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Asteroids and Ophiuroids Associated With Sponge Aggregations as a Key to Marine Habitats. A Comparative Analysis Between Avilés Canyons System and El Cachucho, Marine Protected Area

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This study analyzes the fauna composition of the community of brittle and sea stars associated with sponge aggregations located in Avilés Canyons System and El Cachucho, Marine Protected Area (MPA). Diverse sampling methods were used depending on bottom morphology, such as rock dredges and specific samplers for sedimentary bottoms, mainly beam trawl models. These banks are made up of sponge and coral species that build a very appropriate substrate for the proliferation of benthic species, which together create Vulnerable Marine Ecosystems that are highly relevant for management and conservation. Among these benthic species, echinoderms are of great interest due to their value as indicators of good habitat. In total, 1261 specimens were collected (934 brittle stars and 327 starfishes), belonging to 42 species (28 ophiuroids and 14 asteroids) from INDEMARES AVILÉS, ECOMARG, and SponGES project surveys. Specimens were distributed among four sponge aggregations (F: fields) that were considered according to the sponge records obtained in the same stations (36). These fields were defined and named based on the five most common sponge species: *Aphrocallistes beatrix* and *Regadrella phoenix* (F1: Avilés Canyon); *Pheronema carpenteri* (F2: Intraslope basin of Le Danois Bank); *Asconema setubalense* (F3: Le Danois Bank); and *Neoschrammeniella* aff. *bowerbankii* (F4: Corbiro Canyon). Faunistic results show that *Ophiactis abyssicola* (55.55% occurrence), *Brisinga endecacnemos, Ophiolycus purpureus,* and *Peltaster placenta* (33.33%) were the most frequently found species in F1; *Psilaster andromeda* (80%), *Pseudarchaster parelii* (60%), and *Nymphaster arenatus* (46.67%) in F2; *Ophiura carnea* (71.43%) and *Ophiacantha smitti* (42.86%) in F3; and *Ophiacantha densa,* and *Henricia caudani* (100%) in F4. The asteroid and ophiuroid species collected seem to be composed of four different communities that fit to areas with particular morphological and biological features, related to the presence of species specialized in the use of the resources they can find there. In general, the abiotic factor controlling this structure is depth. This assemblage structure, which favors the dissimilarity between the canyons and the bank, is not so clear, since the deepest stations are located on the intraslope basin of El Cachucho, Marine Protected Area (MPA), therefore, using it *a priori* could lead to misunderstandings. Once the structure of the echinoderm community was known, we compared the expected and obtained results to analyze evidence which should prove the existence of any association between echinoderms and sponges, which enabled us to refute the incongruous hypothesis.

Keywords: Asteroidea, asteroids, Ophiuroidea, ophiuroids, environmental control, sponge aggregations, VMEs

INTRODUCTION

The benthic fauna of the Avilés Canyon System and the El Cachucho, Marine Protected Area (MPA) have been studied from a systematic point of view (mostly in Altuna, 2013; Altuna and Ríos, 2014; Manjón-Cabeza et al., 2014b; García-Guillén et al., 2018; Taboada et al., 2019), and under a general ecosystem approach (Sánchez et al., 2008, 2009, 2014a), providing a complete analysis of habitat scene for management and conservation. These studies were very valuable for these areas to be considered a vulnerable ecosystem and, as such, a protected area by the European Union (92/43/CEE) (Sánchez et al., 2014a,b, 2017; Punzón et al., 2016; Rodríguez-Basalo et al., 2019a). However, specific level studies are scarce, from the biological and ecological approach.

Echinoderms, together with sponges and corals, constitute the most important groups, in both biomass and/or abundance (Sánchez et al., 2008, 2009, 2014a, 2017; Manjón-Cabeza et al., 2014b; García-Guillén et al., 2018), as well as specific richness of the deep seabed. The importance of considering the association between these three groups is considerable, and all these previous studies provide us with a unique opportunity to carry out different kinds of analysis. Moreover, many of these bottoms are made up of sponge and coral species that build a very appropriate substrate for the proliferation of other benthic species. Among these benthic species, echinoderms are of high interest, mostly because of their inherent needs in order to survive (Murillo et al., 2012; Manjón-Cabeza et al., 2014a,b; Andrino-Abelaira, 2015; Gómez-Delgado, 2015; Murillo, 2015; Palma-Sevilla, 2015; Hurtado-García, 2016; Moya, 2016; Mah, 2020), or they are found to be associated to specific communities, leading them to be indicators of good habitat.

Recently, Ríos et al. (2020) studied the community composition and characterization of sponge aggregations in the Cantabrian Sea, showing that these aggregations constitute structuring habitats (3D communities) that function as support for different types of benthic communities (Peña-Cantero and Manjón-Cabeza, 2014, among others) and that certain benthic groups seem to have an intrinsic association with these sponge aggregations.

Based on these results, it should be possible to find an echinoderm reliance, preference, or association with these aggregations, but precise studies on the subject were not carried out, which is the main objective of the present study.

For this purpose, four sampling areas were chosen, two in the canyons and two on El Cachucho, Marine Protected Area (MPA), as well as two groups of echinoderms, starfishes, and brittle stars, because these echinoderm taxa tend to be indicators of different morphological and granulometry bottom features and of the assemblage of benthic communities.

According to this objective, to ascertain whether there exists any link between asteroids and ophiuroids and sponge aggregations on sea beds, we proposed the following hypotheses (**Figure 1**):

1 Although sponge aggregations present different specific compositions, there is not enough evidence to consider that the asteroid/ophiuroid community in canyons is different from on El Cachucho, Marine Protected Area (MPA) (**Figures 1A,C**).
2 These echinoderm species distributions will enable us to define four different echinoderm assemblages related to each sponge field (**Figure 1B**).
3 There are two different taxocoenosis, one in the canyons, and another on El Cachucho, Marine Protected Area (MPA) (**Figure 1D**).

MATERIALS AND METHODS

Study Area and Description of Work Fields

The study area is located in the northern continental margin of the Iberian Peninsula in the Cantabrian Sea (**Figure 2A**), specifically the Avilés Canyon Systems (ACS: **Figure 2B**) and

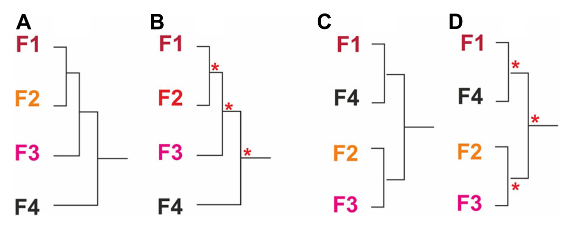

FIGURE 1 | Hypothetical clusters of echinoderm community assemblages **(A–D)**. Asterisks in red illustrates hypothetical strong boundaries segregating significant ($P < 0.001$) clusters (or groups) **(B,D)**.

