

Spatial distribution patterns of the soft corals *Alcyonium acaule* and *Alcyonium palmatum* in coastal bottoms (Cap de Creus, northwestern Mediterranean Sea)

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Abstract Current knowledge on the abundance and distribution patterns of different soft coral species is relatively limited when compared to other benthic suspension feeders such as gorgonians and hard coral species. To overcome this scarcity of information, the distribution patterns of the soft corals *Alcyonium acaule* and *Alcyonium palmatum* were investigated in northwestern Mediterranean benthic communities over a wide geographical (60 km of coastline) and bathymetrical (0–70 m depth) extent using a remotely operated vehicle. *A. acaule* was the most abundant species in the study area with highest recorded density of 18 col m⁻² found at depths of 35–45 m in areas that are

directly exposed to strong near-bottom currents. Conversely, *A. palmatum* was only found as scattered solitary colonies at greater depths in soft bottoms, with maximum density of 2.4 col m⁻². Medium and large colonies of *A. acaule* were preferentially found on sloping and vertical rocky bottoms where they form dense patches. High-density patches of *A. acaule* were preferentially found on vertical rocky bottom, while isolated colonies were preferentially observed on coralligenous substrata as well as on flat soft and maërl substrates. *A. acaule* biomass distribution showed highest values between 40 and 45 m depth, and between 60 and 65 m depth. This suggests that deeper populations are formed by colonies that are bigger than the equivalent shallower ones. Although both species are almost genetically identical, ecologically they are very different. For this reason, conservation plans should consider the differential ecological traits shown by these two soft coral species.

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Introduction

Benthic suspension feeders play an important role in increasing habitat complexity and biodiversity in costal areas and continental margins (Gili and Coma 1998; Buhl-Mortensen et al. 2010). Knowledge of the abundance, distribution patterns, and population ecology of gorgonian (e.g. Kinzie 1973; Yoshioka 1994; Mortensen and Buhl-Mortensen 2004; Watanabe et al. 2009; Gori et al. 2011a) and hard coral species (e.g. Edmunds 2000; Freiwald et al. 2009; Orejas et al. 2009; Rooney et al. 2010) have increased considerably during the last decades. However, less information is currently available about the distribution patterns of soft corals. In tropical areas, soft corals represent a significant part of the total biomass of the

benthic communities (e.g. Benayahu and Loya 1981, 1987; Dinesen 1983; Riegl and Piller 1999), and high abundances of soft corals have also been found in both Polar regions with percentage cover of substrata of up to 75 % (Slattery and McClintock 1995; Slattery and Bockus 1997; Slattery et al. 1997; Post et al. 2011). In other areas, especially in temperate seas, the scarce available data in the literature seems to indicate low cover values (e.g. Atlantic Ocean, Heifetz 2002; Watling and Auster 2005).

In the Mediterranean Sea, *A. acaule* (Linnaeus, 1878) and *Alcyonium palmatum* (Pallas, 1766) can be considered the most abundant soft coral species (Sarà 1969; True 1970; Gili and Ballesteros 1991). Although both species are genetically and morphologically very similar (McFadden et al. 2001), they exhibit different ecological traits (Hartnoll 1977; McFadden 1999). *A. acaule* is known to dwell on hard bottoms from 10 m to at least 45 m depth (Weinberg 1977) and is one of the key ecosystem engineers in the Mediterranean coralligenous community, where it constitutes the intermediate level between encrusting species and erected gorgonians (Ballesteros 2006). *A. acaule* is a long-lived species characterized by low growth rates (Garrabou 1999; Teixidó et al. 2011). Due to the probable lack of asexual reproduction in such species, sexual reproduction with surface brooding of the larvae appears to be the only way local populations can be maintained (Garrabou 1999; Fiorillo et al. 2012). *A. palmatum* is found on soft bottoms from 20 to 200 m depth, fixed to the ground with its sterile stalk on shells, pebbles, or small stones (Weinberg 1977; Gili et al. 1987). This species shows broadcast spawning, so its gametes are directly released into the water column where fertilization takes place (McFadden 1999).

In the last decade, our understanding of shallow (<40 m, e.g. Gili and Coma 1998; Rossi et al. 2006; Ribes et al. 2007; Linares et al. 2008) and deep (>150 m, e.g. Orejas et al. 2009; Bo et al. 2009; Vertino et al. 2010) assemblages of benthic suspension feeders in the Mediterranean Sea has improved substantially as a result of traditional SCUBA diving research and the use of remotely operated vehicles (ROVs) and manned submersibles. However, little attention has been given to the assemblages dwelling at intermediate depths between 40 and 150 m (Gori et al. 2011a). Although video image sampling can never be as precise as studies based on SCUBA diving (Gili and Ballesteros 1991; Virgilio et al. 2006), this methodology allows for surveys over large spatial and bathymetrical extents especially with easily recognizable species (such as *A. acaule* and *A. palmatum*) and significantly minimizes the impacts produced over sessile organisms (Ninio et al. 2003; Matarrese et al. 2004; Rossi et al. 2008). Recently, a few studies using ROVs have provided quantitative information on Mediterranean octocoral assemblages between 40 and

200 m depth (Rossi et al. 2008; Bo et al. 2009, 2011; Gori et al. 2011a, b). These studies demonstrate that many species of gorgonians form deep sublittoral populations that are often denser than their equivalent shallow populations (Bo et al. 2009, 2011; Gori et al. 2011a, b). Furthermore, studies in tropical seas highlight the importance of mesophotic coral ecosystems located at 40–150 m depth, being more productive and rich than previously thought, and significantly different from their shallow-water counterparts (Bongaerts et al. 2010; Kahng et al. 2010).

