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The molluscan fauna of Chella Bank and surroundings (Western Mediterranean Sea)

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Summary: Molluscs of Chella Bank and its surroundings were studied from 21 samples collected with a van Veen grab in the depth range 95-729 m. A total of 299 taxa were identified (77 live-taken), thus increasing by more than 95% the species of molluscs reported in the recently declared site of community importance "Sur de Almería–Seco de los Olivos". Two of the species are new records to Spanish waters and one to the Alboran Sea. The high species richness observed could be related to the location, the hydrological characteristics and the topographical heterogeneity of the area within the Alboran Sea. Four significant groups of samples were discriminated through multivariate analysis of quantitative data of live-taken molluscs: (I) bathyal muddy bottoms with buried rhodoliths; (II) bathyal muddy bottoms with coral rubble; (III) bathyal hemipelagic muddy bottoms and (IV) bathyal sandy bottoms. Molluscs were more diverse on coral framework bottoms than on sedimentary bottoms around Chella Bank. Most of the live-taken species are widely distributed along the Atlantic and Mediterranean Sea, and a few are strictly Mediterranean. The most striking feature was the occurrence of two species with planktotrophic larval development for which Chella Bank is the sole recorded locality in the Mediterranean (*Episcomitra angelesae* and *Mitrella templadoi*) and which elsewhere extremely rare (*Mathilda* spp.).

Keywords: molluscs; deep sea; Chella Bank; Seco de los Olivos; vulnerable marine ecosystem; coral rubble; rhodoliths.

Malacofauna del Banco Chella y alrededores (Mediterráneo occidental)

Resumen: Se estudiaron los moluscos del banco Chella y sus fondos adyacentes a partir de veintiuna muestras cogidas con draga Van Veen entre 95 y 729 m de profundidad. Un total de 299 taxones fueron identificados (77 vivos), incrementando en un 95% el total de moluscos citados en el reciente Lugar de Importancia Comunitaria "Sur de Almería–Seco de los Olivos". Dos especies son nuevas citas para aguas españolas y una para el mar de Alborán. La elevada riqueza específica puede estar relacionada con la localización, las características hidrológicas y la heterogeneidad topográfica de esta zona situada dentro del mar de Alborán. Mediante análisis multivariantes usando datos cuantitativos de la taxocenosis se han diferenciado cuatro grupos de muestras: (I) fangos del batiales con rodolitos enterrados, (II) fangos batiales con restos de corales, (III) fangos hemipelágicos batiales, y (IV) arenas batiales. La mayor diversidad se encontró en los fondos con restos de corales, a diferencia de los fondos sedimentarios situados alrededor del banco Chella. La mayoría de las especies vivas están ampliamente distribuidas por el Atlántico y el Mediterráneo, y muy pocas son estrictamente mediterráneas. Cabe destacar la ocurrencia de algunas especies con desarrollo planctotrófico (*Episcomitra angelesae*, *Mitrella templadoi*) en el banco Chella como única localidad registrada en el Mediterráneo o especies extremadamente raras en otros lugares (*Mathilda* spp.).

Palabras clave: moluscos; mar profundo; banco Chella; Seco de los Olivos; Ecosistemas Vulnerables Marinos; restos de corales; rodolitos.

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INTRODUCTION

The Alboran Sea, located in the transition area between the Mediterranean Sea and the Atlantic Ocean, undergoes complex hydrodynamic processes caused by the mixing of water masses with different characteristics (Rodríguez 1982, Parrilla and Kinder 1987, Vargas-Yáñez et al. 2019). Because of its unique hydrodynamics, partly conditioned by the coastal and seabed morphology, the Alboran Sea has nutrient-enriched upwellings on its margin and is considered one of the areas with the highest biological productivity within the Mediterranean Sea (Rodríguez 1982, 1995, Sarhan et al. 2000). In addition, the Alboran basin contains a wide variety of bottom types and physiographic features along the coastline (e.g. soft bottoms, rocky outcrops and cliffs), as well as in the circalittoral and bathyal zones (e.g. submarine canyons, banks, knolls, carbonated mounds and mud volcanoes) (Muñoz et al. 2008, Palomino et al. 2015; Vázquez et al. 2021). This also promotes a great heterogeneity of benthic habitats and communities that favour the presence of species with different ecological requirements, including some that are highly threatened and vulnerable (Templado 2011, Templado et al. 2021, Rueda et al. 2021). Furthermore, three biogeographical regions converge close to the Alboran Sea, including the temperate Lusitanian region (from the English Channel to the Strait of Gibraltar), the warm Mauritanian region (from the Strait of Gibraltar to Cap Blanc) and the Mediterranean region itself (Ekman 1953, Caballero-Herrera et al. 2021). This biogeographic confluence enables the coexistence of species from the North Atlantic or subtropical northwestern Africa with Mediterranean species, in addition to some endemic species (Gofas 1998, Rueda et al. 2010, Urra et al. 2017, Sitjà et al. 2020). Because of all these features, the Alboran Sea is considered one of the biodiversity hotspots within the Mediterranean basin and the European margin (García Raso et al. 2010, Templado 2011, Rueda et al. 2021).

Molluscs account for 25% of the marine fauna and are one of the most diverse faunal groups in benthic communities (Appeltans et al. 2012). The Iberian margin, favoured by its geographical location and its great variety of benthic habitats from the supralittoral zone to the deep-sea bottoms, hosts more than half of the mollusc species registered within the European Register of Marine Species (http://www.marbef.org/data/erms.php) and therefore the richest molluscan biodiversity for the European margin (Gofas et al. 2017). Molluscs are an appropriate group for the evaluation of the local biodiversity of a specific area, since they are a very well-known faunal group, and several studies allow comparisons with neighbouring areas (Bedulli et al. 2002, Gladstone 2002, Smith 2005). Additionally, they are an important component of benthic communities, playing a key trophic role due to their different feeding strategies and, in some cases, providing an ecosystem service because they can improve water and sediment quality (e.g. filter feeders and deposit feeders) (Gosling 2003). Molluscs also form a fundamental link to upper trophic levels, including humans, who have exploited some mollusc species for centuries (Edgar and Shaw 1995, Pasquaud et al. 2010). Most previous studies on molluscs have focused on those of the infralittoral habitats from the northern Alboran Sea (Salas and Hergueta 1986, Rueda et al. 2009, Urra et al. 2011, 2017, 2018). However, the molluscan assemblages associated with insular and/or deep zones have been poorly studied in the Alboran Sea, with few studies focused on surrounding areas of the Strait of Gibraltar (Salas 1996), the Alboran Island platform (Templado 1993, Peñas et al. 2006), the Djibouti Bank (Gofas et al. 2014) and the trawlable grounds of the shelf and slope (Ciércoles et al. 2018).

The present study was carried out on a submarine knoll of the northeastern Alboran Sea, known as Chella Bank (also known in Spanish as Seco de los Olivos) and its adjacent bottoms. This submarine knoll has been recently integrated into the European Union (EU) Natura 2000 network as a site of community importance (SCI) (ESZZ16003 "Sur de Almería – Seco de los Olivos"). Previous studies in the area have focused on the presence of different habitats and their associated megabenthic species (de la Torriente et al., 2014, 2018, 2019) or specific benthic groups (e.g. brachiopods, bryozoans) (Llompart 1988; Ramalho et al. 2020). However, information on other benthic macro- and micro-fauna, including molluscs, is very scarce and restricted to the presence of a few macrofaunal species (e.g. for molluscs *Episcomitra zonata* (Marryat, 1818), *Ranella olearium* (Linnaeus, 1758), *Octopus vulgaris* Cuvier, 1797 and *Sepia officinalis* Linnaeus, 1758) (Abad et al. 2007, de la Torriente et al. 2014). Formally speaking, Chella Bank does not qualify as a seamount because it is close to the mainland and its elevation above the sea bottom is far less than 1000 m, as defined by Staudigel et al. (2010). However, it retains some seamount characteristics (Von Rad 1974), among which the most important may be the absence of sedimentary input to the upper platform from the mainland, separated by a channel about 350 m deep (Fig. 1).

Increasing knowledge on the biodiversity of different habitats of this SCI will improve our understanding of the role of this submarine elevation for the Alboran Sea and western Mediterranean Sea biodiversity. Moreover, accurate information on the circalittoral and bathyal communities of the Alboran Sea is needed to implement suitable conservation and management measures within the framework of current European Directives (e.g. the Marine Strategy Framework Directive) and the ecosystem approach to fisheries management (Borja et al. 2010, Jennings et al. 2014). Technological progress, mainly in the fisheries sector, is promoting the human exploitation of fish resources into deeper areas that are increasingly distant from the coast, causing severe impacts on the habitats and their associated biodiversity (Clark et al. 2007). Therefore, to achieve a sustainable extraction of resources, it is necessary to study and characterize the deep sea to improve its management and conservation, especially when it harbours vulnerable marine ecosystems (VMEs) such as those occurring on submarine elevations. The main aim of the present study was to improve knowledge of the bi-

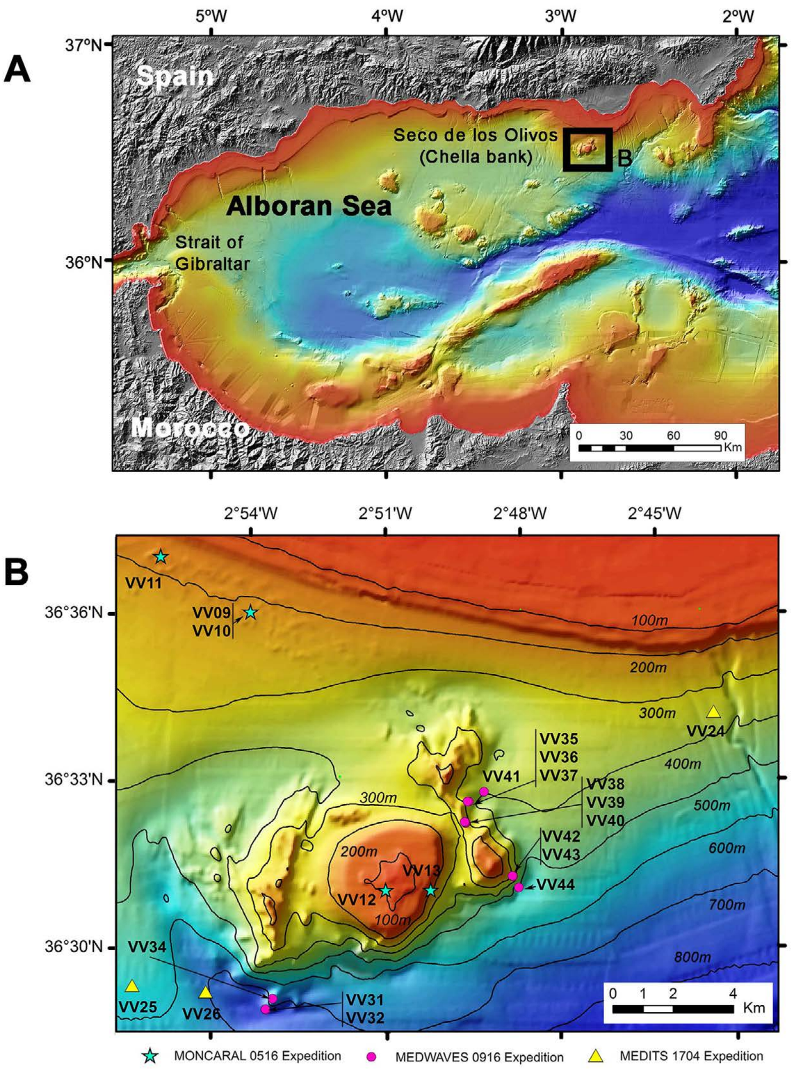

Fig. 1. – A, location of Chella Bank (Seco de los Olivos) within the northeastern Alboran Sea (W Mediterranean Sea); B, bathymetric map of the study area, showing the main morphological features with indication of the sampling stations where van Veen (VV) samples were collected during different expeditions.

odiversity of this SCI and in particular (1) to characterize the molluscan taxocenoses and thanatocenoses and (2) to analyse the affinities of the molluscan fauna with its biogeographical context. This information will also be beneficial for the development of the management plans of this SCI to become a special conservation area in the near future.

MATERIALS AND METHODS

Study area

The study area is located within the SCI "Sur de Almería – Seco de los Olivos", including Chella Bank (36°31.27'N, 2°50.43'W) and its adjacent bottoms (Fig. 1). This seafloor elevation is of volcanic origin and is located on the upper slope of the Almería margin (NE Alboran Sea), with its summit at 76 m depth and its base at 700 m depth (de la Torriente et al. 2014), covering an area in the order of 10000 ha. It is not properly a seamount, which is defined as a rise of more than 1000 m above a seafloor usually located on the oceanic crust (International Hydrographic Organization 2008, Staudigel et al. 2010). Chella Bank has a main edifice or guyot with a subcircular shape and a tabular summit, where abundant rhodolith beds occur (de la Torriente et al. 2014, 2018). This plateau originated in the Quaternary as a result of the abrasion produced during sea level falls in glacial periods (Lo Iacono et al. 2008), and it is currently covered with biogenic carbonate deposits left by the organisms that inhabited the seabed. The seabed is now colonized by sessile filter and suspension feeders such as sponges, gorgonians and aggregations of cold-water corals (CWCs), among other VMEs (Lo Iacono et al. 2012, de la Torriente et al. 2014, 2018).

Other small elevations or pinnacles with steeper slopes are located around the NE and W slopes between 135 and 200 m depth (Muñoz et al. 2008). These areas are dominated by rocky outcrops colonized by communities of large sponges (e.g. *Asconema setubalense* Kent, 1870) and CWC rubble bottoms (Lo Iacono et al.

