Diversity and distribution of bivalve molluscs in the Central Cantabrian Sea and the Avilés Canyons System (Bay of Biscay)

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ABSTRACT

Bivalve molluscs is one of the dominant benthic groups in soft-sediment communities off the Atlantic Ocean, including the European margin and the Bay of Biscay. The current knowledge of deep-sea Euro-Atlantic bivalves and their distribution is still far from comprehensive and has been the scope of several recent publications. We examined the collected bivalve samples from two oceanographic campaigns (COCACE and BIOCANT) carried out in the central Bay of Biscay, including the Avilés Canyons System (ACS), a Site of Community Importance within the Natura 2000 Network. Bivalve specimens were collected from the continental shelf, slope and bathyal zones, ranging in deep from 25 to 4700 m. This is the first study focused on bivalve diversity from the Cantabrian Sea that covers such a wide bathymetric range. Eighty-four live taxa in 36 families were identified; *Cetomya neaeroides* is reported for the first time in the area. We provide photographs showing the shell diagnostic features of all recorded species. The conducted Multivariate Analysis showed three species assemblages: i) samples from shallow waters (continental shelf); ii) intermediate depths (shelf and upper slope) and iii) deep water (slope and abyssal plain). Depth was the main structuring factor that influenced the distribution of the recorded species and the higher species richness was found on the continental shelf. The feeding strategy and the substrate preference appeared as not significant factors in the zonation patterns of the studied bivalves.

1. Introduction

Studies of macrofaunal benthic communities are relevant to assess the biodiversity and the environmental health of marine environments worldwide (Noss, 1990; Martins et al., 2013, 2014). Nowadays, the importance of an accurate knowledge on marine species diversity and distribution is peremptory within the framework of global change and the biodiversity loss (Gamfeld and Roger, 2017). Global warming, marine pollution and other human activities are directly impacting on marine environments across the globe (Padilla and Williams, 2004). Thus, benthic communities change as they adapt to the prevailing situations, altering its species composition and distribution patterns, and some show additional resilience to environmental impacts (Padilla and Williams, 2004; Hily et al., 2008). Multiple environmental factors, such as sediment type, pH, temperature or nutrients, directly affect benthic biodiversity. In such regard, the effects of alteration of these factors can cause severe damage to benthic communities and may even lead to the species extinction (Templado, 2011). Furthermore, our knowledge about the diversity of certain benthic invertebrate groups is still

incomplete, and this is reflected in knowledge gaps in their biogeography and bathymetric distribution patterns (Fernández-Rodríguez et al., 2017, 2019; Arias and Anadón, 2012; Arias et al., 2019). Deep-sea ecosystems, although not being the most diverse ones, are the most extended and widely distributed within the oceans (Valentine et al., 2005; Ramírez-Llodra and Billett, 2006). Deep-sea environments have great biological importance, as evidenced by the complex structural habitats formed by the deep-sea coral reefs and sponge grounds, both considered as biodiversity 'hotspots' and as nurseries for the offspring of many economic-value species (Sánchez et al., 2014; Van Dover et al., 2018; Ríos et al., 2020). On the other hand, these environments are among the most sensitive to human activities, such as marine pollution or commercial trawling (López-Martínez et al., 2007; Van Dover et al., 2018) and therefore they must be target ecosystems for conservation efforts (Sánchez et al., 2014; Ríos et al., 2020). The Avilés Canyons System (ACS) was first designed as an Area of Special interest for Conservation (WWF, ADENA 2005), and subsequently thereafter as a Site of Community Importance (SCI) within the Natura 2000 Network (ESZZ12003, Commission Implementing Decision (EU) 2016/2335).

This regulation was motivated by the presence of vulnerable habitats e.g., deep-sea coral reefs (protected under the European Union Habitats Directive, Habitat 1170: Reefs) and deep-sea sponge grounds (Cristobo et al., 2009), as well as vulnerable species like hakes, goosefishes, and lobsters (Sánchez and Gil, 2000; IEO, 2014). After the declaration of the ACS as a SCI, the area is expected to be declared by the EU as a Special Area of Conservation (SAC) no later than the end of 2022. Consequently, the study of the deep-sea fauna diversity is essential for the elaboration of proper management plans in this area, mainly for the species that constitute marine resources. Within the main groups of marine resources, two phyla of invertebrates stand out, molluscs and crustacean arthropods.

Mollusca is one of the most diverse and widespread phyla in all marine environments worldwide. Furthermore, the study of spatial and temporal molluscan distribution patterns has been commonly considered as a surrogate of the whole marine benthic community (Martins et al., 2014). Within molluscs, bivalves constitute an outstanding class with high ecological and commercial importance (Martins et al., 2014). Filter feeding is the most common feeding strategy found among the members of this class, but there are also other types, such as deposit feeders (e.g., Nuculidae), carnivores (Verticordiidae), xylophagous (Teredinidae) or even species that depend on symbiotic organisms (some species of Cardiidae) or the basibiont secretions (members of Lasaeidae) (Gofas et al., 2011). Bivalves may act as ecosystem engineers (Sousa et al., 2009) and also, as key species in the process of the organic matter recycling (Smyth et al., 2018). Moreover, some bivalve species are bioindicators of neurotoxins, heavy metals and drugs in marine environments (Catry et al., 2017; Cao et al., 2018; Piedade and Nunes, 2020). Despite its great importance at the different stated levels, detailed studies, mainly on deep-sea species, are scarce. Its great diversity, sometimes complex taxonomical identification, and the difficulty of obtaining deep-sea samples, may account for this. The only updated literature about bivalve diversity in the Cantabrian Sea and its surroundings, are the bibliographic compilations of Gofas et al. (2017, 2022), but there are no detailed studies on collected bivalve samples from recent oceanographic campaigns. The aim of this work is to characterize the diversity and distribution of the bivalve molluscs from the Cantabrian Sea, including the ACS and covering a bathymetric range from 25 to 4700 m depth, and to discuss the relationships between the biological and environmental data. This study aims as well to identify the species assemblages and to delineate the specific distribution patterns in relation to depth, substrate and feeding strategies.

2. Material and methods

2.1. Sampling and study area

The different samples belong to two different oceanic campaigns undertaken along the Avilés Canyon System (Fig. 1). The Avilés Canyons System (ACS) is a network of underwater valleys located at the north of the Asturian coast, in the central Cantabrian Sea (Bay of Biscay, northern Spain). This system is composed of three main canyons that begin at the continental shelf (Avilés, El Corbiro, and La Gaviera) and more than twelve secondary canyons that flow into the abyssal plain, at 4700 m depth (Sánchez et al., 2014). The ACS presents one of the richest biological communities of the underwater fauna, characterized by temperate-water species with high biological production due to the strong oceanographic dynamics associated to the continental slope and the canyons (Allen and Durrieu de Madron, 2009; Sánchez et al., 2014).

We considered four different bathymetric areas: continental shelf (to 200 m depth), upper continental slope (200–2000 m depth), lower continental slope (2000–4500 m) and abyssal plain (more than 4500 m) (Gómez Ballesteros et al., 2012; IEO, 2014).

