Chapter 16
Latin America Echinoderm Biodiversity and Biogeography: Patterns and Affinities

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16.1 Introduction

The first attempt to study the diversity and biogeography of echinoderms from Latin America was done by Maluf (1988a, b). She identified 630 species of echinoderms from southern California to southern Peru (Central Eastern Pacific or

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CEP). Two-thirds of all CEP echinoderms occur on the continental shelf (depth <200 m), with a low level of endemism. She found an increase in species richness from higher to lower latitudes, with peaks of richness in the Gulf of California, Panama and the Galápagos Archipelago, places that also have a higher number of endemic species, and are also areas with more research. The Gulf of California had a greater similarity with the tropics than the Pacific side of the Baja California peninsula and southern California, while the oceanic island of Cocos was more similar to the mainland than the Galápagos and Revillagigedo archipelagos. Moreover, she indicated the presence of five faunal transition zones related to large-scale abiotic parameters. Those transition zones were: (1) the Galápagos Islands, (2) Gulf of Guayaquil, (3) Costa Rica–Panama, (4) the mouth of the Gulf of California and (5) Central Baja California outer coast. Seventy percent of all the 265 CEP shelf restricted species were endemic to the region, 12 % were of a Northeast Pacific affinity (Oregonian and Alaska provinces), 5 % had a Southeast Pacific affinity (Magellanic and Peruvian provinces), and 13 % were widespread species. Most species in this last category were transpacific more than circumtropical, and were species associated with reefs and rocky shores (Maluf 1988b).

On the Atlantic side, Price et al. (1999) analyzed a database of presence/absence of the Asteroidea compiled by Clark and Downey (1992) that was based on records collected over 150 years. They determined geographical patterns of diversity and make comparisons between coastal and deep-sea diversity for 26 regions of the Atlantic. For 349 species, they found a higher degree of endemism in coastal waters and a greater level of similarity between regions with increasing depth. However, the number of species between bathymetrical categories was similar: 199 species at depths between 0 and 200 m, 135 and 169 species between 200 and 500 m, and 198 species at depths >500 m. The greatest number of species (81 species) was in the region between Florida and the Yucatan Peninsula, followed by the Bahamas-Caribbean (77 species) and the Caribbean and Guyana basins together with the Gulf of Mexico region (66 species). This last region possessed the highest number of endemic species of all the Atlantic Asteroidea (14 species). Regions like Guyanas-Cape Frío, Cape Frío-Río de la Plata, Río de la Plata-Tierra del Fuego-Falklands islands and the Canary islands had few endemic species (richness: 48, 22, 43, 26 species respectively; endemism: 1, 1, 8, 0 species respectively). According to Price et al. (1999) the disparity in sampling efforts is an important factor which can influence interpretation of geographic patterns.

Alvarado and Cortés (2004), Alvarado et al. (2008, 2010) and Alvarado (2011) studied the diversity of echinoderms in Central America, covering both Pacific and Caribbean coast. On both coasts the class Ophiuroidea was the richest with 85 species on the Pacific side and 79 on the Caribbean coast. Panama was also the richest country in the region on both coasts, with 253 species on the Pacific coast and 154 species on the Caribbean coast. Alvarado et al. (2010) and Miloslavich et al. (2010) made an extensive review of published records on echinoderms of the

Caribbean and reported a total of 433 species. Ophiuroidea was the richest class with 148 species, followed by Asteroidea (116 species). Mexico and Colombia were the richest countries with 182 and 180 species, respectively. In terms of Caribbean ecoregions, the Southwestern Caribbean was richest (283 species), followed by the Western Caribbean (268 species), the Greater Antilles (248 species), the Southern Caribbean (151 species), and lastly the Eastern Caribbean (79 species).

Miloslavich et al. (2011) analyzed the marine biodiversity of South America (including the Pacific coast of Costa Rica and Panama, and excluding the Caribbean coast from Colombia and Venezuela). The best known groups in the region are fish, mollusks, crustaceans, echinoderms, cnidarians, and macroalgae. They divided the region into five subregions: (1) Eastern Tropical Pacific (223 species of echinoderms, 3.3 % of the total species, 4.4 spp./100 km of the coast, 51 % spp. in OBIS–Ocean Biogeographic Information System), (2) Humbolt Current-Chile and Peru (364 species of echinoderms, 3.6 % of the total species, 5.0 spp./100 km of the coast, 38 % spp. in OBIS), (3) Patagonian shelf-Uruguay and Argentina (207 species of echinoderms, 5.5 % of the total species, 3.7 spp./100 km of the coast, 76 % spp. in OBIS), (4) North, South and East Brazilian shelves (254 species of echinoderms, 2.8 % of the total species, 3.4 spp./100 km of the coast, 60 % spp. in OBIS) and (5) tropical west Atlantic-Venezuelan Atlantic, Guyana, Suriname and French Guyana (107 species of echinoderms, 3.9 % of the total species, 5.7 spp./100 km of the coast, 84 % spp. in OBIS). According to their analysis with the OBIS database, echinoderms have a low level of endemism (3.6 %) and seem to have reached a relatively stable number with few new additions. This could be the result of the lack of taxonomic expertise, limited funding for research, lack of collecting effort, and limited access to sampling sites.

Sthör et al. (2012) presented a global biodiversity analysis of the class Ophiuroidea, reporting 2,064 species. They divided Latin America into three regions: East Pacific (EP), South America (SA) and West Atlantic (WA). West Atlantic was the richest region with 335 species with 60.6% of them endemic to the region, followed by EP with 186 species and 62.9 % endemics, and SA with 124 species and 24.2 % endemics. Moreover, according to their depth strata, the bathyal stratum (depths between 200 and 3,500 m) was the richest in the three regions (229 species in WA, 111 species in EP and 102 species in SA), followed by the shelf stratum (depths between 0 and 200 m) (217 spp. in WA, 92 spp. in EP and 79 spp. in SA). The abyssal (depths between 3,500 and 6,000 m) (16 spp. in WA, 28 spp. in EP and 17 spp. in SA) and the hadal strata (depths > 6,500 m) (0 sp. in WA, 1 sp. in EP and SA) were less rich.

On this chapter we analyze the database presented in the appendix of this book. We investigate the current patterns of diversity by country and by class of echinoderms. In addition, we analyze their biogeographical, depth, and habitat or substratum affinities.

Fig. 16.1 Biogeographical regions in central and south American coasts according to Briggs (1995) and Clark and Downey (1992)

16.2 General Oceanographic Variables of Latin America and the Canary Islands

Traditionally, the area has been divided into five biogeographical regions with nine provinces (Briggs 1995) (Fig. 16.1). Western Atlantic Region, from Bermuda (Southern Florida) to Cape Frío (Brazil), which includes the Caribbean, Brazilian and West Indian provinces. In the Pacific Ocean, the Eastern Pacific Region includes the Mexican, Panamanian and Galápagos Provinces, the Eastern South America Region with the Peru-Chilean Province and Easter Island in the central south Pacific. In the Eastern Atlantic, the Canary Islands belong to the Lusitania Region.

Together they cover a wide biogeographical and climate range (Table 16.1). They are affected by the main currents in the Atlantic and the Pacific oceans (Fig. 16.2). Minimum temperature reaches −2 °C South of the Brazilian region and Eastern South America. The highest temperature is reached in the tropical

Table 16.1 Climatic and trophic variables in the water column in the coastal biogeographical provinces of North, Central and South America and the Canary Islands

	Minimum T (°C)[a]	Maximum T (°C)[a]	Mean T (°C)[a]	ST0 (°C)[b]	ST50 (°C)[b]	MLD (m)[b]	Photic Depth (m)[b]	Maximum Chl (mg m^{-3})[a]	Minimum Chl (mg m^{-3})[a]	Mean Chl (mg m^{-3})[a]	Chl (g m^{-1})[b]	Productivity (g C m^{-2} d^{-1})[b]
Caribean	5.3	31.	25.6	26.9	25.8	23.0	44.2	74.3	0.0	0.6	6.6	0.5
West Indian	2.8	31.2	27.3	26.9	25.8	23.0	44.2	74.3	0.0	0.3	6.6	0.5
Brazilian	−2.0	30.5	24.6	27.6	26.7	14.5	38.7	74.3	0.0	0.4	55.8	1.9
EasternSouth America	−2.00	24.7	10.6	8.5	7.1	101.2	30.0	74.3	0.0	1.7		1.3
Canary Islands	16.79	24.7	20.7	21.2	18.0	28.2	28.7	40.9	0.0	0.2	35.0	2.0
Easter Island				16.7	14.2	23.3	43.3				15.7	0.7
Chilean				16.7	14.2	23.3	43.3				15.7	0.7
Galápagos				27.6	24.2	22.5	53.3				4.3	0.3
Panamanian				27.3	21.0	10.2	39.2				11.3	0.9
Mexican				27.3	21.0	10.2	39.2				11.3	0.9

[a] Mean values obtained from monthly satellite data for the period 1982–1991 for sea surface temperature and 2003–2010 for chlorophyll (http://neo.sci.gsfc.nasa.gov)
[b] Data from Longhurst et al. (1995), Longhurst (1998), compiled by Taeger and Lazarus (2010)