2012, de la Torriente et al. 2014, 2018). A carbonated framework composed of dead colonies of CWCs (*Desmophyllum pertusum* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758) is a characteristic habitat among the pinnacles of the main elevation, where small live colonies of the same species have been detected (de la Torriente 2014, 2018). Mixed habitats with sponges and antipatharian corals (e.g. *Leiopathes glaberrima* (Esper, 1792), *Antipathes dichotoma* Pallas, 1766) occur on the bathyal rocky bottoms, hosting a high benthic biodiversity (de la Torriente 2014, 2018). Subfossil reefs of horse-mussels (*Modiolus modiolus* (Linnaeus, 1758)) covered by sediment have been located south of the main elevation and at several isolated points of the secondary elevations, forming biogenic detrital bottoms (de la Torriente 2014). On the southern flank of Chella Bank, the slope reaches 700 m depth and generally contains extensive areas of soft substrates with the presence of decapods of commercial interest (e.g. *Nephrops norvegicus* (Linnaeus, 1758), *Plesionika* spp.) (de la Torriente 2014).

A total of 13 habitat types have been described on and around Chella Bank (de la Torriente et al. 2014, 2018), of which eight are linked to the habitat "Reefs" (1170) of the EU Habitats Directive (Council Directive 92/43/ECC). These are characterized by generally large habitat-forming species such as gorgonians, sponges and CWCs, including *D. pertusum* and *M. oculata*. These two CWCs generate hotspots of structural complexity, biodiversity and biomass in the deep ocean (De Mol et al. 2012) that have persisted for thousands of years (Roark et al. 2009). Unfortunately, this type of habitat is very vulnerable and is currently threatened by human activities such as bottom trawling fishing (Clark et al. 2007). The area around Chella Bank has been heavily frequented by fishermen due to the presence of commercial species and its proximity to the coast (de la Torriente et al. 2014). ROV images have detected the existence of habitats damaged by trawl and longline fishing, especially on the upper part of the main elevation (Lo Iacono et al. 2012). It should also be noted that the red coral *Corallium rubrum* (Linnaeus, 1758)

Table 1. – Location and depth of the sampling stations where van Veen (VV) samples were collected on Chella Bank and its adjacent bottoms during scientific expeditions, with annotations of the bottom types. Codes for each sample during each expedition are displayed.

Expedition	Sample code	Latitude/longitude	Depth (m)	Bottom type
MONCARAL 0516	VV-09	36º36.20' N 2º54.30' W	210	Muddy bottoms with abundant remains of *Posidonia oceanica*
	VV-10	36º36.20' N 2º54.30' W	210	Muddy bottoms with very abundant buried bioclasts and dead rhodoliths
	VV-11	36º36.99' N 2º56.20' W	178	Medium sandy bottoms with little exposed bioclast and dead rhodoliths
	VV-12	36º30.99' N 2º51.00' W	95	Coarse sandy bottoms with very abundant exposed bioclast and rhodoliths
	VV-13	36º31.15' N 2º50.71' W	140	Gravel and very abundant exposed bioclast and rhodoliths
MEDWAVES 0916	VV-31	36°28.85 N 2°53.67' W	729	Hemipelagic muddy bottoms with pteropod shells and foraminifers
	VV-32	36°28.86 N 2°53.68' W	729	Hemipelagic muddy bottoms with pteropod shells and foraminifers
	VV-34	36°29.05 N 2°53.52' W	637	Hemipelagic muddy bottoms with pteropod shells and foraminifers
	VV-35	36°32.55' N 2°49.16' W	320	Medium sandy bottoms with little buried coral rubble
	VV-36	36°32.55' N 2°49.16' W	321	Medium sandy bottoms with little buried coral rubble and bioclasts
	VV-37	36°32.55' N 2°49.16' W	322	Muddy bottoms with abundant buried coral rubble
	VV-38	36°32.20' N 2°49.22' W	250	Muddy bottoms with very abundant exposed coral rubble
	VV-39	36°32.20' N 2°49.22' W	250	Muddy bottoms with very abundant exposed coral rubble
	VV-40	36°32.20' N 2°49.22' W	250	Muddy bottoms with very abundant exposed coral rubble
	VV-41	36°32.76' N 2°48.81' W	381	Hemipelagic muddy bottoms with some bivalve shells
	VV-42	36°31.24' N 2°48.17' W	280	Medium sandy bottoms with some bivalve shells
	VV-43	36°31.24' N 2°48.17' W	280	Medium sandy bottoms with some bivalve shells
	VV-44	36°31.04' N 2°48.04' W	440	Hemipelagic muddy bottoms with scarce buried coral rubble and bioclasts
MED-ITS 1704	VV-24	36°34.19' N 2°43.67' W	344	Hemipelagic muddy bottoms
	VV-25	36°29.29' N 2°56.64' W	567	Hemipelagic muddy bottoms
	VV-26	36°29.17' N 2°55.01' W	578	Hemipelagic muddy bottoms with little buried coral rubble

was overexploited in the past, although this extractive activity is not currently permitted on this submarine elevation. In addition, Chella Bank is located a few miles from one of the main maritime routes of the Mediterranean Sea, and maritime traffic is likely to cause acoustic and chemical pollution due to ballast and tank water cleaning spills (de la Torriente et al. 2014).

Sample collection and laboratory procedures

Sediment and benthic fauna samples were collected from the bank and the adjacent seafloor during three expeditions: (1) MONCARAL 0516 (May–June 2016) on board R/V *Ángeles Alvariño*, under the framework of the MONCARAL project (*Montículos carbonatados del mar de Alborán*); (2) MEDWAVES (Mediterranean out flow water and vulnerable ecosystems) 0916 (September–October 2016) on board R/V *Sarmiento de Gamboa*, under the framework of the EU H2020 ATLAS project (A transatlantic assessment and deep-water ecosystem-based spatial management plan for Europe); and (3) MEDITS 1704 (April 2017) on board R/V *Miguel Oliver*, under the framework of the MEDITS project (Mediterranean international trawl survey). Twenty-one samples (Fig. 1; Table 1) were collected in a wide depth range (95-729 m) using a van Veen grab, a low-impact sampling method. This method was chosen because of the occurrence of VMEs (e.g. CWC banks and sponge and gorgonian aggregations) and the need to cause a minimal impact on them in this already established SCI. The van Veen grab used during the MEDWAVES expedition had dimensions of 30×36 cm, whereas the one used during the MEDITS and MONCARAL expeditions had dimensions of *ca*. 20×29 cm. Two sediment subsamples of 125 g were taken for sedimentological analyses: one preserved at room temperature for grain-size distribution analyses and one preserved frozen at -20°C for geochemical analysis. The remaining sediment was sieved on board with a 0.5 mm sieve to retain the small organisms. The retained material was preserved in 70% ethanol. In the laboratory, fine fractions of all samples were sorted by size fraction (4-2, 2-1 and 1-0.5 mm), which provided most of the species analysed in this study. The molluscs were sorted and identified to the lowest possible taxonomic level following Gofas et al. (2011) and Bouchet and Warén (1980, 1985, 1986, 1993), among other specific research works. In addition, the reference collections of previously processed material from other areas, including Djibouti Bank and the Alboran Sea, which are stored at Departamento de Biología Animal of the Universidad de Málaga, were used for comparison.

The abundance of live-taken specimens of each mollusc species was noted in each sample and the species of the thanatocoenosis were semi-quantified following a rank system used in a similar study of deep-sea molluscs of the Gulf of Cádiz (Utrilla et al. 2020): 1 (1 shell), 2 (from 2 to 5), 3 (from 6 to 30), 4 (from 31 to 100) and 5 (more than 100 shells). The study of the thanatocoenosis generally provides a much more complete faunal list of the species (Ciccolella and Bello 2006), but it was not taken into account for ecological analyses due to potential displacement of shells in space and time (Kidwell 2001, Weber and Zuschin 2013). All taxonomic names were checked and updated using the World Register of Marine Species (http://www.marinespecies.org/). Shells of characteristic specimens were photographed using a Nikon DXM camera mounted on a stereomicroscope, taking a series of views focused on different planes, which were assembled using CombineZ software (Hadley 2006).

The type of larval development was assessed for live-taken species from the characteristics of the larval shell, as detailed by Jablonski and Lutz (1980). A larval shell with two differentiated stages is taken as indicating planktotrophic development, and this also indicates a considerable potential for dispersal. Conversely, a non-planktotrophic development could correspond to (1) species with direct development (without a free pelagic phase) and (2) species known to have a short pelagic non-feeding stage before metamorphosis and settlement. Both of these non-planktotrophic developments should involve a more restricted dispersal capacity, but there are exceptions related to alternative means of dispersal (Wilson 2012).

Bottom type characterization

Bottom type was characterized on the basis of the main granulometric sedimentary components (e.g. mud, sand, gravel), the presence of live/dead rhodoliths and the types of bioclasts (e.g. bivalve, coral remains). Notes on exposed/buried bioclasts were made once the sample was on board.

The grain-size distribution was obtained by wet sieving a sub sample of 100 g in a 63 µm mesh sieve. The coarse fraction was subdivided by dry sieving using a sieve rack and each retained fraction was weighed and transformed into weight percent. The textural classification was performed according to Folk (1954). The geochemical analysis was performed using the loss on ignition method to estimate organic matter and carbonate content of the surficial sediment samples (Heiri et al. 2001).

Characterization of the molluscan fauna

Mollusc taxa were characterized according to their abundance (total number of live-taken individuals and/or the rank system for dead specimens), dominance (percentage of individuals of a particular taxon within the sample) for live-taken samples and frequency (percentage of samples in which a particular taxon is present) for live and dead-taken samples. Abundance data were standardized (individuals/m^2) to enable faunistic comparisons between samples. Kruskal-Wallis tests (a non-parametric analogue of one-way ANOVA) were carried out to test whether ecological indices such as species richness (number of species present in each sample), abundance (number of individuals collected per sample), evenness index (Pielou 1969) and Shannon-Wiener diversity index ($\log_2$, Krebs 1989) were significantly different regarding the significantly different groups

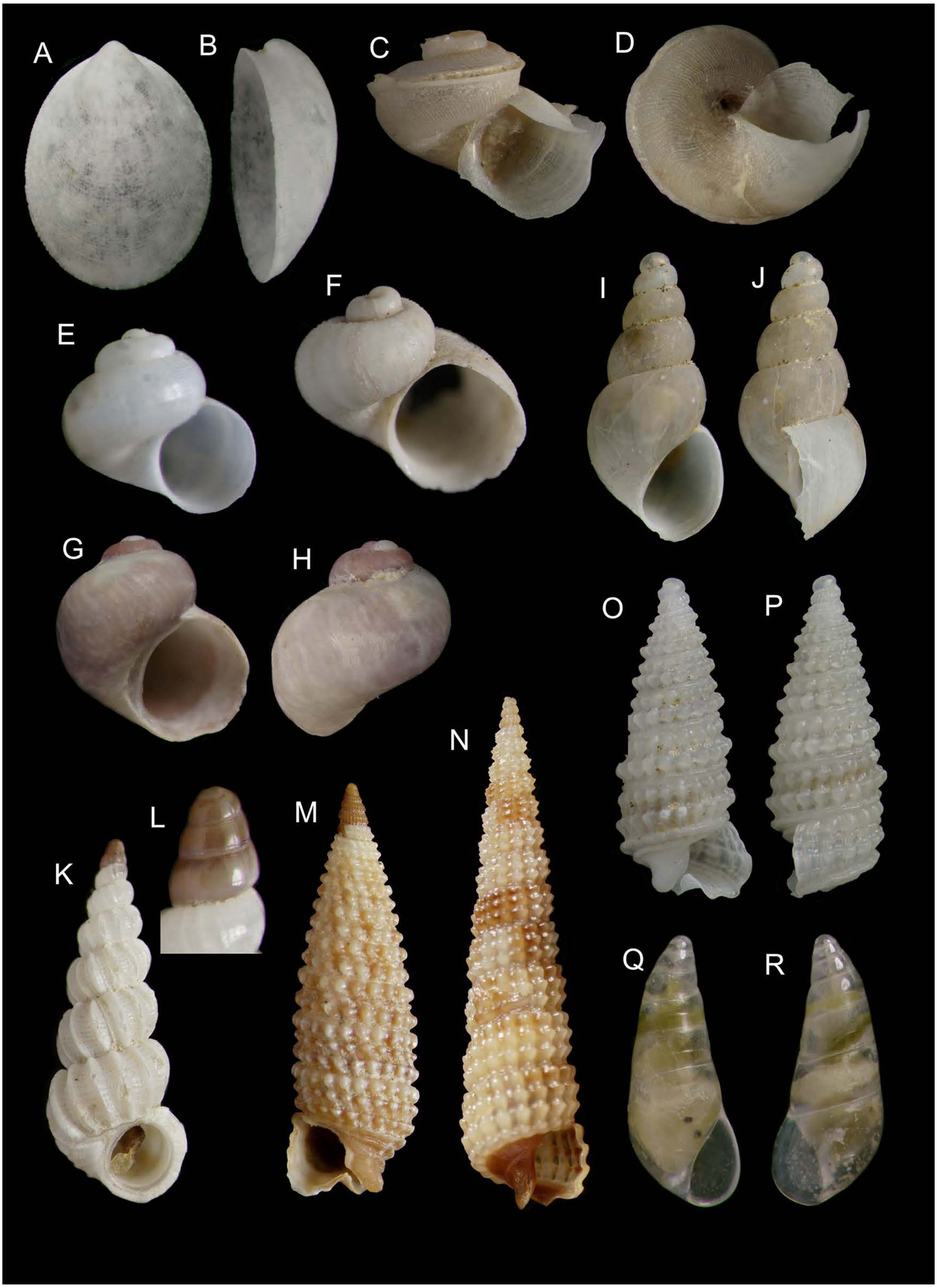

Fig. 2. – Rare or unusual monoplacophorans (A, B) and gastropods (C-R) found on Chella Bank (Seco de los Olivos) and its adjacent bottoms (measurements refer to largest dimension). A, B: *Veleropilina euglypta* (Medwaves VV37; 1.8 mm). C, D: *Anatoma micalii*, new record for Spanish waters (MEDWAVES VV40; 1.9 mm). E: *Anekes paucistriata* (MEDWAVES VV44, 0.9 mm). F: *Granigyra granulifera*, new record for Spanish waters (MEDWAVES VV34; 2.1 mm). G, H: *Tricolia deschampsi*, exclusively found in the thanatocoenosis (MONCARAL VV10; 1.6 mm). I, J: *Talassia dagueneti* (MEDWAVES VV36; 2.4 mm). K, L: *Opalia abbotti* and its protoconch (MEDWAVES VV38; 3.6 mm). M: *Ionthoglossa pseudocanarica* (MEDWAVES VV38; 5.1 mm). N: *Retilaskeya horrida* (MEDWAVES VV38; 9.0 mm). O, P: *Onchodia valeriae* (MEDWAVES VV39; 4.2 mm). Q, R: *Curveulima beneitoi* (MEDWAVES VV40; 1.4 mm).

