Community Composition and Habitat Characterization of a Rock Sponge Aggregation (Porifera, Corallistidae) in the Cantabrian Sea

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Deep-sea sponge-dominated communities are complex habitats considered hotspots of biodiversity and ecosystem functioning. They are classified as Vulnerable Marine Ecosystem and are listed as threatened or declining as a result of anthropogenic activities. Yet, studies into the distribution, community structure and composition of these habitats are scarce, hampering the development of appropriate management measures to ensure their conservation. In this study we describe a diverse benthic community, dominated by a lithistid sponge, found in two geomorphological features of the Cantabrian Sea. Based on the analyses of visual transects using a photogrammetric towed vehicle and samples collected by rock dredge, we characterize the habitat and the associated community in detail. This deep-sea sponge aggregation was found on bedrock. It is dominated by one lithistid sponge, Neoschrammeniella aff.bowerbankii (0.2 ind./m²) and further composed of various sponge species as well as of other benthic invertebrates such as cnidarians, bryozoans and crustaceans. Using a non-invasive methodology (SfM – Structure from Motion) and empirical relationships of individuals size and biomass/volume obtained in laboratory for N. aff.bowerbankii, we were able to estimate a total biomass of 41 kg and volume of 39 l of this species in the surveyed area. This approach allows a fine tune methodology for estimating biomass and volume by image-based-observed area avoiding destructive techniques for this species.

Keywords: sponge grounds, lithistids, demosponges, vulnerable marine ecosystems, ecology, taxonomy, structure from motion, underwater photogrammetry

INTRODUCTION

Sponges constitute an important component of the benthic marine communities, particularly in deeper environments where they play fundamental ecological roles (Pomponi et al., 2019). In areas where they aggregate in high density and biomass they form structurally complex ecosystems (sponge aggregations or grounds) providing habitat, nursery and rearing areas for other organisms...
often augmenting biodiversity levels locally (Murillo et al., 2012; Beazley et al., 2013; Kazanidis et al., 2016; Hawkes et al., 2019). Due to their filter-feeding capacity, they also contribute significantly to the biogeochemical cycles of carbon, nitrogen and silica (Yahel et al., 2007; De Goeij et al., 2008, 2013; Kutti et al., 2013; Cathalot et al., 2015; Maldonado et al., 2019).

The deep-sea ecosystems of the Cantabrian Sea and particularly of the Le Danois Bank (LDB) and Avilés Canyon System (ACS) have been studied in the scope of several projects (ECOMARG, INDEMARES, SponGES, INTEMARES, among others) of the Spanish Institute of Oceanography (IEO) since 2003. Initially, the projects were focused on the characterization of sediments, bathymetry and water masses dynamics, but further developed into an integrated study of the benthic communities and the trophic ecology of these ecosystems (Cartes et al., 2007; Sánchez et al., 2008, 2017; Preciado et al., 2009).

Many of the studies, focusing on Vulnerable Marine Ecosystems (FAO, 2009) of this area have been carried out over the last years, some of which aimed to characterize the sponge-dominated habitat. Protecting and restoring sponge aggregations are considered crucial from an environmental perspective. They are recognized as singular vulnerable habitats that deserve special research attention and legal protection. Deep-water sponge aggregations are now emerging as a key component of deep-sea ecosystems, creating complex habitats hosting many other species (Hogg et al., 2010; Maldonado et al., 2017). Under particular ecological conditions sponges are able to form concentrations or beds of high abundances building habitats for other species and increasing the biodiversity with respect to surrounding areas, especially the associated fauna of other invertebrate and fish (Bett and Rice, 1992; Klitgaard, 1995; Kunzmann, 1996; Bo et al., 2012; Beazley et al., 2013; Fillinger et al., 2013). These evidences indicate that efforts to close areas dominated by deep-sea sponge aggregations to bottom-tending gears will serve to meet the conservation objectives of the UNGA Resolution 61/105, that drew attention to the importance of the benthic megafauna, in vulnerable marine ecosystems. Despite the ecological importance for the deep-sea, sponge aggregations are poorly mapped and understood (Hogg et al., 2010). This lack of knowledge is most evident in deep-sea species due to the complexity of their study.

In the El Cachucho MPA, that include Le Danois Bank and its intraslope basin, the presence of sponges habitats dominated by the hexactinellids Asconema setubalense and Phoronea carpenteri and more recently demosponges habitats for Phakellia ventilabrum, P. robusta, and Geodia barretti have been described (Sánchez et al., 2008, 2009, 2017; García-Alegre et al., 2014).

In the Avilés Canyon System the presence of habitats characterized by different sponge species was also described (Sánchez et al., 2015). These studies were focused mainly on the identification of diversity hotspots and presence of vulnerable species associated with the habitat “1170 Reefs” defined by the EU Habitat Directive (E.C, 2013), toward the creation of a coherent network of Marine Protected Areas in Spain (Rodríguez-Basalo et al., 2019). As a result of these studies, Le Danois Bank and its intraslope basin were designated as a Special Area of Conservation (SAC) category and the Avilés Canyon System as a Site of Community Importance (SCI) and integrated into the Natura 2000 network.

In the Cantabrian Sea, only one other deep-sea sponge aggregation dominated by Artemisia transiens Topsent, 1890, has been reported and characterized, although in a considerably shallower area (Ríos et al., 2018).

However, due to the need to improve the management that applies in these two areas, it is necessary to identify, map and describe other benthic communities which are in these vulnerable habitats to ensure their protection.

Understanding the community composition and the population structure of key habitat-forming species is critical to understand and quantify their ecological roles, and to assess their resilience to disturbance with the aim to develop appropriate management measures to ensure their conservation.

But nowadays, there are still few studies focused on high resolution mapping techniques to determine the distribution patterns and spatial structure of sponge aggregations in the deep-sea (Klitgaard and Tendal, 2004; Chu and Leys, 2010; Kazanidis et al., 2019; Ramiro-Sánchez et al., 2019). Remotely Operated Vehicles (ROVs) and Remotely Operated Towed Vehicles (ROTVs), which integrate video and still cameras, are increasingly used by the scientific community as a means to explore and characterize deep-sea ecosystems in a non-invasive way. In recent years, applied studies have been carried out for mapping deep-sea sponge aggregations in detail based on visual or quantitative analysis of images acquired from different platforms, i.e., ROVs and AUVs (Beazley et al., 2013; Kutti et al., 2013; McIntyre et al., 2016; Powell et al., 2018; Hawkes et al., 2019; Meyer et al., 2019). The application of quantitative image analysis to deep-sea sponge aggregations habitat characterization, in general terms, has not been used to estimate biomass and population size structure.

In order to increase our knowledge about deep-sea sponges, it is essential to know specimens volume and surface area. These data also contribute to describe the population structure and biomass of species of interest. The access to these data is very difficult in the deep-sea. Most of the available methods are invasive or require removing the organisms from their natural habitat, in order to measure these parameters. Recently, approaches using underwater photogrammetry to create digital models of deep-sea communities are providing non-invasive methods to explore morphometry of individual organisms. Techniques based on Structure-from-motion (SfM) allow the reconstruction of digital, true-scale, 3D model (James and Robson, 2012; Westoby et al., 2012). This photogrammetric approach offers the possibility of creating advanced cartographic products of the ocean floor, such as 3D models and very high spatial resolution orthomosaic, in a fast and low-cost way (Kwasnitschka et al., 2013; McCarthy and Benjamin, 2014). Structure-from-Motion (SfM) techniques have been used to determine surface area and volume of corals and marine sponges from in situ images and compare them to measurements obtained in the lab (Lavy et al., 2015).

