7

Marine Biodiversity of Eastern Tropical Pacific Coral Reefs

Jorge Cortés, Ian C. Enochs, Jeffrey Sibaja-Cordero, Luis Hernández, Juan José Alvarado, Odalisca Breedy, José Antonio Cruz-Barraza, Octavio Esquivel-Garrote, Cindy Fernández-García, Alicia Hermosillo, Kirstie L. Kaiser, Pedro Medina-Rosas, Álvaro Morales-Ramírez, Cristian Pacheco, Alejandro Pérez-Matus, Héctor Reyes-Bonilla, Rafael Riosmena-Rodríguez, Celeste Sánchez-Noguera, Evie A. Wieters, and Fernando A. Zapata

---

J. Cortés (✉) · J. Sibaja-Cordero · J.J. Alvarado · O. Breedy · O. Esquivel-Garrote · C. Fernández-García · Á. Morales-Ramírez · C. Sánchez-Noguera
Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica
e-mail: jorge.cortes@ucr.ac.cr

J. Sibaja-Cordero
e-mail: jeffrey.sibaja@ucr.ac.cr

J.J. Alvarado
e-mail: juanalva76@yahoo.com

O. Breedy
e-mail: odaliscab@gmail.com

C. Fernández-García
e-mail: cindyfdez28@gmail.com

Á. Morales-Ramírez
e-mail: alvaro.morales@ucr.ac.cr

C. Sánchez-Noguera
e-mail: celeste08@gmail.com

J. Cortés · J. Sibaja-Cordero · J.J. Alvarado · O. Breedy · O. Esquivel-Garrote · C. Fernández-García · Á. Morales-Ramírez
Escuela de Biología, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica

I.C. Enochs
Atlantic Oceanographic and Meteorological Laboratories (AOML), NOAA, 4301 Rickenbacker Cswy., Miami, FL 33149, USA
e-mail: ian.enochs@NOAA.gov

L. Hernández · H. Reyes-Bonilla
Laboratorio de Sistemas Arrecifales, Universidad Autónoma de Baja California Sur, Carretera al sur km. 5.5 colonia Mezquitito, C.P, 23080 La Paz, Baja California Sur, Mexico
e-mail: lghm@uabcs.mx

J.A. Cruz-Barraza · C. Pacheco
Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (Unidad Académica Mazatlán), Av. Joel Montes Camarena, s/n, 82000 Mazatlán, Sinaloa, Mexico
e-mail: cristian.pachecosolano@gmail.com

A. Hermosillo
Natural History Museum of Los Angeles County, 900 Exposition Blvd, Los Angeles, CA 90007, USA
e-mail: alicia_hg@prodigy.net.mx

K.L. Kaiser
Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, CA 93105, USA
e-mail: kirstie.kaiser@gmail.com

P. Medina-Rosas
Centro Universitario de La Costa, Universidad de Guadalajara, Puerto Vallarta, Jalisco, Mexico
e-mail: pedromedinarosas@gmail.com

A. Pérez-Matus
Subtidal Ecology Laboratory & Marine Conservation Center, Estación Costera de Investigaciones Marinas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile
e-mail: aperez@bio.puc.cl

R. Riosmena-Rodríguez
Programa de Investigación en Botánica Marina, Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, Apartado postal 19-B, 23080 La Paz, Baja California Sur, Mexico
e-mail: riosmena@uabcs.mx

C. Sánchez-Noguera
Leibniz Center for Tropical Marine Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany

E.A. Wieters
Estación Costera de Investigaciones Marinas, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
e-mail: ewieters@bio.puc.cl

F.A. Zapata
Departamento de Biología, Universidad Del Valle, Apartado Aéreo, 25360 Cali, Colombia
e-mail: fernando.zapata@correounivalle.edu.co

P.W. Glynn et al. (eds.), *Coral Reefs of the Eastern Tropical Pacific*,
Coral Reefs of the World 8, DOI 10.1007/978-94-017-7499-4_7

Abstract

The eastern tropical Pacific (ETP) is an isolated oceanic region exposed to extreme oceanographic conditions, including low salinity, low pH, high temperatures during El Niño, and low temperatures during La Niña and seasonal upwelling. The coral reefs in this region have a relatively limited suite of species compared to other coral reef areas of the world, but much like more diverse reefs the species present interact in complex ways. Here we synthezise the knowledge of taxonomic groups of reef organisms from prokaryotes to vertebrates, including algae, sponges, cnidarians, annelids and other worms, molluscs, crustaceans, echinoderms and fishes. We also present summaries on the biodiversity of associated functional groups and habitats, including (a) reef zooplankton and cryptic fauna, and (b) soft benthic environments, rhodolith beds and mesophotic environments. Several factors that structure the biodiversity of ETP coral reefs are explored, including biological, physical and chemical controls. ETP coral reefs are relatively simple systems that can be used as models for studying biodiversity and interactions among species. We conclude this review by highlighting pressing research needs, from very basic inventories to more sophisticated studies of cryptic assemblages, and to investigations on the impacts of natural and anthropogenic effects on ETP coral reef biodiversity.

Keywords

Reef invertebrates • Fishes • Algae • Plankton • Latin America

7.1 Introduction

The eastern tropical Pacific (ETP) is relatively isolated from other regions, yet has an equally diverse range of ecosystems and environments (Fiedler and Lavín 2006; Cortés and Wehrtmann 2009). Climate varies widely across the ETP, ranging from very dry in Baja California, coastal Mexico, northern Central America, southern Ecuador, and most oceanic islands, to very humid in central Costa Rica to northern Ecuador, including Isla del Coco (Amador et al. 2006). Ocean currents that flow within and between the ETP and adjacent regions vary seasonaly, yearly, and on longer time scales. These currents play an important role in the transport and dispersal of marine organisms (see Chap. 16, Lessios and Baums), and changes in nutrient concentrations, salinity and temperature in the region (Fiedler and Talley 2006; Kessler 2006; Lizano 2008).

The ETP region has been divided into separate biogeographic provinces based on the distributions of different taxa. Briggs (1974) divided it into three provinces that include coral reefs: Mexican Province (Gulf of California to Tehuantepec), Panamanian Province (El Salvador to Ecuador), and the Galápagos Islands. Boschi (2000), utilizing decapod crustacean distributions proposed two zoogeographic provinces, namely the Panamic (including the oceanic islands) and the Galápagos Archipelago. Spalding et al. (2007) divided the ETP into 11 ecoregions, and more recently Robertson and Cramer (2009), employing fish distributions, divided the ETP into three provinces, two including coastal areas (Cortez and Panamic) and one the oceanic islands.

7.2 Synopsis of the Biodiversity of ETP Coral Reef Regions

There are few compilations of marine biodiversity from the ETP, and fewer still emcompassing coral reefs. The following examples, listed according to country or region, refer to all coastal and marine ecosystems, including coral reefs where a significant number of the reported species are found (Table 7.1).

Mexico—Reyes-Bonilla et al. (2012) reported 5740 marine species in the Gulf of California, with many of these associated with coral reefs in the southern gulf area. From the current known records from Oaxaca, Bastida-Zavala et al. (2013) reported 2157 species spanning 15 taxonomic groups (ranging from plants to vertebrates). However, it should be recognized that sampling was biased toward some groups. For example, algae and three invertebrate groups (annelids, crustaceans and molluscs) represented over 55 % of the species reported. Since additional taxa are known from adjacent coastal areas, it is highly likely that the number of taxa reported by Bastida-Zavala et al. (2013) is underestimated.

Clipperton—Clipperton Atoll is one of the principal oceanic islands of the ETP (Glynn et al. 1996), with a relatively low biodiversity. This may be attributed to its

Table 7.1 Marine biodiversity of selected eastern tropical Pacific reef regions. Endem, number of endemic species

Regions	Algae	Invertebrates	Fishes	Others[a]	Total	Coral reef	Endem
ETP[1, 2]		85 (corals)				41	26
ETP[3]		2400 (molluscs)				>800	
ETP[3, 4]		850 (crustaceans)					
ETP[5, 6]		722 (echinoderms)					265
ETP[7, 8]			>1300				
Gulf of California, Mexico[9, 10]		4849	891		5740	74 (fishes)	852
Oaxaca, Mexico[11]	242	1153	594	168	2157		several
Mexico-Pacific[12]		76 (sponges)				76	
Clipperton, France[13, 14, 15]	83	576	197		857	290	38
El Salvador[16, 17]		868	100		968		0
Costa Rica-Pacific[18]	156	3379	838	372	4745		85
Golfo Dulce, Costa Rica[19]	11	741	276	199	1028		0
Bahía Culebra, Costa Rica[20, 21]	44	381	82	70	577		0
Isla del Coco, Costa Rica[22]	31	1168	389	100	1688		45
Panama[23]				1157[b]			
Isla Uva, Panama[24, 25]			102			102	
Bahía Honda, Panama[26]			126			88	
Coiba Island, Panama[27]	4	95	69	84	252		
Gorgona Island, Colombia[28]			71				
Ecuador (continental and insular)[29]		862	270	727	1859		
Galápagos Islands, Ecuador[30, 31]		3089	447		3536		565
Costa Rica, Panama, Colombia and Ecuador[32]		5502	1212		6714		122

[a] Foraminifera, phytoplankton, cyanobacteria, fungi, plants, vertebrates other than fishes

[b] Includes both Caribbean and Pacific coasts

Sources [1]Cairns (1991a), [2]Glynn et al. Chap. 6 this book, [3]This chapter, [4]Boschi (2000), [5]Pérez-Ruzafa et al. (2013), [6]Solís-Marín et al. (2013), [7]Robertson and Allen (2008), [8]Eschmeyer (2014), [9]Aburto-Oropeza and Balart (2001), [10]Reyes-Bonilla et al. (2012), [11]Bastida-Zavala et al. (2013), [12]Carballo et al. (2014), [13]Charpy (2009), [14]Payri et al. (2009), [15]Fourriére et al. (2014), [16]Barraza (2000), [17]Barraza (2014a, b), [18]Wehrtmann and Cortés (2009), [19]Morales-Ramírez (2011), [20]Dominici-Arosemena et al. (2005), [21]Cortés J et al. (2012), [22]Cortés (2012), [23]CDB-Panamá (2010), [24]Glynn (2006), [25]Glynn et al. (2014), [26]Dominici-Arosemena and Wolff (2006), [27]Castroviejo (1997), [28]Zapata and Morales (1997), [29]Cruz et al. (2003), [30]Bustamante et al. (2002), [31]Hickman (2009), [32]Miloslavich et al. (2011)

isolation from other land masses and homogeneity of the substrate, which is dominated by steep basaltic rocks and cemented massive corals (Glynn et al. 1996; Charpy 2009; Fourriére et al. 2014). A total of 857 marine species have been reported from Clipperton, and these are predominantly molluscs, fishes and decapods (Table 7.2).

El Salvador—El Salvador, with a relatively short coastal stretch (321 km), consists mainly of sandy beaches and very small coral patches and rocky areas. Only 868 species of invertebrates, mainly molluscs and crustaceans (Barraza 2000, 2014a), and 100 fish species have been reported (Barraza 2014b) from this region.

Costa Rica—The diversity of marine organisms in Costa Rica has been assessed recently by Wehrtmann and Cortés (2009). They reported 4745 species from the Pacific coast of Costa Rica, including 1142 species from Isla del Coco. New records (Cortés 2012) document the occurrence of 1688 species at Isla del Coco, an increase of 32 % in just a few years. Golfo Dulce, an anoxic basin in southern Costa Rica (Hebbeln and Cortés 2001), is also species rich with 1028 described taxa (Morales-Ramírez 2011). Bahía Culebra is a relatively well-studied but small area in northern Costa Rica with 577 documented species (Cortés J et al. 2012). The most speciose groups in Costa Rica are molluscs, fishes and decapods (Wehrtmann et al. 2009).

Panama—Coral reefs occur on the Caribbean and Pacific coasts of Panama, the latter with two contrasting environments, a seasonal upwelling area in the Gulf of Panama and a non-upwelling region in the Gulf of Chiriquí (Glynn 1972a, b; Glynn and Maté 1997; Maté 2003; Guzman et al. 2004, 2008). A total of 1157 species of marine fishes have been reported from both coasts (CDB-Panamá 2010). Glynn (2006) reported 50 species of mostly small cryptic reef fishes and 52 additional species (≥ 15 cm total body length)

Table 7.2 Marine biodiversity of Clipperton Atoll and the biogeographic affinity of nine taxa

Taxon	Coral reef	Biogeographic affinity	Endemics
83 (Algae)[1]	n.r.	81 % West-Central Pacific, 4 % Eastern Pacific, 15 % unidentified species	3
20 (Sponges)[2]	20	90 % Indo-Pacific, 10 % Eastern Pacific	9
22 (Corals)[3]	22	68.4 % Indo-Pacific, 31.6 % Eastern Pacific	0
277 (Molluscs)[4]	n.r.	50 % Indo-West Pacific, 50 % Panamic	0
26 (Polychaetes)[5]	26	42 % Cosmopolitan, 23 % Eastern Pacific, 35 % Panamic	0
14 (Bryozoa)[6]	14	Most with North America	0
190 (Decapods)[7]	95	44 % Indo-West Pacific	19
28 (Echinoderms)[8]	n.r.	46.4 % Indo-Pacific, rest Eastern Pacific	0
197 (Fishes)[9]	106	Most Indo-Pacific	7

n.r. Not reported

Sources [1]Payri et al. (2009), [2]Soest et al. (2011), [3]Flot and Adjeroud (2009), [4]Kaiser (2009), [5]Solís-Weiss and Hernández-Alcántara (2009), [6]Hondt (2009), [7]Poupin et al. (2009), [8]Solís-Marín and Laguarda-Figueras (2009), [9]Fourriére et al. (2014)

observed in swimming transects at the Uva Island coral reef (Glynn et al. 2014). Other than the early taxa-specific reviews in Jones (1972) of marine plants (Earle 1972), crustaceans (Abele 1972), echinoderms (Chesher 1972), and fishes (Robins 1972), no comprehensive reports of the marine biodiversity of Panamanian coral reefs exist. However, several notable advances documenting the biotic richness of reef taxa have been forthcoming in recent decades. One of these, a preliminary inventory of the marine biota of the Coiba Island National Park, reported 252 species ranging from algae to cetaceans (Castroviejo 1997).

Colombia—Colombia, with coasts bordering the Caribbean and ETP, and a marine area of nearly 1,000,000 km^2 encompassing numerous marine habitats, is likely one of the most biologically diverse countries in the Americas (Díaz and Acero 2003). Several Colombian studies (e.g., Alonso et al. 2008) indicate a very high marine biodiversity, but an estimate of the total number of species could not be found.

Ecuador—James (1991) was the first to compile the available information on invertebrate taxonomy and biogeography of the Galápagos Islands. Cruz et al. (2003) reported 1859 species of marine organisms present in continental and insular Ecuador. This contrasts greatly with the 3536 species reported by Hickman (2009) for the Galápagos Islands alone, which was based on an updated list of marine species complied by Bustamante et al. (2002). Of those species, 3089 are invertebrates, predominantly molluscs, crustaceans and echinoderms, and 18.3 % of this fauna is endemic to the Galápagos Islands.

Chile—Two remote volcanic islands on the Easter Fracture Zone are now recognized as belonging to the ETP coral reef region: (1) Rapa Nui or Easter Island (163.6 km^2 in area), located about 4050 km from Tahiti and 3700 km from continental Chile, and (2) Salas y Gómez Island (0.15 km^2 in area), lying about 3210 km west of Chile. Several workers have reported high levels of marine endemism at Rapa Nui (Castilla and Rozbaczylo 1987; DiSalvo et al. 1988; Friedlander et al. 2013), and have also recognized an impoverished coral fauna (Glynn et al. 2007; Veron et al. 2015). Plausible explanations for this are the isolation, small size, and lack of lagoonal ecosystems or protected bays at these oceanic islands.

Multiple countries—Miloslavich et al. (2011) reported 6714 species from Costa Rica, Panama, Colombia and Ecuador. Polychaetes were the most diverse group (1894 species) followed by the usually diverse groups of fishes (1212 spp.), crustaceans (863 spp.) and molluscs (875 spp.). These groups combined made up 47.3 % of the species compiled in this study.

Endemism—Miloslavich et al. (2011) indicated that the percentage of endemics in Costa Rica, Panama, Colombia and Ecuador ranks among the highest globally. This is especially evident among the fishes, with 70 % of the species endemic to the ETP (Robertson and Allen 2008). Cairns (1991a) reported that 41 % of the ahermatypic corals in the Galápagos Islands are endemic, and Hickman (2009) noted that 18.3 % of all marine invertebrates are endemic, ranging from no endemics among the zooxanthellate corals to 71 % of the gorgonians. Carballo et al. (2014) reported a high degree of endemism (29 %) for the sponge fauna of Mexico, but attributed this to a lack of sponge studies elsewhere in the ETP. Finally, Cortés (2012) reported that 2.7 % of the marine organisms at Isla del Coco were endemic to the region, representing 41.2 % of the total number of endemic species known in Costa Rica.

Biogeographically the ETP coral reef fauna has a strong connection with the Central-Western Pacific fauna, although the degree to which this holds true varies considerably among taxa. For example, almost all reef-building corals in the ETP are closely related to those in the Indo-Pacific (Glynn and Ault 2000; see Chap. 5, Glynn et al.), while ETP polychaetes are more closely related to taxa from the American mainland than to species in the Western Pacific (Solís-Weiss and Hernández-Alcántara 2009; Dean et al. 2012). It must be noted, however, that even though ETP reef-building corals have a strong Indo-Pacific affinity, one important ETP reef-builder, *Porites lobata*, is presently isolated from Indo-Pacific populations with no evident gene flow (Baums et al. 2012). Endemism among taxonomic groups also varies within the ETP region. For example, in the Galápagos Islands 71 % of the gorgonians are endemic, while all reef-building corals occur elsewhere (Breedy et al. 2009a; Hickman 2009). The biogeographic affinity of species varies substantially with location. Clipperton Atoll, on the western margin of the ETP, has 277 species of molluscs of which 50 % have Indo-Pacific affinities, and the other 50 % with ties to the Panamic fauna (Kaiser 2009). In contrast, Isla Malpelo, Colombia, at the eastern margin of the ETP, has 341 mollusc species but only 2.6 % of this fauna is related to Indo-Pacific species whereas 97.4 % of the remaining species belong to the Panamic region (Kaiser and Bryce 2001).

In this chapter we consider only the core ETP, traditionally the region between western Mexico and northern Peru. The Rapa Nui bioregion is not included in this review because of its general omission from past ETP biogeographic analyses. The objectives of this chapter are to provide a synthesis of the state of knowledge of ETP coral reef biodiversity, illuminating gaps in our knowledge, and to suggest future lines of research.

7.3 State of Knowledge of ETP Coral Reef Biodiversity

7.3.1 Prokaryotes and Viruses

Little is known concerning ETP reef-associated prokaryotes and viruses; only two published studies are available. In one, water samples were collected for a metagenomic study of the marine planktonic microbiota during the *Sorcerer II* Global Ocean Sampling Expedition (Rusch et al. 2007). Some of these samples were collected near coral reefs in Panama, Costa Rica (Isla del Coco) and the Galápagos Islands, and several species of Archaea and Eubacteria were identified (Rusch et al. 2007). From the same samples, Williamson et al. (2008) recognized viral talC sequences, and P-SSM4-like phages, as well as the cyanobacterium, *Prochlorococcus* sp. Additional studies are needed on these groups and their effects on the health of coral reef organisms.

7.3.2 Macroalgae

In 1945, William R. Taylor published the first and only existing complete key that includes the brown, red and green algae of the ETP, namely the Pacific marine algae of the Allan Hancock Expeditions to the Galápagos Islands (Taylor 1945). Between 1950 and 1965, Elmer Y. Dawson published more than thirty papers describing the marine algal flora of the ETP (Abbott 1966). The introduction of scuba during the 1950s promoted profound changes in the understanding of algal richness throughout the region. Later, from the 1980s to the present, many local and international experts have contributed to our understanding of marine macroalgal biodiversity and ecology, particularly in Mexico, El Salvador, Costa Rica and Panama. More recently, with the advent of molecular biology, there has been even greater resolution of species and their overall richness.

During the past 70 years of ETP macroalgal taxonomy, more than 300 marine species have been documented (Table 7.3). The most diverse group in the region are the red algae, followed by green and brown algae. Algal community diversity in the ETP is dependent on both the geomorphological configuration of the coastline and habitat type (Fernández-García et al. 2011). It is estimated that 60 to 70 % of the ETP macroalgae are associated with coral and rocky reef habitats (Alvarado et al. 2011; Murillo-Muñoz and Peña-Salamanca 2014; Alvarado et al. 2015). Described community richness is also highly dependent on sampling effort and local scientific infrastructure (Fernández-García et al. 2011). For example, in countries such as Mexico, El Salvador, Costa Rica, Panama and Colombia, where local and international phycologists have been studying the marine flora

Table 7.3 Number of ETP marine macroalgal species

	Continental mainland								Oceanic islands			
	MEX[1]	GUA[2]	SAL[2]	NIC[2]	CRC[2]	PAN[2]	COL[3]	ECU[4]	CLI[5]	REV[6]	COC[7]	GAL[8]
Ochrophyta-Phaeophyceae	59	0	14	6	26	25	23	5	11	29	7	46
Chlorophyta	95	5	36	6	44	52	31	8	23	38	10	42
Rhodophyta	78[a]	11	96	12	146	97	81	12	49	123	13	228
Total	232	16	146	24	216	174	135	25	83	190	30	316

Modified from Fernández-García et al. (2011). *MEX* mainland Mexico (Nayarit to Chiapas); *GUA* Guatemala; *SAL* El Salvador; *NIC* Nicaragua; *CRC* Costa Rica; *PAN* Panama; *COL* Colombia; *ECU* Ecuador; *CLI* Clipperton Island (France); *REV* Revillagigedo Islands (Mexico); *COC* Isla del Coco (Costa Rica); *GAL* Galápagos Islands (Ecuador)

[a] There are no updated catalogues of this group; true species richness is expected to be much greater

Sources [1]González-González et al. (1996), Pedroche et al. (2005, 2008); [2]Fernández-García et al. (2011); [3]Schnetter and Bula-Meyer (1982), Bula-Meyer (1995), Peña-Salamanca (2008), Murillo-Muñoz and Peña-Salamanca (2014), [4]Müller-Gelinek and Salazar-Orquera (1996), [5]Sachet (1962), Payri et al. (2009), [6]Serviere-Zaragoza et al. (2007), [7]Fernández (2008), [8]Garske (2002) for decades, there are over a hundred reports of marine macroalgae (Table 7.3). By contrast, in countries such as Guatemala, Nicaragua and Ecuador, there are relatively few local experts, and our knowledge of these regions is less extensive. To further explore macroalgal species diversity and distributions, greater collection effort is needed in these remote and underexplored areas.

Coral reefs in the ETP (<10 m deep) are dominated by algal turf, defined as a typically low lying (several mm to cm high) stratum of algae (Connell et al. 2014) as well as encrusting calcareous and fleshy algae (Fig. 7.1a–d). Algal turfs are composed of a combination of several filamentous and corticated green, red and brown algae. The main turf-forming species are *Asparagopsis taxiformis* (filamentous tetrasporophyte stage), *Polysiphonia, Ceramium, Cladophora, Chlorodesmis*, species within the Order Gelidiales, as well as the red geniculate coralline algae *Jania* and *Amphiroa* (Fig. 7.1a, b). Several fleshy algae such as *Hypnea* sp., *Gracilaria* spp., *Galaxaura rugosa, Halimeda discoidea*, *Codium isabelae*, *Padina mexicana* and *Dictyota humifusa* (present from Mexico to Colombia, Fig. 7.1d), are also present in small patches. From about 12 to 17 m depth, the dominant species are encrusting red coralline algae (*Lithohyllum* spp. and *Lithothamnion* spp.), species in the family Peyssoneliaceae, and *Lobophora* spp. (Fig. 7.1c).

Algal diversity of the ETP is lower than in other tropical regions such as the Caribbean Sea, Indian Ocean and West Pacific Ocean. This depauperate flora could be the result of several factors, including the emergence of the Central American Isthmus (Lessios et al. 2001; Wysor 2004), a geologic event resulting in cooler waters associated with seasonal upwelling and overall changes in current patterns (Glynn 1972a; Cortés 2011) causing local species' extinctions that were previously part of a homogeneous regional flora (Wysor 2004). Other factors structuring species' distributions in the region are the lower prevalence of habitats that favor the presence of certain macroalgal species. For instance, the Caribbean and Indo-Pacific regions possess more extensive carbonate platforms, seagrass ecosystems and well developed coral reefs than are present in the ETP (Cortés 2011).

Another factor in need of further study is the effect of herbivorous fishes on the presence or absence of marine macroalgae across the ETP. Edgar et al. (2011) found that overfishing of predatory fishes in the ETP has led to increased population densities of herbivores, which have contributed to regional declines in algal cover. Two common herbivorous guilds that graze on algae are parrotfishes (Scaridae) and sea urchins such as *Diadema mexicanum* and *Eucidaris galapagensis* (Fig. 7.1e, f). An excess of herbivores, coupled with eutrophication or other types of natural (e.g., ENSO events) and/or anthropogenic disturbances, may lead to the presence of fewer macroalgal species (Glynn and Maté 1997; Smith et al. 2010; Fernández-García et al. 2012).

Finally, it is noted that two marine macroalgae may negatively and directly influence coral reefs in the ETP. *Caulerpa sertularioides* has been observed to competitively exclude other algal species and overgrow corals, thereby reducing biodiversity and calcification (Fernández and Cortés 2005; Smith et al. 2010; Fernández-García et al. 2012). *Acanthophora spicifera* is a well-known invasive species in many Pacific environments such as in Hawaii (Russell 1992) and Baja California Sur, Mexico (Ávila et al. 2012). Recent sampling along the Central American Pacific coast has documented the presence of this alga in El Salvador, Panama and Costa Rica (Fong et al. 2006; Segovia-Prado and Naverrete-Calero 2007; C. Fernández-García, pers. obs.). In Panama, Fong et al. (2006) found that the positive interaction between *A. spicifera* and cyanobacterial epiphytes uncoupled herbivore consumers' control of algal community structure, and hypothesized that the epiphytes maintained the macroalgal dominated patches on coral reefs (see Fong et al., Chap. 11). Presently, however, there are no reported direct impacts of *A. spicifera* at other ETP sites.

7.3.3 Metazoans

7.3.3.1 Porifera

Comprehensive assessment of ETP sponge biodiversity has been scarce until recent years. The earliest surveys were conducted during the Albatross expeditions in the late 19th and early 20th centuries (Wilson 1904; Lendenfeld 1910). Research progressed slowly during the last two decades until renewed interest led to the description and documentation of numerous species in the ETP. Currently, Mexico has received greatest attention where a total of 76 species of coral reef sponges has been reported from the mainland coast (Fig. 7.2) and the Revillagigedo Archipelago (Carballo et al. 2004; Carballo and Cruz-Barraza 2006, 2010), followed by the Galápagos Islands with 38 species reported (Chiriboga et al. 2012). Nine species in the Class Homoscleromorpha have been reported for the ETP (Cruz-Barraza et al. 2014) (Table 7.4).

Clipperton Island has 17 documented species in the Class Demospongiae and two species in the Class Calcarea (Table 7.4). Seven of these sponge species exhibit widespread distributions in the Indo-Pacific, suggesting affinities with the Central and West Pacific regions (Soest et al. 2011). Other ETP areas with reports and descriptions of new species are Costa Rica (mainland and Isla del Coco) (Guzmán 1988; Cortés et al. 2009; Pacheco 2012) and Panama (Laubenfels 1936; Diaz et al. 2005; Caballero-George et al. 2010). In Panama, one study revealed that the morphology of sponge species is more cryptic than in the Caribbean, suggesting an adaptation to potentially higher levels of predation (Wulff 1997).

