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ORIGINAL ARTICLE

Spatial and depth-associated distribution patterns of shallow gorgonians in the Algarve coast (Portugal, NE Atlantic)

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Abstract The ecological role of gorgonians for marine rocky bottoms is worldwide recognized, but the information on the distribution patterns of NE Atlantic temperate species is insufficient, considering current global, regional and local threats. To overcome the lack of information on the spatial distribution patterns of gorgonians in south Portugal, in 2009/2010, the occurrence and abundance of gorgonian species in rocky bottoms were quantified over more than 25 km of coast (37.1°N/8.6°W) down to 30 m depth. *Eunicella labiata, Eunicella gazella, Eunicella verrucosa* and *Leptogorgia sarmentosa* were abundant and frequent in the studied area, while *Leptogorgia lusitanica* was less abundant. All species evidenced a similar depth pattern, that is abundance significantly increased with depth below 15 m. At shallower waters (up to 15 m), the distribution of gorgonians may be constrained by abiotic factors and competition with algae. Indeed, the abundance of gorgonians was negatively correlated with the percentage cover of algae along the depth gradient, but gorgonians and sponges coexist. Competition among gorgonian species also seems to be low in this area because of the similarity in the abundance pattern observed for the most abundant species and also their high association. In NE Atlantic shallow temperate rocky bottoms, the distribution of gorgonians seems to be influenced by environmental factors and biological interactions, namely competition (algae) and coexistence (sponges and other gorgonians).

Keywords Gorgonians · *Leptogorgia* · *Eunicella* · Spatial distribution · Rocky bottoms · Biological interactions

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Introduction

Gorgonians (Octocorallia: Alcyonacea) are colonial organisms characterized by a skeleton, slow growth and long life span. Their three-dimensional structure may modify the physical habitat, by reducing current velocity, stabilizing soft substrata, enhancing sedimentation and local accumulation of fine particles, as well as increasing availability of niches similarly to what is found for other marine animals (e.g. Idjadi and Edmunds 2006; Norling and Kautsky 2007). They are habitat formers (foundation species) facilitating the colonization of other species through positive indirect effects (Bruno et al. 2003; Thomsen et al. 2010) creating habitat cascades. The importance of these facilitation processes for the structure of communities in terms of species abundance and diversity is widely accepted (Thomsen et al. 2010). However, the positive effects deriving from habitat cascades depend on the characteristics of the foundation species, such as size, density and longevity (Bruno et al. 2003). In coastal marine communities, gorgonians are commonly the most abundant habitat formers, sometimes the only conspicuous ones, providing the framework for the community. Because gorgonians are long-lived animals, they may extend these modifications for long time, producing significant effects in marine ecosystems, namely by enhancing local diversity (Cerrano et al. 2009). Furthermore, the ecological role of gorgonians in ecosystem functioning has been widely acknowledged (Ballesteros 2006; Coma et al. 2006; Cupido et al. 2008; Linares et al. 2008b), with a strong emphasis on the role of habitat formers in marine conservation (see Wright and Jones 2006).

Over the last decades, many studies reported that gorgonians are affected by drastic, rapid and lasting disturbances either of natural (e.g. Linares et al. 2005; Coma et al. 2006; Garrabou et al. 2009) or human origin (e.g. Bavestrello et al. 1997; Coma et al. 2004; Chiappone et al. 2005; Cerrano and Bavestrello 2008; Linares et al. 2008b). In order to preserve their ecological role as habitat formers, detailed knowledge on the distribution patterns of abundance of gorgonian species is essential to propose adequate conservation and management measures (Benedet-Cecchi et al. 2003; García-Charton et al. 2008; Costello et al. 2010).

The Algarve coast (southern Portugal, north-eastern Atlantic) presents a rich fauna with biogeographic affinities with the Mediterranean Sea, the Lusitanian, the west African Transition, Northern European Seas and Western Atlantic provinces (sensu Spalding et al. 2007; Souto et al. 2010; Levy et al. 2011), because of the proximity to the Strait of Gibraltar (Baus et al. 2005; and references therein) and the confluence of oceanic currents (Cherubin et al. 2000; Pérez et al. 2001; Coelho et al. 2002; Martins et al. 2002). However, the gorgonian populations of southern Portugal are poorly described, especially compared to the Mediterranean, where in the past few years, several studies have been performed in shallow sub-littoral waters, gathering a large amount of biological and ecological information, and building predictive models to be used in conservation plans (Linares et al. 2007, 2008b; Bramanti et al. 2009). In fact, the most recent study concerning the gorgonian fauna of the Algarve coast reported only 10 different species caught as by-catch by bottom gill nets (Vieira 2008). Therefore, significant knowledge gaps still persist, namely on the abundance patterns in the near shore benthic community (0–30 m), spatial and depth distribution.

In this context, the present study aimed to quantify the occurrence and abundance of the main gorgonian species in the shallow rocky bottoms (0–30 m) of the western Algarve coast ($\approx$25 km of coastline). In order to assess the relationship between the distribution of gorgonians and potential competitors for space and food, the percentage cover of erect algae and sponges were also quantified. If population dynamics of those benthic taxa is governed by competition, it is expected that the abundance of gorgonians and both erect algae and sponges would be inversely correlated.

Materials and methods

Study area

The Algarve coast (Fig. 1) is characterized by heterogeneous coastline and sub-littoral areas. The western part of the Algarve coast comprises rocky formations of several types (e.g. underwater spurs, boulders, low relief rocky areas, submerged rock bottoms) and by different sediment dynamics.

The study area is located in the western Algarve coast extending from Lagos to Portimão (Fig. 1), hereafter designated by Lagos Bay. This area has 20.6 km^2 of rocky bottoms within a total area of 70 km^2 (up to 30 m depth) and covers $\approx$25 km of the Algarve coast, distancing only $\approx$30 km to the westernmost continental part of Europe (Cabo São Vicente, Sagres). In particular, the coast between Ponta da Piedade and Armação de Pêra, where this study was conducted, is morphologically complex presenting rocky areas with cliffs forming small beaches, a large bay with extensive sandy beaches and dunes, including a coastal lagoon (Ria de Alvor) and a small estuary (Rio Arade). The shallow continental shelf (down to $\approx$30 m depth) is generally characterized by rocky outcrops with pockets of rubble and/ or sand (Gonçalves et al. 2010)

In general, the circulation patterns in the Iberian Peninsula are dominated by up-welling (summer) and down-welling (winter) events associated with northerly/southerly winds, coupled to the North Atlantic Oscillation (Sánchez et al. 2007). Sea surface temperature presents marked seasonal variation depending on whether down-welling or up-welling dominates (ranging from 14 to 24 °C, respectively; http://www.hidrografico.pt/), whereas salinity is fairly constant (35.0–36.0).

Species identification

The identification of gorgonian species was based on the studies by Carpine and Grasshoff (1975), Grasshoff (1988; 1992) and González (1993). In the Algarve coast, underwater identification of gorgonians is difficult because of ambiguities in the taxonomy of *Eunicella* and *Leptogorgia*, and therefore, the following criteria were established to identify these species:

Eunicella gazella colonies always white with orange polyps; diameter of the ramets noticeably larger than in *E. verrucosa*; colony surface generally homogeneous with low relief and extensive branching mostly in one dimension.

