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Distribution of meiofaunal abundances in a marine cave complex with secondary openings and freshwater filtrations

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Abstract Submerged sea caves are priority areas for conservation according to the Habitat Directive 92/43/CEE because of their unique biodiversity. A limited number of publications exist about communities living on sediments inside caves, mostly focused on the macrofaunal fraction (>0.5-mm body size). Meiofaunal communities (0.062–0.5-mm body size) have been largely neglected in ecological studies about communities inhabiting sea caves. In the present study, we analysed meiofaunal communities from Los Cerebros cave, a shallow marine cave (3–8 m in depth, 80 m long), with secondary openings in the inner parts and freshwater infiltrations. Sediment samples were taken by scuba divers using cylinders (cores), with known inner diameter. Sampling stations were sampled from the different sections of the cave (entrance, twilight zone, dark zone and jameos). Five surveys were carried out, from June 2003 to February 2005. Nematodes, copepods, and polychaetes dominated overwhelmingly the meiofaunal composition, with the remaining taxonomic groups being scarce. Generalized linear models showed that the high spatial and temporal variability observed among on the abundance of major meiofaunal groups inside the cave was better explained by the surveys, the section of the caves and the presence of freshwater. Higher abundances are observed near the entrance and in the station with regular freshwater input. Nematodes and polychaetes were clearly dominated by species extensively recorded in shallow subtidal sandy sediments on the study area.

Introduction

Sea-flooded caves are very particular marine environments from both evolutionary and ecological perspectives (Iliffe and Kornicker 2009). From an evolutionary point of view, sea-flooded caves often harbor unique lineages of organisms characterized by high levels of adaptation and endemism (Iliffe and Kornicker 2009; Juan et al. 2010) often with unknown marine relatives (Neiber et al. 2011). The most remarkable cases occur amongst arthropods, including Remipedia, Thermosbaenacea, Stygiomysida (Wagner 1994; Meland and Willassen 2007; Hoenemann et al. 2013) and several families of amphipods, copepods and isopods (Wägele 1985; Koenemann and Holsinger 1999; Fosshagen et al. 2001; Iliffe and Botosaneanu 2006; Bauzà-Ribot et al. 2012; Hou et al. 2014). Many of these lineages exhibit disjunct distribution patterns in caves separated by large geographical distance (Koenemann et al. 2009; Wilkens et al. 2009). These patterns have been explained addressing cave colonization events during the Miocene and followed by tectonic vicariance (Iliffe et al. 1984; Wilkens et al. 1986; Humphreys 2000), often with extinction of the marine ancestral populations. Other cave lineages belong to groups that are otherwise exclusively

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known from the deep sea, such as certain sponges (Vacelet et al. 1994; Vacelet and Boury-Esnault 1995; Vacelet 2006), annelids (Pettibone 1985; Núñez et al. 1997; Martínez et al. 2013; Martínez et al. 2014, 2016; González et al. 2015) and crustaceans (Wilkens et al. 1990; Ahyong et al. 2011; Iglikowska and Boxshall 2013). In these cases, cave colonization might be facilitated by the ecological similarities between caves and the deep sea.

Although often categorized as a single habitat, caves harbor a mosaic of ecological conditions with strong differences at both a macro- and micro-scale (Sket 1996; Martínez et al. 2009). Sea-flooded caves are often categorized as marine caves if they hold strong influence from the sea and receive the effects of waves and currents (Riedl and Ozretić 1969; Tilzer 1970); or anchialine if they are isolated from the sea and harbor stratified water bodies with long residence times, sometimes including freshwater layers (Stock et al. 1986; Sket 1996; Wilkens et al. 2009; Bishop et al. 2015). However, these two categories are not always easy to apply to real cases since many marine caves directly connected to the sea become progressively isolated as they extend inland becoming true anchialine environments (van Hengstum and Scott 2011; Yager 2013). These changes are related to the presence of well-characterized gradients from the entrance to the deepest sections, involving a progressive reduction of light as well as availability of allochtonous organic matter (Gili et al. 1986; Fichez 1990, 1991), with conspicuous effects on the fauna dwelling in the different sections (Iliffe 1986). Several studies have focused on characterizing these changes using benthic sessile communities as well as macrofaunal assemblages of crustaceans and foraminifera (Iliffe 1986, 1992; Benedetti-Cecchi et al. 1997, 1998; Gili and Coma 1998; Oertel and Patzner 2007; Bamber et al. 2008; van Hengstum and Scott 2011; Navarro-Barranco et al. 2012, 2014), collectively showing how the abundance of individuals and taxonomic richness is reduced progressively from the entrance. However, studies on similar processes using interstitial meiobenthic communities are scarcer or focus more in single taxonomic groups rather than in overall communities (Palacín and Masalles 1986; Palacín et al. 1992; Núñez et al. 1997; Todaro et al. 2006; Brito et al. 2009). Moreover, scarce studies have dealt with meiofauna responses to salinity variations, especially from stochastic events such as run-offs (Riera et al. 2012). To our knowledge, there are no studies concerning the effects of freshwater filtration on meiofaunal communities inhabiting in caves.

Marine interstitial meiofauna are integrated by a heterogeneous assemblage of metazoans with different phylogenetic affinities that dwell among the sand grains (Giere 2009; Rundell and Leander 2010). Interstitial meiofauna are a very important component of marine diversity due to their taxonomic diversity and high species richness (Curini-Galletti et al. 2012). Despite their different phylogenetic origins, interstitial animals present a set of common adaptations to survive

amongst the sand grains, including small and elongated bodies, a specialized pharyngeal apparatus, direct development, presence of adhesive structures and epidermal ciliation (Giere 2009). These adaptations have evolved convergently in several independent lineages (Di Domenico et al. 2014; Andrade et al. 2015; Martínez et al. 2015), although some cases might represent plesiomorphies that are important to understand the evolution of particular metazoan lineages (Rieger 1980; Worsaae and Rouse 2009; Mwinyi et al. 2010; Laumer et al. 2015). Due to their high abundances, taxonomical diversity and short life cycles, interstitial meiobenthic assemblages are very sensitive to environmental conditions at microscales and exhibit fast time responses to punctual environmental conditions (Schratzberger and Jennings 2002). Therefore, they represent a feasible tool for environmental monitoring and assessment.