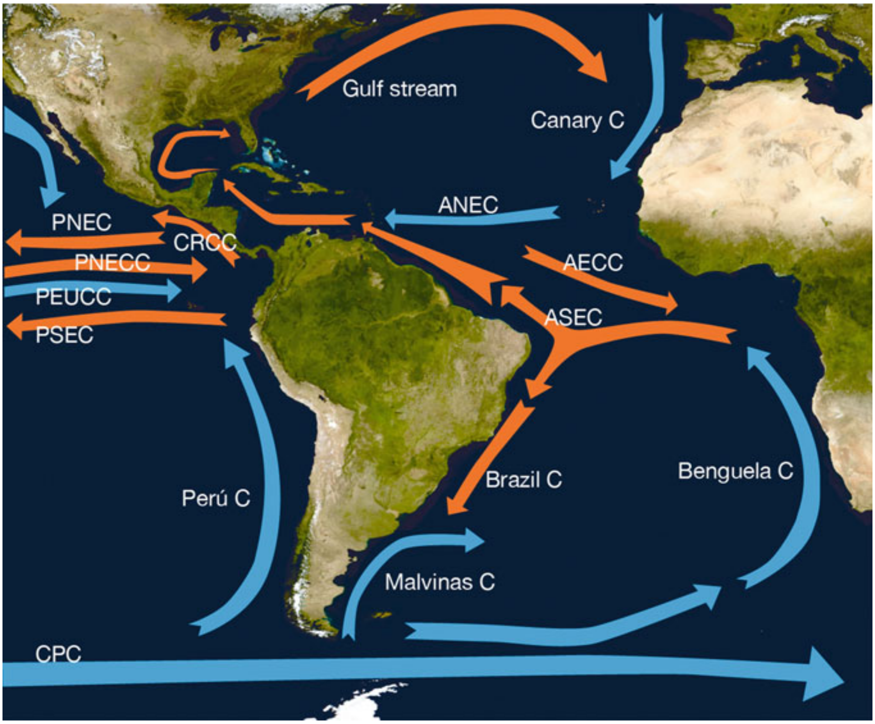


Fig. 16.2 Main current systems affecting the American coasts. *Orange arrows* correspond to warm currents, *blue arrows* correspond to cold currents. *PNEC* Pacific North Equatorial Current, *PNECC* Pacific North Equatorial Countercurrent, *PEUCC* Pacific Equatorial Undercountercurrent, *PSEC* Pacific South Equatorial Current; *CRCC* Costa Rica Costal Current; *CPC* Circumpolar current; *ANEC* Atlantic North Equatorial current; *AECC* Atlantic Equatorial Countercurrent; *ASEC* Atlantic South Equatorial Current

areas of the Pacific and Caribbean, exceeding 31 °C. The thermal range between summer and winter is greater than 25 °C in most areas and reaches 28.4 °C in the West Indies. Canary Islands show less variability, with a range of only 7.8 °C (Fig. 16.3a, b). In general, all the regions are productive. The Brazilian and Canary Islands provinces appear to be among the most productive in the world (1.92 and 2.01 g C $m^{-2}day^{-1}$, respectively) (Taeger and Lazarus 2010). However, in the case of the Canary Islands, this value is reached in the West African upwelling. Productivity in the archipelago is less and maximum chlorophyll concentration does not exceed 40.91 mg m^{-3}. Minimum mean chlorophyll concentration is reached in the Galápagos archipelago, with only 4.29 g m^{-3} (Fig. 16.3c).

The Caribbean, West Indian and Galápagos provinces are characterized by warm waters, with the highest photic depth and with a high mixed layer depth and low chlorophyll concentration and low productivity. The Panamanian and Mexican

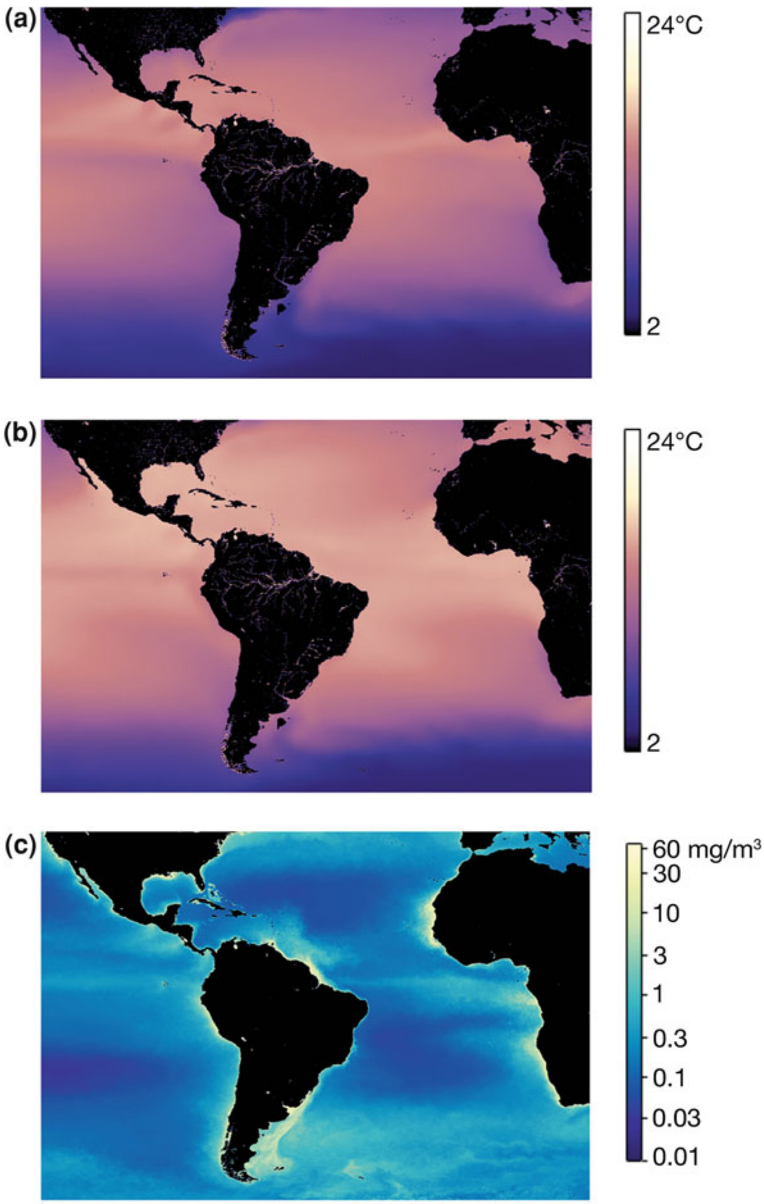


Fig. 16.3 Mean annual minimum (**a**) and maximum (**b**) sea surface temperature (°C) for the period 1982–1992 obtained from monthly satellite images. **c** Mean annual concentration of chlorophyll a (mgm^{-3}) for the period 2003–2010. Data source (http://neo.sci.gsfc.nasa.gov)

provinces share with the former the high temperature and photic depth, but have a narrow mixed layer depth and higher productivity. The Chilean, Easter Island and

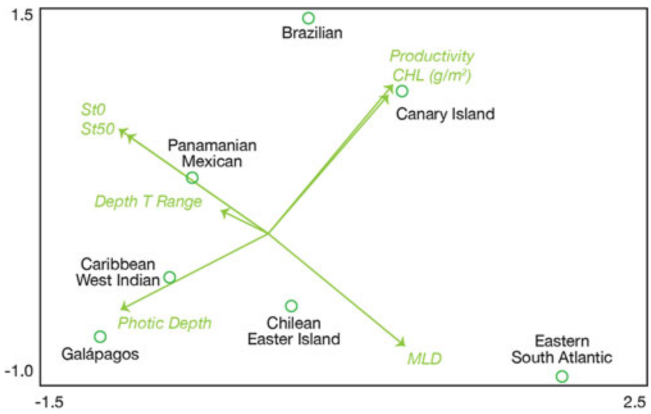


Fig. 16.4 Ordination of North, Central and South American biogeographical regions and environmental variables in a biplot representation of the first axes of the Principal Component Analysis (PCA) performed on the surface water column parameters according to Longhurst (see Table 16.1). Key to abbreviations for environmental variables are in Table 16.1

Eastern South Atlantic provinces are characterized by cold and transparent waters, with the highest mixed layer depth and low productivity (Fig. 16.4).

16.3 Diversity and Biogeographic Affinities

The echinoderm fauna of Latin America and the Canary Islands consist of 1,539 species, 82 species of Crinoidea, 392 species of Asteroidea, 521 species of Ophiuroidea, 242 species of Echinoidea and 302 species of Holothuroidea. Six hundred and twenty-seven species are found only along the Atlantic coasts of Central and South America, 597 species are found only along the Pacific coasts and oceanic islands and 19 species are found only in the Eastern Atlantic, in the Canary Islands.

Species richness is highly variable among the different countries, from 20 species in Easter Island and 23 species along the Caribbean coast of Guatemala to a maximum of 374 species in Cuba (Fig. 16.5a). However, the number of species is highly dependent of the coast length of the countries (Fig. 16.6). The number of species per 10 km of coast is 0.22 in Chile and 66.6 in Malpelo. Among biogeographical provinces (Fig. 16.7) the highest mean value is in the Panamanian province with 11.88 (s.e. $\pm$ 7.4) species per 10 km. However, Permanova analyses do not detect significant differences between provinces ($P = 0.255$).

