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distribution and size
structure of
cold-water coral**

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Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean)

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Abstract

Submarine canyons are known as one of the seafloor morphological features where living cold-water coral (CWC) communities develop in the Mediterranean Sea. We investigated the CWC community of the two westernmost submarine canyons of the Gulf of Lions canyon system: the Cap de Creus Canyon (CCC) and Lacaze Duthiers Canyon (LDC). Coral associations have been studied through video material recorded by means of a manned submersible and a remotely operated vehicle. Video transects have been conducted and analyzed in order to obtain information on (1) coral bathymetric distribution and density patterns, (2) size structure of coral populations, and (3) coral colony orientation with respect to the substrate. *Madrepora oculata* was the most abundant CWC in both canyons, while *Lophelia pertusa* and *Dendrophyllia cornigera* mostly occurred as isolated colonies or in small patches. An important exception was detected in a vertical cliff in LDC where a large *Lophelia pertusa* framework was documented. This is the first record of such an extended *L. pertusa* framework in the Mediterranean Sea. In both canyons coral populations were dominated by medium and large colonies, but the frequent presence of small-sized colonies also indicate active recruitment. The predominant coral orientation with respect to the substrate (90° and 135°) is probably driven by the current regime as well as by the sediment load transported by the current flows. In general no clear differences were observed between the CWC populations from CCC and LDC, despite large differences in particulate matter between canyons.

1 Introduction

Continental margins are the most important areas within the ocean in terms of terrigenous input, biogeochemical cycles and biological production (Walsh, 1991; Valiela, 1995; Levin and Sibuet, 2012). Physical processes occurring at the shelf edge transfer water and particulate matter from the continental shelf to the deep sea (Nittrouer and Wright, 1994), and submarine canyons are the main transport pathways for

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this transfer (Puig et al., 2003; Palanques et al., 2008; Huvenne et al., 2011). Submarine canyons play a fundamental role in shelf-deep ocean exchanges reducing the time and the distances covered by water masses, and consequently enhancing the transfer of organic and inorganic sediments from shallow to deeper waters (Würtz, 2012).

5 Canyons that extend across the continental shelf and approach the coast, intercept and transport down-slope the organic-matter-rich sediments transported along the inner shelf zone (Sánchez-Vidal et al., 2009; Lo Iacono et al., 2011). Given such enhancement of trophic resources, canyons may harbor a significantly increased biodiversity and biomass compared to the open slope adjacent areas (Vetter and Dayton, 1998; De
10 Leo et al., 2010; Huvenne et al., 2011).

The continental shelf and slope of the Gulf of Lions, in the northwestern Mediterranean Sea, is one of the areas of the world oceans with highest canyon density (Würtz, 2012). In the heads of some of these canyons, well developed cold-water coral (CWC) communities have been documented to occur on the rocky bottoms of the
15 canyon flanks (Reyss, 1964a; Orejas et al., 2009; Watremez, 2012). The high structural heterogeneity originated by the growth of CWC provide a complex spatial mosaic of habitats, and promote the presence of a high diverse associated fauna (Henry and Roberts, 2007; Buhl-Mortensen et al., 2010) since CWC can act as potential areas of refuge, breeding and feeding for many deep-sea species, including commercially
20 important fish (Husebø et al., 2002; Costello et al., 2005; Ross and Quattrini, 2007; D'Onghia et al., 2010; Baillon et al., 2012).

25 Occurrence, distribution and abundance of CWC species are strongly influenced by several abiotic factors such as seawater temperature and density, aragonite saturation state, oxygen concentration, presence of appropriate substratum, and water flow regimes (Dullo et al., 2008; Davies et al., 2008; Orejas et al., 2009; Roberts et al., 2009a). Enhanced flows prevent coral smothering by sediments, and play a crucial role in food supply (Roberts et al., 2009b), which has been considered as one of the main governing factors in CWC distribution (Frederiksen et al., 1992; Mortensen et al., 2001; Kenyon et al., 2003; Thiem et al., 2006; Davies et al., 2009). Each canyon

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present unique characteristics (Würtz, 2012) with large differences in the sediment fluxes and hydrodynamic features (Palanques et al., 2006; Canals et al., 2009) that make the availability of food to CWC largely variable among canyons. Such differences affect the abundance and species composition of the fauna (Gili et al., 2000), and could result in different suitability and stability of coral habitats, hence inducing differences among their populations. Both the environmental suitability and the stability of a habitat may be reflected in the distribution patterns of coral colonies, as well as in the size structure of coral populations, because the size structure reflects the factors affecting recruitment, growth, and mortality rates in a particular habitat for a period of time equal to the longevity of the population (Grigg, 1975).

