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Echinoderm diversity in the Caribbean Sea

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Abstract The Caribbean is considered a unique biogeographic province, being one of the top five hotspots in the world for marine and terrestrial biodiversity. The echinoderm research on the Caribbean began in the middle of the nineteenth century, and during the first half of the twentieth century most of the species were described. The number of ecological studies increased in the 1970s that continues until today, mostly focused on *Diadema antillarum*. Based on an extensive review of published records, the Caribbean echinoderm fauna is composed of 433 species, 237 genera, 80 families, 29 orders in five classes, with four endemic species. The richest class is Ophiuroidea with 148 species followed by the class Asteroidea with 116 species. Mexico and Colombia are the richest countries with 182 and 180 species respectively, while Costa Rica and Guatemala are the less diverse with fewer than 50 species. In general terms, the Caribbean is very homogeneous in species composition; however, Colombia and Mexico are the countries more dissimilar in composition with respect to the rest of countries. This semi-enclosed sea represents 6.5% of the total diversity of the phylum worldwide, and is the second most diverse area in tropical America, after Gulf of Mexico. Six species of echinoderms are extracted for commercial use, mostly in Panama, Nicaragua, Colombia, Venezuela and Cuba. However, extraction for the souvenir trade, without any regulation and control, is one of the major threats for some animals—especially the sea star *Oreaster reticulatus*. Research priorities for this group in the Caribbean include exploration of the deep sea, the Central American region and the Lesser Antilles. Moreover, because of its rich biodiversity, research and conservation efforts have to be directed towards its preservation, avoiding illegal extraction, enforcing controls, and improving coastal zone management.

Keywords Echinoderms · Diversity · Richness · Similarity · Historic account · Caribbean

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Introduction

The Caribbean Sea is a large sea, closed off to the west and to the south by the Americas, and partly screened to the north and to the east by the island chains of the Greater and Lesser Antilles (Spalding 2004). The region extends over about 2,754,000 km^2 in which 36–40 politically independent countries and territories can be found (Miloslavich and Klein 2005). Two large currents sweep towards this region from the Atlantic, the North Equatorial Current and Guyana current. A portion of their flow runs between the islands and into the Caribbean Sea, forming a generally westward flow known as the Caribbean current. The rest of the current is deflected to the northwest, fusing with the Gulf Stream (Spalding 2004).

The Caribbean is considered a unique biogeographic region. It is among the top five hotspots in the world for marine and terrestrial biodiversity, and it has many endemic species (Rivera-Monroy et al. 2004). Its complex geological history, begining 130 million years ago (Ma) and involving

emergence of the Isthmus of Panama in the Pliocene (around 3.0–2.8 Ma), had major effects on the marine biodiversity. The separation of the tropical American ocean into two different realms produced isolation and environmental change that resulted in increased evolutionary divergence and radiation of species in extensive coral reefs, mangroves, seagrass beds, deep-shelf ecosystems and partially isolated deep basins and trenches (Collins 1996).

The echinoderm research on the Caribbean began in the middle of the nineteenth century with dredging explorations in Florida and Cuba (Agassiz 1869; Lyman 1869). The first half of the twentieth century increased the number of species described with collections from Puerto Rico (Clark 1901), the Lesser Antilles (Engel 1933), Jamaica (Fointaine 1953a, b, c), and the publication of monographs on groups such as Holothuroidea (Deichmann 1926, 1930, 1940, 1963). During the second half of the twentieth century research increased the number of local records in Cuba (Suárez 1974), Belize (Devaney 1974; Kier 1975; Hotchkiss 1982; Macurda 1982; Hendler and Pawson 2000), Panama (Chesher 1972), Venezuela (Zoppi de Roa 1967; Rodríguez 1969, 1973; Martínez and Mago 1975; Martínez 1987, 1989), Jamaica (Meyer 1973), Honduras (Lessios 1998; Hasbún and Lawrence 2002). During this period information on groups such as Asteroidea (Downey 1973; Clark and Downey 1992) and Crinoidea (Meyer et al. 1978) was augmented. This increase in research is partially a consequence of the work in Panama conducted by the Smithsonian Tropical Research Institution and research in other parts of the Caribbean by the Smithsonian Institution in Washington DC.

During the 1970s, there was an increase in ecological studies that continues to our times, mostly focused on *Diadema antillarum* (Ogden et al. 1973; Sammarco 1980, 1982a, b; Lessios et al. 1984; Lessios 2005; Weil et al. 2005; Mumby et al. 2006; Steiner and Williams 2006; among others). However, one of the most important works was the compilation by Hendler et al. (1995), containing keys, pictures and a detailed description of 144 species. It also contained general comments on their habitat, distribution and biology. In addition to taxonomy, research in the region has focused on topics such as bioerosion (Scoffin et al. 1980; Bak et al. 1984; Griffin et al. 2003; Brown-Saracino et al. 2007), biodiversity (Price et al. 1999), reproduction (Lessios 1981a; Guzmán and Guevara 2002a, b; Guzmán et al. 2003; Montealegre-Quijano and Gómez-Gaspar 2005), aquaculture (Buitrago and Lodeiros-Seijo 2005; Gómez and Gómez 2005), evolution (Lessios 1981b; Lessios *et al.* 2001; Lessios *et al.* 2003; Zigler and Lessios 2004), and competition (Parker and Shulman 1986). The majority of this research was focused on echinods. The Caribbean region likely ranks among the top tropical regions for echinoderms research.

More recently, more research has being carried out, in Colombia (Benavides-Serrato and Borrero-Pérez 2000; Benavidez-Serrato et al. 2005; Borrero-Pérez et al. 2002a, b, 2008), Cuba (Abreu-Pérez et al. 2005; Del Valle-García et al. 2005, 2008), Mexico (Laguarda-Figueras et al. 2005), Hispaniola Island (Herrera-Moreno and Betancourt 2004) and Puerto Rico (Benavides-Serrato 2006). In the past decade scientist from the Instituto de Investigaciones Marinas y Costeras (INVEMAR) have publish most on echinoderm diversity in both shallow and deep water habitats.

The aim of this review is to present an updated list of the echinoderms in the Caribbean region based on information from the literature and museum collections. A list of species is presented indicating their presence in each country, the similarities in species composition, and the possible causes of those patterns of distribution.

Material and methods

I reviewed the echinoderm species composition of the Caribbean coast from the Yucatán Peninsula in Mexico (Quintana Roo State) to Venezuela, including the arc of the Caribbean islands from Cuba to Trinidad & Tobago (Fig. 1). The ecoregions covered by this review included the Eastern Caribbean, Greater Antilles, Southern Caribbean, Southwestern Caribbean and Western Caribbean of the Tropical Northwestern Atlantic Province (Spalding et al. 2007). Existing published echinoderm studies were reviewed (Zoppi de Roa 1967; Chesher 1968, 1970; Flores and Martínez 1970; Serafy 1970; Meyer 1973; Devaney 1974; Martínez and Mago 1975; Meyer and Macurda 1976; Meyer et al. 1978; Caycedo 1978, 1979; Alvarez-Larrauri 1981; Hotchkiss 1982; Macurda 1982; Miller and Pawson 1984; Martínez 1987; Hendler 1988, 1995; Clark and Downey 1992; Hendler et al. 1995; Schoppe 1996; Lessios 1998; Benavides-Serrato and Borrero-Pérez 2000; Hendler and Pawson 2000; Pawson et al. 2001; Borrero-Pérez et al. 2002a, b; Gómez-Gaspar 2002; Gonzalez et al. 2002; Hasbún and Lawrence 2002; Fonseca and Arrivillaga 2003; Herrera-Moreno and Betancourt 2004; Abreu-Pérez et al. 2005; Benavidez-Serrato et al. 2005; Del Valle-García et al. 2005; Laguarda-Figueras et al. 2005; Benavides-Serrato 2006; Alvarado et al. 2008; Borrero-Pérez et al. 2008; Francisco and Pauls 2008), and extracted information from the Geology Collection of the California Academy of Sciences, San Francisco (http://www.calacademy.org/research/izg/iz_coll_db/index.asp). The taxa were validated with the Integrated Taxonomic Information System (http://www.itis.gov/), and the Ophiuroidea (Stöhr and O'Hara 2007) and Asteroidea databases (Mah 2009). For the taxonomic list, the criteria used in Alvarado et al. (2008) were applied.

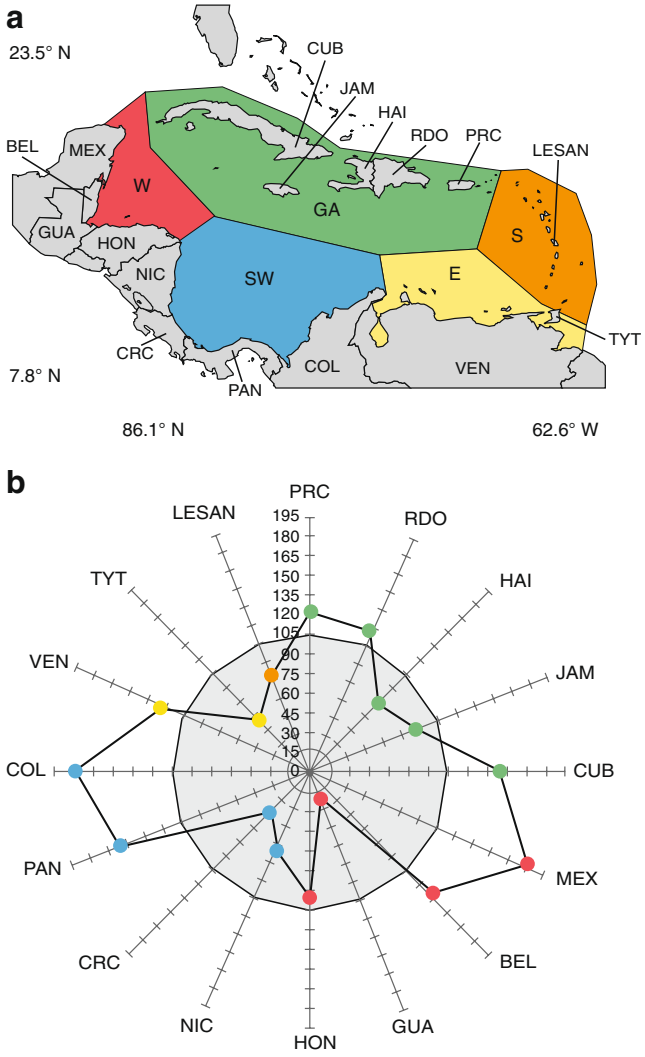

Fig. 1 **a** Caribbean Sea countries and ecoregions. **b** Radial diagram of the number of species of echinoderms (axes) per country on the Caribbean. *Gray circle* countries with under the average number of species. Ecoregions: *W* Western Caribbean (*blue dots*), *SW* Southwestern Caribbean (*green dots*), *GA* Greater Antilles (*red dots*), *E* Eastern Caribbean (*yellow dots*), *S* Southern Caribbean (*orange dots*). *PRC* Puerto Rico, *RDO* Dominican Republic, *HAI* Haiti, *JAM* Jamaica, *CUB* Cuba, *MEX* Mexico, *BEL* Belize, *GUA* Guatemala, *HON* Honduras, *NIC* Nicaragua, *CRC* Costa Rica, *PAN* Panama, *COL* Colombia, *VEN* Venezuela, *TYT* Trinidad & Tobago, *LESAN* Lesser Antillers