The COCACE cruise (Oceanographic Cruise of the Central Cantabrian Sea) took place between 1987 and 1988. Bivalves were collected between 25 and 1400 m depth with a dredge anchor or epibenthic sledge
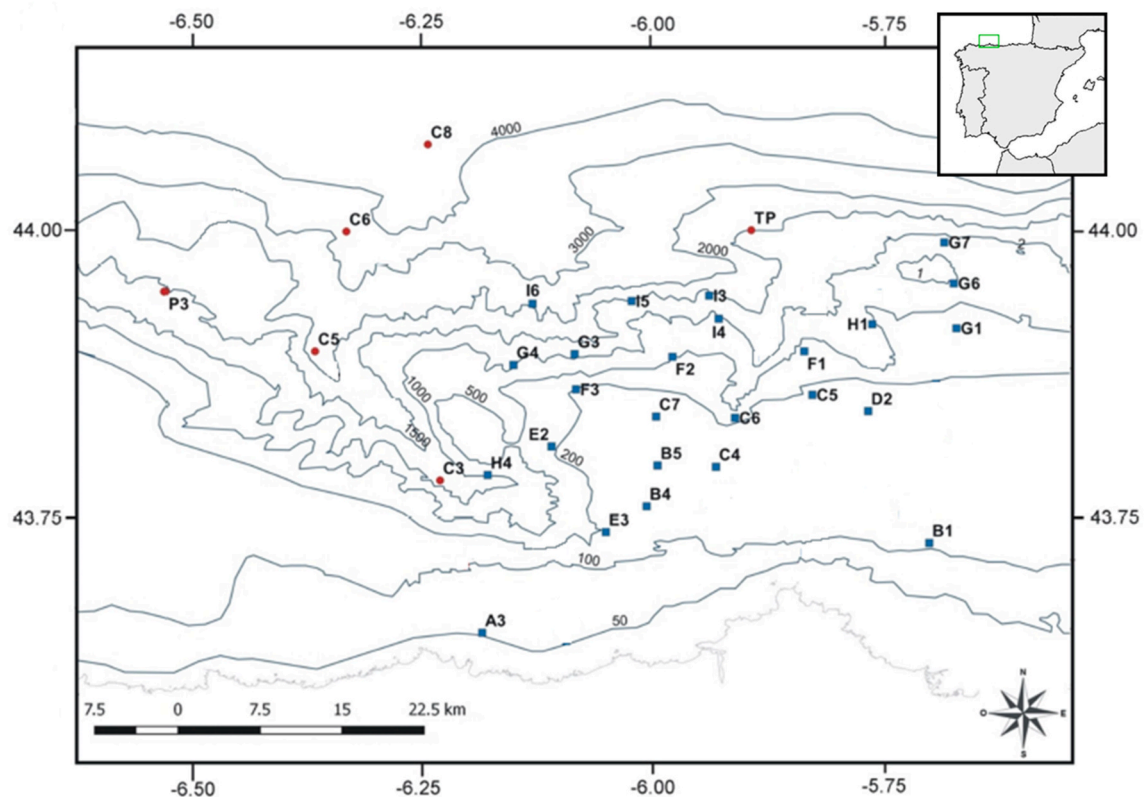

Fig. 1. Geographical distribution of BIOCANT (red circles) and COCACE (blue squares) sampling stations where bivalves were found. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Louzao et al., 2010) (Table 1).

The BIOCANT cruise was undertaken as three different campaigns: BIOCANT I (between the 3–13 March 2012), BIOCANT II (between the 27 September - October 6, 2012) and BIOCANT III (between the 24 April - May 4, 2013). Bivalves were obtained at depths between 1200 and 4700 m, with a Multiple Opening/Closing Net and, a rock dredge and an Agassiz dredge (Romero-Romero et al., 2016) (Table 1).

2.2. Species identification and samples analysis

Most of the samples were originally fixed in formalin isotonic with sea water, and afterwards they were put into alcohol 70%. Nomenclature and systematics used throughout this paper are based on WoRMS (2021). Some of the samples were prepared on aluminium stubs for more detailed observation on the Scanning Electronic Microscope (SEM) JEOL JSM-6610LV at the University of Oviedo.

Similarity among sampling stations was determined considering presence-absence data with the PRIMER v.6 software package (Clarke and Gorley, 2006). A similarity matrix was built with the Bray Curtis similarity coefficient (Bray and Curtis, 1957), and both a multidimensional scaling (MDS) and a Cluster analysis (group-average mode) were carried out with specimens collected alive. The species that characterized the different groups observed in the cluster were detected by means of a SIMPER analysis. Finally, we performed a BIOENV analysis with 999 permutations to study the relationships between the environment variables (type of substrate and depth) and the distribution of the different species studied in each station. The stations were divided into three categories, depending on the main component of the sediment of each station: (i) soft substrate with sands as principal component, (ii) soft substrate with silt as major component, and (iii) hard substrate, as rocks and corals. Regarding feeding strategies, we classified the identified species into the following feeding types to carry out a presence-absence and BIOENV analyses (checking for depth and substrate, same parameters as the former analyses): filter feeders, deposit feeders, carnivores,

bacterial symbiosis and basibiont secretions. With these analyses we aimed to check if the species' type of feeding was relevant for their distribution. These analyses were done following the same methodology explained above (i.e., similarity matrix with Bray Curtis coefficient, 999 permutations in the BIOENV analysis), using presence absence data and abundance. The distribution of the species was checked with the latest works of the sea molluscs of the Iberian Peninsula (Gofas et al., 2017, 2022).

3. Results

3.1. Species diversity

A total of 4851 individuals from 84 taxa, belonging to 36 families and 15 orders (Fig. 2A), were identified (Suppl. Mat. Table 1). Colour photographs, showing diagnostic features of the shell, of all recorded species are provided in Figs. 4–13. The studied samples belonged to 31 sampling stations, located between 25 and 4700 m depth (Table 1). The type of sediment in which the samples were found was heterogeneous: sand, silt, mud, rocks and coral reefs.

Thirty-five % of the studied specimens (1715) belonged to the Veneridae, being the most abundant family from the study area. From the total of identified taxa, 3792 out of the 4851 corresponded to filter feeders (78.17%) and were found from the continental shelf to the abyssal plain. The remaining taxa corresponded to deposit feeders (849 specimens; 17.25%), carnivores (46 specimens; 1,15%) nutrition by symbiotic bacteria (162 specimens; 3.34%) and basibiont secretions (4 specimens; 0.08%) from the Lasaeidae family (*Kurtiella bidentata* (Montagu, 1803) and *Montacuta substriata (Montagu*, 1803) (Fig. 2B).

With regards to their motility, 57 out of 84 taxa identified (69%) were free-living organisms (e.g., *Limopsis cristata* Jeffreys, 1876); 16 specimens (19%) were sessile, living permanently attached to the substrate, either by byssus gland secretions (e.g., mytilids), or by cementing the right valve (e.g., *Spondylus gussoni* O. G. Costa, 1830 and other oyster

Table 1
Data of sampling stations with bivalve occurrence.