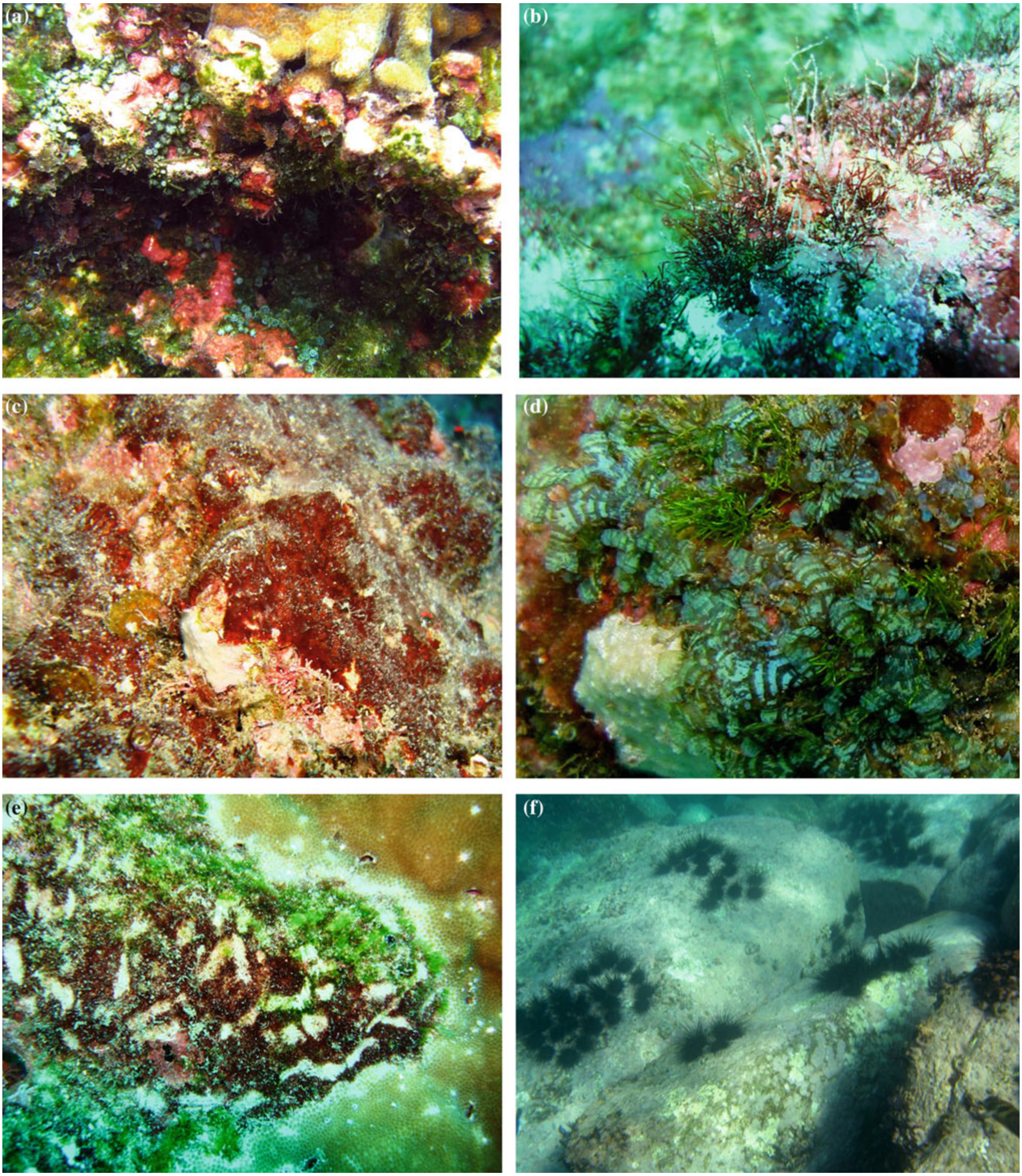

Fig. 7.1 Macroalgae, turf and coralline algae of ETP coral reefs and rocky substrates. **a** A multi-species assemblage of green and red algae, reef base, Coiba Island, Panama; **b** species in the Order Gelidiales, San Juan del Sur, Nicaragua; **c** encrusting Peyssoneliaceae and *Lobophora*, Isla del Coco, Costa Rica; **d** *Dictyota humifusa*, Isla Bolaños, Bahía Salinas, Costa Rica; **e** parrot fish bite marks on turf algae, Isla del Caño, Costa Rica; **f** *Diadema mexicanum* grazing on algae, Acapulco, Mexico. Photographs by Cindy Fernández-García

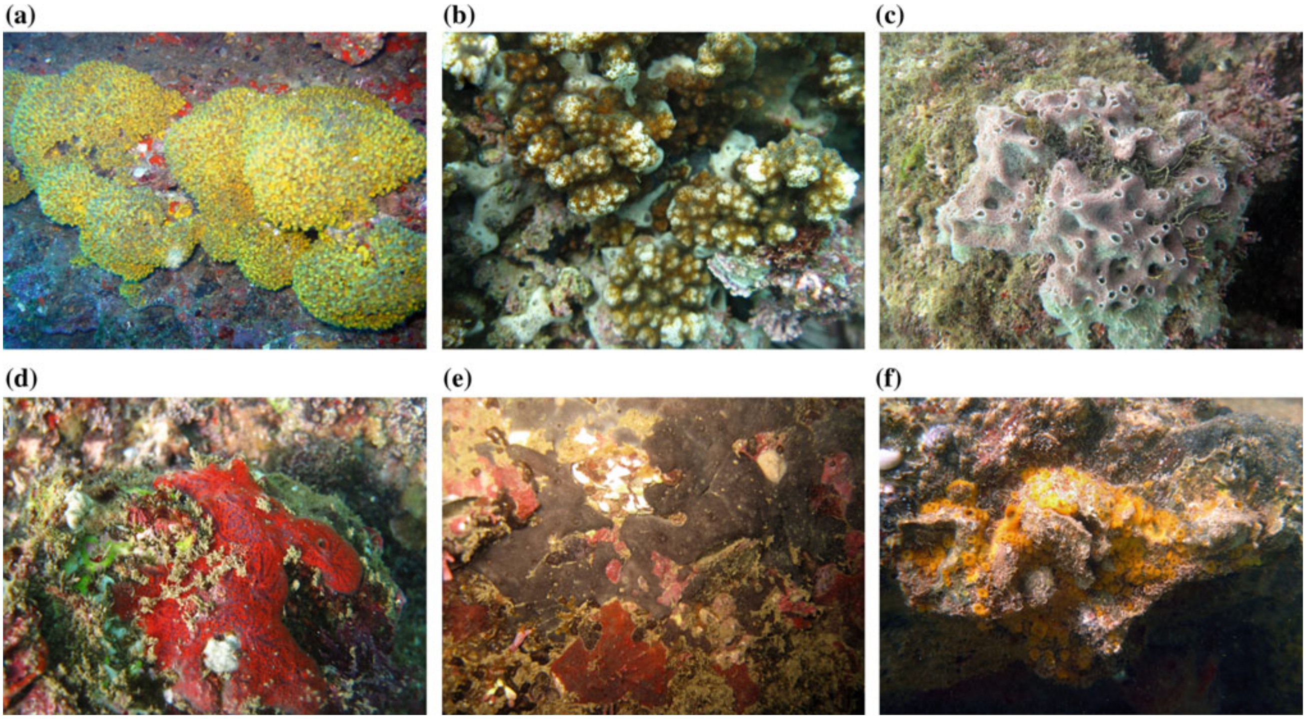

Fig. 7.2 Sponges of the ETP. **a** *Aplysina clathrata,* Isla Isabel; **b** *Callyspongia californiana,* Isla Isabel; **c** *Haliclona caerulea,* Bahía de Huatulco; **d** *Mycale cecilia,* Bahía de Huatulco; **e** *Chondrilla montanusa,* Bahía de Huatulco; **f** *Cliona californiana*, La Paz, Baja California. Photographs by José Antonio Cruz Barraza, all from Mexico

Table 7.4 Number of ETP sponge species by class from coral reef areas

	Continental mainland			Oceanic islands			
	MEX	PAN	CRC	CLI	REV	COC	GAL
Demospongiae	69	17	16	17	4	2	34
Homoscleromorpha	2	1	0	0	4	0	4
Calcarea	0	0	0	2	0	0	0
Total	71	18	16	19	8	2	38

MEX Mexico; *PAN* Panama; *CRC* Costa Rica; *CLI* Clipperton Island; *REV* Revillagigedo Archipelago; *COC* Isla del Coco; *GAL* Galápagos Islands

Other biogeographic regions have received more taxonomic attention than the ETP. In some cases, revisions are necessary to update inaccurately classified ETP species. However, as others have recognized (e.g., Hooper et al. 2002), there has been increased research effort in the field of sponge systematics in recent years.

7.3.3.2 Cnidaria

Hydrozoa

The hydrozoans (Phylum Cnidaria, Class Hydrozoa) are an abundant group of reef organisms but their generally small size and cryptic nature has contributed to the limited knowledge of this group in the ETP. The chief ETP studies are from the late 1930s and 1940s (Fraser 1938a, b, c, 1948). Calder et al. (2003) reported 96 species of hydroids from the Galápagos Islands, representing the most well studied region in the ETP.

The calcareous Hydrozoa (also known as hydrocorals) are better known than their fleshy counterparts and include the Stylasteridae and Milleporidae. Carins' (1986) report on the stylasterids of the Galápagos Islands included 14 species, and nine of these were newly described. Later he reported five additional species, including two new ones from Isla del Coco (Cairns 1991b). Unlike other regions, all ETP species occupy deep waters (200–500 m) and are related to the western Pacific fauna. There is one known exception described from Panama, *Distichopora robusta*, which has been collected between 5 and 25 m depth (Lindner et al. 2004).

The other group of calcareous hydroids belongs to the milleporid family, which potentially contribute to reef-building in Panama (Maté 2003; see Chap. 5, Glynn et al.). Four species have been identified in the ETP, three from the Gulf of Chiriquí, Panama (Glynn and de Weerdt 1991; de Weerdt and Glynn 1991), and one from Clipperton Atoll (Glynn et al. 1996). The populations of the Panamanian species were greatly reduced by El Niño events. Subsequently, one species (*Millepora boschmai*) is thought to have become regionally extinct (Glynn 2011).

Anthozoa

Octocorallia

A total of 111 species of octocorals have been documented from the ETP (Table 7.5). The majority of these species are gorgonians (Order Alcyonacea) within the families Gorgoniidae (three genera; Fig. 7.3a, b, c) Plexauridae (five genera; Fig. 7.3d) and Clavulariidae (one species, *Carijoa riisei*; Fig. 7.3e). Three families of sea pens (Order Pennatulacea) have been reported from the ETP, but very few studies on this group exist (Table 7.6).

Octocoral studies in the ETP began with the expedition *Voyage autour du monde sur La Frégate La Vénus* 1836–1839 (published in 1846, see Breedy and Guzman 2002), where the first specimens of octocorals from Mazatlán, Mexico were collected and described. Following this expedition, a few sporadic records appeared in the literature. Verrill (1868–70) made the most significant contribution in his paper “Notes on Radiata”, synthesizing the existing literature at the time and describing 50 new species. Further contributions have been made in the 20th century by W. Kükenthal, S. J. Hickson and E. Deichmann (see Breedy and Guzman 2002).

From the year 2000 to the present, cooperative research initiatives between the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, and the Smithsonian Tropical Research Institute (STRI, Panama) have significantly enchanced the knowledge of octocoral biodiversity in the ETP. Related contributions include taxonomic reviews (Breedy and Guzman 2002, 2007, 2011; Williams and Breedy 2004; Breedy 2009; Breedy et al. 2009b; Breedy and Cortés 2014), descriptions of new species (Breedy 2001; Breedy and Guzman 2003, 2004, 2008, 2012 2013, 2014; Guzman and Breedy 2008, 2012; Breedy and Cortés 2011) and biogeographic assessments (Vargas et al. 2008). The majority of this work pertains to shallow water habitats (0–40 m) along the coasts of Costa Rica and Panama. As a consequence, during the last 10 years, 15 new species have been described from Panama, and 17 from Costa Rica. Two species from mesophotic reefs (to 50 m depth) have been described, including *Eugorgia siedenburgae* from Hannibal Bank, Panama, and Santa Elena Bay, Costa Rica (Breedy and Guzman 2013), as well as *Eugorgia beebei* from Baja California, Mexico and Paita, Peru (Breedy et al. 2013).

The most speciose family of octocorals is the Gorgoniidae (76 species), with 14 species of *Eugorgia*, 27 of *Leptogorgia* and 35 in the genus *Pacifigorgia*. Plexauridae is the next most abundant family (31 species) with one species of *Adelogorgia*, four each in the genera *Eumuricea* and *Heterogorgia*, six species of *Psammogorgia* and 16 in the genus *Muricea*. Panama has the greatest number of described species of octocorals (64 spp.), followed by Mexico (46 spp.), and mainland Costa Rica (38 spp.) (Table 7.7). Recent records from Nicaragua (24 spp.) and Ecuador (25 spp.) are found in technical reports (Rivera and Martínez 2011; Cortés-Núñez et al. 2012), and from El Salvador (17 spp.) in an unpublished thesis (Segovia-Prado 2012). Preliminary data from Colombia have been published for Malpelo Island (4 spp.; Sánchez et al. 2011) and for Isla Gorgona (13 spp.; Sánchez et al. 2014). Presently, nothing is known of the octocoral species of Guatemala. A survey of the Revillagigedo Archipelago, Mexico (Hull et al. unpub.) indicates the presence of octocorals, although no species list was included. An analysis of collections from Peru contained 16 species (O. Breedy, pers. obs.).

Scleractinia

The scleractinian corals, both hermatypic and ahermatypic, are probably the most extensively studied taxa in the ETP. Forty-seven species each of reef-building corals (see Chap. 5, Glynn et al.; Table 7.8) and azooxanthellate corals, mostly from deep waters (Cairns 1991a; Cortés 2009), are known from the ETP. Veron et al. (2015) concluded that the reef-building corals throughout the ETP are closely related with the exception of the Clipperton fauna, which is taxonomically closer to the Marquesas Islands.

The main hermatypic scleractinian species of the ETP belong to the genera *Pocillopora*, *Porites* and *Pavona* (Cortés 2011; see Chap. 5, Glynn et al.). The pocilloporids are usually abundant in shallow waters (intertidal to 5 m) while massive species of *Porites* and *Pavona* are generally more abundant in deeper waters (>5 m) (Guzmán and Cortés 1989). While regional species composition is often similar, more local community differences are known to exist. For example, coral reefs in the non-upwelling southern areas of Costa Rica have diverse coral assemblages, including all the prominent reef-building scleractinians. However, in the upwelling northern areas, species community composition and structure change, with the most extreme upwelling sites containing only *Pavona gigantea* and *Porites panamensis* (Cortés and Jiménez 2003).

Until recently *Porites lobata* had been considered ubiquitous along the Costa Rican coast and the only reef-building

Table 7.5 Species list of octocorals from the ETP (see text for references)

Family	Species	Country/continental mainland								Oceanic islands		
		MEX	SAL	NIC	CRC	PAN	COL	ECU	PER	COC	MAL	GAL
Aquaumbridae	*Aquaumbra klapferi*									x		
Clavulariidae	*Carijoa riisei*	x	x	x	x	x	x	x	x	x	x	x
	Carijoa multiflora		x									
Gorgoniidae	*Eugorgia ampla*	x				x						
	Eugorgia aurantiaca	x					x					
	Eugorgia beebei	x							x			
	Eugorgia bradleyi				x							
	Eugorgia excelsa	x										
	Eugorgia daniana	x		x	x	x		x				x
	Eugorgia mutabilis	x			x	x						
	Eugorgia multifida	x										
	Eugorgia nobilis	x		x	x	x		x				
	Eugorgia panamensis					x						
	Eugorgia purpurascens			x		x			x			
	Eugorgia querciformis			x								
	Eugorgia rubens	x			x	x			x			
	Eugorgia siedenburgae	x			x	x						
	Leptogorgia aequatorialis							x				
	Leptogorgia alba	x	x	x	x	x	x	x	x	x	x	x
	Leptogorgia californica	x										
	Leptogorgia clavata	x										
	Leptogorgia cofrini			x	x	x						
	Leptogorgia cortesi				x							
	Leptogorgia christiae					x						
	Leptogorgia cuspidata	x	x	x	x	x		x				
	Leptogorgia diffusa		x	x	x	x	x					
	Leptogorgia ena	x										
	Leptogorgia exigua	x		x	x	x			x			
	Leptogorgia filicrispata	x										
	Leptogorgia flexilis	x	x			x						
	Leptogorgia florae					x						
	Leptogorgia fruticosa					x						
	Leptogorgia ignita				x							
	Leptogorgia laxa	x			x	x		x				
	Leptogorgia obscura							x				
	Leptogorgia parva					x						
	Leptogorgia peruana								x			
	Leptogorgia pumila	x		x	x	x		x	x			
	Leptogorgia ramulus	x	x	x		x	x		x			
	Leptogorgia regis	x	x		x	x						
	Leptogorgia rigida	x	x		x	x		x				
	Leptogorgia taboguillae				x	x		x				
	Leptogorgia tricorata									x		

(continued)

Table 7.5 (continued)

Family	Species	Country/continental mainland								Oceanic islands		
		MEX	SAL	NIC	CRC	PAN	COL	ECU	PER	COC	MAL	GAL
	Leptogorgia labiata	x				x						
	Pacifigorgia adamsii	x		x	x	x	x	x	x			
	Pacifigorgia agassizii	x				x						
	Pacifigorgia bayeri				x	x						
	Pacifigorgia cairnsi		x		x	x	x				x	
	Pacifigorgia catedralensis					x						
	Pacifigorgia cribrum	x										
	Pacifigorgia curta				x					x	x	
	Pacifigorgia dampieri											x
	Pacifigorgia darwinii											x
	Pacifigorgia englemanni	x										
	Pacifigorgia eximia				x	x	x					
	Pacifigorgia exilis	x										
	Pacifigorgia gracilis	x				x						
	Pacifigorgia ferruginea					x						
	Pacifigorgia firma			x	x	x	x	x				
	Pacifigorgia flavimaculata				x							
	Pacifigorgia irene		x		x	x	x	x				
	Pacifigorgia labiata	x										
	Pacifigorgia lacerata				x							
	Pacifigorgia pulchra	x										
	Pacifigorgia marviva					x						
	Pacifigorgia media	x	x	x		x						
	Pacifigorgia rubicunda				x	x	x	x				
	Pacifigorgia rubripunctata											x
	Pacifigorgia rutila	x										
	Pacifigorgia samarensis				x							
	Pacifigorgia sculpta			x		x	x					
	Pacifigorgia senta	x			x	x						
	Pacifigorgia symbiotica											x
	Pacifigorgia smithsoniana					x						
	Pacifigorgia stenobrochis	x	x	x	x	x		x	x			
	Pacifigorgia tabogae					x						
	Pacifigorgia tupperi				x							
	Pacifigorgia rubinoffi					x						
	Pacifigorgia douglasii											x
Ellisellidae	*Ellisella limbaughi*	x										
Plexauridae	*Eumuricea acervata*					x						
	Eumuricea tubigera					x						
	Eumuricea horrida								x			
	Eumuricea squarrosa			x		x		x				
	Heterogorgia hickmani							x				x
	Heterogorgia verrucosa			x	x	x	x	x				x

(continued)

Table 7.5 (continued)

Family	Species	Country/continental mainland								Oceanic islands		
		MEX	SAL	NIC	CRC	PAN	COL	ECU	PER	COC	MAL	GAL
	Heterogorgia tortuosa				x	x						
	Heterogorgia papillosa	x										
	Muricea californica	x										
	Muricea crassa					x	x	x				
	Muricea equinata					x						
	Muricea fruticosa				x	x						x
	Muricea fruticosa var. *miser*	x	x	x	x	x		x				
	Muricea austera	x	x		x	x		x				
	Muricea retusa					x						
	Muricea formosa								x			
	Muricea robusta	x										
	Muricea albida					x						
	Muricea hebes			x		x						
	Muricea purpurea	x	x	x		x		x				
	Muricea appressa	x		x		x		x	x			
	Muricea appressa cf. *flavescens*							x				
	Muricea tenella			x		x			x			
	Muricea aspera					x						
	Psammogorgia arbuscula					x						
	Psammogorgia variabilis									x		
	Psammogorgia fucosa	x										
	Psammogorgia teres					x						
	Psammogorgia hookeri								x			
	Psammogorgia sp.		x									
	Adelogorgia telones											x
Total		46	17	24	38	64	14	25	16	6	4	12

MEX Mexico; *SAL* El Salvador; *NIC* Nicaragua; *CRC* Costa Rica; *PAN* Panama; *COL* Colombia; *ECU* Ecuador; *PER* Peru; *COC* Isla del Coco; *MAL* Malpelo; *GAL* Galápagos Islands

species of that genus (*Porites panamensis* forms only small isolated colonies). Genetic analysis, however, has demonstrated that there are two species in the genus, *P. lobata* and *Porites evermanni*. While these species have similar external morphologies, they display different ecological characteristics, with *P. lobata* more susceptible to bleaching, and *P. evermanni* experiencing higher bioerosion and predation rates (Boulay et al. 2014).

Other Anthozoa (Actinaria, Ceriantharia, Zoanthidea, Antipatharia)

While numerous other anthozoan taxa are known from the ETP, the majority of them are poorly studied (Hickman 2008). Most research on sea anemones (Order Actinaria) was conducted in the 19th and early 20th centuries (Verrill 1868–70; Carlgren 1940). Recent work includes Daly and Fautin (2004) and Fautin et al. (2007) in the Galápagos Islands, in which eight species were reported. Excoffon et al. (2009) and Acuña et al. (2012, 2013) reported six species in Costa Rica, and Garese et al. (2009) 14 species from Panama. Tube anemones (Order Ceriantharia) are even less well known; Fautin et al. (2007) reported two species from the Galápagos Islands. The zoanthids (Order Zoanthidea) have been studied recently in the Galápagos Islands (seven species) (Reimer et al. 2008), but not in other areas of the ETP. There are no recent publications on shallow-water black corals (Order Antipatharia), even though they are common at some sites in the ETP (Hickman 2008; J Cortés, pers. obs.).

7.3.3.3 Polychaeta

The reef-inhabiting marine worms (including the Phyla Annelida, Sipuncula, Nemertea, Platyhelminthes, and

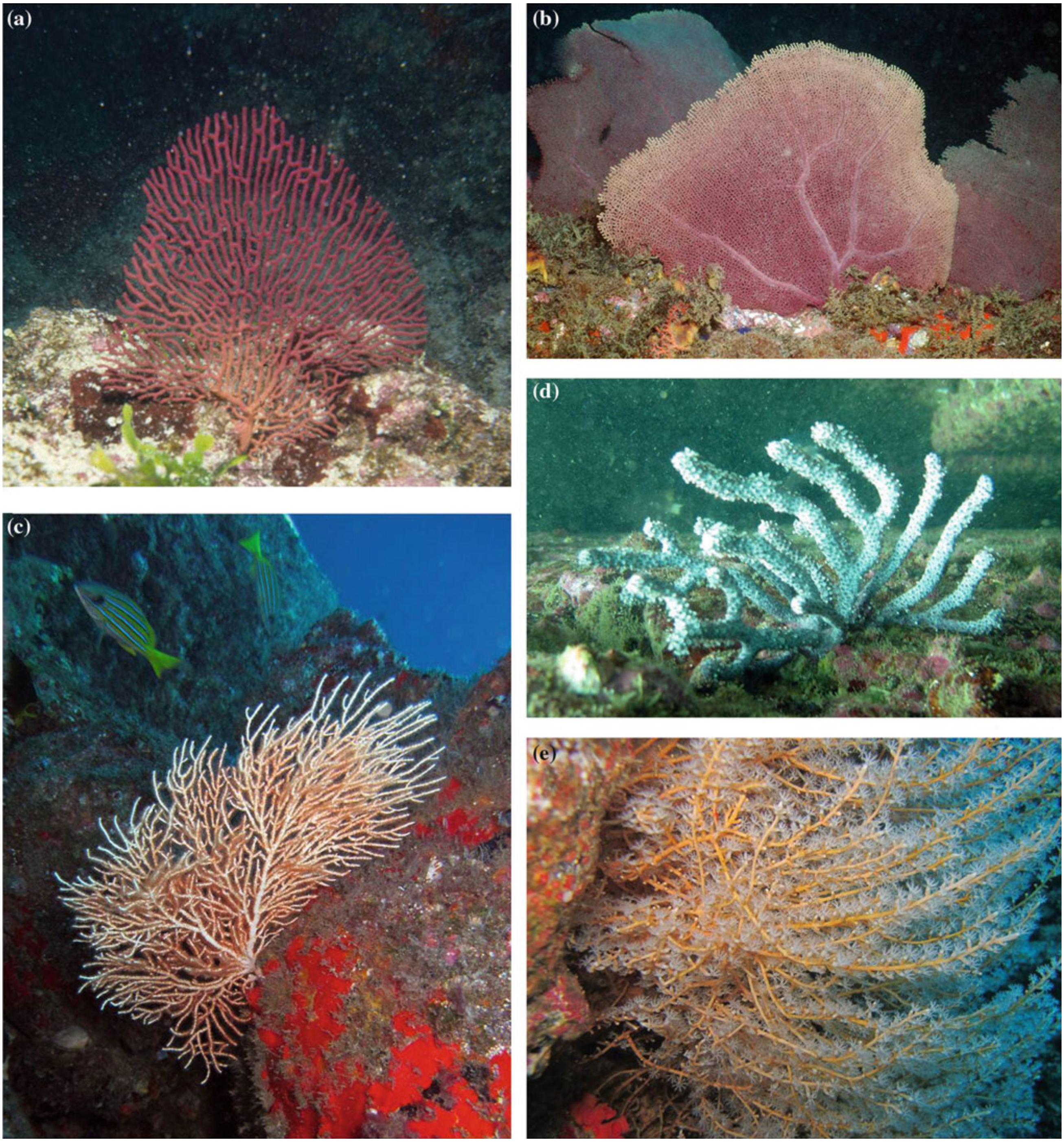

Fig. 7.3 Octocorals of the ETP. **a** *Pacifigorgia stenobrochis*, Isla del Caño, Costa Rica; **b** *Pacifigorgia irene*, Isla Coiba, Panama; **c** *Leptogorgia alba*, Isla del Coco, Costa Rica; **d** *Muricea purpurea*, Bahía Salinas, Costa Rica; **e** *Carijoa riisei*, Isla del Coco, Costa Rica. All photographs by Jorge Cortés except **b** by Graham Edgar

Phoronida) are poorly studied, but play an important role in ecosystem function. Among these worms, the annelids are the dominant group. Dean (2009) cited 19 families and 82 species of coral reef polychaetes (Phylum Annelida, Class Polychaeta), but many were also known to live on other substrates and in different habitats such as soft sediments and rocky bottoms. Bastida-Zavala (1995) recorded 82 species in 21 families inhabiting dead coral, while Blake (1991) noted only ten species in dead and live coral in his checklist for the Galápagos Islands. Enochs and Manzello (2012a) recorded

Table 7.6 Species list of ETP pennatulaceans

Family	Species	Coastal Costa Rica[1]	Oceanic islands	
			Isla del Coco[2]	Galápagos Islands[3]
Pennatulidae	*Ptilosarcus undulatus*		x	x
Renillidae	*Renilla ametystina*	x		
Veretillidae	*Cavernulina* cf. *darwini*			x
Virgulariidae	*Scytalium* sp.			x
Virgulariidae	*Virgularia galapagensis*			x
Virgulariidae	*Stylatula* cf. *elongata*		x	

Sources [1]Breedy (2009), [2]Breedy and Cortés (2008), [3]Hickman (2008)

Table 7.7 Number of species in the most abundant octocoral genera (references in text)

Genus	No. species	Most speciose country
Pacifigorgia	35	Panama (20)
Leptogorgia	27	Panama (17)
Muricea	16	Panama (12)
Eugorgia	14	Mexico (11)
Psammogorgia	6	Panama (2)
Eumuricea	4	Panama (3)
Heterogorgia	4	Costa Rica, Panama Ecuador (2)

Most speciose region and richness indicated in parentheses

Table 7.8 Species richness of ETP hermatypic corals

Country	No. species
Mexico mainland[a]	29
Colombia	28
Panama	27
Costa Rica mainland	25
Revillagigedo	25
Ecuador mainland	23
Galápagos Islands[b]	23
Isla del Coco	22
Clipperton	21
Malpelo	13
El Salvador	11
Nicaragua	10

[a]Includes the Gulf of California
[b]Includes both the northern and southern Galápagos Islands
Source Glynn et al. Chap. 5

21 genera associated with coral exhibiting different degrees of degradation at Playa Larga, Panama, and Dean et al. (2012) reported 62 species from dead coral at Isla del Coco, Costa Rica. A detailed list of polychaetes of the ETP, including species from reef habitats, can be found in Salazar-Vallejo and Londoño-Mesa (2004), and in Dean (2009).

Among the marine worms, the fireworms (Polychaeta: Amphinomidae) are the most conspicuous by their size and coloration. Two species reported from the ETP (Salazar-Vallejo and Londoño-Mesa 2004; Dean 2009) are *Eurythoe complanata* (Fig. 7.4a) and *Notopygos ornata*. The former is considered a cryptic species in the Atlantic Ocean (Barroso et al. 2010), sheltering in crevices and under rocks during the day (Fauchald and Jumars 1979). Other species of this family reported on coral reefs (Dean 2009) are *Chloeia viridis* and *Pherecardia striata*. Species in the family Amphinomidae are traditionally categorized as predators, but *P. striata* also plays an important role as a carrion feeder, and even feeds on the internal organs of injured *Acanthaster planci* (Fauchald and Jumars 1979; Glynn 1984; Jumars et al. 2015). The fireworm *Hermodice carunculata* is common on Caribbean reefs and an active predator of zooxanthellate corals, especially branching species; a single record of this species for the Pacific waters of Costa Rica exists (Treadwell 1941), but the veracity of this record is debated (Dean 2004).

Other families of errant worms are found in coral cavities, in coral rubble, and algae (Dean 2009). Some of these species are known to consume small crustaceans, molluscs or other invertebrates, but others are deposit feeders and omnivores (Jumars et al. 2015). The most active polychaete predators belong to the Eunicidae, and many exhibit endolithic tendencies, boring into coral skeletons with their jaws. *Eunice aphroditois*, *Eunice biannulata* (Fig. 7.4b) and *Palola siciliensis* were found in coral rubble at Playas del Coco, and in dead coral at Isla del Coco, Costa Rica (Dean et al. 2012). The afore-noted species and five more in the genera *Eunice* (*E. antennata*; *E. filamentosa*; *E. reducta*; *E. schemacephala*; and *E. mutilata*) were observed by Bastida-Zavala (1995) at Cabo Pulmo, Mexico. The burrows of these boring taxa are often occupied by additional species, many of them predatory polychaetes in the families Phyllodocidae (*Eulalia* and *Phyllodoce*), as well as scale worms in the family Polynoidae (*Halosydna*, *Harmothoe*, and *Lepidastenia*), including the abundant *Iphione ovata*, a small, ovoid-shaped orange worm that can be found under coral rubble (Fig. 7.4c) (Bastida-Zavala 1995; Dean et al. 2012). Also present are members of the Syllidae with *Haplosyllis*, *Sphaerosyllis, Typosyllis*, and *Exogone* representing genera of high species diversity (Westheide 1974; Bastida-Zavala 1995; Dean 2009). At Isla del Caño and Golfo Dulce, Costa Rica six species of polychaetes in the

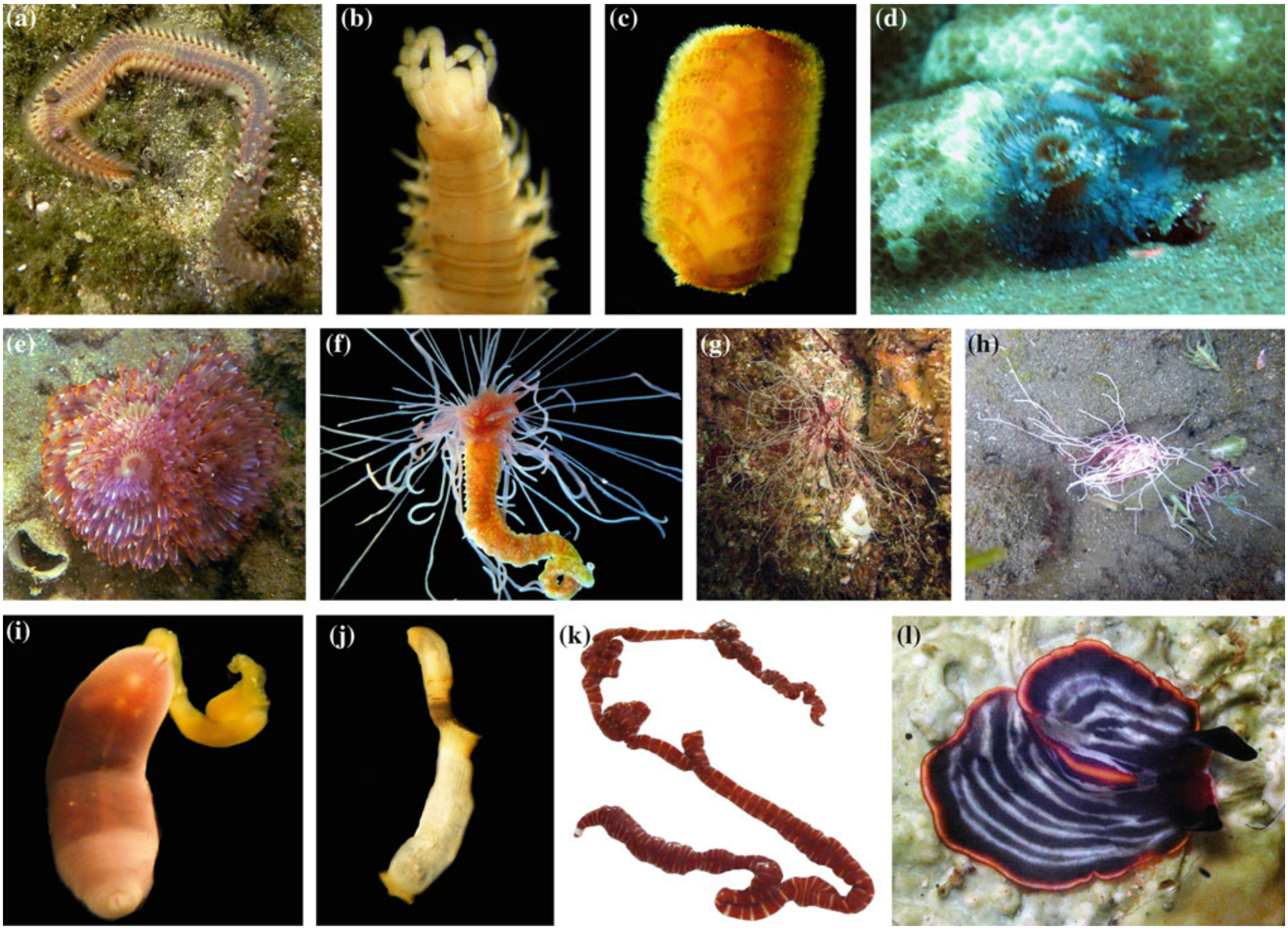

Fig. 7.4 Worms of ETP coral reefs. Polychaetes: **a** *Eurythoe complanata* (Amphinomidae); **b** *Eunice biannulata* (Eunicidae); **c** *Iphione ovata* (Polynoidae); **d** *Spirobranchus giganteus* complex (Serpulidae); **e** *Bispira* sp. (Sabellidae); **f** *Lanice* sp. (Terebellidae); **g** spaghetti worm on dead coral (Terebellidae); **h** *Cirriformia* sp. (Cirratulidae) in a sand crevice; **i** *Thalassema steinbecki* (Echiura: Echiuridae) in dead coral; **j** *Aspidosiphon misakiensis* (Sipuncula: Aspidosiphonidae); **a** to **j** from Isla del Coco, Costa Rica; **k** *Baseodiscus mexicanus* (Nemertea: Valenciniidae) from coral colonies at Cabo Blanco, Costa Rica; **l** *Praestheceraeus bellostriatus* (Platyhelminthes: Euryleptidae) from Sándalo reef, Golfo Dulce, Costa Rica. Photographs **e**, **h** and **l** by Kimberly García-Méndez; **d** and **g** by Jorge Cortés, remainder by Jeffrey Sibaja-Cordero

families Eunicidae, Cirratulidae and Dorvilleidae were found on reefs penetrating both live and dead corals. Species in the families Sabellidae, Spionidae and Flabelligeridae were found sheltering in burrows made by species of eunicids (Fonseca et al. 2006).

