Spatial and temporal variability of sessile benthos in shallow Mediterranean marine caves

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ABSTRACT: Hypotheses on the spatial and temporal distribution of sessile assemblages in submerged marine caves have rarely been tested. Classically, the distribution of cave benthos has been related mainly to the physical gradients along the exterior-interior axis. Using a multifactorial sampling design, we examined the distribution of species assemblages within 3 different caves in Southern Italy. Non-destructive sampling was repeated at 4 different times over a period of 11 mo. Results showed an overall pattern of change in the structure of the assemblages along the exterior-interior axis of the 3 caves (i.e. among sectors). Significant differences in species assemblages, however, were also observed within sectors (i.e. among areas), and changes in assemblages varied inconsistently with time and among caves. This result suggests a high complexity of the processes determining spatio-temporal distribution patterns in marine caves, which are context- and scale-dependent. Results also showed the uniqueness of these assemblages, which has important implications for their conservation and management.

KEY WORDS: Marine caves · Distribution patterns · Sessile benthos · Mediterranean Sea · Conservation

INTRODUCTION

Spatio-temporal variability in the distribution of populations and species assemblages is a common perception in the ecological literature (e.g. Levin 1992, Gaston & McArdle 1993, Boero 1994, Brown 1995, Boero et al. 2004). However, quantitative information on distribution patterns across relevant scales (and understanding of the processes causing or maintaining them) is confined to a small number of habitats and geographic areas and is mainly focussed on either few individual taxa, or sets of interacting species (Schneider 1994, Fraschetti et al. 2005). More quantitative information about the distribution patterns of marine species assemblages over different spatial and temporal scales is needed to support sound habitat management and conservation.

Earlier studies of Mediterranean marine caves showed that unique faunistic and ecological features characterize these habitats (Pérès & Picard 1964, Riedl

1966, Harmelin et al. 1985, Bianchi et al. 1996, Harmelin & Vacelet 1997, Chevaldonné & Lejeusne 2003). Most of these studies provided inventories of biodiversity, and preliminary descriptions of distribution patterns of species assemblages (see Riedl 1966 and references therein).

Surprisingly, in spite of a vast literature describing species composition, distribution patterns and ecological features (Riedl 1966, Ott & Svoboda 1976, Bussotti et al. 2002, Cicogna et al. 2003) few quantitative frameworks have been developed for testing hypotheses on the processes determining spatial and temporal variation of sessile assemblages of submerged marine caves (for exceptions see Gili et al. 1986, Benedetti-Cecchi et al. 1996, 1998). This is most likely due to logistical constraints limiting quantitative investigations: marine caves are less amenable to fieldwork than shallow subtidal and intertidal zones.

In a first attempt to describe the distribution of sessile benthos within marine caves, Riedl (1966)

distinguished 6 faunistic zones mostly on the basis of the distribution of algae and hydroids. Pérès & Picard (1964) described horizontal zonation patterns of cave benthos, identifying 'semi-obscure' (located in the part of the cave that receives light) and 'obscure' biocoenoses (located in the completely dark parts of the cave, with reduced seawater circulation). Species richness, biological cover, and biomass have often been reported to decrease towards the inner parts of the caves (e.g. Laborel & Vacelet 1958, Riedl 1966, Bianchi et al. 1996). Attenuations of light and water movement along the exterior-interior axis were considered as the driving forces for such changes (Riedl 1966, Cinelli et al. 1977, Harmelin et al. 1985, Gili et al. 1986). In fact, the abrupt decrease in water renewal usually determines oligotrophic conditions in the dark cave recesses due to filtering, sedimentation, and degradation of organic particles (Buss & Jackson 1981, Fichez 1990, Palau et al. 1991, Garrabou & Flos 1995 but cf. Airoldi & Cinelli 1997).

Relevant discrepancies between observed distribution patterns of assemblages in these systems and these classical models have often been reported (e.g. Harmelin 1969, Balduzzi et al. 1989, Benedetti-Cecchi et al. 1998, Corriero et al. 2000, Martì et al. 2004a,b). Internal topography, presence or absence of secondary openings, size, exposure, depth, and possible presence of hydrothermal springs were identified as interacting with the main physical gradients inside caves, causing patterns of heterogeneity different from those expected. Little emphasis has generally been given to proper quantification of small-scale patchiness, reflecting the view that in marine caves physical factors are paramount in setting distribution patterns of populations and assemblages, whereas biotic interactions play a major role in more benign environments, where recruitment rates are high (Balduzzi et al. 1989). However, small-scale patchiness is also frequent in submarine caves. Benedetti-Cecchi et al. (1996) revealed large differences in species colonization on a scale of a few metres. Variation in larval and food supply (Airoldi & Cinelli 1996), and post-settlement events have been invoked as processes generating these patterns.

In the Salento Peninsula in SE Italy (Fig. 1a), subtidal habitats are characterized by a substrate (mostly calcarenitic) conducive to the formation of large cavities: in 100 km of rocky coast, about 70 submarine caves have been mapped (see: www.tamug.tamu.edu/cavebiology/Research/research.html). The aim of this study was to conduct a mensurative experiment (Hurlbert 1984) in order to describe the distribution patterns of benthic assemblages in submerged marine caves. We used a structured sampling design to quantify variation in sessile assemblages within and across different positions in caves and their consistency through time. The tested hypotheses about spatial patterns of assemblages were driven by the consideration that, beside the most obvious environmental gradients, other sources of variability need to be properly quantified when describing distribution patterns of benthic organisms in marine caves.