Eunicella verrucosa colonies with colour varying from white to cream, beige or pale orange; polyps varying

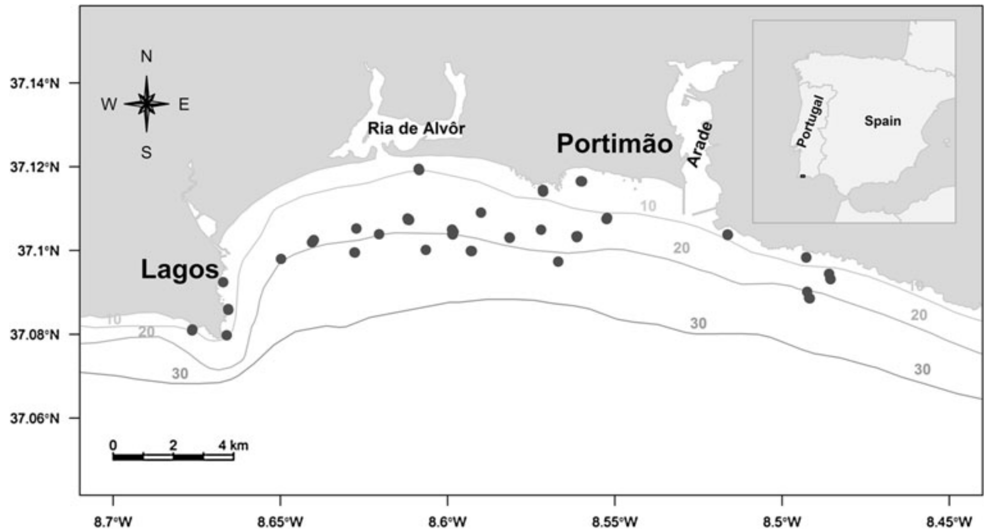

Fig. 1 Location of the sampling sites (*filled circle*) in Lagos Bay

from white to orange; heterogeneous surface with "bumps" (verrucae), usually larger in size than *E. gazella*.

Eunicella labiata large species; colonies divided in two main branches immediately after the base of the colony, with less branches than *E. verrucosa* and *E. gazella*; colours are usually darker than in the previous species, ranging from cream to dark brown; colonies are often broken, loosing one of the main branches; conspicuous verrucae observed all over the colony, usually lighter.

Eunicella singularis erect colonies with few long branches always in upright position; colonies always white coloured; colony surface generally smooth with low relief.

Leptogorgia lusitanica bush-like colonies growing in only one dimension, perpendicular to dominant currents; terminal branches thinner than the central ones; extremely variable in colour, generally presenting two colours, usually wine red/purple and yellow, sometimes white and blue, and other times uniform in colour (generally white or yellow); the central branches of the colony usually lack polyps in the surface facing the currents.

Leptogorgia sarmentosa bush-like colonies growing in one or more dimensions; usually of uniform but variable colour (yellow, red, brick orange, rarely white, rarely green); polyps usually present in all surfaces of the branches.

Underwater photographs of the most common gorgonian species from the study area are presented in Fig. 2.

Spatial and depth distribution of the main gorgonian species

In order to describe the patterns of spatial and vertical distribution of gorgonian species, a total of 69 sites were sampled by means of underwater transects by scuba diving 5 × 1 m belt transects (horizontal), 3 replicates at each site (in total 207 sampling units) from May 2009 to June 2010. Sampling sites were randomly selected, but restricted to rocky substrata, explaining the spatial gaps. In this area, gorgonians are rarely found in soft bottoms, therefore sampling effort was directed towards rocky bottoms only. The bathymetric distribution of the gorgonian species was analysed considering the average depth of each sampling unit and estimating the median density at 6 depth levels: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m and 25–30 m. The number of transects conducted at each depth level was different (see Table 1). Sampling was restricted to 30 m due to scuba diving safety rules and dive time constraints.

Interaction between gorgonians and other benthic groups

In order to assess interaction effects between gorgonians and potential competitors for space and food, the abundance of erect algae (macroalgae and turf) and sponges was quantified. While conducting the censuses of the gorgonian populations, the number of sponges was counted at each transect, and the percentage cover of erect algae was quantified using quadrats (1 × 1 m, 3 replicates).

Statistical analyses

The distribution of gorgonian species indicated that only five out of seven species were frequent in the study area (see Results). Therefore, the comparison of the density of gorgonians at different depth levels was undertaken for the overall gorgonian assemblage (all gorgonians) and for the most frequent species (*L. sarmentosa, L. lusitanica, E. gazella, E. labiata* and *E. verrucosa*) using parametric