In the present study, we describe the effect of distance from the entrance on the abundance of major meiofaunal groups in Los Cerebros cave, on the west coast of Tenerife (Canary Islands, NE Atlantic Ocean). Los Cerebros cave is relatively large and harbors a combination of endemic species (Ortea 1995; Pérez Dionis et al. 2011; Martínez et al. 2013) and typical marine assemblages (Martínez et al. 2004; Álvarez et al. 2005; Riera et al. 2007; Schmidt-Rhaesa et al. 2013). The cave is exposed to waves and currents, which produce turbulence and perturbation on the sediments, potentially affecting the distribution of meiofauna along the cave. We explore any pattern of variability (spatial, temporal and environmental) through multivariate analyses, to infer if the variation can be explained by any of the environmental parameters or, instead, if only seasonality or spatial patchiness are responsible for changes.

Materials and methods

Sampling localities, working hypothesis and experimental design

This study was carried out in Los Cerebros cave, a marine cave located on the west coast of Tenerife (maximum age of the island, 12 Ma; coordinates: 28°10′N/16°48′W; Fig. 1). The cave is a lava tube with a complex structure. The entrance opens at 8 m and leads to two galleries extending *ca*. 80 m inland. The average depth of the passages is 5–8 m. Two terrestrial collapse entrances, locally known as jameos, open at the dead ends of the two main galleries, facilitating the indirect presence of light in these areas. Freshwater flows near one of these dead ends and mixes with the marine waters inside the cave. The water column of the cave is not stratified, as it is affected by waves and currents. These currents carry a significant amount of particulate organic matter, which sustains a rich community of sessile organisms (Álvarez et al.
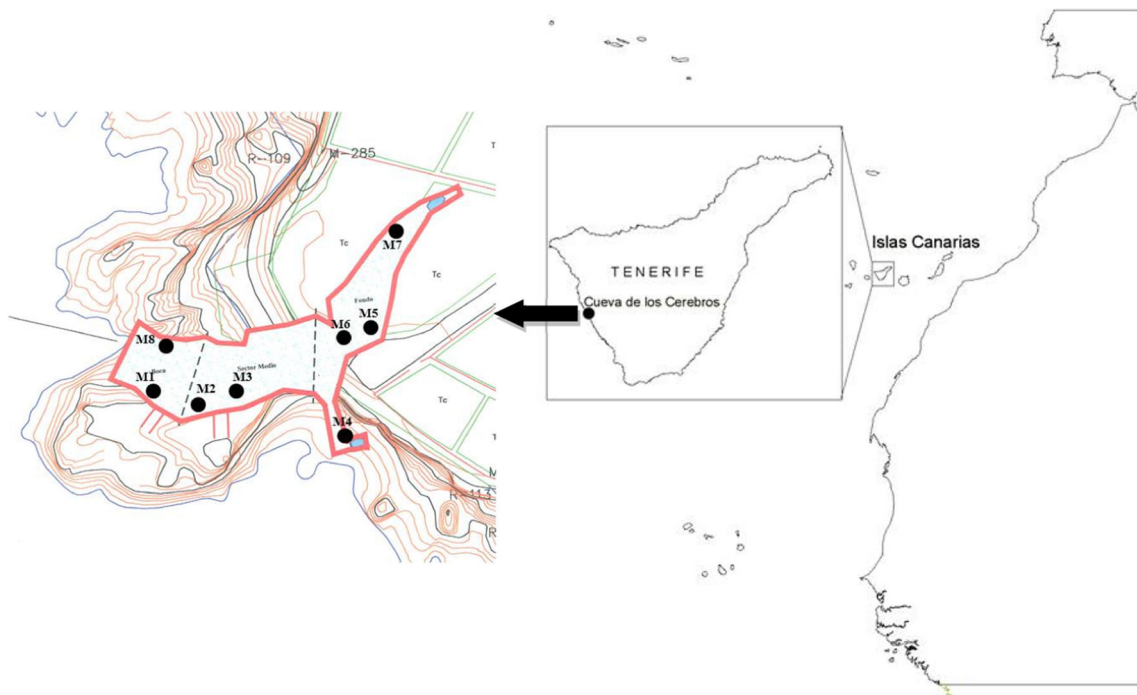
Fig. 1 Map of the study area, showing the cave system of "Los Cerebros"

2005). Marine medium sandy sediments are deposited at the entrance and bottom of the main passages, whereas gravel and boulders occupy certain areas of the middle sections (Martínez et al. 2004, 2013).

Table 1 Summary of abundances of total meiofauna and all taxonomic groups in each of the field surveys

	June 03	October 03	February 04	June 04	February 05
Total Abundance	1863	1906	1442	2005	4008
Nematoda	**684**	**761**	**239**	**208**	**1103**
Copepoda	**439**	**439**	**230**	**371**	**624**
Polychaeta	**156**	**195**	**311**	**297**	**566**
Oligochaeta	**154**	**112**	**91**	**88**	**295**
Ostracoda	**128**	**114**	**128**	**339**	**305**
Gammaridea	**101**	**56**	**115**	**170**	**206**
Priapulida	**82**	**147**	**99**	**145**	**186**
Cumacea	**71**	**50**	**150**	**236**	**453**
Isopoda	18	8	7	31	36
Sipunculida	2	0	14	12	21
Turbellaria	9	14	37	37	51
Gastrotricha	6	0	0	0	0
Chaetognatha	3	0	0	5	2
Tanaidacea	2	1	4	7	48
Kinorhyncha	2	2	1	0	7
Anthozoa	3	0	2	19	69
Nemertina	2	2	2	2	9
Acarii	1	2	1	1	1
Nauplius	0	1	0	0	0
Aplacophora	0	2	4	6	4
Ophiuroidea	0	0	5	17	8
Gastropoda	0	0	1	4	8
Echinoidea	0	0	1	2	1
Misidacea	0	0	0	2	0
Porifera	0	0	0	3	0
Bivalvia	0	0	0	3	1
Picnogonida	0	0	0	0	4