MATERIALS AND METHODS

Study site. Three marine caves characterized by a similar morphology (simple horizontal tunnels, single semi-submerged entrance, presence of air chambers and similar groundwater seeps) were studied near Santa Maria di Leuca (Southern Apulia, SE Italy; Fig. 1b): 'Grotta Piccola del Ciolo' (hereafter CIO; about 100 m long); 'Grotta di Marinella' (hereafter MAR; about 65 m long); and 'Galleria della Principessa' (hereafter PRI; about 85 m long). The caves were located along a 4 km long portion of a continuous rocky coast, and provided a random subset of shallow (about 6 to 8 m depth) blind caves in the region. The internal topography of the 3 caves is characterized by a longitudinal axis, parallel to the principal fracture planes characterizing these calcareous cretaceous rocks.
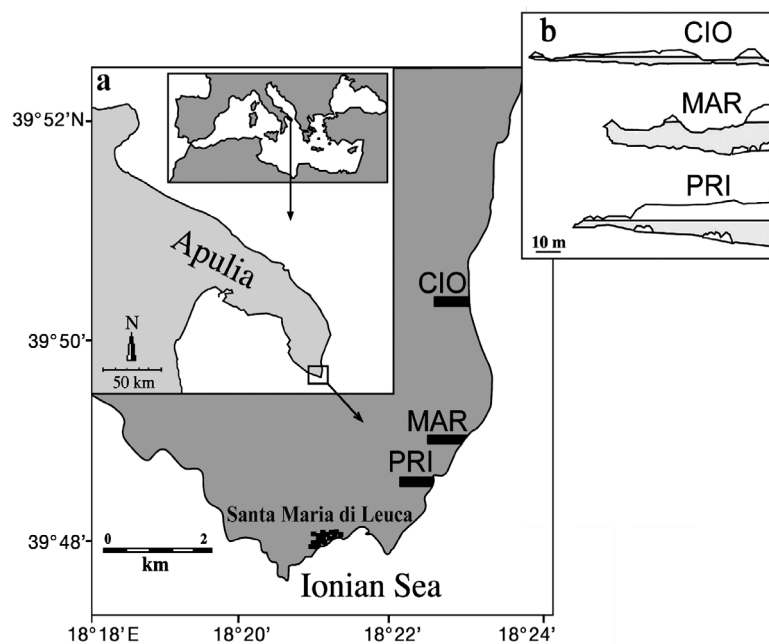

Fig. 1. Caves in the study: (a) geographical location in the Apulia Peninsula, SE Italy; (b) side views, longitudinal axis. CIO: 'Grotta Piccola del Ciolo'; MAR: 'Grotta di Marinella'; PRI: 'Galleria della Principessa'

Sampling procedures and design. Photographic samples were taken on rocky walls of the caves using a Nikonos V underwater camera with a close-up lens and 2 electronic strobes. In each of the 3 caves, 5 sectors were selected, 0, 10, 20, 40 and 60 m from the entrance (hereafter S0, S10, S20, S40, S60). Three random areas of 3 m^2 each were identified at each sector, and 8 random 16 × 23 cm photo-quadrats were taken in each area. Samples were always taken from vertical surfaces, at least 1 m above the coarse-sandy substrate. Sampling was repeated on 4 randomly selected occasions in July and November 2000, and February and June 2001 (hereafter T1, T2, T3 and T4, respectively), yielding a total of 1440 units of observation (slides).

The slides were analyzed under a binocular microscope by superimposing a transparent grid subdivided into 24 equal-sized squares. The abundance of sessile organisms (algae and invertebrates) on each slide was determined visually (Dethier et al. 1993, Benedetti-Cecchi et al. 1996) by assigning a score ranging from 0 to 4 to each taxon within each square and adding up these 24 values. Organisms filling less than 0.25 square were given an arbitrary value of 0.5. Final values were expressed as percentages. Destructive samples were also collected and specialists assisted in the taxonomic identification of organisms.

The sampling design consisted of 4 factors: Time (T, 4 levels, random), Cave (C, 3 levels, random, crossed with T), Sector (S, 5 levels, fixed, crossed with T and C) and Area (A, 3 levels, random nested in S), with n = 8 replicates per combination of factors.

Multivariate statistical analyses. The multivariate data set included 94 taxa. A distance-based permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) was done to test for the significance of terms involved in the full model. The analysis used 4999 random permutations of appropriate units (Anderson & ter Braak 2003) and was based on $\log_{10}(x+1)$ transformed data. Terms found to be significant in the analysis were examined individually using appropriate pair-wise comparisons. For each time, differences among caves, among sectors and among areas within sectors were represented by non-metric multidimensional scaling (nMDS) ordinations plotting centroids of each area. Centroids were calculated using principal coordinates (see Anderson 2001 for details). All nMDS plots were obtained using the multivariate package PRIMER (Plymouth Marine Laboratory). As most of the variability in PERMANOVA was explained by the C × S interaction term (see associated MS value in Table 2), 3 separate canonical analyses of principal coordinates (CAP) (Anderson & Willis 2003) were done to show differences in the structure of assemblages across sectors at each of the 3 caves. Distinctness of groups was assessed using leave-one-out allocation success (Lachenbruch & Mickey 1968). Individual taxa that might be responsible for any group differences seen in the CAP plots were investigated by calculating product-moment correlations of original variables (taxa) with the 2 canonical axes (r_1 and r_2). These correlations were then plotted as arrows in projection biplots. Only those taxa having relatively strong correlations (i.e. with arrow length of $\sqrt{r_1^2 + r_2^2} \geq 0.5$) were included in the plots.

Univariate statistical analyses. Four-way analyses of variance (ANOVA) were used to examine spatial patterns for single response variables (number of species, total cover). Prior to analyses, the homogeneity of variances was tested using Cochran's test (Underwood 1997). If transformations did not remove heterogeneous variances, the analyses were done on untransformed data but α was set at 0.01 to compensate for the increased likelihood of Type I error. The Student-Newman-Keuls' (SNK) test was used for multiple comparisons of the means (Underwood 1997). Pooling procedures were also used when appropriate according to Winer et al. (1991). ANOVAs were done using the GMAV5 program (University of Sydney).