In compliance with the EU Habitats Directive, follow-up surveys are being performed to further characterize and monitor the identified habitats including the deep-sea sponges
aggregations. Such efforts are linked to the objectives of the EU-funded SponGES project which aims to develop an integrated ecosystem-based approach to preserve and sustainably use vulnerable sponge ecosystems of the North Atlantic. Through the SponGES project some of these areas (Le Danois Bank and Avilés Canyon System in the Cantabrian sea) were revisited since there was evidence that a sponge aggregation dominated by a lithistid sponge species was present. The importance of this group of sponges has been recently highlighted by Maldonado et al. (2015) which reported large aggregations of *Leiodermatium pfeifferae* (Carter, 1876) with extensive signs of habitat damage in the Mediterranean Sea.

Thus, the main aim of this study was to (a) characterize and describe the habitat of a benthic community dominated by a lithistid sponge, and (b) establish morphometric relationships of this species to estimate population structure parameters from underwater imagery, in the Avilés Canyon System and Le Danois Bank. This study is the first descriptive and quantitative analysis of lithistid aggregations in the Cantabrian Sea and contributes to our understanding of the population structure of this species as well as the composition of the overall benthic community in the area.

**MATERIALS AND METHODS**

**Study Area**

The Cantabrian Sea central area is characterized by a complex topography, including, deep-sea canyons and seamounts, and a very narrow continental shelf. Within it, two small areas have been selected for our study for having high numbers of *Neoschrommeniella aff. bowerbankii* (Figure 1A).

The western study area corresponds to the so-called El Corbiro Canyon (ECC) (Figure 1B), which forms part of the Avilés Canyon System (ACS). The ACS is a complex region of canyons and valleys comprising three main canyons of different morpho-structural characteristics: Avilés, El Corbiro, and La Gaviera canyons. The ACS has been integrate into the Natura 2000 as a Site of Community Importance (SCI) (Boletín Oficial del Estado, 2014). The continental shelf is generally narrow; the width varies from 12 km (where the head of the Avilés Canyon is incised) to 40 km. The ACS extends from the continental shelf to the abyssal plain, at 4800 m depth, and is controlled by the tectonic regime of the area. The El Corbiro Canyon is characterized by a V-shaped profile and a pronounced axial incision at its head that starts at 176 m depth on the continental shelf. Its head is made up of several gullies, particularly on the eastern wall, that converge to form the main channel (Gomez-Ballesteros et al., 2014). In our study, we have identified a rocky outcrop located on the west side of the canyon head, suitable for the settlement of lithistids. The strong currents over the canyon and his strong slope are responsible for the scarce sedimentary cover in the area.

The second study area is Le Danois Bank (LDB), a large seamount (marginal shelf) located on the Cantabrian Sea central area at 5°W longitude and 44°N latitude (Figure 1A). The Bank presents an elongated form about 72 km long in an E-W direction and about 15 km wide from north to south; it has an almost flat summit with a minimum depth of 424 m, and is separated 25 km from the continental shelf by a deeper intraslope basin (Van Rooij et al., 2010). This structure is a “horst” type, presenting a dissymmetry between its northern and southern flanks. The northern side of Le Danois Bank has a steep continental slope with a relief of 3600 m; its base is located at a 4400 m depth on the Biscay abyssal plain. The sedimentary cover is scarce in the bank summit and particularly in its western flank (Figure 1C), where the rocky outcrops and boulders are quite abundant. Gorgonian forests and deep-sea sponge aggregations are two of the most important habitats of ecological values in the Le Danois Bank and its intraslope basin. These types of habitats are included in the EU Habitat Directive that urges national governments to ensure the conservation and protect these vulnerable ecosystems. In this way, “El Cachucho” became the first Marine Protected Area (MPA) in Spain, and was included in the Natura 2000 network in 2011 (Boletín Oficial del Estado, 2011).

**Data Collection**

**Oceanographic Cruises**

Data were collected at 27 stations (Supplementary Table 1) during five expeditions within the framework of the different projects, namely INDEMARES AVILES_0511, ESMAREC_0514, SponGES_0617, ECOMARG_0717 and ECOMARG_2019 (see details in funding). The surveys were carried out onboard the R/V Vizconde de Eza (SGM) in May 2011, the R/V Ángeles Alvarino (IEO) in May 2014, in June and July 2017 and the R/V Ramón Margalef (IEO) in July 2019.

**Sampling**

Sampling on hard substrate was conducted using a rock dredge RD (80 × 30 cm; 10 mm mesh size net) towed on the seafloor during 5−15 min at a speed of 1.5 knots (Figure 2A).

The sampling stations to collect sponges (2 on each study area) were selected after studying the data provided by the multibeam echosounder or after previous visualization of images from photogrammetric towed vehicle, following gradient of deep and geological structures: DR7_AVILES0511 and DR4_SponGES0617 in ECC; DR9_SponGES0617 and DR15_SponGES0617 in LDB.

Collected material was sorted onboard, and when large catches were obtained, a representative sub-sample was kept (Figures 2D,E).

The collected biological material was photographed, anesthetized and preserved in 96% ethanol for further study in the laboratory. Identifications were performed to the lowest taxonomic level possible from the analyses of taxon-specific morphological features using specialized literature such as Bowerbank (1866), Sollas (1888), Hooper and van Soest (2002), and Cárdenas et al. (2018) (Porifera); Alder (1856), Stephens and Hickson (1909), Gravier (1920), Zibrowius (1978, 1980), Zibrowius and Cairns (1992), Molodtsova (2006), Cairns and Bayer (2009), Altuna (2013), Altuna and Ríos (2014), Addamo et al. (2016), and Cairns and Taylor (2019) (Cnidaria); Thomson (1872), Keebler (1896), Mortensen (1935), Cherbonnier (1969), Clark (1980), Paterson (1985), Clark and Downey (1992), and others.
FIGURE 1 | (A) The Cantabrian Sea central area. (B) El Corbio Canyon and sampling zone. (C) Le Danois Bank western area and sampling stations (squares for rock dredge and dots for ROTV). (D) Video transects in El Corbio Canyon. In red the transect analyzed with SfM (TV17, ECOMARG, 2017).
Southward and Campbell (2006), Míguez (2009), Manjón-Cabeza et al. (2014), and Fernández-Rodríguez et al. (2019) (Echinodermata); and Jullien and Calvet (1903), Calvet (1907, 1931), Rioja (1931), Zariquiey (1968), D’Hondt (1974), Brunton and Curry (1979), Rouse and Pleijel (2001), Louisy (2002), Wisshak et al. (2009), Velasco et al. (2013), Lloris (2015), Negri and Corselli (2016), and Álvarez-Campos et al. (2018) (others).

A total of 668 organism were sampled (339 in ECC and 329 in LDB) and compared with 6321 underwater images analyzed. In ECC we collected 111 specimens of Neoschrammeniella aff. bowerbankii and in LDB we collected 10 specimens.

Spicules on Porifera and other skeletal structures, with taxonomic value, were prepared and cleaned with bleach, distilled water and ethanol. Skeletal arrangement and spicules of Neoschrammeniella aff. bowerbankii were examined with a ZEISS SEM at Bergen University (Suplement A). Taxonomic assignments followed the classification proposed by Morrow and Cárdenas (2015) and the World Porifera Database1 for Porifera, and the World Register of Marine Species (WORMS2) for other invertebrates.

**ROTV Underwater Images**

The images analyzed in this study were obtained at LDB and ECC during the ESMAREC_0514, SponGES_0617, ECOMARG_0717, and ECOMARG_2019 surveys, using the Remotely Operated Towed Vehicle (ROTV) Politolana (Figures 2B,C). The vehicle can be operated up to a maximum of 2000 m in depth and transects were carried out navigating to 0.8 — 1.0 knot of speed at 2 — 4 m over the sea floor. This ROTV acquires simultaneously still pictures and HD video, and synchronizes it with environmental variables (pressure, temperature, and salinity). The Politolana uses telemetry to send and receive data in real-time from the equipment that composes the monitoring system: altimeter, CTD, positioning system and cameras (Sánchez and Rodríguez, 2013).

