J. Mar. Biol. Ass. U.K. (2004), **84**, 557–572
Printed in the United Kingdom

Benthic assemblages in two Mediterranean caves: species diversity and coverage as a function of abiotic parameters and geographic distance

Ruth Martí*[‡], Maria J. Uriz*, Enric Ballesteros* and Xavier Turon[†]

*Centre d'Estudis Avançats de Blanes, CSIC, Accés Cala Sant Francesc, 14, 17300 Blanes (Girona), Spain.
[†]Department of Animal Biology, Faculty of Biology, University of Barcelona, Diagonal Ave. 645, 08028 Barcelona, Spain.
[‡]Corresponding author, e-mail: ruth@ceab.csic.es

Benthic assemblages of two Mediterranean submarine caves were compared. Species coverage and number of species were lower in internal (dark) communities than external. This feature was specially marked in the less illuminated cave. Ordination analyses performed on species coverage per community for each cave separately, distinguished several benthic communities from the outermost to the innermost zone of each cave. Cluster analyses on species coverage, taking into account all communities in both the caves, established similarities among communities: algal-dominated communities clustered according to the level of light received independently of the cave they inhabited, while animal-dominated communities were more similar within each cave than between the caves. Moreover, among the abiotic parameters measured irradiance was the only factor that clearly diminished from the entrance to the innermost zone in both the caves. In contrast, water movement and particulate organic matter varied differently in each cave. Results indicate that the different topography, depth and geographic location of the two caves determine water movement, light penetration and nutrient availability along the caves. These factors are responsible for determining species abundance and diversity, as well as species growth habit in each community.

INTRODUCTION

Submarine caves show patterns comparable worldwide in structure and type of communities. A common feature is a decrease in species richness, biomass and coverage of benthic organisms from the outermost to the innermost part of the cave (see Harmelin, 1985 and references therein). The usual explanation for this gradient is a reduced water turnover towards the inner part (Fichez, 1991), although experiments comparing the dissolution of plaster balls failed to substantiate this hypothesis (Balduzzi et al., 1989; Zabala et al., 1989). Likewise, no stagnation of water in microlayers over wall boundaries has been detected by dye diffusion (Zabala et al., 1989). Other physico-chemical gradients (salinity, temperature, density, dissolved oxygen and chlorophyll) that could explain this zonation were not detected either (Gili et al., 1986; Zabala et al., 1989). Light is, in all cases, the factor that clearly decreases from the external to the innermost zone of all the caves. For planktonic organisms, a strong decrease in the number of individuals from external to internal zones reported in a Mediterranean cave (Palau et al., 1991) may be explained by simple diffusion-sedimentation processes (Garrabou & Flos, 1995). However, this result is inconsistent with the lack of decrease in particulate organic matter (POM) reported for the same cave (Gili et al., 1986; Zabala et al., 1989), although it might be explained by the importance of the tripton part of the seston (not considered in planktonic studies) (Palau et al., 1991). Moreover, it has been suggested that the organic content of the particles inside the caves is lower than that of the particles outside them, so the quality of the food supply potentially available to suspension-feeders would be higher in the external zones of the caves (Fichez, 1991).

Here we attempt to compare species coverage and richness of the flora and fauna in the different communities established in two Mediterranean caves. Using photography we were able to study large areas in the caves and to encompass spatial heterogeneity. Moreover, values of abiotic parameters (irradiance, water movement and POM) were obtained for comparative purposes. Samples were collected in spring and autumn to allow for possible seasonal variation in species presence and/or abundance.

From the comparison of these two caves with contrasting topographical and trophic conditions we aimed to identify the factors determining community structure and variation along the caves, and establish whether the seasonality reported in open littoral communities of the Mediterranean also applies to the inner communities of the caves.

MATERIALS AND METHODS

Study sites

The caves are located in the north-western Mediterranean (Iberian Peninsula): the Cabrera Archipelago (Balearic Islands, oligotrophic sea) and the Medes Islands (Catalan coast, a relatively eutrophic zone). The two caves (Figure 1) have in common the limestone nature of the substrate and the mainly rocky nature

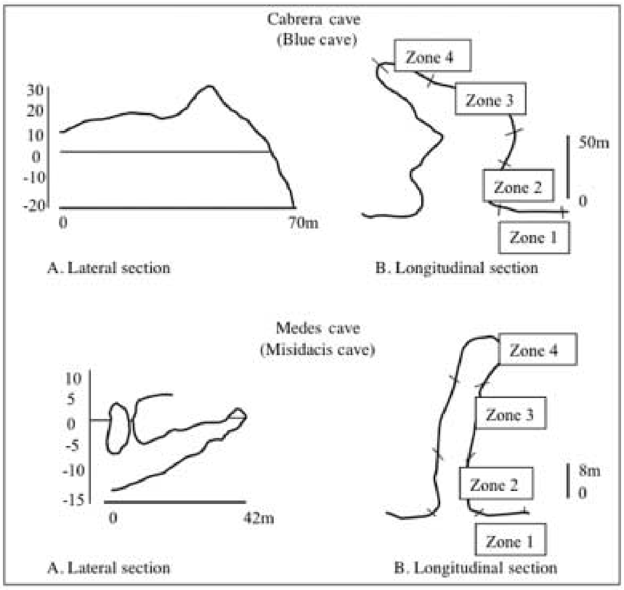

Figure 1. Cave morphology and location of the zones studied.

of the floor, with low amounts of sediment, in contrast to what is commonly found in the caves. They differ in topography and trophic characteristics.

Assemblage assessment

A longitudinal, 2 m wide transect was set up from the cave entrance to the innermost zone in both the caves. The species inventories and the measurement of physical parameters were performed by SCUBA diving along each transect. In the Cabrera cave the transect was located at 6 m depth and in the Medes cave at about ~10 m depth, which represented the mean depth of the respective caves. The study was performed in June and November 1996.

A semi-quantitative inventory of the benthic species was drawn up according to the method described in Braun Blanquet (1979). Species abundance was assessed *in situ*, and samples were collected when necessary for later taxonomic identification in the laboratory.

The semi-quantitative inventories distinguished several communities throughout the caves. Once the main communities (zones) had been established, the physical and biological parameters of each zone were studied.

Physical parameters

Irradiance

Light in each zone was measured in June and November using a SPQA Li-Cor provided with a data-logger Li-Cor LI-1000. The values are referred to the subsurface light.

Water motion and temperature

Water motion in the established zones of both the caves was derived from measurement of weight losses of calcium sulphate balls (1.5 cm in diameter) (Muus, 1968). A wire was passed through each ball and the wires were included in a flexible resin, which was attached to the walls. In a variety of sea conditions, four sets of five balls were maintained for two days on the walls of each zone, in June and November. Five additional balls were left underwater in the cave in a closed container for the same period, as a control for $CaSO_4$ dissolution in static conditions. Balls were dried for 24 h at 100°C after collection and then weighed. Losses of $CaSO_4$ in control balls were subtracted from losses measured in the balls placed on the walls. The results are expressed in mg of $CaSO_4$ lost per hour.

Water temperature was measured in each zone in both seasons.

Particulate organic matter (POM)

Seawater was collected with a Niskins sampler in each zone of both the caves, in June and November. Two litres of water were filtered on precombusted GF/F glass fibre filters of 0.22-μm pore diameter. Afterwards, filters were exposed to hydrochloric acid vapour for 48 h to eliminate the inorganic material, dried and analysed with a C:H:N Autoanalyser Eager 200. Final concentrations are expressed in μg/litre.

Community structure

Sampling

To assess seasonal coverage of the most abundant species, 20 pictures were taken at random in each zone in both the caves, in June and November 1996. The pictures, covering ~310 cm^2 each, were taken with a Nikonos-V camera and a 28 mm objective provided with a Nikonos close-up lens.

All seaweeds and animals in each picture were outlined and identified to the species level (whenever possible). The outlines were later digitalized and analysed with Sigma Scan Image software (Jandel) to measure the total area and number of individuals of each species (which corresponds to the number of patches for sponges and other encrusting organisms).

Coverage and number of species

The percentage cover of each species in the 20 pictures taken per zone and season was calculated. The values were added to obtain the percentage cover of each species in the whole area sampled per zone (6200 cm^2). A log-linear model comparing the number of species per taxon in each zone was performed for each cave.

Ordination

Detrended correspondence analyses (DCAs) were performed on species coverage to study the spatial distribution of the benthic species in each of the four zones previously defined in both the caves. This analysis provided a graph of the distance(s) between the zones on the basis of differences in species composition and abundance. The percentage cover per species was the variable analysed. The percentage of bare rock was also taken into account, since it varied strongly between zones.

The analyses used the software program PC-ORD version 4 (McCune & Mefford, 1999). Outliers were previously eliminated using the Sorensen (Bray–Curtis) distance. The down weighting of rare species option was selected to avoid their possible influence on ordination.

