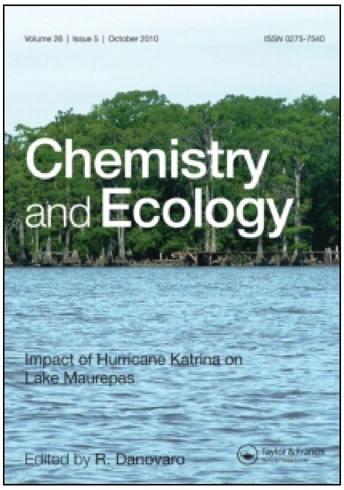

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EPIBENTHIC COMMUNITIES IN A MARINE SHALLOW AREA WITH HYDROTHERMAL VENTS (MILOS ISLAND, AEGEAN SEA)

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A quantitative study of sessile macroepibenthos was carried out in Palaeochori Bay (Milos Island, Aegean Sea) using underwater, framed, still photographs. Images of sessile epibenthos were collected from four different rocky shoals at 10–35 m depth: shoal CR, where continuous vent activity was evident, and shoals E, ST and S, without evident vent activity. At each site images were taken from four stations with different slopes. Three replicate photo-samples were collected at each station. Correspondence analysis showed that the distribution of epibenthic communities was mainly related to 'normal' environmental gradients such as slope, distance from the shore and depth. No clear, univocal effect of venting was recognized. However, small differences between the vent and non-vent sites were detected under overhangs, where vent effects could be locally amplified due to the entrapment of venting fluids.

Keywords: Epibenthos; Cover; Multivariate analysis; Hydrothermal vents; Milos; Mediterranean Sea

1 INTRODUCTION

Although only recently investigated, shallow hydrothermal vents have been known from the Mediterranean Sea since at least the XIX century, when Dumas (1860) described the gaseous manifestations in the Caldera of Panarea (Aeolian Islands, Italy) called 'bollitore' (= boiler) by the local inhabitants. Shallow water vents are less spectacular than many of their deep sea counterparts, even though the former frequently produce large volumes of free gas (gasohydrothermal vents) with temperatures of more than 100 °C and toxic chemicals such as heavy metals and H_2S (Dando *et al.*, 1995a; Aliani *et al.*, 1998; Stüben and Glasby, 1999; Hannington *et al.*, 2001). Macroscopic evidences of their presence are the white or coloured minero-bacterial mats found around the vent fluid outflows. Minerals found in these mats include elemental sulphur, silicates, arsenic and iron compounds. The bacteria are sulphur- or iron-oxidisers and photosynthetic cyanobacteria. Mats of diatoms are also present on the fringes of the venting (Dando *et al.*, 2000).

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In the Mediterranean Sea there are examples of these mats, such as the filamentous sulphur-oxidising bacteria and elemental sulphur forming a 'hairy' cover to the ceiling of some submarine caves at Palinuro, in the Tyrrhenian Sea (Bianchi *et al.*, 1994; Southward *et al.*, 1996, Mattison *et al.*, 1998) and the white and yellow mats over hydrothermal brine seeps through shallow sediments at Milos Island, in the Aegean Sea (Dando *et al.*, 1995a). Wide and conspicuous bacterial mats present on soft sediments (Desbruyères *et al.*, 1994; Thiermann *et al.*, 1997) make the investigation of the vent gradients easier than on rocky substrata.

Venting in shallow water has been shown to induce changes in both the composition and structure of benthic communities (Tarasov *et al.*, 1990; Kamenev *et al.*, 1993; Dando *et al.*, 1995b). However, most of these studies took into account soft bottom communities only (Thiermann *et al.*, 1994; Dando *et al.*, 1995b).

By contrast, rocky bottoms at shallow water vents have received less attention. The subtidal hydrothermal vents at Milos have been among the first to be studied in detail. Previous studies by our own research group dealt with a general description of the communities (Cocito *et al.*, 2000) and faunal diversity (Morri *et al.*, 1999). Detailed descriptions have been given of the distribution of the most interesting higher taxa, including hydroids (Morri and Bianchi, 1999), algae (Sartoni and De Biasi, 1999), serpuloidean polychaetes (Bianchi and Morri, 2000), anthozoans (Morri *et al.*, 2000), and sponges (Pansini *et al.*, 2000). In the present paper we investigate, for the first time, the quantitative structure of the epibenthic communities of rocky bottoms off Paleochori Bay, on the south-eastern coast of Milos. In particular, we compare substratum cover by the major space occupiers at one rocky shoal where vent emission was obvious and three rocky shoals where no venting activity was detected.

2 METHODS

2.1 Study Site

Milos Island is part of the Cyclades Archipelago in the Aegean Sea. Venting affects an area of about 35 km^2 of seabed (Dando *et al.*, 1995a) extending from the intertidal down to 240 m water depth off Milos.

The sampling area, for the present study, was in the subtidal, off the $\sim$1.4 km wide Palaeochori Bay. The seabed of the Bay is mostly sandy, with rocks outcropping in places. Hydrothermal activity appears to be more intense in the north-west and in the centre of the bay, where extensive 'white patches' of mineral-microbial mats and hydrothermal brine seepage occur (Thiermann *et al.*, 1997; Dando *et al.*, 1998). Near these brine seeps the temperature can reach up to 120 °C at 10 m depth. The seagrasses *Posidonia oceanica* and *Cymodocea nodosa*, which largely covered the seabed of the bay, were absent where the sediment temperature was 2 °C higher than ambient (Aliani *et al.*, 1998).

The chemistry of the hydrothermal fluids has been investigated by different authors who described a mixture of hydrothermal brine seeping through the sediment together with flows of both low and high salinity water (Fitzsimons *et al.*, 1997; Stüben and Glasby, 1999). The gas outflow is mainly CO_2 with significant amounts of CH_4, H_2 and H_2S (Dando *et al.*, 1995a). The pH of the venting fluids at 10 m offshore ranges between 5.5 and 6.9 and the fluid is diluted with freshwater, probably from the vapour phase, by about 20% with respect to seawater (the mean chloride concentration of the venting water is 475 mM). At a distance of more than 50 m offshore the venting water is less diluted and only enriched in metals by up to 3-fold compared to the local seawater (D. Stüben and R. Köbl, personal communication).

