Mar Biodiv
DOI 10.1007/s12526-009-0032-5

ORIGINAL PAPER

Echinoderm (Echinodermata) diversity in the Pacific coast of Central America

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Received: 20 May 2009 / Revised: 17 August 2009 / Accepted: 10 November 2009

Abstract We present a systematic list of the echinoderms of Central America Pacific coast and offshore island, based on specimens of the National Museum of Natural History, Smithsonian Institution, Washington D.C., the Invertebrate Zoology and Geology collections of the California Academy of Sciences, San Francisco, the Museo de Zoología, Universidad de Costa Rica, San José and published accounts. A total of 287 echinoderm species are recorded, distributed in 162 genera, 73 families and 28 orders. Ophiuroidea (85) and Holothuroidea (68) are the most diverse classes, while Panama (253 species) and Costa Rica (107 species) have the highest species richness. Honduras and Guatemala show the highest species similarity, also being less rich. Guatemala, Honduras, El Salvador y Nicaragua are represented by the most common nearshore species. Due to their coastal heterogeneity, Costa Rica and Panama are the richest places, with Panama also being the place where more research has been done. The current composition of echinoderms is the result of the sampling effort made in each country, recent political history and the coastal heterogeneity.

Keywords Eastern Tropical Pacific · Similarity · Richness · Taxonomic distinctness · Taxonomic list

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Introduction

The Pacific coast of Central America is located on the Panamic biogeographic province on the Eastern Tropical Pacific (ETP), from the gulf of Tehuantepec, México, to the gulf of Guayaquil(16°N to 3°S), Ecuador (Briggs 1974). The province is under the influence of the Intertropical Convergence Zone (ITCZ), characterized by high irradiance, variable winds and high precipitation (Amador et al. 2006). The depth of the mix layer is shallow (30–40 m) and with a permanent thermocline (Longhurst 1998), localized near the surface (25 m) (Brenes et al. 1990). Productivity is considered as moderate to high, due to the presence of upwelling areas such as the Costa Rica Thermal Dome, and the seasonal upwellings in the gulfs of Tehuantepec, Papagayo and Panama (Bakun et al. 1999). The coast is characterized by extensive mangrove systems, isolated coral reefs of limited development, and essentially no seagrasses (Cortés 2007).

The knowledge of the Central America echinoderm fauna is scarce and dispersed. Alvarado and Cortés (2004) divided the research on this group in the region into two periods. The first, from the mid-nineteenth century to the mid-twentieth century, was characterized by expeditions from North America and Europe, and is the time that most

Published online: 10 December 2009

of the local species were described. The second period, from the mid-twentieth century to the early twenty-first century, was characterized by widespread interest in the ecology and is dominated by studies done mostly in evolution and phylogeography (Lessios 2005).

In a general approach to the ETP, Maluf (1988a, b) did a synthesis of the echinoderm distribution and composition from California to Peru. She reported 630 species, and richness peacks in the Gulf of California, Panama and the Galapagos Archipelago, although the two former as places with high sampling effort. Then Maluf (1988b) compared species similarity and indicated that Central America, from Guatemala to Costa Rica, is a separate unit. She also indicated that the zone between Panama and Costa Rica posses a high degree of endemism and is a transition point, while Panama, Colombia and Ecuador had a greater affinity. Alvarado and Cortés (2004) compared Caribbean and Pacific echinoderms at the Phylum level in each Central American country and found 315 species, with Panama and Costa Rica the richest places. However, in this study, the similarities were calculated without any coast differentiation or discrimination of the presence of the oceanic island, Isla del Coco, that belongs to Costa Rica. This fact does not allow a detailed evaluation of the richness of the Central American Pacific coast.

The objective of this paper is to present an updated list of the echinoderms of each country bordering the Pacific Central America with information coming from scientific collections and literature review, and discuss the taxonomic distinctness and composition similarity for each class.

Methods

We revised the echinoderm species composition of the Pacific coast of mainland Central America: Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica and Panama. Information was obtained from echinoderms collections at the National Museum of Natural History, Smithsonian Institution, Washington D.C., the Invertebrate Zoology and Geology Collection of the California Academy of Sciences, San Francisco (http://www.calacademy.org/research/izg/iz_coll_db/index.asp), the Museo de Zoología at the Universidad de Costa Rica, and published records (Fisher 1928; Nielsen 1931; Boone 1933; H.L. Clark 1940, 1948; Ziesenhenne 1940, 1942; Deichmann 1941, 1958; A. H. Clark 1946; Aberson and Engel 1960; Chesher 1972; Maluf 1988a; Kerstitch 1989; Solís-Marín 1998; Alvarado and Fernández 2005; Barraza and Hasbún 2005; Lessios 2005; Alvarado and Cortés 2008).

For the taxonomic list, we have adopted the criteria of the following authors: for the Class Crinoidea: A.H. Clark (1947, 1950), Clark and Clark (1967); Class Asteroidea: A.M. Clark (1989, 1993, 1996); Class Ophiuroidea: Matsumoto (1915), Fell (1960); Class Echinoidea: Mortensen (1928, 1935, 1940, 1943, 1948, 1950, 1951); and for Class Holothuroidea: Pawson and Fell (1965).

Similarities in species composition for each country were estimated with Pearson similarity index (Field et al. 1982) using a presence/absence matrix per class and for the complete phylum, and we traced a dendrogram and non-metric multidimensional scaling (NMDS) to determine group similarities. We estimated the average taxonomic distinctness (Δ^+) and its variance (Λ^+) (Clarke and Warwick 2001), as measure of diversity. This index measures the taxonomic distance between each pair of individuals, defined by a Linnean classification tree, and is considered as one of the most precise indicators of biodiversity in a strict sense (Warwick and Clarke 2001). We used five taxonomic levels: species, genus, family, order, and class, with the following weights $\omega=20$ (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 analyses were performed with Systat 8.0 and PRIMER 6.0.

Results

The list of echinoderms from Central America includes 287 species, 162 genera, 73 families, 28 orders, and five classes (Table 1). In the Central American Pacific, the richest class was Ophiuroidea with 85 species followed by Holothuroidea with 68 species and Echinoidea and Asteroidea with 63 each (Table 2). Panama is the richest country with 253 species, followed by Costa Rica. El Salvador and Nicaragua have moderate richness, while Guatemala and Honduras are the poorest with less than 20 (Table 3). The Crinoidea was only represented in Panama. Asteroidea was reported in just four countries while the other three classes are present in the entire region (Table 3).