In order to embrace a complete characterization of the distribution and ecology of benthic suspension feeders, it is essential that current research accounts for the whole bathymetric range of species' distributions. In fact, abundance, distribution patterns, demographic traits, biomass, genetic connectivity, and trophic and reproductive ecology may differ in shallow and deep populations (Rossi et al. 2008; Bo et al. 2009; Constantini et al. 2011; Gori et al. 2011b, 2012). This kind of extensive approach is also important for the establishment of management and conservation plans inside and outside marine protected areas, especially in soft-bottom communities that are suffering the destructive effects of different benthic fishing gears (e.g. bottom trawling and benthic long-lines, Thrush and Dayton 2002). Not surprisingly, a high percentage of the bycatch species produced by these fishing techniques are megabenthic soft-bottom species such as *A. palmatum* (Mallol 2005).

The aims of the present study are (1) to quantify the occurrence and abundance of the two most important soft coral species of the western Mediterranean benthic communities over a large geographical (60 km of coastline) and bathymetrical (0–70 m depth) extent, (2) to explore the variation of biomass of *A. acaule* along the entire bathymetrical range, and (3) to assess the possible ecological relationships between abundance and colony size of *A. acaule* and bottom features to provide baseline data for efficient management and conservation policies in coastal areas.

Materials and methods

Study area

The study area is located in the north-western region of the Western Mediterranean Sea, in the southernmost part of the Gulf of Lions (Cap de Creus, 42°19'12"N; 003°19'34"E; Fig. 1). A general east-to-west water circulation occurs in the area due to the Northern Current, which flows in a NE to SW path along the shelf-break (Millot 1990; DeGeest et al. 2008). The northern winds (Tramuntana and Mistral),

dominant in winter months, reach speeds up to 10 m s^{-1} and occur 41 and 28 % of the year, respectively (Ulses et al. 2008). Both wind regimes transport coastal water and suspended sediments towards the south-west (DeGeest et al. 2008; Ulses et al. 2008). According to these characteristics and the specific features of Cap de Creus (see Fig. 1), the study area was sub-divided into seven sub-areas (A to G). The southern coast (sub-area A) is the most sheltered section with respect to the dominant winds, whereas the eastern coast of the cape (sub-areas B, C, and D) is only affected by the less frequent south-easterly and easterly marine winds, which occur <6 % of the time (Ulses et al. 2008). The north face of the cape (sub-areas E and F) is directly exposed to the main winds and wave action in the area (Ulses et al. 2008) as well as to strong near-bottom currents, which accelerate around the cape (DeGeest et al. 2008). Conversely, the northern coast (sub-area G) is partially sheltered from the direct influence of this current, and depositional processes predominate in this area (DeGeest et al. 2008).

Sampling procedure

A total of 76 video transects perpendicular to the coastline were recorded during 21 days of fieldwork between October and November 2004. Transects were video

recorded with the ROV Phantom XTL equipped with a SONY FCB S3000P 3CCD camera (700 horizontal lines), a depth sensor, a compass, and two parallel laser beams that provided scale to define a fixed width of the transects (0.5 m) for subsequent video analysis. Videos were recorded on videotapes in DV format. Each transect was recorded starting from the deepest point and proceeding towards the coastline with a constant speed of approximately 0.4 knots. The initial depth of each transect varied between 12 and 71 m depending on the geographical characteristics of each location. Maximum depth assessed in this study was selected to cover almost the entire sub-littoral zone in the study area, from the littoral to the start of the continental shelf. Transect length ranged between 92.6 and 907.1 m, and a total distance of 28.3 km along the seabed was recorded (see Gori et al. 2011a, b; Sardà et al. 2012 for further details).

Video analysis

All footage was digitalized prior to its analysis, transferring all the information from tape to hard discs, and video analysis was performed using Apple's Final Cut Pro software. Sequences where the ROV was not moving were discarded in order to correctly estimate the total length of each transect, assuming a constant speed. The first step to quantitatively analyse the valid footage was to identify the sequences where image quality was poor due to bad visibility or distance from the bottom. The remaining useful sequences comprised 86.1 % of the total recorded material, which corresponded to a total distance of 24.5 km and an area of approximately 12.2 km^2 . Starting from the beginning of each transect, sampling units of 2.5 m^2 (0.5 m width and 5 m long) were defined along each transect. Non-useful sequences due to bad visibility or distance from the seabed were discarded from the analysis. The sampling unit area of 2.5 m^2 was chosen using the minimal area proposed by Weinberg (1978) based on species–area curves, who estimated that a sample size of 2 m^2 should be considered large enough to sample for sessile invertebrates in the rocky coralligenous community of the Mediterranean Sea.