Dominant groups are highlighted in bold

**Fig. 2** Percentages of dominance and frequency of meiofaunal taxonomic groups in "Los Cerebros" cave
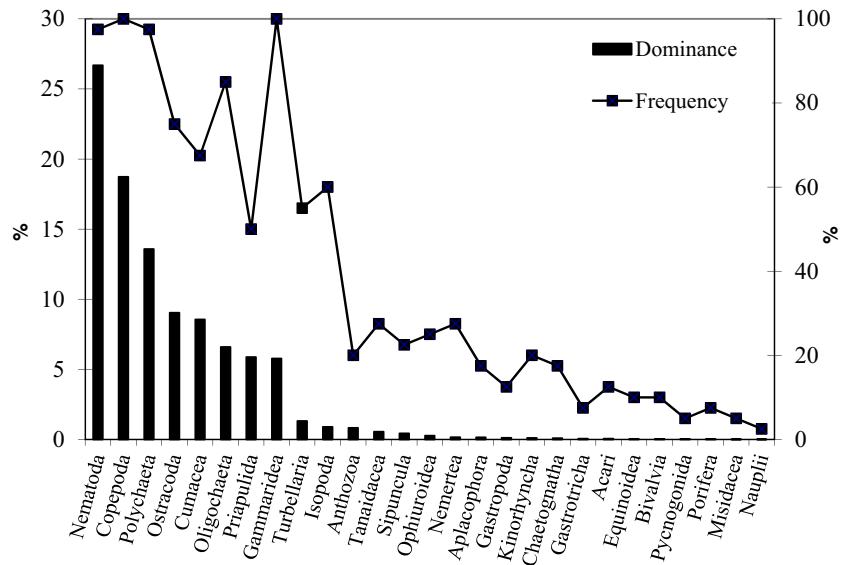
We sampled at eight stations situated at increasing distance from the entrance of the cave and at different regions of the cave, namely entrance, twilight zone, dark zone and jameos (i.e. secondary entrances; Fig. 1). Sediment cores (3.6 in inner diameter, 10 cm² surface) were hammered into the sediment to a depth of 30 cm randomly (1 m apart) for meiofauna analysis. Sampling was conducted throughout five field surveys throughout 3 years [June 2003 (1st), October 2003 (2nd), February 2004 (3rd),

June 2004 (4th) and February 2005 (5th)]. The type of sediment (sand or gravel) and the presence of light and freshwater was also noted. Light formed a gradient along the cave, with the entrance being illuminated (stations M1 and M8), the mid-section and the jameos areas being twilight (stations M2–M4), with the stations M5 and M6 being always in darkness. Freshwater was consistently registered at the bottom of the cave (station M7).

Fig. 3 Overall abundance of meiofauna considering the variables with higher explanatory powers according to the generalized linear model analyses (see Table 1)
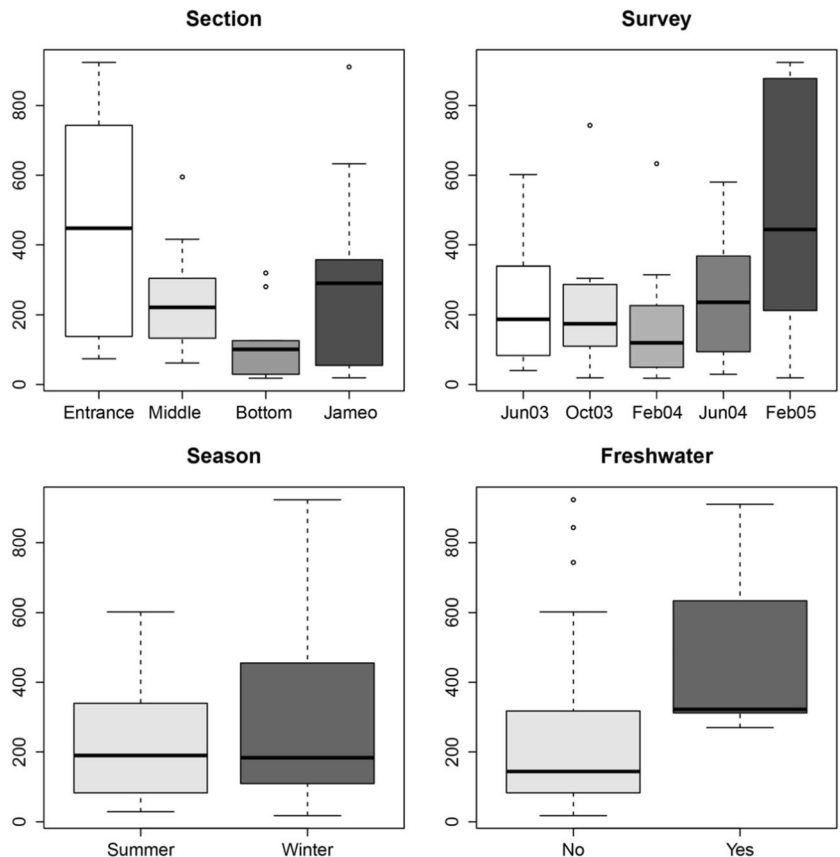
Fig. 4 Abundance of the dominant meiofaunal groups (dominance > 5 %) according to the explanatory variables with higher explanatory powers according to the generalized linear model analyses (see Table 1)
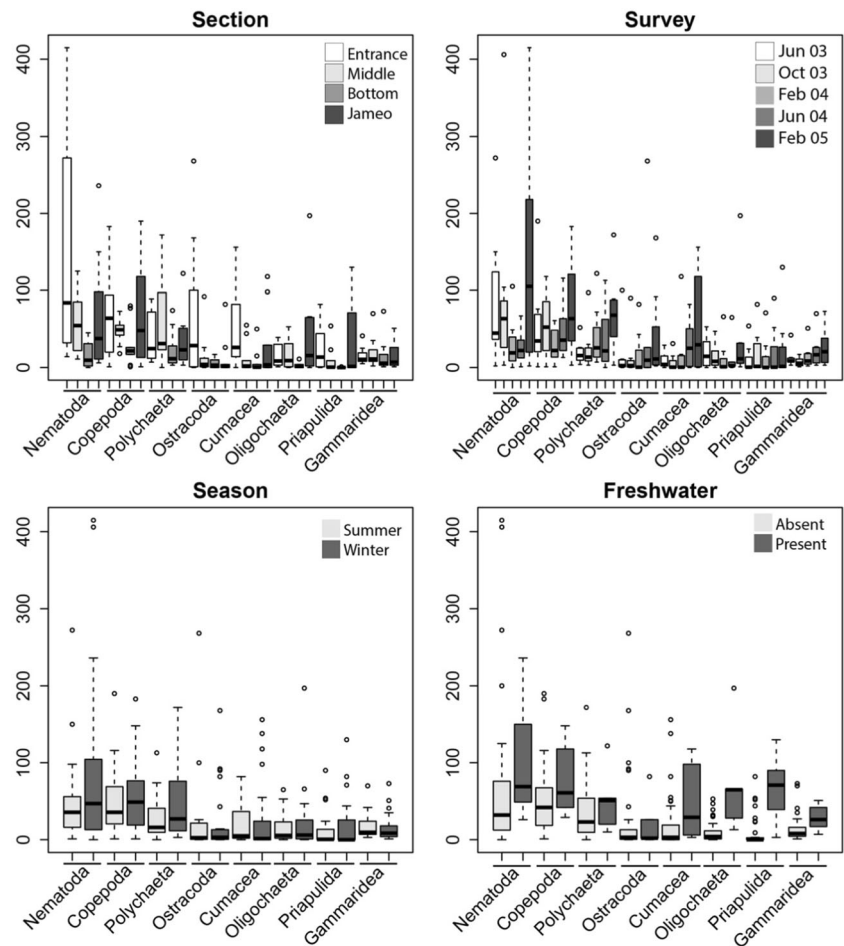
Analysis of meiofauna