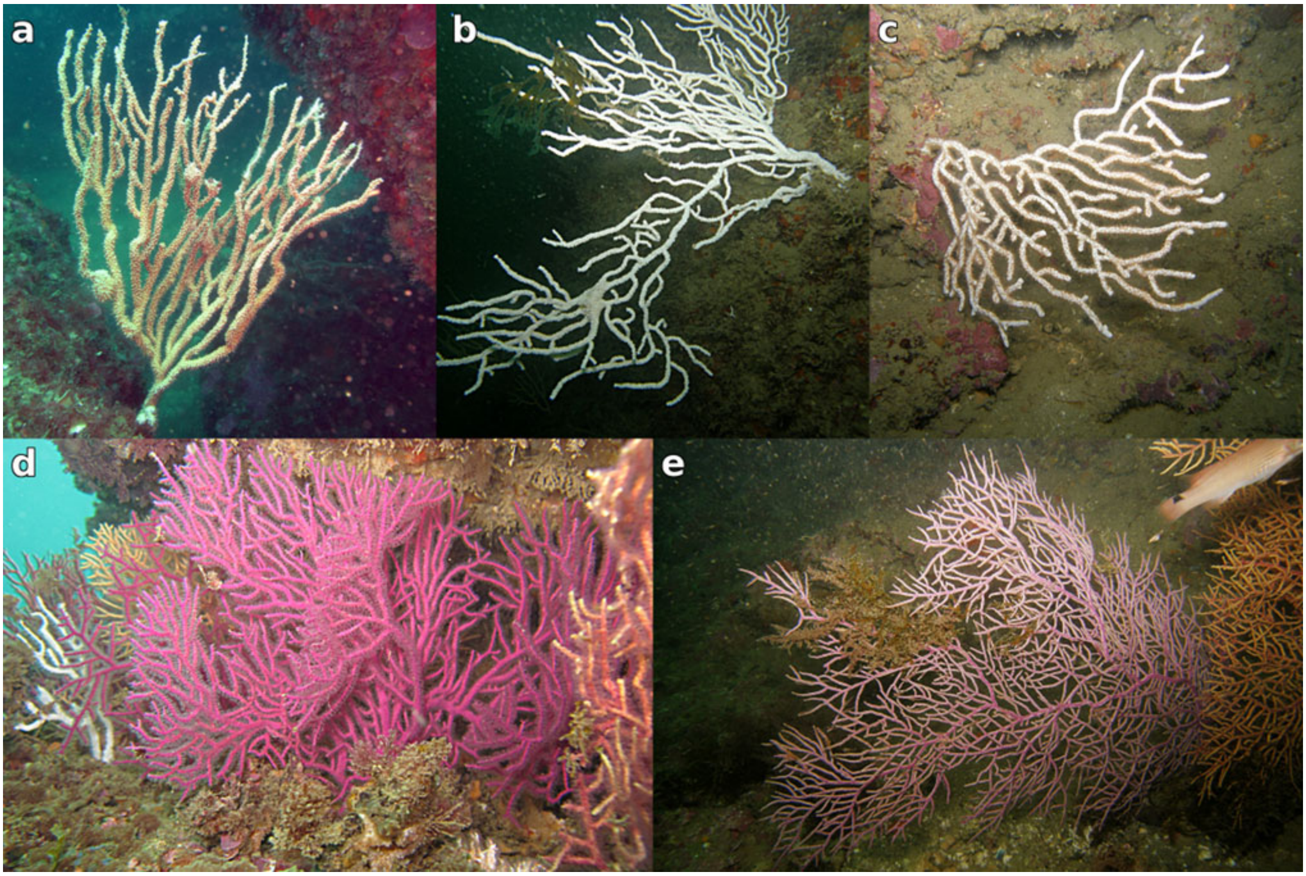

Fig. 2 Main gorgonian species found in Lagos Bay. **a** *E. labiata*, **b** *E. verrucosa*, **c** *E. gazella*, **d** *L. sarmentosa*, **e** *L. lusitanica*. Photos **b**, **c**, **d**, **e** by Pedro Veiga

(one-way ANOVA) or nonparametric methods (Kruskal–Wallis' H test) whenever ANOVA assumptions were not met. In both cases, pairwise multiple comparisons were used: Tukey Honestly Significant Differences (Tukey HSD) and Behrens-Fisher nonparametric multiple test (Berhens-Fisher) (Munzel and Hothorn 2001), respectively. The number of transects was not constant at each depth level, resulting in an unbalanced design, therefore depth levels with fewer samples (0–5 m and 25–30 m) were discarded to improve the power of the statistical tests. The correlation between depth and density of gorgonians was tested by means of an exponential regression using the $\log_e(1 + y)$ transformation of the dependent variable.

Non-metric multidimensional scaling was used to analyse differences in the distribution and abundance patterns of gorgonian assemblages using the modified Gower dissimilarity index with transformed data ($\log_2(x) + 1$). The modified Gower index excludes joint absences and is able to detect changes in composition, with the advantage of being directly interpretable as the average change in orders of magnitude between two sampling units (Anderson et al. 2006). The choice of the base of the logarithm emphasizes compositional change or changes in abundance. By using $\log_2$ transformation, the modified Gower index is weighted towards a compositional change equal to a doubling in abundance (Anderson et al. 2006), which places more emphasis on changes in relative abundance. To analyse the contribution of each species to the discrimination of the compared assemblages, the indicator value (IndVal) was used (Dufrêne and Legendre 1997). On the other hand, the ecological association of gorgonians was quantified using the Ochiai measure based on binary data (presence-absence data) (Janson and Vegelius 1981). This measure presents minimum coexistence values of 0 when the two species are never found together and maximum coexistence values of 1 when both species always occur together (Janson and Vegelius 1981).

The correlation between the abundance of gorgonians and potential competitors was assessed using linear regression. All statistical analyses were performed using the open source software R version 12.1 (R Development Core Team 2010).

Table 1 Gorgonian presence and frequency of occurrence at the different depth levels for the whole gorgonian assemblage (all gorgonians) and each species separately

Depth level	*t*	All gorgonians		Species	*twg*	(%)	Colonies		Density (colonies per 5 square metres)		
		twg	(%)				*n*	(%)	Mean	SE	Maximum
0–5	9	0	(0.0)	–	0	(0.0)	0	(0.0)	–	–	–
5–10	63	11	(17.5)	*E. labiata*	4	(6.3)	6	(16.7)	0.1	0.50	3
				E. verrucosa	5	(7.9)	12	(33.3)	0.2	0.75	5
				L. lusitanica	2	(3.2)	2	(5.6)	0.0	0.03	1
				L. sarmentosa	8	(12.7)	16	(44.4)	0.3	0.76	7
10–15	24	16	(66.7)	*E. gazella*	3	(12.5)	3	(6.1)	0.1	0.00	1
				E. labiata	7	(29.2)	14	(28.6)	0.6	0.44	4
				E. verrucosa	7	(29.2)	12	(24.5)	0.5	0.42	4
				L. lusitanica	2	(8.3)	2	(4.1)	0.1	0.13	1
				L. sarmentosa	7	(29.2)	18	(36.7)	0.8	0.65	5
15–20	72	69	(95.8)	*E. gazella*	50	(69.4)	260	(24.1)	3.6	0.72	34
				E. labiata	61	(84.7)	484	(44.9)	6.7	0.85	29
				Eunicella sp.	1	(1.4)	1	(0.1)	0.0	–	1
				E. verrucosa	48	(66.7)	181	(16.8)	2.5	0.59	19
				L. lusitanica	16	(22.2)	26	(2.4)	0.4	0.23	4
				L. sarmentosa	35	(48.6)	125	(11.6)	1.7	0.57	15
20–25	30	29	(96.7)	*E. gazella*	23	(76.7)	153	(14.4)	5.1	1.78	38
				E. labiata	29	(96.7)	327	(30.7)	10.9	2.43	55
				E. verrucosa	26	(86.7)	264	(24.8)	8.8	2.19	39
				L. lusitanica	9	(30.0)	30	(2.8)	1.0	0.60	6
				L. sarmentosa	24	(80.0)	291	(27.3)	9.7	2.18	42
25–30	9	9	(100.0)	*E. gazella*	7	(77.8)	44	(17.3)	4.9	1.97	15
				E. labiata	8	(88.9)	74	(29.1)	8.2	1.80	16
				E. singularis	1	(11.1)	3	(1.2)	0.3	–	3
				E. verrucosa	9	(100.0)	86	(33.9)	9.6	2.44	22
				L. lusitanica	6	(66.7)	12	(4.7)	1.3	0.37	3
				L. sarmentosa	8	(88.9)	35	(13.8)	3.9	1.08	9

t, number of transects sampled; *twg*, transects with gorgonians; *n* number of colonies

Results

Distribution patterns of gorgonian species

Occupancy and abundance

In Lagos Bay, gorgonians were present in 64.7 % of the 207 sampling units, totalling 2481 colonies belonging to seven *taxa* (Table 1). Four species, *E. labiata, E. verrucosa, L. sarmentosa* and *E. gazella*, were responsible for 96.9 % of the total abundance. *E. labiata* was the most frequent (52.7 % of transects) and abundant species (36.5 % of the total). *E. verrucosa, E. gazella, L. sarmentosa*, were also were also frequent (39.6–45.9 % of the transects) and abundant (18.5–22.4 % of the total abundance). *L. lusitanica* was found in 16.9 % of the transects but accounted only for 2.9 % of the abundance. *E. singularis* was rare as only three colonies were accounted in a single transect.

