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Avilés Canyon System: Increasing the benthic biodiversity knowledge

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ABSTRACT

Macro and megafauna were studied in the Avilés Canyon System (ACS), southern Bay of Biscay (Cantabrian Sea), during several oceanographic cruises carried out from 2009 to 2017. The biodiversity of ACS is summarized and its description is herein updated after sampling surveys of several programmes (ECOMARG, INDEMARES, SponGES, INTEMARES) conducted by the Spanish Institute of Oceanography (IEO).

This study has updated previous knowledge in the canyon area from past national and international projects, their reports and publications as well as data collected in the context of regional projects designed to gain new insight into the diversity of marine invertebrates and fishes from the ACS. Samples were taken using a range of sampling gears (Rock dredge, Beam trawl, Trawl gear GOC-73, Suprabenthic sledge, Box corer and Remoted operated vehicle), from 55 to 2291 m in depth. A total of 1015 species were identified at the ACS: 98 Porifera, 153 Cnidaria, 14 Brachiopoda, 22 Bryozoa, 97 Mollusca, 151 Annelida, 315 Arthropoda, 74 Echinodermata and 91 Chordata. New records for the Bay of Biscay fauna include 13 Porifera species, 17 Cnidaria, 7 Mollusca, 8 Arthropoda, 3 Echinodermata and 4 Chordata. Also the bathymetric range of some species has been extended. As a result of the research projects carried out in the area in the last fifteen years, important information is now available which suggests that the ACS houses a large number of species with a high ecological value, that it represents a biodiversity hotspot in terms of the presence of sponge aggregations and coral reefs in certain regions, and that it sustains important fisheries due to the abundance of commercial species. Given the relevance of the species and habitats occurring in the ACS, there is a need to implement a conservation and management plan of the area in order to maintain habitats in good state of preservation.

1. Introduction

Research in submarine canyons has increased considerably in recent years thanks to the improvement of technologies on oceanographic

vessels, such as submarine remotely operated vehicles (ROVs). This interest has also been triggered by economic interests in the deep sea, such as the exploitation of resources or the laying of submarine cables. The headwaters of the canyons are areas of particular interest in fishery

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resources because they harbour a high biodiversity of benthic species, and can become areas of complex management due to the presence of protected species or habitats (Punzón et al., 2016). These complex large geologic landforms are sinuous valleys with V or U-shaped cross sections, often with steep slopes and rocky overhangs like the better-known large land canyons (Shepard, 1963). This is the case of the Avilés Canyon System (ACS), located in the Central Cantabrian Sea, in the southern Bay of Biscay, in which complex geomorphological structures of main and tributary canyons, are combined with a great variety of habitats and vulnerable marine ecosystems, which harbour a very high species richness. Particularly at the head of the main canyon of Avilés, an important artisanal fleet coming from Asturian fishing ports (Cudillero, Luarca, Avilés and Gijón), exploits the fishing resources which are of vital importance for the economy of the coastal populations. The management of these resources must be done in a sustainable way to ensure the maintenance of good environmental status and hence the importance of knowing the biodiversity that these canyons harbour.

The ACS remained off the track of the great explorations during the nineteenth century which still provide a significant part of our knowledge on the deep water benthos in the Atlantic area. Importantly, the HMS Lightning (1868) and HMS Porcupine (1869) expeditions showed that animal life existed down to depths of 4000 m. Later, the HMS Challenger expedition (1872–1876) with Charles Wyville Thomson as chief scientist, circled the Bay of Biscay and sampled for the first time in Cape Finisterre (Spain). The Caudan expedition in 1895 (Koehler, 1896) explore the deep-sea fauna of Bay of Biscay and collected some new species, but in the eastern part of this area. The earliest important oceanographic expeditions focused on deep-sea research in the Bay of Biscay were onboard the French vessels *Travailleur* and *Talisman*. They produced over 100 scientific publications with descriptions of 176 new species (Dolan, 2020) still considered valid today. The dredging carried out by the *Travailleur* along the coast of Spain did not reach the ACS and remained north of the Asturian coast off Tazones in the 1880 campaign, while the 1882 campaign began east of the Avilés Canyon and procured several relevant samples in stations 1–5 and 69–70 (Norman, 1880; Milne-Edwards, 1881, 1882; Dolan, 2020). Among the first big cruises that mention species collected in the vicinity of the ACS are the expeditions of Prince Albert I of Monaco aboard the *Hirondelle* in 1886 (Topsent, 1892; Jourdan, 1895; Pictet and Bedot, 1900; Studer, 1901). Expeditions between 1934 and 1939 aboard the research vessel *Président Théodore Tissier* discovered the Le Danois Bank (commonly known by Cantabrian fishermen as “El Cachucho”) and the results were published in the book “Les Profondeurs de la Mer” (Le Danois, 1948); however, they did not make any reference to the ACS, located further west. The BIOGAS (Biology of Biscay Bay) programme was promoted by the French oceanographic agency IFREMER with cruises in 1972–1974 and 1977–1981, but its goal was to make a long-term survey of the deeper areas and the ACS was not taken into consideration (Laubier and Monnot, 1985). Since 1983, when the Spanish Institute of Oceanography (IEO) cruises began, samples started to be regularly taken from the ACS, mainly aimed at evaluating demersal fishery resources with specific sampling in different years in the DEMERSALES (Olaso, 1990) and ECOMARG oceanographic expeditions. The COCACE project of the University of Oviedo (1987–88) was seminal to the studies of the benthic fauna in the ACS, and even today results concerning species collected in those campaigns are still being published. As a result of those samplings, Álvarez-Claudio (1993) carried out a doctoral thesis on cnidarians and published several papers (Álvarez-Claudio, 1994a, b, c, 1995a, b, c). Derived from these studies, scientists detected for the first time in the area the presence of the cold-water coral *Madrepora oculata* (Louzao et al., 2010). *Desmophyllum pertusum* (better known under its former name *Lophelia pertusa*) was collected in this area in the *Travailleur* expedition of 1882 and cited by Zibrowius (1980).

From 2010 to 2012, the LIFE+ INDEMARES project “Inventory and designation of marine Natura 2000 areas in the Spanish Sea” promoted the study of ten areas, (including the ACS), for their potential inclusion

in the Natura 2000 Network of Spanish jurisdictional waters (Sánchez-Delgado et al., 2014a). Exhaustive sampling campaigns were carried out in the area, some of which coincided in time with the BIO-CANT/DOSMARES Project (University of Oviedo). As a result, the ACS was formally proposed as a candidate Site of Community Importance (SCI) in December 2014 (Ministerio de Agricultura, Alimentación y Medio Ambiente, 2014) and was adopted in the ninth update of the list for the Atlantic biogeographical region in November 2015. More recently, emphasis has been placed on the study of communities and habitats with the presence of cold-water corals and sponge aggregations, through the SponGES and INTEMARES projects. Many other papers have been published with a focus on marine invertebrates, including Porifera (Cristobo et al., 2009; Ríos et al., 2018; Taboada et al., 2020; Santín et al., 2021), Cnidaria (Altuna, 2012a, b, c, d, 2013a, b; Altuna and Ríos, 2014a, b, 2021; Tu et al., 2015; Molodtsova et al., 2019; Poliseno et al., 2021), Mollusca (Ibarrola et al., 2011; Gofas et al., 2017; Arias et al., 2019), Annelida (Lourido et al., 2014), Echinodermata (García-Guillén et al., 2022a, b, this issue), Fernández-Rodríguez et al., 2017, 2018, 2019), Crustacea (Frutos et al., 2012, 2017), and Chordata (Sánchez, 1993; Sánchez et al., 2002, 2003, 2005; Sánchez and Olaso, 2004; Sánchez and Serrano, 2003; Rodríguez-Cabello et al., 2013; Isbert et al., 2015) and also general information has been generated from this area (OCEANA, 2009, 2011), which proves the increase of interest in the ACS by the scientific community. In addition, some previous studies have studied the distribution and abundance of macrobenthos or habitats in the Cantabrian Sea and included part of the study area (Olaso, 1990; Sánchez et al., 2012a, b, 2013, 2014a, Sánchez et al., 2014a; Serrano et al., 2006a, 2006b, 2011, 2012; Lourido et al., 2014). Some of the latest works published in the area have assessed the microbial diversity associated with sponge aggregations (Busch et al., 2020), the connectivity and genetic diversity of the species (Taboada et al., 2020, 2021), the growth and importance of the structuring species (Ríos et al., 2020; Prado et al., 2021; Rodríguez-Basalo et al., 2021) or the fauna associated with three-dimensional biogenic constructions (Manjón-Cabeza et al., 2021). An effort has been made to study several taxonomic groups, also looking at small cryptic species such as encrusting sponges, bryozoans and crustaceans among others. The objective of the present research is thus to update the biodiversity data of the ACS in terms of the macro- and megafauna present, using the information generated in projects in which authors have been involved since 2010 that could help to implement a conservation and management plan of the area in order to maintain habitats in good state of preservation.

The ecological relevance of the ACS, has been valued by the Government of Spain through the Ministry of Environment as one of the ten areas that will be protected and integrated within the European Natura 2000 network (Sánchez-Delgado et al., 2014a). As shown in this paper, this is a wide area with very high biodiversity values that also has a very important economic importance for the riverside populations of central and western Asturias; the characterization of its fisheries has recently been updated (Punzón et al., 2016) and shows the fishing activity including gear, target species, and working area in the ACS.

2. Material and methods

2.1. The study area

In the Cantabrian Sea, in the southern part of the Bay of Biscay, there is a wide array of submarine canyons of great scientific interest for their special characteristics in terms of dimensions, morphology, diversity and bathymetric range. These canyons start from the edge of the continental shelf and reach the Biscay Abyssal Plain at almost 5000 m deep. From east to west, the main canyons of the Cantabrian Sea are Capbreton, Santander, Llanes, Lastres, Avilés Canyon System (ACS) and Navia.

The ACS consists of three main canyons, Avilés, the largest, La Gaviera and El Corbiro in the east, and another twelve tributary

canyons. The Avilés Canyon is characterized by a V-shaped bottom, its head is at a depth of about 128 m, and it reaches the abyssal plain at 4766 m. The Gaviara Canyon is one of the main tributaries of the ACS and is characterized by a U-shaped irregular bottom, while the Corbiro Canyon is characterized by a V-shaped bottom. The geomorphology of the area is really complex (Gómez-Ballesteros et al., 2014) with different physiographic domains such as a narrow continental shelf, two continental slopes, the abyssal plain and the submarine canyons. In addition, there are some structural highs: El Canto Nuevo, a seamount on the continental slope, and El Agudo de Fuera, a rocky outcrop on the upper continental slope in the northeast of the study area. More recently, channels of the canyons and their tributaries have been characterized, by application of a process of hydrological hierarchization through ArcGIS tools (Díez et al., 2021).

The ACS was declared SIC on the basis that it hosts one of the few cold-water coral reefs in the Iberian Peninsula (habitat 1170 in Annex 1 of the EU Habitats Directive). In the last five years, studies in the area have highlighted the importance of structuring species that form aggregations, such as sponges, which are directly linked to maintaining and increasing biodiversity with respect to surrounding areas (SponGES Project, 2020). Furthermore, vulnerable and emblematic species such as the cetaceans *Tursiops truncatus* (Montagu, 1821) and *Physeter macrocephalus* Linnaeus, 1758 and the turtle *Caretta caretta* (Linnaeus, 1758), some of the very few marine species included in Annex 2 of the Habitats Directive, use the ACS as a transit zone on their migratory routes and provide additional support for the inclusion in the SCI list.

2.2. Expeditions and sampling gears

Samples used in the present study were collected on the following oceanographic vessels and expeditions: R/V *Cornide de Saavedra* (IEO) in the expeditions ECOMARG 09 (14th to July 30, 2009), R/V *Vizconde de Eza* (SGM) in INDEMARES-AVILES 0410 (19th April to May 13, 2010) and INDEMARES-AVILES 0511 (from 1st to May 20, 2011); R/V *Thalassa* (IFREMER/IEO) in INDEMARES 0710 (16th July to August 28, 2010); R/V *Ramón Margalef* (IEO) in INDEMARES-AVILES 0412 (28th April to May 7, 2012) and R/V *Ángeles Alvariño* (IEO) in INDEMARES-AVILES 0912 (22nd September to October 7, 2012) and SponGES 0617 (9th to June 25, 2017). Specimens were collected from a total of 197 stations using 6 different types of sampling gears (Supplementary material-Table 1). In our study we did not include data from IEO annual cruises DEMERSALES which are mainly focused on investigating the biodiversity of species present in soft bottoms from the continental shelf. This study is aimed at the biodiversity associated with underwater canyons and the hard substrate in the continental shelf, linked to habitat 1170.

The present work is based on different multidisciplinary surveys, and samples were collected with gears and samplers suitable for every type of substrate (Fig. 1): Rock dredge (RD) in hard bottoms, Beam trawl (BT) and Trawl gear GOC-73 (GOC) in soft bottoms; Box-corer (BC) for the study of endobenthos; Suprabenthic sledge (SS) for surveying suprabenthic fauna (Frutos, 2006); and images and specimens obtained using the Remote operated vehicle *Liropus* 2000 (ROV) (model Super Mohawk II) from the IEO operated by the contractor ACSM. Underwater imagery was obtained with a high-resolution camera and geo-referenced by means of a transponder (HiPAP 500) attached to the ROV that conveyed the positions of the ROV in relation to the research vessel. The vessel was equipped with a dynamic positioning system able to maintain a specified position, and the ROV was settled on the seafloor when acquiring high magnification images or taking samples.

3. Material

The specimens of these seven expeditions were collected in sedimentary bottoms with BT, GOC, BC and SS, and in hard bottoms with RD and ROV. The taxonomic classification follows that of the World

Table 1

List of the species identified up to genus level and collected in the Avilés Canyon System during the seven research cruises within the ECOMARG, INDEMARES and SponGES projects. Depth ranges are indicated. *: New records for the Bay of Biscay.

Species	Depth range (m)
Phylum Porifera	
Class Hexactinellida	
Order Amphidiscosida	
<i>Phoronema carpenteri</i> (Thomson, 1869)	1008–1744
Order Lyssacosida	
<i>Asconema setubalense</i> Kent, 1870	317–1476
<i>Regadrella phoenix</i> Schmidt, 1880	593–1660
Order Sceptulophora	
<i>Aphrocallistes beatrix</i> Gray, 1858	626–1325
* <i>Periphragella lusitanica</i> Topsent, 1890	1476–2291
Class Demospongiae	
Order Agelasida	
* <i>Hymerhabdia typica</i> Topsent (1892)	86
Order Axinellida	
<i>Axinella infundibuliformis</i> (Linnaeus, 1759)	128–266
<i>Axinella</i> sp.	553
* <i>Axinella vellerea</i> Topsent, 1904	128
<i>Phakellia robusta</i> Bowerbank, 1866	103–928
<i>Phakellia ventilabrum</i> (Linnaeus, 1767)	55–1228
<i>Janulum spinispiculum</i> (Carter, 1876)	340–776
<i>Janulum</i> sp.	266–593
<i>Hymeraphia stellifera</i> Bowerbank, 1864	128
<i>Hymeraphia</i> sp.	103
<i>Halicnemis patera</i> Bowerbank, 1864	110–342
<i>Halicnemis verticillata</i> (Bowerbank, 1866)	103–340
<i>Halicnemis gallica</i> (Topsent, 1893)	128–143
<i>Paratimea</i> sp.	103–1228
Order Biemnida	
<i>Rhabdermia</i> sp.	776
Order Bubarida	
<i>Acanthella erecta</i> (Carter, 1876)	462
<i>Bubaris vermiculata</i> (Bowerbank, 1866)	86–560
<i>Bubaris</i> sp.	103–340
* <i>Monocrepidium vermiculatum</i> Topsent, 1898	128
<i>Sulcastrella</i> sp.	695
Order Desmacellida	
<i>Desmacella informis</i> (Stephens, 1916)	893
<i>Desmacella</i> spp.	462–908
Order Haplosclerida	
<i>Haliclona (Flagellia) porosa</i> (Fristedt, 1887)	128
<i>Haliclona (Gellius) spp.</i>	55–1228
<i>Petrosia (Petrosia) ficiformis</i> (Poiret, 1789)	128–1244
<i>Xestospongia friabilis</i> (Topsent, 1892)	128–1525
* <i>Siphonodictyon infestum</i> (Johnson, 1889)	55–908
<i>Siphonodictyon</i> sp.	533–828
Order Poecilosclerida	
* <i>Acanthancora aenigma</i> (Lundbeck, 1910)	593
<i>Acanthancora</i> sp.	266–772
<i>Antho (Acarinia) sp.</i>	342
<i>Asbestopluma</i> sp.	776–2291
<i>Cladorhiza abyssicola</i> Sars, 1872	908–2291
<i>Chondrocladia (Chondrocladia) robertballardi</i> Cristobo, Rios, Pomponi & Xavier, 2015	1228–1525
<i>Clathria</i> spp.	128–828
<i>Coelosphaera</i> sp.	533–593
<i>Coelosphaera (Histodermion) sp.</i>	462–551
<i>Crella</i> sp.	908–2291
<i>Desmacidon fruticosum</i> (Montagu, 1814)	103–143
<i>Diacarnus</i> sp.	108–128
<i>Discorhabdella tuberoscapitata</i> (Topsent, 1890)	340
* <i>Guitarra solorzanoi</i> Cristobo, 1998	86–143
<i>Hamacantha (Hamacantha) johnsoni</i> (Bowerbank, 1864)	790–893
<i>Hamacantha (Vomerula) falcata</i> (Bowerbank, 1874)	551–790
<i>Hamacantha</i> spp.	340–1165
<i>Hymedesmia (Hymedesmia) paupertas</i> (Bowerbank, 1866)	86–1228
<i>Hymedesmia</i> spp.	55–1165
<i>Hymedesmia (Stylopus) spp.</i>	128–928
<i>Iophon</i> sp.	1228
<i>Iotroata</i> sp.	143
<i>Latrunculia</i> spp.	317–990

