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Malacofauna from soft bottoms in the Cerro Gordo marine cave (Alboran Sea): biodiversity and spatial distribution

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Abstract

A study has been carried out for the first time of the molluscan fauna of the Cerro Gordo submarine cave in the Spanish part of the Alboran Sea. The depth of the cave bottom ranges from 16 m at its entrance, to sea level at its innermost section. Replicate soft-bottom samples were collected from three different stations along the horizontal gradient of the cave. Additional samples were collected on photophilous hard bottoms next to the cave entrance in order to assess the origin of cave bioclasts. The cave sediments contained 158 species of molluscs (23 collected alive and 155 recorded as shells), more than in Mediterranean cave sediments elsewhere. Species richness and abundance of molluscs decreased from the outermost to the innermost part of the cave. No cave-exclusive species were found, possibly due to the scarcity of caves in the Alboran Sea, but many of the recorded species are known from other Mediterranean caves. The lack of adult individuals for most of the living species inside the cave, suggests that these do not constitute self-maintaining populations. Finally, our results suggest that bioclasts found in the sediment do not derive from the outside of the cave nor from the sediment itself, but mostly from the communities inhabiting the walls and ceiling of the cave.

Keywords: Marine cave; Mollusc; Soft-bottom communities; Taxonomy; Alboran Sea.

Introduction

As one of the most remarkable habitats of coastal areas, marine caves have attracted wide scientific interest for the development of biodiversity, and ecological and evolutionary studies (Cattaneo-Vietti *et al.*, 2003; Navarro-Barranco, 2015). Marine caves show marked gradients in their environmental conditions (e.g. light, water movement and trophic supply) on a small spatial scale (Zabala *et al.*, 1989; Fichez, 1990). For this reason, they are often used as model systems in ecological studies to assess the effects of environmental variables on the distribution of marine organisms, their physiological responses or their biotic interactions (Zabala *et al.*, 1989; Martí *et al.*, 2004, 2005; Bussotti *et al.*, 2006). As a result of their unique topography and environmental conditions, coupled with relative confinement, marine caves support differentiated biotic communities, sometimes including endemic and relict species (Hofrichter, 2001; Bussotti *et al.*, 2006; Navarro-Barranco *et al.*, 2013). Moreover, marine caves offer exceptional opportunities to study deep-sea organisms, since the communities inhabiting these dark, oligotrophic and temporally stable environments often resemble those found in bathyal systems (Harmelin *et al.*,

1985; Logan & Zibrowius, 1994; Vacelet *et al.*, 1994). It has also been proved that submarine caves host species regarded as “living fossils” (Kase & Hayami, 1994).

Marine caves play an important ecological and socioeconomic role in marine ecosystems, functioning as biodiversity and genetic reservoirs, nursery areas and valuable tourist attractions, among others (Di Franco *et al.*, 2010; Gerovasileiou & Voultsiadou, 2012; Ouerghi *et al.*, 2019). Nevertheless, the ecological and human-valued services provided by marine caves are at risk due to the low resilience of their communities to environmental changes. Among the main factors threatening marine cave communities are coastal pollution, development of coastal infrastructures, alien species and climate change (Chevaldonné & Lejeusne, 2003; Parravicini *et al.*, 2010; Guarnieri *et al.*, 2012; Gerovasileiou *et al.*, 2016; Nepote *et al.*, 2017; Montefalcone *et al.*, 2018; Ouerghi *et al.*, 2019). For these reasons, marine caves are among the protected marine ecosystems in European waters (EU, 1992; EU, 2008; UNEP-MAP-RAC/SPA, 2015).

The Mediterranean basin is one of the regions with a better knowledge of its marine caves worldwide, but there is an uneven distribution of data, both in terms of the geographical regions and the taxonomical groups con-

sidered. Large areas (such as the Alboran Sea and northern Africa) and small mobile organisms inhabiting cave sediments have been traditionally overlooked (Giakoumi *et al.*, 2013; Gerovasileiou & Voultsiadou, 2014). Most Mediterranean studies dealing with cave malacofauna have been carried out in Italy and the northwestern Mediterranean region (see Cattaneo-Vietti, 2003; Bianchi & Morri, 2003 and references therein). According to these studies, the existence of exclusive stygobiont taxa is uncertain and the abundance of deep-water species is scarce. Those studies conducted in sedimentary bottoms highlighted the high diversity of molluscan species and dominance of empty shells in comparison with living individuals (approximately 85% of the species were exclusively found as dead material in both studies) (Monteiro-Marques, 1981; Huelin, 1981). Akoumianaki & Hughes (2004) described the spatial patterns of the molluscan fauna inhabiting cave sediments and, in contrast to the common pattern described in marine caves, no biotic impoverishment of the soft-bottom community was found towards the end of the cave. This pattern was attributed to the unusual presence of sulphur-water springs in its aphotic chambers. Further studies are necessary in order to estimate the molluscan biodiversity of these remarkable environments, as well as exploring the constancy of their ecological patterns.

The present work constitutes the first comprehensive study of the molluscan fauna from soft bottoms in the submarine caves of the Alboran Sea. Our main objectives were to: (1) characterize the malacofauna of both the biocoenosis and thanatocoenosis from the sedimentary bottoms of the cave of Cerro Gordo, as well as to identify the ecological affinities of the recorded species; and (2) evaluate their patterns (abundance, species richness and species composition) along the horizontal gradient of the cave. Regarding the first objective, it was expected that few (if any) of the species would be exclusive cave-dwellers or deep-sea taxa. We also hypothesized that the origin

of most of the molluscan bioclasts could be species living outside the cave or on the cave-walls (rather than species inhabiting the cave sediment). According to our initial hypothesis concerning the second objective, a significant decrease in the number of species and individuals was expected towards the inner confined areas of the cave.

Materials and Methods

Study area

The Cerro Gordo cave (36.7383° N, 3.7769° W) is located in the Maro-Cerro Gordo nature reserve, an approximately 12 km-long stretch of protected coastline between the provinces of Malaga and Granada (southern Spain) (Fig. 1). This region shows an unusually high biodiversity due to its biogeographical position (which allows the presence of species with both Mediterranean and Atlantic affinities), hydrodynamic conditions (e.g. existence of deep water upwellings) and heterogeneity of habitats (Delgado, 1990; Cebrián & Ballesteros, 2004).

The Cerro Gordo cave is the largest and most interesting cave in the area, as shown from previous studies on its crustacean and sessile fauna (e.g. Navarro-Barranco *et al.*, 2012, 2015; Sempere-Valverde *et al.*, 2019). It has an approximately 100 m-long ascending profile, from 16 m deep at its entrance, to sea level at its innermost section. There are two areas inside the cave separated by a narrowing at a distance of 25 m from the entrance (Fig. 1). The arch-like entrance (of approximately 15 m maximum width and height) is oriented southward. The amount of light and the action of waves inside the cave are attenuated by a large boulder situated in front of the entrance. The first chamber, where light can still be perceived, hosts a rich sciaphilous sessile community characteristic of semi-dark caves. Cnidarians such as the orange coral *Astroides calycularis* (Pallas, 1766), the hydroid *Eudendrium* sp.,