2.2 Sampling

Epibenthic communities were investigated in June 1996 using underwater framed still photography (Littler and Littler, 1985). Images were taken by diving on four different rocky shoals in depths of 10–35 m. Continuous vent activity was evident at the shoal CR, while no vent activity was seen at the remaining shoals E, ST and S (Fig. 1). A detailed description of each site is reported in Cocito *et al.* (2000). At each site, images were taken at 4 photo-stations, each with a different slope, *i.e.*, (sub)horizontal (0–30°), inclined (30–70°), (sub)vertical (70–90°) and overhanging (>90°). Three replicate photo-samples were taken randomly at each station, for a total of 48 images (4 sites × 4 stations × 3 replicate samples). The photographs were taken with a UW Nikonos camera equipped with a wide-angle lens (15 mm) and an electronic flash unit. The frame was maintained parallel to the lens at a distance of 60 cm by a metal rod connected to the UW camera stirrup, photographing a constant area of 0.7 m^2. Samples of species which were difficult to recognize were collected, for later identification in the laboratory, immediately after the picture was taken. The slides were analysed under a binocular microscope for taxonomic identification and then stored on Kodak PhotoCDs. The image processing software NihImage (a public domain image processing and analysis program developed at the U.S. National Institutes of Health) was used to calculate cover of the species. Area measurements were performed by outlining the species border using a freehand selection tool. The program computed the area, automatically outputting a cover matrix.

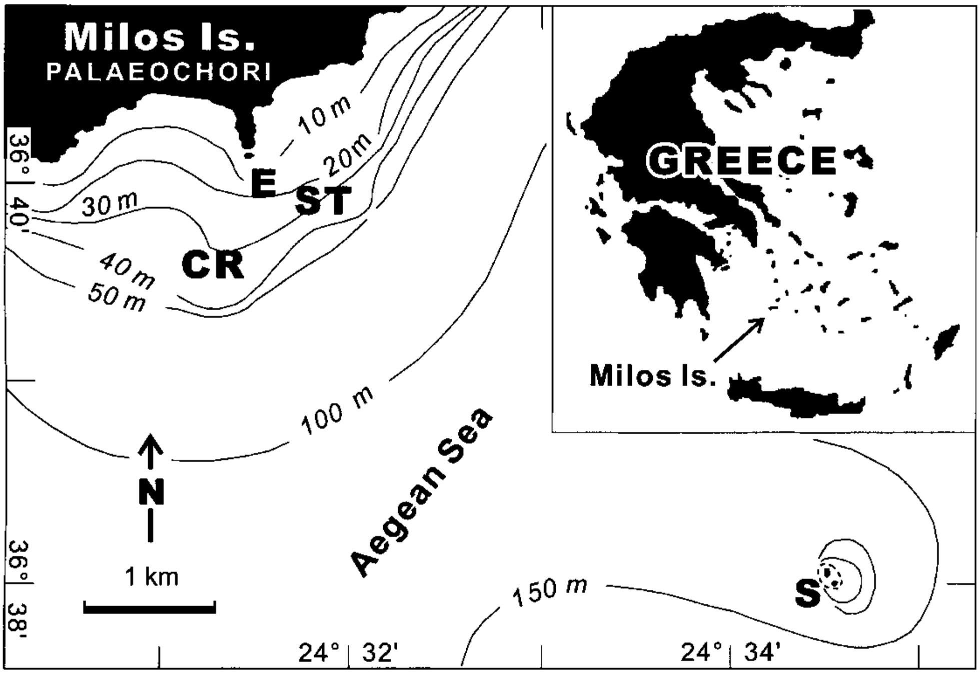

FIGURE 1 Study area and location of the four sites (E, ST, CR and S) where sessile epibenthic assemblages were studied.

2.3 Data Analysis

Differences in mean cover values were tested statistically by one-way ANOVA and compared by the Tuckey test. The matrix of cover values, after arcsin($x^{1/2}$) transformation, was first subjected to Cluster Analysis (with group-average linkage) by the Van Der Maarel's similarity coefficient to identify groups of species and define epibenthic communities, and then subjected to Correspondence Analysis to explore the underlying ecological gradients. The scores of the station points on the I and the III axes were presented using Tuckey's box-and-whisker diagrams, while correlation between axes scores and environmental variables (slope, distance from the coast) was tested by the non-metric Spearman rank correlation coefficient.

3 RESULTS

3.1 Species and Species-groups

A total of 58 macroepibenthic species was identified from the 48 photo-samples. They belonged to 6 major taxa: algae (24 species), porifera (16), bryozoans (7), cnidarians (5), polychaetes (3) and ascidians (3); the term 'algal mat' was used to indicate small, unidentified algal species forming a homogeneous turf covering the substratum (Tab. I). Epibenthos covered the substratum in almost all the stations, showing no significant difference in the degree of cover between sites, despite some bare rock (7–24%) at site E.

Algae and sponges were the most common taxa at all the sites (Fig. 2). The mean algal cover at the sites ranged from 48% to 78%. On horizontal substrata, *e.g.* at site ST, algae covered the substratum almost completely (99% cover). Decreasing algal cover values were observed with increasing slope.

Porifera were the second major taxon and occurred at all the sites with mean cover values from 13% (E) to 45% (ST). Their distribution showed an opposite trend to that of the algae: they were dominant on overhangs and abundant on vertical substrata.

The cover by algae and sponges showed significant differences between sites ($F = 3.95$, $p = 0.014$, and $F = 3.79$, $p = 0.017$, respectively). Significant differences (Tuckey test) were found between ST and CR and ST and S, when comparing algal cover, and between ST and E and ST and S, when comparing sponges.

For the remaining taxa (indicated as 'others' in Fig. 2), the only significant difference was between CR and E. Bryozoans, the most abundant taxon included in 'others', were almost absent at the vent site (CR) and generally scarce on horizontal substrata. They were abundant on vertical and on overhanging substrata, especially at site E where they covered up to 50% of the substratum.

Cluster Analysis defined six groups of species (Fig. 3). Groups 1, 2 and 5 were mostly, or exclusively, dominated by algae, groups 3, 4 and 6 by animals.

Group 1 comprised only algae, mainly Fucophyceae. This assemblage occurred especially on horizontal substrata of site S at 10 m depth, where *Sargassum vulgare* was the dominant species. On all the horizontal substrata the species of the first group were widely present (over 70% of total species), by contrast on inclined substrata their cover ranged from 5% to 27%.

Group 2, which included the largest number of species, was dominated by the algal mat, photophilic algae, such as *Acetabularia acetabulum*, *Padina pavonica* and *Stypopodium schimperi*, and the sponge *Ircinia variabilis.* Species of this group were largely found at shallow stations where they covered up to 99% of the substratum. On horizontal and inclined substrata of sites S and ST only a few species belonging to this group were found.

TABLE I List of sessile organisms, ordered alphabetically by code, recognised on the framed UW photographs taken off Palaeochori Bay, Milos.