I used the year of publication of the description of each currently valid species to examine patterns in the rate of species descriptions over time, and to construct species accumulation curves for the entire described fauna. I followed the criteria from Zapata and Robertson (2007), to predict the total fauna size using the logistic model in the PAST computer program.

Composition similarities for each country were estimated by a presence/absence matrix per class and for the complete phylum. With those matrixes, I applied a Euclidean distance similarity matrix and I compared the diversity of echinoderms with a cluster tree and non-metric multidimensional scaling (nMDS). I estimated the average taxonomic distinctness (Δ^+) and its variation (Λ^+) (Clarke and Warwick 2001). This index evaluated the taxonomic distance between each pair of individuals, defined by a Linnaean classification tree, and could be used with a presence/absence matrix without taking into consideration the sampling methodology used. This index is considered as one of the most precise indicators in a strict biodiversity sense (Clarke and Warwick 2001). It was used on five taxonomic levels: species, genus, family, order and class, with their respective weights ω=20 (species in the same genera), 40 (same family but different genus), 60 (same order but different family), 80 (same class but different order) and 100 (different class). The statistical analysis was performed with the PRIMER 6.0 software.

Results

The list of echinoderms of the Caribbean includes 433 species, 237 genera, 80 families, 29 orders and five classes (Table 1), with four endemic species. The richest class was Ophiuroidea with 148 species, followed by the class Asteroidea with 116 species, then Echinoidea and Holothuroidea with 76 and 63 species respectively, and finally the class Crinoidea with 30 species (Table 2). Mexico and Colombia are the richest countries with 182 and 180 species respectively, followed by Panama with 155 species and Cuba with 145 species (Table 3). Eight countries possess between 100 and 182 species, six between 50 and 99 species, and only two countries possess less than 50 species, Costa Rica and Guatemala with 44 and 23 species respectively. There is an average of 105 species per country (Table 3). The average number of species per kilometer (spp./km) of coastline is 0.13±0.07 spp./km, Belize being the richest country with 0.26 spp./km, and Cuba, Haiti, and Venezuela the poorest with 0.04 spp./km. The average number of spp./km^2 of Economic Exclusive Zone (EEZ) is 0.0022 spp./km^2 of EEZ. Based on this metric, Guatemala is the richest country with 0.0140 spp./km^2 of EEZ, followed by Honduras (0.0052 spp./km^2), and Venezuela and Jamaica are the poorest with 0.0003 spp./km^2 of EEZ (Table 3).

Among the Class Crinoidea, the Dominican Republic (RDO) is the richest country with 17 species, followed by Panama and Jamaica with 15 each (Table 3), while Trinidad & Tobago and Guatemala are the poorest with three and two respectively. *Davidaster discoidea* and *D. rubiginosa* were reported from 12 countries, while eight species were reported only from one country. The genera *Davidaster* and *Democrinus* were the most diverse with three species each.

Table 1 Taxonomic classification of the echinoderm fauna from Caribbean countries. *PRC* Puerto Rico, *RDO* Dominican Republic, *HAI* Haiti, *JAM* Jamaica, *CUB* Cuba, *MEX* Mexico, *BEL* Belize, *GUA* Guatemala, *HON* Honduras, *NIC* Nicaragua, *CRC* Costa Rica, *PAN* Panama, *PAN* Colombia, *VEN* Venezuela, *TYT* Trinidad & Tobago, *LESAN* Lesser Antillers, *NCA* no country assigned; *X* indicates presence

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Class Crinoidea																	
Order Comatulida																	
Family Colobometridae																	
Analcidometra armata (Pourtàles, 1869)			X	X		X	X		X		X	X					
Oligometra caribbea A.H. Clark, 1908												X					
Family Comasteridae																	
Comactinia echinoptera (Müller, 1840)	X	X	X	X	X	X		X	X	X	X	X					
Comactinia meridionalis (L. Agassiz, 1865)	X	X	X	X	X				X	X		X	X				
Davidaster discoidea (Carpenter, 1888)	X		X	X		X	X	X	X	X	X	X	X			X	
Davidaster insolitus A.H. Clark, 1917												X					
Davidaster rubiginosus (Pourtàles, 1867)	X	X	X	X	X	X	X		X		X	X	X	X			
Leptonemaster venustus A.H. Clark, 1909	X		X	X	X	X			X			X		X		X	
Nemaster grandis A.H. Clark, 1911				X		X			X	X		X		X			
Neocomatella alata (Pourtàles, 1878)		X															
Neocomatella pulchella (Pourtàles, 1867)	X			X						X		X	X	X		X	
Family Charitometridae																	
Crinometra brevipinna (Pourtàles, 1867)		X		X		X				X				X	X	X	
Family Antedonidae																	
Antedon bifida (Pennant, 1777)														X			
Coccometra hagenii (Pourtàles, 1867)	X																
Coccometra nigrolineata A.H. Clark, 1908		X	X			X											
Ctenantedon kinziei Meyer, 1972						X	X					X				X	
Hypalometra defecta (Carpenter, 1888)				X								X					
Polimetra prolixa (Sladen, 1881)				X													
Trichometra cubensis (Pourtàles, 1867)	X				X					X			X				
Zenometra columnaris (Carpenter, 1881)					X												
Family Atelecrinidae																	
Atelecrinus balanoides Carpenter, 1881	X					X							X		X	X	
Family Thalassometridae																	
Stylometra spinifera (Carpenter, 1881)				X		X	X		X					X			
Family Tropiometridae																	
Tropiometra carinata (Lamarck, 1816)				X										X	X	X	
Order Isocrinida																	
Family Isocrinidae																	
Endoxocrinus parrae (Gervais, 1835)	X	X			X	X			X				X				
Cenocrinus asteriscus (Linnaeus, 1775)				X													
Neocrinus decorus (Wyville-Thomson, 1864)				X		X			X					X		X	
Order Cyrtocrinida																	
Family Holopodidae																	
Holopus rangii d'Orbigny, 1837	X			X		X										X	

Order Millericrinida																			
Family Bourgueticrinidae																			
Democrinus brevis A.H. Clark, 1909												X		X					
Democrinus conifer (A.H. Clark, 1909)					X	X			X	X		X					X		
Democrinus rawsoni (Pourtàles, 1874)				X						X		X					X		
Class Asteroidea																			
Order Paxillosida																			
Family Luidiidae																			
Luidia alternata alternata (Say, 1825)	X	X	X	X					X			X	X	X					
Luidia barbadensis Perrier, 1881		X	X	X						X			X	X					
Luidia clathrata (Say, 1825)	X	X	X	X			X		X	X		X	X	X					
Luidia heterozona barimae John & Clark, 1954													X	X					
Luidia ludwigi scotti Bell, 1917		X											X	X					
Luidia sarsi elegans Perrier, 1875													X						
Luidia senegalensis (Lamarck, 1816)	X		X	X	X	X			X	X	X	X	X	X			X		
Family Astropectinidae																			
Astropecten acutiradiatus Tortonese, 1956														X					
Astropecten alligator Perrier, 1881				X					X	X			X						
Astropecten americanus Verrill, 1880										X			X						
Astropecten antillensis Lütken, 1860	X												X	X					
Astropecten articulatus (Say, 1825)	X		X	X		X	X	X	X	X	X	X	X	X			X		
Astropecten brasiliensis Müller & Troschel, 1842														X					
Astropecten caribemexicanensis Caso, 1990		X																	
Astropecten cingulatus Sladen, 1883		X								X	X	X							
Astropecten comptus Verrill, 1915		X																	
Astropecten duplicatus Gray, 1840	X	X	X	X		X	X		X	X					X				
Astropecten marginatus Gray, 1840			X	X							X		X	X					
Astropecten nitidus Verrill, 1915		X		X					X	X			X						
Blakiaster conicus Perrier, 1881				X					X										
Dipsacaster antillensis Halpern, 1968													X						
Persephonaster echinulatus H.L. Clark, 1941		X							X	X		X	X						
Persephonaster leptactis H.L. Clark, 1941	X																		
Persephonaster patagiatus H.L. Clark, 1941					X	X				X		X		X					
Plutonaster agassizi agassizi (Verrill, 1880)													X						
Plutonaster efflorescens (Perrier, 1884)	X		X			X								X					
Psilaster cassiope Sladen, 1889													X	X					
Tethyaster grandis (Verrill, 1899)		X		X									X						
Tethyaster vestitus (Say, 1825)		X										X	X	X					
Family Goniopectinidae																			
Goniopecten demonstrans Perrier, 1881						X	X					X	X	X					
Prionaster elegans Verrill, 1899		X								X			X	X					
Family Porcellanasteridae																			
Styracaster elongatus Koehler, 1907																			X
Thoracaster cylindratus Sladen, 1883		X	X											X					
Order Notomyotida																			
Family Benthopectinidae																			

