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Diversity of Deep-Sea Echinoderms From Costa Rica

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Echinoderms are a highly diverse group and one of the most conspicuous in the deep sea, playing ecological key roles. We present a review about the history of expeditions and studies on deep-sea echinoderms in Costa Rica, including an updated list of species. We used literature and information gathered from the databases of the California Academy of Sciences, the Benthic Invertebrate Collection of the Scripps Institution of Oceanography, the National Museum of Natural History, the Museum of Comparative Zoology and the Museo de Zoología from the Universidad de Costa Rica. A total of 124 taxa (75 confirmed species) have been collected from the Costa Rican deep sea, 112 found in the Pacific Ocean, 13 in the Caribbean Sea, and one species shared between the two basins. We report 22 new records for the Eastern Tropical Pacific, 46 for Central American waters, and 58 for Costa Rica. The most specious group was Ophiuroidea with 37 taxa, followed by Holothuroidea (34 taxa), Asteroidea (23 taxa), Echinoidea (17 taxa), and Crinoidea (11 taxa). The highest number of species (64) was found between 800 m and 1200 m depth. Only two species were found deeper than 3200 m. Further efforts on identification will be required for a better comprehension of the diversity of deep-sea echinoderms. Limited research has been done regarding the biology and ecology of deep-sea echinoderms in Costa Rica, so additional approaches will be necessary to understand their ecological functions.

Keywords: Central America, Eastern Tropical Pacific, Caribbean, last frontier, new records, Ophiroidea, Holothuroidea

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INTRODUCTION

Costa Rica is located in the Central American Isthmus facing the Caribbean Sea and the Pacific Ocean, it has an oceanic island 500 km offshore (Isla del Coco), and a marine extension covering 572,877 km^2, that is more than 11-fold its land area, making it the largest country on Central America (Cortés, 2008; Cortés, 2016a; Cortés, 2016b; Cortés, 2016c). Recent studies estimated that over 60% of the total area of the country is below 2,000 m depth, and over one-third below 3,000 m (Cortés and Benavides-Varela, in prep.). Eastern Tropical Pacific (ETP) deep waters (below 200 m) constitute a particularly important ecosystem in Costa Rica, since they represent about 90% of the whole territory and the last frontier in the international scientific agendas (Cortés, 2019; Rojas-Jiménez et al., 2020; Azofeifa-Solano and Cortés, 2021).

Few explorations have been done on the Costa Rican Caribbean (Alvarado et al., 2013; Cortés, 2016c; Cambronero-Solano et al., 2019). The continental shelf is relatively narrow, with a total area of 2,310 km², and an Exclusive Economic Zone (EEZ) of 28,064 km² (Cortés, 2016c; Cortés and Benavides-Varela, in prep.). In the nearshore area, there are mangrove forests, seagrass beds, coral reefs, rocky shores, and sandy beaches, further offshore the bottom is overall sandy, but muddy near river mouths, also some shallow calcareous mounds have been observed (Cortés, 2016c).

The Costa Rican Pacific area is much larger than the Caribbean, covering 544,813 km², hosting a greater variety of deep-sea environments (Cortés, 2016a; Cortés, 2016b). There are mesophotic ecosystems (Cortés, 2019), methane seeps (Sahling et al., 2008; Levin et al., 2012; Levin et al., 2015), seamounts (Auscavitch, 2020), deep areas of fluid discharge (Wheat et al., 2019), extensive abyssal plains (Agassiz, 1898; Townsend, 1901) and a large deep pelagic region. The extensive Coco Submarine Volcanic Range (CSVR, also called Cocos Ridge) has been explored too (Neuhaus, 2004; Alvarado-Induni, 2021).

For Costa Rica, there have been registered ~306 echinoderm species (Alvarado et al., 2017; Cambronero-Solano et al., 2019; Chacón-Monge et al., 2021), of the 420 reported species for Central America (Alvarado and Fabregat-Malé, 2021). Most of them inhabit shallow water or intertidal environments, mainly related to coral and rocky reefs, sand, and mudflats (Solís-Marín et al., 2013). Most collecting efforts have been carried out on Coco, Caño, and Murciélago islands in the Pacific Ocean, while on the Caribbean it has been between Punta Cahuita and Punta Mona (Alvarado et al., 2017; Chacón-Monge et al., 2021). However, the real status of the deep-sea echinoderm's fauna has not been evaluated. Deep-water biodiversity assessments have always been a challenge due to the complexity and cost in logistic operations (Costello and Chaudhary, 2017). In this paper, we undertook the task of compiling the available information in the literature and museum collections about deep-sea echinoderms collected in Costa Rica. In this way, we are aiming to have a better understanding of the deep-sea fauna contribution to the total echinoderm diversity in Costa Rican waters. Likewise, to be able to identify areas or groups that require a greater sampling effort for future collections and research.

MATERIAL AND METHODS

To compile the list of deep-sea echinoderms collected in Costa Rica, a literature search was carried out to corroborate records, ecological investigations, and further aspects of deep-sea Costa Rican echinoderms. In addition, the following databases of biological collections were visited: 1) California Academy of Sciences (CAS: http://researcharchive.calacademy.org/research/izg/); 2) Benthic Invertebrate Collection, Scripps Institution of Oceanography (SIO: https://scripps.ucsd.edu/benthic-invertebrate-collection); 3) National Museum of Natural History, Smithsonian Institution (NMNH: http://collections.nmnh.si.edu/); 4) Museum of Comparative Zoology, Harvard University (MCZ: https://mcz.harvard.edu/database; and 5) Museo de Zoología, Universidad de Costa Rica (MZUCR).

A list of deep-water echinoderms collected in Costa Rican waters was elaborated (**Table 1**), following the phylogenetic order for the five classes of Echinodermata according to the World Register of Marine Species (WoRMS, WoRMS Editorial Board, 2022), including the taxonomy, location, depth, status as new record for the country or Central America, the reported depth range (if available), and the references. A map of the Costa Rican Exclusive Economic Zones was constructed using ArcGIS Desktop 10.8, plotting the location, species richness, and abundance of specimens (**Figure 1**). We followed the definition for the deep sea as oceanic waters and seabed below 200 m depth (UNESCO, 2009).

The biogeographic affinity of the echinoderm species was estimated based on the Ocean Biodiversity Information System (www.obis.org) and WoRMS (WoRMS Editorial Board, 2022). We used the classification of marine biogeographic realms proposed by Costello et al. (2017). We found biogeographic affinities for only 120 species. Based on this affinity, a presence/absence matrix was developed, and a Bray-Curtis similarity matrix was made. A Non-metric Multi-Dimensional Scaling was elaborated, and we overlay vectors using a Pearson correlation based on the realms indicated by the Similarity Percentages - species contributions analysis (SIMPER). These analyzes were performed in PRIMER 7.0.

RESULTS

A total of 124 taxa of deep-sea echinoderms have been collected in Costa Rica, 75 identified to species level with certainty (**Tables 1, 2**), the remaining 49 representing morphospecies (i.e. morphologically similar individuals). There are 112 taxa for the Pacific Ocean and 13 for the Caribbean Sea, with only one shared

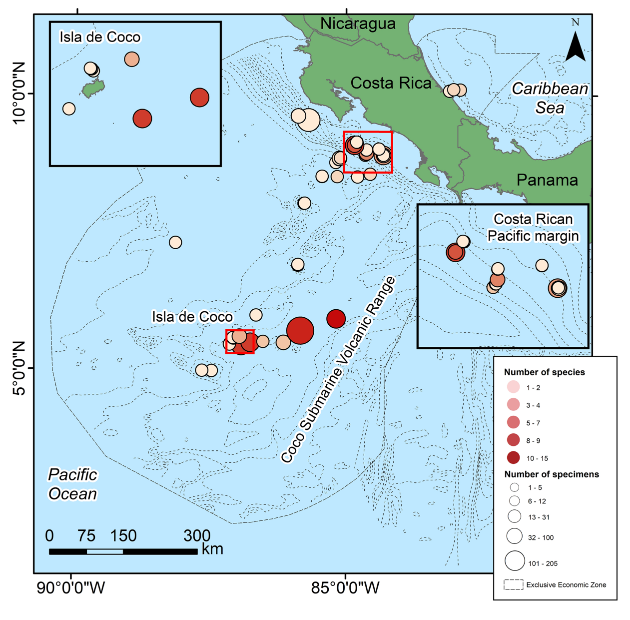

FIGURE 1 | Sampling localities of deep-sea echinoderms recorded on museum collections (Scripps Institution of Oceanography, National Museum of Natural History of Smithsonian Institution, Museum of Comparative Zoology of Harvard University, Museo de Zoología Universidad de Costa Rica) from the Costa Rican Economic Exclusive Zone.

