

## Soft-bottom crustacean assemblages in Mediterranean marine caves: the cave of Cerro Gordo (Granada, Spain) as case study

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**Abstract** Although marine caves are priority conservation areas according to the Directive 92/43/CEE of the European Community, there is a lack of studies dealing with their soft-bottom communities. For a case study, we selected the Cerro Gordo cave at 15 m depth. Three different zones were defined: a semi-dark 25-m long entrance area, a dark intermediate area of 35 m, and the final zone at 90 m from the entrance. Sediment samples were taken from these zones as well as from outside the cave (control) by SCUBA diving. Six rectangular cores of  $10 \times 250 \text{ cm}^2$  were collected in each site for macrofaunal study, and three more replicates were taken to analyze physico-chemical parameters. The granulometry showed a clear gradient from medium sands outside the cave to silt and clay in the inner zone. Measurements of the crustacean assemblages showed that the number of species and abundance were significantly higher outside the cave (30–40 species,  $>4,000 \text{ ind m}^{-2}$ ) than inside (5–10 species,  $<1,000 \text{ ind m}^{-2}$ ). Multivariate analyses showed a clear difference in species composition between outside and inside the cave. Caprellids, tanaids, cumaceans, and decapods were only found outside the cave, while gammarids and

isopods were present both outside and inside the cave. The gammarid *Siphonoecetes sabatieri* and the tanaid *Apseudes latreilli* were the dominant species outside the cave, while the gammarids *Harpinia pectinata*, *Harpinia crenulata*, and *Harpinia ala* were dominant inside. The present study represents an increase in depth range and geographic distribution for *Kupellonura mediterranea* and *Monoculodes packardii*. This is the first description of soft-bottom crustacean communities from submarine caves of southern Spain.

**Keywords** Crustaceans · Peracarids · Amphipods · Marine caves · Mediterranean · Soft bottoms

### Introduction

Marine cave assemblages have aroused great interest over the last decades (Benedetti-Cecchi et al. 1996). This environment is attractive to taxonomists and ecologists for several reasons. It is a simplified and oligotrophic system, depending entirely on energy input from the surrounding productive coastal area. There are strong alterations in the distribution of organisms, which reflect marked gradients in the environmental conditions. These special conditions of light deficiency, oligotrophy and low hydrodynamics enable the presence of species in that shallow environment, which are otherwise restricted to deeper water. Moreover, the investigation of marine caves often provides the facility to discover new and endemic species, due to the isolation of cave communities (Ott and Svoboda 1976; Harmelin et al. 1985; Ros et al. 1989). For all these reasons, submarine caves are unique and vulnerable ecosystems (Sarà 1976), protected by the European Community (Habitat Directive 92/43 EEC). However, the study of marine cave

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communities has focused primarily on the benthic communities of hard substrates, while very little effort has been devoted to the study of soft-bottom communities. The bottom of underwater caves is often formed by muddy sediment. Its suspension, which can result in an almost complete loss of visibility, is one of the greatest dangers to divers advancing into caves.

All cave studies have revealed a marked horizontal zonation within the animal communities on the walls (Laborel and Vacelet 1959; Sarà 1961; Riedl 1966; Pérès 1967; Cinelli et al. 1978; Balduzzi et al. 1989; Bibiloni and Gili 1982; Harmelin et al. 1985; Gili et al. 1986, 1987; Zabala et al. 1989; Bibiloni et al. 1989; Fichez 1990; Benedetti-Cecchi et al. 1996, 1998; Harmelin 1997; Bell 2002; Bussotti et al. 2006; Marti et al. 2004a, b; Dennito and Licciano 2006; Denitto et al. 2007; Moscatello and Belmonte 2007). A common feature in these studies is a decrease in species richness, biomass and coverage of benthic organisms from the outermost to the innermost part of the cave. The proposed explanations for these features are the physical gradients inside the cave (light, oxygen, salinity, etc.), the trophic supply gradient and the limited capacity of the larvae for dispersion and settlement (Harmelin et al. 1985; Zabala et al. 1989; Fichez 1990). All these factors may also apply to soft-bottom communities, but until now possible changes in soft substrate assemblages along the gradient of shallow submarine caves have not been investigated.

Peracarid crustaceans are among the most diverse and abundant organisms in soft-bottom benthic fauna (Fincham 1974; Dauvin et al. 1994; Prato and Biantolino 2005; Lourido et al. 2008). They also play an important role in structuring benthic assemblages (Duffy and Hay 2000), and their abundance and species diversity may serve as indicators of environmental conditions (Alfonso et al. 1998; Corbera and Cardell 1995; Gómez-Gesteira and Dauvin 2000; Guerra-García and García-Gómez 2004). For anchialine caves, Iliffe (2005) indicated that this group makes up 90% of species. Furthermore, many new taxa are being described from marine caves, and sediments of these caves are still largely unexplored. It is difficult to find caves with a defined gradient of sediments from the outer to the inner zones. Consequently, the cave of Cerro Gordo, more than 100 m long, is an adequate site to study, for the first time, the soft-bottom crustacean communities in a Mediterranean cave gradient.