The acoustic positioning system Kongsberg HIPAP 502 was used to obtain the absolute position of the underwater vehicle. It is based on Super (Ultra) Short Base Line (SSBL) principle that establishes a three-dimensional position of the transponder. An SSBL system measured the horizontal and vertical angles together with the range to the ROTV. Then, OFOP (Ocean Floor Observation Protocol) software (Huetten and Greinert, 2008) processed the coordinate observation files and merges them with additional sensor data. Finally a complete data set for each ROTV trajectory deployment is obtained allowing georeferencing image data.

The photographs were revised for habitat characterization and description of associated communities. The ROTV Politolana is provided with a Nikon D90 camera with a Subtronic strobe. Four parallel laser beams spaced 25 cm apart and integrated in the still camera provided scale for photographs. Each 10 s the equipment takes a picture, obtaining representative data of the habitat and benthic communities to be characterized (Sánchez and Rodriguez, 2013; Sánchez et al., 2017).

The video-transect was used to generate an orthomosaic and to measure population of N. aff. bowerbankii sizes. It was recorded in July 2017 at ECC during the ECOMARG_2017 survey (TV17), in a range of depths going from 500 to 800 m (Figure 1D). A full-HD video-camera (Sony HD-700-CX) with two LED lights (12600 lumens/6000° Kelvin) attached to the image system. Two parallel laser beams spaced 20 cm apart

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1http://www.marinespecies.org/porifera/
2http://www.marinespecies.org
provided scale for videos and constant distances to validate results. The video transect analyzed in this study was about 450 m long and ran close to steep slope in ECC. The optical sensors show a portion of around 3 m of the seafloor, this area is referred to as the swath. This footprint varies depending of height over the seafloor and its bathymetry. The area covered and analyzed using this photogrammetric approach was 1450 m$^2$.

**Sponge Density Estimation and Faunal Identification**

The pictures analyzed are scaled in the PescaWin software (Sánchez, 2015). This allows estimating the surface covered by each photograph and sponge density. In each photograph all macro and megafauna were labeled, and identified to the lowest taxonomic level possible. When the external characteristics made it impossible to identify to the species level, observed specimens were assigned to morphotypes. All records were stored in a database of the IEO that allows multiple data queries on existing species throughout the Central Cantabrian Sea, their geographical location, the type of substrate, water depth, etc.

**Lithistid Morphometry**

Morphometric parameters such as biomass (drained weight), surface area, perimeter and thickness were measured for 41 specimens of *Neoschrammeniella aff. bowerbankii* collected at ECC ($N = 35$) and LDB ($N = 6$) covering a range of individual’s sizes (Figure 3). Obtained measurements were used to establish size (perimeter) – volume – biomass (drained weight) relationships. The volume was calculated for 25 samples from ECC by measuring the liquid displacement (Jokiel et al., 1978; Hughes, 2005). Weight, surface, area, perimeter and thickness were measured in all samples.

**Image Morphometry**

The measurement of the morphometry of *N. aff. bowerbankii* specimens was made using an orthomosaic of images covering 450 m of video-transect. This orthomosaic is obtained using a photogrammetric reconstruction approach. This methodology was done decomposing video-sections in thousands of geo-positioned overlapping images processed using photogrammetric Pix4D Mapper Pro software (Pix4D SA, Switzerland). Pix4D uses the Structure-from-Motion (SfM) approach. SfM is the process of estimating the 3-D structure of a scene from a set of 2-D images. It requires point correspondences between images and finds corresponding points by matching features. Pix4D software also uses a dense image matching, an automated process based on dense image matching technology (Tola et al., 2010). Integration of the point measurements, camera calibration, and the position data given by the cameras, the software provides 3D dense point clouds (Figure 4), Digital Surface Models (DSM) and orthomosaics. Since all the information is geo-referenced in a cartographic system (UTM-WGS84), all the geographic layers obtained can be included in a GIS environment thus allowing the subsequent morphometric analysis.

Constant distances between laser pointers projected on the frames were used to evaluate the reconstruction of the geometric model. In this way, the geometric uncertainty of the model and errors associated to measurements over the orthomosaic were estimated.

Thousand five hundred video-frames were used as image input in the photogrammetric adjustment of the 3D block, only 11 images were discarded. The size of 203 specimens of *N. aff. bowerbankii* were measured; the area covered by each specimen was selected as a suitable parameter of size and the area covered by the video section was also measured. The direct measurement of this parameter is possible using a complete orthomosaic with a
very high spatial resolution (0.16 cm/pixel) of the area. Using the QGis software, the area enclosed within each lithistid's perimeter was calculated (Figure 5).

These image-based perimeter data were compared with in situ data measured in the laboratory for evaluation of the equivalence of the samples. To verify this similarity, the Mann Whitney test was used. This test can be used to investigate whether two independent samples from different populations have the same distribution. Then, empirical relationships between in situ morphometric (perimeters) and biological parameters (drained weight biomass and volume) were established for this species. This empirical relationship can be applied to infer biomass from image morphometric data.

RESULTS

Here, we report the discovery of a benthic community dominated by a lithistid sponge in two areas of the Cantabrian Sea, providing a characterization of this community and its habitat. We also established the empirical relationship for Neoschrammeniella aff. bowerbankii surface area with drained weight biomass and volume, improving our knowledge in the relationship between 2D and 3D metrics for this species, in addition to inferring biomass data per unit of surface present in a specific area or aggregation both in weight and in volume occupied by the specimens.

We annotated 509 specimens seen in the videos at 23 stations, between 486 and 672 m depth and we collected 121 samples at 4 stations of RD, between 551 and 695 m depth (Supplementary Table 1).

Benthic Community Composition

In these study cases, 3691 animals belonging to eight Phyla were observed (Figure 6). In the El Corbio Canyon area, 20 sponge morphotypes were identified from the video and photographs of the photogrammetric towed vehicle. These included the habitat-forming lithistid sponge Neoschrammeniella aff. bowerbankii,
Axinellida (Phakellia robusta and P. hirondellei and other fun shape sponges), Tetractinellida, (Pachastrella monilifera, P. ovisternata, P. cf. nodulosa), Verongiida (Hexadella sp.), Halichondriidae (Topsentia sp.), Desmacellida (Desmacella spp.), Haplosclerida and Poecilosclerida (Hymedesmia (Hymedesmia) paupertas, and other Hymedesmia spp.) and other small or encrusting sponges (see Table 1). We also recorded other invertebrates, including the solitary Scleractinian Desmophyllum spp., the black coral Parantipathes hirondelli, the echiurid Bonellia viridis, the asteroid Henricia sp. and the cnidarians Cerianthus spp. However, there were a number of species not easily distinguished and impossible to identify only by video.

In Le Danois Bank, several species of Demospongiae and Hexactinellida were present alongside N. aff. bowerbankii contributing to the 3D structure of the community. Analysis of the samples collected and annotation of the video transects confirmed that there are a number of erect, massive or encrusting species that play an important role because of their size, volume or abundance: erect and fan-shaped species as Phakellia hirondellei and Phakellia robusta; massive Tetractinellida, with three large Geodiid species: Geodia cf. barretti, G. pachydermata, Geodia sp. and the presence of three species of the genus Pachastrella were frequently recorded. In this area, we also collected other Tetractinellida such as Characella pachastrelloides, Calthropella (Calthropella) geodioides and Calthropella (Calthropella) durissima these last ones smaller than the previous ones. Hymedesmia (Hymedesmia) paupertas is one of the most common species recognizable using ROTV by its characteristic encrusting shape and bright blue color. The Hexactinellid Aphrocallistis beatrix was also detected not forming a biogenic framework, but as solitary individuals. Some specimens of Phoronema carteri were observed but in soft bottoms near the N. aff. bowerbankii community.

In ECC, we collected more cnidarians (colonies or individuals) (44 samples) than in LDB (9 samples), where the most abundant are two different species of Cerianthus Anthozoa, the scleractinian Desmophyllum spp. and Balanophyllia (Balanophyllia) thalassae, the Alcyonacea Callogorgia verticillata, Paramuricea cf. placomus and Anthomastus sp., these two only present in LDB.