Samples were fixed in 4 % formalin solution. A 0.5-mm sieve was used to separate macrofauna and the residue collected from a 0.063-mm sieve. The residue was posteriorly separated into taxonomic groups under a binocular microscope, and preserved in 70 % ethanol (Higgins and Thiel 1988). Nematodes and polychaetes were mounted in glycerine for taxonomic identification. These specimens were examined with a Leica DMLB microscope equipped with Nomarski interference contrast.

Statistical analysis

We investigate the changes in the abundance of meiofauna along the different sections of the cave using generalized linear models (GLMs), calculated with the function GLM implemented in R (Zuur et al. 2007). Variable responses were total abundance, and abundance of those groups exhibiting a >5 % dominance, i.e. Nematoda, Copepoda, Polychaeta, Oligochaeta, Ostracoda, Cumacea, Priapulida and Gammaridea. As explanatory variables, we consider five factors: (i) survey (five levels, random: survey 1–5), (ii) section

(four levels, fixed: entrance, twilight zone, dark zone and jameos), (iii) light (three levels, fixed: light, twilight and dark), (iv) habitat (two levels, fixed: sand, gravel), and (v) freshwater (two levels, fixed: presence, absent). Our null hypothesis predicts random variation of densities of meiofaunal groups (number of individuals per taxonomic group and core), amongst different sampling surveys, whereas gradients would predict an overall reduction of abundances from the entrance to the bottom. Higher heterogeneity at the jameos zone is expected due to the presence of indirect light and freshwater flows. Polychaeta and Oligochaeta are treated as independent groups, following the standards of other ecological studies, despite them representing, in fact, the same clade. Boxplots used to describe the changes of abundance according to the most important factors were prepared using the function boxplot implemented in R (Murrell 2005; R Team 2008).

Differences in meiofauna community structure with varying distance to the entrance of the cave (entrance, twilight, dark and jameos zones) were tested by means of a permutational multivariate analysis of variance (PERMANOVA) calculated using the function adonis from the R-package vegan (Dixon and Palmer 2003). We included all the factors from the best GLM for total abundances selected using model average

Table 2 Top generalized linear models ordered by the AICc value for the total abundance of meiofauna as well as the abundances of each of the eight most dominant meiofaunal groups

Models	(Int)	Survey	Freshwater	Habitat	Light	Section	Df	AICc	Delta	AICw
Total abundance										
Model 1	5.92	+	+		+	+	9	3862.13	0.00	0.45
Model 2	5.92	+	+			+	9	3862.13	0.00	0.45
Model 3	5.89	+	+	+		+	10	3864.98	2.85	0.11
RI		**1.00**	**1.00**	0.11	0.45	**1.00**				
Nematoda										
Model 1	5.19	+	+		+	+	9	1459.30	0.00	0.46
Model 2	5.19	+	+			+	9	1459.30	0.00	0.46
Model 3	5.16	+	+	+		+	10	1462.72	3.42	0.08
RI		**1.00**	**1.00**	0.08	0.46	**1.00**				
Copepoda										
Model 1	0.42	+	+		+	+	9	1284.62	0.00	0.24
Model 2	0.42	+	+			+	9	1284.62	0.00	0.24
Model 3	0.42	+	+		+		8	1284.81	0.09	0.23
Model 4	0.41	+	+	+	+		9	1284.96	0.34	0.21
Model 5	0.41	+	+	+		+	10	1287.02	2.40	0.07
RI		**1.00**	**1.00**	0.28	0.68	0.56				
Polychaeta										
Model 1	2.98	+	+		+	+	9	1009.17	0.00	0.46
Model 2	2.98	+	+			+	9	1009.17	0.00	0.46
Model 3	2.97	+	+	+		+	10	1012.74	3.58	0.08
RI		**1.00**	**1.00**	0.08	0.46	**1.00**				
Ostracoda										
Model 1	0.37	+	+		+	+	10	1508.85	0.00	1
RI		**1.00**	**1.00**	0.00	**1.00**	**1.00**				
Cumacea										
Model 1	3.25	+	+	+		+	10	895.38	0.00	0.44
Model 2	2.94	+	+		+	+	9	896.26	0.88	0.28
Model 3	3.25	+	+			+	9	896.26	0.88	0.28
RI		**1.00**	**1.00**	0.44	0.28	**1.00**				
Oligochaeta										
Model 1	2.74	+	+		+	+	9	648.42	0.00	0.38
Model 2	2.74	+	+			+	9	648.42	0.00	0.38
Model 3	2.50	+	+	+		+	10	649.26	0.84	0.25
RI		**1.00**	**1.00**	0.25	0.38	**1.00**				
Priapulida										
Model 1	3.13	+	+	+		+	10	787.02	0.00	0.44
Model 2	2.69	+	+		+	+	9	787.91	0.90	0.28
Model 3	2.69	+	+			+	9	787.91	0.90	0.28
RI		**1.00**	**1.00**	0.44	0.28	**1.00**				
Gammaridea										
Model 1	2.36	+	+	+		+	9	553.48	0.00	0.45
Model 2	2.36	+	+		+	+	9	553.48	0.00	0.45
Model 3	2.45	+	+			+	10	556.30	2.83	0.11
RI		**1.00**	**1.00**	0.11	0.45	**1.00**				