Another common coral reef polychaete family is the Serpulidae, often called Christmas tree worms because of their multi-colored radial crowns. These sedentary annelids construct their calcareous tubes in dead or live corals. Notable examples include *Hydroides* spp., and the *Spirobranchus giganteus* species complex, often referred to as *Spirobranchus incrassatus* (Fig. 7.4d) (Fiege and Ten Hove 1999; Bastida-Zavala 2008).

The Sabellidae or fan worms are sessile and live in mucus tubes in coral crevices or cavities. Sabellids are solitary or gregarious worms and belong to the suspension-feeding guild (Jumars et al. 2015). Two common genera in the ETP (Dean 2004) are *Bispira* (Fig. 7.4e) and *Hypsicomus*. Capa and López (2004) recorded 11 species in the genera *Amphicorina*, *Amphiglena*, *Branchiomma*, *Notaulax*, *Megalomma* and *Pseudopotamilla* living on dead coral (*Pocillopora*) at Coiba Island, Panama. At Cabo Pulmo, Mexico this family was represented by the genera *Chome*, *Euchone*, *Megalomma* and *Pseudopotamilla* (Bastida-Zavala 1995).

Two additional families consist of conspicuous, sedentary species on ETP coral reefs. The Terebellidae (spaghetti worms), including the genera *Lanice, Lanicides* or *Eupolymia* (Fig. 7.4f, g), can be recognized by elongate, usually white tentacles arising from a coral hole or depression. The Cirratulidae, including species in the genus *Cirriformia*, can be recognized by white and reddish tentacles and branchial filaments emerging from crevices or sand patches on coral reefs (Fig. 7.4h). A total of 15 species in this genus is listed for the ETP in Salazar-Vallejo and Londoño-Mesa (2004). These species are surface deposit or suspension feeders (Jumars et al. 2015), and were reported as occurring on ETP coral reefs by Westheide (1977), Bastida-Zavala (2008) and Dean (2009).

Dean et al. (2010a) reported the occurrence of the spoon worm *Thalassema steinbecki* (Fig. 7.4i), now in the subclass Echiura of Annelida sensu Ruggiero et al. (2015), from calcareous rock at Isla del Coco. This echiuran is known to burrow into coral rubble and can be found from Baja California to Ecuador. Fisher (1946) reported specimens of this species from a mud and coral rock habitat with gorgonians and coralline algae in Baja California. Additional records of this species in the ETP include specimens from the intertidal zone (Dean et al. 2010a), and congeneric species are known from rocky and soft bottom habitats (Fisher 1946).

7.3.3.4 Other Marine Worms (Sipuncula, Nemertea, Platyhelminthes, Phoronida)

Many peanut worm species (Phylum Sipuncula) are deposit feeders and are known to bore actively into coral rubble and to occupy preexisting cavities (Fonseca et al. 2006; Dean et al. 2010a). Dean et al. (2010a) found the species *Antillesoma antillarum*, *Aspidosiphon* (*Aspidosiphon*) *misakiensis* (Fig. 7.4j), *Aspidosiphon* (*Aspidosiphon*) *elegans*, *Aspidosiphon* (*Paraspidosiphon*) *fischeri*, *Phascolosoma* (*Phascolosoma*) *agassizii*, *Phascolosoma* (*Phascolosoma*) *nigrescens*, and *Phascolosoma scolops* associated with coral rubble at Isla del Coco. Dean (2001) also reported the species *Siphonosoma vastum* and *P.* (*P.*) *nigrescens* inhabiting coral fragments at Isla del Caño, Costa Rica, and *A.* (*A.*) *elegans* from coral rubble at Sándalo, Golfo Dulce. Pepe (1985) reported the sipunculans *A. antillarum*, *A.* (*P.*) *fischeri* and *Phascolosoma* sp. from coral rubble at Playas de Coco. Fourteen species of sipunculans were reported from the Costa Rican coast, and *A. antillarum*, *Aspidosiphon* (*Paraspidosiphon*) *parvulus*, *P.* (*P.*) *nigrescens*, and *Siphonosoma vastum* were collected from corals or coral rubble (Cutler et al. 1992; Dean 2001). Other substrates with sipunculans were sands, sandstone, limestone and the undersides of rocks (Dean 2001). Cutler (1994) additionally mentioned the presence of *Aspidosiphon* (*Paraspidosiphon*) *coyi*, *A.* (*P.*) *fischeri*, *A. antillarum*, *Phascolosoma perlucens*, *Thysanocardia catharinae* and *Themiste hennahi* from coastal localities in the Gulf of California, Panama, Ecuador, Galápagos, and Peru; information on habitats was not given. Fonseca et al. (2006) and Dean (2009) reported the above-noted species inhabiting hard bottoms.

Presently, our knowledge of the Nemertea (ribbon worms) occupying reefs is limited (Kirsteuer 1969; Thiel and Kruse 2001). From others studies, it is known that the heteronemerteans prey mainly on polychetes, while the hoplonemerteans consume crustaceans and carrion (Thiel and Kruse 2001). Coe (1940) reported on13 species of ribbon worms from southern California to Ecuador, but only provided a direct reference to the reef-affinity of *Baseodiscus delineatus*, *Baseodiscus mexicanus*, *Baseodiscus punnetti* and *Notospermus geniculatus* (reported as *Lineus geniculatus*) in the Gulf of California. Among these species, *B. mexicanus* is named the zebra worm for its maroon or red and white rings encircling the body (Fig. 7.4k). It attains lengths of 20 cm to 4 m, and occurs on the Pacific coast of the Americas and in the Galápagos Islands (Kajihara et al. 2012).

Flatworms (Phylum Platyhelminthes) associated with live coral, coral rubble, and rocky reefs are primarily polyclads (for other flatworms in the ETP, see Westheide 1991). These worms are usually colorful and often mistaken for nudibranchs. Polyclads are poorly studied in the ETP, although many can be found on coral and rocky reefs. For example, Hyman (1953) mentioned four species of polyclads from rocky substrates in the Galápagos Islands, and Enochs and Manzello (2012a) collected 11 flatworm species from a coral reef in Panama. A specimen of *Praestheceraeus bellostriatus*, or a closely related species (Fig. 7.4l), was found in a *Psammocora stellata* coral patch at Golfo Dulce, Costa Rica (K García-Méndez, pers. comm.). *P. bellostriatus* occurs in California and in the Sea of Cortez (as *Prostheceraeus bellostriatus* in Kerstitch and Bertsch 2007), and is recognized by alternating black and white longitudinal lines (Newman and Cannon 2003; Kerstitch and Bertsch 2007). Presently, no other flatworms have been reported on ETP coral reefs.

Finally, worms in the phylum Phoronida, referred to as horseshoe worms due to the shape of their lophophore, are known from coral reefs but remain poorly studied. *Phoronis hippocrepia* was once the only species in this phylum reported from the ETP. It is known to burrow into coral rubble (Bailey-Brock and Emig 2000; Emig 2009). This species was found in the Miraflores Locks, Panama Canal by Emig (1982). Dean et al. (2010b) reported a second species, *Phoronopsis albomaculata*, that occurs on sandy substrates.

7.3.3.5 Mollusca

The Mollusca is one of the most species-rich phyla of marine invertebrates and representatives may be found across many diverse marine ecosystems, including coral reefs. Many of the mollusc species associated with coral reefs are considered charismatic and have important values, including economic, biomedical, biological and ecological.

Keen (1971) reported more than 2400 species of gastropods and almost 800 species of bivalves from different environments on the west coast of the Americas. The number of known molluscs has increased in the last four decades as many new species have been described, mostly from the micromolluscs (0.45–11 mm, Geiger 2012) and in the subclass Opisthobranchia. Nearly a fourth (>800) of the gastropods, bivalves, cephalopods and opisthobranchs reported from the ETP are known to inhabit coral reefs. Gastropoda is the most species rich class among these, with more than 600 species, followed by Bivalvia with more than 200 species. Currently there are ten known species of Polyplacophora and eight species of Cephalopoda. The number of species reported is as much a function of the physical diversity of the area as the sampling effort. Considering that there are numerous areas of the coastline and islands in the ETP where the molluscan fauna has never been sampled, it is likely that numbers of described species will increase as regions and habitats are further explored.

Molluscs are found associated with numerous substrates (see some examples in Fig. 7.5) including both live and dead coral, coral debris, rocky and sandy substrates, intertidal zones, algal fields and seagrass communities (Landa-Jaime et al. 2013). Thus, higher habitat diversity within a given coral reef may encourage higher molluscan diversity. Table 7.9 shows the numbers of molluscs recorded for coral reef areas of the ETP. Gastropods are the most abundant and diverse taxa, representing 68 % of the total number of species, though it must be noted that studies may be biased towards this class. The next most species rich groups are the bivalves (17 % of spp.) and the opisthobranchs (13 % of spp.); the low percentage of Opisthobranchia is likely due in part to their cryptic nature and the difficulty of studying them in situ. Detailed information on these taxa is available from a limited number of areas (Gosliner 1991; Hermosillo and Camacho-García 2006; Hermosillo et al. 2006; Glynn et al. 2008; Camacho-García 2009).

The Galápagos Islands have the highest numbers of described species of molluscs (800 taxa) associated with coral reefs in the ETP (Kaiser 1997), followed by Isla Coiba (Vega and González 2001, 2002; Hermosillo and Valdés 2004; Hermosillo and Camacho-García 2006) and Isla del Coco (Cortés 2012; Kaiser unpub. data), with more than 500 species each. The Islas Revillagigedo, Clipperton Atoll, Isla de Malpelo, and Islas Marías have approximately 300 species each (for specific values and references see Table 7.9).

There are some mainland Mexican sites that are especially well known for mollusc diversity, as they have been studied for more than ten years. Tenacatita reef is one such site and researchers have catalogued more than one hundred species of associated molluscs (Landa-Jaime et al. 2013). Another exhaustive study completed at Bahía de Banderas, listed one hundred and forty-eight species of opisthobranchs, as a result of intensive field work over a three year period (Hermosillo and Valdés 2004; Behrens and Hermosillo 2005; Hermosillo et al. 2006). Extensive studies of the molluscan fauna of Isla

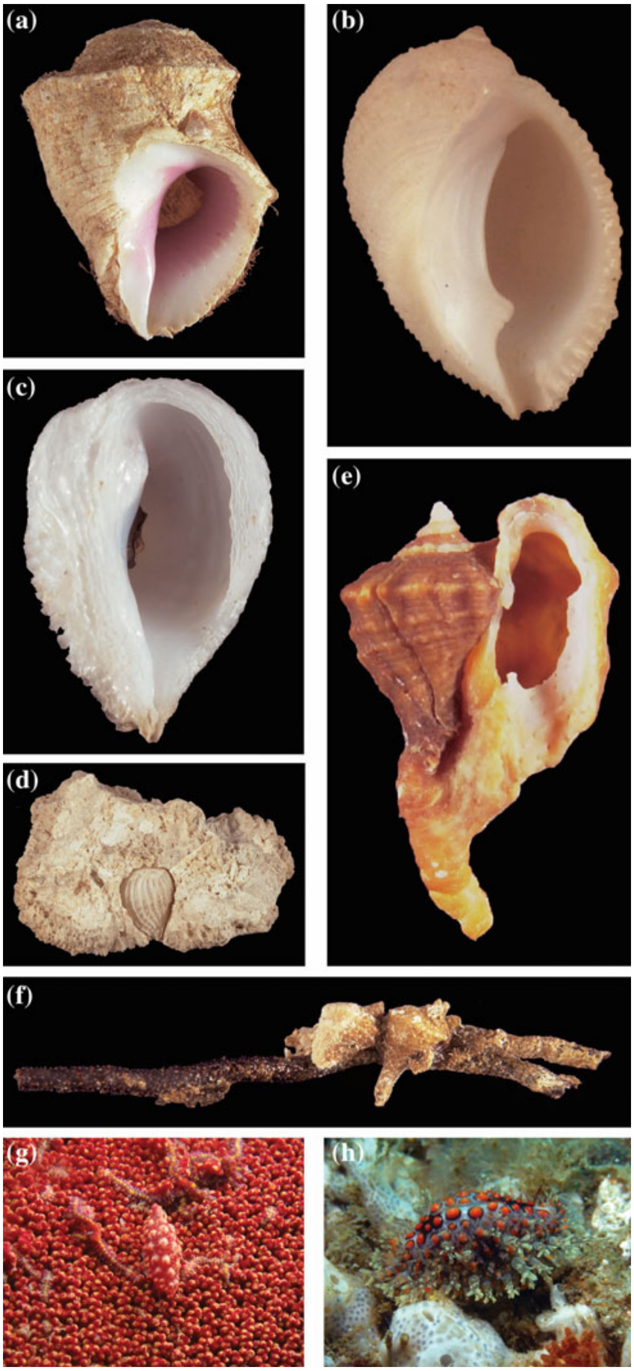

Fig. 7.5 Selected gastropod molluscs associated with ETP coral reefs, with dead or live corals. **a** Ventral view of *Coralliophila neritoidea*; **b** *Quoyula madreporarum*; **c** *Reliquiaecava robillardi* ventral view and **d** inside a coral skeleton; **e** *Rhizochilus antipathum* ventral view and **f** attached to a black coral; **g** ovulid on a gorgonian colony; **h** *Jenneria pustulata* associated with *Pocillopora* corals. Photographs by Patricia Sadeghian, Île Clipperton, except **g** and **h** by Pedro Medina-Rosas, Islas Marías, Mexico

Table 7.9 Number of species of reef-associated molluscs by ETP area

	MEX[1]	SAL[3]	ALI[4]	MAR	REV	CLI[14]	COI	COC[19]	MAL[21]	GAL[14]
Bivalvia	24	1	9	34[6]	77[9]	42	218[16]	78	46	212
Gastropoda	87	6	32	179[7]	204[10]	212	236[17]	446[20]	256	605
Opisthobranchia	148[2]	–	7[5]	52[8]	42[11]	37[15]	85[18]	22	–	34[22]
Polyplacophora	11	–	–	–	8[12]	1	1[17]	8	6	13
Cephalopoda	1	–	–	–	1[13]	1	–	6	3	8
Total	271	7	48	265	332	293	540	560	311	872

MEX Mainland Mexico (Opisthobranchia from Bahía de Banderas, all others from Tenacatita); *SAL* El Salvador; *ALI* Rocas Alijos, Mexico; *MAR* Islas Marías, Mexico; *REV* Islas Revillagigedo, Mexico; *CLI* Île Clipperton, France; *COI* Isla Coiba, Panama; *COC* Isla del Coco, Costa Rica; *MAL* Isla de Malpelo, Colombia; *GAL* Islas Galápagos, Ecuador

Sources [1]Landa-Jaime et al. (2013), [2]Hermosillo et al. (2006), Behrens and Hermosillo (2005), [3]Hernández (1992), [4]McLean and Coan (1996), Kaiser (2006), [5]Hermosillo (2009a), [6]Bernard et al. (1991), Kaiser unpub. data, [7]Small (1998), Kaiser unpub. data, [8]Hermosillo (2009b), [9]Strong and Hanna (1930), Villalobos (1960), González-Nakawaga and Sánchez-Nava (1986), Bernard et al. (1991), Bautista-Romero et al. (1994), Mille-Pagaza et al. (1994), Emerson (1995), [10]Strong and Hanna (1930), Villalobos (1960), González-Nakawaga and Sánchez-Nava (1986), Chávez-Hernández and Bretado-Aguirre (1990), Holguín-Quiñones et al. (1992), Bautista-Romero et al. (1994), Holguín-Quiñones (1994), Mille-Pagaza et al. (1994), [11]Hermosillo and Gosliner (2008), Behrens et al. (2009), [12]Ferreira (1983), [13]Holguín-Quiñones et al. (1992), [14]Kaiser (2007), [15]Millen and Hermosillo (2012), [16]Vega (2001), [17]Vega (2002), [18]Hermosillo and Valdés (2004), Hermosillo and Camacho-García (2006), [19]Cortés (2012), [20]Cortés (2012), Kaiser unpub. data, [21]Kaiser and Bryce (2001), [22]Gosliner (1991)

del Coco and Isla de Malpelo have reported incidental finds of opisthobranchs (Camacho-García 2009; Rodríguez-Sevilla et al. 2009; Cortés 2012). However, no species lists have presently been published on the opisthobranch fauna of El Salvador, or many other locations in the ETP.

7.3.3.6 Crustacea (Decapoda)

More than 850 species of decapod crustaceans have been recorded from the ETP (Boschi 2000), the majority of which are crabs belonging to the Infraorder Brachyura. Most of the information comes from the coasts of Mexico (Fig. 7.6), Costa Rica, Panama, and Colombia, likely due to greater investment in marine research in these countries. For example, of all of the decapod species known from the ETP, 634 occur in the tropical Mexican Pacific (Hendrickx 1993), representing 77 % of the ETP decapod crustaceans. In Costa Rican waters, there are 438 species (53 % of spp.) according to Vargas and Wehrtmann (2009), and on the Colombian Pacific coast, Lemaitre and Álvarez-León (1992) recorded 378 species (45 % of spp.). Little is known of the decapod species of western Guatemala, El Salvador and Nicaragua, except that some commercially important species are exploited for human consumption, such as shrimps (Penaeoidea), lobsters (Palinuridae), and swimming crabs (Portunidae). While the decapod fauna of the ETP is dominated by brachyuran crabs (Boschi 2000), those exclusively associated with corals (mostly live corals) comprise roughly 120 species and are dominated by caridean shrimps (Table 7.10).

Inventories of decapods in the ETP, including coral associated faunas, began with expeditions from the late 19th and mid 20th centuries (*Albatross, Zaca, Velero*, among others) (Garth 1992; Wicksten and Hendrickx 1992). Most of these early studies included descriptions of new species and annotations to species' ranges. It was not until the late 1970s that ecological investigations were carried out with coral-associated crustaceans. On Panamanian reefs (8°N), Abele (1974) noted that the richness of crustacean species is higher on coralline substrates than in sandy or mangrove habitats. Gotelli and Abele (1983) showed that the number of coral-associated species was correlated with coral colony size. On the Pacific coast of Colombia (2°58′N), research on coral-associated decapods has been less extensive. However, studies made by von Prahl et al. (1978) and Castro (1982) noted the importance of symbiotic decapods as promoters of coral health. In Mexico, Ramírez-Luna et al. (2002) demonstrated that abundance and diversity of coral-associated crabs at Huatulco (16°N) was low in the wet season (from May to October). In two studies conducted by Hernández et al. (2009, 2013), 60 coral-associated decapod species were collected along the tropical Mexican Pacific (from 15°N to 26°N), and 11 of these were considered to be coral symbionts. Alvarado and Vargas-Castillo (2012) recorded 35 species of invertebrates from *Pocillopora* corals at Bahía Culebra, Costa Rica (10°36′N), and 18 (nearly 50 %) were decapod crustaceans. Pocilloporid corals have an Indo-Pacific origin (Cortés 1997) and many of their coral-associated decapod symbionts mirror this biogeographic connection (Garth 1974).

There are differences between crustaceans associated with live and dead corals. Enochs and Manzello (2012a) noted higher species richness associated with dead versus live coral substrates, and the dead coral species' assemblage seems to be more closely related to crustaceans associated with rocky than coral substrates. This is an interesting topic worthy of further research.

Fig. 7.6 Selected ETP coral-associated decapods. **a** *Trapezia digitalis*, Revillagigedo Islands; **b** *Calcinus californiensis*, Ixtapa; **c** *Harpiliopsis spinigera*, Huatulco; **d** *Trizopagurus magnificus*, Ixtapa; **e** *Alpheus lottini*, Ixtapa; **f** *Stenorhynchus debilis*, Acapulco. Photographs by Luis Hernández, all from Mexico

Table 7.10 Total ETP species richness of decapod crustaceans and numbers of species associated with corals

	Total no. species[1]	No. with corals[2]
Anomura	165	31
Brachyura	411	38
Caridea	161	50
Others	88	3
Total	825	122

Sources [1]Boschi (2000), [2]Abele (1974), Prahl et al. (1978), Gotelli and Abele (1983), Lemaitre and Álvarez (1992), Hernández et al. (2009, 2013); Enochs et al. (2011), Alvarado and Vargas-Castillo (2012)

7.3.3.7 Echinodermata

A total of 722 species of echinoderms has been reported from the ETP, encompassing 214 ophiuroids, 195 asteroids, 174 holothuroids, 118 echinoids, and 21 crinoids (Solís-Marín et al. 2013a). Of these, only 93 (13 %) inhabit coral reef environments (sensu Solís-Marín et al. 2013a) (Fig. 7.7). These numbers will likely increase with further collections and assessments. The groups with the highest numbers of reef species are the ophiuroids and holothurians, with 31 and 30 species, respectively (Solís-Marín et al. 2013a). Additionally, 16 species of echinoids and asteroids are known from reefs in the region (Solís-Marín et al. 2013a). There are no reports of crinoids inhabiting coral reefs in the ETP.

The most species rich echinoderm fauna in the ETP is known from Mexico, but only 29 % of Mexican echinoderms occur on coral reefs (Table 7.11). This relatively low percentage of coral reef species is similar in Panama (24 %), the Galápagos Islands (27 %), Ecuador (30 %), and at Isla del Coco (35 %). In other areas, the proportion of reef-dwelling echinoderms is notably higher, for example, El Salvador (60 %), Nicaragua (58 %), Revillagigedo Archipelago (58 %), Costa Rican mainland (49 %), Malpelo Island (42 %), and Colombia (41 %) (Table 7.11). This is likely indicative of a greater research effort in more accessible continental environments relative to remote regions and oceanic islands. Considering El Salvador and Nicaragua, those species that are presently reported are the most conspicuous and easy to identify, suggesting a high likelihood that additional species are present but as yet unaccounted for (Alvarado et al. 2010, 2013).

Of the 93 species of reef-associated echinoderms in the ETP, only six have been reported from 11 sampled regions (Table 7.11). Those species are the asteroid *Phataria unifascialis* (Fig. 7.7a), the holothuroid *Isostichopus fuscus* (Fig. 7.7d), the echinoids *Echinometra vanbrunti* and *Diadema mexicanum* (Fig. 7.7f), and the ophiuroids *Ophiocoma alexandri* and *O. aethiops*. The seastar corallivore *Acanthaster planci* (Fig. 7.7b) is present at eight of the eleven regions, only absent in El Salvador, Nicaragua and the Ecuadorian mainland (Solís-Marín et al. 2013a). Another six species are reported from ten of the 11 regions, including the asteroid *Nidorellia armata*, the ophiuroid *Ophiactis savignyi*, the holothuroid *Holothuria* (*Halodeima*) *kefersteini* (Fig. 7.7c) and the echinoids *Eucidaris thouarsii*, *Tripneustes depressus* (Fig. 7.7e) and *Toxopneustes roseus*. Although the total number of studies on reef echinoderms in the ETP is limited, five species, *D. mexicanum*, *Eucidaris galapagensis, E. thouarsii*, *A. planci* and *I. fuscus*, are especially important ecologically as bioeroders, corallivores and in bioturbation, and have been widely studied (Alvarado et al. 2013; Benavides-Serrato et al. 2013; Coppard and Alvarado 2013; Solís-Marín et al. 2013b; Sonnenholzner et al. 2013).

7.3.3.8 Fishes

Over 1300 species of marine fishes have been described from shallow-waters (<100 m depth) in the ETP (Robertson and Allen 2008; Eschmeyer 2014). Based on previous analysis of new species descriptions during the 50 years before 2004, the total number of described fishes in the region increased at a rate of 4.7 new species per year during this time (Zapata and Robertson 2007). Nearly 49 % of the species described in this period inhabit soft bottom habitats while 38 % live in reef (either rocky or coral) habitats. New species likely to be found in soft bottom or reef habitats will tend to be small and restricted in both their geographic and depth distribution, relatively localized towards the center of the ETP region, and from relatively deep waters (Zapata and Robertson 2007).

Currently, the entire shallow water marine fish fauna in the region is composed of 111 species of sharks or rays and 1193 species of bony fishes. Nearly 47 % of the species can be found associated with rocky or coral reefs and adjacent rubble, sandy or water-column habitats. Of these, 25 elasmobranchs and 482 bony fishes (39 % of the fauna) can occur on coral or rocky reefs, but only 353 of them (27 % of the total fish fauna) are found exclusively on either type of reef. However, only 157 species (12 % of all species) can be found associated with corals (not necessarily on reefs since isolated coral colonies are common), and a subset of these (115 species) occurs exclusively on coral reefs (Robertson and Allen 2008). Given the scarcity and small size of coral reefs in the ETP region, it is not surprising that the majority of the exclusive reef fish fauna is found on rocky reefs only (238 species) while only a handful (6 species) are found associated only with corals. This, however, seems to be an artifact of the extremely restricted geographic distribution of these few species, five of which are endemic to the only coral reef atoll in the ETP (Clipperton Atoll: Robertson and Allen 2008).

Therefore, nearly all of the fishes found on coral reefs in the ETP are also found on rocky reefs but not vice versa. Thus, throughout the remainder of this section we will use the term "reef fishes" to refer in general to fishes found on either rocky or coral reefs, while the term “coral reef fishes” will be used to refer to the subset of reef fishes found on coral reefs. The ETP region has been separated for millions of years from the Indo-West Pacific by the 4000–7000 km wide East Pacific Barrier and from the Caribbean by the Isthmus of Panama (Glynn and Ault 2000; Robertson et al. 2004; Robertson and Allen 2008). This isolation of the ETP is reflected in its high level of endemism, 16 % of genera and 70 % of species of marine fishes are endemic to the region (Robertson and Allen 2008). This is also generally the case for reef fishes, 73 % of which are endemic to the ETP (Table 7.12). However, among the coral reef fish component the level of endemism is lower (55 % of 115 reef fishes associated with corals). This reduction in regional endemism can be partially explained by faunal enrichment due to immigration from the Indo-West Pacific region: nearly 43 % of the 115 reef-exclusive fishes found on coral reefs are presumed to be Indo-West Pacific immigrants (Robertson et al. 2004). However, only 31 of these species are considered to have resident populations in the ETP (Robertson and Allen 2008). In contrast, faunal enrichment from the Indo-West Pacific is low among the rocky-reef exclusive component, although there is some peripheral enrichment from the adjacent Californian (17 species) and Peruvian (20 species) warm temperate regions, which lack coral reefs (Table 7.12). Therefore, discounting the vagrant Indo-West Pacific species, the entire coral reef fish fauna in the ETP is just below 100 species.