Table 1 (continued)

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Benthopecten simplex simplex (Perrier, 1884)		X			X												X
Cheiraster (Barbadosaster) echinulatus (Perrier, 1875)		X		X			X			X			X	X			
Cheiraster (Cheiraster) planus Verrill, 1915		X				X			X				X		X		
Cheiraster (Cheiraster) sepitus (Verrill, 1885)	X												X	X			
Cheiraster (Christopheraster) blakei A.M. Clark, 1981	X	X				X	X		X				X				
Cheiraster (Christopheraster) mirabilis (Perrier, 1881)	X		X			X				X			X				
Pectinaster gracilis Verrill, 1915									X								
Order Valvatida																	
Family Poraniidae																	
Marginaster pectinatus Perrier, 1881	X	X											X				
Family Asterinidae																	
Asterina folium (Lütken, 1859)		X	X				X					X	X	X			
Asterina hartmeyeri Döderlein, 1910	X	X	X			X									X	X	
Asterinopsis pilosa (Perrier, 1881)																X	
Paxillasterina pompom A.M. Clark, 1983												X					
Stegnaster wesseli (Perrier, 1875)						X							X	X	X	X	
Leilaster radians (Perrier, 1881)		X															
Family Goniasteridae																	
Anthenoides piercei Perrier, 1881	X	X		X			X			X			X	X	X	X	
Apollonaster yucatanensis Halpern, 1970		X											X				
Astroceramus brachyactis H.L. Clark, 1941	X												X	X			
Ceramaster grenadensis (Perrier, 1881)				X	X				X	X							
Circeraster americanus (A.H. Clark, 1916)		X								X					X		
Cladaster rudis Verrill, 1899																	X
Diplasiaster productus (A.H. Clark, 1917)														X			
Floriaster maya Downey, 1980		X															
Goniaster tessellatus (Lamarck, 1816)		X												X			
Litonotaster intermedius (Perrier, 1884)					X												
Nymphaster arenatus (Perrier, 1881)		X			X				X	X		X	X	X			
Paragonaster grandis H.L Clark, 1941	X	X															
Peltaster placenta (Müller & Troschel, 1842)	X				X												
Plinthaster dentatus (Perrier, 1884)									X	X		X	X	X	X		
Pseudarchaster gracilis gracilis (Sladen, 1889)		X		X	X			X	X	X			X				
Rosaster alexandri (Perrier, 1881)	X												X				
Tosia parva Perrier, 1881		X		X									X				
Family Oreasteridae																	
Oreaster reticulatus (Linnaeus, 1758)	X	X	X	X	X		X	X	X	X	X	X	X	X			
Family Asteropsidae																	
Poraniella echinulata (Perrier, 1881)	X		X				X				X	X				X	
Family Mithrodiidae																	
Mithrodia clavigera (Lamarck, 1816)	X	X								X							
Family Ophidiasteridae																	
Copidaster lymani A.H. Clark, 1948	X						X					X					

Linckia bouvieri Perrier, 1875	X	X															
Linckia guildingi Gray, 1840	X	X	X	X	X	X	X	X			X	X		X			
Linckia nodosa Perrier, 1875		X															
Narcissia trigonaria Sladen, 1889		X										X					
Ophidiaster bullisi (Downey, 1970)																X	
Ophidiaster guildingi Gray, 1840	X	X	X	X			X					X				X	
Tamaria floridae (Perrier, 1881)							X										
Tamaria halperni Downey, 1971		X			X								X				
Order Velatida																	
Family Caymanostellidae																	
Caymanostella spinimarginata Belyaev, 1978					X	X							X				
Family Solasteridae																	
Laetmaster spectabilis (Perrier, 1881)	X																
Lophaster furcifer (Düben & Koren, 1846)	X																
Solaster caribbaeus Verrill, 1915																X	
Solaster notophrynus Downey, 1971																X	
Family Pterasteridae																	
Calyptraster coa Sladen, 1882																X	
Calyptraster personatus (Perrier, 1894)					X								X			X	
Hymenaster lamprus H.L. Clark, 1923						X											
Hymenaster rex Perrier, 1885									X								
Pteraster abyssorum (Verrill, 1895)					X	X			X								
Pteraster acicula Downey, 1970	X											X	X				
Pteraster militarioides (O.F. Müller, 1776)	X		X							X			X			X	
Pteraster personatus Sladen, 1891													X				
Pteraster rugosus H.L. Clark, 1941	X		X													X	
Family Korethrasteridae																	
Remaster palmatus (Perrier, 1881)	X						X									X	
Order Spinulosida																	
Family Echinasteridae																	
Echinaster brasiliensis Müller & Troschel, 1840	X								X			X					
Echinaster echinophorus (Lamarck, 1816)	X		X	X		X				X				X			
Echinaster guyanensis A.M. Clark, 1992				X	X	X		X	X	X		X	X	X			
Echinaster modestus Perrier, 1881		X	X	X		X	X			X				X		X	
Echinaster sentus (Say, 1825)	X	X	X		X	X	X		X								
Echinaster serpentarius Müller & Troschel, 1842		X											X				
Echinaster spinulosus Verrill, 1869							X		X	X		X					
Henricia antillarum (Perrier, 1881)		X				X			X	X						X	
Henricia downeyae A.M. Clark, 1987					X												
Henricia sexradiata (Perrier, 1881)																	X
Order Forcipulatida																	
Family Asteriidae																	
Sclerasterias contorta (Perrier, 1881)														X		X	
Sclerasterias tanneri (Verrill, 1895)									X								
Stephanasterias albula (Stimpson, 1853)													X				
Family Labidiasteridae																	

Table 1 (continued)

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Coronaster briareus (Verrill, 1882)		X											X				
Family Pedicellasteridae																	
Pedicellaster pourtalesi Perrier, 1881										X							
Family Zoroasteridae																	
Doraster constellatus Downey, 1970									X			X	X				
Mammaster sigsbeei (Perrier, 1894)									X				X			X	
Zoroaster fulgens Wyville-Thomson, 1873					X							X	X				
Order Brisingida																	
Family Brisingidae																	
Brisinga costata Verrill, 1888					X									X			
Brisinga cricophora Sladen, 1889																X	
Midgardia xandaros Downey, 1972									X								
Novodinia pandina (Salden, 1889)	X																
Novodinia antillensis (A.H. Clark, 1934)			X														
Stegnobrisinga splendens H.L. Clark, 1926									X					X			
Family Freyellidae																	
Colpaster scutigerula Sladen, 1889									X								
Class Ophiuroidea																	
Order Phrynophiurida																	
Family Ophiomyxidae																	
Ophiomyxa flaccida (Say, 1825)	X	X	X		X		X	X	X			X	X	X	X	X	
Ophiomyxa brevicauda Verrill, 1899	X																
Ophiomyxa stimpsonii (Lyman, 1875)													X				
Ophiomyxa tumida Lyman, 1883													X				
Ophiobyrsa serpens Lyman, 1883							X										
Ophiosyzygus disacanthus H.L. Clark, 1911													X				
Ophioblenna antillensis Lütken, 1859			X				X					X					
Family Asteronychidae																	
Asteronyx loveni Müller & Troschel, 1842		X												X			
Family Asteroschematidae																	
Asterochema intectum Lyman, 1878		X															
Asterochema oligactes (Pallas, 1788)													X				
Family Gorgonocephalidae																	
Astrocaneum herrerai (Oersted & Lütken, 1856)		X															
Astrocnida isidis (Duchassaing, 1850)													X				
Astrophyton muricatum (Lamarck, 1816)	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	
Asteroporpa annulata Oesrsted & Lütken, 1856	X	X	X										X				
Schizostella bifurcata A.H. Clark, 1952			X				X										
Order Ophiurida																	
Family Ophiuridae																	
Amphiophiura fasciculata (Lyman, 1883)		X															
Amphiophiura metabula H.L. Clark, 1915													X				
Amphiophiura oedignatha H.L. Clark, 1915													X				

Amphiophiura oligopora (H.L. Clark, 1913)		X															
Amphipholizona delicata H.L. Clark, 1915													X				
Anthophiura ingolfi Fasmer, 1930		X															
Astrophiura permira Sladen, 1879		X															
Ophiambix devaneyi Paterson, 1985													X				
Ophioceramis januarii Lütken, 1856		X															
Ophiolepis elegans Lütken, 1859	X	X	X			X			X			X	X	X	X	X	
Ophiolepis gemma Hendler &Turner, 1987	X	X					X										
Ophiolepis impressa Lütken, 1859	X	X	X	X			X		X		X	X	X	X		X	
Ophiolepis kieri Hendler, 1979	X											X					
Ophiolepis paucispina (Say, 1825)	X	X	X		X	X	X					X			X	X	
Ophiolepis pawsoni Hendler, 1988							X										
Ophiomastus secundus Lyman, 1878													X				
Ophiomusium acuferum Lyman, 1875		X											X			X	
Ophiomusium eburneun Lyman, 1869													X				
Ophiomusium lymani Wyville-Thomsom, 1873		X															
Ophiomusium testudo Lyman, 1875													X				
Ophiomusium validum Ljungman, 1872													X				
Ophiosphalma planum (Lyman, 1878)		X															
Ophiostriatus atlanticus (Mortensen, 1933)													X				
Ophiozonella nivea Lyman, 1875		X															
Ophiura acervata (Lyman, 1869)													X	X			
Ophiura falcifera (Lyman, 1869)													X				
Ophiura fallax Cherbonnier, 1959		X															
Ophiura tenera (Lyman, 1883)													X				
Family Ophioleucidae																	
Ophiernus adspersus Lyman, 1875		X															
Family Ophiocomidae																	
Ophiocoma echinata (Lamarck, 1816)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Ophiocoma paucigranulata Devaney, 1974		X					X				X						
Ophiocoma pumila Lütken, 1859	X	X	X	X	X	X	X		X			X		X	X	X	
Ophiocoma wendti Müller &Troschel, 1842	X	X	X	X	X	X	X		X		X	X		X	X	X	
Ophiocomella ophiactoides (H.L. Clark, 1901)	X	X	X	X		X	X					X		X	X	X	
Ophiopsila fulva Lyman, 1878													X				
Ophiopsila hartmeyeri Koehler, 1913	X	X									X		X	X			
Ophiopsila riisei Lütken, 1859	X	X	X		X		X					X		X			
Ophiopsila vittata H.L. Clark, 1918		X					X					X					
Family Ophionereididae																	
Ophiochiton ternispinus Lyman,1883		X															
Ophionereis dolabriformis John & A.M. Clark, 1954													X				
Ophionereis olivacea H.L. Clark, 1901	X	X	X				X					X		X			
Ophionereis reticulata (Say, 1825)	X	X	X	X	X	X	X		X		X	X		X	X	X	
Ophionereis squamulosa Koehler,1913	X	X	X		X		X					X			X		
Ophionereis vittata Hendler, 1995	X						X					X				X	
Family Ophiodermatidae																	
Bathypectinura heros (Lyman, 1879)		X							X	X		X	X				