RESULTS

Taxonomic composition

The 94 taxa belonged to 9 phyla (Table 1). The organisms that were not identified at the species level were aggregated into higher taxonomic groups. Moreover, several algae, sponges and bryozoans were not easily identifiable and were aggregated in 8 morphological groups (Steneck & Dethier 1994): turf-forming algae subdivided into filamentous green algae (genera *Cladophora* and *Chaetomorpha*) and filamentous dark algae (including *Ceramium* spp. and *Polysiphonia* spp.), thin tubular sheet-like algae (*Rhodymenia pseudopalmata* and *Nithophyllum* spp.), encrusting coralline algae (*Lithophyllum frondosum*, *Lithophyllum incrustans*, *Mesophyllum alternans*), encrusting sponges (including *Didiscus styliferus* and *Jaspis johnstonii*), massive sponges (*Cacospongia* spp., *Spongia* spp., *Sarcotragus foetidus*), thin encrusting bryozoans, and thick encrusting bryozoans (the latter including the species *Hippaliosina depressa*).

Specifically, the most represented groups were sponges with a total of 40 identified taxa, followed by algae with 14 taxa, bryozoans with 12 taxa, cnidarians (Hydrozoa and Anthozoa) with 10 taxa and molluscs (Bivalvia and vermetid Gastropoda) with 9 taxa.

Table 1. Taxa recorded inside the 3 caves and corresponding abbreviations

Rhodophyceae		*Dendroxea lenis*	Dlen	**Polychaeta**	
Amphiroa sp.	Amph	*Diplastrella* sp.	Dipl1	Serpuloidea	Serp
Encrusting corallines	Coral	*Dysidea* sp.	Dys1	**Bivalvia**	
Gelidiales	Gelid	*Erylus euastrum*	Eeua	*Arca noae*	Anoa
Peyssonneliaceae	Peyss	*Ircinia variabilis*	Ivar	*Chama gryphoides*	Cgry
Sphaerococcus coronopifolius	Scor	*Merlia normani*	Mnor	*Gastrochaena dubia*	Gdub
Phaeophyceae		*Myrmekioderma spelaea*	Mspe	*Lima lima*	Llim
Dictyota dichotoma	Ddic	*Oscarella* sp.	Osc1	*Lithophaga lithophaga*	Llith
Halopteris filicina	Hfil	*Paraplysilla spinifera*	Par	Ostraeidae	Ostr1
Padina pavonica	Ppav	*Penares helleri*	Phel	*Pygnodonta cochlear*	Pcoc
Chlorophyceae		*Petrosia ficiformis*	Pfici	*Spondylus gaederopus*	Sgae
Colpomenia sinuosa	Csin	*Phorbas fictitius*	Pfict	**Gastropoda**	
Palmophyllum crassum	Pcras	*Phorbas tenacior*	Pten	*Vermetus* sp.	Verm
Valonia macrophysa	Vmac	*Placospongia decorticans*	Pdec	**Cirripedia**	
Turf-forming algae		*Plakina* sp.	Plak	Balanidae	Bar
Filamentous dark algae	FDA	Porifera sp. 1	Por1	**Bryozoa**	
Filamentous green algae	FGA	Porifera sp. 2	Por2	Encrusting thin bryozoans	EB1
Thin tubular sheet-like algae	TTS	Porifera sp. 3	Por3	Encrusting thick bryozoans	EB2
Foraminifera		*Reniera sarai*	Rsar	Celleporidae	Cell
Miniacina miniacea	Mmin	*Reniera* sp.1	Ren1	Cthenostomata	Cthe
Porifera		*Sarcotragus spinulosus*	Sspi	*Frondipora* sp.	Frond
Encrusting sponges	ES	*Spirastrella cunctatrix*	Scun	*Lichenophora radiata*	Lrad
Massive sponges	MS	Spirastrellidae	Spir	*Margaretta cereoides*	Mcer
Agelas oroides	Aoro	*Sycon* sp.	Syc	*Myriapora truncata*	Mtru
Aaptos aaptos	Aaap	*Terpios fugax*	Tfug	*Pentapora* sp.	Pent1
Acanthella acuta	Aacu	**Hydrozoa**		Scrupocellaridae	Scrup
Axinella sp.	Axin	Hydroids	Hydr	*Sertella septentrionalis*	Ssep
Chondrosia reniformis	Cren	**Anthozoa**		*Watersipora cucullata*	Wcuc
Clathria toxivaria	Ctox	Anthozoa sp.	Anth	**Ascidiacea**	
Clathrina sp. 1	Cla1	*Caryophyllia smithii*	Csmi	Ascidia sp.	Asc
Clathrina clathrus	Cla	*Cereus pedunculatus*	Cped	*Aplidium conicum*	Acon
Cliona celata	Ccel	*Cladocora caespitosa*	Ccae	*Cystodytes dellechiaje*	Cdel
Cliona schmidti	Csch	Clavulariidae	Clav	*Didemnum lahillei*	Dlah
Cliona spp.	Cli1	*Leptopsammia pruvoti*	Lpru	*Diplosoma listerianum*	Dlist
Corticium candelabrum	Ccan	*Madracis pharensis*	Mpha	*Pyura dura*	Pdur
Crambe crambe	Ccra	*Parazoanthus axinellae*	Paxi		
		Polycyathus muellerae	Pmue		

Multivariate analyses

PERMANOVA detected a significant $T \times C \times A(S)$ interaction, indicating that differences in assemblage structure among areas within sectors varied across caves inconsistently with time (Table 2). Post hoc comparisons of assemblages among areas within each $T \times C \times S$ combination revealed significant differences in 50 out of 60 sets of 3 tests each. Lack of differences among areas occurred mainly in CIO at S0 (T1), S10 (T4), S20 (T2, T3 and T4), S40 (T2) and S60 (T3 and T4); and in MAR and PRI at S40 (T2 and T1, respectively).