In this study, video analysis methods have been employed to compare the state of CWC populations in the Cap de Creus Canyon (CCC) and Lacaze-Duthiers Canyon (LDC), in the Gulf of Lions. Both canyons present well-developed CWC communities, but differ in terms of main hydrodynamic features and particulate fluxes (Palanques et al., 2006, 2012; Ogston et al., 2008; Sanchez-Vidal et al., 2009; Pasqual et al., 2010). The same methodology was employed in both canyons to compare: (1) the distribution of the CWC species, (2) the size structure of the coral populations, and (3) the relationships among coral colony size, depth and their position with respect to the substrate. Moreover, since protection measures will be put in place in both the studied canyons (Madurell et al., 2012; Watremez, 2012), the results of this study will also represent a before-protection assessment for monitoring programs aiming to evaluate the effectiveness of protection measures.

2 Materials and methods

2.1 Research areas and target species

The Gulf of Lions is a crescent-shaped continental margin, with continental shelf width reaching a maximum of ~ 70 km. The shelf break is found at ~ 120 m water depth and

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the slope is incised by numerous submarine canyons that extend down to the continental rise at more than 2000 m water depth. CCC and LDC are the westernmost submarine canyons of the Gulf of Lions margin (Fig. 1). High-resolution multibeam bathymetries from the heads of both submarine canyons were available and have been used in this study (Fig. 2). CCC incises a narrow shelf (< 14 km), while at LDC head region the shelf is wider (~35 km). The CCC axis has a northwest to southeast orientation and has a single canyon head thalweg (Fig. 2a). The northern flank of the canyon displays a smooth morphology, with rounded gullies and scars, with depositional regime prevailing in this sector. In contrast, the southern flank of the canyon is characterized by the prevalence of hard rocky outcrops and steep walls, with a predominant erosive regime (De Geest et al., 2008; Puig et al., 2008). The main reason for the contrast in morphology and sedimentary regimes between the flanks likely resides in the varying hydrodynamic regimes, with the strong bottom currents and high suspended sediment loads associated with cascading events entering the canyon preferentially via the southern flank (Canals et al., 2006; Puig et al., 2008). The detailed morphological features at the head of CCC are described in Lastras et al. (2007). The LDC head displays a north-northwest to south-southeast orientation and has three main step branches that converge at ~400 m water depth into a main canyon axis (Fig. 2b). The canyon is incised up to ~550 m below the canyon rims and displays a large thalweg up to ~600 m width, showing a prevailing depositional regime along the axis (Courp and Monaco, 1990). The southern flank shows a regular aspect until ~600 m depth, with sub-vertical sectors, up to 25° steep, and a general absence of erosive features such as landslide scars and gullies. The northern flank morphology denotes a more long term and large scale erosive regime, with retrograding scars reaching the edge of the flank, and two well-developed tributary valleys. Below the axis depth of ~600 m, the canyon flanks show a clear asymmetry. The southern flank is less steep and displays a more complex morphology, alternating sub-horizontal terraces to steep sectors with retrograding scars and gullies. The northern flank is in contrast steeper and show smooth and well-rounded landslide scars and less incised gullies. Highly energetic

hydrodynamic and sedimentary processes, mainly linked to cold dense shelf water cascading events, have been monitored in both canyons during the past decade. Observations documented similar temperatures for both canyons ($< 12^{\circ}\text{C}$), faster down-canyon current velocities in CCC than in LDC (80 vs. 60 cm s^{-1}), and higher suspended sediment concentrations (> 68 vs. 9.4 mg L^{-1}) and fluxes ($52\text{ g m}^{-2}\text{ s}^{-1}$ vs. $5\text{ g m}^{-2}\text{ s}^{-1}$) in CCC than in LDC head (Palanques et al., 2006, 2012; Ogston et al., 2008), indicating that the CCC acts as a preferential conduit of dense shelf waters and associated suspended particles towards the slope region. The presence of CWCs in CCC and LDC has been previously documented (Pruvot, 1895; Reyss, 1964b, 1972–1973; Pérès and Piccard, 1964; Reyss and Soyer, 1965). In both canyons these communities are dominated by the scleractinian coral *Madrepora oculata*, while the presence of *Lophelia pertusa* and *Dendrophyllia cornigera* is through isolated colonies or small patches (Orejas et al., 2009; Watremez, 2012).