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Lissodendoryx (Ectydoryx) sp.</i>	143
* <i>Melonanchora emphysema</i> (Schmidt, 1875)	128
<i>Mycale sp.</i>	128
<i>Myxilla sp.</i>	2291
<i>Plocamione hystrix</i> (Ridley & Duncan, 1881)	593–2291
<i>Plocamione dirrhopalina</i> Topsent, 1927	143
<i>Plocamionida ambigua</i> (Bowerbank, 1866)	551–928
<i>Podospongia lovenii</i> Barboza du Bocage, 1869	266
<i>Spirorhabdia vidua</i> (Schmidt, 1875)	340
<i>Tedania sp.</i>	86–908
Order Polymastiida	
<i>Polymastia penicillus</i> (Montagu, 1814)	128–143
<i>Polymastia spp.</i>	86–1525
* <i>Tentorium cf. levantinum</i> Ilan, Gugel, Galil & Janussen, 2003	1476–1533
Order Suberitida	
<i>Spongosorites sp.</i>	462–908
* <i>Stylocordyla pellita</i> (Topsent, 1904)	128–143
<i>Topsentia sp.</i>	695
Order Tethyida	
<i>Timea spp.</i>	55–843
Order Tetractinellida	
<i>Calthropella (Calthropella) geodioides</i> (Carter, 1876)	533–776
<i>Erylus sp.</i>	462–551
* <i>Geodia megastrella</i> Carter, 1876	342–2291
<i>Geodia nodastrella</i> Carter, 1876	649–776
<i>Geodia pachydermata</i> (Sollas, 1886)	551–2291
<i>Geodia spp.</i>	143–2291
<i>Characella pachastrelloides</i> (Carter, 1876)	593–1228
<i>Nethea amygdaloides</i> (Carter, 1876)	103–893
* <i>Pachastrella cf. nodulosa</i> Cárdenas & Rapp, 2012	695
<i>Pachastrella monilifera</i> Schmidt, 1868	342–776
<i>Pachastrella ovisternata</i> Lendenfeld, 1894	342–776
<i>Poecillastra compressa</i> (Bowerbank, 1866)	86–776
<i>Corallistes sp.</i>	551
<i>Leiodermatium sp.</i>	929
<i>Neoschrammeniella aff. bowerbankii</i> (Johnson, 1863)	533–695
* <i>Thenea schmidtii</i> Sollas, 1886	695–1525
<i>Thrombus abyssi</i> (Carter, 1873)	769–1228
<i>Vulcanella aberrans</i> (Maldonado & Uriz, 1996)	593–908
<i>Vulcanella gracilis</i> (Sollas, 1888)	828–908
<i>Craniella cranium</i> (Müller, 1776)	86
<i>Craniella sp.</i>	700
Order Trachycladida	
<i>Trachycladus minax</i> (Topsent, 1888)	128–462
Order Verongiida	
<i>Hexadella cf. crypta</i> Reveillaud, Allewaert, Pérez, Vacelet, Banaigs & Vanreusel, 2012	551–990
<i>Hexadella sp.</i>	695–700
Class Homoscleromorpha	
Order Homosclerophorida	
<i>Plakina sp.</i>	317
Phylum Cnidaria	
Class Anthozoa	
Order Spirularia	
<i>Cerianthus lloydii</i> Gosse, 1859	300–790
Orden Actiniaria	
<i>Actinauge richardi</i> (Marion, 1906)	361–578
<i>Phelliactis cf. hertwigii</i> Simon, 1892	1008–1244
<i>Phelliactis sp.</i>	1161
Orden Antipatharia	
<i>Allopathes sp.</i>	790–932
<i>Antipathes dichotoma</i> Pallas, 1766	274
<i>Bathypathes cf. patula</i> Brook, 1889	932
<i>Leiopathes spp.</i>	649–1533
<i>Parantipathes hirondelle</i> Molodtsova, 2006	266–1818
* <i>Stauropathes arctica</i> (Lütken, 1871)	1476
<i>Stichopathes cf. gravieri</i> Molodtsova, 2006	342–1533
<i>Stichopathes sp.</i>	533–2291
* <i>Trissopathes grasshoffi</i> Molodtsova, Altuna & Hall-Spencer, 2019	615–928
Order Scleractinia	
<i>Fungiacyathus (Fungiacyathus) fragilis</i> G.O Sars, 1872	1744
<i>Madrepora oculata</i> Linnaeus, 1758	342–1660
<i>Aulocyathus atlanticus</i> Zibrowius, 1980	893
<i>Caryophyllia (Caryophyllia) abyssorum</i> Duncan, 1873	593–984
<i>Caryophyllia (Caryophyllia) atlantica</i> (Duncan, 1873)	1533

Table 1 (continued)

Species	Depth range (m)
<i>Caryophyllia (Caryophyllia) calveri</i> Duncan, 1873	462–828
<i>Caryophyllia (Caryophyllia) sarsiae</i> Zibrowius, 1974	700–1533
<i>Caryophyllia (Caryophyllia) seguenzae</i> Duncan, 1873	1473
<i>Caryophyllia (Caryophyllia) smithii</i> Stokes & Broderip, 1828	128–893
<i>Desmophyllum dianthus</i> (Esper, 1794)	551–2291
<i>Desmophyllum pertusum</i> (Linnaeus, 1758)	342–1473
<i>Paracyathus pulchellus</i> (Philippi, 1842)	128
<i>Premocyathus cornuformis</i> (Pourtales, 1868)	1008
<i>Solenosmilia variabilis</i> Duncan, 1873	767–2291
<i>Stephanocyathus (Stephanocyathus) moseleyanus</i> (Sclater, 1886)	1244–1473
<i>Stephanocyathus (Odontocyathus) nobilis</i> (Moseley, 1876)	1473–1533
<i>Vaughanella concinna</i> Gravier, 1915	908–1660
* <i>Deltocyathus eccentricus</i> Cairns, 1979	1473
<i>Deltocyathus moseleyi</i> Cairns, 1979	593–908
* <i>Flabellum (Flabellum) chunii</i> Marenzeller, 1904	1473
<i>Flabellum (Ulocyathus) alabastrum</i> Moseley, 1876	1473–1660
<i>Flabellum (Ulocyathus) macandrewi</i> Gray, 1849	828
<i>Javania cailleti</i> (Duchassaing & Michelotti, 1864)	1476–2291
<i>Monomyces pygmaea</i> (Risso, 1826)	55
<i>Balanophyllia (Balanophyllia) thalassae</i> Zibrowius, 1980	462–764
<i>Dendrophyllia cornigera</i> (Lamarck, 1816)	86–551
<i>Eguchipsammia cornucopia</i> (Pourtales, 1871)	593–767
<i>Enallopsammia rostrata</i> (Pourtales, 1878)	990–2291
Order Corallimorpharia	
<i>Corynactis viridis</i> Allman, 1846	55–88
* <i>Sideractis glacialis</i> Danielssen, 1890	776
Order Zoantharia	
<i>Epizoanthus paguriphilus</i> Verrill, 1883	535–1510
<i>Epizoanthus papillosus</i> Johnston, 1842	355–535
<i>Epizoanthus sp.</i>	615–1660
* <i>Vitrumanthus vanderlandi</i> Kisse et al., 2021	843–1177
Order Alcyonacea	
<i>Chelidonisis aurantiaca</i> Studer, 1890	469–990
<i>Alcyonium cf. glomeratum</i> (Hassall, 1843)	55
<i>Alcyonium sp.</i>	1476–2291
* <i>Anthomastus gyratus</i> Molodtsova, 2013	2291
<i>Anthomastus spp.</i>	767–932
<i>Anthelia sp. 1</i>	799–843
<i>Anthelia sp. 2</i>	593
<i>Acanella arbuscula</i> (Johnson, 1862)	535–1525
<i>Lepidisis sp.</i>	1244
<i>Callogorgia verticillata</i> (Pallas, 1766)	469–1018
<i>Narella versluysi</i> (Hickson, 1909)	695–990
* <i>Prinnoa resedaeformis</i> (Gunnerus, 1763)	1177–1150
* <i>Thouarella (Euthouarella) grasshoffi</i> Cairns, 2006	1576–1660
<i>Acanthogorgia armata</i> Verrill, 1878	128–1464
<i>Acanthogorgia cf. pico</i> Grasshoff, 1973	469–500
<i>Acanthogorgia sp.</i>	790–1533
* <i>Dendrobrachia bonsai</i> López-González & Cunha, 2010	615
<i>Muriceides sceptrum</i> (Studer, 1891)	769
<i>Muriceides spp.</i>	790–1533
<i>Paramuricea biscaya</i> Grasshoff, 1977	1476–1660
<i>Placogorgia graciosa</i> (Tixier-Durivault & d'Hondt, 1975)	615–932
<i>Placogorgia sp.1</i>	700
<i>Placogorgia sp.2</i>	790
<i>Placogorgia sp.3</i>	1161
<i>Swiftia cf. dubia</i> (Thomson, 1929)	266–1660
<i>Swiftia sp.</i>	1244
<i>Anthothela sp.</i>	700–1464
<i>Lateothela grandiflora</i> (Tixier-Durivault & d'Hondt, 1975)	700–1177
<i>Hemicorallium niobe</i> (Bayer, 1964)	928
* <i>Pleurocorallium occultum</i> (Tu, Altuna & Jeng, 2015)	767
<i>Paragorgia cf. johnsoni</i> Gray, 1862	1533
<i>Sarcodictyon catenatum</i> Forbes in Johnston, 1847	143–342
<i>Pseudotelestula humilis</i> (Thomson, 1927)	649–1161
<i>Telestula sp.</i>	772
<i>Trachythela sp.</i>	1510–2291
Order Pennatulacea	
<i>Anthoptilum grandiflorum</i> (Verrill, 1879)	1464
<i>Funiculina quadrangularis</i> (Pallas, 1766)	535–1473
<i>Kophobelemnion stelliferum</i> (Müller, 1776)	342–1008
<i>Protoptilum cf. thomsonii</i> Kölliker, 1872	589
<i>Pennatula aculeata</i> Danielssen, 1860	828
<i>Pennatula phosphorea</i> Linnaeus, 1758	135

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Ptilella grandis</i> (Ehrenberg, 1834)	1228–1525
* <i>Umbellula huxleyi</i> K�lliker, 1880	1051
Class Hydrozoa	
Order Anthoathecata	
<i>Zanclaea cf. implexa</i> (Alder, 1856)	558
<i>Eudendrium cf. islandicum</i> Schuchert, 2000	941
<i>Eudendrium cf. rameum</i> (Pallas, 1766)	941
<i>Eudendrium</i> spp.	615–1036
<i>Stenohelia maderensis</i> (Johnson, 1862)	688–1161
Order Leptothecata	
<i>Campanularia hincksii</i> Alder, 1856	53–799
<i>Clytia gracilis</i> (Sars, 1850)	572
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	500
<i>Clytia</i> sp.	469
<i>Obelia bidentata</i> Clark, 1875	469
<i>Obelia dichotoma</i> (Linnaeus, 1758)	88–266
<i>Obelia</i> sp.	53
<i>Egmondella</i> sp.	2291
<i>Cirrholovenia tetranema</i> Kramp, 1959	1161
<i>Halecium beanii</i> (Johnston, 1838)	1018
<i>Halecium cf. delicatulum</i> Coughtrey, 1876	53
<i>Halecium labrosum</i> Alder, 1859	941
<i>Halecium muricatum</i> (Ellis & Solander, 1786)	500–810
<i>Halecium tenellum</i> Hincks, 1861	572
<i>Acryptolaria conferta</i> (Allman, 1877)	88–990
<i>Bedotella armata</i> (Pictet & Bedot, 1900)	469–799
<i>Cryptolaria pectinata</i> (Allman, 1888)	342–990
<i>Filellum cf. serratum</i> (Clarke, 1879)	128–615
<i>Lafoea dumosa</i> (Fleming, 1820)	53–1464
* <i>Zygophylax africana</i> Stechow, 1923	615–790
<i>Zygophylax</i> sp.	1473
<i>Zygophylax biarmata</i> Billard, 1905	535–767
* <i>Zygophylax leloupi</i> Ramil & Vervoort, 1992	615
<i>Zygophylax sibogae</i> Billard, 1918	615–932
<i>Symplectoscyphus bathyalis</i> Vervoort, 1972	700–941
<i>Moderia rotunda</i> (Quoy & Gaimard, 1827)	700–941
<i>Stegolaria geniculata</i> (Allman, 1888)	615–1660
<i>Stegopoma bathyale</i> Vervoort, 1966	700–1018
* <i>Stegopoma plicatile</i> (M. Sars, 1863)	559–941
<i>Aglaophenia kirchenpaueri</i> (Heller, 1868)	55
<i>Aglaophenia lophocarpa</i> Allman, 1877	128–500
<i>Aglaophenia tubulifera</i> (Hincks, 1861)	53–88
<i>Cladocarpus sigma</i> (Allman, 1877)	53–990
<i>Lytocarpia myriophyllum</i> (Linnaeus, 1758)	88–500
* <i>Streptocaulus dollfusi</i> (Billard, 1924)	266–469
<i>Streptocaulus multiseptatus</i> (Bale, 1915)	266
<i>Antennella secundaria</i> (Gmelin, 1791)	128–572
<i>Halopteris catharina</i> (Johnston, 1833)	55
<i>Polyplumaria flabellata</i> Sars, 1874	53–1150
<i>Kirchenpaueria bonnevieae</i> (Billard, 1906)	88–700
<i>Kirchenpaueria pinnata</i> (Linnaeus, 1758)	615
<i>Nemertesia antennina</i> (Linnaeus, 1758)	2291
* <i>Nemertesia falcicula</i> (Ramil & Vervoort, 1992)	469–1161
<i>Nemertesia perrieri</i> (Billard, 1901)	266–535
<i>Nemertesia</i> sp.1	790
<i>Nemertesia</i> sp.2	88–266
<i>Plumularia setacea</i> (Linnaeus, 1758)	500–572
<i>Schizotricha frutescens</i> (Ellis & Solander, 1786)	266–1161
<i>Sertularella cf. fusiformis</i> (Hincks, 1861)	55
<i>Sertularella gayi</i> (Lamouroux, 1821)	53–1151
<i>Sertularella</i> sp.	53–500
<i>Diphasia alata</i> (Hincks, 1855)	88–695
<i>Diphasia margareta</i> (Hassall, 1841)	53–572
<i>Diphasia nigra</i> (Pallas, 1766)	88
<i>Thuiaria articulata</i> (Pallas, 1766)	55
Class Scyphozoa	
Order Coronatae	
<i>Nausithoe punctata</i> K�lliker, 1853	88
<i>Nausithoe sorbei</i> Jarms, Tiemann & Altuna Prados, 2003	799–800
<i>Nausithoe</i> sp.	469–893
Phylum Brachiopoda	
Class Craniata	
Order Craniida	
<i>Novocrania anomala</i> (M�ller, 1776)	103–342
Class Rhynchonellata	

Table 1 (continued)

Species	Depth range (m)
Order Rhynchonellida	
<i>Hispanirhynchia cornea</i> (Fischer in Davidson, 1886)	1150–1818
Order Terebratulida	
<i>Dallina parva</i> Cooper, 1981	800
<i>Dallina septigera</i> (Lov�n, 1846)	984–1533
<i>Dyscolia wyvillei</i> (Davidson, 1878)	1018–1177
<i>Eucalathis ergastica</i> Fischer and Oehlert, 1890	626–1150
<i>Eucalathis</i> sp.	800
<i>Fallax dalliniformis</i> Atkins, 1960	700–1533
<i>Gryphus vitreus</i> (Born, 1778)	1244
<i>Macandrevia cranium</i> (O. F. M�ller, 1776)	128–695
<i>Megeteria truncata</i> (Linnaeus, 1767)	55–776
<i>Platidia anomioides</i> (Scacchi & Philippi in Philippi, 1844)	55–1325
<i>Stenosarina davidsoni</i> Logan, 1998	928–1533
<i>Terebratulina retusa</i> (Linnaeus, 1758)	86–843
Phylum Bryozoa	
Class Gymnolaemata	
Order Cheilostomatida	
<i>Alderina imbellis</i> (Hincks, 1860)	342
<i>Anarthropa monodon</i> (Busk, 1860)	103
<i>Breoganipora cf. bicanalifera</i> Souto, Berning & Ostrovsky, 2016	86–342
<i>Buskea dichotoma</i> (Hincks, 1862)	342
<i>Caberea</i> sp.	342
<i>Cellaria</i> sp.	342
<i>Cribrilaria venusta</i> (Canu & Bassler, 1925)	86
<i>Jubella enucleata</i> Jullien, 1882	462–908
<i>Notoplites jeffreysii</i> (Norman, 1868)	551
<i>Omalosecosa ramulosa</i> (Linnaeus, 1767)	86
<i>Porella laevis</i> (Fleming, 1828)	342
<i>Reteporella couchii</i> (Hincks, 1878)	143
<i>Reteporella cf. incognita</i> Hayward & Ryland, 1996	551
<i>Schizomavella (Schizomavella) linearis</i> (Hassall, 1841)	143
<i>Schizomavella (Calvetomavella) neptuni</i> (Jullien, 1882)	551
<i>Schizomavella (Schizomavella) hastata</i> (Hincks, 1862)	143
<i>Schizoporella cornualis</i> Hayward & Ryland, 1995	128
<i>Schizotheca tuberigera</i> (Jullien in Jullien & Calvet, 1903)	462
<i>Smittina cervicornis</i> (Pallas, 1766)	86
<i>Smittoidea reticulata</i> (MacGillivray, 1842)	128–143
<i>Straechmella buski</i> Lagaaij, 1952	103
Order Cyclostomatida	
<i>Disporella hispida</i> (Fleming, 1828)	462
Phylum Mollusca	
Class Gastropoda	
Order Cephalaspidea	
<i>Cylichna cylindracea</i> (Pennant, 1777)	200–499
Order [unassigned] Caenogastropoda	
<i>Cerithiella metula</i> (Lov�n, 1846)	908
<i>Cerithiopsis scalaris</i> Locard, 1891	86
<i>Claviscala richardi</i> (Dautzenberg & de Boury, 1897)	893–984
* <i>Cylindriscala mirifica</i> (P. Fischer, 1886)	1473
* <i>Cylindriscala</i> sp.	1476
<i>Epitonium trevelyanum</i> (G. Johnston, 1841)	510
Order Cephalaspidea	
<i>Retusa umbilicata</i> (Montagu, 1803)	156
<i>Scaphander lignarius</i> (Linnaeus, 1758)	355–1228
<i>Scaphander punctostriatus</i> (Mighels & C. B. Adams, 1842)	984–1473
Order indet.	
<i>Acteon tornatilis</i> (Linnaeus, 1758)	200
Order Lepetellida	
<i>Emarginula christiaensi</i> Piani, 1985	828
<i>Emarginula fissura</i> (Linnaeus, 1758)	128
* <i>Emarginula tuberculosa</i> Libassi, 1859	800
<i>Puncturella asturiana</i> (P. Fischer, 1882)	266–1660
Order Littorinimorpha	
<i>Aporrhais pespelecani</i> (Linnaeus, 1758)	128
<i>Aporrhais serresiana</i> (Michaud, 1828)	355–1464
<i>Euspira fusca</i> (Blainville, 1825)	355–626
<i>Galeodea rugosa</i> (Linnaeus, 1771)	510–578
<i>Ranella olearium</i> (Linnaeus, 1758)	700
<i>Schilderina achatidea</i> (Gray, 1837)	128
<i>Torellia delicata</i> (Philippi, 1844)	810
Order Neogastropoda	
<i>Brocchinia cf. clenchi</i> Petit, 1986	1473
<i>Buccinum humphreysianum</i> Bennett, 1824	510
* <i>Colus aurariae</i> Fraussen, Rosado, Afonso & Monteiro, 2009	510