Table 1 (continued)

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Ophioderma anitae Hotchkiss, 1982							X										
Ophioderma appressum (Say, 1825)	X	X	X	X	X	X	X		X		X	X	X	X	X	X	
Ophioderma brevicaudum Lütken, 1856	X	X	X	X	X		X					X		X		X	
Ophioderma brevispinum (Say, 1825)	X	X	X	X	X	X	X				X	X		X		X	
Ophioderma cinereum Müller & Troschel, 1842	X	X	X	X	X	X	X		X		X	X		X	X	X	
Ophioderma ensiferum Hendler & Miller, 1984	X						X										
Ophioderma guttatum Lütken, 1859	X	X				X	X								X		
Ophioderma panamense Lütken, 1859												X					
Ophioderma phoenium H.L. Clark, 1918	X	X	X	X			X					X			X		
Ophioderma rubicundum Lütken, 1856	X	X	X	X		X	X					X	X	X	X	X	
Ophioderma squamosissimum Lütken, 1856	X		X				X										
Ophiopaepale goesiana Ljungman, 1872													X				
Ophiurochaeta littoralis (Koehler, 1913)							X										
Family Hemieuryalidae																	
Hemieuryale pustulata Von Martens, 1867							X					X					
Sigsbeia conifera Koehler, 1914	X						X					X					
Sigsbeia murrhina Lyman, 1878							X										
Ophiochondrus convolutus Lyman, 1869													X				
Family Ophiacanthidae																	
Ophiolimna littoralis Kolbe, 1899	X																
Ophiocamax fasciculata Lyman, 1853				X					X	X		X	X				
Ophiocamax hystrix Lyman, 1878													X				
Ophiacantha echinulata Lyman, 1878													X				
Ophiacantha mesembria H.L. Clark, 1915													X				
Ophiacantha ophiactoides H.L. Clark, 1901				X													
Ophiacantha oligacantha H.L. Clarck, 1918				X													
Ophiocanthella troscheli (Lyman, 1878)		X															
Ophiomitra valida Lyman, 1869													X				
Ophiotrema gracilis Koehler, 1914													X				
Ophiomitrella laevipellis (Lyman, 1883)													X				
Ophiomitrella glabra (H.L. Clark, 1901)				X			X										
Ophiomyces frutectosus Lyman, 1869													X				
Ophiopristis hirsuta (Lyman, 1875)													X				
Ophiopristis sertata (Lyman, 1869)		X											X				
Ophiotreta valenciennesi rufescens Koehler, 1896													X				
Family Ophiactidae																	
Hemipholis elongata (Say, 1825)	X		X				X					X			X		
Histampica duplicata (Lyman,1875)													X				
Ophiactis algicola H.L. Clark, 1933		X	X			X	X					X			X		
Ophiactis dispar Verrill, 1899												X					
Ophiactis lymani Ljungman, 1871															X		
Ophiactis muelleri Lütken, 1856												X		X			
Ophiactis quinqueradia Ljungman, 1871	X	X	X	X			X					X					

Ophiactis rubropoda Singletary, 1973		X																	
Ophiactis savignyi (Müller & Troschel, 1842)	X	X	X	X	X		X		X			X	X	X	X				
Family Ophiolepididae																			
Ophiothyreus goesi Ljungman, 1872											X			X					
Family Amphiuridae																			
Amphilimna mirabilis (H.L. Clark, 1941)														X					
Amphilimna olivacea (Lyman, 1869)		X											X	X					
Amphiodia atra (Stimpson, 1852)														X	X				
Amphiodia planispina (Von Martens, 1867)	X		X										X	X					
Amphiodia pulchella (Lyman, 1869)	X	X	X			X	X						X				X	X	
Amphiodia riisei (Lütken, 1869)													X						
Amphiodia trychna H.L. Clark, 1918	X	X	X	X			X						X		X		X		
Amphiodia violacea (Lütken, 1856)							X												
Amphioplus abditus (Verrill, 1871)													X						
Amphioplus coniortodes H.L. Clark, 1918	X	X													X				
Amphioplus sepultus Hendler, 1995	X																		
Amphioplus thrombodes H.L Clark, 1918	X																		
Amphioplus tumidus (Lyman, 1878)														X					
Amphipholis gracillima (Stimpson, 1852)	X		X				X										X		
Amphipholis januarii Ljungman, 1867	X		X				X						X				X		
Amphipholis pachybactra H.L. Clark, 1918													X				X		
Amphipholis squamata (Delle Chiaje, 1828)	X	X	X				X	X	X				X		X				
Amphiura fibulata Koehler, 1913	X	X					X												
Amphiura flexuosa Ljungman, 1867			X																
Amphiura incisa Lyman, 1883													X						
Amphiura otteri Ljungman, 1872														X					
Amphiura palmeri Lyman, 1882		X	X												X				
Amphiura rathbuni Koehler, 1914														X	X				
Amphiura stimpsoni Lütken, 1859	X	X	X		X	X	X										X	X	
Ophiocnida scabriuscula (Lütken, 1849)	X	X	X			X							X		X		X	X	
Ophionema intricata Lütken, 1869			X														X		
Ophionephthys limicola Lütken, 1869	X		X				X						X					X	
Ophiophragmus cubanus (A.H. Clark, 1917)	X						X												
Ophiophragmus filograneus (Lyman, 1875)							X												
Ophiophragmus pulcher H.L. Clark, 1918	X	X	X				X						X						
Ophiophragmus riisei (Lütken, 1859)			X		X	X							X	X					
Ophiophragmus septus (Lütken, 1859)	X		X				X										X		
Ophiophragmus wurdemani Lyman, 1860															X				
Ophiostigma isocanthum (Say, 1825)	X	X	X				X					X	X	X	X		X	X	
Ophiostigma siva Hendler, 1995			X			X	X						X						
Family Ophiochitonidae																			
Ophioplax ljungmani Lyman, 1875														X					
Family Ophiotrichidae																			
Ophiothrix angulata (Say, 1825)	X	X	X	X	X		X						X	X	X				
Ophiothrix brachyactis H.L Clark, 1915	X	X	X												X		X		
Ophiothrix cimar Hendler, 2005												X	X						

Table 1 (continued)

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Ophiothrix lineata Lyman, 1860	X	X					X				X	X					
Ophiothrix oerstedii Lütken, 1856	X	X	X	X	X	X	X					X	X	X	X	X	
Ophiothrix pallida Ljungman, 1872										X							
Ophiothrix stri Hendler, 2005											X	X					
Ophiothrix suensoni Lütken, 1856	X	X	X	X	X		X				X	X	X	X			
Ophiothrix synoecina Schoppe, 1996													X				
Class Echinoidea																	
Order Cidaroida																	
Family Cidaridae																	
Eucidaris tribuloides (Lamarck, 1816)	X	X	X	X	X	X	X	X	X	X	X	X	X	X			
Cidaris abyssicola (A. Agassiz, 1869)		X															
Cidaris rugosa (H.L. Clark, 1907)		X					X										
Calocidaris micans (Mortensen, 1903)		X														X	
Genocidaris maculata A. Agassiz, 1869		X															
Stylocidaris affinis (Philippi, 1845)	X	X								X		X	X				
Stylocidaris lineata Mortensen, 1910				X					X	X			X				
Tretocidaris bartletti (A. Agassiz, 1880)				X					X				X				
Porocidaris purpurata (Wyville-Thomson, 1875)										X							
Order Echinothuroida																	
Family Echinothuriidae																	
Araeosoma belli (Mortensen, 1903)		X		X						X			X				
Araeosoma fenestratum (Wyville-Thomson, 1872)				X									X				
Calveriosoma hystrix Wyville-Thomson, 1872		X															
Hygrosoma petersi (A. Agassiz, 1880)		X			X												
Phormosoma placenta (Wyville-Thomson, 1872)					X				X	X		X	X				
Order Diadematoida																	
Family Diadematidae																	
Diadema antillarum (Philippi, 1845)	X	X	X	X	X		X	X	X	X	X	X	X	X			
Centrostephanus longispinus rubricingulus H.L. Clark, 1921		X		X													
Astropyga magnifica A.H. Clark, 1934	X	X	X	X		X						X	X	X		X	
Family Aspidodiadematidae																	
Aspidodiadema jacobyi A. Agassiz, 1880		X		X			X			X			X				
Plesiodiadema antillarum (A. Agassiz, 1880)					X											X	
Family Pedinidae																	
Caenopedina cubensis A. Agassiz, 1869							X										
Order Salenioida																	
Family Saleniidae																	
Salenia goesiana Loven, 1874				X													
Salenocidaris profundi (Duncan, 1877)					X												
Salenocidaris varispina (A. Agassiz, 1877)					X												
Order Arbacioida																	
Family Arbaciidae													X				
Arbacia punctulata (Lamarck, 1816)	X	X		X			X					X		X	X		