The highest diversity (species richness (S), average taxonomic distinctness ($\Delta+$), total taxonomic distinctness ($s\Delta+$), average phylogenetic diversity (Phi+) and total phylogenetic diversity (sPhi+)) is in Caribbean and West Indian countries (Atlantic coasts of Mexico, Guatemala and Cuba). This suggests they could be the

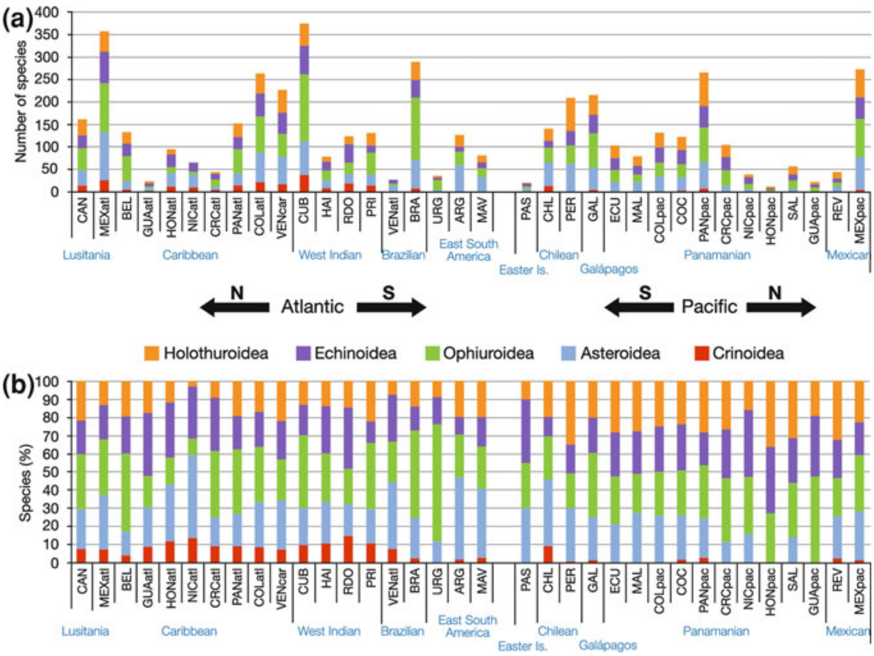


Fig. 16.5 Number of species (*up*) and percentage (*down*) of the five classes of echinoderms along the Pacific and Atlantic coasts of North, Central and South American countries and the Canary Islands. *MEX* Mexico; *REV* Revillagigedo Archipelago; *GUA* Guatemala; *SAL* El Salvador; *HON* Honduras; *NIC* Nicaragua; *CRC* Costa Rica; *COC* Cocos Island; *PAN* Panama; *COL* Colombia; *MAL* Malpelo Island; *GAL* Galápagos Archipelago; *ECU* Ecuador; *PER* Perú; *CHL* Chile; *PAS* Eastern Islands. *BEL* Belize; *VEN* Venezuela; *BRA* Brazil; *URG* Uruguay, *ARG* Argentina; *MAV* Malvinas Islands; *CUB* Cuba; *HAI* Haiti; *RDO* Dominican Republic, *PRI* Puerto Rico; *CAN* Canary Islands; atl: Atlantic; car: Caribbean; pac: Pacific

origin of North Atlantic and Eastern Tropical Pacific echinoderm faunas. Currently, both areas (Caribbean and West Indies) are quite similar in temperature regimes (maximum 31.21 °C in both areas, minimum 5.28 and 2.80 °C, mean 25.61 and 27.25 °C in the Caribbean and West Indian respectively), but differ in chlorophyll concentration (0.64 and 0.28 mg m^{-3} respectively).

On the other hand, there are significant differences (Permanova P = 0.001) in the percentage of the five classes of echinoderms between provinces (Fig. 16.5b). Ophiuroidea is the dominant class in most regions, except in the Chilean province that is dominated by Asteroidea, the Easter Island province that is dominated by Echinoidea and the Mexican province that is dominated by Holothuroidea. Crinoidea is always the least abundant class. Their absence in the Easter Island region and scarcity in the Eastern South America, Galápagos, Panamanian and Mexican provinces should be noted. The absence of Crinoidea has been also emphasized in other Atlantic archipelagos like Cabo Verde (Pérez-Ruzafa et al. 1999). It is also

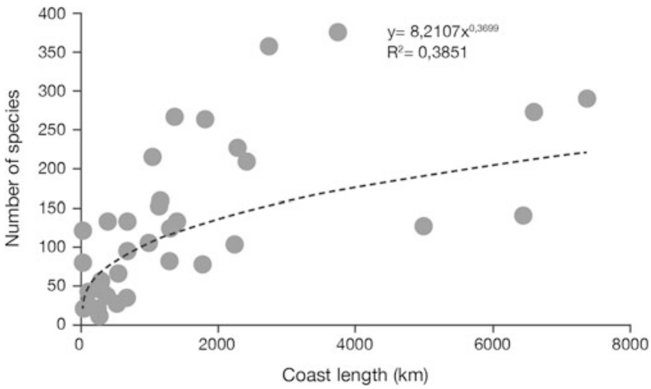


Fig. 16.6 Relationship between the number of echinoderm species and shore length of the Pacific and Atlantic coasts of the North, Central and South American countries and the Canary Islands

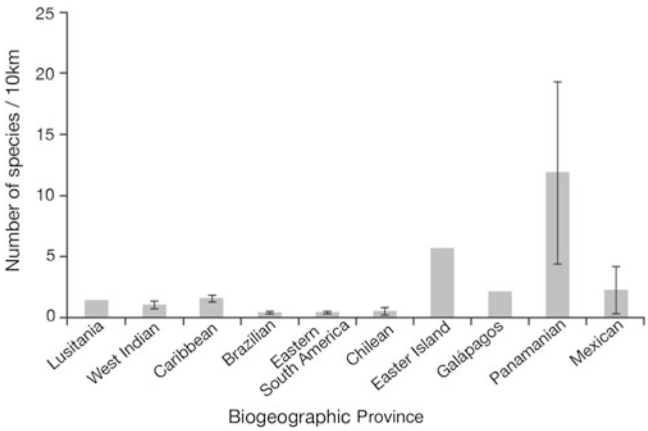


Fig. 16.7 Standardized species richness per 10 km shore length in the biogeographical provinces of North, Central and South American countries and in the Canary Islands. Error *bars* correspond to s.e. of the mean

worthwhile to note the negative relationship that exists between the dominance of holothurians in the faunas and the presence of crinoids (Fig. 16.8).

The echinoderm fauna of the different countries is consistent with their belonging to one of the above mentioned regions and provinces. NMDS analyses, performed with Bray-Curtis similarity calculated on species presence-absence (Bray and Curtis 1957), spatially distributed the countries according to their geographic location and importance to a given province (Fig. 16.9). The plot shows two well-established clusters. One includes the Panamanian, Galápagos and

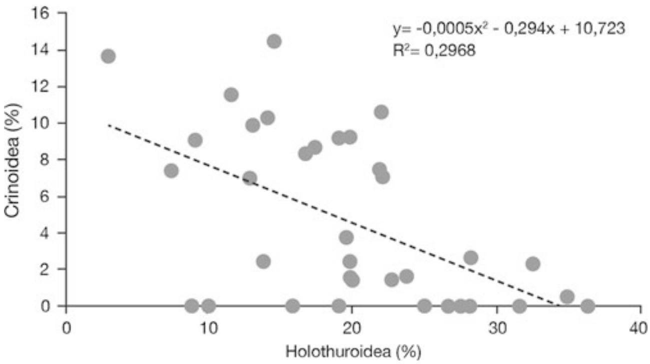


Fig. 16.8 Negative relationship between the percentage of species of crinoids and holothurians of the North, Central and South American countries and in the Canary Islands

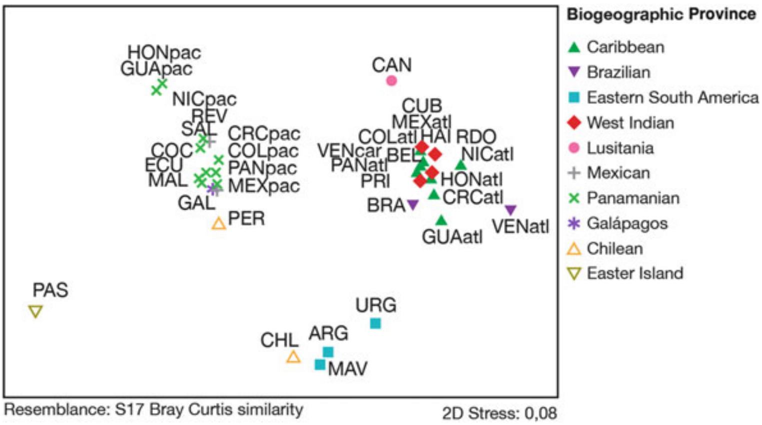


Fig. 16.9 Multivariate analysis nMDS plot of distance-related echinoderm species assemblage structure from Latinamerica based on species composition data and Bray-Curtis similarity measure. The faunal similarity between biogeographical provinces is represented by the relative distance. *MEX* Mexico; *REV* Revillagigedo Archipelago; *GUA* Guatemala; *SAL* El Salvador; *HON* Honduras; *NIC* Nicaragua; *CRC* Costa Rica; *COC* Cocos Island; *PAN* Panama; *COL* Colombia; *MAL* Malpelo Island; *GAL* Galápagos Archipelago; *ECU* Ecuador; *PER* Perú; *CHL* Chile; *PAS* Eastern Islands. *BEL* Belize; *VEN* Venezuela; *BRA* Brazil; *URG* Uruguay, *ARG* Argentina; *MAV* Malvinas Islands; *CUB* Cuba; *HAI* Haiti; *RDO* Dominican Republic, *PRI* Puerto Rico; *CAN* Canary Islands; atl: Atlantic; car: Caribbean; pac: Pacific

