Mar Biol (2011) 158:143–158
DOI 10.1007/s00227-010-1548-8

ORIGINAL PAPER

Spatial distribution patterns of the gorgonians *Eunicella singularis*, *Paramuricea clavata*, and *Leptogorgia sarmentosa* (Cape of Creus, Northwestern Mediterranean Sea)

**Andrea Gori · Sergio Rossi · Elisa Berganzo ·
Joan Lluis Pretus · Mark R. T. Dale ·
Josep-Maria Gili**

Received: 18 March 2010 / Accepted: 14 September 2010 / Published online: 10 October 2010

Abstract Most of the current knowledge on Mediterranean gorgonians is restricted to investigations of those populations found within shallow sublittoral waters, and only limited data are available for populations located below scuba depth. To overcome this lack of information, the occurrence and abundance of the gorgonians *Eunicella singularis*, *Paramuricea clavata*, and *Leptogorgia sarmentosa* were investigated in northwestern Mediterranean benthic communities over a wide geographical (60 km of coastline) and bathymetrical (0–70 m deep) extent using a remotely operated vehicle (ROV). The greatest occurrence and abundances of *E. singularis* and *P. clavata* were concentrated in areas that are directly exposed to strong near-bottom currents. *E. singularis* was the most common and abundant species and displayed great plasticity and amplitude in its environmental preferences. Conversely, *P. clavata* showed a very patchy distribution that was associated with vertical rocky walls. Only isolated colonies of *L. sarmentosa* were observed in the study area. Hot spots of abundance of *E. singularis* and *P. clavata* were identified below a depth of 40 m, which demonstrates the importance of studying the distribution of benthic species over a wide geographical and bathymetrical extent.

Introduction

Characterizing and explaining the spatial variation of the abundance of species is a central question in ecology (Ives and Klopfer 1997; Currie 2007), and an understanding of the distribution patterns of species in space and time is of significant importance in the establishment of management and conservation plans (Ives and Klopfer 1997; Fortin and Dale 2005). Although variation in environmental factors is often considered the most significant factor in determining abundance patterns within a species (Whittaker 1975; Brown et al. 1995), spatial patterns can also arise in the absence of environmental variations (Ives and Klopfer 1997; Currie 2007) due to biological interactions among organisms (Borcard et al. 1992; Frelich et al. 1993) and historical factors such as low-frequency disturbances.

Communicated by R. H. Richmond.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-010-1548-8) contains supplementary material, which is available to authorized users.

A. Gori (✉) · J.-M. Gili
Institut de Ciències del Mar, Consejo Superior de
Investigacións Cientificas, Passeig Maritim
de la Barceloneta 37-49, 08003 Barcelona, Spain
e-mail: gori@icm.csic.es; agori.mail@gmail.com

S. Rossi
Institut de Ciència i Tecnologia Ambientals,
Universitat Autònoma de Barcelona, UAB Campus Cn s/n,
08193 Cerdanyola del Vallès, Barcelona, Spain

E. Berganzo
Centre de Recerca Ecològica i Aplicacions Forestals,
Universitat Autònoma de Barcelona, UAB Campus Cn s/n,
08193 Cerdanyola del Vallès, Barcelona, Spain

J. L. Pretus
Departament d'Ecologia, Facultat de Biologia,
Universitat de Barcelona, Avinguda Diagonal 645,
08028 Barcelona, Spain

M. R. T. Dale
University of Northern British Columbia,
3333 University Way, Prince George, BC V2N 4Z9, Canada

In sessile marine invertebrates, the spatial distribution is determined by the combined effects of biological (Glynn 1976; Neudecker 1979; Sheppard 1979) and environmental factors (Glynn 1976; Adjeroud 1997) that can affect the birth, growth, and death rates of individuals in single-species populations (Hutchinson 1953). Recruitment determines the spatio-temporal distribution patterns of new individuals (Chiappone and Sullivan 1996; Edmunds 2000; Baird et al. 2003) and is influenced by the characteristics of the reproductive cycle of the species, the dispersal abilities of the larvae, the features of the substrate, hydrodynamic patterns, and stochasticity. Recruitment is patchy in time and space across a variety of scales (Dunstan and Johnson 1998; Edmunds 2000). Environmental factors, the food supply, biological interactions (intra and inter-specific), and perturbations determine the survival of new individuals and affect biological processes such as growth and reproduction. The interaction between the recruitment and survival of individuals determines the spatial patterns of the distribution of sessile organisms (Gaines and Roughgarden 1985; Dunstan and Johnson 1998). It has been pointed out that in sessile marine organisms, this interaction frequently results in patchy distribution patterns (Sebens 1991) and spatially structured populations (Karlson 2006). Such patterns will have a fundamental influence both on future processes within each species (feeding, growth, reproduction, intra-specific competition) and on their interactions with other species (predation, inter-specific competition) (Dale 1999) because the spatial structure determines ecological processes in the short term, and ecological processes modify the spatial structure in the long term (Illian et al. 2008).

Among the benthic sessile invertebrates of Mediterranean sublittoral communities, gorgonian corals play an important role as ecosystem engineers (Jones et al. 1994) by providing biomass, structural complexity, and biodiversity in benthic communities (True 1970; Gili and Ros 1985; Gili et al. 1989; Ballesteros 2006). Three species of gorgonians are most abundant in the Western Mediterranean Sea: *Eunicella singularis* (Esper 1794), *Paramuricea clavata* (Risso 1826), and *Leptogorgia sarmentosa* (Linnaeus 1758) (Carpine and Grasshoff 1975; Weinberg 1976). In contrast, *Eunicella cavolinii* (Koch, 1887) has been found to be very common only in the eastern part of the Western Mediterranean Sea, whereas it is absent or very rare along the coasts located west of Marseille (Weinberg 1976).

Our understanding of the ecology of these species has improved during the last two decades (e.g., Mistri and Ceccherelli 1993; Coma et al. 1995; Linares et al. 2007; Ribes et al. 2007), and previous studies have indicated likely environmental parameters that influence the ecological range of each species (Weinberg 1978a, 1979, 1980). Thus far, the majority of studies have been conducted on shallow water populations of gorgonians (depths of less than 40 m), whereas limited information is available for rocky coast assemblages that are present in deeper waters (Virgilio et al. 2006; Rossi et al. 2008). Although gorgonians are known to be present in Western Mediterranean deep sublittoral zone (Rossi 1959; Carpine and Grasshoff 1975; Weinberg 1976), coastal rocky habitats below depths of 40 m are poorly understood because they lie below scuba depth, and most submersible-based research is conducted at depths below 150 m (Sink et al. 2006, Virgilio et al. 2006). Thus, there is a paucity of information on the habitats in the 50–150 m deep range (Sink et al. 2006).

In recent years, the development of remotely operated vehicles (ROVs) has allowed quantitative sampling and detailed observations in areas that could not be sampled using traditional methods (scuba, trawl) due to the depth or the roughness of the terrain (Mortensen and Buhl-Mortensen 2004; Rossi et al. 2008). In addition, video surveys have the advantage of sampling large areas without affecting benthic communities (Bianchi et al. 2004; Mortensen and Buhl-Mortensen 2004). Such a large spatial extent is a central requirement for the correct estimation of general patterns of species distributions, because observations conducted over smaller extents may not reflect the patterns and processes occurring over larger scales (Gotelli and Ellison 2004). The slow population dynamics of gorgonians make them susceptible to many direct and indirect anthropogenic effects, such as ship anchoring and fishing activities (Harmelin and Marinopoulos 1994; Bavestrello et al. 1997), diving (Linares et al. 2008c), and mass mortalities (Cerrano et al. 2000; Perez et al. 2000; Linares et al. 2005; Garrabou et al. 2009). Therefore, a detailed and wide-ranging knowledge of the abundance distributions of each species is fundamental to assess ongoing human effects and to propose scientifically valid conservation and management measures (Fraschetti et al. 2002; Benedetti-Cecchi et al. 2003). To date, knowledge is lacking regarding the abundance of gorgonians in the Mediterranean benthic community below depths of 40 m, the general patterns of the distribution of each species over its entire bathymetrical range, and the depth ranges in which the main densities of each species are concentrated. To approach these questions, the aims of the present study were (1) to quantify the occurrence and abundance of the main gorgonian species in northwestern Mediterranean benthic communities over a large geographic (60 km of coastline) and bathymetrical (0–70 m deep) extent, (2) to assess the spatial distribution patterns of their abundance, and (3) to discuss the main environmental determinants of such distributions.

Materials and methods

Study area

The study area is located in the northwestern region of the Western Mediterranean Sea, south of the Gulf of Lions, and it comprises the Cape of Creus (42°19′12″ N; 03°19′34″ E) and the coast up to the boundary with France (Fig. 1). More than 60 km of coast were sampled by means of 76 video transects perpendicular to the coastline. The study area was sub-divided into seven sub-areas (A to G). The general circulation pattern in the area is dominated by the Northern current, which flows southwestward and thus creates an overall east-to-west circulation (Millot 1990; DeGeest et al. 2008). The wind regime in the study area is characterized by frequent and strong northern winds (Mistral and Tramuntana 28% and 41% of the time, respectively) and rare southeasterly and easterly marine winds (<6% of the time) (Ulses et al. 2008). Both Mistral and Tramuntana wind regimes transport coastal water and suspended sediment toward the southwest (DeGeest et al. 2008; Ulses et al. 2008). Consequently, the southern coast (sub-area A) is the most sheltered section of the surveyed coast. The eastern coast of the cape (sub-areas B, C, and D) is not influenced by direct near-bottom currents and is only affected by the infrequent winds from the east (Ulses et al. 2008; DeGeest 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 study area (Ulses et al. 2008), as well as to a strong near-bottom current that accelerates around the cape (DeGeest et al. 2008). Finally, the northern coast (sub-area G) is not influenced by direct near-bottom currents, and the deposition of sediments predominates in this section of the surveyed coast (DeGeest et al. 2008).