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Colus gracilis</i> (da Costa, 1778)	510–1228
<i>Colus jeffreysianus</i> (P. Fischer, 1868)	355–2291
* <i>Coralliophaga lithophagella</i> (Lamarck, 1819)	507
<i>Coralliophila richardi</i> (P. Fischer, 1882)	700
<i>Coralliophila monterosatoi</i> (Locard, 1897)	593
<i>Kryptos koehleri</i> (Locard, 1896)	984–1533
<i>Mitrella canariensis</i> (d'Orbigny, 1840)	128
<i>Neptunea contraria</i> (Linnaeus, 1771)	
<i>Pagodula cossmanni</i> (Locard, 1897)	1228
<i>Pagodula echinata</i> (Kiener, 1839)	510–538
<i>Spirotropis cf. confusa</i> (Seguenza, 1880)	538
<i>Spirotropis monterosatoi</i> (Locard, 1897)	1473
<i>Tritia reticulata</i> (Linnaeus, 1758)	1660
<i>Trophonopsis barvicensis</i> (G. Johnston, 1825)	984
<i>Trophonopsis muricata</i> (Montagu, 1803)	195
<i>Troschelia berniciensis</i> (W. King, 1846)	700–1525
<i>Turrisiphon fenestratus</i> (W. Turton, 1834)	510–1228
<i>Typhlomangelia nivalis</i> (Lovén, 1846)	1473–1660
Order Seguenziida	
<i>Calliotropis vaillanti</i> (P. Fischer, 1882)	983–1473
Order Trochida	
<i>Calliostoma leptophyma</i> Dautzenberg & H. Fischer, 1896	700–1228
<i>Calliostoma maurolici</i> (G. Seguenza, 1876)	767–1228
<i>Callumbonella suturalis</i> (Philippi, 1836)	510–1238
<i>Cantrainea peloritana</i> (Cantraine, 1835)	533–1228
Class Bivalvia	
Order Adapedonta	
<i>Hiatella arctica</i> (Linnaeus, 1767)	55–342
Order Arcida	
<i>Asperarca nodulosa</i> (O. F. Müller, 1776)	266–1150
<i>Bathyrarca philippiana</i> (Nyst, 1848)	462
<i>Glycymeris glycymeris</i> (Linnaeus, 1758)	86
<i>Limopsis aurita</i> (Brocchi, 1814)	593–984
<i>Limopsis minuta</i> (Philippi, 1836)	503–1008
Order Cardiida	
<i>Gari costulata</i> (W. Turton, 1822)	168
<i>Papillicardium minimum</i> (Philippi, 1836)	168
Order Carditida	
<i>Abra longicallus</i> (Scacchi, 1835)	552–1238
<i>Astarte sulcata</i> (da Costa, 1778)	128–340
Order indet.	
<i>Allogramma formosa</i> (Jeffreys, 1882)	552–942
<i>Cardiomya cadiziana</i> M. Huber, 2010	1473
<i>Cardiomya costellata</i> (Deshayes, 1835)	168–1008
<i>Cardiomya striata</i> (Jeffreys, 1876)	1008
<i>Halicardia flexuosa</i> (A. E. Verrill & S. Smith, 1881)	1818
Order Limida	
<i>Acesta excavata</i> (Fabricius, 1779)	342–800
<i>Lima marioni</i> P. Fischer, 1882	533–1228
<i>Limea crassa</i> (Forbes, 1844)	657
Order Littorinimorpha	
<i>Cabestana cutacea</i> (Linnaeus, 1767)	128
Order Lucinida	
<i>Axinulus croulinensis</i> (Jeffreys, 1847)	156–1318
<i>Genaxinus eumyrius</i> (M. Sars, 1870)	1130
<i>Thyasira succisa</i> (Jeffreys, 1876)	457–1470
Order Mytilida	
<i>Gregariella fischeri</i> (E.A. Smith, 1885)	800
<i>Modiolula phaseolina</i> (Philippi, 1844)	128
Order Nuculanida	
* <i>Malletia pianii</i> (Van Aartsen and Giannuzzi-Savelli, 1991)	1008
<i>Saccella commutata</i> (Philippi, 1844)	157–208
<i>Yoldiella lucida</i> (Lovén, 1846)	740
Order Ostreida	
<i>Neopyncnodonte cochlear</i> (Poli, 1795)	128–143
<i>Neopyncnodonte zibrowii</i> Gofas, C. Salas & Taviani, 2009	551–636
Order Pectinida	
<i>Pododesmus patelliformis</i> (Linnaeus, 1761)	110
<i>Pododesmus squama</i> (Gmelin, 1791)	103
<i>Delectopecten vitreus</i> (Gmelin, 1791)	342–1476
<i>Heteranomia squamula</i> (Linnaeus, 1758)	110
<i>Pseudamussium peslutrae</i> (Linnaeus, 1771)	342
<i>Karnekampia sulcata</i> (O. F. Müller, 1776)	551–828
<i>Spondylus gussonii</i> O.G. Costa, 1830	533–928
Order Venerida	

Table 1 (continued)

Species	Depth range (m)
* <i>Chama circinata</i> Monterosato, 1878	128
<i>Coralliophaga lithophagella</i> (Lamarck, 1819)	
<i>Gouldia minima</i> (Montagu, 1803)	86–128
<i>Timoclea ovata</i> (Pennant, 1777)	128–356
<i>Venus casina</i> Linnaeus, 1758	86–143
Class Polyplacophora	
Order Chitonida	
<i>Placiphorella atlantica</i> (Verrill & S. I. Smith, 1882)	1151
Order Lepidopleurida	
<i>Hanleya hanleyi</i> (Bean, 1844)	593
Class Scaphopoda	
Order Dentaliida	
<i>Antalis agilis</i> (M. Sars in G.O. Sars, 1872)	112–1881
<i>Antalis inaequicostata</i> (Dautzenberg, 1891)	612–964
<i>Antalis novemcostata</i> (Lamarck, 1818)	462–612
<i>Fissidentalium capillosum</i> (Jeffreys, 1877)	510–1533
Order Gadilida	
<i>Cadulus jeffreysi</i> (Monterosato, 1875)	612–1470
<i>Entalina tetragona</i> (Brocchi, 1814)	740–942
Phylum Annelida	
Order Sipuncula	
<i>Aspidosiphon (Aspidosiphon) muelleri muelleri</i> Diesing, 1851	195–1150
<i>Aspidosiphon</i> sp.	843
<i>Golfingia (Golfingia) cf. iniqua</i> (Sluiter, 1912)	986–1473
<i>Golfingia (Golfingia) muricaudata</i> (Southern, 1913)	1228
<i>Golfingia (Golfingia) vulgaris vulgaris</i> (de Blainville, 1827)	626–1008
<i>Nephasoma (Nephasoma) eremita</i> (Sars, 1851)	593
<i>Onchnesoma steenstrupii steenstrupii</i> Koren & Danielssen, 1876	156–1318
<i>Phascalion (Isomya) tuberculosum</i> Théel, 1875	700
<i>Phascalion (Phascalion) strombus strombus</i> (Montagu, 1804)	984–1228
<i>Sipunculus (Sipunculus) norvegicus</i> Danielssen, 1869	1008–1660
<i>Sipunculus (Sipunculus) cf. nudus</i> Linnaeus, 1766	128
Class Polychaeta	
Order Eunicida	
<i>Aponuphis bilineata</i> (Baird, 1870)	83–208
<i>Aponuphis brementi</i> (Fauvel, 1916)	144–200
<i>Eunice norvegica</i> (Linnaeus, 1767)	593–2291
<i>Eunice pennata</i> (Müller, 1776)	1173
<i>Eunice vittata</i> (Delle Chiaje, 1828)	157–195
<i>Hilbigneris gracilis</i> (Ehlers, 1868)	83–1881
<i>Hyalinoecia</i> spp.	128–1473
<i>Lumbrinerides crassicephala</i> (Hartman, 1965)	942–1318
<i>Ninoe armoricana</i> Glémarec, 1968	1017
<i>Paucibranchia bellii</i> (Audouin and Milne Edwards, 1833)	144–462
<i>Paradiopatra calliopa</i> Arvantisidis & Koukouras, 1997	170
<i>Paradiopatra capbretonensis</i> Aguirrezabalaga, Ceberio & Paxton, 2002	780–1183
<i>Paradiopatra</i> sp.	144–389
<i>Paradiopatra florencioi</i> Arias & Paxton, 2015	1004–1206
<i>Parorgia caeca</i> (Webster and Benedict, 1884)	112–389
<i>Protodorvillea kefersteini</i> (McIntosh, 1869)	112–1881
<i>Schistomeringos neglecta</i> (Fauvel, 1923)	195–554
<i>Schistomeringos rudolphi</i> (Delle Chiaje, 1828)	612
<i>Scoletoma laurentiana</i> (Grube, 1863)	156
Order Indet.	
<i>Aricidea (Acmira) catherinae</i> Laubier, 1967	83–657
<i>Aricidea (Acmira) cerrutii</i> Laubier, 1966	83–208
<i>Aricidea (Acmira) laubieri</i> Hartley, 1981	156–457
<i>Aricidea (Aricidea) capensis</i> Day, 1961	503
<i>Aricidea (Aricidea) pseudoarticulata</i> Hobson, 1972	83–356
<i>Aricidea (Aricidea) wassi</i> Pettibone, 1965	83–612
<i>Aricidea (Strelzovia) abyssalis</i> Laubier & Ramos, 1974	170
<i>Aricidea (Strelzovia) antennata</i> Annenkova, 1934	389–1206
<i>Aricidea (Strelzovia) claudiae</i> Laubier, 1967	157–458
<i>Aricidea (Strelzovia) maialenae</i> Aguirrezabalaga & Gil, 2009	389–1004
<i>Aricidea (Strelzovia) mariannae</i> Katzmam & Laubier, 1975	170–1184
<i>Aricidea (Strelzovia) monicae</i> Laubier, 1967	356–458
<i>Aricidea (Strelzovia) nekanae</i> Aguirrezabalaga & Gil, 2009	457–503
<i>Chirimia biceps biceps</i> (Sars, 1861)	462–554
<i>Cirrophorus branchiatus</i> Ehlers, 1908	157–200
<i>Cossura soyeri</i> Laubier, 1964	389–1206
<i>Galathowenia oculata</i> (Zachs, 1923)	157–1130
<i>Galathowenia scotiae</i> (Hartman, 1978)	1183
<i>Heteromastus filiformis</i> (Claparède, 1864)	964–1206
<i>Levinsenia flava</i> (Strelzov, 1973)	156–1470

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Levinsenia gracilis</i> (Tauber, 1879)	356–1318
<i>Levinsenia oculata</i> (Hartman, 1957)	657
<i>Magelona filiformis</i> Wilson, 1959	83–458
<i>Magelona minuta</i> Eliason, 1962	144–168
<i>Mediomastus fragilis</i> Rasmussen, 1973	112–603
<i>Microclymene tricirrata</i> Arwidsson, 1906	144
<i>Notomastus latericeus</i> Sars, 1851	144–1206
<i>Ophelina abbranchiata</i> Støp-Bowitz, 1948	356–1318
<i>Ophelina acuminata</i> Örsted, 1843	603–740
<i>Ophelina cylindricaudata</i> (Hansen, 1879)	156–1183
<i>Ophelina modesta</i> Støp-Bowitz, 1958	356
<i>Owenia fustiformis</i> Delle Chiaje, 1844	168
<i>Paradoneis abbranchiata</i> Hartman, 1965	964–1881
<i>Paradoneis bathyilvana</i> Aguirrezabalaga & Gil, 2009	356–389
<i>Paradoneis ilvana</i> Castelli, 1985	195
<i>Paradoneis lyra</i> (Southern, 1914)	170
<i>Paradoneis mikeli</i> Aguirrezabalaga & Gil, 2009	457–1183
<i>Paraphinome jeffreysii</i> (McIntosh, 1868)	657
<i>Paraonis myriamiae</i> Katzmam & Laubier, 1975	356–1017
<i>Paraonis fulgens</i> (Levinsen, 1884)	83
<i>Phylo grubei</i> (McIntosh, 1910)	499
<i>Pista cristata</i> (Müller, 1776)	168–503
<i>Scalibregma inflatum</i> Rathke, 1843	195–1173
Order Phyllozoa	
<i>Ancistrosyllis groenlandica</i> McIntosh, 1878	157–1318
<i>Ephesiella abyssorum</i> (Hansen, 1878)	1130
<i>Eumida sanguinea</i> (Örsted, 1843)	195
<i>Euthalenessa oculata</i> (Peters, 1854)	168
<i>Exogone naidina</i> Örsted, 1845	112
<i>Exogone (Exogone) sorbei</i> San Martín, Ceberio & Aguirrezabalaga, 1996	612–657
<i>Exogone verugera</i> (Claparède, 1868)	200–1033
<i>Neopolynoe chondrocladiae</i> (Fauvel, 1943)	1166–1525
<i>Paraxogone campoyi</i> (San Martín, Ceberio & Aguirrezabalaga, 1996)	1206
<i>Paraxogone caribensis</i> (San Martín, 1991)	457–1183
<i>Paraxogone hebes</i> (Webster and Benedict, 1884)	156–389
<i>Paraxogone wolfi</i> (San Martín, 1991)	503–1881
<i>Glycera celtica</i> O'Connor, 1987	112–168
<i>Glycera lapidum</i> Quatrefages, 1866	112–1881
<i>Glycera oxycephala</i> Ehlers, 1887	83–208
<i>Glycera unicornis</i> Lamarck, 1818	356–603
<i>Glyphohesione klatti</i> Friedrich, 1950	83–462
<i>Goniada maculata</i> Örsted, 1843	156–356
<i>Haplosyllis spongicola</i> (Grube, 1855)	195–503
<i>Harmothoe antilopes</i> McIntosh, 1876	208–462
<i>Laetmonice filicornis</i> Kinberg, 1856	535–1228
<i>Malmgrenia lunulata</i> (Delle Chiaje, 1830)	144–195
<i>Neoleanira tetragona</i> (Örsted, 1845)	503
<i>Odontosyllis fulgurans</i> (Audouin and Milne Edwards, 1833)	83
<i>Palposyllis prosostoma</i> Hartmann-Schröder, 1977	112
<i>Parapionosyllis brevicirra</i> Day, 1954	503–942
<i>Parapionosyllis cabezali</i> Parapar, San Martín & Moreira, 2000	1130
<i>Pholoe inornata</i> Johnston, 1839	457–1184
<i>Pilargis verrucosa</i> Saint-Joseph, 1899	457–637
<i>Psamathe fusca</i> Johnston, 1836	195
<i>Pseudexogone dineti</i> (Katzmann, Laubier & Ramos, 1974)	499–503
<i>Sphaerosyllis bulbosa</i> Southern, 1914	112–195
<i>Sphaerosyllis hystrix</i> Claparède, 1863	112
<i>Sphaerosyllis parabolosa</i> San Martín and López, 2002	170–356
<i>Sphaerosyllis pirifera</i> Claparède, 1868	170–1470
<i>Sphaerosyllis taylora</i> Perkins, 1981	112–168
<i>Sthenelais boa</i> (Johnston, 1833)	83–170
<i>Sthenelais limicola</i> (Ehlers, 1864)	168
<i>Streptosyllis campoyi</i> Brito, Núñez & San Martín, 2000	112
<i>Syllis garciai</i> (Campoy, 1982)	503–1183
<i>Syllis parapari</i> San Martín & López, 2000	657
Order Sabellida	
<i>Ditrupe arietina</i> (O. F. Müller, 1776)	168
<i>Euchone incolor</i> Hartman, 1965	144–1881
<i>Jasmineira caudata</i> Langerhans, 1880	83–612
<i>Jasmineira elegans</i> Saint-Joseph, 1894	144–1184
Order Spionida	
<i>Aonidella dayi</i> López-Jamar, 1989	1173–1184
<i>Aonides paucibranchiata</i> Southern, 1914	112–503

Table 1 (continued)

Species	Depth range (m)
<i>Auospio dibranchiata</i> Maciolek, 1981	457–1881
<i>Laonice sarsi</i> Söderström, 1920	740
<i>Prionospio caspersi</i> Laubier, 1962	457–499
<i>Prionospio cirrifera</i> Wirén, 1883	83–1173
<i>Prionospio dubia</i> Day, 1961	144–740
<i>Prionospio ehlersi</i> Fauvel, 1928	156–1033
<i>Prionospio fallax</i> Söderström, 1920	144–1183
<i>Prionospio multibranchiata</i> Berkeley, 1927	200
<i>Prionospio steenstrupi</i> Malmgren, 1867	503–1004
<i>Spiophanes bombyx</i> (Claparède, 1870)	83–1183
<i>Spiophanes kroyeri</i> Grube, 1860	112–1881
<i>Spiophanes wigleyi</i> Pettibone, 1962	156–780
Order Terebellida	
<i>Ampharete funmarchica</i> (M. Sars, 1865)	156–603
<i>Amphicteis gunneri</i> (M. Sars, 1835)	157–208
<i>Auchenoplax crinita</i> Ehlers, 1887	144–503
<i>Bradabysa villosa</i> (Rathke, 1843)	603
<i>Caulerionella bioculata</i> (Keferstein, 1862)	112–168
<i>Chaetozone gibber</i> Woodham and Chambers, 1994	144–208
<i>Chaetozone setosa</i> Malmgren, 1867	499–1173
<i>Diplocirrus glaucus</i> (Malmgren, 1867)	170
<i>Eclysippe vanelli</i> (Fauvel, 1936)	144–1470
<i>Glyphanostomum pallescens</i> (Théel, 1879)	1184
<i>Kirkegaardia dorsobranchialis</i> (Kirkegaard, 1959)	156–657
<i>Lagis koreni</i> Malmgren, 1866	168–603
<i>Lanice conchilega</i> (Pallas, 1766)	200–462
<i>Melinna cristata</i> (M. Sars, 1851)	1130–1881
<i>Melinna palmata</i> Grube, 1870	356–458
<i>Sosane sulcata</i> Malmgren, 1866	83–200
<i>Sosane wireni</i> (Hessle, 1917)	457–1130
<i>Tanseimarua vestis</i> (Hartman, 1965)	740–1004
<i>Terebellides stroemii</i> Sars, 1835	156–1206
Phylum Arthropoda	
Class Pycnogonida	
Order Pantopoda	
<i>Colossendeis colosseae</i> Wilson, 1881	1457–1525
<i>Colossendeis macerrima</i> Wilson, 1881	1464
<i>Nymphon cf. leptochelae</i> Sars, 1888	1244
<i>Bathypallenopsis</i> sp.	1510
Class Malacostraca	
Order Decapoda	
<i>Gennadas elegans</i> (Smith, 1882)	355–1473
<i>Penaeopsis serrata</i> Spence Bate, 1881	361
<i>Hymenopenaeus debilis</i> SI Smith, 1882	293–307
<i>Solenocera membranacea</i> (Risso, 1816)	292–620
<i>Robustosergia robusta</i> (SI Smith, 1882)	989–997
* <i>Uroptychus cartesi</i> Baba & Macpherson, 2012	1150
<i>Uroptychus concolor</i> (A. Milne Edwards & Bouvier, 1894)	700–1228
<i>Uroptychus rubrovittatus</i> (A. Milne Edwards, 1881)	893–1017
<i>Sternostylus formosus</i> (Filhol, 1884)	700–1228
<i>Galathea dispersa</i> Bate, 1859	195
<i>Galathea intermedia</i> Lilljeborg, 1851	202–293
<i>Galathea machadoi</i> Barrois, 1888	551–776
<i>Munida intermedia</i> A. Milne Edwards and Bouvier (1899)	293–931
<i>Munida perarmata</i> A. Milne Edwards and Bouvier (1894)	342–1225
<i>Munida sarsi</i> Huus, 1935	202–462
<i>Munidopsis acutispina</i> Benedict, 1902	776
<i>Munidopsis serricornis</i> (Lovén, 1852)	649–1476
* <i>Munidopsis similis</i> SI Smith, 1885	2291
<i>Munidopsis vaillantii</i> (A. Milne Edwards, 1881)	626–1151
* <i>Paralomis bouvieri</i> Hansen, 1908	1660
<i>Paralomis microps</i> Filhol, 1884	1228
<i>Anapagurus laevis</i> (Bell, 1845 [in Bell, 1844–1853])	202–1473
<i>Pagurus alatus</i> JC Fabricius, 1775	292–1060
<i>Pagurus carneus</i> (Pocock, 1889)	700
<i>Pagurus excavatus</i> (Herbst, 1791 [in Herbst, 1791–1796])	293
<i>Pagurus prideaux</i> Leach, 1815 [in Leach, 1815–1875]	194–401
<i>Parapagurus nudus</i> (A. Milne-Edwards, 1891)	2291
<i>Parapagurus pilosimanus</i> SI Smith, 1879	530–1595
<i>Nephropsis atlantica</i> Norman, 1882	1050–1220
<i>Nephrops norvegicus</i> (Linnaeus, 1758)	389–677
<i>Calocaris macandreae</i> Bell, 1846 [in Bell, 1844–1853]	620–1150
<i>Atelecycclus rotundatus</i> (Olivieri, 1792)	128–266
<i>Cymonopus granulatus</i> (Norman in C. W. Thomson, 1873)	786–930
<i>Cymonopus normani</i> Lankester, 1903	1225–1525