M. oculata has polyps of 3–5 mm diameter and forms colonies of 30–50 cm height; it has been found at depths of 55–1950 m (Zibrowius, 1980). *L. pertusa* polyps measure approximately 10 mm in diameter and forms colonies of more than 130 cm height (Gass and Roberts, 2006), which can build reefs as high as 33 m (Mortensen et al., 2001); it has been found at depths of 40–3000 m (Zibrowius, 1980; Fosså et al., 2002; Cairns, 2007). *D. cornigera* has large polyps 20–40 mm in diameter and forms colonies of 15–20 cm height; it can be found at depths of 200–800 m, but locally as shallow as 30 m (Castric-Fey, 1996).

2.2 Video surveys and analyses

Video surveys in CCC were conducted in September 2007 by the manned submersible JAGO (400 m operation depth, equipped with 1080 horizontal lines resolution colour video camera, and a pair of parallel laser beams mounted 50 cm apart). Video surveys in LDC were conducted in November 2008 and June 2009 by the remotely operated vehicle (ROV) Super Achille (800 m operation depth, equipped with 700 horizontal lines resolution colour video camera, and a pair of parallel laser beams mounted 6 cm apart).

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of the colonies with respect to the substrate was tested in each site by means of a chi-square test performed with the R-language function `chisq.test`, with simulated p-value calculated by Monte Carlo simulation based on 9999 replicates when expected frequencies were < 5 . The relationship between colony size, depth and its orientation with respect to the substrate was explored by means of a correspondence analysis performed with the R-language function `ca` which is available in the `ca` library (Nenadić and Greenacre, 2007). Colony size and orientation were included as dummy (zero/one) variables, while depth was coded as a fuzzy variable using four fuzzy categories (Aşan and Greenacre, 2011; Greenacre, 2013). The definition of the four fuzzy depth categories depends on the data set being analyzed. The mean depths in the four fuzzy categories (D1 to D4) are as follows: for *M. oculata* in CCC, 194 m, 208 m, 260 m and 290 m; for *M. oculata* in LDC, 248 m, 264 m, 345 m and 428 m; for *L. pertusa* in LDC, 289 m, 344 m, 495 m and 526 m. This allows the continuous variable depth to be included with the other two categorical variables to explore their joint association in one ordination plot.

3 Results

In a total of 4447 linear m of sea bottom explored in CCC, 790 colonies of *Madrepora oculata*, 16 colonies of *Lophelia pertusa*, and 62 colonies of *Dendrophyllia cornigera* were recorded in 7 of the 10 explored sites (Fig. 2, Table 1). *M. oculata* occurred in the canyon from 180 to 320 m depth (Fig. 3). The few observed colonies of *L. pertusa* were located in the same depth range as *M. oculata*, however most of them occurred in the deeper part of this range (Fig. 3). Colonies of *D. cornigera* were observed from 160 to 300 m depth, with a dense patch located at 190 m depth (Fig. 3). In a total of 8362 linear m of sea bottom explored in LDC, 555 colonies of *M. oculata*, 97 colonies of *L. pertusa*, and 6 colonies of *D. cornigera* were recorded in 6 of the 8 explored sites (Fig. 2, Table 1). *M. oculata* occurred from 220 to 380 m depth, with a few deeper colonies reaching a maximum depth of 540 m (Fig. 3). Colonies of *L. pertusa* were mainly located

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from 320 to 380 m depth and from 500 to 540 m depth, with only some colonies occurring in shallower areas (Fig. 3). The few observed colonies of *D. cornigera* occurred between 220 and 260 m depth, with some deeper colonies located between 550 and 520 m depth (Fig. 3).

5 In the 7 sites where *M. oculata* was documented in CCC, its populations were mainly dominated by medium and large colonies (Fig. 4). Skewness was significantly negative for two populations (T4 and T7), showing the dominance of the largest classes (Table 2). Very large colonies were observed in 3 sites, being rather abundant in one of them (T3) where they accounted for 14.5% of the colonies. Occurrence of small colonies of *M. oculata* was variable among sites in CCC, and only in two populations (T2 and T6) they represented more than 20% of the colonies. On the other side, in the 10 6 sites where *M. oculata* was documented in LDC, its populations were mainly dominated by medium colonies (Fig. 4), skewness was significantly negative for one population (T14), and only one very large colony of *M. oculata* was observed (T16). Small colonies accounted for more than 20% of the colonies in 5 of the sites in LDC, and dominated in one of them (T13) where they accounted for 69.7% of the colonies. In the 15 two sites where *L. pertusa* was abundant, its populations were dominated by medium and large or very large colonies (Fig. 4). In LDC, a massive coral framework structure was observed (T16) on a vertical rocky wall with outcrops at 320–330 m depth, faced to 20 10–40° heading, and with an estimated length of approximately 20 m. This framework was mainly composed by live *L. pertusa* (Fig. 5), with presence of some *M. oculata* colonies, and was not considered in the size structure and colony orientation analyses since it was not possible to determine the number of colonies forming the framework, due to the entanglement of branches from different colonies.