Sampling procedure

Fieldwork was conducted over a total of 21 days in October and November 2004. Transects were video recorded with the ROV Phanthom XTL equipped with a SONY FCB S3000P 3CCD (700 horizontal lines) camera, a depth sensor, a compass, and two parallel laser beams that provide a scale to define a fixed width of the transects (0.5 m) for subsequent video analysis. Videos were recorded on video tapes in DV format. In each sampled location, seabed video recording was started at the deepest point of the transect and proceeded toward the shallows until the ROV surfaced close to shore (except in the case of a few transects that were terminated before reaching the sea surface). The ROV speed was constant (approximately 0.4 knots) during all transects. The initial depth of each transect varied between 12 and 71 m depending on the geographical characteristics of each location. The maximum depth assessed in this study was selected to cover almost all of the sublittoral zone in the study area, from the littoral to the start of the continental shelf. The transect length ranged from 92.6 m to 907.1 m, and a total distance of 28.3 km along the seabed was recorded.

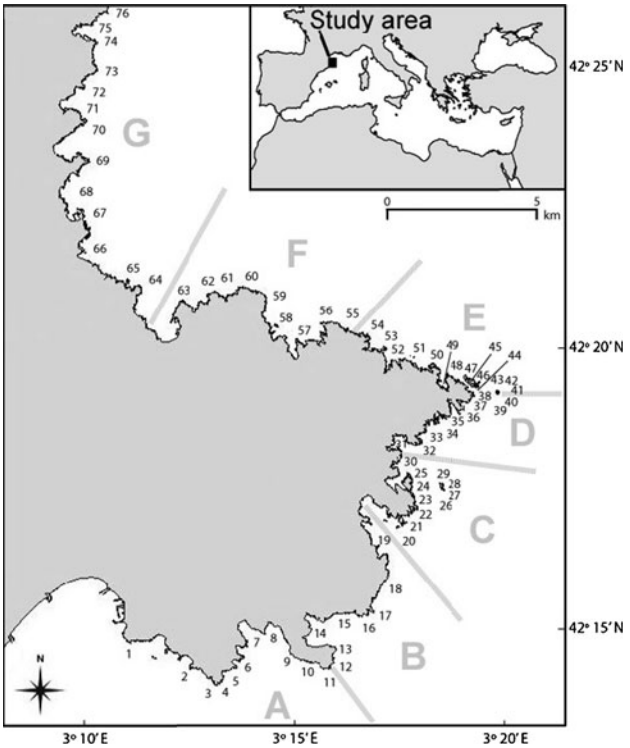

Fig. 1 Map of the study area showing the study sites and the seven sub-areas (*a*–*g*)

Video analysis

Videos were transferred from tapes to a hard disk, and video analysis was performed with Final Cut software (Apple). Pauses in the movement of the ROV were eliminated from each video to correctly estimate the total length of each transect, assuming a constant speed. In the initial stage of the video analysis, sequences for which the video record was not useful were identified (i.e., regions of poor visibility, or periods during which the ROV was at a high altitude from the seabed). The remaining useful sequences comprised 86.1% of the total recorded material and 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 m^2 (0.5 m width and 4 m long) were defined every 10 m along each transect. Sampling units that correlated with an unusable section of the video record were discarded from the analysis. The sampling unit area was chosen to be comparable with previous studies that estimated a minimum sample size of 1.75 m^2 for *Eunicella singularis* and 1.5 m^2 for *Paramuricea* *clavata* (Coma et al. 2006; Linares et al. 2008a) and a representative area of 2.0 m^2 for invertebrates in the rocky substrata of the Mediterranean (Weinberg 1978b).

A total of 2326 useful sampling units were obtained from the 76 transects. In each of these units, the gorgonian abundance was assessed by counting the number of colonies of *Eunicella singularis*, *Paramuricea clavata*, and *Leptogorgia sarmentosa*. Each sampling unit was also characterized according to environmental variables (percentage of the abundance of each seabed substrate type, seabed slope class, and the average depth) and spatial variables (geographical coordinates, transect and sub-area to which the sampling unit belongs, distance along the coast from the southern first transect, and distance from the coastline). The seabed substrate types were classified into the following categories: soft bottoms (mud, sand and detritic), maerl (species of coralline algae growing loosely in beds of fragmented nodules), pebbles, rock, coralline rock, and *Posidonia oceanica* cover. Each video frame was assigned to only one seabed substrate type, and in video frames with the simultaneous presence of more than one substrate type, only the most abundant substrate type was recorded. Similarly, according to previous studies investigating Mediterranean assemblages (Weinberg 1979, Virgilio et al. 2006), the seabed slope in each video frame 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.

Data treatment

The presence of gorgonians 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 densities observed in each sampling unit in relation to its position on a geographically referenced map using Quantum GIS 0.11 software (Quantum GIS Development Team 2009). The position of each sampling unit was estimated from the recorded geographical coordinates of the initial and final points of each transect. Using Passage 2 software (Rosenberg 2008), the Gi* statistic was used to identify the locations of highest abundance (hot spots) (Getis and Ord 1996). This statistic provides a measure of the density variation within a fixed distance (1,000 m) from each sampling unit in relation to the density magnitude within the entire study area. The bathymetrical distribution of each species was studied in each sub-area, taking into account the average depth of each sampling unit and estimating the median density at depth intervals of 5 m. The spatial and bathymetrical distribution of young (colonies <5 cm height) and adult colonies of *Eunicella singularis* were plotted separately due to the large number of young colonies found for this species. Young colonies were considered as the smallest colonies that could be distinguished by the video analysis (2–5 cm in height); they are non-reproductive colonies (Ribes et al. 2007) that have no ramifications and are <10% of the maximum height of the species (Weinberg 1976; Linares et al. 2008a).

The relationships among gorgonian abundance and environmental and spatial variables were analyzed by redundancy analysis (RDA) (ter Braak 1994) using the ordination software Canoco 4.5 (ter Braak and Smilauer 2002). RDA assumes a linear model for the relationship between the response of each species and the ordination axes. The eigenvalue of an ordination axis in RDA is the proportion of the total variance explained by that axis and indicates its relative importance. Gorgonian densities, as quantitative data, were included as response variables; substrate type, seabed slope, and depth were included as environmental variables; geographical coordinates, transects, sub-areas, distance along the coast, and distance from the coastline were included as spatial variables. Forward selection of environmental and spatial variables was used to ascertain the minimum set of variables that best explained the species density. The statistical significance of the environmental and spatial variables in the RDA was determined using a Monte Carlo permutation test with 999 permutations. All of the multivariate analyses were performed using log-transformed data, and the species were centered and standardized. Because spatial structure is a source of spurious correlations due to the spatial autocorrelation between variables (Legendre and Legendre 1998; Currie 2007), we partialled out the spatial component of the species matrix variation using partial redundancy analysis (Borcard et al. 1992; Peres-Neto et al. 2006). According to this method, four fractions of variance can be identified: (a) variance explained by the environmental variables independently of any spatial structure, (b) the spatial structure of the species data that is shared by environmental variables, (c) the spatial pattern of the species data that is not shared by environmental variables, and (d) the unexplained variance (Borcard et al. 1992; Peres-Neto et al. 2006). The amount of each fraction was calculated using the R-language function Varpart, which is available in the Vegan library (Oksanen et al. 2005) of the R software platform (R Development Core Team 2007). A species matrix was created by considering only the sampling units in which gorgonian species were present. For this matrix, two RDAs were generated that were respectively constrained by the sets of environmental and spatial variables to ascertain the minimum set of environmental and spatial variables that best explained the species density data. Subsequently, a partial RDA was generated for the species matrix, constrained by the previously selected environmental variables while controlling for the effects of the previously selected spatial variables. The results of the partial RDA were interpreted to identify the environmental factors that better explain the variation in the presence and abundance of the species after controlling for the effects of the spatial structure.

Results

Occupancy and abundance

Gorgonians were recorded in 20.9% of the total number of 2326 sampling units, and a total of 5100 colonies were observed along all of the transects. *Eunicella singularis* was the most frequent and abundant species, representing 86.1% of the total gorgonian colonies observed and occurring in 18.7% of the sampling units. Young colonies of *E. singularis* accounted for 18.3% of the colonies of this species and were observed in 8.2% of the sampling units. *Paramuricea clavata* was the second most frequent and abundant species, and it accounted for 12.6% of the observed colonies and was present in 3.4% of the total sampling units. *Leptogorgia sarmentosa* represented 1.3% of the total observed colonies and occurred in 2.2% of the total sampling units. *E. singularis* showed the highest maximum density (37.0 colonies m^{-2}), which was twice the maximum density determined for *P. clavata* (18.5 colonies m^{-2}). *L. sarmentosa* showed lower and more constant density values (0.5–1.5 colonies m^{-2}) (Table 1).

Spatial and bathymetrical distribution

The north coast of the Cape of Creus showed the highest presence of gorgonians species with the highest densities (Fig. 2; Table 1). *Eunicella singularis* was the only species that was present throughout the entire study area. This species showed the highest frequency of occurrence and the highest densities on the north side of the cape, and in a few locations on the south coast of the cape. Across all of the other sub-areas, even though *E. singularis* was present at lower densities, it remained the most abundant of the studied species (Fig. 2a, b; Table 1). Adult colonies of *E. singularis* appeared to be widely distributed (Fig. 2a, Online Resource 1), whereas young colonies were more concentrated in areas with high densities of adult colonies (Fig. 2b, Online Resource 2). The distribution of *Paramuricea clavata* was also concentrated on the north coast, where it displayed the highest densities, whereas this species was present in only a few locations along the south and east coasts (Fig. 2c, Online Resource 3, Table 1). The distribution of this species appeared to be restricted, because it was present only in some contiguous locations. In contrast, *Leptogorgia sarmentosa* was the only species that was more common on the east side of the cape, where it showed the highest frequency of occurrence and abundance, although it was widely present along the entire coast as isolated colonies (Fig. 2d, Online Resource 4, Table 1).