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Goneplax rhomboides</i> (Linnaeus, 1758)	293–620
<i>Dicranodromia mahieuxii</i> A. Milne-Edwards, 1882	810
<i>Paromola cuvieri</i> (Risso, 1816)	389–928
<i>Ebalia cranchii</i> Leach, 1817 [in Leach, 1815–1875]	202–293
<i>Ebalia nux</i> A. Milne-Edwards, 1883	168–786
<i>Ebalia tuberosa</i> (Pennant, 1777)	143–401
<i>Scyramathia carpenteri</i> (C.W. Thomson, 1873)	786–1178
<i>Dorhynchus thomsoni</i> C.W. Thomson, 1873	700–1513
<i>Inachus leptochirus</i> Leach, 1817 [in Leach, 1815–1875]	293–401
<i>Eurynome aspera</i> (Pennant, 1777)	202
<i>Ergasticus clouei</i> A. Milne-Edwards (1882)	617
<i>Geryon trispinosus</i> (Herbst, 1803 [in Herbst, 1799–1804])	558–1100
* <i>Bathynectes longipes</i> (Risso, 1816)	55
<i>Bathynectes maravigna</i> (Prestandrea, 1839)	143–908
<i>Liocarcinus marmoreus</i> (Leach, 1814 [in Leach, 1813–1815])	202
* <i>Liocarcinus zariquieyi</i> (Gordon, 1968)	86
<i>Macropipus tuberculatus</i> (P. Roux, 1830 [in P. Roux, 1828–1830])	292–361
<i>Polybius henslowii</i> Leach, 1820 [in Leach, 1815–1875]	194–1178
<i>Monodaeus couchii</i> (R.Q. Couch, 1851)	202–626
<i>Alpheus glaber</i> (Olivi, 1792)	170–401
<i>Alpheus macrocheles</i> (Hailstone, 1835)	776–828
<i>Caridion gordonii</i> (Spence Bate, 1858)	776
<i>Philocheles echinulatus</i> (M. Sars, 1862)	293–603
<i>Philocheles sculptus</i> (Bell, 1847 [in Bell, 1844–1853])	168
<i>Pontophilus norvegicus</i> (M. Sars, 1861)	462–1060
<i>Pontophilus spinosus</i> (Leach, 1816)	292–401
<i>Nematocarcinus exilis</i> (Spence Bate, 1888)	1476
<i>Acanthephyra pelagica</i> (Risso, 1816)	608–1473
<i>Acanthephyra purpurea</i> A. Milne-Edwards (1881)	989–997
<i>Ephyrina figueirai</i> Crosnier & Forest, 1973	925–1473
<i>Systellaspis debilis</i> (A. Milne-Edwards, 1881)	558–1473
<i>Dichelopandalus bonnieri</i> Caullery, 1896	292–1060
<i>Pandalina brevis</i> (Rathke, 1843)	207–211
<i>Pandalina profunda</i> Holthuis, 1946	355–786
<i>Plesionika heterocarpus</i> (A. Costa, 1871)	292–293
<i>Plesionika martia</i> (A. Milne-Edwards, 1882)	389–925
<i>Pasiphaea ecarina</i> Crosnier, 1969	1421
<i>Pasiphaea multidentata</i> Esmark, 1866	558
<i>Pasiphaea sivado</i> (Risso, 1816)	207–1473
<i>Pasiphaea tarda</i> Krøyer, 1845	558–1457
<i>Psathyrocaris infirma</i> Alcock & Anderson, 1894	462–500
<i>Processa canaliculata</i> Leach, 1815 [in Leach, 1815–1875]	144–401
<i>Processa noveli</i> Al-Adhub & Williamson, 1975	355
<i>Pentacheles laevis</i> Spence Bate, 1878	1510–1525
<i>Polycheles typhlops</i> Heller, 1862	293–1060
<i>Stereomastix sculpta</i> (S.I. Smith, 1880)	890–1457
<i>Odontozona edwardsi</i> (Bouvier, 1908)	776
Order Euphausiacea	
<i>Euphausia krohnii</i> (Brandt, 1851)	207–538
<i>Meganctiphanes norvegica</i> (M. Sars, 1857)	355–930
<i>Nematobrachion boopis</i> Calman, 1905	365–1024
<i>Nematoscelis megalops</i> G.O. Sars, 1883	355–1473
<i>Nyctiphanes couchii</i> (Bell, 1853)	207–538
<i>Stylocheiron longicorne</i> G.O. Sars, 1883	365–380
<i>Stylocheiron maximum</i> Hansen, 1908	462–677
Order Lophogastrida	
<i>Eucopeia hanseni</i> Nouvel, 1942	534–997
<i>Gnathophausia zoea</i> Willemoes-Suhm, 1873	361–1513
<i>Lophogaster typicus</i> M. Sars, 1857	293–355
Order Mysida	
<i>Boreomysis arctica</i> (Krøyer, 1861)	399–1050
<i>Boreomysis megalops</i> G.O. Sars, 1872	365–380
<i>Boreomysis tridens</i> G.O. Sars, 1870	989–1050
<i>Anchialina agilis</i> (G.O. Sars, 1877)	144–168
<i>Haplostylus lobatus</i> (Nouvel, 1951)	156–603
<i>Amblyops spiniferous</i> Nouvel and Lagardère, 1976	462–538
<i>Amblyops trisetosus</i> Nouvel and Lagardère, 1976	462–500
<i>Chunomysis diadema</i> Holt & Tattersall, 1905	462–500
<i>Dactylamblyops goniops</i> Tattersall, 1907	989–997
<i>Dactylorhynchus dimorphus</i> Nouvel and Lagardère, 1976	462–500
<i>Erythropus neapolitanus</i> Colosi, 1929	368–369
<i>Paramblyops rostratus</i> Holt & Tattersall, 1905	365–997
<i>Parapseudomma calloptura</i> (Holt & Tattersall, 1905)	365–538
<i>Parerythropus obesus</i> (G.O. Sars, 1864)	989–997

Table 1 (continued)

Species	Depth range (m)
<i>Pseudomma affine</i> G.O. Sars, 1870	399–529
<i>Pseudomma kruppi</i> W. Tattersall, 1909	462–500
<i>Pseudomma nanum</i> Holt & Tattersall, 1906	534–538
<i>Mysidetes farrani</i> (Holt & Tattersall, 1905)	462–786
<i>Leptomysis cf. megalops</i> Zimmer, 1915	207–211
<i>Mysidopsis parva</i> Zimmer, 1915	365–380
<i>Mysidella biscayensis</i> Lagardère & Nouvel, 1980	462–538
Order Amphipoda	
<i>Cleonardopsis carinata</i> K.H. Barnard, 1916	462–500
<i>Apolochus neapolitanus</i> (Della Valle, 1893)	207–211
<i>Amphilochooides boeckii</i> G.O. Sars, 1895	462–538
<i>Amphilochooides serratipes</i> (Norman, 1869)	462–997
<i>Gitana cf. sarsi</i> Boeck, 1871	207–211
<i>Gitana</i> sp.B	989–1024
<i>Epimeria (Epimeria) cornigera</i> (Fabricius, 1779)	981–1238
<i>Epimeria (Epimeria) parasitica</i> (M. Sars, 1858)	293–620
<i>Eusirella elegans</i> Chevreux, 1908	462–500
<i>Eusirus biscayensis</i> Bonnier, 1896	989–997
<i>Eusirus longipes</i> Boeck, 1861	207–500
<i>Eusirus</i> sp.B	989–997
<i>Rhachotropis caeca</i> Ledoyer, 1977	462–538
<i>Rhachotropis faeroensis</i> Stephensen, 1944	462–997
<i>Rhachotropis gracilis</i> Bonnier, 1896	462–997
<i>Rhachotropis palporum</i> Stebbing, 1908	1019–1024
<i>Rhachotropis rostrata</i> Bonnier, 1896	462–997
<i>Laphystiopsis planifrons</i> G.O. Sars, 1893	989–997
<i>Leucothoe incisa</i> Robertson, 1892	207–369
<i>Liljeborgia pallida</i> (Spence Bate, 1857)	195–740
<i>Arrhis mediterraneus</i> Ledoyer, 1983	462–1024
<i>Bathymedon acutifrons</i> Bonnier, 1896	462–1024
<i>Bathymedon longirostris</i> Jaume, Cartes & Sorbe, 1998	462–1024
<i>Bathymedon monoculodiformis</i> Ledoyer, 1983	462–538
<i>Halicreion aequicornis</i> (Norman, 1869)	462–997
<i>Monoculodes cf. latissimus</i> Stephensen, 1931	989–997
<i>Monoculodes packardii</i> Boeck, 1871	462–1024
<i>Oediceroides pilosa</i> Ledoyer, 1983	1173
<i>Oediceropsis brevicornis</i> (Liljeborg, 1865)	355–786
<i>Periculodes longimanus</i> (Spence Bate and Westwood, 1868)	83–997
<i>Synchelidium haplocheles</i> (Grube, 1864)	144
<i>Synchelidium maculatum</i> Stebbing, 1906	83–780
<i>Westwoodilla caecula</i> (Spence Bate, 1857)	144–458
<i>Stenothoe valida</i> Dana, 1852	503
<i>Stilipes</i> sp.A	462–500
<i>Ampelisca aequicornis</i> Bruzelius, 1859	462–1470
<i>Ampelisca brevicornis</i> (Costa, 1853)	168–499
<i>Ampelisca gibba</i> G.O. Sars, 1883	144–1173
<i>Ampelisca pusilla</i> G.O. Sars, 1891	534–538
<i>Ampelisca spinifer</i> Reid, 1951	144–1184
<i>Ampelisca spinipes</i> Boeck, 1861	503–1184
<i>Ampelisca tenuicornis</i> Liljeborg, 1856	144–462
<i>Ampelisca typica</i> (Spence Bate, 1856)	83–1470
<i>Ampelisca uncinata</i> Chevreux, 1887	534–538
<i>Byblis guernei</i> Chevreux, 1887	462–942
<i>Argissa hamatipes</i> (Norman, 1869)	462–1024
<i>Nototropis vedlomensis</i> (Spence Bate & Westwood, 1862)	83–208
<i>Cyphocaris anonyx</i> Boeck, 1871	368–997
<i>Lepechinella manco</i> Barnard, 1973	462–997
<i>Lysianassa cf. plumosa</i> Boeck, 1871	462–500
<i>Melphidippa</i> sp.B	462–997
<i>Melphidippella macra</i> (Norman, 1869)	368–369
<i>Halice abyssii</i> Boeck, 1871	1019–1024
<i>Halicoides anomalus</i> Walker, 1896	989–1024
<i>Nicippe tumida</i> Bruzelius, 1859	355–997
<i>Harpinia antennaria</i> Meinert, 1890	168–538
<i>Harpinia laevis</i> G.O. Sars, 1891	534–1881
<i>Harpinia pectinata</i> (Sars, 1891)	1017–1318
<i>Harpinia serrata</i> G.O. Sars, 1879	657–1184
<i>Metaphoxus simplex</i> (Spence Bate, 1857)	462–1318
<i>Podopriion bolivari</i> Chevreux, 1891	462–500
<i>Scopelochirus hopei</i> (Costa in Hope, 1851)	207–997
<i>Trischizostoma nicaeense</i> (Costa, 1853)	365–997
<i>Hippomedon denticulatus</i> (Spence Bate, 1857)	83–356
<i>Lepidopereum typhlops</i> Bonnier, 1896	989–997
<i>Metambasia faeroensis</i> Stephensen, 1923	462–1024
<i>Paracentromedon crenulatus</i> (Chevreux, 1900)	534–1033

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Tryphosa nana</i> (Krøyer, 1846)	207–997
<i>Tryphosella</i> cf. <i>sarsi</i> Bonnier, 1893	195–380
<i>Tryphosites alleni</i> Sexton, 1911	462–997
<i>Tryphosites longipes</i> (Spence Bate and Westwood, 1861)	365–964
<i>Sophrasynce robertsoni</i> Stebbing & Robertson, 1891	458
<i>Mediterexis mimonectes</i> (Ruffo, 1975)	368–1024
<i>Stegocephaloides auratus</i> (G.O. Sars, 1883)	207–997
<i>Ilerastrae ilergetes</i> (J.L. Barnard, 1964)	462–538
<i>Pseudotiron bouvieri</i> Chevreux, 1895	207–538
<i>Syrrhoë affinis</i> Chevreux, 1908	462–500
<i>Syrrhoites pusilla</i> Enequist, 1949	365–538
<i>Syrrhoites</i> sp.A	989–997
<i>Syrrhoites walkeri</i> Bonnier, 1896	989–997
<i>Centromedon laevis</i> (Bonnier, 1896)	989–1024
<i>Ichnopus spinicornis</i> Boeck, 1861	112–355
<i>Tmetonyx similis</i> (G.O. Sars, 1891)	168
<i>Carangolia barnardi</i> Jaume & Sorbe, 2001	462–1024
<i>Urothoe elegans</i> Spence Bate, 1857	356–1318
<i>Themisto compressa</i> Goës, 1866	207–1024
<i>Primno brevidens</i> Bowman, 1978	534–538
<i>Vibilia armata</i> Bovallius, 1887	368–1024
<i>Scina borealis</i> (G.O. Sars, 1883)	989–997
<i>Carangoliopsis spinulosa</i> Ledoyer, 1970	462–500
<i>Liropus cachuchoensis</i> Guerra-García, Sorbe & Frutos, 2007	989–1024
<i>Parvipalpus linea</i> Mayer, 1890	503
<i>Parvipalpus major</i> Carausu, 1941	207–538
<i>Phtisica marina</i> Slabber, 1769	201–211
<i>Pseudoprotella phasma</i> (Montagu, 1804)	793–1090
<i>Chevreuxius grandimanus</i> Bonnier, 1896	462–1024
<i>Siphonocetes</i> sp.	207–538
<i>Bonnierella abyssorum</i> (Bonnier, 1896)	462–1024
<i>Centraoecetes striatus</i> (Myers & McGrath, 1979)	462
<i>Gammaropsis maculata</i> Johnston, 1828	195
<i>Megamphopus cornutus</i> Norman, 1869	1173
<i>Laetmatophilus tuberculatus</i> Bruzelius, 1859	462–500
<i>Unciolella lunata</i> Chevreux, 1911	1019–1024
<i>Bathyporeia sarsi</i> Watkin, 1938	83
<i>Apherusa bispinosa</i> (Spence Bate, 1857)	399–529
<i>Apherusa ovalipes</i> Norman & Scott, 1906	201–211
<i>Eriopisa elongata</i> (Bruzelius, 1859)	1004
<i>Animoceradocus semiserratus</i> (Spence Bate, 1862)	195
<i>Maerella tenuimana</i> (Spence Bate, 1862)	195
<i>Othomaera othonis</i> (H. Milne Edwards, 1830)	168–195
<i>Abludomelita aculeata</i> (Chevreux, 1911)	207–211
<i>Abludomelita gladiosa</i> (Spence Bate, 1862)	195
Order Cumacea	
<i>Bathycuma brevirostre</i> (Norman, 1879)	989–1024
<i>Bodotria arenosa</i> Goodsir, 1843	83–211
<i>Bodotria scorpioides</i> (Montagu, 1804)	112
<i>Iphinoe serrata</i> Norman, 1867	144–156
<i>Cyclaspis longicaudata</i> G.O. Sars, 1865	534–538
<i>Cyclaspoides sarsi</i> Bonnier, 1896	1019–1024
<i>Diastylis cornuta</i> (Boeck, 1864)	462–500
<i>Diastylodes bacescoi</i> Fage, 1940	462–538
<i>Diastylodes biplicatus</i> (G.O. Sars, 1865)	168–538
<i>Diastylodes serratus</i> (G.O. Sars, 1865)	368–369
<i>Leptostylis macrura</i> G.O. Sars, 1869	462–1024
<i>Makrokyllindrus (Adiastylis) josephinae</i> (G.O. Sars, 1871)	462–1318
<i>Makrokyllindrus (Adiastylis) longipes</i> (G.O. Sars, 1871)	462–1130
<i>Makrokyllindrus (Adiastylis) tubulicauda</i> (Calman, 1905)	1019–1173
<i>Vemakylindrus hastatus</i> (Hansen, 1920)	462–1024
<i>Hemilamprops cristatus</i> (G.O. Sars, 1869)	462–1024
<i>Mesolamprops denticulatus</i> Ledoyer, 1983	462–500
<i>Platysympus typicus</i> (G.O. Sars, 1869)	1019–1024
<i>Platytyphlops orbicularis</i> (Calman, 1905)	462–997
<i>Eudorella</i> cf. <i>truncatula</i> (Bate, 1856)	389–997
<i>Leucon (Crymoleucon)</i> sp.A	989–997
<i>Leucon (Leucon) affinis</i> Fage, 1951	534–538
<i>Leucon (Macrauloeucon) siphonatus</i> Calman, 1905	462–997
<i>Campylaspis glabra</i> Sars, 1878	368–538
<i>Campylaspis horridoides</i> Stephensen, 1915	462–500
<i>Campylaspis macrophthalma</i> Sars, 1878	157–389
<i>Campylaspis rostrata</i> Calman, 1905	657–1318
<i>Campylaspis squamifera</i> Fage, 1929	462–538
<i>Campylaspis sulcata</i> Sars, 1870	368–369

Table 1 (continued)

Species	Depth range (m)
<i>Campylaspis verrucosa</i> Sars, 1866	462–500
<i>Campylaspis vitrea</i> Calman, 1906	989–997
<i>Cumella (Cumella) pygmaea</i> G.O. Sars, 1865	144
<i>Cumellopsis puritani</i> Calman, 1906	462–538
<i>Nannastacus atlanticus</i> (Bacescu & Muradian, 1972)	462–500
<i>Procampylaspis armata</i> Bonnier 1896	462–997
<i>Procampylaspis ommidion</i> Jones, 1984	989–997
<i>Styloptocuma gracillimum</i> (Calman, 1905)	462–997
<i>Pseudocuma (Pseudocuma) simile</i> G.O. Sars, 1900	83
Order Isopoda	
<i>Chelator</i> sp.	462–997
<i>Eugerdia</i> sp.	207–1024
<i>Cornuamesus biscayensis</i> (Chardy, 1975)	462–500
<i>Cornuamesus longiramus</i> (Kavanagh & Sorbe, 2006)	462–500
<i>Ischnomesus</i> sp.	989–997
<i>Janira maculosa</i> Leach, 1814	195
<i>Janirella hessleri</i> Chardy, 1975	780–1184
<i>Belonectes parvus</i> (Bonnier, 1896)	462–538
<i>Disconectes latirostris</i> (G. O. Sars, 1883)	368–500
<i>Ilyarachna longicornis</i> (G.O. Sars, 1864)	365–1024
<i>Ilyarachna polita</i> Bonnier, 1896	989–997
<i>Lipomera (Paralipomera)</i> sp.A	368–1024
<i>Lipomerinae</i> sp.A	1019–1024
<i>Munnopsurus atlanticus</i> (Bonnier, 1896)	207–997
<i>Munnopsurus</i> sp.C	462–997
<i>TythSCOPE megalura</i> (G.O. Sars, 1872)	989–1024
<i>Notoxenoides</i> sp.A	462–500
<i>Paramunna bilobata</i> (G.O. Sars, 1866)	365–538
<i>Leptanthura</i> sp.	989–997
<i>Aegiochus ventrosa</i> (M. Sars, 1859)	1464
<i>Aega bicarinata</i> Leach, 1818	776
<i>Eurydice</i> sp.	989–997
<i>Metacirrolana hansenii</i> (Bonnier, 1896)	989–997
<i>Natatolana borealis</i> (Lilljeborg, 1851)	355–620
<i>Politolana sanchezi</i> Frutos & Sorbe, 2010	462–617
<i>Gnathia</i> sp.	365–1024
<i>BathycOpea typhlops</i> Tattersall, 1905	462–538
<i>Cymodoce truncata</i> Leach, 1814	195
Order Tanaidacea	
<i>Apseudes grossimanus</i> Norman & Stebbing, 1886	457–1881
<i>Agathotanaia ingolfi</i> Hansen, 1913	534–997
<i>Cryptocopoides</i> sp.	462–538
<i>Leptognathia manca</i> Sars, 1882	112–1318
<i>Araphura brevimanus</i> (Lilljeborg, 1864)	157–780
<i>Typhlotanaia aequiremis</i> (Lilljeborg, 1864)	554–1033
Order Leptostraca	
<i>Sarsinebalia typhlops</i> (G. O. Sars, 1870)	534–997
Class Thecostraca	
Order Balanomorpha	
<i>Bathylasma hirsutum</i> (Hoek, 1883)	1513–1660
Order Calanticomorpha	
* <i>Aurivillialepas calycula</i> (Aurivillius, 1898)	776–928
<i>Gruvelialepas</i> sp.A	1421–2291
* <i>Scillaelepas grimaldii</i> (Aurivillius, 1898)	1018–1228
<i>Smilium acutum</i> (Hoek, 1883)	1387–2291
Order Scalpelloomorpha	
<i>Arcoscalpellum incisum</i> (Aurivillius, 1898)	984
<i>Arcoscalpellum michelottianum</i> (Seguenza, 1876)	1228
Order Verrucomorpha	
* <i>Altiverruca obliqua</i> (Hoek, 1883)	1525
<i>Metaverruca recta</i> (Aurivillius, 1898)	1476–1533
<i>Metaverruca trisulcata</i> (Gruvel, 1900)	1525
Phylum Echinodermata	
Class Crinoidea	
Order Comatulida	
<i>Leptomera celtica</i> (M'Andrew & Barrett, 1857)	510–1660
Class Asteroidea	
Order Brisingida	
<i>Brisinga</i> cf. <i>endecacnemus</i> Asbjørnsen, 1856	510–1476
<i>Hymenodiscus</i> cf. <i>coronatus</i> (Sars, 1871)	626–942
<i>Novodinia pandina</i> (Sladen, 1889)	942–1660
Order Forcipulatida	
<i>Marthasterias glacialis</i> (Linnaeus, 1758)	55–128
<i>Neomorphaster margaritaceus</i> (Perrier in Milne-Edwards, 1882)	510–1473

