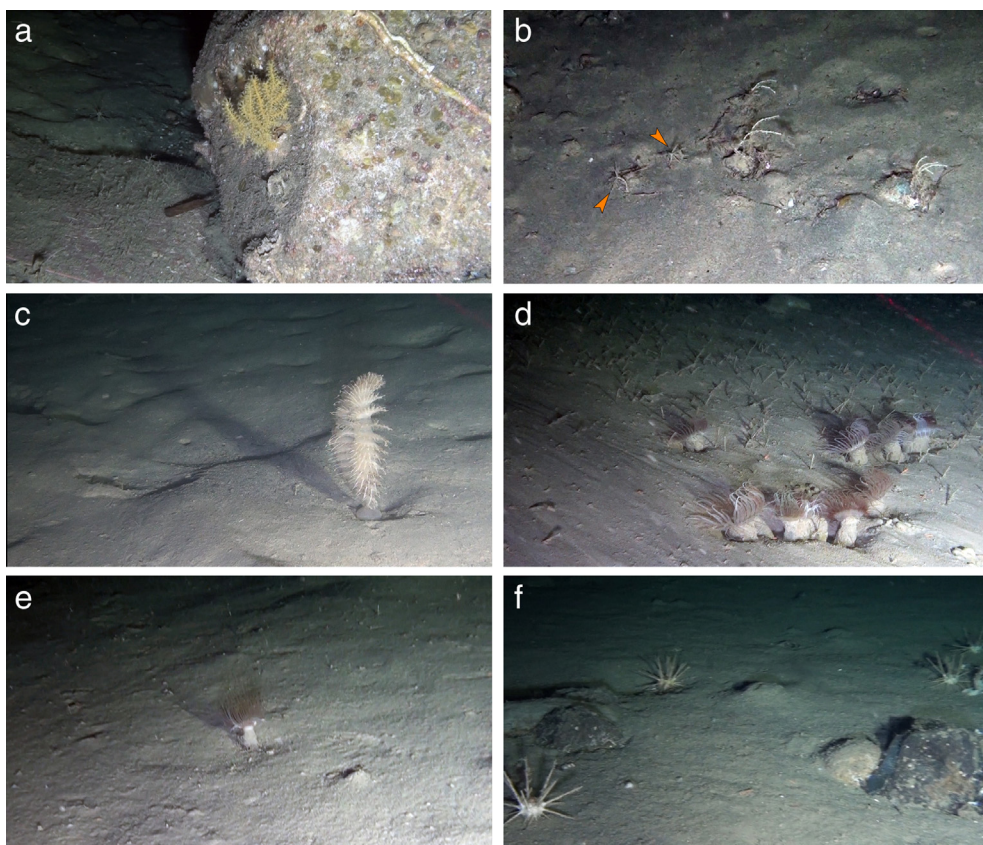
**Fig. 5.** ROV images showing some benthic taxa recorded in the areas studied. (a) *Acanthogorgia hirsuta,* Messina Canyon, −146 m; (b) *Swiftia dubia* and cf. *Praxillura maculata* (indicated by orange arrows), Sant'Agata Canyon, −304 m; (c) *Pteroides spinosum*, Petrace Canyon, −135 m; (d) Ceriantharia and Polychaeta Sabellidae, Gioia Canyon, −485 m; (e) Ceriantharia, Caulonia Canyon, −511 m; (f) *Cidaris cidaris*, Tremestieri, −375 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
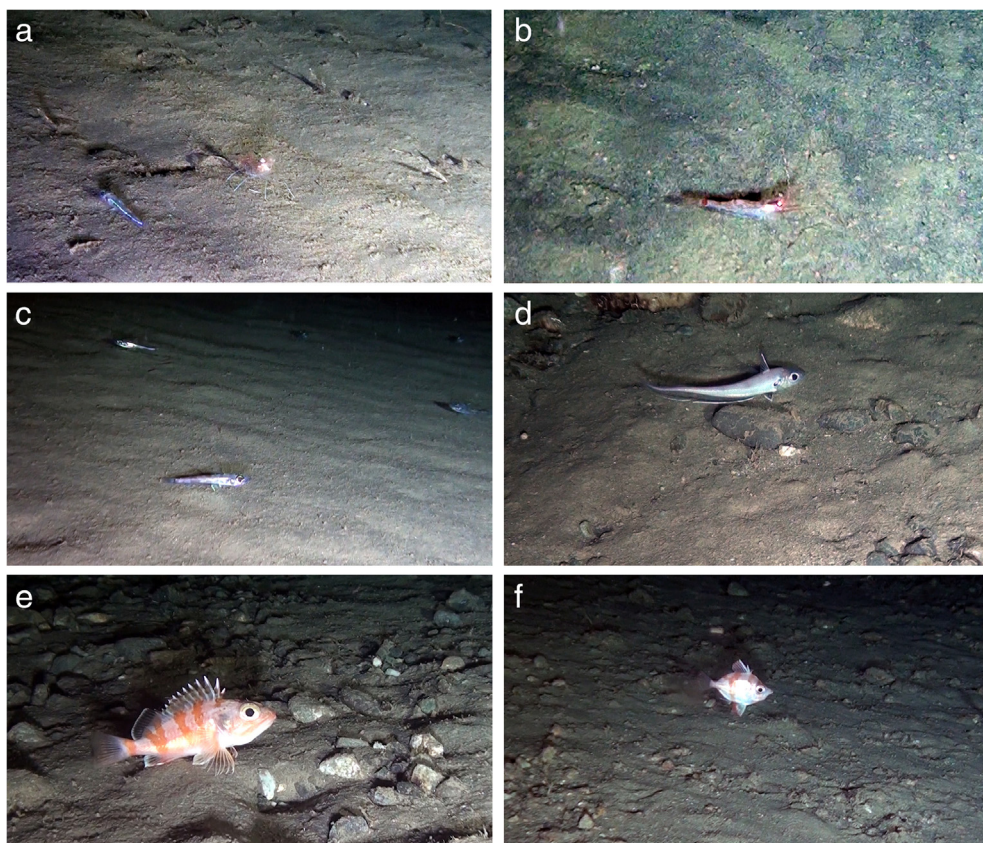
