Marine Biodiversity Records

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Decapod crustaceans associated with macroinvertebrates in Pacific Costa Rica

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Abstract

Decapod crustaceans are a diverse group that exploits various types of habitats in Costa Rica, where they represent 8.1% of the marine diversity of the country. This group includes families containing species with strictly symbiotic behavior, e.g., the Palaemonidae and Pinnotheridae. Despite the high diversity of decapods and the importance of symbionts in marine ecosystems, very little research has been done regarding symbiosis in Costa Rica and the Central American region. The objective of the present study is to present a check list of the species of decapods that are associated with macroinvertebrates in Pacific Costa Rica. The research was carried out using different sources, including a literature review, the Crustaceans Collection of the Zoology Museum of the University of Costa Rica, and field surveys between 1970 and 2019 along the Pacific coast of Costa Rica, and Isla del Coco, 500 km offshore. One-hundred associations are reported, of 74 species of symbiotic decapods with six host phyla. Seventy-four associated with Cnidaria, 15 with Echinodermata, four each with Annelida and Mollusca, two with Chordata, and one with Porifera. In total, there were 14 new reports of decapods occurring on Isla del Coco and four new reports of decapods for Costa Rica: *Pseudocoutierea elegans, Raytheres clavapedatus*, *Tulearіocaris holthuisi,* and *Calyptraeotheres pepeluisi*. These results highlight the need to conduct more detailed studies to determine the real diversity and ecological importance of the associations between marine organisms.

Keywords: Isla del Coco, Coral reefs, Biodiversity, Palaemonidae, Pinnotheridae, Symbiosis

Introduction

The diversity of decapod crustaceans is directly correlated with the abundance of habitats exploited by these organisms, including continental waters, intertidal zones, coral reefs, the deep sea and even the body cavities of other marine organisms (Bruce 1976; Martin and Davis 2001; Macedo et al. 2012; Sal Moyano et al. 2012; Baeza 2015). The different species expend a great deal of energy in habitat selection because the location that they choose should not only allow them to survive, but also to reproduce (Anthony and Cannolly 2004). In their search for shelter, many of these animals are exposed to the presence of spatially and temporarily limited resources. Some of these resources include aggregations of seastars, sea urchins, mussels, algal mats, and kelp forests, among others (Baeza et al. 2002; Ory et al. 2013). The characteristics of the habitat, predation and interspecific competition encourage great specificity of habitat selection and are even considered to be drivers of symbiotic relationships (Montfrans et al. 2003; Baeza 2007; Ory et al. 2013). Symbiosis is a very common type of interaction in marine ecosystems (Thiel and Baeza 2001; Sotka 2005; Baeza 2007; Glynn 2013). It has been defined as "the living together of unlike organisms" (De Bary 1879). Other definitions include the factor of time, since these associations can extend through a part or the entirety of the lifecycle of one or both organisms (Starr et al. 2009).

In Costa Rica, there are 591 species of decapods, 8.1% of the known marine biodiversity of the country

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in both oceans (Vargas and Wehrtmann 2009; Wehrtmann et al. 2009). The families in this group with the greatest species richness in Pacific Costa Rica are Xanthidae (45 spp.), Porcellanidae (44 spp.), Majidae (43 spp.), Alpheidae (34 spp.), Ocypodidae (28 spp.) and Palaemonidae (23 spp.) (Vargas and Wehrtmann 2009). Similarly, of the 1688 marine species reported for Isla del Coco, 8.2% are decapods (Cortés 2012). Some decapod species are adapted for symbiotic behavior. Among the most well-known groups for establishing associations with other species are the families Palaemonidae, Alpheidae, Pinnotheridae and Porcellanidae (Baeza 2007). The decapods that live in association with other animals in Costa Rica have been scarcely studied and in most publications they are only mentioned in species lists with no indication of their association with other organisms. The objective of the present study is to present a compilation of species of decapod crustaceans associated with macroinvertebrates in the Pacific of Costa Rica.

Materials and methods

Study sites

This study includes specimens collected in different locations, associated with different biological substrates, along the Pacific coast of Costa Rica, including from the north, Bahía Salinas and Gulf of Papagayo; to the Central Pacific coast: Gulf of Nicoya; and to the south: Golfo Dulce; as well as different sites around Isla del Coco National Park (Fig. 1, Table 1). These sites have different levels of protection and the health status of their ecosystems differs considerably (Cortés 2016a, b).