| CAMPAIGN	STATIONS	COORDINATES N W	DEPTHS (m)	SUBSTRATE	DATE	CAPURE METHOD
COCACE	A1	43°40′54″ 05°49′20″	36	Fine sand	September 18, 1987	A/E
COCACE	A3	43°35′20″ 06°09′30″	60	Fine sand with shell rests	June 01, 1987	A/E
COCACE	B1	43°42′00″ 05°42′30″	113	Gross sand with stones	September 17, 1987	A/E
COCACE	B2	43°38′18″ 06°05′21″	86	Sand	September 17, 1987	A/E
COCACE	B3	43°41′24″ 06°01′4″	117	Med. size sand, shell rests and stones	July 05, 1987	A/E
COCACE	B5	43°43′48″ 05°58′48″	121	Gross sand with coral rests	June 03, 1987	A/E
COCACE	C4	43°45′00″ 05°54′36″	130	Gross sand with madreporites rests	April 26, 1987	A
COCACE	C6	43°48′36″ 05°54′36″	154	Fine sand with boulders	December 20, 1987	A/E
COCACE	C7	43°48′36″ 05°58′48″	146	Medium size sand	December 19, 1987	A/E
COCACE	D2	43°48′36″ 05°45′00″	161	Fine sand	June 29, 1987	A/E
COCACE	E3	43°42′36″ 06°04′12″	190	Fine sand with pebbles	December 20, 1987	A/E
COCACE	F1	43°53′24″ 05°48′36″	249	Fine sand	September 17, 1987	A/E
COCACE	F2	43°52′48″ 05°58′12″	300	Fine sand	December 19, 1987	A/E
COCACE	F3	43°51′36″ 06°04′48″	227	Sand with stones	June 02, 1987	A/E
COCACE	G1	43°55′48″ 05°39′36″	468	Very fine sand	April 28, 1987	A/E
COCACE	G2	43°51′22″ 05°52′43″	322	Fine sand	November 22, 1987	A/E
COCACE	G6	43°58′12″ 05°40′12″	533	Very fine sand with stones	February 23, 1988	A/E
COCACE	G7	44°01′48″ 05°40′12″	850	Very fine sand, stones and coral rests	February 23, 1988	A
COCACE	H1	43°55′12″ 05°44′24″	198	Fine sand with shell rests	November 22, 1987	A/E
COCACE	H4	43°46′12″ 06°10′12″	790	Gross silt	June 02, 1987	A
COCACE	H5	43°51′30″ 06°09′38″	586	Very fine silt	November 21, 1987	A/E
COCACE	I3	43°57′36″ 05°54′00″	1400	Fine silt with stones	December 17, 1987	A/E
COCACE	I4	43°54′36″ 05°54′00″	720	Very fine sand	December 17, 1987	A/E
COCACE	I6	43°55′12″ 06°06′36″	1186	Fine silt with boulders	July 04, 1987	A/E
COCACE	SP	43°33′36″ 05°40′48″	15–25	Sand with stones and shells	September 23, 1986	A/E
BIOCANT	C3′	43°46′22″ 06°12′37″	1200	Rocky	October 01, 2012	AG
BIOCANT	C5′	43°54′18″ 6°20′30″	2100	Sand and boulders	01/10/12–05/10/12	AG
BIOCANT	C6′	44°01′41″ 6°17′41″	3000	Silty sands and	May 03, 2012	AG
BIOCANT	C8	44°08′29″ 6°14′18″	4700	Sandy-muddy and gravel	28/04/13–30/04/13	AG
BIOCANT	P3	43°58′01″ 6°30′57″	1200	Cold-water coral bank	05/03/12–30/04/13	AG
BIOCANT	TP	44°02′05″ 5°53′59″	1500	Cold-water coral bank	11/03/12–04/10/12	AG
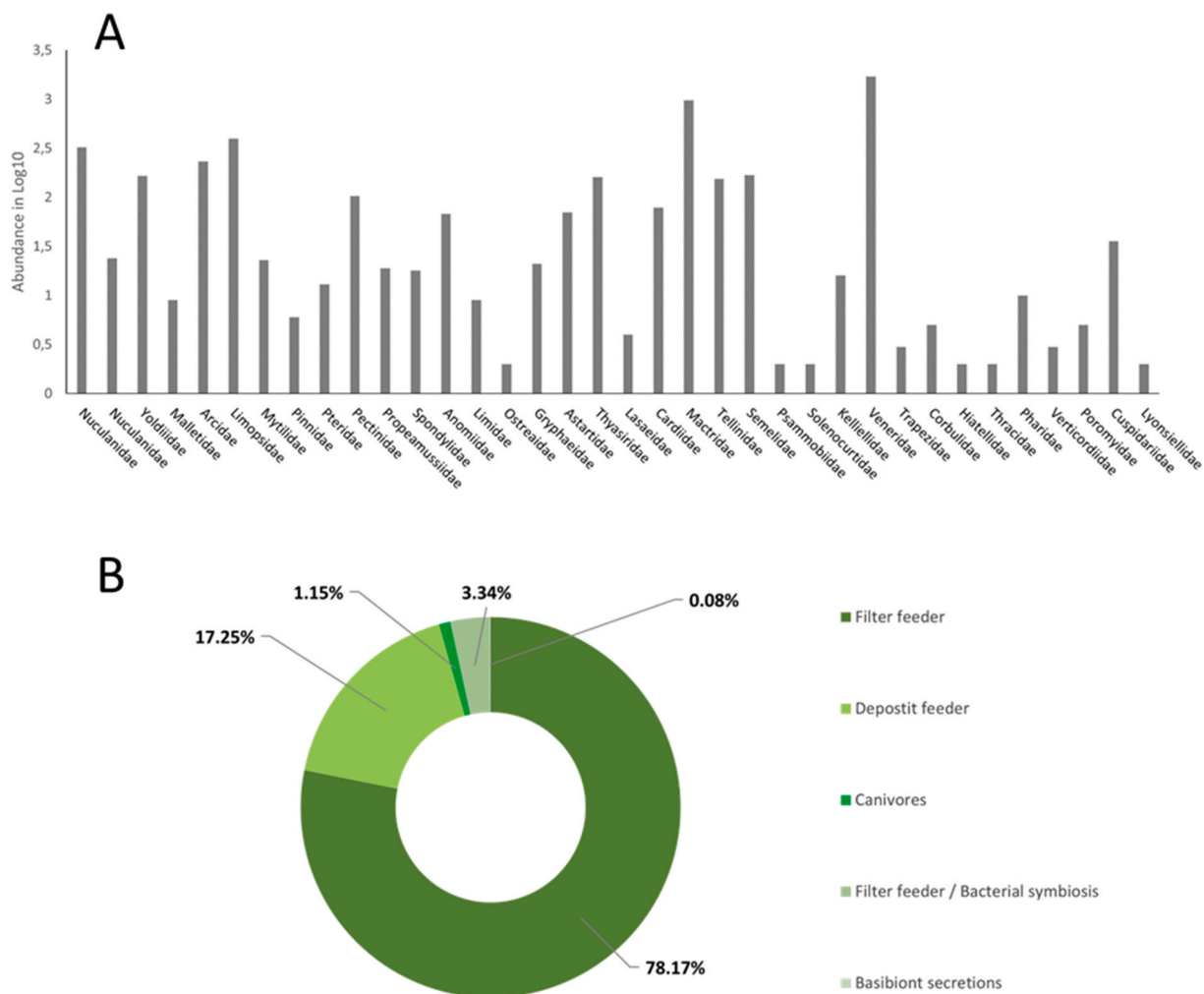
Fig. 2. A. Total abundance (Log10) of each bivalve family considering live samples from campaigns. **B.** Percentage distribution of the feeding strategies of each live bivalve samples for each campaign.
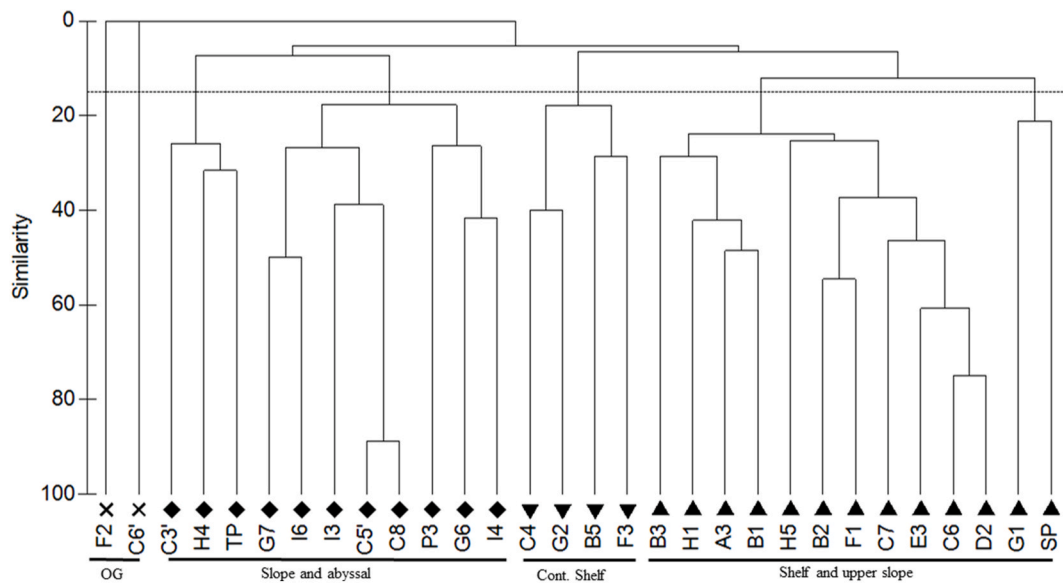

Fig. 3. Cluster dendrogram based on the similarity of the live bivalve fauna among samples. Symbols identify the different assemblages as defined by branches in the dendrogram (see the text for assemblage characteristics).