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Zoroaster fulgens</i> Wyville Thomson, 1873	535–1464
Order Paxillosida	
<i>Astropecten irregularis</i> (Pennant, 1777)	266–510
<i>Luidia sarsii</i> Düben & Koren in Düben, 1844	510–578
<i>Persephonaster patagiatus</i> (Sladen, 1889)	510–1473
<i>Plutonaster bifrons</i> (Wyville Thomson, 1873)	1464–1473
<i>Pseudarchaster parelii</i> (Düben & Koren, 1846)	1051
<i>Psilaster andromeda</i> (Müller & Troschel, 1842)	535–1464
* <i>Radiaster tizardi</i> (Sladen, 1882)	1228
Order Notomyotida	
<i>Benthopecten simplex</i> (Perrier, 1881)	1244
<i>Pontaster tenuispinus</i> (Düben & Koren, 1846)	510–552
Order Spinulosida	
<i>Henricia caudani</i> (Koehler, 1895)	551–1244
* <i>Henricia sexradiata</i> (Perrier, 1881)	700
Order Valvatida	
<i>Anseropoda placenta</i> (Pennant, 1777)	128
<i>Ceramaster grenadensis</i> (Perrier, 1881)	342–1150
<i>Nymphaster arenatus</i> (Perrier, 1881)	510–1464
<i>Odontaster mediterraneus</i> (von Marenzeller, 1893)	700
<i>Peltaster placenta</i> (Müller & Troschel, 1842)	342–928
<i>Plinthaster dentatus</i> (Perrier, 1884)	1228–1473
<i>Porania (Porania) pulvillus</i> (O.F. Müller, 1776)	1244
<i>Poraniomorpha (Poraniomorpha) hispida</i> (M. Sars, 1872)	551
Order Velatida	
<i>Pteraster militaris</i> (O.F. Müller, 1776)	551
Class Ophiuroidea	
Order Euryalida	
<i>Asteronyx loveni</i> Müller & Troschel (1842)	844–908
Order Amphilepidida	
<i>Asteroschema inornatum</i> Koehler, 1906	578–1476
<i>Amphilepis norvegica</i> (Ljungman, 1865)	538–783
<i>Amphiura (Amphiura) grandisquama</i> Lyman, 1869	538–790
<i>Amphiura filiformis</i> (O.F. Müller, 1776)	342–538
<i>Amphiura griegi</i> Mortensen, 1920	342
<i>Histampica duplicata</i> (Lyman, 1875)	1473
<i>Ophiactis abyssicola</i> (M. Sars, 1861)	593–2291
<i>Ophiactis balli</i> (W. Thompson, 1840)	266–626
<i>Ophiothamnus affinis</i> Ljungman, 1872	930–1473
<i>Ophiothrix</i> spp.	342–893
Order Ophiacanthida	
<i>Ophiacantha abyssicola</i> G.O. Sars, 1872	769–1476
<i>Ophiacantha aristata</i> Koehler, 1895	462–1464
<i>Ophiacantha bidentata</i> (Bruzelius, 1805)	593–1473
<i>Ophiacantha lineata</i> Koehler (1896)	1228–1464
<i>Ophiacantha smitti</i> Ljungman, 1872	844–1244
<i>Ophiomitrella globifera</i> (Koehler, 1895)	1164–2291
<i>Ophionyxca serpentaria</i> Lyman, 1883	1228–1244
Order Ophioscolecida	
<i>Ophionyces grandis</i> Lyman, 1879	984
Order Ophiurida	
<i>Amphiophiura bullata</i> (Thomson, 1877)	1473
<i>Ophiocten affinis</i> (Lütken, 1858)	355–984
<i>Ophiomusa lymani</i> (Wyville Thomson, 1873)	1476–1533
<i>Ophiura (Dictenophiura) carnea</i> Lütken, 1858	355–783
<i>Ophiura ophiura</i> (Linnaeus, 1758)	355
<i>Ophiuroglypha irrorata irrorata</i> (Lyman, 1878)	1476–2291
Class Echinoidea	
Order Cidaroida	
<i>Cidaris cidaris</i> (Linnaeus, 1758)	535–1244
<i>Histocidaris purpurata</i> (Thomson, 1872)	1008–1464
<i>Stereocidaris ingolfiana</i> Mortensen, 1903	1228–1473
Order Echinothurioida	
<i>Araeosoma fenestratum</i> (Thomson, 1872)	533–1244
<i>Calveriosoma hystrix</i> (Thomson, 1872)	1228–1244
<i>Phormosoma placenta</i> Thomson, 1872	535–1473
Order Camarodonta	
<i>Echinus melo</i> Lamarck, 1816	55–1051
<i>Gracilechinus acutus</i> (Lamarck, 1816)	125–1051
* <i>Gracilechinus affinis</i> (Mortensen, 1903)	530
<i>Gracilechinus alexandri</i> (Danielsen & Koren, 1883)	1228
<i>Gracilechinus elegans</i> (Düben & Koren, 1844)	510–1476
Order Spatangoida	
<i>Spatangus purpureus</i> O.F. Müller, 1776	86
Class Holothuroidea	

Table 1 (continued)

Species	Depth range (m)
Order Dendrochirotida	
<i>Psolus rufus</i> Fernández-Rodríguez, Arias, Borrell, Anadón, Massin & Acuña, 2017	1476–2291
<i>Psolus tessellatus</i> Koehler, 1896	593–2291
<i>Stereoderma kirchsbergii</i> (Heller, 1868) Panning, 1949	462
Order Elaspodida	
<i>Benthogone rosea</i> Koehler, 1895	1051–1464
<i>Laetmogone violacea</i> Théel, 1879	535–1228
Order Holothuriida	
<i>Holothuria (Panningothuria) forskali</i> Delle Chiaje, 1823	55–103
Order Molpadida	
<i>Molpadia musculus</i> Risso, 1826	560–1744
Order Synallactida	
<i>Bathylotes natans</i> (M. Sars, 1868)	1008–1473
<i>Parastichopus regalis</i> (Cuvier, 1817)	125–128
<i>Parastichopus tremulus</i> (Gunnerus, 1767)	535–1244
Phylum Chordata	
Class Actinopteri	
Order Acanthuriformes	
<i>Capros aper</i> (Linnaeus, 1758)	194–357
Order Alepocephaliformes	
<i>Alepocephalus bairdii</i> Goode & Bean, 1879	925–1473
<i>Alepocephalus rostratus</i> Risso, 1820	925–1457
<i>Xenodermichthys copei</i> (Gill, 1884)	558–1473
Order Anguilliformes	
<i>Conger conger</i> (Linnaeus, 1758)	194–578
<i>Nemichthys scolopaceus</i> Richardson, 1848	1007–1457
<i>Nettastoma melanura</i> Rafinesque, 1810	925–1051
<i>Pseudoplichthys splendens</i> (Lea, 1913)	558
<i>Synaphobranchus kaupii</i> Johnson, 1862	558–1473
Order Argentiniformes	
<i>Argentina sphyraena</i> Linnaeus, 1758	194–292
Order Aulopiformes	
<i>Bathypterois dubius</i> Vaillant, 1888	786–1473
<i>Chlorophthalmus agassizi</i> Bonaparte, 1840	357–389
Order Beryciformes	
<i>Beryx decadactylus</i> Cuvier, 1829	578
<i>Hoplostethus atlanticus</i> Collett, 1889	925
<i>Poromitra capito</i> Goode & Bean, 1883	1007
Order Callionymiformes	
<i>Callionymus lyra</i> Linnaeus, 1758	194
<i>Callionymus maculatus</i> Rafinesque, 1810	293
Order Carangiformes	
<i>Trachurus trachurus</i> (Linnaeus, 1758)	194–293
Order Gadiformes	
<i>Coelorinchus caelorhincus</i> (Risso, 1810)	292–677
<i>Coelorinchus labiatus</i> (Köhler, 1896)	1457–1473
<i>Coryphaenoides carapinus</i> Goode & Bean, 1883	1457
<i>Coryphaenoides mediterraneus</i> (Giglioli, 1893)	1457
<i>Coryphaenoides rupestris</i> Gunnerus, 1765	677–1457
<i>Gadiculus argenteus</i> Guichenot, 1850	194–677
<i>Gadomus arcuatus</i> (Goode & Bean, 1886)	1457
<i>Gadomus dispar</i> (Vaillant, 1888)	1051
<i>Gaidropsarus macrophthalmus</i> (Günther, 1867)	293–620
<i>Gaidropsarus vulgaris</i> (Cloquet, 1824)	786
<i>Halargyreus johnsonii</i> Günther, 1862	530–1457
<i>Hymenocephalus italicus</i> Giglioli, 1884	558–1007
<i>Lepidion lepidion</i> (Risso, 1810)	530–1457
<i>Malacocephalus laevis</i> (Lowe, 1843)	194–677
<i>Melanonus zugmayeri</i> Norman, 1930	925
<i>Merluccius merluccius</i> (Linnaeus, 1758)	194–677
<i>Micromesistius poutassou</i> (Risso, 1827)	194–677
<i>Molva macrophthalma</i> (Rafinesque, 1810)	357–578
<i>Mora moro</i> (Risso, 1810)	578–1051
<i>Nezumia aequalis</i> (Günther, 1878)	530–1457
<i>Nezumia sclerorhynchus</i> (Valenciennes, 1838)	786
<i>Phycis blennoides</i> (Brünnich, 1768)	292–1051
<i>Trachyrinchus scabrus</i> (Rafinesque, 1810)	558–1457
<i>Trisopterus minutus</i> (Linnaeus, 1758)	194
Order Lophiiformes	
<i>Lophichthys budegassa</i> Spinola, 1807	292–357
<i>Lophius piscatorius</i> Linnaeus, 1758	194–1051
Order Mulliformes	
<i>Mullus surmuletus</i> Linnaeus, 1758	194
Order Myctophiformes	

(continued on next page)

Table 1 (continued)

Species	Depth range (m)
<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	578–608
<i>Lampanyctus crocodilus</i> (Risso, 1810)	677–1457
<i>Lampanyctus pusillus</i> (Johnson, 1890)	578
<i>Myctophum punctatum</i> Rafinesque, 1810	530
<i>Notoscopelus kroeyeri</i> (Malm, 1861)	608–620
Order Notacanthiformes	
<i>Aldrovandia phalacra</i> (Vaillant, 1888)	1051
<i>Halosaurus ovenii</i> Johnson, 1864	1012
<i>Notacanthus bonaparte</i> Risso, 1840	558–1457
Order Ophidiiformes	
<i>Cataetx alleni</i> (Byrne, 1906)	930
Order Perciformes	
<i>Chelidonicichthys cuculus</i> (Linnaeus, 1758)	194
<i>Helicolenus dactylopterus</i> (Delaroche, 1809)	194–608
<i>Melanostigma atlanticum</i> Koefoed, 1952	558–1051
<i>Paraliparis membranaceus</i> Günther, 1887	530–617
<i>Scorpaena loppei</i> Cadenat, 1943	194
<i>Trigla lyra</i> Linnaeus, 1758	292–357
Order Pleuronectiformes	
<i>Arnoglossus imperialis</i> (Rafinesque, 1810)	194
<i>Bathysolea profundicola</i> (Vaillant, 1888)	355–1060
<i>Lepidorhombus bosci</i> (Risso, 1810)	194–1015
<i>Lepidorhombus whiffiagonis</i> (Walbaum, 1792)	194–357
<i>Microchirus variegatus</i> (Donovan, 1808)	292–361
Order Scombriformes	
<i>Aphanopus carbo</i> Lowe, 1839	578–1007
Order Stomiiformes	
<i>Argyropelecus hemigymnus</i> Cocco, 1829	361–1457
<i>Chauliodus sloani</i> Bloch & Schneider, 1801	1051
<i>Cyclothone braueri</i> Jespersen & Tåning, 1926	578
<i>Cyclothone microdon</i> (Günther, 1878)	1007
<i>Maurolicus muelleri</i> (Gmelin, 1789)	293
<i>Polymetne corythaeola</i> (Alcock, 1898)	608
<i>Sigmops elongatus</i> (Günther, 1878)	1015
Order Zeiformes	
<i>Neocyttus helgae</i> (Holt & Byrne, 1908)	1457
Class Elasmobranchii	
Order Carcharhiniformes	
<i>Galeus melastomus</i> Rafinesque, 1810	292–1051
* <i>Galeus murinus</i> (Collett, 1904)	1457–1473
<i>Scyliorhinus canicula</i> (Linnaeus, 1758)	194–578
Order Rajiformes	
<i>Dipturus oxyrinchus</i> (Linnaeus, 1758)	1457
* <i>Neoraja caerulea</i> (Stehmann, 1976)	1457
* <i>Neoraja iberica</i> Stehmann, Sèret, Costa & Baro, 2008	510–530
* <i>Rajella kukujevi</i> (Dolganov, 1985)	1051
Order Squaliformes	
<i>Centrophorus squamosus</i> (Bonnaterre, 1788)	1051
<i>Centroscymnus coelolepis</i> Barbosa du Bocage and de Brito Capello, 1864	1457
<i>Deania calcea</i> (Lowe, 1839)	925–1457
<i>Deania profundorum</i> (Smith & Radcliffe, 1912)	578–1007
<i>Etmopterus princeps</i> Collett, 1904	1007–1457
<i>Etmopterus pusillus</i> (Lowe, 1839)	558–1051
<i>Etmopterus spinax</i> (Linnaeus, 1758)	530–677
<i>Scymnodon ringens</i> Barbosa du Bocage and de Brito Capello, 1864	530–1007
Class Holoccephali	
Order Chimaeriformes	
<i>Chimaera monstrosa</i> Linnaeus, 1758	361–1457
<i>Hydrolagus mirabilis</i> (Collett, 1904)	677–1457

Register of Marine Species (WoRMS, 2022). The complete names of all species with authority and year are given in Table 1 and for this reason their repetition throughout the manuscript is avoided. Specimens were photographed, preserved in ethanol and identified based on their morphological characteristics using specialized literature for each taxon and the appropriate protocols and techniques for their visualization.

In order to assess the representativeness of the fauna collected in this sampling effort, we extracted, for each of the major phyla, the total number of species recorded for Northern Demarcation (NOR)" (e.g. Spanish part of Bay of Biscay and Galicia) in the "Lista patrón española de especies marinas (LPEM)", elaborated by a panel of experts

nationwide and officially published in February 2017 by the then Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente. We then filtered this list for species pertaining to the World Register of Deep-Sea species (Glover et al., 2022), a subset of the WoRMS database which comprises species which normally occur below 500 m depth. These two numbers (total LPEM for NOR and fraction of those registered as deep sea) provide a bracket for the number of species expected to be present in the area of interest.

4. Results

In the ACS a total of 1015 macro- and megabenthic species were identified, included in the following phyla: 98 Porifera (from 86 to 2291 m in depth), 153 Cnidaria (55–2291 m), 14 Brachiopoda (55–1818 m), 22 Bryozoa (86–908 m), 97 Mollusca (55–2291 m), 151 Annelida (83–2291 m), 315 Arthropoda (55–2291 m), 74 Echinodermata (86–2291 m) and 91 Vertebrata (194–1473 m) (Table 1).