Code	*Species (Phylum)*
Aaa	*Aaptos aaptos* (Porifera)
Aac	*Acetabularia acetabulum* (Chlorophyta)
Ada	*Axinella damicornis* (Porifera)
ama	algal mat
Aor	*Agelas oroides* (Porifera)
Apu	*Acrosymphyton purpuriferum* (Rhodophyta)
Ari	*Amphiroa rigida* (Rhodophyta)
Ave	*Axinella verrucosa* (Porifera)
Bme	*Beckerella mediterranea* (Rhodophyta)
Cba	*Cystoseira barbata* (Phaeophyta)
Cbr	*Cystoseira brachycarpa* (Phaeophyta)
Cbu	*Codium bursa* (Chlorophyta)
Ccr	*Crambe crambe* (Porifera)
Cef	*Codium effusum* (Chlorophyta)
Cin	*Caryophyllia inornata* (Cnidaria)
Cni	*Cliona nigricans* (Porifera)
cor	encrusting corallines (Rhodophyta)
Cre	*Chondrosia reniformis* (Porifera)
Cve	*Chrysymenia ventricosa* (Rhodophyta)
Dav	*Dysidea avara* (Porifera)
Dma	*Didemnum maculosum* (Tunicata)
Dve	*Dasycladus vermicularis* (Chlorophyta)
Fpe	*Flabellia petiolata* (Chlorophyta)
Hpa	*Halocynthia papillosa* (Tunicata)
Hsc	*Halopteris scoparia* (Phaeophyta)
Htu	*Halimeda tuna* (Chlorophyta)
Hym	*Hymeniacidon* sp (Porifera)
Ior	*Ircinia oros* (Porifera)
Iva	*Ircinia variabilis* (Porifera)
Lpr	*Leptopsammia pruvoti* (Cnidaria)
Lvi	*Liagora viscida* (Rhodophyta)
Mli	*Mycale lingua* (Porifera)
Mph	*Madracis pharensis* (Cnidaria)
Mtr	*Myriapora truncata* (Bryozoa)
Pcr	*Palmophyllum crassum* (Chlorophyta)
Pey	*Peyssonnelia* spp (Rhodophyta)
Pfi	*Petrosia ficiformis* (Porifera)
Pfu	*Pseudochlorodesmis furcellata* (Chlorophyta)
Pmo	*Phyllangia mouchezi* (Cnidaria)
Ppa	*Padina pavonica* (Phaeophyta)
Pte	*Phorbas tenacior* (Porifera)
Ptr	*Parasmittina tropica* (Bryozoa)
Ptu	*Protula tubularia* (Annelida)
Rhy	*Rhynchozoon neapolitanum* (Bryozoa)
Rse	*Reteporella septentrionalis* (Bryozoa)
Rvi	*Reptadeonella violacea* (Bryozoa)
Sac	*Sargassum acinarium* (Phaeophyta)
Sce	*Smittina cervicornis* (Bryozoa)
Sdy	*Salmacina dysteri* (Annelida)
Ser	Serpulidae spp (Annelida)
Sfo	*Sarcotragus foetidus* (Porifera)
Slo	*Schizoporella longirostris* (Bryozoa)
Sof	*Spongia officinalis* (Porifera)
Ssa	*Schizobrachiella sanguinea* (Bryozoa)
Ssc	*Stypopodium schimperi* (Phaeophyta)
Svu	*Sargassum vulgare* (Phaeophyta)
Syd	*Sydnium* sp (Tunicata)
Vma	*Valonia macrophysa* (Chlorophyta)
Zpr	*Zanardinia prototypus* (Phaeophyta)

Note: The code is the one used in Figs. 3–5.

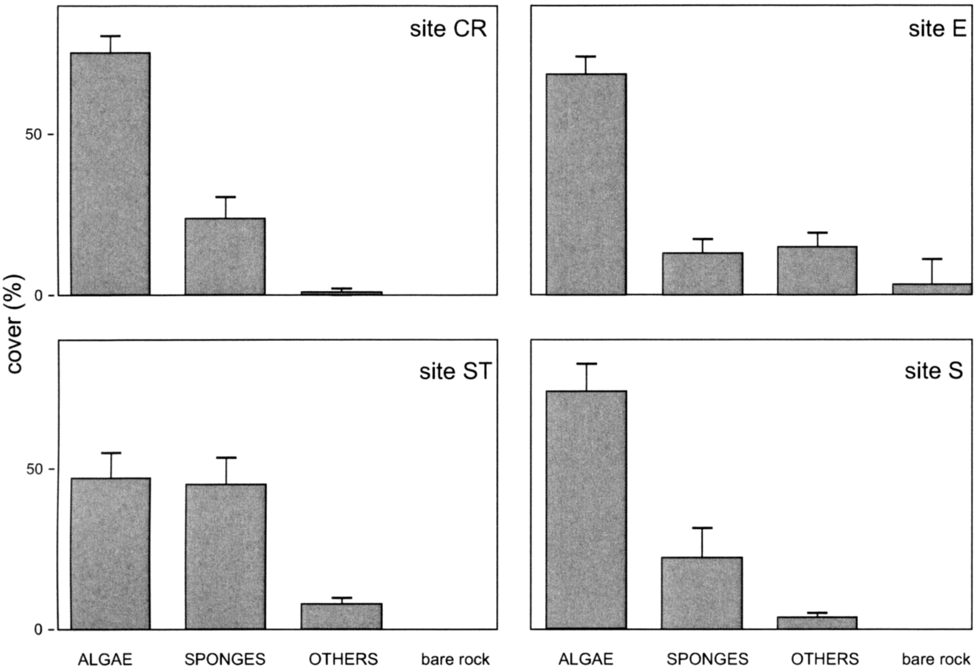

FIGURE 2 Percent cover of primary space occupiers and bare rock (means + SE) at the four sites.

The most conspicuous species belonging to group 5 was the brown alga *Sargassum acinarium*. Species of this group occurred on vertical substrata from 10 to 35 m depth at all the sites but ST. The crustose red alga *Peyssonnelia* spp, one of the most abundant species in this group, showed the widest distribution, being recorded at almost all the sites. It was very abundant at site ST on inclined substrata, where it represented 50% of the cover.

Group 3 was dominated by sponges (*Ircinia oros*, *Chondrosia reniformis*) and scleractinians (*Leptopsammia pruvoti*, *Phyllangia mouchezii*) preferring vertical substrata. *Palmophyllum crassum*, a species well adapted to dim light conditions, was the only alga in this group. This assemblage colonized overhangs (15% of average total cover) and vertical substrata (12% of average total cover) from 10 to 30 m depth, and was especially important on vertical substrata at site ST (40% of average total cover).

In group 4, sponges were again conspicuous but scleractinians were largely replaced by bryozoans (*Myriapora truncata*, *Smittina cervicornis*, *Reteporella septentrionalis*) which typically colonized crevices and overhangs from 10 to 30 m depth. They covered up to 93% of the substratum at deeper stations. Lastly, group 6 was characterized by encrusting species of bryozoans (*Schizoporella longirostris*, *Reptadeonella violacea*), sponges (*Crambe crambe*) and coralline algae. This assemblage was present on vertical substrata of all the sites. It was conspicuous in shallow (10 m) crevices at site E.