Locations along the northern coast (Bahía Salinas, Bahía Cuajiniquil, Islas Murciélago and Bahía Culebra) are under the influence of a seasonal coastal upwelling (McCreary et al. 1989; Alfaro et al. 2012). The coral ecosystems in Bahía Cuajiniquil in the Gulf of Santa Elena are dominated by the genus *Pocillopora*, and the species *Porites panamensis* and *Pavona gigantea*, while the reefs in Bahía Salinas are basically made up of *P. gigantea* (Cortés et al. 2010). In the reefs of Bahía Culebra, coral cover is under 1%; this ecosys-

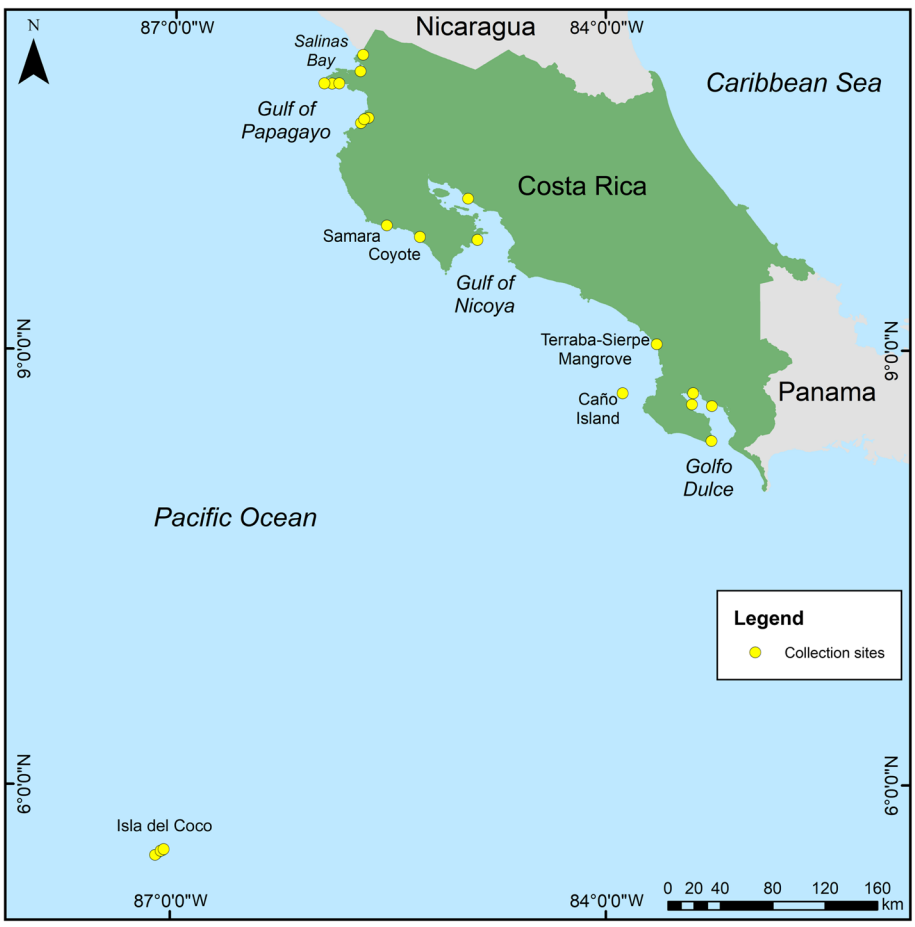

Fig. 1 Collection sites mentioned in the text and Tables

Table 1 Hosts, associated decapods, sites, depth and year of collections

Host Phylum	Host Group	Host Species	Associated species	Site	Abundance	Depth (m)	Year
Porifera	Demospongidae	*Halichondria* sp.	*Panopeus chilensis*	Punta Morales, Golfo de Nicoya, Puntarenas	Abundant	Intertidal	2014
Cnidaria	Scleractinia	*Pavona gigantea*	*Opecarcinus crescentus*	Isla del Caño, Puntarenas	Abundant	6	1992
		Pavona gigantea	*Opecarcinus crescentus*	Islas Pelonas, Bahía Culebra, Guanacaste	Abundant	16	1992
		Pavona gigantea	*Opecarcinus crescentus*	Playa Pochote, Guanacaste	Abundant	NI	1994
		Pocillopora damicornis	*Ala cornuta*	Playa Blanca, Bahía Culebra, Guanacaste	Rare	3	2003–2004
		Pocillopora damicornis	*Alpheus lottini*	Islas Palmitas, Bahía Huevo, Guanacaste	Abundant	6–10	1997
		Pocillopora damicornis	*Alpheus lottini*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Amphithrax tuberculatus*	Playa Blanca, Bahía Culebra, Guanacaste	Rare	3	2003–2004
		Pocillopora damicornis	*Cycloxanthops vittatus*	Playa Blanca, Bahía Culebra, Guanacaste	Rare	3	2003–2004
		Pocillopora damicornis	*Fennera chacei*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Hapalocarcinus marsupialis*	Islas Palmitas, Bahía Huevo, Guanacaste	Rare	6	1991
		Pocillopora damicornis	*Harpiliopsis depressa*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Heteractaea lunata*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Pachycheles biocellatus*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Pagurus lepidus*	Playa Blanca, Bahía Culebra, Guanacaste	Rare	3	2003–2004
		Pocillopora damicornis	*Petrolisthes haigae*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Teleophrys cristulipes*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Trapezia bidentata*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Trapezia corallina*	Playa Blanca, Bahía Culebra, Guanacaste	Abundant	3	2003–2004
		Pocillopora damicornis	*Trizopagurus magnificus*	Playa Blanca, Bahía Culebra, Guanacaste	Rare	3	2003–2004
		Pocillopora damicornis	*Williamstimpsonia stimpsoni*	Playa Blanca, Bahía Culebra, Guanacaste	Rare	3	2003–2004
		Pocillopora sp.	*Alpheus lottini*	Bahía Thomas, Cuajiniquil, Guanacaste	Abundant	2	2016
		Pocillopora sp.	*Brachycarpus biunguiculatus*	Bahía Thomas, Cuajiniquil, Guanacaste	Abundant	2	2016
		Pocillopora sp.	*Domecia hispida*	Bahía Santa Elena, Guanacaste	Rare	NI	1994
		Pocillopora sp.	*Hapalocarcinus marsupialis*	Isla del Caño, Puntarenas	Rare	8–10	1986
		Pocillopora sp.	*Harpiliopsis depressa*	Bahía Santa Elena, Guanacaste	Abundant	NI	1994
		Pocillopora sp.	*Hemus finneganae*	Playa Matapalo, Guanacaste	Very abundant	6–14	2008
		Pocillopora sp.	*Lipaesthesius leeanus*	Playa Matapalo, Guanacaste	Rare	6–14	2008
		Pocillopora sp.	*Stenorhynchus debilis*	Playa Matapalo, Guanacaste	Very abundant	6–14	2008
		Pocillopora sp.	*Trapezia bidentata*	Bahía Thomas, Cuajiniquil, Guanacaste	Abundant	2	2016
		Pocillopora sp.	*Trapezia cymodoce*	Bahía Santa Elena, Guanacaste	Abundant	NI	1994
		Porites lobata	*Alpheus floridanus*	Parque Nacional Isla del Coco	Rare	NI	2004
		Porites lobata	*Pachygrapsus transversus*	Parque Nacional Isla del Coco	Very abundant	NI	2004

Table 1 Hosts, associated decapods, sites, depth and year of collections *(Continued)*