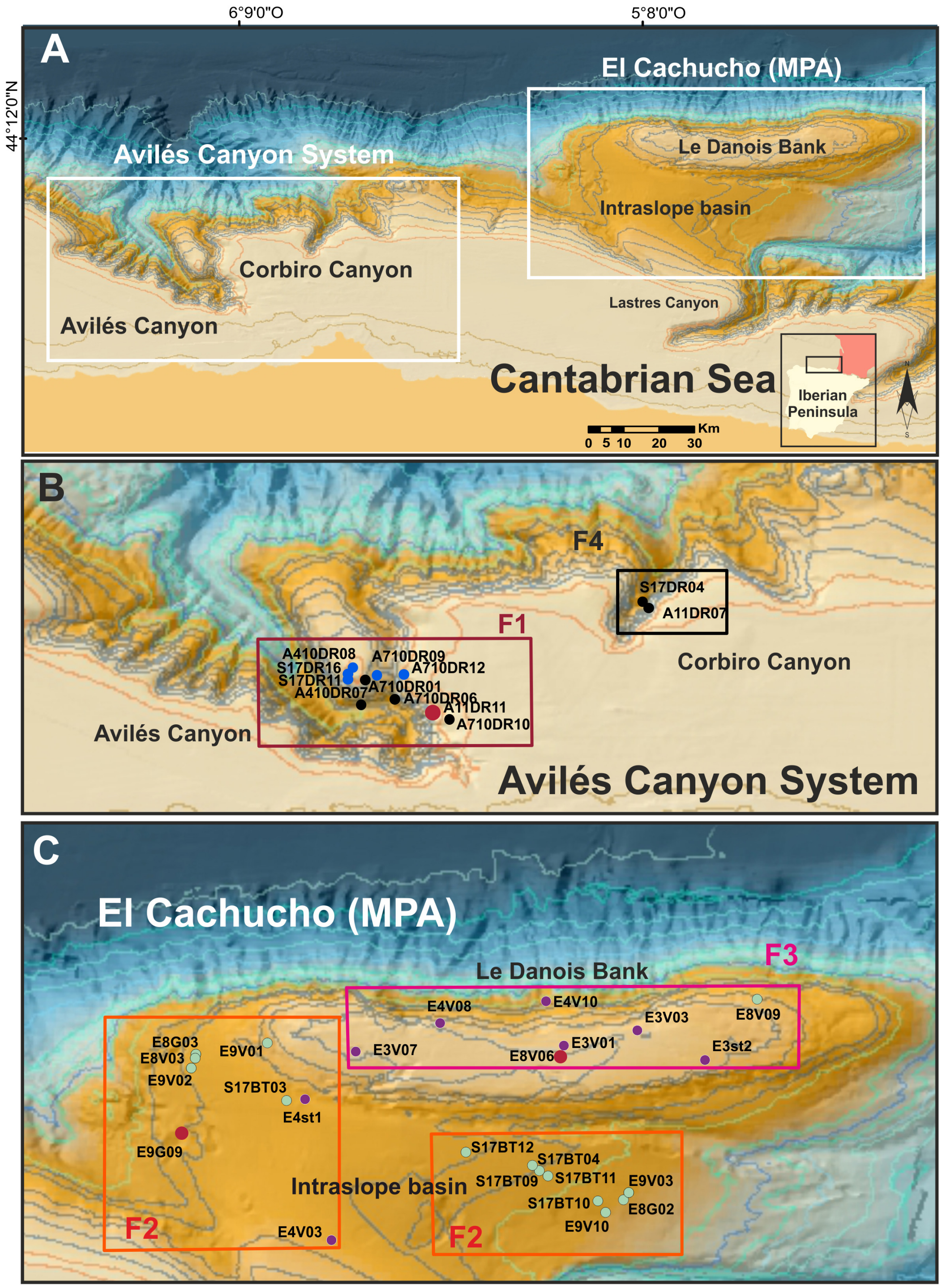

FIGURE 2 | (A) Central Cantabrian Sea, sampling area. **(B)** Avilés Canyon System. Delimited field samling area described as F1: Avilés Canyon field; F4: Corbiro Canyon field**. (C)** El Cachucho, Marine Protected Area (MPA). Field sampling: F2: Intraslope basin and southern Bank Break; F3, Top of the Bank. Rectangle colors define the stations integrated in each sponge field, and dot colors are related to the cluster (Baroni-Urbani similarity coefficient) significant group, G1: purple; G2: black; G3: green; G4: blue (see **Figure 7**).

El Cachucho, Marine Protected Area (MPA) (LDB: **Figure 2C**), which present peculiar geomorphological and habitat features described in several previous papers (Ballesteros et al., 2006; Sánchez et al., 2008, 2009; Van Rooij et al., 2010). These features together with station locations were analyzed and georeferenced by ArcGIS 10.7.

TABLE 1 | Stations positions (DD: decimal degrees), trawl sampling methods, surveys per station included in the present study and depth (m: meters).

Station label	Latitude (DD)	Longitude (DD)	Depth (M)	Species richness (S)	Organic matter (O.M).	Fine sands	Coarse sands	Mud	Trawl type	Survey
A11DR07	43.88	−5.91	551	6	5.08038	78.613029	6.904155	14.482851	Rock dredge	Avilés 0511
A11DR11	43.74	−6.11	560	1	2.780715	73.069511	19.273928	7.657844	Rock dredge	Avilés 0511
A410DR07	43.77	−6.18	1150	1	2.993144	66.57946	13.330684	20.091095	Rock dredge	Avilés 0410
A410DR08	43.78	−6.20	844	10	2.083293	69.159325	19.163313	11.677369	Rock drege	Avilés 0410
A710DR01	43.78	−6.17	810	3	2.821625	74.323586	8.588992	17.087648	Rock drege	Avilés 0710
A710DR06	43.75	−6.15	649	2	4.18501	74.114952	8.779974	17.110119	Rock dredge	Avilés 0710
A710DR09	43.75	−6.19	626	3	6.769381	42.594917	13.366544	44.047024	Rock dredge	Avilés 0710
A710DR10	43.73	−6.10	342	6	2.359874	68.493271	27.756544	3.750027	Rock dredge	Avilés 0710
A710DR12	43.78	−6.14	843	4	3.400344	78.122818	1.736524	20.140703	Rock dredge	Avilés 0710
E3St2	44.08	−4.79	498	2	3.141706	69.795197	2.381698	27.851824	Otter trawlBaca	Ecomarg 03
E3V01	44.07	−4.87	486	3	3.225364	77.87632	6.198897	15.925241	Beam trawl	Ecomarg 03
E3V03	44.10	−4.85	577	8	3.645695	61.037514	3.799862	35.144951	Beam trawl	Ecomarg 03
E3V07	44.06	−5.09	612	1	3.660562	82.994209	1.983048	15.023699	Beam trawl	Ecomarg 03
E4St1	44.01	−5.14	828	3	6.145019	39.749054	0.928039	59.323273	Otter trawl/ Beam trawl	Ecomarg 04
E4V03	43.86	−5.10	636	1	5.6551	38.509182	0.925954	60.564735	Beam trawl	Ecomarg 04
E4V08	44.09	−5.00	458	1	3.484327	85.281425	2.524338	12.194761	Beam trawl	Ecomarg 04
E4V10	44.11	−4.89	819	3	6.150105	57.747826	1.677681	40.583981	Beam trawl	Ecomarg 04
E8G02	43.91	−4.81	1238	4	10.11529	9.439515	0.15593	90.408005	GOC trawl	Ecomarg 08
E8G03	44.06	−5.25	940	2	5.896505	62.467136	2.061242	35.472809	GOC trawl	Ecomarg 08
E8V03	44.05	−5.25	955	3	6.064717	58.448795	2.08347	39.468407	Beam trawl	Ecomarg 08
E8V06	44.05	−4.87	556	1	3.339893	75.221672	7.423264	17.354637	Beam trawl	Ecomarg 08
E8V09	44.11	−4.67	573	2	3.219686	75.022011	2.718862	24.390215	Beam trawl	Ecomarg 08
E9G09	43.97	−5.26	964	1	7.393692	48.521889	1.885192	49.593349	GOC trawl	Ecomarg 09
E9V01	44.07	−5.18	761	6	5.278858	68.415642	2.189937	29.397015	Beam trawl	Ecomarg 09
E9V02	44.04	−5.26	972	6	6.302202	55.234425	2.100391	42.665234	Bou de Vara	Ecomarg 09
E9V03	43.91	−4.80	1205	12	9.854292	9.733132	0.148228	90.120399	Beam trawl	Ecomarg 09
E9V10	43.89	−4.83	1222	11	10.491391	8.616531	0.121215	91.268669	Beam trawl	Ecomarg 09
S17BT03	44.01	−5.16	862	6	6.196742	44.040867	1.274781	54.68409	Beam trawl	Sponges 0617
S17BT09	43.93	−4.89	1100	4	6.421437	18.751524	0.670461	80.56958	Beam trawl	Sponges 0617
S17BT10	43.90	−4.83	1050	4	6.944242	16.984913	0.441254	82.566994	Beam trawl	Sponges 0617
S17BT11	43.90	−4.83	1220	9	9.654444	9.915883	0.123678	89.96283	Beam trawl	Sponges 0617
S17BT12	43.96	−4.97	1225	6	9.730149	9.778616	0.1232	90.100792	Beam trawl	Sponges 0617
S17BT4	43.94	−4.90	890	7	6.117696	47.858704	1.853494	50.285255	Beam trawl	Sponges 0617
S17DR04	43.87	−5.90	695	1	4.790974	79.049644	7.526987	13.423498	Rock dredge	Sponges 0617
S17DR11	43.77	−6.20	1177	1	1.879759	64.495148	21.688709	13.81614	Rock dredge	Sponges 0617
S17DR16	43.78	−6.20	1018	10	1.994119	66.795364	20.510435	12.694198	Rock dredge	Sponges 0617

This work focuses on two canyon heads, Avilés Canyon (AC) and the Corbiro Canyon (CC) (**Figure 2B**), and Le Danois Bank and its intraslope basin (**Figure 2C**), based on sponge aggregation types of settlements described by different authors (Prado et al., 2019; Rodríguez-Basalo et al., 2019b; Ríos et al., 2020). Four sponge fields were established according to sponge species**:** F1 (AC), *Aphrocallistes Beatrix* Gray, 1858, and *Regadrella phoenix* Schmidt, 1880; F2

TABLE 2 | Fauna composition.