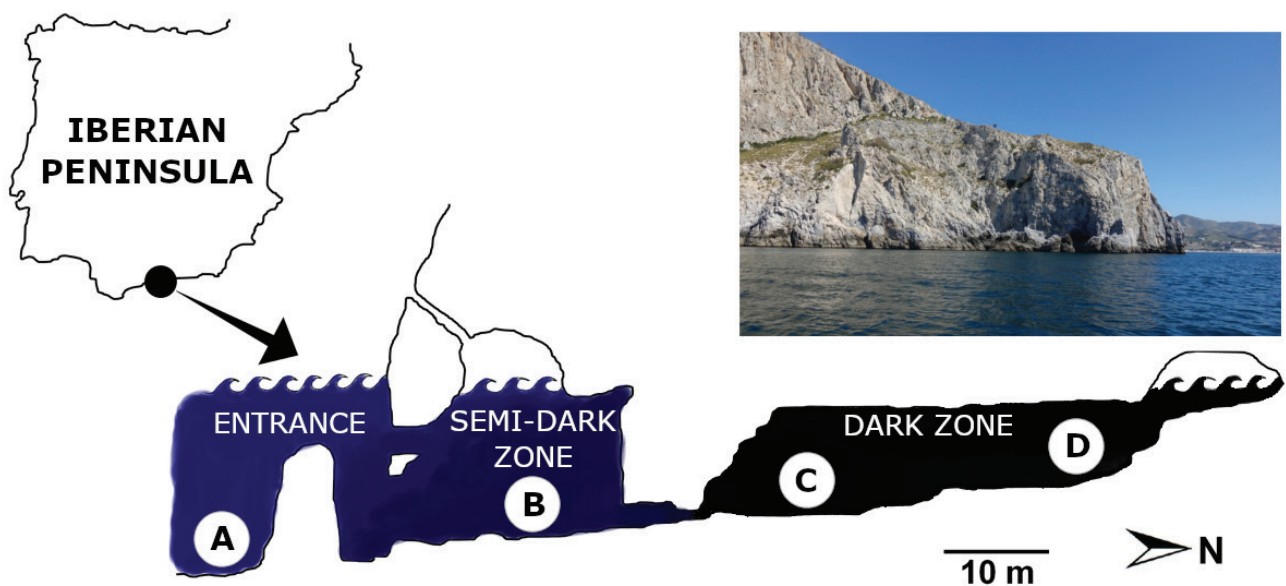


Fig. 1: Location and longitudinal section of the Cerro Gordo cave. Adapted from Navarro-Barranco (2015).

and the yellow encrusting anemone *Parazoanthus axinellae* (Schmidt, 1862) are abundant. Other frequent species are the sponges *Sarcotragus fasciculatus* (Pallas, 1766), *Oscarella lobularis* (Schmidt, 1862), and *Chondrosia reniformis* Nardo, 1847, annelids of the *Filograna/Salmacina* complex, bryozoans such as *Pentapora fascialis* (Pallas, 1766) and *Myriapora truncata* (Pallas, 1766) (Navarro-Barranco, 2015; Sempere-Valverde *et al.*, 2019). In this area, the bottom is heterogeneous, mainly consisting of medium and coarse sand (Navarro-Barranco *et al.*, 2012). In the inner dark zone, water flow and light are reduced or absent and cave walls are mainly covered by encrusting sponges, serpulids and brachiopods. Some fish species, such as *Phycis phycis* (Linnaeus, 1766), *Conger conger* (Linnaeus, 1758), *Sciaena umbra* (Linnaeus, 1758), *Apogon imberbis* (Linnaeus, 1758) or large swarms of mysids, are also present. Here, sediments are mainly composed of silt and clay and inhabited by an impoverished community (at least for crustaceans) (Navarro-Barranco *et al.*, 2012). Finally, there is a marked decrease in encrusting species towards the innermost part of the cave in accordance with the increasing influence of freshwater inputs. A detailed description of the cave, as well as an underwater video itinerary of the cave, is available in Sanchez-Tocino (2019).

Sampling design and data collection

Sediment samples were collected on 11 March, 2019 using SCUBA diving equipment at three different zones of the cave (stations B, C and D) and using 10 cm square-mouth tubs with a depth of 3 cm. The first centimetres of the soft bottom were collected so that the total surface area sampled was 10 cm × 20 cm and the volume was 600 cm³. Four replicates were collected at each station. Additionally, four samples were collected by scraping a wall surface of 20 cm × 20 cm (using a net and a hard brush) near the entrance (station A) in order to evaluate the contribution from the outer assemblages to the cave thanatocoenosis.

All the samples were washed on a 0.5 mm mesh sieve and fixed with 70% ethanol. The sediment fraction >0.5 mm was examined under a Nikon C-LEDS stereomicroscope to separate live specimens and shells, as well as other invertebrate hard parts. In some cases, an ultrasonic cleaner was used to open bivalve shells and to recognize live individuals from empty shells. Photographs of selected species of interest were taken with a Nikon DXM camera attached to a Nikon SMZ1000 stereomicroscope. Focus-stacking was used for smaller individuals under higher magnification by means of CombineZM software (Hadley, 2006).

Statistical analyses

Potential differences in species richness and abundance values along the horizontal gradient of the Cerro Gordo cave were explored through analysis of variance

(ANOVA). The study design included a single fixed factor (Station) with three levels (stations B, C and D) and four replicates in each one. Separate analyses were conducted for biocoenosis and thanatocoenosis data. Normality (Kolmogorov-Smirnov test) and homogeneity of variances (Cochran test) were verified prior to ANOVA. In those cases where data did not fulfil the homoscedasticity requirement, they were transformed by the square root of $x+1$. When variances remained heterogeneous, untransformed data were analyzed, as ANOVA is robust enough to support conclusions based on these assumptions (particularly in a balanced design), but level of significance was set at 0.01 in order to reduce Type I errors (Underwood, 1997). When ANOVA results showed significant differences for the factor considered (Station), individual differences between pairs of stations were examined using the Student-Newman-Keuls (SNK) post-test (Underwood, 1997). Univariate analyses were performed using the GMAV5 program (Underwood *et al.*, 2002).

Spatial patterns of the molluscan assemblage were also explored using multivariate analyses, based on a triangular matrix of Bray-Curtis similarity among replicates (Bray & Curtis, 1957). As for the previously described analyses, multivariate analyses were performed separately for thanatocoenosis and biocoenosis data. Cluster analyses of the samples were conducted, together with a SIMPROF permutation test, to assess clusters of samples with a significant internal structure ($p < 0.05$). Moreover, possible differences in community structure were tested using PERMANOVA analysis (Anderson, 2001, 2005) following the same design previously described. When the analysis showed a significant influence of the factor 'Station', these differences were examined individually using pairwise comparisons (pairwise testing). Multivariate analyses were performed using PERMANOVA+ for the PRIMER v6 statistical package (Clarke & Gorley, 2001).

Finally, in order to obtain information about the source of shells in the thanatocoenosis within the cave, an additional multivariate analysis was performed including both thanatocoenosis and biocoenosis data from stations B, C and D, and data from the species on the walls of the external zone of the cave (station A). Because heterogeneity in the sampling methods prevents an adequate quantitative comparison between these communities, data from each replicate were standardized to the total number of individuals. The data matrix was used to generate a triangular Bray-Curtis similarity matrix and replicates were ordered by nMDS (non-metric Multi-Dimensional Scaling) analysis (Clarke & Gorley, 2001).

Results

A total of 172 species of molluscs was identified at the four stations (three inside the cave and station A outside), including 109 gastropods, 61 bivalves and 2 chitons (38, 19 and 1 species were represented by at least one live individual, respectively) (Annex I).

Some individuals or shells remained identified at ge-

nus level only, since they were lacking key characters (e.g. juveniles or degraded shells). Eulimidae (*Curveulima* or *Vitreolina* spp.) are easily differentiated when alive by having different echinoderm hosts but their shells are notably featureless. Individuals here attributed to *Diodora* spp. mostly belong to *Diodora gibberula* (Lamarck, 1822), but some of them could be juveniles of *D. graeca* (Linnaeus, 1758). Oysters could belong to *Neopycnodonte cochlear* (Poli, 1791) or *Ostrea stentina* (Payraudeau, 1826), but the defining characters were not clear in the shells collected. However, the intense brown colour of the interior of the shells points to *N. cochlear*.