TABLE 1 | Taxonomic list of deep-sea echinoderms from Costa Rican waters.

Class	Order	Family	Scientific name	P	C	PC	Depth range Costa Rica (m)	CR new report	CA new report	Reported depth range (Solís-Marín et al., 2013)	References
Crinoidea	Comatulida	Antedonidae	cf. *Antedon* sp.	X			1246-1390	X	X	n.d.	SIO; Summers et al., 2014
			Fariometra parvula	X			1788-1789			n.d	Hartlaub, 1895; A.H. Clark, 1917
		Bathycrinidae	*Bathycrinus mendeleevi*	X			1371	X	X	n.d., ETP new report	SIO
		Bourgueticrinidae	*Bourgueticrinus* sp.	X			3031	X	X	n.d., ETP new report	SIO
		Comasteridae	*Neocomatella pulchella*		X		1095^{+}			3-695	Cambronero-Solano et al., 2019
		Thalassometridae	*Thalassometra agassizii*	X			1030-1180			596-1429	SIO
		Zenometridae	*Psathyrometra fragilis*?	X			644-1908	X	X	n.d., ETP new report	SIO
			Psathyrometra sp.	X			644-1148	X	X	n.d	SIO
	Hyocrinida	Hyocrinidae	*Calamocrinus diomedae*	X			$714\text{-}2209^{+}$	X		717-1431	SIO; Roux, 2004
			Calamocrinus sp.	X			1158	X	X	717-1158	SIO
			Hyocrinus sp.	X			1087-1807	X	X	n.d.	SIO
Asteroidea	Spinulosida	*Echinasteridae*	*Henricia* sp.	X			1071	X	X	0-2001	SIO
	Paxillosida	Astropectinidae	*Astropecten benthophilus* $_{\epsilon}$	X			1408			1408	USNM; MCZ; Ludwig, 1905
			Leptychaster inermis	X			1143-1408			732-1593	Ludwig, 1905; Fisher, 1928
			Persephonaster armiger	X			1951			n.d., ETP new report	Ludwig, 1905
			Tethyaster canaliculatus $_{\epsilon}$	X			1908^{+}	X		23-300	SIO
			Thrissacanthias penicillatus	X			1000	X	X	55-1503	SIO
			Thrissacanthias sp.	X			1119-1281	X	X	n.d.	MZUCR
		Porcellanasteridae	*Porcellanaster ceruleus*	X			1408-2149			1158-6035	USNM; Ludwig, 1905
			Eremicaster pacificus	X			2149			1463-5780	USNM; Ludwig, 1905
		Pseudarchasteridae	*Pseudarchaster* spp.	X			1119-1281	X		98-3575	MZUCR
	Notomyotida	Benthopectinidae	*Cheiraster* (*Cheiraster*) *planus*		X		485-596			226-1339	Cambronero-Solano et al., 2019
			Pectinaster agassizi	X			1789-1951			790-2323	USNM; Ludwig, 1905
			Benthopecten acanthonotus	X			1157-1454	X		1800-1936	SIO
			Benthopecten spinuliger $_{\epsilon}$	X			1789-1847			1618-2323	USNM; Ludwig, 1905
	Valvatida	Asterinidae?	cf. *Patiria*	X			950	X	X	n.d.	SIO
		Goniasteridae	*Bathyceramaster elegans* $_{\epsilon}$	X			1789	X	X	1789, ETP new report	USNM; Ludwig, 1905
			cf. *Ceramaster* sp.	X			910-1000	X	X	n.d.	SIO
			Evoplosoma claguei?	X			1097	X	X	n.d.	SIO
			cf. *Hippasteria* cf. *phrygiana*	X			910^{+}	X	X	0-400	SIO
			Nymphaster diomedeae $_{\epsilon}$	X			1000-1408			702-1810	SIO; USNM; Ludwig, 1905: Fisher, 1928
			Pillsburiaster ernesti $_{\epsilon}$	X			2149			2149	USNM; Ludwig, 1905
	Velatida	Caymanostellidae	*Belyaevostella* sp.	X			967-1005	X	X	n.d., ETP new report	SIO
			Caymanostella sp.	X			974-1887	X	X	n.d., ETP new report	SIO

(Continued)

TABLE 1 | Continued.

Class	Order	Family	Scientific name	P	C	PC	Depth range Costa Rica (m)	CR new report	CA new report	Reported depth range (Solís-Marín et al., 2013)	References
Ophiuroidea	Euryalida	Asteronychidae	*Astrodia plana* $_{\epsilon}$	X			1807-2109	X		717-3058	SIO
		Euryalidae	*Asteroschema* sp.	X			1097-1854	X		350-1271	SIO
			Asteroschema sublaeve	X			1119-1281	X		1271	MZUCR
			Ophiocreas sp.	X			1097-1886^{+}	X	X	n.d	SIO
		Gorgonocephalidae	*Gorgonocephalus* cf. *chilensis*	X			665	X	X	4-900	SIO
			Gorgonocephalus diomedeae	X			1009	X		1271	SIO
			Gorgonocephalus sp.	X			1004-1040			n.d.	SIO
	Ophiacanthida	Ophiacanthidae	*Ophiacantha quadrispina*	X			156-273			183-549	MZUCR
			Ophiacantha similis	X			130-1180*			717-1097	SIO
			Ophiacantha sp.	X			606-1908			0-5203	SIO
			Ophiochondrus sp.	X			967-1751	X	X	n.d.	SIO
			Ophiambix sp.	X			988-2091	X	X	n.d., ETP new report	SIO
		Ophiotomidae	*Ophiomitra* sp.	X			741-745	X	X	n.d., ETP new report	SIO
			Ophiotoma paucispina	X			2149			1643-4082	Lütken & Mortensen, 1899
			Ophiotreta sp.	X			1009	X	X	n.d., ETP new report	SIO
	Ophioscolecida	Ophioscolecidae	*Ophiolycus* sp.?	X			997-998	X	X	n.d., ETP new report	SIO
	Ophioleucida	Ophioleucidae	*Ophioleuce gracilis*	X			1751-1908	X	X	n.d., ETP new report	SIO
	Ophiurida	Ophiuridae	*Ophiocten hastatum*	X			1157-1847			1159-2877	USNM; SIO; Lütken & Mortensen, 1899
			Ophiura flagellata	X			1662			128-2014	SIO
			Ophiura sp.	X			1000-1866			n.d.	SIO
			Ophiura (*Ophiura*) *nana*	X			1650			1650	USNM; Lütken & Mortensen, 1899
		Ophiopyrgidae	*Amphiophiura abcisa*	X			245			245-3714	USNM; MCZ; Lütken & Mortensen, 1899
			Amphiophiura paucisquama $_{\epsilon}$	X			820			n.d.	MZUCR
			Ophiuroglypha irrorata irrorata	X			1951-2149			405-5869	USNM; Lütken & Mortensen, 1899
			Ophiuroglypha sp.	X			974-1866			0-5869	SIO
			Stegophiura sp.	X			1791-1800	X	X	n.d.	SIO
		Ophiomusaidae	*Ophiomusa faceta?*	X			1009	X	X	n.d.	SIO
			Ophiomusa lymani	X			1408-2149			51-2906	USNM; SIO; Lütken & Mortensen, 1899
		Ophiosphalmidae	*Ophiosphalma glabrum*	X			1157-3400			878-5203	USNM; SIO; Lütken & Mortensen, 1899
		Amphilepididae	*Amphilepis patens*	X			1157-1454	X		304-4087	SIO
	Amphilepidida	Amphiuridae	*Amphiura koreae*	X			1157-1454	X	X	n.d.	SIO
			Amphiura serpentina	X			1157-1454	X		770-1865	SIO
			Amphiura seminuda	X			1157-1454	X	X	9-4096	SIO
		Ophiothamnidae	*Histampica duplicata*	X			156-256			125-2870	MZUCR
		Hemieuryalidae	*Ophiozonella alba* $_{\epsilon}$	X			1408-2149			1408-2487	USNM; Lütken & Mortensen, 1899
		Ophiolepididae	*Ophiolepis* sp.	X			1157-1454	X		0-230.	SIO
		Ophiacanthidae	*Ophiolimna bairdi*	X			1157-1454	X	X	n.d.	SIO

(Continued)

TABLE 1 | Continued.