Class	Order	Family	Species
Phylum Porifera			
Demo spongiae	Verongiida	Ianthellidae	*Hexadella* sp.
	Tetractinellida	Geodiidae	*Geodia barretti* Bowerbank, 1858
			Geodia megastrella Carter, 1876
			Geodia nodastrella Carter, 1876
			Geodia pachydermata (Sollas, 1886)
			Penares sp.
		Corallistidae	*Neoschrammeniella* aff. *bowerbankii* (Johnson, 1863)
		Pachastrellidae	*Characella pachastrelloides* (Carter, 1876)
			Pachastrella nodulosa Cárdenas and Rapp, 2012
			Pachastrella ovisternata Lendenfeld, 1894
	Axinellida	Axinellidae	*Phakellia robusta* Bowerbank, 1866
	Bubarida	Desmanthidae	*Sulcastrella* sp.
	Tetractinellida	Siphonidiidae	*Siphonidium* sp.
		Theneidae	*Thenea schmidti* Sollas, 1886
	Suberitida	Halichondriidae	*Topsentia* sp.
	Poecilosclerida	Cladorhizidae	*Cladorhiza abyssicola* Sars, 1872
		Podospongiidae	*Podospongia lovenii* Barboza du Bocage, 1869
Hexac tinellida	Sceptrulophora	Aphrocallistidae	*Aphrocallistes beatrix* Gray, 1858
	Lyssacinosida	Rossellidae	*Asconema setubalense* Kent, 1870
	Amphidiscosida	Pheronematidae	*Pheronema carpenteri* (Thomson, 1869)
	Lyssacinosida	Euplectellidae	*Regadrella phoenix* Schmidt, 1880
Phylum Echinodermata			
	Paxillosida	Astropectinidae	*Plutonaster bifrons* (Wyville Thomson, 1873)
			Psilaster andromeda (Müller & Troschel, 1842)
		Pseudarchasteridae	*Pseudarchaster parelii* (Düben and Koren, 1846)
	Notomyotida	Benthopectinidae	*Pontaster tenuispinus* (Düben and Koren, 1846)
	Valvatida	Goniasteridae	*Ceramaster grenadensis* (Perrier, 1881)
			Peltaster placenta (Müller and Troschel, 1842)
Asteroidea			*Nymphaster arenatus* (Perrier, 1881)
		Poraniidae	*Poraniomorpha hispida* (M. Sars, 1872)
		Pterasteridae	*Pteraster militaris* (O.F. Müller, 1776)
	Spinulosida	Echinasteridae	*Henricia* sp.
			Henricia caudani (Koehler, 1895)

(Continued)

TABLE 2 | Continued

Class	Order	Family	Species
	Forcipulatida	Zoroasteridae	*Zoroaster fulgens* Wyville Thomson, 1873
	Brisingida	Brisingidae	*Brisinga endecacnemos* Asbjørnsen, 1856
			Novodinia pandina (Sladen, 1889)
	Amphilepidida	Amphiuridae	*Amphiura* sp.
			Amphiura filiformis (O.F. Müller, 1776)
			Amphiura grandisquama Lyman, 1869
			Amphiura griegi Mortensen, 1920
		Ophiactidae	*Ophiactis* sp.
			Ophiactis abyssicola (M. Sars, 1861)
			Ophiactis balli (W. Thompson, 1840)
			Ophiactis nidarosiensis Mortensen, 1920
			Ophiactis virens (M. Sars, 1859)
		Ophiothamnidae	*Ophiothamnus affinis* Ljungman, 1872
Ophiuroidea		Ophiotrichidae	*Ophiothrix* spp.
	Euryalida	Asteronychidae	*Asteronyx loveni* Müller And Troschel, 1842
			Astrodia tenuispina (Verrill, 1884*)*
	Ophiacanthida	Ophiacanthidae	*Ophiacantha abyssicola* G.O. Sars, 1872
			Ophiacantha aristata Koehler, 1895
			Ophiacantha bidentata (Bruzelius, 1805)
			Ophiacantha sp.
			Ophiacantha densa Farran, 1913
			Ophiacantha lineata Koehler, 1896
			Ophiacantha smitti Ljungman, 1872
			Ophiochondrus armatus (Koehler, 1907)
		Ophiotomidae	*Ophiotreta valenciennesi* (Lyman, 1879)
		Ophiobyrsidae	*Ophiophrixus spinosus* (Storm, 1881)
		Ophiomyxidae	*Ophiomyxa serpentaria* Lyman, 1883
	Ophiurida	Ophiopyrgidae	*Ophiopleura inermis* (Lyman, 1878)
		Ophiuridae	*Ophiocten affinis* (Lütken, 1858)
			Ophiura carnea Lütken, 1858
			Ophiura ophiura (Linnaeus, 1758)
	Ophioscolecida	Ophioscolecidae	*Ophiolycus purpureus* (Düben and Koren, 1846)
		Ophiohelidae	*Ophiomyces grandis* Lyman, 1879

Phylum Porifera and Echinodermata species and their classification position.

(intraslope basin of LDB), *Pheronema carpenteri* (Thomson, 1869); F3 (LBD), *Asconema setubalense* Kent, 1870; and F4 (CC), *Neoschrammeniella* aff. *bowerbankii* (Johnson, 1863; **Figures 2B,C**).

These four species were studied based on previous knowledge of the study area (García-Alegre et al., 2014; Sánchez et al., 2014a) and the criteria by which vulnerable marine ecosystems such as sponge grounds are considered (Hogg et al., 2010; Maldonado et al., 2016): they support high biodiversity of other species, are fragile and unlikely to recover from trawl damage, and are limited to discrete areas with suitable environmental conditions.

Sampling was carried out using different trawl gear and surveys, as described in previous studies (Sánchez et al., 2008; Rapp, 2019). A total of 36 stations (**Table 1**) meeting the afore-described criteria requirements were selected.

Material

The biological material consisted of 1261 specimens: 934 ophiuroids and 327 asteroids. Specimens were photographed and conserved in ethanol and identified based on their morphological characteristics using specialized literature (Mortensen, 1927, 1933; Lieberkind, 1935; Paterson, 1985; Clark and Downey, 1992; Southward and Campbell, 2006), and the appropriate protocols for their visualization (light microscopy or SEM).

Data Analysis

Echinoderm and sponge occurrence frequencies were calculated (to analyze the general faunal composition). Echinoderm species were classified into four categories according to their frequency across stations, which is a surrogate for evaluating their importance in the community: the most common species (50% of stations), very common species (between 25 and 50%), common species (between 25 and 10%), and rare or accidental species (<5%) (Mora, 1980; Manjón-Cabeza and García Raso, 1994; Manjón-Cabeza and Ramos, 2003, among others). To investigate the structure of echinoderms, assemblage similarities, related to sponge aggregations, were computed by a hierarchical cluster analysis (classification) using the UPGMA agglomerative algorithm (Sneath and Sokal, 1973; RMACOQUI ver. 1.0 software Olivero et al., 2011; RStudio Ver. 0.99.473) made on the similarity matrix of the Baroni-Urbani coefficients calculated from presence/absence data (Baroni-Urbani and Buser, 1976). The robustness of each cluster was supported by a test of biological significance of the boundaries between echinoderm assemblages. Strong and weak boundaries were defined between assemblages following (McCoy et al., 1986, $P < 0.001$). A strong boundary separates two significantly different clusters (red node number in **Figure 7**). A weak boundary (green asterisk in **Figure 7**) measures the homogeneity of species distribution between stations. When boundaries are not significant, it means that species are randomly distributed. Boundary analysis followed Olivero et al. (1998, 2011).

Stations were identified using Canonical Correspondence Analysis **(CCA)** computed from the presence/absence matrix and based on the eigenvalues of χ^2 distances between all data points (Ter Braak and Prentice, 1988; Hennebert and Lees, 1991; Legendre and Legendre, 1998), using PAST (paleontological statistics, ver. 3.25 computer program (Hammer et al., 2001).

Three analyses were performed**: (CCA1)** only with% sponge occurrence as the biotic variable; **(CCA2)** with all non-correlated abiotic variables, in this case only depth and granulometry (latitude and longitude were discarded) and biotic variable (% sponge occurrence); **(CCA3)** only abiotic variables (granulometry and depth). These were used to define ordination axes on which echinoderm data (with both stations and specimens) were plotted. Environmental variables were plotted as well as correlations with ordination axes.

RESULTS

General Faunal Composition

The faunal composition of the study area presented 42 echinoderm species (28 ophiuroids and 14 starfishes) and 21 sponge species (**Table 2** and **Figures 3–6**). *Ophiolycus purpureus, Ophiophrixus spinosus,* and *Ophiotreta valenciennesi* were new records for the area and as such will be included in the "Echinodermata Spanish Check List" (2020 in press, update of Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente, 2017).

