Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact

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ABSTRACT: The occurrence and density of 3 cold-water coral (CWC) species (*Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera*) were investigated in the Cap de Creus canyon (northwestern Mediterranean) by conducting and analysing 22 video survey transects. Species distribution patterns were also investigated at 3 spatial extents (km, 100s of m and m) across 3 of the transects using spatial statistics. Additionally, the locations of snagged benthic long-line fishing gear were logged across these 3 transects. Video surveys were carried out by both remotely operated vehicles (ROVs) and the JAGO manned submersible. CWCs were present in 15 of the 22 survey transects, predominantly those covering areas with hard substrate (boulders or hardrock outcrops). *M. oculata* was the most abundant CWC species in the survey transects, whereas *L. pertusa* and *D. cornigera* were much more sparsely distributed, with only isolated colonies observed in the majority of transects. *M. oculata* showed a significant contagious distribution pattern across the analysed transects, with several scales of spatial pattern and patch size being detected, whereas *L. pertusa* and *D. cornigera* were not found in sufficient numbers to apply spatial statistics. Different covariance patterns were found across the transects between snagged fishing gear and the presence of *M. oculata*. Further investigation of this relationship and the level of hazard posed by long-line fishing to *M. oculata* colonies is required prior to development of a protective management strategy.

KEY WORDS: Cold water corals · Submarine canyons · ROVs · Manned submersible · Population density · Spatial statistic · Spatial patterns · Patch size

INTRODUCTION

Over the last 2 decades, a significant body of research has focused upon improving our understanding of cold-water coral (CWC) distribution along continental margins (e.g. Roberts et al. 2006, Hall-Spencer et al. 2007, Schroeder 2007, Wareham & Edinger 2007, Freiwald et al. 2009). However, within the Mediterranean Sea, investigations have been more moderate and have focused mostly on CWC distributions within the central and eastern basins (e.g. Tursi et al. 2004, Taviani et al. 2005a,b, Freiwald et al. 2009). CWC distribution in the

northwestern basin is poorly described in the literature; a general description of the white coral biocoenosis from Pérès & Picard (1964) and a description by Reyss (1971) of the benthic macrofauna communities from the Cap de Creus and Lacaze-Duthiers canyons, comprise the only published investigative data.

Little quantitative information is available on the spatial distribution patterns of CWCs (but see Mortensen & Buhl-Mortensen 2004, Parrish 2007) at large (km), middle (100s of m) and small (m) spatial extents (term used after Dungan et al. 2002 definition). A major difficulty in acquiring information on CWC distribution

has historically been the absence of appropriate technology to sample and survey at the depths at which they are commonly found (Gage & Bett 2005). In recent years, improvements in remotely operated vehicle (ROV) and manned submersible design and surveying techniques have provided scientists with the opportunity to carry out accurate, quantitative *in situ* investigations of CWC distribution, as well as demographic studies of major species. Appropriate analytical methods for assessing spatial patterns in natural marine communities are generally undeveloped, with few exceptions (but see Yoshioka & Yoshioka 1989). Statistical methods developed and applied previously in the field of terrestrial plant ecology could potentially be applicable for assessment of benthic species distribution (Dale 1979, 1999). Compared to facies and faunal analysis, spatial statistics permit a multi-scale quantification of species distribution patterns (such as the degree of aggregation, scale of any observable distribution patterns, patch and gap sizes, etc.). Spatial patterns in the abundance of a species are the result of past processes (e.g. reproduction, feeding, inter- and intraspecific interactions) and play a major role in determining future processes (Dale 1999).

Species distribution patterns are not exclusively determined by 'natural' factors. Progressively, human influence is playing a role in shaping marine benthic populations and communities. CWC communities have been impacted by bottom trawling (e.g. Hall-Spencer et al. 2002, 2007, Le Goff-Vitry & Rogers 2005, Mortensen et al. 2005, Waller & Tyler 2005, Edinger et al. 2007), with other fishing methods and gears (such as those used in benthic long-line fishing) also of concern (Lumsden et al. 2007).

In the present study we aim to improve the level of knowledge of CWC distribution within the northwestern Mediterranean by presenting the findings of an investigation into the occurrence and densities of 3 CWC species (*Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera*) within a submarine canyon in the region. Additionally, we assessed spatial distribution patterns in *M. oculata* abundance within the canyon using spatial statistics. We also investigated the level of potential anthropogenic impact on CWC communities within the canyon by quantifying the amount of benthic long-line fishing gear and other anthropogenic material observed within the canyon. These data can be used to aid the decision-making process when deciding whether or not to establish marine protected areas in the canyon in the future. To assess these CWC distributions, we worked with ROVs and the manned submersible JAGO (Leibniz Institute of Marine Sciences [IFM-GEOMAR], Christian-Albrechts Universität, Kiel), and applied spatial statistic tools to achieve reliable quantitative data.

MATERIALS AND METHODS

Research area. The survey was conducted in the Cap de Creus canyon (northwestern Mediterranean), the most westerly of the Gulf of Lions submarine canyon system (Fig. 1) and a bathymetrically complex region with significant sediment input from the Rhone and many other small rivers. The canyon axis has a northwest to southeast orientation incising on the continental shelf with maximal depths reaching 2200 m. The preferential direction of the coastal currents and the narrowing of the shelf towards the west results in the majority of off-shelf sediment transport on this margin running through the Cap de Creus canyon. Sediment fluxes observed in this canyon are much higher than in the eastern and central Mediterranean submarine canyons (Palanques et al. 2006). Additionally, the Cap de Creus canyon is more frequently affected by periodic arrivals of dense shelf water cascades, an oceanographic phenomenon occurring each winter in the Gulf of Lions (Durrieu de Madron et al. 2005), which make the Cap de Creus canyon head a unique environment in the northwestern Mediterranean. This oceanographic phenomenon results in rapid drops in temperature at depth. Commonly, a drop of 2 to 3°C occurs over a few days; for example, during winter 2003–2004 in the Cap de Creus canyon, bottom temperatures varied from maximal peaks of 15.5°C down to minimal values of 11.6°C, with an average of 13.4°C (Palanques et al. 2006). Through these cascading events, shelf waters carrying large quantities of dissolved and particulate organic matter are rapidly advected 100s of m downward, with these cascades acting as a significant natural carbon sequestration and deep-sea ecosystem fuelling mechanism (Canals et al. 2006). This high throughput of organic material along the Cap de Creus canyon is thought to be essential for the maintenance of its associated deep-sea ecosystems and the high local biodiversity (Canals et al. 2009).