Because species coverage varied from June to November, especially in the most external zones dominated by seaweeds, the ordination analyses were carried out separately for each sampling season. However, as the general pattern was similar in both seasons, only the analyses from June are shown here.

An analysis was first performed for all samples of each cave separately (80 samples, 20 pictures per zone). A second analysis was performed for the animal-dominated zones (Zones 3 and 4 of the Cabrera cave and Zones 2, 3 and 4 of the Medes cave) of each cave separately since they appeared clumped in the first analysis.

Classification

Cluster analyses were conducted on percentage cover per taxonomic group to assess the relationships between zones of the two caves in the two seasons. Bare rock was not considered for these analyses.

Hierarchical clustering with group-average linking, based on similarity matrices (Bray–Curtis coefficient) was used. Data were previously transformed to double root (4th root), which down weights the importance of the very abundant species so that the less dominant, and even the rare species, contribute to similarity between samples. The PRIMER (Plymouth Routines in Multivariate Ecological Research) package for the analyses (Clarke & Warwick, 1994) was used.

A preliminary analysis was done using the percentage cover per high taxonomic entity (from Phylum to Class depending on the group) as the variable. Using the groups found in this analysis, more accurate analyses were carried out on the percentage cover per species.

RESULTS

Assemblage assessment

Species composition and abundance (semi-quantitative inventories) as well as changes in growth habit of the same species (for example massive forms at the cave entrance becoming thinly encrusting forms at the innermost parts), allowed us to distinguish four differentiated zones in each cave, which corresponded to four different communities (Pérès & Picard, 1964).

In the Cabrera cave (Figure 1A), Zone 1 corresponded to a photophilic seaweed community, and Zone 2 to a sciaphilic seaweed community. The former, facing west, was located just outside the cave. The sciaphilic community faced north-west and was located at the cave entrance. Zone 3 corresponded to a semi-dark cave community and Zone 4 represented a dark community in several aspects (see Discussion) (terminology according to Pérès & Picard, 1964).

The narrow shape of the Medes (Figure 1B) cave and its deeper location as compared to the Cabrera cave results in a darker nature of its communities. Zone 1 faced south-east out of the cave and had a hemisciaphilic seaweed community. The communities inhabiting Zones 2 and 3 corresponded to a semi-dark cave community. Although Zone 3 was darker, both zones had similar species composition, although the species showed different growth habits. The assemblage dwelling on Zone 4 represented a dark-cave community. The cave ended with a zone almost free of macroinvertebrates.

The three communities of seaweeds in the two caves can be therefore positioned along a gradient of light: photophilic, hemisciaphilic and sciaphilic.

Physical parameters

Irradiance

The irradiance values in each zone of both the caves are reported in Table 1. In the Cabrera cave, Zone 1 (located outside the cave) was well illuminated (Table 1). Zone 2 received nearly 3% of the subsurface light. In the two innermost zones no light was detected at 11 a.m. At sunset some light was detected in Zone 4 due to the west facing of the cave.

The two innermost zones of the Medes cave were dark throughout the day (Table 1). Zone 2 received some light from a pit that opens to the outside just above it and from the entrance to the cave. Zone 1, although it was placed outside the cave (as in the Cabrera cave), received less light than Zone 1 in the Cabrera cave, since it was deeper.

Water motion and temperature

In the Cabrera cave, Zone 3 had the lowest water motion in both seasons while Zone 2 showed the highest

Table 1. *Irradiance in each zone of both the caves. The mean values are referred to the subsurface light (0 m depth). There were no appreciable differences between seasons.*

		% of irradiance	
Season	Zone	Cabrera cave	Medes cave
June	1	42.8	19.5
and	2	2.7	0.076
November	3	0.0036	0
	4	0	0

Table 2. *Water motion expressed in mg $CaSO_4$ lost per hour. The values correspond to means and standard errors of four sets of measures per season including different sea conditions.*

	mg $CaSO_4$/h	
Season and zone	Cabrera cave	Medes cave
June		
1	125.6 (±38.6)	293.5 (±8.9)
2	175.2 (±75.5)	101.0 (±17.1)
3	90.2 (±31.4)	116.0 (±20.1)
4	117.5 (±56.1)	160.3 (±27.3)
November		
1	129.2 (±46.3)	145.4 (±49.5)
2	184.9 (±75.1)	35.0 (±21.2)
3	70.0 (±31.5)	40.3 (±27.0)
4	151.3 (±45.5)	50.6 (±31.8)

Table 3. *Particulate organic carbon and nitrogen (μg/l) in the water in the four zones of the two caves and in the two seasons.*

Season and zone		Cabrera cave		Medes cave	
		Carbon	Nitrogen	Carbon	Nitrogen
June					
	1	834	76	1175	67
	2	818	88	1206	151
	3	1226	87	1614	104
	4	1251	81	1313	113
November					
	1	896	93	2102	210
	2	870	89	2250	256
	3	1282	101	2495	317
	4	1336	99	2284	286

(Table 2). Zones 1 and 4 were always within the range of values of Zones 2 and 3. However, while water movement in Zone 1 was comparable in both seasons, water motion in Zone 4 was higher (~30%) in November than in June.

In the Medes cave, comparison between seasons was precluded due to very different sea conditions (much rougher in June). The zone outside the cave (Zone 1) always had the highest water motion, followed by the innermost zone. Zones 3 and 2 had similar water motion, in both cases lower than Zones 1 and 4.

The temperature values registered indicated that there were no differences between zones or seasons within each cave. The average temperature was 19°C in the Cabrera cave and 17°C in the Medes cave.

Particulate organic matter (POM)

The results shown in Table 3 for POM content are merely illustrative, since water samples were taken only once per season. The values, however, are useful for assessing within-cave trends.

In the Cabrera cave, the organic matter concentration was similar in both seasons for all zones. Nitrogen concentration, as expected, was lower in absolute values than carbon concentration. Carbon concentration was higher in the two innermost zones of the cave than in the two external ones.

In the Medes cave, a gradient of POM along the cave was evident. Zone 3 had the highest concentration of carbon, followed by Zone 4, Zone 2 and finally Zone 1. Nitrogen concentration was also lower outside the cave (Zone 1), while inside the cave Zone 2 showed the highest value. Concentrations were higher in November than in June.

Community structure
Coverage

The coverage of all species from the two caves is listed in Table 4 (see Appendix for list of species and authorities).

In the Cabrera cave there were no outstanding differences in species coverage between seasons in any zone (Figure 2). Zone 1 was clearly dominated by seaweeds and the substratum was totally covered. In Zone 2, although seaweeds were still the dominant group and the substratum was also totally covered, other taxonomic groups (sponges, cnidarians and bryozoans) represented 12–18% of the total coverage. Zones 3 and 4 lacked seaweeds and were dominated by filter- and suspension-feeders. In both zones a large amount of bare rock was present, being more abundant in Zone 4.

The differences between Zones 3 and 4 were mainly due to the faunal composition. While in Zone 3, bryozoans, cnidarians and sponges were abundant, the last group was the most important in terms of coverage. In Zone 4 sponges clearly dominated and cnidarians and bryozoans were poorly represented.

In the Medes cave (Figure 2) there were large differences in taxon abundance with respect to the Cabrera cave. Only the external zone (1) was dominated by seaweeds. The remaining zones inside the cave were dominated by animals. The traits common to the internal Zones (2, 3, and 4) were the dominance of sponges and the high proportion of bare rock (up to 73% in June in Zone 4), although their respective percentages varied among zones.

When comparing the caves, differences became evident. First, Zones 1 and 2 in the Cabrera cave were dominated by seaweeds while only Zone 1 was in the Medes cave.

Zones 2, 3, and 4 of the Cabrera cave were roughly equivalent in composition to Zones 1, 2, and 3 of the Medes cave, respectively. Finally, the equivalent of Zone 4 from the Medes cave was not present in the Cabrera cave. The low animal cover of Zone 4 in the Medes cave was an indicator of its extreme confinement.

Number of species

In the Cabrera cave (Figure 3) the differences in the number of species between the two external zones (1 and 2) and the similarity in this parameter in the two internal zones (3 and 4) are noteworthy. This pattern was not observed for the percentage cover (Figure 2). A log-linear model comparing the number of species per taxon in each zone detected significant ($P<0.001$) differences in species composition between zones. In Zone 1 the number of seaweed species was higher in both seasons than that of the remaining taxonomic groups. Moreover, in November there were ten more seaweed species than in June. In Zone 2 seaweeds were also the dominant group in number of species but the sum of animal species was higher than in Zone 1. In November the number of seaweed species decreased with respect to June. Zones 3 and 4 were similar with the dominant groups, ranked from the richest to the poorest, being: sponges, bryozoans, cnidarians and polychaetes. The number of sponge species in Zone 4 was the highest but no noticeable differences were found for other taxonomic groups.