of samples detected in multivariate analyses. These multivariate analyses were based on quantitative similarities of live-taken taxa (Bray and Curtis 1957) to assess similarity between samples. A fourth-root transformation pre-treatment was applied on the quantitative data of each live-taken mollusc taxon in each sample in order to minimize the contribution of very abundant taxa to the analyses. A cluster of the samples was obtained using the Bray-Curtis similarity index and the unweighted pair group method with an arithmetic mean agglomerative algorithm (UPGMA) (Sneath and Sokal 1973). A permutation procedure, the similarity profile routine (SIMPROF), tested for the significance of groups of samples (Clarke et al. 2008). The identification of the taxa characterizing each group (displaying significant differences with the SIMPROF test) was performed through a similarity percentage analysis (SIMPER) with a 90% cut-off for low contributions. All these analyses were carried out with the PRIMER v.6 (Plymouth Routines In Multivariate Ecological Research) software from Plymouth Marine Laboratory, UK (Clarke and Gorley 2006) and the SPSS software v.16. Some of these multivariate analyses have been used for detecting similarities and differences between groups of benthic samples collected with van Veen dredges (De Leonardis et al. 2008, Sciberras et al. 2009, Doğan et al. 2016).

Affinities with the biogeographical context

Distribution patterns were analysed for 73 live-taken taxa that were identified to species level whose distribution pattern is known from the scientific literature (Gofas et al. 2017). The geographical sectors considered in the analyses presented in this study are (1) the Mediterranean Sea (MED), excluding those species that are not reported east of the Alboran Sea; (2) the Ibero-Moroccan Gulf (IB) (also known as Gulf of Cádiz in some studies), including the southern margin of Portugal, the Gulf of Cádiz (SW Spain) and Morocco; (3) West Europe, from Portugal to the southern margin of the United Kingdom; (4) Northern Europe, from the southern margin of the United Kingdom to Scandinavia; (5) the Canary Islands, including Madeira and/or the Lusitanian seamounts (Gorringe, Josephine, Ampère and Seine, among other banks); and (6) West Africa, from the western Sahara to the tropical western African margin.

Chorotypes of molluscs were analysed following the method described by Olivero et al. (2011) using the RMacoqui 1.0 software (http://rmacoqui.r-forge.r-project.org/). The similarity between species distribution was classified hierarchically according to the presence/absence of species using the Baroni-Urbani and Buser (1976) similarity index and the UPGMA (Sneath and Sokal 1973). The resulting clusters were assessed for statistical significance using G tests of independence (Sokal and Rohlf 1981) (see more details in Olivero et al. 2011).

RESULTS

Molluscan fauna

A total of 282 taxa identified to species level were found on Chella Bank and its adjacent bottoms (Table 2) and 17 additional taxa, pending identification,

Table 2. – List of molluscs found on Chella Bank and its adjacent bottoms. N, Abundance; %D, Dominance; %F, Frequency; Rank, Rank abundance range in samples (1, one shell collected; 2, 2-5; 3, 6-30; 4, 31-100; 5, >100 shells); Larvae, type of larval development of live-taken species (SP, short planktonic; PK, planktotrophic; DI, direct development; ?, unknown larval development; --, unidentified).

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
	Class APLACOPHORA							
	Solenogastres unidentified	7	1.22	19.05				--
	Caudofoveata unidentified	3	0.52	9.52				--
Prochaetoder-matidae	*Prochaetoderma* sp.	4	0.7	14.29				--
	Class POLYPLACOPHORA							
Leptochitonidae	*Leptochiton* spp.	4	0.7	9.52				--
	Class MONOPLACOPHORA							
Neopilinidae	*Veleropilina euglypta* (Dautzenberg & H. Fischer, 1897)				1	1	4.76	
	Class GASTROPODA							
Lepetidae	*Propilidium exiguum* (W. Thompson, 1844)				59	1-4	33.33	
Scissurellidae	*Scissurella costata* d'Orbigny, 1824				159	1-5	28.57	
Anatomidae	*Anatoma aspera* (Philippi, 1844)	3	0.52	9.52	67	1-4	38.10	SP
	Anatoma micalii Geiger, 2012	8	1.39	9.52				SP
Fissurellidae	*Emarginula adriatica* O. G. Costa, 1830	3	0.52	9.52	90	1-4	23.81	SP
	Diodora graeca (Linnaeus, 1758)				3	1-2	9.52	

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
	Emarginula rosea Bell, 1824				15	2-4	19.05	
	Emarginula tenera Locard, 1891				5	3	4.76	
	Emarginula tuberculosa Libassi, 1859				8	3	4.76	
	Fissurisepta granulosa Jeffreys, 1883				1	1	4.76	
Lepetellidae	*Lepetella espinosae* Dantart & Luque, 1994				49	3-4	14.29	
Trochidae	*Callumbonella suturalis* (Philippi, 1836)				9	1-3	23.81	
	Clelandella miliaris (Brocchi, 1814)				12	1-3	9.52	
	Gibbula guttadauri (Philippi, 1836)				1	1	4.76	
	Jujubinus montagui (Wood, 1828)				6	1-3	9.52	
	Jujubinus spp.				256	3-5	14.29	
Calliostomatidae	*Calliostoma* spp.				5	1-2	19.05	
Chilodontaidae	*Danilia tinei* (Calcara, 1839)				44	1-3	33.33	
Eucyclidae	*Putzeysia wiseri* (Calcara, 1842)				5	1-2	14.29	
Skeneidae	*Cirsonella romettensis* (Granata-Grillo, 1877)				22	1-3	23.81	
	Dikoleps marianae Rubio, Dantart & Luque, 1998				31	2-4	14.29	
	Dikoleps templadoi Rubio, Dantart & Luque, 2004				117	3-4	14.29	
	Skenea serpuloides (Montagu, 1808)				93	1-4	19.05	
Seguenzioidea	*Anekes paucistriata* Warén, 1992				7	1-3	9.52	
	Anekes sculpturata Warén, 1992				64	4	4.76	
	Granigyra granulifera Warén, 1992				1	1	4.76	
	Adeuomphalus ammoniformis Seguenza, 1876	1	0.17	4.76	16	3	4.76	SP
Turbinidae	*Bolma rugosa* (Linnaeus, 1767)				1	1	4.76	
Colloniidae	*Cantrainea peloritana* (Cantraine, 1835).				9	3	4.76	
Phasianellidae	*Tricolia pullus* (Linnaeus, 1758)				1	1	4.76	
	Tricolia deschampsi Gofas, 1993				1358	1-5	23.81	
Cerithiidae	*Bittium latreillii* (Payraudeau, 1826)				70	1-4	19.05	
	Bittium simplex (Jeffreys, 1867)				1	1	4.76	
	Bittium spp.				385	1-5	9.52	
Turritellidae	*Turritella communis* Risso, 1826				19	3	9.52	
	Turritella turbona Monterosato, 1877				4	2	9.52	
Triphoridae	*Strobiligera brychia* (Bouchet & Guillemot, 1978)	1	0.17	4.76	13	2-3	14.29	PK
	Marshallora adversa (Montagu, 1803)				1	1	4.76	
	Metaxia metaxa (Delle Chiaje, 1828)				5	1-2	19.05	
	Ionthoglossa pseudocanarica (Bouchet, 1985)				3	1-2	9.52	
	Strobiligera flammulata Bouchet & Warén, 1993				1	1	4.76	
	Triphoridae unidentified				40	2-3	23.81	
Cerithiopsidae	*Krachia cylindrata* (Jeffreys, 1885)	1	0.17	4.76	1	1	4.76	PK
	Onchodia valeriae (Giusti Fr., 1987)	1	0.17	4.76	21	2-3	14.29	PK
	Cerithiopsidae unidentified				765	2-5	19.05	
	Cerithiopsis diadema Monterosato, 1874				3	1-2	9.52	
	Cerithiopsis fayalensis R. B. Watson, 1880				1	1	4.76	
Newtoniellidae	*Retilaskeya horrida* (Monterosato, 1874)	1	0.17	4.76				PK
Epitoniidae	*Epitonium algerianum* (Weinkauff, 1866)	1	0.17	4.76	5	1-2	19.05	PK
	Opalia abbotti Clench & R. D. Turner, 1952				4	1-2	9.52	
	Epidendrium dendrophylliae (Bouchet & Warén, 1986)				3	2	4.76	
	Epitonium celesti (Aradas, 1854)				20	1-3	33.33	

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
	Epitonium clathratulum (Kanmacher, 1798)				12	2-3	14.29	
	Epitonium hispidulum (Monterosato, 1874)				3	1-2	9.52	
	Epitonium linctum (de Boury & Monterosato, 1890)				9	2-3	14.29	
	Epitonium pseudonanum Bouchet & Warén, 1986				4	1-2	14.29	
	Iphitus tenuisculptus (Seguenza, 1876)				2	1	9.52	
	Iphitus tuberatus Jeffreys, 1883				15	2-3	14.29	
	Punctiscala cerigottana (Sturany, 1896)				1	1	4.76	
Eulimidae	*Sticteulima jeffreysiana* (Brusina, 1869)	2	0.35	9.52	16	2-3	19.05	PK
	Vitreolina curva (Monterosato, 1874)	10	1.74	14.29	17	1-3	19.05	SP
	Aclis ascaris (W. Turton, 1819)				11	3	4.76	
	Aclis attenuans Jeffreys, 1883				15	1-3	33.33	
	Aclis trilineata R. B. Watson, 1897				103	1-4	14.29	
	Curveulima beneitoi Peñas & Rolán, 2006	7	1.22	9.52				DI
	Curveulima sp.				6	2	9.52	
	Eulima bilineata Alder, 1848				159	1-4	47.62	
	Haliella stenostoma (Jeffreys, 1858)				2	2	4.76	
	Melanella alba (da Costa, 1778)				1	1	4.76	
	Melanella frielei (Jordan, 1895)				4	1-2	9.52	
	Melanella lubrica (Monterosato, 1890)				1	1	4.76	
	Melanella petitiana (Brusina, 1869)				1	1	4.76	
	Melanella spp.				15	2-3	9.52	
	Pelseneeria minor Koehler & Vaney, 1908				16	3	4.76	
Vanikoridae	*Megalomphalus azoneus* (Brusina, 1865)				2	1	9.52	
	Talassia dagueneti (de Folin, 1873)	3	0.52	9.52	156	2-5	33.33	DI
Rissoidae	*Alvania cimicoides* (Forbes, 1844)	1	0.17	4.76	272	1-4	61.90	PK
	Alvania tomentosa (Pallary, 1920)	1	0.17	4.76	153	1-4	52.38	DI
	Alvania cancellata (da Costa, 1778)				281	3-5	14.29	
	Alvania electa (Monterosato, 1874)				77	1-4	28.57	
	Alvania hispidula (Monterosato, 1884)				3	2	4.76	
	Alvania punctura (Montagu, 1803)				310	1-5	19.05	
	Alvania testae (Aradas & Maggiore, 1844)				262	1-5	47.62	
	Alvania zetlandica (Montagu, 1815)				89	1-4	42.86	
	Alvania zylensis Gofas & Warén, 1982				1	1	4.76	
	Manzonia crassa (Kanmacher, 1798)				1	1	4.76	
	Obtusella intersecta (S. Wood, 1857)				4	2	4.76	
	Pseudosetia amydralox Bouchet & Warén, 1993				7	1-2	14.29	
	Pusillina radiata (Philippi, 1836)				7	1-3	9.52	
Iravadiidae	*Ceratia proxima* (Forbes & Hanley, 1850)				11	1-3	14.29	
	Hyala vitrea (Montagu, 1803)				18	1-3	38.10	
Anabathridae	*Pisinna glabrata* (Megerle von Mühlfeld, 1824)				38	3-4	9.52	
Barleeiidae	*Barleeia unifasciata* (Montagu, 1803)				193	3-5	9.52	
Caecidae	*Caecum clarkii* Carpenter, 1859				9	1-3	9.52	
	Caecum subannulatum de Folin, 1870				1	1	4.76	
Naticidae	*Euspira fusca* (Blainville, 1825)	3	0.52	14.29	58	3-4	19.05	PK
	Tectonatica rizzae (Philippi, 1844)				4	1-2	9.52	
Ovulidae	Ovulidae unidentified	1	0.17	4.76				--