3.2 Correspondence Analysis

From the Correspondence Analysis (CA), four axes were statistically significant ($p < 0.05$) according to Lebart's tables (59 taxa × 48 stations). Total variance associated to these axes was 46%. The distribution of station- and species-points on the plane of CA defined by the first two axes (Fig. 4) showed a parabolic arc dispersion, a frequent phenomenon

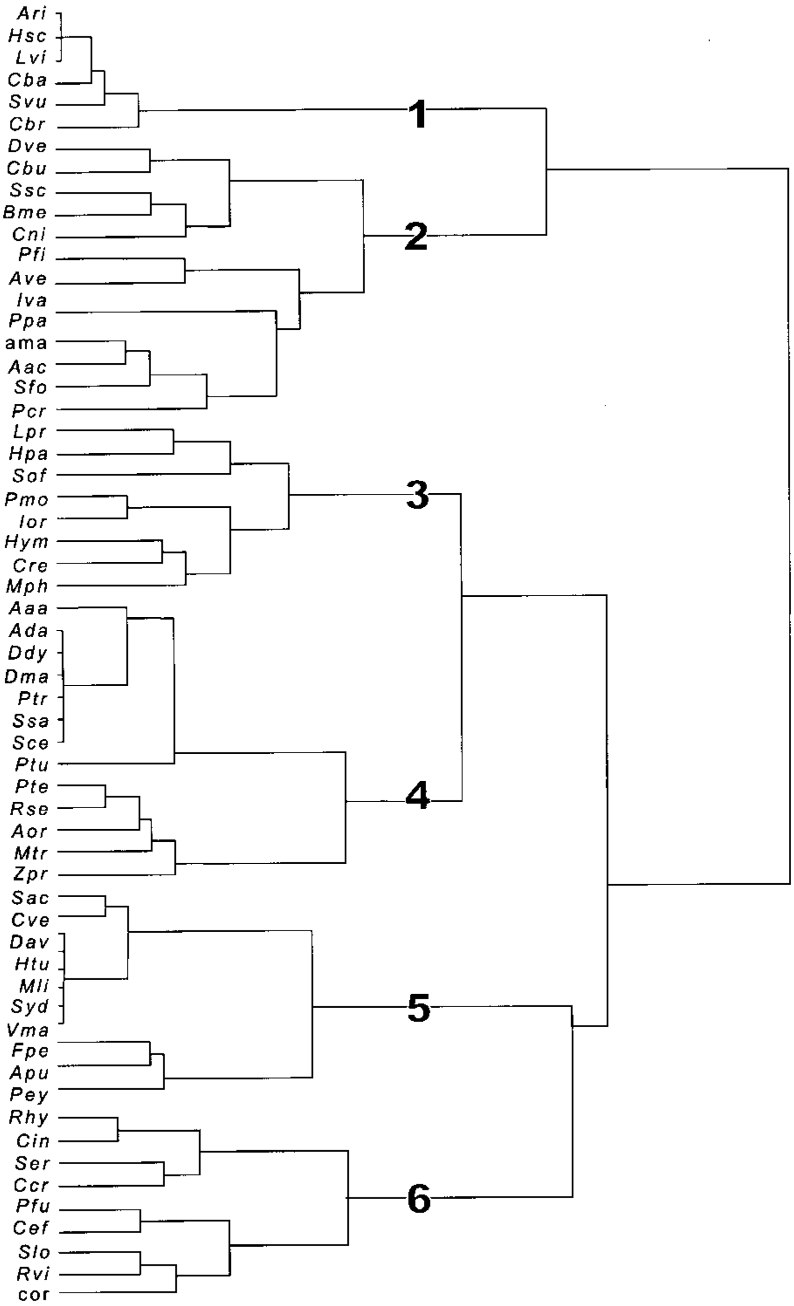

FIGURE 3 Species groups resulting from cluster analysis based on cover data (arcsine transformed, van der Maarel coefficient, average linkage). Bold numbers identify species groups (see text). Species codes according to Table I.

under CA that derives from the quadratic dependence of the second axis on the first. This distribution, known as Guttmann effect, generally occurs when systems with an underlying fundamentally uni-dimensional phenomenon are examined.

All groups dominated by animals (4, 3, 6) showed negative values along the x-axis. They were clearly separated by algae-dominated groups located on the right-hand side of the plot.