The bathymetrical distribution of *Eunicella singularis* ranged from depths of 6 to 67 m (Figs. 3, 4). *E. singularis* was frequent on the north face of the cape (sub-areas E and F) and showed high densities within all depth ranges, achieving a maximum depth of 67 m. In the northern part of the study area (sub-area G), this species was frequent at all depths, showing small median density values but very high maximum values. In the other sub-areas (A to D), *E. singularis* was frequent at depths between 15 and 25 m, but on the east coast of the cape (sub-areas C and D) the species displayed high median and maximum density values below a depth of 40 m (Fig. 3). The occurrence of young colonies of *E. singularis* was very variable among the sub-areas, but in sub-areas E, F, and G they were more frequent and presented a distribution in the same depth range in which the adult colonies presented high-density values (Fig. 4). The bathymetrical distribution of *Paramuricea clavata* ranged from a depth of 15 to 62 m but was mainly restricted to depths from 20 to 50 m, where the species showed the highest density and frequency of occurrence in sub-areas D, E and F (Fig. 5). In sub-area F, the deepest depth of this species was observed, with medium densities and frequencies of occurrence. *Leptogorgia sarmentosa* was documented at depths from 11 to 61 m, and it consistently showed low densities and frequencies of occurrence. In sub-areas C and D, this species was slightly more frequent, and the highest density values were observed; only a few isolated colonies were found in the other sub-areas (Fig. 6).

Hot spots (identified as the sampling units that displayed the highest 10% of the Gi* values) of *Eunicella singularis* and *Paramuricea clavata* were concentrated on the north side of the cape (Fig. 2), which represented the area with the highest values of abundance within the entire study area. The bathymetrical distribution of the hot spots showed that the highest abundances of *E. singularis* were concentrated between depths of 32.5 and 47 m (first and third quartile) with a median at a depth of 39 m for adult colonies and between 31 and 55.7 m (first and third quartile) with a median at 40.2 m for young colonies. For *P. clavata*, the bathymetrical distribution of the hot spots ranged between depths of 26.1 and 40.1 m (first and third quartile) with a median at 33 m. In contrast, hot spots of *Leptogorgia sarmentosa* were identified on the east side of the cape (Fig. 2) and in shallower waters between a depth of 16 and 31.5 m (first and third quartile) with a median at 25 m.

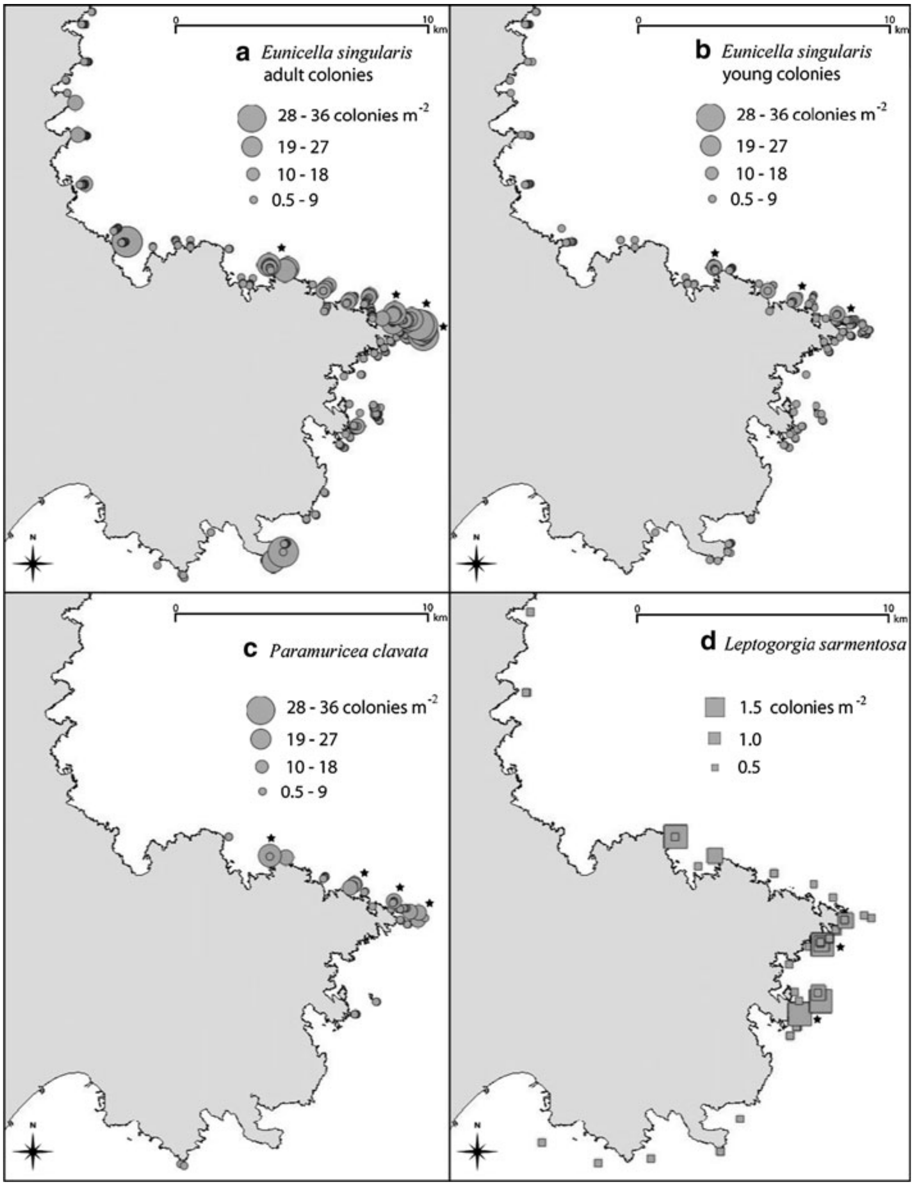

Fig. 2 Spatial distribution of *Eunicella singularis* adult (**a**) and young (**b**) colonies, *Paramuricea clavata* (**c**), and *Leptogorgia sarmentosa* (**d**) in the study area. *Squares* are used instead of *bubbles* in (**d**) to highlight the lower magnitude of the density values. *Black stars* indicate hot spots of species abundance, which were identified as the sampling units that displayed the highest 10% of the Gi* values. The spatial distribution of each species can be displayed on Google Earth by means of Online Resources 1 to 4

Relationship with environmental variables

The variation of the species matrix resulted partitioned as follows: (a) non-spatial environmental variation, 10.0%; (b) spatially structured environmental variation, 11.1%; (c) spatial species variation that is not shared by environmental variables, 19.2%; and (d) unexplained variation and stochastic fluctuations, 59.7%. Environmental variables explained 21.1% of the variance in the species matrix, but 50.7% of this amount could also be predicted by the spatial structure, which showed that the species and environmental data had a fairly similar spatial structure. The variance explained by the spatial variables that could not be related to the measured environmental variables (fraction c) could be due to unmeasured environmental variables or to biotic processes. The unexplained variance (fraction d) was probably due to some overlooked factors (e.g., historical factors, food availability), to an incomplete description of the spatial structure or to a large amount of random variation (Borcard et al. 1992). The first two axes of the partial RDA controlled for the spatial structure, explained 12.8% of the species data variance; the first axis explained 6.8%. Six environmental variables were statistically significant according to the Monte Carlo permutation test ($P < 0.05$) (Fig. 7). The seabed substrate types clearly divided *Leptogorgia sarmentosa*, which appeared to be strongly associated with soft bottoms and maerl (Fig. 7a, d), from *Eunicella singularis*, which was associated with a rocky substrate (Fig. 7a, b). The slope of the seabed was strongly significant in determining the presence and abundance of *Paramuricea clavata* (Fig. 7a, c).

Table 1 Gorgonian presence and spatial distribution in the study area. Occupancy (frequency of occurrence in the set of sampling units) 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		Colonies		Max Density
	Number	With gorgonians	(%)		Number	(%)	Number	(%)	(colonies m^{-2})
A	411	20	(4.9)	*E. singularis*	14	(3.4)	109	(84.5)	20.5
				P. clavata	2	(0.5)	15	(11.6)	4.5
				L. sarmentosa	5	(1.2)	5	(3.9)	0.5
B	233	23	(9.9)	*E. singularis*	22	(9.4)	172	(99.4)	30.5
				P. clavata	0	(0.0)	0	(0.0)	0.0
				L. sarmentosa	1	(0.4)	1	(0.6)	0.5
C	332	68	(20.5)	*E. singularis*	53	(16.0)	206	(81.7)	15.0
				P. clavata	8	(2.4)	28	(11.1)	4.0
				L. sarmentosa	13	(3.9)	18	(7.1)	1.5
D	342	73	(21.3)	*E. singularis*	58	(17.0)	593	(86.6)	28.5
				P. clavata	11	(3.2)	67	(9.8)	10.0
				L. sarmentosa	20	(5.8)	25	(3.6)	1.5
E	403	128	(31.8)	*E. singularis*	120	(29.8)	1,598	(81.4)	34.0
				P. clavata	39	(9.7)	360	(18.3)	17.5
				L. sarmentosa	5	(1.2)	5	(0.3)	0.5
F	236	54	(22.9)	*E. singularis*	51	(21.6)	794	(81.4)	30.0
				P. clavata	19	(8.1)	174	(17.8)	18.5
				L. sarmentosa	4	(1.7)	7	(0.7)	1.5
G	369	119	(32.2)	*E. singularis*	117	(31.7)	920	(99.7)	37
				P. clavata	0	(0.0)	0	(0.0)	0.0
				L. sarmentosa	3	(0.8)	3	(0.3)	0.5