Fig. 6. ROV images showing some crustaceans and fish recorded in the areas studied. (a) *Plesionika antigai,* Petrace Canyon, −229 m; (b) *Plesionika gigliolii*, Sant'Agata Canyon, −518 m; (c) *Chlorophtalmus agassizii*, Tremestieri, −378 m; (d) *Coelorinchus caelorhincus*, San Gregorio Canyon, −255 m; (e) *Helicolenus dactylopterus*, San Gregorio Canyon; −258 m; (f) *Capros aper*, Messina Canyon, −142 m.
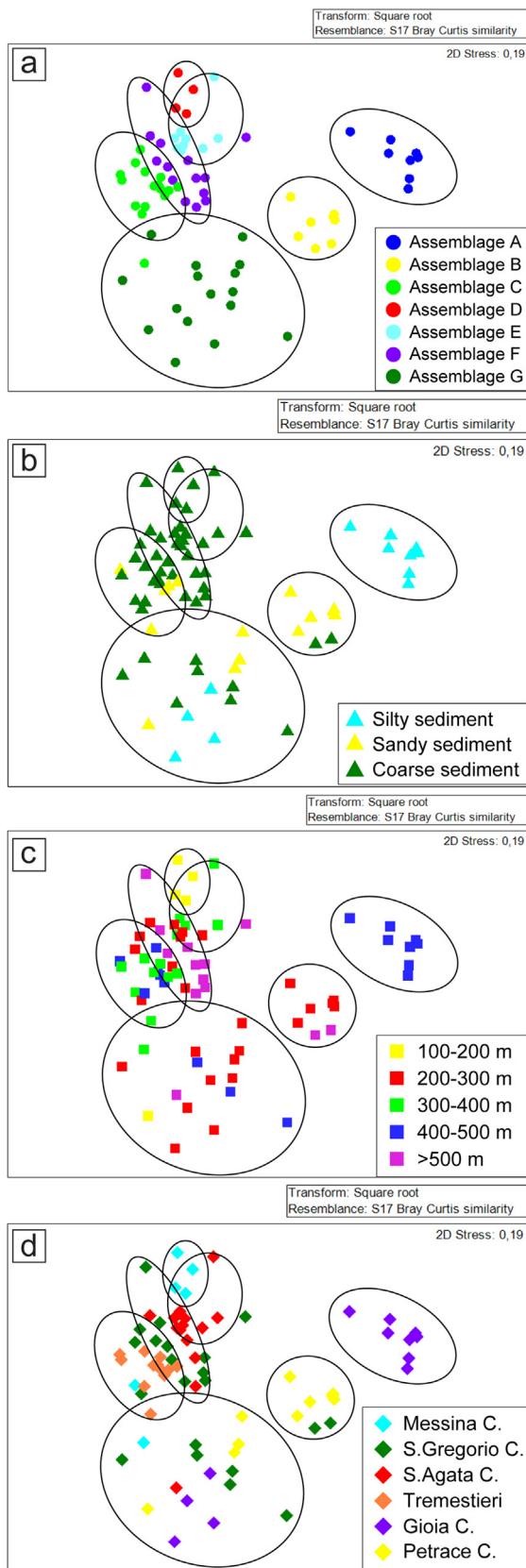
Fig. 7. Non-metric multi-dimensional scaling (MDS) plot of the 100-m long sampling units labelled by (a) assemblage from cluster and SIMPROF analysis, (b) seafloor class, (c) depth range and (d) submarine canyon.