Fig. 4. A-D Nuculidae A. *Nucula nucleus* (Linnaeus, 1758), COCACE, C7, 146 m, 6 mm. **B.** *Nucula nitidosa* Winckworth, 1930, COCACE, A3, 60 m, 8 mm. **C.** *Ennucula tenuis* (Montagu, 1808), COCACE, G1, 468 m, 5 mm. **D.** *Ennucula corbuloides* (Seguenza, 1877), COCACE, I3, 1400 m, 3 mm. **E Nuculanidae E.** *Saccella commutata* (Philippi, 1844), COCACE, C6, 154 m, 4 mm. **F Malletidae F.** *Malletia pianni* (van Aartsen and Giannuzzi-Savelli, 1991), COCACE, I4, 1400 m, 8 mm. **G-I Arcidae G.** *Bathyarca pectunculoides* (Scacchi, 1835), COCACE, H4, 790 m, 4 mm. **H.** *Bathyarca philippiana* (Nyst, 1848), COCACE, G1, 468 m, 5 mm. **I.** *Asperarca nodulosa* (O. F. Müller, 1776), COCACE, A3, 60 m, 6 mm. Scale bars = 3 mm.

like species). The remaining 11 taxa (12%) presented both lifestyles through their life history, such as *Delectopecten vitreus* (Gmelin, 1791).

The oval venus, *Timoclea ovata* (Pennant, 1777), was the most frequent species found (appearing in 12 out of 31 sampling stations), and also the most abundant one (with 974 specimens). This mobile filter feeder was found in all types of sediments between 60 and 790 m depth. The saltwater clam, *Mactra stultorum* (Linnaeus, 1758), was the second most abundant species, with 792 specimens found only in one station at 25 m.

3.2. New species records from the Cantabrian Sea

3.2.1. Tagelus adansonii (Bosc, 1801) (Fig. 11A)

Big, solid and inflated shell, between 5 and 7 cm long, anterior margin truncated and posterior margin rounded. Hinge formed by two small hinge teeth on both valves. Whitish in colour, changing into olive brown the further it gets from the umbo, melting with growth lines. Two specimens were collected alive from one sampling station: COCACE-SP, 25 m depth, with sandy sediment mixed with conchiferous rests.

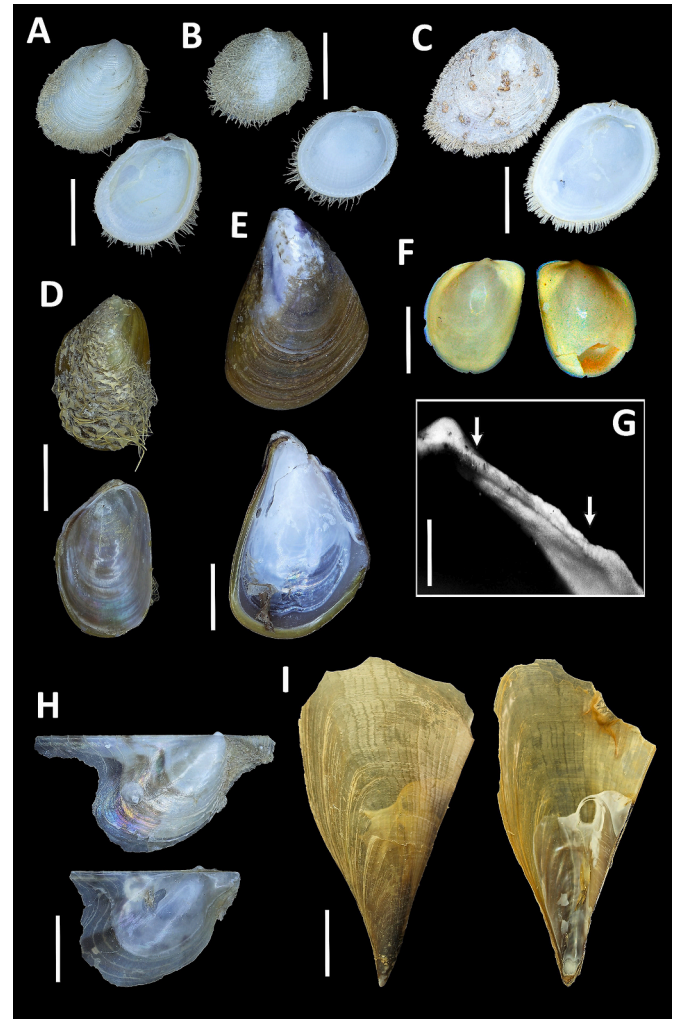This species is originally distributed along the mangrove biomass of

Fig. 5. A-C Limopsidae A. *Limopsis minuta* (Philippi, 1836), COCACE, G6, 533 m, 8 mm. **B.** *Limopsis cristata* Jeffreys, 1876, COCACE, I6, 1186 m, 4 mm. **C.** *Limopsis aurita* (Brocchi, 1814), COCACE, H4, 790 m, 10 mm. **D-G Mytilidae D.** *Modiolula phaseolina* (Philippi, 1844), COCACE, B3, 117 m, 6 mm. **E.** *Mytilus galloprovincialis* Lamarck, 1819, COCACE, A3, 60 m, 8 mm. **F.** *Dacrydium ockelmanni* Matson & Warén, 1977, BIOCANT, C8, 4700 m, 2 mm. **G.** *D. ockelmanni,* micrograph of the hinge of the right valve showing the teeth. **H Pteriidae H.** *Pteria hirundo* (Linnaeus, 1758), COCACE, B3, 117 m, 9 mm. **I Pinnidae I.** *Atrina fragilis* Pennant, 1777, COCACE, B1, 113, m, 152 mm. Scale bars: B, D-E = 3 mm; A, C, H = 5 mm; F = 1 mm; G = 250 μm; I = 50 mm.

eastern Africa, the Gulf of Guinea and the Islands of Bijagós (Haroun et al., 2018; Catry et al., 2017). This may represent a punctual introduction to the Cantabrian Sea (this statement will be explored in the Discussion section).

3.2.2. Cetomya neaeroides (Seguenza, 1877) (Fig. 13A)

Fine, oval shaped and little inequivalve shell, reaching 1.5 cm. Slightly prominent umbo. Sculpture formed by faint growth lines and small granules arranged on radial rows. Elongated and slightly sunken ligament, left valve with protuberant posterior dorsal margin and with prominent hinge on the right valve. Inside of the shell shiny. Three specimens were collected from two sampling stations: BIOCANT-P3, 1200 m depth, and BIOCANT-TP, 1500 m depth, both of coral substrate.