In the Medes cave (Figure 3), the similarity of the three internal zones (2, 3 and 4), which clearly differ from the external zone (1), is evident. As in the Cabrera cave, a log-linear model comparing the number of species per taxon in each zone revealed a significant ($P<0.001$) difference between zones. In Zone 1, the number of seaweed species equalled the sum of the species of the other taxonomic groups; in both seasons algae were the dominant group followed by sponges. In Zones 2, 3 and 4, sponges were the group with the highest number of species and Zone 2 had the highest value. Bryozoans, cnidarians and

Table 4. *Species coverage (%) from 20 pictures taken at random per zone in the Cabrera cave and in the Medes cave in June and November.*

Species	June				November			
Cabrera cave	Zone 1	Zone 2	Zone 3	Zone 4	Zone 1	Zone 2	Zone 3	Zone 4
Chlorophyta								
Acetabularia acetabulum	0.01							
Acetabularia parvula					0.01			
Anadyomene stellata	0.15				0.35			
Cladophora pellucida		0.09						
Cladophora sp.					0.15	0.08		
Codium bursa	0.04				0.25			
Flabellia petiolata	0.09	5.39			0.54	8.34		
Halimeda tuna	0.03	0.02			0.05			
Palmophyllum crassum		6.16				5.78		
Pseudochlorodesmis furcellata	0.12	1.09			0.01			
Valonia utricularis		0.06			0.01	0.03		
Phaeophyta								
Aglaozonia sp.		0.02						
Cystoseira balearica	10.63				2.06			
Cystoseira compressa	0.65				0.01			
Dictyopteris polypodioides	2.73				2.94	0.002		
Dictyota dichotoma	0.20	0.03			0.14			
Dictyota dichotoma var. *intricata*	23.81				2.51			
Halopteris filicina		3.74				1.03		
Halopteris scoparia	15.38				1.30			
Lobophora variegata	0.18	0.38			5.48	3.34		
Padina pavonica	22.89				6.47			
Sphacelaria cirrosa					0.45			
Taonia atomaria	0.93	0.05						
Unid. filamentous brown algae		0.12						
Rhodophyta								
Amphiroa cryptarthrodia		0.06			0.14	0.10		
Amphiroa rigida	0.91				2.88			
Boergeseniella fruticulosa	0.10				0.11			
Botryocladia boergesenii		0.004				0.01		
Botryocladia botryoides		0.004			0.09			
Contarinia squamariae		0.12				0.07		
Corallina elongata	0.40				0.43	0.003		
Cryptonemia lomation					0.004			
Delesseriaceae unid.		0.12				0.53		
Falkenbergia sp.	0.61	0.09			0.22			
Gloiocladia furcata		0.10			0.004	0.31		
Haliptilon virgatum	9.19	0.25			36.95	0.46		
Hydrolithon farinosum		1.83	0.004			3.77	0.004	
Laurencia gr. *obtusa*					0.002			
Lithophyllum cabiochae		0.27						
Melobesiae unid.			0.64			0.24	0.89	
Mesophyllum alternans	0.49	7.95			2.11	3.08		
Neogoniolithon brassica-florida	7.44				28.59			
Peyssonnelia rosa-marina		32.31				44.90		
Peyssonnelia squamaria	0.30	13.38			0.30	9.47		
Plocamium cartilagineum		0.19				0.02		
Polystrata fosliei					1.80	0.05		
Rhodymenia ardissonei						0.004		
Tricleocarpa sp.		0.001			0.08	0.01		
Unid. filamentous red algae		2.37						
Wurdermannia miniata					1.86			
Granuloreticulosa								
Miniacina miniacea		0.04	0.08	0.47			0.12	0.12
Porifera								
Acanthella acuta		0.20	0.06			0.15	0.10	
* *Agelas oroides*			1.29	1.61			0.98	1.61
* *Axinella damicornis*		0.60	1.49	1.39		0.48	2.63	1.39
Cacospongia mollior		0.08						
Chondrosia reniformis		0.03	1.92	0.001			1.51	0.004

(Continued)

Table 4. *(Continued)*.

Species	June				November			
Cabrera cave	Zone 1	Zone 2	Zone 3	Zone 4	Zone 1	Zone 2	Zone 3	Zone 4
Clathrina clathrus		0.01		0.003		0.004		
Clathrina sp.				0.01				
Cliona celata					0.03			
Cliona sp.	0.01	0.18						
Cliona viridis	0.01							
* *Crambe crambe*	0.46	1.13	0.01	1.05	0.03	0.18	0.02	1.05
* *Darwinella* sp.				0.01				0.01
* *Dendroxea lenis*			1.37	5.59			0.71	5.59
* *Diplastrella bistellata*			0.40	6.66			0.27	6.66
* *Dictyonella* sp.			2.49	0.85			0.75	0.85
* *Dysidea avara*		0.09		0.63		0.07		0.63
Erylus euastrum		0.14	3.84	1.24		0.20	0.91	2.78
Eurypon sp.			0.17	0.43			0.28	0.32
Hexadella pruvotii			0.03	0.64			0.06	1.07
Hippospongia communis			0.01				0.01	0.18
**Hymedesmia* sp. 1			0.89	1.01			0.18	1.01
**Hymedesmia* sp. 2	0.14			1.75				1.75
**Hymedesmia* sp. 4				10.62				10.62
Ircinia fasciculata							0.21	
Ircinia oros			0.82				0.53	
Ircinia variabilis			1.26	0.45		0.04	4.88	1.30
Leucosolenia variabilis			0.001	0.01				0.001
Microciona cf. *ascendens*			0.01					
**Microciona* sp.				0.46				0.46
Myceliospongia araneosa			0.14	0.40			0.30	0.26
Oscarella tuberculata			0.87	0.11			0.92	0.21
* *Petrosia ficiformis*				0.04				0.04
Phorbas fictitius		0.07	0.07		0.22		0.09	
Phorbas tenacior		0.06	2.34	1.43			2.21	3.22
Pione vastifica	0.001							
Pleraplysilla spinifera		0.32	1.47	0.34		0.20	2.30	0.25
Raspaciona aculeata			0.48	0.21			0.85	0.46
Reniera fulva			0.02	0.002				
Reniera mucosa		0.19		0.03				0.01
* *Spirastrella cunctatrix*			4.62	6.44			3.12	6.44
Spongia virgultosa			0.16		0.01			
Terpios fugax		0.01	0.04	0.01		0.02	0.01	0.03
Topsentia garciae			0.24	0.10			0.35	0.34
Cnidaria								
Aglaophenia sp.	0.12				0.08			
Balanophyllia europaea	0.11				0.20			0.01
Caryophyllia inornata		0.20	0.003			0.17		
Clavularia crassa		0.36			0.12	0.43		
Cornularia cornucopiae		0.01				0.25		
Eudendrium sp.		0.47				0.01		
Hydrozoan unid.						0.27		
Hoplangia durotrix		0.06		0.42				0.06
Leptopsammia pruvoti		1.78	0.06	0.26	0.03	0.61	0.01	0.17
Maasella edwardsi					0.06			
Parerythropodium coralloides								0.00
Parazoanthus axinellae			9.33	1.21			13.85	2.57
Polycyathus muellerae		3.55	0.10	0.43		3.14	0.73	1.11
Polychaeta								
Protula sp.		0.09	0.87	0.003		0.03	0.07	
Salmacina dysteri				0.02				
Serpula vermicularis	0.40		0.01	0.002				0.68
Serpulidae sp. 1				0.01				
Serpulidae sp. 2			0.43	0.24			0.21	0.08
Serpulidae sp. 3			0.05	1.09				0.73
Serpulidae sp. 4			0.02	0.20			0.01	

Bryozoa								
Annectocyma indistincta		0.10						
Annectocyma sp.			0.002			0.01	0.004	
Bryozoan sp.1			0.08	0.05		0.02	0.02	0.02
Bryozoan sp.2			0.05					
Bryozoan sp.3						0.33		
Bryozoan sp.4			0.01					
Bryozoan sp.5				0.33			0.01	0.19
Bryozoan sp.6								0.01
Bryozoan sp.7		0.13		0.01				
Bryozoan sp.8		1.19						
Bugula calathus		0.01		0.36				0.18
Cellaria sp.				0.001	0.01			
Celleporina sp.						0.02		
Chlidonia pyriformis				0.01		0.04		
Crisia sp.1		0.39						
Crisia sp.2						0.07		
Crisia sp.3						1.48		
Crisia sp.4		0.16						
Crisia sp.5		0.32						
Crisia sp.6	0.003							
Frondipora verrucosa		0.03	0.39	0.58		0.01	0.64	0.71
Lichenopora radiata			0.03	0.04			0.05	0.02
Margaretta cereoides			0.12				0.02	
Myriapora truncata		4.74			0.01	3.16		
Puellina gattyae		0.09						
Reptadeonella violacea		0.12			0.30			
Rynchozoon sp.						0.12		
Schizomavella sp.1				0.31				0.05
Schizomavella sp.2			5.37	1.94			5.41	3.01
Schizomavella sp.3		0.01	0.89	0.34	0.06		1.12	0.10
Scrupocellaria sp.			3.41	0.42			3.86	0.10
Sertella sp.		1.21	5.97	0.55		0.25	6.84	0.43
Smittina cervicornis		0.10	0.56				0.44	
Mollusca								
Bittium reticulatum		0.003						
Calliostoma sp.			0.03					
Lima hians		0.01	0.05					
Lithophaga lithophaga		0.03		0.01		0.03	0.14	0.03
Patella sp.					0.01			
Brachiopoda								
Argyrotheca cordata				0.01				0.01
Echinodermata								
Paracentrotus lividus					0.14			
Tunicata								
Ascidia mentula				0.01				
Botrylloides leachii							0.01	
Didemnum sp. 1			0.02			0.04	0.02	
Didemnum sp. 2				0.03				0.01
Lissoclinum perforatum	0.01	0.04		0.11	0.08			0.07
Pyura dura							0.13	
Unidentified	1.48	5.27	7.66	0.95	0.20	6.43	10.42	0.74
Bare rock		0.06	37.23	46.05			30.81	40.34