Table 3
Results of DistLM analyses on megafaunal species composition and environmental variables. * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001.

(a) Marginal test

Environmental variable	Pseudo-F	P	Explained variation (%)
Canyon	8.797	0.0001***	38.93
Seafloor class	9.7	0.0001***	21.22
Depth	3.184	0.0041**	4.18
Slope	1.946	0.551	2.6
Aspect	2.038	0.036*	2.72

(b) Step-wise sequential test

Environmental variable	AIC	Pseudo-F	P	Explained variation (%)	Cumulative explained variation (%)
+Canyon	576.89	8.797	0.0001***	38.93	38.93
+Depth	572.58	5.972	0.0001***	4.93	43.86
+Aspect	571.28	3.01	0.005**	2.41	46.27

nMDS plots in Fig. 7 illustrate the relative distance of sampling units pertaining to different assemblages (Fig. 7a) and associated to different seafloor type (Fig. 7b), depth range (Fig. 7c) and canyon system (Fig. 7d). The plots showed that most of the assemblages associated with coarse sediment are separated from those associated with fine sediments (Fig. 7b) and indicated that the greatest difference in taxa composition can be found between the assemblages colonizing the Messina Strait canyons and those distributed in the Gioia and Petrace canyons (Fig. 7d).

The linear model selected by DistLM explained the 46.3% of the variation in megabenthic assemblages composition and identified the canyon system, depth and aspect as variables that significantly contributed to the observed differences (ρ[perm] < 0.01) (Table 3). The canyon variable contributed the highest percentage of variance explained (38.9%), followed by depth (4.9%)

and aspect (2.4%). Despite the DistLM marginal tests (Table 3) showed seafloor class alone to explain a quite high proportion of variation (21.2%), this factor was not included in the best solution of the model. By forcing inclusion of the variable seafloor class in the model we obtained a higher AIC, while it added only an additional 0.9% to the explained variation (data not shown).

The dbRDA ordination plot (Fig. 8) showed that the variable canyon system mainly structured the samples along the first axis, separating the assemblages occurring in Gioia and Petrace canyons (characterized by prevalent silty and sandy seafloor, respectively) from those distributed in the Messina Strait's canyons (mainly associated to coarse sediment). Depth and aspect showed minor positive correlation to the second axis, as represented by the short vectors' length.

The species accumulation curves obtained for different seafloor classes and submarine canyons (Fig. 9) showed that almost all the curves did not reach an asymptote, as a consequence of limited sampling. However, the analysis of the curves indicated that the highest species richness was found for assemblages colonizing coarse sediments, whereas sampling units associated with sandy and silty seafloor had lower species richness (Fig. 9a). The enhancement of megabenthic diversity resulting from the presence of increased seafloor heterogeneity in coarse sediments is indicated by comparing species accumulation curves for different canyons (Fig. 9b). Higher species richness was observed for assemblages colonizing San Gregorio and Sant'Agata canyons, followed by groups from Gioia and Petrace Canyon. Relatively lower species richness was observed at the Messina Canyon head and at the erosive channels off Tremestieri. The lowest species richness was observed in the Caulonia Marina Canyon.
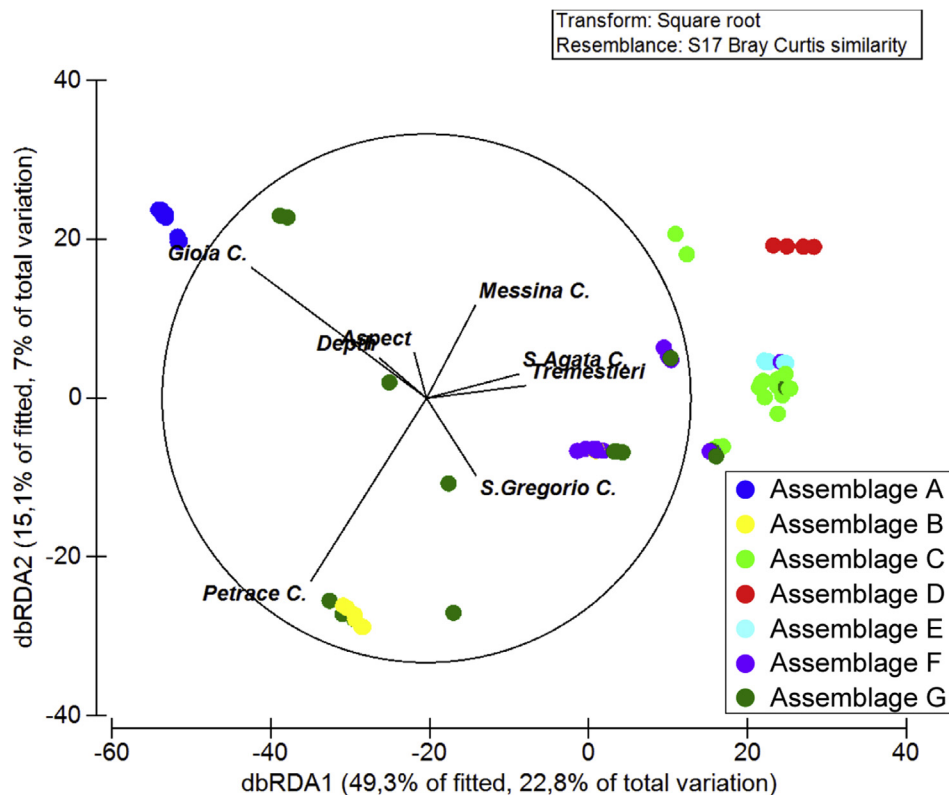
Fig. 8. Distance-based redundancy analysis (dbRDA) plot showing ordination of the DistLM model. Samples are labelled by the cluster and SIMPROF assemblage and the lengths of overlaid vectors indicate the relative influence of the fitted predictor variables.