Two sponge species, *Thenea schmidtii* and *Pachastrella ovisternata,* were the most common, while very common ones were: *Regadrella phoenix*, *Geodia pachydermata, Neoschrammeniella* aff. *bowerbanki, Podospongia loveni, Characella pachastrelloides,* and *Phakellia robusta,* present in more than half of occurrence of the stations (**Figures 3**, **5**). In the case of echinoderm species, occurrence was more evenly spread between them. They were classified as: very common species (between 25 and 50%): *Psilaster andromeda* and *Pseudarchaster parelii;* common species (between 25 and 10%): *Ophiactis abyssicola*, *Henricia caudani*, *Nymphaster arenatus*, *Ophiacantha smitti*, *Ophiothamnus affinis*, *Ophiacantha abyssicola*, *Brisinga endecacnemos*, *Ophiura carnea*, *Zoroaster fulgens*, *Plutonaster bifrons*, *Ophiomyces grandis*, *Ophiopleura inermis*, *Peltaster placenta*, and *Pontaster tenuispinus*; and rare or accidental species (<5%): the rest (**Figures 4**, **6**).

Work Field Faunal Features

Sponge (S) and echinoderm (E) composition of each field are shown in **Figure 3**. **F1** (***Aphrocallistes* and *Regadrella* aggregation**) presented nine sponge species, the most frequent of which were *Aphrocallistes beatrix* (77.78%) followed by *Regadrella phoenix* (22.22%) and *Pachastrella ovisternata* (22.22%) (**Figures 3A–S**). Twenty-three echinoderm species were recorded, 12 of which were exclusive (**Figure 3B**): the most commonly occurring echinoderm species was *Ophiactis abyssicola* (55.5%) (**Figures 4A–E**). **F2** (***Pheronema* aggregation**) was represented by *Pheronema carpenteri* with 92% of sponge species occurrence (**Figure 4A-S**), while the echinoderm community consisted of 24 species, nine of which were only present in F2 (**Figure 3B**). In this case the most common species were *Psilaster andromeda* with 75% and *Pseudarchaster parelii* with 56.25% occurrence, respectively. **F3 (*Asconema* aggregation):** Two sponges, *Asconema setubalense, Podospongia loveni,* established a new field with 40% occurrence. Regarding echinoderms, 12 species were distinguished, three of which

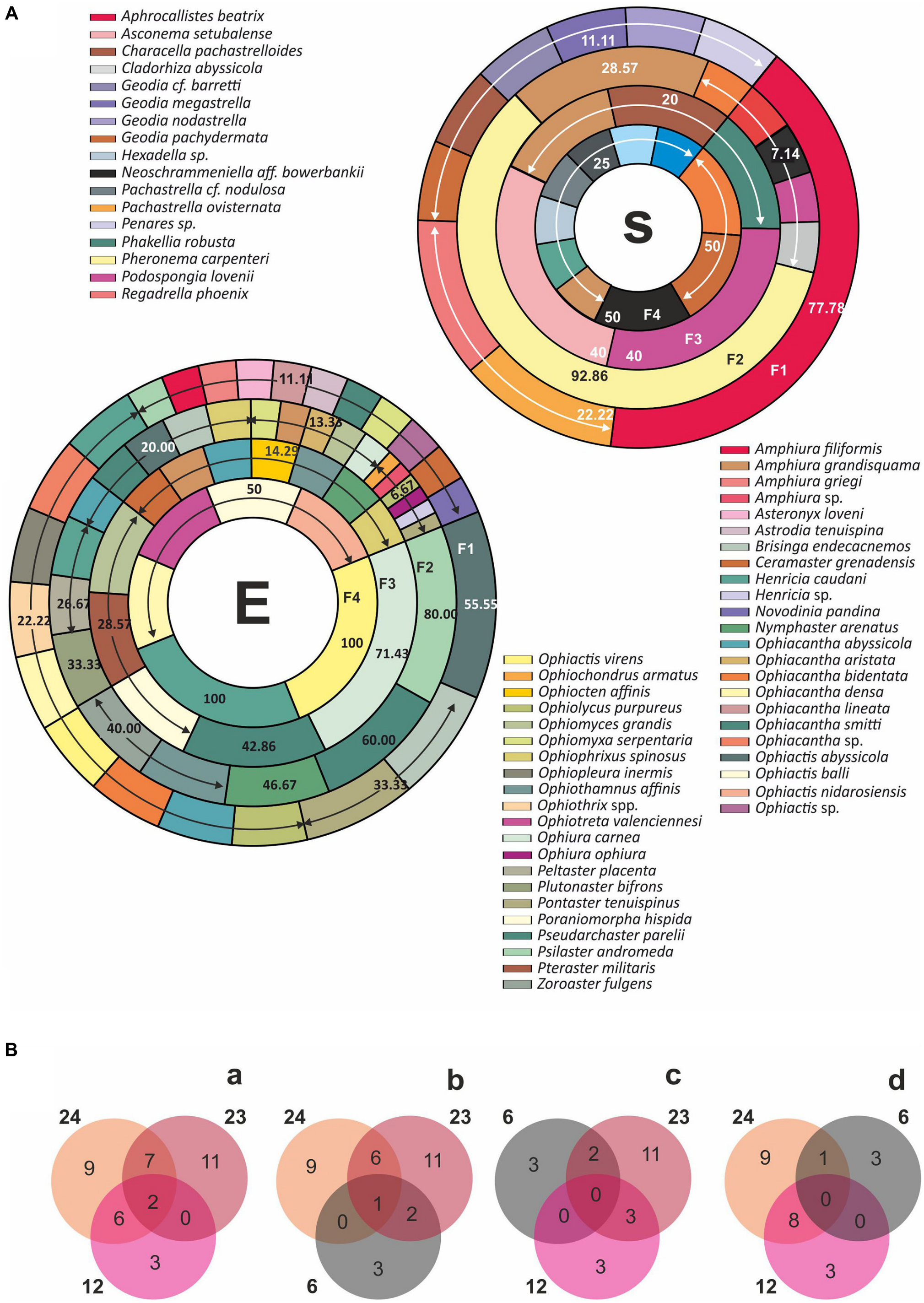

FIGURE 3 | (A) Species richness by field. **(B)** Faunal composition. S: sponges; E: echinoderms, based on occurrence percentages related to the whole area of study.

were exclusive. Echinoderm composition was 14 species, 10 of which were starfish, and four of which were very rare brittle stars (in terms of occurrence). The species featured were *Ophiura carnea* with 55.56% and *Ophiacantha smitti* with 33.33%. **F4** (***Neoschrammeniella*** **aggregation):** the most frequent sponges (50%) were *Neoschrammeniella* aff. *bowerbankii*, *Pachastrella ovisternata,* and *Geodia pachydermata*. Six echinoderm species made up this field, three of which were exclusive. *Ophiacantha densa* and *Henricia caudani,* were recorded in all stations of this field.