Biocoenosis composition and spatial patterns

Living individuals were mostly bivalves, and extremely rare in all samples, with a total of 172 individuals (from a total of 3,782 molluscan individuals and shells collected in the soft bottoms) belonging to 23 different species (73 individuals and 16 species in station B, 88 individuals and 8 species in station C, and only 11 individuals of two species in station D). Univariate analyses showed that the differences among stations (both in terms of species richness and abundance of individuals) were significant (Table 1; Fig. 2). According to post-hoc results, all stations showed significant differences in their species richness values, while stations B and C showed a similar number of individuals but significantly higher

than those recorded at the innermost station.

Most of the living individuals were juveniles, except for *Nucula perminima* (Monterosato, 1875) which has an adult size not exceeding one millimetre, and one individual of *Diodora gibberula* from zone D. The dominant living species at station B were *Kurtiella bidentata* (Montagu, 1803), *Gouldia minima* (Montagu, 1803) (Fig. 3), *Lucinella divaricata* (Linnaeus, 1758), *Nucula hanleyi* (Winckworth, 1931), the last three mainly represented by juveniles. At station C, juveniles of *Tellina compressa* (Brocchi, 1814) (Fig. 3) were by far the most abundant (76 individuals), followed by *Nucula hanleyi* and *Abra alba* (Wood, 1802). *Nucula perminima* (10 individuals) and *Diodora gibberula* (one adult) were present at the inner station D (Fig. 4); the latter is a species which lives on hard substrate and eats sponges, and is believed to have accidentally fallen from the cave ceiling. PERMANOVA analyses support the existence of significant differences in the structure of the community among all stations (Table 2). According to cluster analyses, replicates from station D (the innermost one) showed low similarity among them, which is most likely due to the high influence of stochastic variations in such impoverished communities (each replicate only accounts for a few individuals of one or two species) (Fig. 5A). Replicates of the intermediate zone (C) constitute a significantly homogeneous group, with 60% similarity, which may be determined by the dominance of *Tellina compressa*. The presence of a replicate from station B within this group would be due to

Table 1. Results of ANOVA and SNK analysis for the number of living individuals and live-collected species. d.f. = degrees of freedom; MS = mean of squares; F = F statistic; P = level of significance.

Source of variation	Abundance				Species richness		
	d.f.	MS	F	P	MS	F	P
Station	2	416.6	9.88	0.005	30.3	19.16	< 0.001
Residuals	9	42.2			1.6		
SNK analyses		(B = C) > D			B > C > D		

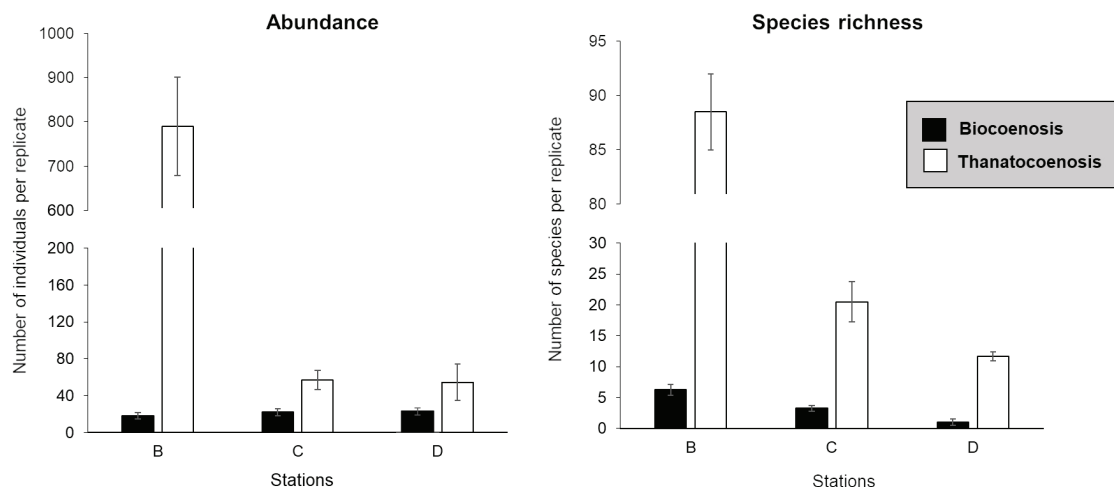


Fig. 2: Average (\pm Standard deviation) number of molluscan individuals or shells, and number of species in the biocoenosis and thanatocoenosis of each cave station.



Fig. 3: Species represented by living individuals in the sediment of the Cerro Gordo cave, stations B and C. A-B: *Tellina compressa*, set of ultra-juveniles (replica C2 and detail of an individual, size 2.1 mm); C: *Tellina compressa* adult valve (replica C4, size 14 mm); D: *Phaxas pellucidus* (replica C4, size 7.5 mm); E-G: *Ctena decussata* (replica B1, size 1.2 mm and 3.6 mm); H-J: *Gouldia minima* (replica B4, size 6.5 mm and 4.2 mm).

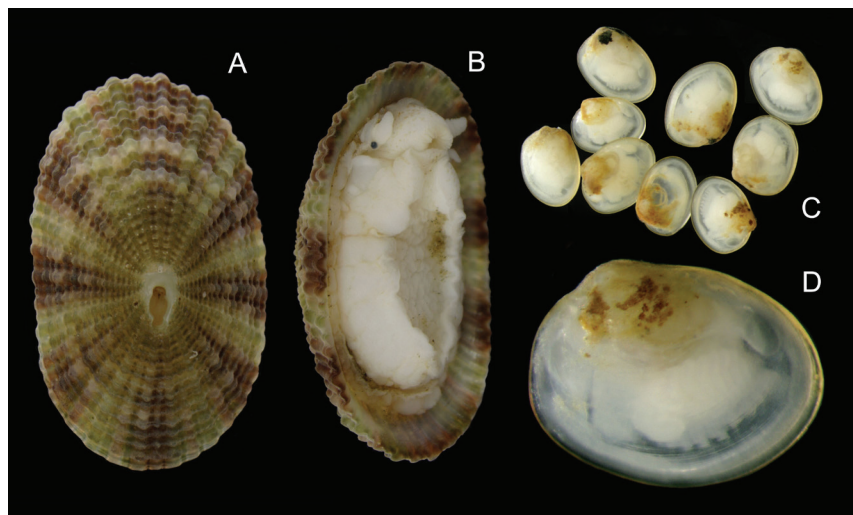


Fig. 4: Species represented by living individuals in the sediment of the Cerro Gordo cave, station D. A-B: *Diodora gibberula* (replica D4, size 10 mm). C-D: *Nucula perminima*, set of individuals from replica D2, and magnified view of a specimen, size 1.0 mm.

the presence of *T. compressa* on that replicate as well. The remaining three replicates from the semi-dark area (station B), dominated by *Kurtiella bidentata*, *Lucinella divaricata* and *Gouldia minima*, constitute another homogeneous cluster with a high degree of similarity.

Thanatocoenosis composition and spatial patterns

The number of shells and species in the thanatocoenosis was higher, but in agreement with the spatial patterns observed for the biocoenosis (Fig. 2). ANOVA analyses showed a significant biotic impoverishment towards the innermost section of the cave (Table 3). The semi-

Table 2. Results of PERMANOVA and Pairwise analysis for quantitative data of molluscs in the biocoenosis and thanatocoenosis inside the Cerro Gordo cave. d.f. = degrees of freedom; MS = mean of squares; Pseudo F = pseudo F statistic; P = level of significance.