Including samples collected with RD and analyzed images with ROTV. The species richness is very similar in both areas (Figure 7), but slightly higher in LDB for almost all the taxonomic groups, with the phylum Porifera being dominant (35.44% ECC – 38.64% LDB), and consisting nearly entirely of species belonging to the class Demospongiae. As for Cnidarians (17.72% ECC – 20.45% LDB), they are also found in both areas, but images show that they are more frequent in the surrounding areas than in the habitat occupied by the sponges. Mollusca (6.33% ECC – 2.27%
### TABLE 1 | Species in associated fauna (AF) and co-occurrence (CO) in populations of *Neoschrammeniella aff. boweberanki* in El Corbiro Canyon (SCA) and Le Danois Bank (LDB).

| Phylum | Species | AF | El Corbiro Canyon (ECC) | Le Danois Bank (LDB) |
|--------|---------|----|-------------------------|----------------------|
|        |         |    | CO – DR | CO – TF | CO – DR | CO – TF |
| Porifera | Antho sp. | X | X | X | X | X |
| Demospongiae | Axinellida indet. | X | X | X | X | X |
|            | Axinella sp. | X | X | X | X | X |
|            | *Calthropella (Calthropella) geodioides* (Carter, 1876) | X | X | X | X | X |
|            | *Calthropella (Calthropella) durissima* Topsent, 1892 | X | X | X | X | X |
|            | *Caminella pustula* (Cárdenas et al., 2018) | X | X | X | X | X |
|            | *Characella pachastrelloides* (Carter, 1876) | X | X | X | X | X |
|            | *Clathria sp.* | X | X | X | X | X |
|            | *Coelosphaera (Histodermion) sp.* | X | X | X | X | X |
|            | *Desmacella sp.* | X | X | X | X | X |
|            | Demospongiae indet. | X | X | X | X | X |
|            | *Geodia anceps* (Vosmaer, 1894) | X | X | X | X | X |
|            | *Geodia cf. barretti* | X | X | X | X | X |
|            | *Geodia nodastrella* Carter, 1876 | X | X | X | X | X |
|            | *Geodia pachydermata* (Sollas, 1886) | X | X | X | X | X |
|            | *Geodia sp.* | X | X | X | X | X |
|            | *Haliclona (Flagella) sp.* | X | X | X | X | X |
|            | *Haliclona (Gellius) sp.* | X | X | X | X | X |
|            | *Halocnemus sp.* | X | X | X | X | X |
|            | *Haploclerida indet.* | X | X | X | X | X |
|            | *Hexactinellida indet.* | X | X | X | X | X |
|            | *Hymedesminia (Hymedesminia) pauperta* (Bowerbank, 1866) | X | X | X | X | X |
|            | *Hymedesminia sp.* | X | X | X | X | X |
|            | *Janulium spiniculium* (Carter, 1876) | X | X | X | X | X |
|            | *Latrunculia sp.* | X | X | X | X | X |
|            | *Microcionidae indet.* | X | X | X | X | X |
|            | *Pachastrella cf. nodolosa* | X | X | X | X | X |
|            | *Pachastrella monilifera* Schmidt, 1868 | X | X | X | X | X |
|            | *Pachastrella ovisternata* Lendenfeld, 1894 | X | X | X | X | X |
|            | *Pachastrella sp.* | X | X | X | X | X |
|            | *Pachastrellidae indet.* | X | X | X | X | X |
|            | *Phakellia hirondellei* Topsent, 1890 | X | X | X | X | X |
|            | *Phakellia robusta* Bowerbank, 1866 | X | X | X | X | X |
|            | *Plocamione hystrix* (Ridley and Duncan, 1881) | X | X | X | X | X |
|            | *Plocamionida sp.* | X | X | X | X | X |
|            | *Polymastia sp.* | X | X | X | X | X |
|            | *Sceptrella sp.* | X | X | X | X | X |
|            | *Siponodictyon sp.* | X | X | X | X | X |
|            | *Spirorhabdia vitia* (Schmidt, 1875) | X | X | X | X | X |
|            | *Spongiosorites sp.* | X | X | X | X | X |
|            | *Sulcastrella sp.* | X | X | X | X | X |
|            | *Tentorium semilobatus* (Schmidt, 1870) | X | X | X | X | X |
|            | *Tetraclitellida indet.* | X | X | X | X | X |
|            | *Thena schmidtii* (Sollas, 1886) | X | X | X | X | X |
|            | *Thrombus sp.* | X | X | X | X | X |

(Continued)
| Phylum       | Species                        | AF        | El Corbiro Canyon (ECC) | Le Danois Bank (LDB) |
|--------------|--------------------------------|-----------|-------------------------|----------------------|
|              |                                | CO – DR   | CO – TF                 | CO – DR   | CO – TF |
| Cnidaria     | Cnidaria indet.                |           |                         | X         |
| Anthozoa     | Balanophyllia (Balanophyllia) thalassae Zibrowius, 1980 | X         | X                       | X         | X       |
|              | Caryophyllia sp.               |           |                         | X         |
|              | Deltocysthus moseleyi Cairns, 1979 |         |                         | X         |
|              | Dendrophyllia cornigera (Lamarck, 1816) |         |                         | X         |
|              | Desmophyllum dianthus (Esper, 1794) |         | X                       | X         | X       |
|              | Desmophyllum pertusum (Linnaeus, 1758) |         | X                       | X         | X       |
|              | Desmophyllum sp.               |           |                         | X         |
|              | Scleractinia indet.            |           |                         | X         |
|              | Acanthogorgia armata Verrill, 1878 |         |                         | X         |
|              | Acanthogorgia sp.              |           |                         | X         |
|              | Anthomastus sp.                |           |                         | X         |
|              | Callogorgia verticillata (Pallas, 1766) |         | X                       | X         | X       |
|              | Gersemia sp.                   |           |                         | X         |
|              | Narella versatilis (Stephens and Hickson, 1909) |         | X                       | X         |
|              | Paramuricea cf. placornus      |           |                         | X         | X       |
|              | Paramuricea sp.                |           |                         | X         |
|              | Placogorgia sp.                |           |                         | X         |
|              | Stolonifera indet.             |           |                         | X         |
|              | Swiftia dubia (Thomson, 1929)  |           |                         | X         |
|              | Viminella flagellum (Johnson, 1863) |         |                         | X         |
|              | Actinaria indet.               |           | X                       | X         |
|              | Antipatharia indet.            |           |                         | X         |
|              | Allopathes sp.                 |           | X                       | X         |
|              | Leiopathes sp.                 |           |                         | X         |
|              | Paramuricea hirondelle Malodtsova, 2006 |         |                         | X         |
|              | Schizopathes sp.               |           |                         | X         |
|              | Cerianthus sp.                 |           |                         | X         |
| Hydrozoa     | Epizoanthus sp.                |           |                         | X         |
|              | Hydrozoa indet.                |           |                         | X         |
|              | Campanularia hincksi Alder, 1856 |         | X                       | X         |
|              | Diphasia alata (Hincks, 1855)  |           |                         | X         |
|              | Lafoea dumosa (Fleming, 1820)  |           |                         | X         |
|              | Stenohelia maderensis (Johnson, 1862) |         |                         | X         | X       |
| Brachiopoda  | Macandrevia sp.                |           | X                       | X         |
|              | Platidia sp.                   |           |                         | X         |
|              | Terebratulina retusa (Linnaeus, 1758) |         |                         | X         |
| Bryozoa      | Buguloidea indet.              |           |                         | X         |
|              | Diaporella sp.                 |           |                         | X         |
|              | Reteporella sp.                |           |                         | X         |
| Sipuncula    | Sipuncula indet.               |           |                         | X         |