The aims of this study were (1) to identify the crustacean species that inhabit the soft bottom of Cerro Gordo cave and (2) to determine their distribution and abundance along the environmental gradient of the cave in order to assess whether soft-bottom communities present patterns that are similar to those found for the hard-bottom animal communities on the walls of the cave.

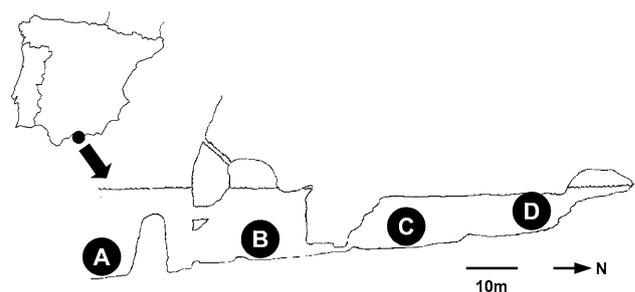
## Materials and methods

### Study area

The study was conducted at the Cerro Gordo cave, a karstic submarine cave located on the coast of Granada (south Spain, Alboran Sea, 33°43'46"N, 3°45'56"O) (Fig. 1). Because of upwelling events, which bring nutrient-rich water from the deep, this area is characterized by very diverse benthic communities. The cave is more than 100 m long and presents a large submerged single entrance. A marked narrowing of the cave 25 m from the entrance separates two topographic areas. The first area, extending from the entrance to the narrowing, is a hall, with 15 m wide and 15 m high, with an air chamber on the top. Light, although reduced, is still present in this hall. The second area is a rectilinear, blind-ending tunnel more than 75 m long, representing the dark area. The depth decreases along the tunnel until the tunnel reaches an air chamber at its end, where there are freshwater springs. Sampling stations were referred as A, B, C and D. Station A was located outside the cave, in a sandy bottom area near the entrance. Station B was located in the semi-dark area, between 15 and 20 m from the entrance. The other two sampling stations were in the dark area, one at about 60 m from the entrance and the other at the end of the cave, in an area under freshwater influence (Fig. 1).

### Sample collection and analyses

The sample collection was carried out in February 2001, using a hand-held rectangular core of 0.025 m<sup>2</sup> to a depth of 10 cm by SCUBA diving. Six replicate core samples were taken at each station for the crustacean study. Samples were washed through a 0.5-mm mesh sieve with seawater and fixed with ethanol stained with rose bengal. In the laboratory, each sample was examined using binocular microscopes. All crustacean specimens were counted and identified to species level where possible. Species diversity for each sample and the associated evenness component  $J'$



**Fig. 1** Location and longitudinal section of Cerro Gordo cave, showing the sampling stations (a–d)

(Pielou 1966) were calculated applying the ( $\log_2$ ) Shannon–Weaver diversity index ( $H'$ ) (Shannon and Weaver 1963).

Together with the macrofaunal samples, three more sediment cores were collected at each station for physico-chemical analyses of the sediments. All samples were immediately stored frozen until the laboratory analyses. Granulometric parameters were determined following the method proposed by Guitián and Carballas (1976). For the chemical analysis, the sediments were air-dried, crushed and sieved (2 mm) first. Aliquots of sediment samples were also ground to  $<60 \mu\text{m}$  prior to determination of major, minor and trace element concentrations. Organic matter (OM) was analyzed by dichromate oxidation and titration with ferrous ammonium sulphate (Walkley and Black 1934). Kjeldahl-N was determined by the method described by Hesse (1971). Total major, minor and trace element concentrations in sediments ( $<60 \mu\text{m}$ ) were determined by Inductively Coupled Plasma-Optical Emission Spectrometer (ICP-OES Varian ICP 720-ES axially viewed) following aqua-regia digestion in a microwave oven (Microwave Laboratory Station Mileston ETHNOS 900). The term 'total' accounts for the aqua-regia digestion, but it does not completely destroy silicates. The accuracy of the analytical methods was assessed by carrying out analyses of the BCR (Community Bureau of Reference) samples: BCR 320R (channel sediment) and soil sample reference ISE 872 from the Wageningen Evaluating Programs for Analytical Laboratories, International Soil-analytical Exchange (WEPAL; ISE).

#### Statistical analyses

Biological, chemical and granulometric data were not normally distributed (Kolmogorov–Smirnov test) and did not feature homogeneity of variance (Levene test). Thus, we opted to use Kruskal–Wallis analysis to detect differences between stations. If differences existed, Tamhane post hoc tests were used for post hoc comparisons. The univariate statistical analyses were carried out using the SPSS 17.0 statistic program.

Cluster analyses were conducted on abundance per taxonomic group to assess the relationship between stations. Hierarchical clustering with group-average linking, based on similarity matrices (Bray–Curtis coefficient), was used. Data were previously square root-transformed to reduce the importance of extreme values. To the same end, cluster analyses were conducted with the granulometric and chemical data. In such cases, the clustering with group-average linking was based on euclidean distances matrices. These analyses were done using the PRIMER package (Clarke and Gorley 2001).