Class	Order	Family	Scientific name	P	C	PC	Depth range Costa Rica (m)	CR new report	CA new report	Reported depth range (Solís-Marín et al., 2013)	References
Holothuroidea	Apodida	Chiridotidae	*Chiridota*?	X			1408			n.d.	SIO
	Dendrochirotida	Cucumariidae	*Abyssocucumis abyssorum*	X			2149			3241-4000	USNM; Ludwig, 1894
		Psolidae	*Psolus* aff. *diomedeae* $_{\epsilon}$	X			1157-1454^{+}			13-302	USNM; SIO
		Ypsilothuriidae	*Ypsilothuria bitentaculata*	X			974-1866			255-4082	SIO
	Elasipodida	Elpidiidae	*Achlyonice* sp.	X			1886-1869	X	X	n.d.	SIO
			cf. *Peniagone* sp.	X			1859-1868	X	X	n.d.	SIO
			Peniagone vitrea	X			1789-2149			1160-4507	USNM; Ludwig, 1894
		Laetmogonidae	*Benthogone*? sp.	X			1854-1886			n.d., ETP new report	SIO
			Pannychia sp.	X			924-1908			n.d	SIO
			Pannychia moseleyi	X			1408			199-2599	USNM; Ludwig, 1894
			Psychronaetes sp.	X			1097-1982	X	X	3852-4289	SIO
		Pelagothuriidae	*Pelagothuria natatrix* $_{\epsilon}$	X			982-1650			0-4505	SIO; Ludwig, 1894; Selig et al., 2019
		Psychropotidae	*Benthodytes sanguinolenta*	X	X	X	385-3453^{+}			P=978-2323; C=914-3100	USNM; SIO; Ludwig, 1894; Cambronero-SOlano et al., 2019
	Holothuriida	Mesothuriidae	*Mesothuria multipes* $_{\epsilon}$	X			2149			725-4064	USNM; Ludwig, 1894
			Zygothuria láctea		X		704-1292			484-5100	Cambronero-Solano et al., 2019
		Caudinidae		X			1782			0-2850	SIO
	Molpadida	Molpadiidae	*Molpadia granulata* $_{\epsilon}$	X			2690			2690-5869	Ludwig, 1894
			Molpadia musculus	X			1951-2149			37-6134	USNM
	Synallactida	Deimatidae	*Deima validum pacificum*	X			1789-2149			1618-2487	USNM; Ludwig, 1894
			Deima validum validum		X		1017-1300			914-2780	Cambronero-Solano et al., 2019
			Orphnurgus vitreus	X			1847	X	X	n.d., ETP new report	USNM
			Oneirophanta setigera	X			2149	X	X	3667-4088	USNM; Ludwig, 1894
		Synallactidae	*Bathyplotes natans*		X		496-1308			210-1644	Cambronero-Solano et al., 2019
			Bathyplotes sp.		X		677-1908			n.d.	USNM; SIO
			Oloughlinius macdonaldi $_{\epsilon}$	X			2149^{+}	X	X	1644	USNM; Ludwig, 1894
			Synallactes cf. *chuni*	X			1000	X	X	n.d., ETP new report	SIO
			Synallactes sp.	X			910-1065			n.d.	SIO
	Persiculida	*incertae sedis*	*Benthothuria funebris*		X		1225			n.d.	Cambronero-Solano et al., 2019
			cf. *Hadalothuria* sp.	X			1065	X	X	n.d., ETP new report	SIO
			Hansenothuria sp.		X		742-1481			n.d.	Cambronero-Solano et al., 2019
		Gephyrothuriidae	*Paroriza pallens*		X		385-1481			n.d.	Cambronero-Solano et al., 2019
			Paroriza sp.		X		987-1046	X	X	n.d., ETP new report	USNM
		Pseudostichopodidae	*Pseudostichopus mollis*	X			245-1951			100-5203	USNM, Ludwig, 1894
			Pseudostichopus peripatus	X			1789			1158-3667	USNM
			Pseudostichopus sp.	X			1951			n.d.	USNM

(Continued)

TABLE 1 | Continued.

Class	Order	Family	Scientific name	P	C	PC	Depth range Costa Rica (m)	CR new report	CA new report	Reported depth range (Solís-Marín et al., 2013)	References
Echinoidea	Cidaroida	Cidaridae	*Centrocidaris doederleini* $_{\epsilon}$	X			265			87-550	SIO; Cortés & Blum, 2008
		Histiocidaridae	*Histocidaris variabilis*	X			571	X	X	n.d., ETP new report	SIO
	Camarodonta	Strongylocentrotidae?		X			1782	X	X	0-1200	SIO
	Echinothurioida	Echinothuriidae	*Araeosoma leptaleum*	X			964-1271	X	X	740-1046	SIO
			Tromikosoma cf. *tenue*	X			2067	X	X	n.d., ETP new report	SIO
			Tromikosoma hispidum	X			2067-2149			1820-3375	SIO; USNM; A. Agassiz, 1904
	Aspidodiadematoida	Aspidodiadematidae	*Aspidodiadema hawaiiense*	X			1003	X	X	n.d., ETP new report	SIO
			Plesiodiadema?	X			1807-2109			n.d.	SIO
			Plesiodiadema horridum $_{\epsilon}$	X			1650-2149			1625-3381	USNM, A. Agassiz, 1898; 1904
	Pedinoida	Pedinidae	*Caenopedina hawaiiensis*	X			758-2209	X	X	n.d., ETP new report	SIO
			Caenopedina diomedeae	X			759-966	X		723-850	SIO
	Salenioida	Saleniidae	*Salenocidaris miliaris*	X			2149			1159-3376	A. Agassiz, 1898; 1904
	Clypeasteroida	Clypeasteridae	*Clypeaster euclastus*		X		1050^{+}			36-530	Cambronero-Solano et al.,2019
		Asterostomatidae	*Phrissocystis aculeata*	X			1951	X	X	n.d., ETP new report	USNM; A. Agassiz, 1898; 1904
	Spatangoida	Brissidae	*Brissopsis elongata*		X		302-329			3-270	USNM
		Loveniidae	*Araeolampas hastata* $_{\epsilon}$	X			1847			1785-3376	MCZ; A. Agassiz, 1898; 1904
		Macropneustidae	*Argopatagus aculeata* $_{\epsilon}$	X			1951			1952	A. Agassiz, 1898
		Aeropsidae	*Aeropsis fulva*	X			2149			1455-5200	A. Agassiz, 1898
			TOTAL	**112**	**13**	**1**		**58**	**46**		

*CR, Costa Rica; CA, Central America; P, Pacific; C, Caribbean; PC, Pacific and Caribbean; n.d, no data; ETP, Eastern Tropical Pacific; CAS, California Academy of Sciences; SIO, Scripps Institution of Oceanography; NMHN, National Museum of Natural History, Smithsonian Institution; MCZ, Museum of Comparative Zoology, Harvard University; MZUCR, Museo de Zoología, Universidad de Costa Rica. + = deeper depth range; * = shallower depth range.* **ϵ***: Eastern Tropical Pacific endemic.*

species between the two basins (the holothuroid *Benthodytes sanguinolenta*). We found 22 new reports for the Eastern Tropical Pacific, 46 for Central America, and 58 for Costa Rica (57 on the Pacific Ocean and one in the Caribbean Sea) (**Table 1**). With this, we reached a total of 364 species of echinoderms for Costa Rica, 78% of the total species registered in Central America (466). 34% of the echinoderm species of Costa Rica are deep-sea species.