4.1. Phylum Porifera

The analysis of this phylum for the ACS, based on 1875 samples collected, detected the class Demospongiae (84%) as the most abundant one followed by Hexactinellida (15%) and Homoscleromorpha and Calcarea (1%). The Class Demospongiae was dominated by the orders Poecilosclerida (27%), Tetractinellida (24%), Axinellida (15%), Haplosclerida (6%), Desmacellida (3%), among others. Poecilosclerida include many encrusting species as the blue *Hymedesmia* (*Hymedesmia*) *paupertas* the most abundant species on rocky and coral substrates as well as *Hamacantha* (*Hamacantha*) *johnsoni*, *Hamacantha* (*Vomerula*) *falcula* and *Plocamionida ambigua*. Also noteworthy is the presence of carnivorous sponges such as *Chondrocladia* (*Chondrocladia*) *robertballardi* and *Cladorhiza abyssicola* or *Asbestopluma* sp. which were mainly found between 776 and 2291 m depth, in the Gaviera Canyon and at the NE of the Avilés Canyon. Tetractinellida represented also an important group with ecological implications in benthic ecosystems, since some species in this order are relatively large in size and can form dense aggregations. Among the most important species in terms of biomass and specific richness, we found *Geodia megastrella* (342–2291 m), *Geodia pachydermata* (551–2291 m), *Characella pachastrelloides* (593–1228 m), *Poecillastra compressa* (86–776 m) and *Pachastrella ovis-ternata* (593–776 m), species that were particularly abundant in the Avilés and Corbiro Canyons heads, in the Gaviera Canyon and El Agudo de Fuera. Also, *P. compressa* was found in El Canto Nuevo and in the massive rocky outcrop at the eastern part, from AC head, of the continental shelf. *Neoschrammeniella* cf. *bowbankii* was only found in rocky walls at the Corbiro Canyon between 533 and 695 m depth. Among Axinellida it is worth mentioning the presence of sponge aggregations of species of the genus *Phakellia*, including *Phakellia ventilabrum*, with a preference for rocky circalitoral bottoms, and *Phakellia robusta*, found down to 1000 m in the study area. In the Class Hexactinellida the best represented orders were Amphidiscosida (63%) due to the presence of the nest sponge *Pheronema carpenteri*, preferentially located in soft bottoms between 1008 and 1744 m, and Sceptulophora (22%) due to the presence of *Aphrocallistes beatrix* (626–1325 m) associated to the cold water corals and developing on coral rubble as substrate and *Peri-phragella lusitanica* (1476–2291 m). The order Lyssacinoida (11%) also played an important role in the ACS with species such as *Asconema setubalense* (317–1476 m) and *Regadrella phoenix* (593–1660 m). A total of 15 new records for the phylum Porifera were recorded in the ACS, which are also new records for the Bay of Biscay (Table 1): *Acanthancora aenigma*, *Acanthancora* cf. *schmidti*, *Axinella vellerea*, *Guitarra solorzanoi*, *Hymerhabdia typica*, *Melonanchora emphysema*, *Monocrepidium vermiculatum*, *Siphonodictyon infestum*, *Stylocordyla pellita*, *Tentorium* cf. *levantinum*, *Pachastrella* cf. *nodulosa* and *Thenea schmidtii* distributed principally at the W of the Avilés Canyon, in the rocky outcrop of the continental shelf, in the Corbiro Canyon head and between El Agudo de

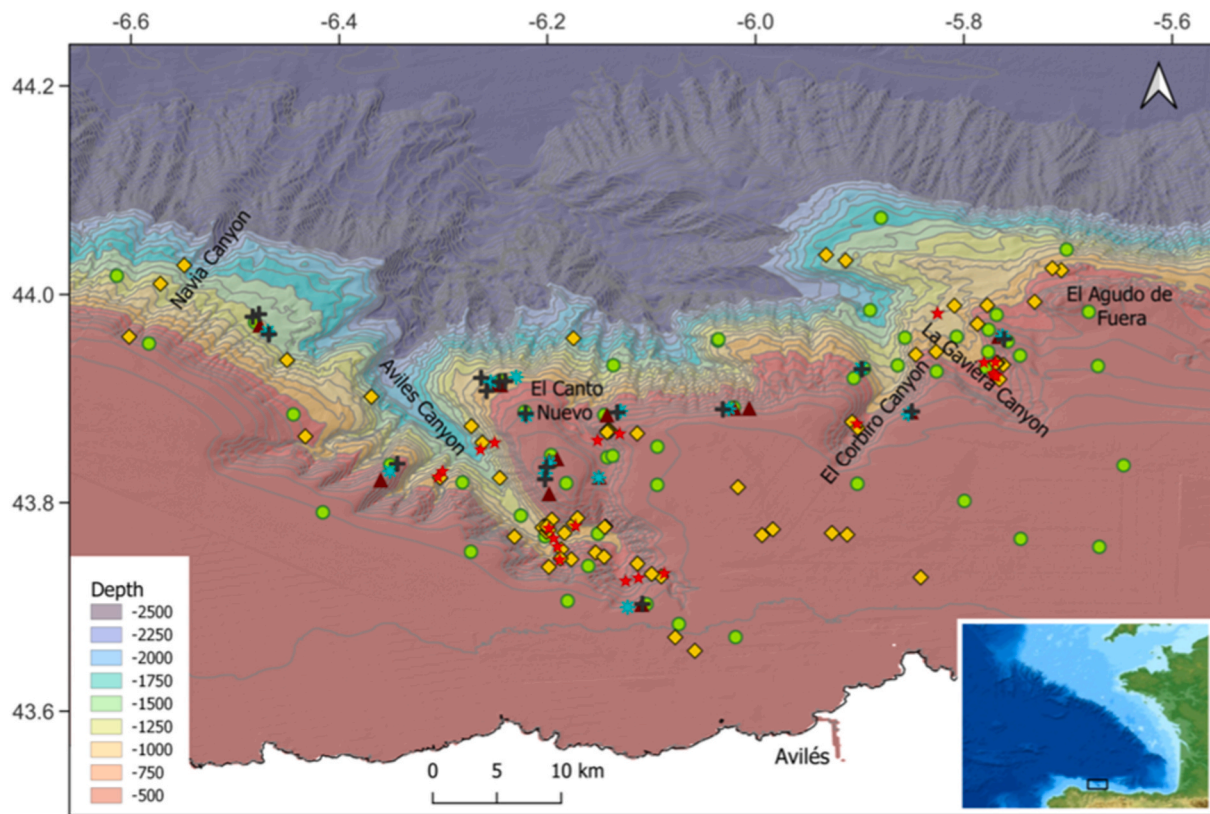


Fig. 1. Sampling effort in the Avilés Canyon System. Rock dredge (yellow diamond), Beam trawl (black cross), GOC (blue aster), Box-Corer (green dot), Suprabenthic sledge (maroon triangle) and ROV (red star). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

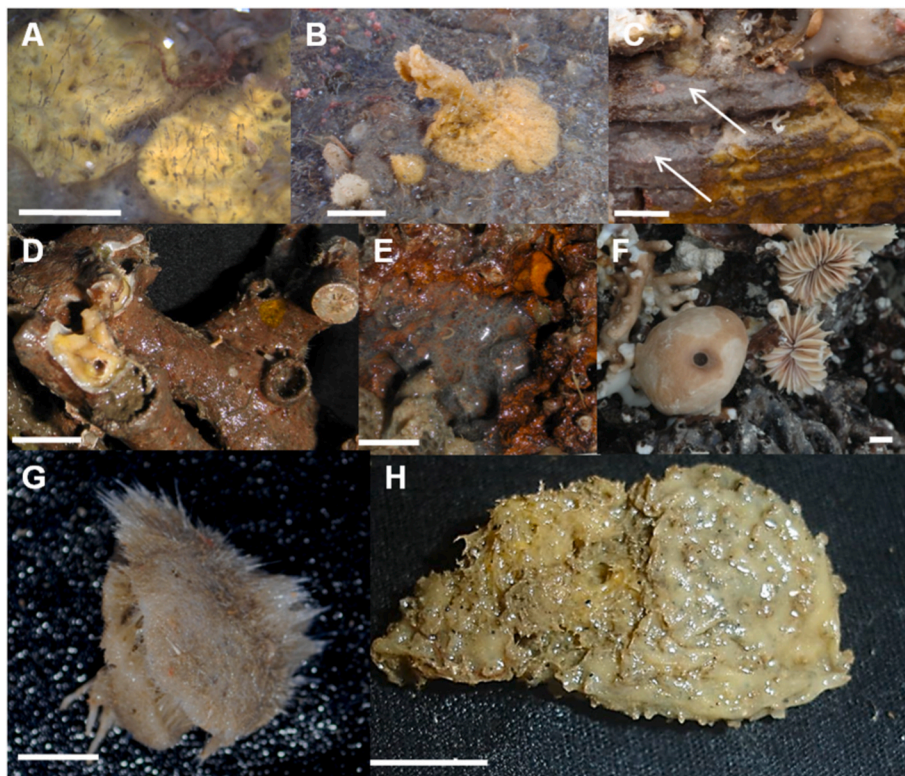


Fig. 2. Porifera. Some of the new records in the ACS. A. *Hymerhabdia typica*. B. *Axinella vellerea*. C. *Monocrepidium vermiculatum*. D. *Siphonodictyon infestum*. E. *Acanthancora aenigma*. F. *Geodia megastrella*. G. *Thenea schmidtii*. H. *Guitarra solorzanoi*. Scale bars: 1 cm. Pictures were taken onboard immediately after sampling.

Fuera and La Gavieta Canyon. The above mentions *P. lusitanica*, *G. megastrella* and *G. pachydermata* should also be included in this list of new records of sponge species (Fig. 2).

4.2. Phylum Cnidaria

A total of 43 octocorals were identified in this study at least to genus level. The order Alcyonacea comprised the largest number of species (35), more than the order Pennatulacea (8). Thirteen more species are known from the literature which makes a total of 56 species in the ACS. Importantly, there are still 11 more species pending identification, including new genera and species. Findings of interest for octocorals are new records for the Iberian fauna, *Anthomastus gyratus* (Fig. 3) and *Thouarella grasshoffi*, for the Spanish fauna, *Primnoa resedaeformis* and the description of a new species, *Pleurocorallium occultum* (Fig. 3). Future taxonomic studies on material collected from the ACS will focus on the southernmost record of *Trachythela*, a new genus for the Iberian fauna, as well as in the description of new species from the genera *Anthelia*, *Anthothela*, *Swiftia* and *Telestula*. The seven species of pennatulaceans reported here belong to seven different genera. With the exception of *Umbellula huxleyi*, they are mostly well known species from the Bay of Biscay. *Kophobelemnonm stelliferum* was especially abundant, present in 12 stations (342–1008 m).

Regarding hexacorals, only members of the order Scleractinia were studied in detail, which allowed the identification of 28 species. Another 5 species are known from the literature. The reef-builders *Desmophyllum*

pertusum and *Madrepora oculata*, which frequently co-occur, stand out for their bionomic importance and abundance. *Flabellum chunii* and *Deltocyathus eccentricus*, are remarkable findings, both new for the Bay of Biscay and northernmost records in the NE Atlantic. It is also noteworthy the occurrence of *Aulocyathus atlanticus*, *Caryophyllia atlantica*, *Fungia-cyathus fragilis*, *Javania cailleti* and *Monomyces pygmaea*, all of them hexacorals infrequently recorded in the Bay of Biscay. The high number of species typical of soft bottoms is also significant (12), with a good representation of the genera *Deltocyathus* (2) and *Flabellum* (3).

The study of other orders of hexacorals as Actiniaria, Zoantharia and Ceriantharia is only preliminary. Their biodiversity, according to the morphotypes, is not very high except for the Actiniaria. This impression has been corroborated in the literature review, with 10, 3 and 2 known species in the ACS respectively (Table 1). Within the IEO material there were no less than 15 Actiniaria species, of which only 2, typical of soft bottoms, have been identified: *Actinauge richardi* and *Phelliactis* cf. *hertwigi*. In the canyon there were zoanthids living on rocks, white coral banks, epibionts of other organisms or forming carcinoecia. *Epizoanthus* sp. was common on white coral being spread over a wide bathymetric range; *Epizoanthus papillosus* and *E. paguriphilus*, form carcinoecia, while *Vitrumanthus vanderlandi*, never reported previously from Spanish waters, lives associated to the sponge *Aphrocallistes beatrix*. The hexacoral order Corallimorpharia comprises a small number of species in European waters, and this is reflected in the inventory of the ACS, with only a shallow-water species (*Corynactis viridis*, Plataforma la Marona, 55 m) and a bathyal one associated to the white coral reef frame (*Sideractis glacialis*, 776 m). Six Antipatharia were identified to species level and another 3 specimens were identified to genus. Among the collected material, there are 1–2 additional species and 2 more were mentioned in the literature. Consequently the antipatharian fauna in the ACS might comprise at least 12–13 species, which is half of the known fauna in the Bay of Biscay and adjacent areas. Worth to mention here the recently described *Trissopathes grasshoffi* reported from a bathymetric range of 615–928 m and *Stauropathes arctica*, found at a depth of 1476 m in the deeper western branch of Avilés Canyon, being the southernmost known record of the species (Fig. 3). The species *Stichopathes* cf. *gravieri* was frequent, being collected in 17 stations within a wide bathymetric range of 342–1533 m. The genera *Leiopathes* and *Parantipathes*, as well as an unidentified threadlike species of *Stichopathes*, were also well represented in the area.

There is an important knowledge of the order Leptothecata (Class Hydrozoa) in the Bay of Biscay with abundant previous information in the ACS. The hydroid fauna reaches 88 known species, 60 of which have been collected from the IEO expeditions, 16 previously unknown species in the area were recovered. The Lafoeidae (especially *Acryptolaria*, *Cryptolaria*, *Zygophylax*), the Plumularioidea (mainly *Aglaophenia*, *Cladocarpus*, *Nemertesia*, *Polyplumaria*) and Sertularioidea (genera *Sertularella* and *Diphasia*) were abundant in the ACS. New records were also registered: for the Iberian fauna (*Symplectoscyphus bathyalis*), for the Spanish coasts (“*Stegopoma plicatile*”- possible group of cryptic species, see Schuchert et al., 2017, *Zygophylax leloupi*), for the Bay of Biscay (*Nemertesia falcicula*, *Streptocaulus dollfusi*) (Fig. 3), and for the European waters (*Zygophylax africana*). Interestingly, the hydrocoral *Stenohelia maderensis*, whose presence in the canyon was already known, was collected in 13 stations in a bathymetric range of 688–1161 m.

Scyphozoan polyps were found occasionally in the ACS on different types of hard substrates including coral debris. At least 3 species were identified: two of them typically of the bathyal (*Nausithoe sorbei*, *Nausithoe* sp.) while *Nausithoe punctata* is normally found in shallower waters in La Marona platform as a sponge endobiont.

4.3. Phylum Brachiopoda

In our material of Brachiopoda, 14 species were identified from the ACS: the craniid *Novocrania anomala*, with 1 specimen with excellent shell preservation (Fig. 4B), the rhynchonellide, *Hispanirhynchia cornea*,

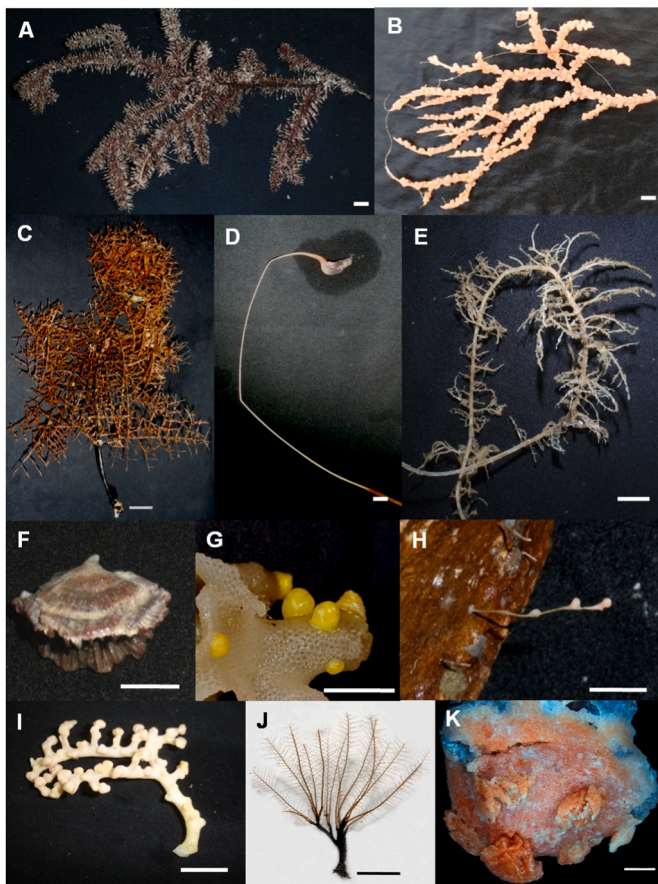


Fig. 3. Cnidaria. Some of the new records in the ACS. A. *Trissopathes grasshoffi*. B. *Primnoa resedaeformis*. C. *Stauropathes arctica*. D. *Umbellula huxleyi*. E. “*Stegopoma plicatile*”. F. *Flabellum chunii*. G. *Vitrumanthus vanderlandi*. H. *Dendrobrachia bonsai*. I. *Pleurocorallium occultum*. J. *Nemertesia falcicula*. K. *Anthomastus gyratus*. Scale bars: 1 cm. C. 2 cm. K. 0.2 cm. Pictures (excluding K) were taken onboard immediately after sampling.

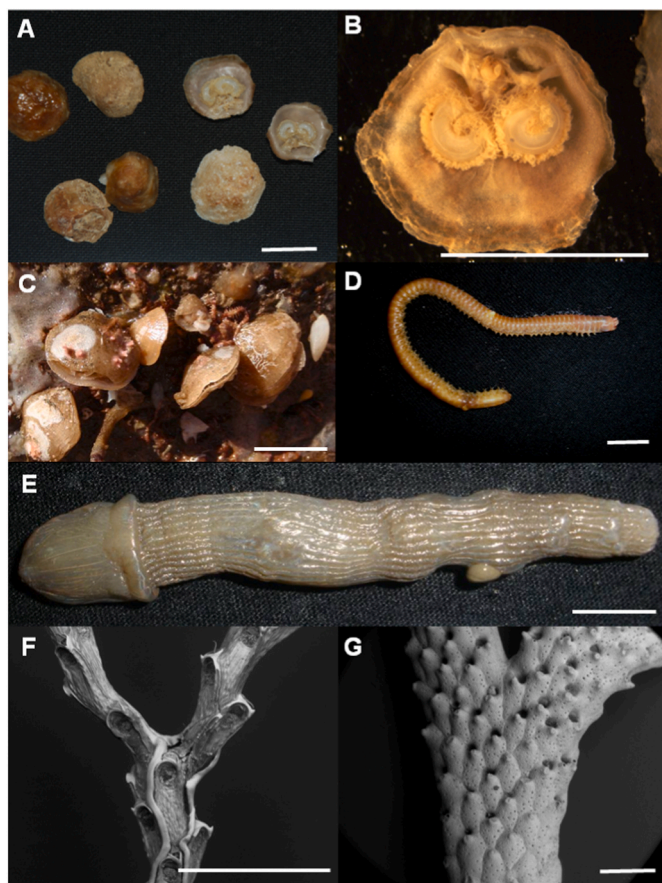


Fig. 4. Pictures of some species from the ACS area, **Brachiopoda**, A-B. *Novocrania anomala*. C. *Megerlia truncata*. **Annelida, Polychaeta** D. *Eunice* sp. **Sipuncula** E., *Sipunculus (Sipunculus) norvegicus*. **Bryozoa**, F. *Jubella enucleata*. G. *Buskea dichotoma*. Scale bars: 1 cm.

6 terebratulidines, *Gryphus vitreus*, *Stenosarina davidsoni*, *Terebratulina retusa*, *Eucalathis ergastica*, *Eucalathis* sp. and *Dyscolia wyvillei*. Six terebratellidines, *Macandrevia cranium*, *Fallax dalliniformis*, *Dallina septigera*, *Dallina parva*, *Megerlia truncata* (Fig. 4C) and *Platidia anomioides*, all of them are very common in the Bay of Biscay. The specimens assigned in this study to the terebratulid species *G. vitreus*, *S. davidsoni*, *Fallax dalliniformis* and its homeomorphic species *D. septigera* are only tentatively assigned as further study of the internal morphology is still in progress. The samples have been collected over a wide range of depths, from 55 m (*M. truncata* and *P. anomioides*) to 1818 (*H. cornea*). Most of them, show a wide bathymetric range (>500 m): *P. anomioides* (55–1325), *M. truncata* (55–776), *T. retusa* (86–843), *M. cranium* (128–695), *E. ergastica* (626–1150), *F. dalliniformis* (700–1533), *S. davidsoni* (928–1533), *D. septigera* (984–1533) and *H. cornea* (1150–1818) (Table 1).

In our samples, the most abundant species have been *M. truncata*, *M. cranium*, *E. ergastica* and *H. cornea*, while the rarest, of which only one specimen has been collected, are *Dallina parva* and *Dyscolia wyvillei*.

The brachiopods were more diverse in the many stations sampled on the epibathyal or shallow water zone of the continental shelf at the NW of Avilés and beginning of Avilés Canyon, in different types of sand, boulders and/or coral debris [e.g. *N. anomala*, *T. retusa*, *M. truncata* and *E. ergastica*]. They were relatively abundant and diverse in boulders, fine sand and coral banks (they use the skeletal remains as a substrate for fixation) of the NE slope of the La Gaviera Canyon, in the mesobathyal Zone [e.g. *E. ergastica*, *M. truncata* and *P. anomioides*], decreasing rapidly in diversity and abundance as it deepens into the continental slope, NE of La Gaviera Canyon [e.g. *M. cranium*, *G. vitreus*, *D. septigera*, *F. dalliniformis* and *S. davidsoni*] and on the rocky substrates or coral

banks on the north western slope of the Avilés Canyon [e.g. *H. cornea* and *M. cranium*].