3.4. Interactions between megafauna and litter

The ROV video analyzed in this study provided numerous examples of interactions between benthic and demersal fauna and marine litter (Fig. 10). In some cases these interactions were clearly harmful to sessile organisms such as the Alcyonacea *Swiftia dubia* or the Echinoidea *Cidaris cidaris* which showed their fragile appendices entangled in plastic items (Fig. 10a and b). In other cases the organisms were observed exploiting litter in several ways. Large litter items could be used as growing substrate by sessile species, such as *Acanthogorgia hirsuta* that was observed to colonize bricks in San Gregorio Canyon (Fig. 10c). Large items were also used as aggregation sites, especially for some taxa such as *Cidaris cidaris* and *Pleisionika* sp. which were often observed in correspondence of litter accumulations in the canyons off Tremestieri (Fig. 10d) or on single litter items in San Gregorio Canyon. Moreover, possible useful interactions with litter were observed for other species. In fact, *Paromola cuvieri* was observed carrying fragments of plastic with their fifth pereiopods in Caulonia Canyon (Fig. 10e); some fishes used different litter items as shelter, like *Coelorinchus caelorhincus* and *Helicolenus dactylopterus* which were seen entering inside plastic bags (Fig. 10f–g) while *Macroramphosus scolopax* was recorded quietly swimming inside litter accumulation (Fig. 10h).

4. Discussion

4.1. Influence of environmental factors on megafauna distribution

Multivariate analyses indicate that the variability of the mega-benthic assemblages across the study areas can be related to differences in seafloor type, depth and canyon system. The relevance of seafloor type and depth in structuring benthic assemblages is well-acknowledged (Kostylev et al., 2001; Beaman and Harris, 2007; Buhl-Mortensen et al., 2009; Miller et al., 2012; Quattrini et al., 2015; Ross et al., 2015; Pierdomenico et al., 2017). Indeed, in this study the largest differences

in taxa composition were found between the assemblages distributed over the soft bottoms of the Gioia-Petrace canyon system and those colonizing coarse-grained seafloor along the channelized features in the Messina Strait, as evident from the nMDS and dbRDA plots. This is also supported by qualitative observation on Caulonia canyon assemblages that are more similar to those observed in the Gioia Canyon, in agreement with its prevalent silty composition. However, it is noteworthy that the best solution of DistLM model selected the canyon system as the main factor driving the distribution of megafauna in the study areas, while excluding the seafloor type. The model also suggest that the depth has a lower but significant influence, that could explain local variability in assemblages composition within the same canyon (Smith and Lindholm, 2016), as for instance observed in Gioia and Sant'Agata canyons (Fig. 4).

The DistLM outcome can be related to the fact the seafloor type is already encompassed within canyon parameter, being primarily the result of the geological setting and linked sedimentary processes acting within each specific canyon (Puig et al., 2014). However, the canyon parameter can be considered as surrogate for a series of other environmental variables, mostly related to hydrological patterns, frequency and types of sedimentary gravity flows. These processes influence the quantity and quality of organic matter and the intensity of physical disturbance within the studied canyons. All these parameters, although not quantified in this study, are identified as important driver of benthic communities distribution within submarine canyons (McClain and Barry, 2010; Cunha et al., 2011; Hunter et al., 2013). For this reason, the canyon parameter overwhelms the significance of the seafloor type in explaining the variability of megafauna distribution.

In fact, in active shelf-indenting canyons such as those analyzed in this study, the enhanced sediment transport processes may trigger multiple and cascading effects, influencing habitat heterogeneity, regulating the quantity and quality of food delivered from coastal areas to deep-sea bottoms, and determining the level and frequency of physical disturbance to which benthic and bentho-pelagic fauna is exposed
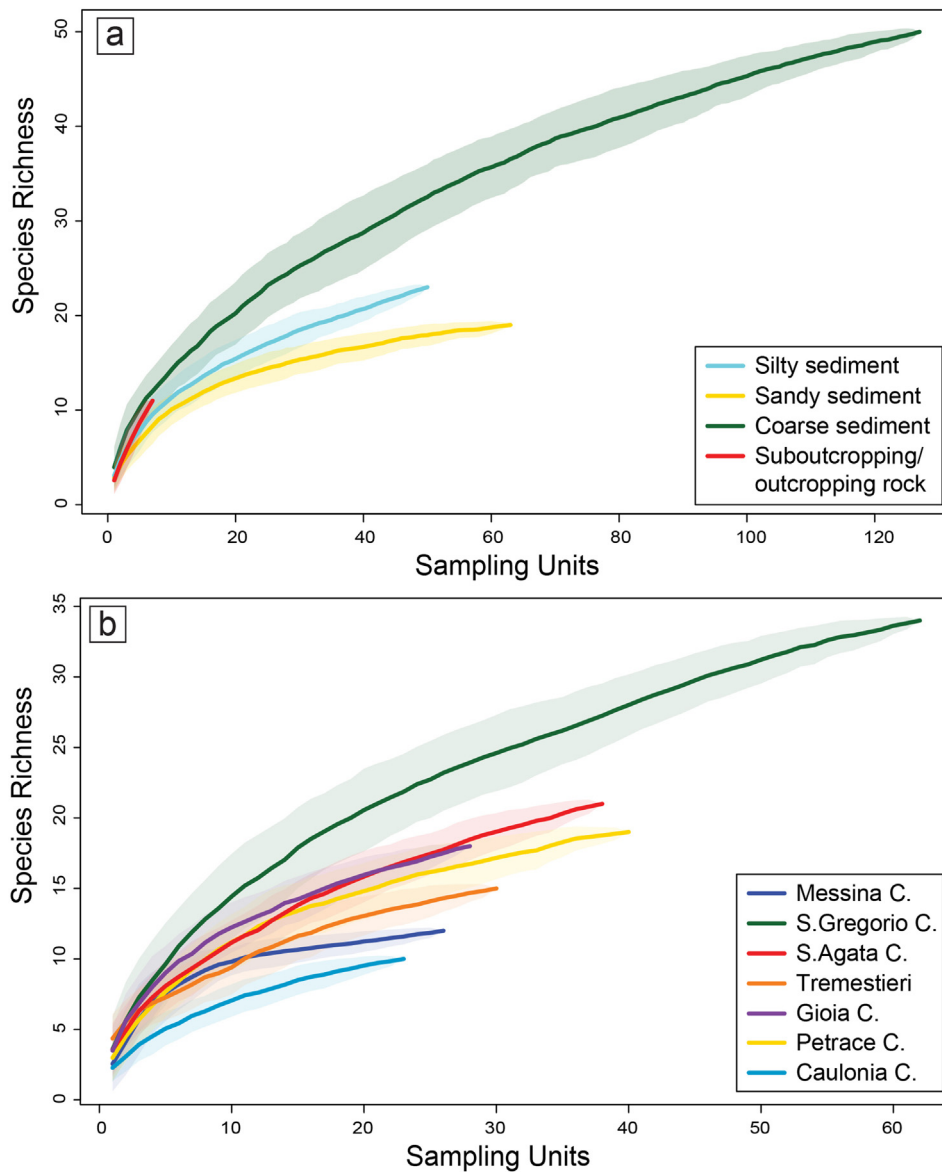
Fig. 9. Mean species accumulation curves calculated for (a) different seafloor classes and (b) different submarine canyons. Colored areas around the curves represent the confidence intervals from standard deviation.