Discussion

The occurrence and abundance of gorgonians in the study area are consistent with previous data from other locations within the Western Mediterranean Sea (Table 2). Although differences in the applied methodology posed difficulties in making comparisons among studies, the density values documented for the Mediterranean species (Table 2) are comparable to those reported for tropical (Kinzie 1973; Lasker and Coffroth 1983; Yoshioka and Yoshioka 1989a; Chiappone et al. 2003) and temperate species (Grigg 1975, 1977). Conversely, research conducted in deep-sea (Mortensen et al. 1995; Mortensen and Buhl-Mortensen 2004) and polar areas (Orejas et al. 2002) demonstrated a much lower occurrence and abundance of gorgonians in those regions. In contrast with the high diversity of species in tropical gorgonian communities (Lasker and Coffroth 1983; Yoshioka and Yoshioka 1989b; Chiappone et al. 2003), the Mediterranean gorgonian assemblages are mostly monospecific, and the coexistence of multiple species has been observed only sporadically (*Eunicella singularis* and *Paramuricea clavata* on rocky walls, and deep horizontal rocky bottoms; *Leptogorgia sarmentosa* and *E. singularis* on shallow rocky bottoms). Indeed, the three gorgonian species exhibit different spatial distribution patterns. *E. singularis* is widely distributed throughout the studied area as well as in other locations in the Western Mediterranean Sea (Weinberg 1979, 1980; Linares et al. 2008b), where it can be considered the most common and abundant gorgonian species (Table 2). Its distribution is mainly driven by the requirement for hard bottom substrates without a slope angle preference, and high densities of *E. singularis* are also observed on vertical walls independently of the light exposure. Conversely, *P. clavata* presented a strongly patchy distribution that was mainly associated with vertical rocky walls (Fig. 7) (Carpine and Grasshoff 1975; Weinberg 1976; Linares et al. 2008a), and this strong association could be the main explanation for the observed confinement of populations of this species to a few sites (Fig. 2). According to Linares et al. (2008a), the extensive distribution of *E. singularis* might be related to its tolerance to a wide range of environmental conditions, in contrast to the contagious distribution of *P. clavata*, which seems to be highly dependent on the vertical slope of the rocky bottom and on low light conditions. The lower maximum densities reported in this study in comparison with other locations (Table 2) might reflect a constraint of the video technique employed, which

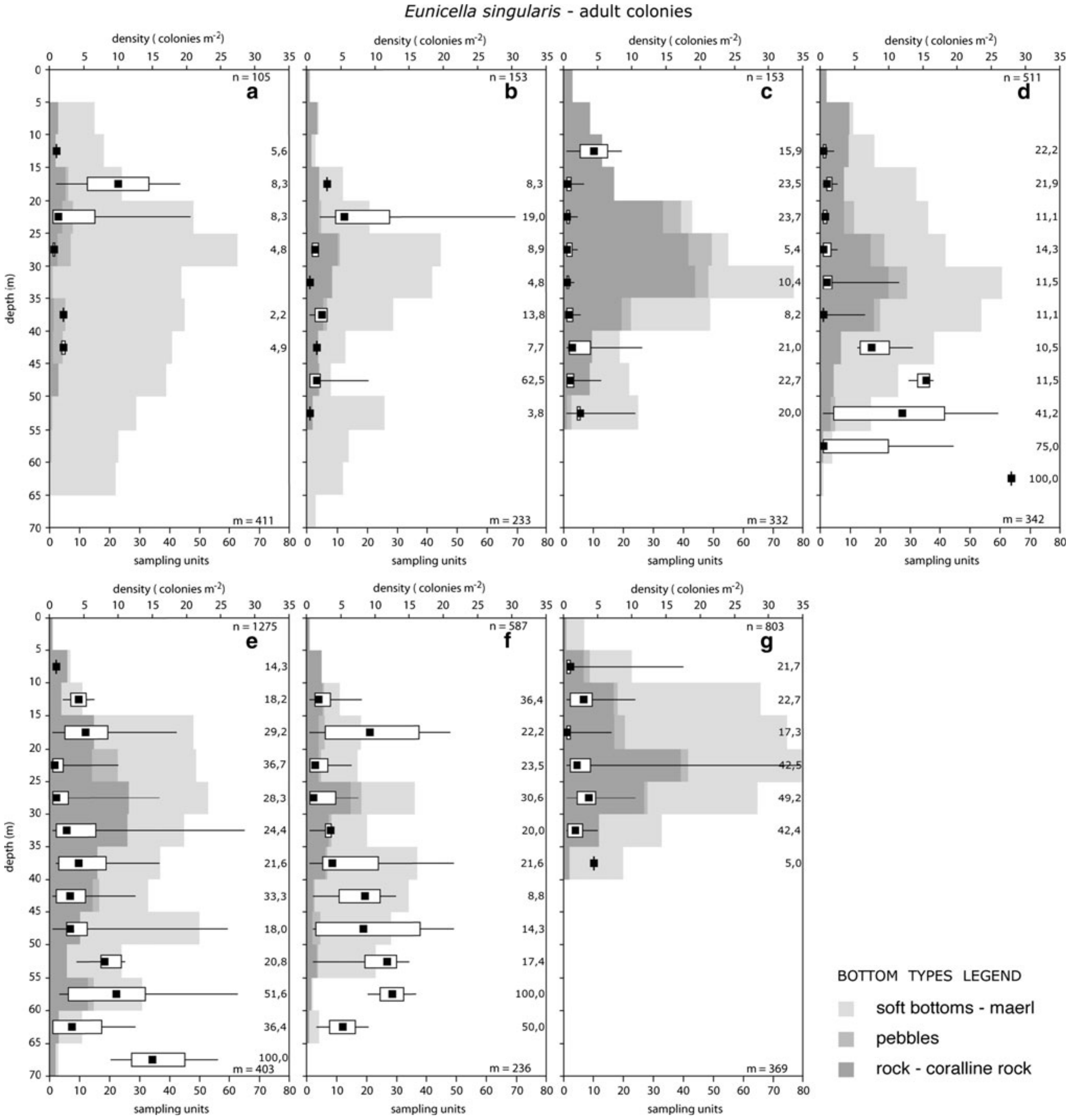

Fig. 3 *Eunicella singularis*—Bathymetrical distribution of the density of adult colonies in each sub-area (**a**–**g**): the *black square* indicates the median value; the *box* indicates the first and third quartiles; and the *line* indicates the range between minimum and maximum values. *Gray-scale histograms* represent the total number of sampling units for each substrate type (see legend) over the studied bathymetrical range. *Numbers* presented in brackets indicate the percentage of sampling units with presence of the species. Total number of colonies (*n*) and sampling units (*m*) are indicated for each sub-area

allows an extended sampling coverage but loses accuracy in measuring density when compared to other methods. However, the observed range of variability in the density of both species in the Cape of Creus area is within the same order of magnitude as the variability previously reported for different locations in the Western Mediterranean Sea (Tables 1, 2) (Coma et al. 2006; Linares et al. 2005, 2008a; Cupido et al. 2008), which suggests that this is the natural range of the density of these species over a large extent. The scattered distribution of *L. sarmentosa*, with few