Total fish species richness estimates on coral reefs based on visual censuses generally agree with the notion that the ETP coral reef fish fauna is “depauperate” (Ekman 1953; Sale 1980; Thresher 1991). For example, while only 71 species were observed during 99 visual censuses made during one year at a single ~10 ha coral reef at Gorgona Island, Colombia, a log-normal abundance-distribution model fitted to these data predicted the occurrence of 102 species on this reef (Zapata and Morales 1997). Dominici-Arosemena and Wolff (2006) observed a total of 88 species at four coral reef sites in the Gulf of Chiriquí, two dominated by massive corals and two by branching corals. Benfield et al. (2008) observed a total of 79 species on 45 coral reefs and coral communities at Las Perlas Archipelago in Panama. Alvarez-Filip et al. (2006) observed a total of 62 species on the coral reef at Cabo Pulmo, Gulf of California. Estimates based on visual counts, however, generally underestimate the cryptic fish fauna, which can represent a relatively large proportion of the total

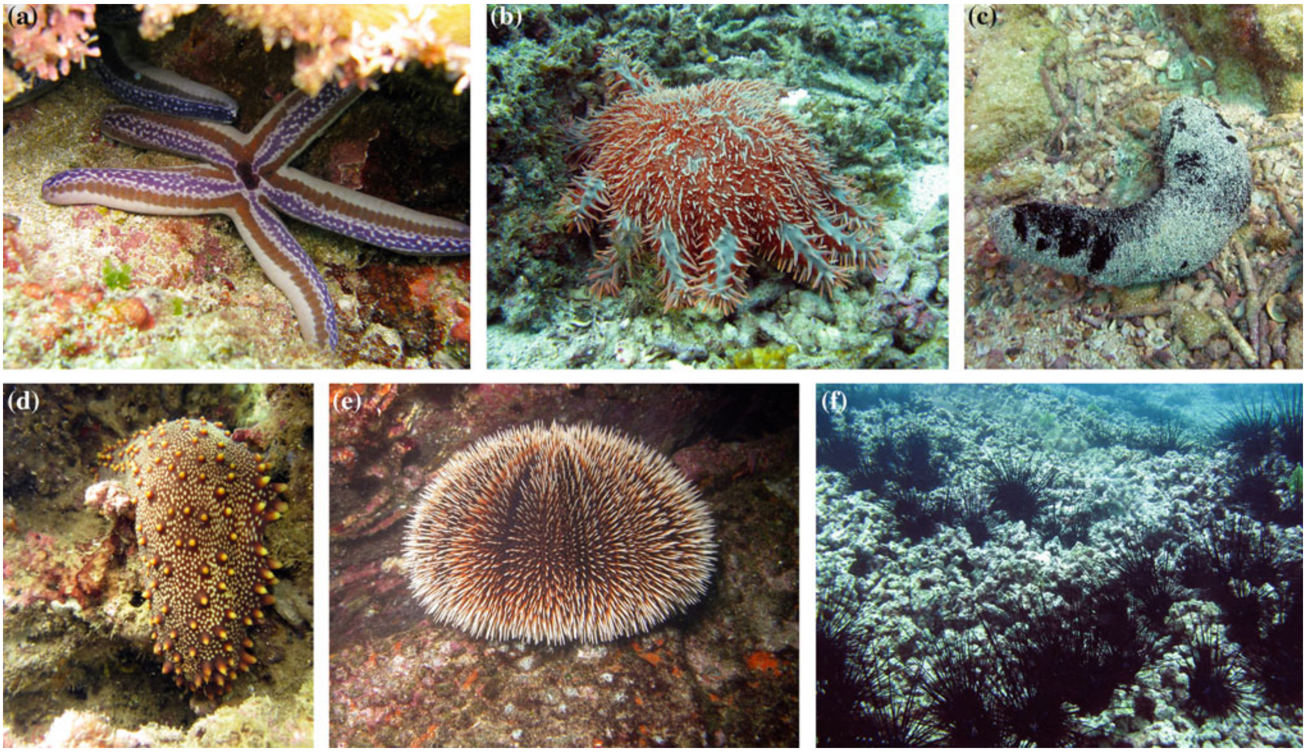

Fig. 7.7 Common echinoderms of ETP coral reefs. **a** *Phataria unifascialis,* Islas Tortuga, Costa Rica; **b** *Acanthaster planci*, Isla Espíritu Santo, Mexico; **c** *Holothuria* (*Halodeima*) *kefersteini*, Galápagos Islands, Ecuador; **d** *Isostichopus fuscus*, Golfo Dulce, Costa Rica; **e** *Tripneustes depressus*, Galápagos Islands, Ecuador; **f** *Diadema mexicanum*, Bahía Culebra, Costa Rica. Photographs by Cindy Fernández-García (**a**), Juan José Alvarado (**b**, **f**), Ángel Chiriboga (**c**, **e**), and Jeffrey Sibaja-Cordero (**d**)

Table 7.11 Numbers of ETP echinoderm species associated with coral reefs, by class for each country or region

	Country-continental mainland							Oceanic islands			
	MEX	SAL	NIC	CRC	PAN	COL	ECU	REV	COC	MAL	GAL
Asteroidea	13	4	2	6	9	13	5	5	8	10	10
Ophiuroidea	25	11	8	17	21	16	5	4	9	7	17
Echinoidea	13	6	7	10	9	11	11	5	11	10	11
Holothuroidea	28	13	5	18	24	15	10	11	15	7	20
Total spp. associated with reefs	79	34	22	51	63	55	31	25	43	34	58
Total echinoderm spp. in region	274	57	38	105	267	133	104	43	123	81	216

MEX Mexico; *SAL* El Salvador; *NIC* Nicaragua; *CRC* Costa Rica; *PAN* Panama; *COL* Colombia; *ECU* Ecuador; *REV* Revillagigedo Archipelago; *COC* Isla del Coco; *MAL* Isla Malpelo; *GAL* Galápagos Islands
Sources Pérez-Ruzafa et al. (2013), Solís-Marín et al. (2013a)

Table 7.12 Number of ETP fish species per family that occur exclusively on coral and rocky reefs

Family	Coral and rocky reefs			Rocky reefs only			Total
	ETP	IP	Other	ETP	IP	Other	
Acanthuridae^a		10		2			12
Antennariidae	2	2					4
Aplodactylidae						1	1
Apogonidae^a	5					1	6
Aulostomidae		1					1
Balistidae	2	2	2				6
Blenniidae^a	3			6		3	12
Bythitidae				13			13
Carapidae					1		1
Carcharhinidae		1					1
Chaenopsidae				23			23
Chaetodontidae^a	1	5		2			8
Cirrhitidae	1	2					3
Gobiesocidae				28		1	29
Gobiidae	4			19		1	24
Haemulidae	1			3		2	6
Holocentridae^a	4^b	2					6
Kyphosidae				4		4	8
Labridae^a	6^b	2		3		4	15
Labrisomidae				40		2	42
Lutjanidae	1			1			2
Microdesmidae				3			3
Monacanthidae		1	1				2
Muraenidae	5	11		4		3	23
Myrocongridae				1			1
Ophidiidae	1						1
Oplegnathidae						1	1
Ostraciidae		1					1
Pomacanthidae	4^b						4
Pomacentridae^a	8^b			10		4	22

(continued)

Table 7.12 (continued)

Family	Coral and rocky reefs			Rocky reefs only			Total
	ETP	IP	Other	ETP	IP	Other	
Priacanthidae		1		1		2	4
Scaridae[a]		1		3	1		5
Sciaenidae				4		3	7
Scorpaenidae	1	1		3			5
Serranidae[a]	11[b]			9		8	28
Syngnathidae		1		1			2
Tetraodontidae	1	4					5
Tripterygiidae	2			13			15
Zanclidae		1					1
Total	63	49	3	196	2	40	353

Species are divided in two groups: those that occur both on coral and rocky reefs (except for six species occurring only on coral reefs, indicated by a superscript) and those restricted to rocky reefs. In each habitat, species are subdivided into biogeographic categories as follows: ETP, endemic to the ETP; IP, Indo-West Pacific immigrant; Other, other regions including Californian, Circumtropical, E to W migrant, Peruvian, and Western Atlantic/Eastern Pacific

[a] Bellwood (1996, 1997) coral reef fish consensus families (i.e., families present on coral reefs everywhere). Other consensus families (Carangidae and Mullidae) also occur on ETP reefs but are not exclusive reef inhabitants

[b] Species occurring exclusively on coral reefs are: *Myripristis gildi* (Holocentridae), *Thalassoma robertsoni* (Labridae), *Holacanthus limbaughi* (Pomacanthidae), *Stegastes baldwini* (Pomacentridae), *Epinephelus clippertonensis* and *Pseudogramma axelrodi* (Serranidae)

Sources Robertson et al. (2004), and Robertson and Allen (2008)

fish fauna in particular microhabitats (e.g., up to 36 % on coral rubble; Glynn 2006). Comparisons of visual counts and collections using rotenone and clove oil made on isolated live coral colonies at Gorgona Island, indicated that visual counts underestimated overall species richness by 28–36 % and number of individuals by 16–35 % (Alzate et al. 2014).

In spite of the dominance of rocky-reef habitats and the depauperate nature of the ETP coral reef fish fauna, its taxonomic structure does not differ significantly from that of more diverse fish assemblages in coral-rich regions (Robertson 1998). Secondary colonization of rocky reef habitats and subsequent adaptation by a fish fauna that originally evolved on coral reefs may explain this pattern (Dominici-Arosemena and Wolff 2006). Alternatively, rocky-reef habitats may offer sufficient resources to fulfill the requirements of coral reef fishes. Whatever the cause, all of the 11 families of fishes that are characteristic of coral reef fish assemblages everywhere (referred to as coral-reef-fish consensus families: Bellwood 1996, 1997) have representatives in the ETP (Table 7.12). However, the most species-rich families of ETP reef fishes are either restricted to rocky habitats, for example, weed blennies (family Labrisomidae with 42 species), clingfishes (Gobiesocidae, 29 spp.) and tube blennies (Chaenopsidae, 23 spp.), or have few representatives on coral reefs, e.g. gobies (Gobiidae) with four species on coral reefs out of 24 species on reefs). Other families have variable representation on coral reefs. For instance, 11 species of grouper (Serranidae) occur on coral reefs out of 28 species occurring on any type of reef. Similarly, 16 out of 23 moray eels (Muraenidae), 8 out of 22 damselfishes (Pomacentridae), and 8 out of 15 wrasses (Labridae) occur on coral reefs (Table 7.12). Some families relatively rich in coral reef species are composed of a large proportion of Indo-West Pacific immigrants, most notably the surgeonfishes (Acanthuridae) and the moray eels (Muraenidae). Other families, while poor in species, have a large Indo-West Pacific component, e.g., the hawkfishes (Cirrhitidae), and yet others are represented by a single Indo-West Pacific immigrant species, e.g., Aulostomidae, Ostraciidae and Zanclidae (Robertson and Allen 2008).

While fish families typical of coral reefs everywhere (i.e., Bellwood's consensus families) have representatives in the ETP, few of those species are either numerically dominant or ecologically important (Fig. 7.8). For instance, two of the five most abundant species (the snapper *Lutjanus viridis* and the hawkfish *Cirrhitichthys oxycephalus*; Zapata and Morales 1997) and two of the most ecologically important species on a coral reef at Gorgona Island, Colombia (the pufferfish *Arothron meleagris* and the triggerfish *Pseudobalistes naufragium*; Guzmán 1988; Palacios et al. 2014), do not belong to Bellwood's consensus families (Bellwood 1996, 1997). Only in some cases, such as in the damselfishes (Pomacentridae), can species in Bellwood's consensus families be either very abundant (e.g., *Chromis atrilobata*; Zapata and Morales 1997) or ecologically important (e.g.,

Fig. 7.8 Some numerically dominant (*left column*) and ecologically important (*right column*) fishes from Gorgona Island, Colombia coral reefs. **a** Scissortail damselfish, *Chromis atrilobata* (Pomacentridae); **b** Guineafowl puffer, *Arothron meleagris* (Tetraodontidae); **c** Cortez rainbow wrasse, *Thalassoma lucasanum* (Labridae); **d** Blunthead triggerfish, *Pseudobalistes naufragium* (Balistidae); **e** Blue and gold snapper, *Lutjanus viridis*, (Lutjanidae); **f** Acapulco damselfish, *Stegastes acapulcoensis* (Pomacentridae). All photographs by Fernando A. Zapata

Stegastes acapulcoensis; Wellington 1982a, b). Rarely, a single species from a coral reef fish consensus family is both numerically dominant and ecologically important in an ETP coral reef, although it might be argued that abundant species are always ecologically important (e.g., the wrasse *Thalassoma lucasanum*).

A noteworthy feature of the ETP reef fish fauna is the relatively distinctive composition of the oceanic island assemblages. The five oceanic islands or archipelagos in the region (Galápagos, Malpelo, Coco, Clipperton and Revillagigedo islands) are sufficiently isolated to exhibit both a significant degree of local endemism and a reduction in species richness. Only 64 % of the exclusively reef-associated fish species occur on islands and, individually, each of the islands or archipelagos exhibit between 1 and 4.5 % local endemism. An additional 5 % of the reef fishes are endemic to more than one oceanic island (Robertson and Allen 2008). Overall, 18 % of the reef-associated fish species are endemic to ETP oceanic islands and including other environments the level of endemism is 22 % on oceanic islands. Such a level of endemism led Robertson and Cramer (2009), in their re-evaluation of fish faunal relationships in the ETP, to propose the existence of an Oceanic Island Province. In contrast to the full set of reef species, those found exclusively on coral reefs exhibit different patterns. For instance, the reduction in species richness is minimal (only 3 out of 115 species do not occur on oceanic island coral reefs), but local endemism on oceanic islands is lower than in the full set of reef fishes (<1 % on each island except at Clipperton Atoll, where it is 4 %). However, endemism on multiple oceanic islands is higher (9 %) than in the entire reef fish fauna.

Latitudinal variation in species richness has been previously examined for the continental shoreline component of the endemic ETP fish fauna (Mora and Robertson 2005). This analysis found a major species richness peak between Panama and Costa Rica and a second, smaller one, in the lower Gulf of California, Mexico. However, when considering only species that occur exclusively on either coral or rocky reefs (including those on islands), the major peak in species richness is located on the south-eastern tip of the Baja California Peninsula, with secondary high-diversity areas along the south-western coast of the Mexican mainland and in the Costa Rica and Panama area. When considering the subset of species found on coral reefs only, the peak in species richness is located in the Gulf of Chiriquí, Panama, where coral reefs are most abundant (Maté 2003; Robertson and Allen 2006).

7.4 Reef-Associated Communities and Habitats

Several interdependent communities and habitat niches make up coral reef ecosystems. In this section we discuss two communities that are integral parts of ETP coral reefs: zooplankton and the cryptofauna. Zooplankton inhabits coral reef structures closely (emergent or demersal zooplankton, see below) as well as the overlying water column, and is a necessary food source for corals and other reefs organisms. Numerous reef species also contribute importantly to plankton communities during early stages of dispersal and immigration (settlement events). Some species of zooplankton have been found only in reef environments, suggesting that reefs may harbor a distinct zooplankton assemblage whose functional and energetic roles are still poorly understood. The reef cryptofauna is composed of a diverse assemblage of organisms that dwell within reef frameworks and sediments, and are therefore rarely visible on the reef's surface. These assemblages are just beginning to be studied in the ETP. In addition, we summarize present knowledge on soft benthic environments, rhodolith beds, and mesophotic environments neighboring coral reefs. Most of the sediment in reef-associated soft benthic environments in the ETP comes from freshwater run-off and from the coral reefs themselves, mainly as a product of bioerosion. The organisms living in these sediments are important sources of food for some reef fishes. Rhodolith beds are understudied habitats commonly associated with ETP coral reef ecosystems, and are important nursery grounds for several reef species. Much like rhodolith beds, mesophotic environments are very poorly known, and contrary to other ocean regions, there is little evidence of a strong connection between shallow and deep reef habitats.

7.4.1 Reef Zooplankton

Eastern tropical Pacific coral reefs are typically species poor relative to other reef regions, and some do not occur in nutrient poor waters. Although the roles of zooplankton in coral reef communities are not yet well known (Roman et al. 1990), zooplankton represents an important trophic link between primary producers and higher trophic levels, including scleractinian corals and fishes (Porter 1974; Robichaux et al. 1981; Hamner et al. 1988; Sorokin 1990; Sedberry and Cuellar 1993).

Emery (1968) established the term "emergent zooplankton," to refer to the zooplankton living over and within reef substrates. This plankton remains associated with the benthos during the day and migrates into the water column at night (Ohlhorst 1982). A complex and dynamic mix of pelagic zooplankton, eggs and larvae may also be found in the water above reef habitats (Carleton et al. 2001). The abundance and seasonality of coral reef zooplankton have been linked to various environmental conditions (Glynn 1973; McWilliam et al. 1981), reef morphology (Lefevre 1984), and habitat patchiness (Greenblatt 1982). The presence of some groups has been correlated with differences in substrate composition (Alldredge and King 1977; Porter and Porter 1977; Birkeland and Smally 1981), lunar cycles (Alldredge and King 1980), and predation intensity (Holzman et al. 2005; Motro et al. 2005; Yahel et al. 2005).

Information concerning the horizontal distribution of zooplankton is scarce (Morales and Murillo 1996). Some studies, however, have demonstrated the importance of the net import of zooplankton to reef ecosystems (Ferraris 1982). Others have described the differences in abundance, composition and behavior between the diverse community of resident, reef-dwelling zooplankton and the community occupying waters outside of reefs (Echelman and Fishelson 1990; Carleton 1993). Nevertheless, quantitative data on variations in the abundance, type, and distribution of coral reef zooplankton on spatial scales of centimeters to meters and temporal scales of one to several hours are rare (Jacoby and Greenwood 1989; Yahel et al. 2005). Early studies concerned with the abundance, diversity, flux and fate of zooplankton as it approaches and crosses a windward coral reef suffered from the limitations of traditional sampling procedures in reef environments and a poor understanding of fine scale physical oceanographic processes near reefs (Carleton 1993). More recent methods used for the study of zooplankton associated with coral reefs, including nets, benthic traps, core samplers, bags, video footage and suction devices (Heidelberg et al. 2004), have allowed for a better understanding of zooplankton dynamics. Although each method provides information about a specific subset of the zooplankton community, such as the pelagic or demersal component (Alldredge and King 1977), each has limitations (reviewed by Sorokin 1990).

Compared to studies on the Great Barrier Reef and in the Caribbean Sea (Heidelberg et al. 2004), information on zooplankton associated with coral reef ecosystems in the ETP is limited (Table 7.13). Studies in Pacific Panama have quantified the important role of zooplankton as a source of food for corals. This work suggested that coral feeding is facultative and that rates can vary widely (Palardy et al. 2005, 2006). Wellington (1982a) concluded that corals were largely phototrophic, but some species under shading could compensate for the reduction in phototrophic nutrition by feeding on plankton. Grottoli and Wellington (1999) determined the effects of light and zooplankton on skeletal $\delta^{13}C$ values in the ETP corals *Pavona clavus* and *Pavona gigantea*. They found that decreases in light or increases in zooplankton abundances resulted in decreases in skeletal $\delta^{13}C$ levels, thus establishing a preliminary basis for reconstructing past environmental changes in irradiance and zooplankton prevalence using coral records.

Work off the Pacific coast of Colombia, including areas encompassing coral reefs, has examined the taxonomy, spatial distribution, and abundance of ichthyoplankton, plankton productivity and composition, as well as the abundance and diversity of hyperiid amphipods (Giraldo et al. 2006; Escarria et al. 2007; Valencia and Giraldo 2009). In this region, copepods (56.8 % of spp.) and appendicularians (16.9 % of spp.) were the dominant taxa. Also collected were 35 species and 14 families of fish larvae, as well as 20 species of amphipods.

Several studies are available on the reef zooplankton from Costa Rica's Pacific coast. Guzmán and Obando (1988) reported on the composition of zooplankton from coral reefs at Isla del Caño. In this study, copepods were the dominant group, accounting for 40–70 % of the total zooplankton abundance. These workers also found that the abundances of other groups changed at night, in some cases reaching higher levels than the copepods. A detailed study of the isopod *Excorallana tricornis occidentalis* from the same samples indicated a nocturnal migration into the water column and changes in density throughout the year (Guzmán et al. 1988). In coral reef studies at Bahía Culebra, Costa Rica, copepods were numerically dominant among the zooplankton sampled with traps over colonies of *Pavona clavus* and *Pavona gigantea* (Morales-Ramírez, unpub. data). In this study a new monstrilloid copepod was discovered, namely *Cymbasoma concepcione* (Suárez-Morales and Morales-Ramírez 2003).

The first synthesis of zooplankton at Isla del Coco was published by Morales-Ramírez (2008). He reported 136 species, including the species of ichthyoplankton previously reported by Fernández-Leiva (1996). Three coral reefs at Isla del Coco were sampled between 2009 and 2012, and copepods were again the dominant group, with abundances accounting for between 56 and 75 % of the total number of individuals collected, including two new species of monstrilloid copepods (Suárez-Morales and Morales-Ramírez 2009). Other groups such as chaetognaths and larvaceans could, depending on water temperature and food availability, exhibit abundances similar to those of copepods (Esquivel-Garrote 2015). The emergent zooplankton associated with coral reefs was captured with nets and traps during vertical migration to the surface in the evening, and a change in the population structure of zooplankton was observed on these reefs according to the time of day (Esquivel-Garrote 2015).

Studies on the ecology and relationships of the demersal zooplankton among corals and reef communities in the ETP are few compared to other regions; therefore, more research is needed on the diversity, distribution, composition, abundance and trophic role of zooplankton on coral reefs in the ETP region.

7.4.2 Cryptofauna

The term cryptofauna refers to animals that shelter within reef frameworks (Ginsburg 1983; Kobluk 1988; Glynn and Enochs 2011) (Fig. 7.9). Their shelters are structurally diverse, ranging from large framework cavities to thin cracks under loose rubble fragments, and from voids between coral

Table 7.13 Coral reef zooplankton studies in the ETP

Site	Country	Sampling method	Depth (m)	Dominant groups	Study objective
Isla del Caño[1]	Costa Rica	Net (280 μm)	Surface	Copepoda Mysidacea Crab zoea	Diversity and abundance of zooplankton
Isla del Coco[2]	Costa Rica	Net (200 μm-500 μm)	Surface	Copepoda Chaetognatha Appendicularia	Diversity and abundance of zooplankton
Isla Contadora[3]	Panama	Bucket	1–6	Isopoda Crab Zoea Amphipoda	Corals feeding on zooplankton
Isla Contadora[4]	Panama	Net (50 μm)	0–6	Copepoda Isopoda Amphipoda	Corals feeding on zooplankton
Isla Gorgona[5]	Colombia	Net (250 μm)	0–50	Ichthyoplankton	Ichthyoplankton taxa
Isla Gorgona[6]	Colombia	Net (250 μm)	0–50	Copepoda Appendicularia	Plankton productivity
Punta Cruces, Cabo Marzo[7]	Colombia	Net (250 μm)	0–50	Amphipoda	Abundance and diversity of amphipods

Sources [1]Guzmán and Obando (1987), [2]Esquivel-Garrote (2015), [3]Palardy et al. (2005), [4]Palardy et al. (2006), [5]Escarria et al. (2007), [6]Giraldo et al. (2006), [7]Valencia and Giraldo (2009)

Fig. 7.9 Collage of cryptofauna extracted from coral reef frameworks and rubble in the Gulf of Chiriquí, Panama. Photographs by Ian C. Enochs

branches to burrows into mounding coral colonies. Compared to the reef surface the cryptic habitat generally experiences reduced irradiance and water flow, which can influence the distribution of both photosynthetic flora (Kobluk 1988) and sessile suspension feeding fauna alike (Buss and Jackson 1981; Richter et al. 2001). This can, in turn, affect the distribution of a suite of motile cryptic herbivores and invertivores, respectively. The cryptic habitat is also unique in that it confers upon its occupants a degree of protection from large surface predators (Bakus 1966), though many of the cryptofauna may be predators themselves (Glynn 2006, 2013; Enochs 2012).

The animals that occupy the cryptic reef habitat are incredibly diverse, accounting for the majority of reef metazoan biodiversity (Reaka-Kudla 1997). Despite this, the cryptofauna community is understudied relative to surface reef fauna. This holds true for the ETP, though structurally complex pocilloporid reefs and associated rubble fields provide ideal habitats for a diverse cryptofauna assemblage. Investigation of ETP cryptic reef fauna, ecology and biodiversity has focused primarily on associates of living *Pocillopora damicornis* (e.g., Abele 1976; Alvarado and Vargas-Castillo 2012). Recent work (Glynn 2006, 2011; Enochs et al. 2011; Enochs 2012; Enochs and Manzello 2012a), however, has expanded investigation to the multi-phyletic assemblage associated with dead coral, reef frameworks, and rubble. Cryptic communities associated with each of these habitats have been shown to be diverse. For example, Abele (1979) collected more than 55 species of decapods from living *Pocillopora* colonies in the Pearl Islands, Panama and 37 species from colonies at Uva Island, Panama. Glynn (2006) also collected 23 species of cryptic fishes from Uva Island. Alvarado and Vargas-Castillo (2012) identified 35 species from 448 cryptic individuals collected from *P. damicornis* at Playa Blanca, Bahía Culebra, Costa Rica. Enochs and Manzello (2012a) collected more than 289 cryptic species from live and dead coral at Playa Larga, Isla Contadora, in the Gulf of Panama.

7.4.3 Soft Benthic Environments

Coral reefs are one of the main sources of carbonate sediments in soft sandy benthic environments in the ETP. These sediments are the product of erosive processes, both by abiotic factors and by eroding invertebrates (e.g., echinoids, annelids, molluscs and crustaceans) and fishes (e.g., Scaridae, Tetraodontidae, and Balistidae) (Glynn 1997). The sand produced creates intertidal and subtidal soft benthic environments (adjacent to or within the coral reef), where a characteristic benthic fauna lives (Westheide 1991; Sibaja-Cordero et al. 2013). Few studies have been carried out on the benthic fauna of sandy bottoms on or near coral reefs of the ETP.

The meiofauna (metazoans in the size range 63–500 μm) of the Galápagos Islands was studied at 35 intertidal sites composed of carbonate sands (Ax and Schmidt 1973; Schmidt 1978; Westheide 1991). Westheide (1991) recorded 390 species of meiofauna from the archipelago. While the Platyhelminthes were highly species rich (79 spp.) and abundant (50 % of indiv.), other groups, including polychaetes (100 spp.), molluscs and peracarids, were also prominent. Poorly known groups were the Gastrotricha (23 spp.), Acoelomorpha (16 spp.), Nemertea (7 spp.), Gnathostomulida (4 spp.) and Kinorhyncha (1 sp.). Meiofaunal abundances were found to be highest in the warmer equatorial months (Westheide 1991).

Guzmán et al. (1987) studied the dynamics of meiofaunal groups in the sediments at Isla del Caño, Costa Rica. In this study the most abundant groups were the Foraminifera (21.2 %), Copepoda (19.7 %), Nematoda (19.1 %) and Gastropoda (16.5 %). Community composition shifted with season, likely due to the input of organic matter during the rainy months. The highest diversity was observed in heterogeneous carbonate sediments. No other studies on meiofauna are presently known from coral reefs in the ETP.

Studies of reef sediment-dwelling macrofauna (animals >500 μm) are also limited. Examples include studies on the taxonomy of polychaetes from the sublittoral sandy substrates of the coral reefs at Mali Rock and Granito de Oro, Coiba Island, Panama (Aguado and López 2003; Aguado and San Martín 2004, 2006; López et al. 2005). This fauna includes nine species of the family Paraonidae, including one new species (Aguado and López 2003), four species of the family Pisionidae, including one new species (Aguado and San Martín 2004), 19 species of the family Syllidae, including a probable new species (Aguado and San Martín 2006), and nine species of the family Capitellidae, including one new species (López et al. 2005).

Other studies of the macrofauna associated with coral colonies have been performed in the Las Perlas Archipelago, Panama. For example, Mair et al. (2009) reported 201 invertebrate taxa from the sand and sandy-shell bottoms (<30 m depth) near coral colonies. The crustacean families Ampeliscidae, Anthuridae, Ogyridae, Processidae, Pasiphaeidae, and Squillidae were prominent with higher densities in mixed sediments rather than in other benthic substrates. The annelids of the families Nepthyidae, Lubrinereidae, Orbiniidae and Goniadidae, and bivalves of the family Tellinidae were dominant in calcareous sands (Mair et al. 2009).

Valencia et al. (2014) sampled the soft bottom benthos (10 m depth) at Gorgona Island, Colombia, and collected 73 species belonging to 58 families, primarily polychaetes and crustaceans. The sediments contained more carbonates (>50 %) at the stations near the dead Remanso coral reef and the Playa Blanca live reef. Other stations near the live coral reefs of Azufrada, Farrallones and Planchón contained less than 9 % carbonates. The species composition of the benthic fauna indicated that stations in close proximity to coral reefs were different from those located elsewhere. Communities near the dead reef were unique with coarse sediments dominated by both suspension (Ampeliscidae, amphipods) and deposit (Spionidae, polychaete worms) feeders. A previous study by Cortés FA et al. (2012) demonstrated similar patterns with high densities and species richness at El Remanso, Gorgona Island.

Sibaja-Cordero (2012) recorded 267 taxa in sediments primarily produced by the erosion of reef carbonates (<80 m depth; Sibaja-Cordero et al. 2014) at Isla del Coco, Costa Rica. These macrofauna were evidently dependent on detrital trophic inputs from nearby coral reefs and insular terrestrial sources. The stations with sand substrates at the coral reefs of Chatham Bay revealed 18–34 taxa, at Weston Bay 24–26 taxa, and at Wafer Bay 7–31 taxa. Community composition changed with depth, with shallow reef substrates dominated by surface deposit and suspension feeders, such as the polychaete *Magelona californica* and the bivalve *Gouldia californica*, respectively (Sibaja-Cordero 2012). Isla del Coco has a marked thermocline around 50 m depth; at this depth Sibaja-Cordero et al. (2012) observed a reduction in the diversity of polychaetes and other changes in the species composition of the sediments.

Finally, the macrofauna associated with the carbonate sediments of Isla del Coco demonstrated a high species richness of molluscs compared with other soft bottom habitats near the Costa Rican mainland. Sibaja-Cordero et al. (2013) reported 40 species of molluscs from Cocos Island, including 11 new records and one new species of Caecidae (*Caecum cocoensei* Sibaja-Cordero et al. 2014). A total of about 180 species of macrobenthos inhabits the sediments at Isla del Coco (Sibaja-Cordero 2012).

7.4.4 Rhodolith Beds

Rhodolith or mäerl beds (Fig. 7.10a, b) are associated with rocky (Foster 2001; Foster et al. 2007) and coral reefs (Littler and Littler 2008) in the ETP. These communities are made up of aggregations of free-living, non-geniculate coralline red algae (Woelkerling 1988; Foster et al. 2013). Individual rhodoliths usually grow around a rock, coral, shell or any other element that serves as a nucleus for their development. They are composed of erect calcified branches (Fig. 7.10b) that usually grow in a consistent number of concentric cellular layers (McConnnico et al. 2014). Rhodoliths display a wide variety of growth forms ranging from fruticose to lumpy and are discoid or irregularly shaped, averaging approximately six cm in diameter (Riosmena-Rodriguez et al. 1999). Individual rhodoliths, as well as rhodolith communities, can be composed of a single species or a combination of species (Yabur-Pacheco et al. 2007; Steller et al. 2009; Riosmena-Rodríguez et al. 2010; Hernández-Kantún et al. 2014).