#### Results

A total of 36 crustacean species were recorded from the four stations of the study. These comprised 24 amphipod species, four cumaceans, four isopods, two tanaids and two decapods (Table 1). The exterior zone was dominated by the amphipods *Siphonoecetes sabatieri* and *Metaphoxus fultoni*, the tanaid *Apseudes latreilli* and the decapod *Diogenes pugilator*. These four species comprised 74% of the specimens. The most abundant species inside the cave were three species of the genus *Harpinia*: *Harpinia ala*, *H. crenulata* and *H. pectinata*. *H. pectinata*, which has a shallower distribution, was the only one found in all stations, including the one outside the cave. *Harpinia crenulata* was present in the three stations inside the cave, and *H. ala* only occurred in the dark part of the cave. Other interesting deep-water species found inside the cave were the amphipod *Monoculodes packardi* and the isopod *Kupellonura mediterranea*. Amphipods were the dominant group in abundance and number of species for all stations (Fig. 2). However, the number of amphipod species and individuals was lower inside the cave. Species of the suborder Gammaridea were able to colonize the interior of the cave, while species of the suborder Caprellidea were only present in the exterior area. The other crustacean group inhabiting the cave sediment was the order Isopoda. Although its dominance was higher in the inner part of the cave, this group also presented a decrease in richness and abundance inside the cave. Tanaidacea, Cumacea and Decapoda were only present in the external station. Richness, abundance and diversity values clearly decreased towards the inner part of the cave. By contrast, evenness increased slightly in station D (Fig. 3). The Kruskal–Wallis analysis revealed that these differences among stations were significant for number of species, number of individuals and diversity values, but not for the evenness. The Tamhane post hoc test results were different in each case (Table 2).

The granulometric data indicated a progressive increase in the finer fractions in the inner areas of the cave (Fig. 4). The Kruskal–Wallis analysis showed the existence of significant differences in the silt and clay composition among stations ( $W = 10.38$ ;  $p = 0.016$ ). Tamhane post hoc test supported the existence of three groups of samples: samples from the exterior zone (A), from the semi-dark zone (B) and from the dark zone of the cave (C and D). Concerning chemical analyses, univariate tests showed significant differences between stations for all variables, with the exception of organic matter, nitrogen and phosphorus. Although there were some differences between elements in the results obtained by the Tamhane post hoc tests, most tests showed significant differences between all the stations

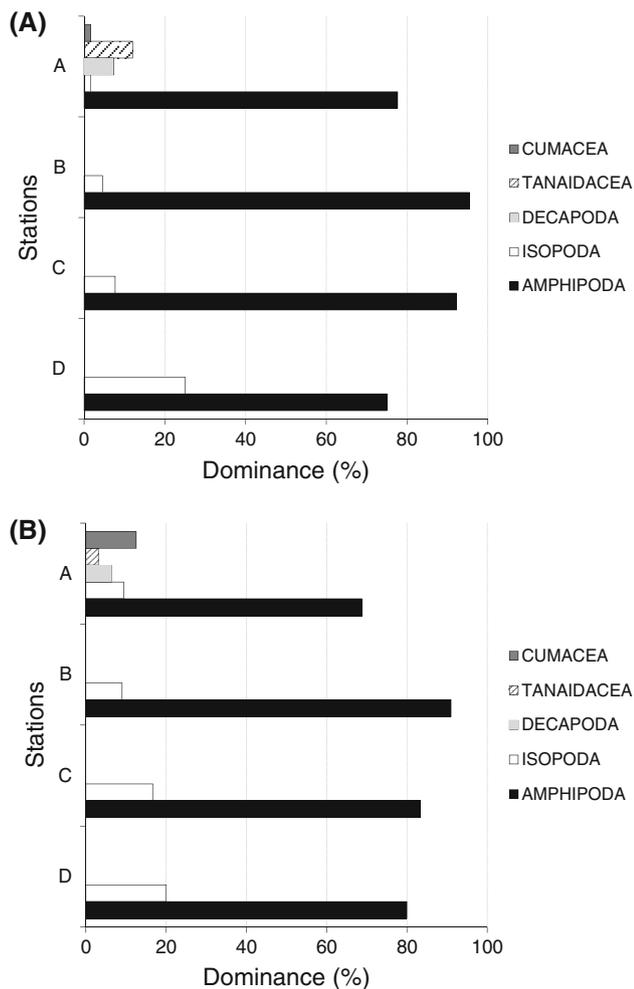
**Table 1** List of crustacean species recorded at Cerro Gordo cave and relative abundances (number of individuals per m<sup>2</sup> ±SE) in the four stations