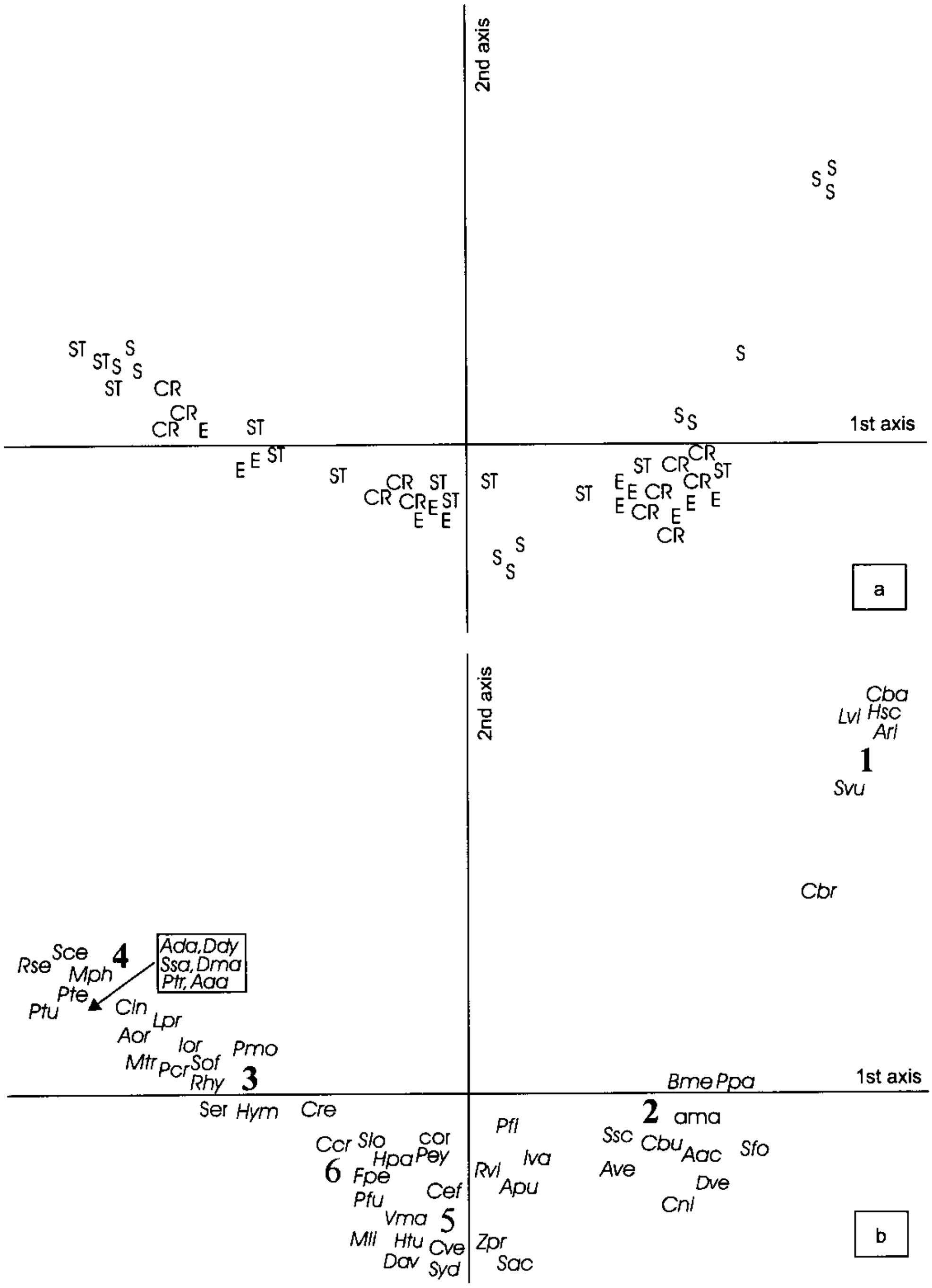

FIGURE 4 Ordination plot on the plane formed by the first and second axes extracted by CA on arcsine transformed cover data. 1st axis explains 17.6% of the total variance, 2nd axis 11.3%. Image-points (a) and species-points (b) are plotted separately for the sake of clarity. Images are indicated simply by their site name, species are coded as in Table I. Bold numbers in (b) are the centroids of the species groups resulting from cluster analysis (see Fig. 3).

The fifth group contributed poorly to axis 1, acting like a *trait d'union* between animal and algal communities. The strictly sciaphilic elements, such as *Reteporella septentrionalis* and *Smittina cervicornis*, which mainly characterize group 4, were gradually replaced by algae or animals preferring dim light conditions (*Palmophyllum crassum*, *Petrosia ficiformis*, *Crambe crambe*) or inhabiting vertical substrata without direct light exposition (*Schizoporella longirostris*). These species describe the transition towards group 1, strictly composed of fucophycean algae such as *Cystoseira barbata* and *C. brachycarpa.*

The triangular cloud dispersion shown by station-points on the plane of the third and fourth axes (Fig. 5) indicated the existence of two different ecological gradients, separately expressed by each of the axes.

The third axis opposed group 5, dominated by species occurring mostly at site S, to groups 4 and 2, comprising species mainly recorded at sites ST and E. *Sargassum acinarium*, mainly recorded at the site S, and *Sarcotragus foetidus*, mainly characterizing the coastal site E, represented the opposite poles of the gradient. Groups 1, 3, 6 were located in an intermediate position. The species belonging to these groups showed a wide distribution among sites.

The fourth axis opposed groups 1 and 6 to group 4, with groups 3, 2 and 5 in between. *Codium effusum*, *Pseudochlorodesmis furcellata* and *Schizoporella longirostris*, preferring low or moderate depth, were contrasted to *Cariophyllia inornata*, *Smittina cervicornis* and *Madracis pharensis*, which prefer deeper or darker habitats.

3.3 CA Axes Interpretation

Station-points were distributed on the plane of the first and second axes according to the slope of the stations which they represent (Fig. 6). The correlation between the first axis and the slope was statistically significant (Spearman Coefficient $r = -0.857$, $p < 0.001$).

The second axis conferred the parabolic curvature (Fig. 7), thus introducing a kind of 'intensity' effect to the gradient expressed by the first axis (Benzecri 1980; Fresi *et al.*, 1983). Such an arching curve occurs when the abundance relationships among species are non-linear, so two axes are required to represent the underlying gradient (Ludwig and Reynolds, 1988). The quadratic dependence within the axes was expressed by the equation $y = 0.9579\ x^2 + 0.1637\ x - 0.7109$ ($p < 0.05$), and both species-points (dots) and station-points (crosses) were scattered along the parabolic arc following a decreasing slope of the substratum: overhang, vertical, inclined, and horizontal (from left to right).

Along the third axis (Fig. 8), stations were distributed according to the increasing distance from the coast (Spearman Coefficient $r = -0.473$, $p < 0.001$).

To interpret the fourth axis, the station-point scores were grouped either according to depth or presence of vent activity (Fig. 9). In both cases, the resulting differences were highly significant [1-way ANOVA: $p = 0.008$ for (a) $p = 0.002$ for (b)].

Other signs of possible vent-effect were looked for, comparing the vent and non-vent sites for the variations of cover values (mean values) in each group and for the different slopes (Fig. 10). Both horizontal and inclined substrata were dominated by group 2, without significant differences between the vent and non-vent sites. On vertical substrata a more complicated community pattern was observed. This was mainly characterized by groups 5 and 6, although groups 2, 3 and 4 were also represented. Again, no significant differences were present between the vent and non-vent sites.

Under overhangs, both the vent and non-vent sites were dominated by group 4. The differences in cover were not significant. The most interesting differences concerned groups 3 and 5, dominated by scleractinians/sponges and by sciaphilic algae, respectively. Both were significantly more abundant at the vent site ($F = 5.69$, $p = 0.038$ and $F = 30.59$, $p < 0.001$, respectively).