Podocidaris sculpta A. Agassiz, 1869	X												X				
Coelopleurus floridanus A. Agassiz, 1871		X		X			X					X	X				
Order Temnopleuroida																	
Family Toxopneustidae																	
Lytechinus euerces H.L. Clark, 1912		X		X	X		X										
Lytechinus callipeplus H.L. Clark, 1912													X				
Lytechinus variegatus (Lamarck, 1816)	X	X	X	X	X	X	X	X	X		X	X	X	X			
Lytechinus williamsi Chesher, 1968	X	X		X	X		X					X	X				
Pseudoboletia maculata Troschel, 1869														X		X	
Tripneustes ventricosus (Lamarck, 1816)	X	X	X	X	X		X		X		X	X	X	X			
Family Temnopleuridae																	
Trigonocidaris albida (A. Agassiz, 1869)				X									X				
Order Echinoida																	
Family Echinidae																	
Echinus gracilis A.Agassiz, 1869		X															
Family Echinometridae																	
Echinometra lucunter (Linnaeus, 1758)	X	X	X	X	X	X	X	X	X	X	X	X	X	X			
Echinometra viridis A. Agassiz, 1863	X	X	X	X	X		X	X	X		X	X	X	X			
Order Holectypoida																	
Family Echinoneidae																	
Echinoneus cyclostomus Leske, 1778	X	X		X	X		X		X		X	X	X				
Order Clypeasteroida																	
Family Clypeasteridae																	
Clypeaster chesheri Serafy, 1970		X		X					X			X	X				
Clypeaster cyclopilus H.L.Clark, 1941														X			
Clypeaster euclastus H.L. Clark, 1941				X					X				X	X			
Clypeaster lamprus A.H. Clark, 1914				X					X	X			X	X			
Clypeaster luetkeni Mortensen, 1948					X								X				
Clypeaster prostratus Ravenel, 1848									X				X	X			
Clypeaster ravenelii (A.Agassiz, 1869)		X															
Clypeaster rosaceus (Linnaeus, 1758)	X	X	X	X	X	X	X		X			X	X	X			
Clypeaster speciosus Verrill, 1870											X						
Clypeaster subdepressus (Gray, 1825)	X	X		X		X	X					X	X	X			
Family Fibulariidae																	
Echinocyamus grandiporus Mortensen, 1907		X											X				
Family Mellitidae																	
Encope aberrans Martens, 1867		X															
Encope emarginata (Leske, 1778)							X	X				X	X	X			
Encope michelini L. Agassiz, 1841	X	X												X			
Leodia sexiesperforata (Leske, 1778)	X	X	X	X		X	X		X		X	X	X	X		X	
Mellita quinquiesperforata (Leske, 1778)	X		X	X		X			X	X	X	X	X	X			
Order Spatangoida																	
Family Asterostomatidae																	
Heterobrissus hystrix (A. Agassiz, 1880)									X	X			X				
Linopneustes longispinus (A. Agassiz, 1878)				X					X	X			X				
Palaeobrissus hilgardi (A. Agassiz, 1883)				X									X				

Table 1 (continued)

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Palaeopneustes cristatus A. Agassiz, 1873				X					X				X				
Palaeopneustes tholoformis Chesher, 1968				X									X				
Family Brissidae																	
Brissopsis atlantica Mortensen, 1907									X	X	X	X	X			X	
Brissopsis elongata Mortensen, 1907			X	X			X		X			X	X	X			
Brissopsis mediterranea Mortensen, 1913					X								X				
Brissus unicolor (Leske, 1778)	X	X		X	X		X		X		X	X	X	X			
Meoma ventricosa ventricosa (Lamarck, 1816)	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	
Plagiobrissus grandis (Gmelin, 1788)	X	X	X	X		X	X					X	X				
Plethotaenia spatangoides (A. Agassiz, 1883)										X							
Family Loveniidae																	
Homolampas fragilis (A. Agassiz, 1869)													X				
Family Schizasteridae																	
Agassizia excentrica A. Agassiz, 1869				X			X			X		X	X				
Brisaster fragilis (Düben & Koren, 1846)								X									
Hypselaster limicolus (A. Agassiz, 1878)									X				X				
Moira atropos (Lamarck, 1816)	X		X	X			X		X			X	X	X			
Paraster doederleini Chesher, 1972				X			X		X	X		X					
Paraster floridensis (Kier & Grant, 1965)				X			X		X			X					
Schizaster orbignyanus A.Agassiz, 1880													X	X			
Order Cassidulida																	
Family Echinolampadidae																	
Conolampas sigsbei (A. Agassiz, 1878)				X					X	X							
Echinolampas depressa Gray, 1851		X															
Family Cassidulidae																	
Cassidulus caribaearum Lamarck, 1881		X		X			X					X					
Class Holothuroidea																	
Order Dendrochirotida																	
Family Phyllophoridae																	
Neothyonidium parvum (Ludwig, 1881)			X									X					
Stolus cognatus (Lampert, 1885)	X	X										X		X			
Phyllophorus occidentalis (Ludwig, 1875)	X	X	X									X		X	X	X	
Thyone deichmannae Madsen, 1941												X			X		
Thyone inermis Heller, 1868	X											X			X		
Thyone pseudofusus Deichmann, 1930		X					X					X			X	X	
Thyone sabanillaensis Deichmann, 1930													X				
Thyone tanyspeira Pawson, 1976									X								
Family Cucumariidae																	
Acaudina suspecta Cherbonnier & Féral, 1981													X				
Cucumaria pulcherrima (Ayres, 1854)													X				
Duasmodactyla seguroensis (Deichmann, 1930)		X	X			X								X			
Euthyonacta solida (Deichmann, 1930)		X															
Leptopentacta deichmannae Domantay, 1953													X				

Ocnus pygmaeus (Théel, 1886)		X	X											X	X		
Ocnus surinamensis (Semper, 1868)	X		X	X		X						X		X		X	
Ocnus suspectus (Ludwig, 1874)	X	X	X			X	X					X				X	
Pentacta pygmaea (Théel, 1886)														X			
Thyone cognata (Lampert, 1885)					X												
Thyonella gemmata (Pourtàles, 1851)	X	X										X					
Thyonella pervicax (Théel, 1886)		X										X					
Family Sclerodactylidae																	
Euthyonidiella destichada (Deichmann, 1930)	X		X				X					X		X			
Euthyonidiella trita (Sluiter, 1910)		X	X			X								X			
Sclerodactyla briareus (Lesueur, 1824)														X			
Pseudothyone belli (Ludwig, 1886)		X	X				X					X			X		
Family Psolidae																	
Lissothuria antillensis Pawson, 1967							X										
Lissothuria braziliensis (Theél, 1886)													X				
Order Elasipodida																	
Family Psychropotidae																	
Benthodytes sanguinolenta (Theél, 1882)									X								
Benthodytes typica Théel, 1882					X												
Order Aspidochirotida																	
Family Stichopodidae																	
Astichopus multifidus (Sluiter, 1910)	X	X	X	X		X						X	X	X			
Eostichopus arnesoni Cutress & Miller, 1982			X					X									
Isostichopus macroparentheses (H.L. Clark, 1922)		X				X	X										
Isostichopus badionotus (Selenka, 1867)	X	X	X	X	X	X	X		X			X		X	X	X	
Family Holothuriidae																	
Actinopyga agassizi (Selenka, 1867)	X	X	X	X	X	X	X	X	X		X						
Holothuria (Cystipus) cubana Ludwig, 1874	X	X	X	X			X					X		X			
Holothuria (Cystipus) occidentalis Ludwig, 1874				X					X								
Holothuria (Cystipus) pseudofossor Deichmann, 1930	X	X	X			X	X						X	X			
Holothuria (Halodeima) floridana Pourtàles, 1851	X	X	X			X	X		X			X				X	
Holothuria (Halodeima) grisea Selenka, 1867	X	X	X		X	X	X					X	X	X		X	
Holothuria (Halodeima) mexicana Ludwig, 1875	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	
Holothuria (Platyperona) parvula (Selenka, 1867)			X	X		X							X	X	X	X	
Holothuria (Platyperona) rowei Pawson & Gust, 1981							X										
Holothuria (Semperothuria) densipedes Clark, 1901			X														
Holothuria (Semperothuria) surinamensis Ludwig, 1874	X	X	X			X	X							X	X	X	
Holothuria (Selenkothuria) glaberrima Selenka, 1867	X		X	X	X	X			X			X	X		X	X	
Holothuria (Theelothuria) princeps Selenka, 1867		X	X	X										X			
Holothuria (Theelothuria) imperator Deichmann, 1930		X															
Holothuria (Thymiosycia) arenicola Semper, 1868	X	X	X	X		X	X	X	X			X	X			X	
Holothuria (Thymiosycia) impatiens (Forskål, 1775)	X	X	X			X	X					X	X	X	X	X	
Holothuria (Thymiosycia) thomasi Pawson & Caycedo, 1980	X	X	X	X	X		X		X			X				X	
Order Molpadiida																	
Family Molpadiidae																	
Molpadia cubana Deichmann, 1940												X					

Table 1 (continued)

	CUB	MEX	PRC	RDO	HAI	JAM	BEL	GUA	HON	NIC	CRC	PAN	COL	VEN	TYT	LESAN	NCA
Molpadia parva (Théel, 1882)												X	X				
Order Apodida																	
Family Synaptidae																	
Epitomapta roseola (Verrill, 1873)		X				X	X					X					
Euapta lappa (Müller, 1850)	X	X	X	X		X	X				X	X			X	X	
Protankyra ramiurna Heding, 1928			X														
Leptosynapta inswe Pawson, 1976							X										
Leptosynapta tenuis (Ayres, 1851)		X															
Leptosynapta multigranula H.L. Clark, 1924		X					X										
Leptosynapta nannoplax Pawson, 1976							X										
Leptosynapta parvipatina H.L. Clark, 1924												X			X		
Leptosynapta roseogradia Pawson, 1976							X										
Eupatinapta acanthia (A.H. Clark, 1899)												X					
Synaptula hydriformis (Lesueur, 1824)	X	X	X			X	X		X	X	X	X				X	
Family Chiridotidae																	
Chiridota rotifera (Pourtàles, 1851)	X	X	X	X		X	X					X		X	X	X	

Colombia was the richest country for the class Asteroidea with 51 species followed by Mexico with 44 species. For this class, *Astropecten* is the most diverse genus with 12 species. *Astropecten articulatus* and *Oreaster reticulatus* are reported from 13 countries, and 38 species are reported for only one country. *Laetmaster spectabilis* is endemic to Cuba. Four species were reported for international waters: *Styracaster elongatus, Benthopecten simplex simplex, Cladaster rudis* and *Henricia sexradiata*.