25 In both canyons, colonies of *M. oculata* were mainly orientated at 90° with respect to the rocky substrate, at all sites (Fig. 6, Table 2). In CCC, the rest of the colonies were mainly orientated at 135° and 0°, and only few colonies were orientated at 180° under rocky outcrops. In LDC the rest of the colonies were mainly orientated at 135°, and only a small number of colonies were orientated at 180° and 0° with respect to the

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substrate. Colonies of *L. pertusa* were primarily orientated at 90° with respect to the substrate, with the rest of the colonies mainly orientated at 0° (Fig. 6).

The correspondence analyses performed for the *M. oculata* colonies in both canyons and *L. pertusa* in LDC are shown in Fig. 7. In CCC the largest size colonies of *M. oculata* were preferentially orientated at 0° with respect to the substrate, and at shallower depths, whereas the smallest colonies were preferentially orientated at 90° and at deeper depths. In LDC, the relationship between depth and size was the opposite, both for *M. oculata* and *L. pertusa*, with smaller colonies found in shallower depths and larger colonies at deeper depths. As far as orientation is concerned, smaller and medium colonies of *M. oculata* tended to be preferentially oriented to 180° and 135°, while large colonies were oriented to 0°. These associations in LDC were similar for *L. pertusa*, the only difference being that large colonies tended to be preferentially oriented at 135°.

4 Discussion

In both canyons *Madrepora oculata* was the most abundant CWC species, while *Lophelia pertusa* and *Dendrophyllia cornigera* were present with much lower abundances. In CCC *M. oculata* was almost 45 fold more abundant than *L. pertusa* and 12 fold more than *D. cornigera*. Likewise in LDC *M. oculata* was almost 10 fold more abundant than *L. pertusa* and 100 fold more than *D. cornigera*. This dominance of *M. oculata* has already been documented also for the central Mediterranean (Taviani et al., 2005; Freiwald et al., 2009; Vertino et al., 2010), but contrasts with the dominance of *L. pertusa* in the north Atlantic CWC communities (e.g. Mortensen et al., 1995; Rogers, 1999; Fosså et al., 2002; Roberts et al., 2009b). The factors determining these differences are still unclear, but dominance of *M. oculata* in the Mediterranean Sea could be related to its wider tolerance to environmental conditions (Weinberg et al., 2009). However, the observation of an extensive coral framework mostly composed of live *L. pertusa* colonies developing on a cliff in LDC (Fig. 5), demonstrates that CWC frameworks also

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in deep-sea gorgonians (Mortensen and Buhl-Mortensen, 2005; Watanabe et al., 2009), as well as in temperate and tropical gorgonian and scleractinian species (Edmunds, 2000; Harmelin and Garrabou, 2005; Linares et al., 2008). In some of these species it has been shown that several years of extremely low recruitment rates alternate with sporadic high recruitment peaks (Yoshioka, 1996; Hughes et al., 1999; Edmunds, 2000; Garrabou and Harmelin, 2002; Bramanti et al., 2005). However, long-lived species have been shown to be buffered against such fluctuations in recruitment (Garrabou and Harmelin, 2002; Linares et al., 2007; Santangelo et al., 2007; Bramanti et al., 2009), while the survival of large and high reproductive colonies is the key factor for population persistence (Gotelli, 1991; Lasker, 1991; Linares et al., 2007). Although the lack of information on CWC reproductive ecology in Mediterranean Sea, the observed abundance of small colonies indicates active recruitment in both canyons. Based on the growth rates obtained in aquaria incubations, the small sized colonies observed in this study might be 5–6 yr old (Orejas et al., 2008, 2011).