PERMANOVA also detected a significant $T \times C \times S$ interaction, indicating that differences in assemblage structure across sectors varied with time and among caves (Table 2). Pairwise comparisons of sectors within each $T \times C$ combination (12 sets with 5 groups compared within each set, Table 3) revealed consistent significant differences between the assemblages at S0 (i.e. the entrance of the caves) and those at the inner parts of the caves (S40 and S60). Differences in assemblage structure among intermediate sectors (e.g. the comparisons S10 vs. S20 and/or S20 vs. S40) varied greatly across caves and times and were in some cases not interpretable (e.g. at PRI, T3).

nMDS plots of area centroids at the 4 sampling times reflected these general results (Fig. 2). A clear gradient of assemblage structure along the exterior-interior axis of each of the 3 caves was evident from all plots. With the only exception of PRI, where separation between S0 and S10 was less clearly depicted, areas within S0 were always distinct from areas in S40 and S60. Differences among intermediate sectors were less clear, with points referring to areas in different sectors often overlapping (Fig. 2).

Assemblage differences along the external-internal gradients were also highlighted by the CAP analyses (Table 4). The percentage of allocation success (i.e. all points correctly allocated into each group) was maximum at all sectors except S40 in CIO and at S0 and S60

Table 2. PERMANOVA based on Bray-Curtis dissimilarities of $\log_{10}(x+1)$-transformed data from 94 variables. p-values were obtained using 4999 permutations of given permutable units. Terms already involved in significant higher order interactions were not analyzed. **p < 0.01; ***p < 0.001

| Source of variation	df	SS	MS	F	p	MS$_{denom}$
Time = T	3	46822.9449	15607.6483			
Cave = C	2	285575.0448	142787.5224			
Sector = S	4	1306823.7668	326705.9417			
Area(A) = A(S)	10	29643.1769	2964.3177			
T × C	6	72540.9071	12090.1512			
T × S	12	78150.5525	6512.5460			
T × A(S)	30	113402.0648	3780.0688			
C × S	8	341975.5763	42746.9470			
C × A(S)	20	58056.4046	2902.8202			
T × C × S	24	150419.3346	6267.4723	1.4735	0.0116**	T × C × A(S)
T × C × A(S)	60	255204.2938	4253.4049	3.3176	0.0002***	Residual
Residual	1260	1615431.7963	1282.0887			
Total	1439	4354045.8635				
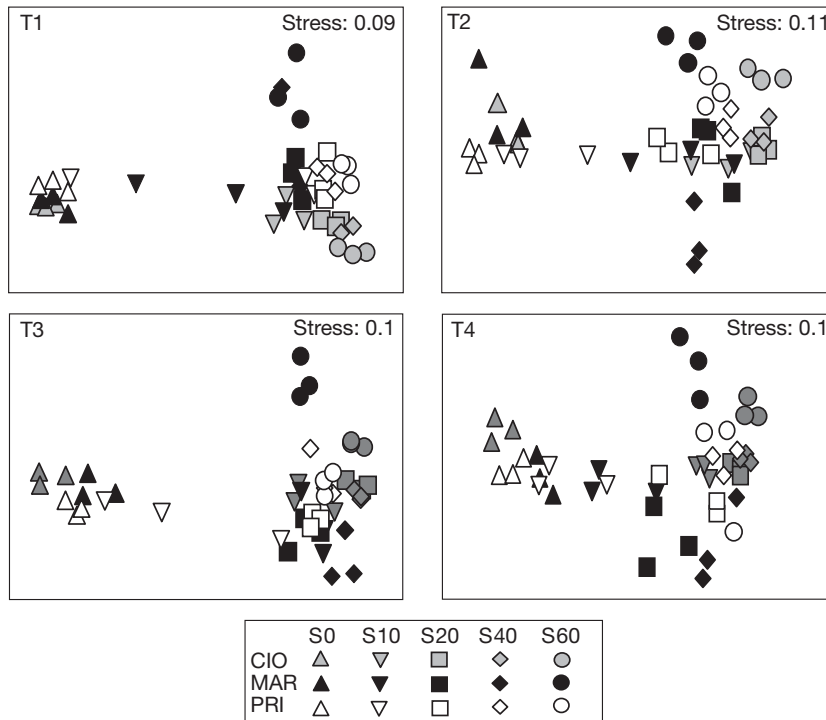
Fig. 2. nMDS plots showing differences of sessile benthos assemblages among caves, among sectors and among areas at the 4 sampling times (T1: July 2000; T2: November 2000; T3: February 2001; T4: June 2001). Each point represents the centroid of assemblages from 8 replicates based on the Bray-Curtis dissimilarities on $\log_{10}(x+1)$- transformed data. S0, S10, S20, S40, S60: sector 0, 10, 20, 40, 60 m from cave entrance, respectively

of filamentous green algae, filamentous dark algae, red algae of the order Gelidiales, encrusting coralline and Peyssonneliaceae, and the encrusting green alga *Palmophyllum crassum* characterized the assemblages at all caves. The group of thin tubular sheet-like algae characterized the assemblage at CIO and PRI while *Sphaerococcus coronopifolius* and *Valonia macrophisa* characterized the assemblage at MAR and PRI. With respect to invertebrates, boring sponges of the genus *Cliona* spp. contributed to discriminate S0 in CIO and MAR, the boring bivalve *Gastrochaena dubia* and the group of the encrusting thin bryozoans were important in CIO and MAR, respectively, whereas invertebrates were not important taxa in the entrance to PRI.