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
	Pseudosimnia carnea (Poiret, 1789)				1	1	4.76	
Atlantidae	*Atlanta peronii* Lesueur, 1817				2	2	4.76	
Capulidae	*Capulus ungaricus* (Linnaeus, 1758)				29	1-3	28.57	
Aporrhaidae	*Aporrhais serresiana* (Michaud, 1828)				5	1-2	19.05	
Muricidae	*Orania fusulus* (Brocchi, 1814)	1	0.17	4.76	1	1	4.76	PK
	Coralliophila brevis (Blainville, 1832)				1	1	4.76	
	Coralliophila panormitana (Monterosato, 1869)				2	2	4.76	
	Coralliophila spp.				14	1-2	28.57	
	Hirtomurex squamosus (Bivona, 1838)				7	1-2	14.29	
	Pagodula echinata (Kiener, 1839)				7	3	4.76	
	Trophonopsis barvicensis (Johnston, 1825)				3	2	4.76	
Fasciolariidae	*Pseudofusus pulchellus* (Philippi, 1840)				3	1-2	9.52	
Nassariidae	*Tritia recidiva* (von Martens, 1876)				21	1-3	38.10	
	Tritia ovoidea (Locard, 1886)				2	1	9.52	
Columbellidae	*Mitrella templadoi* Gofas, Luque & Urra, 2019	1	0.17	4.76	25	2-3	23.81	PK
	Amphissa acutecostata (Philippi, 1844)				3	1	14.29	
Chauvetiidae	*Chauvetia recondita* (Brugnone, 1873)	2	0.35	9.52	64	1-4	23.81	DI
Mitridae	*Episcomitra angelesae* Caballero-Herrera, Gofas & Rueda, 2022				2	1	9.52	
Cystiscidae	*Gibberula turgidula* (Locard & Caziot, 1900)	14	2.44	23.81	595	1-5	47.62	DI
Granulinidae	*Granulina occulta* (Monterosato, 1869)				61	1-4	23.81	
Borsoniidae	*Drilliola loprestiana* (Calcara, 1841)	1	0.17	4.76	47	1-3	33.33	PK
	Drilliola emendata (Monterosato, 1872)				5	1-2	9.52	
Mitromorphidae	*Mitromorpha columbellaria* (Scacchi, 1836)				2	1	9.52	
	Mitromorpha wilhelminae (van Aartsen, Menkhorst & Gittenberger, 1984)				19	1-3	19.05	
Mangeliidae	*Bela atlantidea* (Knudsen, 1952)				2	1	9.52	
	Bela nuperrima (Tiberi, 1855)				21	1-3	33.33	
	Benthomangelia macra (R. B. Watson, 1881)				2	2	4.76	
	Kurtziella serga (Dall, 1881)				1	1	4.76	
	Mangelia costata (Pennant, 1777)				35	2-3	28.57	
	Sorgenfreispira brachystoma (Philippi, 1844)				4	1-2	9.52	
Raphitomidae	*Gymnobela abyssorum* (Locard, 1897)				18	1-3	33.33	
	Pleurotomella demosia (Dautzenberg & Fischer, 1896)	1	0.17	4.76	5	1-2	9.52	PK
	Pleurotomella gibbera Bouchet & Warén, 1980				8	1-3	19.05	
	Raphitoma aequalis (Jeffreys, 1867)				8	1-2	14.29	
	Raphitoma echinata (Brocchi, 1814)				28	1-3	23.81	
	Raphitoma spp.				15	1-3	23.81	
	Leufroyia erronea Monterosato, 1884				3	2	4.76	
	Teretia teres (Reeve, 1844)				32	1-3	33.33	
	Taranis moerchii (Malm, 1861)				4	1	19.05	
Architectoni-cidae	*Discotectonica discus* (Philippi, 1844)	1	0.17	4.76				PK
	Pseudomalaxis zanclaeus (Philippi, 1844)				1	1	4.76	
	Solatisonax alleryi (Seguenza G., 1876)				4	2	4.76	
	Solatisonax hemisphaerica (Seguenza, 1876)				1	1	4.76	
	Spirolaxis clenchi Jaume & Borro, 1946				6	1-2	19.05	
Mathildidae	*Mathilda cochlaeformis* Brugnone, 1873				76	1-4	23.81	

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
	Mathilda coronata Monterosato, 1875				1	1	4.76	
	Mathilda retusa Brugnone, 1873				4	1-2	9.52	
Cimidae	*Cima cuticulata* Warén, 1993				1	1	4.76	
	Graphis gracilis (Monterosato, 1874)				16	1-3	19.05	
Hyalogyrinidae	*Hyalogyra zibrowii* Warén, 1997				17	1-3	9.52	
Pyramidellidae	*Megastomia* cf. *conoidea* (Brocchi, 1814)	1	0.17	4.76	49	1-4	28.57	SP
	Tibersyrnola unifasciata (Forbes, 1844)	1	0.17	4.76	18	1-3	19.05	SP
	Eulimella bogii van Aartsen, 1994				5	3	4.76	
	Eulimella cerullii (Cossmann, 1916)				26	1-3	19.05	
	Eulimella cossignaniorum van Aartsen, 1994				4	2	4.76	
	Eulimella neoattenuata Gaglini, 1992				12	1-3	19.05	
	Eulimella scillae (Scacchi, 1835)				7	1-2	19.05	
	Eulimella ventricosa (Forbes, 1844)				201	3-4	38.10	
	Jordaniella truncatula (Jeffreys, 1850)				1	1	4.76	
	Megastomia conspicua (Alder, 1850)				24	4	4.76	
	Odostomella bicincta (Tiberi, 1868)				25	1-3	23.81	
	Odostomella doliolum (Philippi, 1844)	1	0.17	4.76	73	1-4	38.10	SP
	Odostomia acuta Jeffreys, 1848				1	1	4.76	
	Odostomia spp.				10	1-3	14.29	
	Odostomia suboblonga Jeffreys, 1884				45	3-4	14.29	
	Parthenina dollfusi (Kobelt, 1903)				3	2	4.76	
	Parthenina flexuosa (Monterosato, 1874)				102	1-4	57.14	
	Parthenina interstincta (J. Adams, 1797)				7	3	4.76	
	Parthenina palazzii (Micali, 1984)				1	1	4.76	
	Parthenina suturalis (Philippi, 1844)				1	1	4.76	
	Syrnola minuta H. Adams, 1869				3	1-2	9.52	
	Tiberia minuscula (Monterosato, 1880)				2	2	4.76	
	Tragula fenestrata (Jeffreys, 1848)				2	2	4.76	
	Turbonilla acutissima Monterosato, 1884				15	3	9.52	
	Turbonilla amoena (Monterosato, 1878)				7	2	14.29	
	Turbonilla cf. *jeffreysii* (Jeffreys, 1848)				35	1-4	14.29	
	Turbonilla micans (Monterosato, 1875)	1	0.17	4.76	22	1-4	9.52	SP
	Turbonilla sp. (*T. magnifica* sensu Jeffreys)				37	3	14.29	
Acteonidae	*Crenilabium exile* (Jeffreys, 1870)	3	0.52	9.52	35	1-4	28.57	SP
	Acteon monterosatoi Dautzenberg, 1889				20	1-4	14.29	
Colpodaspididae	*Colpodaspis pusilla* M. Sars, 1870				4	2	9.52	
Diaphanidae	*Diaphana cretica* (Forbes, 1844)				4	1-2	14.29	
	Diaphana minuta T. Brown, 1827				2	2	4.76	
Philinidae	*Hermania scabra* (O. F. Müller, 1784)				4	1-5	47.62	
	Philine intricata Monterosato, 1884				8	1-3	9.52	
	Philine striatula Monterosato, 1874				17	1-3	23.81	
	Rhinodiaphana ventricosa (Jeffreys, 1865)				3	2	4.76	
Retusidae	*Retusa laevisculpta* (Granata-Grillo, 1877)				26	3	9.52	
	Retusa mammillata (Philippi, 1836)				34	3-4	9.52	
	Retusa umbilicata (Montagu, 1803)				2	2	4.76	
Alacuppidae	*Roxania utriculus* (Brocchi, 1814)				2	2	4.76	

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
Cylichnidae	*Cylichna cylindracea* (Pennant, 1777)				6	1-2	23.81	
Rhizoridae	*Volvulella acuminata* (Bruguière, 1792)				1	1	4.76	
Cavoliniidae	*Cavolinia inflexa* (Lesueur, 1813)				5	1-2	9.52	
	Diacria trispinosa (Blainville, 1821)				1	1	4.76	
	Cavolinia gibbosa (d'Orbigny, 1835)				1	1	4.76	
Cliidae	*Clio cuspidata* (Bosc, 1801)				4	2	9.52	
	Clio pyramidata Linnaeus, 1767				89	1-4	38.10	
Limacinidae	*Heliconoides inflatus* (d'Orbigny, 1835)				22	1-3	19.05	
	Limacina lesueurii (d'Orbigny, 1836)				10	1-3	9.52	
	Limacina retroversa (J. Fleming, 1823)				5	1-2	14.29	
Peraclidae	*Peracle reticulata* (d'Orbigny, 1835)				1	1	4.76	
Pleurobranchidae	Pleurobranchidae unidentified				3	1-2	9.52	
	Class SCAPHOPODA							
Dentaliidae	*Antalis panorma* (Chenu, 1843)	3	0.52	14.29	45	1-4	23.81	SP
	Antalis novemcostata (Lamarck, 1818)				1	1	4.76	
	Antalis sp.				34	1-4	9.52	
Gadilidae	*Cadulus jeffreysi* (Monterosato, 1875)	6	1.05	19.05	49	2-4	14.29	SP
Entalinidae	*Entalina tetragona* (Brocchi, 1814)				15	2	28.57	
	Class BIVALVIA							
Nuculidae	*Nucula perminima* Monterosato, 1875	1	0.17	4.76	16	3	4.76	SP
	Nucula nucleus (Linnaeus, 1758)				24	1-4	14.29	
	Nucula sulcata Bronn, 1831	6	1.05	19.05	33	1-4	33.33	SP
	Ennucula aegeensis (Forbes, 1844)	5	0.87	19.05	47	1-4	23.81	SP
	Ennucula decipiens (Philippi, 1844)	3	0.52	14.29	11	2	19.05	SP
Nuculanidae	*Ledella messanensis* (Jeffreys, 1870)	2	0.35	4.76	75	2-4	14.29	SP
	Saccella commutata (Philippi, 1844)	33	5.75	14.29	445	1-5	38.10	SP
Yoldiidae	*Yoldiella philippiana* (Nyst, 1845)	16	2.79	28.57	358	2-5	61.90	SP
Sareptidae	*Pristigloma minima* (Seguenza, 1877)				51	1-4	23.81	
Arcidae	*Asperarca nodulosa* (O. F. Müller, 1776)	6	1.05	14.29	60	1-4	38.10	SP
	Bathyarca pectunculoides (Scacchi, 1835)	8	1.39	14.29	412	2-5	42.86	SP
	Bathyarca philippiana (Nyst, 1848)	4	0.7	9.52	164	1-5	38.10	SP
	Anadara gibbosa (Reeve, 1844)				3	1-2	9.52	
	Arca tetragona Poli, 1795				433	2-5	19.05	
Noetiidae	*Striarca lactea* (Linnaeus, 1758)	1	0.17	4.76				SP
Glycymerididae	*Glycymeris* spp.				21	1-4	9.52	
Limopsidae	*Limopsis angusta* Jeffreys, 1879	13	2.26	14.29	101	1-4	33.33	DI
	Limopsis aurita (Brocchi, 1814)	1	0.17	4.76	67	1-4	33.33	DI
	Limopsis minuta (Philippi, 1836)				3	2	4.76	
Mytilidae	*Dacrydium hyalinum* (Monterosato, 1875)	44	7.67	19.05	446	1-5	28.57	DI
	Gregariella semigranata (Reeve, 1858)	1	0.17	4.76	127	5	4.76	PK
	Modiolula phaseolina (Philippi, 1844)	1	0.17	4.76	479	1-5	28.57	SP
	Crenella arenaria Monterosato, 1875				1	1	4.76	
Pectinidae	*Aequipecten opercularis* (Linnaeus, 1758)				2	1	9.52	
	Delectopecten vitreus (Gmelin, 1791)				1	1	4.76	
	Manupecten pesfelis (Linnaeus, 1758)				3	1-2	9.52	
	Palliolum incomparabile (Risso, 1826)				19	1-3	9.52	