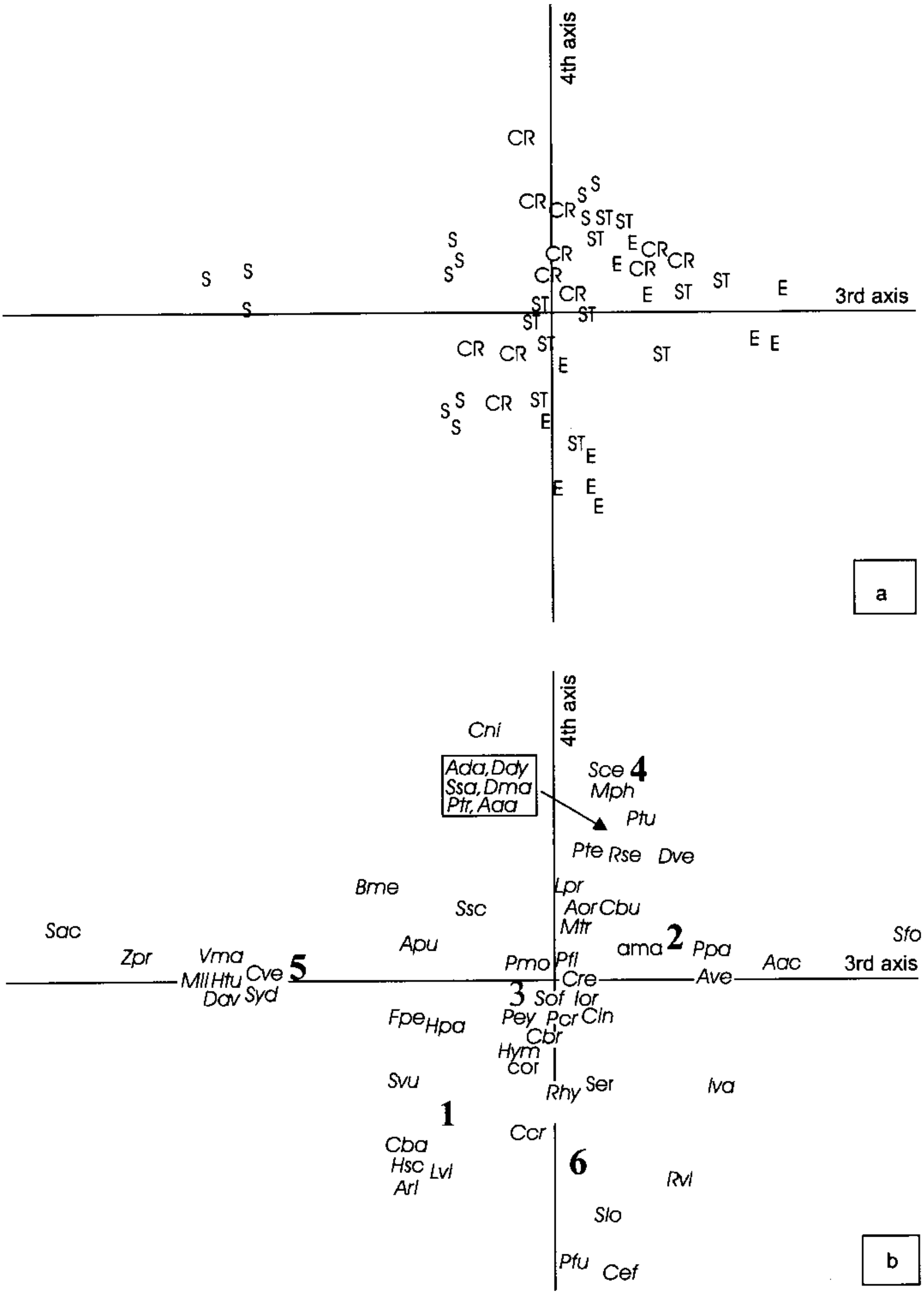

FIGURE 5 Ordination plot on the plane formed by the third and fourth axes extracted by CA on arcsine transformed cover data. 3rd axis explains 10.2% of the total variance, 4th axis 7.5%. Image-points (a) and species-points (b) are plotted separately for the sake of clarity. Images are simply indicated by their site name, species are coded as in Table I. Bold numbers in (b) are the centroids of the species groups resulting from cluster analysis (see Fig. 3).

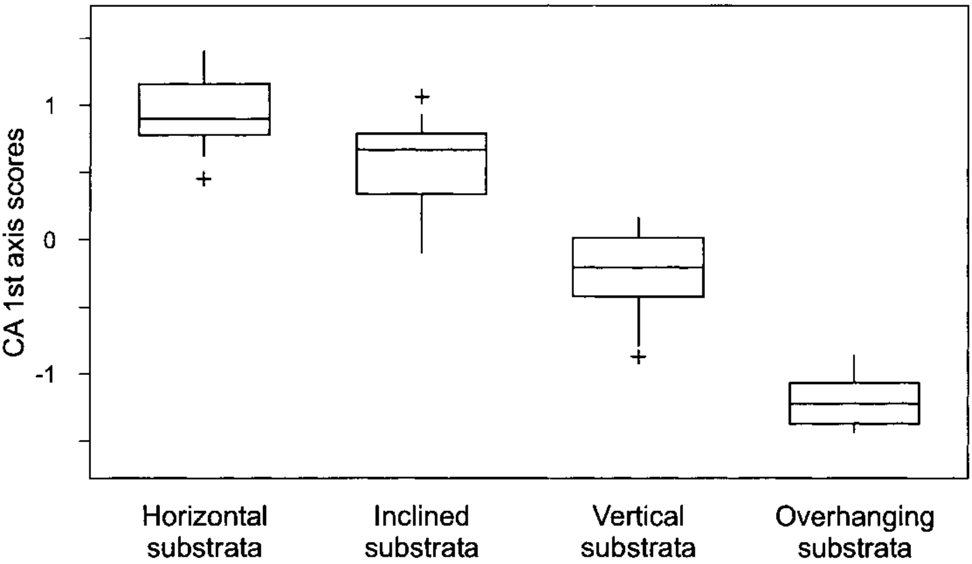

FIGURE 6 Box-whisker diagrams of the distribution of image-point scores on the first axis extracted by CA, according to the slope of the substratum at the relevant photo station. Rank correlation is very significant (Spearman $r = -0.857$, $p = 0.000$).

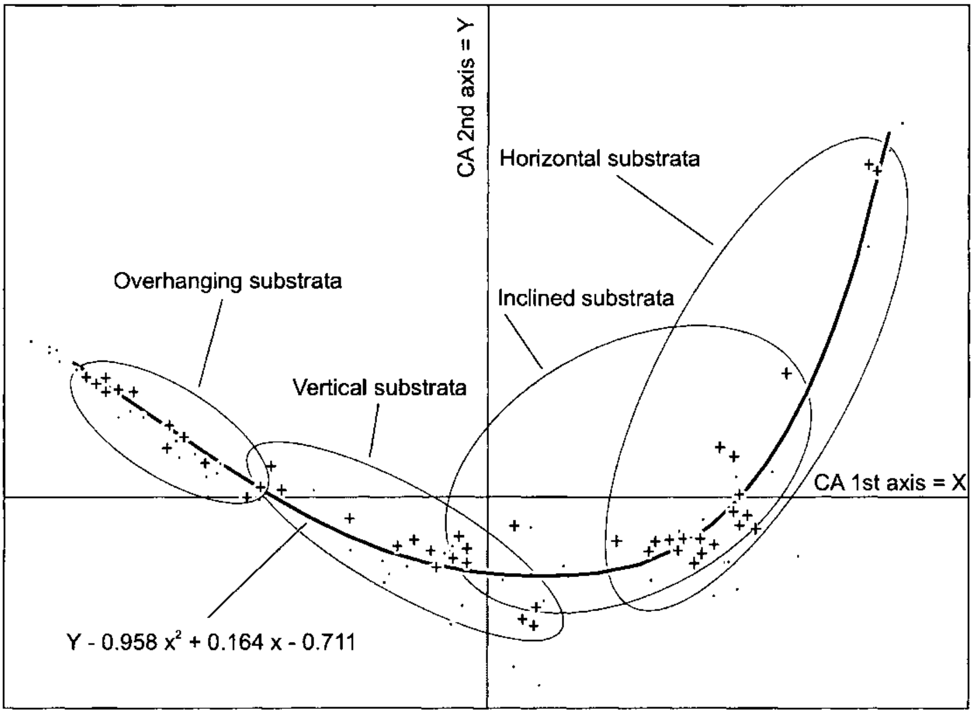

FIGURE 7 Parabolic relation between the first two axes extracted by CA. Quadratic dependence of the second axis on the first is very significant ($r = 0.883$, $p = 0.000$).