In more than one cave, a set of taxa was found which characterized the intermediate sectors (S10, S20 and S40). The boring bivalve *Lithophaga lithophaga* and the sponges *Clathria toxivaria*, *Phorbas tenacior*, *Terpios fugax* and *Spirastrella cunctatrix* were common to all 3 caves, while the anthozoan *Polycyathus muellerae* and a group of encrusting thick bryozoans characterized assemblages only in CIO and MAR intermediate sectors. Other sponges including *Agelas oroides*, *Dendroxea lenis*, *Erylus euastrum*, *Penares helleri* and the group of encrusting sponges were important in all 3 caves, but in PRI they characterized assemblages at S40 and S60. The sponge *Cliona celata* was associated with the most internal sector (S60) in MAR, and with intermediate sectors (S10 and S20) in PRI. The sponge *Diplastrella* sp. and the group of polychaetes Serpuloidea characterized the inner sectors in all 3 caves. The sector S60 was characterized by *Myrmekioderma spelaea* only in CIO and PRI, and by *Placospongia decorticans* and *Aaptos aaptos* only in MAR and PRI.

Several characterizing taxa were found exclusively in one cave. In CIO, these were the sponges *Clathrina*

in MAR. The lowest allocation success was achieved for the S10 groups in MAR and PRI. Particularly in the MAR data, the assemblage structures at S10 and S20 were not distinguishable from the analysis.

Several single variables were correlated with canonical axes in the CAP plots (Fig. 3). At S0, the groups

Table 3. Results of multivariate pairwise comparisons between the 5 sectors at each cave and time (T1: July 2000; T2: November 2000; T3: February 2001; T4: June 2001) (following the significant T × C × S term shown in Table 2). See Fig. 1 for full cave names

Cave	T1	T2	T3	T4
CIO	0≠10=20=40≠60 10≠40	0≠10=20=40≠60	0≠10=20=40≠60	0≠10=20=40≠60 10≠40
MAR	0≠10=20=40≠60	0≠10=20=40≠60	0≠10=20=40≠60	0≠10=20=40≠60
PRI	0=10≠20≠40≠60 10=20=40=60	0=10≠20=40=60	0=10≠20≠40≠60 10=20≠40≠60 20=40≠60 40=60	0=10≠20≠40=60 60=20

clathrus in the intermediate sectors, and *Clathrina* sp. 1, *Corticium candelabrum*, *Plakina* sp., *Reniera sarai*, and *Reniera* sp. at S60. In MAR, exclusive taxa were found at S10, S20, and S40; the sponge *Merlia normani*, the anthozoan *Leptopsammia pruvoti*, the gastropod *Vermetus* sp., the bryozoan *Watersipora cucullata*, and a suite of species belonging to the families Scrupocellaridae and Celleporidae. In PRI, assemblages at S10 and S20 were characterized by the sponge *Phorbas fictitius*, the anthozoan *Parazoanthus axinellae* and the ascidian *Cystodytes dellechiaje*.

Univariate analyses

The analysis of mean number of taxa detected the significance of the interaction terms T × C × A(S) and T

× C × S (Table 5), indicating differences among and within sectors that changed interactively with time and across caves.

SNK tests and visual inspection of graphs (Fig. 4) suggested that the mean number of taxa did not change in parallel with the exterior-interior axis of the caves. At MAR, the lowest values were recorded at S60 at all sampling times. Such a pattern, however, was reversed at CIO, where the richness of taxa was lowest at S0. Differences were also not interpretable according to the axis at PRI, where the highest mean number of taxa was recorded at S20, the lowest at S0.

The analysis of percent substrate cover by algae and sessile animals detected a significant T × C × A(S) interaction term, suggesting significant differences among areas that varied across sectors and caves, inconsistently with time (Table 5). The analyses also highlighted the significance of the term C × S (Table 5), suggesting that changes in percentage cover among sectors were not consistent across caves. Comparisons of sectors within each level of the factor Cave indicated a clear pattern of reduction in substrate cover from the entrance to the inner part of the cave only at MAR (Fig. 5). At both CIO and PRI, differences in percent cover among sectors were complex and not interpretable according to the exterior-interior axis.

Table 4. Results of CAP analyses examining effects of sector within each of the 3 caves (see Fig. 1). m: no. of PCO axes used in the CAP procedure; % var: percentage of total variance explained by PCO axes; δ^2_1 and δ^2_2 the squared canonical correlations for the 2 canonical axes; % All. Succ.: percentage of points correctly allocated into each group