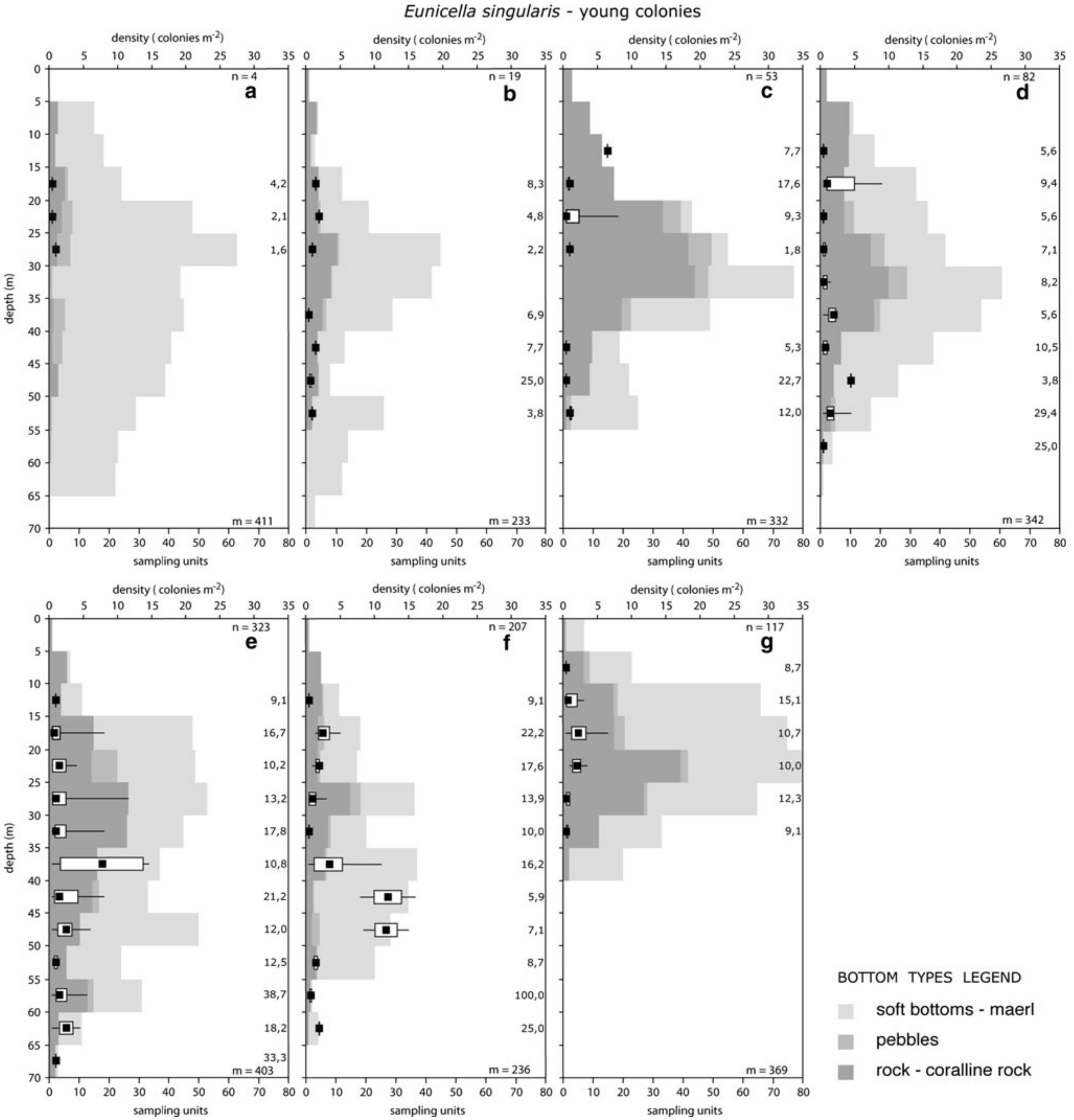

Fig. 4 *Eunicella singularis*—Bathymetrical distribution of the density of young colonies in each sub-area (**a**–**g**): the *black square* indicates the median value; the *box* indicates the first and third quartiles; and the *line* indicates the range between minimum and maximum values. *Gray-scale histograms* represent the total number of sampling units for each substrate type (see legend) over the studied bathymetrical range. *Numbers* presented in brackets indicate the percentage of sampling units with presence of the species. Total number of colonies (*n*) and sampling units (*m*) are indicated for each sub-area

colonies that were mainly dispersed on soft bottoms and maerl, is consistent with previous observations of this species (Carpine and Grasshoff 1975; Weinberg 1976; Gili et al. 1989; Mistri and Ceccherelli 1993; Rossi and Gili 2009). However, the low-density values determined for the Cape of Creus are different from those of other locations in which dense populations (up to 17 colonies m^{-2}) have been recorded (Weinberg 1979; Mistri 1995).

The highest occurrences and abundances of *Eunicella singularis* and *Paramuricea clavata* were concentrated on

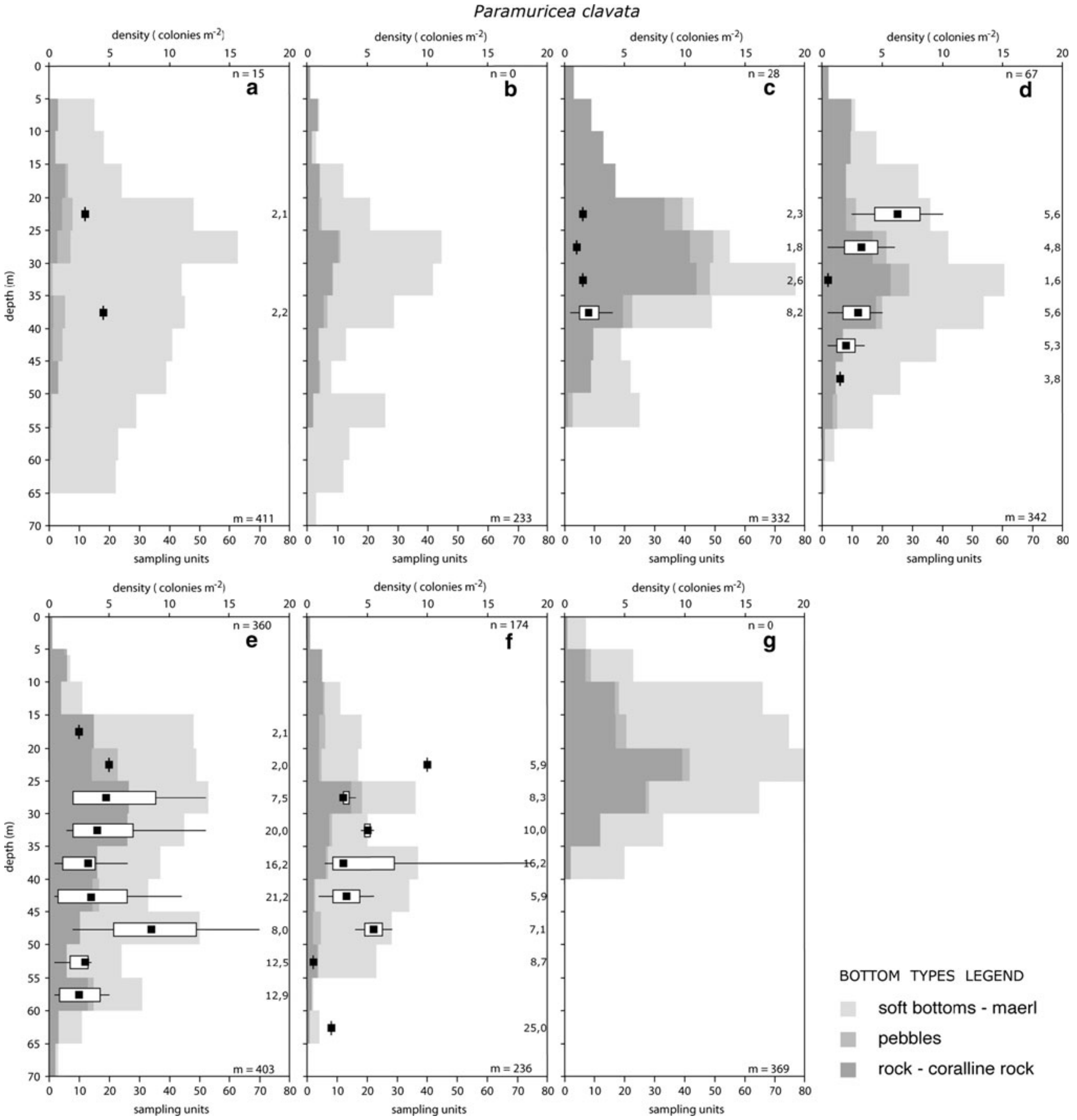

Fig. 5 *Paramuricea clavata*—Bathymetrical distribution of the density of colonies in each sub-area (**a**–**g**): the *black square* indicates the median value; the *box* indicates the first and third quartiles; and the *line* indicates the range between minimum and maximum values. *Gray-scale histograms* represent the total number of sampling units for each substrate type (see legend) over the studied bathymetrical range. *Numbers* presented in brackets indicate the percentage of sampling units with presence of the species. Total number of colonies (*n*) and sampling units (*m*) are indicated for each sub-area

the northern coast of the Cape of Creus in the area directly exposed to the main near-bottom currents, wind and wave action (Millot 1990; DeGeest et al. 2008; Ulses et al. 2008; Rubio et al. 2009). In contrast, hot spots of *Leptogorgia sarmentosa* were located along the more sheltered east side of the cape, where there is a turbulent circulation but no strong near-bottom currents (DeGeest et al. 2008; Ulses et al. 2008). Hydrodynamic patterns are a key factor in understanding the distribution of benthic suspension feeders (Gili and Ballesteros 1991; Wildish and Kristmanson 1997), and higher densities are often found in areas exposed to higher hydrodynamism and particulate organic