Species	Stations			
	A	B	C	D
<b>Amphipoda</b>				
<i>Ampelisca brevicornis</i> (Costa, 1853)	33 ± 16	0	0	0
<i>Ampelisca serraticaudata</i> (Chevreux, 1888)	47 ± 30	13 ± 8	0	13 ± 13
<i>Ampelisca truncata</i> (Bellan-Santini & Kaim-Malka, 1977)	20 ± 13	0	0	0
<i>Amphilocheus spencebatei</i> (Stebbing, 1876)	20 ± 13	0	0	0
<i>Argissa stebbingi</i> (Bonnier, 1896)	13 ± 13	0	0	0
<i>Bathyporeia guilliamsoniana</i> (Bate, 1857)	100 ± 36	0	0	0
<i>Cheirocratus sundevallii</i> (Rathke, 1843)	13 ± 8	0	0	0
<i>Harpinia ala</i> (Karaman, 1987)	0	0	93 ± 33	7 ± 6
<i>Harpinia crenulata</i> (Boeck, 1871)	0	240 ± 45	87 ± 42	27 ± 20
<i>Harpinia pectinata</i> (Sars, 1891)	13 ± 8	653 ± 145	447 ± 120	13 ± 8
<i>Hippomedon massiliensis</i> (Bellan-Santini, 1965)	13 ± 8	7 ± 6	0	0
<i>Lembos</i> sp.	87 ± 47	0	0	0
<i>Leucothoe oboa</i> (Karaman, 1971)	20 ± 9	20 ± 13	0	0
<i>Maera</i> sp.	7 ± 6	0	0	0
<i>Methaphoxus fultoni</i> (Scott, 1890)	387 ± 189	7 ± 6	0	0
<i>Monoculodes acutipes</i> (Ledoyer 1983)	0	0	7 ± 6	0
<i>Monoculodes packardi</i> (Boeck, 1871)	7 ± 6	0	7 ± 6	0
<i>Pariambus typicus</i> (Krøyer, 1844)	47 ± 16	0	0	0
<i>Perioculodes longimanus</i> (Bate & Westwood, 1868)	153 ± 40	7 ± 6	0	0
<i>Photis longipes</i> (Della-Valle, 1893)	147 ± 52	173 ± 103	0	0
<i>Phtisica marina</i> (Slabber, 1769)	113 ± 74	0	0	0
<i>Pontocrates arenarius</i> (Bate, 1858)	20 ± 18	7 ± 6	0	0
<i>Siphonoecetes sabatieri</i> (Rouville, 1894)	2,213 ± 938	0	0	0
<i>Urothoe elegans</i> (Bate, 1857)	73 ± 28	7 ± 6	0	0
<b>Cumacea</b>				
<i>Campyloopsis</i> sp.	7 ± 6	0	0	0
<i>Cumea</i> sp.	27 ± 20	0	0	0
<i>Dyastilis</i> sp.	7 ± 6	0	0	0
<i>Iphinoe</i> sp.	33 ± 12	0	0	0
<b>Decapoda</b>				
<i>Diogenes pugilator</i> (Roux, 1929)	320 ± 53	0	0	0
Juvenile	13 ± 13	0	0	0
<b>Isopoda</b>				
<i>Cymodoce truncata</i> (Leach, 1814)	7 ± 6	0	0	0
<i>Euridyce</i> sp.	60 ± 42	0	0	0
<i>Paranthura nigropunctata</i> (Lucas, 1846)	7 ± 6	0	0	0
<i>Kupellonura mediterranea</i> (Barnard, 1925)	0	53 ± 52	20 ± 9	53 ± 9
<b>Tanaidacea</b>				
<i>Apseudes latreilli</i> (Milne-Edwards, 1828)	547 ± 158	0	0	0
<i>Tanaopsis graciloides</i> (Lilljeborg, 1864)	7 ± 6	0	0	0

except for stations C and D (Table 3). The trends observed along the horizontal transect also varied. For Al, As, Ba, Co, Cr, Cu, Fe, K, Li, Mn, Ni, Pb, V and Zn, there was an increase in their concentrations towards the inner part of

the cave. In contrast, we obtained an opposite trend for B, Ca, Cd, Mg, Na, S and Sr (Fig. 5).

The cluster analyses performed for the biological, granulometric and chemical data also showed the existence



**Fig. 2** Dominance (%) of different groups for the different sampling stations, calculated with respect to number of species (a) and number of individuals (b)

of the three distinct groups mentioned above (Fig. 6). The first group included the samples of station A, with sediments dominated by medium sands and a faunistic composition clearly different from that inside the cave, with less than 20% of similarity. The second group was represented by samples from the semi-dark area (station B). The samples from this zone, where the most abundant sediment fraction was the very fine sands, appeared very close in the three cluster analyses (more than 60% of similarity in their taxonomic composition). Finally, a third group included the samples of stations C and D (the dark zone). This area had the lowest values of richness, abundance and diversity, and its sediments were composed mainly of silt and clay.

## Discussion

All the analyses showed a zonation in the Cerro Gordo cave. The photic (exterior) area, the semi-dark area and the