Rhodolith beds have been known in the ETP (Fig. 7.10a) since the pioneering taxonomic studies of Dawson (1960) in the Gulf of California. In recent years, rhodolith beds have been observed in other regions of the ETP including Panama (Littler and Littler 2008; Reijmer et al. 2012), Costa Rica (Solano-Barquero 2011; Robinson et al. 2013), the Pacific coast of Baja California (Ávila and Riosmena-Rodríguez 2011; Riosmena-Rodríguez et al. 2012; Robinson et al. 2013; Hinojosa-Arango et al. 2014), the Galápagos Islands (Halfar and Riegl 2013), Nicaragua (Robinson et al. 2013), and the tropical Mexican Pacific coast (Peralta-García and Rosas-Alquicira 2014).

Rhodolith beds are ecologically important because their complex three-dimensional structure provides microhabitats and shelter that sustain a rich diversity of algae, invertebrates, and fishes, some of which are commercially important or endemic (Steller et al. 2003; Hinojosa-Arango and Riosmena-Rodríguez 2004; Solano-Barquero 2011). Reyes-Bonilla et al. (1997) reported the presence of five species of unattached hermatypic corals, and James et al. (2006) described free-living bryozoans within rhodolith communities in the Gulf of California. New records (Hernández-Kantún et al. 2010; Solano-Barquero 2011) and new species of exclusively rhodolith-associated organisms (Cho and Riosmena-Rodríguez 2008) have been reported. Solano-Barquero (2011) has documented the presence of 145 morphospecies of algae and animals associated with rhodolith beds at Isla del Coco National Park, Costa Rica. Rhodolith beds also provide a habitat for the recruitment of hundreds of species (Steller and Cáceres 2009; Amado-Filho et al. 2010; Solano-Barquero 2011), as evidenced from diverse larvae collected in these communities by Riosmena-Rodríguez and Medina (2010).

7.4.5 Mesophotic Environments

The mesophotic or ‘twilight zone’ has been defined as water depths between 30–40 and 150 m (Menza et al. 2008; Kahng et al. 2014). Mesophotic coral reefs (MCR) or mesophotic coral ecosystems occur throughout the tropics (Hinderstein et al. 2010; Kahng et al. 2010, 2014; Bridge et al. 2013). In the ETP, however, MCRs or prominent zooxanthellate coral communities have not been observed at coastal sites. The deepest ETP zooxanthellate corals typically occur between 10 to 30 m depth, near the thermocline where they can form refuge populations (see Chap. 17, Smith et al.). This absence of MCRs is not due to a lack of exploration since deep areas in the Galápagos Islands (Cairns 1991a), Costa Rica (Cortés and Blum 2008; Starr et al. 2012) and Panama (Cunningham et al. 2013) have been surveyed. In the Galápagos Islands and at Isla del Coco, Costa Rica, only azooxanthellate ahermatypic corals have been observed in deeper habitats (Cairns 1991a; Cortés and Blum 2008). Nonetheless, the occurrence of abundant coral populations at some oceanic island sites, such as Clipperton Atoll (Glynn et al. 1996) and Easter Island (Glynn et al. 2003), to depths of 30–60 m, are worth further scrutiny. At mesophotic depths in the Galápagos Islands, kelp forests

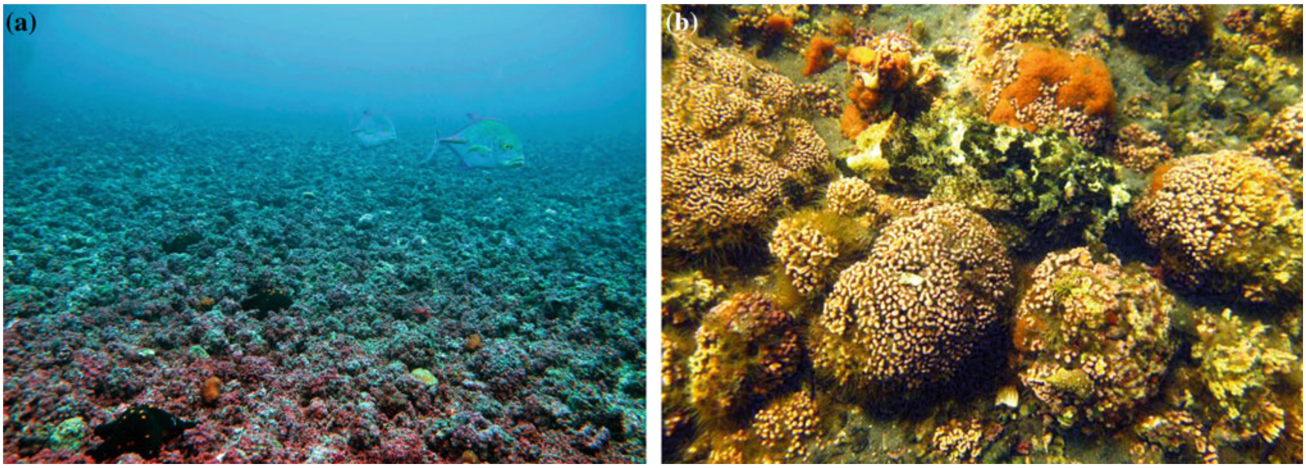

Fig. 7.10 **a** Rhodolith bed at 25 m depth, Isla del Coco, Costa Rica, in 2012; **b** closeup view of rhodoliths, Bahía Magdalena, Mexico. Photographs by Cindy Fernández-García (**a**) and Rafael Riosmena-Rodríguez (**b**)

(*Eisenia galapagensis*) have been documented at some sites (Graham et al. 2007), but have not been found in other areas of the ETP. Recently, a mesophotic octocoral (*Eugorgia siedenburgae*), not associated with euphotic coral reefs, was described from Panama (Breedy and Guzmán 2013).

In other coral reef regions there is a gradual transition of species assemblages from shallow to deep reefs (Kahng et al. 2014), but not in the ETP. At Isla del Coco, Sibaja-Cordero et al. (2012) reported an abrupt separation of the deep (>50 m) and shallow fauna. These workers examined polychaete diversity in soft sedimentary enviroments and demonstrated a difference in species composition and even of families above and below 50 m depth. The possible difference between the ETP mesophotic area and other regions is the characteristic permanent shallow thermocline at roughly 50 m depth (Fiedler and Talley 2006; see Chap. 3 Fiedler and Lavín). This shallow thermocline often results in water-quality conditions at mesophotic depths being much different than those in shallow water. In the ETP, mesophotic depths often have marked declines in temperature and pH, while nutrients are substantially elevated (D'Croz and O'Dea 2007; Manzello et al. 2008; Manzello 2010a). More studies are necessary to better document and understand these regional differences, and to guage the level of connectivity between shallow and deep habitats in the ETP.

7.5 Factors Affecting Biodiversity

7.5.1 Biological Effects

7.5.1.1 Live Coral

In a study of fish communities spanning three decades and highly dynamic fluctuations in benthic coral cover at Uva Island, Gulf of Chiriquí, Panama, Glynn et al. (2014) recorded a parabolic relationship between percent live coral and the species richness of reef-associated fishes. The highest species richness occurred at roughly 20 % live coral cover. This relationship between fish species richness and benthic cover is likely related to the diversity of available habitat and nutritional resources. Dominici-Arosemena and Wolff (2006) analyzed fish communities across a suite of rocky and coral reef habitats, also in the Panamanian Gulf of Chiriquí. Similar to the Glynn et al. (2014) study, they recorded a correlation between fish community richness and substrate heterogeneity, but did not find a significant relationship between coral cover and species richness. Live coral, therefore, provides important shelter and food for a suite of species such as corallivores. Other species utilizing different feeding strategies (e.g., herbivores, non-corallivorous invertivores) are more dependent on other benthic communities (e.g., algae, sponges) and are more often present when their food sources are as well. It should be noted that while high coral cover is not necessary for and may even inhibit highly diverse reef fish communities, it is ultimately responsible for habitat formation and its structure, independent of whether it is alive or dead, and is therefore vital for supporting diverse reef flora and fauna.

Similar to fish communities, there are numerous cryptic invertebrates that are obligate associates of live coral. Perhaps the most conspicuous and well studied of these are the coral guard crabs (*Trapezia* spp.) and the snapping shrimp (*Alpheus lottini*) that associate with live pocilloporid corals. These species are known to defend aggressively their host corals from corallivores such as the crown-of-thorns seastar (*Acanthaster planci*) (Glynn 1976). These crustacean "guards" live in male/female pairs and actively exclude conspecific crabs (Castro 1978). The interactions of crabs and shrimps are complex, and evidence suggests that the association on a coral colony is orchestrated by the shrimps' adoption of the crab's behaviors, eventually resulting in a stable yet territorially-established community (Vannini 1985). Their aggressive behavior can also extend toward other cryptic coral inhabitants (Preston 1973; Abele and Patton 1976; Lassig 1977), though congeneric aggression may be less pronounced and less important in structuring species' distributions (Gotelli and Abele 1983). Nevertheless, it is possible that these behaviors may alter localized diversity through territorial exclusion.

The coral itself is perhaps of equal or greater importance in restricting the biodiversity of its cryptic associates. Corals employ a variety of defensive mechanisms (e.g., nematocysts, mucus) that make them inhospitable to some taxa that would otherwise shelter within their branches (Kirsteuer 1969; Lang and Chornesky 1990). Furthermore, the live coral habitat can be relatively homogeneous, providing relatively few unique niches and thereby limiting diversity (Tews et al. 2004). Enochs and Manzello (2012a) collected more than 289 species of cryptic fauna belonging to six phyla from live and dead coral substrates on a pocilloporid reef in the Gulf of Panama. They employed individual-based rarefaction to standardize sampling effort and fitted six different models to their data. While the community richness estimates of these models varied greatly, they consistently predicted more species associated with dead vs live coral substrates. Many of the species collected on live coral in their study were known obligate commensals, specially adapted to tolerate the defensive characteristics of their hosts and capitalize from the food sources they provide (Patton 1974, 1994). In a similar study conducted at Uva Island, in the Panamanian Gulf of Chiriquí, Enochs and Hockensmith (2009) experimentally induced coral mortality and monitored cryptofauna settlement and colonization relative to live corals. Communities settling on dead coral substrates were less similar than those settling on live corals, at both one and two years after mortality, indicating potentially higher species diversity in dead coral habitats (Enochs and Hockensmith 2009).

At greater distances from coral, the influence of live coral on cryptic community biodiversity becomes more tenuous. To investigate this relationship, Enochs et al. (2011) created cryptic reef habitats from baskets of dead reef framework and covered them with either live or dead coral substrates. They found no significant influence on community richness, diversity, or on the multivariate species assemblages of the underlying experimental habitat. By contrast, in other reef regions a significant positive correlation between coral cover and the generic richness of the more conspicuous benthic invertivore fauna has been established (Idjadi and Edmunds 2006). More investigation is necessary to determine to what extent and at what scales these relationships hold in the ETP.

7.5.1.2 Predation

In addition to influencing actual species numbers, predation plays a role in the behavior and physical location of the majority of the metazoan species on ETP reefs. While coral reefs are known for their great biodiversity and have often been described as the "rainforests of the sea," swimming over the surface of a pocilloporid reef will reveal at first glance fewer species than might be expected. Those species that are conspicuous often possess highly evolved anti-predatory traits such as venom, repellants, and hard skeletal features. This pattern highlights the high level of predation on reef surfaces, a factor that also strongly influences behavior (Castro 1978), and has driven many of the more "palatable" species into the cryptic recesses of reef frameworks and sediments (Bakus 1966). Indeed, the number of species (>289) of small invertebrates and fishes collected by Enochs and Manzello (2012a) from a reef framework on one reef at Isla Contadora in the Gulf of Panama is likely a gross underestimation of true metazoan biodiversity but an order of magnitude or more greater than that readily recognizable on the reef surface.

The influence of predation on species diversity is complex. Given especially high predation levels, or exceptionally vulnerable species, predation can lead to species elimination and decreased diversity. Glynn (1985) described a scenario where El Niño-related mortality of pocilloporid corals would make previously inaccessible and more desirable coral prey available for *Acanthaster* predators. Glynn hypothesized that *Acanthaster* would quickly consume these species and thereby reduce coral species diversity in that area. At lower abundances, however, *Acanthaster* has been hypothesized to increase the diversity of its coral prey. Porter (1972) measured coral diversity at two reefs with very low (1 indiv. per 50,000 m^2, Islas Secas) and moderate (1 indiv. per 50 m^2, Isla Uva) abundances of *A. planci*. He found that the moderate levels of *Acanthaster* were correlated with higher coral diversity and that while all coral species were present at both sites, the site with more predation had greater evenness; a higher relative abundance of the rarer species. While apparently contradictory, the aforementioned studies and hypotheses are both in keeping with the intermediate disturbance hypothesis (Connell 1978). High abundances of *Acanthaster* can cause widespread mortality and ultimately reduce species numbers whereas the absence of disturbance from *Acanthaster* can result in homogeneous stands of fast-growing and competitively dominant coral species such as *Pocillopora*. Infrequent and patchy consumption of coral provides substrate for less common and slower-growing species to become established and grow, thereby increasing site biodiversity.

7.5.1.3 Competition

Competition among species is a ubiquitous feature of reefs (e.g., Lang and Chornesky 1990) and manifests from the common utilization of resources such as food and shelter. For instance, the damselfish *Stegastes acapulcoensis* aggressively defends territories that it establishes in protected shallow reef environments (Wellington 1982b). Once established, these fish will chase away other fishes and exclude sea urchins from the immediate vicinity (Glynn 1988; Eakin 1996). Additionally, *S. acapulcoensis* will preferentially bite at flat coral colonies as it expands and maintains the algal lawn from which it feeds. This can eventually lead to colony mortality and can restrict the distribution of pavonid corals to deeper regions where the damselfish are less abundant (Wellington 1982b). In this manner, territorial exclusion and mortality can lower biodiversity at small scales, among and within zones on a given reef. By contrast, studies from the western Pacific have shown that damselfishes can increase the diversity of algae within their territories (Hixon and Brostoff 1981; Sammarco 1983) and enhance cryptofauna populations (Klumpp et al. 1988).

We have already mentioned the aggressive territorial nature of some species of live coral associates, and this strong affinity for their coral hosts may be rooted in both nutritional requirements (Stimson 1990) and escape from predation (Castro 1978). Huber and Coles (1986), however, presented evidence that the aggressive behavior of trapeziid crabs often results in space occupation greatly in excess of their nutritional demands. As such, the subtle influences of competition on ETP reef biodiversity may be inextricably linked to other ecological relationships and difficult to identify. Further research is therefore needed to examine the degree to which the utilization of a common resource structures species distributions and biodiversity on reefs in the ETP.

7.5.2 Physical Effects

7.5.2.1 Substrate Structure

Substrate structure is likely one of the most studied physical influences on reef community biodiversity, and this holds true in the ETP. Nowhere is this relationship more apparent than among the cryptofauna (>2 mm) that associate directly with their substrate. To investigate experimentally the relationship between substrate porosity and cryptic community diversity, Enochs et al. (2011) created artificial reef frameworks from pocilloporid rubble. Replicate framework habitats were created from two different sizes of rubble, resulting in two treatments: low-porosity/small-rubble and high-porosity/larger-rubble. Cryptofauna community richness was higher in low porosity replicates where higher numbers of individuals were collected, likely due to the greater density of substrate in the same volume of habitat. Comparison of diversity indices (Fisher's α, Shannon's H′), however, revealed a more diverse community associated with high porosity frameworks. These habitats likely contained a greater variety of shelters, more diverse sessile food sources, and allowed organisms with larger body sizes to settle within them.

Enochs and Manzello (2012a) collected naturally occurring cryptofauna from the pocilloporid skeletal habitat along a continuum of erosion and degradation, from intact solid framework to thin veneers of rubble. In order to standardize measurements across these various substrates and the differing sampling procedures, the authors used both rarefaction and non-parametric richness estimators to calculate total community richness at infinite sampling effort. Undisturbed framework sheltered the least species rich community, had the most homogeneous living space, and was covered with a relatively uninterrupted layer of live coral. Areas with higher levels of erosion and lower coral cover had incrementally more species of cryptofauna associated with them, likely due to more diverse and heterogeneous habitat.

Glynn (2006) examined fish communities, both cryptic and surface dwelling, and recorded more species associated with artificial substrates of greater structural complexity and higher relief. This study represents an analysis of communities associated with more extreme levels of habitat erosion than that in the aforementioned studies (Enochs et al. 2011; Enochs and Manzello 2012a). Simulated reef structures were relatively low-relief and composed of fragments of coral rubble, whereas the degraded structure was flat, two-dimensional sand and small rubble fragments. As such, Glynn (2006) picks up where the Enochs and Manzello studies leave off, and ultimately lends insight into the complete loss of reef habitat and the coincident decline in community diversity (Enochs and Manzello 2012b).

Relationships between substrate structure and biodiversity also extend to communities that are not exclusively cryptic in nature. For example, Dominici-Arosemena and Wolff (2006) found a positive correlation between the species richness of reef-associated fishes and the benthic complexity of their coral and rocky reef habitats. These workers also considered aspects of the habitat's porosity and found a significant correlation between richness and the number, variability, and size of holes in the substrates. While it is likely that some of the fish species they considered exhibit cryptic tendencies, it is equally likely that numerous other species associate with these habitat characteristics because of more subtle and indirect relationships, for example pursuing cryptic prey.

7.5.2.2 Other Environmental Influences

The interaction of current flow and coral reef biodiversity is poorly understood. This relationship has been investigated in the Gulf of Panama using artificial reef frameworks deployed at two sites of different current speed and exposure (Enochs et al. 2011). Cryptofauna communities at the more exposed, high-flow site were more species rich and had greater biodiversity (Fisher's α, Shannon's H′) than those in the protected low-flow site. This could be due to a variety of factors, including access to a greater supply of pelagic larvae and the settlement of rare species (Palardy and Witman 2011) or to a greater diversity of prey items available to sessile filter-feeding species (Leviten and Kohn 1980).

Depth is correlated with coral species' distributions on ETP reefs, with relatively homogeneous stands of pocilloporid corals in shallow areas, giving way to more massive species in deeper regions (Wellington 1982a; Guzmán and Cortés 1989). This may, in part, be related to differential dependence on autotrophy versus heterotrophy among species, and the capability of massive coral morphologies to rely on particulate feeding to offset reduced light at depth (Wellington 1982a). It is cautioned, however, that nutritional requirements cannot explain this zonation alone and that both physical (e.g., wave action, tidal exposure, salinity) and biological factors (e.g., competition, predation) may also play a role (Guzmán and Cortés 1989). As previously mentioned, Wellington (1982b) has shown that the behavior of fishes plays a part in structuring this gradient, where massive species in shallow areas are more susceptible to damselfish-inflicted mortality and *Pocillopora* colonies in deeper waters are subjected to a greater degree of predation from corallivorous pufferfishes and grazing parrotfishes. Differences in communities associated with depth and reef zonation have also been observed in other ETP taxa. For example, Gotelli and Abele (1983), investigating crustacean-associates of living *Pocillopora*, observed statistically different species/area relationships between communities present on shallow reef flats versus the deeper reef flanks. These workers concluded, however, that this relationship was likely driven by the density of individuals, which was higher on the reef flat than in deeper reef zones.

7.5.2.3 Disturbance

Abele (1979) examined decapod associates of *Pocillopora damicornis* in the dynamic upwelling Gulf of Panama and the more stable nonupwelling Gulf of Chiriquí. Abele found higher species richness (55 vs. 37 species) in the thermally fluctuating gulf, largely due to the presence of generalists. By contrast, there were greater numbers of obligate coral associates in the thermally constant environment. Abele hypothesized that the higher biodiversity in the periodically upwelling Gulf of Panama was due to mortality of territorial and obligate symbionts, caused by low temperature exposure and subsequent disturbance of their coral food sources. This allowed for the subsequent colonization of opportunistic, non-obligate commensals and thereby increased regional diversity.

If environmental disturbances are too extreme or too frequent they can result in localized or even global extinction if the distribution of the species is limited to the extent of the disturbance. This may have been the case with *Millepora boschmai* in the ETP, which was reported to have been rendered extinct by the 1982–83 ENSO event at the time of its taxonomic description in 1991 (de Weerdt and Glynn 1991). Subsequent searches within its originally reported distribution revealed several colonies (Glynn and Feingold 1992), which were eventually killed in the subsequent 1997–98 ENSO (Glynn 2000). While specimens have since been discovered in Indonesia (Razak and Hoeksema 2003), no living colonies have been documented from the ETP, thereby supporting the suggestion that this represents a disturbance-induced regional extinction.

Enochs and Manzello (2012b) synthesized findings from previously published work (Enochs 2012; Enochs and Manzello 2012a) and created a conceptual model for how the species richness and trophic potential of cryptofauna would respond to coral mortality and erosion, charting community response to reef disturbance and habitat loss. They predicted increased cryptofauna richness following the disruption and partial mortality of previously undisturbed homogeneous stands of *Pocillopora*. Richness is expected to rise further still as dead frameworks are eroded, providing diverse habitats and substrates for benthic communities to colonize and develop. During this time, however, community abundances and trophic potential will likely decrease as important live coral food sources are lost and the quantity of habitat space declines. Ultimately, collapse in both richness and abundance is posited as reef habitat degrades into sand. The effective management of live coral populations is therefore critical for maintaining reef habitat and biodiversity alike (Enochs and Manzello 2012b).

7.5.3 Chemical Effects

The ocean's carbonate chemistry experiences changes due to a combination of biological and physical processes, as well as human-induced ocean acidification (OA). Any alteration of the balance of this system will impact marine biogeochemical cycles, ecosystems and their constituent organisms (Kleypas et al. 2006; Fabry et al. 2008; Doney et al. 2009; Feely et al. 2009; Kleypas and Yates 2009). Of the affected taxa, calcifying organisms are particularly sensitive to changes in pH and carbonate saturation state (Ω) (Kleypas et al. 2006; Kuffner et al. 2008; Dove et al. 2013; van Woesik et al. 2013). Besides the scleractinian corals, some calcifying reef organisms previously mentioned in this chapter (e.g., coralline algae and rhodoliths, polychaete worms, molluscs, crustaceans and echinoderms) can also be negatively impacted to different degrees by changes in seawater carbonate chemistry (Kleypas and Yates 2009; Ragazzola et al. 2012; Wittmann and Pörtner 2013; Fabricius et al. 2015; Gómez et al. 2015). Thus, community composition and diversity could well experience marked changes due to future OA conditions.

Due to the occurrence of seasonal upwelling events in the ETP (McCreary et al. 1989; Millero 2007), coral reefs from this region are naturally exposed to low-pH and low-Ω conditions (Manzello 2008, 2010a, b; Manzello et al. 2008; Rixen et al. 2012; see Chap. 18, Manzello et al.). This results in a potential disadvantage to calcification and, ultimately, for reef accretion as well. Coral reefs are widely recognized as the most threatened ecosystems by OA (Kleypas and Yates 2009) and it is expected that under the ETP's unusual biogeochemical conditions that reefs in this region will be strongly impacted by OA (Kleypas et al. 2006; Manzello et al. 2008; Veron 2008; Manzello 2010a). For example, accelerated carbonate dissolution combined with a reduction in calcification could preclude coral reef accretion within the next few decades (Hoegh-Guldberg 1999; Feely et al. 2004; Hoegh-Guldberg et al. 2007; Silverman et al. 2009). Furthermore, reef ecosystems and associated biota may experience the deleterious impacts of OA via numerous other pathways. For example, increased levels of CO_2 have been shown to cause branching corals to lose their zooxanthellae (Kaniewska et al. 2012), resulting in coral bleaching that could lead to massive mortality events (Anthony et al. 2008). By means of such effects, unfavorable carbonate chemistry could lead to a loss in the complexity of reef structures and a reduction in associated biodiversity, potentially leading to a decline in reef resilience (Kleypas and Yates 2009; Kroeker et al. 2011). Sensitivity and tolerance of marine organisms to OA will differ from one group to the next (Fabry et al. 2008; Gattuso et al. 2011; Kroeker et al. 2013), and these differences have the potential to trigger phase shifts in coral ecosystems (Hall-Spencer et al. 2008; Fabricius et al. 2011). Therefore, coral reefs as we know them today may disappear, leading to macroalgae- or octocoral-dominated communities instead of the current scleractinian coral ecosystems (Veron 2008; Silverman et al. 2009; Gómez et al. 2014; Johnson et al. 2014; see Chap. 11, Fong et al.).

In summary, OA could impact coral reef biodiversity in the ETP, not only by reducing the complexity of reef structures, but also by changing their community composition, including reef benthos and all other associated species. Published studies on this topic in the ETP are scarce, and the best-studied areas are in Panama and the Galápagos Islands (Manzello 2008, 2010a; Manzello et al. 2008), with an additional contribution from the Pacific coast of Costa Rica (Rixen et al. 2012). Nevertheless, there are several ongoing projects in the ETP, and it is expected that forthcoming findings will improve our knowledge of this issue.

7.6 ETP Reefs as a Model for Studying Biodiversity

The ETP is one of the most isolated ocean regions (Glynn and Ault 2000; Cortés 2011), separated from the Central Pacific by the East Pacific Barrier (Grigg and Hey 1992), and from the Caribbean after the uplift of the Central American Isthmus (Coates et al. 1992). The closure of the Central American Seaway resulted in extreme conditions with ENSO disturbance events and cold episodes due to seasonal upwelling (Cortés 1997, 2011). In addition, sea level fluctuations during glacial-interglacial periods, low pH, and cooling during the Little Ice Age have limited reef growth in the ETP (Glynn et al. 1983; Manzello 2010b; Cortés 2011). The contemporary ETP coral fauna derives mostly from the Central and Western Pacific (Cortés 1986; Glynn and Ault 2000; see Chap. 5, Glynn et al.). Coral reefs in the ETP are small, isolated, and constructed by a few coral species, and could be considered as the minimum expression of a structural reef (Cortés 1997), with some reefs constructed solely of one or two species (Cortés 2011). These reefs, however, harbor diverse and complex communities of associated organisms, have a long growth history, and occur adjacent to diverse and interdependent communities and habitats (Guzmán and Cortés 1993; Cortés et al. 1994; Glynn 2004; Cortés 2011).

ETP coral reefs are ideal systems for investigating biological and environmental factors influencing coral reef biodiversity. Relative to reef ecosystems in the Western Pacific and Caribbean, they are less diverse, with fewer described species of fishes, corals, molluscs, and crustaceans (Roberts et al. 2002). Given the enormity and complexity of highly diverse reef communities, this comparatively simple system can facilitate work that would not be feasible at other localities (e.g., Enochs and Manzello 2012a). Furthermore, there is a long history of taxonomic work in the ETP, for example, the expeditions of the US Fish Commission, New York Zoological Society, California Academy of Sciences, and the Allan Hancock Foundation (see Cortés 2008, for an example of the history of research at one ETP oceanic island). Additionally, there are taxonomic studies available for the identification of many taxa (e.g., Keen 1971; Wells 1983; Hickman 1998, 1999, 2008; Hickman and Zimmerman 2000; Breedy and Guzman 2002, 2007, 2011; Carballo et al. 2004; Allen et al. 2005; Robertson and Allen 2008; Breedy et al. 2009b; Littler and Littler 2010; Breedy and Cortés 2014). While excellent taxonomic work is currently ongoing in the region (e.g., Wehrtmann and Cortés 2009; Breedy and coworkers; Carballo and collaborators) and the biodiversity of some localities has received an exceptional amount of attention (e.g., the Galápagos Islands by C. P. Hickman), still other areas of the ETP remain open for further exploration and taxonomic attention.

Facilitating the investigation of factors influencing reef biodiversity is the morphology of many ETP reefs, namely those formed by pocilloporid corals. These reefs develop distinct zones that can be mapped and subsequently sampled in a stratified random manner (Eakin 1996; Enochs 2012). Substrates within these zones are relatively homogeneous compared to structurally diverse Caribbean and Western Pacific coral communities, allowing replicate sampling and zone-specific inference. Living pocilloporid corals and dead framework are relatively homogeneous but structurally complex, providing abundant shelter for diverse assemblages of associated cryptofauna.

Pocilloporid corals are present across the Pacific and have been used as model systems (especially *P. damicornis*) to study the ecology and diversity of coral-associated fauna (e.g., Grassle 1973; Kropp and Birkeland 1981; Black and Prince 1983; Gotelli and Abele 1983; Chang et al. 1987). Though especially prominent in the ETP, large clonal stands of *Pocillopora* and the resulting reef frameworks are known from other parts of the world, e.g., western Arabian Sea (Glynn 1993), Gulf of Aden (Kemp and Benzoni 1999), and western Australia (Miller and Ayre 2004). For these reasons research on the biodiversity of ETP reef communities is not limited in its applicability to the ETP; it may also be applied in some instances to systems across large geographic scales.

Finally, ETP reefs are distributed across pronounced gradients in nutrients, temperature, and carbonate chemistry (D'Croz and O'Dea 2007; Manzello et al. 2008; Cortés 2011; see Chap. 5, Glynn et al.). These naturally occurring conditions are closely related to predicted extreme conditions under climate change scenarios and can inform scientists on how anthropogenic stressors will likely structure the reefs of the future. Combined with the relatively depauperate nature of the reef-associated biota and the spatially homogeneous yet structurally complex framework habitat, ETP coral reefs are ideal natural laboratories for studying reef biodiversity and the factors that affect it.

7.7 Research Needs and Closing Remarks

While there are areas in the ETP that are presently considered to be more biotically diverse than others, more studies are necessary as the local species richness of select taxa is likely correlated with sampling effort (Cruz et al. 2003; Wehrtmann et al. 2009). The detailed study of particular groups can increase the known diversity of given sites significantly. For example, previously only nine species in six families of polychaetes were known from Isla del Coco (Dean et al. 2012). As a result of further sampling and analysis, at least 106 species in 35 families are known to occur there. Of these, 92 are new records for Costa Rica and 40 are new records for Central America (Dean et al. 2012). Even more species have been identified since (J.A. Sibaja-Cordero pers. comm. 2014). Additional inventories and compilations such as those conducted in Costa Rica (Wehrtmann and Cortés 2009) and Oaxaca, Mexico (Bastida-Zavala et al. 2013) are needed for a better understanding of the richness of the ETP region and to develop a basis to gauge expected changes in biodiversity. Furthermore, regional workshops should be instituted and supported to improve taxonomic capabilities in the ETP region.

Recent studies of taxonomically cryptic or sibling taxa have demonstrated that species richness is presently greatly underestimated (Knowlton 1993). Not recognizing the full diversity of a taxon can have important implications in the understanding of ecological function, biogeography, resilience, and conservation (Bickford et al. 2007). This issue is especially apparent in the ETP as evidenced by a recent discovery of cryptic species in the genus *Porites*, one of the principal reef-building coral genera (Boulay et al. 2014). What was formerly known as *P. lobata* is actually two species, *P. lobata* and *P. evermanni*, with similar colony morphology, but different reproductive modes and responses to bleaching stress events (Boulay et al. 2014).