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
	Pseudamussium clavatum (Poli, 1795)				2	2	4.76	
	Pseudamussium peslutrae (Linnaeus, 1771)				2	1	9.52	
	Pseudamussium sulcatum (Müller O. F., 1776)				42	1-4	33.33	
	Talochlamys multistriata (Poli, 1795)				4	2	4.76	
Propeamussiidae	*Similipecten similis* (Laskey, 1811)	1	0.17	4.76	43	1-3	28.57	SP
	Cyclopecten hoskynsi (Forbes, 1844)				14	2-3	9.52	
	Parvamussium fenestratum (Forbes, 1844)	2	0.35	9.52	44	1-4	33.33	SP
Spondylidae	*Spondylus gussonii* O. G. Costa, 1830				7	1-2	23.81	
Anomiidae	*Heteranomia squamula* (Linnaeus, 1758)	18	3.14	9.52	298	1-2	14.29	SP
	Pododesmus patelliformis (Linnaeus, 1761)				1	1	4.76	
Limidae	*Lima lima* (Linnaeus, 1758)				1	1	4.76	
	Limaria loscombi (G. B. Sowerby I, 1823)				1	1	4.76	
	Limatula subauriculata (Montagu, 1803)	1	0.17	4.76	185	1-5	28.57	SP
	Limatula gwyni (Sykes, 1903)				58	2-4	14.29	
	Limea crassa (Forbes, 1844)				95	1-4	38.10	
Gryphaeidae	*Neopycnodonte cochlear* (Poli, 1795)				6	2	9.52	
Astartidae	*Goodallia triangularis* (Montagu, 1803)	6	1.05	9.52	120	1-4	23.81	DI
	Astarte sulcata (da Costa, 1778)				11	1-3	23.81	
	Digitaria digitaria (Linnaeus, 1758)				15	2-3	14.29	
Carditidae	*Cardita calyculata* (Linnaeus, 1758)				1	1	4.76	
Lucinidae	*Myrtea spinifera* (Montagu, 1803)	1	0.17	4.76	1	1	4.76	SP
Thyasiridae	*Axinulus alleni* (Carrozza, 1981)	4	0.7	4.76	10	1-2	19.05	SP
	Axinulus croulinensis (Jeffreys, 1847)	15	2.61	38.10	30	1-3	42.86	SP
	Mendicula ferruginosa (Forbes, 1844)	35	6.1	52.38	147	2-4	71.43	SP
	Thyasira biplicata (Philippi, 1836)	1	0.17	4.76	60	1-4	47.62	SP
	Thyasira granulosa (Monterosato, 1874)	2	0.35	4.76	8	1-3	19.05	SP
	Thyasira obsoleta (Verrill & Bush, 1898)	10	1.74	28.57	10	1-3	19.05	SP
	Thyasira subovata (Jeffreys, 1881)	1	0.17	4.76	42	4	4.76	SP
	Thyasira succisa (Jeffreys, 1876)	2	0.35	4.76	31	1-4	23.81	SP
	Genaxinus eumyarius (M. Sars, 1870)				1	1	4.76	
Basterotiidae	*Atopomya dolobrata* (P. G. Oliver, 2013)				1	1	4.76	
Lasaeidae	*Kellia suborbicularis* (Montagu, 1803)	10	1.74	14.29	46	3-4	9.52	SP
	Kelliopsis jozinae van Aartsen & Carrozza, 1997	5	0.87	14.29	111	1-4	28.57	?
	Kurtiella bidentata (Montagu, 1803)	1	0.17	4.76	15	1-3	23.81	PK
	Kurtiella tumidula (Jeffreys, 1866)				2	2	4.76	
	Montacuta substriata (Montagu, 1808)	1	0.17	4.76	26	1-3	33.33	SP
	Epilepton parrussetense Giribet & Peñas, 1999				4	2	4.76	
	Tellimya ferruginosa (Montagu, 1808)				4	2	9.52	
Cardiidae	*Parvicardium minimum* (Philippi, 1836)	14	2.44	23.81	695	1-5	42.86	SP
Tellinidae	*Arcopella balaustina (*Linnaeus, 1758)	1	0.17	4.76	28	2-3	23.81	SP
	Tellina compressa Brocchi, 1814	2	0.35	4.76				SP
Semelidae	*Abra longicallus* (Scacchi, 1835)	10	1.74	42.86	110	1-4	47.62	SP
	Ervilia castanea (Montagu, 1803)				15	3	9.52	
Hiatellidae	*Hiatella arctica* (Linnaeus, 1767)	1	0.17	4.76	324	2-5	47.62	SP
Kelliellidae	*Kelliella miliaris* (Philippi, 1844)	172	29.97	52.38	1630	1-5	71.43	SP
Trapezidae	*Coralliophaga lithophagella* (Lamarck, 1819)	4	0.7	14.29	4	1-2	14.29	PK

		Taxocoenosis			Thanatocoenosis			
Family	Taxa	N	%D	%F	N	Rank	%F	Larvae
Ungulinidae	*Diplodonta intermedia* Biondi-Giunti, 1859				43	4	4.76	
Chamidae	*Chama circinata* Monterosato, 1878				6	3	4.76	
Veneridae	*Venus casina* Linnaeus, 1758				3	1-2	9.52	
	Venus nux Gmelin, 1791				2	1	9.52	
	Globivenus effossa (Philippi, 1836)				51	3-4	9.52	
	Clausinella fasciata (da Costa, 1778)				1	1	4.76	
	Timoclea ovata (Pennant, 1777)	5	0.87	4.76	161	1-4	38.10	SP
	Gouldia minima (Montagu, 1803)				9	3	4.76	
	Pitar mediterraneus (Aradas & Benoit, 1872)				35	1-3	14.29	
Xylophagaidae	*Xylophaga dorsalis* (W. Turton, 1819)				2	1	9.52	
	Xylophaga praestans E. A. Smith, 1903				5	1-2	14.29	
Poromyidae	*Poromya granulata* (Nyst & Westendorp, 1839)				4	1-2	14.29	
Cuspidariidae	*Cardiomya costellata* (Deshayes, 1835)				32	1-3	42.86	
	Cuspidaria rostrata (Spengler, 1793)				5	1-2	14.29	
	Tropidomya abbreviata (Forbes, 1843)				3	1	14.29	
Total		574			16743			

could each comprise one or more species. A total of 77 taxa were represented by 573 live-taken individuals (ind.), and 288 taxa were detected in the thanacoenosis from 16741 shells analysed. Of these, 11 taxa were only represented by live-taken specimens, including five gastropods (*Anatoma micalii, Curveulina beneitoi, Retilaskeya horrida, Discotectonica discus* and one unidentified Ovulida) and two bivalves (*Striarca lactea* and *Tellina compresa*) as well as the taxa belonging to Solenogastres and Polyplacophora (1 species each) and Caudofoveata (at least two species). Conversely, 222 taxa (74.2% of the total) were only represented by shells, Gastropoda and Bivalvia being the most diverse classes.

All molluscan classes were represented in the studied samples, with the exception of Cephalopoda. The best represented classes were Gastropoda with 201 taxa (29 live-taken with 76 ind.) and Bivalvia with 88 taxa (42 live-taken with 470 ind.). The least represented classes included Scaphopoda with 5 taxa (2 live-taken with 9 ind.); Caudofoveata, including at least two different genera with 7 live-taken individuals; Solenogastres, with 7 live-individuals (unidentified); and finally, Polyplacophora with 4 live-taken individuals (unidentified) and one Monoplacophora shell (*Veleropilina euglypta*). The most diverse bivalve families were Thyasiridae (8 spp.), Nuculidae and Lasaeidae (4 spp.) among the live-taken molluscs and Pyramidellidae (4 spp.) and Eulimidae (3 spp.) among the gastropods.

The top-dominant live-taken taxa were the bivalves *Kelliella miliaris* (172 ind., D=29.97%), *Dacrydium hyalinum* (44 ind., D=7.67%), *Mendicula ferruginosa* (35 ind., D=6.10%) and *Saccella commutata* (33 ind., D=5.7%) (Table 2). Moreover, *K. miliaris* and *M. ferruginosa* were the most frequently collected taxa in the samples (52.38%F, respectively). On the other hand, 36 taxa were represented by a single individual (i.e. singletons), including the bivalves *Modiolula phaseolina*, *Hiatella arctica* and *Limatula subauriculata* and the gastropods *Alvania cimicoides, Alvania tomentosa* and *Odostomella doliolum*.

The most diverse classes in the thanatocoenosis were Gastropoda, with 196 taxa (65.3% of the total) and Bivalvia with 86 taxa (28.7% of the total). The most abundant species were the bivalves *K. miliaris* and *Parvicardium minimum*, together with the gastropods *Tricolia deschampsi* and those of the family Cerithiopsidae (Table 2). However, the most frequently collected species included the bivalves *K. miliaris*, *M. ferruginosa* and *Y. philippiana* and the gastropod *A. cimicoides* (Table 2). Finally, 45 non–live-taken taxa were represented by a single shell, including 33 gastropods (e.g. *Mathilda coronata* and *Parthenina palazzii*), 10 bivalves (e.g. *Pododesmus patelliformis* and *Atopomya dolobrata*), one scaphopod (*Antalis novemcostata*) and the monoplacophoran.

Rare species

Anatoma micalii and *Granigyra granulifera* are recorded for the first time in Spanish waters and *Anekes paucistriata* for the first time in the Alboran Sea (Fig. 2). Other species are not new, but are seldom recorded: e.g. the eulimid *Curveulima beneitoi* (Fig. 2) (so far only known from its type locality in the Alboran platform), the columbellid *Mitrella templadoi* (Fig. 3) (recently described by Gofas et al. 2019 from the Strait of Gibraltar and the Meteor group seamounts of the northeastern Atlantic), the pyramidellid *Parthenina palazzii,* and three species of the genus *Mathilda* (Fig. 3). *Episcomitra angelesae* (Fig. 2) was described very recently, partly using the present material (Caballero-Herrera et al. 2022).

Affinity between samples

Four main groups of samples (similarity >0.2) were detected in multivariate analyses of live-taken molluscs (Fig. 4), one of them corresponding to the samples collected on buried carbonate mounds located close to the shelf break northwards of Chella Bank, and the other three to samples collected on Chella Bank. Two samples (VV12 and VV13) displayed no similarity to any group and were not considered further. The four groups were supported by the SIMPROF test ($\pi = 2.68$, $p < 0.005$). The typifying taxa (according to SIMPER) within each groups of samples are displayed in Table S1 (Supplementary material).

Group I (VV09, VV10, VV11) (Upper bathyal muddy bottoms with buried rhodoliths)

This group of samples was collected on buried carbonate mounds located close to the mainland shelf break northwest of Chella Bank at 178-210 m depth. The sediment was composed predominantly of mud (>60%), except in sample VV11, which contained a greater percentage of coarse and medium sand (>30%, respectively). These samples showed an intermediate percentage of organic matter (%OM) (4.3±0.2%, mean±standard error) and one of the highest carbonate contents (%CO_3, 22.9±6.9%) in comparison with other groups of samples. They were characterized by the presence of remains of dead rhodoliths within the sediment, and the abundance of dead shells of *Tricolia deschampsi* (Fig. 2) (a species always found living among rhodoliths but not detected alive in any of the samples) was noteworthy. A total of 16 live-taken molluscan species were found, with the bivalves *Kelliella miliaris, Saccella commutata* and *Parvicardium minimum* as the top dominant taxa (Fig. 5, Table S2).

Group II (VV38, VV39, VV40) (Upper bathyal muddy bottoms with exposed coral rubble on the flanks of Chella Bank)

This group corresponded to samples collected on the NE flank of the main elevation of Chella Bank between the pinnacles (*ca*. 250 m depth). The seabed was characterized by the presence of abundant exposed coral rubble corresponding mostly to the cold-water coral *M. oculata*, together with a wide variety of invertebrates inhabiting the coral rubble matrix, including crinoids, ophiurids (e.g. *Ophiothrix* sp.) and solitary corals such us *Caryophyllia* sp. The main sediment component was mud (>75%), with an intermediate %OM (4.9±0.17) and the lowest %CO_3 (5.6±0.4) (Kruskal-Wallis for %CO_3 comparisons: $\chi 2=9.7$, $p<0.05$). There were 31 live-taken species, with the bivalves *Dacrydium hyalinum*, *Mendicula ferruginosa*, *Heteranomia squamula* and *Limopsis angusta* and the gastropod *Vitreolina curva* as the top dominant species (Fig. 5, Table S2).

Group III (VV24, VV25, VV26 VV31, VV32, VV34, VV41, VV44) (Upper and middle bathyal muddy hemipelagic bottoms on the flanks of Chella Bank and adjacent bottoms).

This group was composed of eight samples located on bathyal muddy bottoms on the periphery of the main elevation of Chella Bank along a wide bathymetrical range (334-729 m depth). The seabed was mainly characterized by muddy hemipelagic sediments (>90%) with the presence of planktonic pteropod and foraminifera shells and showed the highest %OM (5.7±0.8%) (Kruskal-Wallis for OM comparisons: χ^2= 12.2, $p<0.05$) and intermediate %CO_3 (7.2±2.1). A total of 23 live-taken molluscs species were found, with the bivalves *Thyasira obsoleta, Axinulus croulinensis, Mendicula ferruginosa* and *Kelliella miliaris* as the top dominant species (Fig. 5, Table S2).

Group IV (VV35, VV36, VV37, VV42, VV43) (Upper Bathyal sandy bottoms on the flanks of Chella Bank)

This group was detected northeast of Chella Bank at 280-320 m depth. The seabed was generally characterized by sandy sediment (>50%) and the presence of buried bioclasts, including some coral rubble. The sediment displayed the lowest %OM (2.9±0.2%) (Kruskal-Wallis for OM comparisons: χ^2= 12.2, $p<0.05$) and intermediate %CO_3 (12.5±1.1%). There were 26 live-taken species, with the gastropod *Gibberula turgidula,* the bivalves *Yoldiella philippiana* and *Bathyarca pectunculoides* and the scaphopod *Cadulus jeffreysi* as the top dominant species (Fig. 5, Table S2).

Ungrouped samples (VV12, VV13)

These two samples were taken at the summit of Chella Bank at 95 and 140 m depth, respectively, at the shallowest sampling stations of the study area. Sample VV12 was composed predominantly of coarse sand (51.44%) with very abundant bioclasts and live rhodoliths. It contained 4.4% OM and showed the highest %CO_3 (51.7%) of all samples (Kruskal-Wallis for %CO_3 comparissons: χ^2= 9.7, $p<0.05$). The live-taken molluscan fauna was represented by the bivalves *Goodallia triangularis*, *Modiolula phaseolina* and *Striarca lactea,* and the gastropods *Anatoma aspera* and *Talassia dagueneti* (Table S2, supplementary material). On the other hand, sample VV13 was composed predominantly of gravel (70.7%) with very abundant exposed bioclasts but dead rhodoliths with a size ranging between 7 and 10 cm. Four live-taken gastropod species dominated, including *Curveulima beneitoi*, *Chauvetia recondita, Sticteulima jeffreysiana* and *Orania fusulus* (Table S2, Supplementary material).