Remaining values had a delta value > 4, and an Akaike weight of < 0.1. Akaike weights may be interpreted as the relative probability that a particular model would have the best fit for another set of data drawn from the same underlying processes. The response variables in the most complex model (of a total of 30 models) depended on "~ survey + presence of freshwater + habitat + light + section". The symbol "+" represents the explanatory variables kept in the selected model. Relative importance (RI) for each selected variable is giving in a scale from 0 to 1. Parameters with high relative importance values (= 1.00) are highlighted in bold

AICc Akaike information criterion corrected; *AICw* Akaike information criterion weight

(see above), which included the factors "section" (fixed factor) and "survey" (fixed factor), "habitat" (fixed factor) and "freshwater" (fixed factor). To visualize affinities in meiofauna assemblage structure, a nm-MDS (non-metric multidimensional scaling) ordination was carried out on square-rooted transformed abundance data via the Bray–Curtis similarity index (Clarke and Warwick 1994) using the function metaMDS included in the R package vegan (Dixon and Palmer 2003). A similarity percentage analysis calculated with the R function simper (Clarke 1993) was used to compute the percentage contribution of each meiofauna taxonomic group to the dissimilarities between all pairs of sampling sectors (entrance, twilight, dark zone and jameos sections).

Results

A total of 11,224 individuals (ind) belonging to 26 taxonomic groups, plus the larval stage "nauplius", were collected

Table 3 Multivariate ANOVA (PERMANOVA) of meiofauna community structure considering the best model for the abundance, which includes "sector" (entrance, twilight zone, dark zone and jameos sections), "survey" (June 2003, October 2003, February 2004, June 2004 and February 2005), "habitat" (sand, pebbles), and "freshwater" (absence, presence)

	MS	Pseudo-F	p
Sector (Se)	0.451	2.733	0.005**
Survey (Su)	0.233	1.410	0.120
Habitat	0.268	1.626	0.127
Freshwater	0.829	5.026	0.001***
Residual	4.951		
Total	8.333		

throughout the 5 field surveys. Nematodes and copepods were the most abundant groups making up the 26.7 % (2995 ind) and 18.7 % (2103 ind) of the overall abundance, respectively. In contrast, 17 taxonomic groups were scarce, with low abundances (<100 ind; Table 1). The percentage of dominance and the frequency of occurrence were globally correlated if all meiofaunal groups are considered (Fig. 2).

Consistent temporal variations were recorded throughout the study period, with highest abundances in the last survey (February 2005; Fig. 3). Meiofaunal densities showed spatial variability among the three sections of the cave, reaching the highest abundances at the entrance (4489 ind), followed by the deepest sector (4207 ind). However, meiofaunal abundances varied greatly among field surveys, with highest densities in inner sections of the cave in the second (June 2003), the fourth (February 2004) and the last (February 2005) survey. The lowest densities were recorded in the middle section (2528 ind) in all surveys (Fig. 3).

Meiofaunal composition also varied temporally along the study period, especially among the most abundant taxonomic groups, i.e. nematodes, copepods, and polychaetes.
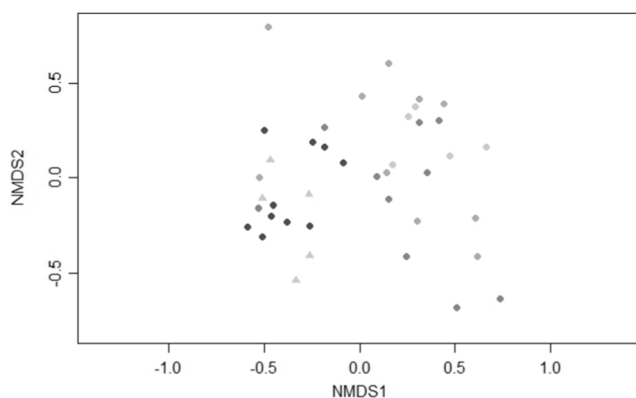
Fig. 5 n-MDS of meiofauna community at "Los Cerebros" cave. Sections "entrance", "middle", "bottom" and "jameo" are represented in grey colours from light grey ("entrance") to black ("jameo") . Presence of freshwater was represented by polygons. Circles: absence of freshwater; triangles: presence of freshwater

Nematodes obtained the highest abundances in June 2003, October 2003 and February 2005. In the remaining surveys, they were the second (February 2004) and the third (June 2004) most abundant group, being overcome by polychaetes and copepods and polychaetes, respectively (Fig. 4). The remaining groups showed little variability, mostly related to the highest abundances recorded in February 2005 (Fig. 4).