This species has been previously reported near the Gulf of Cádiz (Utrilla et al., 2020) and around the Canary and Azores Islands (Krylova, 2006). It is the first record of the species in the Cantabrian Sea and the Bay of Biscay.
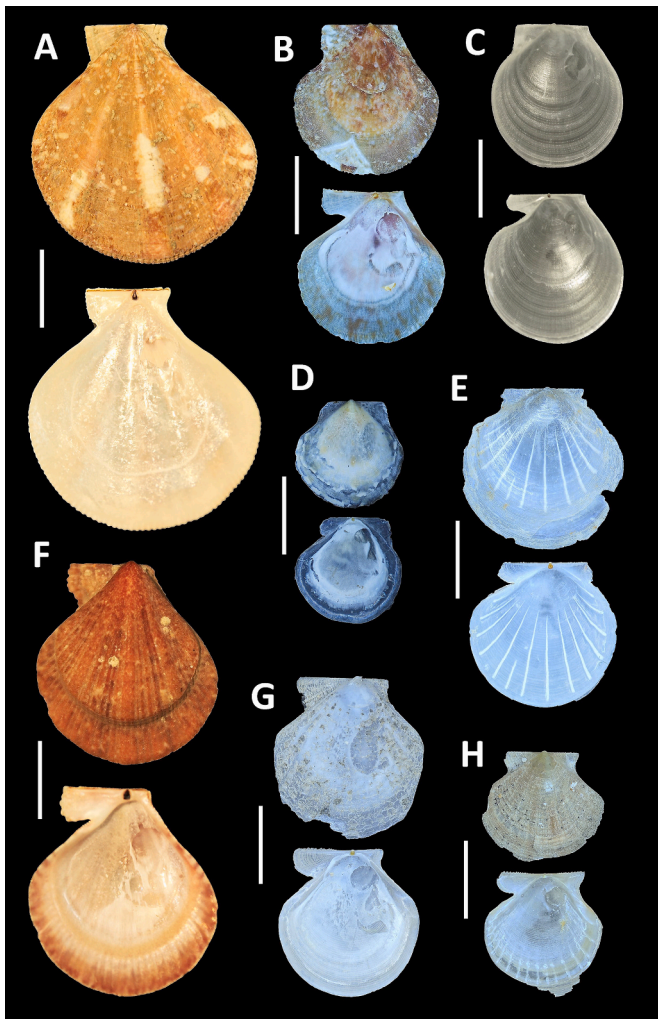
Fig. 6. A-D Pectinidae; A. *Pseudamussium clavatum* (Poli, 1791), COCACE, F3, 227 m, 31 mm. **B.** *Palliollum incomparabile* (Risso, 1826), COCACE, C7, 146 m, 10 mm. **F.** *Palliollum tigerinum* (O. F. Müller, 1776), COCACE, B3, 117 m, 21 mm. **C.** *Delectopecten vitreus* (Gmelin, 1791), BIOCANT, P3, 1200 m, 19 mm. **E-H Propeamussiidae E.** *Similipecten similis* (Laskey, 1811), COCACE, H1, 198 m, 5 mm. **F.** *Parvamussium propinquum* (E. A. Smith, 1885), BIOCANT, TP, 1500 m, 20 mm. **G.** *Cyclopecten antiquatus* (Philippi, 1844), COCACE, G1, 468 m, 8 mm. **H.** *Parvamussium fenestratum* (Forbes, 1844), COCACE, F3, 227 m, 5 mm. Scale bars: A, D = 10 mm; B–C, E-H = 5 mm.

3.3. Characterization of benthic assemblages

The presence-absence MDS analysis and the abundance analysis (Cluster, MDS and BIOENV) of the different live organisms do not show any statistical significance and did not make any informative assemblage. The data of presence-absence. Cluster and its BIOENV analysis, carried out with the live individuals, had a statistical relevance, showing three assemblages and two outgroups (Fig. 3).

3.3.1. Continental shelf
This group includes shallow water stations from the continental shelf (121-322- m depth) with sandy sediment, including coral remains, conchiferous and stones (Table 1). The average similarity within this assemblage was 23.35%. Eleven species were found in these stations, with *Modiolula phaseolina* (Philippi, 1844) the most frequent species of this group.

3.3.2. Shelf and upper slope
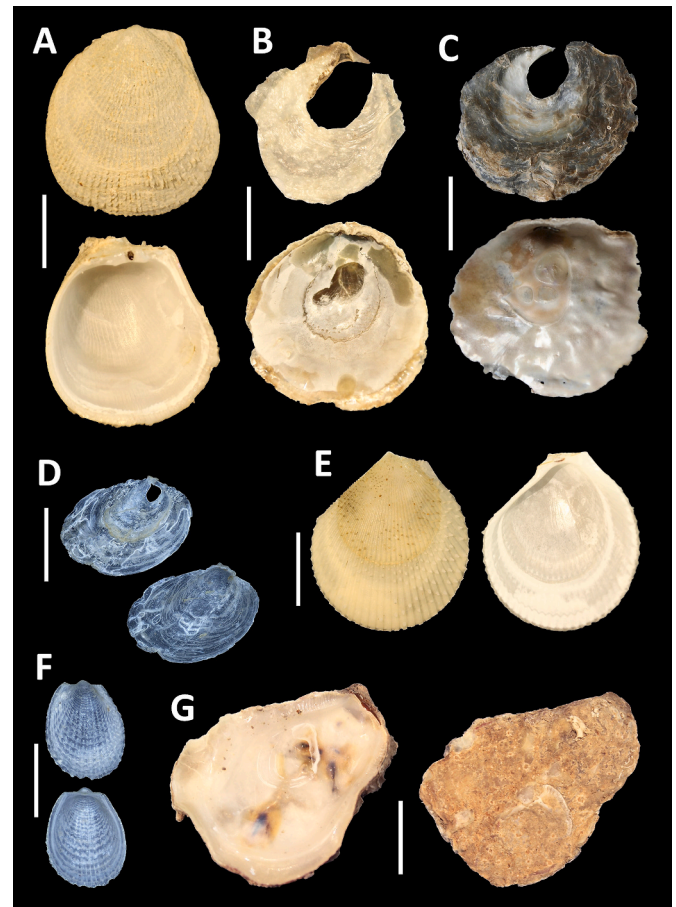This group was comprised of 13 stations from the continental shelf

Fig. 7. A Spondylidae A. *Spondylus gussonii* O. G. Costa, 1830, COCACE, H4, 790 m, 15 mm. **B-D Anomiidae B.** *Pododesmus patelliformis* (Linnaeus, 1761), COCACE, C4, 130 m, 30 mm. **C.** *Anomia ephippium* Linnaeus, 1758, COCACE, B5, 121 m, 30 mm. **D.** *Heteranomia squamula* (Linnaeus, 1758), I4, 720 m, 6 mm. **E-F Limidae E.** *Lima marioni* P. Fischer, 1882, COCACE, H4, 790 m, 33 mm. **F.** *Limea crassa* (Forbes, 1844), COCACE, I4, 720 m, 2 mm. **G.** *Ostra stentina* Payraudeau, 1826, COCACE, B5, 121 m, 36 mm. Scale bars: B–C,E, G = 10 mm; A, D = 6 mm; F = 2 mm.

and upper slope (25–586 m depth), with sandy sediments together with coral remains, conchiferous and stones, except from one station (H5) with lime substrate (Table 1). The average similarity between them is 25.76%. This assemblage had the highest species richness, with 55 different species, with *T. ovata* the most representative species of this group.

3.3.3. Slope and abyssal
This assemblage was composed of 11 stations from the continental slope and abyssal plain, with depth between 533 and 4700 m. Nine of these stations belonged to the upper continental slope, with a sandy substrate mixed with stones, coral and lime (Table 1). One station belonged to the lower continental slope (C5'), with sandy substrates, and the last one (C8) belonged to the abyssal plain. The stations of this group had an average similarity of 18.06%. This assemblage had a species richness of 39, being *Yoldiella* sp. the most representative taxa of this group.