The multibeam bathymetry conducted by Fugro Engineers, AOA Geophysics and the University of Barcelona (see Lastras et al. 2007 for details) showed morphological complexity of the canyon, particularly the striking differences between the northern and southern canyon flanks (Fig. 2). The northern flank displays a smooth morphology, with rounded gullies and scars, suggesting that in recent years a depositional regime has prevailed in this sector. Sediment accumulation rates recorded from the northern flank reach values up to 1.5 mm yr^{-1}, probably due to advection via nepheloid layer transport controlled by regional southward currents (DeGeest et al. 2008). In contrast, the broad areas with hardrock outcrops, step walls and erosive morphological features that are evident on the southern flank of the Cap de Creus canyon
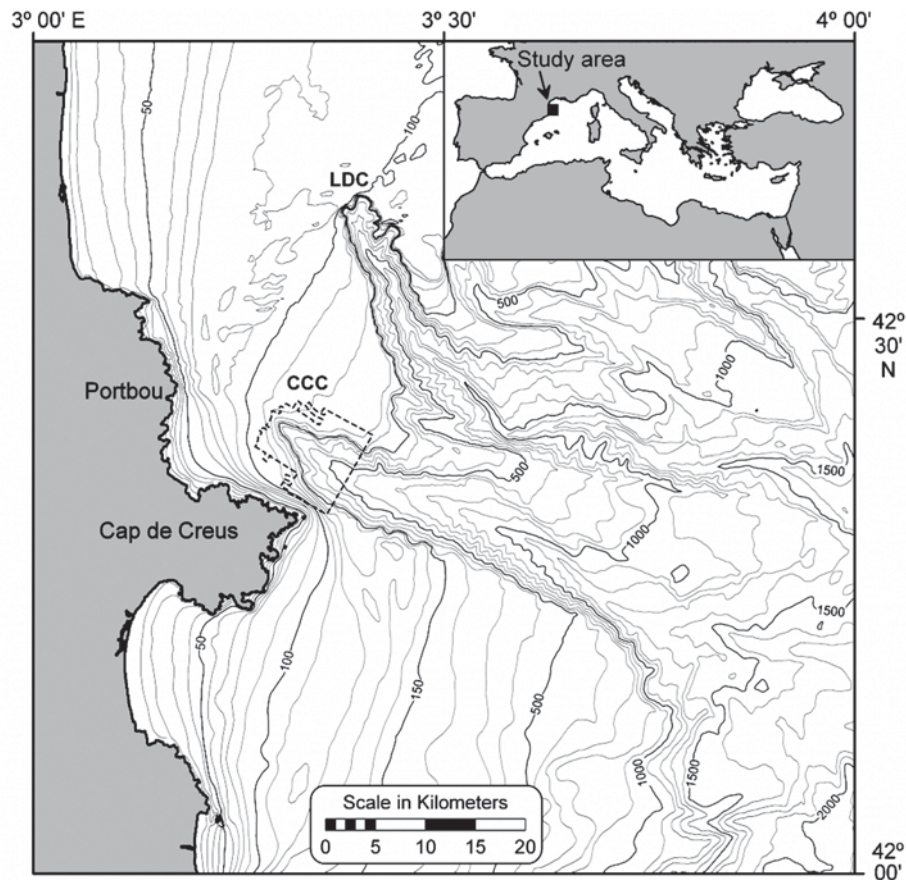
Fig. 1. Bathymetric map and location of the study area in the western sector of the Gulf of Lions, showing the Lacaze-Duthiers canyon (LDC) and the Cap de Creus canyon (CCC). The area delimited with a dashed line at the head of the CCC corresponds to coverage of the multibeam bathymetry illustrated in Fig. 2

indicate an ongoing, predominantly erosive regime (Puig et al. 2008). Accumulation rates in this area are very low and very coarse sands have been collected along the shelf edge and upper canyon rim (DeGeest et al. 2008). The main cause of the contrast in flank morphology is likely to be the varying hydrodynamic situation in the area, with the strong bottom currents and high suspended sediment loads associated with the cascading events entering the canyon preferentially via the southern flank (Puig et al. 2008).

Video surveys. Sampling was conducted in October 2005, July 2006 and September 2007 by video survey (see Table 1) from the RV 'García del Cid'. The first 2 survey campaigns (October 2005 and July 2006) were conducted by ROVs, a Falcon Sea Eye and Phantom HD2+2, both rated to 300 m water depth and equipped with colour video cameras (700 horizontal lines resolution). The third survey campaign (September 2007) was conducted by the manned submersible JAGO (400 m operation depth, cruising speed 1 knot, equipped with CTD, manipulator and 1080 horizontal lines resolution colour video camera). Positioning of the

JAGO transects was achieved using the LinkQuest TrackLink 1500 HA system and the transponder TN 1510B. The multibeam bathymetry data was used to locate the transects, with the aim of surveying hard bottom areas as far as possible. Throughout the dives, a pair of parallel laser beams mounted 50 cm apart allowed determination of a 1.5 m wide region of the seabed. This 1.5 m width was used to produce 1.5 m wide transects covering each dive, within which the densities of the 3 target species could be assessed.

A total of 22 video surveys were conducted (see Table 1), 12 with ROV and 10 with JAGO; all were carried out in the upper canyon area. The video durations produced during the ROV dives varied between 2 and 5 h, covering a seabed distance of ~500 to 5000 m. JAGO dives were shorter, with 2 to 4 h of video produced for each survey transect covering traverses of ~500 and 1500 m. The dives carried out by ROV were recorded on digital video tapes, whereas high-definition video tapes were used to record the JAGO video data. All video material was transferred from tapes to hard disk prior to analysis.
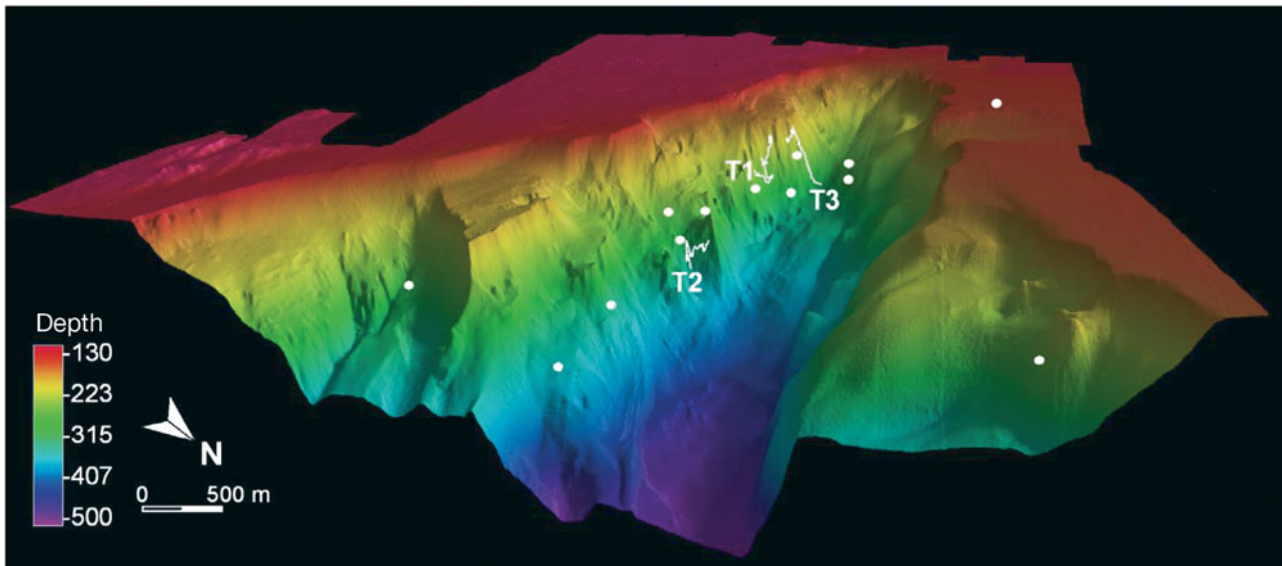
Fig. 2. Three-dimensional bathymetry of the Cap de Creus canyon (CCC) head illustrating the location of cold-water corals (white dots) in the CCC during the 3 conducted ROV (2) and JAGO (1) surveys (October 2005, July 2006 and September 2007), and the statistically analyzed JAGO video tracks (T1, T2 and T3) in the southern canyon flank

Video analysis. The video analysis was carried out with Final Cut software (Apple). Occurrence of the 3 CWC species (*Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera*) in the canyon was investigated by logging the locations of corals recorded on each of the video transects (from ROVs and JAGO).