Comparison of different nested GLMs using Akaike information criteria (AIC) showed that two models predicted equally well the variation of total meiofauna as well as the variation of the abundances of major groups. Model 1, included the variables "survey", "freshwater", "light" and, "section"; and model 2, with "survey", "freshwater" and "section". The only exceptions to that were found for the total abundance of Cumacea and Gammaridea, better explained by "survey", "freshwater", "habitat" and "section". The model average amongst nested models indicated that the variables with the highest relative importance (RI = 1.00, Table 2) in predicting the variations in abundances are "survey", "freshwater" and "section"; exceptions were for Copepoda, for which "survey" and "freshwater" have the highest relative importance; and Ostracoda, the variation of which was better explained by "survey", "freshwater", "light" and "section". A summary of the better models for each group is shown in Table 2.

Total abundance of meiofauna was higher at the cave entrances during the February 2005 survey (Fig. 3), and in the station with freshwater filtrations. Higher abundances at the entrances of the cave were also observed for all dominant meiofaunal groups individually, except for Copepoda, Oligochaeta and Priapulida, which were more abundant near the jameos; and Polychaeta, with maximum abundances at the twilight section (Fig. 4). Regarding survey and freshwater, maximum abundances were also found in February 2005 and in the station with freshwater consistently for all the dominant meiofaunal groups.

Meiofauna assemblage structure varied consistently among the four cave sections (entrance, twilight, dark zone and jameos; pseudo-F = 2.733, p = 0.0005). Temporal variations of meiofauna structure were not significant throughout the study period (Pseudo-F = 1.410, p = 0.120). Differences in seabed composition did not affect significantly to meiofauna assemblage structure (Pseudo F = 1.626, p = 0.001), but freshwater inputs underpinned consistent changes on meiofauna (Pseudo-F = 5.026, p = 0.001; Table 3, Fig. 5).

Dissimilarities in meiofauna composition among the sections ranged from 44.75 % (entrance–twilight section) to 50.31 % (entrance–dark zone). Differences are explained by the highest abundances of nematodes at the entrance (10.48 % of overall abundance), cumaceans (6.10 %) and ostracods (5.84 %). The latter two taxonomic groups were scarce at the middle and the inner sections. The twilight section was characterized by harboring the highest polychaete abundances (6.69 %) and the jameos by the highest oligochaete

Table 4 List of free-living marine nematodes identified from sampling stations collected in Los Cerebros cave

Order	Family	Species
Araeolaimida	Comesomatidae	*Sabatieria* sp.
Araeolaimida	Comesomatidae	*Setosabatieria triangularis* Riera, Núñez & Brito, 2006
Araeolaimida	Diplopeltidae	*Araeolaimus elegans* de Man, 1888
Chromadorida	Cyatholaimidae	*Marylynnia* sp.
Chromadorida	Selachinematidae	*Richtersia* sp.
Chromadorida	Selachinematidae	*Synonchiella* sp.
Desmodorida	Desmodoridae	*Desmodora* sp.
Desmodorida	Desmodoridae	*Onyx* sp.
Desmodorida	Desmodoridae	*Spirinia parasitifera* Bastian, 1865
Desmodorida	Draconematidae	*Draconema* sp.
Enoplida	Anticomidae	*Anticoma* sp.
Enoplida	Enchelidiidae	*Calyptronema* sp. nov.
Enoplida	Enchelidiidae	*Eurystomina ornata* (Eberth, 1863)
Enoplida	Enchelidiidae	*Symplocostoma tenuicolle* (Eberth, 1863)
Enoplida	Ironidae	*Thalassironus* sp.
Enoplida	Leptosomatidae	*Cylicolaimus magnus* Villot, 1875
Enoplida	Leptosomatidae	*Synonchus fasciculatus* Cobb, 1893
Enoplida	Oncholaimidae	*Adoncholaimus* aff. *panicus*Cobb, 1930
Enoplida	Oncholaimidae	*Adoncholaimus* aff. *Papillatus* Kreis, 1932
Enoplida	Oncholaimidae	*Oncholaimus campylocercoides*De Connick & Schuurmans Stekhoven, 1933
Enoplida	Oncholaimidae	*Pontonema* cf. *simile* (Southern, 1914)
Enoplida	Oncholaimidae	*Viscosia* aff. *abyssorum* Warwick & Buchanon, 1970
Enoplida	Oxystominidae	*Halalaimus* aff. *capitulatus* Boucher, 1978
Enoplida	Thoracostomopsidae	*Mesacanthion diplechma* (Southern, 1914)
Monhysterida	Linhomoeidae	*Linhomoeus* sp.1
Monhysterida	Linhomoeidae	*Linhomoeus* sp. 2
Monhysterida	Linhomoeidae	*Paralinhomoeus* sp.
Monhysterida	Linhomoeidae	Linhomoeidae sp1
Monhysterida	Siphonolaimidae	*Siphonolaimus* sp.
Monhysterida	Xyalidae	*Paramonohystera* sp.
Plectida	Ceramotematidae	*Dasynemoides* sp.
Triplonchida	Rhabdodemaniidae	*Rhabdodemania minor* (Southern, 1914)

abundances (4.1 %). The lowest abundances were found in the dark zone (bottom) of the cave.

Species composition of Nematoda and Polychaeta

A total of 32 meiofaunal nematode species were identified in Los Cerebros cave, belonging to 7 orders (Araeolaimida, Chromadorida, Desmodorida, Enoplida, Monhysterida, Plectida and Triplonchida) and 18 families (Table 4). Half of the species were determined to a genus level and *ca.* 9–10 species belonged to previously undescribed species. Most of the species are typical of shallow subtidal sandy seabeds from the Canary Islands, including several putative new species.