Chilean provinces to the tip of the Eastern South American region. Another cluster well separated region includes the Caribbean, West Indian, Lusitanica and Brazilian provinces. Earlier studies (Maluf 1988a, 1991) and results presented here suggest that the echinoderm faunas of the Panamic, Galápagos and the Chilean provinces are biogeographically related. There is a low level of association among echinoderm species from the Chilean fauna and Eastern South American

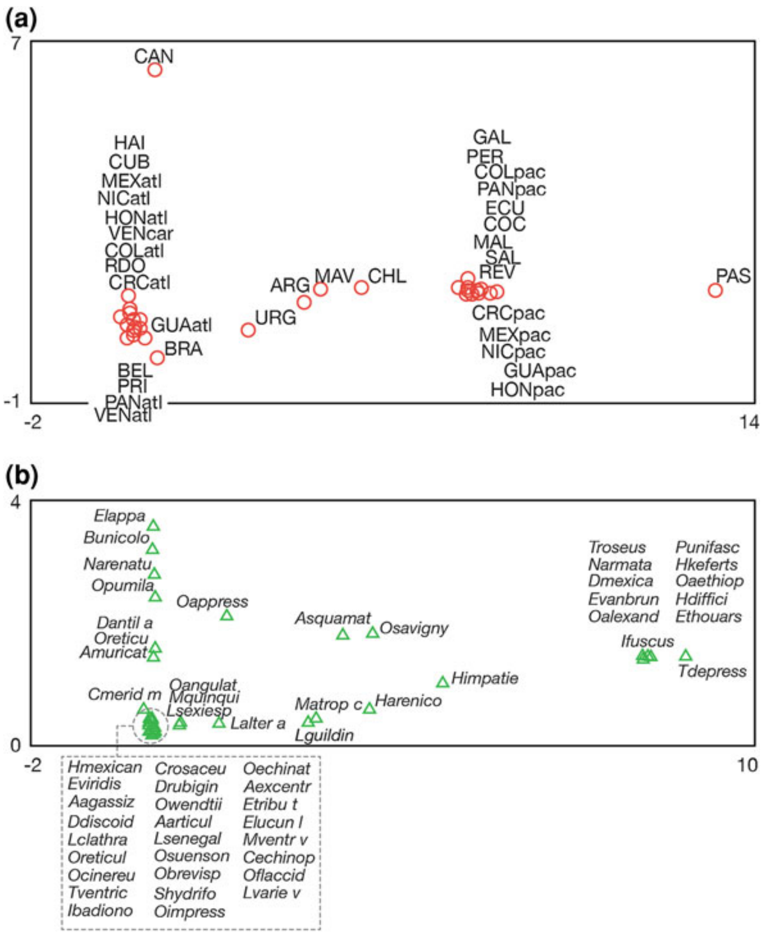


Fig. 16.10 **a** Ordination of countries in the representation of the first axes of the Detrended Correspondence analysis (DCA) performed on the echinoderm species matrix. **b** Ordination of species in the representation of the first axes of the Detrended Correspondence analysis (DCA) performed on the echinoderm species matrix. Only species with a weight >40 % on the axis are represented. *MEX* Mexico; *REV* Revillagigedo Archipelago; *GUA* Guatemala; *SAL* El Salvador; *HON* Honduras; *NIC* Nicaragua; *CRC* Costa Rica; *COC* Cocos Island; *PAN* Panama; *COL* Colombia; *MAL* Malpelo Island; *GAL* Galápagos Archipelago; *ECU* Ecuador; *PER* Perú; *CHL* Chile; *PAS* Eastern Islands. *BEL* Belize; *VEN* Venezuela; *BRA* Brazil; *URG* Uruguay, *ARG* Argentina; *MAV* Malvinas Islands; *CUB* Cuba; *HAI* Haiti; *RDO* Dominican Republic, *PRI* Puerto Rico; *CAN* Canary Islands; atl: Atlantic; car: Caribbean; pac: Pacific

biogeographic region. Chile is closer to Argentina and the Malvines than to Peru. In fact, there are two biogeographical provinces, the Peru-Chilean and the South America or Magellan.

The first two axis of the Detrended Correspondence Analyses (DCA), also performed on country species composition, also show a geographical ordination,

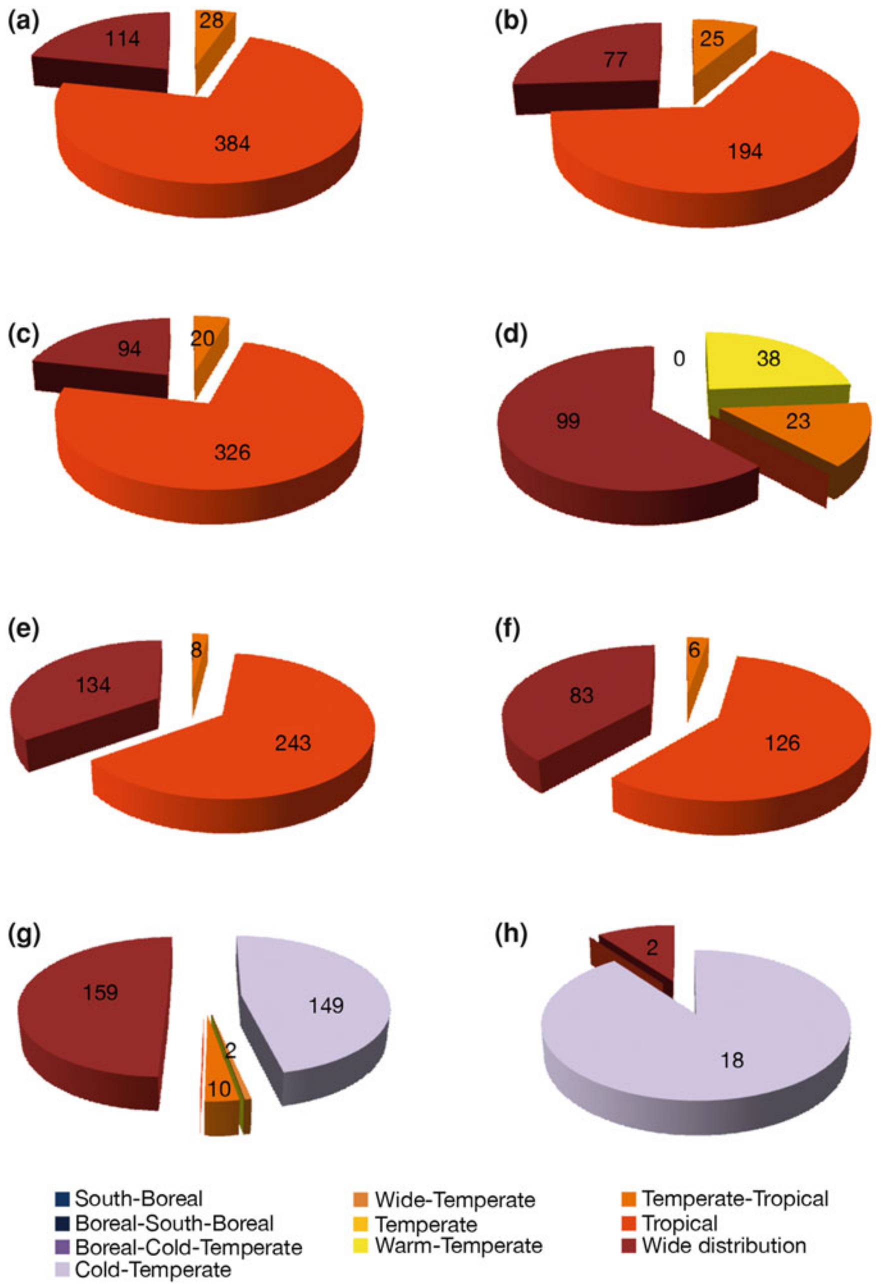


Fig. 16.11 Composition of the echinoderm faunal assemblages of the biogeographical provinces of North, Central and South America and the Canary Islands according to the thermal distribution range of the species inventoried. **a** Caribbean, **b** Brazilian, **c** West Indian, **d** Canary Is. (Lusitania), **e** Panamanian, **f** Galápagos, **g** Chilean, **h** Easter Island