Another area in need of further research is the biogeography of ETP marine organisms. As mentioned in the introduction to this chapter, several taxa have been studied, revealing a strong Indo-Pacific affinity. For example, in fishes, a relatively well-studied group, biogeographic inferences can be made with a high degree of confidence (Robertson et al. 2004; Robertson and Cramer 2009). This sort of analysis is not yet possible with other groups. Vega et al. (2012), for example, attempted to determine the biogeographic affinities of ETP sponges, but concluded that more studies are needed to establish species' distributions before geographic relationships can be determined. Biogeographic studies combined with genetic analyses (Hellberg 2009) will help determine the connectivity of populations, information which is critically important in management and conservation. In a detailed analysis of invertebrates from the Galápagos Islands, Hickman (2009) found that some groups are under-represented with respect to continental areas, while others are over represented. He attributed these differences to the relative isolation of the islands, taxon-specific dispersal capabilities, the spatial distribution of particular habitats, and patterns of ocean circulation. Additional research of this genre is needed to understand the distribution and ecology of the contemporary ETP biota.

In the future, biogeographic analyses of the ETP marine fauna should include Rapa Nui (Easter Island) and Salas y Gómez Island, which exist at the southeastern-most limits of coral reef distribution in the Pacific. Most ETP studies exclude these islands. In an updated review of 88 published articles and 10 web databases, Fernández et al. (2014) reported the occurrence at Rapa Nui of 964 species, including 143 algal species (56 % red algae), 605 marine invertebrate species (68 % crustaceans and molluscs) and 216 fish species (6 % chondrichthyans). Rapa Nui is characterized by a high degree of endemism. For example, >30 % of sponges and molluscs as well as >20 % of reef fishes are endemic to the region (Randall and Cea 2011), and examples of restricted ranges in other groups are reported as well (Fernández et al. 2014). This synthesis by Fernández et al. (2014) is an excellent starting point for biogeographic comparisons with the core ETP. A recent study by Veron et al. (2015) reinforces the validity of a connection between Rapa Nui and the remainder of the ETP. In their analysis of the affinity of zooxanthellate corals by ecoregions, Rapa Nui is closer to the core ETP region than is Clipperton Atoll, despite its closer geographic proximity.

Coral reefs at Rapa Nui are constructed predominantly by only two species (*Pocillopora verrucosa* and *Porites lobata*), which comprise nearly 80 % of the total benthic cover (Wells 1972; Glynn et al. 2003, 2007; Wieters et al. 2014). Wieters et al. (2014) reported consistent increases in coral abundance in shallow habitats at Rapa Nui over the past 15 years, since the ENSO bleaching/mortality event in 2000 (Wellington et al. 2001). Top-down effects on this recovery are unlikely because the naturally depauperate fish assemblages and high fishing pressure likely contribute to low fish abundances, small body sizes, and a skewed trophic structure (Friedlander et al. 2013). It is hypothesized that the reported higher abundance of sea urchins (*Diadema savignyi*) increases the likelihood of coral larval settlement, colonization and re-growth. The coral reefs at Rapa Nui are therefore likely resilient systems, potentially capable of maintaining normal ecosystem function in spite of perturbation (Wieters et al. 2014).

Coral reefs across the ETP are impacted by a variety of natural disturbances and anthropogenic stressors (see Chap. 8, Glynn et al.; Chap. 20, Cortés and Reyes-Bonilla). Such conditions are expected to negatively impact the biodiversity of ETP coral reefs. Accordingly, monitoring programs must be implemented to establish present-day baselines and to track changes in biodiversity over time. Presently, only zooxanthellate corals, and select fishes and macro-invertebrates are monitored in the ETP and, while commendable, this approach is lacking in scope (Cortés et al. 2010; Zapata et al. 2010; Glynn et al. 2014).

In closing we cite Rogers (2013), who has captured the essence of coral reef vitality and the possibility of long-term persistence: “The biodiversity of coral reefs is the basis for their remarkable beauty and for the benefits they provide to society. The extraordinary complexity of these ecosystems makes it both more difficult to predict their future and more likely they will have a future.”

Acknowledgements We thank Peter W. Glynn and Derek P. Manzello for the invitation to contribute this chapter to the eastern Pacific coral reef book. J. Cortés thanks the Vicerrectoría de Investigación, Universidad de Costa Rica, for the internship received (2014) to work on this and other manuscripts. J.C. also acknowledges the extra help by Luis Hernández in reviewing the complete text, and helping with tables and figures. F.A. Zapata thanks D.R. Robertson, Smithsonian Tropical Research Institute (STRI) for providing access to his Online Information System on the Shore Fishes of the Tropical Eastern Pacific during a time when the website was closed for maintenance. K.L. Kaiser, P. Medina-Rosas and A. Hermosillo thank D.R. Robertson for allowing us to participate in the Expeditions aboard the *RV Urracá* to Panama, Costa Rica, El Salvador, Isla del Coco, Costa Rica, and Clipperton Atoll, sponsored by STRI, and, to Clipperton Atoll by the National Geographic Society (Grant NGS 5831–96); also our thanks to the Santa Barbara Museum of Natural History (SBMNH), Malacology Department, for use of their facilities. A special thanks to Patricia Sadeghian (SBMNH) for her assistance in photography. E. Wieters and A. Pérez-Matus thank the Fondo Nacional de Ciencia y Tecnología, Chile (Fondecyt # 1130167). We thank Peter W. Glynn, Derek P. Manzello and Michael J. Kramer for their detailed reviews and suggestions, and Benjamin Grassian for help with the final figures. Michael P.C. Fuller and Tyler B. Smith offered helpful editorial suggestions.

References

Abbott IA (1966) Elmer Yale Dawson (1918–1966). J Phycol 2:129–132

Abele LG (1972) Comparative habitat diversity and faunal relationships between the Pacific and Caribbean Panamanian decapod Crustacea: a preliminary report, with some remarks on the crustacean fauna of Panamá. Bull Biol Soc Washington 2:125–137

Abele LG (1974) Species diversity of decapod crustaceans in marine habitats. Ecology 55:156–161

Abele LG (1976) Comparative species richness in fluctuating and constant environments: coral-associated decapod crustaceans. Science 192:461–463

Abele LG (1979) The community structure of coral-associated decapod crustaceans in variable environments. In: Livingston RJ (ed) Ecological processes in coastal and marine systems. Plenum Press, New York, pp 265–287

Abele LG, Patton WK (1976) The size of coral heads and the community biology of associated decapod crustaceans. J Biogeogr 3:35–47

Aburto-Oropeza O, Balart EF (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. PSZNI: Mar Ecol 22:283–305

Acuña FH, Cortés J, Garese A (2012) Occurrence of the sea anemone *Telmatactis panamensis* (Verrill, 1869) (Cnidaria: Anthozoa:

Actiniaria) at Cocos Island National Park. Costa Rica. Rev Biol Trop 60(Suppl 3):201–205

Acuña FH, Garese A, Excoffon AC, Cortés J (2013) New records of sea anemones (Anthozoa: Actiniaria) from Costa Rica. Rev Biol Mar Oceanogr 48:177–184

Aguado MT, López E (2003) Paraonidae (Annelida: Polychaeta) del Parque Nacional de Coiba (Pacífico, Panamá), con la descripción de una nueva especie de *Aricidea* Webster, 1879. Rev Chilena Hist Nat 76:363–370

Aguado MT, San Martín G (2004) Pisionidae (Polychaeta) from Coiba National Park with the description of a new species and two new reports of *Pisione*. J Mar Biol Assoc UK 84:73–79

Aguado MT, San Martín G (2006) Sílidos (Syllidae: Polychaeta) del Parque Nacional de Coiba. Rev Biol Trop 54:725–743

Alldredge A, King JM (1977) Distribution, abundance and substrate preference of demersal reef zooplankton at Lizard Island lagoon, Great Barrier Reef. Mar Biol 41:317–333

Alldredge A, King JM (1980) Effects of moon light on the vertical migration pattern of demersal zooplankton. J Exp Mar Biol Ecol 44:133–156

Allen G, Steene R, Humann P, DeLoach N (2005) Reef fish identification—tropical Pacific. New World Publications, Inc., Jacksonville, Florida, p 480

Alonso D, Ramírez L, Segura-Quintero C, Castillo-Torres P, Diaz JM, Walschburger T (2008) Prioridades de conservación in situ para la biodiversidad marina y costera de la plataforma continental del Caribe y Pacífico colombiano. Santa Marta, Colombia, INVEMAR, TNC, UAESPNN, p 20

Alvarado JJ, Solis-Marin FA, Ahearn C (2010) Echinoderm (Echinodermata) diversity in the Pacific coast of Central America. Mar Biodiv 40:45–56

Alvarado JJ, Aguirre-Rubí J, Ayala A, Buitrago F, Fernández-García C, Reyes-Bonilla H, Sánchez A (2011) Characterization of the coral communities of San Juan del Sur, south Pacific Nicaragua. Bull Mar Sci 87:129–146

Alvarado JJ, Vargas-Castillo R (2012) Invertebrados asociados al coral constructor de arrecifes *Pocillopora damicornis* en Playa Blanca, Bahía Culebra. Costa Rica. Rev Biol Trop 60(Suppl 2):77–92

Alvarado JJ, Baraza E, Sancho-Mejía T (2013) Central American echinoderms: diversity, ecology and future perspectives. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm research and diversity in Latin American. Springer, Berlin, pp 67–106

Alvarado JJ, Beita A, Mena S, Fernández-García C, Guzmán-Mora AG (2015) Ecosistemas coralinos del Área de Conservación Osa, Costa Rica: estructura y necesidades de conservación. Rev Biol Trop 63 (Suppl 1):219–259

Alvarez-Filip L, Reyes-Bonilla H, Calderón-Aguilera LE (2006) Community structure of fishes in Cabo Pulmo reef, Gulf of California. Mar Ecol 27:253–262

Alzate A, Zapata FA, Giraldo A (2014) A comparison of visual and collection-based methods for assessing community structure of coral reef fishes in the tropical eastern Pacific. Rev Biol Trop 62 (Suppl 1):359–371

Amado-Filho GM, Maneveldt GW, Pereira-Filho GH, Manso RCC, Bahia RG, Barros-Barreto MB, Guimarães SMPB (2010) Seaweed diversity associated with a Brazilian tropical rhodolith bed. Cienc Mar 36:371–391

Amador J, Alfaro EJ, Lizano OG, Magaña V (2006) Atmospheric forcing in the eastern tropical Pacific: a review. Progr Oceanog 69:101–142

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. Proc Nat Acad Sci USA 105:17,442–17,446

Ávila E, Riosmena-Rodríguez R (2011) A preliminary evaluation of shallow-water rhodolith beds of Bahía Magdalena, Mexico. Brazilian J Oceanogr 59:365–375

Ávila E, Méndez-Trejo MC, Riosmena-Rodríguez R, López-Vivas JM, Sentíes A (2012) Epibiotic traits of the invasive red seaweed *Acanthophora spicifera* in La Paz Bay, south Baja California (eastern Pacific). Mar Ecol 33:470–480

Ax P, Schmidt P (1973) Interstitielle fauna von Galapagos. I. Einfihrung. Mikrof Meeresb 20:1–38

Bailey-Brock JH, Emig CC (2000) Hawaiian Phoronida (Lophophorata) and their distribution in the Pacific region. Pac Sci 54:119–126

Bakus GJ (1966) Some relationships of fishes to benthic organisms on coral reefs. Nature 210:280–284

Barraza E (2000) Comentarios sobre la diversidad de macroinvertebrados marinos de El Salvador. Publicación ocasional Ministerio del Medio Ambiente y Recursos Naturales 2, p 15

Barraza E (2014a) Invertebrados marinos de El Salvador. Ministerio del Medio Ambiente y Recursos Naturales, San Salvador, El Salvador, p 96

Barraza E (2014b) Peces estuarinos y marinos de El Salvador. Ministerio del Medio Ambiente y Recursos Naturales, San Salvador, El Salvador, p 66

Barroso RM, Klautau AM, Solé-Cava Paiva PC (2010) *Eurythoe complanata* (Polychaeta: Amphinomidae), the 'cosmopolitan' fireworm, consists of at least three cryptic species. Mar Biol 157:69–80

Bastida-Zavala JR (1995) Poliquetos (Annelida: Polychaeta) del arrecife coralino de Cabo Pulmo-Los Frailes, B.C.S, Mexico. Rev Zool 6:9–29

Bastida-Zavala JR (2008) Serpulids (Annelida: Polychaeta) from the eastern Pacific, including a brief mention of Hawaiian serpulids. Zootaxa 1722:1–66

Bastida-Zavala JR, García-Madrigal M del S, Rosas-Alquicira EF, López-Pérez RA, Benítez-Villalobos F, Meraz-Hernando JF, Torres-Huerta AM, Montoya-Márquez A, Barrientos-Luján NA (2013) Marine and coastal biodiversity of Oaxaca, Mexico. Check List 9:329–390

Baums IB, Boulay JN, Polato NR, Hellberg ME (2012) No gene flow across the Eastern Pacific Barrier in the reef-building coral *Porites lobata*. Mol Ecol 21:5418–5433

Bautista-Romero J, Reyes-Bonilla H, Lluch-Cota DB, Lluch-Cota SE (1994) Aspectos generales sobre la fauna marina. In: Ortega-Rubio A, Castellanos-Vera A (eds) La Isla Socorro, reserva de la biósfera Archipiélago de Revillagigedo, México. Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, México, pp 247–265

Behrens DW, Hermosillo A (2005) Eastern Pacific nudibranchs: a guide to the opisthobranchs from Alaska to Central America. California, Sea Challengers, p 137

Behrens DW, Gosliner TM, Hermosillo A (2009) A new species of dorid nudibranch (Mollusca) from the Revillagigedo Islands of the Mexican Pacific. Proc California Acad Sci, Ser 4, 60:423–429

Bellwood DR (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. Coral Reefs 15:11–19

Bellwood DR (1997) Reef fish biogeography: habitat associations, fossils and phylogenies. In: Proceedings of 8th International Coral Reef Symposium, vol 1, Panamá, pp 379–384

Benavides-Serrato M, Borrero-Pérez GH, Cantera J, Cohen-Renjifo M, Neira R (2013) Echinoderms of Colombia. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm research and diversity in Latin America. Springer, Berlin, pp 145–182

Benfield S, Baxter L, Guzmán HM, Mair JM (2008) A comparison of coral reef and coral community fish assemblages in Pacific Panama and environmental factors governing their structure. J Mar Biol Assoc UK 88:1331–1341

Bernard FR, McKinnell SM, Jamieson GS (1991) Distribution and zoogeography of the Bivalvia of the eastern Pacific Ocean. Canadian Spec Publ Fish Aquat Sci 112:60

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22:148–155

Birkeland C, Smalley TL (1981) Comparison of demersal plankton from comparable substrates from a high island and an atoll. In: Proceedings of 4th International Coral Reef Symposium, vol 1, Manila, pp 437–442

Black R, Prince J (1983) Fauna associated with the coral *Pocillopora damicornis* at the southern limit of its distribution in Western Australia. J Biogeogr 10:135–152

Blake JA (1991) The polychaete fauna of the Galápagos Islands. In: James MJ (ed) Galápagos marine invertebrates. Topics in Geobiology. Plenum Press, New York, pp 75–96

Boschi E (2000) Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. Rev Invest Des Pesq 13:1–63

Boulay JN, Hellberg ME, Cortés J, Baums IB (2014) Unrecognized coral species diversity masks differences in functional ecology. Proc Roy Soc B 281:20131580. doi:10.1098/rspb.2013.1580

Breedy O (2001) A new species of *Pacifigorgia* from the eastern Pacific (Coelenterata: Octocorallia: Gorgoniidae). Bull Biol Soc Washington 10:181–187

Breedy O (2009) Octocorals. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 161–167, Species List: Compact Disc pp 108–111

Breedy O, Cortés J (2008) Octocorals (Coelenterata: Anthozoa: Octocorallia) of Isla del Coco, Costa Rica. Rev Biol Trop 56(Suppl 2):71–77

Breedy O, Cortés J (2011) Morphology and taxonomy of a new species of *Leptogorgia* (Cnidaria: Octocorallia: Gorgoniidae) in Cocos Island National Park, Pacific Costa Rica. Proc Biol Soc Washington 124:62–69

Breedy O, Cortés J (2014) Gorgonias (Anthozoa: Octocorallia: Gorgoniidae) de las aguas someras del Pacífico Norte de Costa Rica. Rev Biol Trop 62(Suppl 4):43–62

Breedy O, Guzman HM (2002) A revision of the genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae). Proc Biol Soc Washington 115:782–839

Breedy O, Guzman HM (2003) The genus *Pacifigorgia* (Octocorallia: Gorgonacea) in Costa Rica (Coelenterata: Octocorallia: Gorgoniidae). Zootaxa 281:1–60

Breedy O, Guzman HM (2004) New species of the gorgonian genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae) from the Pacific of Panamá. Zootaxa 541:1–15

Breedy O, Guzman HM (2007) A revision of the genus *Leptogorgia* Milne Edwards & Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. Zootaxa 1407:1–90

Breedy O, Guzman HM (2008) *Leptogorgia ignita*, a new shallow-water coral species (Octocorallia: Gorgoniidae) from the tropical eastern Pacific. J Mar Biol Assoc UK 88:893–899

Breedy O, Guzman HM (2011) A revision of the genus *Heterogorgia* Verrill, 1868 (Coelenterata: Octocorallia: Plexauridae. Zootaxa 2995:27–44

Breedy O, Guzman HM (2012) A new species of *Leptogorgia* (Cnidaria: Anthozoa: Octocorallia) from Golfo Dulce, Pacific Ocean, Costa Rica. Zootaxa 3182:65–68

Breedy O, Guzman HM (2013) A new species of the genus *Eugorgia* Verrill, 1868 (Cnidaria: Octocorallia: Gorgoniidae) from mesophotic reefs in the eastern Pacific. Bull Mar Sci 89:735–743

Breedy O, Guzman HM (2014) A new species of alcyonacean octocoral from the Peruvian zoogeographic region. J Mar Biol Assoc UK 94:493–498

Breedy O, Hickman CP Jr, Williams GC (2009a) Octocorals in the Galapagos Islands. Galapagos Res 66:27–31

Breedy O, Guzman HM, Vargas S (2009b) A revision of the genus *Eugorgia* Verrill, 1868 (Coelenterata: Octocorallia: Gorgoniidae). Zootaxa 2151:1–46

Breedy O, Williams G, Guzman HM (2013) Two new species of gorgonian octocorals from the tropical eastern Pacific biogeographic region (Cnidaria, Anthozoa, Gorgoniidae). ZooKeys 350:75–90

Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. Nature Clim Chan 3:528–530

Briggs JC (1974) Marine zoogeography. McGraw-Hill, New York, p 475

Bula-Meyer G (1995) Macroalgas de la Isla Gorgona (Pacífico Colombiano) con nuevos registros y una explicación de la baja diversidad y biomasa. In: Pinto P (ed) La Isla Gorgona, nuevos estudios biológicos. Editorial Guadalupe Ltda, Bogotá, Colombia, pp 23–45

Buss LW, Jackson JBC (1981) Planktonic food availability and suspension-feeder abundance: evidence of in situ depletion. J Exp Mar Biol Ecol 49:151–161

Bustamante RH, Wellington GM, Branch GM, Edgar GJ, Martinez P, Rivera F, Smith F, Witman J (2002) Outstanding marine features. In: Bensted-Smith R (ed) A biodiversity vision for the Galapagos Islands. Charles Darwin Foundation and World Wildlife Fund, Puerto Ayora. Galápagos, Ecuador, pp 60–71

Caballero-George C, Bolaños J, Ochoa E, Carballo JL, Cruz JA, Arnold E (2010) Protocol to isolate sponge-associated fungi from tropical waters and an examination of their cardioprotective potential. Curr Trends Biotech Pharm 4:881–899

Cairns SD (1986) Stylasteridae (Hydrozoa: Hydroida) of the Galapagos Islands. Smithsonian Contr Zool 426:1–42

Cairns SD (1991a) A revision of the ahermatypic Scleractinia of the Galápagos and Cocos Islands. Smithsonian Contr Zool 504:1–45

Cairns SD (1991b) New records of Stylasteridae (Hydrozoa: Hydroida) from the Galápagos and Cocos Islands. Proc Biol Soc Washington 104:209–228

Calder DR, Mallinson JJ, Collins K, Hickman CP (2003) Additions to the hydroids (Cnidaria) of the Galápagos, with a list of species reported from the islands. J Nat Hist 37:1173–1218

Camacho-García, Y (2009) Benthic opisthobranchs. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 371–386, Species List: Compact Disc pp 330–347

Capa M, López E (2004) Sabellidae (Annelida: Polychaeta) living in blocks of dead coral in the Coiba National Park, Panamá. J Mar Biol Assoc UK 84:63–72

Carballo JL, Cruz-Barraza JA (2006) The genus *Timea* (Porifera: Hadromerida) in the Eastern Pacific Ocean: revision of type material, new species and intraspecific variability. Cah Biol Mar 47:301–320

Carballo JL, Cruz-Barraza JA (2010) A revision of the genus *Mycale* (Poecilosclerida: Mycalidae) from the Mexican Pacific Ocean. Contrib Zool 79:165–194

Carballo JL, Cruz-Barraza JA, Gómez P (2004) Taxonomy and description of clionaid sponges (Hadromerida, Clionaidae) from the Pacific Ocean of Mexico. Zool J Linn Soc 141:353–397

Carballo JL, Gómez P, Cruz-Barraza JA (2014) Biodiversidad de Porifera en México. Rev Mexicana Biodiv, Supl 85:S143–S153

Carleton JH (1993) Zooplankton and coral reefs: an overview. SPUMS J 23:102–107

Carleton JH, Brinkman R, Doherty PJ (2001) Zooplankton community structure and water flow in the lee of Helix Reef (Great Barrier Reef, Australia). Mar Biol 139:705–717

Carlgren O (1940) Eastern Pacific expeditions of the New York Zoological Society. XIX. Actiniaria from the Gulf of California. Zoologica 25:211–219

Castilla JC, Rozbaczylo N (1987) Invertebrados marinos de Isla de Pascua y Sala y Gómez. In: Castilla JC (ed) Islas oceánicas chilenas: conocimiento científico y necesidades de investigación. Ediciones Universidad Católica de Chile, Santiago, pp 167–189

Castro P (1978) Movements between coral colonies in *Trapezia ferruginea* (Crustacea: Brachyura), an obligate symbiont of scleractinian corals. Mar Biol 46:237–245

Castro P (1982) Notes on symbiotic decapod crustaceans from Gorgona Island, Colombia, with a revision of the eastern Pacific species of *Trapezia* (Brachyura, Xanthidae), symbionts of scleractinian corals. An Inst Invest Mar Punta de Betín 12:9–17

Castroviejo S (1997) Flora y fauna del Parque Nacional de Coiba (Panama): inventario preliminar. AECI, Madrid, p 534

CDB-Panamá (2010) Cuarto Informe Nacional de Panamá ante el Convenio sobre la Diversidad Biológica. Autoridad Nacional del Ambiente, Panamá, República de Panamá, p 110

Chang KH, Chen YS, Chen CP (1987) Xanthid crabs in the corals, *Pocillopora damicornis* and *P. verrucosa* of southern Taiwan. Bull Mar Sci 41:214–220

Charpy L (ed) (2009) Clipperton, environnement et biodiversité d'un microcosme océanique. MNHN, Paris & IRD, Marseille. Patrimoines Naturels 68, p 420

Chávez-Hernández E, Bretado-Aguirre J (1990) Contribución al conocimiento de los gasterópodos macroscópicos litorales de Isla Socorro, Archipiélago de Revillagigedo, México. Mem VIII Simp Int Biol Mar, Universidad Autónoma de Baja California, Ensenada, México, pp 150–155

Chesher RH (1972) The status of knowledge of Panamanian echinoids, 1971, with comments on other echinoderms. Bull Biol Soc Washington 2:139–158

Chiriboga Á, Ruiz D, Banks S (2012) CDF Checklist of Galapagos sponges. In: Bungartz F, Herrera H, Jaramillo P, Tirado N, Jiménez-Uzcátegui G, Ruiz D, Guézou A, Ziemmeck F (eds) Charles Darwin Foundation Galapagos Species Checklist. Charles Darwin Foundation, Puerto Ayora, Galapagos. http://checklists.galadarwin.webfactional.com/marine-invertebrates/porifera/

Cho TO, Riosmena-Rodriguez R (2008) *Ceramium periconicum* sp. nov. (Ceramiaceae, Rhodophyta): a new subtidal species from Baja California Sur, Mexico. Bot Mar 51:307–312

Coates AG, Jackson JBC, Collins LS, Cronin TM, Dowsett HJ, Bybell LM, Jung P, Obando JA (1992) Closure of the Isthmus of Panama: the near-shore marine records of Costa Rica and western Panama. Geol Soc Amer Bull 104:14–28

Coe WR (1940) Revision of the nemertean fauna of the Pacific coasts of North, Central, and Northern South America. Allan Hancock Pac Exp 2:247–323

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Connell SD, Foster MS, Airoldi L (2014) What are algal turfs? Toward a better description of turfs. Mar Ecol Prog Ser 495:299–307

Coppard S, Alvarado JJ (2013) Echinoderm diversity in Panama: 146 years of research across the isthmus. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm research and diversity in Latin America. Springer, Berlin, pp 107–144

Cortés FA, Solano OD, Ruiz-López JA (2012) Variación espacio-temporal de la fauna macrobentónica asociada a fondos blandos y su relación con factores ambientales en el Parque Nacional Natural Gorgona, Pacífico colombiano. Bol Invest Mar Cost 41:323–353

Cortés J (1986) Biogeografía de corales hermatípicos: el istmo centroamericano. An Inst Cienc Mar Limnol, UNAM 13:297–304

Cortés J (1997) Biology and geology of eastern Pacific coral reefs. Coral Reefs 16:S39–S46

Cortés J (2008) Historia de la investigación marina de la Isla del Coco, Costa Rica. Rev Biol Trop 56(Suppl 2):1–18

Cortés J (2009) Stony corals. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 169–173, Species List: Compact Disc pp 112–118

Cortés J (2011) Eastern Tropical Pacific coral reefs. In: Hopley D (ed) The encyclopedia of modern coral reefs: structure, form and process. Springer, Berlin, pp 351–358

Cortés J (2012) Marine biodiversity of an eastern tropical Pacific oceanic island, Isla del Coco. Costa Rica. Rev Biol Trop 60(Suppl 3):131–185

Cortés J, Blum S (2008) Life to 450 m depth at Isla del Coco. Costa Rica. Rev Biol Trop 56(Suppl 2):189–206

Cortés J, Jiménez C (2003) Corals and coral reefs of the Pacific of Costa Rica: history, research and status. In: Cortés J (ed) Latin American coral reefs. Elsevier Science B.V, Amsterdam, pp 361–385

Cortés J, Macintyre IG, Glynn PW (1994) Holocene growth history of an eastern Pacific fringing reef, Punta Islotes, Costa Rica. Coral Reefs 13:65–73

Cortés J, der Hal N van, Soest RWM van (2009) Sponges. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 137–142, Species List: Compact Disc pp 83–93

Cortés J, Jiménez CE, Fonseca AC, Alvarado JJ (2010) Status and conservation of coral reefs in Costa Rica. Rev Biol Trop 58(Suppl 1):33–50

Cortés J, Vargas-Castillo R, Nivia-Ruiz J (2012) Marine biodiversity of Bahía Culebra, Guanacaste, Costa Rica: published records. Rev Biol Trop 60(Suppl 2):39–71

Cortés-Núñez J, Sánchez-Noguera C, Breedy-Shadid O, Pacheco-Solano C (2012) Los Ecosistemas marinos del Refugio de Vida Silvestre La Flor y del Corredor Biológico Paso del Istmo, Rivas, Nicaragua. Proyecto Investigación Marino-Costero: Asegurando las bases científicas y educativas para la protección y manejo de tortugas marinas en los RVS La Flor y Río Escalante-Chococente. CIMAR, Paso Pacífico, DANIDA, Managua, Nicaragua, p 52

Cruz M, Gabor N, Mora E, Jiménez R, Mair J (2003) The known and unknown about marine biodiversity in Ecuador (continental and insular). Gayana 67:232–260

Cruz-Barraza JA, Vega C, Carballo JL (2014) Taxonomy of family Plakinidae (Porifera: Homoscleromorpha) from eastern Pacific coral reefs, through morphology and cox1 and cob mtDNA data. Zool J Linn Soc 171:254–276

Cunningham S, Guzman HM, Bates R (2013) The morphology and structure of the Hannibal Bank fisheries management zone, Pacific Panama using acoustic seabed mapping. Rev Biol Trop 61:1967–1979

Cutler EB (1994) The Sipuncula. Their systematics, biology, and evolution. Comstock Publishing Association, Ithaca, New York, p 480

Cutler NJ, Cutler EB, Vargas JA (1992) Peanut worms (Phylum Sipuncula) from Costa Rica. Rev Biol Trop 40:153–158

Daly M, Fautin DG (2004) *Anthopleura mariscali*, a new species of sea anemone (Cnidaria: Anthozoa: Actiniaria) from the Galápagos Islands. Zootaxa 416:1–8

Dawson EY (1960) Marine red algae of Pacific Mexico. Part 3. Cryptonemiales. Corallinaceae subf. Melobesioideae. Pac Nat 2:3–125

D'Croz L, O'Dea A (2007) Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. Estuar Coast Shelf Sci 73:325–340

de Weerdt WH, Glynn PW (1991) A new and presumably now extinct species of *Millepora* (Hydrozoa) in the eastern Pacific. Zool Med Leiden 65:267–276

Dean HK (2001) Marine biodiversity of Costa Rica: the phyla Sipuncula and Echiura. Rev Biol Trop 49(Suppl 2):85–90

Dean HK (2004) Marine biodiversity of Costa Rica: Class Polychaeta (Annelida). Rev Biol Trop 52(Suppl 2):131–181

Dean HK (2009) Polychaetes and echiurans. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 181–191, Species List: Compact Disc pp 122–159

Dean HK, Sibaja-Cordero JA, Cortés J, Vargas R, Kawauchi GY (2010a) Sipunculans and echiurans of Isla del Coco (Cocos Island), Costa Rica. Zootaxa 2557:60–68

Dean HK, Sibaja-Cordero JA, Cortés J (2010b) Occurrence of the phoronid *Phoronopsis albomaculata* in Cocos Island, Costa Rica. Pac Sci 64:459–462

Dean HK, Sibaja-Cordero JA, Cortés J (2012) Polychaetes (Annelida: Polychaeta) of Cocos Island National Park, Pacific Costa Rica. Pac Sci 66:347–386

Díaz JM, Acero A (2003) Marine biodiversity in Colombia: achievements, status of knowledge, and challenges. Gayana 67:261–274

Diaz MC, van Soest RWM, Guzmán HM (2005) *Aplysina chiriquiensis*, a new pedunculate sponge from the Gulf of Chiriquí, Panamá, Eastern Pacific (Aplysinidae, Verongida). Zootaxa 1012:1–12