Host Phylum	Host Group	Host Species	Associated species	Site	Abundance	Depth (m)	Year
		Porites lobata	*Paracallianidea laevicauda*	Parque Nacional Isla del Coco	Rare	NI	2004
		Porites lobata	*Parapinnixa cortesi*	Chatham Bay, Parque Nacional Isla del Coco	Rare	NI	2004
		Porites lobata	*Petrolisthes artifrons*	Parque Nacional Isla del Coco	Rare	NI	2004
		Porites lobata	*Uca* (*Petruca*) *panamensis*	Parque Nacional Isla del Coco	Rare	NI	2004
		Porites lobata	*Pomatogebia rugosa*	Parque Nacional Isla del Coco	Abundant	NI	1988–1989
		Tubastraea coccinea	*Platypodiella rotundata*	Isla San José, Islas Murciélago, Guanacaste	Abundant	30	2010
	Antipatharia	*Antipathes* sp.	*Periclimenes murcielagensis*	San Pedrito, Islas Murciélago, Guanacaste	Rare	25	1996
		Antipathes sp.	*Waldola schmitti*	San Pedrito, Islas Murciélago, Guanacaste	Rare	25	1996
		Lillipathes ritamariae	*Coralaxius galapagensis*	Parrita, Puntarenas	Rare	1000	2009
		Myriopathes panamensis	*Eupilumnus xantusii*	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Myriopathes panamensis	*Gnathophyllum panamense*	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Myriopathes panamensis	*Iridopagurus occidentalis*	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Myriopathes panamensis	*Lipkemedaeus spinulifer*	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Myriopathes panamensis	*Pachycheles velerae*	Everest, Parque Nacional Isla del Coco	Abundant	70–80	2009
		Myriopathes panamensis	*Periclimenes murcielagensis*	Peñon Abrazo de la Muerte, Islas Murciélago, Guanacaste	Rare	30	1999
		Myriopathes panamensis	*Pilumnus stimpsonii*	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Myriopathes panamensis	*Quadrella nitida*	Peñon Abrazo de la Muerte, Islas Murciélago, Guanacaste	Rare	30	1999
		Myriopathes panamensis	*Stenorhynchus debilis*	Everest, Parque Nacional Isla del Coco	Abundant	70–80	2009
		Myriopathes panamensis	*Synalpheus* sp.	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Myriopathes panamensis	*Veleronia sympathes*	Everest, Parque Nacional Isla del Coco	Abundant	70–80	2009
		Myriopathes panamensis	*Waldola schmitti*	Peñon Abrazo de la Muerte, Islas Murciélago, Guanacaste	Rare	30	1999
	Octocorallia	*Eugorgia mutabilis*	*Megalobrachium tuberculipes*	Los Potreros, Puerto Jiménez, Puntarenas	Abundant	Intertidal	2013
		Eugorgia mutabilis	*Neopontonides henryvonprahli*	Los Potreros, Puerto Jiménez, Puntarenas	Rare	11	2013
		Eugorgia mutabilis	*Orthochela pumila*	Los Potreros, Puerto Jiménez, Puntarenas	Rare	Intertidal	2013
		Eugorgia mutabilis	*Pseudoveleronia laevifrons*	Los Potreros, Puerto Jiménez, Puntarenas	Abundant	Intertidal	2013
		Eugorgia mutabilis	*Typton* sp.	Los Potreros, Puerto Jiménez, Puntarenas	Rare	11	2013
		Leptogorgia cortesi	*Hippolyte* sp.	Punta Islotes, Golfo Dulce, Puntarenas	Rare	NI	1997
		Leptogorgia cortesi	*Periclimenes infraspinis*	Punta Islotes, Golfo Dulce, Puntarenas	Rare	NI	1997
		Leptogorgia cortesi	*Periclimenes* sp.	Punta Islotes, Golfo Dulce, Puntarenas	Rare	NI	1997
		Leptogorgia cuspidata	*Raytheres clavapedathus*	San Pedrito, Islas Murciélago, Guanacaste	Rare	NI	1994
		Muricea sp.	*Pseudocoutierea elegans*	Everest, Parque Nacional Isla del Coco	Abundant	70–80	2009
		Muricea sp.	*Quadrella nitida*	Everest, Parque Nacional Isla del Coco	Rare	70–80	2009
		Muricea sp.	*Quadrella nitida*	Rodolitos, Parque Nacional Isla del Coco	Rare	50	2009
		Pacifigorgia irene	*Megalobrachium*	Playa Matapalo, Península de Osa, Puntarenas	Rare	11	2013

Table 1 Hosts, associated decapods, sites, depth and year of collections *(Continued)*