A total of 4559 useful sampling units were obtained from the 76 transects. In each of these units, the abundance of the target species was assessed by means of counting the number of colonies of *A. acaule* and *A. palmatum*. Furthermore, colony size, seabed substrate type, and seabed slope were recorded only for a subsample of the observed *A. acaule* colonies for which all these variables could be clearly determined from the video images. Maximum height and number of fingers (Weinberg 1977) were used as a proxy for colony size. The seabed substrate types were classified into the following categories: soft bottoms (mud,

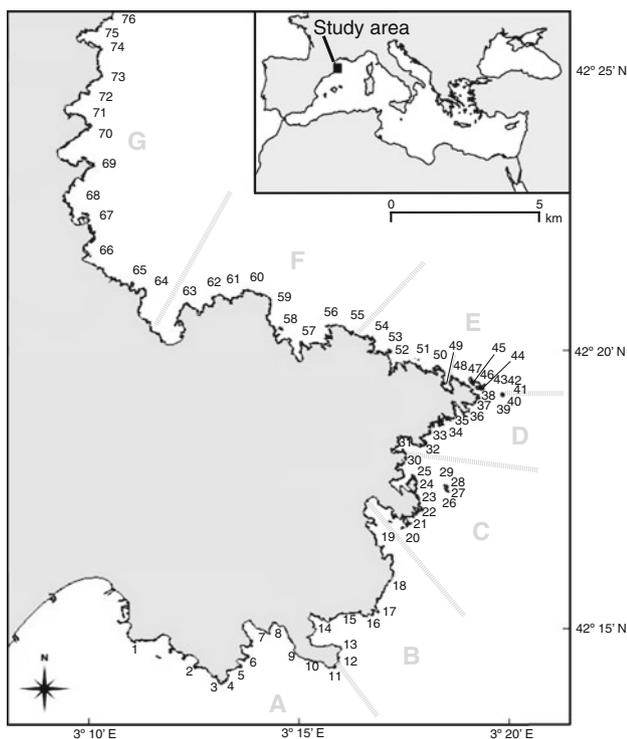


Fig. 1 Map of the study area showing the study sites and the seven selected sub-areas (A–G)

sand, and detritic), maërl (species of coralline algae growing loosely in beds of fragmented nodules), pebbles, rock, and coralline rock (Sardá et al. 2012). The seabed slope was classified as flat (0° – 30°), sloping (30° – 80°), or vertical (80° – 90°). The slope was estimated by looking at the distance between the two parallel laser beams on the video screen and the depth sensor data (further details in Gori et al. 2011a).

Data treatment

The presence of the target species was quantified both by occupancy (frequency of occurrence in the set of sampling units) and by abundance (number of colonies per sampling unit). The spatial distribution of each species was studied by mapping the density observed in each sampling unit with respect to its position on a geographically referenced map using QUANTUM GIS 1.7.4 software (Quantum GIS Development Team 2009). The position of the sampling units was estimated from the recorded geographical coordinates of the initial and final point of each transect. The G_i^* statistic was applied using the Passage 2 software (Rosenberg 2008) to identify the locations with the highest abundances. Sampling units displaying the highest 10 % of the G_i^* values are identified as hot spots (Getis and Ord 1996). This statistic provides a measure of the variation within a fixed distance (1,000 m) from each sampling unit in relation to the density within the entire study area. The bathymetric distribution was studied in each sub-area taking into account the depth of each sampling unit and estimating the median density at depth intervals of 5 m. It was only possible to determine the relationship between colony size and biomass for *A. acaule*, for which 35 colonies were sampled spanning the entire size range (from 1 to 26 fingers or from 1 to 10 cm maximum height) by SCUBA diving. The maximum height and number of fingers of each colony were determined before the colonies were dried in an oven (96 h at 40°C) and weighed to establish the relationship that was used to convert colony size to dry weight. Maximum height showed moderate fit with biomass (maximum height = $-1.97 + 1.26$ biomass; $R^2 = 0.56$, p value <0.001), whereas the number of fingers exhibited a stronger fit with biomass (number of fingers = $-0.27 + 0.39$ biomass; $R^2 = 0.87$, p value <0.001). This last equation was used to convert the colony size for the sub-sample of the *A. acaule* colonies, for which it was possible to count the number of fingers by the video images ($n = 610$ colonies), into biomass and to examine the variation of *A. acaule* biomass with increasing depth.

In the same way, the relationship between colony size, colony density, seabed substrate type, and seabed slope was explored in the same sub-sample of *A. acaule* colonies ($n = 610$) by means of a variation of multiple

correspondence analysis (Greenacre 2007), performed with the R-language functions in the ca library (Nenadić and Greenacre 2007) of the R software platform (R Development Core Team 2012). The variables colony size and colony density were first coded into three fuzzy categories each, which conserve all the information in the variables while reducing them to a categorical scale (Asan and Greenacre 2011; Greenacre 2013). In the case of colony density, the first category codes “crisply” (i.e. as a 0–1 dummy variable) the isolated colonies for which density equals 1, while the remaining two categories code densities greater than 1 into low and high categories “fuzzily”. The fuzzy coding obviates the need to define specific intervals for low, medium, and high values of these variables and allows size and density to be analysed simultaneously with the other categorical variables, substrate and slope. Multiple correspondence analysis is an exploratory multivariate method, which allows for the representation of the different classes of the categorical variables, so that the classes extending out in similar directions from the centre of the plot are the most related. The significance of the associations between the four categorical variables (colony density, colony size, seabed substrate type, and seabed slope) was estimated using permutation testing, based on 10,000 permutations (e.g. Good 2000).

Results

Occupancy and abundance

A total of 708 colonies of the two target species (648 *A. acaule* and 60 *A. palmatum*) were observed along all transects, occurring in 24.6 % of the number of sampling units. *A. acaule* was the most frequent and abundant species in the study area, representing 91.5 % of the total number of colonies observed, occurring in 20.1 % of the sampling units, and showing a maximum density of 18.4 col m^{-2} . Conversely, *A. palmatum* only accounted for the remaining 8.5 % of the total colonies observed, occurred in 5.1 % of the sampling units, and showed a maximum density of 2.4 col m^{-2} .