Species	June				November			
Medes cave	Zone 1	Zone 2	Zone 3	Zone 4	Zone 1	Zone 2	Zone 3	Zone 4
Chlorophyta								
Cladophora pellucida	0.02				0.04			
Cladophora sp.	0.11				1.33			
Flabellia petiolata	0.56				2.27			
Halicystis parvula	0.001	0.001						
Halimeda tuna	0.07				0.06			
Pseudochlorodesmis furcellata	0.003							

(*Continued*)

Table 4. *(Continued).*

Species	June				November			
Medes cave	Zone 1	Zone 2	Zone 3	Zone 4	Zone 1	Zone 2	Zone 3	Zone 4
Phaeophyta								
Aglaozonia sp.	0.28				0.24			
Colpomenia sinuosa	0.12							
Dictyopteris polypodioides					0.02			
Dictyota dichotoma	1.05				0.06			
Dictyota dichotoma v. *intricata*	5.27							
Dictyota fasciola	1.81				0.04			
Halopteris filicina	1.36				3.41			
Halopteris scoparia	1.35							
Padina pavonica	0.01							
Taonia atomaria	24.57							
Rhodophyta								
Amphiroa beauvoisii					0.05			
Amphiroa cryptarthrodia	0.01				0.14			
Asparagopsis armata	3.57							
Bornetia secundiflora	0.01							
Corallina elongata	2.37				11.27			
Falkenbergia rufolanosa	33.35				45.20			
Hydrolithon farinosum	0.25							
Jania rubens	0.08				0.09			
Lithophyllum dentatum	0.13							
Lithophyllum incrustans	1.78				1.47			
Melobesiae unid.		0.03				0.02		
Mesophyllum alternans	2.65				11.35			
Peyssonnelia rosa-marina	0.20				1.47			
Peyssonnelia squamaria	0.81				3.34			
Plocamium cartilagineum	0.52				0.44			
Rhodophyllis divaricata	0.003							
Rhodymenia ardissonei		0.20						
Unid. filamentous red algae					8.65			
Granuloreticulosa								
Miniacina miniacea		0.001						0.14
Porifera								
Aaptos aaptos		0.04	0.72	0.01		0.41	0.12	0.45
Acanthella acuta		0.38				0.07		
Agelas oroides		1.67	0.20	0.04		2.50	1.54	0.03
Aplysina cavernicola		0.05	1.62	0.53		0.41	2.06	0.75
Axinella damicornis		0.01				0.30		0.03
Cacospongia mollior					0.01			
Chelanoplysilla noevus		0.004	0.001			0.14	0.004	
Chondrosia reniformis		0.003		0.01			0.01	0.03
Clathrina sp. 1	0.001	0.06	0.29	0.90	0.05	0.09	0.40	1.02
Clathrina clathrus		2.48	2.40	0.57	0.001	1.90	1.28	0.70
Clathrina sp. 2				0.01				
Cliona schmidti				0.01			0.001	0.001
Clionia celata	0.01				0.01			
Clionia viridis	0.01	0.003			0.01		0.06	
Crambe crambe	0.98				1.90	0.001		
Crella mollior		0.05	0.18	0.08		0.10	0.11	0.22
Dendroxea lenis	0.01	11.49	15.71	7.70	0.01	7.49	11.48	12.52
Diplastrella bistellata		8.57	9.34	0.89		10.14	10.70	3.30
Dictyonella sp.		0.23				1.09		0.07
Dysidea avara		1.05	0.75			1.76	0.46	0.003
Erylus euastrum		0.07	0.20	0.92		0.15	1.31	2.38
Eurypon sp.1		0.28			0.26	0.09		
Eurypon sp.2			0.03					
Hemimycale columella					0.01			
Hexadella pruvotii		0.002	0.01	0.02		0.39	0.002	
Hymedesmia sp. 1		0.07	0.06	0.85		0.27	0.11	2.46
Hymedesmia sp. 2			0.13	0.06			0.06	
Hymedesmia sp. 4			0.70	0.003		0.24		0.01

0.32

Ircinia fasciculata	0.18				0.30			
Ircinia oros		0.34	0.03	0.26	0.001	0.50	0.17	0.08
Ircinia variabilis		0.36	1.46	1.51		0.45	1.00	1.78
Leucosolenia variabilis	0.001					0.002		
Microciona sp.		0.08				0.04	0.02	
Mycale sp.		0.04	0.01			0.35	0.12	
Myceliospongia araneosa		0.04	2.05	0.03		0.12	1.08	1.82
Oscarella sp.								0.001
Oscarella tuberculata		0.26				0.02		
Petrosia ficiformis		6.19	2.57	0.02		6.57	3.29	0.57
Phorbas fictitius	0.04				0.03			
Phorbas tenacior	0.02	0.59	2.32		0.02	2.85	1.80	0.14
Pione vastifica	0.01							
Pleraplysilla spinifera		2.13	0.89	0.04		1.00	0.39	0.09
Reniera mucosa		6.21	3.77	0.84		3.71	3.75	2.02
Reniera sarai						0.003	0.19	
Reniera sp.		0.05						
Spirastrella cunctatrix		5.69				5.53	0.004	
Spongia virgultosa	0.01	1.08	0.58	0.07	0.002	2.60	1.05	0.16
Sycon elegans		0.003					0.001	0.01
Sycon sp.				0.01				
Terpios fugax		0.01				0.02	0.001	0.01
Topsentia garciae		0.02		0.01		0.13		
Cnidaria								
Aglaophenia kirchenpaueri	0.01				0.03			
Alcyonium acaule					0.01			
Balanophyllia regia		0.02	0.02	0.00	0.03	0.01	0.01	
Caryophyllia inornata			0.002				0.003	
Corallium rubrum	0.06	0.47				0.19	0.01	0.07
Cornularia cornucopiae	0.01				0.09			
Eudendrium sp.	0.04				0.01			
Eunicella singularis					0.02			
Hydrozoan unid.		0.003						
Hoplangia durotrix		0.02	0.09	0.02		0.09	0.06	0.17
Leptopsammia pruvoti		1.73	0.42	0.004		2.12	0.89	0.37
Polycyathus muellerae		0.10				0.00		
Sertularella ellisi	0.01				0.04			
Sertularella sp.					0.02			
Polychaeta								
Myxicola aesthetica			0.01	0.03		0.01	0.001	0.02
Protula sp.		0.07	1.02		0.07	0.03	0.33	0.05
Salmacina dysteri	0.03	0.34				0.37		
Serpula vermicularis	0.01	0.06			0.03	0.02	0.02	0.01
Serpulidae sp. 1		0.16	0.03	0.14		0.09		0.16
Serpulidae sp. 2				0.01				
Serpulidae sp. 3				0.11				0.05
Serpulidae sp. 4		0.01	0.47				0.21	0.003
Serpulidae sp. 5							0.01	
Spirorbis sp.		0.02	0.32	4.35		0.003	0.40	0.73
Bryozoa								
Bryozoan sp. 1		0.01						
Bryozoan sp. 2		1.43		3.63			0.20	3.05
Bryozoan sp. 3	0.05							
Bryozoan sp. 4		0.06	0.01					
Celleporina sp.				0.01		0.001		0.001
Chlidonia pyriformis			0.01					
Crisia sp.	0.03				0.15			
Disporella hispida		0.06				0.07		
Frondipora verrucosa		0.04						
Idmidronea atlantica		0.04						
Lichenopora radiata			0.002	0.01		0.01	0.002	0.002
Myriapora truncata	0.001							
Parasmittina tropica		0.14				0.03		
Schizomavella cuspidata		0.73				1.07		
Schizomavella linearis		0.06				1.23		
Schizomavella sp. 1			0.01					
Schizomavella sp. 2			0.01				0.70	

(*Continued*)

Table 4. *(Continued)*.