Host Phylum	Host Group	Host Species	Associated species	Site	Abundance	Depth (m)	Year
			tuberculipes				
		Pacifigorgia irene	*Neopontonides henryvonprahli*	Playa Matapalo, Península de Osa, Puntarenas	Rare	11	2013
		Pacifigorgia irene	*Orthochela pumila*	Playa Matapalo, Península de Osa, Puntarenas	Rare	11	2013
		Pacifigorgia irene	*Pseudoveleronia laevifrons*	Playa Matapalo, Península de Osa, Puntarenas	Rare	11	2013
		NI	*Nemausa sinensis*	Dos Amigos, Parque Nacional Isla del Coco	Rare	NI	2001
		NI	*Neopontonides henryvonprahli*	Islas Palmitas, Bahía Huevo, Guanacaste	Rare	NI	1997
		NI	*Pseudoveleronia laevifrons*	Sámara, Guanacaste	Rare	NI	1997
		NI	*Pseudoveleronia laevifrons*	Dos Amigos, Parque Nacional Isla del Coco	Rare	NI	2001
		NI	*Quadrella nitida*	Dos Amigos, Parque Nacional Isla del Coco	Rare	NI	2001
		NI	*Veleronia serratifrons*	Bahía Salinas, Guanacaste	Rare	NI	1997
		Pennatulacea	*Euceramus transversilineatus*	Punta Sortija, Bahía Santa Elena, Guanacaste	Rare	NI	2013
	Hydrozoa	*Stylaster marenzelleri*	*Munida* sp.	Everest, Parque Nacional Isla del Coco	Rare	86	2014
		Stylaster marenzelleri	*Pseudocoutierea elegans*	Everest, Parque Nacional Isla del Coco	Abundant	86	2014
Mollusca	Gastropoda	*Crepidula* sp.	*Calyptraeotheres pepeluisi*	Punta Morales, Golfo de Nicoya, Puntarenas	Rare	Intertidal	2014–2016
	Bivalvia	*Pinctada mazatlanica*	*Pontonia margarita*	Isla Tortuga, Golfo de Nicoya, Puntarenas	Rare	2–18	1993–2018
		Pinctada mazatlanica	*Pontonia margarita*	Parque Nacional Isla del Coco	Rare	8	2014
		Pinna rugosa	*Pontonia simplex*	Playa Iguanita, Bahía Culebra, Guanacaste	Very rare	NI	1995
		Sacosstrea palmula	*Austinotheres angelicus*	Punta Morales, Golfo de Nicoya, Puntarenas	Very abundant	Intertidal	2012–2014
Annelida	Polychaeta	*Lanicola* sp.	*Glassella costaricana*	Punta Morales, Golfo de Nicoya, Puntarenas	Abundant	Intertidal	1992
		NI	*Tetrias scabripes*	Bajo Manuelita, Parque Nacional Isla del Coco	Rare	66	2009
		Onuphidae	*Pinnixa longipes*	Punta Islotes, Golfo Dulce, Puntarenas	Rare	10	2014
		Onuphidae	*Polyonyx nitidus*	Punta Islotes, Golfo Dulce, Puntarenas	Rare	10	2014
Echinodermata	Asteroidea	*Asteropsis carinifera*	*Calyptraeotheres* sp.	Bahía Culebra, Guanacaste	Rare	12	2014–2016
		Asteropsis carinifera	*Pachycheles biocellatus*	Bahía Culebra, Guanacaste	Abundant	12	2014–2016
		Asteropsis carinifera	*Zenopontonia soror*	Bahía Culebra, Guanacaste	Abundant	12	2014–2016
		Astropecten regalis	*Minyocerus kirki*	Manglar de Térraba-Sierpe, Puntarenas	Rare	8	2013
		Nidorellia armata	*Zenopontonia soror*	Bahía Salinas, Guanacaste	Abundant	3–8	2014–2016
		Nidorellia armata	*Zenopontonia soror*	Bahía Culebra, Guanacaste	Abundant	3	2014–2018
		Pentaceraster cumingi	*Zenopontonia soror*	Isla Tortuga, Golfo de Nicoya, Puntarenas	Abundant	6	2013
		Pentaceraster cumingi	*Zenopontonia soror*	Golfo Dulce, Puntarenas	Abundant	2–16	2014
		Pentaceraster cumingi	*Zenopontonia soror*	Bahía Cuajiniquil, Golfo de Santa Elena	Abundant	25	2014–2016
		Pentaceraster cumingi	*Zenopontonia soror*	Bahía Culebra, Guanacaste	Abundant	2–12	2014–2018
		Pharia pyramidata	*Zenopontonia soror*	Bahía Culebra, Guanacaste	Abundant	4–6	2014–2016
		Phataria unifascialis	*Zenopontonia soror*	Nicuesa, Golfo Dulce, Puntarenas	Abundant	2.5	2014
		Phataria unifascialis	*Zenopontonia soror*	Bahía Culebra, Guanacaste	Abundant	4–6	2014–2016
	Echinoidea	*Astropyga pulvinata*	*Tuleariocaris holthuisi*	Bahía Culebra, Guanacaste	Abundant[a]	6–8	2013–2014
		Centrocidaris	*Pseudocoutierea elegans*	Parque Nacional Isla del Coco	Abundant	85–103	2009, 2013,

Table 1 Hosts, associated decapods, sites, depth and year of collections *(Continued)*

Host Phylum	Host Group	Host Species	Associated species	Site	Abundance	Depth (m)	Year
		doederleini					2016
		Diadema mexicanum	*Stenorhynchus debilis*	Isla Tortuga, Golfo de Nicoya, Puntarenas	Abundant	2–15	2014–2019
		Diadema mexicanum	*Tuleariocaris holthuisi*	Bahía Culebra, Guanacaste	Abundant[a]	2–8	2014
		Encope micropora	*Dissodactylus nitidus*	Bahía Salinas, Guanacaste	Rare	NI	2005
		Lanthonia longifissa	*Dissodactylus nitidus*	Playa Costa de Oro, Coyote, Guanacaste	Rare	NI	2010
		Tripneustes depressus	*Gnathophylloides mineri*	Bahía Wafer, Parque Nacional Isla del Coco	Rare	15	2016
Chordata	Ascidiacea	*Rhopalaea birkelandi*	*Ascidonia pusilla*	Playas del Coco, Bahía Culebra, Guanacaste	Rare	Shallow	1970
		NI	*Ascidonia pusilla*	Isla Bolaños, Bahía Salinas, Guanacaste	Rare	NI	2012

NI No information
[a]Seasonally abundant, otherwise rare

tem is in a phase shift, where some macroalgae have increased their abundance and become dominant, e.g., *Caulerpa sertularioides* (Fernández-García et al. 2012; Arias-Godínez et al. 2019). Several collections were done at the Islas Murciélago, an archipelago in Área de Conservación Guanacaste (Cortés 2017). In the Gulf of Nicoya, specimens were obtained from the coral communities of Isla Tortuga, where coral cover is below 5% and of low diversity (Alvarado et al. 2018), as well as from the intertidal mudflat of Punta Morales, where polychaete worms and ostracods predominate (Vargas 1987). Punta Nicuesa is a coral community with one of the highest covers of live coral along the southern Pacific coast (up to 83.4%) (Alvarado et al. 2015). Isla del Coco is the site with the greatest protection in Pacific Costa Rica; coral cover there is reported to be 18.64 ± 3.55% (Alvarado et al. 2016a; Cortés 2016b).