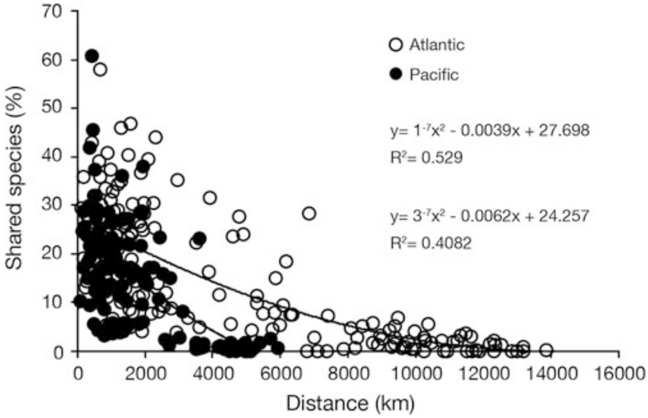
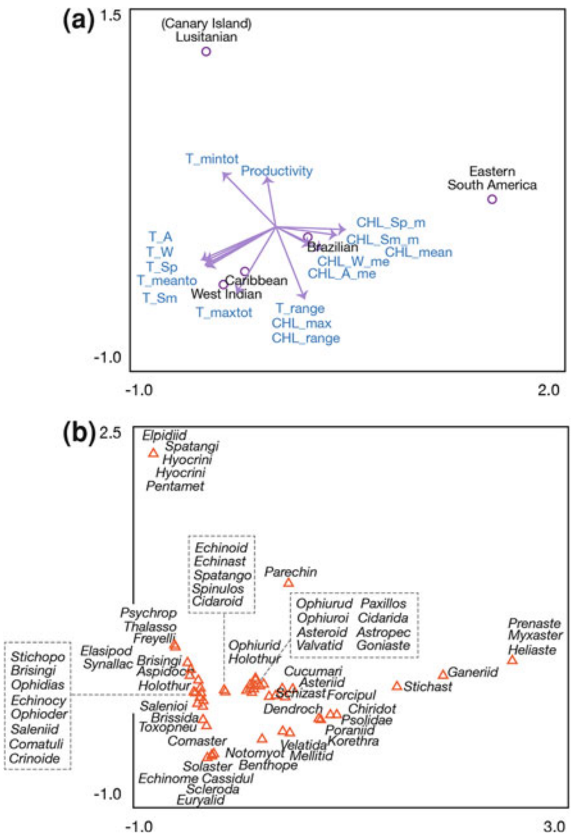


Fig. 16.12 Number of echinoderm species shared by two countries as a function of the distance between them. Distances have been calculated using the geographical coordinates at the *midpoint* of their *shorelines*

Fig. 16.13 Ordination of samples (biogeographical areas) and environmental variables (**a**) and families (**b**) in the representations of the first axes of the canonical correspondence analysis (CCA) performed on the matrix containing the number of species representing the echinoderm orders and families in the different Atlantic biogeographical provinces



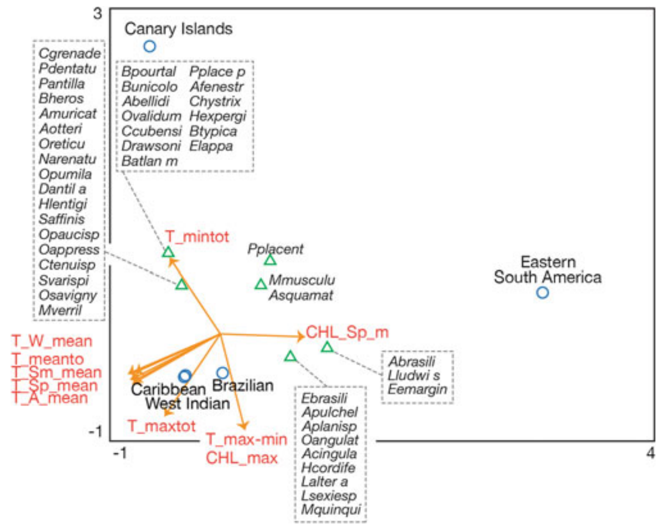


Fig. 16.14 Ordination of samples (biogeographical areas) and environmental variables (**a**) and species (**b**) in the representations of the first axes of the canonical correspondence analysis (CCA) of Atlantic echinoderm species matrix using environmental data as explanatory variables. Key of abbreviations for environmental variables and species are in Table 16.1

with North Atlantic locations on the second axis, Pacific countries on the positive part of the first axis, and Southern Atlantic, and Southern Pacific countries as a transition between the two main groups. The first axis, which determines the separation of Atlantic and Pacific faunas and the gradient throughout the Magellan region explain 29.6 % of total variance. The second axis explains only an additional 3.8 % (Fig. 16.10a).

The species represented in Fig. 16.10b are those that have a weight on the axis higher than 40 %. The positive part of axis 1 is represented by species exclusive to the Pacific and with a wide distribution in this ocean, like the sea urchins *Toxopneustes roseus*, *Diadema mexicanum Echinometra vanbrunti*, *Eucidaris thouarsii*, *Tripneustes depressus*, the sea stars *Nidorellia armata*, *Ophidiaster alexandri, Phataria unifascialis*, the ophiuroids *Ophiocoma aethiops* and the holothuroids *Holothuria (Halodeima) kefersteini, Holothuria (Platyperona) difficilis, Isostichopus fuscus*.

The left extreme of axis 1 is characterized by exclusively Atlantic species. In the lower part of the axis 2 are widely distributed species and exclusively from the western Atlantic coasts, like the crinoids *Comactinia meridionalis meridionalis, Davidaster discoideus*, the ophiuroids *Ophionereis reticulata*, the sea star *Luidia clathrata*, the sea urchin *Echinometra viridis* or the holothuroids *Holothuria (Halodeima) mexicana, Actinopyga agassizii.*

Between both extremes are ubiquitous species, widely distributed in both oceans, like the ophiuroids *Ophiactis savignyi* and *Amphipholis squamata*, the

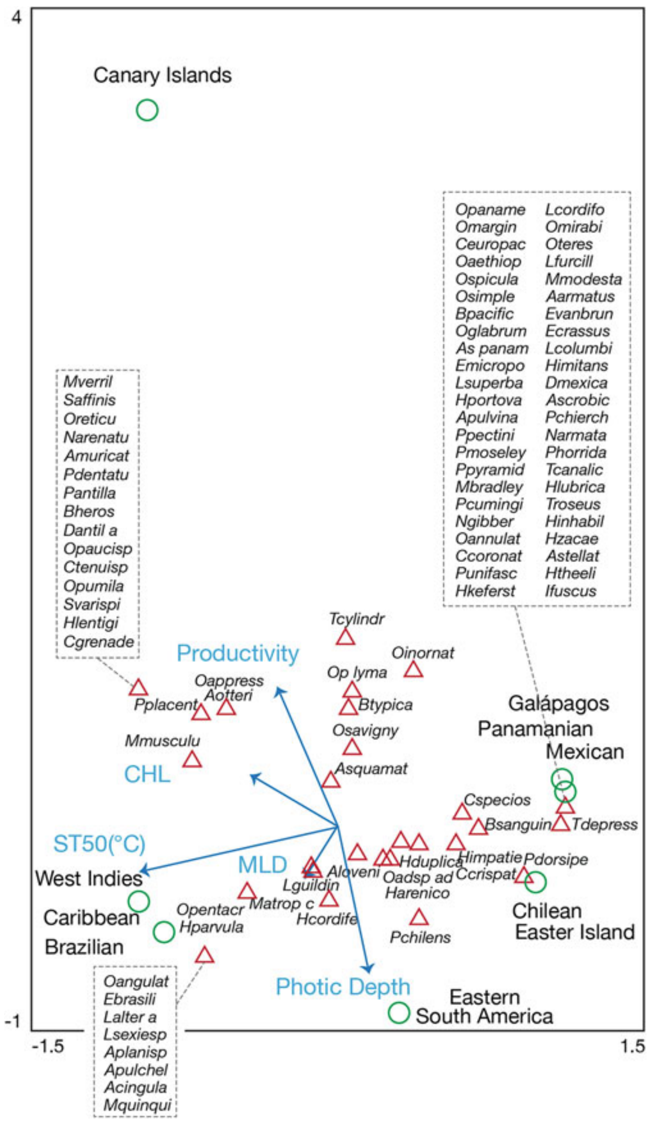


Fig. 16.15 Ordination of samples (biogeographical areas) and environmental variables (**a**) and species (**b**) in the representations of the first axes of the canonical correspondence analysis (CCA) of Atlantic and Pacific echinoderm species matrix using environmental data as explanatory variables. Key of abbreviations for environmental variables and species are in Table 16.1

holothuroids *Holothuria (Thymiosycia) arenicola* and *Holothuria (Thymiosycia) impatiens*, and the sea star *Linckia guildingi*.