The preferential orientations with respect to the substrate (90° and 135°) of *M. oculata* and *L. pertusa* colonies in both canyons are probably related to the main currents as well as to the sediment transported by them. These orientations of corals could represent a compromise between protection from the sediment, and exposure to the water flow to ensure feeding. Thus the large amounts of sediments transported through the canyons (Heussner et al., 2006; Palanques et al., 2006; Canals et al., 2009) may prevent locations at 0° orientation (i.e., upright position), which is the most common orientation in the north-east Atlantic CWC populations, where sedimentation levels are very low (Mortensen et al., 2001). A 90° orientation is also frequent for the Mediterranean red coral (*Corallium rubrum*) colonies in deep sublittoral (50–80 m) areas (Rossi et al., 2008), while a dominance of upright (0°) orientated colonies has been documented in CWC areas, where corals settle preferentially on the top of features or on the up-current flank of elevations (Genin et al., 1986; Mortensen et al., 2001; Reed et al., 2006; Freiwald et al., 2009; Vertino et al., 2010). In LDC the frequency of colonies with upright orientation was slightly higher than in CCC, which might be related to the lower

sediment flux observed in LDC compared to the CCC (Palanques et al., 2006, 2012; Pasqual et al., 2010). On the other hand, the frequent 90° orientation of coral colonies in both canyons might explain the observed low frequency of very large colonies, since whenever a certain large size is exceeded, strong currents and the own weight of the corals may detach or break down these larger colonies.

Overall, no clear differences were observed in the CWC populations located in CCC and LDC, despite the main differences between canyons in terms of hydrodynamic conditions and especially fluxes of particulate matter (Palanques et al., 2006, 2012; Pasqual et al., 2010). This suggests that the particle flux in LDC, although lower than in CCC, is probably large enough to ensure suitable environmental conditions for the development of mature CWC populations. On the other hand, the lower sedimentation rates documented in LDC could act as a positive factor for the development of the CWC communities, which are more affected in CCC by the very high sedimentation rates (Palanques et al., 2006). In a similar way, also the weaker currents documented in LDC could promote coral feeding, since slow flows (2.5 cm s^{-1}) were shown to maximize capture rates in *Lophelia pertusa* (Purser et al., 2010). The higher frequency of lost long lines fishing gears found in CCC with respect to LDC (Orejas et al., 2009; Watremez, 2012) suggest that this canyon could be more affected by anthropogenic impacts. Long line fishing gears have been frequently observed entangled in coral colonies, and this fisheries impact has already been recognized as a cause of coral mortality (Hourigan et al., 2007; Orejas et al., 2009). Since protection measurements are planned for both canyon heads in the near future (Madurell et al., 2012; Watremez, 2012), a future comparison of CWC distribution patterns and population structure with the results of this study will allow to assess recovery rates of CWC populations, and to evaluate the effectiveness of the protection measures.

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Table 2. Skewness of the size structures, and chi-square test on colony orientation in the studied populations of *Madrepora oculata* and *Lophelia pertusa* in the Cap de Creus Canyon (CCC) and Lacaze-Duthiers Canyon (LDC); significant p-values are indicated with one (p-value < 0.05), two (p-values < 0.01) or three asterisks (p-value < 0.001).

Canyon	Species	Transect	Size structure		Colony orientation		
			Skewness	p-value	χ^2	p-value	
Cap de Creus Canyon (CCC)	<i>Madrepora oculata</i>	T1	-0.43	0.2084	89.94	< 0.001	***
		T2	-0.04	0.8992	205.22	< 0.001	***
		T3	0.07	0.7664	104.03	< 0.001	***
		T4	-1.07	0.0052	84.37	< 0.001	***
		T5	-0.18	0.7580	15.83	0.0012	**
		T6	-0.06	0.9320	23.2	< 0.001	***
		T7	-1.32	< 0.001	39.25	< 0.001	***
Lacaze-Duthiers Canyon (LDC)	<i>Madrepora oculata</i>	T11	0.03	0.9781	42.00	< 0.001	***
		T12	-0.16	0.6494	54.22	< 0.001	***
		T13	0.86	0.1585	36.21	< 0.001	***
		T14	-0.64	0.0486	96.02	< 0.001	***
		T15	0.23	0.6744	18.44	< 0.001	***
		T16	0.20	0.4042	168.78	< 0.001	***
			<i>Lophelia pertusa</i>	T11	-0.19	0.7738	25.67
T16	0.32			0.4463	23.58	< 0.001	***