3.3.4. Outgroup
The station C6' and F2 only have one species each; *Limopsis* sp. and Pectinidae sp. respectively C6' (3000 m) has sandy sediment with gravel and F2 (300 m) had a sandy sediment. The BIOENV analysis showed that depth was the main structuring agent (Rho = 0.408; p-value = 0.001), but the combination of both variables (substrate and depth) had also
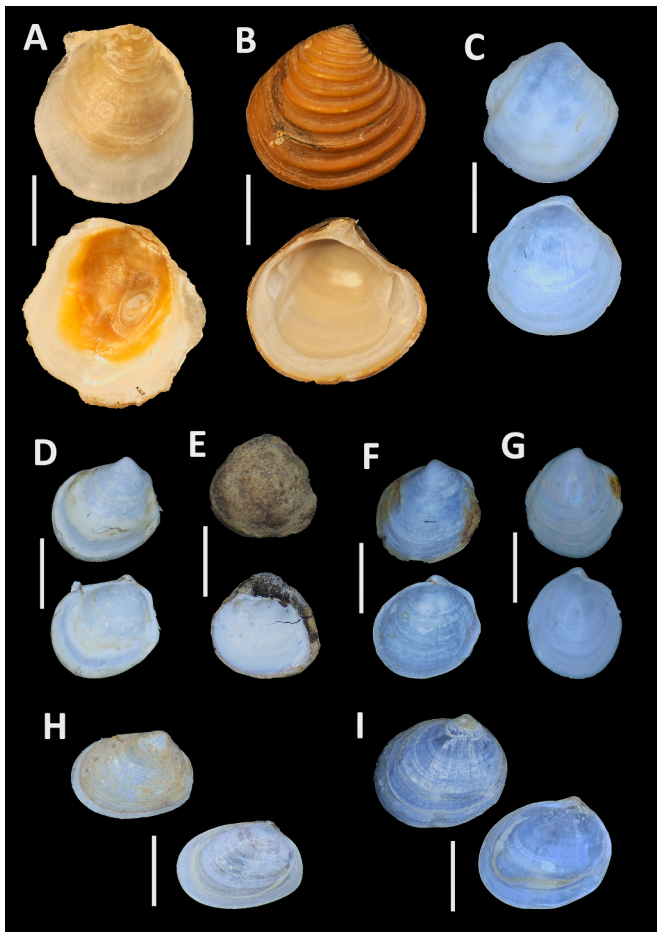
Fig. 8. A Gryphaeidae; A. *Neopycnodonte cochlear* (Poli, 1795), COCACE, C7, 146 m, 13 mm. **B Astartidae; B.** *Astarte sulcata* (da Costa, 1778), COCACE, A3, 60 m, 13 mm.**C-G Thyasiridae; C.** *Thyasira flexuosa* (Montagu, 1803), COCACE, G1, 468 m, 2 mm. **D.** *Thyasira succisa* (Jeffreys, 1876), COCACE, G6, 533 m, 2 mm. **E.** *Mendicula ferruginosa* (Forbes, 1844) BIOCANT, C8, 4700 m, 8 mm. **F.** *Axinulus brevis* (Verril & Bush, 1898), BIOCANT, C5′, 2100 m, 2 mm. **G.** *Axinulus croulinensis* (Jeffreys, 1847), COCACE, G1, 461 m, 2 mm. **H–I Lasaeidae; H.** *Kurtiella bidentata* (Montagu, 1803), COCACE, B2, 86 m, 1 mm. **I.** *Montacuta substriata* (Montagu, 1808), COCACE, B3, 117 m, 2 mm. Scale bars: A-B = 6 mm; C = 4 mm; D-I = 1 mm.

Fig. 9. A-D Cardiidae A. *Acanthocardia echinata* (Linnaeus, 1758), COCACE, A3, 60 m, 38 mm. **B.** *Acanthocardia paucicostata* (G. B. Sowerby II, 1834), COCACE, SP, 25 m, 11 mm. **C.** *Parvicardium pinnulatum* (Conrad, 1831), COCACE, H1, 198 m, 4 mm. **D.** *Papillicardium minimum* (Philippi, 1836), COCACE, C7, 146 m, 2 mm. **E.** *Mactra stultorum* (Linnaeus, 1758), COCACE, SP, 25 m, 5 mm. **F.** *Spisula elliptica* (T. Brown, 1827), COCACE, B3, 117 m, 5 mm. **G.** *Spisula subtruncata* (da Costa, 1778), COCACE, A3, 60 m, 7 mm. **H.** *Lutraria lutraria* (Linnaeus, 1758), COCACE, SP, 25 m, 8 mm. Scale bars: A-B = 20 mm; C = 2 mm; D = 1 mm; E-H = 3 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

high correlation values (Rho = 0.408; p-value = 0.001). The type of substrate presented lower correlation values (Rho = 0.320; p-value = 0.001). Regarding the BIOENV analysis carried out with the presence-absence data of the different feeding strategies among stations, neither the substrate (Rho = 0.210; p-value = 0.15) nor depth (Rho = 0.272; p-value = 0.15) were significant structuring agents for the distribution of the different feeding strategies of bivalves on this study.

4. Discussion

The diversity, ecology and distribution patterns of the Cantabrian Sea bivalves and their relationship with abiotic factors were studied from samples collected by two large oceanographic campaigns, COCACE and BIOCANT. We found one species that clearly constitutes a new records of the Cantabrian Sea and the Bay of Biscay: *C. neaeroides*. This species has been previously reported from the southern Iberian Peninsula (Pino et al., 2020; Zenetos et al., 2005; Krylova, 2006; Gofas et al., 2011, 2017; Catry et al., 2017; Haroun et al., 2018; Utrilla et al., 2020). Here, we are extending its known distribution range to the Cantabrian Sea, constituting its northernmost distribution to date. Additionally, a second species, *Ta. adansonii,* may represent a punctual introduction in
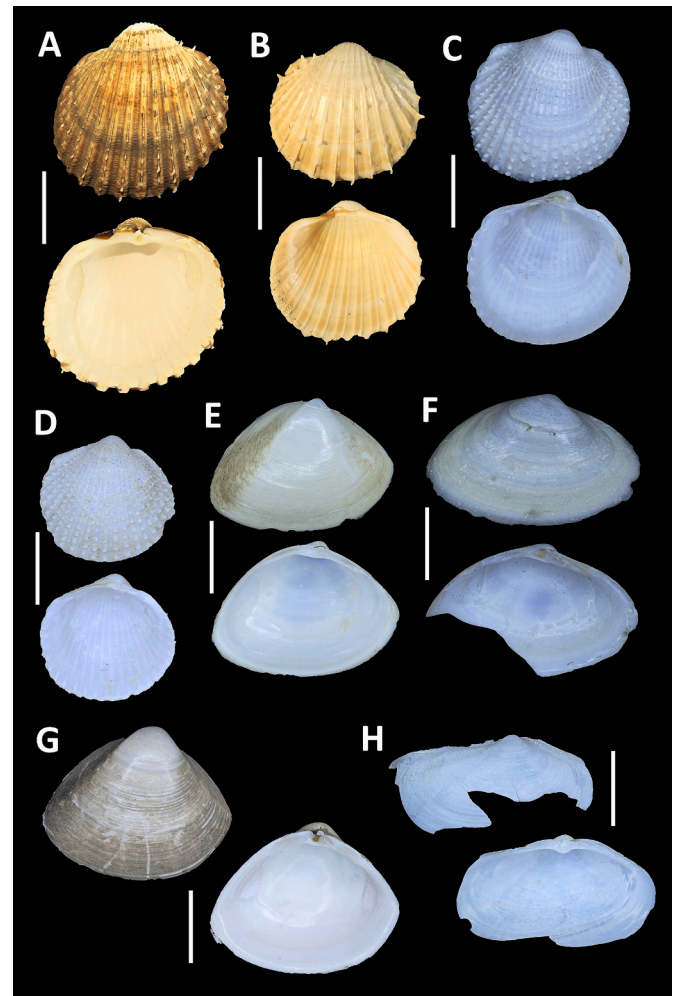
the Cantabrian Sea. This species commonly occurs associated with mangroves from the African Atlantic (Catry et al., 2017; Haroun et al., 2018). The finding of *Ta. adansonii* in the Cantabrian Sea may be a human mediated introduction *via* shipping. The station SP, in which the species was found, is close to the Musel Port, a commercial and freight port with regular routes with northern and equatorial Africa. Considering *Ta. adansonii* habitat requirements, the long-term survival and settlement of the species in the area seems unlikely. However, the former explanation seems less plausible for *C. neaeroides*, collected from the lower continental slope (1200–1500 m depth). Probably, this species have been overlooked in previous studies, due to the high fragility of its shells or the rarity of its presence. Other factors, like the 'tropicalization' or the 'meridionalization' are known to facilitate the spreading of some species originally from warmer areas to temperate ones, and their subsequent establishment in the receiving ecosystems (Palmer et al., 2007; Arias and Crocetta, 2016). Particularly, the Cantabrian Sea is an interesting area to study both phenomena, being a transitional zone between two different ecoregions (one with predominantly boreal biota and one
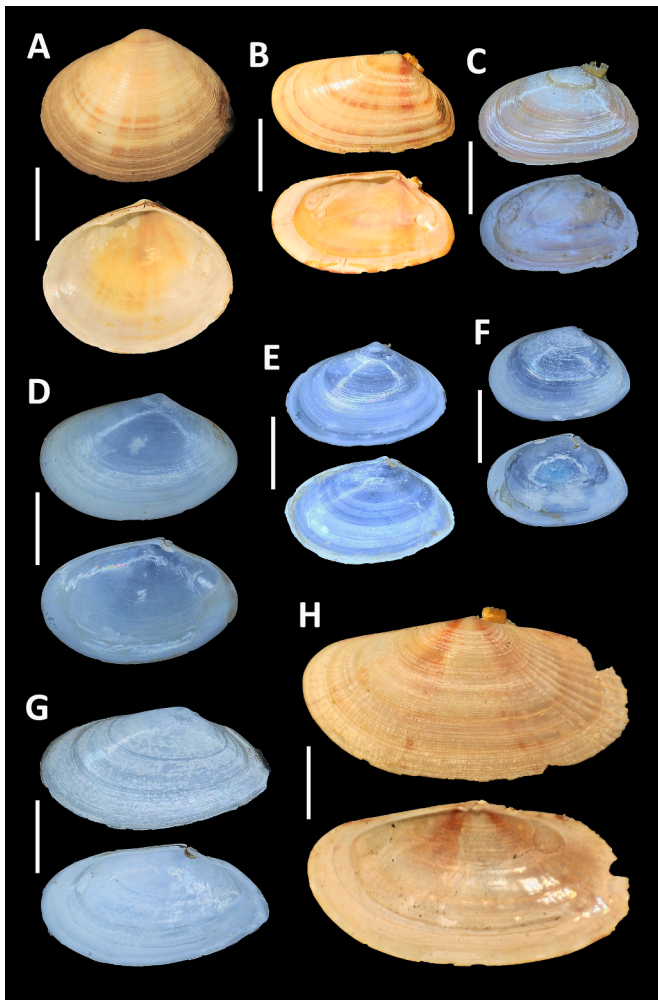
Fig. 10. A–C Tellinidae; A. *Arcopella balaustina* (Linnaeus, 1758), COCACE, B1, 113 m, 18 mm. **B.** *Moerella donacina* (Linnaeus, 1758), COCACE, B3, 117 m, 9 mm. **C.** *Oudardia compressa* (Brocchi, 1814), COCACE, C7, 146 m, 8 mm. **D–G Semelidae; D.** *Abra alba* (W. Wood, 1802), COCACE, SP, 25 m, 7 mm. **E.** *Abra longicallus* (Scacchi, 1835), COCACE, G1, 468 m, 5 mm. **F.** *Abra nitida* (O. F. Müller, 1776), COCACE, C7, 146 m, 4 mm. **G.** *Abra prismatica* (Montagu, 1808), COCACE, C7, 146 m, 7 mm. **H Psammobiidae; H.** *Gari costulata* (W. Turton, 1822), COCACE, B1, 113 m, 9 mm. Scale bars: A-C, H = 10 mm; D-G = 3 mm.