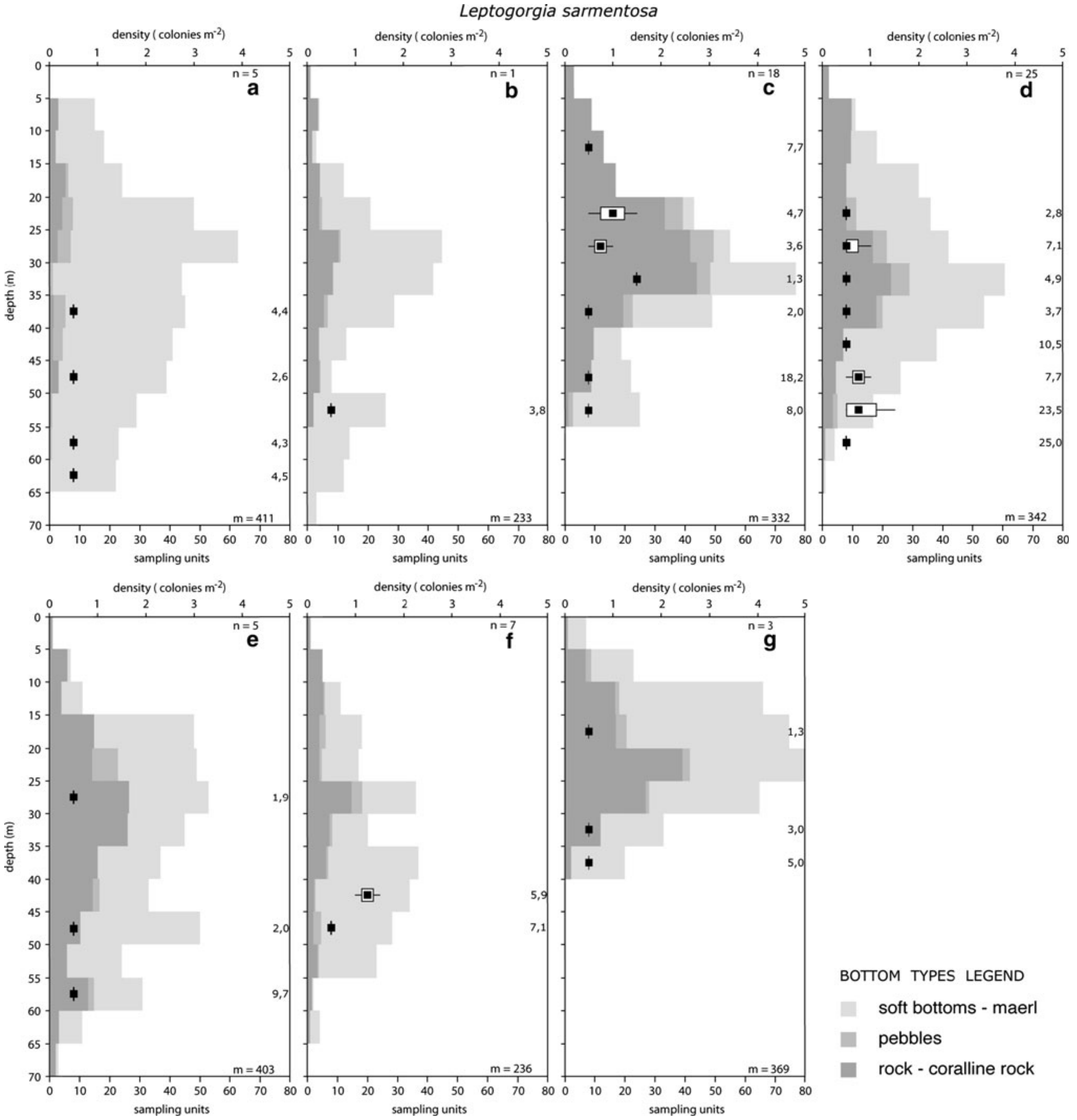

Fig. 6 *Leptogorgia sarmentosa*—Bathymetrical distribution of the density of colonies in each sub-area (**a**–**g**): the *black square* indicates the median value; the *box* indicates the first and third quartiles; and the *line* indicates the range between minimum and maximum values. *Gray-scale histograms* represent the total number of sampling units for each substrate type (see legend) over the studied bathymetrical range. *Numbers* presented in brackets indicate the percentage of sampling units with presence of the species. Total number of colonies (*n*) and sampling units (*m*) are indicated for each sub-area

matter concentrations (Cocito et al. 1997). The influence of topography on current patterns, and consequently on the food supply, is thought to determine the distribution of gorgonians and cold-water corals on both large and small scales (Cocito et al. 1997; Wildish and Kristmanson 1997; Mortensen and Buhl-Mortensen 2004). The diet of *P. clavata* consists mainly of microzooplankton (Coma et al. 1994; Ribes et al. 1999), and the preference for a moderate-high current regime and only moderate resuspension could explain the distribution of this species on vertical rocky walls. Shallow colonies of *E. singularis* host zooxantellae, and consequently, their distribution might be mainly

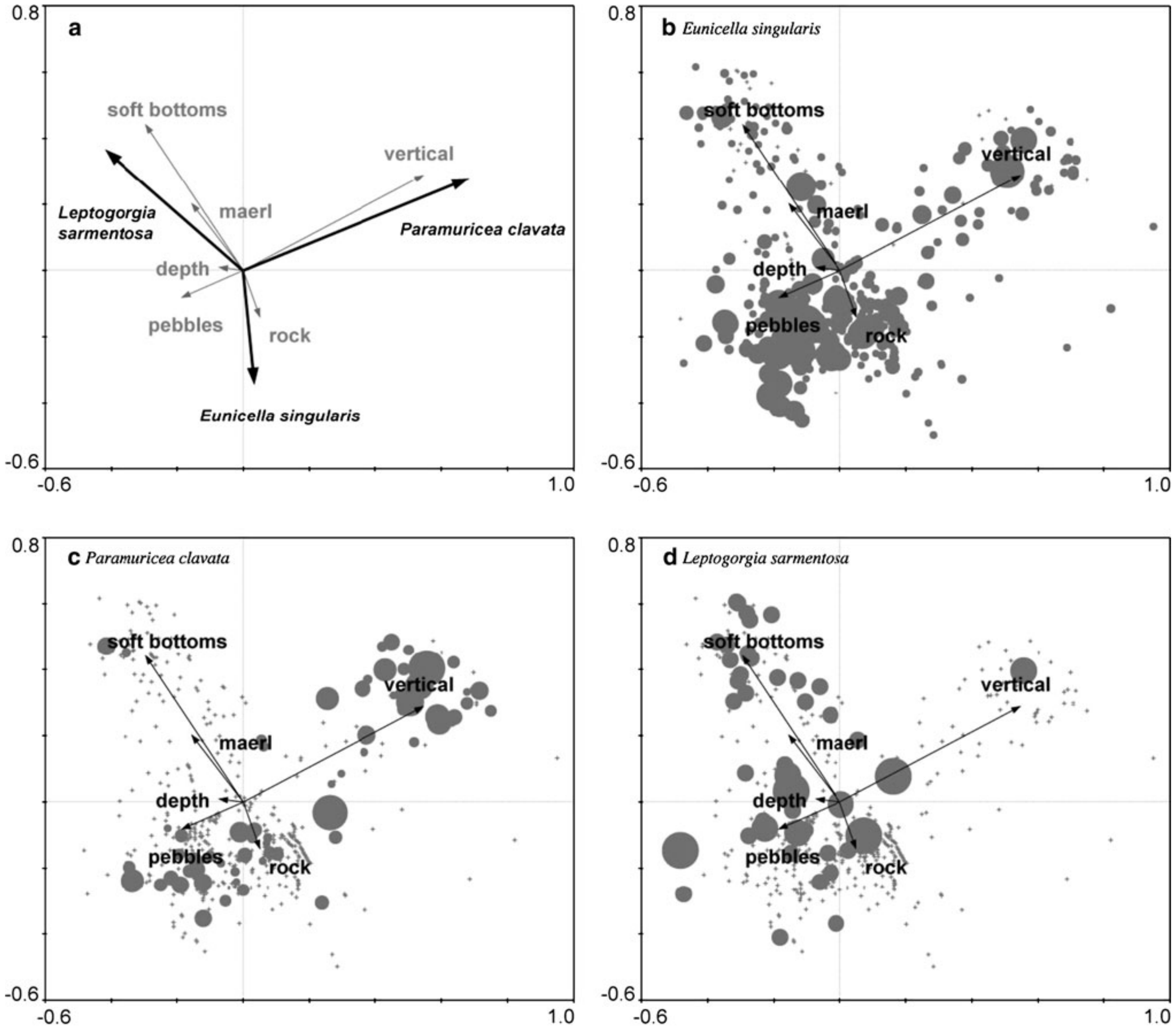

Fig. 7 Partial redundancy analysis (RDA): (**a**) biplot showing the ordination of gorgonian species and the roles of the significant environmental variables; (**b**, **c**, **d**) attribute plots of the abundance of each species in the two-dimensional space determined by the partial RDA. *Crosses* represent empty sampling units, whereas in those units in which the species is present, the *circle* diameter is proportional to the species abundance from the minimum up to the maximum value (*Eunicella singularis*: 0.5–37 colonies m^{-2}; *Paramuricea clavata*: 0.5–18.5 colonies m^{-2}; *Leptogorgia sarmentosa*: 0.5–1.5 colonies m^{-2})

related to light exposure; in contrast, data regarding the diet of deep sublittoral *E. singularis* colonies is lacking. The distribution of *L. sarmetosa* on soft bottoms might be related to a higher degree of resuspension (Rossi et al. 2003), which correlates with the increased importance of resuspended particles in the diet of this species (Ribes et al. 2003; Rossi et al. 2004).

The amount of variation accounted for by space alone shows that the substrate type, seabed slope, and depth were insufficient to completely explain the observed spatial structure of gorgonian abundance. This strictly spatial variation may be due to some overlooked environmental factors, or it may reflect some contagious biological process (Borcard et al. 1992). A short dispersal range of the larvae and settlement near the parental colony has been observed in *Eunicella singularis* (Théodor 1967; Weinberg and Weinberg 1979) and *Paramuricea clavata* (Coma et al. 1995; Linares et al. 2007, 2008c), and the effect of variability in the dispersion capability of larvae on the resulting spatial structure has been reported for tropical gorgonians and corals (Carlon and Olson 1993; Jordán-Dahlgren 2002; Baird et al. 2003). Many young colonies of *E. singularis* were observed along the Cape of Creus, whereas populations of *P. clavata* and *Leptogorgia sarmentosa* consisted

Table 2 Maximum densities reported for the studied gorgonian species in other locations in Western Mediterranean Sea

Species	Maximum density (colonies m^{-2})	Geographic location	Author
Eunicella singularis	56.4	Cape of Creus	Linares et al. (2008a)
	4.76	Montgrí	Linares et al. (2008a)
	41.91	Medes Islands	Linares et al. (2008a)
	47.55	Tarragona	Linares et al. (2008a)
	1.67	Valencia	Linares et al. (2008a)
	18.6	Gandia	Linares et al. (2008a)
	41.25	Cape of Palos	Linares et al. (2008a)
	>50	Banyuls-sur-Mer	Weinberg (1976)
	>84	Banyuls-sur-Mer	Weinberg (1978b, 1979)
Paramuricea clavata	52	Cape of Creus	Linares et al. (2008a)
	52.5	Medes Islands	Linares et al. (2008a)
	30.82	Tamariu	Linares et al. (2008a)
	53.13	Columbretes Islands	Linares et al. (2008a)
	37.33	Cape of Palos	Linares et al. (2008a)
	59	Port-Cros (Ilot de Gabinière)	Linares et al. (2005)
	38	Port-Cros (Montrémian)	Linares et al. (2005)
	32	Medes Islands	Coma et al. (1994)
	55.8	Medes Islands	Coma et al. (1995)
	>55	Banyuls-sur-Mer	Weinberg (1978b, 1979)
	46	Banyuls-sur-Mer	Weinberg (1976)
	33	Gulf of La Spezia (Tino Island)	Cupido et al. (2008)
	52	Gulf of La Spezia (Tinetto Island)	Cupido et al. (2008)
	50	Gulf of La Spezia (Tinetto Shoal)	Cupido et al. (2008)
Leptogorgia sarmentosa	>12	Banyuls-sur-Mer	Weinberg (1976)
	17	Banyuls-sur-Mer	Weinberg (1978b, 1979)

almost exclusively of adult colonies. These results agree with the extremely rare recruitment reported for *P. clavata* (Linares et al. 2008a) and *L. sarmentosa* (Rossi and Gili 2009) and the very low survival of new *P. clavata* settlers (Linares et al. 2008b). The observed large number of young *E. singularis* colonies seems to indicate a high survival of its recruits (Linares et al. 2008a) and continuous recruitment over time (Ribes et al. 2007; Linares et al. 2008a). Conversely, the distribution patterns of *P. clavata* and *L. sarmentosa* seem to be more dependent on periodic occurrences of successful recruitments.