DiSalvo L, Randall J, Cea A (1988) Ecological reconnaissance of the Easter Island sublittoral marine environment. Natl Geogr Res 4:451–473

Dominici-Arosemena A, Wolff M (2006) Reef fish community structure in the tropical eastern Pacific (Panamá): living on a relatively stable rocky reef environment. Helgol Mar Res 60:287–305

Dominici-Arosemena A, Brugnoli-Olivera E, Cortés-Núñez J, Molina-Ureña H, Quesada-Alpízar M (2005) Community structure of eastern Pacific reef fishes (Gulf of Papagayo, Costa Rica). Tecnociencia 7:19–41

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Ann Rev Mar Sci 1:169–192

Dove SG, Kline DI, Pantos O, Angly FE, Tyson GW, Hoegh-Guldberg O (2013) Future reef decalcification under a business-as-usual CO_2 emission scenario. Proc Nat Acad Sci USA 110:15,342–15,347

Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. Coral Reefs 15:109–119

Earle SA (1972) A review of the marine plants of Panamá. Bull Biol Soc Washington 2:69–97

Echelman T, Fishelson L (1990) Surface zooplankton dynamics and community structure in the Gulf of Aqaba (Eilat), Red Sea. Mar Biol 107:179–190

Edgar GJ, Banks SA, Bessudo S, Cortés J, Guzmán HM, Henderson S, Martinez C, Rivera F, Soler G, Ruiz D, Zapata FA (2011) Variation in reef fish and invertebrate communities with level of protection from fishing across the eastern tropical Pacific seascape. Global Ecol Biogeogr 20:730–743

Ekman S (1953) Zoogeography of the Sea. Sidgwick and Jackson, London, p 418

Emerson WK (1995) A zoogeographic summary of the marine mollusks of the Revillagigedo Islands (tropical eastern Pacific ocean). Festivus 27:3–18

Emery AR (1968) Preliminary observations on coral reef plankton. Limnol Oceanogr 13:293–303

Emig CC (1982) Nouvelles localisations de phoronidiens. Téthys 10:287–290

Emig CC (2009) Phoronids. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 409– 411, Species list: Compact Disc pp 383–384

Enochs IC (2012) Motile cryptofauna associated with live and dead coral substrates: implications for coral mortality and framework erosion. Mar Biol 159:709–722

Enochs IC, Hockensmith G (2009) The effects of coral mortality on the community composition of cryptic metazoans associated with *Pocillopora damicornis*. In: Proceedings of 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, pp 1375–1379

Enochs IC, Manzello DP (2012a) Species richness of motile cryptofauna across a gradient of reef framework erosion. Coral Reefs 31:653–661

Enochs IC, Manzello DP (2012b) Responses of cryptofaunal species richness and trophic potential to coral reef habitat degradation. Diversity 4:94–104

Enochs IC, Toth LT, Brandtneris VW, Afflerbach JA, Manzello DP (2011) Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. Mar Ecol Prog Ser 438:105–118

Escarria E, Beltrán-León BS, Giraldo A, Zapata F (2007) Ichthyoplankton in the National Park Isla Gorgona (Pacific Ocean of Colombia) during September 2005. Inves Mar 35:127–133

Eschmeyer WN (2014) Catalog of fishes: genera, species, references. http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Accessed 5 Jul 2014

Esquivel-Garrote O (2015) Abundancia, diversidad, biomasa y composición del zooplancton, asociado a los parches de arrecife coralino en el Parque Nacional Isla del Coco (PNIC), Pacífico de Costa Rica. Thesis, Universidad de Costa Rica, San Pedro, San José, Costa Rica, p 70

Excoffon AC, Acuña FH, Cortés J (2009) The sea anemone *Nemanthus californicus* (Cnidaria, Actiniaria, Nemanthidae) from Costa Rica: re-description and first record outside the type locality. Mar Biodiv Rec 2:e142. doi:10.1017/S1755267209990601

Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, De'ath G, Okazaki R, Muehllehner N, Glas MS, Lough JM (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nat Clim Chang 1:165–169

Fabricius KE, Kluibenschedl A, Harrington L, Noonan S, De'ath G (2015) In situ changes of tropical crustose coralline algae along carbon dioxide gradients. Sci Rep 5:9537. doi:10.1038/srep09537

Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J Mar Sci 65:414–432

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychete feeding guilds. Ocean Mar Biol Ann Rev 17:193–284

Fautin DG, Hickman CP Jr, Daly M, Molodtsova T (2007) Shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria) and tube anemones (Cnidaria: Anthozoa: Ceriantharia) of the Galápagos Islands. Pac Sci 61:549–573

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305:362–366

Feely RA, Doney SC, Cooley SR (2009) Ocean acidification: present conditions and future changes in a high-CO_2 world. Oceanography 22:36–47

Fernández C (2008) Flora marina del Parque Nacional Isla del Coco, Costa Rica. Pacífico Tropical Oriental. Rev Biol Trop 56(Suppl 2):57–69

Fernández C, Cortés J (2005) *Caulerpa sertularioides*, a green alga spreading aggressively over coral reef communities in Culebra Bay, North Pacific of Costa Rica. Coral Reefs 24:10

Fernández M, Pappalardo P, Rodríguez-Ruiz MC, Castilla JC (2014) Synthesis of the state of knowledge about species richness of macroalgae, macroinvertebrates and fishes in coastal and oceanic waters of Easter and Salas y Gómez islands. Latin Amer J Aquat Res 42:760–802

Fernández-García C, Riosmena-Rodríguez R, Wysor B, Tejada O, Cortés J (2011) Checklist of the Pacific marine macroalgae of Central America. Bot Mar 54:53–73

Fernández-García C, Cortés J, Alvarado JJ, Nivia-Ruiz J (2012) Physical factors contributing to the benthic dominance of the alga *Caulerpa sertularioides* (Caulerpaceae, Chlorophyta) in the upwelling Bahía Culebra, north Pacific of Costa Rica. Rev Biol Trop 60 (Suppl 2):93–107

Fernández-Leiva S (1996) Taxonomía del ictioplancton en la Isla del Coco. Thesis, Universidad de Costa Rica, San Pedro, San José, Costa Rica, Costa Rica, p 175

Ferraris JD (1982) Surface zooplankton at Carrie Bow Cay Belize. In: Rützler K, McIntyre IG (eds) The Atlantic barrier reef ecosystem at Carrie Bow cay Belize I. Structure and communities. Smithsonian Institution, Washington DC, pp 143–151

Ferreira AJ (1983) The chiton fauna of the Revillagigedo Archipelago, Mexico. Veliger 25:307–322

Fiedler PC, Lavín MF (2006) Introduction: a review of eastern tropical Pacific oceanography. Prog Oceanogr 69:94–100

Fiedler PC, Talley LD (2006) Hydrography of the eastern tropical Pacific: a review. Prog Oceanogr 69:143–180

Fiege D, Ten Hove HA (1999) Redescription of *Spirobranchus gaymardi* (Quatrefages, 1866) (Polychaeta: Serpulidae) from the Indo-Pacific with remarks on the *Spirobranchus giganteus* complex. Zool J Linn Soc 126:355–364

Fisher WK (1946) Echiuroid worms of the North Pacific Ocean. Proc US Nat Mus 96:215–292

Flot JF, Adjeroud M (2009) Les coraux de Clipperton. In: L Charpy (ed) Clipperton, environnement et biodiversité d'un microcosme océanique. Patrim Nat 68:155–162

Fong P, Smith TB, Wartian MJ (2006) Epiphytic cyanobacteria maintain shifts to macroalgal dominance on coral reefs following ENSO disturbance. Ecology 87:1162–1168

Fonseca ACE, Dean HK, Cortés J (2006) Non-colonial coral macro-borers as indicators of coral reef status in the south Pacific of Costa Rica. Rev Biol Trop 54:101–115

Foster MS (2001) Rhodoliths: between rocks and soft places. J Phycol 37:659–667

Foster MS, McConnico LM, Lundsten L, Wadsworth T, Kimbal T, Brooks LB., Medina-López M, Riosmena-Rodríguez R, Hernández-Carmona G, Vásquez-Elizando RM, Johnson S, Steller DL (2007) Diversity and natural history of a *Lithothamnion muelleri-Sargassum horridum* community in the Gulf of California. Cienc Mar 33:367–384

Foster MS, Amado-Filho GM, Kamenos NA, Riosmena-Rodríguez R, Steller DL (2013) Rhodoliths and rhodolith beds. Smithsonian Contr Mar Sci 39:143–155

Fourriére M, Reyes-Bonilla H, Rodríguez-Zaragoza FA, Crane N (2014) Fishes of Clipperton Atoll, Eastern Pacific: checklist, endemism, and analysis of completeness of the inventory. Pac Sci 68:375–395

Fraser CM (1938a) Hydroids of the 1934 Hancock Pacific expeditions. Allan Hancock Pac Exped 4:1–105

Fraser CM (1938b) Hydroids of the 1936 and 1937 Allan Hancock Pacific Expeditions. Allan Hancock Pac Exped 4:107–127

Fraser CM (1938c) Hydroids of the 1932, 1933, 1935, and 1938 Allan Hancock Pacific expeditions. Allan Hancock Pac Exped 4:129–153

Fraser CM (1948) Hydroids of the Allan Hancock Pacific expeditions since March, 1938. Allan Hancock Pac Exped 4:179–335

Friedlander AM, Ballesteros E, Beets J, Berkenpas E, Gaymer CF, Gorny M, Sala E (2013) Effects of isolation and fishing on the marine ecosystems of Easter Island and Salas y Gómez Island, Chile. Aquat Conserv 23:515–531

Garese A, Guzman HM, Acuña FH (2009) Sea anemones (Cnidaria, Anthozoa: Actiniaria and Corallimorpharia) from Panama. Rev Biol Mar Oceanogr 44:791–802

Garske LE (2002) Macroalgas marinas. In: Danulat E, Edgar GJ (eds) Reserva Marina de Galápagos. Línea Base de la Biodiversidad, Fundación Charles Darwin/Servicio del Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador, pp 419–439

Garth JS (1974) On the occurrence in the eastern tropical Pacific of Indo-west Pacific decapod crustaceans commensal with reef-building corals. In: Proceedings of 2nd International Coral Reef Symposium, vol 1, Brisbane, pp 397–404

Garth JS (1992) The brachyuran crabs of the Revillagigedo Islands, Colima, Mexico, with remarks on insular endemism in the Eastern Tropical Pacific. Proc San Diego Soc Nat Hist 24:1–6

Gattuso JP, Bijma J, Gehlen M, Riebesell U, Turley C (2011) Ocean acidification: knowns, unknowns and perspectives. In: Gattuso JP, Hanson L (eds) Ocean acidification. Oxford University Press, Oxford, p 326

Geiger DL (2012) Monograph of the little slit shells. Vol 1. Introduction, Scissurellidae. pp 1–728. Vol 2. Anatomidae, Larocheidae, Depressizonidae, Sutilizonidae, Temnocinclidae. pp. 729–1291. Santa Barbara Museum of Natural History Monographs Number 7. Santa Barbara Museum of Natural History: Santa Barbara, California

Ginsburg RN (1983) Geological and biological roles of cavities in coral reefs. In: Barnes D (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, QLD, Australia, pp 148–153

Giraldo A, Valencia B, Ramírez D (2006) Productividad planctónica y condiciones oceanográficas locales en la Isla Gorgona durante julio 2006. Bol Invest Mar Cost 40:185–201

Glynn PW (1972a) Observations on the ecology of the Caribbean and Pacific coasts of Panamá. Bull Biol Soc Washington 2:13–29

Glynn PW (1972b) Pacific coral reefs of Panamá: structure, distribution and predators. Geol Rundsch 61:483–519

Glynn PW (1973) Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: part 2. Plankton community with evidence for depletion. Mar Biol 22:1–21

Glynn PW (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol Monogr 46:431–456

Glynn PW (1984) An amphinomid worm predator of the crown-of-thorns sea star and general predation on asteroids in eastern and western Pacific coral reefs. Bull Mar Sci 35:54–71

Glynn PW (1985) Corallivore population sizes and feeding effects following El Niño (1982–1983) associated coral mortality in Panama. In: Proceedings of 5th International Coral Reef Congress, vol 4, Tahiti, pp 183–188

Glynn PW (1988) El Niño warning, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. Galaxea 7:129–160

Glynn PW (1993) Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. Atoll Res Bull 379:1–66

Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 69–98

Glynn PW (2000) El Niño-Southern Oscillation mass mortalities of reef corals: a model of high temperature marine extinctions? In: Insalaco E, Skelton PW, Palmer TJ (eds) Carbonate platform systems: components and interactions. Geological Society, London, pp 117–133

Glynn PW (2004) High complexity food webs in low diversity eastern Pacific reef-coral communities. Ecosystems 7:358–367

Glynn PW (2006) Fish utilization of simulated coral reef frameworks versus eroded rubble substrates off Panama, eastern Pacific. Proceedings of 10th International Coral Reef Symposium, vol 1, Okinawa, pp 250–256

Glynn PW (2011) In tandem reef coral and cryptic metazoan declines and extinctions. Bull Mar Sci 87:1–28

Glynn PW (2013) Fine-scale interspecific interactions on coral reefs: functional roles of small and cryptic metazoans. Smithsonian Contr Mar Sci 39:229–248

Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19:1–23

Glynn PW, de Weerdt WH (1991) Elimination of two reef-building hydrocorals following the 1982–83 El Niño warming event. Science 253:69–71

Glynn PW, Enochs IC (2011) Invertebrates and their roles in coral reef ecosystems. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Berlin, pp 273–325

Glynn PW, Feingold JS (1992) Hydrocoral species not extinct. Science 257:1845

Glynn, PW, Maté JL (1997) Field guide to the Pacific coral reefs of Panamá. Proceedings of 8th International Coral Reef Symposium, vol 1, Panamá, pp 145–166

Glynn PW, Druffel EM, Dunbar RB (1983) A dead Central American coral reef tract: possible link with the Little Ice Age. J Mar Res 41:605–637

Glynn PW, Veron JEN, Wellington GM (1996) Clipperton Atoll (eastern Pacific): oceanography, geomorphology, reef-building coral ecology and biogeography. Coral Reefs 15:71–99

Glynn PW, Wellington GM, Wieters EA, Navarrete SA (2003) Reef-building coral communities of Easter Island (Rapa Nui), Chile. In: Cortés J (ed) Latin American coral reefs. Elsevier Science, Amsterdam, pp 474–494

Glynn PW, Wellington GM, Riegl B, Olson DB, Borneman E, Wieters EA (2007) Diversity and biogeography of the scleractinian coral fauna of Easter Island (Rapa Nui). Pac Sci 61:67–90

Glynn PW, Enochs IC, McCosker JE, Graefe AN (2008) First record of a pearlfish, *Carapus mourlani*, inhabiting the aplysiid opisthobranch mollusc *Dolabella auricularia*. Pac Sci 62:593–602

Glynn PW, Enochs IC, Afflerbach JA, Brandtneris VW, Serafy JE (2014) Eastern Pacific reef fish responses to coral recovery following El Niño disturbances. Mar Ecol Prog Ser 495:233–247

Gómez CE, Paul VJ, Ritson-Williams R, Muehllehner N, Langdon C, Sánchez JA (2015) Responses of the tropical gorgonian coral *Eunicea fusca* to ocean acidification conditions. Coral Reefs 34:451–460

González-González J, Gold-Morgan M, León-Tejera H, Candelaria C, León-Alvarez D, Serviere Zaragoza E, Fragoso D (1996) Catálogo onomástico (nomenclátor) y bibliografía indexada de las algas bentónicas marinas de México. UNAM, Cuad Inst Biol 29:1–492

González-Nakawaga O, Sánchez-Nava S (1986) Nota de moluscos como fauna de acompañamiento de crustáceos de la Isla Clarión, México. Inv Oceanogr BC 3:153–182

Gosliner T (1991) The opisthobranch gastropod fauna of the Galápagos Islands. In: James MJ (ed) Galápagos marine invertebrates: taxonomy, biogeography and evolution in Darwin's Islands. Plenum Press, New York, pp 281–305

Gotelli NJ, Abele LG (1983) Community patterns of coral-associated decapods. Mar Ecol 13:131–139

Graham MH, Kinlan BP, Druehl LD, Garske LE, Banks S (2007) Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. Proc Nat Acad Sci USA 104:16,576–16,580

Grassle JF (1973) Variety in coral reef communities. In: Jones OA, Endean R (eds) Biology and geology of coral reefs II. Biology 1. Academic Press, New York, pp 247–270

Greenblatt PR (1982) Small-scale horizontal distributions of zooplankton taxa. Mar Biol 67:97–111

Grigg RW, Hey R (1992) Paleoceanography of the tropical eastern Pacific Ocean. Science 255:172–178

Grottoli AG, Wellington GM (1999) Effect of light and zooplankton on skeletal δ^{13}C values in the eastern Pacific corals *Pavona clavus* and *Pavona gigantea*. Coral Reefs 18:29–41

Guzmán HM (1988) Distribución y abundancia de organismos coralívoros en los arrecifes coralinos de la Isla del Caño, Costa Rica. Rev Biol Trop 36:191–207

Guzman HM, Breedy O (2008) *Leptogorgia christiae* (Octocorallia: Gorgoniidae) a new shallow gorgonian from Pacific Panama. J Mar Biol Assoc UK 88:719–722

Guzman HM, Breedy O (2012) *Pacifigorgia marviva* (Anthozoa: Octocorallia) a new species from Coiba National Park, Pacific Panama. J Mar Biol Assoc UK 92:693–698

Guzmán HM, Cortés J (1989) Coral reef community structure at Caño Island. Pacific Costa Rica. PSZNI: Mar Ecol 10:23–41

Guzmán HM, Cortés J (1993) Los arrecifes coralinos del Pacífico Oriental Tropical: revisión y perspectivas. Rev Biol Trop 41:535–557

Guzmán HM, Obando VL (1988) Diversidad y abundancia diaria y estacional del zooplancton marino de la Isla del Caño, Costa Rica. Rev Biol Trop 36:139–150

Guzmán HM, Obando VL, Cortés J (1987) Meiofauna associated with a Pacific coral reef in Costa Rica. Coral Reefs 6:107–112

Guzmán HM, Obando VL, Brusca RC, Delaney PM (1988) Aspects of the population biology of the marine isopod *Excorallana tricornis occidentalis* Richardson, 1905 (Crustacea: Isopoda: Corallanidae) at Caño Island, Pacific Costa Rica. Bull Mar Sci 43:77–87

Guzman HM, Guevara CA, Breedy O (2004) Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island). Environ Conserv 31:111–121

Guzman HM, Benfield S, Breedy O, Mair JM (2008) Broadening reef protection across the marine conservation corridor of the eastern tropical Pacific: distribution and diversity of reefs in Las Perlas Archipelago, Panama. Environ Conserv 35:46–54

Halfar J, Riegl B (2013) From coral framework to rhodolith bed: sedimentary footprint of the 1982/1983 ENSO in Galápagos. Coral Reefs 32:985

Hall-Spencer JM, Rodolfo-Metalpa R, Martin S, Ransome E, Fine M, Turner SM, Rowley SJ, Tedesco D, Buia MC (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454:96–99

Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, planktivorous fishes and water currents on a windward reef face, Great Barrier Reef, Australia. Bull Mar Sci 42:459–479

Hebbeln D, Cortés J (2001) Sedimentation in a tropical fjord: Golfo Dulce, Costa Rica. Geo-Marine Lett 20:142–148

Heidelberg KB, Sebens KP, Purcell JE (2004) Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. Coral Reefs 23:263–276

Hellberg ME (2009) Gene flow and isolation among populations of marine animals. Ann Rev Ecol Evol Syst 40:291–310

Hendrickx ME (1993) Crustáceos decápodos del Pacífico mexicano. In: Salazar-Vallejo SI, González NE (eds) Biodiversidad marina y costera de México. Comisión Nacional para el uso y conocimiento de la Biodiversidad y CIRQRO, México, pp 271–318

Hermosillo A (2009a) A note on the opisthobranch mollusks of Rocas Alijos. Festivus 41:118–119

Hermosillo A (2009b) The opisthobranch fauna of Islas Tres Marías, Mexican Pacific. Festivus 41:3–9

Hermosillo A, Camacho-García YE (2006) A note on the opisthobranchs of Parque Nacional de Coiba, Panama (tropical eastern Pacific). Festivus 38:95–98

Hermosillo A, Gosliner TM (2008) The opisthobranch fauna of Archipiélago de Revillagigedo, Mexican Pacific. Festivus 40:25–34

Hermosillo A, Valdés A (2004) Two new dorids (Mollusca: Opisthobranchia) of Bahía de Banderas and La Paz, México. Proc California Acad Sci 55:550–560

Hermosillo A, Behrens DW, Ríos-Jara E (2006) Opistobranquios de México. Guía de babosas marinas del Pacífico, Golfo de California y las islas oceánicas. Dirección de Artes Escénicas y Literatura, Universidad de Guadalajara-CONABIO, México, p 143

Hernández L, Balart EF, Reyes-Bonilla H (2009) Checklist of reef decapod crustaceans (Crustacea: Decapoda) in the southern Gulf of California, Mexico. Zootaxa 2119:39–50

Hernández L, Ramírez-Ortiz G, Reyes-Bonilla H (2013) Coral-associated decapods (Crustacea) from the Mexican tropical Pacific coast. Zootaxa 3609:451–464

Hernández MA (1992) Inventario preliminar de moluscos marinos de la costa de El Salvador. Secretaría Ejecutiva del Medio Ambiente, San Salvador, El Salvador, p 172

Hernández-Kantún J, Riosmena-Rodríguez R, López-Vivas JM, Pacheco-Ruíz I (2010) Range extension for *Kallymenia* spp. (Kallymeniaceae: Rhodophyta) associated with rhodolith beds, new records from the Gulf of California, México. Mar Biodiv Rec 3:e84 doi:10.1017/S1755267210000783

Hernández-Kantún JJ, Riosmena-Rodríguez R, Adey WH, Rindi F (2014) Analysis of the cox 2-3 spacer region for population diversity and taxonomic implications in rhodolith-forming species (Rhodophyta, Corallinales). Phytotaxa 190:331–354

Hetzinger S, Halfar J, Riegl B, Godinez-Orta L (2006) Sedimentology and acoustic mapping of modern rhodolith beds on a non-tropical carbonate shelf (Gulf of California, Mexico). J Sediment Res 76:670–682

Hickman CP (1998) A field guide to sea stars and other echinoderms of Galápagos. Sugar Spring Press, Lexington, Virginia, p 83

Hickman CP (1999) A field guide to marine molluscs of Galápagos. Sugar Spring Press, Lexington, Virginia, p 150

Hickman CP (2008) A field guide to corals and other radiates of Galápagos. Sugar Spring Press, Lexington, Virginia, p 172

Hickman CP (2009) Evolutionary responses of marine invertebrates to insular isolation in Galapagos. Galapagos Res 66:32–42

Hickman CP, Zimmerman TL (2000) A field guide to crustaceans of Galápagos. Sugar Spring Press, Lexington, Virginia p156

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on "mesophotic coral ecosystems: characterization, ecology, and management". Coral Reefs 29:247–251

Hinojosa-Arango G, Riosmena-Rodríguez R (2004) Influence of rhodolith-forming species and growth-form on the associated fauna of rhodolith beds in the Central-West Gulf of California. Mexico. PSZNI: Mar Ecol 25:109–127

Hinojosa-Arango G, Rioja-Nieto R, Suárez-Castillo AN, Riosmena-Rodríguez R (2014) Using GIS methods to evaluate rhodolith and *Sargassum* beds as Critical Habitats for commercially important marine species in Bahía Concepción, B.C.S., México. Cryptogamie, Algologie 35:49–65

Hixon MA, Brostoff WN (1981) Fish grazing and community structure of Hawaiian reef algae. Proceedings of 4th International Coral Reef Symposium, vol 2, Manila, pp 508–514

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Holguín-Quiñones O (1994) Comunidades bentónicas marinas. In: Ortega-Rubio A, Castellanos-Vera A (eds) La Isla Socorro, Reserva de la Biósfera Archipiélago de Revillagigedo. Publ Esp 8, CIBNOR, La Paz, México, pp 225–245

Holguín-Quiñones O, Mille-Pagaza S, Pérez-Chi A (1992) Resultado de las campañas de muestreo de 1991 para el estudio del bentos marino de Isla Socorro, Revillagigedo, Colima, México. Zool Inf 24:1–20

Holzman R, Reidenbach MA, Monismith SG, Koseff JR, Genin A (2005) Near-bottom depletion of zooplankton over a coral reef II: relationships with zooplankton swimming ability. Coral Reefs 24:87–94

Hondt, J-L d' (2009) Les bryozoaires. In: Charpy L (ed) Clipperton, environnement et biodiversité d'un microcosme océanique. Patrim Nat 68:271–276

Hooper JNA, Kennedy JA, Quinn RJ (2002) Biodiversity "hotspots", patterns of richness and endemism, and taxonomic affinities of tropical Australian sponges (Porifera). Biodiver Conserv 11:851–885

Huber ME, Coles SL (1986) Resource utilization and competition among the five Hawaiian species of *Trapezia* (Crustacea, Brachyura). Mar Ecol Prog Ser 30:21–31

Hyman LH (1953) Some polyclad flatworms from the Galapagos Islands. Allan Hancock Pac Exp 15:183–210

Idjadi JA, Edmunds PJ (2006) Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. Mar Ecol Prog Ser 319:117–127

Jacoby CA, Greenwood JG (1989) Emergent zooplankton in Moreton Bay, Queensland, Australia: seasonal, lunar, and die1 patterns in emergence and distribution with respect to substrata. Mar Ecol Prog Ser 51:131–154

James DW, Foster MS, O'Sullivan J (2006) Bryoliths (Bryozoa) in the Gulf of California. Pac Sci 60:117–124

James MJ (ed) (1991) Galápagos marine invertebrates: taxonomy, biogeography, and evolution in Darwin's Islands. Plenum Press, New York, p 474

Johnson MD, Price NN, Smith JE (2014) Contrasting effects of ocean acidification on tropical fleshy and calcareous algae. PeerJ 2:e411. doi:10.7717/peerj.411

Jones ML (1972) The Panamic biota: some observations prior to a sea-level canal. Bull Biol Soc Washington 2:270

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. Ann Rev Mar Sci 7:1–20

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) A review of community ecology of mesophotic coral ecosystems. Coral Reefs 29:255–275

Kahng SE, Copus JM, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Curr Opin Environ Sust 7:72–81

Kaiser KL (1997) The Recent molluscan marine fauna of the Islas Galápagos. Festivus 24:1–67

Kaiser KL (2006) Additional mollusk species from Rocas Alijos. México. Festivus 38:22

Kaiser KL (2007) The Recent molluscan fauna of Île Clipperton (tropical Eastern Pacific). Festivus 39:1–162

Kaiser, KL (2009) Les mollusques. In: Charpy L (ed) Clipperton, environment et biodiversité d'un microcosme océanique. Patrim Nat 68:217–234

Kaiser KL, Bryce CW (2001) The Recent molluscan marine fauna of Isla de Malpelo, Colombia. Festivus 33:1–149

Kajihara H, Yoshida R, Uyeno D (2012) First record of *Baseodiscus mexicanus* (Bürger, 1893) (Nemertea: Heteronemertea) from Japanese waters. Check List 8:754–755

Kaniewska P, Campbell PR, Kline DI, Rodriguez-Lanetty M, Miller DJ, Dove S, Hoegh-Guldberg O (2012) Major cellular and physiological impacts of ocean acidification on a reef building coral. PLoS ONE 7(4):e34659. doi:10.1371/journal.pone.0034659

Keen MA (1971) Sea shells of Tropical West America: Marine Molluscs from Baja California to Peru. Stanford University Press, Stanford, California, p 1064

Kemp JM, Benzoni F (1999) Monospecific coral areas on the northern shore of the Gulf of Aden, Yemen. Coral Reefs 18:280

Kerstitch A, Bertsch H (2007) Sea of Cortez marine invertebrates. A guide for the Pacific Coast, México to Perú, 2nd ed. Sea Challengers, Monterey, California, p 124

Kessler WS (2006) The circulation of the eastern tropical Pacific: a review. Prog Oceanogr 69:181–217

Kirsteuer E (1969) Quantitative and qualitative aspects of the nemertean fauna in tropical coral reefs. In: Proceedings of 1st International Coral Reef Symposium, vol 1, Mandapam Camp, pp 363–371

Kleypas JA, Yates KK (2009) Coral reefs and ocean acidification. Oceanography 22:108–117

Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine CL, Robbins L (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Report of a Workshop held, St. Petersburg, Florida, NSF, NOAA, USGS, 18–20 Apr 2005

Klumpp DW, McKinnon AD, Mundy CN (1988) Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. Mar Ecol Prog Ser 45:95–108

Knowlton N (1993) Sibling species in the sea. Annu Rev Ecol Syst 24:189–216

Kobluk DR (1988) Cryptic faunas in reefs: ecology and geologic importance. Palaios 3:379–390

Kroeker KJ, Micheli F, Gambi MC, Martz TR (2011) Divergent ecosystem responses within a benthic marine community to ocean acidification. Proc Nat Acad Sci USA 108:14,515–14,520

Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajos L, Singh GS, Duarte CM, Gattuso JP (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interactions with warming. Glob Chan Biol 19:1884–1896

Kropp RK, Birkeland C (1981) Comparison of Crustacea associates on *Pocillopora verrucosa* from a high island and an atoll. In: Proceedings of 4th International Coral Reef Symposium, vol 1, Manila, pp 627–632

Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT (2008) Decreased abundance of crustose coralline algae due to ocean acidification. Nat Geosci 1:114–117

Landa-Jaime V, Michel-Morfín E, Arciniega-Flores J, Castillo-Vargasmachuca S, Saucedo-Lozano M (2013) Mollusks associated to the coral reefs of Tenacatita, Jalisco, in the central Mexican Pacific. Rev Mexicana Biodiv 84:1121–1136

Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals: a review of mechanisms and effects. In: Dubinsky Z (ed) Coral reefs, ecosystems of the world, vol 25. Elsevier, Amsterdam, pp 209–252

Lassig BR (1977) Communication and coexistence in a coral community. Mar Biol 42:85–92

Laubenfels MW de (1936) A comparison of the shallow-water sponges near the Pacific end of the Panama Canal with those at the Caribbean end. Proc US Natl Mus 83:441–466

Lefevre M (1984) Répartition de la biomasse zooplanctonique autour de l'île de Moorea, Polynésie Française. J Rech Oceanogr 9:20–22

Lemaitre R, Álvarez-León R (1992) Crustáceos decápodos del Pacífico colombiano: Lista de especies y consideraciones zoogeográficas. An Inst Inv Mar Punta Betín 21:33–76