Spatial and bathymetric distribution

Alcyonium acaule was present almost throughout the whole study area (Fig. 2a), with the highest frequency of occurrence and the highest density concentrated on the northern side of the cape and in a few locations on the eastern coast (Table 1). On the other hand, *A. palmatum* was generally represented as isolated or very sparse colonies (Fig. 2b), mainly concentrated in the area around the central part of the cape (Table 1). The bathymetric

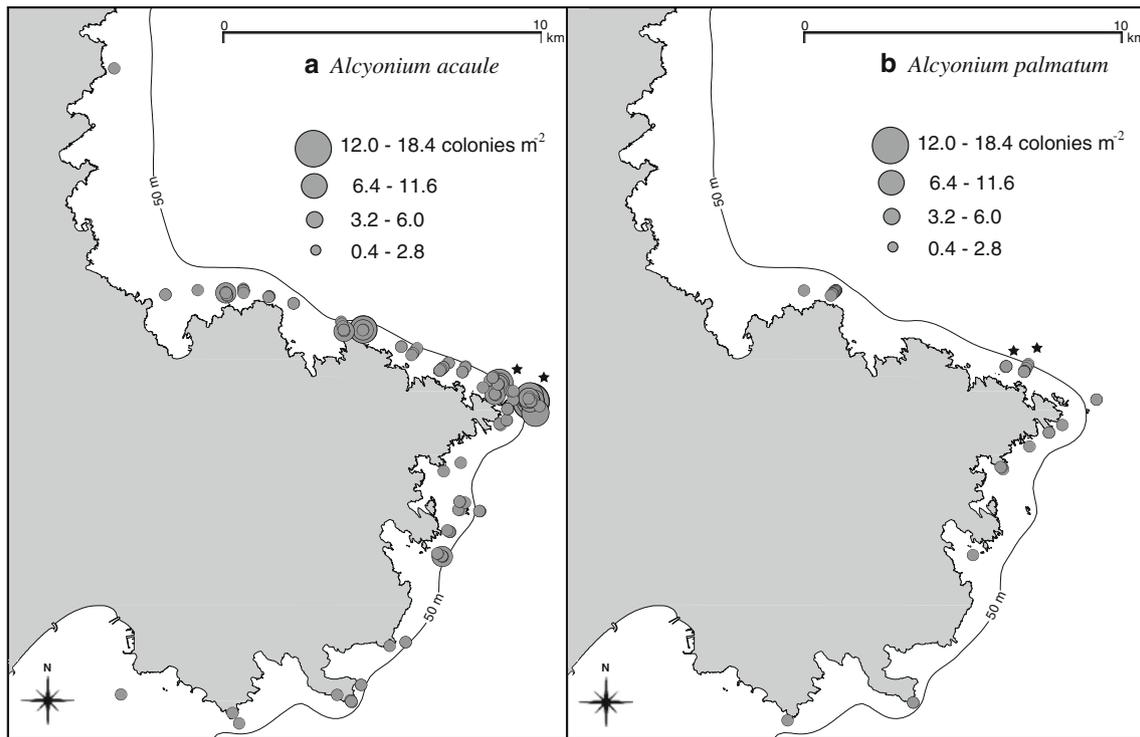


Fig. 2 Spatial distribution of *Alcyonium acaule* (a) and *Alcyonium palmatum* (b) in the study area. Black stars indicate hot spots of species abundance, which were identified as the sampling units that

displayed the highest 10 % of the G_i^* values. The spatial distribution of each species can be displayed on Google Earth by means of the Online Resource 1 and 2

Table 1 Presence and spatial distribution of *Alcyonium* species in the study area. Occupancy (frequency of occurrence in the set of sampling units from the transects in each sub-area) is given for each

sub-area and species; abundance (number of colonies) and maximum density of each species is given per each sub-area

Sub-area	Sampling units		Species	Sampling units with species Number (%)	Colonies Number (%)	Max density (colonies m ⁻²)
	Number	With species (%)				
A	804	11 (1.4)	<i>A. acaule</i>	8 (1.0)	11 (73.3)	0.8
			<i>A. palmatum</i>	3 (0.4)	4 (26.7)	0.8
B	456	6 (1.3)	<i>A. acaule</i>	5 (1.1)	8 (88.9)	1.2
			<i>A. palmatum</i>	1 (0.2)	1 (11.1)	0.0
C	630	23 (3.7)	<i>A. acaule</i>	23 (3.7)	42 (100.0)	6.0
			<i>A. palmatum</i>	0 (0.0)	0 (0.0)	0.0
D	663	17 (2.6)	<i>A. acaule</i>	12 (1.8)	30 (78.9)	7.5
			<i>A. palmatum</i>	7 (1.1)	8 (21.1)	0.8
E	776	79 (10.2)	<i>A. acaule</i>	67 (8.6)	392 (94.0)	18.4
			<i>A. palmatum</i>	13 (1.7)	25 (6.0)	2.4
F	453	53 (11.8)	<i>A. acaule</i>	38 (8.4)	162 (88.0)	10.0
			<i>A. palmatum</i>	16 (3.5)	22 (12.0)	0.8
G	777	3 (0.4)	<i>A. acaule</i>	3 (0.4)	3 (100.0)	0.4
			<i>A. palmatum</i>	0 (0.0)	0 (0.0)	0.0

distribution of *A. acaule* ranged from depths of 16–67 m (Fig. 3). This species is more frequent and abundant on the northern face of the cape (sub-areas E and F), with highest densities recorded between 30 and 45 m depth,

although relatively high numbers were also observed from 50 to 65 m (sub-area E) and from 20 to 35 m depth (sub-area F) (Fig. 3). In the other sub-areas (from A to D), *A. acaule* was present at almost all depths, although