Previous knowledge on the bathymetrical distribution of *Eunicella singularis* (depths of 7 to 54 m) and *Paramuricea clavata* (5 to 100 m depth) was based mainly on irregular observations (Laborel et al. 1961; Carpine and Grasshoff 1975; Weinberg 1976), but to date, there is still very little quantitative information on the bathymetrical distribution patterns of these species (Bo et al. 2009). Our results demonstrated a high abundance of *P. clavata* at depths from 25 to 50 m (Fig. 5) and high densities of *E. singularis* from 15 to 70 m (Figs. 3, 4). *E. singularis* colonies that were present at depths shallower than 30–35 m displayed the common candlestick-like colony morphology, with a few long and straight branches that run parallel to one another and exhibit a dirty grayish-white color (Weinberg 1976). Conversely, colonies present at depths deeper than 30–35 m displayed a more variable colony morphology and bright white color (Théodor 1969; Weinberg 1976), and they should be considered as *E. singularis aphyta,* as previously described by Théodor (1969). Further studies are needed to elucidate the classification of these colonies as a subspecies or variety (Théodor 1969; Carpine and Grasshoff 1975, Weinberg 1976). The observation of high-density populations of *P. clavata* and *E. singularis* at locations below 40 m depth, highlight as the research on Mediterranean gorgonians to date has focused only on a fraction of the species populations (the shallower ones). To achieve a complete understanding of the ecology of the main Mediterranean gorgonians species, it will now be important to explore the ecological characteristics of the deep sublittoral gorgonian populations, the possible connectivity with shallow populations, and the properties of these spatially structured population systems (Thomas and Kunin 1999). New studies are necessary to explore whether these deep sublittoral populations are exposed to more stable environmental conditions and whether these populations might play a role in the re-colonization of the shallower areas in which gorgonians are exposed more frequently to less stable conditions and to frequent perturbations. This aspect appears to be extremely important in light of the episodes of mass mortality that have affected the shallow populations of gorgonians in the Western Mediterranean (e.g., Cerrano et al. 2000; Perez et al. 2000; Linares et al. 2005; Cupido et al. 2008; Garrabou et al. 2009) and in consideration of the sporadic mortality events caused by perturbations, such as the extremely strong storm that severely affected many shallow populations of *E. singularis* and *P. clavata* along the Catalan coast in December 2008 (Linares, personal communication). The reported deep sublittoral populations of *E. singularis* and *P. clavata* demonstrate the importance of studying the distribution of benthic species over a great spatial and bathymetrical range and highlight how ROV studies can provide information that is complementary to that obtained by scuba divers.

Acknowledgments The authors would like to thank R Hernandez for his suggestions during the video laboratory assembly, PR Peres-Neto and D Borcard for their valuable updates on the variance partitioning method, JL Riera for his precious help with the software R. We are grateful to C Orejas for her useful comments which helped improving the manuscript, to S Requena for her help with the software QUANTUMGIS, and to A Purser, E Nebreda and C Dominguez for the revision of the English. Andrea Gori has been financed by a I3P contract of the Consejo Superior de Investigaciones Cientificas (Ref. I3P-BPD2005), and Sergio Rossi by a Ramón y Cajal contract (RyC-2007-01327). This work is part of the 2003–2004 INTERREG project between Catalonia-Languedoc Rouissillon “Pirineus Mediterrànis: La muntanya que uneix” of the CSIC and CNRS.

References

Adjeroud M (1997) Factors influencing spatial patterns on coral reefs around Moorea, French Polynesia. Mar Ecol Prog Ser 159:105–119

Baird AH, Babcock RC, Mundy CP (2003) Habitat selection by larvae influences the depth distribution of six common coral species. Mar Ecol Prog Ser 252:289–293

Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogr Mar Biol Annu Rev 44:123–195

Bavestrello G, Cerrano C, Zanzi D, Cattaneo-Vietti R (1997) Damage by fishing activities to the gorgonian coral *Paramuricea clavata* in the Ligurian Sea. Aquat Conserv 7:253–262

Benedetti-Cecchi L, Bertocci I, Micheli F, Maggi E, Fosella T, Vaselli S (2003) Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. Mar Environ Res 55:429–458

Bianchi CN, Pronzato R, Cattaneo-Vietti R, Benedetti Cecchi L, Morri C, Pansini M, Chemello R, Milazzo M, Fraschetti S, Terlizzi A, Peirano A, Salvati E, Benzoni F, Calcinai B, Cerrano C, Bavestrello G (2004) Hard bottoms. Biol Mar Mediterr 11:185–215

Bo M, Bavestrello G, Canese S, Giusti M, Salvati E, Angiolillo M, Greco S (2009) Characteristics of a black coral meadow in the twilight zone of the central Mediterranean Sea. Mar Ecol Prog Ser 397:53–61

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055

Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. Ecology 76:2028–2043

Carlon BD, Olson RR (1993) Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. J Exp Mar Biol Ecol 173:247–263

Carpine C, Grasshoff M (1975) Les gorgonaires de la Méditerranée. Bull Inst Océanogr Monaco 71:1–140

Cerrano C, Bavestrello G, Bianchi CN, Cattaneo-Vietti R, Bava S, Morganti C, Morri C, Picco P, Sarà G, Schiaparelli S, Siccardi A, Sponga F (2000) A catastrophic mass- mortality episode of gorgonians and other organisms in the Ligurian Sea (north western Mediterranean), summer 1999. Ecol Lett 3:284–293

Chiappone M, Sullivan KM (1996) Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. Bull Mar Sci 58:555–569

Chiappone M, Dienes H, Swanson DW, Miller SL (2003) Density and gorgonian host- occupation patterns by flamingo tongue snails (*Cyphoma gibbosum*) in the Florida Keys. Caribbean J Sci 39:116–127

Cocito S, Sgorbini S, Bianchi CN (1997) Zonation of a suspension-feeder assemblage on a temperate rocky shoal: the influence of water current and bottom topography. In: Hawkins LE, Hutchinson S (eds) The response of marine organisms to their environments. University of Southampton, UK, pp 183–192

Coma R, Gili JM, Zabala M, Riera T (1994) Feeding and prey capture cycles in the aposymbiontic gorgonian *Paramuricea clavata*. Mar Ecol Prog Ser 115:257–270

Coma R, Ribes M, Zabala M, Gili JM (1995) Reproduction and cycle of gonadal development in the Mediterranean gorgonian *Paramuricea clavata*. Mar Ecol Prog Ser 117:173–183

Coma R, Linares C, Ribes M, Díaz D, Garrabou J, Ballesteros E, Zabala M (2006) Consequences of a mass mortality in populations of *Eunicella singularis* (Cnidaria: Octocorallia) in Menorca (NW Mediterranean). Mar Ecol Prog Ser 327:51–60

Cupido R, Cocito S, Sgorbini S, Bordone A, Santangelo G (2008) Response of a gorgonian (*Paramuricea clavata*) population to mortality events: recovery or loss? Aquat Conserv 18:984–992

Currie DJ (2007) Disentangling the roles of environment and space in ecology. J Biogeogr 34:2009–2011

Dale MRT (1999) Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge, p 324

DeGeest AL, Mullenbach BL, Puig P, Nittrouer CA, Drexler TM, Durrieu de Madron X, Orage DL (2008) Sediment accumulation in the western Gulf of Lions, France: the role of Cap de Creus canyon in linking shelf and slope sediment dispersal systems. Cont Shelf Res 28:2031–2047

Dunstan PK, Johnson CR (1998) Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. Coral Reefs 17:71–81

Edmunds PJ (2000) Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. Mar Ecol Prog Ser 202:113–124

Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, p 365

Fraschetti S, Terlizzi A, Micheli F, Benedetti-Cecchi L, Boero F (2002) Marine protected areas in the Mediterranean Sea: objectives, effectiveness and monitoring. PSZNI Mar Ecol 23:190–200

Frelich LE, Calcote RR, Davis M, Pastor J (1993) Patch formation and maintenance in an old-growth hemlock-hardwood forest. Ecology 74:513–527

Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc Natl Acad Sci 82:3707–3711

Garrabou J, Coma R, Chevaldonné P, Cigliano M, Diaz D, Harmelin JG, Gambi MC, Kersting DK, Lejeune C, Linares C, Marschal C, Pérez T, Ribes M, Romano JC, Teixido N, Serrano E, Torrents O, Zabala M, Zuberer F, Cerrano CA (2009) Mass mortality in NW Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob Change Biol 15:1090–1103

Getis A, Ord JK (1996) Local spatial statistics: an overview. In: Longley P, Batty M (eds) Spatial analysis: modelling in a GIS environment. GeoInformation International, Cambridge, pp 261–277