Regarding ecological parameters, the highest values of species richness (S) and Shannon-Wiener diversity H'(log_2) index were detected in Group II (S=17±2.1 spp.; H'(log_2)=3.4±0.2) (Kruskal-Wallis S, χ^2=8.84, $p<0.05$); H'(log2), χ^2=8.57, $p<0.05$), whereas the highest abundance (N) value was detected in Group I (1310±603.7 ind.) (Kruskal-Wallis N, χ^2=12.179, $p<0.05$). On the other hand, the lowest S and N values were observed in Group III (S=6.9±1.1

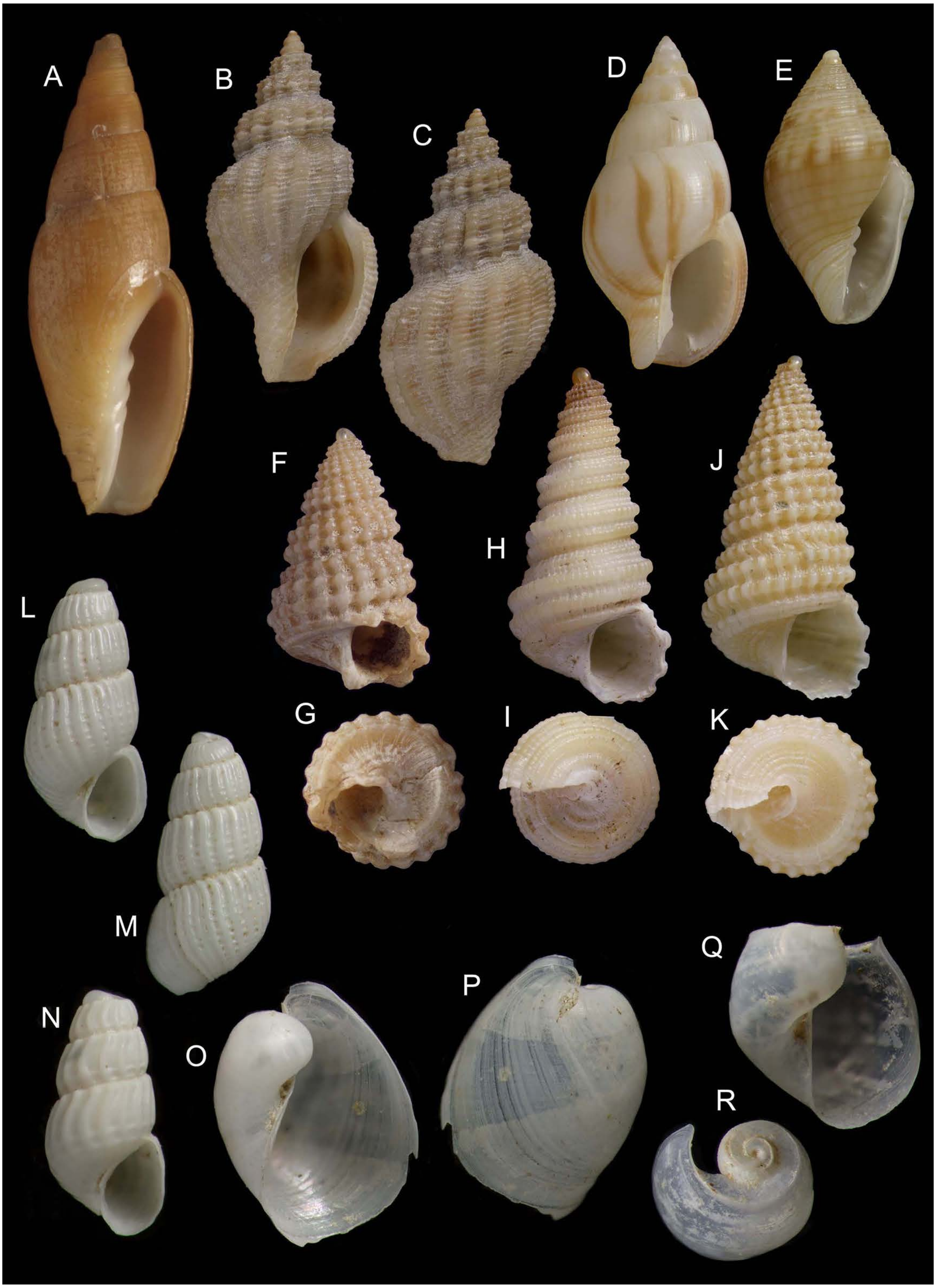

Fig. 3. – Rare or unusual gastropods found on Chella Bank (Seco de los Olivos) and its adjacent bottoms. A: *Episcomitra angelesae*, MEDWAVES VV39; 22 mm). B, C: *Leufroyia erronea* (MEDWAVES VV40; 10.9 mm). D: *Mitrella templadoi* (MEDWAVES VV38; 9.1 mm). E: *Mitrolumna wilhelminae* (MONCARAL VV12; 7.2 mm). F, G: *Mathilda coronata* (MEDWAVES VV38; 5.4 mm). H, I: *Mathilda cochleaeformis* (MEDWAVES VV39; 8.4 mm). J, K: *Mathilda retusa* (MEDWAVES VV39; 8.9 mm). L, M: *Parthenina palazzii* (MEDWAVES VV43; 1.8 mm). N: *Parthenina flexuosa* (MEDWAVES VV43; 1.6 mm). O, P: *Rhinodiaphana ventricosa* (MEDWAVES VV35; 2.8 mm). Q, R: *Colpodaspis pusilla* (MEDWAVES VV38; 1.4 mm).

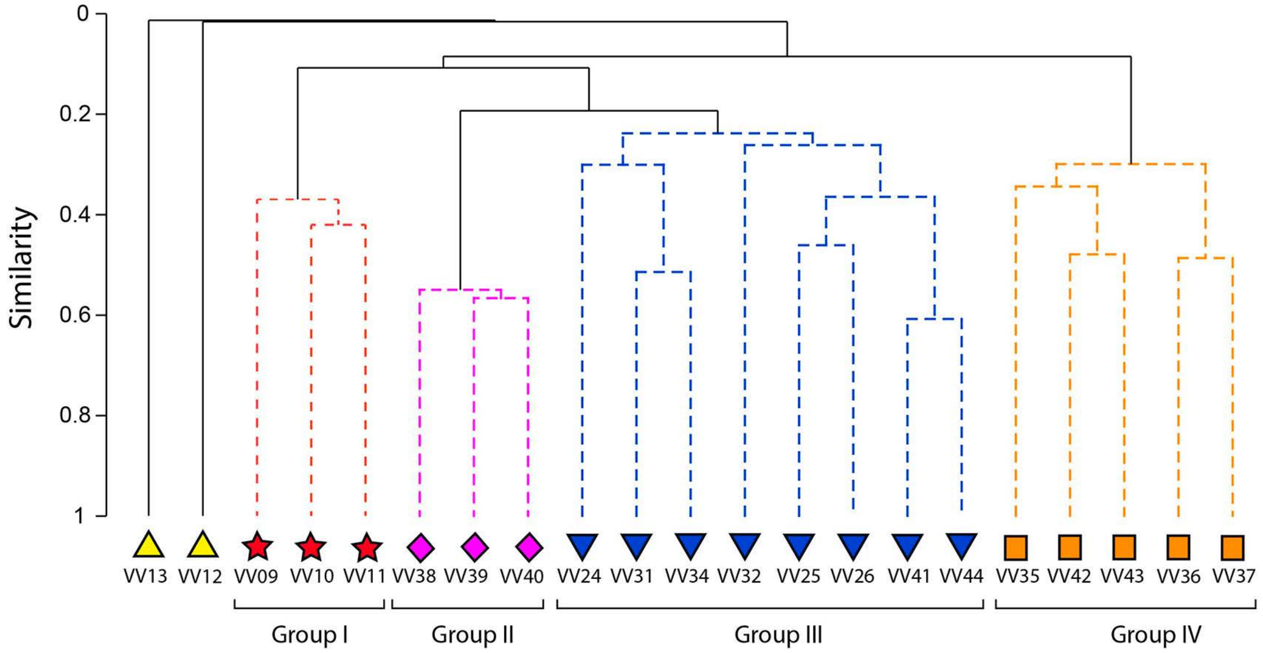

Fig. 4. – Cluster based on Bray-Curtis similarity index and abundance data of live-taken molluscs species (fourth root transformed) collected on Chella Bank (Seco de los Olivos) and its adjacent bottoms. Continuous lines indicate significant differences between samples or group of samples in SIMPROF test ($p < 0.005$).

spp.; N=136±27.1 ind.), although this group displayed the highest evenness index value (J'=0.95 ±0.02) (Kruskal-Wallis J', χ^2=10.24, $p<0.05$). The lowest H'(log_2) and J' values were observed in the group I (H'(log_2)=1.8±0.6; J'= 0.6±0.2).

Affinities with the biogeographical context

Most of the mollusc species from Chella Bank and its adjacent bottoms considered in the analyses display a wide distributional range in the Atlantic Ocean and are also present in the Mediterranean Sea. Three major chorotypes and another group of species with a gradual distribution pattern were identified (Fig. 6, Table 3).

Chorotype 1 (C1) shares 40 species widely distributed along the Atlantic Ocean and Mediterranean Sea: 14 of them are present in all the localities (e.g. *Heteranomia squamula, Myrtea spinifera, Anatoma aspera*), 8 are widely distributed and absent in Northern Europe (e.g. *Gregariella semingranata, Striarca lactea, Epitonium algerianum*), 13 are absent in West Africa (e.g. *Asperarca nodulosa, Bathyarca philippiana, Alvania cimicoides*) and 4 are also widely distributed but not present in West Africa and Northern Europe (*Thyasira succisa, Drilliola lopestriana, Vitreolina curva* and *Talassia dagueneti*).

Chorotype 2 (C2) is formed by 14 species distributed along the Mediterranean Sea and showing different combinations of distribution patterns along the Atlantic location. They are particularly absent in the Canary Islands (e.g. *Nucula sulcata, Mendicula ferruginosa* and *Thyasira biplicata*), absent in the Canary Islands and West Africa (e.g. *Kelliella miliaris, Kurtiella bidentata* and *Thyasira granulosa*) or absent in the Canary Islands, West Africa and Northern Europe (e.g. *Chauvetia recondita, Krachia cylindrata* and *Alvania tomentosa*).

Chorotype 3 (C3) is represented by 14 species with a more restricted distribution close to the Alboran Sea. Of these, there are only two strictly Mediterranean species, the bivalves *Kelliopsis jozinae* and *Nucula perminima*; six of them are reported in the Mediterranean and also in the Ibero-Moroccan Gulf but not in the rest of the Atlantic Ocean (e.g. *Dacrydium hyalinum, Ennucula aegeensis* and *Anatoma micalii*); two are present in the Ibero-Moroccan Gulf and the Canary Islands but not in the Mediterranean (*Limopsis angusta* and *Onchodia valeriae*); and three species are present along the Canary Islands, the Ibero-Moroccan Gulf and the Mediterranean Sea (*Emarginula adriatica, Retilaskeya horrida* and *Pleurotomella demosia*).

Another five species were clustered together showing occasional occurrence at different Atlantic locations and the Alboran Sea but not in the rest of the Mediterranean (*Ennucula decipiens, Mitrella templadoi* and *Strobiligera brychia*); were endemic to the Alboran Sea (the gastropod *Curveulima beneitoi*); or were restricted to the Alboran basin and West Europe (the gastropod *Adeuomphalus ammoniformis*).

The most predominant type of larval development was short planktonic (70% of the total of the live-taken species), followed by planktotrophic development (22%) and direct development (8%). This ratio was not found to differ significantly between the chorotypes.

DISCUSSION

This study has considerably increased the knowledge on molluscs for the recently declared SCI "Sur de Almería – Seco de los Olivos", adding more than