For the asteroids, *Luidia* is the most diverse genus with 9 species, and *Nidorellia armata* and *Phataria unisfacialis* are reported from most countries (four). Of the 63 species, 51 are reported for just one country, most of them at Panama.

Within Ophiuroidea, Panama and Costa Rica were the richest countries with 73 and 37 species, respectively, while Honduras was the poorest (Table 3). *Amphiodia* was the most diverse genus with 9 species, and *Ophiolepis grisea, Ophiocoma aethiops* and *O. alexandri* were the only species reported for the entire region. For this class, 56 species were reported only for one country.

With respect to Echinoidea, Panama was the richest with 60 species, followed by Costa Rica with 28 (Table 3). *Encope* was the most diverse genus with 6 species, while

Table 1 Taxonomic classification of the echinoderm fauna on the Central America Pacific countries

	G	ES	H	N	CR	P
CLASS CRINOIDEA						
ORDER Millericrina						
Family Hyocrinidae						
Calamocrinus diomedae A. Agassiz, 1890						X
Order Comatulida						
Family Antedonidae						
Florometra magellanica (Bell, 1882)						X
Psathyrometra bigradata (Hartlaub, 1895)						X
CLASS ASTEROIDEA						
ORDER Paxillosida						
Family Luidiidae						
Luidia armata Ludwig, 1905						X
Luidia asthenosoma Fisher, 1906						X
Luidia columbiae (Gray, 1840)						X
Luidia ferruginea Ludwig, 1905						X
Luidia foliolata Grube, 1865		X		X		X
Luidia latiradiata (Gray, 1871)		X		X		X
Luidia phragma H.L. Clark, 1917						X
Luidia superba A.H. Clark, 1917						X
Luidia tessellata Lütken, 1859					X	X
Family Astropectinidae						
Astropecten armatus Gray, 1840		X			X	X
Astropecten exiguus Ludwig, 1905						X
Astropecten fragilis Verrill, 1867						X
Astropecten regalis de Loriol, 1899					X	X
Dystater gilberti Fisher, 1905						X
Leptychaster inermis (Ludwig, 1905)						X
Plutonaster abyssicola Ludwig, 1905						X
Tethyaster canaliculatus (A.H. Clark, 1916)						X
Family Porcellanasteridae						
Eremicaster pacificus (Ludwig, 1905)						X
Eremicaster crassus gracilis (Sladen, 1833)						X
Family Goiopectinidae						
Ctenodiscus crispatus (Retzius, 1805)						X
Order Notomyotida						
Family Benthopectinidae						
Benthopecten cognatus (Ludwig, 1905)						X
Benthopecten pectinifer (Ludwig, 1905)						X
Benthopecten spinuliger (Ludwig, 1905)						X
Pectinaster agassizii (Ludwig, 1905)						X
Order Valvatida						
Family Goniasteridae						
Nymphaster diomedeae Ludwig, 1905						X
Pseudarchaster pectinifer Ludwig, 1905						X
Pseudarchaster verrilli Ludwig, 1905						X
Family Asterodiscididae						
Amphiaster insignis Verrill, 1868		X				X
Pauliella aenigma Ludwig, 1905					X	
Family Oreasteridae						
Nidorellia armata (Gray, 1840)		X		X	X	X
Pentaceraster cumingi (Gray, 1840)					X	X
Family Asteropsidae						
Asteropsis carinifera (Lamarck, 1816)					X	X
Family Ophidiasteridae						
Leiaster analogus Fisher, 1913						X
Leiaster teres (Verrill, 1871)						X
Linckia guildingi Gray, 1840						X
Ophidiaster ludwigi de Loriol, 1900						X
Pharia pyramidatus (Gray, 1840)		X			X	X
Phataria unifascialis (Gray, 1840)		X		X	X	X
Tamaria obstipa Ziesenhenne, 1942					X	
Family Mithrodidae						
Mithrodia bradleyi Verrill, 1867						X
Family Acanthasteridae						
Acanthaster ellisi (Gray, 1840)						X
Acanthaster planci (Linnaeus, 1758)					X	X
Family Asterinidae						
Meridiastra modesta (Verrill, 1870)						X
Order Spinulosida						
Family Solasteridae						
Lophaster validus (Ludwig, 1905)						X
Family Pterasteridae						
Hymenaster platyacanthus Ludwig, 1905						X
Hymenaster purpureus Ludwig, 1905						X
Hymenaster quadripinosus Fisher, 1905						X
Hymenaster violaceus Ludwig, 1905						X
Family Poraniidae						
Poraniopsis inflata (Fisher, 1905)						X
Family Echinasteridae						
Echinaster (Othilia) aculeata (Gray, 1840)				X	X	
Order Forcipulatida						
Family Zoroasteridae						
Cnemidaster wyvilli Sladen, 1889						X
Zoroaster longispinus Ludwig, 1905						X
Zoroaster magnificus Ludwig, 1905						X
Family Heliasteridae						
Heliaster cumingii (Gray, 1840)				X		
Heliaster microbrachius Xantus, 1860						X
Heliaster morrisoni A.H. Clark, 1946						X
Heliaster solaris A.H. Clark, 1920					X	
Family Asteriidae						
Hydrasterias diomedeae Ludwig, 1905						X
Pisaster ochraceus (Brandt, 1835)						X
Sclerasterias alexandri (Ludwig, 1905)						X
Order Brisingida						
Family Brisingidae						
Astrolirus panamensis (Ludwig, 1905)						X
Freyella pacifica Ludwig, 1905						X
Freyella insignis Ludwig, 1905						X
CLASS OPHIUROIDEA						
ORDER Phrynophiurida						
Family Ophiomyxidae						
Ophiomyxa panamensis Lütken & Mortensen, 1899						X
Family Asteronychidae						
Asteronyx loveni Müller & Troschel, 1842						X

Table 1 (continued)