(Continued)
| Phylum       | Species                                | AF | El Corbiro Canyon (ECC) | Le Danois Bank (LDB) |
|-------------|----------------------------------------|----|-------------------------|----------------------|
|            |                                        |    | CO – DR | CO – TF | CO – DR | CO – TF |
| Mollusca    |                                        |    |         |         |         |         |
| Solenogastres | Solenogastres indet.                   |    |         | X       |         |         |
| Polyplacophora | Hanleya hanleyi (Bean, 1844)           |    |         |         |         |         |
| Gastropoda  | Calliostoma leptopylema Dautzenberg and Fischer, 1896 |    | X       | X       |         |         |
|             | Emarginula sp.                         |    |         |         |         |         |
| Bivalvia    | Spondylus gussoni Costa, 1830 [*1829*] |    |         |         | X       |         |
|             | Kamekampia sulcata (Müller, 1776)      |    |         |         | X       |         |
|             | Neopycnodonte zibrowi Wissel et al., 2009 |    |         |         | X       |         |
| Cephalopoda | Eledone sp.                            |    |         |         | X       |         |
| Annelida    |                                        |    |         |         |         |         |
|             | Amphipomidae indet.                    |    |         |         |         |         |
|             | Bonellia vindi Rolando, 1822           |    | X       | X       | X       |         |
|             | Eunicidae indet.                      |    | X       | X       |         |         |
|             | Haplosyllis sp.                       |    |         |         |         |         |
|             | Hesionidae indet.                     |    |         |         |         | X       |
|             | Hyalinoecia tubicola (Müller, 1776)   |    |         |         |         | X       |
|             | Maldanidae indet.                     |    | X       | X       | X       |         |
|             | Phylodocidae indet.                   |    |         |         |         |         |
|             | Polynoidae indet.                     |    | X       | X       |         |         |
|             | Syllis sp.                            |    | X       | X       | X       |         |
|             | Terebellidae indet.                   |    |         |         |         | X       |
|             | Trypanosyllis sanchezi (Álvarez-Campos et al., 2018) |    |         |         |         | X       |
|             | Trypanosyllis sp.                     |    |         |         | X       |         |
|             | Vermilopsis sp.                       |    |         |         | X       |         |
| Arthropoda  | Crustacea                              |    |         |         |         |         |
|             | Dichelopandalus bonnier Caullery, 1896 |    |         |         |         | X       |
|             | Munida perarmata Milne-Edwards and Bouvier, 1894 |    | X       | X       |         | X       |
|             | Bathynectes maravigna (Prestandrea, 1839) |    | X       | X       | X       |         |
|             | Polybius henslowi Leach, 1815–1875     |    |         |         |         | X       |
|             | Pagurus sp.                           |    |         |         |         | X       |
|             | Uroptychus sp.                        |    |         |         |         | X       |
| Echinodermata |                                        |    |         |         |         |         |
| Echinoidea  | Araeopoma fenestratum (Thomson, 1872)  |    | X       | X       | X       | X       |
|             | Cidaris cidaris (Linnaeus, 1758)       |    | X       | X       | X       |         |
|             | Phormosoma placenta Thomson, 1872     |    |         |         |         |         |
| Asteridea   | Brisinga endecaemnas Asbjørnsen, 1856  |    |         |         |         |         |
|             | Ceraster sp.                          |    |         |         |         |         |
|             | Culcitoasis borealis (Süssbach and Breckner, 1911) |    |         |         |         | X       |
|             | Henricia caudata (Koeber, 1895)       |    | X       | X       | X       | X       |
|             | Novodinia pandina                      |    |         |         |         |         |
|             | Peltaster placenta (Müller and Troschel, 1842) |    |         |         |         | X       |
|             | Porania sp.                           |    |         |         |         | X       |
|             | Pterasteridae indet.                  |    |         |         |         |         |
|             | Asteroida indet.                      |    |         |         |         | X       |
| Ophiuroidea | Ophiuroidea                           |    |         |         |         |         |
| Crinoidea   | Ophiura valenciennesi (Lyman, 1879)   |    |         |         | X       |         |
|             | Koehlermetra porrecta (Carpenter, 1888) |    | X       |         | X       |         |
|             | Leptometra celtica (M‘Andrew and Barrett, 1857) |    |         |         | X       |         |
|             | Crinoidea indet.                      |    |         |         |         | X       |
| Holothuroidea |                                            |    |         |         |         |         |
|             | Benthogone rosea Koeber, 1895          |    |         |         |         | X       |
|             | Parastichopus tremulus (Gunnerus, 1767) |    |         |         |         | X       |
|             | Psolidium cf. complanatum             |    |         |         |         | X       |
|             | Psolus sp.                            |    |         |         |         | X       |

(Continued)
LDB), Crustacea (3.8% ECC – 5.69% LDB); Annelida (12.66% ECC – 12.5% LDB) and Echinodermata (12.66% ECC – 14.77% LDB) are other groups well represented in the area, with high density of the taxon Echinoidae.

The presence of Brachiopoda (5 ECC) and Sipuncula (5 ECC – 9 LDB) was only detected with the specimens collected by the RD.

**Habitat Characterization**

In the two Cantabrian Sea areas we studied, habitats have a similar structure and taxonomic composition with only slight differences. In ECC the aggregation of *Neoschrammeniella aff. bowerbankii* occurs on the west wall (Figures 1B,D) attached by their bases on a rocky bottom with a steep slope between 520 and 760 m in depth (Figure 8A).

The massive skeletons have a very hard consistency neither disaggregate nor easily dissolved after sponge death; they persist attached to the bottom and they are an available substrate for other organisms. Sponge densities estimated by image analysis were 0.43 indiv./m² in the TF17_ECOMARG_0717 transect (ECC) and 0.05 indiv./m² in the TF9_ESMAREC_0514 transect (LDB). Individuals were not clustered nor densely aggregated as in other deep-sea sponge aggregations. They presented an average distance of 79.6 cm between individuals (with minimum distances of 8.30 and maximum distances of 212.40 cm).

In LDB, the aggregation occurs mainly on the rocky ridges of the western and SW flanks of the seamount (Figure 1C), at 477–760 m in depth (Figure 8B). The substrate type is quite different in both areas. In ECC, we find that the area is continuous and well defined and is formed by bedrock covered with a thin layer of mud, with a slope range of 45–60°. At LDB, facies are formed by rock ridges, large boulders and mixed sediments producing a more patchy habitat both along the seamount and inside our study area. The water temperature at the seafloor during the survey periods was 10.30–10.86°C in ECC and 10.50–11.14°C in LDB. The salinity ranged between 35.56–35.72 ppm in ECC and 35.59–35.66 ppm in LDB.

**Neoschrammeniella aff. bowerbankii**

**Morphometry**

The form of the collected samples in the Cantabrian Sea is a small cup in the case of the younger specimens and the shape of a round tray with undulated margin in that of the adults. Dimensions (height, width) varied between 3.1 × 4.1 in the smallest and 19.5 × 19.6 in the largest collected specimens, with wall thickness ranging from 1.2 to 2.8 cm. The perimeter varies from 10.10 to 64.7 cm.

Morphometric parameters (perimeter, thickness, weight, and volume) obtained in the laboratory for 41 specimens allowed us to establish logarithmic morphometric relationships, with high adjustment for perimeter – drained weight ($R^2 = 0.93$) and perimeter – volume ($R^2 = 0.91$) for *Neoschrammeniella aff. bowerbankii* (Figures 9B,C).

The size of 203 *Neoschrammeniella aff. bowerbankii* specimens were obtained through manual digitized perimeter and area enclosed measurements. Both specimens measured in the laboratory and those measured on the image orthomosaic belonged to the same study area, the El Corbiro Canyon, in ACS, at two different stations, separated at 678m.

The lithistid perimeter data of the two samples sets (measured in the lab and from the images) have been compared to verify their similarity, using Mann Whitney test (Figure 9A). The result shows that $U$-value is 3352; the Z-Score is 0.53167 and the $p$-value is 0.59612. Subsequently, we cannot reject the null hypothesis at 5% significance, indicating not significant differences between the obtained measurements.