In the Costa Rican deep sea, the most diverse class is Ophiuroidea with 37 taxa and 22 confirmed species, all from the Pacific (**Table 2**), with the families Ophiacanthidae and Ophiopyrgidae as the most specious (five taxa each). The Holothuroidea is the second in richness, with 35 taxa in 19 species, the Synallactidae had most of the taxa (five), followed by Laetmogonidae and Deimatidae (four each). Asteroidea and Echinoidea have 24 and 18 taxa, respectively (14 and 15 confirmed species, respectively). For the asteroids, the families Goniasteridae and Astropectinidae were the richest (six taxa each). While Echinothutiridae and Aspidodiadematidae were the most specious families in Echinoidea (three taxa each). Finally, Crinoidea have 10 taxa and five confirmed species, where Hyocrinidae is the richest family (three genera) (**Table 1**, **2**).

According to their distribution and diversity (**Figure 1**), the greatest collecting effort has been around the CSVR,

TABLE 2 | Number of deep-sea echinoderms taxa at different taxonomic levels from Costa Rican waters.

Class	Orders	Families	Genus	Species	Morphospecies	Caribbean	Pacific
Crinoidea	2	7	9	5	5	1	10
Asteroidea	5	8	21	14	10	1	23
Ophiuroidea	6	17	25	22	15	0	37
Holothuroidea	7	15	25	19	16	9	27
Echinoidea	8	13	13	15	3	2	16
Total	28	60	93	75	49	13	112

Isla del Coco, the seamount subduction zone, and along the continental margin (9°4'26.09"-8°36'37.88"N and 85°14'11.77"-84°17'050"W) on the Pacific side, and in front of the Port of Limón (10°4'35.77"N-82°54'9.38"W) on the Caribbean coast. Other areas of the country have been scarcely sampled, like the extensive abyssal plains of the Pacific and most of the EEZ in the Caribbean (**Figure 1**).

The greatest number of taxa by depth range (**Figure 2**) was found between 800 and 1200 m with 64 taxa, followed by 52 and 51 taxa between 1600-2000 m and 1200-1600 m, respectively. The holothuroid *Benthodytes sanguinolenta* and the ophiuroid *Ophiosphalma glabrum* were the species with the largest bathymetric distribution range (385-3453 m and 1157-3400 m, respectively), and the only two species found deeper than 3200 m. One species of ophiuroid, *Ophiacantha similis*, had a shallower deep range than previously reported, while the holothuroids, *Psolus* aff. *diomedeae*, *Benthodytes sanguinolenta, Oloughlinius macdonaldi*, and the echinoid, *Clypeaster euclastus*, had deeper depth ranges than previously reported (**Table 1**).

Most taxa of deep-sea echinoderms collected in Costa Rica are vouchered in the collections at SIO (73 species) and the NMNH (35 species) (**Figure 3**). Otherwise, the MZUCR and MCZ have six taxa and three species respectively. No reports were found in the CAS database. Additionally, we found 49 records in the literature (**Table 1**), mostly all deposited in museum collections, except for the echinoderms reported by Cambronero-Solano et al. (2019) for the Caribbean Sea.

About 78% of the species present in the Costa Rican deep sea have a biogeographic affinity with the Eastern Tropical Pacific realm (**Table 3**), 23 species are endemic to this region (**Table 1**). Other regions with higher biogeographic affinity are the North Pacific (40%), followed by Tropical Indo-Pacific & coastal Indian Ocean (36%), Western Tropical Atlantic (35%), offshore Western Pacific and South Australia with 33% both. By class, most of the species have an ETP affinity, there are also several species that can be found in other regions (**Table 3**; **Figure 4**).

DISCUSSION

Historical Perspectives

The Costa Rican coastal areas have been relatively well studied, but not so the deep regions (Cortés, 2009; Cortés, 2016a; Cortés, 2016b; Cortés, 2016c). In the Caribbean, few studies have been carried out, and only two publications mentioned echinoderms collected below 200 m depth (Voss, 1971; Cambronero-Solano et al., 2019). In 1971, the R/V John Elliot Pillsbury, cruised to Central America, sampling off the Costa Rican Caribbean coast at two deep stations (Voss, 1971). Voss (1971) reported "small ophiuroids" (Ophiuroidea) and three "large sea biscuits" (Echinoidea: Spatangoida) from a "gray muddy bottom".

In 2011, the R/V Miguel Oliver, under the Central America Fisheries and Aquaculture Organization (OSPESCA), trawled into two areas of the Costa Rican Caribbean. Trawls ranged from 385 to 1,481 m and found six new echinoderm reports for Costa Rica (Cambronero-Solano et al., 2019). Holothuroids made up 99% of the total biomass, mainly comprised of *Benthodytes sanguinolenta* (60%) (Cambronero-Solano et al., 2019).

The deep waters of the Costa Rican Pacific were first studied in the late 19^{th} century, when the United States Fisheries Committee visited the area with the steamer USS Albatross, with Alexander Agassiz as Chief Scientist (Agassiz, 1898; Townsend, 1901; Agassiz, 1904). They sampled near Isla del Coco between February and March 1891 and carried dredging and trawling on abyssal plains at 12 stations (#3362-3373), ranging from 95 m to 3433 m (Azofeifa-Solano and Cortés, 2021). From the material collected during the Albatross expeditions, Ludwig (1894; 1905), Hartlaub (1895); Agassiz (1898; 1904), Lütken and Mortensen (1899), and Clark (1917) described many Central American deep-sea echinoderms (Alvarado et al., 2013). Ludwig (1894) worked on Holothuroidea and recorded 11 species from Costa Rican deep waters. Hartlaub (1895) reported one comatulid Crinoidean species. In the preliminary report on the Echini, Agassiz (1898) registered five Costa Rican deep-sea urchin species, later he added one species (Agassiz, 1904). Lütken and Mortensen (1899) worked on Ophiuroidea and reported eight species from Costa

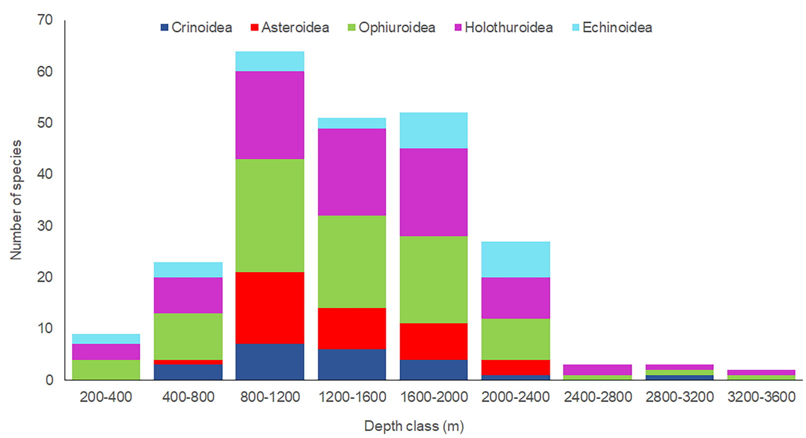

FIGURE 2 | Bathymetric variation in deep sea echinoderm species richness by class

TABLE 3 | Biogeographic distribution of Costa Rican deep sea echinoderms species based on the Ocean Biodiversity Information System (www.obis.org) and the World Register of Marine Species (www.marinespecies.org), and according to the marine biogeographic realms proposed by Costello et al. (2017).