Spatial and depth distribution

Generally, gorgonians were present in the entire study area, without any evidence of spatial segregation (Fig. 3).

In Lagos Bay, gorgonians were found from 7.5 to 27 m (the maximum depth sampled). The depth range of all species presented similar upper limits, with *L. sarmentosa* occurring from 7.5 m, *E. verrucosa* from 8.0 m, *E. labiata* and *L. lusitanica* from 8.7 m and *E. gazella* from 11.6 m. The increase of gorgonians' abundance with depth was evident and common to the most frequent and abundant species (Fig. 4). Up to 15 m, gorgonians were rare or presented very low abundance. At depths deeper than 15 m, all species increased in abundance and showed similar trends.

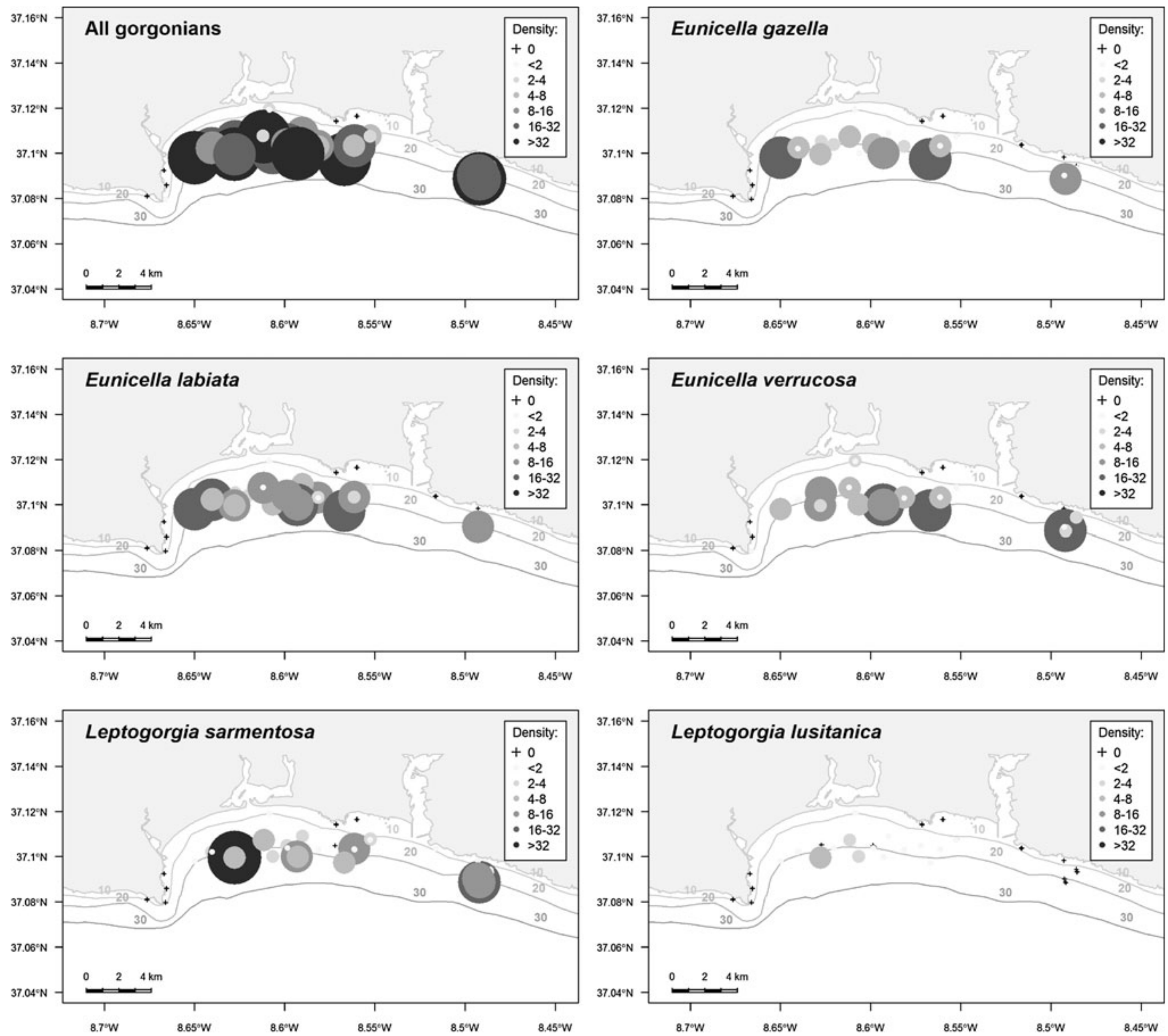

Fig. 3 Spatial distribution of gorgonian species in Lagos Bay. The size of the bubbles reflects the abundance of the gorgonians at each transect. Density is presented as colonies per 5 square metres

At 20–25 m, more than colonies per 5 square metres were found in Lagos Bay. All species showed large variation in abundance at 15–20 m and 20–25 m, especially the most abundant and frequent ones (Fig. 4).

Significant differences were found in the abundance of all species at different depth levels (Table 2). For the most abundant and frequent species, *E. labiata*, significant differences were found between depth levels below and above 15 m (Table 2). The second most abundant species, *E. verrucosa*, showed significant differences between 10–15 m and 20–25 m, whereas *L. sarmentosa* showed differences between 20–25 m (its highest abundance) and the shallower depth levels (up to 15 m). *E. gazella* was absent above 10 m and rare at 10–15 m, increasing significantly its abundance with depth. *L. lusitanica* exhibited low abundance but still the same increasing pattern with depth. Its abundance was significantly higher at depths below 15 m, even though apparently decreasing at 25–30 m.

An exponential trend was detected between depth and gorgonian's abundance for the bathymetric range of this study (Fig. 5). All regressions were highly significant ($P < 0.001$) and presented high coefficients of determination ($r^2 = 0.438$–0.787, except for *L. lusitanica* with 0.221). The increase of 1 m in depth is associated with a 10.3–11.0 % increase in the number of colonies of *L. sarmentosa, E. gazella* and *E. verrucosa*, with *E. labiata* showing the highest percentage (15.5 %) and *L. lusitanica*