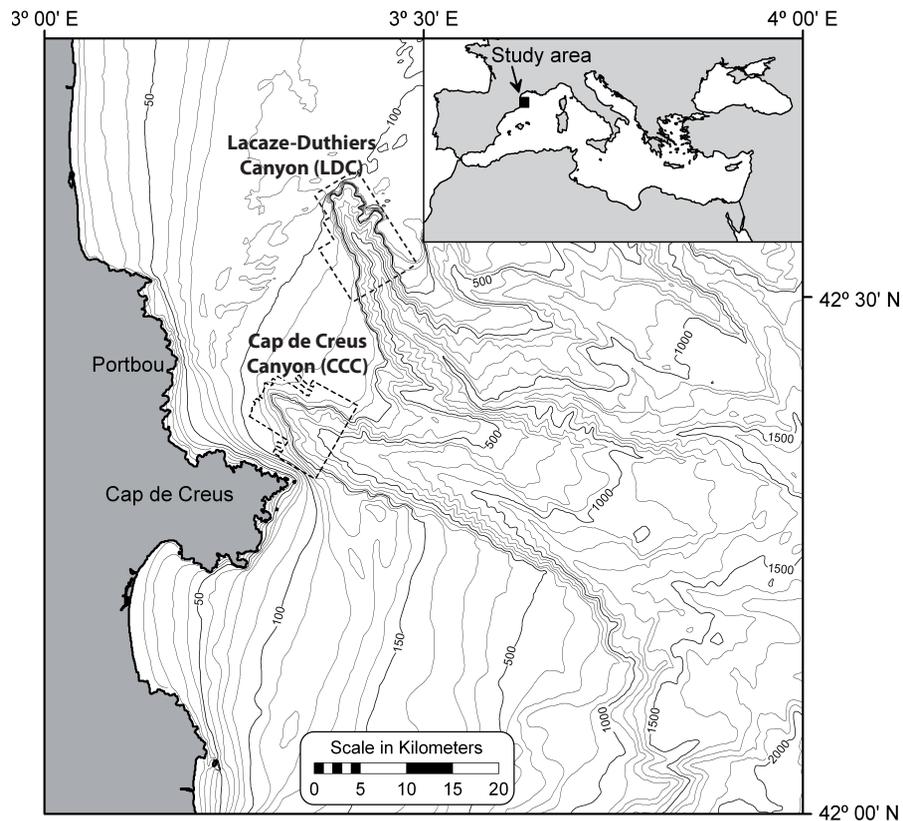


Fig. 1. Bathymetric map and location of the study areas in the western sector of the Gulf of Lions, showing the Cap de Creus Canyon (CCC) and the Lacaze-Duthiers Canyon (LDC). The areas delimited with a dashed line correspond to coverage of the multibeam bathymetries illustrated in Fig. 2.

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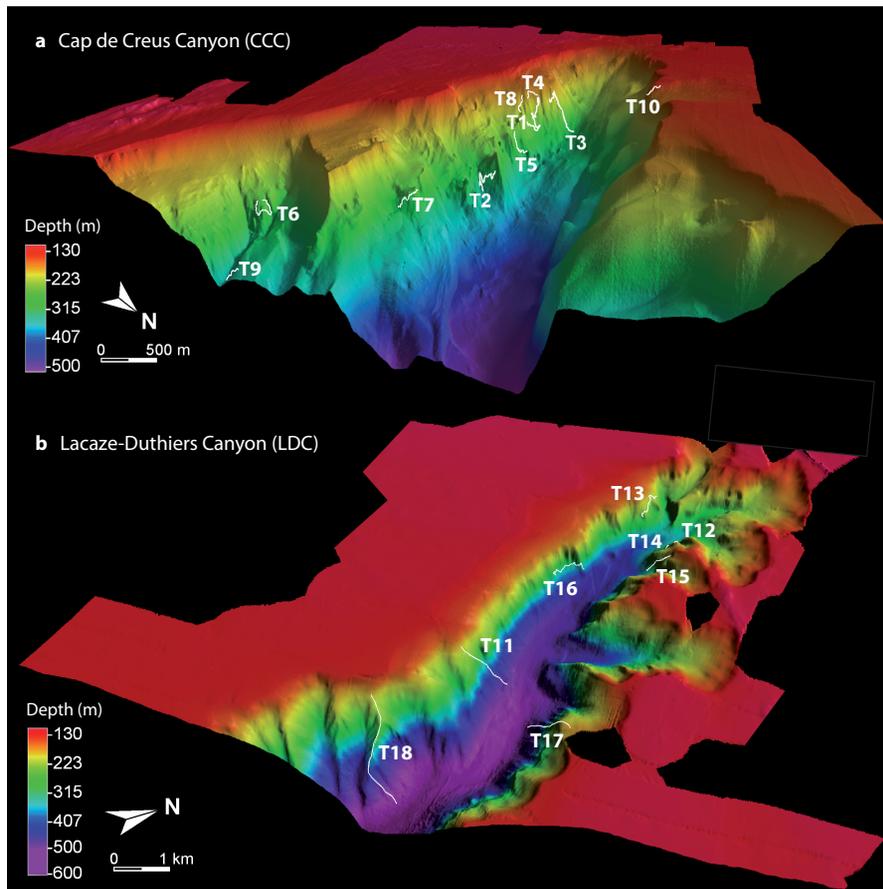


Fig. 2. Three-dimensional bathymetries illustrating the locations of the video tracks (T1 to T18) in **(a)** the Cap de Creus Canyon (CCC) and **(b)** the Lacaze-Duthiers Canyon (LDC).