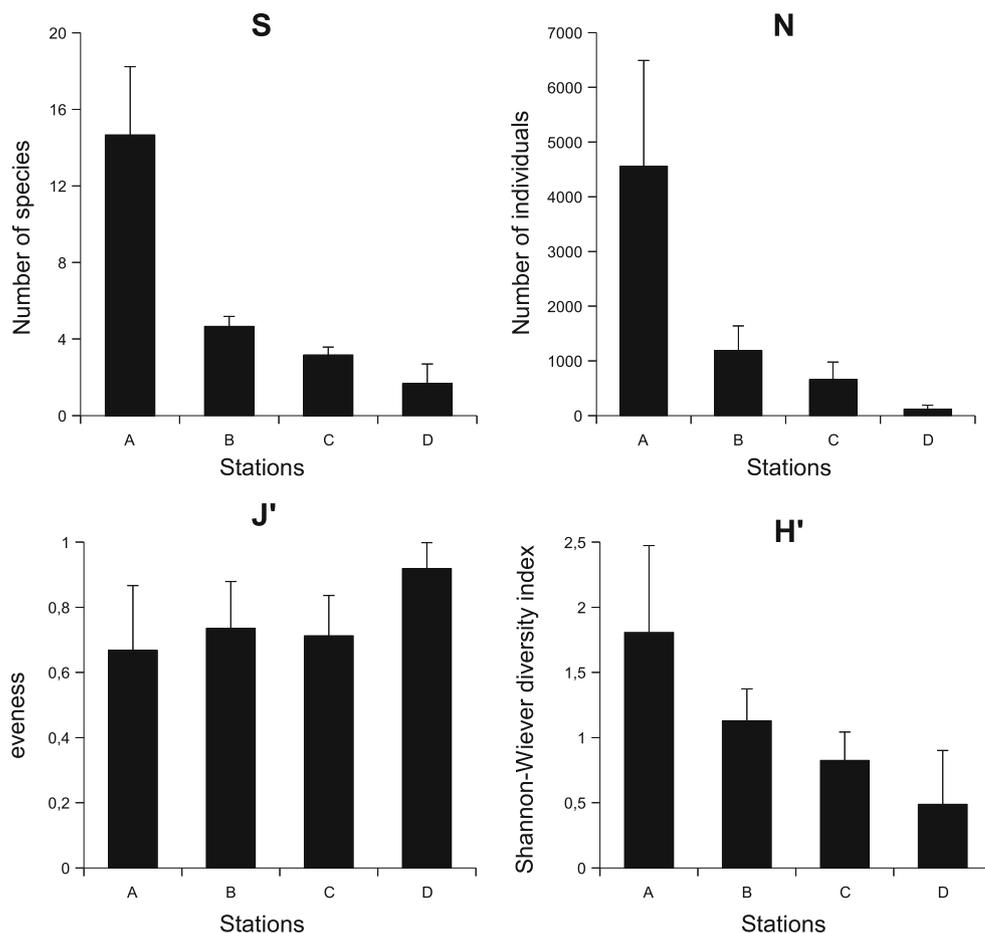
dark area were clearly different in both taxonomic composition and physico-chemical characteristics. These three biocoenoses are generally recognized in Mediterranean marine caves and have been identified for both mobile and hard-bottom cave communities (Riedl 1966; Pérès 1967; Bibiloni and Gili 1982; Balduzzi et al. 1989; Gili et al. 1986; Gili and Macpherson 1987; Bibiloni et al. 1989; Fichez 1990; Marti et al. 2004a; Bussotti et al. 2006; Denitto et al. 2007; Moscatello and Belmonte 2007; Bussotti and Guidetti 2009). Nevertheless, it was unknown so far whether a similar pattern of zonation also applies to soft substrate communities.

The data obtained for the exterior station corresponded to those previously reported for this area (Sanchez-Moyano et al. 2005). More interesting results were obtained for inside the cave, where many rare species could be recorded. *K. mediterranea* was described by Barnard (1925) and redescribed in detail by Wägele (1981) and Kensley (1987). This species was so far known only from 70 to 880 m depth and from the coasts of Naples, Sicily and the Ligurian Sea. Thus, our finding shows a huge increase in both depth range and geographic distribution of *K. mediterranea*. Another deep-water species found in the Cerro Gordo cave was *M. packardii*, which had a known bathymetric distribution between 90 and 2,616 m depth (Ruffo 1993). So our findings represent the shallowest occurrence of this species so far.

The dominance of the amphipoda over other crustacean taxa is a common feature (Sanchez-Moyano et al. 2005). The presence of isopoda and amphipoda inside the cave was not surprising as both have a great capacity to live in most marine habitats. Kensley (1998) indicated that isopods show their highest diversity in the deep sea (a marked oligotrophic environment with predominantly muddy sediment, like cave environments). Interestingly, caprellids, cumaceans, decapods and tanaids were absent in the inner area of the cave. All these groups have been reported from muddy sediments (e.g. Guerra-García and García-Gómez 2004; Lourido et al. 2008) so that factors others than granulometry may account for these findings.

The results showed a clear decline in richness, abundance and diversity of the crustacean soft-bottom community from the exterior to the inner dark parts of the cave. This trend has been observed for many groups such as suspension and filter feeders (sponges, cnidarians, bryozoans and tunicates) (Bibiloni and Gili 1982; Gili et al. 1986; Balduzzi et al. 1989; Bibiloni et al. 1989; Harmelin 1997; Benedetti-Cechi et al. 1998; Corriero et al. 2000; Bell 2002; Martí et al. 2004a; Bussotti et al. 2006), large decapods (Gili and Macpherson 1987), meiofauna (Todaro et al. 2006), planktonic organisms (Garrabou and Flos 1995; Moscatello and Belmonte 2007), polychaetes (Denitto and Licciano 2006), fishes (Bussotti et al. 2002, 2003;