	G	ES	H	N	CR	P
Astrodia plana (Lütken & Mortensen, 1899)						X
Family Asteroschematidae						
Asteroschema sublaeve Lütken & Mortensen, 1899						X
Family Gorgonocephalidae						
Astrocaneum spinosum (Lyman, 1875)					X	X
Astrodictyum panamense (Verrill, 1867)						X
Gorgonocephalus diomedeae Lütken & Mortensen, 1899						X
Order Ophiurida						
Family Ophiacanthidae						
Ophiacantha contigua Lütken & Mortensen, 1899						X
Ophiacantha costata Lütken & Mortensen, 1899						X
Ophiacantha inconspicua Lütken & Mortensen, 1899						X
Ophiacantha spinifera Lütken & Mortensen, 1899						X
Ophiacantha cosmica Lyman, 1878						X
Ophiacantha phragma Ziesenhenne, 1940						X
Ophiotoma paucispina (Lütken & Mortensen, 1899)	X					X
Ophiophthalmus normani (Lyman, 1879)					X	
Family Hemieuryalidae						
Sigsbeia laevis Ziesenhenne, 1940						X
Sigsbeia lineata Lütken & Mortensen, 1899						X
Family Amphiuridae						
Amphichondrius granulatus Nielsen, 1932						X
Amphichondrius laevis Ziesenhenne, 1940	X					
Amphilepis patens Lyman, 1879						X
Amphiodia grisea (Ljungman, 1867)						X
Amphiodia occidentalis (Lyman, 1860)						X
Amphiodia oerstedii (Lütken, 1856)		X			X	X
Amphiodia platyspina Nielsen, 1932						X
Amphiodia sculptilis Ziesenhenne, 1940				X		
Amphiodia tabogae Nielsen, 1932					X	X
Amphiodia urtica (Lyman, 1860)					X	
Amphiodia vicina H.L. Clark, 1940					X	
Amphiodia violacea (Lütken, 1856)					X	
Amphioplus dalea (Lyman, 1879)						X
Amphipholis elevata Nielsen, 1932						X
Amphipholis geminata (Le Conte, 1851)		X			X	X
Amphipholis granulata (Lütken & Mortensen, 1899)						X
Amphipholis platydisca Nielsen, 1932		X			X	X
Amphipholis pugetana (Lyman, 1860)					X	
Amphipholis puntarenae (Lütken, 1856)					X	X
Amphipholis squamata (Delle Chiaje, 1828)				X	X	X
Amphiura diomedeae Lütken & Mortensen, 1899					X	X
Amphiura gymnogastra Lütken & Mortensen, 1899						X
Amphiura gymnopora Lütken & Mortensen, 1899						X
Amphiura polyacantha Lütken & Mortensen, 1899						X
Amphiura serpentina Lütken & Mortensen, 1899						X
Ophiocnida hispida (Le Conte, 1851)						X
Ophiophragmus marginatus (Lütken, 1859)					X	
Ophiophragmus ophiactoides Ziesenhenne, 1940					X	

Table 1 (continued)

	G	ES	H	N	CR	P
Ophiophragmus paucispinus Nielsen, 1932						X
Ophiophragmus tabogensis Nielsen, 1932					X	
Family Ophiactidae						
Hemipholis elongata (Say, 1825)						X
Hemipholis gracilis Verrill, 1867		X		X	X	X
Ophiactis savignyi (Müller & Troschel, 1842)						
Ophiactis simplex (Le Conte, 1852)				X	X	X
Family Ophiotrichidae						
Ophiothela gracilis Nielsen, 1932					X	X
Ophiothela mirabilis Verrill, 1867		X			X	X
Ophiothrix spiculata Le Conte, 1851		X		X	X	X
Family Ophiocomidae						
Ophiocoma aethiops Lütken, 1859	X	X	X	X	X	X
Ophiocoma alexandri Lyman, 1874	X	X	X	X	X	X
Ophiocomella sexradia (Duncan, 1887)						X
Family Ophiochitonidae						
Ophiochiton carinatus Lütken & Mortensen, 1899						X
Family Ophionereididae						
Ophionereis annulata (Le Conte, 1851)		X			X	X
Ophionereis dictyota Ziesenhenne, 1940					X	X
Ophionereis dubia (Müller & Troschel, 1842)						X
Ophionereis nuda Lütken & Mortensen, 1899						X
Family Ophiodermatidae						
Diopederma daniana (Verrill, 1867)	X	X			X	X
Ophioderma appressum (Say, 1825)					X	
Ophioderma panamense Lütken, 1859		X		X	X	X
Ophioderma teres (Lyman, 1860)		X		X	X	X
Ophioderma variegatum Lütken 1856				X	X	X
Ophiopaepale diplax (Nielsen, 1932)					X	X
Family Ophiuridae						
Gymnophiura mollis Lütken & Mortensen, 1899						X
Ophiocten hastatum Lyman, 1878					X	X
Ophioglypha tumulosa Lütken & Mortensen, 1899						X
Ophiolepis crassa Nielsen, 1932						X
Ophiolepis grisea H.L. Clark, 1940	X	X	X	X	X	X
Ophiolepis hispida Le Conte, 1851						X
Ophiolepis plateia Ziesenhenne, 1940					X	
Ophiolepis simplex Le Conte, 1851						X
Ophiolepis variegata Lütken, 1856		X			X	X
Ophiosphalma glabrum (Lütken & Mortensen, 1899)						X
Ophiomusium lymani Thomson, 1873						X
Ophionema hexacantha Nielsen, 1932						X
Ophiura irrorata (Lyman, 1860)						X
Ophiura plana (Lütken & Mortensen, 1899)	X					X
Ophiozona pacifica (Lütken, 1856)					X	X
Family Ophioleucidae						
Ophiernus adspersus Lütken & Mortensen, 1899						X
Ophiernus seminudum Lütken & Mortensen, 1899						X
CLASS ECHINOIDEA						
ORDER Cidaroida						
Family Cidaridae						
Aporocidaris milleri (A. Agassiz, 1898)						X

Table 1 (continued)