Densities (colonies m^{-2}) of these species were quantified through a detailed analysis of 3 (T1, T2 and T3) video transects (see Table 1, Fig. 2) recorded with the manned submersible JAGO. The initial phase of video analysis consisted of 2 stages. Firstly, during the JAGO dives the submarine would pause for either sample collection or to photograph fauna in detail—these pauses were eliminated from the transects prior to processing. Secondly, the JAGO data contained areas of poor quality data, where visibility was poor mainly due to sediment resuspension or distance from the seabed; these sections of video were also removed prior to analysis. Useful video sequences comprised a total distance of 1543 m. All colonies of the target species appearing within the central 1.5 m of the video transect data were recorded.

Three different substrate types (soft sediment, rocky boulders and hardrock outcrops) were identified along each transect. Dominant substrate type was logged throughout each transect, with a substrate being considered dominant when covering >50% of the transect width.

Anthropogenic impact was similarly logged, with occurrences of fishing gear or other man-made detritus logged throughout each video transect.

Statistical analyses. Data were analyzed by applying spatial statistics with the PASSaGE 2.0 software package (Rosenberg 2008). Species distribution along the transects was displayed in density plots. Significance of deviation from a random distribution (after Lincoln et al. 1982) was analyzed with the 1-dimensional version of Ripley's K-function, plotted as L-function: L(*t*) = *t* – K(*t*)/2 (Ripley 1976, 1981, Haase 1995, Haase et al. 1996, Fortin & Dale 2005). In Ripley's K-function, the number of neighboring colonies within a distance (*t*) of each coral colony is counted; for colonies located near the transect border, an edge correction was applied (Fortin & Dale 2005). To test the null hypothesis that there was a complete spatial randomness in coral distributions along the transects, a number of randomised transects were generated for comparison. These random transects were generated by repositioning all the observed colonies randomly along each transect. For statistical significance (95% CI), the values of the statistic (Ripley's K-function) at the limit of 2.5% of the tails of 99 of these randomizations were used. Should the sample statistic be found within the bounds of the confidence interval at any point, then the null hypothesis could not be rejected. A significantly positive deviated sample statistic indicates a regular (after Lincoln et al. 1982) distribution, whereas a significant negative deviation suggests a contagious (after Lincoln et al. 1982) distribution pattern (Fortin & Dale 2005). To determine the scale of the spatial pattern, three-term local quadrat variance (3TLQV) was calculated (Hill 1973, Dale 1999). Each transect was transformed into a grid of contiguous quadrats (1 × 1.5 m) and species density inside each quadrat was calculated. The 3TLQV examines the average of squared differences

among trios of adjacent block size, by subtracting twice the total of the middle block from the sum of the 2 that surround it. The resulting variance is plotted as a function of block size and peaks are indicative of pattern at that scale (Dale 1999). To identify the more frequent average smaller phase (patch or gap) sizes of the pattern, the two-term form of the new local variance (NLV) was used. As with the 3TQLV, this statistic is applied to a grid of contiguous quadrats obtained from each transect, and peaks in the plot of variance as a function of block size are interpreted as average patch or gap sizes (Galiano 1982, Dale 1999). For a correct interpretation of the results, Ludwig & Reynolds (1988) suggest that 3TLQV and NLV should not be interpreted for block sizes >10% of the transect length in order to maintain reasonable precision (Dale 1999). This limit was applied in this work.

Spatial statistics assume homogeneity of the study area (Ripley 1981, Dale 1999). In the survey region, seabed topography and composition were not homogeneous; nevertheless, we performed the statistical analysis over the entire transect area in order to quantify a selection of the characteristics of the spatial distribution pattern of *Madrepora oculata* colonies (aggregation degree, scale of the pattern, patch and gap sizes). By additionally logging substrate type across each transect, we were able to determine whether any *M. oculata* distribution patterns made evident by the statistical analysis were related to substrate change. On a more local scale, regions of the analysed transects with homogenous substrate were

analysed in detail using the same statistical methods. The aim of this focused study was to assess whether or not, at the local scale, factors other than substrate type (e.g. hydrography, biotic interactions) could play a role in coral distribution patterns. Three ~75 m long transect sections were analysed at this local scale (T1: 428 to 550 m; T2: 84 to 160 m; T3: 205 to 267 m).

The scale of association between *Madrepora oculata* colonies and benthic long-line fishing gears was assessed using the three-term local quadrat covariance (3TLQC) method, which calculated variance as a function of block size for *M. oculata* (Var A) and benthic long-line fishing gears (Var B), and for their combined densities (Var A+B), where Cov = Var A+B – Var A – Var B (Kershaw 1960, Dale 1999). Positions of peaks, whether positive or negative, in produced covariance graphs as a function of block size indicated the scale of any positive or negative association between the coral and the fishing gear (Dale 1999, Fortin & Dale 2005).

RESULTS

Occurrence of CWCs was detected at 15 (68%) of the 22 surveyed locations. Most of these stations were located in the southern flank of the canyon between approximately 180 to 300 m depth (Table 1, Fig. 2).

A total of 528 colonies were recorded in the 3 JAGO transects analyzed (T1, T2 and T3). The most frequent species in all transects was *Madrepora oculata*, which represented 93.7% of total CWC colonies. *Lophelia per-*

Table 1. Location of transects (ROV and submersible JAGO) in the Cap de Creus canyon during the 3 surveys. Analysed JAGO transects (T1, T2 and T3) are shaded