Along the axis 2 are anfiatlantic species, shared by the American coasts and the Canary Islands, like the ophiuroids *Astrophyton muricatum, Ophiocoma pumila*,

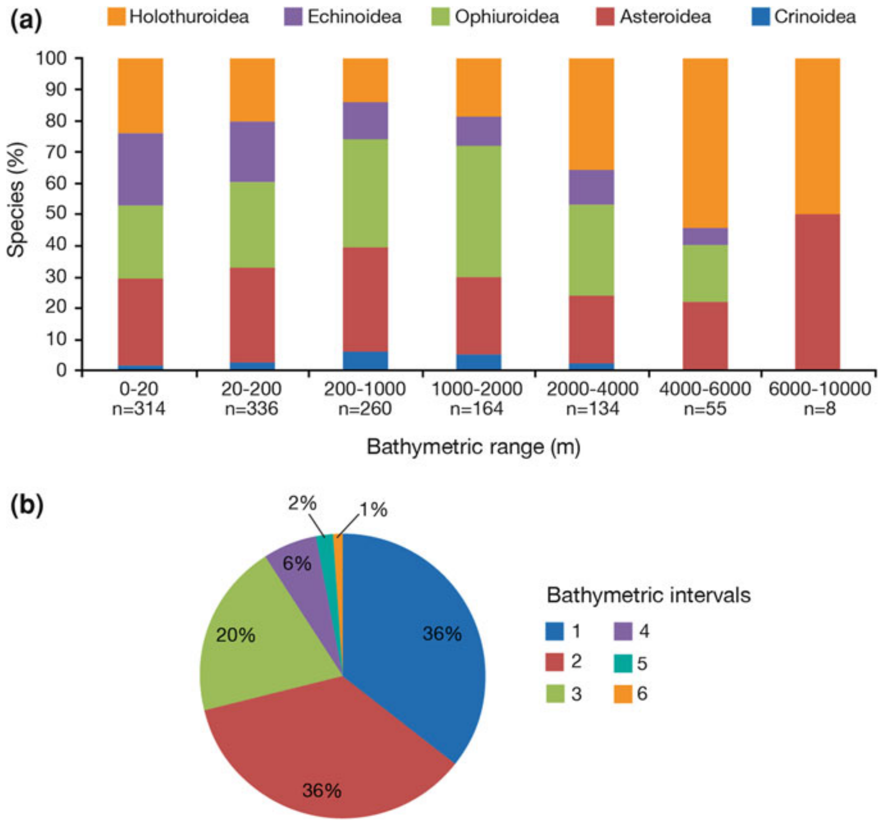


Fig. 16.16 **a** Percentage of echinoderm species per class by bathymetric range in the Pacific taxonomic list and **b** percentage of species present in one to six bathymetric intervals. N = 620 species

the sea stars *Oreaster reticulatus*, *Nymphaster arenatus*, the sea urchins *Diadema antillarum antillarum, Brissus unicolor* and the holothuroid *Euapta lappa*.

Cosmopolitan species are an important component in all the biogeographical regions (Fig. 16.11). Except the Chilean and the Easter Island provinces, which are dominated by cold temperate species. The Central and South American regions are dominated by tropical species and to a lesser extent, temperate species with a wide distribution range. In the Canary Islands, the warm temperate component is also important.

Similarity between country faunas depends on climatic and trophic conditions and on geographical proximity. The number of shared species is highly dependent on the distance separating two countries (Fig. 16.12). The diminishing proportion of shared species between two areas with increasing geographical distance is an obvious feature of natural systems (Hengeveld 1990; Huston 1994; Rosenzweig 1995; Brown and Lomolino 1998; Hubbell 2001).

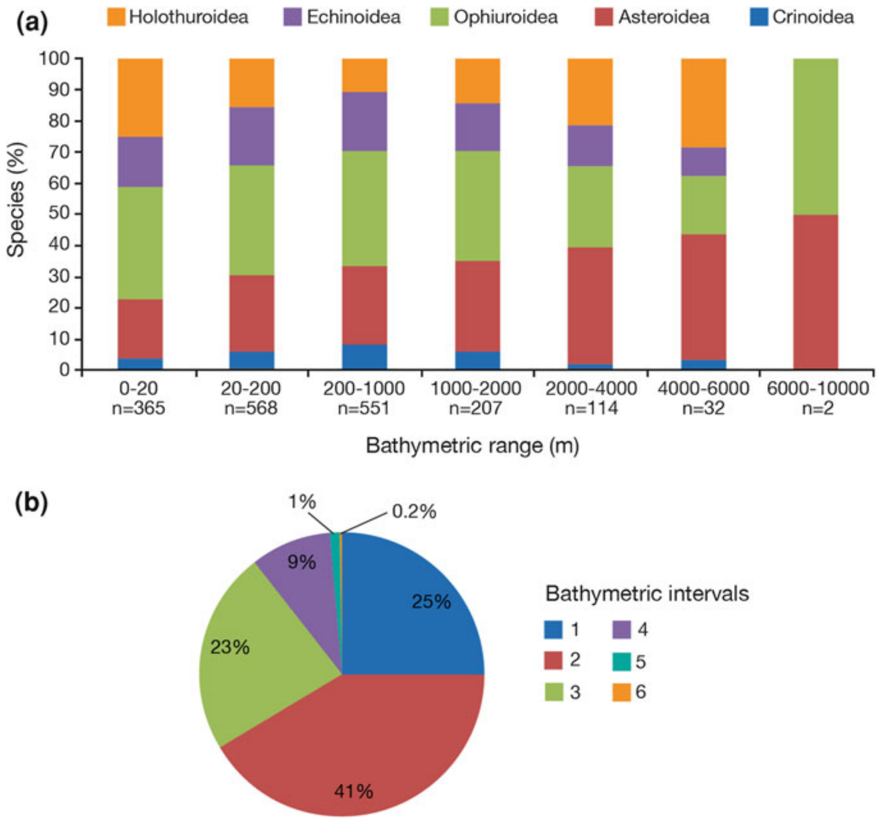


Fig. 16.17 **a** Percentage of echinoderm species per class by bathymetric range in the Caribbean and Atlantic taxonomic list and **b** percentage of species present in one to six bathymetric intervals. N = 836 species

There are more islands in the Atlantic region (i.e. the Lesser Antilles). Geographical distance between islands might be an important source of similarity in terms of species richness and taxonomic composition. Two islands may share the same number of species not because they are similar in area and/or in diversity because they are geographically close (Rosenzweig 1995), which allows individuals to move easily from one island to the other.

Canonical Correspondence analyses performed on the number of species representing the echinoderm orders and families in the different biogeographical provinces (Fig. 16.13) are consistent with the previous non-canonical analyses on species presence-absence data and climatic conditions. Figure 16.13 shows the results obtained for Atlantic provinces. The environmental variables used were mean seasonal and mean, minimum, maximum and range of variation annual values obtained from monthly satellite data for sea surface temperature (1982–1991) and for chlorophyll (2003–2010). Productivity values were obtained

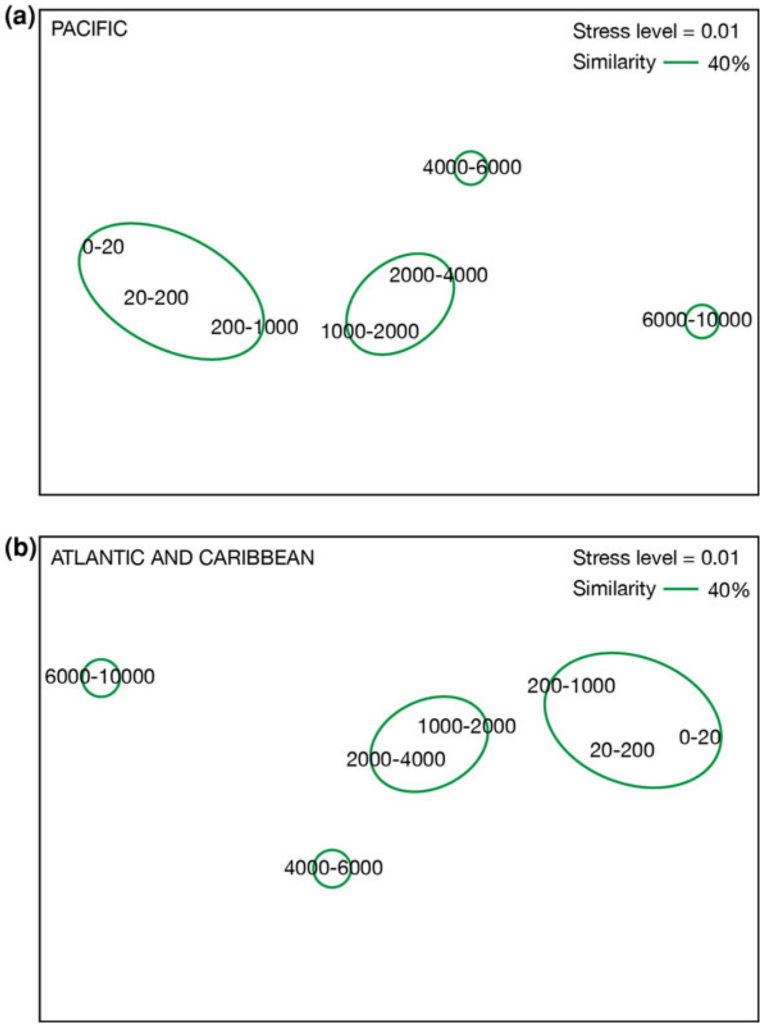


Fig. 16.18 Multivariate analysis nMDS *plot* of distance-related echinoderm species assemblage structure from **a** the Pacific taxonomic list and **b** the Caribbean and Atlantic taxonomic list, based on species presence/absence matrix by bathymetric interval using Bray-Curtis similarity measure

from Longhurst et al. (1995), Longhurst (1998), compiled by Taeger and Lazarus (2010) (Table 16.1).