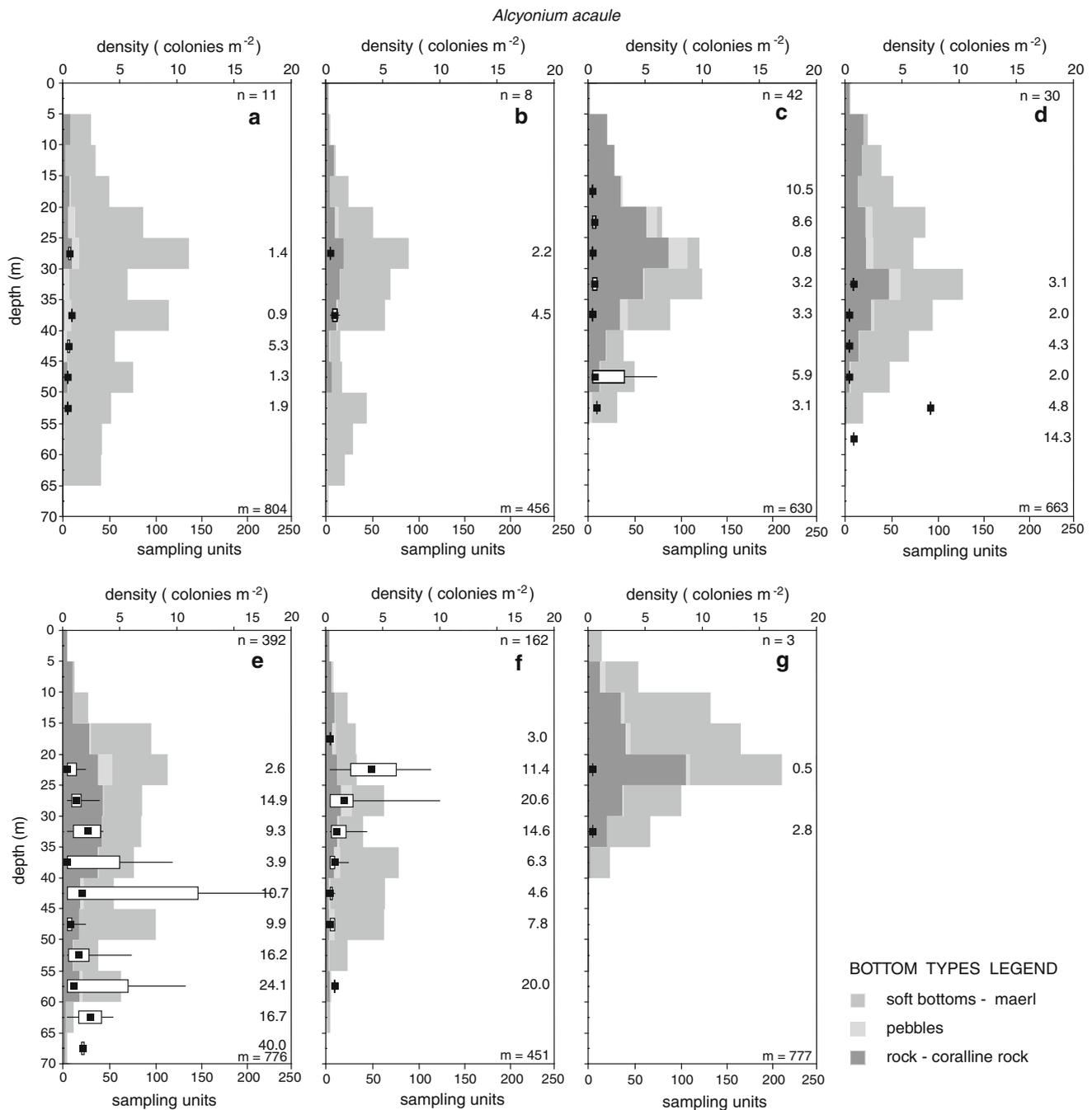


Fig. 3 *Alcyonium acaule*—Bathymetric distribution of colony density in each sub-area (a–g): the *black square* indicates the median value; the *box* indicates the first and third quartiles; and the *line* indicates the range between minimum and maximum values. *Grey-scale* histograms represent the total number of sampling units for each

substrate type (see legend) over the studied bathymetrical range. *Numbers* shown at the end of the *bars* indicate the percentage of sampling units where the species was present. Total number of colonies (*n*) and sampling units (*m*) are indicated for each sub-area

values showed comparatively lower densities and occupancies (Fig. 3). The bathymetric distribution of *A. palmatum* ranged between 28 and 60 m depth, but it was mainly restricted to depths from 35 to 55 m, also showing the highest frequency of occurrence in sub-areas E and F

(Fig. 4). Hot spots of *A. acaule* were concentrated on the northern side of the cape (Fig. 2) between depths of 25 and 39.6 m (first and third quartile) with the median at 36 m. In the same way, hot spots of *A. palmatum* were identified on the northern side of the cape (Fig. 2)