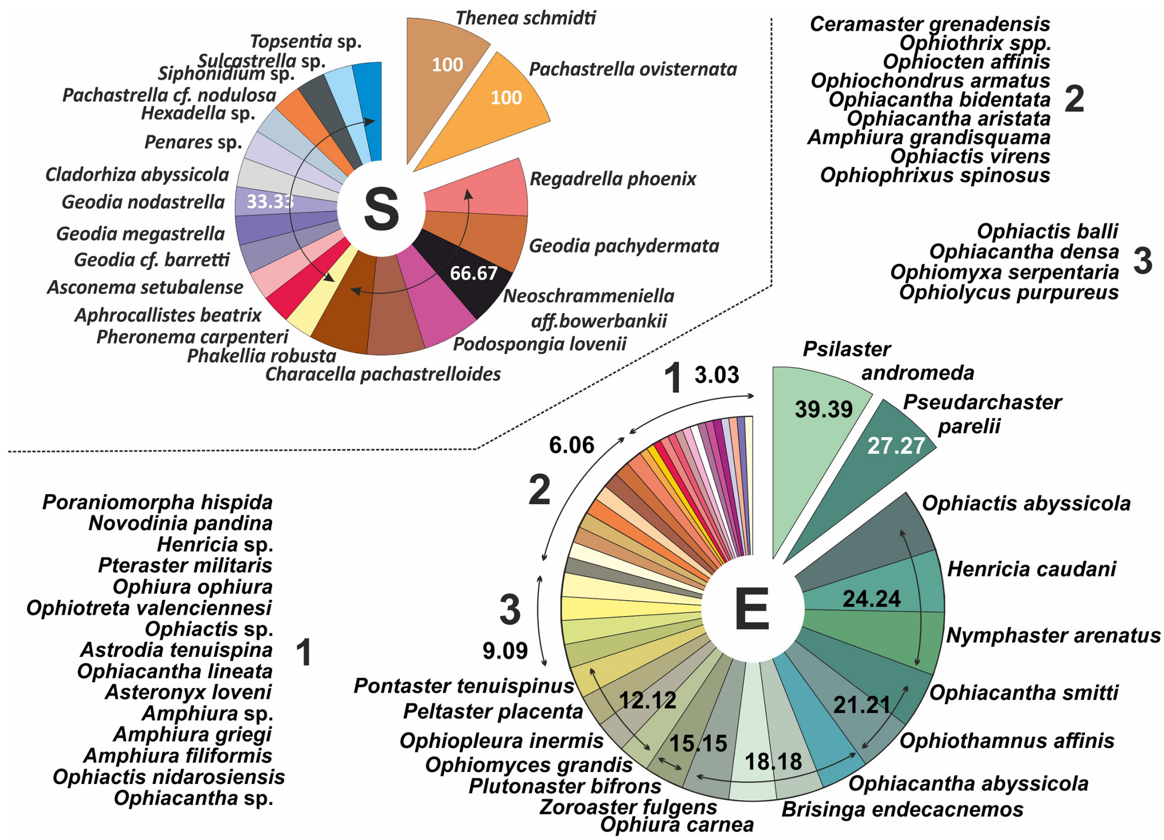

FIGURE 4 | Faunal composition predefined sponge field (see "Materials and Methods" section). **S:** sponges; **E:** echinoderms, based on occurrence percentage related to the total number of stations included in each defined sponge field.

Structure of Echinoderm Assemblages

Classification Analysis

Presence-absence species matrix, and occurrence percentage used for data analysis (**Table 3**). Cluster results display a clear discontinuity between different station groups (**Figure 7**, see dot colors), revealing the existence of four distinctive assemblages (G1, G2, G3, and G4), divided by strong boundaries (red nodes), while three stations did not match up with any other.

However, G3 and G4 represent very homogeneous groups because of the weak boundary found on nodes 22 and 28 (green nodes). **G3** was composed of stations from work field F2, except E8V09 which belongs to F3. The most frequent species in this group were starfishes, such as *Psilaster andromeda* (85.71%), *Pseudarchaster parelii* (64.29%), *Nymphaster arenatus* (50%), *and Zoroaster fulgens* (42.85%). Only one brittle star should be mentioned, *Ophiothamnus affinis* (42.86%). **G4**, on the same cluster branch as G3, consists of stations exclusively from F1. In these cases, the most commonly occurring were *Ophiactis abyssicola*, (100%), followed by *Brisinga endecacnemos*, *Ophiacantha abyssicola*, *Ophiacantha bidentata*, *Ophiochondrus armatus*, *Ophiolycus purpureus,* and *Ophiophrixus spinosus*, present in 40% of stations.

G2 contains four stations from F1 and two stations from F4. In this case there was no evidence of homogeneity, but it was a consolidated group (node 31; $P < 0.00001$) as well as G1. This group was mainly composed of *Henricia caudani* and *Ophiactis balli* (**Figure 6E**) (both 50% occurrence), followed by *Ceramaster grenadensis*, *Ophiacantha densa,* and *Peltaster placenta* (33.33%).

G1 also presents a mix of stations from F2 (2) and F3 (6). It was made up of a group with a high dissimilarity with the rest, consisting exclusively of ophiuroid species. The most frequent species was *Ophiura carnea.*

Reliability of Setting to Preset Fields

Percentage fit of the different cluster groups to the working fields are: **G1**, 75% of **F3** stations; **G2**, 33.33% of **F4** (considering G2 is the only group with F4 stations); **G3,** 94.33% of **F2;** and **G4** representing 100% of **F1**stations.

Ordination Analysis

Results from CCA analysis are shown in **Table 4** (**Figures 8**, **9**). **CCA1** was carried out only with sponge frequency as a biotic variable and echinoderms were ordered according to these, which was not significant (**Table 4**). However, when granulometry was taken into account **(CCA2)** (**Figure 8**), the CCA results became significant despite the very low% explanation. In the case of **CCA3,** only granulometry and depth significance were taken into account, showing the highest significance (**Table 4** and **Figure 9**).

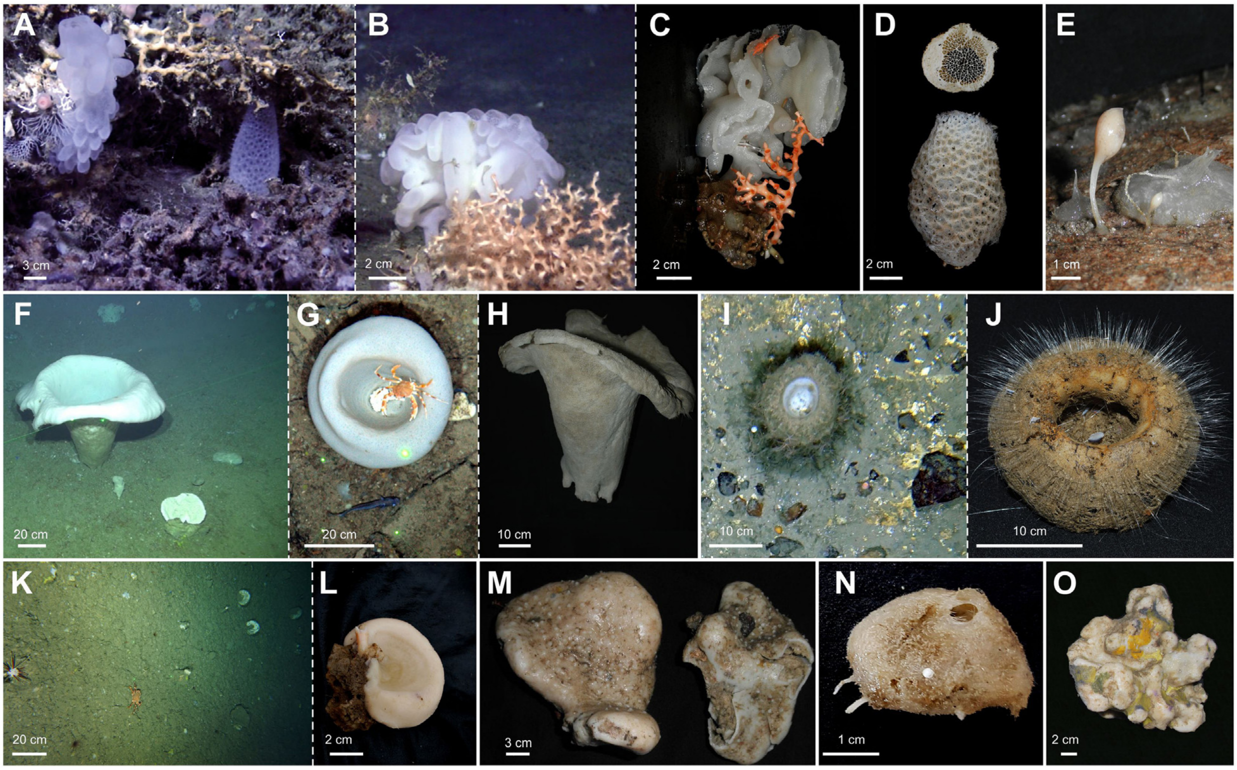

FIGURE 5 | Habitats and species of 3D large sponge aggregations in the Cantabrian sea. **(A)** *Aphrocallistes beatrix* with *Regadrella phoenix* "*in situ*" Avilés Canyon System. Scale bar 3 cm. **(B)** *Aphrocallistes beatrix* "*in situ*" Avilés Canyon System. Scale bar 2 cm. **(C)** *Aphrocallistes beatrix* view of the same specimen. Scale bar 2 cm. **(D)** *Regadrella phoenix.* Scale bar 2 cm. **(E)** *Podospongia lovenii*. Scale bar 1 cm. **(F,G)** *Asconema setubalense* "*in situ,*" Le Danois Bank. Scale bar 20 cm. **(H)** *Asconema setubalense.* Scale bar 10 cm. **(I)** *Pheronema carpenteri* "*in situ,*" Le Danois Bank. Scale bar 10 cm. **(J)** *Pheronema carpenteri.* Scale bar 10 cm. **(K)** *Neoschrameniella* aff. *bowerbankii* "*in situ*" in El Corbiro Canyon.Scale bar 20 cm. **(L)** *Neoschrameniella* aff. *bowerbankii.* Scale bar 2 cm. **(M)** *Geodia pachydermata.*Scale bar 3 cm. **(N)** *Thenea schmidti.* Scale bar 1 cm. **(O)** *Pachastrella ovisternata.* Scale bar 2 cm.

DISCUSSION

Echinoderm Assemblages and Control of Their Environmental Variables

The echinoderm community seems to be composed of four different communities that fit to areas with particular morphological and biological features, related to the presence of species specialized in the use of the resources they can find there (Sánchez et al., 2008; Ríos et al., 2020).