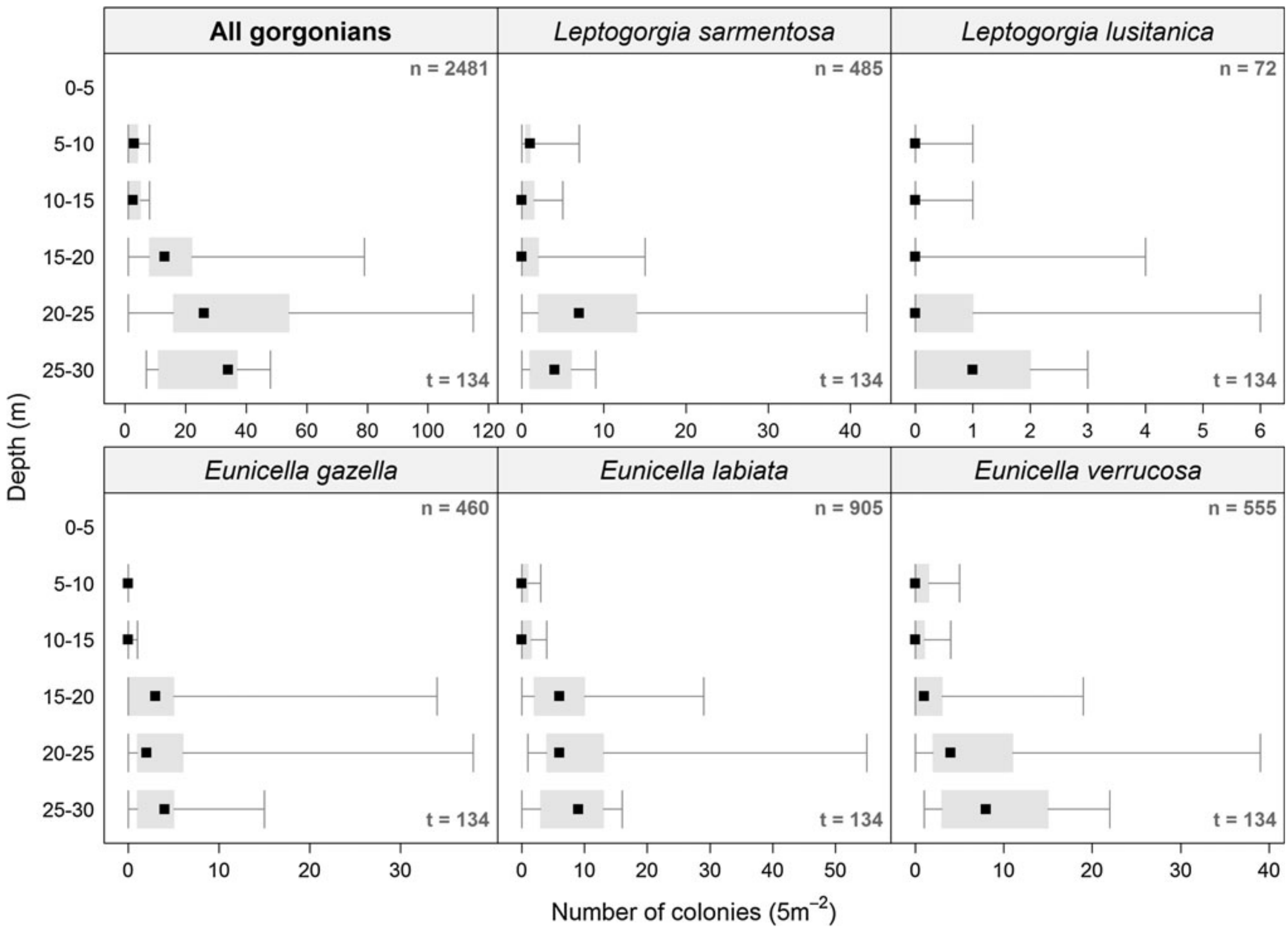

Fig. 4 Depth distribution of gorgonian species' abundance in Lagos Bay. Data correspond to transects grouped into depth levels. The *black square* represents the median; the *box* indicates the first and third quartiles; and the *line denotes* the range. Total number of colonies (*n*) and samples (*t*) are indicated for each species

presenting a much lower value (3.0 %). The rates of increase in the two latter species were significantly different from the remaining (*L. lusitanica*, ANCOVA, $P < 0.001$; *E. labiata*, ANCOVA, $P < 0.05$).

The non-metric multidimensional scaling diagram (Fig. 6) shows a depth gradient from left to right, reflecting differences in abundance within each depth level. The composition and structure of the gorgonian assemblages in Lagos Bay presented significant differences (Permanova, Pseudo $F = 4.07$, $P < 0.001$), due to higher abundances at deeper sites. However, the generally low indicator values (IndVal 0.31–0.44; $P > 0.05$) showed that the composition of the assemblages was similar at all depth levels and most species (except *E. singularis*) occurred in several depth levels. The assemblage was characterized by a dynamic alternation in species rankings with *E. labiata* being in the top two ranks along the studied depth range and *L. sarmentosa* alternating from first to fourth in rank. The low abundance of *L. lusitanica* was reflected in its rank position, fifth at all depth levels.

Four species were highly associated, coexisting in a large number of the samples. *E. labiata, E. verrucosa, E. gazella* and *L. sarmentosa* presented high values of the Ochiai measure (0.68–0.85), whereas *L. lusitanica* showed lower values (0.46–0.58) and *E. singularis* presented extremely low levels of association with the remaining gorgonian species (0–0.19).

Interactions between gorgonians and other biota

The distribution of erect algae (mainly Chlorophyta and Phaeophyta) and sponges in Lagos Bay is also depth-dependent. The abundance of erect algae (dominated by *Dictyota dichotoma*, *Asparagopsis armata*, *Halopteris filicina*, *Gelidium latifolium* and *Peyssonnelia rubra*) declined along the depth gradient. On the other hand, sponges clearly increased their abundance with depth (Fig. 7). This group was dominated by encrusting forms such as *Phorbas fictitius*, *Scopalina lophyropoda*, *Cliona viridis*, *Axinella damicornis* and *Chondrosia reniformis* and massive erect forms such as

Table 2 Results of Kruskal–Wallis' H (*H*) for the abundance of gorgonians at each depth level

Species	*H*	*P*	Behrens-Fisher test				
All gorgonians	46.30	<0.001		5–10	10–15	15–20	20–25
			5–10		*	***	***
			10–15			***	***
			15–20				NS
			20–25				
E. gazella	37.45	<0.001		5–10	10–15	15–20	20–25
			5–10		NS	***	**
			10–15			***	*
			15–20				NS
			20–25				
E. labiata	46.57	<0.001		5–10	10–15	15–20	20–25
			5–10		*	***	***
			10–15			***	***
			15–20				NS
			20–25				
E. verrucosa	36.44	<0.001		5–10	10–15	15–20	20–25
			5–10		NS	***	***
			10–15			*	***
			15–20				NS
			20–25				
L. lusitanica	11.16	0.0109		5–10	10–15	15–20	20–25
			5–10		NS	**	NS
			10–15			NS	NS
			15–20				NS
			20–25				
L. sarmentosa	22.72	<0.001		5–10	10–15	15–20	20–25
			5–10		NS	***	**
			10–15			NS	*
			15–20				NS
			20–25				

Results of the multi–comparison tests using Berhens-Fisher are also given

NS not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Crella elegans and *Axinella polypoides*. A significant negative correlation (linear regression, $r^2 = 0.439$, $F_{1,11} = 8.605$, $P < 0.05$) between the percentage cover of erect algae, and the number of gorgonian colonies was found in Lagos Bay, whereas a positive correlation (linear regression, $r^2 = 0.769$, $F_{1,11} = 36.67$, $P < 0.05$) was detected between sponges and gorgonians (Fig. 7).