Collection

Collection of specimens was carried out in a targeted way. The available environments of most sites were explored from the intertidal zone to ~ 30 m deep, including mudflats, sandy beaches and rocky shores, coral and rocky reefs, rhodolith beds and subtidal soft bottoms. Different organisms that are known to be decapod hosts were collected and accommodated in separate plastic bags. Each of the collected specimens underwent a detailed visual inspection and the water was filtered to separate possible decapod symbionts. In general, echinoids, asteroids, holothuroids, octocorals and scleractinian corals were collected and externally inspected, while the interiors of the bivalves were inspected. Occasionally, sponges and annelids were collected. Most of the samples were collected manually in the intertidal zone and by scuba diving in the subtidal environments (Table 1). In the case of Isla del Coco, samples from two dives in the submarine *DeepSee* (Cortés and Blum 2008; Cortés 2019) that explored rocks in deep locations (between 60 and 280 m) were inspected. The sampling was opportunistic, which means that search efforts were not the same to all sites.

Our results include a species list of collected decapods associated with other organisms along the Pacific of Costa Rica, and their relative abundance. In addition, information is included from specimens collected in the Costa Rican Pacific, both on the coast and in Isla del Coco, which were in the collection of the Zoology Museum, University of Costa Rica (MZUCR, for its abbreviation in Spanish). These collections were carried out between 1970 and 2019; they included the intertidal zone, scuba diving to 40 m, dives of the submarine *DeepSee* to depths between 60 and 280 m and a dive of the submarine *ALVIN* to 1000 m deep (Tables 1 and 2). The list that is presented also includes the decapod associations that have previously been reported in the literature for Pacific Costa Rica. Species identification were done using Rathbun (1918, 1930, 1931), Holthuis (1951), Haig (1960), Williams (1986), Kim and Abele (1988), Kropp (1989), Ramos (1995), Castro (1996), Hendrickx (1999), Vargas (2000), Thoma et al. (2005), Marín and Anker (2009), Campos and Hernández-Ávila (2010). All names are according to WoRMS (http://www.marinespecies.org, last accessed 14 December 2020).

Results

One-hundred associations are reported, which include 74 species of decapods are guests of six phyla of hosts (Table 1). The phylum with the most associated decapods was Cnidaria, with 74 species i.e., 74% of the total), followed by Echinodermata with 15 species, and four each with Annelida and Mollusca, two with Chordata,