The density of this species as assessed by the video is 0.2 indiv./m². Using the surface data enclosed in the perimeters of the lithistids measured by digitizing on the orthomosaic image, a histogram with the population size distribution of *N. aff. bowerbankii* was obtained showing that specimens range from 7 to 497 cm² (Figure 9D). Applying the relationships established with the in situ samples and empirical lab measures, we can infer the drained weight biomass and volume of each of the copies of *N. aff. bowerbankii* measured in the images and the total weight (41.13 kg) and volume (39.34 l) of the aggregation of lithistids present in the area, without the need for extractive sampling.

**DISCUSSION**

The biology and ecology of present-day lithistid fauna remain poorly known (Carvalho et al., 2015; Maldonado et al., 2015). With this study we focus on the knowledge of lithistid aggregation in the Cantabrian Sea at two Natura 2000 sites.
Deep-sea sponge aggregations have been considered a type of habitat under the OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic (Christiansen, 2010). The document mentions grounds of Astrophorids and Hexactinellida, and in particular the genera *Geodia* and *Pheronema*, which are the predominant habitat-forming species in the NE Atlantic. Hogg et al. (2010), in the frame of the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), report outlines of what is known about deep-water sponge grounds habitats and Maldonado et al. (2015), reported a distinct reef-like type from the Mediterranean, the monospecific formation built by the lithistid demosponge *Leiodermatium pfeifferae*. Other regions where lithistids dominate the fauna are the tropical
and subtropical Atlantic (Pomponi et al., 2001; Maldonado et al., 2017) and the south of New Caledonia (Lévi, 1991) and New Zealand (Kelly, 2007; Kelly et al., 2007).

The study area is subject to some management measures in the context of the Natura 2000 Framework, the “El Cachucho” MPA, that include Le Danois Bank, and the Site of Community Importance (SCI) Avilés Canyon System. For both Natura 2000 areas the main environmental value that has conditioned its protection policies is the presence of the habitat “1170 Reefs” of the European Habitat Directive (E.C, 2013). The sponge aggregations located on hard bottoms are included in this classification of vulnerable habitats on which it is mandatory for the European countries to establish conservation measures. In this sense, the knowledge of the habitats structured by lithistids sponges is essential to provide managers with indicators for monitoring the degree of the habitat’s recovery in order to know the success of management measures and to ensure their adequate protection. Within the implementation of Marine Strategy Framework Directive (MSFD, E.C, 2008) it would be good to monitor those indicators that could help assess the environmental status of this vulnerable habitat. The methodologies described in this work will facilitate future monitoring of the MPAs using different indicators within the descriptor “Biological Diversity,” such as the species distribution, the size and condition of their populations and some indicators in relation of deep-sea sponge aggregations (as distributional range, pattern and area covered) and condition of the typical species and communities (Borja et al., 2011, 2014). Among the indicators of “Sea-floor Integrity” descriptor of MSFD (Rice et al., 2012), the most suitable are estimates of the type, abundance, biomass
and the real extent of the biogenic substrate as well as all those indicators related to benthic community condition such as the presence of species on the seabed particularly sensitive and/or tolerant to human activities. Considering just those indicators in successive surveys and applying ground-truth sampling and photogrammetric techniques in representative biotopes of deep-sea sponge aggregations (using fixed sampling stations), the monitoring could be affordable and provide reliable results (Sánchez et al., 2017).

On the basis of the environmental characteristics required for the settlement of these sponges it is possible to obtain high resolution maps of their spatial distribution and identify potential impacts of anthropogenic uses. These approaches have already been used successfully in the study area by providing detailed maps needed for effective protection of gorgonians forest, deep-sea sponge aggregations and cold-water corals (Sánchez et al., 2014, 2017; Rodríguez-Basalo et al., 2019). The present study of the lithistids sponges should be taken into consideration for the design of the new management plan of the ACS.

The approach presented here to obtain the size of sponges demonstrate the consistency and reliability of SFM methodology. This is especially relevant in deep-sea environments where the access to the sizes of species is limited. The obtained results, giving a quadratic mean error of 0.10 cm in distance (using laser beam constant distance) and a retroprojection error of 0.154 pixels in image block adjustments, show very low values of geometric uncertainty, which validate the application of this approach for the measurement of parameters related to the size of sessile organism living on the sea bottom. Mean retroprojection errors values of less than 2 pixels were assumed as indicators of the effectiveness of SFM programs for creating highly accurate 3D reconstructions of underwater habitats (Burns and Delparte, 2017).

The relationship between surface area (2D) and volume (3D) metrics estimated using SFM, are particularly relevant when estimating the ecosystem services and functions performed by corals (House et al., 2018).

Surface area can be used as an indicator of structural habitat availability, which is an important ecosystem service of coral reefs and sponges (Santavy et al., 2013). The SFM technique shows a great potential for characterization and monitoring habitats and benthic communities. Thanks to the non-destructive nature it can be used in vulnerable habitats and protected areas, across multiple depths, scales, and reef types (Bythell et al., 2001; Cocito et al., 2003; Courtney et al., 2007; Burns et al., 2015a,b; Prado et al., 2019; Price et al., 2019). The high resolution cartographic outputs can increase the speed, scale and accuracy of species morphometric assessment. In addition, the methodologies based on SFM are quantitative and replicable, so these techniques, therefore allows detailed, spatially explicit observation of community change through time rather than purely typical qualitative descriptions (Ferrari et al., 2016).

“For sponges (Porifera), the amount of food available is directly proportional to the amount they can pump. All the mechanisms which could lead to induced current, depend on the flow regime around the sponge, the morphology of the sponge (mound-shaped or cylindrical) and the direction the apertures open into the flow” (Leys et al., 2011). It is, therefore key to fine-tune methodologies to evaluate the shape and size of the specimens of the different species. The relationship of these parameters to filtration rates is a complex matter in the deep-sea that has so far rarely been addressed, with the exception of some experiments conducted with monitoring hoods placed on-site (Yahel et al., 2007; Maldonado et al., 2012, 2017; De Goeij et al., 2017). The progress in relating size (surface area) to volume and even biomass measurements (weight or volume) is essential to be able to understand basic processes of the biology of the species.

The accuracy of the adjustments obtained in the ratio of the size measures (perimeters) to weight and volume (R2 greater than 0.9 in both cases) make us consider a robust and logical relationship between the size of the specimens and the biomass and volume they provide in the habitat. These aspects are key not only for sponge aggregations but also for coral reefs, in this case with morphotype specific conversion parameters, the surface area and volume scale consistently with planar area (House et al., 2018) based on the SFM method. But this approach is still rarely mentioned in literature.

Photogrammetry provides accurate estimates of the surface and perimeters and the establishment of the relationship between in situ measurements and image-based measurements describing a relationship between lab conenchymal surface versus mesh surface calculation for Paramuricea clavata (Palma et al., 2018) but no known similar approximation has been made for lithistid sponge aggregations.

Common methods for measuring surface, area and volume of marine organisms include water displacement (Jokiel et al., 1978) and paraffin dipping (Stimson and Kinzie, 1991; Veal et al., 2010) and require in all cases the extraction of the specimens from seafloors. The use of extractive methodologies is usually banned for highly vulnerable species or in areas of special conservation. It is thus very important to develop and validate non-invasive methodologies to obtain morphometric parameters of the different species and subsequently, establish the empirical relationships between biological characteristics and the morphometry of the specimens. The morphometric measurements of a species can be determined using non-invasive methods and by applying obtained empirical relations, important information can be inferred from the biology of highly unknown benthic species.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found at: https://doi.pangaea.de/10.1594/PANGAEA.910127.