**Fig. 3** Mean values  $\pm$  SD of numbers of species/sample (S), number of individuals/m<sup>2</sup> (N), evenness (*J'*) and diversity (*H'*) for the sampling stations a–d



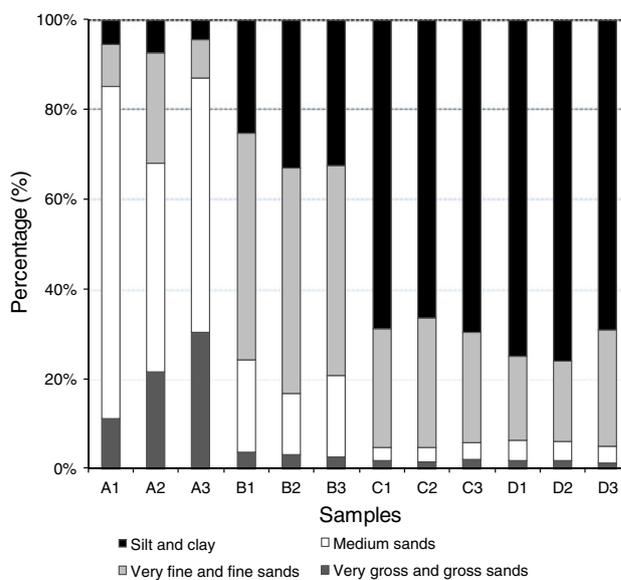
**Table 2** Kruskal–Wallis and Tamhane post hoc results on biological data per station

	Kruskal–Wallis statistic	Tamhane post hoc
S	21.2***	A $\neq$ B $\neq$ C = D
N	20.6***	A $\neq$ B = C = D; B $\neq$ D
J'	0.68 n.s.	
H'	15.6**	A = B = C = D; A $\neq$ C; A $\neq$ D

S number of species, N abundance, *J'* evenness, *H'* Shannon diversity  
 \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

Bussotti and Guidetti 2009), etc. However, this trend has not been reported for the macro-infauna so far.

There are very few investigations dealing with the macro-infauna of submarine caves, and it is difficult to compare their results with those of the present study. Monteiro-Marques (1981) made a taxonomical description of macro-infauna assemblages from some submarine caves from southern France. As their samples were washed through a 1-mm mesh sieve, most crustaceans were not taken into account. Akoumianaki and Hughes (2004) studied the Grotta Azzurra (Italy) and did not find any decrease in macro-infauna abundance or diversity inside



**Fig. 4** Percentage of the different granulometric fractions in the sediment per sample

the cave. A possible explanation for this could be the existence of sulphur springs at the end of the cave, which provided an additional source of food for an otherwise

**Table 3** Kruskal–Wallis and Tamhane post hoc results on chemical data per station

	Kruskal–Wallis statistic	Tamhane post hoc
OM	8.556 n.s.	
N	8.735 n.s.	
P	3.359 n.s.	
Al	10.385*	A ≠ B ≠ C = D
As	10.385*	A = B = C ≠ D; A ≠ C A ≠ D
B	10.385*	A ≠ B ≠ C = D
Ba	9.974*	A = B ≠ C = D
Ca	9.462*	A ≠ B ≠ C = D
Cd	9.974*	A ≠ B ≠ C = D
Co	10.385*	A ≠ B ≠ C = D
Cr	10.385*	A ≠ B ≠ C = D
Cu	10.385*	A ≠ B ≠ C = D
Fe	10.385*	A ≠ B ≠ C = D
K	10.385*	A ≠ B = C ≠ D
Li	10.385*	A ≠ B ≠ C = D
Mg	7.000 n.s.	
Mn	9.667*	A = B ≠ C = D
Na	9.667*	A = B ≠ C = D
Ni	10.385*	A ≠ B ≠ C = D
Pb	10.385*	A = B ≠ C ≠ D
S	9.462*	A ≠ B ≠ C = D
Sr	9.462*	A = B ≠ C = D
V	10.385*	A ≠ B ≠ C = D
Zn	9.974*	A ≠ B ≠ C = D