Discussion

The present study detected a clear depth pattern in the distribution of all gorgonian species in Lagos Bay. According to Weinberg (1978), the two main factors affecting the octocorallia communities are irradiance and presence of sediment in the substrate. The amount of light reaching an underwater surface is related to depth, even though it depends on several factors, namely transparency and suspended particles (Gili et al. 1989). Depth, slope and the interaction of these two factors have been reported as presenting a marked positive effect in Anthozoa species distribution (Gili et al. 1989). Indeed, many studies highlighted major variations of physical (e.g. currents, sedimentation) and chemical variables (organic matter content) along the depth gradient, with consequences for the distribution of marine communities (e.g. Garrabou et al. 2002; McArthur et al. 2010).

For most species, the general pattern found indicated increasing abundances with depth within the analysed depth range. The present study also revealed that the 15 m bathymetric seems to be an important turning point in the distribution of most gorgonian species in Lagos Bay, which can be related to higher irradiance above this depth but also to higher surf impact. Indeed, in the Algarve, the lower beach profile limit (closure depth), where wave action is able to disturb the sea bottom, is around 10 m below mean

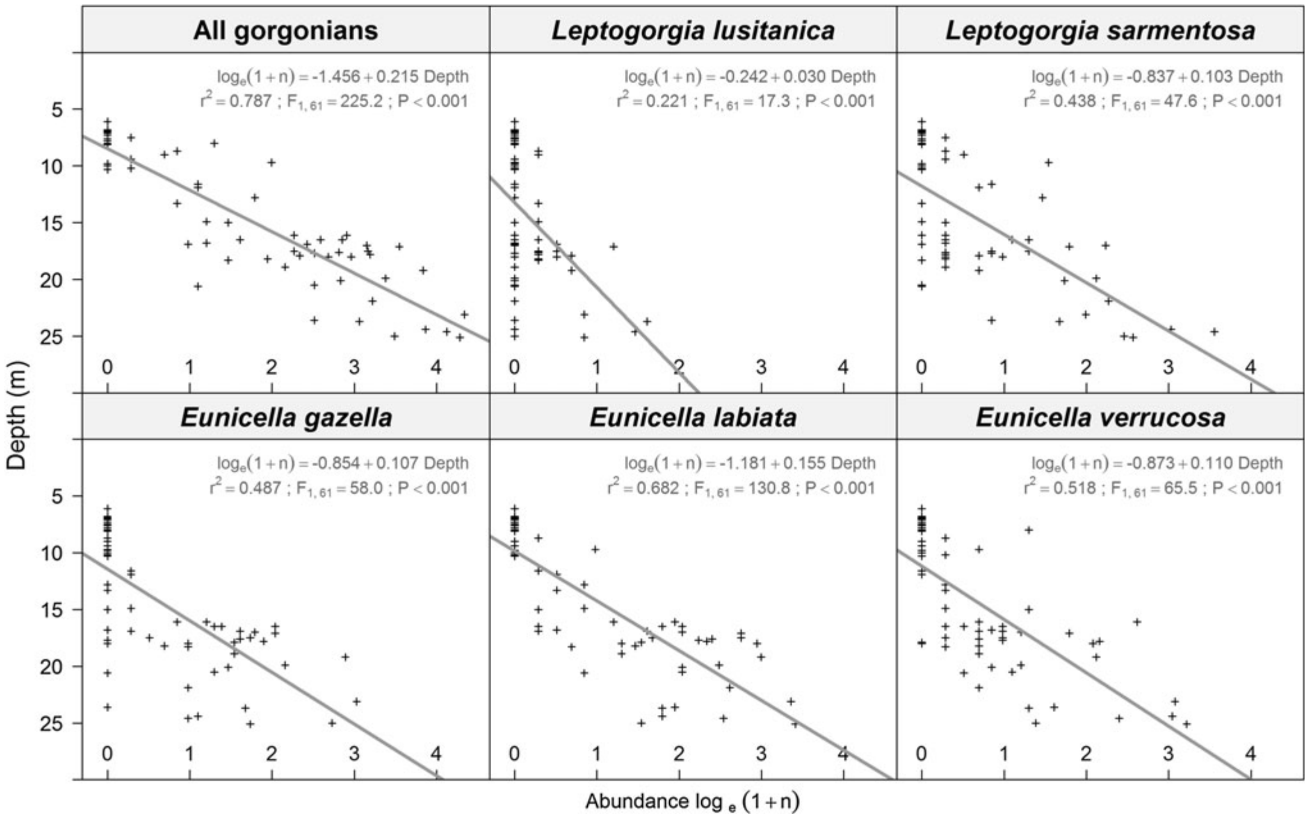

Fig. 5 Relationship between depth and abundance of gorgonians in Lagos Bay. The regression equation is presented for each species. The axes of the graphs were rotated for improving the visualization of the depth gradient

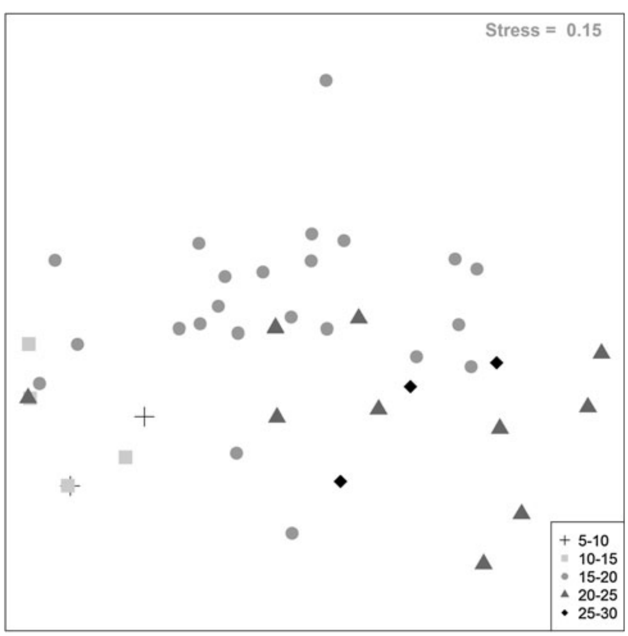

Fig. 6 Non-metric multidimensional scaling plot of the gorgonian assemblage data from Lagos Bay (modified Gower index of dissimilarity using $\log_2(x) + 1$ transformed data)

sea level (Dolbeth et al. 2007; Almeida et al. 2011), which is known to influence the patterns of benthic communities (Dolbeth et al. 2007; Carvalho et al. 2011). The turbulence from surf can detach gorgonians but also increase the rates of contact with substrate or neighbouring conspicuous fauna and flora, leading to colony tissue damage due to abrasion. The upper depth distribution limit of the dominant gorgonians in Lagos Bay was very similar suggesting that they are determined by abiotic conditions as observed elsewhere (Zabala and Ballesteros 1989; Linares et al. 2008a), especially the high water motion of shallower coastal areas. The combination of both factors (strong irradiance and surf) was already reported as being determinant in the distribution of western Mediterranean gorgonian species (Weinberg 1978).