AUTHOR CONTRIBUTIONS

All the authors conceived and designed the study. EP, PR, and FS analyzed the data. EP, FS, PR, and AR-B contributed to the
photogrammetry and structure from motion techniques. FS and JC led the ship surveys. PR, EP, and AR-B processed the video and image material. FS, JC, and JX acquired the funding. FC, AR-B, PR, and TI identified the fauna. All the authors helped to collect process and map field data, prepared the figures and tables, reviewed drafts of the manuscript, and helped to writing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00578/full#supplementary-material

REFERENCES

Addamo, A. M., Vertino, A., Stolariki, J., García-Jiménez, R., Tavani, M., and Machordam, A. (2016). Merging scleractinian genera: the overwhelming genetic similarity between solitary Desmophyllum and colonial Lophelia. BMC Evolut. Biol. 16:108. doi: 10.1186/s12862-016-0654-8

Alder, J. (1856). A notice of some new genera and species of British hydroid zoophytes. Ann. Magaz. Nat. History 18, 12–14. doi: 10.1080/0022293580697652

Altuna, A. (2013). Scleractinia (Cnidaria: Anthozoa) from ECOMARG 2003, 2008 and 2009 expeditions to bathyal off northwest and northwestern Spain (northeast Atlantic). Zootaxa 3641, 101–128. doi: 10.11646/zootaxa.3641.2.1

Altuna, A., and Ríos, P. (2014). Scleractinia (Cnidaria: Anthozoa) from INDEMARES 2010–2012 expeditions to the Avilés Canyon System (Bay of Biscay, Spain, northeast Atlantic). Helgol Mar. Res. 68, 399–430. doi: 10.1007/s10152-014-0398-z

Álvarez-Campos, P., Taboada, S., San Martín, G., Leiva, C., and Riesgo, A. (2018). Phylogeographic relationships and evolution of reproductive modes within flattened syllids (Annelida: Syllidae) with the description of a new genus and six new species. Invertebr. Syst. 32, 224–251. doi: 10.1017/ISI1711

Asbjørnsen, P. C. (1856). Description d’un nouveau genre des Astéries in Sars, P. S. Fauna Litt. Norw. 1, 150-158.

Bean, T. C. (1844). British Marine Conchology; Being a Descriptive Catalogue, Arranged According to the Lamarckian System, of The Salt Water Shells of Great Britain. London: Edward Lumley.

Beazley, L. I., Kenchington, E. L., Murillo, F. J., and Sacau, M. (2013). Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. ICES J. Mar. Sci. 70, 1471–1490. doi: 10.1093/icesjms/fst124

Bett, B. J., and Rice, A. L. (1992). The influence of hexactinellid sponge (Phoronea carpenteri) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic). Ophelia 36, 217–226. doi: 10.1080/00306369.1992.10430372

Bo, M., Bertolino, M., Bastesrrello, G., Canese, S., Giusti, M., Angiolillo, M., et al. (2012). Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. Hydrobiologia 687, 163–177. doi: 10.1007/s10750-011-0964-1

Boletín Oficial del Estado (2011). 8 de Diciembre de 2011. Boletín Oficial del Estado (BOE-A-2011-19246).

Burns, J. H. R., and Delparte, D. (2017). “Comparison of commercial structure-from-motion photogrammetry software used for underwater three-dimensional modeling of coral reef environments,” in The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences. Vol. XLII-2/W3, Náploth, 127–131. doi: 10.5194/isprs-archives-XLII-2-W3-127-2017

Burns, J. H. R., Delparte, D., Gates, R. D., and Takabayashi, M. (2015a). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 3:e1077. doi: 10.7717/peerj.1077

Burns, J. H. R., Delparte, D., Gates, R. D., and Takabayashi, M. (2015b). “Utilizing underwater three-dimensional modeling to enhance ecological and biological studies of coral reefs,” in The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences, XL-5/W5, Italy. doi: 10.5194/isprsarchives-XL-5-W5-61-2015

Burns, J. H. R., and Delparte, D. (2015a). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 3:e1077. doi: 10.7717/peerj.1077

Bythell, J., Pan, P., and Lee, J. (2001). Three-dimensional morphometric measurements of reef corals using underwater photogrammetry techniques. Coral Reefs 20, 193–199. doi: 10.1007/s003380100157

Cairns, S. D. (1979). The deep-water Scleractinia of the Caribbean and adjacent waters. Stud. Fauna Curacao. 57:341.

Cairns, S. D., and Bayer, F. M. (2009). A generic revision and phylogenetic analysis of the Primnoidae (Cnidaria:Octocorallia). Smithsonian Contributions to Zoology, 629. Washington DC: Smithsonian Institution Press, 79. doi: 10.5479/si.00810282.629

Cairns, S. D., and Taylor, M. L. (2019). An illustrated key to the species of the genus Narella (Cnidaria, Octocorallia, Primnoidae). ZooKeys 822, 1–15. doi: 10.3897/zoolkeys.822.29922

Calvet, L. (1907). Bryozoaires. Expeditions scientifiques du “Talisman” pendant les années 1880–1883. Paris 8, 355–495.

Calvet, L. (1931). Bryozoaires provenant des campagnes scientifiques du prince Albert ier de monaco. Rés. Camp. Sci. Prince Monaco 83, 1–152.
Jullien, J., and Calvet, L. (1903). Bryozoaires provenant des campagnes de l’Hirondelle (1886-1888). *Result. Campag. Sci. Acconm. Yacht Albert Prince Souver. Monaco*, 23, 1–188.

Kazanidis, G., Henry, L. A., Roberts, J. M., and Witte, U. F. M. (2016). *Biodiversity of Spongiosorites coralliphaga* (Stephens, 1915) on coral rubble at two contrasting cold-water coral reef settings. *Coral Reefs* 35, 193–208. doi: 10.1007/s00338-015-1355-2

Kazanidis, G., Vad, J., Henry, L. A., Neat, F., Berx, B., Georgoulas, K., et al. (2019). *Seabed Images and Corresponding Environmental Data From Deep-Sea Sponge Aggregations in the Faroe-Shetland Channel Nature Conservation Marine Protected Area*. Amsterdam: PANGAEA, doi: 10.1594/PANGAEA.897604

Kelly, M. (2007). *The Marine Fauna of New Zealand. Porifera: Lithistid Demospongiae (Rock Sponges)*. The Marine Fauna of New Zealand. Wellington: National Institute of Water and Atmospheric Research (NIWA).

Kelly, M., Ellwood, M., Tubbs, L., and Buckrider, J. (2007). “The lithistid Demospongiae in New Zealand waters: species composition and distribution,” in *Porifera Research: Biodiversity, Innovation and Sustainability*, eds M. R. Custódio, G. Lobo-Hajdu, E. Hajdu, and G. Muricy (Rio de Janeiro: Museu Nacional do Rio de Janeiro, vol série livros), 393–404.

Klitgaard, A. B. (1995). “The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongeae) at the Faroe Islands, northeastern Atlantic.” *Sarsia* 80, 1–22. doi: 10.1080/00364827.1995.10413574

Klitgaard, A. B., and Tendal, O. S. (2004). *Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic*. *Prog. Oceanogr.* 61, 57–98. doi: 10.1016/j.pocean.2004.06.002

Koehler, R. (1895). *Dargrages profundos ejecuta un bord caudan en el golfe de Gascogne. Rapport préliminaire sur les Échinodermes. Revue biologique du Nord de la France*, 7, 439–496.

Koehler, R. (1896). “Échinodermes,” in *Résultats scientifiques de la campagne du “Caudan” dans le golfe de Gascogne — août-septembre 1895*, Vol. 26, ed. R. Koehler (Lyon: Université de Lyon), I–IV. doi: 10.5962/bhl.t1-65730

Kunzmann, K. (1996). Associated fauna of selected sponges (Hexactinellida and Demospongeae) from the Weddell Sea, Antarctica. *Rep. Polar Res. 210*, 1–93.

Kutti, T., Bannister, R. J., and Fossa, J. H. (2013). Community structure and ecological function of deep-water sponge grounds in the Traenadypet MPA—Northern Norwegian continental shelf. *Cont. Shelf Res.* 69, 21–30. doi: 10.1016/j.csr.2013.09.011

Kwasnitschka, T., Hansteent, T. H., Devey, C. W., and Kutterolf, S. (2013). Doing bathymetry from bathymetric data. *Remote Sensing* 5, 1329–1353. doi: 10.3390/rs5081329

Lyman, L. (1879). *Ophiuridae and Astrophylidae of the “Challenger” Expedition. Part II*, Vol. 6. Cambridge, MA: Harvard College, 17–83.