| Date	Vehicle	Position		Depth (m, start–end)	Coral occurrence
		Start	End		
07/10/2005	FALCON Sea Eye (ROV)	42° 22.82N, 3° 17.60E	42° 22.82N, 3° 17.60E	106–105	–
		42° 23.52N, 3° 18.77E	42° 23.26N, 3° 18.70E	193–142	–
08/10/2005		42° 20.67N, 3° 20.86E	42° 20.84N, 3° 19.89E	202–133	+
		42° 18.53N, 3° 23.60E	42° 18.68N, 3° 23.94E	115–119	–
		42° 18.72N, 3° 25.85E	42° 18.35N, 3° 25.54E	197–136	–
09/10/2005		42° 22.84N, 3° 19.62E	42° 23.59N, 3° 18.76E	156–218	+
11/07/2006	Phantom HD2+2 (ROV)	42° 21.76N, 3° 20.54E	42° 22.62N, 3° 19.65E	254–171	+
12/07/2006		42° 23.01N, 3° 19.15E	42° 23.41N, 3° 18.86E	249–251	+
13/07/2006		42° 23.10N, 3° 19.15E	42° 23.26N, 3° 18.88E	224–208	+
14/07/2006		42° 23.36N, 3° 22.29E	42° 23.49N, 3° 21.82E	234–184	+
		42° 23.21N, 3° 23.29E	42° 23.21N, 3° 22.90E	205–212	+
15/07/2006		42° 21.76N, 3° 20.54E	42° 22.62N, 3° 19.65E	220–220	+
08/09/2007	JAGO (manned submersible)	42° 23.10N, 3° 19.14E	42° 23.18N, 3° 18.87E	220–150	–
09/09/2007		42° 23.38N, 3° 18.84E	42° 23.39N, 3° 18.83E	186–190	+
		42° 21.98N, 3° 21.47E	42° 20.97N, 3° 21.58E	390–376	–
10/09/2007		42° 23.21N, 3° 19.01E	42° 23.33N, 3° 18.84E	207–156	+ (T1)
12/09/2007		42° 23.13N, 3° 19.20E	42° 23.20N, 3° 19.26E	252–260	+
13/09/2007		42° 22.71N, 3° 19.75E	42° 22.79N, 3° 19.73E	306–285	+ (T2)
14/09/2007		42° 21.41N, 3° 20.03E	42° 21.39N, 3° 20.04E	235–235	+
15/09/2007		42° 22.14N, 3° 20.28E	42° 22.27N, 3° 20.20E	295–256	+ (T3)
		42° 23.60N, 3° 18.90E	42° 23.43N, 3° 18.79E	285–150	+
16/09/2007		42° 24.04N, 3° 19.48E	42° 24.08N, 3° 19.33E	125–160	–
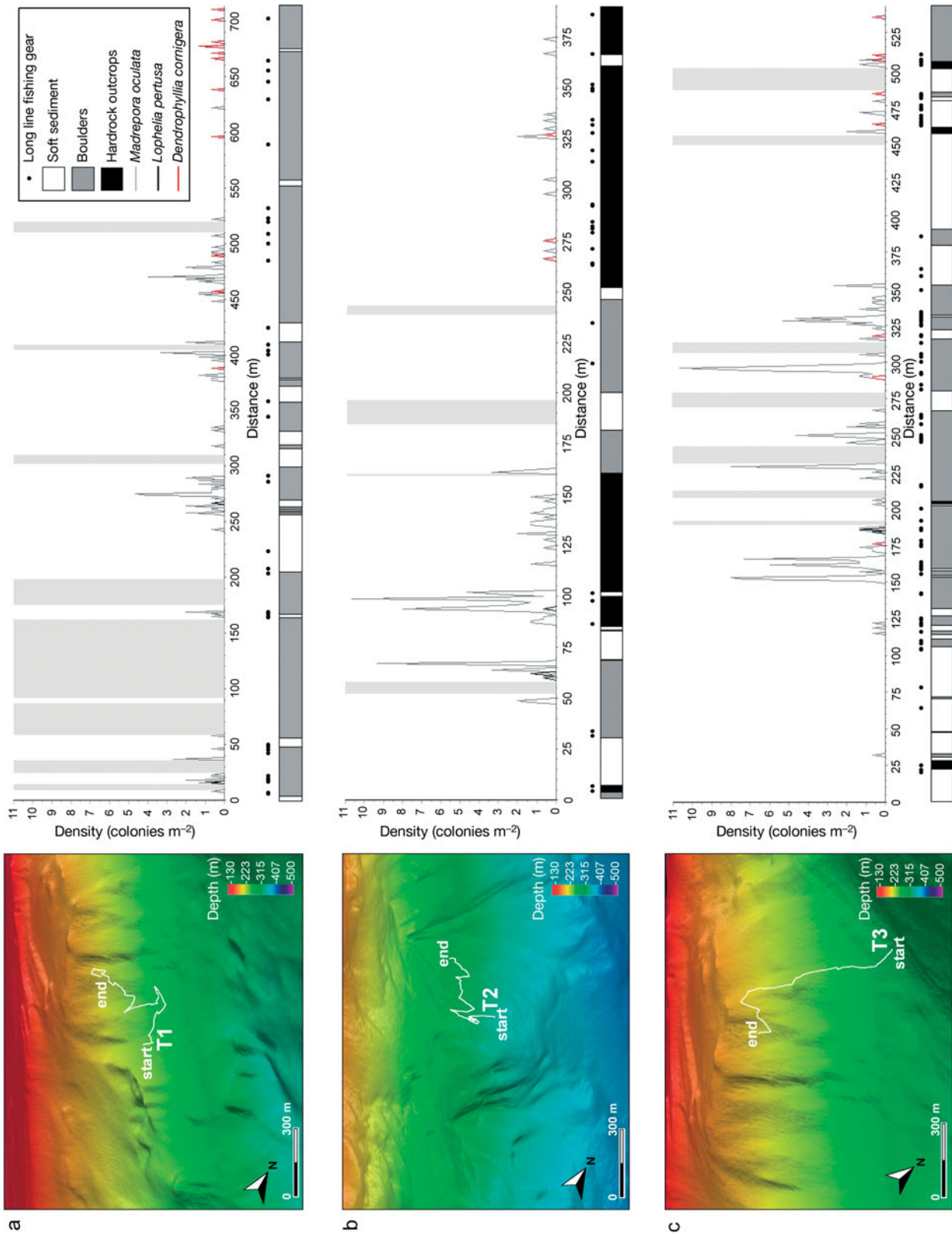
Fig. 3. *Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera*. Left: 3D plots indicating the location of the 3 anayzed video tracks (a: T1, b: T2, c: T3). Right: coral density plots and detection of benthic long-line fishing gears (black dots) and corresponding substrate types (soft sediment, rocky boulders and hardrock outcrops) along these transects. Vertical grey bars indicate locations of video sequences where image quality was not sufficient for interpretation
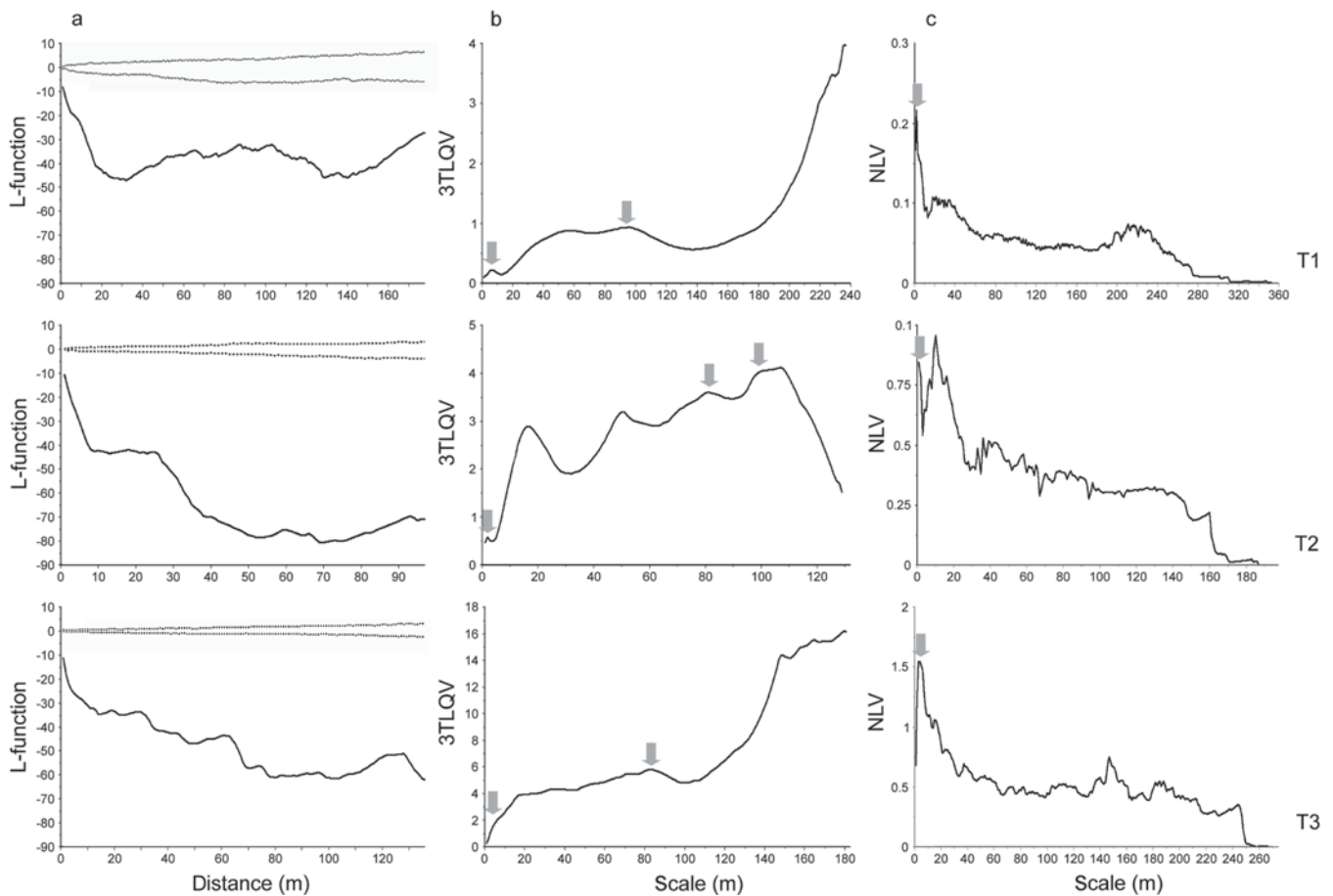
Fig. 4. *Madrepora oculata*. Spatial statistics for transects T1, T2 and T3. (a) L-function (Ripley's K); values below 95 % CI (dotted lines) indicate a statistically significant contagious distribution. (b) Three-term local quadrat variance 93TLQV) as a function of scale (block size); arrows indicate the scale of the spatial pattern coincident for the 3 transects. (c) New local variance (NLV) as a function of scale (size of the smaller phase of the pattern); arrows indicate the most frequent patch sizes for all transects