(Vetter and Dayton, 1999; McClain and Barry, 2010; Paull et al., 2010; Baker et al., 2012; D'Onghia et al., 2015b; Quattrini et al., 2015). Particularly, the physical disturbance of the seafloor associated with sediment gravity flows that may periodically affect the canyons analyzed in this study (Casalbore et al., 2011; Ridente et al., 2014; Tessarolo et al., 2008; Bosman et al., 2017), seems to determine stressing environmental conditions for benthic communities. Noteworthy, ROV dives were performed within the thalweg in the upper reach of the canyons, i.e. the sectors most impacted by sedimentary gravity processes (Puig et al., 2014 and references therein). Such disturbance regime may determine overall low megafaunal abundance and low species richness, with assemblages sometimes exhibiting high dominance of few taxa, which may act as opportunistic species. This is consistent with previous studies showing the disturbance regime created by sediment flows as one of the main drivers influencing communities within active canyons (e.g., Okey 2003; Vetter and Dayton, 1998; Paull et al., 2010; McClain and Barry, 2010).

In our case, the different geological setting and associated variability of sedimentary input and gravity flows within the canyons studied are reflected on the large diversity in seafloor type and geomorphological features observed, and may account for different levels of seabed disturbance to which benthic communities are subjected.

For the Gioia Canyon, the occurrence of small-scale sediment gravity flows able to erode the seafloor (with consequent periodical destruction of benthic habitats) was observed through repeated bathymetric surveys performed in the last years (Bosman et al., 2017), representing a main disturbance factor for benthic fauna at the canyon head. This is suggested by the almost total absence of sessile benthos in the Gioia Canyon at 250 m depth (ROV-20), where the assemblage was dominated by mobile species such as shrimps (mostly *Pleisionika* spp. and *Parapeneus longirostris*) and Holothuroidea (*Parastichopus regalis*). These taxa tolerate well the high sedimentation rates and also take advantage of the large amounts of detritus that are frequently funneled in the canyon. A lower level of disturbance at greater depths (470–480 m) allows the colonization by dense population of Polychaeta Sabellidae and Ceriantharia observed in the deeper dive (ROV-21). This can be related to the fact that the frequency of sedimentary gravity flows decrease with the increasing distance from the canyon head and consequently with the depth. However, it is possible that large-scale
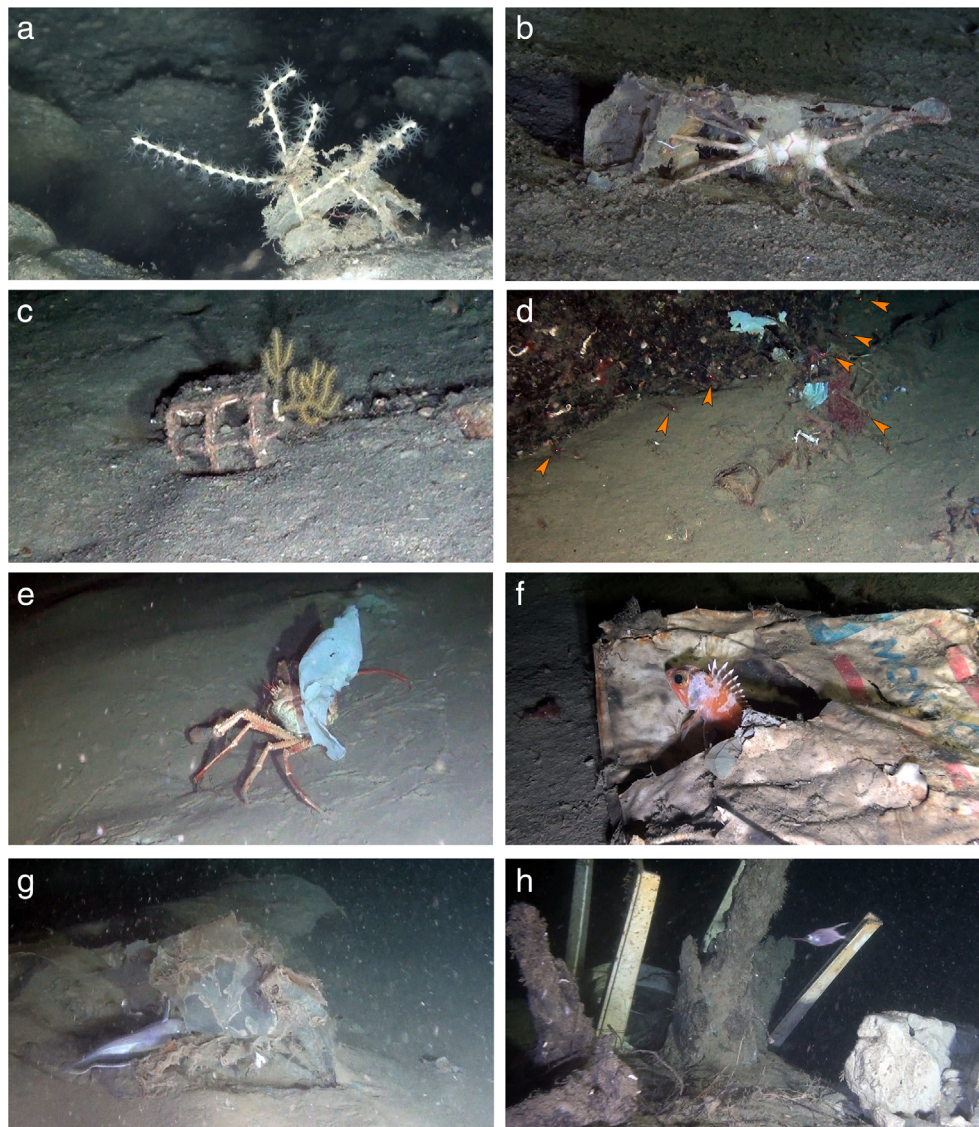