The first two axes account for 46.6 and 30.3 %, respectively, of the total variance of species-environment relation. The first axis represents a gradient from the Caribbean and West Indies to the south. The positive extreme of the first axis is associated with the Eastern South America region and highest mean chlorophyll concentration in all seasons and the lowest temperatures. It is represented by the

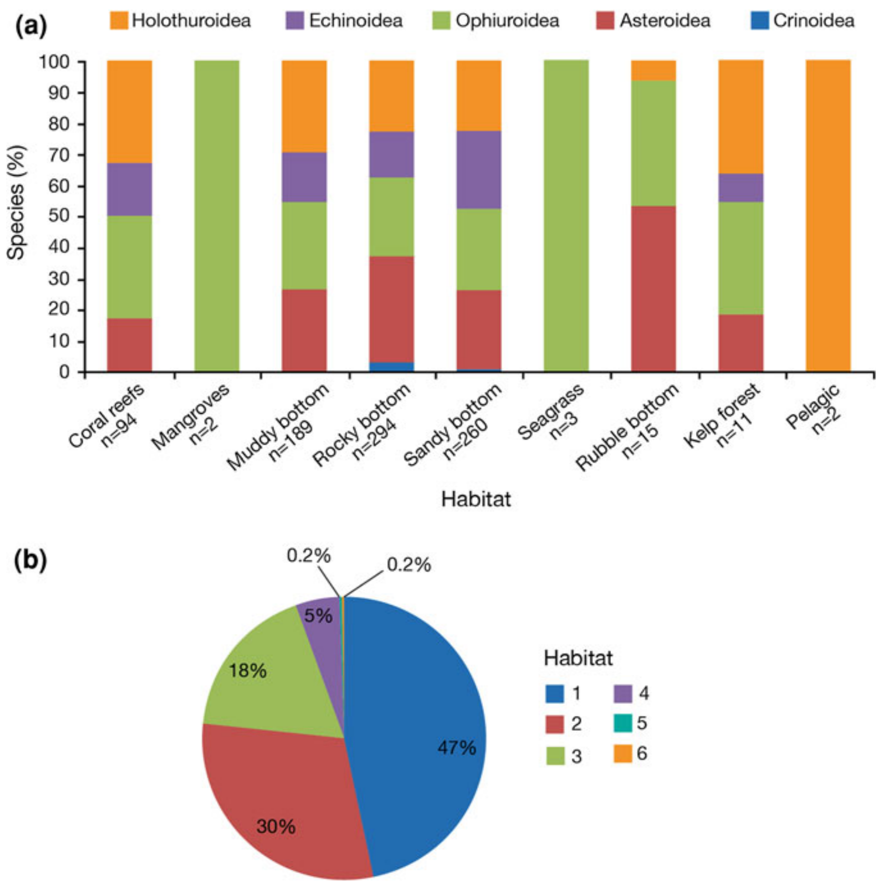


Fig. 16.19 **a** Percentage of echinoderm species per class by habitat type in the Pacific taxonomic list and **b** percentage of species presents in one to seven habitat types. N = 473 species

families Heliasteridae, Stichasteridae, Ganeriidae, Myxasteridae and Prenasteridae. The Myxasteridae is exclusive to the Eastern South America region and the Prenasteridae is shared with the Chilean province.

In the negative part of this axis, associated with highest temperatures and low chlorophyll concentration, are families with a wide distribution in the Atlantic but absent in the Eastern South America region like Echinocyamidae. Some of them like Brisingida, Ophidiasteridae, Saleniidae, Stichopodidae, Ophiodermatidae or the class Crinoidea are even present along Pacific coasts. This indicates their tropical origin and ancient links, prior to closure of the Isthmus of Panama. In general, these families are represented by different species in each ocean. For example, the sea star family Ophidiasteridae, is present in the area with 29 species, 14 in the Pacific, five in the Western Atlantic and nine in the Anfiatlantic. None is shared between the Atlantic and Pacific coasts. Congeneric species are *Ophidiaster*

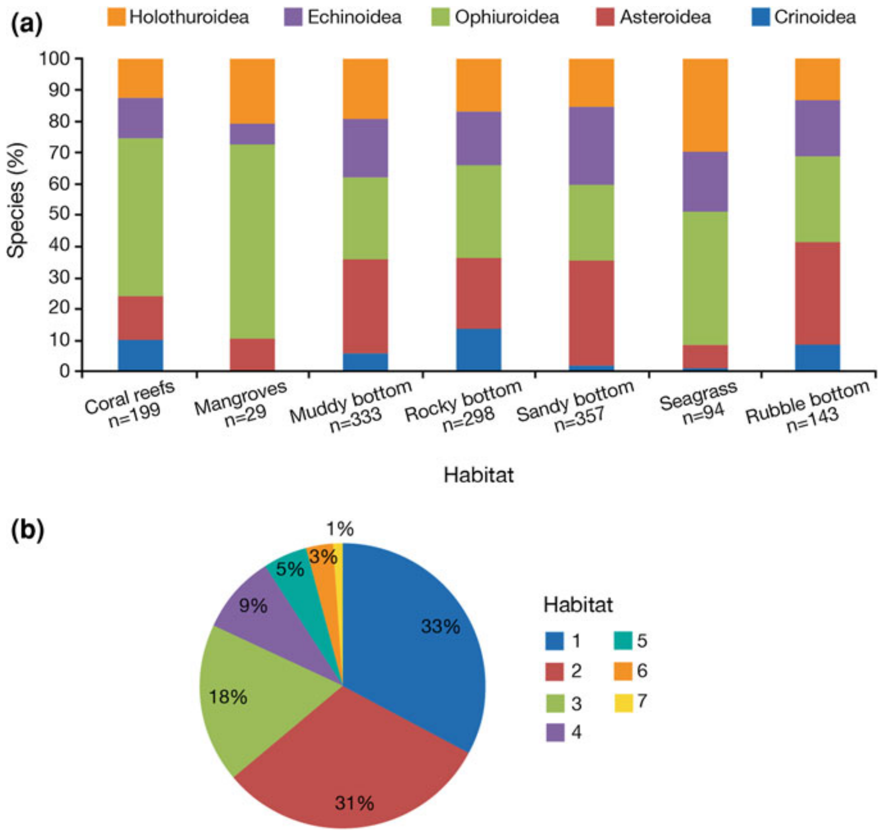


Fig. 16.20 **a** Percentage of echinoderm species per class by habitat type in the Caribbean and Atlantic taxonomic list and **b** percentage of species presents in one to seven habitat types. N = 630 species

alexandri, Ophidiaster bayeri, Tamaria floridae and *Tamaria halperni* in the Western Atlantic, *Ophidiaster agassizi, Ophidiaster ludwigi* along the Pacific coasts, and *Tamaria obstipa* and *Tamaria stria*. *Ophidiaster guildingii* and *Ophidiaster ophidianus* in the Anfiatlantic. *Narcissia canariensis* and *N. trigonaria* are Anfiatlantic, *Narcissia gracilis* and the subspecies *N. gracilis malpeloensis* occur in the Pacific.

The second axis represents a Western–Eastern gradient. Pentametrocrinidae, Elpidiidae, Hyocrinidae and Spatangidae characterize the positive part of this axis. Pentametrocrinidae is present in the Canary Islands and is not shared with south American regions, Elpidiidae and Hyocrinidae are shared by the Canary Islands and all the Pacific regions except Easter Island, but are absent in the South American coasts. In the same way, Spatangidae is a family shared by the Canary Islands and the Pacific Mexican coast but is absent from the other regions.

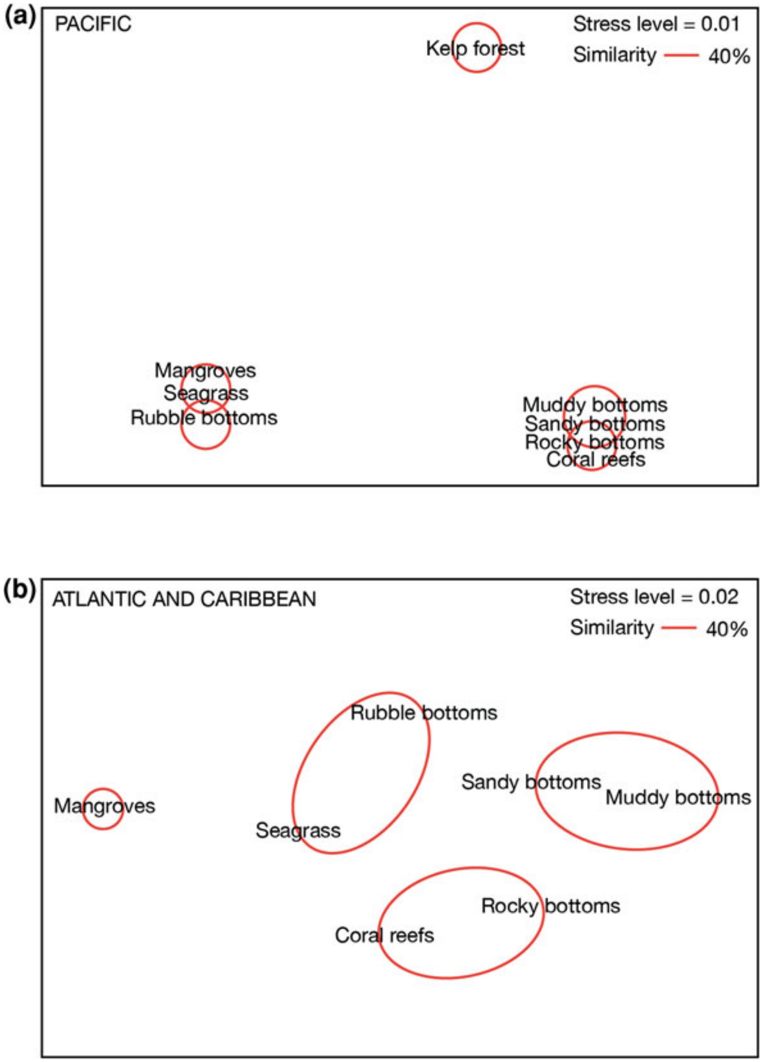


Fig. 16.21 Multivariate analysis nMDS plot of distance-related echinoderm species assemblage structure from the **a** the Pacific taxonomic list and **b** the Caribbean and Atlantic taxonomic list, based on species presence/absence matrix by habitat category using Bray-Curtis similarity measure

The negative part of this axis is represented by the families Solasteridae, Echinometridae, Sclerodactylidae and the order Cassiduloida. All of them are present in the Caribbean, West Indian and Brazilian provinces, and even in the warm Pacific coasts. But they are not present in the Canary Islands or the Eastern South America region. It indicates a common tropical origin, after the separation of western and eastern Atlantic coasts but prior to closure of the Isthmus of Panama.