Species	June				November			
Medes cave	Zone 1	Zone 2	Zone 3	Zone 4	Zone 1	Zone 2	Zone 3	Zone 4
Bryozoa (*continued*)								
Schizomavella sp. 3			0.04				0.10	
Scrupocellaria sp.		5.35	1.31	0.04		0.60	0.22	0.05
Sertella sp.	0.02				0.02	0.01		
Smittina cervicornis		0.59				0.31		
Smittoidea reticulata		0.20				0.01		
Spiralaria gregaria		0.09				0.85		0.40
Mollusca								
Bittium reticulatum								0.001
Bivalvia unid.			0.003					
Coralliophila sp.			0.001				0.003	
Lithophaga lithophaga	2.35		0.01		0.03		0.01	
Brachiopoda								
Argyrotheca cordata							0.002	0.001
Terebratulina sp.			0.01	0.02			0.04	
Crania anomala			0.15	2.31			0.12	0.91
Megerlia truncata			0.001	0.01		0.003	0.001	0.02
Echinodermata								
Paracentrotus lividus	0.42					0.01		
Tunicata								
Clavelina lepadiformis	0.10				0.54			
Cystodytes dellechiajei	0.08	0.12	0.01		0.11	0.42	0.001	
Didemnum sp. 1	0.01	0.05	0.36	0.61		0.04	0.18	0.94
Didemnum sp. 2	0.01							
Didemnum sp. 3			0.03				0.004	0.33
Didemnum sp. 4							0.004	
Diplosoma spongiforme			0.04					
Pyura dura		0.02						
Unidentified	13.21	2.35	1.26	0.12	5.23	0.39	1.95	1.18
Bare rock		35.84	48.28	73.20		40.56	51.55	60.69

Note that in Zone 4 of the Cabrera cave some sponge species (*) have exactly the same coverage in June and November. Although these species in fact decreased in coverage, we consider this decrease an artefact due to the small size of the zone and the intensive sampling for toxicity analyses carried out in June. Some sponge specimens that remained untouched showed an increment in coverage from June to November. We have kept the coverage values of these species for June, as we think that this is the more conservative correction we can apply.

polychaetes were the groups best represented after the sponges.

There were marked seasonal differences in species richness (Figure 3). In the Cabrera cave there was a noticeable increase in the number of species in Zone 1 from June to November, and a decrease in Zones 2, 3 and 4 during the same period. In the Medes cave there was a decrease in the number of species from June to November in Zones 1 and 2, while Zones 3 and 4 showed an increase in the number of species in the same period.

Ordination

The ordination analysis of the samples from the Cabrera cave is graphically represented in Figure 4A,B. The first axis was interpreted as representing the horizontal gradient across the cave from the most external zone (left in the graph) to the innermost zone (right in the graph). Forty-seven per cent of the variation of our pictures was explained by the two first axes. However, almost all the variance (77.6%) was explained by axis I. Notice that the r^2 for axis II is low in all the graphs (Figure 4).

The 20 pictures taken at the most external part of the cave (zone 1), appeared in the analysis as a compact group on the left part of the graph. Clearly separated from the first group, another cluster of 20 samples, which belonged to Zone 2, were represented.

The set of samples on the right of the graph belonged to Zones 3 and 4. These two zones were situated inside the cave, with low levels of light, so the dominant benthic organisms there were invertebrates. No spatial separation of the two zones was obtained in this analysis.

In order to assess whether the lack of resolution between the two internal zones (Zones 3 and 4) was an artefact due to the presence of the other, markedly different zones, another analysis was carried out with only the 40 pictures of these two zones (Figure 4B). After the elimination of the outliers, axis I represented the gradient from Zone 3 to the innermost part of the cave (Zone 4). Most of the samples of Zone 4 can be found on the right part of the graph. Axis I explained 37% of the variance in the samples.

Most of the samples from Zone 3 were grouped on the left. However, the separation of the two zones was not clear cut. This was expected since the species found were

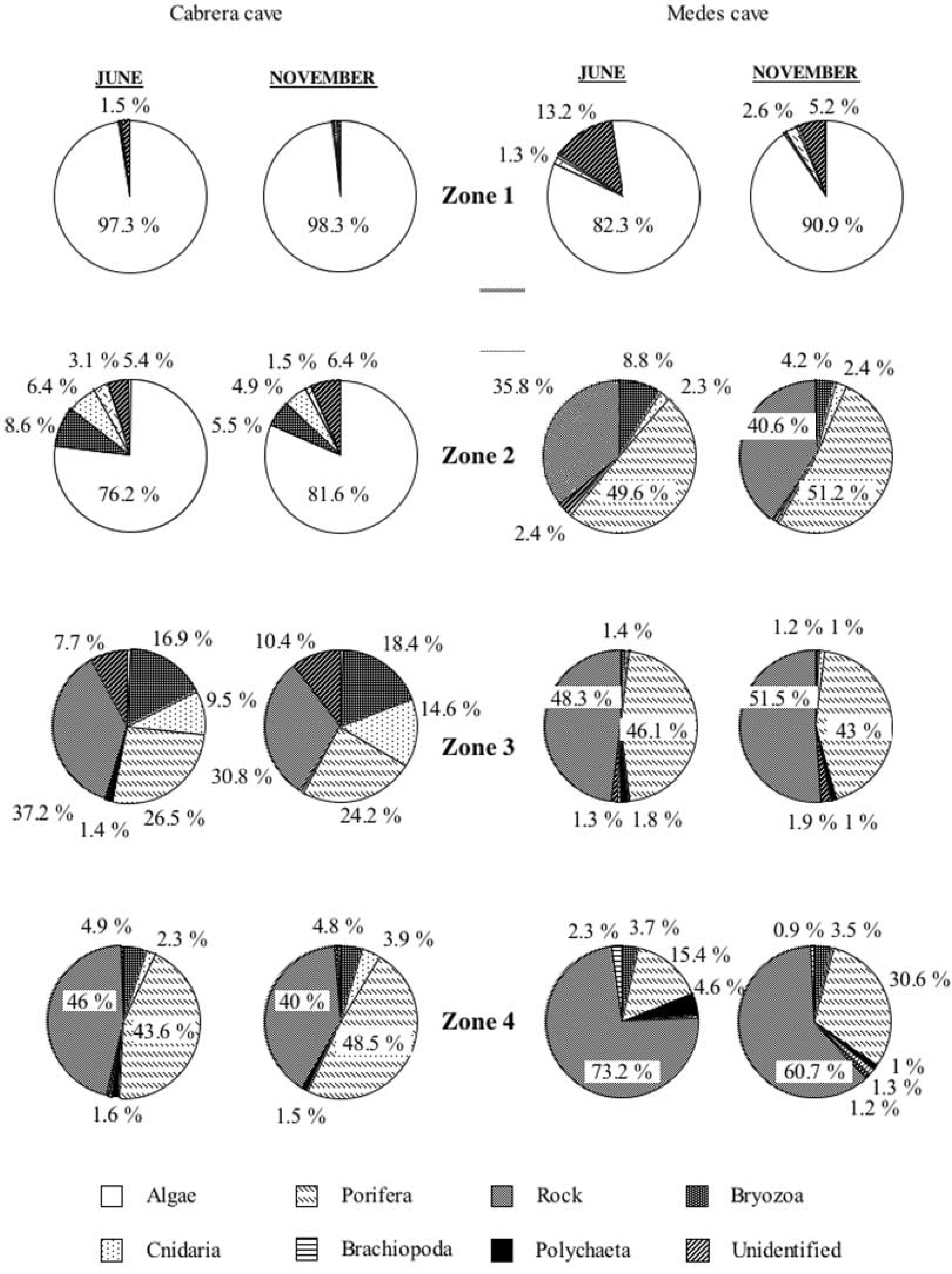

Figure 2. Coverage per high-level taxonomic group in the four zones of the Cabrera cave and the Medes cave in both seasons.