	G	ES	H	N	CR	P
Centrocidaris doderleini (A. Agassiz, 1898)						X
Eucidaris thouarsii (Valenciennes, 1846)		X			X	X
Hesperocidaris asteriscus H.L. Clark, 1948					X	X
Hesperocidaris dubia (H.L. Clark, 1907)					X	X
Hesperocidaris panamensis (A. Agassiz, 1898)					X	X
Hesperocidaris perplexa (H.L. Clark, 1907)						X
Order Echinothurioida						
Family Echinothuriidae						
Araeosoma leptaleum A. Agassiz & H.L. Clark, 1909						X
Tromikosoma hispidum (A. Agassiz, 1898)						X
Tromikosoma panamense (A. Agassiz, 1898)						X
Order Diadematoida						
Family Diadematidae						
Astropyga pulvinata (Lamarck, 1816)		X			X	X
Centrostephanus coronatus (Verrill, 1867)					X	X
Diadema mexicanum A. Agassiz, 1863		X			X	X
Kamptosoma asterias (A. Agassiz, 1881)						X
Family Aspidodiadematidae						
Plesiodiadema horridum (A. Agassiz, 1898)						X
Order Pedinoida						
Family Pedinidae						
Caenopedina diomedeae Mortensen, 1939						X
Order Salenioida						
Family Saleniidae						
Salenocidaris miliaris (A. Agassiz, 1898)						X
Order Arbacioida						
Family Arbaciidae						
Arbacia incisa (A. Agassiz, 1863)		X		X	X	X
Arbacia spatuligera (Valenciennes, 1846)						X
Dialithocidaris gemmifera A. Agassiz, 1898						X
Order Temnopleuroida						
Family Toxopneustidae						
Lytechinus panamensis Mortensen, 1921						X
Lytechinus pictus (Verrill, 1867)						X
Toxopneustes roseus (A. Agassiz, 1863)		X			X	X
Tripneustes depressus A. Agassiz, 1863					X	X
Order Echinoida						
Family Echinometridae						
Caenocentrotus gibbosus (L. Agassiz & Desor, 1846)						X
Echinometra oblonga (Blainville, 1825)						X
Echinometra vanbrunti A. Agassiz, 1863	X	X	X	X	X	X
Order Clypeasteroida						
Family Clypeasteroida						
Clypeaster europacificus H.L. Clark, 1914					X	X
Clypeaster ochrus H.L. Clark, 1914					X	X
Clypeaster rotundus (A. Agassiz, 1863)	X	X	X	X	X	X
Clypeaster speciosus Verrill, 1870						X
Family Dendrasteridae						
Dendraster excentricus (Eschscholtz, 1831)						X
Family Mellitidae						
Encope grandis L. Agassiz, 1841	X	X	X	X		X
Encope laevis H.L. Clark, 1948				X	X	

Table 1 (continued)

	G	ES	H	N	CR	P
Encope michelini L. Agassiz, 1841					X	
Encope micropora L. Agassiz, 1841		X		X	X	X
Encope perspetiva L. Agassiz, 1841					X	X
Encope wetmorei A.H. Clark, 1946					X	X
Melitella stokesi (L. Agassiz, 1841)		X			X	X
Mellita grantii Mortensen, 1948						X
Mellita kanakoffi Durham, 1961					X	X
Mellita longifissa Michelin, 1858	X	X	X	X	X	X
Mellita notabilis H.L. Clark, 1947		X		X		X
Order Cassiduloida						
Family Cassidulidae						
Rhyncholampas pacificus (A. Agassiz, 1863)					X	X
Order Pourtalesoida						
Family Urechinidae						
Urechinus loveni (A. Agassiz, 1898)	X					
Urechinus naresianus A. Agassiz, 1879						X
Family Pourtalesiidae						
Pourtalesia tanneri A. Agassiz, 1898						X
Cystocrepis setigera (A. Agassiz, 1898)						X
Order Spatangoida						
Family Hemiasteridae						
Hemiaster tenuis (A. Agassiz, 1898)						X
Family Schizasteridae						
Agassizia scrobiculata Valenciennes, 1846		X		X	X	X
Brisaster latifrons (A. Agassiz, 1898)						X
Moira clotho (Michelin, 1855)					X	X
Family Aeropsidae						
Aeropsis fulva (A. Agassiz, 1898)						X
Family Brissidae						
Brissopsis columbaris A. Agassiz, 1898						X
Brissopsis pacifica (A. Agassiz, 1898)					X	X
Brissus obesus Verrill, 1867					X	X
Meoma ventricosa frangibilis Chesher, 1970						X
Meoma ventricosa grandis Gray, 1851					X	X
Metalia nobilis Verrill, 1867						X
Plagiobrissus pacificus H.L. Clark, 1940						X
Family Lovenidae						
Homolampas fulva A. Agassiz, 1879						X
Homolampas hastata A. Agassiz, 1898						X
Lovenia cordiformis A. Agassiz, 1872						X
CLASS HOLOTHUROIDEA						
ORDER Dendrochirotida						
Family Psolidae						
Lissothuria ornata Verrill, 1867		X		X		X
Psolidium dorsipes Ludwig, 1886						X
Psolidium ekmani Deichmann, 1941						X
Psolidium gracile Ludwig, 1894						X
Psolidium panamense Ludwig, 1894						X
Psolus digitatus Ludwig, 1894						X
Thyonepsolus beebei Deichmann, 1937					X	X
Family Phyllophoridae						
Euthyonidium ovulum Deichmann, 1938					X	X
Euthyonidium veleronis Deichmann, 1937		X			X	

Table 1 (continued)