Fig. 10. ROV images showing different types of interactions between litter and megafauna. (a and b) *Swiftia dubia* and *Cidaris cidaris* entangled with plastic; (c) *Plesionika* spp. (indicated by orange arrows) on litter accumulations; (d) *Acanthogorgia hirsuta* growing on a brick; (e) *Paromola cuvieri* with carrying plastic; (f) *Macroramphosus scolopax* inside litter accumulation; (g) *Coelorinchus caelorhincus* sheltering in a plastic bag; (h) *Helicolenus dactylopterus* sheltering in a paper bag. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

events are able to flush the entire upper reach of canyon, with a complete destruction of benthic habitats. Similarly, in the Petrace Canyon, where total absence of megafauna was previously reported at the canyon head (Pierdomenico et al., 2016), we observed low abundance of sessile fauna in the shallower dive at 120 m depth (ROV-12). In the deeper dive at 250 m depth (ROV-22), the higher abundance of sessile fauna, mainly constituted by the same species of Polychaeta Sabellidae observed in the Gioia Canyon along with ceriantarians and sea pens, suggest less stressing environmental conditions.

In both canyons, benthic organisms may benefit from the intense bottom currents (that may lead to a greater availability of food) within the thalweg, whose action is supported by the occurrence of megaripple fields and the frequent drift of plastic bags observed on ROV videos. On the other hand, the silty sediment resuspension due to high sedimentation rates combined with the intense oceanographic processes present in the area may represent a further disturbance factor for the benthic communities. In this respect, *Plesionika* spp. often concentrate in the benthic intermediate nepheloid layers related to water mass circulation and turbulence (Puig et al., 2001). Indeed the overall low abundance within the axis of Gioia and Petrace canyons of benthic

suspension feeders particularly vulnerable to sediment resuspension such as sea pens (Greathead et al., 2014), contrasted with the assemblages observed along the canyon margins, dominated by sea pens (*Pennatula rubra*, *Pteroides spinosum*, *Funiculina quadrangularis*, *Kophobelemnon stelliferum*), and octocorals (*Isidella elongata*) (Pierdomenico et al., 2016, 2018).

Similarly to what observed for Gioia and Petrace canyons, a strong seafloor disturbance associated to sediment resuspension and the occurrence of turbidity flows (Tessarolo et al., 2008, also indicated by the occurrence of partially buried pebbles and sea urchin carcasses on ROV videos) can be inferred within the Caulonia Canyon. Such disturbance may explain the extreme faunal paucity and the low biodiversity, especially in the shallower dive at 150 m depth.