In general, the abiotic factor that mainly controls this community structure is depth. In fact, it is very frequent in echinoderm assemblage studies (Manjón-Cabeza and Ramos, 2003; Moya, 2016). This assemblage structure, which favors the dissimilarity between the canyons and El Cachucho, Marine Protected Area (MPA), is not so clear, since the deepest stations are located on the intraslope basin of the bank, therefore, its use *a priori* could lead to misunderstandings (**Figures 8**, **9**).

Group G4 would represent a community associated to deep, hard bottoms covered by coarse sands. The stations fit perfectly at the head of the Avilés Canyon (**Figures 2**, **7**). The taxa making up this community are suspension feeder species, such as brisingid species like *Brisinga endecacnemos* and *Novodina pandina* (Downey, 1986; Clark and Downey, 1992), which take advantage of the pedestals offered by the rock outcrops, or coral patches of *Madrepora oculata* Linnaeus, 1758; and *Desmophyllum pertusum*; Linnaeus, 1758 (Sánchez et al., 2014b). Coral aggregations are used as support by some ophiacanthids such as *Ophiochondrus armatus*, or species of the Genus *Ophiacantha*. However, *Ophiactis abyssicola,* like the rest of species in the *Ophiactis* genus, lives associated with bottoms that have cavities available, such as oscula sponges (Schejter et al., 2012; Sivadas et al., 2014; Çinar et al., 2019), little holes in stones or associated with dead corals or rest of calcareous algae (rhodoliths), which provides them with shelter (Gofas et al., 2014; Manjón-Cabeza et al., 2014c; Palma-Sevilla, 2015).

The community closest to G4 is G3, which is found on the intraslope basin of the Le Danois bank. This affinity is mainly due to species richness (**Figures 3**, **7**). Depth seems to be the abiotic environmental factor controlling these two communities (**Figures 7**, **8**), although other variables should be taken into account, such as the slope. In fact, steep areas could favor the settlement of structuring species (3D) such as *Pheronema carpenteri,* which would determine the echinoderm community (Cristobo et al., 2010; Sánchez et al., 2010, 2014a). In contrast with the rest of the communities studied, the species making up this one are mainly Asteroids, like *Psilaster*

TABLE 3 | Presence/absence species matrix, and occurrence percentage used for data analysis.

Species	Ocurrence (%)	A11DR07	A11DR11	A410DR07	A410DR08	A710DR01	A710DR06	A710DR09	A710DR10	A710DR12	E3St2	E3V01	E3V03	E3V07	E4St1	E4V03	E4V08	E4V10
Amphiura filiformis	3.03	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Amphiura grandisquama	3.03	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Amphiura griegi	3.03	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Amphiura sp.	3.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asteronyx loveni	3.03	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Astrodia tenuispina	3.03	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Brisinga endecacnemos	18.18	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Ceramaster grenadensis	6.06	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Henricia caudani	24.24	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Henricia sp.	3.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Novodinia pandina	3.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphaster arenatus	24.24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha abyssicola	18.18	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Ophiacantha aristata	6.06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha bidentata	6.06	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiacantha sp.	3.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha densa	9.09	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Ophiacantha lineata	3.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha smitti	21.21	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1
Ophiactis abyssicola	24.24	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Ophiactis balli	9.09	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Ophiactis nidarosiensis	3.03	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ophiactis sp.	3.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiactis virens	6.06	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Ophiochondrus armatus	6.06	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiocten affinis	6.06	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Ophiolycus purpureus	9.09	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Ophiomyces grandis	12.12	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
Ophiomyxa serpentaria	9.09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiophrixus spinosus	6.06	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiopleura inermis	12.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiothamnus affinis	21.21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiothrix spp.	6.06	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Ophiotreta valenciennesi	3.03	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura carnea	18.18	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Ophiura ophiura	3.03	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Peltaster placenta	12.12	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Plutonaster bifrons	15.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pontaster tenuispinus	12.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poraniomorpha hispida	3.03	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudarchaster parelii	27.27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psilaster andromeda	39.39	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pteraster militaris	3.03	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoroaster fulgens	18.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(Continued)

TABLE 3 | Continued

Species	E8G02	E8G03	E8V03	E8V06	E8V09	E9G09	E9V01	E9V02	E9V03	E9V10	S17BT03	S17BT04	S17BT09	S17BT10	S17BT11	S17BT12	S17DR04	S17DR11	S17DR16
Amphiura filiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura grandisquama	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphiura griegi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Asteronyx loveni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astrodia tenuispina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brisinga endecacnemos	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1
Ceramaster grenadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Henricia caudani	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
Henricia sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Novodinia pandina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nymphaster arenatus	0	0	0	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	0
Ophiacantha abyssicola	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1
Ophiacantha aristata	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Ophiacantha bidentata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha sp.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha densa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacantha lineata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiacantha smitti	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Ophiactis abyssicola	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1
Ophiactis balli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiactis nidarosiensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiactis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiactis virens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiochondrus armatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiocten affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiolycus purpureus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiomyces grandis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ophiomyxa serpentaria	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
Ophiophrixus spinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiopleura inermis	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Ophiothamnus affinis	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0
Ophiothrix spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiotreta valenciennesi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura carnea	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ophiura ophiura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltaster placenta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Plutonaster bifrons	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0
Pontaster tenuispinus	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Poraniomorpha hispida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudarchaster parelii	1	1	1	0	0	0	1	1	0	1	1	0	1	0	0	1	0	0	0
Psilaster andromeda	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0
Pteraster militaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoroaster fulgens	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0

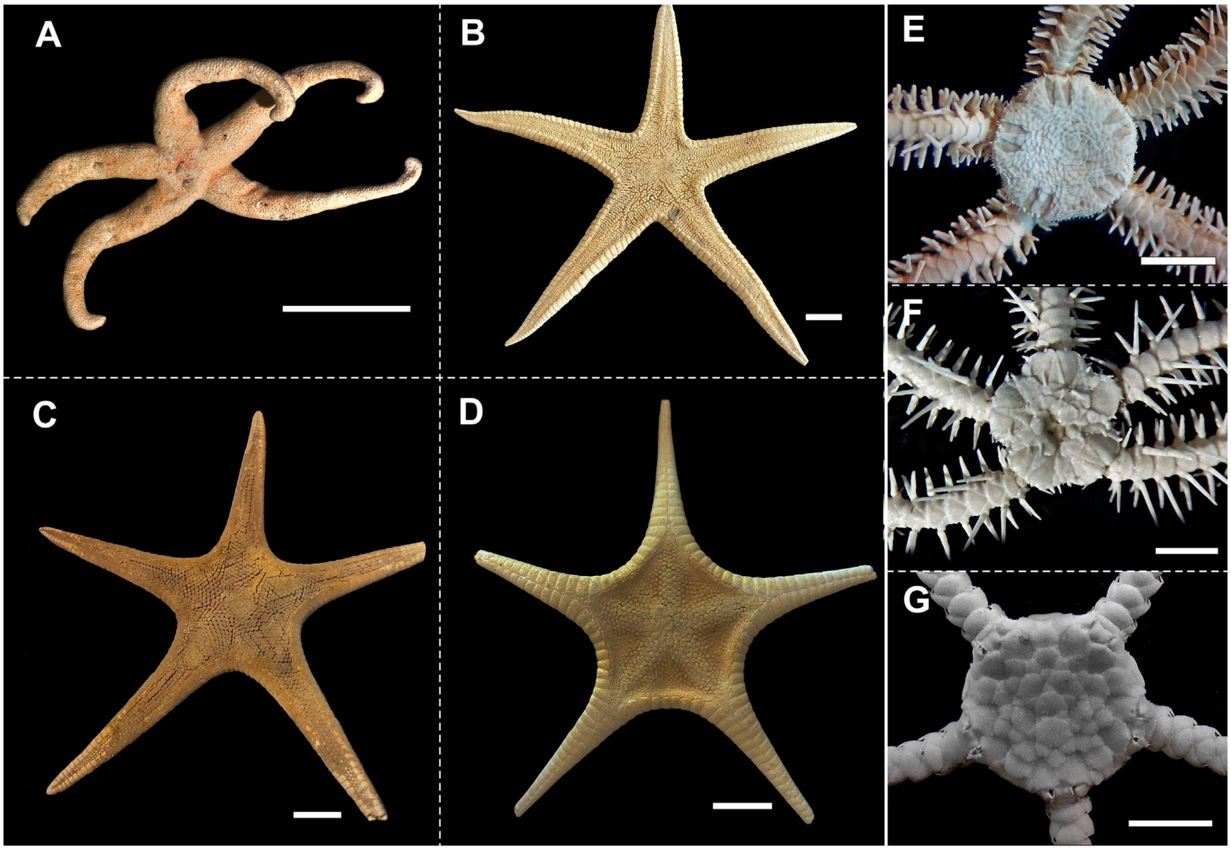

FIGURE 6 | Images of characteristic echinoderm species from each field. **(A)** *Henricia caudani*. Scale bar 2 cm. **(B)** *Psilaster andromeda*. Scale bar 1 cm. **(C)** *Pseudarchaster parelii*. Scale bar 2 cm. **(D)** *Nymphaster arenatus*. Scale bar 2 cm. **(E)** *Ophiactis balli*. Scale bar 0.15 cm. **(F)** *Ophiactis abyssicola*. Scale bar 0.2 cm. **(G)** *Ophiura carnea*. Scale bar 0.2 cm.

andromeda, *Pseudarchaster parelii*, *Nymphaster arenatus*, and *Zoroaster fulgens*, and others of lesser occurrence such as *Plutonaster bifrons* and *Pontaster tenuispinus*. This community is the most homogeneous one, and the one with the greatest specific richness. In this case, the abiotic factor mainly affecting species composition is the presence of fine sands with a high content of organic matter, preferred by sand burrow species such as those belonging to the Genus *Amphiura* (Sánchez et al., 2008).