	G	ES	H	N	CR	P
Pentamera beebei Deichmann, 1938					X	
Pentamera chierchia (Ludwig, 1887)					X	X
Pentamera zacae Deichmann, 1938		X				
Thyone bidentata Deichmann, 1941		X				X
Phyllophorus aculeatus Ludwig, 1894						X
Family Sclerodactylidae						
Afrocucumis ovulum (Selenka, 1867)		X				
Apentamera lepra Deichmann, 1941						X
Neothyone gibber (Selenka, 1867)					X	X
Neothyone gibbosa Deichmann, 1938		X			X	
Neothyone panamensis (Ludwig, 1887)						X
Family Cucumaridae						
Abyssocucumis abyssorum (Théel, 1886)						X
Cucumaria flamma Solís & Laguarda, 1999					X	X
Pseudocnus californicus (Semper, 1868)	X	X	X	X	X	X
Pseudocnus dubiosa (Semper, 1868)					X	
Leptopentacta nina Deichmann, 1941						X
Neocucumis panamensis Heding & Panning, 1954						X
Neocucumis veleronis (Deichmann, 1941)				X		X
Pentacta panamensis Verrill, 1867						X
Allothyone mexicana (Deichmann, 1941)						X
Order Dactylochirotida						
Family Ypsilothuriidae						
Ypsilothuria bitentaculata (Ludwig, 1893)						X
Order Aspidochirotida						
Family Holothuridae						
Actinopyga mauritiana (Quoy & Gaimard, 1833)						X
Holothuria (Cystipus) inhabilis Selenka, 1867						X
Holothuria (Cystipus) rigida (Selenka, 1867)					X	X
Holothuria (Halodeima) atra (Jaeger, 1833),					X	X
Holothuria (Halodeima) hilla Lesson, 1830					X	X
Holothuria (Halodeima) inornata Semper, 1868	X				X	
Holothuria (Halodeima) kefersteini (Selenka, 1867)		X			X	
Holothuria (Lessonothuria) pardalis Selenka, 1867			X		X	X
Holothuria (Mertensiothuria) leucospilota (Brandt, 1835)						X
Holothuria (Platyperona) difficilis Semper, 1868	X	X	X	X	X	X
Holothuria (Selenkothuria) lubrica Selenka, 1867		X			X	X
Holothuria (Selenkothuria) portovallartensis Caso, 1954					X	X
Holothuria (Semperothuria) imitans (Ludwig, 1875)				X	X	X
Holothuria (Semperothuria) languens (Selenka, 1867)					X	X
Holothuria (Thymiosycia) arenicola (Semper, 1868)					X	X
Holothuria (Thymiosycua) impatiens (Forskål, 1775)		X			X	X
Holothuria (Theelothuria) princeps Selenka, 1867						X
Labidodemas americanum Deichmann, 1938		X			X	
Labidodemas maccullochi (Deichmann, 1958)					X	X
Family Stchopodidae						
Isostichopus fuscus (Ludwig, 1875)	X	X	X	X	X	X
Family Synallactidae						
Mesothuria multipes (Ludwig, 1893)						X

Table 1 (continued)

	G	ES	H	N	CR	P
Pelopatides suspecta Ludwig, 1894						X
Pseudostichopus peripatus (Sluiter, 1901)						X
Synallactes aenigma Ludwig, 1894						X
Synallactes alexandri Ludwig, 1894						X
Order Elasipodida						
Family Psychropotidae						
Benthodytes sanguinolenta Théel, 1882						X
Family Elpidiidae						
Peniagone papillata Hansen, 1975						X
Peniagone vitrea Théel, 1882						X
Family Pelagothuriidae						
Pelagothuria natatrix Ludwig, 1894						X
Order Apodida						
Family Synaptidae						
Euapta godefroyii (Semper, 1868)					X	X
Protankyra brychia (Verrill, 1885)						X
Synapta abyssicola Ludwig, 1894						X
Family Chiridotidae						
Chiridota aponocrita H.L. Clark, 1920						X
Epitomapta tabogae Heding, 1928						X
Order Molpadia						
Family Molpadidae						
Molpadia granulata (Ludwig, 1894)						X
Molpadia intermedia (Ludwig, 1894)						X
Molpadia musculus Risso, 1826						X
Ankyroderma spinosum Ludwig, 1894						X
Family Caudinidae						
Paracaudina chilensis chilensis (J. Müller, 1850)					X	

G Guatemala, *ES* El Salvador, *H* Honduras, *N* Nicaragua, *CR* Costa Rica, *P* Panama

X Presence

Echinometra vanbrunti, Clypeaster rotundus and *Mellita longifissa* were reported for the entire region. In this class, 34 species are known in only one country. As with the previous class, Panama was the richest country for Holothuroidea with 68 species, while Guatemala and Honduras were the poorest (Table 3). *Holothuria* was the most diverse genus with 16 species, while *Pseudocnus californicus, Holothuria (Platyperona) difficilis* and *Isostichopus fuscus* appeared in all the countries. Of this class, 40 species have been observed in a single country.

The dendrograms generated one large group and a separated unit (Figs. 1a and 2b, gray shading), with Panama as the richest country. The group has an isolated element (Costa Rica) with an intermediate diversity, while El Salvador and Nicaragua, and Guatemala and Honduras, are joined and have less diversity (Fig. 2a gray shading). Similar patterns were observed at the class level. Guatemala and Honduras were associated in all comparisons (Figs. 1b-e and 2b-e) as the least diverse countries. Panama is always

Table 2 Number of echinoderms at different taxonomic leves in the Pacific coast of Central America

Class	Orders	Families	Genera	Species
Crinoidea	1	2	3	3
Asteroidea	6	21	38	63
Ophiuroidea	2	15	40	85
Echinoidea	12	20	41	63
Holothuroidea	6	15	37	68
Total	27	73	159	282

separated (similitude percentages 4.3–15.9% with the rest of the region), as well as Costa Rica (30.4%), although this tends to have a higher percentage of similitude with El Salvador (33%) (Table 4).

With respect to the taxonomic distinctness index (Δ^+) (Fig. 3), all countries fall inside the 95% confidence limit except Panama and Costa Rica (Fig. 3a). Guatemala, Honduras, Nicaragua and El Salvador, besides having few species, possess the most common and widely distributed species of the region, while Panama has 161 species that are only founded in that country, and Costa Rica has just 17. Guatemala, El Salvador and Nicaragua have 2 species each which are only found on their coasts, while Honduras has none. Taxonomically, Panama is a rich country with a higher taxonomic variation, while Costa Rica has a lower taxonomic distinctivness because it is represented by many species in few taxonomic hierarchies. The rest of the countries are moderately diverse, possessing few species, the most common and widely distributed, representing a higher variation in genera, families, and orders (Fig. 3b). The behavior of this index is congruent with the behavior of the similitude analysis (Figs. 1a and 2a) and the common species percentages (Table 4).

Discussion

The Pacific coast of Central America is one of the most diverse and rich echinoderm areas of the Eastern Tropical Pacific (Table 5), and Panama is one of the richest countries of the region (Table 3). Central America is the second region for crinoids (after Galapagos) and the first in the other groups (Table 5). However, this high richness is due to the amount of species present in Panama and Costa Rica.