With respect to the Class Ophiuroidea, Mexico, Colombia, Belize and Panama exhibited the highest species richness with 63, 62, 58 and 56 species respectively, while Nicaragua and Guatemala were the least diverse with six and four species each (Table 3). *Ophioderma* was the most diverse genus with 11 species. *Ophiocoma echinata* was the only species reported in the entire region (16 countries or territories), while *Astrophyton muricatum* was reported from 15 countries and *Ophioderma appressum* from 14. For this class 71 species were reported from only one country, and the species *Ophiothrix synoecina* is endemic to Colombia, and *O. stri* and *O. cimar* are endemic to Costa Rica and Panama.

With respect to Echinoidea, Colombia was the richest country with 47 species, followed by the Dominican Republic with 41 (Table 3). *Clypeaster* was the most diverse genus with ten species; *Meoma ventricosa ventricosa* was reported in 15 countries and *Echinometra lucunter* and *Eucidaris tribuloides* in 14. In this class, 18 species were reported from only one country.

Mexico was the richest country for the Holothuroidea with 32 species, followed by Panama and Puerto Rico with 30 species each, while Guatemala, Costa Rica, and Nicaragua were the least diverse (Table 3). *Holothuria* was the most diverse genus with 16 species; *Holothuria (Halodeima) mexicana* was reported for 15 countries and *Isostichopus badionotus* for 12. Within this class, 23 species were reported for only one country.

Initially, the publication of echinoderm species descriptions in the Caribbean Sea was slow (Fig. 2a, b), with an average of 0.47 species described per year between 1740 and 1840. Between 1840 and 1920, there was a substantial increase (3.83 species described per year), followed by a slower rate between 1920 and the present, with 0.91 species described per year. Taking the entire period of 1740 to 2010, there were on average 1.61 species described per year. According to the logistic model (Fig. 2b), the curve will be reaching an asymptote in the next 50 years, with seven probable undescribed species to be named.

Colombia and Mexico, the most diverse countries, are the most dissimilar in comparison relative to the rest of the region (Figs. 3, 4, *gray areas*). The difference is primarily due to the composition of Asteroidea (Figs. 3c, 4c), Ophiuroidea (Figs. 3d, 4d) and Echinoidea (Figs. 3e, 4e),

Table 2 Species, genera, families and orders of Caribbean echinoderms

Class	Order	Family	Genus	Species
Crinoidea	4	10	23	30
Asteroidea	7	23	68	116
Ophiuroidea	2	16	63	148
Echinoidea	11	21	53	76
Holothuroidea	5	10	30	63
Total	29	80	237	433

and to the influences from other regions like the Gulf of Mexico, Florida and Brazil. In general terms, the Caribbean is very homogenous in species composition between countries (Figs. 3, 4).

The taxonomic distinctness index (Δ^+) indicated that most of the countries are inside the 95% confidence limit of composition; Panama, Cuba, Mexico and Colombia (Fig. 5) being closer to the average of distinctness. Guatemala possesses few species (23 spp.) but exhibits a high value of distinctness (Δ^+), because those species represent many different groups with few representatives in each one, making the taxonomic distance greater. In Guatemala, each class is represented more or less equally by two to eight species, with very low variation (Fig. 5b). On the other hand, Trinidad & Tobago, which also has few species (55 spp.), has a lower distinctness value (Δ^+), because the species are unequally represented. The 55 species are dominated by two groups, Ophiuroidea (29 spp.) and Holothuroidea (15 spp.), while the other classes possess fewer species, so the average taxonomic distance is lower (Fig. 5a), with a greater variation (Fig. 5b).

Discussion

The Caribbean Sea is a marine province rich in echinoderm species. It has 433 species, representing 6.5% of the total diversity of the phylum, according to numbers presented by Pawson (2007). This region possesses almost 10% of the world's Ophiuroidea, and between 4 and 6% of the other classes. The Caribbean is second in the tropical Americas with respect to species numbers, after the Gulf of Mexico (522 species; Pawson et al. 2009). The Caribbean ranks above other regions like Brazil (329 species; Hadel et al. 1999), the Pacific of Central America (287; Alvarado et al. 2010), Baja California and the Gulf of California (231 species; Solís-Marín et al. 2005; Honey-Escandón et al. 2008), and the Galapagos Archipelago (198 species; Maluf 1991).

The Caribbean, with an apparent well-known echinoderm fauna (Fig. 2b), is highly homogeneous in composition, due mostly to the current patterns and the semi-closed nature of the region (Spalding 2004). This sea has been recognized as one of the most important coral reef biogeographic provinces (Spalding et al. 2001), with many

Table 3 Number of echinoderm species per class in each country. Coastline information taken from the *The world fact book* (https://www.cia.gov/library/publications/the-world-factbook/geos) and Economic Exclusive Zone (EEZ) information was taken from www.seaaroundus.org/eez/eez.aspx

Country	Crinoidea	Asteroidea	Ophuiroidea	Echinoidea	Holothuroidea	Total	Coastline (km)	No. spp./km of coastline	EEZ (km^2)	ssp./km^2 EEZ
Mexico[a]	7	44	63	36	32	182	905	0.20	88,874	0.0020
Colombia	7	51	62	47	13	180	1,760	0.10	472,891	0.0004
Panama	15	25	56	29	30	155	1,295	0.12	143,442	0.0011
Cuba	11	35	55	21	23	145	3,755	0.04	350,751	0.0004
Belize	5	18	58	27	26	134	516	0.26	35,351	0.0038
Venezuela	10	36	34	24	20	124	2,800	0.04	470,666	0.0003
Puerto Rico	7	22	48	14	30	121	501	0.24	205,529	0.0006
Dominican Republic	17	22	23	41	14	117	1,280	0.09	255,898	0.0005
Honduras	11	30	14	29	11	95	644	0.15	18,151	0.0052
Jamaica	15	20	20	10	21	86	1,022	0.08	258,137	0.0003
Lesser Antilles	11	21	23	7	17	79	–	–	–	–
Haiti	8	19	19	19	8	73	1,771	0.04	126,760	0.0006
Nicaragua	9	29	6	19	2	65	503	0.13	87,930	0.0007
Trinidad & Tobago	3	7	29	1	15	55	362	0.15	74,199	0.0007
Costa Rica	4	7	16	13	4	44	212	0.21	25,090	0.0018
Guatemala	2	5	4	8	4	23	150	0.15	1,642	0.0140
No country assigned	0	4	0	0	0	4	–	–	–	–

[a] Shore line and economic exclusive zone are from Quintana Roo State

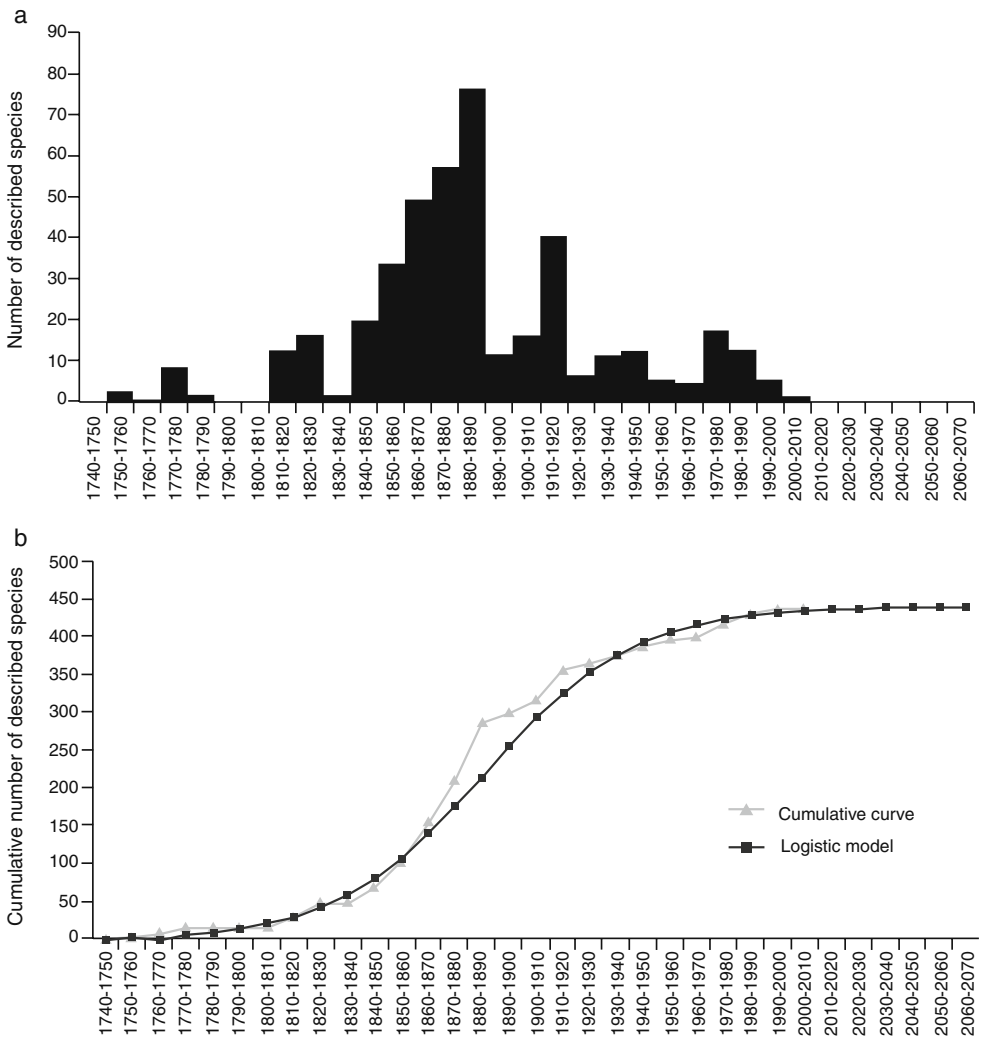

Fig. 2 **a** Number of new species of echinoderms from the Caribbean described by decade. **b** Accumulation curves of species descriptions for the total (*gray line*) and with the fitted logistic model (*black line*)

cryptic habitats ideal for the development of the Ophiuroidea, which is the most diverse in the region. Moreover, additional species will probably be described when the deep areas of the Caribbean are studied, altering the predictive species description curve in Fig. 2b.