tusa (1.7 % total CWC colonies) and *Dendrophyllia cornigera* (4.6 % total CWC colonies) were less common (Table 2). Presence of *M. oculata* was 1 order of magnitude higher in areas with hard substrate bottom types, i.e. boulders (0.44 ± 0.33 [SD] colonies m^{-2}) and hardrock outcrops (0.41 ± 0.40 colonies m^{-2}), than in regions with soft bottom substrates (0.07 ± 0.09 colonies m^{-2}). *L. pertusa* was only observed on boulders (0.01 ± 0.01 colonies m^{-2}). *D. cornigera*, although more commonly found on boulders (0.02 ± 0.01 colonies m^{-2}), was also observed on hardrock outcrops (0.005 ± 0.01 colonies m^{-2}).

Although densities of *Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera* varied between species, the densities for each species did not vary much between transects (Table 2, Fig. 3). *M. oculata* was the CWC present in highest density across the 3 transect regions, varying from 0.11 ± 0.44 to 0.30 ± 0.44 colonies m^{-2}, with maximal values of 10.67 colonies m^{-2}. *D. cornigera* density was much lower than *M. oculata* across all transects, varying only moder-

ately between transects, from 0.01 ± 0.09 to 0.01 ± 0.67 colonies m^{-2}, with a maximal value of 1.33 colonies m^{-2}. *L. pertusa* was observed to have the lowest and most variable density between transects, from 0.002 ± 0.035 to 0.01 ± 0.08 colonies m^{-2}, with a maximal value of 1.33 colonies m^{-2}. The low densities of *L. pertusa* and *D. cornigera* (Table 2, Fig. 3) rendered the spatial statistics inapplicable; thus a detailed analysis on the aggregation degree and spatial patterns was conducted only for *M. oculata*.

The distribution of *Madrepora oculata* was significantly different from complete spatial randomness in all transects and at all scales. The significant negative deviation from randomness, after applying Ripley's K-function, indicated a contagious distribution of *M. oculata* colonies (Fig. 4a).

The 3TLQV analysis showed several scales in the spatial pattern of *Madrepora oculata* colonies (Fig. 4b). Some scales of spatial pattern were detected in all transects (<5 m and ~80 to 90 m). In transects T2 and
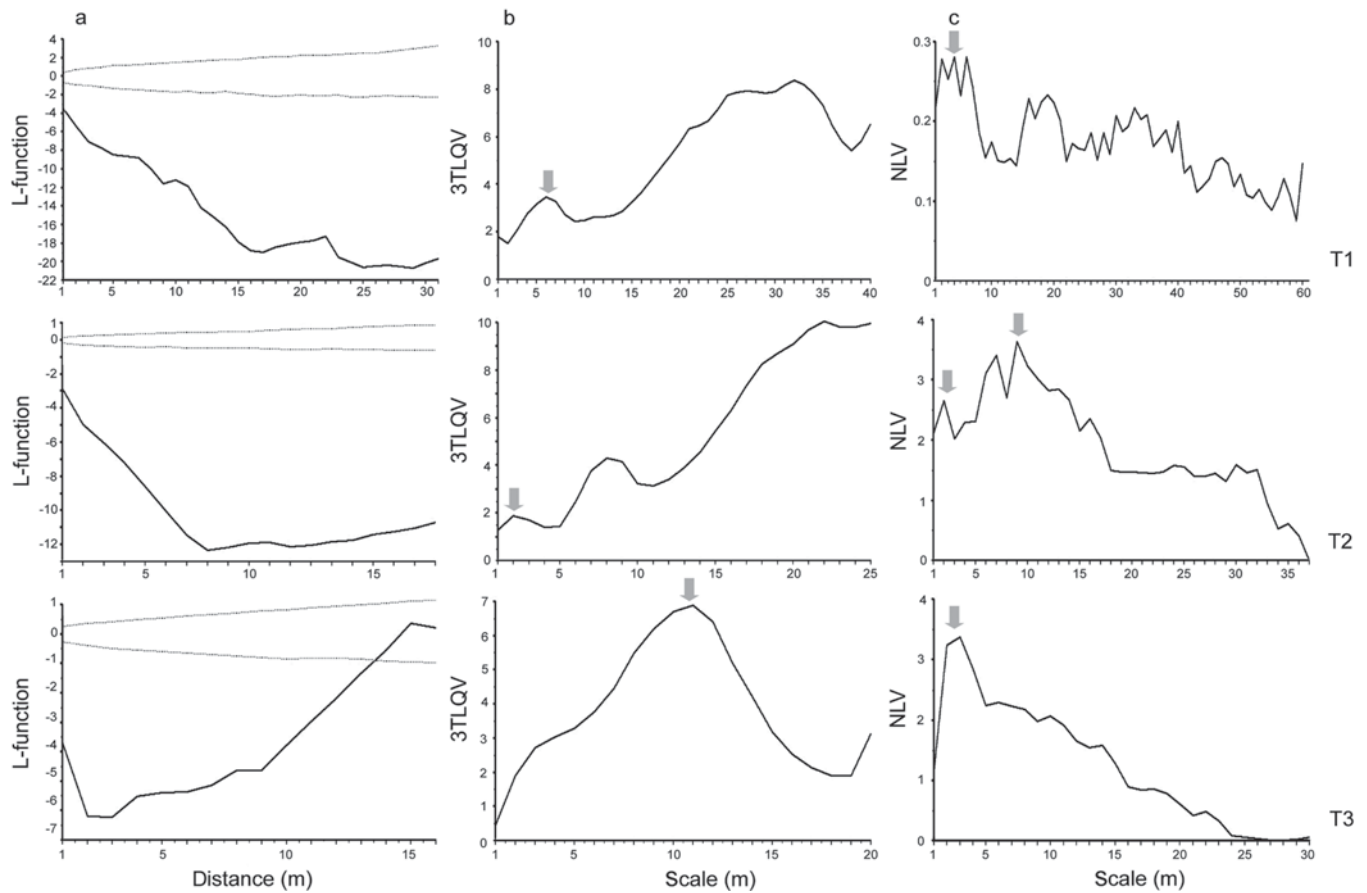
Fig. 5. *Madrepora oculata*. Spatial statistics across selected sections of transects with homogenous substrate: T1 (428 to 550 m), T2 (84 to 160 m) and T3 (205 to 267 m). (a) L-function (Ripley's K), scale represents fragment distance; values below 95% CI (dotted lines) indicate a statistically significant contagious distribution. (b) Three-term local quadrat variance (3TLQV) as a function of scale (block size of the aggregation pattern); arrows: the main aggregation levels for each transect. (c) New local variance (NLV) as a function of scale (size of the smaller phase of the pattern); arrows: the most frequent patch sizes for each transect

T3 intermediate scales (at ~20 m and ~100 m) were detected, whereas in transects T1 and T2 a further pattern scale was found at ~50 m (Fig. 4b).