The Pacific coast of Guatemala and the northern part of El Salvador consists of sandy beaches, with mangrove forests with sand bars (Cortés 2007). At Los Cóbanos, in El Salvador, there is a change in orientation of the coast and low rocky outcrops and platforms appear; Guatemala and Honduras have no coral reefs, and at El Salvador, coral communities are limited to Los Cóbanos (Reyes-Bonilla and Barraza 2003). The entrance to the Gulf of Fonseca, shared by El Salvador, Honduras and Nicarguara, has high energy sandy beaches and is surrounded by rocky outcrops, while the inner section has extensive mangrove forests (Jiménez 1994; Cortés 2007). This northern part of the Central America coast has only a few islands located in the Gulf of Fonseca (Cortés 2007). The Pacific coast of southern Nicaragua, Costa Rica and Panama consists of a combination of rocky points, sandy beaches, cobble beaches, deltas and several gulfs, many islets and islands (i.e. 250 islands and islets in the Perlas Archipelago; Guzmán et al. 2008), ranging from a few square meters to several tens or hundreds of square kilometers, especially in Panama. Costa Rica and Panama have many coral reefs, being the last place where the largest and well-developed reefs occur (Cortés and Jiménez 2003; Maté 2003; Cortés 2007). The difference in richness among the countries in Central America could be the result of this coastal contrast having given rise to different environments for more species, but also due to a biased sampling effort in the mentioned areas.

When we compared the coastline of each country, we noticed that the longer ones are located in Panama and Costa Rica with 1,690 and 1,160 km, respectively. The rest of countries possessed shorter coastlines, 64 km for Honduras, 250 km for Guatemala, 307 km for El Salvador and 358 km for Nicaragua. In the number of species per coastline kilometer, Honduras is the richest country (0.172

Table 3 Number of echinoderm species per class in each country

Class/Country	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panamá	Central American Pacific
Crinoidea	0	0	0	0	0	3	3
Asteroidea	0	6	0	6	13	58	63
Ophiuroidea	7	14	3	11	37	73	85
Echinoidea	5	13	4	9	28	60	63
Holothuroidea	4	13	4	5	29	59	68
Total	16	46	11	31	107	253	282
Coastline (km)	250	307	64	358	1,160	1,690	3,829
Spp. km^{-1} of coastline	0.064	0.150	0.172	0.086	0.092	0.150	0.074

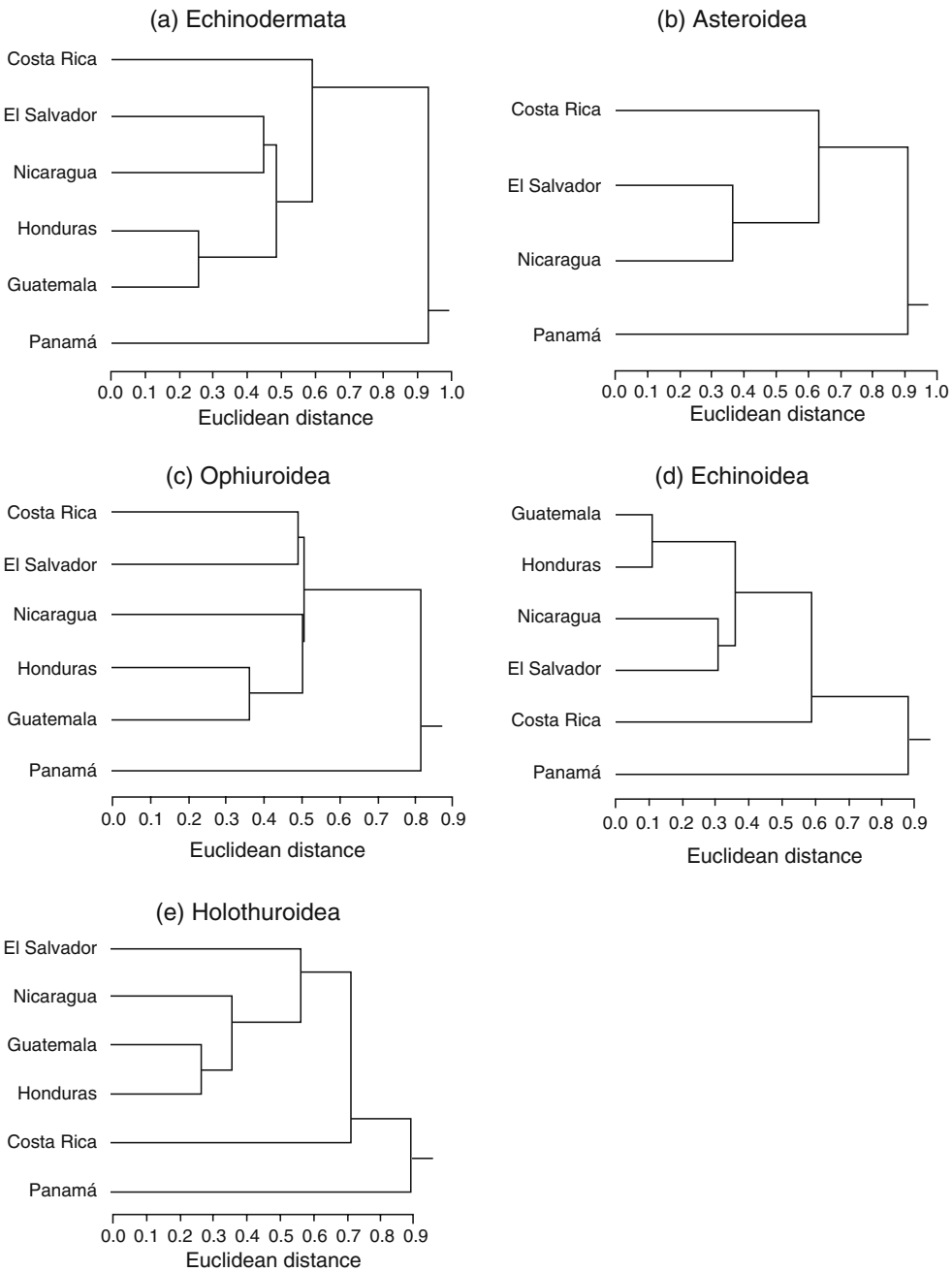

Fig. 1 Dendograms (Euclidian distance) based on species presence/absence Pearson correlation matrix: **a** Echinodermata, **b** Asteroidea, **c** Ophiuroidea, **d** Echinoidea, **e** Holothuroidea; between the Central America countries

spp. km^{-1}), followed by El Salvador and Panama each with 0.150 spp. km^{-1}, Costa Rica, Nicaragua and, again as the least diverse, Guatemala with 0.064 spp. km^{-1} of coastline (Table 3). The low diversity of Guatemala is probably due to its shorter and more homogeneous coast, consisting of long high energy sandy beaches with low environmental heterogeneity (Cortés 2007).