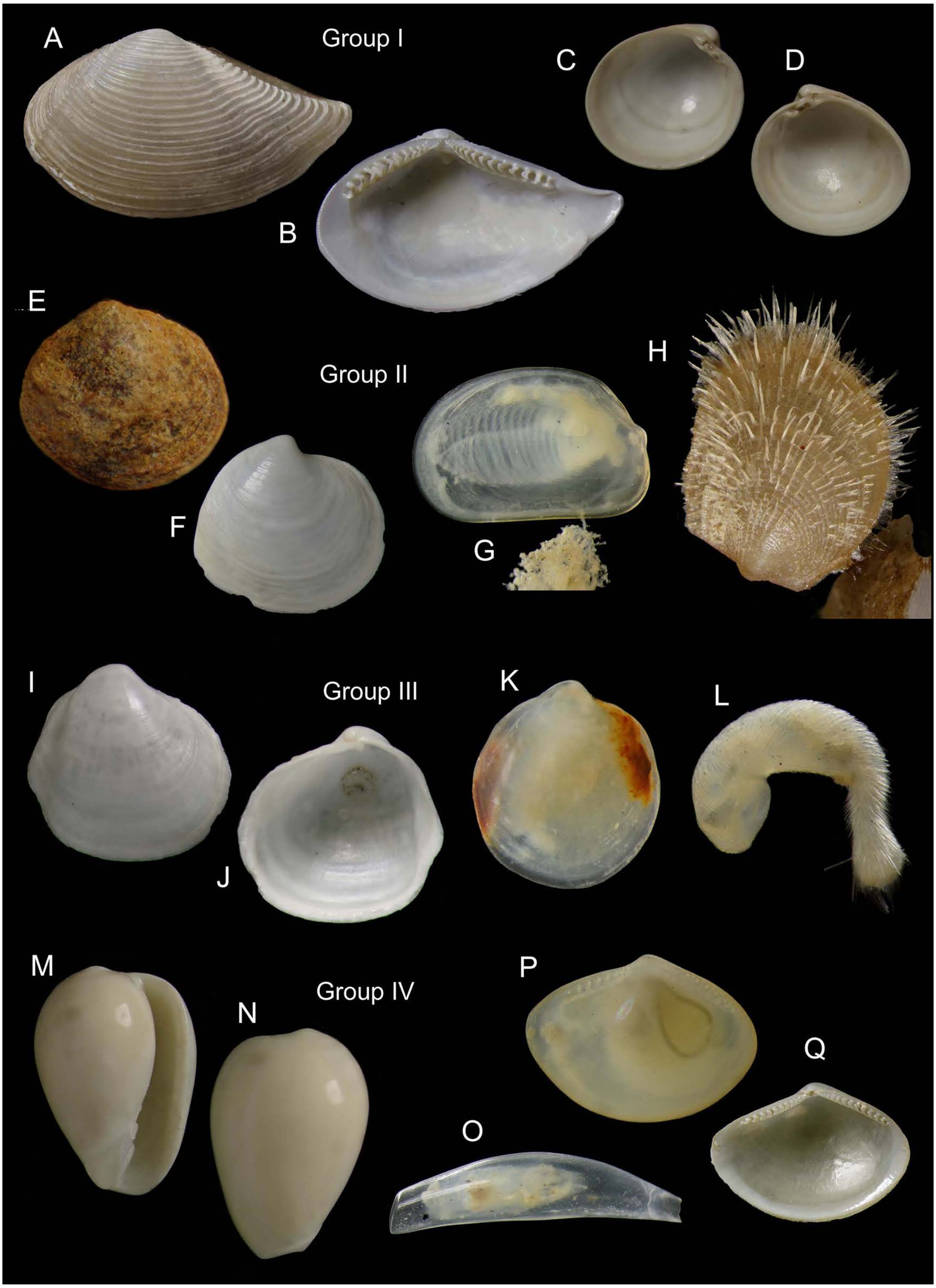

Fig. 5. – Some characteristic species (bivalves, A-K, P-Q; gastropod, M-N; caudofoveate, L; scaphopod, O) of the four groups of samples identified on Chella Bank (Seco de los Olivos) and its adjacent bottoms. A, B: *Saccella commutata* (MONCARAL VV09; 5.5 and 5.1 mm). C, D: *Kelliella miliaris* (MONCARAL VV10; 1.6 and 1.7 mm). E: *Mendicula ferruginosa*, live-taken specimen with thick oxide crust (MEDITS VV25; 1.3 mm). F: *M. ferruginosa* from thanatocoenosis, without the crust (MEDWAVES VV34; 2.4 mm). G: *Dacrydium hyalinum*, byssally attached to a sediment particle (MEDWAVES VV38; 2.0 mm). H: *Limopsis angusta*, byssally attached to a coarse particle (MEDWAVES VV40; 2.7 mm). I, J: *Thyasira obsoleta* (MEDWAVES VV34; 1.5 mm). K: *Axinulus croulinensis* (MEDWAVES VV34; 1.6 mm). L: Class Caudofoveata, *Prochaetoderma* sp. (MEDWAVES VV32; 1.4 mm). M, N: Class Gastropoda, *Gibberula turgidula* (MEDWAVES VV42; 2.1 mm). O: Class Scaphopoda, *Cadulus jeffreysi* (MEDWAVES VV35; 3.2 mm). P, Q: *Yoldiella philippiana* (MEDWAVES VV36; 3.6 and 2.9 mm).

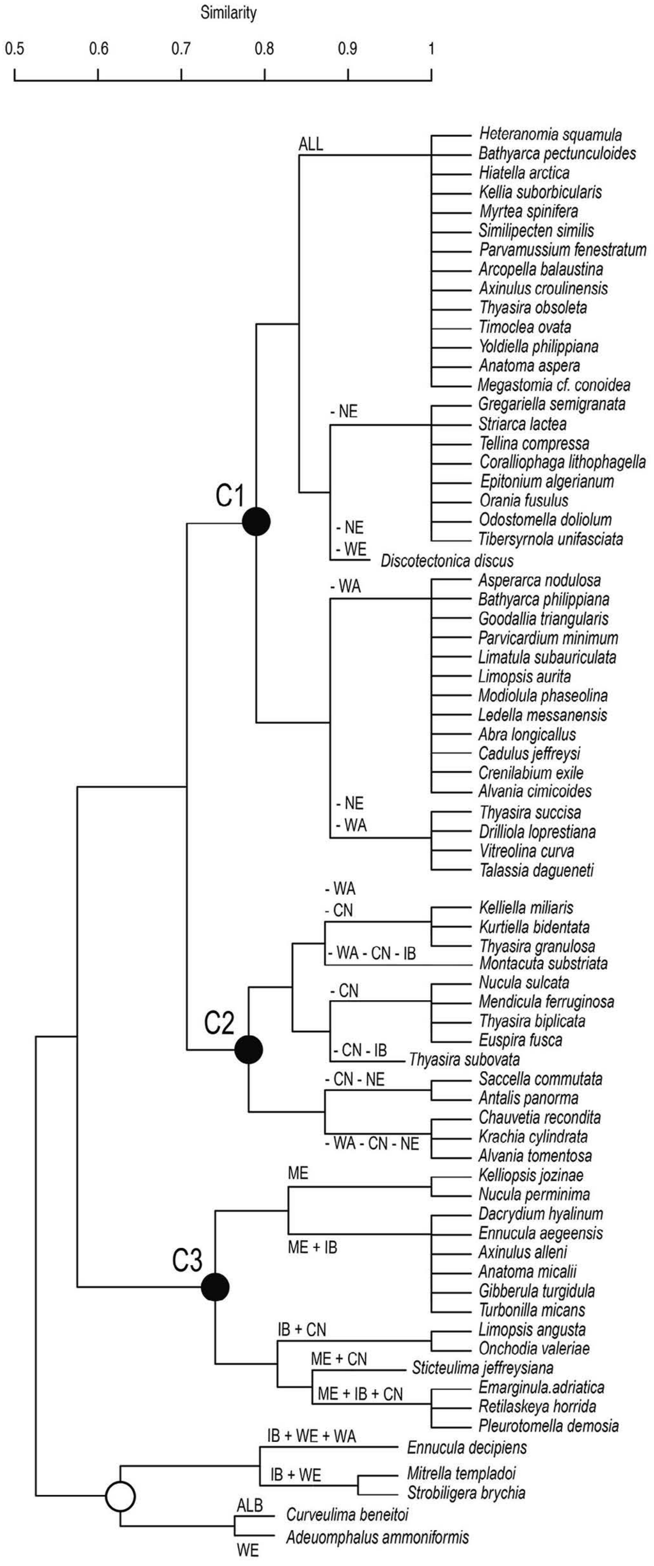

Fig. 6. – Cluster of live-taken molluscs species collected on Chella Bank (Seco de los Olivos) and its adjacent bottoms from different geographic areas using presence/absence data and the Baroni-Urbani and Buser (1976) similarity index. (ALB, Alboran Sea; CN, Canary Islands, Madeira and Lusitanian seamounts; IB, Ibero-Moroccan Gulf; ME, Mediterranean; NE, North Europe; WA, West Africa; WE, West Europe; ALL, all geographic areas; +, presence; -, absence). Black point indicates chorotypes 1, 2 and 3, respectively, and white point corresponds to a group of species with a gradual pattern distribution.

Table 3. Parameters for chorotypes and gradual patterns in Figure 6. IH is the internal homogeneity index. IH >0 and a significant G (independence G-test, with p-value) indicate that the cluster can be considered a chorotype. Otherwise, the cluster is a group of species with a gradual distribution pattern.

	IH	G	P
Chorotype 1	0.55	392.602	0
Chorotype 2	0.439	53.282	0
Chorotype 3	0.558	130.036	0
Gradual pattern	0.223	2.023	0.155

95% to the previously reported species. The absence of cephalopods could be linked to the sampling method used here (van Veen grab), which is not appropriate for collecting those highly mobile organisms, whereas other studies using bottom otter trawling added appropriate data of this group for the northern Alboran Sea (Abad et al. 2007; Ciércoles et al. 2018). Previous studies listed 13 species on Chella Bank (de la Torriente et al. 2014), including seven cephalopod species and the giant deep-sea oyster *Neopycnodonte zibrowii*, which forms small concretions in deep vertical rocky walls (Abad et al. 2007, de la Torriente et al. 2014). Moreover, gastropods included in the Berna and/or Barcelona Convention and catalogued as vulnerable species in the *Libro Rojo de los Invertebrados de Andalucía* (Red Book of the Invertebrates of Andalusia) were reported by de la Torriente et al. (2014), including *Charonia lampas* (Linnaeus, 1758), *Episcomitra zonata*, *Ranella olearium* and *Zonaria pyrum* (Gmelin, 1791). The richness of mollusc species found on Chella Bank and its adjacent bottoms confirms the importance of this marine protected area (MPA) as a biodiversity hotspot within the context of the Alboran Sea and the western Mediterranean Sea, which is a priority area for the conservation of the marine biodiversity integrated in the EU Natura 2000 network (de la Torriente et al. 2014, Mateo Ramírez et al. 2021).

The high diversity of molluscs reported on Chella Bank and its adjacent bottoms is in agreement with the extraordinary biodiversity of other faunal groups that occur on this bank, such as gorgonians, corals, sponges, echinoderms and bryozoans (de la Torriente et al. 2014, 2018; Ramalho et al. 2020). Many of these benthic organisms have three-dimensional structures which provide architectural complexity and refuge for several species, including molluscs such as Epitoniidae, Muricidae (*Coralliophilla* spp.) and Solenogastres, where they find shelter, food and/or spawning areas (Gofas et al. 2011, Rossi et al. 2017). Molluscs are considered key indicators (surrogates) of the biodiversity of other taxa (Reyers et al. 2000) and are therefore a suitable group for evaluating the biodiversity of a particular marine area (Reyers et al. 2000, Mellin et al. 2011).

The samples analysed here were collected with a traditional sampling technique, the van Veen grab, which is a sediment sampler with a very small sampling area (ca. 0.1 m^2) that has a low impact on the seabed, a factor which is crucial for studying biodiversity in VMEs. Despite the limited sampled area and the fact that samples were mostly collected in the bathyal zone, a high number of species was found. The combination of different sampling techniques, whenever it is possible, is the most appropriate methodology for studying benthic communities, because then the species of different ecosystem compartments (i.e. epibenthic and infaunal) can be collected. For instance, Utrilla et. al (2020) used a combination of sampling methods (e.g. box-corer dredge, shipek grab, benthic dredge and beam-trawl) to study deep molluscan assemblages at Gazul mud volcano and adjacent areas in the northeastern Gulf of Cádiz, where they reported a total of 232 species. In the infralittoral zone of the northern Alboran Sea, Rueda et al. (2009) studied the fauna of molluscs associated with *Zostera marina* beds (12-16 m) by combining a small Agassiz trawl and quadrates taken with scuba-diving techniques, and reported a total of 162 species. The present study documents a significant number of mollusc species (299 taxa) for this SCI using a single sampling method, but the number is certainly underestimated and, for instance, the large species reported from video footages by de la Torriente et al. (2014) are missing. Moreover, the small total area sampled (1.84 m^2) represents a very small fraction of the studied bottoms and of the fauna that inhabit them, so any conclusion on the relationships of the studied fauna with environmental characteristics may be venturesome. Therefore, further sampling using low-impact sampling techniques may improve knowledge on the total faunistic list of molluscs of the SCI, the different assemblages that they form and the role of environmental variables on the spatial distribution of these species and assemblages. Nevertheless, the present work still provides a baseline of benthic molluscs associated with certain types of bottoms that are still poorly studied in bathyal areas of some parts of the Mediterranean Sea, in this case the Alboran Sea.

The study of the thanatocoenosis was given special consideration in this study, and this considerably increased the faunal list with the rare species that occur at low density and/or are difficult to collect (Kidwell 2001, Albano and Sabelli 2011). Examples of this fauna include species inhabiting stone cracks (e.g. *Coralliophaga lithophagella*) and rocky bottoms (e.g. *Arca tetragona* and *Neopycnodonte cochlear*), those living on vertical walls (e.g. *N. zibrowii*) that were not sampled in this study but observed in ROV images recorded during the MEDWAVES expedition, and epibionts such as species of the family Eulimidae, some of them parasites of echinoderms. Species only found in low numbers in the thanatocoenosis, such as *Pisinna glabrata* and *Cardita calyculata* (both inhabiting the infralittoral zone) are very probably extinct on Chella Bank. However, the presence of other shells may represent indicators of the actual existence in the area of species (e.g. *Aporrhais serresiana* and *N. cochlear*) that are common and abundant in similar environments of the Alboran Sea (Gofas et al. 2011, Ciércoles et al. 2018). The same probably applies to the *Mathilda* species, which are epibiotic on Zoantharians and usually occur at low densities, so they are very difficult to capture alive with a small dredge sampler (Gofas et al. 2011).

In addition, the thanatocoenosis provides information on species that lived in the past (Kidwell 2001), such as the pteropod *Limacina retroversa,* which has been reported as a Mediterranean "cold host" during glacial periods and interpreted as an element of a thanatocoenosis that is now extinct in the Mediterranean Sea (Malatesta and Zarlenga 1986). Another example is the gastropod *Tricolia deschampsi* (Fig. 2), which is a characteristic species of bottoms with calcareous algae (Gofas et al. 2011), being mostly represented in the thanatocoenosis from samples collected on buried carbonate mounds close to the shelf break, where muddy bottoms with buried rhodoliths occur (Sánchez-Guillamón et al. 2022). This corresponds to an ancient occurrence on carbonate mounds of maërl-rhodolith bottoms from the glacial Pleistocene, when the sea level was lower than nowadays (Sánchez-Guillamón et al. 2022). However, *T. deschampsi* could still occur on Chella Bank since well-preserved shells were also found at the top of the bank (95 m depth), where live rhodoliths beds occur but could not be sufficiently sampled in this study.