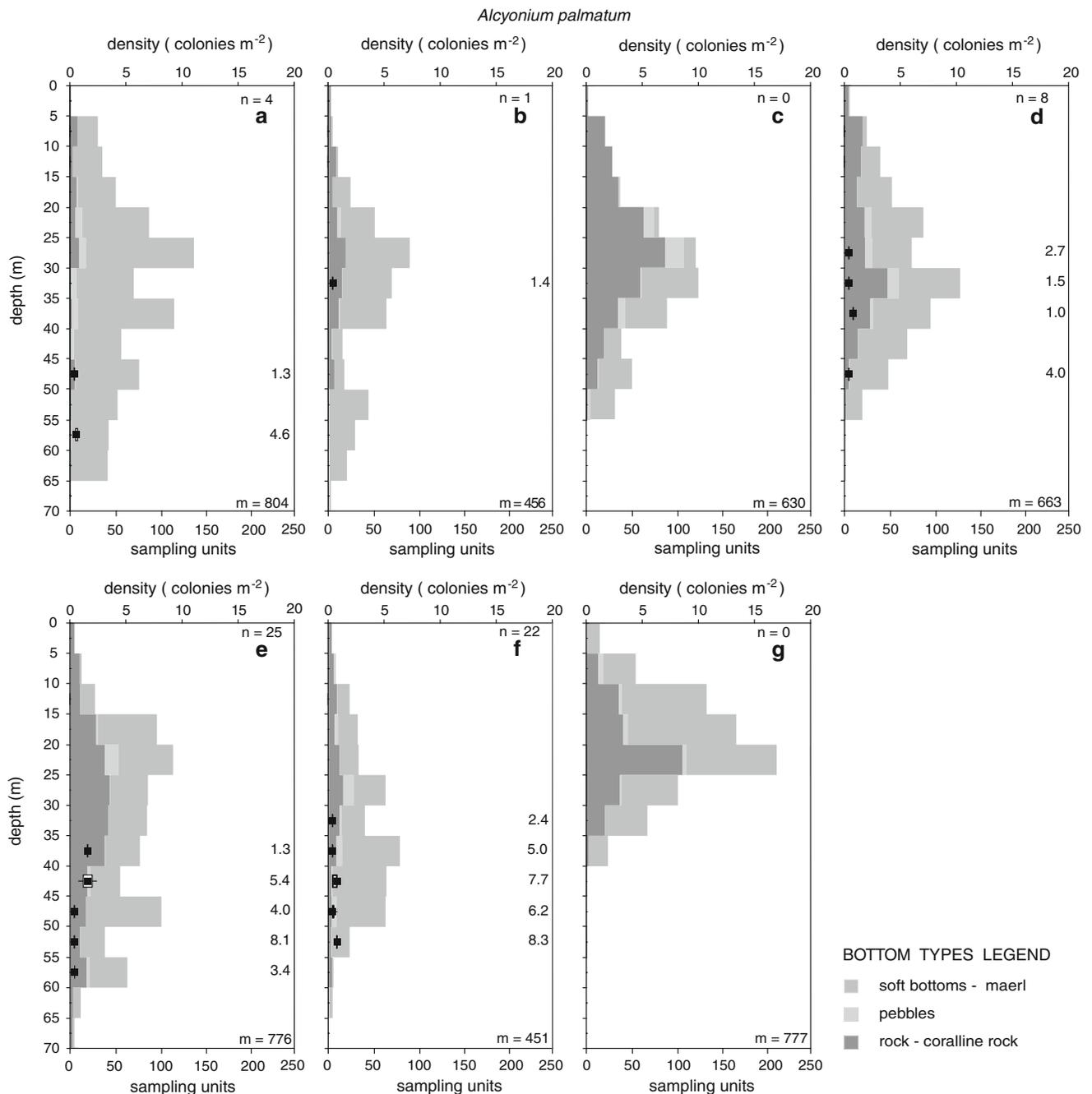


Fig. 4 *Alcyonium palmatum*—Bathymetric distribution of colony density in each sub-area (a–g): the *black square* indicates the median value; the *box* indicates the first and third quartiles; and the *line* indicates the range between minimum and maximum values. *Grey-scale* histograms represent the total number of sampling units for each

substrate type (see legend) over the studied bathymetrical range. *Numbers* shown at the end of the *bars* indicate the percentage of sampling units where the species was present. Total number of colonies (*n*) and sampling units (*m*) are indicated for each sub-area

between depths of 42 and 50 m (first and third quartile) with the median at 49 m. For the entire study area, the analysis of *A. acaule* biomass in relation to depth indicated that deeper populations tend to sustain bigger colonies than shallower ones, since biomass was higher between 40 and 45 m depth, and peaked again between 60 and 65 m depth (Fig. 5).

Relationship among colony size, density, and bottom features

The multiple correspondence analysis for the *A. acaule* colonies was represented in a bi-dimensional plot and captured 58.6 % of the total adjusted inertia of the data (Fig. 6), using an adjustment procedure similar to that