The zone between Guatemala and Nicaragua has been called the "Pacific Central American Gap" (Springer 1958), since it separates the two main areas of coral occurrence in the region (Glynn and Ault 2000): the tropical coast of Mexico and the rocky areas of Costa Rica to South America. This stretch of coastline is relatively homogeneous with few rocky points as protected areas (with the exception of Golfo de Fonseca). This results in low viability for echinoderm larvae recruitment to coral and rocky reefs. Los Cobanos coral reef, in El Salvador, breaks this coast pattern (Reyes-Bonilla and Barraza 2003). Contrary to this pattern, Costa Rica and Panama possessed a higher environmental heterogeneity which is manifested in the number of species reported in this work.

Maluf (1988b) indicated similar numbers of species for Central America, indicating that Panama was the most diverse. She indicated the richness of each country on the

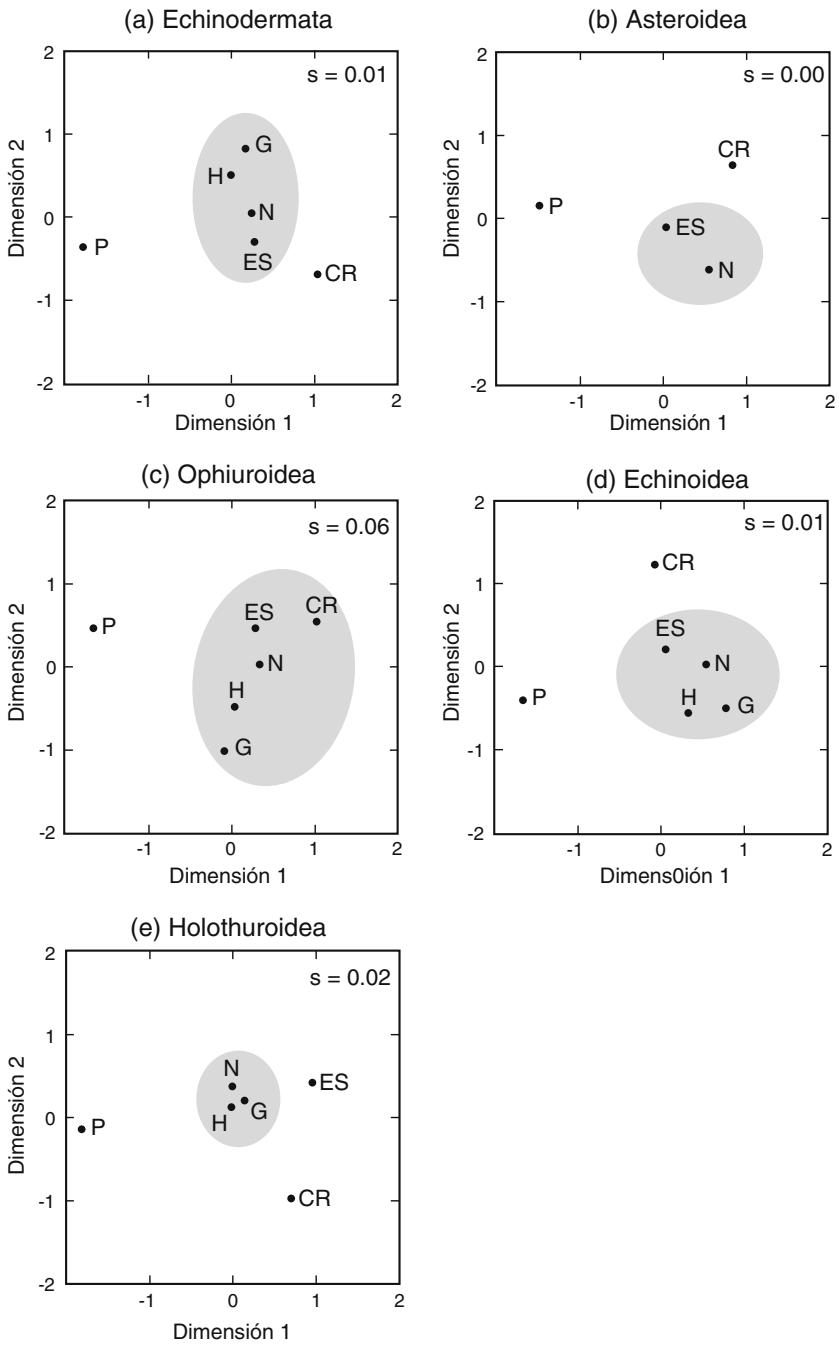

Fig. 2 Non-metric multiple dimensional scaling (NMDS) based on species presence/absence Pearson correlation matrix: **a** Echinodermata, **b** Asteroidea, **c** Ophiuroidea, **d** Echinoidea, **e** Holothuroidea; between the Central America countries. *G* Guatemala, *ES* El Salvador, *H* Honduras, *N* Nicaragua, *CR* Costa Rica, *P* Panamá. *S* Stress level

Table 4 Number and percent (%) of species of echinoderms shared between the Central America countries

	Guatemala	Honduras	Nicaragua	Costa Rica	Panamá
El Salvador	11 (21.6)	10 (21.3)	23 (42.6)	38 (33.0)	41 (15.9)
Guatemala		10 (62.5)	10 (27.0)	11 (9.8)	13 (5.1)
Honduras			10 (31.3)	10 (9.3)	11 (4.3)
Nicaragua				24 (21.1)	27 (10.5)
Costa Rica					84 (30.4)