Table 2 Decapods associated with other invertebrates on Pacific Costa Rica

#	Species	Infraorder	Family	MZUCR
1	*Trizopagurus magnificus* (Bouvier, 1898)	Anomura	Diogenidae	NC
2	*Munida* sp. Leach, 1820		Munididae	3521
3	*Iridopagurus occidentalis* (Faxon, 1893)		Paguridae	2483
4	*Pagurus lepidus* (Bouvier, 1898)		Paguridae	NC
5	*Euceramus transversilineatus* (Lockington, 1878)		Porcellanidae	3266
6	*Megalobrachium tuberculipes* (Lockington, 1878)		Porcellanidae	3312, 3408
7	*Minyocerus kirki* Glassell, 1938		Porcellanidae	3327
8	*Orthochela pumila* Glassell, 1936		Porcellanidae	3312
9	*Pachycheles velerae* Haig, 1960		Porcellanidae	2746
10	*Pachycheles biocellatus* (Lockington, 1878)		Porcellanidae	3709–03
11	*Petrolisthes artifrons*[a] Haig, 1960		Porcellanidae	2552
12	*Petrolisthes haigae* Chace, 1962		Porcellanidae	NC
13	*Polyonyx nitidus* Lockington, 1878		Porcellanidae	3413
14	*Coralaxius galapagensis* Kensley, 1994	Axiidea	Axiidae	2733, 2738
15	*Paracallianidea laevicauda*[a] (Gill, 1859)		Callianideidae	2552
16	*Hapalocarcinus marsupialis* Stimpson, 1859	Brachyura	Criptochiridae	1652, 1924
17	*Opecarcinus crescentus* (Edmondson, 1925)		Criptochiridae	1646, 1801, 1957
18	*Domecia hispida* Eydoux & Souleyet, 1842		Domeciidae	1929
19	*Pachygrapsus transversus* (Gibbes, 1850)		Grapsidae	2552
10	*Stenorhynchus debilis* (Smith, 1871)		Inachoididae	3461
21	*Ala cornuta* (Stimpson, 1860)		Mithracidae	NC
22	*Amphithrax tuberculatus* (Stimpson, 1860)		Mithracidae	2364
23	*Hemus finneganae* Garth, 1958		Mithracidae	2607
24	*Nemausa sinensis*[a] (Rathbun, 1892)		Mithracidae	2413
25	*Teleophrys cristulipes* Stimpson, 1860		Mithracidae	NC
26	*Uca* (*Petruca*) *panamensis* (Stimpson, 1859)		Ocypodidae	2552
27	*Eupilumnus xantusii*[a] (Stimpson, 1860)		Oziidae	2744
28	*Panopeus chilensis* H. Milne Edwards & Lucas, 1843		Panopeidae	3272
29	*Pilumnus stimpsonii*[a] Miers, 1886		Pilumnidae	3466
30	*Austinotheres angelicus* (Lockington, 1877)		Pinnotheridae	1627, 2831, 2832, 2833, 3068, 3069
31	*Calyptraeotheres pepeluisi*[b] E. Campos and Hernández-Ávila, 2010		Pinnotheridae	3279
32	*Calyptraeotheres* sp.[b] E. Campos, 1990		Pinnotheridae	3709–01
33	*Dissodactylus nitidus* Smith, 1870		Pinnotheridae	2859, 3052
34	*Glassella costaricana* (Wicksten, 1982)		Pinnotheridae	1883, 2564, 2605, 2606, 2685, 2911, 3107, 3115, 3194, 3271, 3311, 3452, 3453, 3506, 3530
35	*Parapinnixa cortesi* B. P Thoma, Heard & Vargas, 2005		Pinnotheridae	2552
36	*Pinnixa longipes* (Lockington, 1876)		Pinnotheridae	3413
37	*Raytheres clavapedatus*[b] (Glassell, 1935)		Pinnotheridae	2604
38	*Tetrias scabripes* Rathbun, 1898		Pinnotheridae	2821