Gili JM, Ballesteros E (1991) Structure of cnidarian populations in Mediterranean sublittoral communities as a result of adaptation to different environmental conditions. Oecol Aquat 10:243–254

Gili JM, Ros J (1985) Study and cartography of the benthic communities of Medes Islands (NE Spain). PSZNI Mar Ecol 6:219–238

Gili JM, Murillo J, Ros JD (1989) The distribution pattern of benthic Cnidarians in the Western Mediterranean. Sci Mar 53:19–35

Glynn PW (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol Monogr 46:431–456

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates, Sunderland, p 510

Grigg RW (1975) Age structure of a longevous coral: a relative index of habitat suitability and stability. Am Nat 109:647–657

Grigg RW (1977) Population dynamics of two gorgonian corals. Ecology 58:278–290

Harmelin JG, Marinopoulos J (1994) Population structure and partial mortality of the gorgonian *Paramuricea clavata* (Risso) in the North-western Mediterranean (France, Port-Cros Island). Mar Life 4:5–13

Hutchinson GR (1953) The concept of pattern in ecology. Proc Acad Nat Sci Philadelphia 105:1–12

Illian J, Penttinen A, Stoyan H, Stoyan D (2008) Statistical analysis and modelling of spatial point patterns. Wiley, Chichester, p 560

Ives AR, Klopfer ED (1997) Spatial variation in abundance created by stochastic temporal variation. Ecology 78:1907–1913

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jordán-Dahlgren E (2002) Gorgonian distribution patterns in coral reef environments of the Gulf of Mexico: evidence of sporadic ecological connectivity? Coral Reefs 21:205–215

Karlson RH (2006) Metapopulation dynamics and community ecology of marine systems. In: Kritzer JP, Sale PF (eds) Marine metapopulations. Academic Press, Burlington, pp 457–515

Kinzie RA (1973) The zonation of west Indian gorgonians. Bull Mar Sci 23:93–155

Laborel J, Pérès JM, Picard J, Vacelet J (1961) Étude directe des fonds des parages de Marseille de 30 à 300 m avec la soucoupe plongeante Cousteau. Bull Inst Océanogr Monaco 1206:1–16

Lasker HR, Coffroth MA (1983) Octocoral distributions at Carrie Bow Cay, Belize. Mar Ecol Prog Ser 13:21–28

Legendre P, Legendre L (1998) Numerical ecology, 2nd English edn. Elsevier, Amsterdam, p XV + 853

Linares C, Coma R, Díaz D, Zabala M, Hereu B, Dantart L (2005) Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. Mar Ecol Prog Ser 305:127–137

Linares C, Doak DF, Coma R, Díaz D, Zabala M (2007) Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology 88:918–928

Linares C, Coma R, Garrabou J, Díaz D, Zabala M (2008a) Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. J Appl Ecol 45:688–699

Linares C, Coma R, Mariani S, Díaz D, Hereu B, Zabala M (2008b) Early life history of the Mediterranean gorgonian *Paramuricea clavata*: implications for population dynamics. Invertebr Biol 127:1–11

Linares C, Coma R, Zabala M (2008c) Restoration of threatened red gorgonian populations: an experimental and modelling approach. Biol Conserv 141:427–437

Millot C (1990) The Gulf of Lions' hydrodynamics. Cont Shelf Res 19:885–894

Mistri M (1995) Population structure and secondary production of the Mediterranean Octocoral *Lophogorgia ceratophyta* (L.1758). PSZNI Mar Ecol 16:181–188

Mistri M, Ceccherelli V (1993) Growth of the Mediterranean gorgonian *Lophogorgia ceratophyta* (L., 1758). PSZN I Mar Ecol 14:329–340

Mortensen PB, Buhl-Mortensen L (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Mar Biol 144:1223–1238

Mortensen PB, Hovland M, Brattegard T, Farestveit R (1995) Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64° N on the Norwegian shelf: structure and associated megafauna. Sarsia 80:145–158

Neudecker S (1979) Effects of grazing and browsing on the zonation of coral in Guam. Ecology 60:666–672

Oksanen J, Kindt R, Legendre P, O'Hara RB (2005) Vegan: community ecology package. Version 1.7-81. http://cran.r-project.org

Orejas C, López-González PJ, Gili JM, Teixidó N, Gutt J, Arntz WE (2002) Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea. Mar Ecol Prog Ser 231:101–114

Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625

Perez T, Garrabou J, Sartoretto S, Harmelin JG, Francour P, Vacelet J (2000) Mortalité massive d'invertébrés marins: un événement sans précédent en Méditerranée nord-occidentale. CR Acad Sci III 323:853–865

Quantum GIS Development Team (2009) GNU General Public License. http://qgis.osgeo.org

R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051- 07-0. URL. http://www.R-project.org

Ribes M, Coma R, Gili JM (1999) Heterogeneous feeding in benthic suspension feeders: the natural diet and grazing rate of the temperate gorgonian *Paramuricea clavata* (Cnidaria: Octocorallia) over a year cycle. Mar Ecol Prog Ser 183:125–137

Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Mar Ecol Prog Ser 254:141–150

Ribes M, Coma R, Rossi S, Micheli M (2007) Cycle of gonadal development in *Eunicella singularis* (Cnidaria: Octocorallia): trends in sexual reproduction in gorgonians. Invertebr Biol 126:307–317

Rosenberg MS (2008) PASSaGE: pattern analysis, spatial statistics, and geographic exegesis. Version 2. http://www.passagesoftware.net

Rossi L (1959) Le specie di *Eunicella* (Gorgonaria) del Golfo di Genova. Res Ligusticae 118:203–225

Rossi S, Gili JM (2009) The cycle of gonadal development of the soft bottom-gravel gorgonian *Leptogorgia sarmentosa* in the NW Mediterranean sea. Invertebr Reprod Dev 53:175–190

Rossi S, Grémare A, Gili JM, Amouroux JM, Jordana E, Vétion G (2003) Biochemical characteristics of settling particulate organic matter at two north-western Mediterranean sites: a seasonal comparison. Est Coast Shelf Sci 58:423–434

Rossi S, Ribes M, Coma R, Gili JM (2004) Temporal variability in zooplankton prey capture rate of the passive suspension feeder *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), a case study. Mar Biol 144:89–99

Rossi S, Tsounis G, Orejas C, Padrón T, Gili JM, Bramanti L, Teixidó N, Gutt J (2008) Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). Mar Biol 154:533–545

Rubio A, Barnier B, Jordà G, Espino M, Marsaleix P (2009) Origin and dynamics of mesoscale eddies in the Catalan Sea (NW Mediterranean): insight from a numerical model study. J Geophys Res 114. doi:10.1029/2007JC004245

Sebens KP (1991) Habitat structure and community dynamics in marine benthic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London, pp 211–234

Sheppard CRC (1979) Interspecific aggression between reef corals with reference to their distribution. Mar Ecol Prog Ser 1:237–247

Sink KJ, Boshoff W, Samaai T, Timm PG, Kerwath SE (2006) Observations of the habitats and biodiversity of the submarine canyons at Sodwana Bay. S Afr J Sci 102:466–474

ter Braak CJF (1994) Canonical community ordination. Part I: basic theory and linear methods. Ecoscience 1:127–140

ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, p 500

Théodor J (1967) Contribution a l'étude des gorgones (VII): écologie et comportement de la planula. Vie Milieu 18:291–301

Théodor J (1969) Contribution a l'étude des gorgones (VIII): *Eunicella stricta aphyta* sous-espèce nouvelle sans zooxanthelles proche d'une espèce normalement infestée par ces algues. Vie Milieu 20:635–638

Thomas CD, Kunin WE (1999) The spatial structure of populations. J Anim Ecol 68:647–657

True MA (1970) Étude quantitative de quatre peuplements sciaphiles sur substrat rocheux dans la région marseillaise. Bull Inst Océanogr Monaco 69:1–48

Ulses C, Estournel C, Bonnin J, Durrieu de Madron X, Marsaleix P (2008) Impact of storms and dense water cascading on shelf-slope exchanges in the Gulf of Lion (NW Mediterranean). J Geophys Res 113. doi:10.1029/2006JC003795

Virgilio M, Airoldi L, Abbiati M (2006) Spatial and temporal variations of assemblages in a Mediterranean coralligenous reef and relationships with surface orientation. Coral Reefs 25:265–272

Weinberg S (1976) Revision of the common Octocorallia of the Mediterranean circalittoral. I. Gorgonacea. Beaufortia 24:63–104

Weinberg S (1978a) Mediterranean octocorallian communities and the abiotic environment. Mar Biol 49:41–57

Weinberg S (1978b) The minimal area problem in invertebrate communities of Mediterranean rocky substrata. Mar Biol 49:33–40

Weinberg S (1979) Autecology of shallow-water Octocorallia from Mediterranean rocky substrata, I. The Banyuls area. Bijdr Dierkd 49:1–15

Weinberg S (1980) Autecology of shallow-water Octocorallia from Mediterranean rocky substrata, II. Marseille, Côte d'Azur and Corsica. Bijdr Dierkd 50:73–86

Weinberg S, Weinberg F (1979) The life cycle of a gorgonian: *Eunicella singularis* (Esper, 1794). Bijdr Dierkd 48:127–140

Whittaker RH (1975) Communities and ecosystems, 2nd edn. MacMillan Publishing Co, New York, p 185

Wildish D, Kristmanson D (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambridge, p 409

Yoshioka PM, Yoshioka BB (1989a) A multispecies, multiscale analysis of spatial pattern and its application to a shallow-water gorgonian communities. Mar Ecol Prog Ser 54:257–264

Yoshioka PM, Yoshioka BB (1989b) Effects of wave energy, topographic relief and sediment transport on the distribution of shallow-water gorgonians of Puerto Rico. Coral Reefs 8:145–152