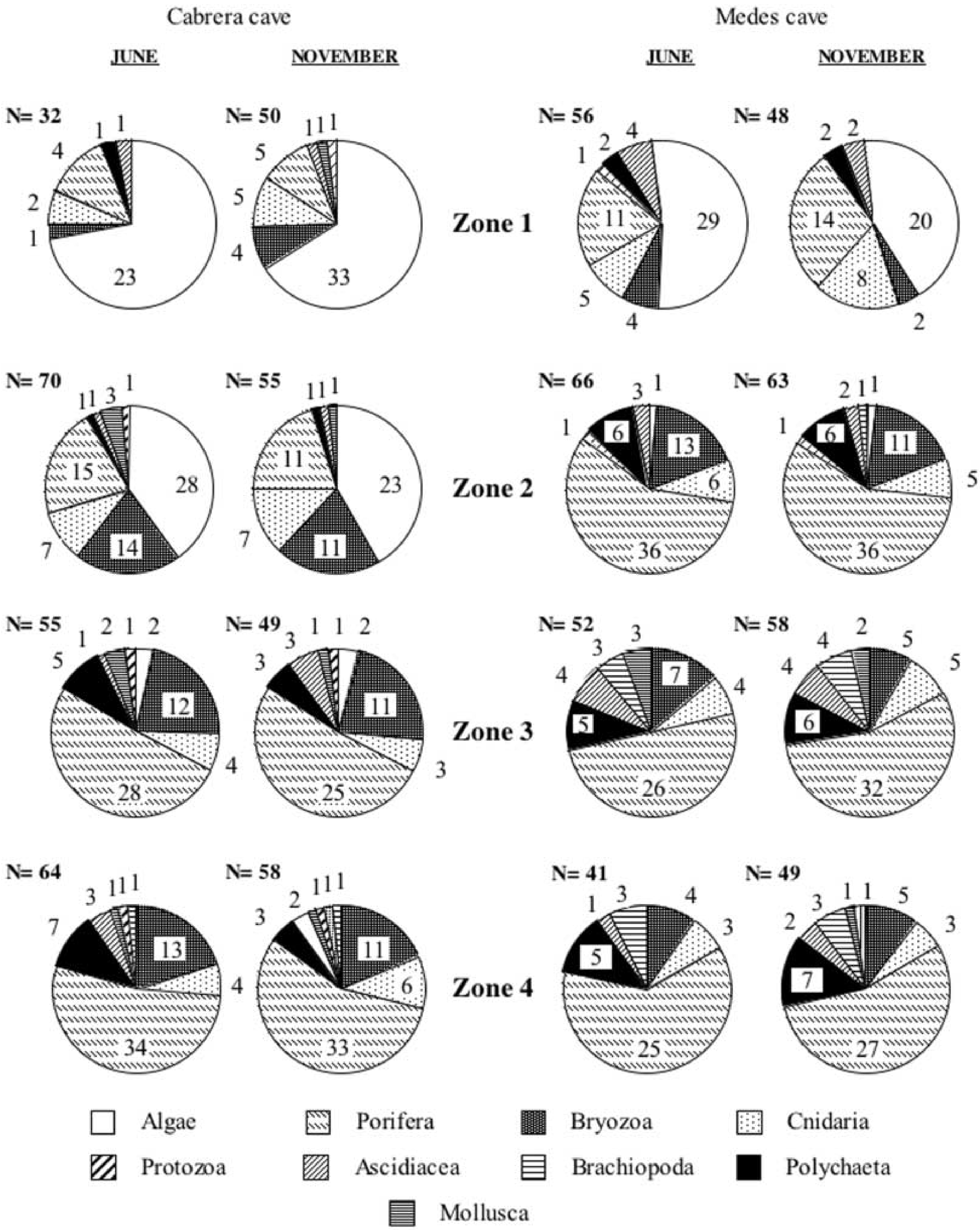

Figure 3. Number of species per high-level taxonomic group in the four zones of the Cabrera cave and the Medes cave in both seasons. Bold values indicate species richness.

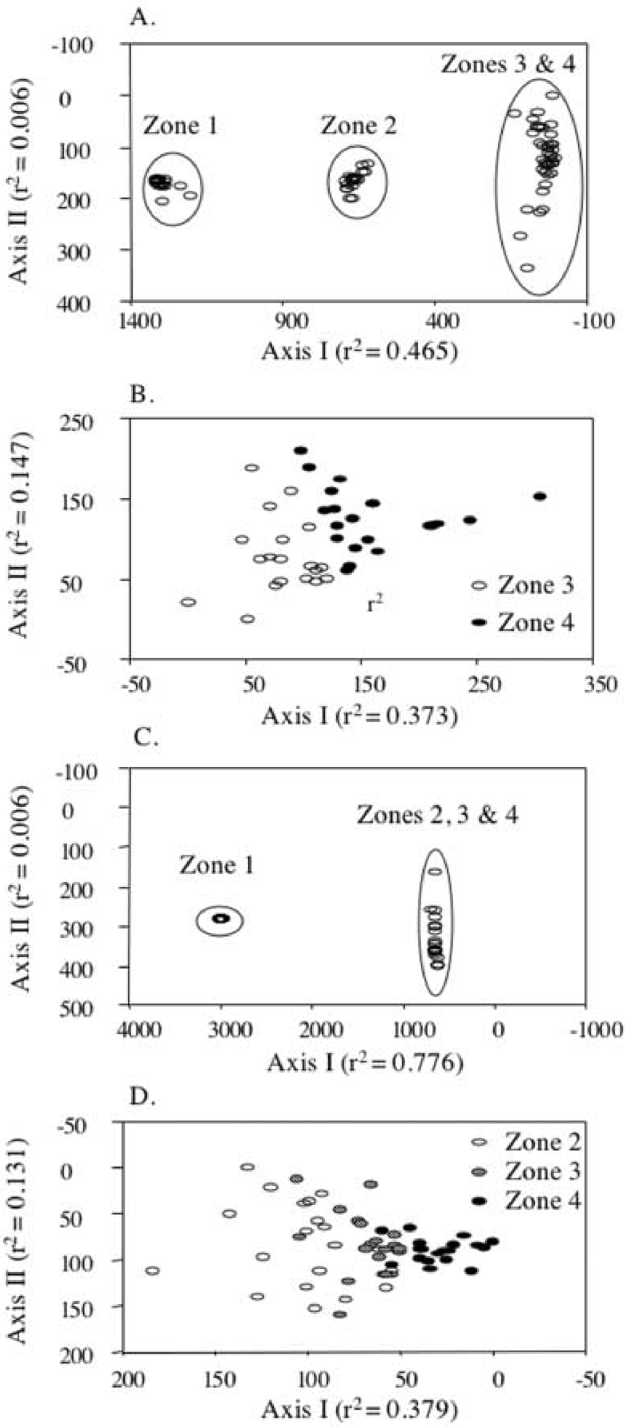

Figure 4. Detrended correspondence analyses (DCAs) representation of all samples (A) and samples of Zones 3 and 4, exclusively (B), from the Cabrera cave and DCAs representation of all samples (C) and samples of Zones 2, 3 and 4, exclusively (D) from the Medes cave. Data represent coverage values in June.

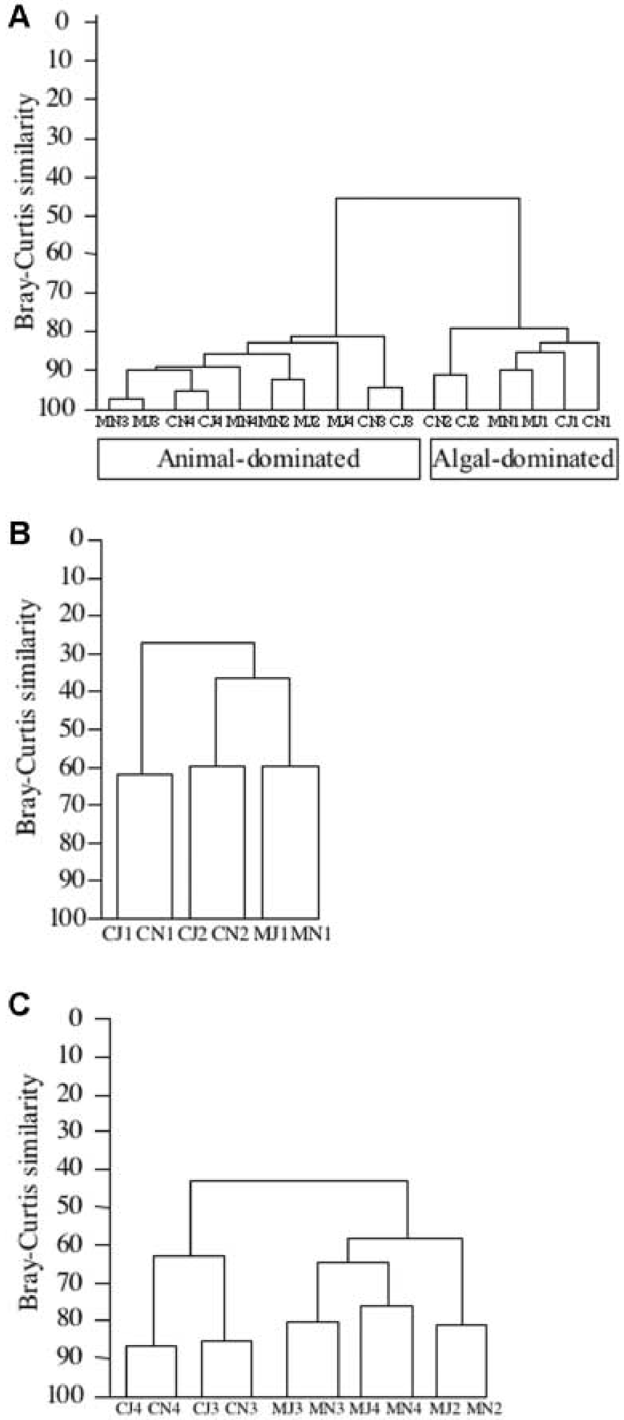

Figure 5. Cluster analysis of zones from both the caves using the percentage cover per high-level taxonomic group (A). Cluster analysis of the algal-dominated zones (B) and animal-dominated zones (C), using the percentage cover per species. Data were transformed to 4th root. C, the Cabrera cave; M, the Medes cave; J, June; N, November. Numbers denote cave zones.

similar in both zones. Axis II distributed samples according to species abundance and amount of bare rock.