Class	Species	Biogeographic distribution
Crinoidea	cf. *Antedon* sp.	4,3,5,9,11,13,15,16,17,18,19,20,21,23,28,30
	Fariometra parvula	12
	Bathycrinus mendeleevi	13
	Bourgueticrinus sp.	n.d.
	Neocomatella pulchella	11
	Thalassometra agassizii	12
	Psathyrometra fragilis?	13
	Psathyrometra sp.	7,9,10,12,17,20,26,28
	Calamocrinus diomedae	12,26
	Calamocrinus sp.	12,26
	Hyocrinus sp.	7,12,22
Asteroidea	*Henricia* sp.	worldwide
	Astropecten benthophilus	12
	Leptychaster inermis	7,12
	Persephonaster armiger	19
	Tethyaster canaliculatus	12
	Thrissacanthias penicillatus	7,12,20
	Thrissacanthias sp.	7,12,20
	Porcellanaster ceruleus	3,11,12,13,16,17,18,20,23,26,28
	Eremicaster pacificus	7,12,13,17
	Pseudarchaster spp.	worldwide
	Cheiraster (*Cheiraster*) *planus*	11
	Pectinaster agassizi	7,12
	Benthopecten acanthonotus	7,12
	Benthopecten spinuliger	12
	cf. *Patiria*	7,10,12,20,29
	Bathyceramaster elegans	12
	cf. *Ceramaster* sp.	worldwide
	Evoplosoma claguei?	7,12
	cf. *Hippasteria* cf. *phrygiana*	3,4,7,10,11,12,18,20,21,24,28,29,30
	Nymphaster diomedeae	12
	Pillsburiaster ernesti	12
	Crossaster borealis?	7,12
	Belyaevostella sp.	16
	Caymanostella sp.	7,12,28,11,13,16,26
Ophiuroidea	*Astrodia plana*	12
	Asteroschema sp.	7,10,11,12,13,15,16,18,25,28
	Asteroschema sublaeve	7,12
	Ophiocreas sp.	11,13,15,16,17,21,26,27,28
	Gorgonocephalus cf. *chilensis*	24,25,28,30
	Gorgonocephalus diomedeae	12
	Gorgonocephalus sp.	7,6,11,12,13,16,18,20,21,22,24,25,28,29
	Ophiacantha quadrispina	12
	Ophiacantha similis	12
	Ophiacantha sp.	wordlwide
	Ophiochondrus sp.	5,11,16,21,24,30
	Ophiambix sp.	11,13,18,20,22,28
	Ophiomitra sp.	3,11,12,13,16,18,20
	Ophiotoma paucispina	12
	Ophiotreta sp.	11,12,13,15,16,17,19,20,22,23,26,28,29
	Ophiolycus sp.?	3,4,13,16,24,26,28,30,4,3
	Ophioleuce gracilis	n.d
	Ophiocten hastatum	3,7,11,12,18,20,21,26,28,30
	Ophiura flagellata	7,12,13,16,20,26,27,28,30
	Ophiura sp.	worldwide
	Ophiura (*Ophiura*) *nana*	12
	Amphiophiura abcisa	10,12
	Amphiophiura paucisquama	12
	Ophiuroglypha irrorata irrorata	3,7,10,11,12,16,18,19,20,22,26,27,28
	Ophiuroglypha sp.	worldwide
	Stegophiura sp.	3,4,7,8,12,13,16,17,18,20,25,26,28,29
	Ophiomusa faceta?	13

(Continued)

TABLE 3 | Continued.

Class	Species	Biogeographic distribution
	Ophiomusa lymani	3,7,8,11,12,13,15,16,20,22,23,26,27,28
	Ophiosphalma glabrum	7,10,12,13,15,16,22,28
	Amphilepis patens	7,12,20
	Amphiura koreae	20,29
	Amphiura serpentina	7,12
	Amphiura seminuda	10,12
	Histampica duplicata	3,9,11,12,13,15,16,17,18,28
	Ophiozonella alba	12
	Ophiolepis sp.	3,9,11,12,13,15,16,17,21,23,27,28
	Ophiolimna bairdi	3,7,12,11,16,18,20,26,28
	Ophiomitra sp.	11,12,13,16,18,20
Holothuroidea	*Chiridota*?	worldwide
	Abyssocucumis abyssorum	3,7,12,18,25,26,28,30
	Psolus aff. *diomedeae*	12
	Ypsilothuria bitentaculata	3,5,7,10,12,13,16,18,20,21,25,26,28
	Achlyonice sp.	3,12,20,21,26,28,30
	cf.*Peniagone* sp.	3,7,10,12,16,18,19,20,22,23,26,28,30
	Peniagone vitrea	7,12,22,26,28
	Benthogone? sp.	3,13,16,18,21,27,28
	Pannychia sp.	6,7,9,10,12,13,20,26,28,30
	Pannychia moseleyi	6,7,9,10,12,13,20,26,28
	Psychronaetes sp.	11,12,22
	Pelagothuria natatrix	12
	Benthodytes sanguinolenta	11,12
	Mesothuria multipes	12
	Zygothuria lactea	3,11,18
	Molpadia granulata	12
	Molpadia musculus	3,4,5,6,7,8,11,12,13,16,18,21,23,26,28,30
	Deima validum pacificum	n.d.
	Deima validum validum	3,11,12,13,18,22,23,26,27,28
	Orphnurgus vitreus	9,12,13
	Oneirophanta setigera	12,17,22,28
	Bathyplotes natans	3,4,9,11,12,13,18,21,26,28
	Bathyplotes sp.	3,4,7,9,10,12,13,16,17,18,20,21,24,25,26,28,30
	Oloughlinius macdonaldi	12
	Synallactes cf. *chuni*	20
	Synallactes sp.	3,7,10,11,12,13,20,21,22,24,26,27,28
	Benthothuria funebris	3,8,11,18
	cf. *Hadalothuria* sp.	13,20
	Hansenothuria sp.	11,12
	Paroriza pallens	3,18,21,27
	Paroriza sp.	3,5,11,13,18,21,22
	Pseudostichopus mollis	7,10,12,13,25,26,28,30
	Pseudostichopus peripatus	3,7,9,11,12,13,18,20,21,22,26,28,30
	Pseudostichopus sp.	3,7,9,10,11,12,13,20,22,23,26,27,28,30
Echinoidea	*Centrocidaris doederleini*	12
	Histocidaris variabilis	9
	Araeosoma leptaleum	7,12
	Tromikosoma cf. *tenue*	7,13,15,20
	Tromikosoma hispidum	10,12
	Aspidodiadema hawaiiense	9
	Plesiodiadema?	11,12,13,21,22,26,27
	Plesiodiadema horridum	12
	Caenopedina hawaiiensis	9,28
	Caenopedina diomedeae	7,12
	Salenocidaris miliaris	13
	Clypeaster euclastus	11
	Argopatagus aculeata	12
	Brissopsis elongata	11
	Araeolampas hastata	12

(Continued)

TABLE 3 | Continued.

Class	Species	Biogeographic distribution
	Argopatagus aculeata	12
	Aeropsis fulva	7,10,12,20

Realms: 1) Inner Baltic Sea; 2) Black Sea; 3) NE Atlantic; 4) Norwegian Sea; 5) Mediterranean; 6) Artic; 7) North Pacific; 8) North American Boreal; 9) Mid-Tropical North Pacific Ocean; 10) South-east Pacific; 11) Tropical W Atlantic; 12) Tropical E Pacific; 13) Tropical Indo-Pacific and Coastal Indian Ocean; 14) Red Sea; 15) Tasman Sea and SW Pacific; 16) Tropical Australia and Coral Sea; 17) Mid South Tropical Pacific; 18) Offshore and NW Atlantic; 19) Offshore Indian Ocean; 20) Offshore W Pacific; 21) Offshore S Atlantic; 22) Offshore mid-E Pacific; 23) Tropical E Atlantic; 24) Argentina; 25) Chile; 26) South Australia; 27) South Africa; 28) New Zealand; 29) North West Pacific; 30) Southern Ocean; n.d., no data.

Rican deep sea. Finally, Ludwig (1905) reported 14 deep-sea species of Asteroidea for Costa Rican deep sea.

In 1925, during the oceanographic expedition of the Zoological Society of New York, with the yacht Arcturus led by William Beebe, deep-sea stars were collected from one station close to Isla del Coco (Fisher, 1928).