Fig. 11. A Solenocurtidae A. *Tagelus adansonii* (Bosc, 1801), COCACE, SP, 25 m, 7 mm. **B Kelliellidae B.** *Kelliella miliaris* (Philippi, 1844), COCACE, G6, 533 m, 2 mm. **C-G Veneridae C.** *Venus casina* Linnaeus, 1758, COCACE, B1, 113 m, 33 mm **D.** *Chamelea striatula* (da Costa, 1778), COCACE, B2, 86 m, 20 mm. **E.** *Dosinia lupinus* (Linnaeus, 1758), COCACE, B2, 86 m, 14 mm. **F.** *Timoclea ovata* (Pennant, 1777), COCACE, B1, 113 m, 8 mm. **G.** *Pitar mediterraneus* (Aradas & Benoit, 1872), COCACE, D2, 161 m, 7 mm. **H Corbulidae H.** *Varicorbula gibba* (Olivi, 1792), COCACE, C7, 146 m, 5 mm. **I Hiatellidae I.** *Hiatella arctica* (Linnaeus, 1767), COCACE, C7, 146 m, 3 mm. Scale bars: B, H–I = 2 mm; A, C–G: 10 mm.

with subtropical Atlantic biota), and due to the increase in average seawater temperature during the last 50 years (over 0.13 °C per decade) (Díez et al., 2012). Thus, the rising sea temperature may facilitate the settlement of typical Mediterranean or subtropical species in the Cantabrian Sea. This study also gives new ecological information for several species, in terms of bathymetric range distribution and habitat preferences, and highlighted the transitional characteristics of the bivalve communities from this particular northeastern Atlantic sea where boreal and temperate faunas can coexist.

In this study, the highest species richness was found in the shallower areas, which agrees with other studies that conclude that depth is the most important delimiting factor for the presence and distribution of bivalves (Kamenev, 2013). However, there are many other factors that may affect the species distribution in deep-sea ecosystems (Wilson and Hessler, 1987). In the case of bivalves, the food availability is one of the most important factors. Food availability on deep sea areas depends on the remains from the eutrophic areas, where most of the nutrients originated (Danovaro et al., 2014). These nutrients are transported to the heterotrophic areas by the marine streams, which can therefore modify their concentration in these ecosystems (Genin et al., 1992). The
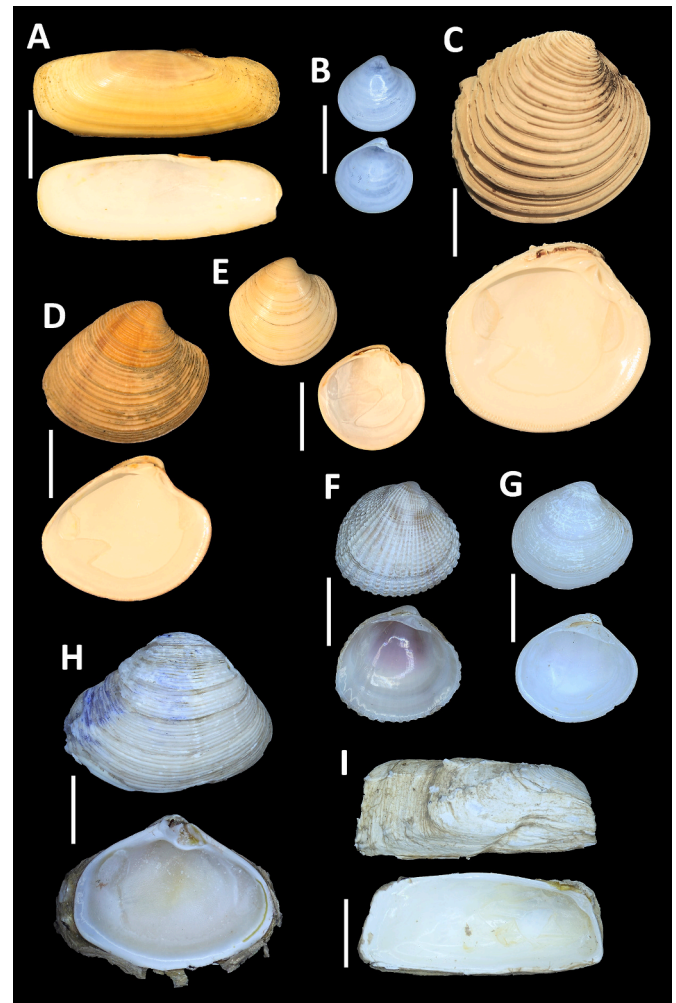
low food availability, together with the low rates of digestibility of some of the proteins of bivalve shells, partially explain the fragility and small size of many deep-sea bivalve species (Allen, 1978). Of the total identified species from the continental slope and the abyssal zone (from 2000 to 4700 m depth), 67.67% of them have fragile and small shells. In contrast, it is worth noting the adaptation of *Mendicula ferruginosa* (Forbes, 1844) to these environments. This small bivalve was found between 468 and 4700 m depth and presents a solid shell due to the presence of ferruginous deposits on its periostracum that provide the shell with a notorious hardness (Gofas et al., 2011).