Source of variation	Biocoenosis				Thanatocoenosis		
	d.f.	MS	Pseudo F	P (perm)	MS	Pseudo F	P (perm)
Station	2	11822	4.805	< 0.001	11061	8.6748	< 0.001
Res	9	2460.3			1275.1		
Pairwise analysis		B ≠ C ≠ D			B ≠ C ≠ D		

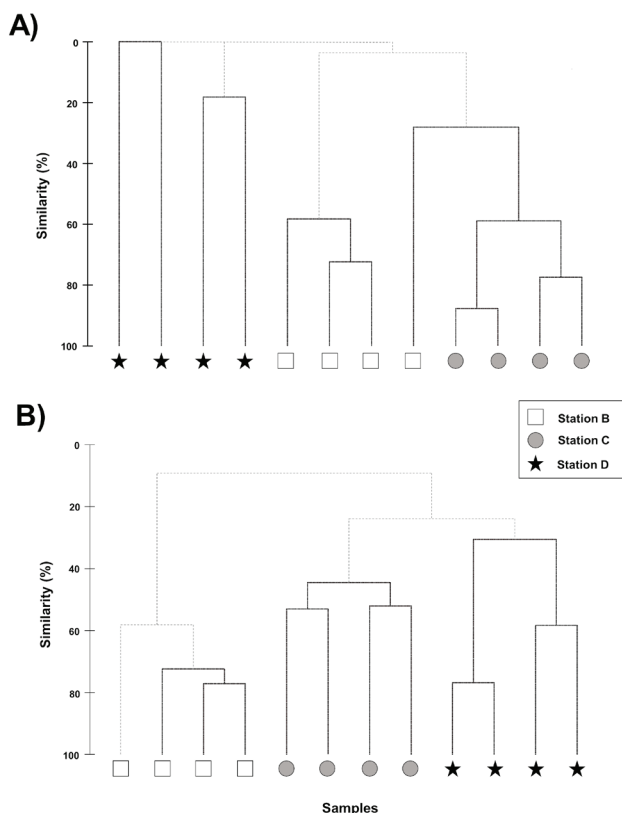


Fig. 5: Dendrogram representing the Bray-Curtis similarity between replicates of the mollusc assemblages from biocoenosis (A) and thanatocoenosis (B) collected in each the cave stations (B, C and D). Dotted lines refer to the existence of significant differences between clusters of homogeneous samples (connected by solid lines).

dark zone showed a higher number of species and shells (3,157 shells belonging to 143 species) compared to the two inner stations.

The most abundant taxa at the semi-dark station B comprised *Alvania* spp., *Bittium reticulatum* (da Costa, 1778), *Skenea serpuloides* (Montagu, 1808), *Emarginula tenera* (Locard, 1891), *Diodora* spp. and the bivalves *Barbatia barbata* (Linnaeus, 1758), *Gregariella semigranata* (Reeve, 1858) (Fig. 6), *Hiatella arctica* (Linnaeus, 1767) and *Gouldia minima* (Fig. 3). The number of shells and species decreased in the dark section of the cave: 228 shells from 46 species at station C and 225 shells from 27 species at station D. Station C was characterized by *Gregariella semigranata*, *Tellina compressa*, *Gouldia minima* and *Emarginula tenera*. The two most abundant species at the innermost section of station D were *Emarginula tenera* and *Crenella arenaria* (Monterosato, 1875) (Fig. 7), the latter almost exclusively found there (with 39 out of a total of 42 shells); valves of *Barbatia barbata* were also abundant. Common brachiopod species originating from the cave walls, such as *Megathiris truncata* (Gmelin, 1791), *Argyrotheca cuneata* (Risso, 1826), *Argyrotheca cistellula* (Wood, 1841), *Joania cordata* (Risso, 1826) or *Novocrania anomala* (O.F. Müller, 1776), were very common as empty shells in the sediment of the dark area (Fig. 7).

According to multivariate analyses, the ‘Station’ factor had a significant influence on the structure of the thanatocoenosis and those groups highlighted by cluster and SIMPROF analyses were well defined and corresponded to the different stations considered in the present study. The multidimensional scaling (MDS) (Fig. 8) considering all the replicates of the present study, showed no overlapping between the thanatocoenosis samples and those of biocoenosis replicates collected either inside or outside the cave. Replicate samples of living assemblages were grouped together in accordance with their position along the horizontal cave gradient (stations A, B, C or D), while thanatocoenosis samples were located in the centre.

Table 3. Results of ANOVA and SNK analysis for abundance data and species richness of molluscs in the thanatocoenosis. Abundance data were transformed by the square root of x + 1. d.f. = degrees of freedom; MS = mean of squares; F = F statistic; P = level of significance.

Source of variation	Abundance				Species richness		
	d.f.	MS	F	P	MS	F	P
Station	2	560.8	63.46	< 0.001	7060.8	229.62	< 0.001
Residuals	9	8.8			30.8		
SNK analyses		B > (C = D)			B > (C = D)		

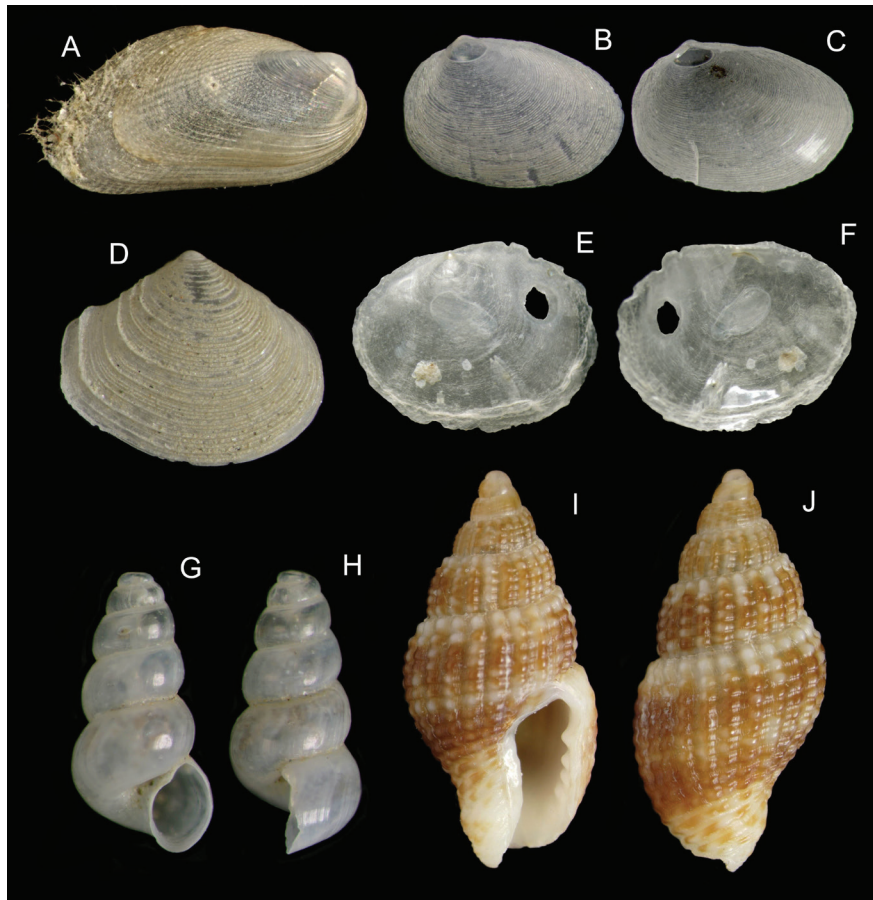


Fig. 6: Some species found in stations B and C in the thanatocoenosis of the Cerro Gordo cave. A: *Gregariella semigranata* (replica C2, size 2.4 mm); B-C: *Coracuta obliquata* (replica B1, size 1.9 mm); D: *Tellina serrata* (replica C1, size 2.1 mm); E-F: *Heteranomia squamula* (replica B2, size 1.9 mm); G-H: *Mifsudia melitensis* (replica B1, size 1.5 mm); I-J: *Anachis aliciae* (replica B2, size 8.2 mm).