4.4. Phylum Bryozoa

Twenty two species of bryozoans were identified based on the study of 113 specimens sorted from samples collected in 10 localities along the study area. Only one species belonged to the Order Cyclostomatida, while the other 21 species belonged to the Order Cheilostomatida, represented by 12 families and 18 genera. Attending to the morphology of the colony, 52.2% of the species presented erect colonies and 47.8% encrusting ones. However, this data might be due to the sampling methods used, leading to a relatively small number of specimens and species identified for this habitat, as more species were expected to be present in the study area. Four species, *Jubella enucleata* (Fig. 4F), *Buskea dichotoma* (Fig. 4G), *Breoganipora* cf. *bicanalifera* and *Reteporella couchi* represented the 48% of all colonies studies, all them presenting erect and conspicuous. Again, this could be a sampling artefact.

4.5. Phylum Mollusca

A total of 97 species of molluscs were identified, of which 48 were gastropods, 41 bivalves, 6 scaphopods and 2 chitons. Species with uncertain identification were not included in the list.

The gastropod *Colus aurariae* (Fig. 5C) and the bivalve *Malletia pianii* (Fig. 5F) are new to Spanish waters. Other species are new to Iberian waters (the gastropods *Cylindriscala mirifica* –Fig. 5B– previously known from the Canary Islands and *Cylindriscala* sp. –Fig. 5A–) or to the MSFD (Marine Strategy Framework Directive) Northern Demarcation (the bivalves *Coralliophaga lithophagella* –Fig. 5D– and *Chama circinata* –Fig. 5E). A gastropod of the family Triphoridae, possibly new to science, was found on the elevation situated E of La Gaviera Canyon at 462 m.

On the deeper part of the continental shelf, near the head of the canyons, sedimentary bottoms harboured mostly infaunal bivalves (*Astarte sulcata*, *Venus casina*, *Timoclea ovata*, *Gouldia minima*) and few gastropods (e.g. *Actaeon tornatilis*); the epifaunal bivalves *Neopyncnodonte cochlear* and *Chama circinata* were found on the hard bottoms in the same bathymetric range.

The biogenic edifices involving “white corals” *Desmophyllum pertusum* and *Madrepora oculata* harboured a suite of very characteristic species: the gastropods *Calliostoma maurolicci*, *C. leptophyma*, *Emarginula christiaensi*, and the epifaunal bivalves *Asperarca nodulosa*, *Spondylus gussoni*, *Delectopecten vitreus* and *Lima marioni*. These species do not depend on the living coral, but they use the skeletal remains as a substrate for fixation (bivalves) or grazing on sessile invertebrates

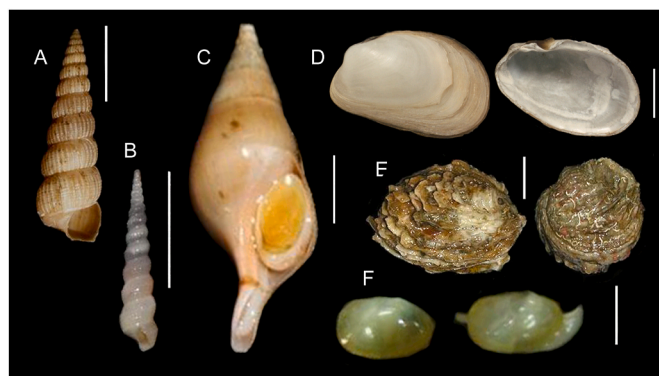


Fig. 5. **Mollusca**. Some of the new records in the ACS. A. *Cylindriscala* sp. B. *Cylindriscala mirifica*. C. *Colus aurariae*. D. *Coralliophaga lithophagella*. E. *Chama circinata*. F. *Malletia pianii*. Scale bars: 1 cm. Pictures were taken onboard immediately after sampling.

(gastropods).

The sedimentary bottoms of the continental slope were the habitat of the gastropods *Aporrhais serresianus*, *Galeodea rugosa*, *Buccinum humphreysianum*, the bivalve *Abra longicallus* and the scaphopod *Antalis agilis*.

The large oyster *Neopycnodonte zibrowii* was found on steep rocky bottoms below 500 m depths often in association with another large epifaunal bivalve, *Acesta excavata*.

4.6. Phylum Annelida

Annelida, with a total of 151 species, is a common taxon in the ACS. The most abundant polychaete families were Spionidae, Paraonidae, Ampharetidae, Sabellidae, Capitellidae, Syllidae, Maldanidae, Onuphidae and Cirratulidae. The most speciose families were Syllidae (31 species), Paraonidae (30), Spionidae (23), Ampharetidae (20), Onuphidae (12), Lumbrineridae (10), and Terebellidae (10). Regarding the species, the dominant ones were *Eclysippe vanelli*, *Levinsenia flava*, *Prionospio cirrifera*, *Aricidea (Aricidea) wassi*, *Euchone incolor*, *Glycera lapidum* and *Prionospio fallax*. Furthermore, 5 species were present on more than 20 sampling stations: *G. lapidum*, *L. flava*, *P. fallax*, *E. incolor* and *Notomastus latericeus*.

In the Order Sipuncula, formerly considered a separated Phylum before the evidence of the molecular analyses (Rouse et al., 2022) a total of 132 specimens were collected in 42 stations, by using mainly the BC, RD and BT gears. Eleven species were identified included in 6 genera: *Aspidosiphon*, *Golfingia*, *Nephasoma*, *Onchnesoma*, *Phascolion* and *Sipunculus*. The 75% of the species belonged to the Family Golfingiidae and the remaining 18% and 7% in the Families Aspidosiphonidae and Sipunculidae respectively. All the identified species were previously known from the Bay of Biscay, being the most frequent *Onchnesoma steenstrupii steenstrupii* and *Aspidosiphon (Aspidosiphon) muelleri muelleri*, recorded in 24 and 9 sampling sites respectively.

The abundance of annelids decreased with depth in the area. The highest abundance values appeared in shallower stations (<500 m depth), while the lowest values were recorded at deeper stations. There was also a decrease in species richness with depth. From the bathymetric point of view, the dominant species were grouped as follows: the paraonid *Aricidea (Aricidea) wassi* inhabits the shallowest bottoms of the ACS, between 83 and 612 m deep. The spionids *Prionospio cirrifera* and *P. fallax* and the capitellid *Notomastus latericeus* is preferentially found at greater depths, being found in the present study at depths between 83 and 144 m up to 1206 m deep. The two most dominant species, the ampharetid *Eclysippe vanelli* and the paraonid *Levinsenia flava*, were collected between 144 and 1470 m, while the species *Euchone incolor* (Family Sabellidae) and *Glycera lapidum* (Family Glyceridae) reached the widest and deepest bathymetric range in the entire study, with samples collected between 112 and 1881 m depth.

4.7. Phylum Arthropoda

In the ACS, 315 species belonging to 121 families in the phylum Arthropoda were identified. They were mostly represented by 311 crustaceans species (98.7% of the total species) and 4 pycnogonids. Malacostraca was the dominant group with 301 species, whereas Thecostraca contributed with 10 species. Amphipods was the most speciose taxon (114 species) followed by decapods (81), cumaceans (38), isopods (30), mysids (21), euphausiids (7), tanaids and lophogastrids (6 and 3 species, respectively). Cirripeds were represented by 10 species of which Calanticomorpha and Verrucomorpha contribute with 4 and 3 species, respectively.

Despite crustacean species reported here are well-known fauna widely distributed in the northeastern Atlantic and the Bay of Biscay, 1 genus and 11 species are new to science: the amphipods *Gitana* sp. B, *Eusirus* sp. B, *Stilipes* sp. A (see Frutos and Sorbe (2022), this issue), *Melphidippa* sp. B, and *Syrrhoites* sp. A, the cumacean *Leucon*

(*Crymoleucon*) sp. A, the isopods *Lipomera (Paralipomera)* sp. A, Lipomerinae sp. A, *Munnopsurus* sp. C, *Notoxenoides* sp. A and the cirriped *Gruvelialepas* sp. A.

The decapods *Uroptychus cartesi*, *Munidopsis similis*, *Bathynectes longipes* and *Liocarcinus zariqueyi* being reported for the first time in the Bay of Biscay whereas the amphipod *Liropus cachuchoensis*, the isopods *Cornuamesus longiramus*, *Politolana sanchezi*, species recently described in the southeastern Bay of Biscay, are extending their geographical distribution westwards. It is noteworthy the occurrence of *Uroptychus cartesi* and *Stilipes* sp. A into the S Bay of Biscay after being recently described in the Galicia Bank (type locality).

Special records are the occurrence of the NW Atlantic *Munidopsis similis* in the ACS, reporting the first record of the species in the NE Atlantic, or *Paralomis microps* recorded for the second time after being described; whereas *Paralomis bouvieri*, *Liocarcinus zariqueyi* and *Bathynectes longipes* point out its occurrence in the southern Bay of Biscay. Additionally, records of amphipods, cumaceans and isopods are improving the knowledge on deep-sea peracarid species no reported in the area so far.

Cirripeds listed occurred below 776 m depth. Deep-sea species of this group have a wide distribution in the NE Atlantic, some of them (*Arcoscappelum michelottianum*, *Smilium acutum* and *Metaverruca recta*), considered as cosmopolitan. While *Altiverruca obliqua*, *Aurivillialepas calycula*, *Scillaelepas grimaldii* and the new *Gruvelialepas* sp. A recorded here for the first time in the Bay of Biscay, the other species have been already reported there and thus extend their geographical distribution (Fig. 6).

4.8. Phylum Echinodermata

In the present study a total of 8224 echinoderm specimens belonging to 74 species were studied. Ophiuroids represented the most diverse Class (43.9% of species) followed by asteroids (27.5%), although they both groups might have been underestimated since they are under further taxonomic review. The rest of classes are represented as follows: 15.4% holothuroids, 13.2% echinoids, and 7.7% crinoids.

Class Ophiuroidea was the most abundant (86.48%) and frequent (28.68%). These differences among classes, are due to specimen numbers of two species of ophiuroids: *Ophiocten affinis* (Fig. 7A), and *Ophiothamnus affinis*, which occurred at very high abundances (4101 and 1850 specimens respectively), but they were not very frequent as they preferentially occurred in dense aggregations in soft bottoms, being less frequent at canyons. In contrast, *Ophiactis abyssicola* (Fig. 7B) was the most frequent species within echinoderms in the ACS mostly found in association with hard bottoms which occupy a big surface of the studied canyon system. Other species with special relevance are *Araeosoma fenestratum* (Fig. 7C), *Cidaris cidaris* (Fig. 7D), *Brisinga cf. endecacemos*, *Hymenodiscus cf. coronatus*, and *Ophiacantha bidentata*, the latter normally associated to “white corals”.

4.9. Phylum Chordata

A total of 91 species of fishes were recorded. The 81% corresponded to teleost fishes and 19% to chondrichthyans. Among teleost fishes the order with the highest number of species was Gadiformes followed by Pleuronectiformes, Scorpaeniformes and Stomiiformes. Regarding chondrichthyans, 65% of the species were sharks followed by 23% rajidae species and 12% chimaeras. The main orders of chondrichthyans were Squaliformes (n = 8), Rajiformes (n = 4) and Carcharhiniformes (n = 3). Taking into account that most of the information comes from bottom trawl surveys, most of the fish species are of demersal or benthic behavior, leaving the pelagic species scarcely represented.

5. Discussion

The >1000 species registered in this study (within an area of 6300



Fig. 6. Arthropoda. Pictures of some deep-sea crustacean species from the ACS area. Cirripeds: A. *Alтивerruca obliqua*. B. *Arcoscalpellum michelottianum*. C. *Aurivillialepas calycula*. D. *Scillaelepas grimaldii*. Decapods Anomura: E. *Munidopsis similis*. F. *Urotychus cartesi*. G. *Galathea machadoi*. H. *Paralomis microps*. I. *Paralomis bouvieri*. Decapods Brachyura: J. *Liocarcinus zariquieyi*. Amphipods: K. *Lepechinella manco*. L. *Rhachotropis rostrata*. M. *Cleonardopsis carinata*. N. *Pseudotiron bouvieri*. Cumacean: O. *Cyclaspis longicaudata*. Isopoda: P. *Tythocope megalura*. Scale bars: A, G = 1 mm; C, E, F, J = 5 mm; B, D, H, I = 1 cm. Pictures E, K–P were taken onboard immediately after sampling. Authors: Teodoro P. Ibarrola (A, B), Alejandra Calvo (C–D, F–J), Javier Cristobo (E), Inmaculada Frutos (K–P).

km²) represent roughly half of the deep-sea species recorded in the NOR demarcation (with a total extent 306499 km²). According to this numbers, the ACS might represent a good choice as a priority for conservation since despite having a limited geographic extension it harbours a relatively high proportion of marine species. It is important to note, though, that the species numbers recorded here are underestimated for some groups like Mollusca (where most species are small,

in the size range 1–5 mm, and have not yet been sorted from sediment samples), or fishes (many of which are bathypelagic and have not been investigated here), nevertheless still amounting to about one-third of the expected species in the deep-sea.

Available data for other comparable areas are fragmentary and/or strongly biased between unequally sampled groups. For instance, for the Galicia Bank, one of the best studied INDEMARES areas, [Bañón et al.](#)

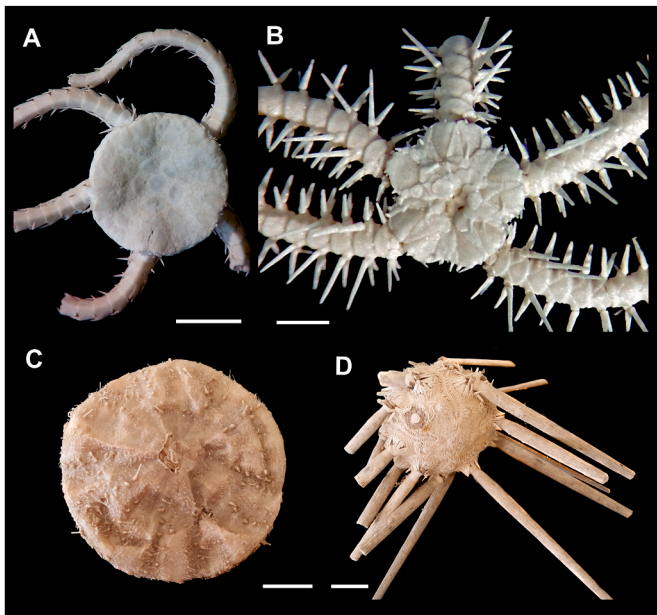


Fig. 7. Echinodermata. Some of the most relevant species of echinoderms in ACS: A. *Ophiocten affinis*. B. *Ophiactis abyssicola*. C. *Araeosoma fenestratum*. D. *Cidaris cidaris*. Scale bars: A = 0.25 cm; B = 0.16 cm; C, D = 2 cm.

(2016) listed 139 species of marine fishes through >30 years of surveys, Gofas et al. (2021) listed 212 species of Mollusca (although this was the result of very fine sorting of sediment samples down to 0.5 mm), while Souto et al. (2016) listed 25 species of Bryozoans (only Cheilostomes). In any case, the species number at the ACS is expected to largely exceed those numbers if similar methods and efforts were applied.

Here we present the most comprehensive study on the distribution and bathymetric range of macro- and megabenthic marine species present in the ACS. The extensive multi-gear sampling carried out (using samples from expeditions between 2009–2017) and the collaborative effort of several specialists working on different taxonomic groups, allowed an update on the knowledge of this benthic fauna respect to previous records (Table 1). The use of different and specific samplers for each type of substrate resulted in greater success in the collection of more elusive species. One of the main objectives in each of the expeditions was the identification and description of vulnerable habitats and species contemplated in various protection regulations. In addition to the new records, the presence of dominant species that increase the complexity of habitats and biodiversity in relation to the nearby areas of the canyon is confirmed.

Among **Porifera**, four species (*Aphrocallistes beatrix*, *Asconema setubalense*, *Pheronema carpenteri* and *Neoschrameniella* aff. *bowerbankii*) are known to form extensive sponge aggregations that give three-dimensional structure to the habitats where they form sponge aggregations in the ACS, such as *Geodia* spp. and *Phakellia* spp. (Ríos et al., 2018, 2020; Maldonado et al., 2017). With the implementation of MSFD and Natura 2000, sponge aggregations as *Neoschrameniella* aff. *bowerbankii* located on hard bottoms of El Corbiero Canyon, or *Aphrocallistes beatrix* in the head of Avilés Canyon are now included in the classification of the habitat “1170 Reefs” of the European Habitat Directive and they thus considered as vulnerable habitats on which it is mandatory for the European countries to establish conservation measures.

Cnidarians are a very important part of the canyon fauna not only because of their abundance, but also because of the sessile character of most species and their capacity for habitat formation, constituting substrate or refuge for many other animals. This is particularly true for some scleractinians that are essential in the formation of cold water coral reefs, well represented in some sectors of the ACS as the La Gaviera

Canyon (see Sánchez et al., 2014a). Up to 153 species of benthic cnidarians were identified, which are the 71% of those that are known in the canyon (Table 1). In turn, the 216 known species including a review of the literature, are close to half of the total benthic fauna known from the southern sector of the Bay of Biscay and Galicia (Altuna, 2015, 406 species). The amount is very important, considering that the littoral fauna was not sampled in the IEO surveys, which in the Cantabrian Sea is rich in actinarians and hydrozoans. Interestingly, a significant part of the deep-sea fauna of the Bay of Biscay and NW Iberian Peninsula was present in the ACS. For example, 33 scleractinians are known from ACS, which is a 73% of those mentioned below 50 m depth in the aforementioned area (Altuna and Ríos, 2014b, updated).

Knowledge on the cnidarians fauna has increased not only for the ACS fauna with 69 previously unknown species added, but also at the scale of the Bay of Biscay, the Iberian Peninsula, Spain, and European waters (Altuna, 2012b, c, d, e; Altuna and Ríos, 2014a, b; Tu et al., 2015). In addition, an evaluation of the material not identified so far allows estimating about 40–42 additional species, mainly among Actiniaria (ca. 15), Alcyonacea (ca. 11) and Zoantharia (ca. 6). There are also new species and genera to be described, principally alcyonacea. According to this, we estimate that the Alcyonacea is, after the Leptothecata, the order with the greatest number of species in the whole canyon, agreeing with the general picture of the Bay of Biscay with their highest diversification at bathyal depths (see Altuna, 2015).