Here, the most structuring factor of recorded bivalve distribution was the depth, one of the most important in marine bivalves, together with the sediment type (Perez-Nevarez, 1995). Some species need a solid substrate to attach its lower valve, as is the case of animals that live attached to the substrate at least during some phases of its life (e.g. *S. gussonii*). Although the substrate type of the sampled localities was heterogeneous, in general terms it was thicker in the shallow areas (continental shelf) and its granulometry tended to decrease along with
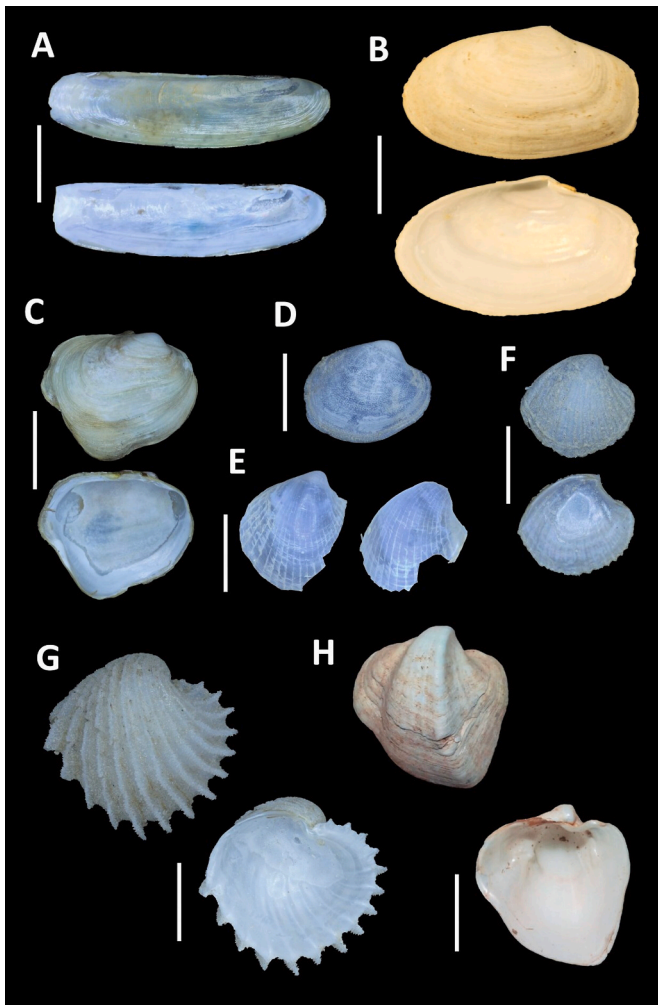
Fig. 12. **A Pharidae A.** *Phaxas pellucidus* (Pennant, 1777), COCACE, A3, 60 m, 5 mm. **B Thraciidae B.** *Thracia phaseolina* (Lamarck, 1818), COCACE, B1 113 m, 13 mm. **C.Trapezidae C.** *Coralliophaga lithophagella* (Lamarck, 1819), COCACE, G2, 322 m, 7 mm. **D-E Lyonsiellidae D.** *Lyonsiella abyssicola* (Sars G. O., 1872), COCACE, I3, 1400 m, 2 mm. **E.** *Policordia gemma* (A. E. Verrill, 1880), BIOCANT, TP, 1500 m, 5 mm. **F–H Verticordiidae F.** *Haliris granulata* (Seguenza, 1860), COCACE, E3, 190 m, 3 mm. **G.** *Spinosipella acutecostata* (Philippi, 1844), COCACE, I4, 720 m, 7 mm. **H.** *Halicardia flexuosa* (A. E. Verrill & S. Smith, 1881), BIOCANT, P3, 1200 m, 35 mm. Scale bars: A-B = 5 mm; C–F = 2 mm; G-H = 3.

Fig. 13. **A-B Poromyidae; A.** *Cetomya neaeroides* (Seguenza, 1877), BIOCANT, TP, 1500 m, 13 mm. **B.** *Poromya granulata* (Nyst & Westendorp, 1839), BIOCANT, P3, 1200 m, 8 mm. **C–F Cuspidariidae; C.** *Cuspidaria rostrata* (Spengler, 1793), COCACE, D2, 161 m, 6 mm. **D.** *Cardiomya cadiziana* M. Huber, 2010, COCACE, H4, 790 m, 8 mm. **E.** *Cardiomya costellata* (Deshayes, 1835) COCACE, D2, 161 m, 5 mm. **F.** *Cuspidaria cuspidata* (Olivi, 1792), COCACE, C6, 154 m, 8 mm. Scale bars = 4 mm.

depth; this pattern has been previously reported in other studies (e.g. Gómez-Ballesteros et al., 2014). Despite the apparent importance of the type of substrate for the occurrence of bivalves (Perez Nevarez, 1995), we found less effect of the substrate on the species distribution than the depth one. The large bathymetric range sampled (from 25 to 4700 m depth) may have masked the possible effect of the substrate type on the distribution of bivalve species. This is consistent with the observations made by Fernández-Rodríguez et al. (2019) on the holothurian fauna from the same study area and bathymetric range.

5. Conclusions

Depth appears as the main factor that influences the diversity and distribution of bivalves from the Cantabrian Sea. The species richness decreases with depth, with the continental shelf stations being the most speciose ones. From the 84 live taxa identified in this study, *C. neaeroides* constitutes a new record from the Bay of Biscay and *Ta. adansonii* is a punctual introduction in the Cantabrian coast. Our results evidence our
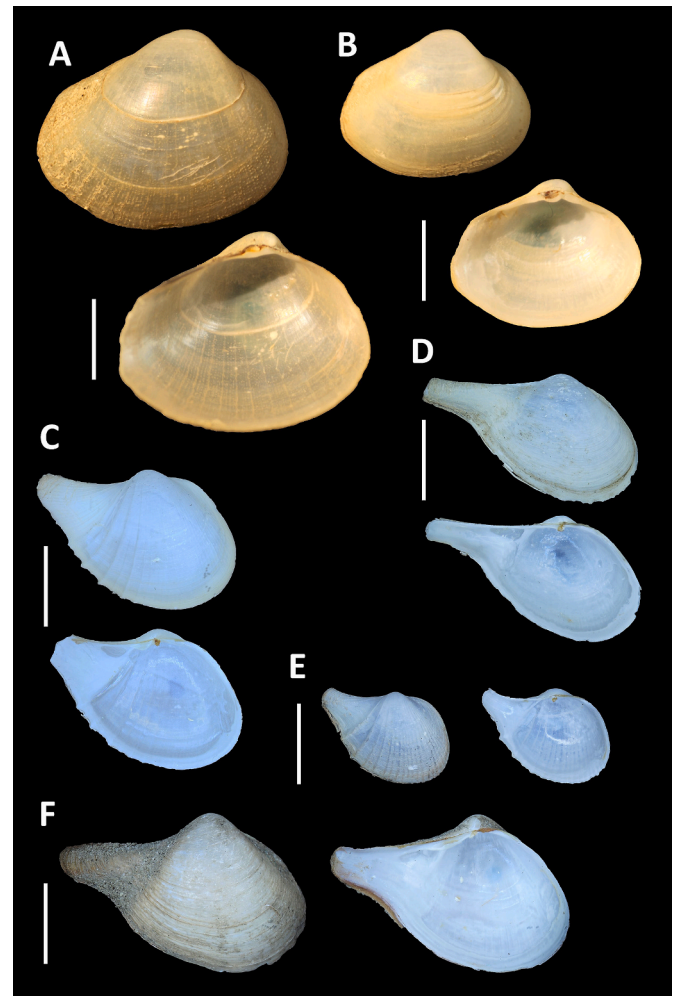
still incomplete knowledge on European marine malacofauna and the need of more studies that taxonomically address the molluscan diversity. We provide new information about the bivalve communities from the ACS that is highly valuable for the ongoing protection of this Special Area for Conservation within the Natura 2000 Network.

CRediT authorship contribution statement

R. López-Alonso: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **O. Sánchez:** Writing – review & editing, Methodology, Investigation, Formal analysis. **I. Fernández-Rodríguez:** Writing – review & editing, Methodology, Investigation, Formal analysis. **A. Arias:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107907.

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