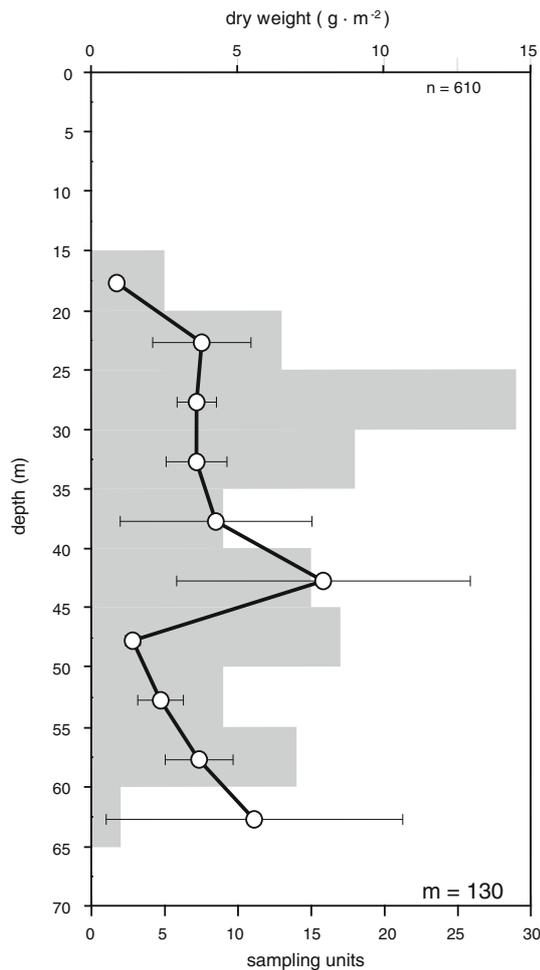


Fig. 5 Relationship between biomass and depth for *Alcyonium acaule*. Biomass (g m^{-2}) is depicted by a black line (mean \pm SD), whereas grey-scale histograms represent the total number of sampling units over the studied bathymetrical range. Total number of colonies (n) and sampling units (m) are indicated

described by Greenacre (2007). All two-way associations between the four categorical variables (colony density, colony size, seabed substrate, and seabed slope) were highly significant ($p < 0.001$ for all associations, except for the association between density and size, which is $p = 0.007$). High-density patches of *A. acaule* were preferentially found on vertical rocky bottom, while isolated colonies were preferentially observed on coralligenous substrata as well as on flat soft and maërl substrates. Colony size was more variable, and only slightly correlated with the other variables, with larger colonies preferentially found on rocky and coralligenous bottoms.

Discussion

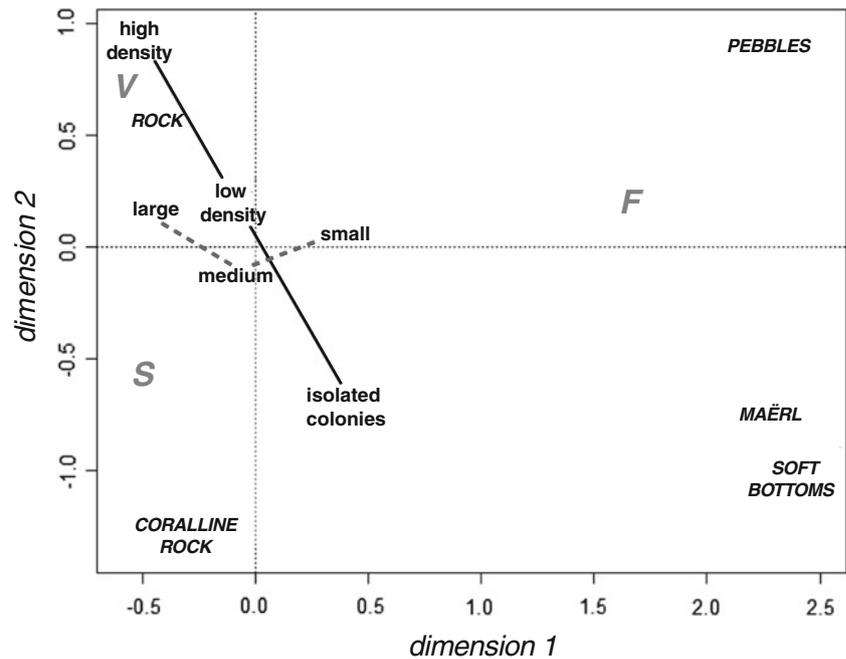
The two soft coral species studied in this work exhibit very different spatial distribution patterns of their abundances.

A. acaule was widely distributed throughout the whole study area, with highest densities on the northern coast of Cap de Creus (subareas E and F). The densities of *A. acaule* are similar to those found for other large benthic suspension feeders dwelling on hard bottoms in Western Mediterranean (e.g. the gorgonians *Eunicella singularis* ($18\text{--}56 \text{ col/m}^2$) and *Paramuricea clavata* ($19\text{--}53 \text{ col/m}^2$), Linares et al. 2008; Gori et al. 2011a) and in tropical seas (Lasker and Coffroth 1983; Yoshioka and Yoshioka 1989). The extensive distribution of *A. acaule* suggests a tolerance to a wide range of environmental conditions (e.g. hydrodynamics, water temperature, seston concentration), making it the most common and abundant soft coral species in Mediterranean sublittoral benthic communities (True 1970; Weinberg 1977; Gili and Ros 1985; Garrabou 1999). In contrast to the extensive distribution and the high densities observed for *A. acaule*, only solitary colonies of *A. palmatum* were recorded in the studied area, showing maximum densities, similar to those found for another soft-bottom suspension feeder in the same study area, the gorgonian *Leptogorgia sarmentosa* (Gori et al. 2011a). Although low densities were recorded throughout most regions of Cap de Creus, a slightly higher frequency was observed on the northern coasts of the cape (sub-area E).

The differential distribution patterns and abundances observed in the two studied soft coral species could be influenced by their differential modes of reproduction. Broadcast spawning increases larval dispersal favouring species that develop on the abundant mobile sandy bottoms of the continental shelf, which would be the case of *A. palmatum* (Sebens 1983; Coma and Lasker 1997). On the contrary, surface brooding of larvae is considered a possible mechanism to reduce larval dispersal in order to maximize the probability of larvae settling on an adequate substrate (Kahng et al. 2011). This mode of reproduction could explain the high-density patches of *A. acaule*, with maximum densities in the same order of magnitude than those observed for the gorgonian *P. clavata*, which is also a surface brooder (Coma et al. 1995). Due to the differential modes of reproduction and to the preferences for different bottom features shown by both species, coexistence in space was not found throughout the whole study area, with monospecific patches the only observed situation. Interestingly, although both species are very close genetically (McFadden et al. 2001), their distributions showed contrasting patterns without sharing the same ecological habitat. In contrast, tropical alcyonacean assemblages show many different soft coral species coexisting in the same habitat, promoting high diversity rates (Dinesen 1983; Benayahu et al. 2003; Lasker and Coffroth 1983).