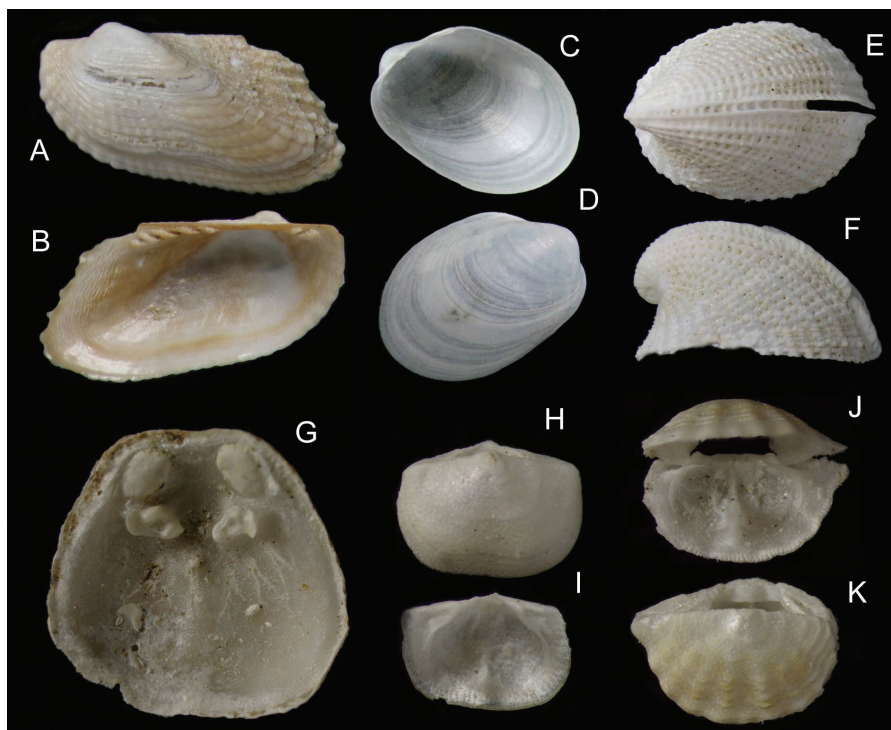


Fig. 7: Some species of molluscs and brachiopods found at the innermost station (D) in the thanatocoenosis of the Cerro Gordo cave. A-B: *Barbatia barbata* (replica D3, size 2.1 mm); C-D: *Crenella arenaria* (replica D2, size 2.1 mm); E-F: *Emarginula tenera* (replica D3, size 2.8 mm); G: *Novocrania anomala* (replica D2, size 8.5 mm); H-I: *Argyrotheca cistellula* (replica D2, size 7 mm and 6 mm); J-K: *Argyrotheca cuneata* (replica D2, size 3.0 mm).

Discussion

Molluscan biodiversity

The number of molluscan species (158 considering both live and dead material) in the Cerro Gordo cave was higher than that reported in previous studies conducted on cave sediments, such as Di Geronimo *et al.* (1997), Huelin (1981) or Monteiro-Marques (1981) (119, 96 and 66 different species, respectively), even though some of these pooled several caves. The number of living species (23) was also higher than that reported by Huelin (1981) (18 species), Akoumianaki & Hughes (2004) (17 species), or Monteiro-Marques (1981) (10 species), although the reduced diversity in the latter case could be explained by the loss of smaller species due to the mesh size used (1 mm). This high species richness could be linked to the aforementioned biogeographical particularities of the study region and the Alboran Sea, which is considered a “hot spot” of biodiversity within the Mediterranean region by Coll *et al.* (2010) and Urrea *et al.* (2017).

According to their ecological affinities, molluscan species can be classified as speleoxenes (species coming from outside the cave and which can be regarded as allochthonous or accidental species), speleophiles (species commonly found in marine caves but which can also be found in other sciaphilous biotopes), and exclusive cave species (Starmühlner, 1968; Di Geronimo *et al.*, 1997; Palazzi & Villari, 2001). Starmühlner doubted that any of the molluscs found in the Mediterranean marine caves could be exclusive, but since then several species such as *Asperarca magdalenae* La Perna, 1998, *Skeneoides digeronimoi* La Perna, 1999, *Lucinoma spelaeum* Palazzi & Villari, 2001 and *Ocenebra vazzanai* Crocetta, Houart & Bonomolo, 2020, have been reported in the Mediterranean Basin (Cattaneo-Vietti, 2003; Crocetta *et al.*, 2020). *Tethyrhynchia mediterranea* Logan, 1994, a cave-dwelling neotenous brachiopod, is also so far reported exclusively from Mediterranean submarine caves in France and Tunisia (Logan & Zibrowius, 1994). No such exclusive

species were found in the present study, and we speculate that the submarine caves in the Alboran Sea are too small and too scarce to sustain viable populations of exclusively speleobiont species and must rely on a pool of more eclectic sciaphilous species. Strangely, some sciaphilous species such as *Acar clathrata* (Defrance, 1816) [= *A. pulchella* (Reeve, 1844)] and *Homalopoma sanguineum* (Linnaeus, 1758), routinely reported (e.g. Cattaneo-Vietti & Russo, 1987; Di Geronimo *et al.* 1997) from Mediterranean caves, were absent, not only from our material from the Cerro Gordo cave, but in the Alboran Sea as a whole (Gofas *et al.*, 2011). This puzzling biogeographic pattern required further research.

Many of the species here reported have been elsewhere considered as speleophiles, such as *Emarginula tenera*, *Barbatia barbata*, or *Fossarus ambiguus* (Linnaeus, 1758) (Starmühlner, 1968; Palazzi & Villari, 2001). As it was expected, some of the species found inside the Cerro Gordo cave are commonly found (Gofas *et al.*, 2011) in deeper waters (approximately 100 m deep); this is the case of *Heteronomia squamula*, *Dacrydium hyalinum* (Monterosato, 1875), *Tellina serrata* Brocchi, 1814, *Crenella arenaria* and *Anachis aliciae* (Pallary, 1900) (Fig. 7). *Neopycnodonte cochlear*, which is possibly present in the cave as juvenile oysters, is also mostly distributed between 50 and 300 m deep (Gofas *et al.*, 2011).

Most of the living individuals recorded inside the cave were juveniles (except for *Nucula perminima* found at the innermost section, Fig 2). This pattern for molluscan cave fauna was already reported by Monteiro-Marques (1981), who found a high dominance of juveniles belonging to the species *Gouldia minima*, *Tellina* sp. and *Thyasira* sp. This finding suggests that mollusc larvae are able to colonize these muddy sediments, but the oligotrophic conditions prevent the survival of these recruits and the development of stable populations. Therefore, this would be an example of source-sink metapopulation dynamics, with cave dwelling “pseudopopulations” relying on the larval input from outside. On a wider scale, it has been hypothesized that this model also applies to the deep Mediterranean