39	*Quadrella nitida* Smith, 1869		Trapeziidae	1963, 2309, 2730, 2737
40	*Trapezia bidentata* (Forskål, 1775)		Trapeziidae	2294, 2852, 3565
41	*Trapezia corallina* Gerstaecker, 1856		Trapeziidae	2851
42	*Trapezia cymodoce*[a] (Herbst, 1801)		Trapeziidae	1929
43	*Trapezia digitalis* Latreille, 1828		Trapeziidae	1010

Table 2 Decapods associated with other invertebrates on Pacific Costa Rica *(Continued)*

#	Species	Infraorder	Family	MZUCR
44	*Cycloxanthops vittatus* (Stimpson, 1860)		Xanthidae	NC
45	*Heteractaea lunata* (Lucas in H. Milne Edwards & Lucas, 1844)		Xanthidae	NC
46	*Lipaesthesius leeanus* Rathbun, 1898		Xanthidae	2607
47	*Lipkemedaeus spinulifer*[a] (Rathbun, 1898)		Xanthidae	3461
48	*Platypodiella rotundata* (Stimpson, 1860)		Xanthidae	2813
49	*Williamstimpsonia stimpsoni* (A. Milne-Edwards, 1879)		Xanthidae	2853–05
50	*Alpheus floridanus*[a] Kingsley, 1878	Caridea	Alpheidae	2552
51	*Alpheus lottini* Guérin-Méneville, 1838 [in Guérin-Méneville, 1829–1838]		Alpheidae	2364, 3565
52	*Synalpheus* sp. Spence Bate, 1888		Alpheidae	3466
53	*Hippolyte* sp. Leach, 1814 [in Leach, 1813–1815]		Hippolytidae	3187
54	*Ascidonia pusilla* Holthuis, 1951		Palaemonidae	3302
55	*Brachycarpus biunguiculatus* (H. Lucas, 1846)		Palaemonidae	3565
56	*Fennera chacei* Holthuis, 1951		Palaemonidae	2851, 2852
57	*Harpiliopsis depressa* (Stimpson, 1860)		Palaemonidae	1929
58	*Gnathophylloides mineri* Schmitt, 1933		Palaemonidae	NC
59	*Gnathophyllum panamense*[a] Faxon, 1893		Palaemonidae	2744
60	*Neopontonides henryvonprahli* Ramos, 1995		Palaemonidae	2234, 3312, 3408, 3434
61	*Periclimenes infraspinis* (Rathbun, 1902)		Palaemonidae	3187
62	*Periclimenes murcielagensis* Vargas, 2000		Palaemonidae	2247, 2308, 2309, 3526
63	*Periclimenes* sp. O.G. Costa, 1844		Palaemonidae	3187
64	*Pontonia margarita*[a] Smith in Verrill, 1869		Palaemonidae	1572, 1682, 3186, 3188
65	*Pontonia simplex* Holthuis, 1951		Palaemonidae	2202
66	*Pseudocoutierea elegans*[a] Holthuis, 1951		Palaemonidae	2731, 3521, 3350
67	*Pseudoveleronia laevifrons*[a] (Holthuis, 1951)		Palaemonidae	2233, 2413, 3312, 3408, 3434
68	*Tulleariocaris holthuisi*[b] Hipeau-Jacquotte, 1965		Palaemonidae	3443, 3444, 3446
69	*Typton* sp. O.G. Costa, 1844		Palaemonidae	3434
70	*Veleronia serratifrons* Holthuis, 1951		Palaemonidae	2233
71	*Veleronia sympathes*[a] (De Ridder & Holthuis, 1979)		Palaemonidae	2727
72	*Waldola schmitti* Holthuis, 1951		Palaemonidae	2247, 2309
73	*Zenopontonia soror* (Nobili, 1904)		Palaemonidae	3445, 3449, 3709–02
74	*Pomatogebia rugosa*[a] (Lockington, 1878)	Gebiidea	Upogebiidae	1770, 1925