Recent description of the **brachiopod** species, lists with synonymies and their bathymetrical and geographical distribution can be found in Álvarez & Emig (2005), Álvarez et al. (2005) and Álvarez et al. (2016). Considering the distribution of *Novocrania turbinata* and *N. anomala*, the taxonomic validity of the morphological characters used to differentiate both species and the data obtained by molecular analyses, Emig (2014) concluded that both species should be considered as synonymous. The specimens attributed here to *Gryphus vitreus* externally resemble those of *Stenosarina davidsoni*. The 14 species identified in this contribution were already recorded from the area while three species previously recorded were not found during this campaigns, *Eucalathis tuberata*, *Megathiris detruncata*, and *Platidia davidsoni* and the species *Megerlia monstrosa* is considered synonym of *Megerlia truncata*. The number of **bryozoan** species recorded during these campaigns (22 spp) can be considered as an underestimation of the number of expected species in the ACS. A total of 143 species of bryozoan are known from the Iberian continental shelf of the Bay of Biscay below 50 m of depth (Souto, personal compilation from literature), despite this is not the best studied area for the bryozoans. Underestimation of bryozoan species could be due to the lack of expert on bryozoan onboard during the sorting of samples, besides the different objectives of the campaign. Previous data from the study area are very scarce with only six species before recorded. Three species identified during this work were previously recorded from the area; *Reteporella couchii*, *Buskea dichotoma* and *Schizomavella neptuni* (D' Hondt (1974); Jullien and Calvet, 1903; Reverter-Gil et al., 2015). While three species previously recorded in the area were not found during these cruises; *Amphiblestrum flemingii*, *Hippoporina polygonia* and *Adeonellopsis distoma* (D' Hondt (1974); Jullien and Calvet, 1903). It is remarkable the presence of the *Breoganipora* cf. *bicanalifera*, since this genus was only previously known from a seamount in deep-water habitats. *Breoganipora* was recently described from an abundant number of specimens collected at the Galicia Bank (Souto et al., 2016) from deep-water stations (between 685 and 1697 m depth) and after that, this genus was recorded from the Hayes Fracture in the Mid-Atlantic ridge from (1447 m), although identification to species level was not possible in this case (Souto and Albuquerque, 2019). The specimens identified here represent the first record of the genus from the continental shelf. Besides, the specimen identified as *Caberea* sp. is currently under study and it could be a new species. Specimen collected in the head of Avilés Canyon is similar in characters to the specimens identified by D' Hondt (1974) as *Caberea boryi* (Audouin, 1826), nevertheless some features as the morphology of the scutum, avicularias, etc. seem not coincide with

descriptions of *C. boryi*; so a detailed revision of previous records from deep waters in the close areas of the Bay of Biscay to this species is necessary.

In **annelids**, this research reveals the presence of 140 species of the class Polychaeta in the ACS, with spionids, paraonids, and ampharetids as the most relevant families in terms of abundance and 11 Sipuncula. It is important to note that the sabellid *Euchone incolor* is considered a casual Non-Indigenous Species (NIS) of polychaete in the Iberian Peninsula (Northatlantic Demarcation) from Warm Western Atlantic native origin (López and Richter, 2017). Polychaetes are the numerically dominant macrofaunal taxon in the deep-sea (Gage and Tyler, 1991; Ramirez-Llodra et al., 2010). In the ACS, these annelids accounted for more than 50% of the total macroinfaunal abundance (Lourido et al., 2014), attaining similar relative abundances to other deep-sea areas, as shown in Table 2. The most numerous families of this faunistic group were mostly the same as have already been recorded in previous studies, with Spionidae, Paraonidae and Cirratulidae standing out among the rest of the families of these deep-sea areas.

In general, macrofaunal abundance decreases with depth in many deep-sea environments (Thistle, 2003), and our results agree with this general pattern reported in other deep-sea areas (Baldrigi et al., 2014 in the west, central and eastern Mediterranean basins; Hessler and Sanders, 1967 in the Gay Head-Bermuda transect; Galéron et al., 2000 in the tropical Northeast Atlantic; Flach et al., 2002 in the Goban Spur in the NE Atlantic Ocean; Levin and Gooday, 2003 in the Northwest Atlantic; Nephin et al., 2014 in the Canadian Beaufort Shelf and Slope in Arctic; Thistle, 2003 in the Gulf of Mexico; Cunha et al., 2011 in three Portuguese submarine canyons in the NE Atlantic): the observed polychaete abundance indices decreased with increasing water depth in the ACS showing significant negative correlations.

Our study revealed the presence of 315 species of phylum **Arthropoda** in the ACS, mainly amphipod (114 species) and decapod (81 species) crustaceans. Our data remarkably extended the 93 taxa previously reported in the area (Louzao et al., 2010), especially for peracarid species. Within peracarids, amphipods are the most speciose taxon followed by cumaceans and isopods, thus confirming the general trends observed in the distribution of peracarid diversity related to depth in the Bay of Biscay (Frutos and Sorbe, 2014, 2017; Sorbe and Elizalde, 2014; Frutos et al., 2017).

In general, the crustaceans herein reported are new occurrences of widespread NE Atlantic species mainly extending the depth range; e.g. the mysid *Chunomysis diadema* (Tattersall and Tattersall, 1951; Nouvel and Lagardère, 1976; Elizalde et al., 1991), but also providing new boundaries for the distribution of peracarid species recently described in the southern Bay of Biscay (Kavanagh and Sorbe, 2006; Guerra-García et al., 2008; Frutos and Sorbe, 2010), or decapods not previously cited there (Macpherson, 1988; D'Udeckem d'Acoz, 1999; Baba et al., 2008; Marco-Herrero et al., 2015; García Raso et al., 2018).

The records in the ACS contribute to extend the distribution of species in the Bay of Biscay all along its margin, with special remarks on *Uroptychus cartesi*, a species treated as a possible "endemic" decapod of the Galicia Bank (Cartes et al., 2014) or the amphipods *Bathymedon monoculodiformis* and *Pseudotiron bouvieri*, species considered as "endemic" from the Mediterranean (Ruffo, 1993) already reported in the southern Bay of Biscay (Bachelet et al., 2003; Frutos et al., 2017).

This continuity of deep-sea crustaceans in the Bay of Biscay was pointed out by Le Danois (1948) in the first study of benthic communities of European margins; which has been corroborated and increased after subsequent studies carried out in the Cantabrian Sea on the continental shelf and upper slope (Serrano et al., 2006a,b, 2008, 2011; Cartes et al., 2007, 2014; Sánchez et al., 2008; Sorbe et al., 2010; Frutos and Sorbe, 2008, 2014, 2017; Frutos et al., 2012, 2017; Rodríguez et al., 2021). Additionally, the comparison of the suprabenthic communities characterizing the Avilés and Capbreton canyons, showed a similar structure of assemblages with 109 species common to both canyons (Frutos et al., 2012).

Table 2

Best represented polychaetes in the deep-sea (A: Ampharetidae; Am: Amphinomidae; Ca: Capitellidae; Ci: Cirratulidae; Co: Cossuridae; Do: Dorvilleidae; Eu: Eunicidae; Fa: Fauveliopsidae; Fl: Flabelligeridae; Gl: Glyceridae; Lu: Lumbrineridae; Ma: Maldanidae; Ne: Nephtyidae; Op: Opheliidae; Or: Orbiniidae; On: Onuphidae; Pa: Paraonidae; Ph: Phyllodocidae; Pl: Pilargidae; Ps: Pisionidae; Sa: Sabellidae; Si: Siboglinidae; Sp: Spionidae; Sy: Syllidae).

Study area	Reference	Polychaete abundances	Best represented polychaete families
Avilés Canyon System (Cantabrian Sea, N Spain)	Lourido et al. (2014)	>50%	Sp, Pa, A, Sa, Ca, Sy, Ma, On, and Ci
West, central and eastern Mediterranean basins	Baldrigi et al. (2014)		Ca, Pa, Co, Eu, Sy, Gl
Three portuguese submarine canyons: Nazaré, Setúbal and Cascais Canyons (NE Atlantic)	Cunha et al. (2011)	42,1%	Sp, A, On, Lu, Si
Campeche Canyon in the SW Gulf of Mexico	Escobar Briones et al. (2008)	43.67%	
Continental slope off the eastern seaboard of the USA	Gage and Tyler (1991)	45%	Am, Pa and Sp have most species
Deep continental margin (Gulf of Guinea)	Galéron et al., 2000	40–76%	Ci, Pa, Sp, Op
Central Pacific abyss	Glover et al. (2002)		Ci, Sp, Pa, Sa, Sy
Gay Head-Bermuda transect	Levin and Gooday (2003)	34–84%	A, Ma, Pa, Ph, Sp, Sy
Cape Hatteras and Charleston Bump	Levin and Gooday (2003)	50%	
North Atlantic Bight margin and Mid-Atlantic Bight margin	Levin and Gooday (2003)	44–47%	Ci, Do, Pa, Sp
Porcupine Abyssal Plain	Levin and Gooday (2003)	35%	Sp, Ci, Sa, Op, Pa
Tagus Abyssal Plain	Levin and Gooday (2003)	58%	Ci, Sp, Pl, Op, Pa
Madeira Abyssal Plain	Levin and Gooday (2003)	49%	Sa, Fl, Pa, Sp, Ps
Rockall Trough	Levin and Gooday (2003)	59.1%	
Slope off Cape Blanc, continental rise southwest of Cap Blanc and Cape Verde Abyssal Plain	Levin and Gooday (2003)	56–67-64%	
Avilés Canyon, N Iberian Shelf	Louzao et al. (2010)	28.8%	
Besós canyon (Catalonian coast, W Mediterranean)	Mamouridis et al. (2011)		A, Pa, Fl
Beaufort Shelf and Slope, Canada	Nephin et al. (2014)		Ne, Ma
Region of the Subtropical Front, Chatham Rise, New Zealand	Probert et al. (2009)		Sp, Pa, Ci, Sy, Or
Mid-Atlantic Ridge, North Atlantic Ocean	Shields and Blanco-Perez (2013)		Sp, Ci, Sy, Gl

The variety of sampling devices used for the present study, allowed to successfully collect fauna from different habitats in both soft- and hard bottoms, consequently extending the bathymetric range of several species. Besides the direct study on the epibenthic fauna associated with deep-sea water corals, mainly *Desmophyllum pertusum* and *Madrepora oculata*, and hexactinellid sponges (i.e. sampling 3-D habitats using non invasive methods), demonstrated that motile fauna that are well-represented in soft-bottom surrounding areas of coral reefs, are also present in close vicinity of these habitats (Sánchez et al., 2013; Frutos et al., 2017).

Three new records of **Echinoderms** have been confirmed, two asteroids and one echinoid species, furthermore a new contribution for

LPEM, included in the *Inventario Español del Patrimonio Natural y la Biodiversidad* (IEPNB) (García-Guillén et al., 2022a,b). Although in ophiuroids more than five new records are expected (Macías-Ramírez, pers. com.), most of these new records were originally described from the Caribbean Sea, and in some cases their distribution is restricted to this area (Perrier, 1881). The amphiatlantic distribution of these species could be due to natural and/or anthropogenic reasons. The Gulf Stream current connects the Caribbean Sea with the Cantabrian Sea. If confirmed, this occurrence should be considered as a new indicator of the Cantabrian Sea tropicalization according to Arias et al. (2014) and Arias and Crocetta (2016). Further studies, including molecular approaches, on these species should be conducted in order to confirm the presence of amphiatlantic distribution of these species and to rule out the possibility of individuals from the Caribbean and Cantabrian Seas being cryptic species.

Regarding **Chordata**, the list of fishes species was less diverse compared to those reported for adjacent waters summarized in the north demarcation (NOR) of the Marine Strategies framework (Báez et al., 2019). However NOR includes also the Galicia Bank (a seamount) and Galicia estuaries (rias) where shallower and even some tropical species have been reported (Bañón et al., 2016; Bañón and Maño, 2021). Despite this the number of fish accounted for 91 which represents the 18% of total species reported in the NOR area. It is also remarkable that fishes are mobile species and thus subjected to present seasonal and ontogenic distribution patterns as well as differences in catchability and therefore the number of species reported is probably an underestimation. With respect to deepwater chondrichthyans some species were recorded for the first time in these waters (ACS) as example *Neoraja iberica* and *N. careula*, *Rajella kukujevi* and *Galeus murinus* (Rodríguez-Cabello et al., 2013). Other species not reported on the list (Table 1) are known to occur in the ACS. In this sense trawl gears are not the most efficient devices for collecting pelagic sharks such as *Prionace glauca*, *Isurus oxyrinchus*, *Alopias* sp., among others. Besides, certain cosmopolitan species are frequently observed but rarely caught such as *Cetorhinus maximus* or *Hexanchus griseus*, etc.

In the three main canyons of the ACS, namely Avilés (AC), La Gavieta (LGC) and El Corbiro (ECC) there are differences not only geomorphologic and physicochemical (Gómez-Ballesteros et al., 2014), but also in terms of the diversity of species that inhabit them. One of the factors responsible for these differences is related to the structuring species found in each of these areas and consequently the associated fauna they host, their specific richness and their biomass.

In the AC, particularly at the head of the canyon where fishing grounds are located, important aggregations of *Aphrocallistes beatrix* sponges have been found growing on the rubble coral. These sponge grounds have not been detected in the other two canyons. This glass sponge was generally covered by the zoantharian *Vitrumanthus vanderlandi*. The echinodermata present in this area and also in the sedimentary substrate are: *Gracilechinus acutus*, *Araeosoma fenestratum*, *Phormosoma placenta*, *Cidaris cidaris*, *Peltaster placenta*, brisingid seastars and Ophiuroidea. Big colonies of the antipatharian *Trissopathes grasshoffi* are colonized by Decapoda, Asteroidea and Alcyonacea.

On the other hand, in LGC, the singularity of this canyon is the presence of two living cold-water coral species, one of them in a carbonate mounds located on the canyon floor and the other on stepped rocky bottoms at both flanks and on the canyon floor. The associated megafauna in LGC is dominated by the phyla Cnidaria, Porifera and Echinodermata, considered components of vulnerable marine ecosystems for being more exposed to impacts by bottom trawling and other human disturbances. The dominant species are *M. oculata* and *D. pertusum* (Sánchez et al., 2014a). The species associated with these cold water coral are the hexactinellids sponges *A. beatrix* and *Regadrella phoenix*, the cnidarians *Narella versluysi*, *Leiopathes* spp., *Parantipathes hirondelle*, *Bathypathes* sp., *Allopathes* sp., *T. grasshoffi* and an unidentified ceriantharian; the asteroids *Brisinga* cf. *endecacnemos*, *Hymenodiscus* cf. *coronatus*, *Novodinia pandina*, *Henricia caudani*, *P. placenta* and the

echinoids *A. fenestratum* and *C. cidaris*. In this area lots waste nets, plastics and fishing ropes were noticed. In the *Montaña Indemares*, the other coral reef, the same species were detected, but with the presence of additional cnidarians as *Lateothela grandiflora* and *Enallopsammia rostrata* or sponges of the genus *Geodia*.

In ECC, one of the most relevant species found was the lithistid sponge *Neoschrammeniella* aff. *bowerbankii* located on the rock walls of this canyon, which develops there important concentrations. Other associated large sponge species found there are *Pachastrella ovisternata*, *Pachastrella* cf. *nodulosa* with *Hexadella* sp. covering its external wall, and also *Phakellia* spp., along with some Antipatharia, *Callogorgia verticillata* and the asteroids *H. caudani* and *Zoroaster fulgens*. If the substrate is composed of coral rubble, it's frequent the presence of echinoids of the genus *Cidaris*, *Araeosoma* and *Phormosoma*, the cnidarians *Acanthogorgia armata*, *Phelliactis* cf. *hertwigii*, an unidentified cerianthid solitary, scleractinians and the sponges *R. phoenix* and *A. beatrix*.

Another important structuring species was located outside these three canyons, in the area of *Mar de Mares*, east of El Canto Nuevo. This is the case of the glass sponge *Asconema setubalense* whose specimens can measure more than 1 m in height, which are sometimes damaged as a result of fishing activities. Different species of the genus *Geodia* have also been reported in this area.

The type of substrate also conditioned the presence of different species in the study area. In the head of the Avilés Canyon (AC), the bottom is a sedimentary/mixed substrate and around of *El Canto de San Pedro*, *Tres Peñas*, *El Calafro*, *El Rebeón* and *La Piedra* fishing grounds, the principal phyla presented were Cnidaria, Porifera and Echinodermata. The most relevant species live in the rock-patchy corals area, linked to the presence of the Habitat 1170, associated with *Madrepora oculata*, *Desmophyllum pertusum*, *Phelliactis* cf. *hertwigii*, *A. beatrix*, *B. endecacnemos* and several species of Antipatharia. In the sedimentary sector there were abundant echinoderms such as *A. fenestratum* or *C. cidaris*, or cnidarians such as an unidentified ceriantharian, *Kophobelemnon stelliferum* or *Funiculina quadrangularis*. On the rocks, incrusting (*Hymedesmia* (*Hymedesmia*) *paupertas*) and fan-shape sponges (*Phakellia* spp.) were also reported. The Decapods *Munida* spp. were also very frequent in both types of sediments. The West flank of El Canto Nuevo in the AC is more sedimentary, with the presence of *A. armata* and *Asteronyx loveni* living on it. Other common fauna here are *Acanella arbuscula*, *Epizoanthus paguriphilus* with *Parapagurus pilosimanus* living associated, *Colus* sp., unidentified cerianthid, *A. fenestratum*, *Zoroaster fulgens*, Crinoidea, Polychaeta and fishes as *Phycis blennoides*, *Xenodermichthys copei*, *Bathypterois dubius* and *Trachyrincus scabrus*. In a part of *La Vallina* fishing ground, at the AC-2W subsidiary branch, the substrate is muddy and very compacted in the walls and prominence of slabs. The fauna here was very different with the presence of sponges as *Chondrocladia* (*Chondrocladia*) *robertballardi* and *Thenea schmidtii*, giant Foraminifera (probably *Syringamina* aff. *fragilissima* – not included in Table 1), the molluscs *Acesta excavata* and *Lima marioni*, the brachiopod *Gryphus vitreus*, Pennatulacea and Polychaeta. In the few stones of this area, incrusting sponges, solitary scleractinians, *Phelliactis* cf. *hertwigii* and the structurant coral *Enallopsammia rostrata* were also detected.

In recent years, the loss of taxonomy specialists who have retired without a replacement by young students, increases the problems in biodiversity studies of many of the phyla of marine fauna; despite this, an important number of species are currently under study and several new species are expected to be described which means that biodiversity values are underestimated.

A quick summary of the species recorded in the Spanish noratlantic area that represent almost half of the Biscay Bay, (Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, 2017) with respect to the studied area in the present work (only 2% of its extension) (Table 3) can give us an idea of the specific richness of the ACS and also of the potentiality of what may remain to be discovered taking into account the lack of studies carried out by below 2000 m.

The advances presented in the knowledge of biodiversity in the ACS

Table 3

Species per Phylum in Noratlantic Demarcation (NOR) of which Deep Sea context in WoRDSS (DeepSea), number reported herein (This work) and proportion of reported DeepSea (% Deep).

Taxa	Porifera	Cnidaria	Brachiopoda	Bryozoa	Mollusca	Annelida	Arthropoda	Echinodermata	Fish	TOTAL
NOR	269	402	16	284	992	830	1062	208	477	4540
DeepSea	47	203	10	73	307	394	515	159	301	2009
This work	98	153	14	22	97	151	311	74	91	1011
Ratio Deep	2.09	0.75	1.40	0.30	0.32	0.38	0.60	0.46	0.30	0.50

have required a very important scientific effort during the past few years (2008–2021) by the expeditions of the Spanish Institute of Oceanography (ECOMARG, INDEMARES, INTEMARES and SponGES Projects). Biodiversity plays a fundamental role in benthic marine ecosystems and this is particularly true for submarine canyons given the diverse communities they house and the anthropogenic impacts they suffer (Punzón et al., 2016). In the near future the management plans of the Site of Community Importance (SCI) of the ACS and its conservation will require an adequate baseline knowledge of the diversity of species, their responses to environmental factors including impacts of invasive species or climate change and interactions. Of great importance for fishery resources will be the protection of biogenic structures that have been found in the ACS (e.g., sponge aggregations and cold-water corals) due to the tridimensional structure they provide, used by a plethora of organisms, resulting in a substantial increase of biodiversity and abundance of associated fauna (Beazley et al., 2013). It will be thus of crucial importance for the increase our capacity to provide rigorous advice to policy makers responsible for managing and protecting biodiversity and convey to fishermen the importance of preserving habitats to make fishing sustainable.

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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.2022.107924>.

All authors have contributed to write the manuscript from the original research group, specifically critical review, commentaries and revision.

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