M’Andrew, R., and Barrett, L. (1857). List of the echinodermata dredged between dronthem and the north cape. *Ann. Mag. Nat. History* 20, 43–44.

Maldonado, M., Aguilar, R., Bannister, R. J., Bell, J. J., Conway, K. W., Dayton, P. K., et al. (2017). “Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns,” in *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*, eds S. Rossi, L. Bramanti, A. Gori, and C. Orejas (Berlin: Springer International Publishing), 145–183. doi: 10.1007/978-3-319-17001-5_24-1

Maldonado, M., Aguilar, R., Blanco, J., García, S., Serrano, A., and Punzón, A. (2015). Aggregated clumps of lithistid sponges: a singular, reef-like benthal habitat with relevant paleontological connections. *Phylo One* 10:e0125378. doi: 10.1371/journal.pone.0125378

Manjón-Cabeza, M. E., Palma-Sevilla, N., Gómez-Delgado, A. I., Andrinio-Abelaira, J., and Ríos, P. (2014). “Échinodermas asombles de Avilés canyons (přéliminary results) (Biscay (INDEMARES)LIPE Project),” in *XVIII Simposio Ibérico de Estudios de Biologia Marina. Libro de resímenes*, eds P. Ríos, L. A. Suárez, and J. Cristobo (Gijón : Centro Oceanográfico de Gijón).

McCarty, I., and Benjamin, J. (2014). Multi-image photogrammetry for underwater archaeological site recording: an accessible, diversifiable approach. *J. Mar. Archaeol.* 9, 95–114. doi: 10.1080/11451704.91277

Mcflytre, D. F., Drewery, J., Eerkes-Medrano, D., and Neat, F. C. (2016). Distribution and diversity of deep-sea sponge grounds on the rosemary bank seamount, NE Atlantic. *Mar. Biol. 163*:143. doi: 10.1007/s00227-016-2913-z

Meyer, H. K., Roberts, E. M., Rapp, H. T., and Davies, A. J. (2019). Spatial patterns of arctic sponge ground fauna and demersal fish are detectable in autonomous underwater vehicle (AUV) imagery. *Deep Sea Res. Part II* 190:10337. doi: 10.1016/j.dsr.2019.103137

Milne-Edwards, A., and Bouvier, E. L. (1894). Considerations générales sur la famille des Galatheides. *Ann. Sci. Nat. Zool.* 16, 191–327.

Miguez, L. I. (2009). *Echinodermos (Crinoidea, Echinoidae et Holothuroidea) Litorales, Batales y Abisales de Galicia*. 864. Ph.D. Thesis, Universidad de Santiago de Compostela, Santiago de Compostela.

Molodstova, T. N. (2006). “Black corals (Antipatharia: Anthozoa: Cnidaria) of North-East Atlantic,” in *Biogeography of the North Atlantic seamounts*, eds A. N. Mironov, A. V. Gebruk, and A. J. Southward (Moscow: KMK Press), 141–151.

Morrow, C., and Cárdenas, P. (2015). Proposal for a revised classification of the Demospongeae (Porifera). *Front. Zool.* 12:7. doi: 10.1186/s12983-015-0099-8

Mortensen, T. (1935). *A Monograph of the Echinidea. II. Bothriocidaroida, Melencinchoida, Lepidocentroida, and Stirodonta*, ed. C. A. Reitzel (London: Oxford University Press), 647.

Müller, O. F. (1776). *Zoologie Danica Prodromus, seu Animalium Daniae et Norvagiae Indigenarum Characteres, Nomina, et Synonyma Imprimis Populairum*, Copenhagen: Hallageri, 274.

Müller, J., and Troschel, F. H. (1842). *System der Asteriden. 1. Asteriæ. 2. Ophiuridæ*. Vieweg: Braunschweig, 12.

Murillo, F. J., Durán Muñoz, P., Cristobo, J., Ríos, P., González, C., Kencinghton, E., et al. (2012). Deep-sea sponge grounds of the Flemish Cap, Flemish Pass and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): Distribution and species composition. *Mar. Biol. Res.* 8, 842–854. doi: 10.1080/17451000.2012.682583

Negri, M. P., and Corselli, C. (2016). Bathyal Mollusca from the cold-water coral biotope of Santa Maria di Leuca (Apulian margin, southern Italy). *Zootaxa* 4186, 1–97. doi: 10.1164/zootaxa.4186.1.1

Pallas, P. S. (1766). *Elencus Zoophytorum Sistens Generum Adnuburations Generaliores et Specierum Cognitarum Succintas Descriptiones, Cum Selectis Auctorum Synonymis*. Haga: Franciscum Varentruppet, 451.

Palma, M., Rivas, M., Pantaleo, U., Pavoni, G., Pica, D., and Cerrano, C. (2018). SMF-based method to assess gorgonian forests (*Paramuricea clavata* (Cnidaria, Octocorallia)). *Remote Sensing* 10:1154. doi: 10.3390/rs10071154
interactions between the Mediterranean outflow water and the upper Cantabrian slope (north Iberian margin). *Mar. Geol.* 274, 1–20. doi: 10.1016/j.margeo.2010.03.001

Veal, C. J., Carmi, M., Fine, M., and Hoegh-Guldberg, O. (2010). Increasing the accuracy of surface area estimation using single wax dipping of coral fragments. *Coral Reefs* 29, 893–897. doi: 10.1007/s00338-010-0647-9

Velasco, E. M., Amez, M. A., and Punzón, A. (2013). *Especies de Interés Pesquero en Galicia, Asturias y Cantabria*. Madrid: Ministerio de Economía y Competitividad, 218.

Verrill, A. E. (1878). Notice of recent additions to the marine fauna of the eastern coast of North America, No. 2. Brief contributions to zoology from the Museum of Yale College, No. 39. *Am. J. Sci. Arts Third Ser.* 16, 371–378.

Vosmaer, G. C. J. (1894). Preliminary notes on some tetractinellids of the Bay of Naples. *Tijdschr. Nederland. Dierkund. Vereeniging* 4, 269–286.

Westoby, M. J., Brasington, J., Glasser, N. F., Hambrey, M. J., and Reynolds, J. M. (2012). Structure–from–Motion photogrammetry: a low-cost, effective tool for geoscience applications. *Geomorphology* 179, 300–314. doi: 10.1016/j.geomorph.2012.08.021

Wisshak, M., López Correa, M., Gofas, S., Salas, C., Taviani, M., Jakobsen, J., et al. (2009). Shell architecture, element composition, and stable isotope signature of the giant deep-sea oyster *Neopycnodonte zibrowii* sp. n. from the NE Atlantic. *Deep Sea Res. I* 56, 374–404. doi: 10.1016/j.dsr.2008.10.002

Yahel, G., Whitney, F., Reiswig, H. M., Eerkes-Medrano, D. I., and Leys, S. P. (2007). In situ feeding and metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep temperate fjord with a remotely operated submersible. *Limnol. Oceanogr.* 52, 428–440. doi: 10.4319/lo.2007.52.1.0428

Zarouquey, A.R. (1968). Crustáceos decápodos ibéricos. *Inves. Pesq.* 52, 1–520.

Zibrowius, H. (1978). Les scléractiniaires des grottes sous-marines en Méditerranée et dans l’Atlantique nor-oriental (Portugal, Madère, Canaries, Azores). *Pubbl. Staz. Zool. Napoli* 40, 516–544.

Zibrowius, H. (1980). Les scléractiniaires de la Méditerranée et de l’Atlantique nord-oriental. *Mém. Inst. Océanogr. Monaco* 11, 1–284.

Zibrowius, H., and Cairns, S. D. (1992). Revision of the northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). *Memoires du Museum National d’Histoire Naturelle. Serie A Zool.* 133:135.

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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