| Cave	m	% var	δ^2_1	δ^2_2	Sector	S0	S10	S20	S40	S60	Total	% All. Succ.
CIO	8	96.62	0.98	0.93	S0	12	0	0	0	0	12	100
					S10	0	12	0	0	0	12	100
					S20	0	0	12	0	0	12	100
					S40	0	0	2	10	0	12	83
					S60	0	0	0	0	12	12	100
											Total	97
MAR	6	80.82	0.93	0.90	S0	12	0	0	0	0	12	100
					S10	2	5	5	0	0	12	42
					S20	0	1	9	2	0	12	75
					S40	0	1	2	9	0	12	75
					S60	0	0	0	0	12	12	100
											Total	78
PRI	6	83.95	0.92	0.83	S0	11	1	0	0	0	12	92
					S10	2	7	3	0	0	12	58
					S20	0	0	11	1	0	12	92
					S40	0	0	1	10	2	12	83
					S60	0	0	0	1	11	12	92
											Total	83
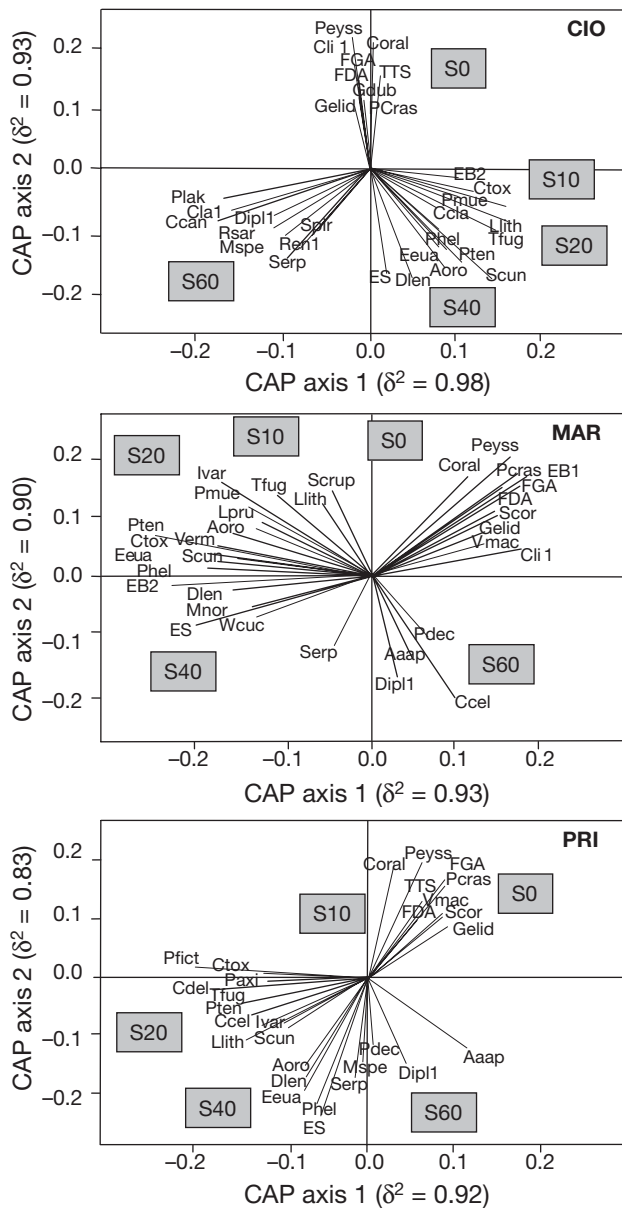
Fig. 3. CAP plots showing canonical axes that best discriminate assemblages at the 5 different sectors. See Table 1 for definition of taxonomical abbreviations

DISCUSSION

The results of this study indicate that the structure of the assemblages changed sharply along the exterior-interior axis of the 3 caves, with some taxa occurring at some distances from the entrance but not at others. Several taxa were recorded from only one cave and, often, different taxa characterized equivalent sectors in the 3 caves. However, the general pattern of differences along the gradient was not consistent in time and across caves and was blurred by differences in assemblage structure occurring among areas within

sectors. Our results therefore suggest that highly complex processes govern such spatio-temporal distribution patterns and that most of the ecological processes commonly invoked as major determinants of the structure of natural assemblages are context- and scale-dependent.

Differences in benthic assemblages along the exterior-interior axis of the 3 caves reflect a common pattern, already reported in the literature by several authors (e.g. Cinelli et al. 1977, Balduzzi et al. 1989, Zabala et al. 1989). Red encrusting and filamentous green algae characterized the entrances of the 3 caves for about 10 m inwards. Probably related to the absence of other successful competitors such as algae, sponges were quantitatively dominant in the intermediate and inner sectors. Moreover, encrusting forms of sponges characterized the innermost sectors of all caves, as observed also by Bell (2002) on the cliff walls of an Atlantic marine cave. We have not provided measures of current velocity inside the caves but the presence of these growth forms, which resist dislodging in fast and turbulent flow regimes (Bell & Barnes 2000) leads us to hypothesize that in some cases fast currents and turbulent flows may characterize even shallow blind caves, in contrast with the classical model of reduced hydrodynamic regime from the entrance towards the inner portions.

Although the horizontal zonation clearly emerges as a main pattern in the 3 caves, a simple gradient alone cannot explain all the variability observed in sessile benthos among areas within sectors. This result is not surprising since all the recent attempts at describing the distribution of populations and species assemblages along environmental gradients unequivocally showed the presence of other sources of variation influencing both spatial and temporal distribution patterns of benthic organisms (Benedetti-Cecchi et al. 1998, Menconi et al. 1999, Benedetti-Cecchi 2001, Giangrande et al. 2003, Terlizzi et al. 2003, in press, Fraschetti et al. 2005). Inside a single cave, Airoldi & Cinelli (1996) detected small-scale spatial variability of fluxes of particulate material. From this perspective, small-scale heterogeneity inside caves (e.g. small protuberances, hollows, flats, silt deposits on walls) may lead to microhabitat complexity affecting recruitment and biological interactions of established organisms (Balduzzi et al. 1989, Benedetti-Cecchi et al. 1996).