On the other hand, **G1** is represented by stations located mostly on Le Danois Bank which has fine sand bottoms with *Asconema setubalense*. These features are very well defined in previous publications where the characteristic habitats of the area are described, and a large occurrence of *Callogorgia veticillata* (Pallás, 1766) is attributed to the upper zone of the bank (Sánchez et al., 2008, 2017). These features, indeed, explain the presence of species as diverse as *Ophiura carnea*, *Ophiomyces grandis, Ophiocten affinis,* and *Ophiothamnus affinis*, which live on sandy bottoms; and species of the Genus *Ophiacantha* and *Ophiothrix* (Granja-Fernández et al., 2014) that have a preference for corals, especially gorgonians.

G2 group does not make much biological sense and its stations seem to be a consequence of the scarcity of stations from F4 in the Corbiro Canyon (only two). Another reason that could explain this artifact would be due to stations from F1, associated would have a similar sponge species contents, and *Aphrocallistes beatrix* were not as frequent as in the rest of stations from Avilés Canyon or in the other way round, *Neoschrammeniella* aff. *bowerbankii*, does not represent any echinoderm association. Therefore, the sea star and brittle star community of Corbiro Canyon should be more profusely studied in the near future.

Does There Exist a Real Association of Echinoderms With Sponge Aggregations?

Once the structure of the echinoderm community was known, we were able to compare the expected and obtained results in order to analyze the evidence which should prove the existence of any association between echinoderms and sponges, which enable us to refute the incongruous hypothesis.

In this way, the results obtained do not conform to any of the proposed hypotheses (**Figures 1**, **7**), and the reasons that would explain this issue are developed below.

(1) Although station fit is quite high in G1, G3, and G4 clusters, the G2 cluster has a very low percentage station affiliation.

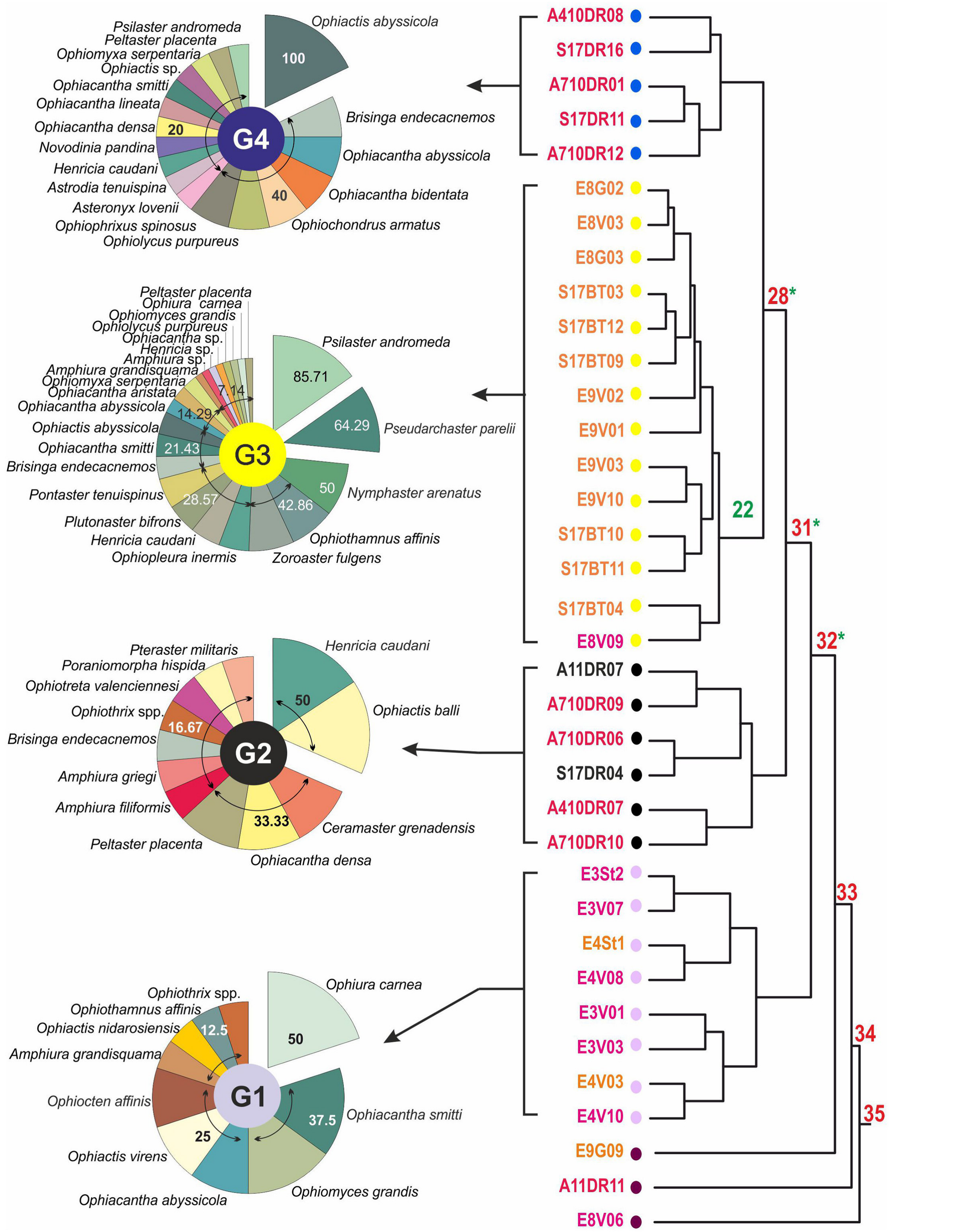

FIGURE 7 | Cluster resulting from Echinoderm species classification (Baroni-Urbani index). Noted group color and dot colors. They are related to the cluster (Baroni-Urbani similarity coefficient) significant group, G1: purple; G2: black; G3: green; G4: blue. Node number in red illustrates strong boundaries segregating significant ($P < 0.001$) clusters (or groups), whereas green asterisks denote where weak boundaries ($P < 0.001$) were found, measuring the homogeneity of species distribution between stations included in these clusters or group. No node number shows non-significant boundaries ($P > 0.001$), in these cases species are randomly distributed (following Olivero et al., 1998, 2011). Sector diagrams show species occurrence percentage related to each significant cluster.

TABLE 4 | Canonical Correspondence analysis values (Eigenvalues, P, Explanation percentage).

	Eigenvalues	*P*	Explanation percentage
CCA1: variables: sponges occurrence %			
Axis I	0.75	*P* > 0.1	18.85%
Axis II	0.67	*P* > 0.01	16.87%
CCA2: variables: sponges occurrence %, depth and granulometry			
Axis I	0.75	*P* < 0.05	19.49%
Axis II	0.66	*P* <0.01	17.15%
CCA3: variables: sponges occurrence %, depth and granulometry			
Axis I	0.61	*P* <0.001	32.93%
Axis II	0.57	*P* < 0.001	30.74%

Minimum of significance: P < 0.05. Gray shadow: not significant Axis.

(2) Asteroid/ophiuroid community assemblages do not fit the sponge species composition.

Given the high percentage of adjustment that some of the fields present, it is possible that these small imbalances can be explained, since fields were delimited on the basis of main sponge species, although this occurrence may vary between stations (**Figures 4**, **8**), and then some of them did not fit the field as we expected.

On the other hand, CCA using only an environmental variable set is more significant than using it in combination with occurrence of sponges. There are two ways to address this question: (1) sponges are not a very good biotic factor to control the echinoderm community; (2) echinoderms depend more on other bottom types (for instance related to granulometry, **Figure 9**), so the variable data set should be improved.