Mexico, Belize, Panama, Colombia and Cuba exhibit the highest species diversity, due in part to the rich coastal habitats, which are the most diverse in the region (Spalding et al. 2001), and to intensity of research in these areas. Relative to species description and publications, Colombia has taken the lead, with a higher sampling effort along all of its Economic Exclusive Zone, with collections from shallow and deep waters (Borrero-Pérez et al. 2002a, b, 2008; Benavidez-Serrato et al. 2005). An important feature of the region is the presence of the Mesoamerican reef, in Mexico, Belize, Guatemala and Honduras. This area could be considered a diversity hot spot.

In terms of ecoregions, the Southwestern Caribbean is the richest (Fig. 6), due to its central location in the region, the current patterns, and the influence of species from the north and the south. The Western Caribbean and the Greater Antilles ecoregions are the most similar due to their proximity but also due to the influence of species from the Gulf of Mexico, Florida and Bahamas. On the other hand, the Southern and Eastern Caribbean ecoregions are influenced by the faunas from Guyana and Brazil. This can also help explain why Mexico and Colombia are located on opposite sides of the nMDS (Fig. 4), having faunal influences from two different regions. All the countries from one ecoregion are very similar in composition (Figs. 3, 4).

The Central American countries like Guatemala, Honduras, Nicaragua and Costa Rica, and the Lesser Antilles are the least studied. It is important to notice that in the case of the Central American countries, the social movements of the 1960s and 1970s shifted the attention to issues other other than science. This combined with the lack of economic resources, research institutions, and reduced science investments have resulted in this lack of knowledge. However, according to Fig. 1b, countries with low species numbers are probably undersampled, especially

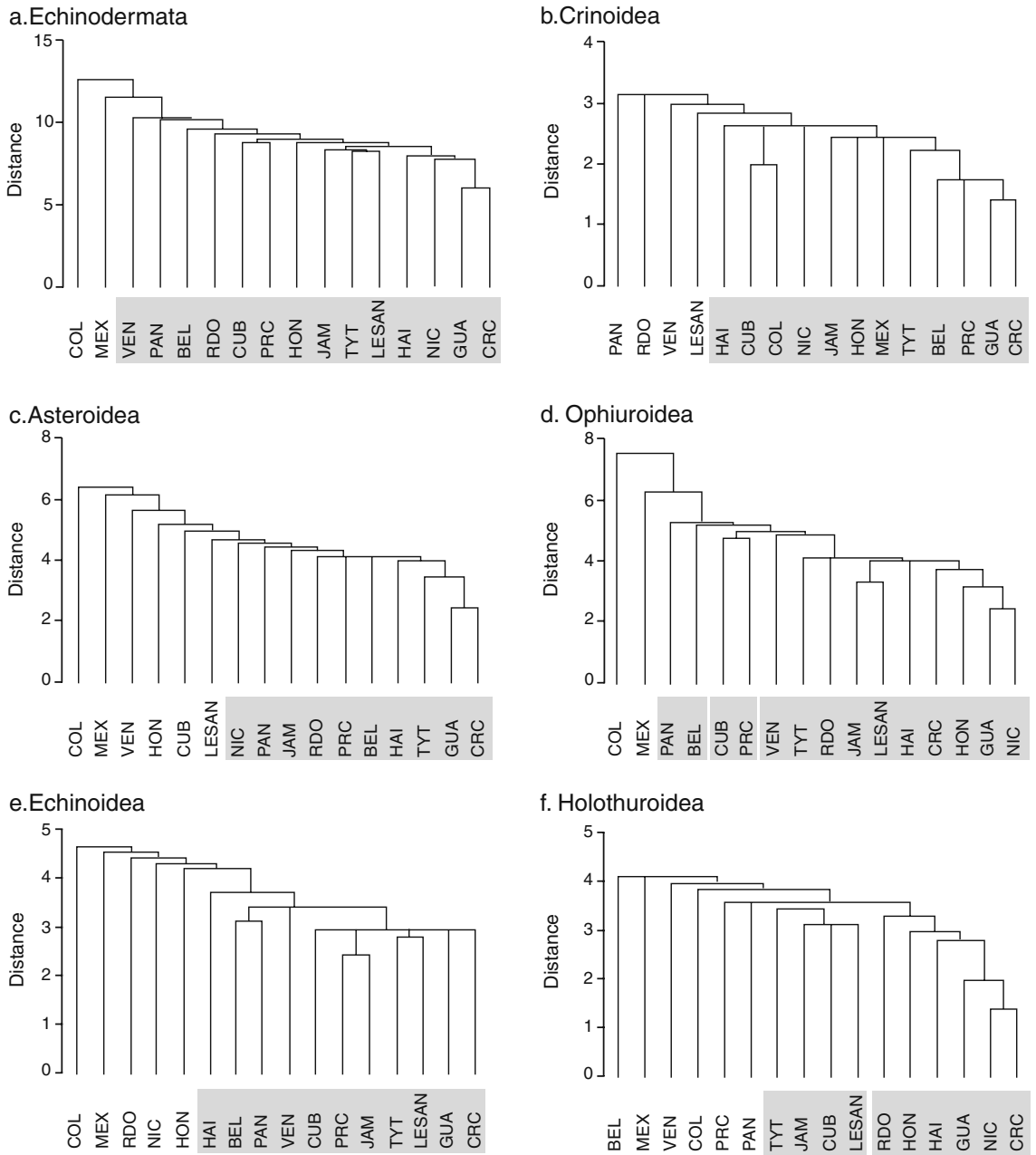

Fig. 3 Cluster tree (Euclidean distance) based on species presence/absence Bray-Curtis resemblance matrix: **a** Echinodermata, **b** Crinoidea, **c** Asteroidea, **d** Ophiuroidea, **e** Echinoidea, **f** Holothuroidea; between the Caribbean countries. *Gray areas* most similar countries

those in close proximity to highly diverse countries. Trinidad & Tobago, the Lesser Antilles, Haiti, Jamaica, Guatemala, Honduras, Nicaragua and Costa Rica are likely undersampled, when compared with the number of species reported from neighboring countries (Fig. 1). However, it is necessary to look at these analyses with care, because in some cases it could reflect the reality of the species richness due to the small size of the coastal zone, the degraded state of some coasts from natural and anthropogenic disturbances, and the lack of complex coastal morphology and habitat diversity.

Along the Caribbean Sea, seven species of echinoderms (four holothuroids and three echinoids) are extracted for commercial use. Among them are the sea cucumbers A*stichopus multifidus, Holothuria mexicana, Actinopyga agassizi,* and *Isostichopus badionotus,* the last being the most intensely harvested (Toral-Granda 2008). Extractions occur primarily in Panama, Nicaragua, Colombia, Venezuela, Mexico and Cuba. The exploitation of sea cucumbers without the use of a calculated fisheries management approach is probably the biggest threat to their populations within the region. For many of the species under legal or