In the Messina Strait the megabenthic assemblages colonizing the canyons differ from those of the Gioia, Petrace and Caulonia canyons mainly for the occurrence of species associated with hard substrates, a greater heterogeneity of faunistic assemblages and for an overall higher abundance of megabenthic fauna. The patchy distribution of different seafloor types within the canyons' thalweg is related to the distinct geomorphic setting of the Messina Strait, where headless canyons

develop at the base of a steep slope apron affected by unconfined sedimentary gravity flows (Ridente et al., 2014). The high-energy regime associated with gravity flows in the Messina Strait is supported by the widespread occurrence on ROV videos of cobbles and large boulders, especially along the thalweg of Sant'Agata, San Gregorio and Messina canyons, on the Calabrian side of the strait. On the other hand, a high spatial heterogeneity of physical disturbance due to unconfined gravity flows allows the colonization of cobbles and boulders by slow-growing species vulnerable to physical disturbance such as alcyonaceans (*Acanthogorgia armata, A. hirsuta, Swiftia dubia*), which may distribute in relatively low disturbed sectors of the slope apron facing the Messina and Sant'Agata canyons. In fact, taxa habitat-makers like Alcyonacea and Scleractinia require stable hard substrates, like the large boulders widespread in the area, for settlement and growth. The almost total absence of taxa, normally widespread in this kind of habitats, like sponges, is more difficult to interpret. It could be explained by a combination of factors like low larval dispersion and the time since when substrates were available for the colonization. The success and the duration of species colonization within a habitat depend not only on environmental conditions, but also on the life history and life cycle of each species (Cardone et al., 2014). Along with taxa associated with hard substrates, the assemblages of the Messina, Sant'Agata and San Gregorio canyons include a diversified soft bottom faunistic component characterized by vagile and sessile taxa with a variety of trophic strategies, suggesting an increased complexity of the habitat (*sensu latu*) (e.g. substrate heterogeneity, food supply, environmental variables). However, the hypothesis that higher seafloor heterogeneity supports larger variability of megabenthic assemblages (De Leo et al., 2010; McClain and Barry, 2010) is, in our case, verified only for San Gregorio Canyon that hosted the largest number of benthic and demersal species (52) among all the canyons studied (Table 2 and Fig. 8). On the contrary, the species richness and species accumulation curves for Sant'Agata Canyon are comparable to those observed in the Gioia and Petrace canyons (where homogenous fine-grained sediment are present), while the Messina and Tremestieri areas have the lowest values (Table 2 and Fig. 8). This setting could be linked to inadequate sampling for the Messina Canyon, whereas in the case of Tremestieri area (where two ROV dives are available) it could be attributed to the strong impact associated to a larger occurrence of sedimentary flows, suggested by a very high abundance of land-based litter.

4.2. Distribution of fish fauna

Regarding the fish fauna distribution, the most frequently observed species are represented by *H. dactylopterus, C. agassizi* and *C. caelorhincus*. The first two fishes are typically sedentary species, strictly linked to the bottom, and abundant on the slope and in canyons as well as in heterogeneous habitats (Uiblein et al., 2003; Costello et al., 2005; Ross and Quattrini, 2007; Sabatini et al., 2007; D'Onghia et al., 2006, 2010, 2011, 2015a; Fabri et al., 2014; Ross et al., 2015). *H. dactylopterus* shows a clear behavioural pattern of sit-and-wait on the seabed, feeding mainly on benthic crustaceans and fishes as well as on plankton organisms (Uiblein et al. 2003; Sulak et al., 2007; Consoli et al., 2010). *C. agassizi* can form dense aggregates on the slope (e.g. D'Onghia et al., 2006) and can be a species indicator of assemblages in submarine canyons (Sabatini et al., 2007), but generally occurred as solitary individuals resting on the seabed (e.g. Ross and Quattrini, 2007). *C. caelorhincus,* as other macrourid fishes, shows the typical behaviour of digging on the seafloor searching for food (Mauchline and Gordon, 1984) and can be found very abundant in complex habitats (e.g. D'Onghia et al., 2010) and canyons (e.g. Baker et al., 2012; Fabri et al., 2014). Video footage of demersal fish and substratum types collected from Logachev Mounds, Rockall Bank and Hebrides Terrace Seamount revealed the presence of *C. caelorhincus* and *H. dactylopterus* in coral reef and transitional substrata, and their relative abundances were significantly affected by depth and substrate type (Milligan et al.,

2016). Recently, *H. dactylopterus* was the most frequent fish species observed in the Nora Canyon (Sardinian waters), resting on seabed, often sheltering close to coral colonies. *C. agassizi, C. caelorhincus* and *B. robustus* were among other fish species recorded in this canyon, the former two species on coral-free bioturbated muddy bottom (Taviani et al., 2017). The latter species, together with the fishes *M. scolopax* and *C. aper,* are species often observed associated to epibenthic megafauna represented by gorgonians and sea pens (Bo et al., 2012, 2014, 2015; Fabri et al., 2014; Ross et al., 2015; Gomes-Pereira et al., 2017; Mastrototaro et al., 2017). In fact, these epibenthic organisms often constitute Essential Fish Habitat for fish species (e.g. Brodeur, 2001; Etnoyer and Warrenchuk, 2007; Baillon et al., 2012; Miller et al., 2012; Gomes-Pereira et al., 2017), but they grow slowly and can live for hundreds of years (Andrews et al., 2002), making their recovery times after disturbance very long.