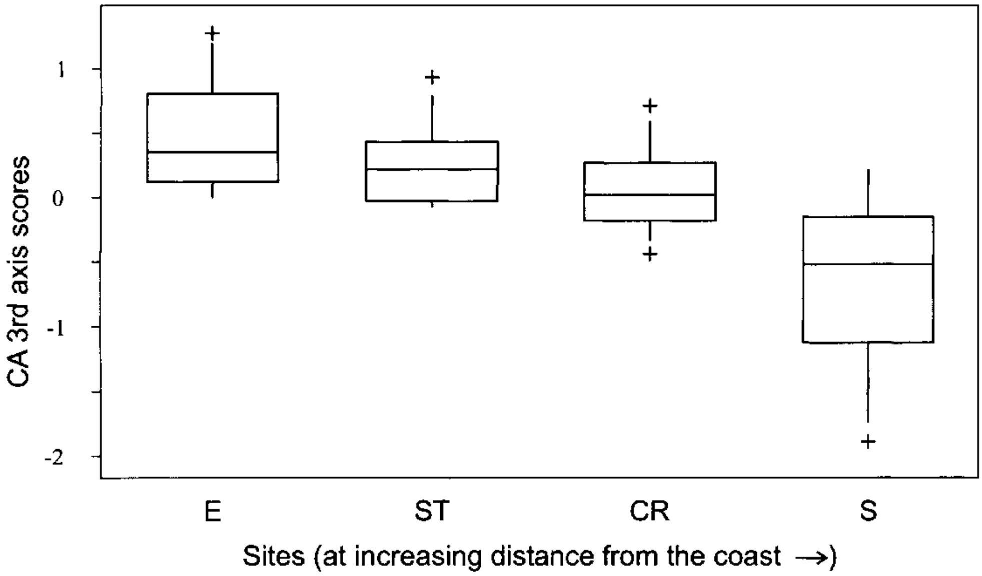

FIGURE 8 Box-whisker diagrams of the distribution of image-point scores on the third axis extracted by CA, ordered by increasing distance of the relevant sites from the coast. Rank correlation is very significant (Spearman $r = -0.473$, $p = 0.000$).

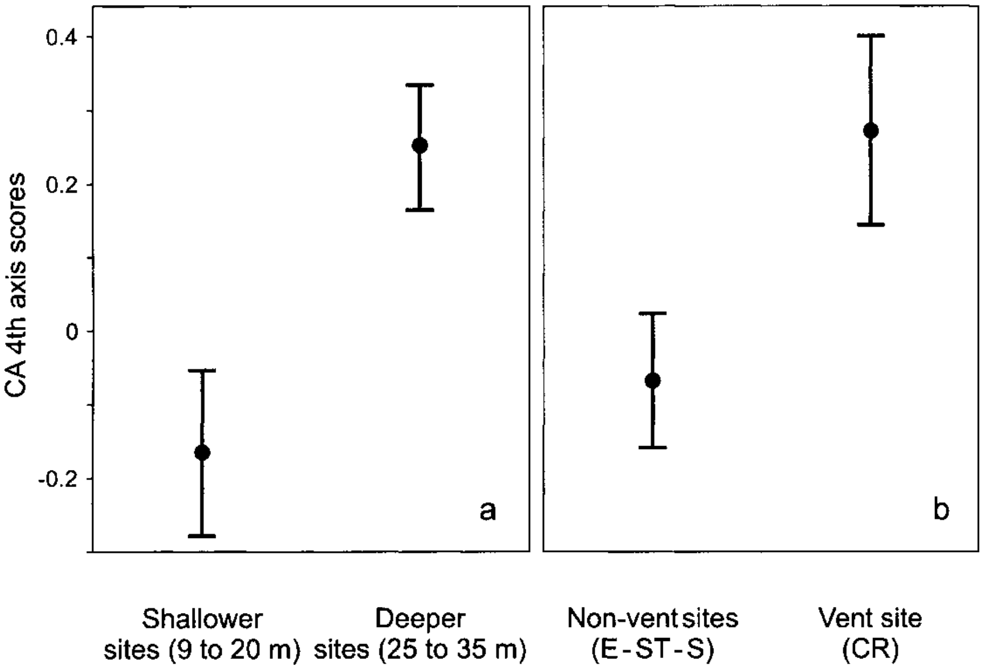

FIGURE 9 Mean (±SE) of image-point scores on the fourth axis extracted by CA, grouped by depth zones (a) or according to the presence of vent activity (b). In both cases differences are highly significant [1-way ANOVA: $p = 0.008$ for (a) $p = 0.002$ for (b)].