Finally, these results enable us to infer that the association of asteroids and ophiuroids with sponge aggregations is conditioned to environmental factors, like granulometry, which control fields such as habitat. Sponge species composition, or the structure they

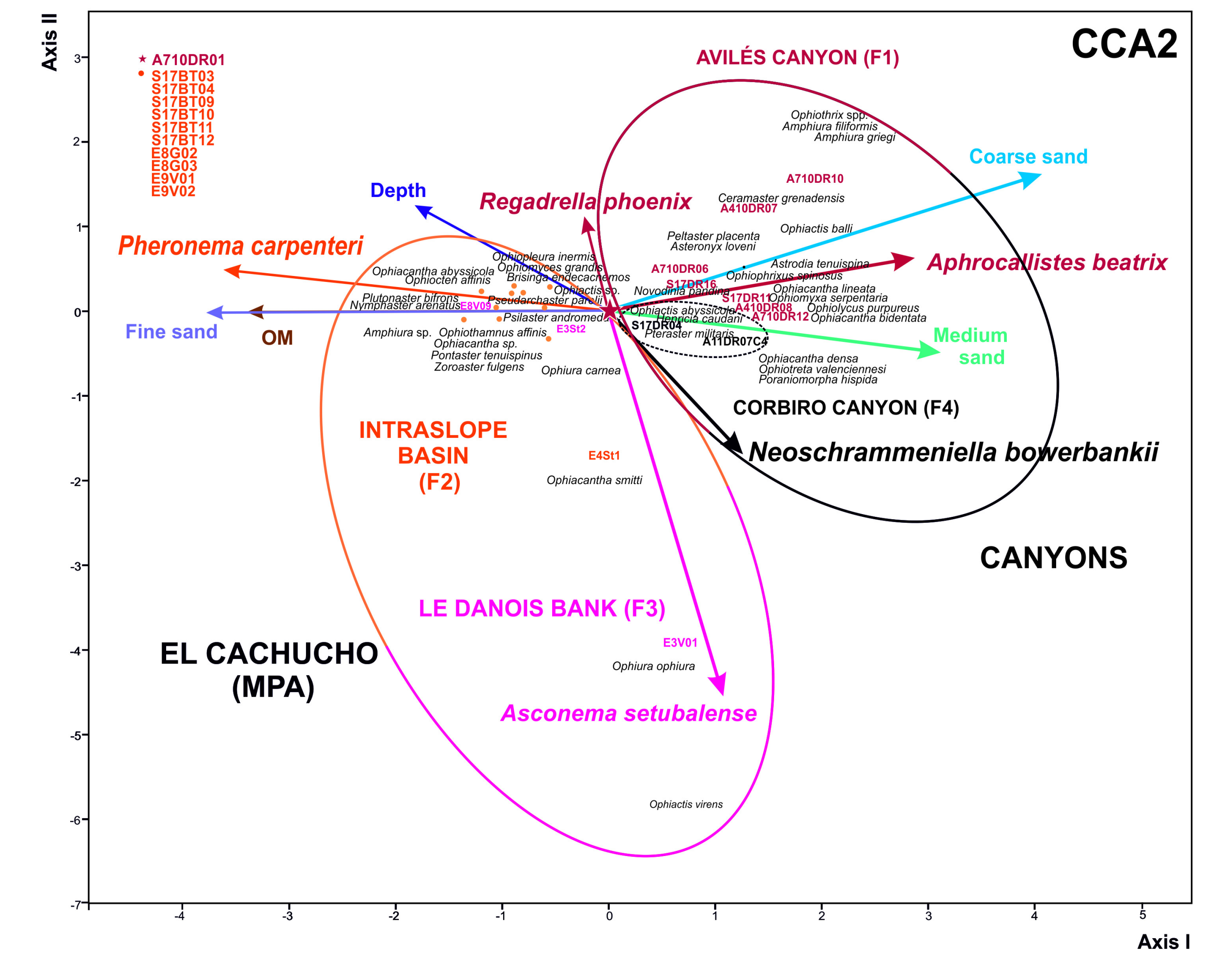

FIGURE 8 | Ordination studies. Canonical Correspondence Analysis **(CCA2).** Physical environmental variables and biotic variable (most relevant sponges): Granulometry characteristics and depth. F1, 2, 3, 4 described in **Figure 2**. Statistical parameters and null hypothesis shown in **Table 4**.

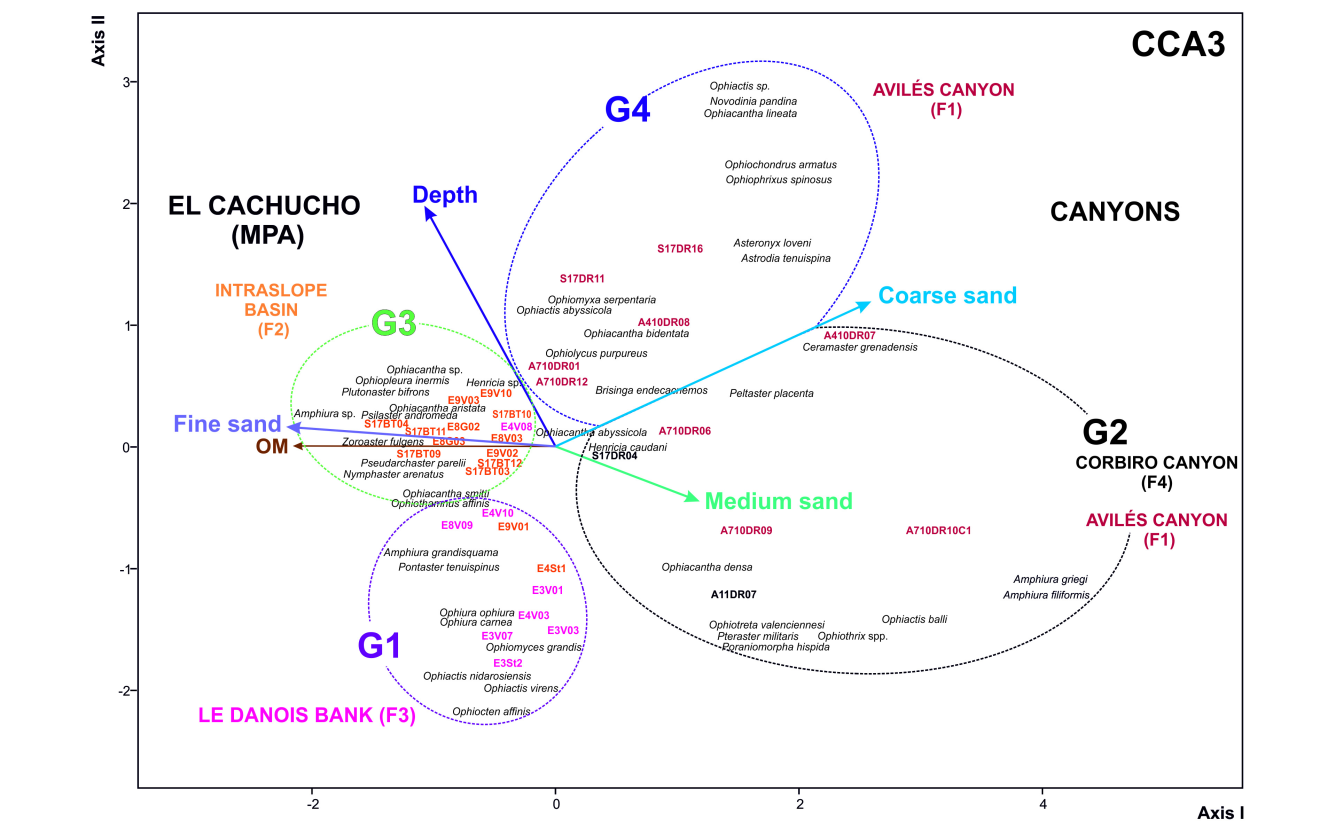

FIGURE 9 | Ordination studies. Canonical Correspondence Analysis **(CCA3).** Physical environmental variables and granulometry characteristics and depth. F1, F2, F3, F4 described in **Figure 2**. CCA3: variables: sponge occurrence%, depth and granulometry. Statistical parameters and null hypothesis shown in **Table 4**.

provide, would not be the main reason for explaining echinoderm assemblage structure.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MM-C and PR conceived and designed the study and wrote the manuscript. PR, TI, AR-B, FS, and JC collected the specimens and the pre-identification major taxa. PR and JC identified the sponges. MM-C, PR, AM-R, and LG-G identified the echinoderms, analyzed the data, prepared the figures and tables, reviewed drafts of the manuscript, and helped to writing the manuscript. MM-C, FS, and JC acquired the funding. All authors contributed to the article and approved the submitted version.

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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.