In the 3 transects there was a clear sharp peak in the NLV plot at around 2 to 5 m, indicating that the most common patches were small (Fig. 4c). However, all transects showed secondary small peaks which corre-

Table 2. *Madrepora oculata*, *Lophelia pertusa* and *Dendrophyllia cornigera*. Mean ± SD (maximal) density for the 3 studied species. T: transect

| | Density (colonies m^{-2}) | | |
	T1	T2	T3
M. oculata	0.11 ± 0.44 (4.67)	0.23 ± 0.99 (10.67)	0.30 ± 1.14 (10.67)
L. pertusa	0.002 ± 0.035 (0.67)	0.01 ± 0.08 (1.33)	0.004 ± 0.06 (1.33)
D. cornigera	0.01 ± 0.09 (1.33)	0.01 ± 0.06 (0.67)	0.01 ± 0.09 (0.67)

sponded to subsequently defined patch sizes, indicating a range of patch sizes in this species.

The distribution of *Madrepora oculata* was also found to be contagious in the small-scale analysis plots representing the homogenous substrate regions of each transect (Fig. 5a). The 3TLQV analysis showed several small scales in the spatial pattern of *M. oculata* colonies (between 2 and 11 m) (Fig. 5b), with some of these scales being coincident with the smallest scales identified in the whole transects (Fig. 4b). Furthermore, the results obtained for the NLV analysis of each of these small homogenous regions was also coincident with the results generated for each whole transect, i.e. the most dense patch sizes are also small (between 2 and 10 m) (Fig. 5c).

A total of 197 benthic long-line fishing gears were recorded across the 3 transects, with an average of 0.06, 0.09 and 0.22 lines m^{-1} at each transect, respectively. The 3TLQC plots showing spatial covariation in *Madrepora oculata* and benthic long-line fishing gear occurrence across the transects is shown in Fig. 6. At a
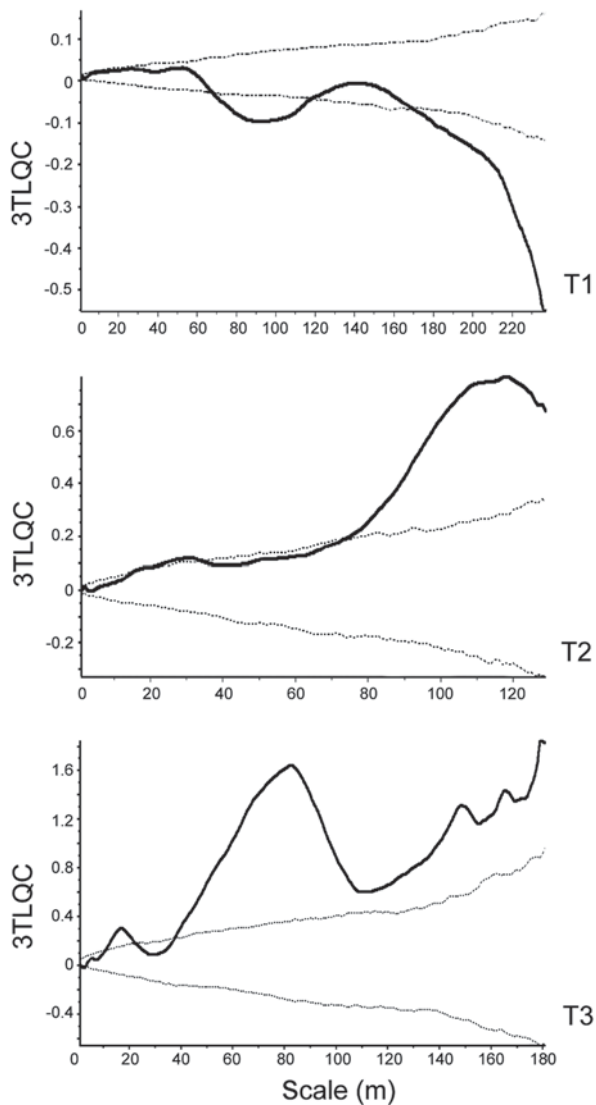
Fig. 6. *Madrepora oculata*. Three-term local quadrat covariance (3TLQC) for *M. oculata* and benthic long-line fishing gear occurrence in the 3 analysed transects (T1, T2 and T3). Values outside 95% CI (dotted lines) indicate a statistically significant spatial covariance. Scale represents the block size

scale of meters, the pattern is random across the 3 transects. At scales of 10s of m (20 to 80 m), the covariance is positive across transects T2 and T3 implying that at this scale, coral occurrence correlates with benthic long-line fishing gear occurrence. In contrast, transect T1 shows a negative covariance at this scale, indicating that wherever corals are present, benthic long line fishing gears are likely to be absent and vice versa.

Some other anthropogenic impacts were sporadically observed and thus counted in the analysed videos: a Roman amphora, a fragment of a fishing net and a plastic fragment.

DISCUSSION

CWC occurrence in the Cap de Creus canyon

CWCs are the most conspicuous animal group in the hard substrate regions of the Cap de Creus canyon flanks. The predominant presence of CWCs in the southern flank of the canyon is directly related to the broad areas of hardrock outcrops and steep walls. Furthermore, this side of the canyon (Fig. 2) is characterized by the arrival of recurrent dense shelf water cascades during winter (Puig et al. 2008), as described in 'Materials and methods'. Therefore, coral occurrence in this area seems to be related to: (1) the energetic current flows carrying periodically nutritive particles in suspension from the shelf environments (Canals et al. 2006) and (2) the reduced sediment accumulation rates caused by the cascading process (DeGeest et al. 2008); both aspects (hydrodynamics and/or food supply, sedimentation pressure) have been documented as determining factors in CWC occurrence in other systems (e.g. Frederiksen et al. 1992, White et al. 2005). Contrary to the erosional features of the southern flank of the canyon, the northern flank is marked by features indicating a prevailing depositional regime with high sedimentation rates (rounded gullies and smoothed scars). These high sediment accumulation rates have resulted in the scarce occurrence of rocky substrates (DeGeest et al. 2008). This is probably the cause of the scarce presence of CWCs on the northern flank. Former observations indicate that scleractinians occur in areas where the interaction between currents and topography can generate high-speed flow (e.g. Frederiksen et al. 1992, White et al. 2005, 2007, Grasmueck et al. 2006, Dorschel et al. 2007, Mienis et al. 2007), which both helps to remove excess sediment and also supply food and larvae (Grigg 1984).

Consequently, even if available substrate is one of the main determining factors of the distribution pattern of *Madrepora oculata* within the canyon, the current regime could play as large a role. This is more likely when the episodic cascading events, or the presence of near-inertial internal waves at the shelf edge of the Gulf of Lions (Millot & Crépon 1981), are taken into account. Although internal waves do not contribute to the main off-shelf sediment transport through the Cap de Creus canyon (Palanques et al. 2008), this hydrographical phenomenon can periodically control the resuspension, advection and mixing of turbid shelf water into the canyon heads (Ogston et al. 2008). This resuspension of light organic matter aggregates by internal waves could provide additional food supply to corals (Frederiksen et al. 1992).