In 1973, the Scripps Institution of Oceanography realized the first expedition to the Eastern Pacific (EP) with the R/V Agassiz, in which some sample stations included deep-sea echinoderms (Luke, 1982; Cortés, 2009). In 1986, a submersible was used at Isla del Coco, the Johnson Sea-Link I of Harbor Branch Oceanographic Institute (HBOI), as part of the SeaPharm Project (a pharmaceutical prospecting expedition). Six dives were done ranging from 105 to 785 m (Cortés, 2008). The crinoid *Calamocrinus diomedae* was collected southeast Isla del Coco at 714 m deep and cataloged in the collections of the HBIO (Roux, 2004). Starting in 2007 a three-person submarine, DeepSee, able to reach 450 m has been used regularly at Isla del Coco. Echinoderms and other taxonomic groups have been video recorded and/or collected (Cortés, 2008; Cortés and Blum, 2008).

Since the 1990's the methane seeps along the Pacific margin have drawn attention, mainly from a geological point of view, but also there are some images of deep-water echinoderms available (Sahling et al., 2008). The methane seeps off the Central Pacific coast of Costa Rica have been studied using the Human Operated Vehicle (HOV) Alvin in 2009-2010, led by Lisa A. Levin, and again in 2017-2018, led by Erik E. Cordes, this last one also included the exploration of several seamounts farther offshore. Echinoderms were collected between 974-1866 m depth, most of the specimens were deposited at SIO.

Based on the 2009-2010 expeditions, Levin et al. (2012) described "hydrothermal seep ecosystems" hosting high densities of ophiuroids (Ophiuridae). Levin et al. (2015) demonstrated the role of authigenic carbonate rocks, providing a unique habitat and food resources for macrofaunal assemblages at seep sites on the Costa Rican margin (400-1850 m). The presence of high densities of ophiuroids is strongly related to overlying water's hydrography. Based on those collections, Summers et al. (2014) described species of Myzostomida (Annelida) which are obligate associates, mostly of echinoderms. One of them, *Pulvinomyzostomum inaki* Summers & Rouse, 2014, was collected on the crinoid *Antedon* sp., at Jaco Scarp in 2009.

In 2019 an expedition led by Erik E. Cordes visited the methane seeps and more seamounts using the ROV SuBastian onboard the R/V Falkor. Echinoderms were video recorded and collected. Selig et al. (2019), reported aggregations of *Pelagothuria* sp. in deep sea regions of minimum oxygen concentration, based on data from R/V Falkor that includes observations from Costa Rica.

Deep-Sea Echinoderm Fauna

According to the compiled information, the main component of the known deep sea echinoderm fauna in Costa Rica inhabits

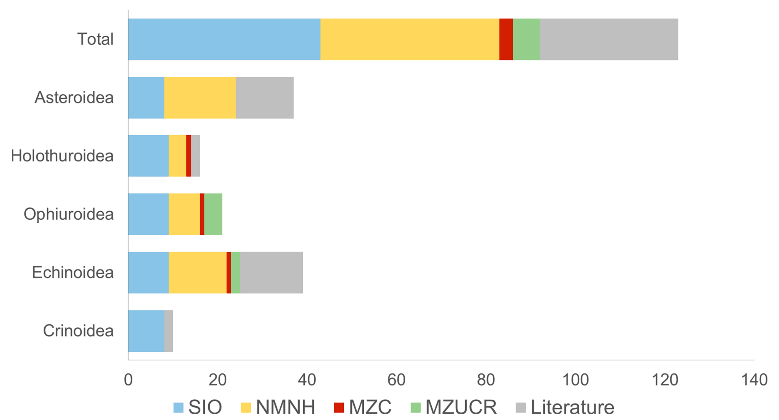

FIGURE 3 | Number of echinoderms species registered by museum collection or literature for Costa Rica deep waters. Scripps Oceanographic Institution (SIO); National Museum of Natural History, Smithsonian Institution (NMNH); Museum of Comparative Zoology, Harvard University (MCZ); Museo de Zoología, Universidad de Costa Rica (MZUCR).

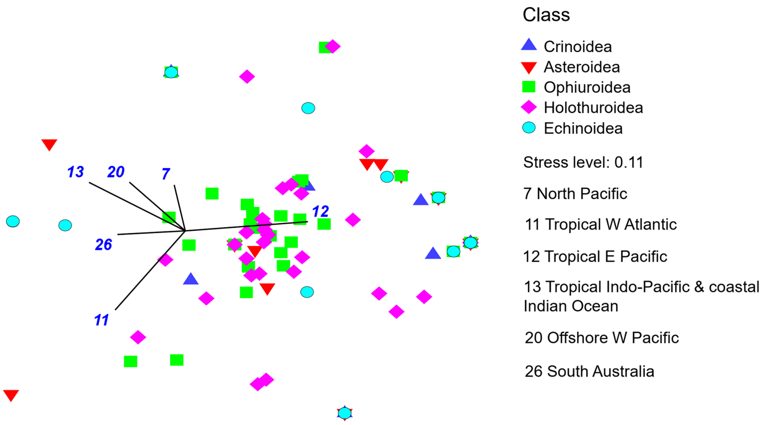

FIGURE 4 | A Non-metric Multi-Dimensional Scaling based on a Bray-Curtis similarity matrix of the presence/absence of the biogeographic affinities of Costa Rica deep sea echinoderms. Vectors indicated the greatest contributions of the realms based on the SIMPER analysis. Number is blue refer to the marine biogeographic realms proposed by Costello et al. (2017) in **Table 3.**

from the bathyal to the abyssal zone (200-3000 m depth). This view could be biased by the exploration approaches, the scientific historic background and the relative representativeness of the deep sea total area covered (particularly scarce in the Caribbean) and their proportional size, but depicts the biogeographic predicted pattern (Mah and Blake, 2012; Stöhr et al., 2012; Pérez-Ruzafa et al., 2013). It is important to recognize that the taxa list reported in this study was obtained from literature and zoological museum databases, in which taxa are classified at the genus level or identified with affinities towards a species. Therefore, further taxonomic efforts are required.

For Crinoids, the genus *Antendon* is reported in the Costa Rican deep sea, but the only species listed near the ETP is *A. bifida* from Chile (Solís-Marín et al., 2013). Similarly, the only *Psathyrometra* reported before was *P. bigradata*, from Panama, Galapagos and Chile (Solís-Marín et al., 2013), but now there is also *P. fragilis* from Costa Rica. For *Calamocrinus*, the only species reported is *Calamocrinus diomedae*, from Panama and Galapagos, while *Hyocrinus foelli* is also the only species reported for the genus, in Mexico (Solís-Marín et al., 2013).

In Asteroidea, at museum collections we found *Thrissacanthias* sp., being *T. penicillatus* the only species reported for Mexico and Peru (Solís-Marín et al., 2013). In other genera, the situation is more complex, as there are different possible species. *Pseudarchaster* has five species in the ETP: *P. discus*, *P. pectinifer*, *P. pulcher*, *P. pusilus*, and *P. verrilli*, scattered from Mexico to Peru. For *Patiria* two species have been identified, *P. chilensis* (Chile-Pascua) and *P. miniata* (Mexico-Revillagigedo), but with bathymetric distributions below 40 m and 300 m respectively, while our specimen was found at 950 m. *Ceramaster* (**Figure 5**) has three species (*C. grenadensis*, *C. patagonicus* and *C. leptoceramus*) while *Henricia* has nine, all with overlapping bathymetric ranges but with geographically isolated records (USA, Mexico, Galapagos, Peru and Chile) (Solís-Marín et al., 2013). *Evoplosoma claguei* is the only reported species for this genus in Mexico, while *Hippasteria* has two, *H. phrygiana* and *H. falklandica*, both from deep waters, but with different geographic distribution, one is present in the Mexican Pacific waters while the other is from Chile (Solís-Marín et al., 2013). Finally, the family Caymanostellidae has been registered for the first time in the ETP. The genus *Belyaevostella* has two recognized species, while the genus *Caymanostella* has five. *Belyaevostella hyugaensis* was described from samples collected on sunken wood from the Southern of Japan (Fujita et al., 1994), while *Belyaevostella hispida* have been described from deep sea Indo-Malaysian region (Aziz and Jangoux, 1984), otherwise *Caymanostella* spp. are widely distributed (**Table 3**).