The representation of ordination analyses for the Medes cave in June is shown in Figure 4C,D. When all zones were included (Figure 4C), the first axis, which explained 41% of the total variance, again represented the horizontal gradient along the cave.

The 20 pictures taken in Zone 1 appeared in the analysis in a compact group on the left part of the graph. Clearly separated from Zone 1, there was a group composed of all the remaining 60 pictures, all of them taken inside the cave.

When the analysis was only performed on the three internal zones (2, 3 and 4) (Figure 4D), axis I again represented the horizontal gradient from the external to the internal zones of the cave, explaining 38% of the variance.

The three zones appeared separated along this axis, although with some overlap. This overlap was expected because, as in the Cabrera cave internal zones, the three zones shared the same species. Species abundance and the increment of bare rock were the two factors that clearly varied among zones. Axis II discriminated samples according to the coverage of the most abundant species and bare rock.

Classification

Two distinct groups were clearly separated in the preliminary cluster analysis performed on high-level taxonomic groups (Figure 5A). The first one comprised all the zones dominated by seaweeds irrespective of cave or season. The second group included all the zones inside the caves (i.e. the darker communities dominated by suspension-feeders). However, relationships within each group were not clear.

A separate analysis on the group comprising the algal-dominated zones (Figure 5B) performed at the species level, showed that Zone 2 of the Cabrera cave was more similar to zone 1 of the Medes cave than to Zone 1 of the Cabrera cave. Thus, two zones belonging to two geographically separated archipelagos were more similar than two zones with spatial continuity. This result highlighted the importance of the amount of light in establishing affinities between different algal communities. Seasonal variation was less important, as the sample of both seasons in each zone clustered together in all cases.

When the animal-dominated communities were analysed at the species level (Figure 5C), the differences in species composition between the two caves became manifest, and the Cabrera and the Medes caves appeared as separate clusters. Again, similarity was higher between seasons for the same zone than between zones.

DISCUSSION

A clear although different pattern of zonation was found in both the caves. In the Cabrera cave the decrease in coverage and number of species and the corresponding increase in bare rock towards the internal zone is less marked than in the Medes cave (also reported by Gili et al., 1986) possibly due to the higher water flow inside. A diminished larval supply might explain the poor colonization of the substratum at the most internal zones of the caves, since larvae of the main benthic taxa living inside the caves (sponges, bryozoans and ascidians) have not been found in the corresponding planktonic compartment (Palau et al., 1991). However, the difficulty in larval identification of several Phyla (mainly sponges, Mariani et al., 2003) casts some doubt on the absence of larvae in these caves.

Sponges were the dominant group in the animal-dominated communities of both the caves. Bryozoans and cnidarians were also relevant in the Cabrera cave. In contrast, cnidarians were scarce and even absent from the innermost zone in the Medes cave, a finding consistent with the progressive disappearance of cnidarians from semi-dark communities to dark communities previously reported (Harmelin, 1985, 1997).

The adaptation of the organisms from different taxonomic groups to life inside the caves relies mainly on their trophic requirements (Harmelin, 1985). Sponges (active filter-feeders) appear to be well adapted to this kind of environment due to their high efficiency in retention of small organic particulates (Simpson, 1984). As a result, they are highly competitive organisms in submarine caves (Harmelin et al., 1985) and clearly dominate semi-dark communities (Vacelet, 1979). Our data confirmed the reported dominance of sponges in the caves, in terms of both species richness and coverage, from the cave entrance to the innermost zone. However, the pattern of sponge abundance was different in the two caves. While the number of sponge species and their coverage clearly decreased from the external to the internal zone in the Medes cave, both descriptors reached the highest values in the innermost zone (Zone 4) of the Cabrera cave. The differences in species composition (only 38 species out of 62 were present in both the caves) may be due to the geographical isolation of both the caves, and the low dispersal capacity of sponges (Harmelin, 1985; Mariani et al., 2003). When we compare the sponge species composition of the caves studied with that of other Mediterranean caves (e.g. Marseilles caves, Pouliquen, 1972; Harmelin & Vacelet, 1997; and Migtigliano cave, Balduzzi et al., 1989), we find that the number of species in common is generally low, and decreases with increasing geographic distance, as previously reported (Alcover et al., 1993).

Detrended correspondence analyses revealed differences between the two caves. In all cases the axis with the highest coefficient of determination was the one that represented the horizontal gradient across the cave, from the most external zone to the innermost one.

The cluster analysis on percentage cover per high taxonomic groups allowed us to differentiate those organisms from the external and internal zones of both the caves. The analysis of the external zones (phytobenthic communities) using species percentage cover clustered the zones on the basis of light availability and not by geographic proximity. The internal zones (animal-dominated communities), on the other hand, were grouped according to the cave they belonged to.

All the results presented here show that light is determinant in explaining differences among algal-dominated communities, but not among the animal-dominated communities. The algal communities are similar between the caves, varying as a function of irradiance. In contrast, animal-dominated communities are more similar within than between the caves, and more intrinsic factors, such as cave typology, that determines water flows and hence differences in food and larval supply, may be more relevant to explain differences among animal-dominated benthic communities from the caves. Although seasonal differences in species abundance and coverage are much less important than differences linked to the caves and zones, there is nevertheless significant seasonal variation even in the innermost zones of the caves, especially with respect to coverage figures.

This research was partially supported by INTERREG-IIIA K115C n 0123 (EU) and CICYT (Comision Interdepartmental de Ciencia y Technología) REN2001-2312-CO3/MAR grants. It also benefited from Governments of Catalonia and Spain fellowships to R. Martí. We gratefully acknowledge M. Bardají, G. Agell and D. Martin for helping in samples and data processing. We also thank the Cabrera National Park for research facilities.

REFERENCES

Alcover, J.A., Ballesteros, E. & Fornós, J.J., 1993. *Història natural de l'Arxipèlag de Cabrera*, CSIC-Editorial Moll. Monografies de la Societat d'Història Natural de les Balears, 2.

Balduzzi, A., Bianchi, C.N., Boero, F., Cattaneo, R., Pansini, M. & Sarà, M., 1989. The suspension feeder communities of Mediterranean sea cave. *Scientia Marina*, **53**, 247–250.

Braun Blanquet, J., 1979. *Fitosociologia. Bases para el estudio de las comunidades vegetales*. Barcelona: Blume Ediciones.

Clarke, K.R. & Warwick, R.M., 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Swindon: Natural Environmental Research Council.

Fichez, R., 1991. Suspended particulate organic matter in Mediterranean submarine cave. *Marine Biology*, **108**, 167–174.

Garrabou, J. & Flos, J., 1995. A simple diffusion–sedimentation model to explain planktonic gradients within a NW Mediterranean submarine cave. *Marine Ecology Progress Series*, **123**, 273–280.

Gili, J.M., Riera, T. & Zabala, M., 1986. Physical and biological gradients in a submarine cave on the Western Mediterranean coast (north-east Spain). *Marine Biology*, **90**, 291–297.

Harmelin, J.G., 1985. Organisation spatiale des communautés sessiles des grottes sous-marines de Méditerranée. *Rapports et Procès-verbaux des Réunions. Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée, Paris*. **29**, 149–153.

Harmelin, J.G., 1997. Diversity of bryozoans in a Mediterranean sublittoral cave with bathyal-like conditions: role of dispersal processes and local factors. *Marine Ecology Progress Series*, **153**, 139–152.

Harmelin, J.G. & Vacelet, J., 1997. Clues to deep-sea biodiversity in a nearshore cave. *Vie Milieu*, **47**, 351–354.

Harmelin, J.G., Vacelet, J. & Vasseur, P., 1985. Les grottes sous-marines obscures: un milieu extrême et un remarquable biotope refuge. *Téthys*, **11**, 214–229.

Mariani, S., Uriz, M.J. & Turon, X., 2003. Methodological bias in the estimations of important meroplanktonic components from near-shore bottoms. *Marine Ecology Progress Series*, **253**, 67–75.

McCune, B. & Mefford, J.M., 1999. *PC-ORD. Multivariate analysis of ecological data*, Version 4. Glenden Beach, Oregon, USA: MjM Software Design.

Muus, B.J., 1968. A field method for measuring exposure by means of plaster balls. *Sarsia*, **34**, 61–68.

Palau, M., Cornet, C., Riera, T. & Zabala, M., 1991. Planktonic gradients along Mediterranean sea cave. *Oecologia Aquatica*, **10**, 299–316.

Pérès, J.M. & Picard, J., 1964. Nouveau manuel de bionomie Benthique de la Mer Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, **31**, 3–137.

Pouliquen, L., 1972. Les spongiaires des grottes sous-marines de la région de Marseille: écologie et systématique. *Téthys*, **3**, 717–758.