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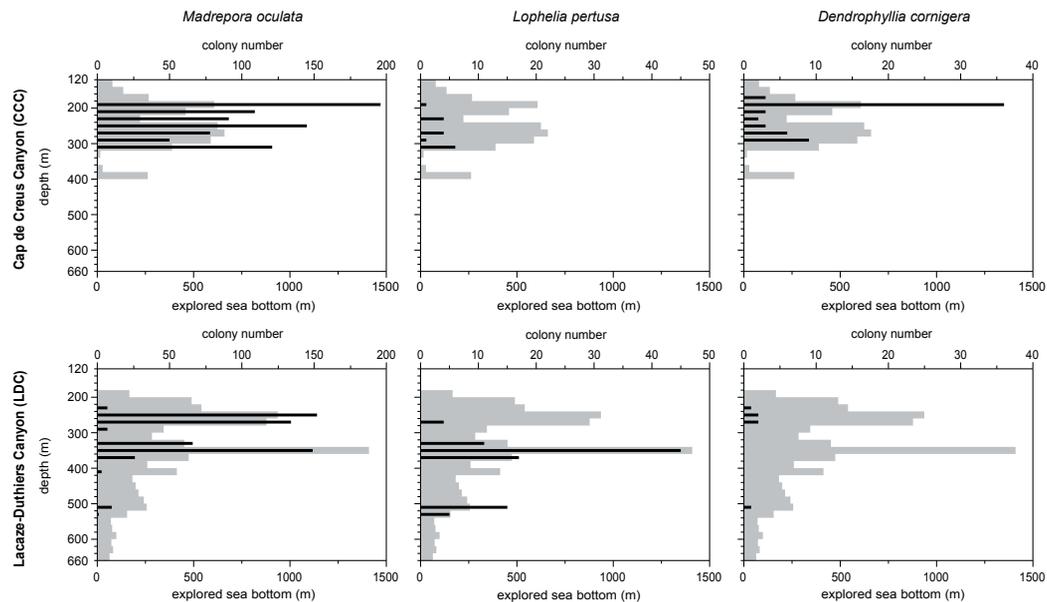


Fig. 3. Bathymetrical distribution of the *Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera* colonies in the Cap de Creus Canyon (CCC) and the Lacaze-Duthiers Canyon (LDC): the black line indicates the number of colonies; gray-scale histograms represent the explored sea bottom (m) over the studied bathymetrical range.

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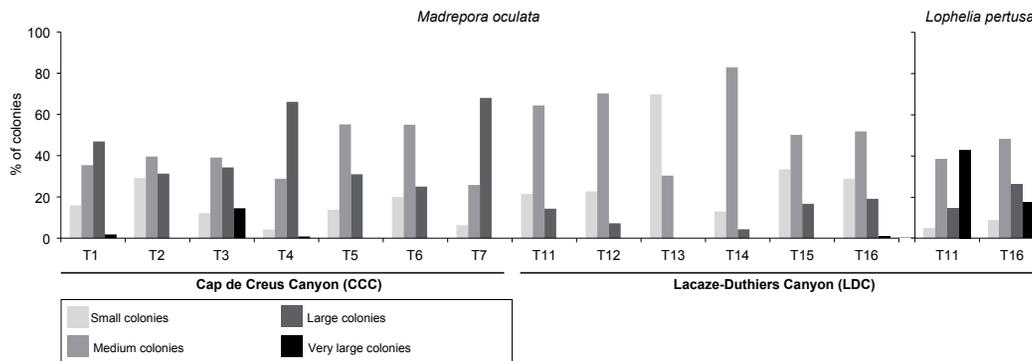


Fig. 4. Size-frequency distribution of *Madrepora oculata* and *Lophelia pertusa* populations in the Cap de Creus Canyon (CCC) and the Lacaze-Duthiers Canyon (LDC).