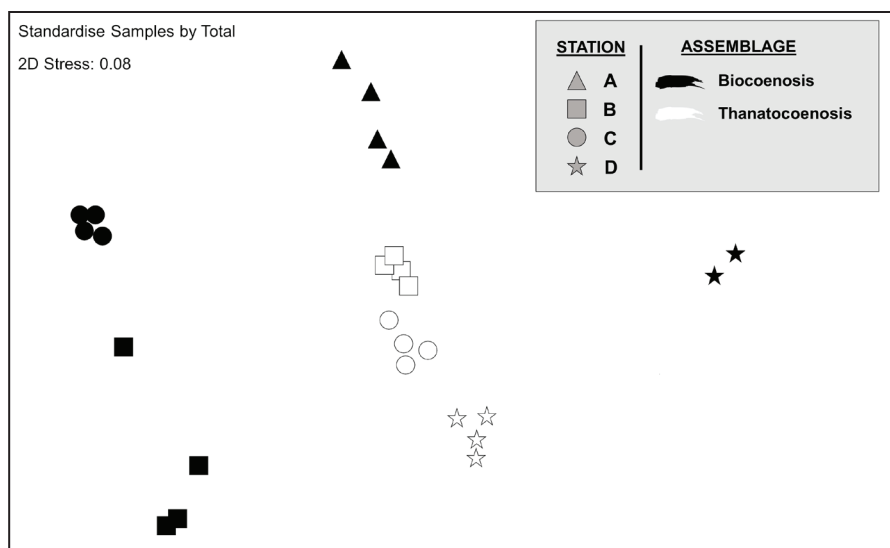


Fig. 8: MDS plot based on similarity (Bray-Curtis index) between replicates of the four stations (A, B, C and D) considering percent abundance data of biocoenosis and thanatocoenosis.

benthos as a whole: "...much of Mediterranean deep-sea fauna consist of reproductively sterile pseudopopulations that are constantly derived through larval inflow from Atlantic mother populations" (Bouchet & Taviani, 1992).

Finally, the present study also provided reports of poorly known species, such as *Aclis ascaris* (Turton, 1819) or *Anachis aliciae*, and/or species scarcely cited in the waters of the Alboran Sea, like *Coracuta obliquata* (Chaster, 1897) and *Heteranomia squamula*. The present study also constitutes the first report of *Mifsudia meliten-sis* (Mifsud, 1998) (only represented in the present study by a single shell found at station B, Fig. 7) for Spanish coasts and the Alboran Sea.

Spatial patterns

Our results highlighted the existence of a biotic impoverishment towards the inner end of the cave in the soft bottom of the Cerro Gordo cave. These results are in agreement with previous studies dealing with the soft-bottom crustaceans in the same cave (Navarro-Barranco *et al.*, 2012), as well as the evidence provided for other taxa such as sponges and cnidarians (Bibiloni *et al.*, 1989; Benedetti-Cechi *et al.*, 1998; Gerovasileiou & Voultsiadou, 2016), bryozoans (Harmelin, 1997), annelids (Denitto & Licciano, 2006) and fishes (Bussotti *et al.*, 2002), among others. The decrease in abundance and species richness is mostly related to the increasing confinement (often associated with reduced hydrodynamics, light intensity and trophic supply) in the inner section of marine caves (Harmelin *et al.*, 1985; Fichez, 1990; Bianchi & Morri, 1994). Navarro-Barranco *et al.* (2012) also attributed the observed reduction in the diversity of soft-bottom crustaceans to the increasing percentages of silt and clay and the influence of freshwater inputs at the inner sections. This explanation could be also applied to the molluscan fauna, although previous studies conducted in the Alboran Sea highlight the high diversity of molluscan species inhabiting soft bottoms dominated by fine and muddy sediments (Urre *et al.*, 2011). Moreover, environmental changes along the horizontal gradient not only determine changes in abundance and species richness, but also in species composition (in both biocoenosis and thanatocoenosis assemblages). This is also an expected pattern, since other studies previously conducted in the Alboran Sea highlighted the importance of environmental factors such as grain size, salinity, temperature, trophic supply, temperature, light availability and water renewal (all of these factors clearly affected by cave position), in driving molluscan composition (Guerra-García & García-Gómez, 2004; Rueda *et al.*, 2009; Urre *et al.*, 2013).

The similarity between the composition of the thanatocoenosis and that of the assemblages inhabiting cave sediments or the photophilous hard substrates outside the cave was low. Although some species found alive outside the cave (e.g. *Chauvetia mamillata* (Risso, 1826), *Bittium* spp., *Pusillina inconspicua* (Alder, 1844), *Jujubinus rus-curianus* (Weinkauff, 1868)) or in the cave sediments (e.g.

Kurtiella bidentata, *Gouldia minima*, *Tellina compressa*) were also found as empty shells, most of the species of the thanatocoenosis were not present anywhere else in the present study. The nMDS results also suggest that sediment thanatocoenosis is not a faithful representation of the molluscan assemblage living in the soft bottom. Many of the numerically dominant species in the thanatocoenosis (e.g. *Barbatia barbata*, *Gregariella semigranata*, *Cardita calyculata* (Linnaeus, 1758), *Hiatella arctica* or *Emarginula tenera*) live on hard substrates. Similarly, all the brachiopod species found abundantly in the sediment of the inner part have been previously recorded on the walls of the Cerro Gordo cave (Sempere-Valverde *et al.*, 2019). Therefore, the main source of the empty mollusc shells in the cave sediment is presumed to be the sessile community inhabiting the walls and ceilings of the cave.

In summary, the present study provides insights into the biodiversity of molluscan assemblages inhabiting marine caves, and particularly the Cerro Gordo cave. Some of the biological patterns highlighted for other cave dwelling groups, such as the biotic impoverishment along the horizontal cave gradient or the presence of deeper species in shallow caves (Balduzzi *et al.*, 1989; Boury-Esnault *et al.*, 1993), also applied to molluscan fauna. The soft-bottom biocoenosis of the cave is mainly composed of juveniles derived from external propagules. On the other hand, most of the bioclasts found in the cave sediment originate from the biotic community developing on cave walls and ceilings. In addition, the high biodiversity and presence of rare and poorly known molluscan species within the Cerro Gordo cave support the currently protected status of the cave. Nevertheless, further studies dealing with its species composition, natural dynamics and anthropogenic threats are needed in order to develop efficient conservation measures. In this sense, the proved response of mollusc assemblages to changes in environmental conditions support the use of this group as a monitoring tool for evaluating the ecological status of marine cave environments.

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Annex I. List of live and dead molluscs found in the four stations of the Cerro-Gordo cave: station A (outside the cave), station B (semi-dark area) and stations C and D (dark areas). “L” indicates individuals collected alive and “S”, shells. Species represented by at least one living individuals appear in this word itself in boldface.

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
POLYPLACOPHORA																												
CHITONIDAE																												
<i>Chiton olivaceus</i> Spengler, 1797															1													
LEPIDOCHITONIDAE																												
<i>Lepidochitona</i> sp.				3																								
BIVALVIA																												
ANOMIIDAE																												
<i>Anomia ehippium</i> Linnaeus, 1758											4									1								
<i>Heteranomia squamula</i> (Linnaeus, 1758)							1																					
<i>Pododesmus patelliformis</i> (Linnaeus, 1761)									1																			
ARCIDAE																												
<i>Arca noae</i> Linnaeus, 1758					6		5		2		4																	
<i>Arca tetragona</i> Poli, 1795					2		7		7		1												1					
<i>Barbatia barbata</i> (Linnaeus, 1758)					65		24		28		25		2		5		1		1		1		4		4		1	
CARDIIDAE																												
<i>Acanthocardia</i> sp.																					1							
<i>Papillicardium papillosum</i> (Poli, 1791)							4				1																1	
<i>Parvicardium scabrum</i> (Philippi, 1844)					1		1																					
CARDITIDAE																												
<i>Cardita calyculata</i> (Linnaeus, 1758)				2	13		7		9		8		2					1										
CHAMIDAE																												
<i>Chama gryphoides</i> Linnaeus, 1758					14		4		3				1							1								
GASTROCHAENIDAE																												
<i>Rocellaria dubia</i> (Pennant, 1777)					1																							
HIATELLIDAE																												
<i>Hiatella arctica</i> (Linnaeus, 1767)			4	4	35		30		26		55		10		4		2		2		1							