Depth distribution in tropical shallow water gorgonians is also mainly governed by light (Sánchez et al. 1998) and other environmental factors affecting light (e.g. bed load, Yoshioka and Yoshioka 1989), mainly because most species are zooxanthellate (Dahlgren 1989; Sánchez et al. 1998). In opposition, shallow water gorgonian assemblages in the Algarve are dominated by azooxanthelate octocorals,

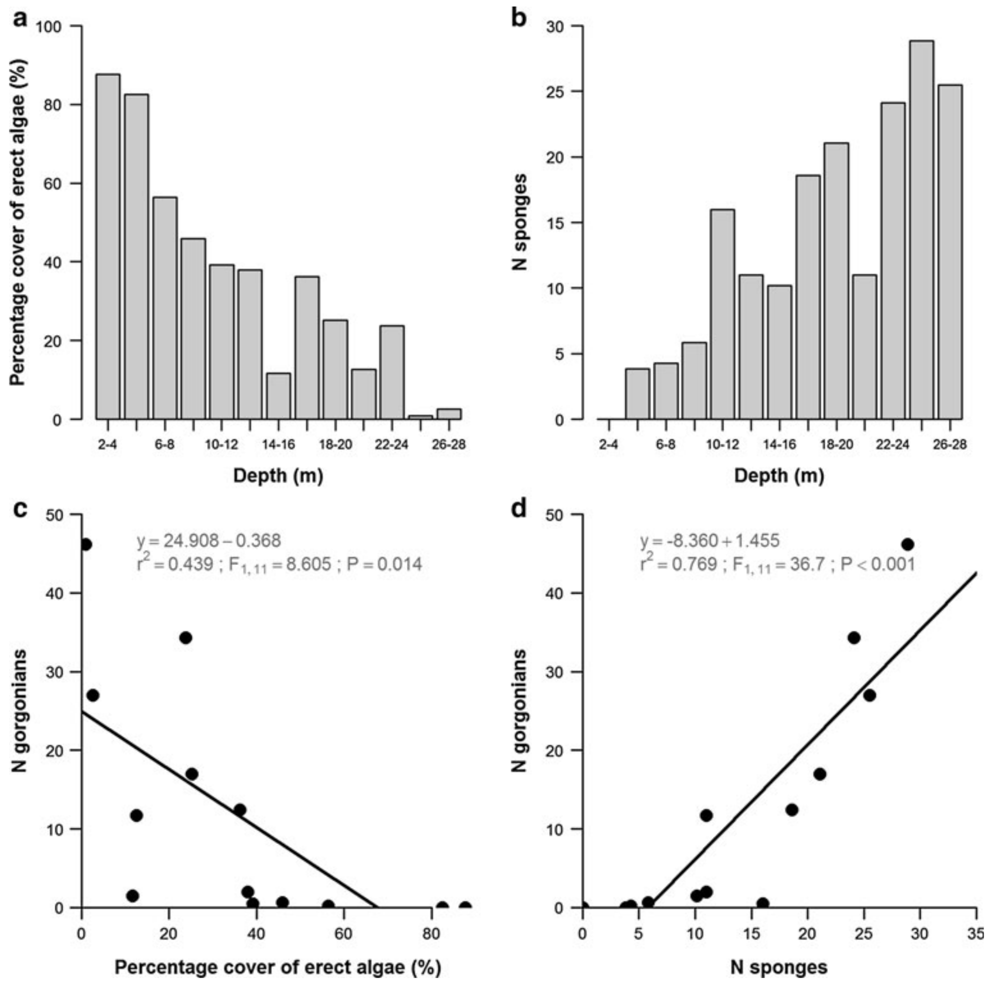

Fig. 7 Percentage cover of erect algae and abundance of sponges along the depth gradient (**a** and **b**, respectively) and linear regressions between these faunal groups and the number of gorgonian colonies in Lagos Bay (**c** and **d**). N-abundance

with the zooxanthelate gorgonian *E. singularis* being rarely sampled (and the presence of zooxanthelae in the few colonies found in the Algarve was not confirmed). Besides, in the present study, erect algae dominated the biocenoses at low depth but rapidly decreased their abundance when light intensity is reduced, and their abundance was inversely correlated to the abundance of gorgonians. In shallow water, algal-dominated benthic communities present species that favour out-competition processes being continuously replaced (Garrabou et al. 2002). In contrast, animal-dominating deeper communities tend to present slow-growth species avoiding competition displacement and enhancing the maintenance of diversity and complexity (Garrabou et al. 2002). However, there is a depth range (12–20 m) where the abiotic conditions seem suitable both for erect algae and gorgonians where competition for space occurs, explaining the negative correlation between the two groups. In fact, anthozoans are unable to compete with large algae where light intensity is high (Zabala and Ballesteros 1989; Gili et al. 1989) supporting the idea that the bathymetric behaviour of gorgonian species in Lagos Bay may be only indirectly linked to light intensity. The present observations are in agreement with the model proposed for the Mediterranean, consisting of three zones: a superficial zone (0–10 m) dominated by erect algae, a mixed zone (10–15 m) co-dominated by erect algae, crustose algae and suspension feeders and a third zone (15–42 m) dominated by suspension feeders (Zabala and Ballesteros 1989).

Sponges and gorgonians in Lagos Bay presented similar distribution patterns with depth and were positively correlated, suggesting that the species belonging to these groups coexist. Massive erect sponges such as *C. elegans* and *A. polypoides* may compete for space with gorgonians, but these are only a part of the sponges assemblage (percentage cover of sponges was not assessed) dominated by encrusting forms that use the available space below erect forms efficiently. Sponges mainly feed on very small particles, such as suspended particles, free-living bacteria and colloidal organic matter (Ruppert and Barnes 1994; Riisgård and Larsen 2010). On the other hand, gorgonians mainly feed on larger particles such as zooplankton and particulate organic carbon. Therefore, passive (gorgonians) and active (sponges) suspension feeders can co-exist (Gili and Coma 1998) as observed in Lagos Bay.

The similarity in depth distribution patterns of gorgonian species and the high association of the most abundant species suggest the coexistence of these slow-growth species. The lower coexistence of *L. lusitanica* with the more abundant species may be due to its lower abundance in Lagos Bay being absent in a high number of samples. In fact, the only case of competition between gorgonians reported for nearby areas concerns the mutual exclusion of *Eunicella cavolinii* and *E. verrucosa* in Mediterranean coralligenous habitats (Carpine and Grasshoff 1975). However, until now, *E. cavolinii* has not been found in the Algarve, and there is no evidence that *E. verrucosa* distribution is being constrained by competition. It is important to notice that the strong associations found between the gorgonian species that are more representative of Lagos Bay should be addressed with care as competition may take place at lower scales (<5 m).

Concerning the gorgonian assemblage composition, four species are well represented in the area, with *E. labiata* being the most abundant and *E. verrucosa, E. gazella* and *L. sarmentosa* presenting similar abundance. The mentioned *Eunicella* species are poorly represented in the Mediterranean, where shallow water gorgonian assemblages are dominated by *Paramuricea clavata, E. singularis* and *L. sarmentosa* (e.g. Ballesteros 2006; Gori et al. 2010). However, the abundance of each dominant species in the Mediterranean is clearly associated with habitat characteristics such as vertical facies, soft bottoms, maerl, pebbles and rocks (Gori et al. 2010), suggesting different ecological requirements. On the contrary, in Lagos Bay, the distributions of the dominant gorgonian species were all well correlated (species occurring at the same sites) suggesting that the rocky areas are relatively homogeneous with respect to available niches for several gorgonian species. However, because the study was restricted to rocky areas, the environmental gradients in several topographic and environmental factors that can affect the distribution of gorgonians are relatively short, minimizing the influence of those factors in the distribution of some species.