For Ophiuroidea, *Ophiocreas* is a new report for Central America and has at least 16 species described. *Asteroschema* (**Figure 5**) and *Gorgonocephalus* have two species reported for the ETP (Solís-Marín et al., 2013); *A. rubrum* from Pascua (below 731 m) and *A. sblaeve* from the USA (1235 m), Guatemala, Panama (1271 m), and Costa Rica (1119-1281 m); *G. chilensis* was registered from Chile (4-900 m) while *G. diomedeae* was found in Panama (1271 m). The worldwide distributed *Ophiacantha* has 25 species present in the ETP, but only *O. phragma* is registered for Costa Rica, at Isla del Coco (Solís-Marín et al., 2013). For *Ophiochondrus*, only *O. stelliger* is reported for Chile, between 73-439 m, while our specimen was collected between 1005-1008 m, and for *Ophiambix* there are about six species and is a genus widely distributed (**Table 3**). *Ophiomitra* has 11 valid species and *Ophiotreta* 17 (Stöhr et al., 2022), both genera are widely distributed (**Table 3**). Ophioscolecidae is a new family for the ETP, where the widely distributed genus *Ophiolycus* has three species (Stöhr et al., 2022). *Ophiura* has 16 species from shallow to deep sea on the ETP, two of them have been identified from Isla del Coco (Solís-Marín et al., 2013). In the family Ophiopyrgidae, both *Ophiuroglypha* and *Stegophiura* are widely distributed genera (**Table 3**), which have about 19 recognized species each (Stöhr et al., 2022), only one registered at Isla del Coco for *Ophiuroglypha* (Solís-Marín et al., 2013) while *Stegophiura* has been found in USA and Mexico. *Ophiomusa* is the unique

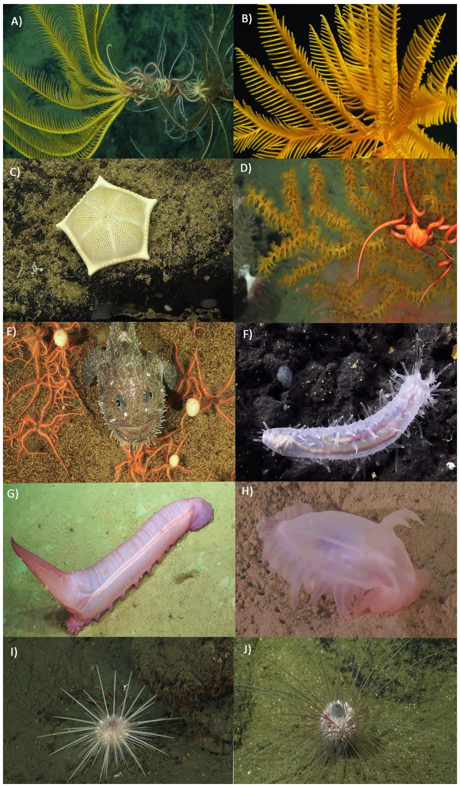

FIGURE 5 | Costa Rican deep-sea echinoderms. **(A)** Antedonidae sp.; **(B)** Antedonidae sp.; **(C)** Ceramaster sp.; **(D)** Asteroschema sp.; **(E)** Ophiacantha sp. and the fish Lophiodes caulinaris (Lophiidae); **(F)** Synallactida sp.; **(G)** Psychropotidae sp.; **(H)** Peniagone sp.; **(I)** Caenopedina sp.; **(J)** Aspidodiadema sp. Images were taken by the HOV Alvin and ROV SuBastian onboard of the Costa Rica expeditions.

genus for the family Ophiomusaidae, but it has about 50 valid and widely distributed species (**Table 3**). Finally, *Ophiolepis* has five species reported from the ETP nevertheless, only *O. crassa*, reach deeps beyond 200 m.

In holothuroids, *Chiridota pisanii* has been the unique species found in the deep sea for the genus in the ETP, but *Psolus* is represented by eight species at wide depths ranges. *P. digitatus* has been listed for Panama, *P. diomedae* is reported for Mexico, Isla del Coco, Panama, and Galapagos, while *P. squamatus* for Mexico and Chile (Solís-Marín et al., 2013). For the genus *Achlyonice*, the only species reported for the ETP is *A. ecalcarea*, while *Peniagone* has seven deep sea species at the ETP. *P. vitrea* has the largest extension range including Isla del Coco, *P. papillata* is also presented in Panama, but others are from Galapagos, Ecuador and Peru (Solís-Marín et al., 2013). The family Laetmogonidae is represented with three genera, *Benthogone* is widely distributed and has three accepted species (**Table 3**). The genus *Pannychia* has two species; *P. taylorae* was described from the Indian Ocean (O'Loughlin et al., 2013), while *P. moseleyi* has been found in Mexico, Panama, Galapagos and Peru. *Psychronaetes hanseni* is monospecific for its genus and was described from the Eastern Central Pacific Ocean (Pawson, 1983). Synallactidae is represented in two genera, *Bathyplotes natans* has been found in the Caribbean deep sea from Costa Rica but also in other countries in Latin America at both Pacific and Atlantic basins and also there have been another three species registered for the ETP (Solís-Marín et al., 2013). *Synallactes* has three species reported for Panama, Colombia, Malpelo, Galapagos, Ecuador and Peru, *S. chuni* has been reported from West Pacific (**Table 3**). *Hadalothuria* and *Hansenothuria* are monospecific genera. *Hadalothuria wolffi* was described from the hadal zone (>6000 m; Hansen, 1956) however, our specimen was found on the mesopelagic zone (~1000 m), whereas *Hansenothuria benti* was described from the Tropical Western Atlantic (Miller and Pawson, 1989). Gephyrothuriidae is a new family in the ETP represented by the genus *Paroriza*, which has four recognized species, only *P. prouhoi* has been reported from Chile. Finally, the genus *Pseudostichopus* registered three species at deep sea in ETP, *P. mcdonaldi* and *P. mollis* were found at Isla del Coco, but the second is more widely distributed (Solís-Marín et al., 2013).

In the case of echinoids, the echinothuriids *Tromikosoma* and *Plesiodiadema* have two species in the region each, and for both they have been previously listed from ETP at similar depths (Solís-Marín et al., 2013). *Tromikosoma hispidum* and *P. horridum* were reported for Isla del Coco and Costa Rica (Solís-Marín et al., 2013).

Regional Comparison

In Latin America, most echinoderm species were found only in one or two bathymetric intervals, Ophiuroidea was dominant from 200 to 2000 m at Pacific and West-Atlantic basins, but Asteroidea and Holothuroidea (respectively) where dominant from 2000 to 6000 m (Pérez-Ruzafa et al., 2013). For Asteroidea as also as Ophiuroidea, it has been suggested a highly conservative morphology in deep sea species and recent molecular analysis are suggesting cryptic and species complexes, thus deep sea and especially abyssal echinoderm diversity is considered underestimated (Mah and Blake, 2012; Stöhr et al., 2012).

Diversity information of deep-sea echinoderm fauna through recent research is scarce (Pawson, 1982; Stöhr and Segonzac, 2005; Mecho et al., 2014; Moles et al., 2015; Calero et al., 2017; Mironov et al., 2018; Setyastuti and Wirawati, 2018; Stöhr and O'Hara, 2021). Strong progress has been made, especially for Colombia, Chile, Brazil, Argentina and Mexico (González et al., 2002; Borrero-Pérez et al., 2003; Benavides-Serrato and Borrero-Pérez, 2010; Campos et al., 2010; Manso, 2010; Massin and Hendrickx, 2011; Borrero-Pérez et al., 2012; Hendrickx et al., 2014; Solís-Marín et al., 2014; Martínez et al., 2014; Martínez et al., 2015; Martínez, 2016; Conejeros-Vargas et al., 2017; Martinez and Penchaszadeh, 2017;Martínez et al., 2017, Rivadeneira et al., 2017; Luna-Cruz and Hendrickx, 2018; Borrero-Pérez et al., 2019; Flores et al., 2019; Pertossi et al., 2019; Martínez et al., 2019;Borrero-Pérez et al., 2020; Martinez et al., 2020; Rivadeneira et al., 2020; Luna-Cruz and Hendrickx, 2020; Catalán et al., 2020; Luna-Cruz and Hendrickx, 2021; Flores et al., 2021).