Continued

Annex I continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
LIMIDAE																												
<i>Lima lima</i> (Linnaeus, 1758)					4						2																	
<i>Limaria hians</i> (Gmelin, 1791)					2		3		4		4										1							
LASAEIDAE																												
<i>Coracuta obliquata</i> (Chaster, 1897)					3				2		1	2														1		1
<i>Kellia suborbicularis</i> (Montagu, 1803)					2		1		2		5																	
<i>Kurtiella bidentata</i> (Montagu, 1803)					11	13	12	9	4	5	9	1							1									
<i>Scacchia ovata</i> Philippi, 1844							3																					
<i>Tellimya ferruginosa</i> (Montagu, 1808)									1																			
LUCINIDAE																												
<i>Loripinus fragilis</i> (Philippi, 1836)					5		1																					
<i>Ctena decussata</i> (O. G. Costa, 1829)					3	1	1		5		1		1		1					1								
<i>Lucinella divaricata</i> (Linnaeus, 1758)					3	3	5	3	1	1	1																	
<i>Myrtea spinifera</i> (Montagu, 1803)											1									1								
MACTRIDAE																												
<i>Spisula subtruncata</i> (da Costa, 1778)					6		6		4		4						3											
MYTILIDAE																												
<i>Crenella arenaria</i> Monterosato, 1875					1				2												5		22		9		3	
<i>Dacrydium hyalinum</i> (Monterosato, 1875)											1												2		1			
<i>Gregariella semigranata</i> (Reeve, 1858)	1	2	4	8	48	1	65		75		62		20		12		4		12		1		1					
<i>Lithophaga lithophaga</i> (Linnaeus, 1758)					2		1		1		2										1		6		8		3	
<i>Modiolus barbatus</i> (Linnaeus, 1758)							1				2																	
<i>Musculus costulatus</i> (Risso, 1826)		6		2					2																			
<i>Musculus subpictus</i> (Cantraine, 1835)		10				1	3																					
NOETIIDAE																												
<i>Striarca lactea</i> (Linnaeus, 1758)					19		9		12		10								1									
NUCULIDAE																												
<i>Nucula perminima</i> Monterosato, 1875									1		2										1		1	9			2	1

Continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
<i>Nucula hanleyi</i> Winckworth, 1931					8				1			4		1	1			1	1									
<i>Nucula nitidosa</i> Winckworth, 1930											1	1											1					
OSTREOIDEA SUPERFAMILY																												
<i>Ostreoidea</i> indeterminate					4		1		3		7										1							
PECTINIDAE																												
<i>Manupecten</i> sp.																	2											
<i>Mimachlamys varia</i> (Linnaeus, 1758)					3		2				2															1		
<i>Pectinidae</i> sp.																			1						1			
<i>Talochlamys multistriata</i> (Poli, 1795)					3		1		1						1													
PHARIDAE																												
<i>Phaxas pellucidus</i> (Pennant, 1777)																				1								
SEMELIDAE																												
<i>Abra alba</i> (W. Wood, 1802)							4				5		1		3	2	3				1							
<i>Abra nitida</i> (O. F. Müller, 1776)							1																					
<i>Ervilia castanea</i> (Montagu, 1803)					3		5		5		3				10		12											1
TELLINIDAE																												
<i>Arcopella balaustina</i> (Linnaeus, 1758)					2																							
<i>Asbjornsenia pygmaea</i> (Lovén, 1846)															1													
<i>Moerella donacina</i> (Linnaeus, 1758)					5	1			1		1																	
<i>Moerella distorta</i> (Poli, 1791)							2		1		1																	
<i>Crenella arenaria</i> Monterosato, 1875					1				2												5		22		9		3	
<i>Tellina serrata</i> Brocchi, 1814											1		1		1												3	
<i>Tellina</i> sp.															2													1
<i>Tellina compressa</i> Brocchi, 1814					1		5		4		5	4	4	11	4	25	2	26		14								
THRACIIDAE																												
<i>Thracia</i> sp.					1																							
THYASIRIDAE																												
<i>Thyasira flexuosa</i> (Montagu, 1803)					1																							

Continued

Annex I continued

SPECIES	STATIONS																												
	A				B								C								D								
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	
UNGULINIDAE																													
<i>Diplodonta rotundata</i> (Montagu, 1803)					1																								
VENERIDAE																													
<i>Gouldia minima</i> (Montagu, 1803)					24	4	22	6	34	4	12	2	1		2		1		1										1
<i>Irus irus</i> (Linnaeus, 1758)					2		1		1		2																		
<i>Pitar rudis</i> (Poli, 1795)					1		1				1																		
<i>Polititapes aureus</i> (Gmelin, 1791)					3		4		2		3																		
<i>Timoclea ovata</i> (Pennant, 1777)					11	2	12	1	10		4				1														
<i>Venus verrucosa</i> Linnaeus, 1758					3		3																						
GASTROPODA																													
AMATHINIDAE																													
<i>Clathrella clathrata</i> (Philippi, 1844)					7		10		14		2																		
APLYSIIDAE																													
<i>Aplysia</i> sp.	1	7																											
BARLEEIIDAE																													
<i>Barleeia unifasciata</i> (Montagu, 1803)													1																
BUCCINIDAE																													
<i>Chauvetia mamillata</i> (Risso, 1826)	1	13	1																										
<i>Chauvetia procerula</i> (Monterosato, 1889)	2																												
<i>Chauvetia recondita</i> (Brugnone, 1873)					1				3		1																		
CAECIDAE																													
<i>Caecum auriculatum</i> de Folin, 1868					2		2		5																				
<i>Caecum subannulatum</i> de Folin, 1870					7		21		21	1	6		3		1						1								
CALLIOSTOMATIDAE																													
<i>Calliostoma laugieri</i> (Payraudeau, 1826)	2	2	2	4																									
<i>Calliostoma</i> sp.					1								7								2								
CALYPTRAEIDAE																													
<i>Calyptrea chinensis</i> (Linnaeus, 1758)					2								3								1								

Continued

Annex I continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
<i>Crepidula moulinsii</i> Michaud, 1829									2																			
CAPULIDAE																												
<i>Capulus ungaricus</i> (Linnaeus, 1758)					2		1																					
CERITHIIDAE																												
<i>Bitium latreillii</i> (Payraudeau, 1826)	1		1	3	10		10		7														1					
<i>Bitium reticulatum</i> (da Costa, 1778)	1		4	33	110		74		54		43				2		1										1	
<i>Cerithium vulgatum</i> Bruguière, 1792							1																					
CERITHIOPSIDAE																												
<i>Cerithiopsis diadema</i> Monterosato, 1874					4		1		4		1																	
<i>Cerithiopsis</i> spp.					7		14		14		9																	
<i>Dizoniopsis concatenata</i> (Conti, 1864)							1		1		1																	
CIMIDAE																												
<i>Graphis albida</i> (Kanmacher, 1798)					2		3		2										1									
<i>Mifsudia melitensis</i> (Mifsud, 1998)					1																							
COLUMBELLIDAE																												
<i>Anachis aliciae</i> (Pallary, 1900)					4		3		1		1																	
<i>Mitrella broderipii</i> (G. B. Sowerby I, 1844)	1	1		1																								
CYSTISCIDAE																												
<i>Gibberula miliaria</i> (Linnaeus, 1758)				1																								
EPITONIIDAE																												
<i>Epitonium muricatum</i> (Risso, 1826)					1		1																					
<i>Epitonium pseudonanum</i> Bouchet & Warén, 1986											1																	
<i>Epitonium pulchellum</i> (Bivona, 1832)							2																					
<i>Opalia</i> sp.							1																					
EULIMIDAE																												
<i>Aclis ascaris</i> (W. Turton, 1819)					1						1		1		1		1											
<i>Curveulima</i> or <i>Vitreolina</i> spp.	1	4		5	34		33		56		16		2		1		1		1									