A total of 70 polychaetes species, 18 of them determined to the genus level, were identified in Los Cerebros cave, belonging to 35 families (Table 5). About 15 species are recorded for the first time in the Canary Islands, 10 of them possibly undescribed species that are currently under taxonomic study. Except for two species, all annelids discovered during this survey belong to marine species, also found in marine sediments in the Canary Islands (Núñez et al. 2005). The species *Leptonerilla diatomeophaga* is exclusively found in anchialine and marine caves in the Canary Islands, including La Corona lava tube (Lanzarote) and Aguadulce cave system (Tenerife; Worsaae et al. 2009). It belongs to a genus mostly represented by cave species distributed in the Mediterranean Sea, the Caribbean Sea and Bermuda (Martínez et al. in press). The species *Axiokebuita cavernicola*, though not recorded through the study period, is endemic from Los Cerebros cave, where it is exclusively

Table 5 List of meiofaunal polychaete species identified from sampling stations collected in Los Cerebros cave

Order	Family	Species
Amphinomida	Amphinomidae	*Linopherus canariensis* Langerhans, 1881
Eunicida	Onuphidae	*Aponuphis bilineata* (Baird, 1870)
Eunicida	Lumbrineridae	*Lumbrineriopsis paradoxa* (Saint-Joseph, 1888)
Eunicida	Dorvilleidae	*Ophryotrocha* sp.
Eunicida	Dorvilleidae	*Schistomeringos rudolphi* (Delle Chiaje, 1828)
Eunicidae	Eunicidae	*Lysidice unicornis* (Grube, 1840)
Orbinida	Nerillidae	*Leptonerilla* cf. *diatomeophaga*
Orbinida	Nerillidae	*Mesonerilla* cf. *intermedia* Wilke, 1953
Orbinida	Nerillidae	*Nerillidium* sp.
Phyllodocida	Syllidae	*Brania* sp.
Phyllodocida	Chrysopetallidae	*Dysponetus caecus* (Langerhans, 1880)
Phyllodocida	Phyllodocidae	*Eulalia mustela* Pleijel, 1987
Phyllodocida	Syllidae	*Erinaceusyllis cryptica* (Ben-Eliahu, 1977)
Phyllodocida	Syllidae	*Eurysyllis tuberculata* Ehlers, 1864
Phyllodocida	Syllidae	*Exogone (Parexogone) mediterranea* San Martín, 1984
Phyllodocida	Sigalionidae	*Fimbriosthenelais zetlandica* (McIntosh, 1876)
Phyllodocida	Goniadidae	*Goniadides cf. carolinae* Day, 1973
Phyllodocida	Hesionidae	*Neogyptis mediterranea* Pleijel, 1993
Phyllodocida	Syllidae	*Miscellania dentata* Martín, Alós & Sardá, 1990
Phyllodocida	Syllidae	*Odontosyllis fulgurans* (Audouin & Milne Edwards, 1833)
Phyllodocida	Syllidae	*Opisthodonta* sp.
Phyllodocida	Syllidae	*Palposyllis prosostoma* Hartmann-Schröder, 1977
Phyllodocida	Syllidae	*Parapionosyllis brevicirra* Day, 1954
Phyllodocida	Pholoidae	*Pholoe* cf. *inornata* Johnston, 1839
Phyllodocida	Pholoidae	*Laubierpholoe* sp.
Phyllodocida	Pisionidae	*Pisione guanche* San Martín, López & Núñez, 1999
Phyllodocida	Syllidae	*Prosphaerosyllis* sp.
Phyllodocida	Phyllodocidae	*Pseudomystides limbata* (Saint-Joseph, 1888)
Phyllodocida	Syllidae	*Erinaceusyllis cf. cryptica*
Phyllodocida	Syllidae	*Sphaerosyllis* sp.
Phyllodocida	Syllidae	*Streptosyllis bidentata*
Phyllodocida	Syllidae	*Streptosyllis websteri*
Phyllodocida	Syllidae	*Streptosyllis campoyi*
Phyllodocida	Syllidae	*Syllides* sp.
Phyllodocida	Syllidae	*Sphaerosyllis* cf. *bulbosa* Southern, 1914
Phyllodocida	Syllidae	*Prosphaerosyllis* aff. *tetralix* (Eliason, 1920)
Phyllodocida	Syllidae	*Syllis gerundensis* (Alós & Campoy, 1981)
Phyllodocida	Hesionidae	*Hesiospina aurantiaca* (M. Sars, 1862)
Phyllodocida	Syllidae	*Perkinsyllis spinisetosa* (San Martín, 1990)
Protodrilida	Protodrilidae	*Claudrilus* sp. (in Martínez et al. 2015)
Protodrilida	Saccocirridae	*Saccocirrus* sp
Sabellida	Sabellidae	Sabellidae sp. 1
Sabellida	Sabellidae	*Fabricia stellaris* (Müller, 1774)
Sabellidae	Oweniidae	*Galathowenia oculata* (Zachs, 1923)
Scolecida	Paraonidae	*Aricidea (Acmira) cerruti* Laubier, 1966
Scolecida	Opheliidae	*Armandia cirrosa* Filipii, 1861
Scolecida	Arenicolidae	*Branchiomaldane* sp.
Scolecida	Capitellidae	*Capitella minima* (Langerhans, 1881)
Scolecida	Paraonidae	*Paradoneis lyra* (Southern, 1914)
Scolecida	Paraonidae	*Paradoneis perdidoensis* (McLelland & Gaston, 1994)

Table 5 (continued)

Order	Family	Species
Scolecida	Capitellidae	*Dasybranchus* cf. *caducus* (Grube, 1846)
Scolecida	Capitellidae	*Heteromastus* sp.
Scolecida	Capitellidae	*Peresiella?* sp.
Scolecida	Opheliidae	*Ophelia* cf. *bicornis* Savigny in Lamarck, 1818
Scolecida	Orbiniidae	*Questa caudicirra* Hartmann, 1966
Scolecida	Paraonidae	*Levinsenia canariensis* (Brito & Núñez, 2002)
Scolecida	Paraonidae	*Levinsenia gracilis*
Spionida	Spionidae	*Aonides* cf. *oxycephala* (Sars, 1862)
Spionida	Spionidae	*Aonides* sp.
Spionida	Spionidae	*Laonice cirrata* (Sars, 1851)
Spionida	Spionidae	*Prionospio* aff. *multibranchiata* Berkeley, 1927
Terebellida	Flabelligeridae	*Brada* sp.
Terebellida	Fauveliopsidae	*Fauveliopsis* sp.
Terebellida	Acrocirridae	*Macrochaeta* cf. *clavicornis* (M. Sars, 1835)
Terebellida	Acrocirridae	*Macrochaeta* sp.
Terebellida	Terebellidae	*Polycirrus* sp.
Terebellida	Cirratulidae	*Aphelochaeta marioni* (Saint-Joseph, 1894)
Terebellida	Terebellidae	*Polycirrus* sp.
Terebellida	Cirratulidae	*Cirriformia filigera* (Delle Chiaje, 1828)

found in the gravel beds found in the middle section of the cave, in complete darkness. The species belongs to a genus with other two species, exclusively known from the deep sea (Martínez et al. 2013, 2014).