The most frequent and abundant species found, *E. labiata*, is relatively common in coralligenous habitats near the Strait of Gibraltar (González 1993), but to the authors' best knowledge, this species has only been reported recently for the Algarve coast (Gonçalves et al. 2007; Vieira 2008), probably resulting from erroneous identifications in the past. Another recent study also reported its occurrence in the Professor Luiz Saldanha Marine Park (Arrábida, Center Portugal) (Rodrigues 2008), where it was frequent but not dominant. Another abundant *Eunicella* species in Lagos Bay, *E. verrucosa* has been described as an Atlantic species with a wide vertical range. In the current study, this species was found from 8 to 27 m, which agrees with data from the Strait of Gibraltar, where it occurs from 6 to 87 m (González 1993). However, in the Mediterranean, this species is only found at deeper waters (35–200 m) because of the competition with *E. cavolinii*, which occurs mainly between 10 and 30 m (Carpine and Grasshoff 1975). The wider bathymetric range observed both in Lagos Bay and the Strait of Gibraltar may be due to the lack of competitive exclusion by *E. cavolinii*, which was not observed in both areas but is common in the Mediterranean. The other species dominating the assemblages in Lagos Bay, *E. gazella*, presented a distribution positively correlated to that of *E. verrucosa*, which once more is in agreement with the findings by González (1993) in the Strait of Gibraltar, where they are also commonly found together.

The dominance of *L. sarmentosa* in the study area may be related to the presence of sediment particles in the rocky bottom. Indeed, this species is clearly associated with areas with frequent but moderate disturbance, where sediment re-suspension is high (Gori et al. 2010), and has been pointed as an indicator of silt (Weinberg 1978; reported as *Leptogorgia ceratophita*). Although it has been reported to inhabit different substrates, namely rocky areas, shells on biodetritic sediments and sandy muddy areas (González 1993), it shows a high correlation with soft bottoms or surfaces where sediments tend to accumulate (Gori et al. 2010). The preferential distribution of *L. sarmentosa* within areas of high sedimentation rates may be related to its feeding requirements, as it is known that re-suspended particles are particularly important for this species' diet (Ribes et al. 2003; Rossi et al. 2004). According to our observations, sediment transport (bed load) is high in the Lagos Bay area, probably because this area is near the Rio Arade estuary, Ria de Alvor (coastal lagoon) and Ribeira de Bensafrim (creek). The habitat conditions in Lagos Bay clearly favour this species as the area is mainly characterized by low relief rocky plateaus with a thick layer of fine sediments that are easily re-suspended (submerged rock bottoms). In the Mediterranean, this species is abundant in sheltered areas with turbulent circulation but without strong near-bottom currents (Gori et al. 2010). Regarding *L. lusitanica*, even though its ecological requirements are still poorly understood, it has been described as preferring habitats with weak to moderate hydrodynamics but clear waters (González 1993). In fact, in other areas of the Algarve coast where sedimentation and turbidity is lower, this species presents higher abundance at similar depths (e.g. Pedra da Greta and Pedra do Barril, authors' unpublished data).

The low abundance and frequency of occurrence of *E. singularis* was already expected, as it is a Mediterranean species with limited distribution outside this area. This species is one of the dominant taxa in the coralligenous communities in the Mediterranean Sea (Ballesteros 2006;

Gori et al. 2010) and dominant in light-rich areas (photophilic communities) where it can be found on horizontal or slightly sloped surfaces, having a marked dependence on light. Indeed, this is the only gorgonian species in the Mediterranean area presenting zooxanthellae, but has been reported from 6 to 67 m. The preferential habitat described for this species is frequent in the study area, but the species was rarely found in Lagos Bay. We hypothesize that the colonies found in the study area are colonizers from Mediterranean populations that under favourable conditions were able to reach and settle in suitable rocky areas of the Algarve coast.

The gorgonian community in Lagos Bay is co-dominated by different species contrasting greatly to what has been reported from the Mediterranean characterized by mono-specific communities. This co-dominance extends beyond the depth limits explored in this study, as recent surveys suggest that gorgonian fauna is abundant and diverse in the south Portugal continental shelf (JG, unpublished data). Studies dealing with gorgonian species distribution on the Mediterranean rarely focused on comparative studies, probably because communities are so strongly dominated by the typical Mediterranean species *P. clavata, E. singularis* and *L. sarmentosa*. The distribution of these species with small overlap due to different habitat requirements and traits (Gori et al. 2010) probably reflects their evolutionary history. The distribution of weaker competitors may be constrained due to density-dependent traits leading to the high dominance by locally adapted species. On the other hand, in Lagos Bay, the co-dominance of several gorgonian species of different origin may reflect not only the confluence of recruits to the area promoted by physical factors but also the complex interactions between species that enhance coexistence. Multi-species coexistence (gorgonians and sponges, in the present study) may be encouraged by neighbourhood interactions (http://www.rensub.com) and local dispersal which increase intra-specific competition relative to inter-specific (Tilman 1994). What is more, gorgonians facilitate the colonization of other species (Bruno et al. 2003; Idjadi and Edmunds 2006; Thomsen et al. 2010) promoting biodiversity, biomass increase and ecological complexity. Reciprocal facilitation can enhance the positive effects and the persistence of foundation species in marine benthic communities (Bozec et al. 2012) with relevance on ecosystem functioning and conservation (Halpern et al. 2007).

Final remarks

The present study provides invaluable information on the spatial and depth distribution of gorgonian species in shallow rocky bottoms near the westernmost part of continental Europe. The key role of gorgonians in the infralittoral rocky communities poses another challenge, the capacity of these animals to cope with both thermal stress but also pathogens under a climate change scenario, an important issue for the future management of coastal marine ecosystems. The present data are also relevant for the establishment and management of future MPAs in southern Portugal, a common management tool in several areas of the world, namely in the Mediterranean, where gorgonians are used as ecological indicators. What is more, "coral gardens", including gorgonian dominated biocenoses in south Portugal and Spain have been recently proposed for the OSPAR (Convention for the Protection of the marine Environment of the North-East Atlantic) list of protected habitats (Anonymous 2011). Therefore, reference data like the one provided by this study may be relevant for future monitoring programmes. In Lagos Bay, the abundance of all gorgonian species increases with depth, showing a strong association to another suspension feeding benthic taxa, the sponges (Porifera). The specific ecological requirements regarding space and food of the two taxonomical groups probably present low overlap, thus competition levels shall be low. However, at shallower depths, gorgonians seem to be out-competed by algae for space, even though the upper limit in the distribution of gorgonians in Lagos Bay is probably mostly related to abiotic factors such as high water movement. Further multidisciplinary studies, with broader spatial and temporal scales but also wider depth ranges, supported by modern technology (e.g. ROVs and remote sensors) should be undertaken in order to elucidate on the abiotic and biotic factors that might be affecting the distribution of these octocorals in the Algarve coast.

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