Lendenfeld R von (1910) Reports on the scientific results of the expedition to the Eastern Tropical Pacific in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross" from 1904–1905. The sponges I. The Geodiidae. Mem Mus Comp Zoöl, Harvard Coll 41:1–259

Lessios HA, Kessing BD, Pearse JS (2001) Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. Evolution 55:955–975

Leviten PJ, Kohn AJ (1980) Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. Ecol Monogr 50:55–75

Lindner A, Cairns SD, Guzmán HM (2004) *Distichopora robusta* sp. nov., the first shallow-water stylasterid (Cnidaria: Hydrozoa: Stylasteridae) from the tropical eastern Pacific. J Mar Biol Assoc UK 84:943–947

Littler DS, Littler MM (2010) Marine plants of Pacific Panama. Smithsonian Tropical Research Institute, Smithsonian Institution. http://biogeodb.stri.si.edu/pacificalgae: Updated on Jan 2010

Littler MM, Littler DS (2008) Coralline algal rhodoliths form extensive benthic communities in the Gulf of Chiriqui, Pacific Panama. Coral Reefs 27:553

Lizano OG (2008) Dinámica de aguas alrededor de la Isla del Coco, Costa Rica. Rev Biol Trop 56(Suppl 2):31–48

López E, Capa M, Aguado MT, Cladera P (2005) Capitellidae (Annelida: Polychaeta) from Coiba National Park, Pacific coast of Panamá with a new species of the genus *Amastigos*. Cah Biol Mar 46:57–67

Mair JM, Cunningham SL, Sibaja-Cordero JA, Guzman HM, Arroyo MF, Merino D, Vargas R (2009) Mapping benthic faunal communities in the shallow and deep sediments of Las Perlas Archipelago, Pacific Panama. Mar Poll Bull 58:375–383

Manzello DP (2008) Reef development and resilience to acute (El Niño warming) and chronic (high-CO_2) disturbances in eastern tropical Pacific: a real-world climate change model. In: Proceedings of 11th International Coral Reef Symposium, Ft Lauderdale, pp 1299–1303

Manzello DP (2010a) Ocean acidification hotspots: spatiotemporal dynamics of the seawater CO_2 system of eastern Pacific coral reefs. Limnol Oceanogr 55:239–248

Manzello DP (2010b) Coral growth with thermal stress and ocean acidification: lessons from the eastern tropical Pacific. Coral Reefs 29:749–758

Manzello DP, Kleypas JA, Budd DA, Eakin CM, Glynn PW, Langdon C (2008) Poorly cemented coral reefs of the eastern tropical Pacific: possible insights into reef development in a high-CO_2 world. Proc Nat Acad Sci USA 105:10,450–10,455

Maté JL (2003) Corals and coral reefs of the Pacific coast of Panamá. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 387–417

McConnico LA, Foster MS, Steller DL, Riosmena-Rodríguez R (2014) Population biology of a long-lived rhodolith: the consequences of becoming old and large. Mar Ecol Prog Ser 504:109–118

McCreary JP, Lee HS, Enfield DB (1989) The response of the coastal ocean to strong offshore winds: with application to circulation in the gulfs of Tehuantepec and Papagayo. J Mar Res 47:81–109

McLean JH, Coan EV (1996) Marine mollusks of Rocas Alijos. In: Schmieder RW (ed) Rocas Alijos. Cordell Expeditions. Kluwer Acad Publ, Dordrecht, Netherlands, pp 305–318

McWilliam PS, Sale PF, Anderson DT (1981) Seasonal changes in resident zooplankton sampled by emergence traps in One Tree Lagoon, Great Barrier Reef. J Exp Mar Biol Ecol 52:185–203

Menza C, Kendall M, Hile S (2008) The deeper we go the less we know. Rev Biol Trop 56(Suppl. 1):11–24

Mille-Pagaza SR, Pérez-Chi A, Holguín-Quiñones O (1994) Fauna malacológica bentónica del litoral de isla Socorro, Revillagigedo, México. Cienc Mar 20:467–486

Millen S, Hermosillo A (2012) Three new species of aeolid nudibranchs (Opisthobranchia) from the Pacific coast of Mexico, Panama, and the Indopacific, with a redescription and redesignation of a fourth species. Veliger 51:145–164

Miller KJ, Ayre DJ (2004) The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. Heredity 92:557–568

Millero FJ (2007) The marine inorganic carbon cycle. Chem Rev 107:308–341

Miloslavich P, Klein E, Díaz JM, Hernández CE, Bigatti G, Campos L, Artigas F, Castillo J, Penchaszadeh PE, Neill PE, Carranza A, Retana MV, Díaz de Astarloa JM, Lewis M, Yorio P, Piriz ML, Rodríguez D, Yoneshigue-Valentin Y, Gamboa L, Martín A (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. PLoS ONE 6:e14631. doi:10.1371/journal.pone.0014631

Mora C, Robertson DR (2005) Causes of latitudinal gradients in species richness: a test with fishes of the tropical eastern Pacific. Ecology 86:1771–1782

Morales A, Murillo MM (1996) Distribution, abundance and composition of coral reef zooplankton, Cahuita National Park, Limon, Costa Rica. Rev Biol Trop 44:619–630

Morales-Ramírez A (2008) Caracterización cualitativa del zooplancton del Área de Conservación Marina Isla del Coco (ACMIC), Océano Pacífico de Costa Rica. Rev Biol Trop 56(Suppl 2):159–169

Morales-Ramírez A (2011) La diversidad marina del Golfo Dulce, Pacífico sur de Costa Rica: amenazas a su conservación. Biocenosis 24:9–20

Motro R, Ayalon I, Genin A (2005) Near-bottom depletion of zooplankton over coral reefs: III. Vertical gradient of predation pressure. Coral Reefs 24:95–98

Müller-Gelinek H, Salazar-Orquera M (1996) Algas marinas del Ecuador. Comisión Asesora Ambiental, Instituto Nacional de Pesca, República de Ecuador, p 187

Murillo-Muñoz M, Peña-Salamanca EJ (2014) Benthic marine algae of Gorgona Island, Colombian Pacific coast. Rev Biol Trop 62(Suppl 1):27–41

Newman LJ, Cannon LRG (2003) Marine flatworms: the world of polyclads. CSIRO Publishing, Melbourne, p 112

Ohlhorst SL (1982) Diel migration patterns of demersal reef zooplankton. J Exp Mar Biol Ecol 60:1–15

Pacheco C (2012) Estudio taxonómico de las esponjas perforadoras (Porifera, Demospongiae) de arrecifes de coral del Pacífico de Costa Rica. Thesis, Universidad de Costa Rica. San Pedro, Costa Rica, p 69

Palacios MM, Muñoz CG, Zapata FA (2014) Fish corallivory on a pocilloporid reef and experimental coral responses to predation. Coral Reefs 33:625–636

Palardy JE, Witman JD (2011) Water flow drives biodiversity by mediating rarity in marine benthic communities. Ecol Lett 14:63–68

Palardy JE, Grottoli AG, Matthews KA (2005) Effect of upwelling, depth, morphology, and polyp size on feeding in three species of Panamanian corals. Mar Ecol Prog Ser 300:79–89

Palardy JE, Grottoli AG, Matthews KA (2006) Effect of naturally changing zooplankton concentrations on feeding rates of two coral species in the eastern Pacific. J Exp Mar Biol Ecol 331:99–107

Patton WK (1974) Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In: Vernberg W (ed) Symbiosis in the sea. University of South Carolina Press, Columbia, South Carolina, pp 219–243

Patton WK (1994) Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef, Australia. Bull Mar Sci 55:193–211

Payri C, Menou J-L, N'Yeurt A (2009) La flore marine du complexe récifal et quelques aspects de la biodiversité et de la géomorphologie de l'île. In: Charpy L (ed) Clipperton, environnement et biodiversité d'un microcosme océanique. Patrim Nat 68:129–141

Pedroche FF, Silva PC, Aguilar-Rosas LE, Dreckmann KM, Aguilar-Rosas R (2005) Catálogo de las algas marinas bentónicas del Pacífico de México. I. Chlorophycota. Universidad Autónoma de Baja California, Baja California, México, p 135

Pedroche FF, Silva PC, Aguilar-Rosas LE, Dreckmann KM, Aguilar-Rosas R (2008) Catálogo de las algas marinas bentónicas del Pacífico de México. UAM, Estado de México, México, II. Phaeophycota, p 146

Peña-Salamanca EJ (2008) Dinámica espacial y temporal de la biomasa algal asociada a las raíces de mangle en la Bahía de Buenaventura, costa Pacífica de Colombia. Bol Invest Mar Cost 37:55–70

Pepe PJ (1985) Littoral endolithic fauna of the Central American Isthmus. Rev Biol Trop 33:191–194

Peralta-García EC, Rosas-Alquicira EF (2014) Range extension and morphological characterization of rhodolith-forming species (Corallinales, Rhodophyta) from shallow water in the Mexican South Pacific. Helgol Mar Res 68:503–513

Pérez-Ruzafa A et al (2013) Chapter 16: Latin America echinoderm biodiversity and biogeography: patterns and affinities. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm research and diversity in Latin America. Springer, Berlin, Heidelberg, pp 511–542

Porter JW (1972) Predation by *Acanthaster* and its effect on coral species diversity. Am Nat 106:487–492

Porter JW (1974) Zooplankton feeding by the Caribbean reef-building coral *Montastraea cavernosa*. In: Proceedings of 2nd International Coral Reef Symposium, vol 1, Brisbane, pp 111–125

Porter JM, Porter KG (1977) Quantitative sampling of demersal zooplankton migrating from different coral reef substrates. Limnol Oceanogr 22:553–556

Poupin J, Bouchard J-M, Albenga L, Cleva R, Hermoso-Salazar M, Solis-Weiss V (2009) Les crustacés décapodes et stomatopodes, inventaire, écologia et zoogéographie. In: Charpy L (ed) Clipperton, environnement et biodiversité d'un microcosme océanique. Patrim Nat 68:163–216

Preston E (1973) A computer simulation of competition among five sympatric congeneric species of xanthid crabs. Ecology 54:469–483

Ragazzola F, Foster LC, Form A, Anderson PSL, Hansteen TH, Fietzke J (2012) Ocean acidification weakens the structural integrity of coralline algae. Glob Chan Biol 18:2804–2812

Ramírez-Luna S, de la Cruz G, Barrientos-Luján N (2002) Variación espacio temporal de Porcellanidae, Majoidae y Xanthoidae asociados a los corales del género *Pocillopora* en bahías de Huatulco, México. In: Hendrickx M (ed) Contribuciones al estudio de los Crustáceos del Pacífico Este, 1:233-254. UNAM, ICMyL, Mazatlán, México

Randall JE, Cea A (2011) Shore fishes of Easter Island. University of Hawaii Press, Honolulu, Hawai'i, p 164

Razak TB, Hoeksema BW (2003) The hydrocoral genus *Millepora* (Hydrozoa: Capitata: Milleporidae) in Indonesia. Zool Verh Leiden 345:313–336

Reaka-Kudla ML (1997) The global biodiversity of coral reefs. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, DC, pp 83–108

Reijmer JJG, Bauch T, Schäfer P (2012) Carbonate facies patterns in surface sediments of upwelling and non-upwelling shelf environments (Panama, East Pacific). Sedimentology 59:32–56

Reimer JD, Sinniger F, Hickman CP Jr (2008) Zoanthid diversity (Anthozoa: Hexacorallia) in the Galapagos Islands: a molecular examination. Coral Reefs 27:641–654

Reyes-Bonilla H, Riosmena-Rodríguez Foster MS (1997) Hermatyic corals associated with rhodolith beds in the Gulf of California, Mexico. Pac Sci 51:328–337

Reyes-Bonilla H, Walther-Mendoza M, Ramírez-Ortiz G (2012) Biodiversidad y turismo ecológico. In: Ibáñez-Pérez RM, Ivanova-Boncheva A (eds) Medio ambiente y política turística en México. Instituto Nacional de Ecología, México, pp 135–148

Richter C, Wunsch M, Rasheed M, Kötter I, Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413:726–730

Riosmena-Rodríguez R, Medina-López M (2010) The role of rhodolith beds in the recruitment of invertebrate species from the southwestern Gulf of California, Mexico. In: Israel A, Einav R, Seckbach J (eds) Seaweeds and their role in globally changing environments. Springer, Berlin, pp 127–138

Riosmena-Rodríguez R, Woelkerling WJ, Foster MS (1999) Taxonomic reassessment of rhodolith-forming species of *Lithophyllum* (Corallinales, Rhodophyta) in the Gulf of California, Mexico. Phycologia 38:401–417

Riosmena-Rodríguez R, Steller DL, Hinojosa-Arango G, Foster MS (2010) Reefs that rock and roll: biology and conservation of rhodolith beds in the Gulf of California. In: Brusca RC (ed) The Gulf of California biodiversity and conservation. University of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, Arizona, pp 49–71

Riosmena-Rodríguez R, López-Calderón JM, Mariano-Meléndez E, Sánchez-Rodríguez A, Fernández-García C (2012) Size and distribution of rhodolith beds in the Loreto Marine Park: their role in coastal processes. J Coast Res 28:255–260

Rivera F, Martínez P (2011) Guía fotográfica de corales y octocorales: Parque Nacional Machalilla y Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena. NAZCA, Instituto de Investigaciones Marinas. Informe Técnico, Conservación Internacional, Ecuador, Ecuador, p 78

Rixen T, Jiménez C, Cortés J (2012) Impact of upwelling events on the sea water chemistry in the Gulf of Papagayo (Culebra Bay). Costa Rica. Rev Biol Trop 60(Suppl 2):187–195

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284

Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? Coral Reefs 17:179–186

Robertson DR, Allen GR (2006) Shorefishes of the tropical eastern Pacific: an information system. Version 2.0. Smithsonian Tropical Research Institute, Balboa, Panama

Robertson DR, Allen GR (2008) Shorefishes of the Tropical Eastern Pacific online information system. Version 1.0.4.53. Smithsonian Tropical Research Institute, Balboa, Panama (available at: www.stri.org/sftep)

Robertson DR, Cramer KL (2009) Shore fishes and biogeographic subdivisions of the tropical eastern Pacific. Mar Ecol Prog Ser 380:1–17

Robertson DR, Grove JS, McCosker JE (2004) Tropical transpacific shorefishes. Pac Sci 58:507–565

Robichaux DM, Cohen AC, Reaka MJ, Allen D (1981) Experiments with zooplankton on coral reefs, or, will the real demersal please come up? PSZNI: Mar Ecol 2:77–94

Robins CR (1972) The state of knowledge of the coastal fish fauna of the Panamic region prior to the construction of an interoceanic sea-level canal. Bull Biol Soc Washington 2:159–166

Robinson NM, Hansen GI, Fernández-García C, Riosmena-Rodríguez R (2013) A taxonomic and distributional study of the rhodolith-forming species *Lithothamnion muelleri* (Corallinales, Rhodophyta) in the Eastern Pacific Ocean. Algae 28:63–71

Rodríguez-Sevilla L, Vargas R, Cortés J (2009) Benthic, shelled Gastropods. In: Werhtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, pp 333–356

Rogers CS (2013) Coral reef resilience through biodiversity. ISRN Oceanogr 2013, Article ID 739034. doi:10.5402/2013/739034

Roman MR, Furnas MJ, Mullin MM (1990) Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef. Mar Biol 105:73–82

Ruggiero MA, Gordon DP, Orrell TM, Bailly N, Bourgoin T, Brusca RC, Cavalier-Smith T, Guiry MD, Kirk PM (2015) A higher level classification of all living organisms. PLoS ONE 10(4): e0119248

Rusch DB et al (2007) The Sorcerer II Global Ocean Sampling Expedition: northwest Atlantic through eastern tropical Pacific. PLoS Biol 5(3):e77. doi:10.1371/journal.pbio.0050077

Russell DJ (1992) The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Bøerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J.Ag. and *Hypnea cervicornis* J. Ag. ICES Marine Science Symposiom, vol. 194, pp 110–125

Sachet MH (1962) Flora and vegetation of Clipperton Island. Proc California Acad Sci 31:249–307

Salazar-Vallejo SI, Londoño-Mesa MH (2004) Lista de especies y bibliografía de poliquetos (Polychaeta) del Pacífico Oriental Tropical. An Inst Biol UNAM Ser Zool 75:9–97

Sale PF (1980) The ecology of fishes on coral reefs. Oceanogr Mar Biol Ann Rev 18:367–421

Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. Mar Ecol Prog Ser 13:1–14

Sánchez JA, Gómez CE, Escobar D, Dueñas LF (2011) Diversidad, abundancia y amenazas de los octocorales de la Isla Malpelo, Pacífico Oriental Tropical, Colombia. Bol Inv Mar Cost 40(Supl Esp):139–154

Sánchez JA, Ardila NE, Andrade J, Dueñas LF, Navas R, Ballesteros D (2014) Octocoral densities and mortalities in Gorgona Island, Colombia. Tropical Eastern Pacific. Rev Biol Trop 62(Suppl 2):209–219

Schmidt P (1978) Interstitielle fauna von Galapagos. XXI. Lebensraum, Umweltfaktoren. Gesamtfauna. Mikrof Meeresb 68:1–52

Schnetter R, Bula-Meyer G (1982) Algas marinas del litoral Pacífico de Colombia. Gantner Verlag, Berlin, p 287

Sedberry GR, Cuellar N (1993) Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboplites aurorubens* (Teleostei, Lutjanidae). US Fish Bull 91:699–709

Segovia-Prado JV, Navarrete-Calero MT (2007) Biodiversidad a nivel de ecosistema en parches de corales hermatípicos (*Porites lobata*, *Pocillopora* sp.) en la zona intermareal de la Playa los Cóbanos, Departamento de Sonsonate, El Salvador. Thesis, Universidad de El Salvador, San Salvador, El Salvador, p 68

Segovia-Prado JV (2012) Comunidades de octocorales (Cnidaria: Octocorallia) en El Salvador, América Central. MSc thesis, Universidad de Costa Rica, San Pedro, San José, Costa Rica, p 126

Serviere-Zaragoza E, Riosmena-Rodríguez R, León-Tejera H, González-González J (2007) Distribución espacial de macroalgas marinas en las Islas Revillagigedo, México. Ciencia y Mar 11:3–13

Sibaja-Cordero JA (2012) Composición de la macrofauna bentónica en substratos sedimentarios del Parque Nacional Isla del Coco. PhD Dissertation, Universidad de Vigo, Vigo, España, Costa Rica, p 306

Sibaja-Cordero JA, Cortés J, Dean HK (2012) Depth diversity profile of polychaete worms in Bahía Chatham, Parque Nacional Isla del Coco, Pacific of Costa Rica. Rev Biol Trop 60(Suppl 3):293–301

Sibaja-Cordero JA, García-Méndez K, Troncoso JS (2013) Additions to the mollusk checklist of Cocos Island National Park, Costa Rica (Eastern Tropical Pacific). Iberus 31:127–163

Sibaja-Cordero JA, Troncoso JS, Gómez-Ramírez E (2014) Recent surface marine sediments of Cocos Island in Costa Rica. Int J Sed Res 29:59–72

Silverman J, Lazar B, Cao L, Caldeira K, Erez J (2009) Coral reefs may start dissolving when atmospheric CO_2 doubles. Geophys Res Lett 36:L05606. doi:10.1029/2008GL036282

Small M (1998) Ten days in May: a trip to Las Islas Tres Marías. Festivus 30:75–82

Smith TB, Fong P, Kennison R, Smith J (2010) Spatial refuges and associational defenses promote harmful blooms of the alga *Caulerpa sertularioides* onto coral reefs. Oecologia 164:1039–1048

Solano-Barquero A (2011) Macrofauna asociada a rodolitos en el Parque Nacional Isla del Coco. Thesis, Universidad de Costa Rica, San Pedro, San José, Costa Rica, p 50

Solís-Marín FA, Laguarda-Figueras A (2009) Les échinodermes. In: Charpy L (ed) Clipperton, environnement et biodiversité d'un microcosme océanique. Patrim Nat 68:235–247

Solís-Marín FA et al. (2013a) Appendix. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm research and diversity in Latin America. Springer, Berlin, pp 543–654

Solís-Marín FA, Honey-Escandón MBI, Herrero-Perezrul MD, Benitez-Villalobos F, Díaz-Martínez JP, Buitrón-Sánchez BE, Palleiro-Nayar JS, Durán-González A (2013b) Echinoderms from Mexico: Biodiversity, distribution and current state of knowledge. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm Research and Diversity in Latin America. Springer, Berlin, pp 11–65

Solís-Weiss V, Hernández-Alcántara P (2009) Les annélides polychètes de la cryptofaune benthique assciées au corail mort. In: Charpy L (ed) Clipperton, environnement et biodiversité d'un microcosme océanique. Patrim Nat 68:249–270

Sonnenholzner J, Brandt M, Francisco V, Hearn A, Luzuriaga M, Guarderas P, Navarro JC (2013) Echinoderms of Ecuador. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm research and diversity in Latin America. Springer, Berlin, pp 183–233

Sorokin YI (1990) Plankton in the reef ecosystems. In: Dubinsky Z (ed) Ecosystems of the world, vol 25., Coral Reefs. Elsevier, Amsterdam, pp 291–327

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583

Starr RM, Cortés J, Barnes CL, Green K, Breedy O (2012) Characterization of deepwater invertebrates at Coco Island National Park and Las Gemelas Seamounts. Costa Rica. Rev Biol Trop 60 (Suppl 3):303–319

Steller DL, Cáceres C (2009) Coralline algal rhodoliths enhance larval settlement and early growth of the Pacific calico scallop *Argopecten ventricosus*. Mar Ecol Prog Ser 396:49–60

Steller DL, Riosmena-Rodríguez R, Foster MS, Roberts C (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of anthropogenic disturbances. Aquat Conserv Mar Freshw Ecosyst 13:S5–S20

Steller DL, Foster MS, Riosmena-Rodríguez R (2009) Living rhodolith bed ecosystems in the Gulf of California. In: Johnson JM, Ledesma-Vazquez J (eds) Atlas of coastal ecosystems in the Gulf of California: past and present. University of Arizona Press, Tucson, Arizona, pp 72–82

Stimson J (1990) Stimulation of fat-body production in the polyps of the coral *Pocillopora damicornis* by the presence of mutualistic crabs of the genus *Trapezia*. Mar Biol 106:211–218

Strong AM, Hanna GD (1930) Marine Mollusca of the Revillagigedo Islands, Mexico. Proc California Acad Sci 19:7–12

Suárez-Morales E, Morales-Ramírez A (2003) A new species of *Cymbasoma* (Crustacea: Copepoda: Monstrilloida) from the Pacific coast of Costa Rica, Central America. Proc Biol Soc Washington 116:206–214

Suárez-Morales E, Morales-Ramírez A (2009) New species of Monstrilloida (Crustacea: Copepoda) from the Eastern Tropical Pacific. J Nat Hist 43:1257–1271

Taylor WR (1945) Pacific marine algae of the Allan Hancock Pacific Expeditions to the Galapagos Islands. Allan Hancock Pac Exped 12:1–528

Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Thiel M, Kruse I (2001) Status of the Nemertea as predators in marine ecosystems. Hydrobiologia 456:21–32

Thresher RE (1991) Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press Inc, San Diego, pp 401–436

Treadwell AL (1941) Eastern Pacific expeditions of the New York Zoological Society. XXIII. Polychaetous annelids from the west coast of Mexico and Central America. Zoologica 26:17–24

Valencia B, Giraldo A (2009) Hipéridos (Crustacea: Amphipoda) en el sector norte del Pacífico oriental tropical Colombiano. Lat Am J Aquat Res 37:265–273

Valencia B, Herrera L, Giraldo A (2014) Estructura de la comunidad y distribución vertical de la macrofauna de fondos blandos en Isla Gorgona, Pacifico Colombiano. Rev Biol Trop 62(Suppl 1):169–188

Vannini M (1985) A shrimp that speaks crab-ese. J Crust Biol 5:160–167

van Soest RWM, Kaiser KL, van Syoc R (2011) Sponges from Clipperton Island, East Pacific. Zootaxa 2839:1–46

van Woesik R, van Woesik K, van Woesik L, van Woesik S (2013) Effects of ocean acidification on the dissolution rates of reef-coral skeletons. PeerJ 1:e208. doi:10.7717/peerj.208

Vargas R, Wehrtmann IS (2009) Decapod crustaceans. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, Text pp 209–228, Species List: Compact Disc pp 167–198

Vargas S, Guzman HM, Breedy O (2008) Distribution patterns of the genus *Pacifigorgia* (Octocorallia Gorgoniidae): track analysis and parsimony analysis of endemicity. J Biogeogr 35:241–247

Vega AJ, González A (2001) Moluscos del Pacífico veragüense, parte I (Clases: Bivalvia y Poliplacophora). Tecnociencia 3:89–107

Vega AJ, González A (2002) Moluscos del Pacífico veragüense, parte II (Gasterópoda). Tecnociencia 4:23–45

Vega C, Hernández-Guerrero J, Cruz-Barraza JA (2012) Biogeografía de esponjas marinas (Phylum Porifera); Estudios en el Pacífico Oriental. CICIMAR Oceánides 27:35–50

Veron JEN (2008) Mass extinctions and ocean acidification: biological constraints on geological dilemmas. Coral Reefs 27:459–472

Veron J, Stafford-Smith M, DeVantier L, Turak E (2015) Overview of distribution patterns of zooxanthellate Scleractinia. Front Mar Sci 1:81. doi:10.3389/fmars.2014.00081

Verrill AE (1868–70) Notes on Radiata in the museum of Yale College, Number 6: Review of the corals and polyps of the West Coast of America. Trans Connecticut Acad Arts Sci, 2nd ed., vol 1, pp 377–558

Villalobos A (1960) Notas acerca del aspecto hidrobiológico de la parte Sur de la Isla. In: Adem J, Cobo E, Blásquez L, Miranda F, Villalobos A, Herrera T, Villa B, Vásquez L (eds) La Isla Socorro. Monogr Inst Geofís 2:155–180

von Prahl H, Guhl F, Grögl M (1978) Crustáceos decápodos comensales del coral *Pocillopora damicornis* L. en la Isla de Gorgona, Colombia. An Inst Inv Mar Punta Betín 10:81–93

Wehrtmann IS, Cortés J (eds) (2009) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin. Text 538 p, List of species in Compact Disk p 500

Wehrtmann IS, Cortés J, Echeverría-Sáenz S (2009) Marine biodiversity of Costa Rica: perspectives and conclusions. In: Wehrtmann IS, Cortés J (eds) Marine biodiversity of Costa Rica, Central America. Springer+Business Media, Berlin, pp 521–533

Wellington GM (1982a) An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia 52:311–320

Wellington GM (1982b) Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. Ecol Monogr 52:223–241

Wellington GM, Glynn PW, Strong AE, Navarrete SA, Wieters E, Hubbard D (2001) Crisis on coral reefs linked to climate change. EOS, Trans Amer Geophys Union 82(1):5

Wells JW (1972) Notes on Indo-Pacific scleractinian corals. Part 8. Scleractinian corals from Easter Island. Pac Sci 26:183–190

Wells JW (1983) Annotated list of the scleractinian corals of the Galápagos. In: Glynn PW, Wellington GM (eds) Corals and coral reefs of the Galápagos Islands. Univ California Press, Berkeley, pp 212–295

Westheide W (1974) Interstitielle fauna von Galapagos XI. Pisionidae, Hesionidae, Pilargidae, Syllidae (Polychaeta). Mikr Meeresb 44:1–146

Westheide W (1977) Interstitielle fauna von Galapagos XVIII. Nereidae, Eunicidae, Dorvilleidae (Polychaeta). Mikr Meeresb 63:357–393

Westheide W (1991) The meiofauna of the Galapagos: a review. In: James MJ (ed) Galapagos marine invertebrates: taxonomy, biogeography, and evolution in Darwin's Islands. Plenum, New York, pp 37–73

Wicksten MK, Hendrickx ME (1992) Checklist of penaeoid and caridean shrimps (Decapoda: Penaeoidea, Caridea) from the Eastern Tropical Pacific. Proc San Diego Soc Nat Hist 9:1–11

Wieters EA, Medrano A, Pérez-Matus A (2014) Functional community structure of shallow hard bottom communities at Easter Island (Rapa Nui). Lat Am J Aquat Res 42:827–844

Williams G, Breedy O (2004) The Panamic genus *Pacifigorgia* (Octocorallia: Gorgoniidae) in the Galápagos Archipelago. Proc California Acad Sci 55:54–87

Williamson SJ, Rusch DB, Yooseph S, Halpern AL, Heidelberg KB, Glass JI, Andrews-Pfannkoch C, Fadrosh D, Miller CS, Sutton G, Frazier M, Venter JC (2008) The Sorcerer II global ocean sampling expedition: metagenomic characterization of viruses within aquatic microbial samples. PLoS ONE 3(1):e1456. doi:10.1371/journal.pone.0001456

Wittmann AC, Pörtner HO (2013) Sensitivities of extant animal taxa to ocean acidification. Nature Clim Change. doi:10.1038/nclimate1982

Wilson HV (1904) The sponges. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands. Mem Mus Comp Zoöl, Harvard Coll 30:1–164

Woelkerling WJ (1988) The coralline red algae: an analysis of the genera and subfamilies of nongeniculate Corallinaceae. British Museum (Natural History)/Oxford University Press, London/Oxford, p 268

Wulff J (1997) Causes and consequences of differences in sponge diversity and abundance between the Caribbean and Eastern Pacific of Panama. In: Proceedings of 8th International Coral Reef Symoposium, vol 2, Panamá, pp 1377–1382

Wysor B (2004) An annotated list of marine Chlorophyta from the Pacific coast of the Republic of Panama with a comparison to Caribbean Panama species. Nova Hedwigia 78:209–241

Yabur-Pacheco R, Riosmena-Rodríguez R (2007) Rhodolith bed composition in the Southwestern Gulf of California, México. Publ Seto Mar Biol Lab Spec Publ Ser 8:37–47

Yahel R, Yahel G, Genin A (2005) Near-bottom depletion of zooplankton over coral reefs: I. Diurnal dynamics and size distribution. Coral Reefs 24:75–85

Zapata FA, Morales YA (1997) Spatial and temporal patterns of fish diversity in a coral reef at Gorgona Island, Colombia. In: Proceedings of 8th International Coral Reef Symposium, vol 1, Panama, pp 1029–1034

Zapata FA, Robertson DR (2007) How many species of shore fishes are there in the tropical Eastern Pacific? J Biogeogr 34:38–51

Zapata FA, Rodríguez-Ramírez A, Caro-Zambrano C, Garzón-Ferreira J (2010) Mid-term coral-algal dynamics and conservation status of a Gorgona Island (tropical Eastern Pacific) coral reef. Rev Biol Trop 58(Suppl 1):81–94