Simpson, T.L., 1984. *The cell biology of sponges*. New York: Springer-Verlag.

Vacelet, J., 1979. La place des spongiaires dans les systèmes trophiques marins. In *Biologie des spongiaires*, vol. 291 (ed. C. Lévi and N. Boury-Esnault), pp. 259–270. Paris: Editions du CRNS.

Zabala, M., Riera, T., Gili, J.M., Barangel, M., Lobo, A. & Peñuelas, J., 1989. Water flow, trophic depletion, and benthic Macrofauna impoverishment in a submarine cave from the western Mediterranean. *Marine Ecology*, **10**, 271–287.

Submitted 22 July 2003. Accepted 20 April 2004.

Appendix. *List of species and authorities*

Div. CHLOROPHYTA
Acetabularia acetabulum (Linnaeus) Silva
Acetabularia parvula Solms-Laubach
Anadyomene stellata (Wulfen) C. Agardh
Cladophora pellucida (Hudson) Kützing
Codium bursa J. Agardh
Flabellia petiolata (Turra) Nizamuddin
Halimeda tuna (Ellis & Solander) Lamouroux
Halicystis parvula Schmitz
Palmophyllum crassum (Naccari) Rabenhorst
Pseudochlorodesmis furcellata (Zanardini) Børgesen
Valonia utricularis (Roth) C. Agardh

Div. PHAEOPHYTA
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier in Castagne
Cystoseira balearica Sauvageau
Cystoseira compressa (Esper) Gerloff & Nizamuddin v. *pustulata* Ercegovic
Dictyopteris polypodioides (Stackhouse) Batters
Dictyota dichotoma (Hudson) Lamouroux
Dictyota dichotoma (Hudson) Lamouroux v. *intricata* (C. Agardh) Greville
Dictyota fasciola (Roth) Howe
Halopteris filicina (Grateloup) Kützing
Halopteris scoparia (Linnaeus) Sauvageau
Lobophora variegata (Lamouroux) Womersley
Padina pavonica (Linnaeus) Thivy
Sphacelaria cirrosa (Roth) C. Agardh
Taonia atomaria (Woodward) J. Agardh

Div. RHODOPHYTA
Amphiroa beauvoisii Lamouroux
Amphiroa cryptarthrodia Zanardini
Amphiroa rigida Lamouroux
Asparagopsis armata Harvey
Boergeseniella fruticulosa (Wulfen) Sprengel
Bornetia secundiflora (J. Agardh) Thuret
Botryocladia boergesenii J. Feldmann
Botryocladia botryoides (Wulfen) J. Feldmann
Contarinia squamariae (Meneghini) Denizot
Corallina elongata Ellis & Solander
Cryptomenia lomation (Bertoloni) J. Agardh
Falkenbergia rufolanosa (Harvey) Scmitz (life-history phase)
Gloiocladia furcata (C. Agardh) J. Agardh
Haliptilon virgatum Ellis & Solander
Hydrolithon farinosum (Lamouroux) Howe
Jania rubens (Linnaeus) Lamouroux
Laurencia obtusa (Hudson) Lamouroux
Lithophyllum cabiochae (Dufour) Furnari, Cormaci & Alongi
Lithophyllum dentatum (Kützing) Foslie *sensu* Hamel & Lemoine
Lithophyllum incrustans Philippi
Mesophyllum alternans (Foslie) Cabioch & Mendoza
Neogonolithion brassica-florida (Harvey) Setchell & Mason
Peyssonnelia rosa-marina Boudouresque & Denizot
Peyssonnelia squamaria (Gmelin) Decaisne
Plocamium cartilagineum (Linnaeus) Dixon
Polystrata fosliei (Weber van Bosse) Denizot
Rhodophyllis divaricata (Stackhouse) Papenfuss

Rhodymenia ardissonei J. Feldmann
Wurdermannia miniata (Sprengel) J. Feldmann & Hamel

Phylum GRANULORETICULOSA
Miniacina miniacena (Pallas, 1766)

Phylum PORIFERA
Aaptos aaptos (Schmidt, 1864)
Acanthella acuta Schmidt, 1862
Agelas oroides (Schmidt, 1864)
Aplysina cavernicola (Vacelet, 1959)
Axinella damicornis (Esper, 1794)
Cacospongia mollior Schmidt, 1862
Chelanoplysilla noevus (Carter,1876)
Chondrosia reniformis Nardo, 1833
Clathrina clathrus (Schmidt, 1864)
Cliona celata Grant, 1826
Cliona schmidti (Ridley, 1881)
Cliona viridis (Schmidt, 1862)
Crambe crambe (Schmidt, 1862)
Crella mollior Topsent, 1925
Dendroxea lenis (Topsent, 1892)
Diplastrella bistellata (Schmidt, 1862)
Dysidea avara (Schmidt, 1862)
Erylus euastrum (Schmidt, 1870)
Hemimycale columella (Bowerbank, 1874)
Hexadella pruvotii Topsent, 1905
Hippospongia communis (Lamarck, 1813)
Ircinia fasciculata (Pallas, 1766)
Ircinia oros (Schmidt, 1864)
Ircinia variabilis (Schmidt, 1862)
Leucosolenia variabilis Haeckel, 1870
Myceliospongia araneosa Vacelet & Perez, 1998
Oscarella tuberculata (Schmidt, 1868)
Petrosia ficiformis (Poiret, 1879)
Phorbas fictitius (Bowerbank, 1866)
Phorbas tenacior (Topsent, 1925)
Pione vastifica (Hanckock, 1849)
Pleraplysilla spinifera (Schulze, 1879)
Raspaciona aculeata (Johnston, 1842)
Reniera fulva Topsent, 1893
Reniera mucosa Griessinger, 1971
Reniera sarai (Pulitzer-Finali)
Spirastrella cunctatrix Schmidt, 1868
Spongia virgultosa (Schmidt, 1868)
Sycon elegans (Bowerbank, 1866)
Terpios fugax Duchassaing & Michelotti, 1864
Topsentia garciae Bibiloni, Uriz & Gili, 1989

Phylum CNIDARIA
Aglaophenia kirchenpaueri (Heller, 1868)
Alcyonium acaule Marion, 1878
Balanophyllia europaea (Risso, 1826)
Balanophyllia regia (Gosse, 1860)
Caryophyllia inornata (Duncan, 1878)
Cladocora caespitosa (Linnaeus, 1767)
Clavularia crassa (Milne-Edwards, 1848)
Corallium rubrum (Linnaeus, 1758)
Cornularia cornucopiae (Pallas, 1766)
Eunicella singularis (Esper, 1791)
Hoplangia durotrix Gosse, 1860
Leptopsammia pruvoti Lacaze-Duthiers, 1897
Maasella edwardsi (Lacaze-Duthiers, 1888)
Parerythropodium coralloides (Pallas, 1766)
Parazoanthus axinellae (Schmidt, 1862)
Polycyathus muellerae (Abel, 1959)
Sertularella ellisi (Milne-Edwards, 1836)

Phylum ANNELIDA
Myxicola aesthetica Koch in Renier, 1847
Salmacina dysteri (Huxley, 1855)
Serpula vermicularis Linnaeus, 1767

Phylum MOLLUSCA
Bittium reticulatum (Da Costa, 1778)
Lima hians (Gmelin, 1790)
Lithophaga lithophaga (Linnaeus, 1758)

Phylum ECTOPROCTA
Annectocyma indistincta (Canu & Bassler, 1929)
Bugula calathus (Norman 1868)
Chlidonia pyriformis (Bertoloni, 1810)
Disporella hispida (Fleming, 1828)
Frondipora verrucosa (Lamouroux, 1821)
Idmidronea atlantica (Canu & Bassler, 1928)
Lichenopora radiata (Audouin, 1826)
Margaretta cereoides (Ellis & Solander, 1786)
Myriapora truncata (Pallas, 1766)
Parasmittina tropica (Waters, 1909)
Puellina gattyae (Landsborough, 1852)
Reptadeonella violacea Johnston, 1847
Schizomavella cuspidata (Hincks, 1880)
Schizomavella linearis (Hassall, 1841)
Smittina cervicornis (Pallas, 1766)
Smittoidea reticulata (MacGillivray, 1842)
Spiralaria gregaria (Heller, 1867)

Phylum BRACHIOPODA
Argyrotheca cordata (Risso, 1826)
Crania anomala (Müller, 1776)
Megerlia truncata (Linnaeus, 1767)

Phylum ECHINODERMATA
Paracentrotus lividus (Lamarck, 1816)

Phylum CHORDATA
Ascidia mentula Müller, 1776
Botrylloides leachi (De Savigny, 1816)
Clavelina lepadiformis (Müller, 1776)
Cystodytes dellechiajei (Della Valle, 1877)
Diplosoma spongiforme (Giard, 1872)
Lissoclinum perforatum (Giard, 1872)
Pyura dura (Heller, 1877)