The role of competition in influencing the distribution of cave benthic assemblages is largely unknown, notwithstanding its recognized importance in affecting natural communities at small spatial scales (Jackson 1977, Buss & Jackson 1979, Sebens 1982). Buss & Jackson (1981) stressed the potential for competition for food in cryptic epibenthic fauna when high levels of depletion occur. Inside caves, Benedetti-Cecchi et

Table 5. Results of analyses of variance on mean number of taxa and percentage cover of benthic organisms. Terms already involved in significant interactions were not analyzed. ns: not significant; **p < 0.01, ***p < 0.001

Source of variation	df	No. of taxa		Total cover	
		MS	*F*	MS	*F*
Time = T	3	127.95		4660.48	
Cave = C	2	294.87		5833.24	
Sector = S	4	1425.26		42350.34	
Area = A(S)	10	37.85		465.51	
T × C	6	34.70		835.34	
T × S	12	31.00		1401.44	
T × A(S)	30	18.78		585.35	
C × S	8	357.89		9844.18	27.80***
C × A(S)	20	16.70		535.74	
T × C × S[a]	24	25.20	1.87**	738.18	1.49
T × C × A(S)	60	13.48	1.87***	495.38	1.83***
Residual	1260	7.21		271.18	
Total	1439				
Cochran Test		0.02[ns]		0.18[ns]	
Transformation		None		None	

[a]MS component pooled in analysis to obtain appropriate denominator

tively displayed and maintain their dominance for an extended period (Connell & Slatyer 1977, Underwood & Denley 1984). Biotic interactions, therefore, may largely contribute to the heterogeneity among (and within) caves.

Trends of total cover were not consistent with previous observations of a progressive decrease in total cover from the entrance towards the inner portions of blind caves (e.g. Harmelin et al. 1985, Gili et al. 1986, Balduzzi et al. 1989, Corriero et al. 2000). Whereas in MAR total cover in the innermost sector was significantly lower than in the outer sectors, high total covers were found in the inner sectors of the CIO and PRI caves. Furthermore, hydroids of the genus *Eudendrium* were also observed in the dark inner reaches of MAR. Boero (1985) and Balduzzi at al.

al. (1996, 1998) revealed the superior competitive ability of the larger organisms (i.e. the sponge *Geodia cydonium*) but also suggested a mechanism of competition through pre-emption of the substratum: once adults gain access to space, they cannot be competi-

(1989) suggested that the penetration of passive suspension-feeders such as hydroids inside marine caves is limited by conditions of insufficient water renewal. Given the presence of these organisms, an abrupt decline of water renewal is unlikely to have occurred
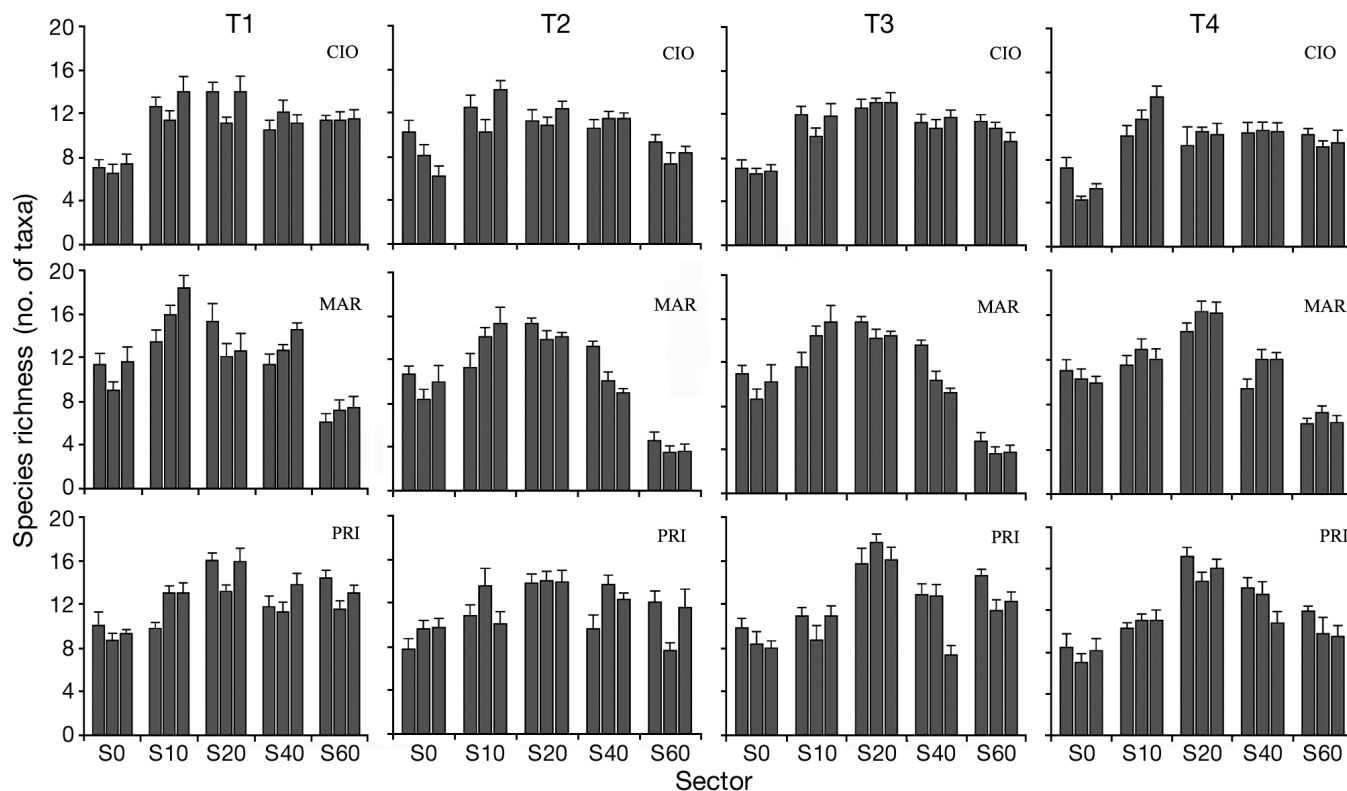