Madrepora oculata distribution pattern in the Cap de Creus canyon

There is a clear relationship between substrate and *Madrepora oculata* density, with the highest *M. oculata* densities being found in regions with hard substrates (Fig. 3). The other 2 studied corals, *Lophelia pertusa* and *Dendrophyllia cornigera*, were present only in the hard substrate areas. This relationship between substrate type and CWC occurrence has been observed elsewhere (Rogers 1990, Davies et al. 2008).

Contagious distributions are common among benthic organisms and, as is found with terrestrial plants, are more common than regular distributions, with random distributions rarely found (Kershaw 1958). The contagious distribution pattern of *Madrepora oculata* in the Cap de Creus canyon (Figs. 4 & 5) is probably the result of interactions between several factors (both physical and biological) with the presence of a hard substrate (boulders and outcrops), high hydrodynamic regime (both the current regime and episodic cascading events) and high nutrient delivery the most significant in determining distribution. Food supply has been observed as an important factor in influencing patch distribution in the deep sea: Grassle & Grassle (1992) and Grassle & Morse-Porteous (1987) argued that localized concentrations of food (such as phytodetritus pulses from surface blooms) and carcass falls are important patch food structures in the deep sea, greatly boosting food availability in areas with a low background productivity. Duineveld et al. (2004) also documented the importance of the food supply from surface waters in understanding local diversity and density in seamounts and deep coral banks.

The observed spatial distribution pattern for *Madrepora oculata* in the Cap de Creus canyon is unbalanced when considering the transects as a whole. Large periodic gaps in *M. oculata* dominate the 3 transects (see Fig. 3), with these gaps mainly correlating with changes in substrate. However, the spatial analysis carried out in the transect regions with homogenous substrate also present contagious *M. oculata* distribution patterns (Fig. 5). For these regions, in which substrate cannot be a factor in determining the distribution pattern, other aforementioned factors (such as current regime and food supply) are most likely responsible for the observed pattern.

After the 3TLQV and the NLV results, we identified 2 common scales within the *Madrepora oculata* distribution pattern across the 3 transects (<5 m and ~80 to 90 m) (Figs. 4b,c & 5b,c). This observation of very similar distribution patterns across the 3 transects suggests that they are likely to be representative of the southern flanks of the Cap de Creus canyon as a whole. However, the identification of other scales of pattern in some of the transects (15, 25, 150 and 215 to 220 m) (Fig. 4b) indicates a degree of local variability.

The smallest scale of pattern found in the canyon corresponds to the smallest patch sizes of *Madrepora oculata* observed in the transects (<5 m). These small patches may be due to: (1) settlement on non-optimal substrate (e.g. on small pebbles in a soft-bottom dominant substrate), (2) patchiness of food or (3) the reproduction strategy of the species. Following the reasoning of Greig-Smith (1961), for gorgonian distributions the dominant patch size (which *for M. oculata* within the canyon is <5 m) represents the spatial scales at which the major ecological process controlling shallow-water gorgonian communities is most fully developed. In the case of the gorgonians studied by Yoshioka & Yoshioka (1989), visual inspections of the habitat suggested that patch sizes correspond to the predominant scales of topographic elevations. Even if the topographical variation was relatively small, involving differences in relief of only a few centimetres, they observed a dramatic effect on gorgonian abundances. A similarly significant change in distribution associated with a minor change in a controlling factor could be expected for the coral species in the present study.

The convex shape of most *Madrepora oculata* patches (Fig. 3) indicates that the highest densities occur in the middle of each patch. This is probably related to active growth of the patches and/or outward expansion. Patches are hydrodynamically significant, reducing current flow within and surrounding the patches, thus increasing the local residence time of particles in suspension. This increased residence time allows local organisms (predominantly the CWCs in this case) longer to capture them (Gili & Coma 1998). Another major factor in determining benthic organism patch size and enlargement rate is strategy of larval dispersal (Lissner et al. 1991). *Lophelia pertusa* and *M. oculata* are observed to be most commonly seasonal broadcasters, with direct release of the gametes into the water column, probably over a limited time period (Brooke & Young 2003, Waller & Tyler 2005). However, recent observations of the presence and survival of *L. pertusa* larvae in aquaria showed a survival time of 7 wk, but an increase in mortality after about 4 to 5 wk, prior to which settlement had not been observed (T. Lundälv pers. comm.). This live larval period exceeds that observed for the CWC *Oculina varicosa*, where ~20 live days has been observed (Brooke & Young 2003). The ecological significance of such 'long-life' larva is high, as the larvae could be transported via benthic currents to locations far from the parental colonies, allowing colonization over significant distance. Rogers (1999) pointed out that larval dispersion should play a paramount role in the degree of spread-

ing of CWC species, as observed in the Stylasterines where the short-lived larvae (produced by both shallow- and deep-water Stylasterines) and their planulae settle close to the parent colonies (Fritchman 1974, Ostarello 1976, Brooke & Stone 2007), determining the population structure as well as the dispersal patterns. This pattern has also been observed in several species of anthozoans (Fautin 2002). In the present study, the presence of isolated colonies (10s of m between) could reflect either the remains of larger colonies (after possible environmental or anthropogenic perturbations) or more recent pioneer colonies (produced sexually or asexually) entering the area. Moreover, it is known that asexual reproduction (fragmentation) is likely to play an important role in scleractinians (Highsmith 1982).

The observed gaps in *Madrepora oculata* coverage of areas with rocky substrate could also be the result of natural perturbations, such as corals breaking under heavy flow or excessive growth, or of anthropogenic impact. The large quantity of benthic long-line fishing gear found within the canyon indicates that the seabed is periodically exposed to dragging lines (Fig. 3). The 3TLQC analysis did not show a clear pattern in the relationship between benthic long-line fishing gear distribution on the seabed and coral density (Fig. 6); however, at a scale of 10s of m in transects T2 and T3 there is a degree of relationship between benthic gear occurrence and coral density. This is perhaps best explained by the larger coral-covered hard substrate regions snagging the long-lines more effectively than the soft sediment or coral-free seabed areas. This entanglement is not uncommon and can be seen in Fig. 7b,d. In T1, however, at a scale of 10s of m, a negative correlation between corals and benthic lines can be
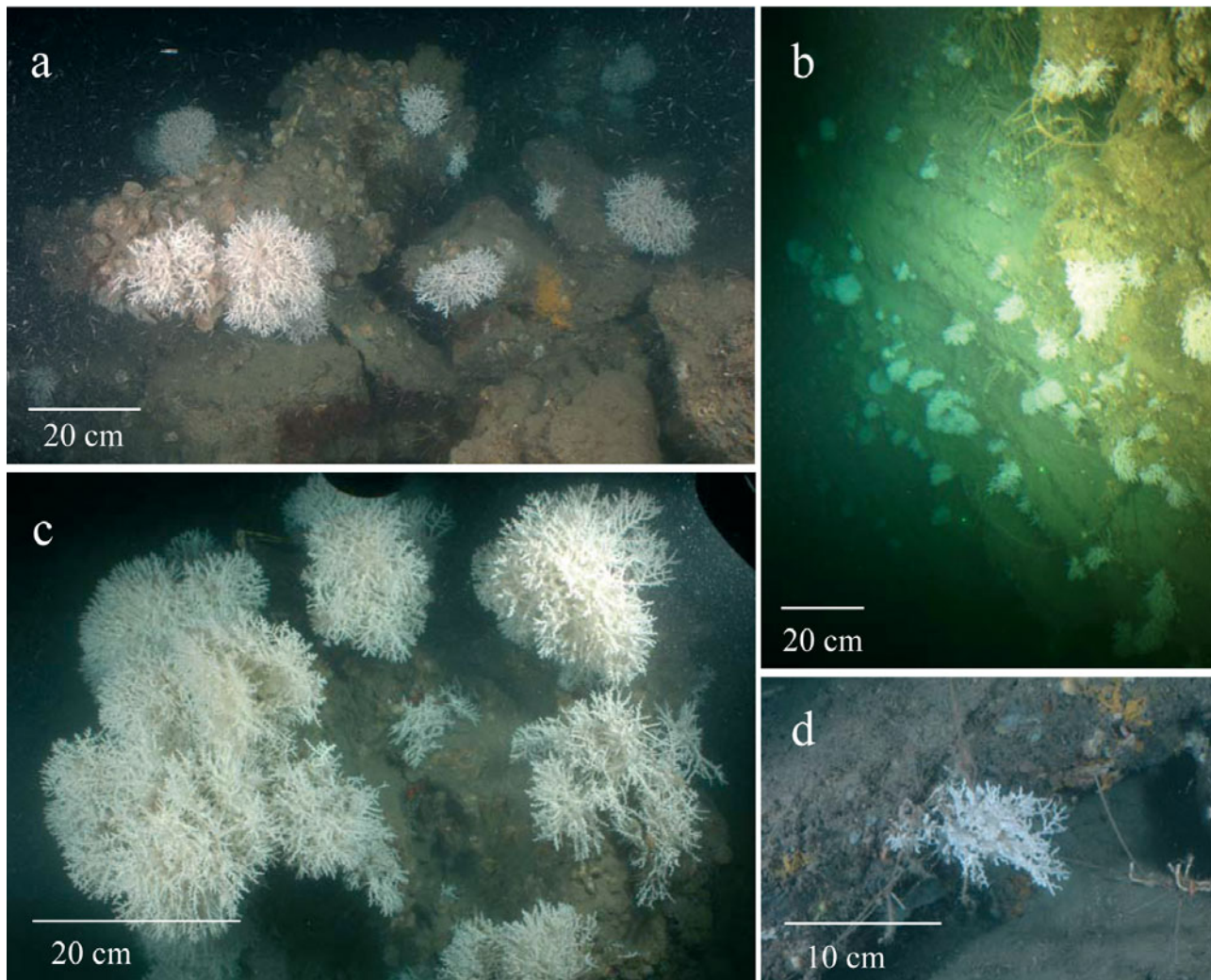