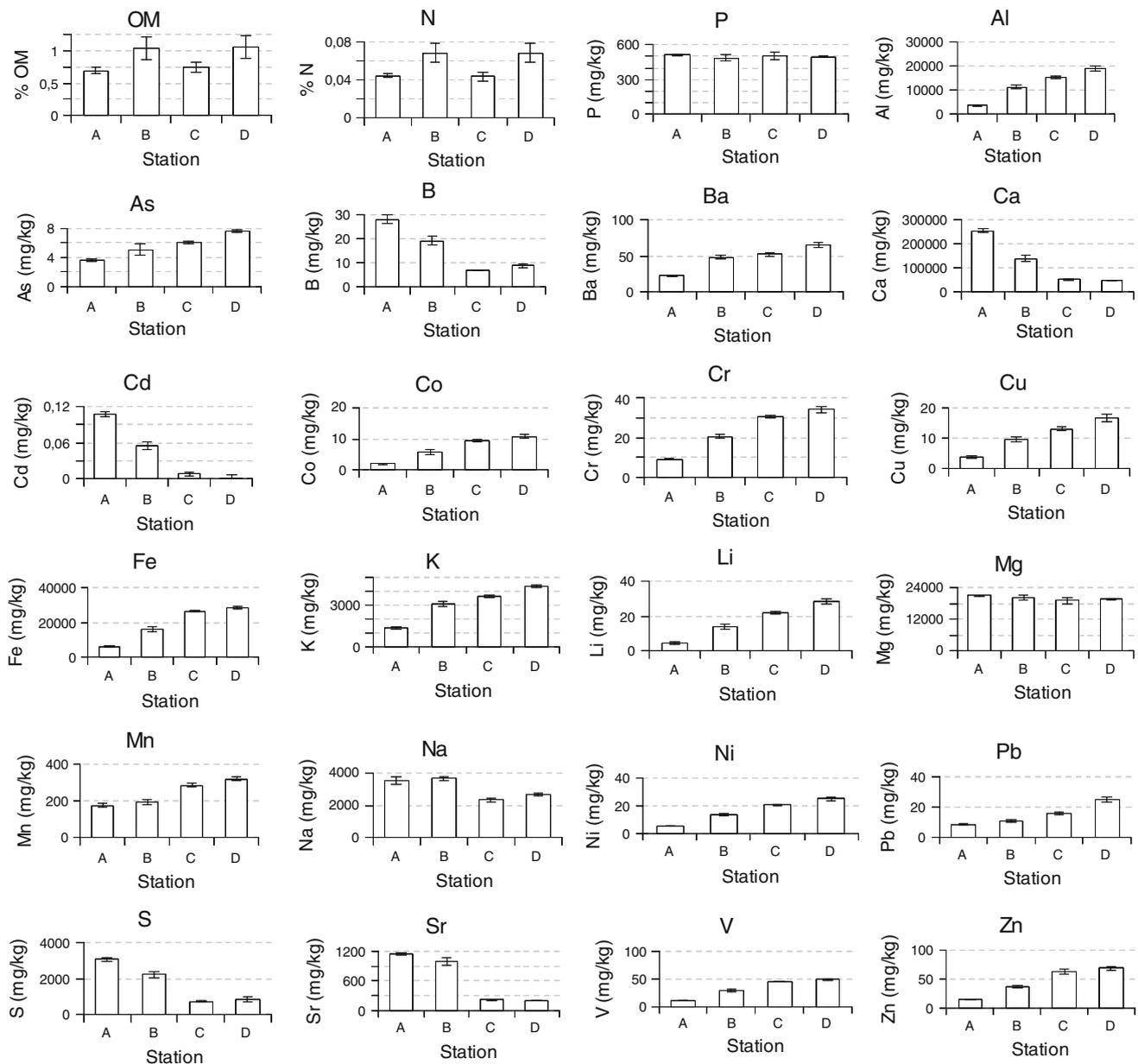
OM organic matter

\*  $p < 0.05$ 

resource-limited cave environment. Thus, to our knowledge, the present study provides the first evidence of a decrease in soft-bottom macro-infauna diversity in Mediterranean marine caves, when compared with communities outside the cave. For hard-bottom communities, this gradient is usually explained by a reduced water turnover towards the inner part of the cave, which generally results in oligotrophic conditions (Harmelin et al. 1985; Fichez 1990). In the Cerro Gordo cave, the gradient in silt and clay percentage in the sediment would support this hypothesis, since it indicates a low water turnover inside the cave. However, despite the extreme confinement and the lack of primary production, we did not find significant differences in organic matter or macro-nutrients between different stations. The reason for this remains unclear. Recently, it has been proposed that mobile animals such as fish (Bussotti et al. 2003) or mysids (Coma et al. 1997) can play a relevant ecological role in caves by introducing organic matter with their daily migrations. We can find some of

these organisms in the Cerro Gordo cave (e.g. *Scyaena umbra*, *Apogon imberbis* and mysid species), but because of their low abundance, they may not have a significant effect. Nevertheless, this issue should be further studied.

There are many other caves where the trophic-depletion hypothesis fails to explain the very poor faunal assemblages of their inner parts, as there is no significant decrease in organic matter. The studies on hard-bottom assemblages suggest the processes determining spatio-temporal distribution patterns in marine caves to be highly complex, being context and scale dependent (Benedetti-Cechi et al. 1998; Bussotti et al. 2006). Thus, many other factors have been proposed to explain the distribution patterns observed (always for hard-bottom communities): physico-chemical gradients with respect to salinity, temperature, density and dissolved oxygen (Gili et al. 1986; Zabala et al. 1989; Harmelin 1997), diffusion-sedimentation processes (Garrabou and Flos 1995), the persistence of microlayer gradients along the walls (Gili et al. 1986), variation in larval settlement and post-settlement events (Benedetti-Cechi et al. 1996; Harmelin 1997; Denitto et al. 2007), biotic interactions between species (Benedetti-Cechi et al. 1996; Martí et al. 2004b, 2005; Turon et al. 2009), presence of hydrothermal springs (Benedetti-Cechi et al. 1996, 1998), the depth and the exposure of the entrance (Corriero et al. 2000; Bell 2002), differences in internal topography (Martí et al. 2004a, b) and presence or absence of secondary openings (Zabala et al. 1989). One of the main explanations for the distribution of crustacean soft-bottom communities in the present study could be grain size. This factor significantly affects the distribution and composition of peracarid assemblages in sediments (Robertson et al. 1989). The number of species tends to be higher in fine and coarse sands than in muddy sediments (Dauvin et al. 1994). So, the decrease in grain size towards the inner part of the cave may explain the richness pattern found. Bamber et al. (2008) compared submarine caves and open habitats at Hong Kong and found that grain size was the factor most associated with the macro-infauna diversity. However, in this study richness and abundance was often higher inside than outside the cave. In contrast, the crustacean diversity found in Cerro Gordo cave was very low, comparable to that found in deep Mediterranean sediments (Bellan-Santini 1990). The factor proposed by Bamber et al. (2008) to explain their results was the high heterogeneity of the sediments in the caves studied: ‘The heterogeneity of the substratum, in a stable environment, may be expected to accommodate a wider diversity of taxa (and of niches), as well as potentially offering habitat conditions which may be rare or absent elsewhere, giving potential to support species not commonly found outside the cave habitat’. Gray (1974) also suggested that heterogeneous sediments provide many microhabitats, which