4.3. Litter interaction with organisms

Physical disturbances of the seafloor are not limited to natural processes but may also be caused by human activities. Specifically, marine litter accumulation on the seafloor is recognized as one of the most significant and growing threat for the health of world's oceans (UNEP, 2009; Galgani et al., 2015). Due their geomorphologic characterics and hydrodynamic processes, submarine canyons act as natural traps, deposits and transport pathways of anthropogenic materials, from the shelf to the abyssal plains and can be considered accumulation zones of land-based marine litter (Orejas et al., 2009; Ramirez-Llodra et al., 2013; Schlining et al., 2013; Fabri et al., 2014; Pham et al., 2014; Cau et al. 2017). Sediment transport process occurring in many Mediterranean canyons can deliver large amount of litter toward deep-sea areas.

ROV observation conducted in this study showed several cases of exploitation of litter by different taxa for multiple purposes, generating complex and controversial responses that need to be better explored.

Although the data collected in the present study do not allow us providing details of impact of litter on the fauna and their interactions, some observations are worth noting. Harmful effects were detected by litter items, generally large plastic objects, as a physical damage to fragile fauna such as cnidarians and echinoderms. It could be probably due to trapping effect of coral branches or sea urchins' spines that remained entangled in the plastic materials, as already detected by *in situ* observation in other deep-sea areas and canyons where different plastic items, particularly discarded fishing gears, heavily impacted the benthic species (Freiwald et al., 2009; Bo et al., 2014; Cau et al., 2017; D'Onghia et al., 2017; Taviani et al., 2017). On the other hand, litter may also provide heterogeneous substrates with additional habitats for benthic and benthopelagic organisms that are able to colonize these artificial surfaces, using litter as shelter and growing substrate. This has a potential influence on the relative abundance of organisms within local assemblages. The relevant presence and aggregation of benthic and benthopelagic mobile fauna on litter accumulations were particularly observed in Tremestieri area, where the echinoid *Cidaris cidaris* and different pandalid species of *Plesionika* genus colonized different types of litter. The pandalid shrimps are generally active predators on macroplankton as well as on benthic resources, but they also present a secondary scavenging activity as the feeding habit (Cartes, 1993). The litter buildup could represent a feeding area and could also promote an opportunistic feeding habit for these species. Most species of the *Plesionika* genus are widely distributed in the Ionian area, particularly on the deep-sea grounds of the Calabrian coast where they spent different phases of their life-cycle (Maiorano et al., 2002, 2010).

The ROV observation of the present study also detected a useful role of litter accumulations as a refuge area for some fish species that can swim undisturbed around and inside different large items or select them as a shelter from eventual predators. For some fishes, such as *H. dactylopterus*, the litter could support the behavioural pattern of resting on

the seabed, while for some others, like for *C. caelorhincus,* the presence of a plastic bag could represent a sudden shelter during swimming, if disturbed by the ROV presence.

Finally, the observation of *Paromola cuvieri* carrying fragments of plastic with their fifth pereiopods confirms its general carrying behaviour which seems to be a common adaptation in this crab for both passive covering behaviour and active behaviour of discouraging competitors or predators (Capezzuto et al., 2012). This species was generally recorded carrying sponges, but it is also known that carrying behaviour could be influenced by the abundance of materials in the environment (Wicksten, 1993). Thus, the wide availability of plastic and other litter items also represents an opportunity to select a different coverage as observed in other studies (Freiwald et al., 2009; Taviani et al., 2017).

5. Conclusion

This study documented the benthic and demersal megafauna distribution dwelling within the thalweg of different active canyons of the central Mediterranean, revealing their relationships with the environmental factors. Results from multivariate statistics showed that megafaunal assemblages were significantly different between different seafloor types, depth ranges and canyon systems. The largest differences in megafauna composition were observed between the assemblages distributed over fine-grained sediments and those colonizing coarse-grained seafloor, overall characterized by higher species richness. However, the distance-based linear modelling indicated that the canyon factor explained more of the spatial variability in megafauna assemblages than other seafloor variables. This evidence suggests that the physical processes specific of each canyon, mostly related to the variability in sediment supply and sedimentary processes but also including hydrodynamic regime and organic matter input, have a prominent role in the spatial distribution of megabenthic assemblages. Effects of the physical disturbance of the seafloor associated with sediment gravity flows that periodically flush the canyons investigated are envisaged especially in the shallower sectors of the soft-bottom canyons (i.e. Gioia, Petrace and Caulonia canyons), resulting in an almost total absence of sessile fauna in these areas and dominance of few mobile species such as shrimps. Conversely, along coarse-grained canyons (i.e. Messina, San Gregorio and Sant'Agata canyons) a higher seafloor heterogeneity seems to support a larger variability of megabenthic assemblages, with species associated to hard substrates that colonize the larger cobbles and boulders. Here, the occurrence of slow-growing species vulnerable to physical disturbance such as alcyonaceans also suggest a higher spatial heterogeneity of physical disturbance.

On the whole, we can also remark that the presented faunal assemblages represent only a small proportion of the regional biodiversity associated with these canyons, because the sampling strategy was mainly addressed to study the areas the most impacted by sedimentary gravity flows (i.e. the canyon thalweg) able to transport land-based litter in deep-water. In this regard, widespread occurrence of marine litter is recorded in all the canyons, along with several cases of interactions between organisms and litter items. Despite harmful effects, such as entanglement, are detected for some species (mostly cnidarians and echinoderms), our observations also indicate usage of litter for multiple purposes including sheltering and growing substrate. Anyway, the complex and controversial interaction between megafauna and litter need to be better explored with further and more detailed analysis, especially considering that the environmental consequences of marine litter pollution are still poorly understood.

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