The same analyses performed on species presence-absence data can be seen in Fig. 16.14 for the Atlantic regions and Fig. 16.15 for Pacific and Atlantic Regions. The figure includes only species fitting more than 50 % of the axis and weighting more than 50 %.

As previously mentioned, the affinities between faunas are a consequence of the combination of climatic and trophic factors, connectivity as a function of distance, current patterns and historical processes. The partition of the variance to see the relative influence of environmental variables and spatial organization (latitude and longitude coordinates) was done following the methodology proposed by Borcard et al. (1992). It shows that the covariation of space and environment reach 62.2 % in the case of Atlantic provinces. The environmental variables alone are responsible for 37.8 % of the variance. The covariation of space and environment of the Atlantic and Pacific regions analyzed together account for only 11.4 % of the variability while environmental variables explain 58.6 % of the variability. There is 14.5 % variation that is purely spatial and an additional 15.5 % is of unexplained variation and stochastic fluctuations or due to historical processes linked to the isolation of the faunas of the Caribbean and tropical Pacific after the closure of the isthmus of Panama.

Furthermore, different environmental factors would be responsible for faunal composition and species distribution at different spatial scales (Barry and Dayton 1991; Levin 1992; Pérez-Ruzafa et al. 2003; Entrambasaguas et al. 2008). Water temperature is considered the most important influence on the global distribution of marine animals and minimum temperature is usually the factor that determines faunal similarities at small geographical scales (Steele 1983; Pérez-Ruzafa and López-Ibor 1988; Pérez-Ruzafa et al. 2003). Factors such as predation (Tegner and Dayton 1981; Sala 1997), settlement and recruitment (Young and Chia 1982; Ebert 1983; Hereu et al. 2004; Hernández et al. 2010), availability of trophic resources (Menge 1992), disease epidemics (Hagen 1999; Dumont et al. 2004), or competitive interactions (Hagen and Mann 1992), physical factors like substrate nature, bottom complexity, depth, wave exposition, etc. (Drouin et al. 1985; Tyler et al. 2000; Entrambasaguas et al. 2008) or harvesting (Pfister and Bradbury 1996; Hasan 2005) are of major importance in explaining small scale species distribution and abundance.

16.4 Bathymetrical and Substrate Distribution

In the Pacific taxonomic list (see appendix) there were 620 species of echinoderms with bathymetric information (Fig. 16.16) that represent 86 % of the species of the list, while in the Caribbean and Atlantic taxonomic list (see appendix) there were 836 species, that represent 92 % of the species on the list (Fig. 16.17). In the Pacific most species were reported at depths between 20 and 200 m (336 species), 30 % in the class Asteroidea (Fig. 16.16a). This class was also the predominant at depths between 0 and 20 m (28 %). The class Ophiuroidea was the predominant at depths between 200–1,000 m (35 %) and 1,000–2,000 m (42 %). The class Holothuroidea was predominant at depths between 2,000–4,000 m (36 %) and 4,000–6,000 m (55 %). Most species on the Pacific list were found only in one or two bathymetric intervals (each 36 %) while just 2 and 1 % were found in five and six bathymetric intervals respectively (Fig. 16.16b). In the Caribbean and Atlantic list most species were also at depths between 20 and 200 m (568 species) (Fig. 16.17a), 35 % in the class Ophiuroidea. This class also predominated at depths between 0–20 m (36 %), 200–1,000 m (37 %) and 1,000–2,000 m (35 %). The class Asteroidea was predominant at depths between 2,000–4,000 m (38 %) and 4,000–6,000 m (41 %). Most of the species on the Caribbean and Atlantic list were found only in two or one bathymetric intervals (41 and 25 %, respectively) while only 1 and 0.2 % were found in five and six bathymetric intervals respectively (Fig. 16.17b).

According to the depth categories in the Pacific and the Caribbean-Atlantic, the similarity analysis showed four groups with 40 % resemblance (Fig. 16.18a, b). The first group is composed by the depths from 0 to 20 m, 20 to 200 m and 200 to 1,000 m. These groups possesses the highest number of species (314, 336, 260 species respectively in the Pacific and 365, 568, 551 species in the Caribbean-Atlantic), Margalef species richness (54.4, 57.5, 46.5 respectively in the Pacific and 61.5, 89.2, 87.1 respectively in the Caribbean-Atlantic) and Shannon diversity (5.7, 5.8, 5.5 respectively in the Pacific and 5.8, 6.3, 6.3 respectively in the Caribbean-Atlantic). The second group is composed by depths from 1,000 to 2,000 m and 2,000 to 4,000 m, that possesses moderate values of number of species (164 and 134 species in the Pacific and 207 and 114 in the Caribbean-Atlantic), Margalef species richness (31.9 and 27.1 in the Pacific and 38.6 and 23.8 in the Caribbean-Atlantic) and Shannon diversity (5.1 and 4.8 in the Pacific and 5.3 and 4.7 in the Caribbean-Atlantic). The other two groups are composed by only one bathymetric interval (4,000–6,000 m and 6,000–10,000 m) and possesses the lowest values of all indices; number of species (55 and 8 species in the Pacific and 32 and 2 in the Caribbean-Atlantic), Margalef species richness (13.4 and 3.3 in the Pacific and 8.9 and 1.4 in the Caribbean-Atlantic) and Shannon diversity (4.0 and 2.0 in the Pacific and 3.4 and 0.6 in the Caribbean-Atlantic). Of the first two groups, the Caribbean-Atlantic always had higher values than the Pacific in all the indices. But in deeper waters (groups 3 and 4), the Pacific was richer than the Caribbean-Atlantic.

There were 473 species of echinoderms (66 % of the total) in the Pacific taxonomic list (see appendix) with habitat or substrate information (Fig. 16.19) In the Caribbean and Atlantic taxonomic list (appendix) there were 630 species (70 % of the total) with habitat or substrate information (Fig. 16.20). Most of the species in the Pacific were on rocky bottoms. Of the 294 species, 30 % are in the class Asteroidea (Fig. 16.19a). This class was also the predominant on rocky and rubble bottom (34 and 53 %, respectively). On coral reefs and in kelp forest, the classes Ophiuroidea (33 and 36 %, respectively) and Holothuroidea (33 and 36 %, respectively) were predominantd. Holothuroidea were predominant on muddy bottoms (30 %). On sandy bottoms, Asteroidea (26 %) and Ophiuroidea (26 %) were predominant. Most of the species in the Pacific list were found in only one habitat (each 47 %) while only 0.2 % were found in five and seven habitats (Fig. 16.19b). In the Caribbean and Atlantic list, most of the species were on sandy bottoms (357 species) (Fig. 16.20a), 33 % in the class Asteroidea. This class also was predominant on rubble (33 %) and muddy (30 %) bottoms. The class Ophiuroidea was predominant on coral reefs (50 %), mangroves (62 %), seagrass (43 %) and rocky bottoms (30 %). Most of the species in the Caribbean and Atlantic lists were found in only one habitat (33 %) while only 3 % and 1 % were found in six and seven habitats respectively (Fig. 16.20b).

There are three groups according to habitat categories in the Pacific (Fig. 16.21a). The first group is composed of coral reefs, muddy, rocky and sandy bottoms. These habitats possess the highest values of total species richness (94–294), Margalef species richness (20.3–51.4) and Shannon Diversity (5.3–5.9). The second group is composed by sea grass, mangroves and rubble bottom. These habitats possess low values of total species richness (2–15), Margalef species richness (1.4–5.2) and Shannon Diversity (0.7–2.7). The third group is composed by the kelp forest that possesses low values of the total species richness (11), Margalef species richness (4.2) and Shannon Diversity (2.3). In the Caribbean-Atlantic, the nMDS indicates the presence of four groups (Fig. 16.21b). The first one is composed of sandy and muddy bottoms that possess the highest values of total species richness (357–333 species respectively), Margalef species richness (60.4–57.1 respectively) and Shannon Diversity (5.9–5.8). The second group is composed of rocky bottoms and coral reefs that possess high to moderate values of total species richness (298–199 species respectively), Margalef species richness (52.1–37.4 respectively) and Shannon Diversity (5.7–5.3 respectively). The third group is composed of seagrass and rubble bottoms with moderate values of total species richness (94–143 species respectively), Margalef species richness (20.5–28.6 respectively) and Shannon Diversity (4.5–4.9 respectively). The last group is composed of mangroves that possess the lowest values of total species richness (29), Margalef species richness (8.3) and Shannon Diversity (3.4).

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