Fig. 4. Spatial and temporal patterns of species richness (mean number of taxa ± SE, n = 8). For each sector, 3 areas were sampled
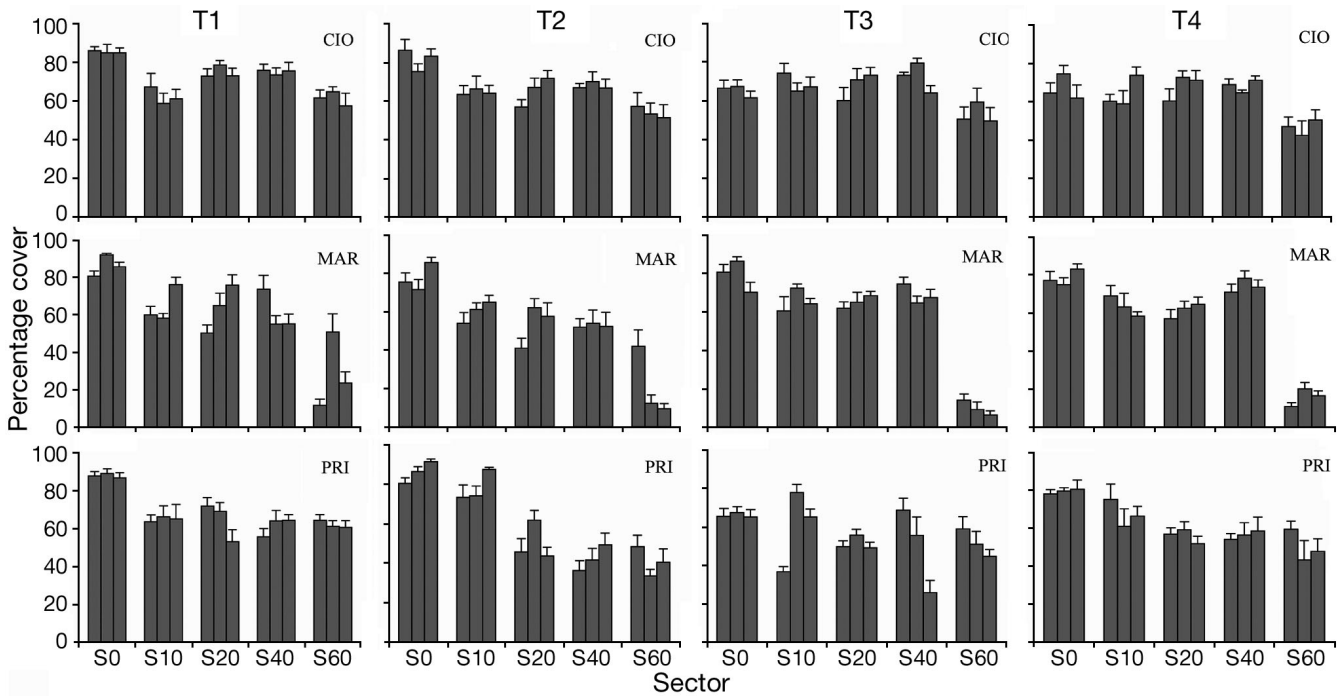
Fig. 5. Spatial and temporal patterns of percentage substratum covered by algae and sessile animals (mean ± SE, n = 8)

and a decline in food availability in the inner part of the cave should be excluded.

The differences among caves might depend on local differences in species distribution outside the caves. Several taxa characterizing the outermost sectors of the 3 caves are common in the subtidal rocky reefs of the same stretch of coast (Fraschetti et al. 2001, Terlizzi et al. in press). However, a suite of taxa was exclusive to each cave and, in general, the organisms most responsible for the high heterogeneity among caves inhabited the inner portions (e.g. the encrusting cheilostome bryozoan *Watersipora cucculata,* the sponges *Corticium candelabrum* and *Placospongia decorticans,* and the ascidian *Cystodites dellechjaie*). Results suggest that peculiar features characterize each cave, and also indicated a substantially low temporal variability in the structure of assemblages. Similar considerations are reported in the literature: Sarà (1978) stressed that assemblages of marine caves generally show a high degree of individuality. Harmelin (1985) suggested that the relative stability of environmental factors in the inner portions of the caves (Riedl 1966, Harmelin et al. 1985, Bianchi et al. 1996) could facilitate the persistence of populations well represented in certain caves but absent or rare in adjacent ones.

The caves we investigated were rather close to each other, so differences in larval dynamics due to large-scale hydrographic processes can be excluded. Species with short-lived larvae can have patchy distribu-

tion, being strongly affected by the location of source populations (Bingham 1992, Fraschetti et al. 2003) but such aspects require further investigation inside caves. For instance, encrusting cheilostome bryozoans are good competitors for space, but they have low recruitment rates (McKinney & Jackson 1989, Herrera et al. 1996); in addition sponge and ascidian larvae are generally reported as short-lived (Svane & Young 1989, Maldonado & Bergquist 2002). Encrusting cheilostome bryozoans (such as the bryozoan *Hippoliosina depressa*) and some sponge species (e.g. *Plakina* sp.) were found in only one cave. Harmelin (1997) suggested that the occurrence of some bryozoan species in caves from the Provence region (France, Mediterranean Sea) could be related to low dispersal capability. Muricy et al. (1996), studying sponges of the genus *Plakina* in the same region, hypothesized that marine caves may function as islands supporting isolated populations.

Uniqueness is an important requisite to set conservation priorities, especially for those ecological systems that, at present, are among the few marine habitats protected by the European Community (Habitat Directive 92/43 EEC). Since, from our results, peculiar benthic assemblages inhabit each cave, much deeper knowledge of these unique systems is needed to make decisions about which and how many caves need protection, so as to include proper representation of species and the relevant ecological processes operating in the different caves.

In conclusion, the present results are consistent with previous findings of the influence of environmental gradients on the distribution of cave benthos, but suggest that generalizations of results from a single cave, are not appropriate since multiple and interactive ecological processes shape cave assemblages in complex ways. Unravelling the interplay of different abiotic and biotic factors acting at different spatial and temporal scales remains a major challenge in these environments.

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