Discussion

The present study showed consistent spatial differences in meiofauna assemblage structure, with the complex nature of this cave being of utmost importance. The presence of several entrances (jameos) and corridors creates an environment without a pattern from the entrance to the insides of the cave. The jameos and corridors create an environment with conditions (trophic supply, lightness, etc.) that favor the development of benthic fauna. No temporal trends have been found in the studied cave and this may be explained by its shallow nature (8 m at the entrance), affected by hydrodynamics that could suspend the sediment and leave only coarse sedimentary types (e.g. gravels). The temporal patterns of rough seas does not fit with seasons, though they are more frequent in autumn and winter.

A decrease of univariate descriptors, i.e. species richness and individual abundances, of faunal communities has been observed from the entrance to the inward end of marine caves (Cicogna 2003; Martí et al. 2004). This feature is commonly explained by the depletion of trophic supply in inner parts of caves (Zabala et al. 1989), but, surprisingly, no decrease of organic matter has been detected in several caves (Navarro-Barranco et al. 2013). An other plausible explanation may be

variations of other environmental variables, such as grain size (Bamber et al. 2008), habitat heterogeneity (Zabala et al. 1989), water turbulence and exposure (Carvalho et al. 2012). In contrast, several studies have revealed that infaunal communities do not respond in the same way (Navarro-Barranco et al. 2013) and community response uniquely depends on the cave characteristics. Thus, soft-bottom communities from caves seem to be context- and scale-dependent, with no well-defined spatio-temporal patterns, as has been reported for hard-bottom communities (Bussotti et al. 2006). In our particular case, the most important parameters explaining the changes in meiofauna abundances were the survey, cave section and freshwater inputs. The importance of survey highlights the temporal variation of abundances of meiofauna in the cave, whereas the section and the presence of freshwater might be related to the presence of organic matter in the sediments dragged inside the cave by waves from the ocean, or introduced by the jameos and the freshwater from surrounding terrestrial areas. Freshwater flowing into the cave might be enriched with organic matter coming from banana plantations.

Meiofauna communities from marine caves have remained overlooked compared to studies based on large-sized biota, e.g. macro- and megafauna (Gerovasileiou and Voultsiadou 2015). Most of the studies are focused on taxonomic aspects (e.g. Núñez et al. 1997, 2009; Worsaae et al. 2009; Curini-Galletti et al. 2012; Schmidt-Rhaesa et al. 2013) or ecology of certain taxonomic groups [e.g. gastrotrichs, (Todaro et al. 2006), tardigrades (Grimaldi De Zio et al. 1982; D'Addabbo et al. 2001; Jørgensen et al. 2014) or nematodes (Ape et al.

2015)]. A limited number of studies regarding overall meiofauna community in caves has been conducted (e.g. Palacín and Masalles 1986; Palacín et al. 1992; Sandulli et al. 1999) and most of them identified meiofaunal specimens to major taxa (e.g. nematodes, copepods, polychaetes, etc.). Thus, scarce information is provided to extract general and consistent patterns of meiofaunal communities within caves; even the high variability among caves makes each cavity a unique ecosystem (Navarro-Barranco et al. 2013). In the present study, a high spatial variability of meiofauna community was observed because of the cave complexity (secondary openings and freshwater inputs) and the influence of hydrodynamics, i.e. tides and rough seas, due to shallow depths (<8 m) and orientation of the entrance. The lack of consistent spatial and temporal trends may be explained by the stochasticity of events (rough seas and freshwater input) that affect directly and indirectly meiofauna abundances.

Most of the ecological studies have been conducted in anchialine caves, with relatively small influence of hydrodynamics (Iliffe et al. 2000) and even in sheltered areas with minor influence of tides, e.g. the Mediterranean Sea (Sandulli et al. 1999; Todaro et al. 2006). To our knowledge, no ecological studies on meiofaunal communities have been focused on caves exposed to hydrodynamics where environmental conditions greatly differ depending on tide height and sea conditions. Moreover, the freshwater input from terrestrial runoffs is periodical throughout the year, with special emphasis during the summer season since most of the runoff comes from the irrigation of plantations on the surrounding land. Freshwater inputs may have sporadic influence in meiofauna assemblages directly through changes in salinity, and indirectly by carrying organic matter to the cave; however, a more exhaustive environment monitoring assessment is necessary to elucidate the importance of this factor structuring the fauna composition of Los Cerebros cave. Above all, the studied cave system may not be considered as anchialine cave since there is continuous connection to the sea, no permanent stratified water column and no oxygen zonation, among other factors that characterize these environments (Gerovasileiou et al. 2016).

In short, communities of polychaetes and nematodes at Los Cerebros cave were characterized by low abundances and species richness. Samples need to be re-examined for in-depth taxonomic identification, but in preliminary tests, the annelid and nematode fractions were dominated by marine species that have been previously recorded in subtidal sandy bottoms of the Canarian Archipelago (e.g. Martínez et al. 2004, 2009, 2013; Riera et al. 2006, 2010, 2011, 2013; Worsaae et al. 2009). The low representation of cave-dwelling species may be explained by the hydrodynamic conditions inside the cave system that affects directly, i.e. erosion and drifting effects of tides and currents, and indirectly, i.e. resuspension of fine-grained sediments and particulate organic matter.

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