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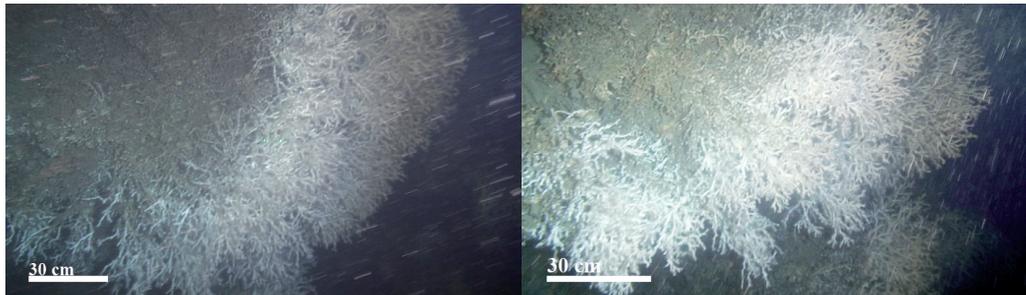


Fig. 5. Massive coral framework structure observed on a vertical rocky wall with outcrops on the southern flank of the Lacaze-Duthiers Canyon (LDC, T16) at 320–330 m depth, faced to 10–40° heading, and with an estimated length of approximately 20 m. This framework was mainly composed by live *Lophelia pertusa*, with presence of some *Madrepora oculata* colonies.

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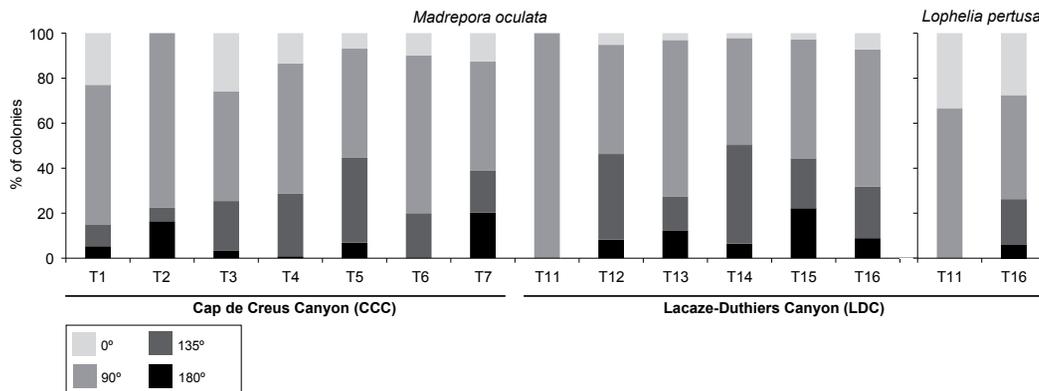


Fig. 6. Orientation of the *Madrepora oculata* and *Lophelia pertusa* colonies with respect to the substrate in the Cap de Creus Canyon (CCC) and the Lacaze-Duthiers Canyon (LDC).

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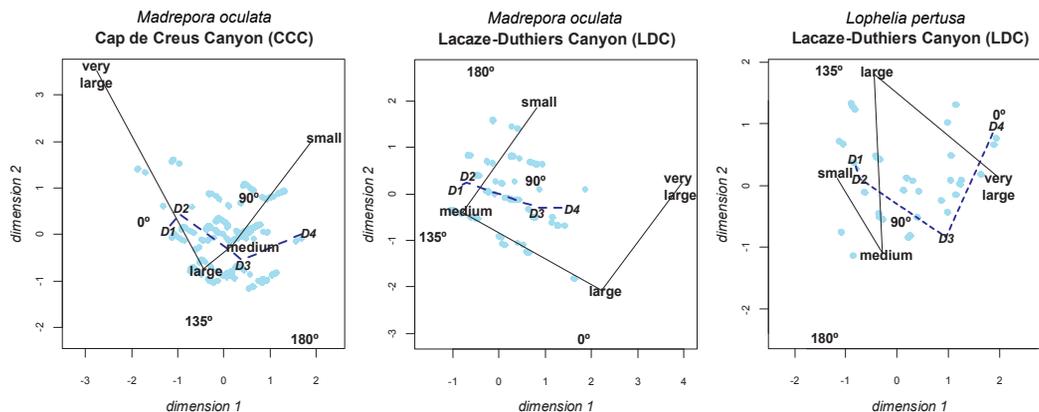


Fig. 7. Correspondence analysis showing the relationship between *Madrepora oculata* and *Lophelia pertusa* colony size, depth and colony orientation with respect to the substrate in the Cap de Creus Canyon (CCC) and the Lacaze-Duthiers Canyon (LDC). Samples are shown by dots; the ordinal categories of size and depth are connected by solid and dashed lines respectively.

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