The deep sea of the Colombian Caribbean has been extensively studied (González et al., 2002; Borrero-Pérez et al., 2003; Benavides-Serrato and Borrero-Pérez, 2010; Borrero-Pérez et al., 2012; Borrero-Pérez et al., 2019; Dueñas et al., 2021). For the Southern Colombian Caribbean region, 16 species of sea cucumbers are found between 596 and 2566 m (Borrero-Pérez et al., 2020), of which only four have been reported for the Costa Rican Caribbean (*B. sanguinolenta*, *Benthothuria funebris*, *Deima validum validum*, and *Paroriza pallens*). For the SeaFlower Biosphere Reserve area (Borrero-Pérez et al., 2019), a region immediately adjacent to the exclusive economic zone of Costa Rica, they found 111 deep-sea echinoderm species, that represents 10 times more species than those reported for the Costa Rican Caribbean (Cambronero-Solano et al., 2019). Dueñas et al. (2021) reported the presence at cold-seep communities in the Colombian Caribbean between 2300 and 3300 m including the sea star family, Solasteridae, and two sea cucumbers, *Chiridota cf. heheva* and *Pseudostichopus* sp. This indicates a high potential for research and discovery of new reports for our waters.

In the ETP, Stöhr and O'Hara (2021) report 17 species of ophiuoids from waters deeper than 400 m as part of the Danish Galathea II Expedition, at stations in Nicaragua and Panama. Of these 17 species, only three are reported in Costa Rican waters in our review (*Astrodia plana*, *Ophiosphalma glabrum*, and *Ophiura flagellata*), which indicates a high potential for an increase in the number of ophiuroids in our region. Manso (2010) reports the presence of 15 species of brittle stars in Chile, of which only three are present in our list (*Gorgonocephalus chilensis*, *Ophiolimna bairdi* and *Ophiomusium lymani*). According to Stöhr et al. (2012), globally, the greatest diversity of ophiuroids occurs in shallow waters between 0 and 200 m deep, with 1313 species. Between 200 and 3500 m they indicate that there are 1297 species. For the ETP, they mention that the greatest diversity occurs between 200 and 3500 m with 111 species, while for shallow waters only 92 species. For the abyssal and hadal zone they indicate 28 and one species, respectively. For the Western Atlantic, the species richness of brittle stars is quite similar between the platform (217) and the bathyal zone (229), and only 16 species for the abyssal zone.

Perhaps the country in the region that has the most complete evaluation of its deep-sea fauna is Mexico (Solís-Marín et al., 2014). This country has 348 species of echinoderms that inhabit deep waters, which corresponds to 54.4% of the total species reported for the country. At the Caribbean and Gulf of Mexico they have been listed 111 and 103 deep sea species respectively (Crinoidea 25, Asteroidea 39, Ophiuroidea 100, Holothuroidea 9, Echinoidea 41) but sharing some species, while for the Pacific coast a total of 188 species are included (Crinoidea 3, Asteroidea 63, Ophiuroidea 61, Holothuroidea 34, Echinoidea 26) (Solís-Marín et al., 2014; Conejeros-Vargas et al., 2017). For the west coast of the Baja California Peninsula, Luna-Cruz and Hendrickx (2021) indicate the presence of 18 species of sea cucumbers between 554 m and 2082 m depth. Probably many of the widespread West-Atlantic or Pacific deep sea Asteroidea and Ophiuroidea present in Mexico are also found in Costa Rica (Pawson et al., 2015; Conejeros-Vargas et al., 2017; Luna-Cruz and Hendrickx, 2021). In Costa Rica, the deep fauna corresponds to 33% of the total diversity of echinoderms, while the Mexican coast and its economic exclusive zone are much larger than those of Costa Rica, and the sampling effort has been greater due to the presence of several oceanographic vessels such as the R/V Puma or R/V Justo Sierra of the National Autonomous University of Mexico, among others.

Threats for Conservation

The deep sea is under increasing pressure from exploration and extraction activities during the last decades, fueled by modern technological advances, depletion of terrestrial and shallow-water resources, growing global population with rising demands for food, energy, and raw materials (Ramírez-Llodra et al., 2011; Norse et al., 2012; Hefferman, 2019), climate change (Levin and Le Bris, 2015; Sweetman et al., 2017), and ocean acidification (Solís-Marín et al., 2014). Deep-sea species and ecosystems are more vulnerable than its shallow-water counterparts, due to the life-history traits of most deep-sea species such as slow growth, delayed maturity, extended longevities, and slow colonization (Cheung et al., 2007). In addition, recovery of deep-sea habitats is slow, studies have found that extraction impacts (scars on the sea bottom) are still visible after 26 years (1989-2015), while some organisms found prior to the extraction have not returned (e.g., sponges, soft corals, or sea anemones) (Hefferman, 2019).

Costa Rica has prohibited oil, gas and mineral exploration and exploitation in the sea until 2050 through the government moratorium decree 36693-MINAET (MINAET, 2010). Nonetheless, the debate on whether Costa Rica should or should not exploit the deep-sea mineral resources has been increasing in media articles and social media recently. The only known fishing activity that exploited resources deeper than 200 m in Costa Rica was shrimp trawling. The target species were the kolibri shrimp (*Solenocera agassizii*), the northern nylon shrimp (*Heterocarpus vicarius*), and to a less extent the three-spined nylon shrimp (*Heterocarpus affinis*) (Wehrtmann and Nielsen-Muñoz, 2009). Data from scientific surveys indicated a decreasing deep-sea shrimp catch while bycatch was increasing (Wehrtmann and Nielsen-Muñoz, 2009; Wehrtmann et al., 2012). These surveys did not record any echinoderm (I. Wehrtmann per. comm.). The shrimp trawling is currently prohibited in Costa Rica (Sala Constitucional, 2013), however, there has been recent and continuous efforts to re-activate this activity. Finally, litter has also been observed in Costa Rican deep-sea waters around Isla del Coco, composed mainly of plastics and lost fishing gear (Naranjo-Elizondo and Cortés, 2018), and in much deeper areas in several locations (J. Cortés per. obs.).

Future Perspectives

The current knowledge on deep-sea echinoderms is limited and more research is needed. Publishing diversity records with taxonomic precision contributes to improve future efforts in research and management and contributes to assess future impacts on the marine ecosystems (Worm et al., 2006; Costello et al., 2013).

Deep-sea research is costly and requires highly specialized vessels, equipment, and trained scientists. These issues preclude research of deep-sea habitats in most developing and undeveloped countries. Companies will continue to be important allies in the exploration of the deep sea, including in Costa Rica (Brewin et al., 2007; Wehrtmann and Nielsen-Muñoz, 2009). Further collaborations with international institutions will be necessary to advance our knowledge on deep-sea echinoderms.

There is no doubt that the deep sea plays a unique and outstanding role on sustaining the health and functioning of the oceans (Sweetman et al., 2017). Deep-sea ecosystems provide habitat provision for commercial species (e.g., tuna, large bill fishes), nutrient cycling, heat absorption, trophic and diversity support services, and carbon sequestration, all of which are vital ecological processes to maintain diversity and humanity (Thurber et al., 2014). Van Dover (2011) suggest that having a coherent conservation, management, and mitigation framework for the deep sea is necessary before undergoing deep-sea resources exploitation. We call for further active action and advocacy for working towards science-based management conservation of the deep sea in Costa Rica, following the precautionary principles since the impacts on the deep sea could be irreversible at human timescale (Roberts, 2002; Waller et al., 2007; Hefferman, 2019).

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

The authors contribute in equal proportions to the elaboration of the work, both in the search for information, analysis, elaboration of figures, and writing. All authors contributed to the article and approved the submitted version.

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