The hydrodynamic regime is considered to be one of the key factors determining the spatial distribution patterns of benthic suspension feeders (Gili and Ballesteros 1991;

Fig. 6 Correspondence analysis of colony size for *Alcyonium acaule* (small, medium, large), density of colonies (isolated colonies, low density, high density), and bottom features (seabed substrate types: soft bottoms, maërl, pebbles, rock, coralline rock; seabed slope: F flat, S sloping, V vertical)



Wildish and Kristmanson 1997). This is particularly true for passive suspension feeders, which depend entirely on the transport of particles by the water current to feed (Wildish and Kristmanson 1997). High densities of passive benthic suspension feeders are often found in areas exposed to moderate or strong hydrodynamic conditions and relatively high particulate organic matter concentrations (Cocito et al. 1997; Mortensen et al. 2001). The northern coast of Cap de Creus (sub-area E and F) is directly influenced by strong northern winds as well as by the near-bottom currents that promote high seston concentrations (Millot 1990; DeGeest et al. 2008; Ulses et al. 2008; Rubio et al. 2009). Thus, the differences in the main physical factors ensure a strong asymmetry between the northern and the southern part of Cap de Creus, promoting higher occurrences of benthic suspension feeders on the more exposed northern coasts of the peninsula. The same spatial distribution was found for the gorgonians *E. singularis* and *P. clavata* in the same study area (Gori et al. 2011a). In line with this result, a similar pattern has been observed in the Medes Islands, where north-facing walls that are exposed to the main winds and currents harbour highly diverse suspension feeder species (Gili and Ros 1985).

The bathymetric distribution of the two studied species seems to be directly influenced by substrate availability. In the study area, the continental shelf begins at around 55–60 m depth, where the substrate is mainly composed of terrigenous coastal muds and detritic littoral sandy muds (Sardá et al. 2012). These kinds of substrate are ideal for *A. palmatum*, while *A. acaule* prefers the rocky substrata

(Weinberg 1977) that dominate at shallower depths (Sardá et al. 2012). The observation of high abundances and biomass of *A. acaule* at locations below the 40 m depth range highlights the fact that research on soft corals in the Mediterranean Sea has mainly focused on a fraction of their overall distributions, most of the attention being paid to shallow populations. Populations of *E. singularis* and *P. clavata* were previously observed at intermediate depths in the same study area (Gori et al. 2011a). These populations are located below the summer thermocline (35–40 metres depth), and consequently experience very different environmental conditions to those found at shallower depths (Garrabou et al. 2002; Rossi et al. 2008; Gori et al. 2012). Food may be more constant below the thermocline (Tsounis et al. 2006; Gori et al. 2012) and stress due to stochastic storms or thermal anomalies is lower (Garrabou et al. 2009), possibly causing an increase in the maximum densities that can be found at those depths.

Consequently, to achieve a complete understanding of the ecology of the Mediterranean soft coral and gorgonian species, it is essential to explore the ecological features of the deep sublittoral populations (Gori et al. 2012), the potential connectivity with shallow populations (Costantini et al. 2011), and the characteristics of these spatially structured systems (Thomas and Kunin 1999). Density of *A. acaule* populations displayed a strong positive correlation with type of substrate and its orientation, where denser patches of this species were usually found on vertical rocky bottoms, suggesting a preference of this species for this type of substratum. In the same study area, the slope of the

seabed was strongly significant in determining the presence and abundance of the gorgonian *P. clavata* (Gori et al. 2011a). However, the less significant correlation between density and colony size observed for *A. acaule* differs from that found for *P. clavata* and *C. rubrum* populations, which are characterized by self-thinning mechanisms due to the strong intraspecific competition, determining a negative correlation between density and size of the colonies (Linares et al. 2008; Rossi et al. 2012).

It is important to note that the results about the bathymetric distribution of *A. palmatum* only refer to its coastal distribution, while maximum densities for this species should be expected on the soft bottoms of the continental shelf, at greater depths than those analysed for this study (Gili and Ros 1985; Dominguez-Carrió unpublished data). The fact that *A. palmatum* dwells on muddy or sandy bottoms makes this species highly vulnerable to the impact of bottom trawling (Demestre et al. 2000; Thrush and Dayton 2002; de Juan et al. 2007), as it has been suggested also for the gorgonian *L. sarmentosa* (Rossi et al. 2011; Gori et al. 2011a). Both species are among the few engineering species (Jones et al. 1994) that dwell on the soft bottoms of the Mediterranean continental shelf, where they contribute to creating structural complexity (Gili et al. 1987). The removal of colonies as a bycatch due to commercial bottom trawling may result in an excessive thinning of populations of these benthic suspension feeders. This in turn may affect their trophic capacity (capability to process particulate organic matter captured from the near-bottom seston) as well as their reproduction success, since an excessive dilution of gametes in the water can drastically reduce the probability of fertilization (Coma and Lasker 1997). For this reason, management and conservation plans should consider the importance of preserving megabenthic species that create three-dimensional structures over both hard and soft substrates. In this sense, the recognition of the actual spatial distribution patterns of *A. acaule* and *A. palmatum* over a great spatial and bathymetrical extent can be useful in setting priorities to efficiently manage marine biodiversity and highlights the way in which ROV studies can provide information that is complementary to that obtained by SCUBA divers.

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