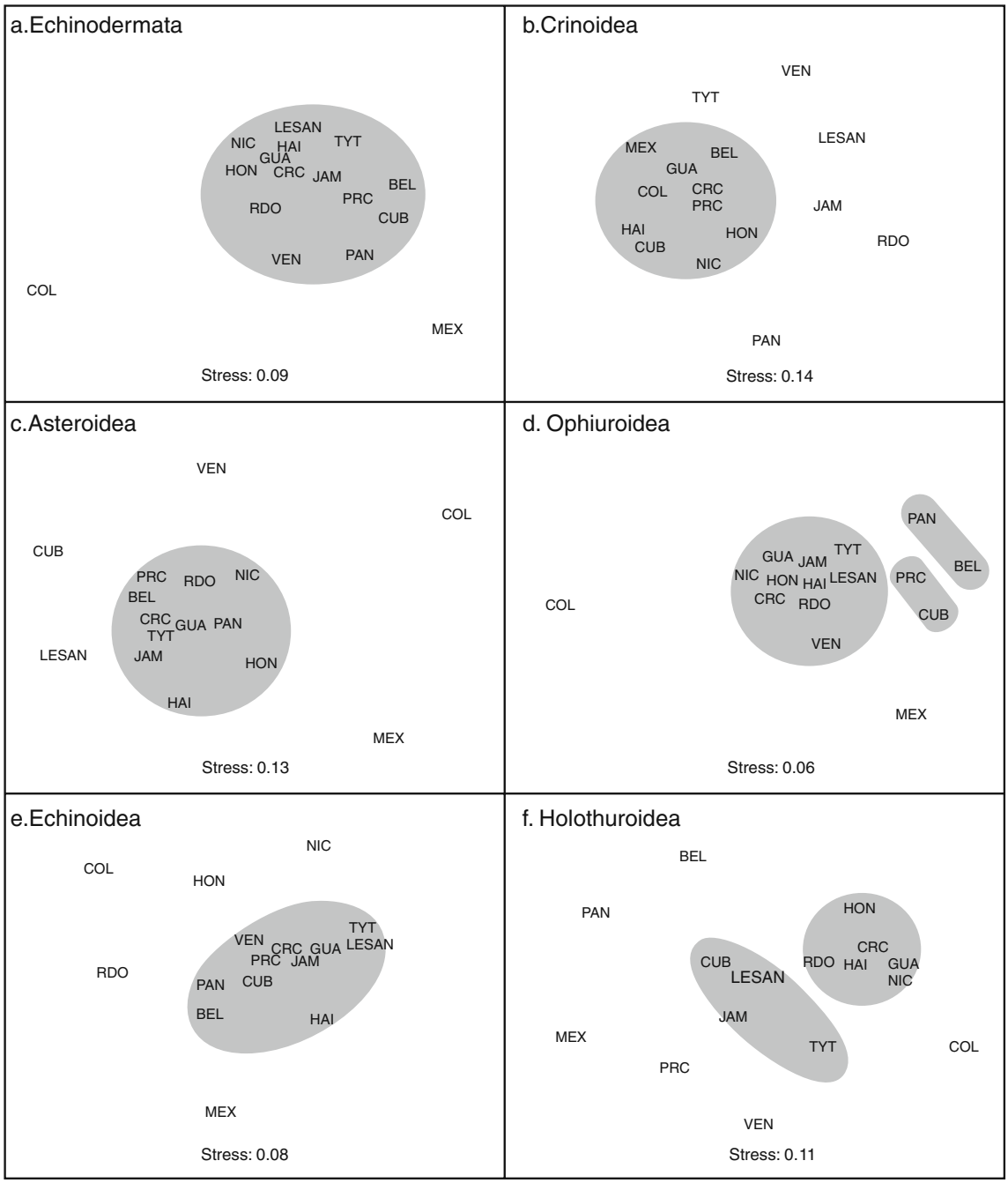

Fig. 4 Non-metric multiple dimensional scaling (NMDS) based on species presence/absence Bray-Curtis resemblance matrix: **a** Echinodermata, **b** Crinoidea, **c** Asteroidea, **d** Ophiuroidea, **e** Echinoidea, **f** Holothuroidea; between the Caribbean countries. *Gray areas* most similar countries

illegal fishing pressures there is little or no scientific information available on the biology, ecology, population abundance and dynamics (Toral-Granda 2008). Moreover, the situation is exacerbated because the majority of sea cucumber exploitations along the Caribbean (Buitrago and Boada 1996; Rodríguez-Millet and Pauls 1998; de la Fuente-Betancourt et al. 2001; Guzmán and Guevara 2002b) started with the consent of the local authorities, but without any knowledge about the ecology of the species (Guzmán et al. 2003). In the case of Panama, this activity is now banned, due to overfishing in 1997, during which 750,000 sea cucumbers were extracted in 30 days (Guzmán and Guevara 2002b).

Along the Caribbean there are small sea urchin fisheries focused on *Echinometra* spp., *Lytechinus variegatus* and *Tripnesutes ventricosus*. Granada and Martinique sea urchin harvests are the largest (Williams 2002). In the Margarita and Coche islands, Venezuela, *L. variegatus* and *E.*

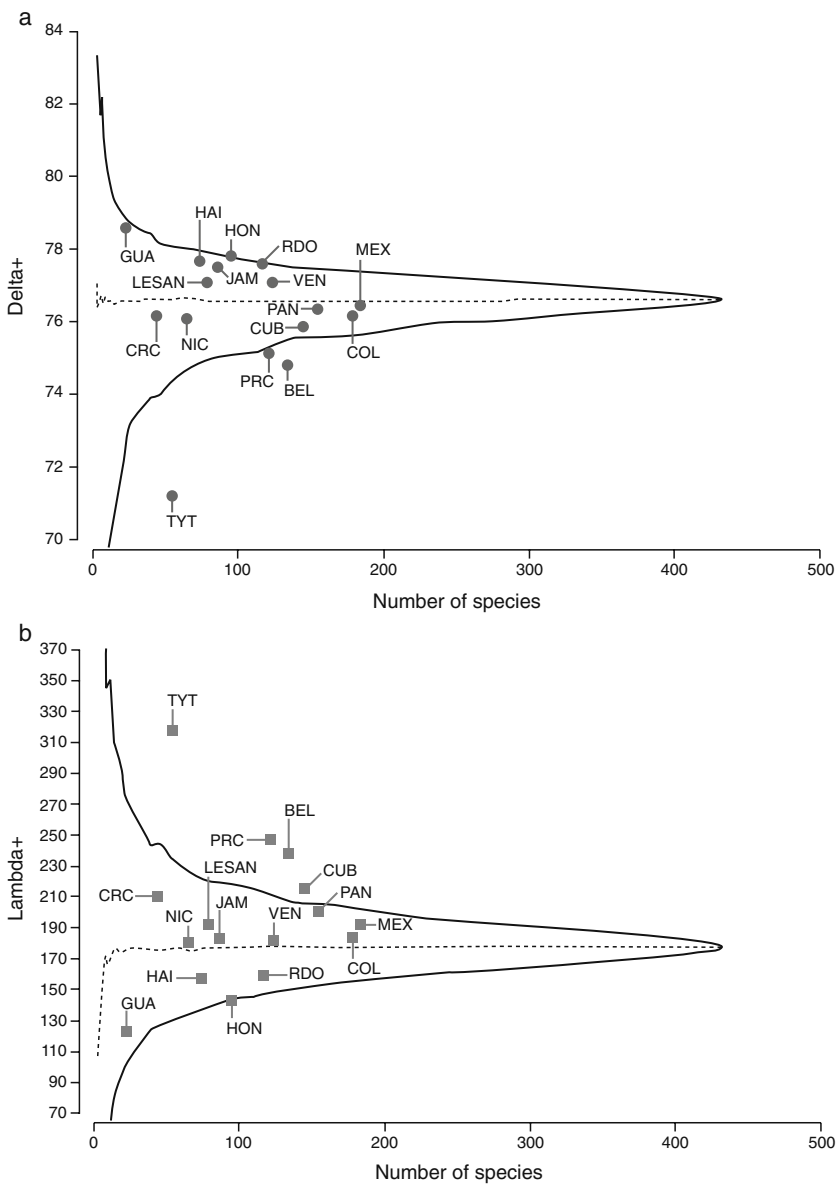

Fig. 5 Taxonomic distinctness index: **a** average (delta: Δ^+), and **b** their variation (lambda: Λ^+) of the Caribbean echinoderms. *Continuous line* 95% confidence limit, *discontinuous line* Δ^+ average value

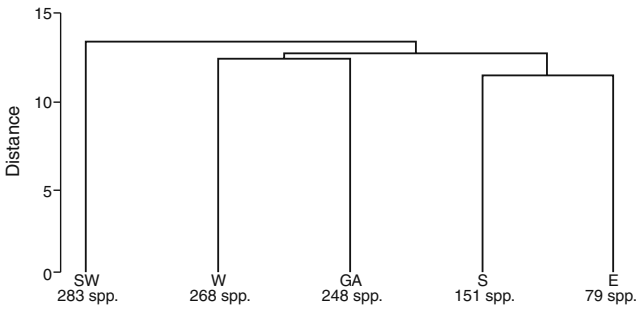

Fig. 6 Cluster tree (Euclidean distance) based on species presence/absence Bray-Curtis resemblance matrix of echinoderms by ecoregion. *W* Western Caribbean, *SW* Southwestern Caribbean, *GA* Greater Antilles, *E* Eastern Caribbean, *S* Southern Caribbean

lucunter are extracted and processed on a small scale for human consumption (Gómez 1999). However, there is the fear that due to their naturally low population numbers these resources could be reduced by overfishing (Gómez and Gómez 2005).

In the case of the souvenir trade, Lunn et al. (2008) analysed the situation in Mexico, finding that annually 87,600 *Oreaster reticulatus* are extracted, with no regulation, and sold at prices between 1.8 and 60 US dollars. Similarly, Sloan (1984) indicated that this seastar might be under threat throughout the Caribbean, where some populations have been devastated. Mexico, Jamaica, Trinidad and Venezuela, among others, allow *Oreaster* extraction without apparent restrictions, which could increase demand in other countries (Guzmán and Guevara 2002a).

Lunn et al. (2008) also mentioned the extraction of other echinoderms like *Astropecten*, *Mellita* and *Tripnesutes* as souvenirs in Mexico. However, there are no complete analyses of the exploitation of echinoderms in other places, like Colombia, Venezuela or Panama, where *Oreaster* as well as other echinoderms are extracted.

The lack of control in echinoderm extraction is a major threat in the Caribbean region. However, the greatest threats to this group of animals come from anthropogenic disturbances like sedimentation and coastal pollution. Sedimentation reduces recruitment success for some key species, such as sea urchins (i.e., *Diadema antillarum*; Vázquez-Domínguez 2003). Moreover, the loss of architectural complexity of the majority of coral reefs on the area (Alvarez-Filip et al. 2009), reduces the availability of substrate for recruitment and development. Agricultural pollution can produce endocrine disruptions in many species, slowing the recovery of critical populations (Rawlins et al. 1998). Coastal development has become a serious threat for endemic and cryptic species of ophiuroids in Colombia, Panama and Costa Rica, where the rock cavities made by sea urchins are being seriously degraded (Hendler 2005; Monroy-López and Solano 2005).

The research priorities for this group of animals in the Caribbean should be focused on the discovery of new species from deep waters, increased research in Central America and the Lesser Antilles, and increased ecological research in groups other than the echinoids. Future studies should also focus on (1) the role of marine protected areas for the recovery of key species, (2) population changes in fishing grounds, and (3) the impact of diseases in the region. Moreover, due to its rich biodiversity, relative to other tropical American waters, research and conservation efforts must be directed toward the preservation and conservation of that diversity, avoiding illegal extraction, enforcing controls, and improving coastal management.

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