The importance of sorting the collected material into different size fractions, with special care for the fine fractions (0.5-1 mm and 1-2 mm) considering molluscs, is a key factor behind the large number of species found in this study. Gofas et al. (2014) documented the retention of over 90% of 156 species of molluscs in the fine fraction of a sample of sediment from Djibouti Bank (Alboran Sea) sieved on a 0.5 mm mesh, and this observation is similar to that from Streftaris and Zenetos (2007). When the benthos (mostly soft bottoms) is sampled with samplers that do not retain the fine fraction, the number of mollusc species drops dramatically, as in the case documented by Ciércoles et al. (2018), who obtained 190 samples with a bottom otter trawl in circalittoral and bathyal soft bottoms of the northern Alboran Sea and reported only 101 molluscs species, mainly macrobenthic and demersal molluscs. Therefore, the methodology of this study is essential for obtaining a more complete assessment of species diversity, as micro-molluscs usually represent a large proportion of the total molluscan diversity (Albano et al. 2011, Gofas et al. 2014). Furthermore, the fine fractions can collect juvenile stages of species that are more difficult to collect when they reach adult sizes (e.g. species belonging to the superfamilies Nuculoidea and Tellinoidea live buried in the sediment).

The high biodiversity reported for Chella Bank and its adjacent bottoms contrasts with the old idea that bathyal areas in the deep Mediterranean Sea are poor from a biodiversity perspective (Bouchet and Taviani 1992). The studies carried out in the last two decades have shown that bathyal areas are not as poor as previously considered (Koutsoubas et al. 2000, Danovaro et al. 2010). The high richness found on Chella Bank, taking into account the small total area sampled with the van Veen grab (1.84 m^2), is comparable to that found in other areas of the Alboran Sea: 156 mollusc species were collected from a single sampling station with a beam-trawl (over 889 m^2 sampled area) on Djibouti Bank (Gofas et al. 2014), and 655 mollusc species were reported around the Alboran Island platform (Peñas et al. 2006) from the supralittoral level down to 450 m depth using different sampling techniques. These are some examples of the extraordinary diversity of molluscs present in deep areas of the Alboran Sea when compared with other deep areas of the Mediterranean basin. For instance, Negri and Corselli (2016) reported only 97 species of molluscs in the thanatocoenosis of 18 samples retrieved with a box-corer at Santa Maria di Leuca (SE Italy). This high biodiversity of the Alboran Sea is probably due to several factors: (i) its location between the Lusitanian and Mauritanian biogeographical regions and the Mediterranean Sea (Ekman 1953, Caballero-Herrera et al. 2021); (ii) its hydrological characteristics, which facilitate the transport of larvae from the Atlantic and the presence of persistent populations of species from the NE Atlantic that do not occur in other parts of the Mediterranean Sea (Gofas et al. 2011, Gallardo-Roldán et al. 2015, Rueda et al. 2021); and (iii) the topographical heterogeneity of the bottom, which favours a wide diversity of habitats and, together with the particular hydrological features of the basin, promotes almost constant upwellings of nutrient-enriched deep waters, thereby enhancing nutrient supply to the ocean upper layers (Sarhan et al. 2000, Rueda et al. 2021, Vázquez et al. 2021).

The highest values of mollusc diversity (i.e. species richness, Shannon-Wiener diversity) were observed in the group of samples from coral rubble (coral framework) bottoms (Group II), whereas the lowest values were found in those collected from the bathyal sedimentary bottoms around Chella Bank (Groups I and III). This type of complex bottoms, in which unusual species like *Episcomitra angelesae* and *Mitrella templadoi* (Fig. 3) were collected, provides a wide variety of ecological niches for species with different ecological requirements and biological interactions (e.g. substrate for attachment, feeding or parasitism and shelter) (Buhl-Mortensen et al. 2010). The results presented in this study confirm and support the importance of bottoms dominated with coral rubble as VMEs and the need for their conservation as they maintain a healthy ecosystem that is less susceptible to environmental changes and species loss, and allow degraded ecosystems to recover (de la Torriente et al. 2020).

From a biogeographical perspective, the malacofauna analysed here is dominated by species with a wide distributional range along the Atlantic Ocean and the Mediterranean Sea. The location of the Alboran Sea between these two basins and the proximity of the African and European biotic regions (Caballero-Herrera et al. 2021) allow the confluence of species with different distribution patterns (Ekman 1953). Almost 10% of the species are distributed in the Atlantic and also present in the Alboran Sea but absent in the rest of the Mediterranean, whereas *ca*. 8% are present in the Mediterranean and Ibero-Moroccan Gulf, and only *ca*. 4% are strictly Mediterranean. This biogeographical pattern is similar to that observed for molluscs from other coastal and circalittoral environments in the Alboran Sea (Rueda et al. 2009, Marina et al. 2012, Gofas et al. 2014). According to these results, the Levantine Intermediate Water, considered to be the second "barrier" (after the sill of Gibraltar) for the incoming deep fauna in the Mediterranean (Bouchet and Taviani 1992), does not seem to be a permanent barrier to the dispersion of some Atlantic bathyal fauna larvae. The most striking feature of the molluscan fauna, however, is the occurrence of a few species with planktotrophic larval development for which Chella Bank is their sole recorded locality in the Mediterranean (*Episcomitra angelesae*, *Mitrella templadoi*) or which are extremely rare elsewhere (*Mathilda* spp.) (Fig. 3).

The in-depth knowledge on the composition of the fauna is important in an area designated as an MPA, especially in deep and poorly explored areas of the Alboran Sea, which has been identified as a biodiversity hotspot for European waters (Templado 2011, Rueda et al. 2021, Mateo Ramírez et al. 2021). Although the present study has contributed significantly to the knowledge of molluscs from Chella Bank and its adjacent bottoms, it probably does not yet provide a suitable representation of the malacofauna of some areas of this SCI, and it is expected that the number of species is still higher than is reported here. A high sampling effort in the shallower areas of the bank, where coralligenous formations and maërl beds occur, is suggested for future expeditions in order to improve the knowledge of this still poorly studied habitat in the Alboran Sea.

The high environmental heterogeneity and habitat diversity present in the SCI "Sur de Almería – Seco de los Olivos" (de la Torriente 2014, 2018) explains the extraordinary list of molluscans reported, showing a good representation of the bathyal molluscans from the Alboran Sea. This list provides additional information, especially for the microbenthic fauna, which significantly increases the ecological importance of conservation in this MPA. It is important to highlight the presence of species which are hard to find in mollusc studies because of their low-density occurrence in marine ecosystems. This could be closely related to the existence of VMEs (de la Torriente 2018, 2020), some of them within the Habitats List of the Barcelona Convention in the framework of the Mediterranean Action Plan of the United Nations Environment Programme (UNEP/IUCN) (Mateo Ramírez et al. 2021). The present study will also increase knowledge of the deep-sea fauna of the Alboran Sea, providing some baseline data for further environmental evaluation and conservation of habitats under the EU Marine Strategy Framework Directive (Directive 2008/56/EC) and the Directive on Establishing a Framework for Maritime Spatial Planning (2014/89/EU).

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SUPPLEMENTARY MATERIAL

Table S1. – Cumulative contributions to the similarity (%Cum) of taxa characterizing the different assemblages detected on Chella Bank and its adjacent bottoms based on SIMPER analyses and multivariate methods (cluster) using abundance data.

Group I: Upper bathyal muddy bottoms with buried rhodoliths		
Average similarity: 38.71		
Species	%Contrib%	%Cum
Kelliella miliaris	43.38	43.38
Saccella commutata	30.41	73.79
Parvicardium minimum	26.21	100
Group II: Upper bathyal muddy bottoms with exposed coral rubble on the flanks of Chella Bank		
Average similarity: 55.57		
Species	%Contrib%	%Cum
Dacrydium hyalinum	14.29	14.29
Mendicula ferruginosa	12.90	27.19
Limopsis angusta	11.75	38.94
Vitreolina curva	9.72	48.66
Asperarca nodulosa	9.32	57.97
Abra longicallus	8.72	66.69
Axinulus croulinensis	8.72	75.40
Coralliophaga lithophagella	8.72	84.12
Heteranomia squamula	4.65	88.77
Anatoma micalii	3.17	91.94
Group III: Upper and middle bathyal muddy hemipelagic bottoms on the flanks and adjacent bottoms of the bank		
Average similarity: 29.57		
Species	%Contrib%	%Cum
Mendicula ferruginosa	25.63	25.63
Axinulus croulinensis	15.02	40.65
Thyasira obsoleta	13.72	54.37
Abra longicallus	10.52	64.89
Kelliella miliaris	9.98	74.87
Prochaetoderma sp.	5.14	80.01
Ennucula aegeensis	4.43	84.44
Euspira fusca	4.03	88.47
Solenogastres unidentified	3.61	92.08
Group IV: Upper Bathyal sandy bottoms on the flanks of Chella Bank		
Average similarity: 34.57		
Species	%Contrib%	%Cum
Gibberula turgidula	38.10	38.10
Yoldiella philippiana	21.07	59.16
Cadulus jeffreysi	17.18	76.34
Antalis panorma	9.11	85.45
Limopsis angusta	3.36	88.82
Mendicula ferruginosa	3.36	92.18

Table S2. – Dominance index (%D) of the top-dominant species of the taxocoenosis and the maximum observed rank (2, 2-5; 3, 6-30; 4, 31-100; 5, >100 shells) of the most representative species of the thanatocoenosis collected in each group of samples.

Goodallia triangularis	33.33	*Alvania cancellata*	5
Anatoma aspera	22.22	*Alvania punctura*	5
Talassia dagueneti	22.22	*Arca tetragona*	5
Modiolula phaseolina	11.11	*Bittium* spp.	5
Striarca lactea	11.11	Cerithiopsidae unidentified	5
		Dacrydium hyalinum	5
		Heteranomia squamula	5
		Hiatella arctica	5
		Modiolula phaseolina	5
		Tricolia deschampsi	5
(ungrouped) VV13			
Taxocoenosis	%D	Thanatocoenosis	Max. Rank
Curveulima beneitoi	66.67	*Bittium latreillii*	3
Chauvetia recondita	11.11	Cerithiopsidae unidentified	3
Orania fusulus	11.11	*Modiolula phaseolina*	3
Sticteulima jeffreysiana	11.11	*Arca tetragona*	2
		Clio pyramidata	2
		Hiatella arctica	2
		Limatula gwyni	2
		Skenea serpuloides	2
		Talassia dagueneti	2
		Timoclea ovata	2
Group I: Upper bathyal muddy bottoms with buried rhodoliths			
Taxocoenosis	%D	Thanatocoenosis	Max. Rank
Kelliella miliaris	68.86	*Alvania testae*	5
Saccella commutata	14.47	*Barleeia unifasciata*	5
Parvicardium minimum	5.26	*Gibberula turgidula*	5
Timoclea ovata	2.19	*Kelliella miliaris*	5
Axinulus alleni	1.75	*Parvicardium minimum*	5
Kelliopsis jozinae	1.32	*Saccella commutata*	5
Goodallia triangularis	1.32	*Tricolia deschampsi*	5
Tellina compressa	0.88	*Yoldiella philippiana*	5
Abra longicallus	0.44	*Aclis trilineata*	4
Kellia suborbicularis	0.44	*Bathyarca pectunculoides*	4
Group II: Upper bathyal muddy bottoms with exposed coral rubble on the flanks of Chella Bank			
Taxocoenosis	%D	Thanatocoenosis	Max. Rank
Dacrydium hyalinum	25.30	*Chauvetia recondita*	4
Mendicula ferruginosa	13.86	*Pseudamussium sulcatum*	4
Heteranomia squamula	10.84	*Alvania tomentosa*	3
Limopsis angusta	7.83	*Asperarca nodulosa*	3
Vitreolina curva	6.02	*Emarginula adriatica*	3
Anatoma micalii	4.82	*Iphitus tuberatus*	3
Danilia tinei	4.82	*Onchodia valeriae*	3
Asperarca nodulosa	3.61	*Strobiligera brychia*	3
Abra longicallus	2.41	Triphoridae unidentified	3
Axinulus croulinensis	2.41	*Vitreolina curva*	3

Group III: Upper and middle bathyal muddy hemipelagic bottoms on the flanks and adjacent bottoms of the bank			
Taxocoenosis	%D	Thanatocoenosis	Max. Rank
Thyasira obsoleta	12.06	*Mendicula ferruginosa*	4
Axinulus croulinensis	10.94	*Alvania cimicoides*	4
Mendicula ferruginosa	9.97	*Abra longicallus*	4
Kelliella miliaris	8.89	*Ledella messanensis*	4
Kellia suborbicularis	7.65	*Yoldiella philippiana*	4
Solenogastres unidentified	5.84	*Kelliella miliaris*	4
Abra longicallus	5.61	*Odostomia suboblonga*	4
Yoldiella philippiana	4.25	*Ennucula aegeensis*	4
Prochaetoderma sp.	4.14	*Clio pyramidata*	4
Ennucula aegeensis	3.40	*Parthenina flexuosa*	3
Group IV: Upper bathyal sandy bottoms on the flanks of Chella Bank			
Taxocoenosis	%D	Thanatocoenosis	Max. Rank
Gibberula turgidula	18.92	*Bathyarca pectunculoides*	5
Yoldiella philippiana	14.86	*Bathyarca philippiana*	5
Bathyarca pectunculoides	9.46	*Gibberula turgidula*	5
Cadulus jeffreysi	8.11	*Alvania cimicoides*	4
Kelliella miliaris	6.76	*Alvania electa*	4
Bathyarca philippiana	5.41	*Anatoma aspera*	4
Antalis panorma	4.05	*Eulimella ventricosa*	4
Dacrydium hyalinum	2.70	*Kelliella miliaris*	4
Leptochiton spp.	2.70	*Limea crassa*	4
Mendicula ferruginosa	2.70	*Yoldiella philippiana*	4