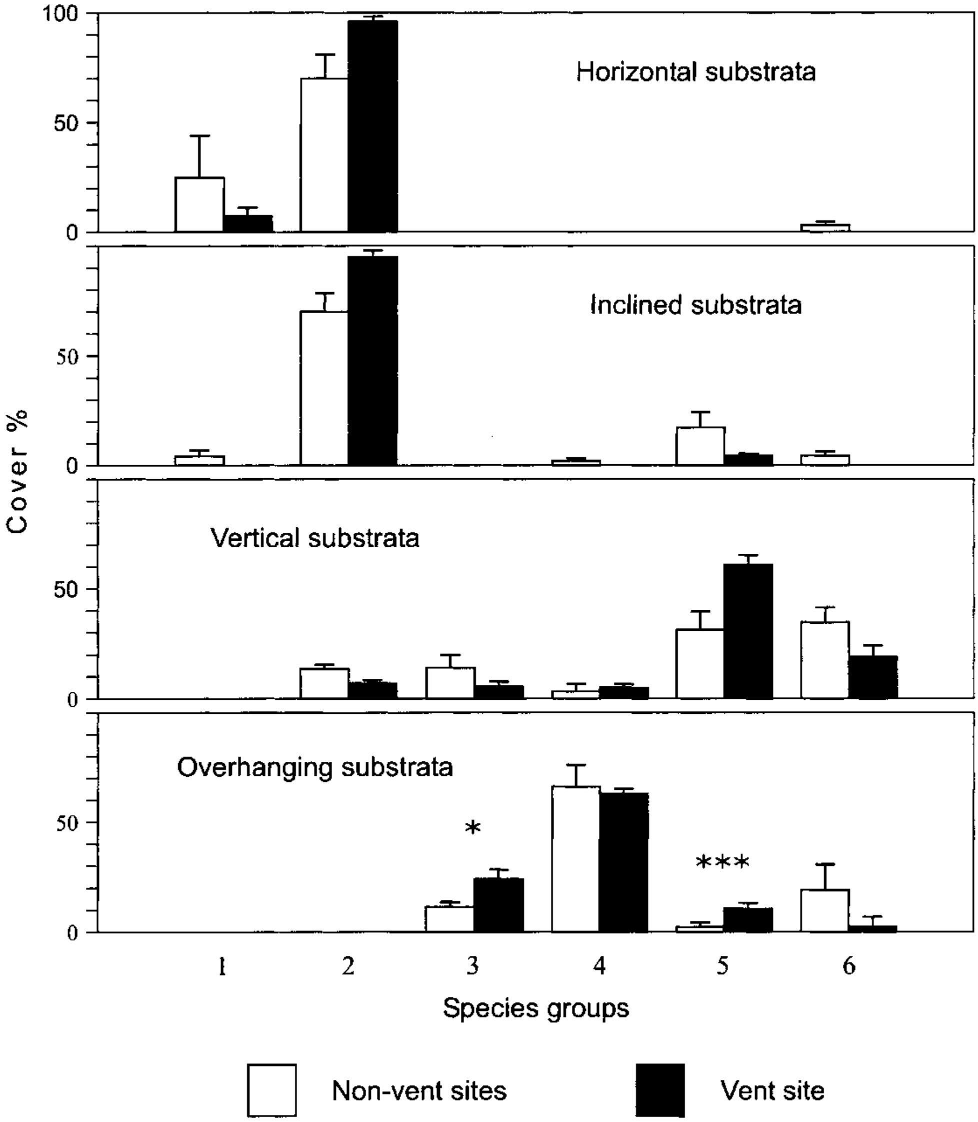

FIGURE 10 Mean percent cover (+SE) of the six species groups (sea text and Fig. 3) on differently sloping substrata. Differences between vent and non-vent sites are significant only in the cases marked with asterisks (1-way ANOVA, *: $p = 0.038$; ***: $p = 0.000$).

4 DISCUSSION

This paper reports the first quantitative data on the composition and distribution of epibenthic communities of hard bottoms in the Palaeochori Bay area. The epibenthic assemblages identified both in vent and non-vent shoals did not differ from those generally described for the Mediterranean Sea (*e.g.*, Ros *et al.*, 1985). The distribution of the epibenthic communities appeared mainly related to the ‘normal’ environmental gradients, in particular slope and distance from the shore. Depth (in the range investigated) showed a lower importance and compounded with vent activity. About the latter there is little comparative literature regarding the quantitative effects on epibenthos.

Moderate effects have been documented in the Aeolian Islands (southern Tyrrhenian Sea) by Acunto *et al.* (1996) who reported that the consequences on algal cover can vary according to different species. At Milos, Aliani *et al.* (1998) revealed a reduction of percentage cover of *Cymodocea nodosa* at a short distance from vents. Cocito *et al.* (2000) observed a severe rarefaction of the epibenthic communities on rocks surrounding the vents, in the presence of diffuse filamentous mat. By contrast, Morri *et al.* (1999) maintained that biodiversity was proportionally higher at the sites closest to hydrothermal vents. Such apparent contradictions are a consequence of the different spatial scales considered in these studies. At large scale, vents may play a role in increasing the number of species with warm-water affinities, as a probable consequence of seawater temperature anomalies (Aliani *et al.*, 2000; De Biasi *et al.*, 2001; De Biasi and Aliani, 2003).

Various points of view have been proposed to interpret community distribution on rocky substrata in a vent area. Physical and chemical factors were first recognized as the main ecological constraints on the community structure of sulphide chimneys at deep sea hydrothermal vents (Sarrazin *et al.*, 1997, 1999). Subsequent experimental manipulation demonstrated the significance of biological factors such as competition, predation and biological disturbance in setting limits to species distribution (Mullineaux *et al.*, 2000).

In our study, at a shallow water site, no clear, unequivocal clues of the effect of venting on the shoal CR have been recognised. Photographs only detect main space occupiers, which may not comprise the main responders to the effects of venting. However, significant differences between vent and non-vent sites were detected in overhangs that, for their morphology, can be considered confined environments (Dando *et al.*, 1995b). Previous research (Dando *et al.*, 1991; Kamenev *et al.*, 1993) indicated that, only in areas with reduced water motion, such as closed bays, depressions, hollows and crevices, may vent activity induce significant changes in composition and distribution of benthic communities. At shallow water gasohydrothermal vents, on soft bottoms, the large gas volume increases the circulation of seawater through the sediment, due to entrainment, so that only a very small fraction of the vented water is from the hydrothermal end-member (Dando *et al.*, 2000). This very dilute hydrothermal fluid is then further diluted by the overlying water so that the effects on epibenthos on the surrounding rocks are likely to be small. The one exception to this is when enriched fluids are released as a result of seismic activity (Dando *et al.*, 1995c). Although the hydrothermal brines seeping through the sand in Palaeochori Bay are highly enriched in reducing gases and metals (Fitzsimons *et al.*, 1997), their high density means that they stay on the seabed and are unlikely to have a direct effect on the epibenthos of hard substrata. However, these brines have a profound influence on the community structure of the infauna due to the high temperatures and high sulphide concentrations within the sediment (Dando *et al.*, 1995b; Thiermann *et al.*, 1997).

In the present study, epibenthic assemblages dominated by sponges and scleractinians (third group) showed significantly higher cover values in overhangs at the vent site. Sponges and scleractinians were more abundant and larger in size than usually in a submarine cave with hydrothermal vents at Palinuro, Tyrrhenian Sea (Morri *et al.*, 1994; Bianchi *et al.*, 1998). Similarly, Tarasov *et al.* (1999) found a considerable effect of hydrothermalism on filter-feeding epifaunal communities of New Guinea dominated by corals and sponges. Both corals and sponges grew well in hydrothermally influenced water off Ambitle Island, Papua New Guinea (Pilcher and Dix, 1996; Pilcher *et al.*, 1999) and sponges grew in warm water close to vent outlets at Kolbeinsey, Iceland (Fricke *et al.*, 1989). Filter feeders, which depend on particulate matter present in the water column for feeding, may take advantage of suspended organic matter commonly abundant near vents (Airoldi and Cinelli, 1997; Miquel *et al.*, 1998).

In contrast, the significantly higher cover by sciaphilic algae (fifth group) on overhangs at the vent site was previously unreported in the literature on shallow hydrothermal vents. Nutrient enrichment may be invoked as a possible cause, although no increase in phytoplankton production could be observed in hydrothermally influenced seawater at Milos (Robinson, 2000).

Our results evidence that the effects of hydrothermalism in shallow water are complex, and particularly subtle on rocky substratum communities. Epibenthic organisms act as foundation species (Bruno *et al.*, 2003), shaping submarine landscape and generating habitats for the associate mobile fauna. Several studies in the Mediterranean Sea indicate that the 'biological conditioning' of the substratum operated by the epibiota may greatly influence the associated fauna (Abbiati *et al.*, 1987, 1991; Sardá, 1991; Simboura *et al.*, 1995; Chemello and Milazzo, 2002). Although weak, the effects of hydrothermalism on the sessile epibenthos are therefore likely to reverberate through the whole hard substratum community (Hunter *et al.*, 1992), but no indication of such a cascade process is available at this stage of our knowledge: further study is clearly required.

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