Continued

Annex I continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
<i>Eulima glabra</i> (da Costa, 1778)					1																							
<i>Melanella boscii</i> (Payraudeau, 1826)					1																							
FASCIOLARIIDAE																												
<i>Fusinus</i> sp.					1				3																			
FISSURELLIDAE																												
<i>Emarginula huzardii</i> Payraudeau, 1826					3		2		1																			
<i>Emarginula tenera</i> Locard, 1891					41		29		26		16		12		8		12		5		9		58		44		7	
<i>Diodora</i> spp.					26		31		23		9		1		1		2		1		1		5		4		1	1
MANGELIIDAE																												
<i>Bela nebula</i> (Montagu, 1803)									1																			
<i>Mangelia unifasciata</i> (Deshayes, 1835)							2				1																	
<i>Mangelia vauquelini</i> (Payraudeau, 1826)				1																								
MITROMORPHIDAE																												
<i>Mitromorpha columbellaria</i> (Scacchi, 1836)					1		1		1																			
MURICIDAE																												
<i>Ocenebra nicolai</i> (Monterosato, 1884) or sp.					6						7																	
<i>Ocenebrina aciculata</i> (Lamarck, 1822)	4	2	1	6	1																							
<i>Ocenebra erinaceus</i> (Linnaeus, 1758)		1																										
<i>Ocenebra</i> sp.							1		9																			
<i>Muricopsis</i> sp.	1				19		12		22		7																	
NASSARIIDAE																												
<i>Tritia incrassata</i> (Strøm, 1768)	2	7	1	5	14		3		6		4					1												
<i>Tritia pygmaea</i> (Lamarck, 1822)											1																	
<i>Tritia reticulata</i> (Linnaeus, 1758)												1						1										
NATICIDAE																												
<i>Euspira macilenta</i> (Philippi, 1844)									1																			
<i>Euspira nitida</i> (Donovan, 1804)					2																							

Continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
OMALOGYRIDAE																												
<i>Ammonicera fischeriana</i> (Monterosato, 1869)	1																											
<i>Ammonicera</i> sp.		1																										
<i>Omalogyra</i> sp.		4																										
PHASIANELLIDAE																												
<i>Tricolia miniata</i> (Monterosato, 1884)							1																					
PHILINIDAE																												
<i>Philine intricata</i> Monterosato, 1884														1														
<i>Philine iris</i> Tringali, 2001			2			3	4	1																				
PISANIIDAE																												
<i>Aplus scaber</i> (Locard, 1891)					13	10	10	2																				
<i>Aplus</i> sp.														1												1		
PLANAXIDAE																												
<i>Fossarus ambiguus</i> (Linnaeus, 1758)					2		2																					
PLEUROBRANCHIDAE																												
<i>Pleurobranchidae</i> indeterminate					5	2																						
PYRAMIDELLIDAE																												
<i>Brachystomia</i> sp.					3																							
<i>Folinella excavata</i> (Phillippi, 1836)					3	4	5	1																				
<i>Megastomia conoidea</i> (Brocchi, 1814)	1						1																					
<i>Odostomella doliolum</i>						2																						
<i>Odostomia</i> sp.						3	2					1																
<i>Odostomia striolata</i> Forbes & Hanley, 1850					21	20	20	5																				
<i>Odostomia turrata</i> Hanley, 1844					1																							
<i>Parthenina emaciata</i> (Brusina, 1866)		1		1													1											
<i>Parthenina interstincta</i> (J. Adams, 1797)				5																								
<i>Parthenina monozona</i> (Brusina, 1869)	1	4	1		1		1	1									1											
<i>Pyrgolidium internodulum</i> (S. V. Wood, 1848)							2										1											

Continued

Annex I continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
<i>Spiralinella incerta</i> (Milaschewich, 1916)							1																					
<i>Pyrgostylus striatulus</i> (Linnaeus, 1758)					1																							
RAPHITOMIDAE																												
<i>Raphitoma aequalis</i> (Jeffreys, 1867)							1																					
<i>Raphitoma linearis</i> (Montagu, 1803)			1						1																			
<i>Raphitoma leufroyi</i> (Michaud, 1828)											1																	
RETUSIDAE																												
<i>Pyrunculus ovatus</i> (Jeffreys, 1871)							1		4		2																	
<i>Retusa truncatula</i> (Bruguière, 1792)									1																			
<i>Retusa umbilicata</i> (Montagu, 1803)																										1		
RINGICULIDAE																												
<i>Ringicula conformis</i> Monterosato, 1877					1						1																	
RISSOIDAE																												
<i>Alvania beanii</i> (Hanley in Thorpe, 1844)					1		6				1																	
<i>Alvania cancellata</i> (da Costa, 1778)	2				44		35		41		16																	
<i>Alvania carinata</i> (da Costa, 1778)									1																			
<i>Alvania cimex</i> (Linnaeus, 1758)					4		1		1		1																	
<i>Alvania lineata</i> Risso, 1826	2	3	1	7	1				2		1																	
<i>Alvania nestaresi</i> Oliverio & Amati, 1990				1	110		75		141		15																	
<i>Alvania punctura</i> (Montagu, 1803)					9		10		15		3				1													
<i>Alvania scabra</i> (Philippi, 1844)	2	4		7			1		2																			
<i>Alvania tenera</i> (Philippi, 1844)	1								1																			
<i>Alvania zetlandica</i> (Montagu, 1815)					1				1																			
<i>Crisilla semistriata</i> (Montagu, 1808)					15		9	1	14		10				1									1				
<i>Crisilla</i> sp.							1																					
<i>Manzonia crassa</i> (Kanmacher, 1798)					3		1		2																			
<i>Obtusella intersecta</i> (S. Wood, 1857)					2		3		3		1																	
<i>Pusillina inconspicua</i> (Alder, 1844)		9		10	11		14		20		8				1													

Continued

Annex I continued

SPECIES	STATIONS																											
	A				B								C								D							
	1L	2L	3L	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L	1S	1L	2S	2L	3S	3L	4S	4L
<i>Pusillina philippi</i> (Aradas & Maggiore, 1844)					3		3		3		2						1											
<i>Setia amabilis</i> (Locard, 1886)	1																											
RISSOINIDAE																												
<i>Rissoina bruguieri</i> (Payraudeau, 1826)					3		1		1																			
SCISSURELLIDAE																												
<i>Scissurella costata</i> d'Orbigny, 1824									1																			
<i>Sinezona cingulata</i> (O. G. Costa, 1861)					2				1																			
SIPHONARIIDAE																												
<i>Williamia gussoni</i> (Costa O. G., 1829)			2																									
SKENEIDAE																												
<i>Skenea serpuloides</i> (Montagu, 1808)					42		19		31		11				1													
TRIPHORIDAE																												
<i>Marshallora adversa</i> (Montagu, 1803)													1		5													
<i>Metaxia metaxa</i> (Delle Chiaje, 1828)					1		1											1										
<i>Triphoridae</i> indeterminate					55		28		9		12																	
TROCHIDAE																												
<i>Jujubinus ruscurianus</i> (Weinkauff, 1868)	2	4		3			5		7						3													
<i>Jujubinus striatus</i> (Linnaeus, 1758)							1		3		1				3		1											
TURRITELLIDAE																												
<i>Turritella turbona</i> Monterosato, 1877											1																	
VANIKORIDAE																												
<i>Megalomphalus azoneus</i> (Brusina, 1865)					4		3																					
Total					992	26	787	21	898	11	480	15	64	12	80	28	52	29	32	19	24	0	103	9	74	0	24	2