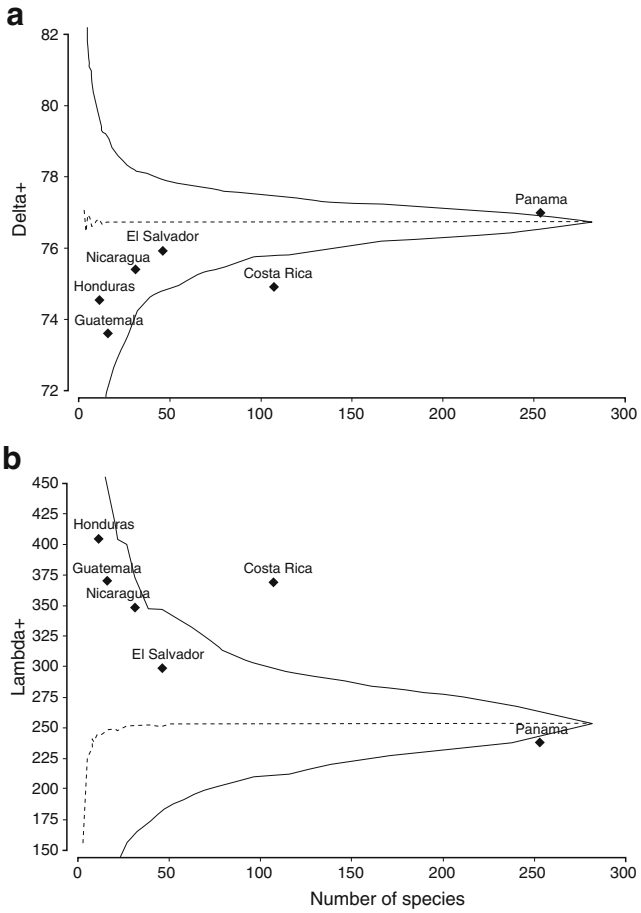

Fig. 3 Taxonomic distinctness index: **a** average (delta: Δ^+), and **b** their variation (lambda: Λ^+) of the Central America Pacific echinoderms. *Continuous line* 95% confidence limit; *discontinuous line* Δ^+ average value

basis of distribution ranges, predicting values between 125 and 150 species for Guatemala, El Salvador and Nicaragua. However, these numbers may be overestimations because of the lack of suitable substrates for the majority of the organisms. It is possible that the discontinuity of species richness that Maluf mentioned between the Gulf of California-Baja and Costa Rica is a response to a current pattern similar to those observed for corals (Glynn and Ault 2000). Moreover, the coastal upwellings of Papagayos (northern Costa Rica and southern Nicaragua) and Tehuantepec (Mexico) generate barriers that probably make larval recruitment difficult due to lower temperatures (12°C), and the fact that the strong currents that move away from the coast (Glynn 1974). On the other hand, the Panama basin is surrounded by the Cocos and Carnigie ridge (Fiedler and Lavín 2006; Lizano 2008), which extends from the gulfs of Nicoya and Guayaquil to the Galapagos Archipelago, and rise from depths of 3,000 m to less than 200 m, thus becoming a physical and biogeochemical barrier for deep water organisms between the basin of Panama from Guatemla and Peru (McClain et al. 2002; Fiedler and Lavín 2006). This could explain why Maluf (1988b) found a higher similarity between Costa Rica, Panama, Colombia and Ecuator.

As shown by Maluf (1988a) and Alvarado and Cortés (2004), our study indicates that Panama is the richest country in the Central American Pacific, followed by Costa Rica, and determines its low similitude with the remaining countries. This pattern is similar on the Caribbean coast where Panama is the richest country, followed in this case by Belize (Alvarado et al. 2008). This may be because it is the most studied in the region. In other countries, research has being scarce mainly due to three reasons: (1) lack of specialists, (2) lack of resources, and (3) the unstable political situation over the past 30 years. The taxonomic distinctness index indicates that this country is represented by many species reported only for Panama, while in the other countries the species reported are the most common, and generally the ones that live in shallow waters.

In agreement with Maluf (1988a), it is probable that the number of species in the rest of the countries will increase according to the distribution ranges along the ETP. However, we would expect lower numbers due to the geomorphologic

Table 5 Echinoderms richness per class in selected regions and countries in the Eastern Tropical Pacific

Class/Country or region	Pacific Baja California and Gulf of California	Mexican Central Pacific	Colombian Pacific	Revillagigedo Archipelago	Isla del Coco	Malpelo Island	Galápagos Archipelago	Central America
Crinoidea	0	1	0	0	2	0	5	3
Asteroidea	56	26	19	9	35	23	44	63
Ophiuroidea	80	43	18	12	30	18	74	85
Echinoidea	45	23	17	10	30	19	37	63
Holothuroidea	50	36	12	13	27	24	38	68
Total	231	129	66	44	124	84	198	282
References[a]	1, 2	2, 3	4	2	5	6	7	8

[a] *1* Solís-Marín et al. 2005; *2* Honey-Escandón et al. 2008; *3* Benítez-Villalobos et al. 2008; *4* Neira-Ortíz and Cantera 2005; *5* Alvarado 2009; *6* Cohen-Rengifo 2008; *7* Maluf 1991; *8* This study

and oceanographic conditions mentioned earlier. It is important to increase the research effort in transitional zones in El Salvador and Nicaragua, and at Golfo Dulce, Costa Rica, with its unique environment as a tropical-like fjord (Hebbeln and Cortés 2001). It should be a priority to measure the connectivity of Galapagos, Panama, and Costa Rica and the Gulf and Baja California as centers of high biodiversity, in order to establish management measures that will assure the production and transport of larvae in the future, taking into consideration the pressures of coastal development and the impacts of global warming.

Acknowledgements We thank those who facilitated our literature search or access to museum collections. We also thank R. Vargas and M. Springer from the Museo de Zoología, Universidad de Costa Rica, A. Durán González from the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. FASM thanks PAPIIT-UNAM (IN 226308). J.J.A. thanks CONICYT, MCIT and CONACYT. The manuscript was enriched by comments from J. Cortés, H. Reyes-Bonilla and two anonymous reviewers.

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