Fig. 7. *Madrepora oculata.* Coral colonies on the southern flank of the canyon (a) growing on boulders at 250 m depth; (b) on a rocky outcrop at 300 m depth; (c) dense populations on boulders at 250 m depth; (d) entangled in long-line fishing gear at 200 m depth

seen (Fig. 6); it is therefore difficult to present any firm conclusions about the potential threat of benthic longline fishing gears to the corals in this area. However, further investigations should be carried out in more canyon locations to explore the possible relationship between coral occurrence and lost fishing equipment, particularly as this type of fishing has been observed to have a negative impact on CWC communities in other areas (Lumsden et al. 2007).

CWC in the Mediterranean Sea

Madrepora oculata is the dominant CWC in the Cap de Creus system. This is in contrast with dominances found in other better documented CWC ecosystems, such as on the NE Atlantic shelf where *Lophelia pertusa* is the dominant species, or the NW Atlantic where *L. pertusa* and *Oculina varicosa* are most dominant (Reed 1992, Breeze et al. 1997, Fosså et al. 2000, Gass 2002). CWC ecosystems elsewhere in the Mediterranean Sea are mostly dominated by *M. oculata* and *L. pertusa* (Pérès & Picard 1964, Pérès 1982, Tursi et al. 2004, Taviani et al. 2005a, Freiwald et al. 2009); however, a dominance of *M. oculata* has been reported in some regions, such as off Thassos (Freiwald et al. 2009), Santa Maria di Leuca (Taviani et al. 2005a, Freiwald et al. 2009) and Malta (Freiwald et al. 2009).

By comparing the results of the present study with published papers on *Madrepora oculata*-dominated CWC banks within the Mediterranean (Tursi et al. 2004, Taviani et al. 2005a, Freiwald et al. 2009), the populations found in the southern flank of the Cap de Creus canyon seem to comprise one of the most developed *M. oculata*-dominated ecosystems. This is supported particularly by the density data (Table 2, Fig. 3) and photographs of some locations within the Cap de Creus canyon (Fig. 7).

The presence of *Lophelia pertusa* (which was first discovered alive in the Mediterranean as recently as 2000, Tursi et al. 2004) in these communities is very scarce (Table 2, Fig. 3). This is true for other CWC sites in the east and central Mediterranean (Tursi et al. 2004, Taviani et al. 2005a,b, Freiwald et al. 2009). The reasons for these low densities of *L. pertusa* in the Mediterranean (limited to some isolated colonies in the Cap de Creus canyon) is still unknown. Nevertheless, it is likely that the living white coral biocoenosis in the Mediterranean Sea consists of relicts from past flourishing times (Pérès & Picard 1964, Pérès 1982). The most likely causes of the dramatic decrease in occurrence of Mediterranean CWCs have been attributed to the major changes in oceanographic and geologic conditions which occurred during the Holocene sea level rise (Pérès 1982, Delibrias & Taviani 1984). During the start of the Holocene sea level rise, changes in climatic conditions produced a strong increase in Mediterranean water temperatures, modifying the environmental conditions that were present and favourable to CWCs during the last glacial maximum (Delibrias & Taviani 1984) to those less favourable. Based on ^{14}C dating, Delibrias & Taviani (1984) estimated that the major decline of CWC abundance in the Mediterranean Sea took place during the period ranging from 30 to 15 kyr BP. Other researchers have suggested different dates: McCulloch et al. (2006) dated the demise of CWCs in the Mediterranean to the end of the Younger Dryas (10.5 kyr BP), which was a cool period occurring during the last sea level rise and characterized by more glacial-like conditions. At the end of the Younger Dryas, the combined effect of a rapid 6 to 8°C rise in ocean temperatures and high sediment influx from river discharge by glacial melt water pulses may have promoted the CWC recession (McCulloch et al. 2006).

The idea that homoeothermic conditions within the Mediterranean Sea are responsible for the general scarcity of CWC communities is given support by the documented *in situ* temperature tolerance limits for *Lophelia pertusa*, which range from 4 to 13°C (Freiwald 2002). This means that *L. pertusa* within the Mediterranean is living close to its upper temperature limit. In the Cap de Creus canyon, the maximal documented temperature peak recorded at 300 m water depth is 15.5°C (Palanques et al. 2006). Temperature tolerance seems to be wider for *Madrepora oculata*, which is able to function at temperatures up to 20°C (Keller & Os'kina 2008). The low abundances of *Dendrophyllia cornigera* in the Cap de Creus canyon are not surprising, as this species is not reef-forming and the densities we found agree well with previous observational records in other regions (Le Danois 1948), although recent research documented that *D. cornigera* could reach high densities in some locations (Sánchez et al. 2009). However, new data showed that CWCs also existed during the Holocene in the Mediterranean Sea (Ruggeberg et al. 2008). In Wienberg et al. (2009), the authors discuss the temperature and current speed tolerances of *M. oculata*, *L. pertusa* and *D. cornigera* in the Gulf of Cadiz during the interglacial and glacial periods. They found that both *M. oculata* and *D. cornigera* coped better with temperature and flow rate changes than *L. pertusa*.

In conclusion, this new insight in the distribution of CWCs in the Cap de Creus canyon in the northwest Mediterranean, and the high densities reported in the southern flank of the canyon, will be of significant use in planning future marine protected areas and management measures in order to preserve the CWC communities in this area.

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