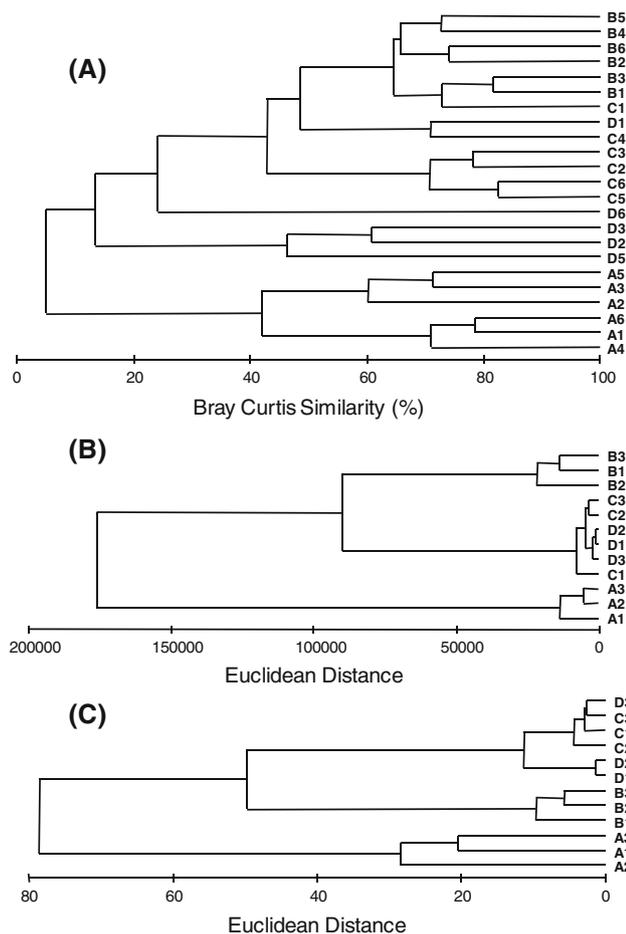
**Fig. 5** Mean concentration  $\pm$  SD of the different chemical variables per station; *OM* organic matter

may support a greater diversity of species than homogeneous sediments do. On the other hand, it has been suggested that the composition of organic matter may change along the cave, with the fraction easier to degrade being less abundant in the inner parts of the cave (Fichez 1991).

There was an increase in the concentration of most elements towards the inner part of the cave. The reason for this was probably the high capacity of muddy sediments to retain elements, and especially heavy metals (Guerra-García 2001). Many studies have indicated abundance and diversity of peracarid species may serve as indicators of environmental conditions because these animals are highly sensitive to hydrocarbon and heavy metals pollution

(Guerra-García and García-Gómez 2004). Thus, the increase in the concentrations of heavy metals, such as aluminium and lead, may also be responsible for the decline of richness and abundance of crustaceans. In karstic caves, water salinity is a major factor too. Although the salinity values obtained in the dark area of the cave were not very low, the supply of freshwater is highly variable, being especially abundant after rains. Therefore, variations of salinity may also contribute to the low diversity in the inner part of the cave, but probably do not affect the semi-dark area, where diversity is also low.

Furthermore, larvae have great difficulty in reaching and colonizing the dark inner parts of caves. This may be



**Fig. 6** Cluster analysis of samples using the abundance of each species (a), the chemical data (b) and the granulometric data (c)

another important factor responsible for the impoverishment of cave faunas (Harmelin 1997; Denitto et al. 2007). Since the communities of the dark inner parts of caves are usually composed of deep-water species, the arrival of these organisms depends on both biotic (the existence of a pool of deep-water organisms in the region with enough dispersal capacity) and abiotic factors (the hydrodynamic conditions in the area and inside the cave) (Harmelin 1997). Peracarids, the dominant crustaceans in the present study, lack dispersive larvae (direct development), and the dispersion of adults by bed-load transport or drift in the water column may be rather limited inside the cave. It would be interesting to conduct experimental studies on recolonization patterns inside the cave.

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