MZUCR Catalogue number of the Zoology Museum, University of Costa Rica, *NC* Not catalogued
[a]New reports for Isla del Coco = 14
[b]New reports for Costa Rica = 4

and one with Porifera. The host order with the greatest diversity of associated decapods was Scleractinia (Table 1). The species that showed the most associations with different hosts was *Zenopontonia soror*, which was found in five species of seastars (Table 1). This species was recently reported new to Costa Rica by Vargas-Castillo and Cortés (2019). The shrimp *Pseudocoutierea elegans* was found in hosts from three groups (Octocorallia, Hydrozoa, and Echinoidea). On the other hand, *Tetrias scabripes* was found associated solely with polychaetes (Table 1).

Of the associations recorded 59% were rare, that is, we observed them in a few occasions or with few individuals. While 36% of the associations were observed many times and with several members of the symbiont species on the host. Four relations were very abundant, three of them, *Hemus finneganae, Stenorhynchus debilis* and *Pachygrapsus transversus* with hard corals, and *Austinotheres angelicus* with a bivalve. On the other extreme was *Pontonia simplex* of which we found only one specimen in a bivalve. *Tulleariocaris holthuisi*, associated with two species of

sea urchins, was seasonally abundant but rare at other times. A species that was abundant was always abundant, with very few exceptions, *Megalobrachium tuberculipes* and *Pseudoveleronia laevifrons* were abundant in one species of octocoral, *Eugorgia mutabilis*, but not in other octocorals. Symbiotic species were usually associated to the same species or group of related species, being an exception *P. elegans* that was abundant in an octocoral, a calcareous hydroid and a sea urchin (Table 1).

In total, 74 species of symbiotic decapods have been discovered in Pacific Costa Rica, 13 anomurans, two axiidids, 34 brachyurans, 24 carideans, and one gebiidid (Table 2). The family with the most symbiotic species was Palaemonidae (20 spp.), followed by the families Pinnotheridae and Porcellanidae, with nine species each. The genus with the most species was *Trapezia* with four, followed by *Periclimenes* with three. Fourteen new reports of decapods were recorded for Isla del Coco along with the occurrence of four new decapod records for Pacific Costa Rica, *Calyptraeotheres pepeluisi* Campos and Hernández-Ávila 2010, *Raytheres clavapedatus* (Glassell, 1935), *Tuleariocaris holthuisi* Hipeau-Jacquotte 1965 and *Pseudocoutierea elegans* Holthuis 1951. This is the first time that the genus *Calyptraeotheres* is reported in Costa Rica (Table 2).

In the following section, the associations are detailed according to the type of host (Table 1).

Porifera

In this study, only the species *Panopeus chilensis* is reported to be associated with an intertidal sponge, genus *Halichondria*. However, this is probably because the few studies on sponges have not focus on documenting the associated organisms.

Cnidaria

Fifty-six species of decapods, distributed in five orders, 23 families and 50 genera, were found associated with 21 species of cnidarians. *Opecarcinus crescentus* has only been found in *Pavona gigantea*, while Alvarado and Vargas-Castillo (2012) reported 16 species of decapods associated with *Pocillopora damicornis*, all of which are typically found with this host. Six additional species are reported associated to *Pocillopora* sp. Seven species were found living on *Porites lobata* and one, *Platypodiella rotundata*, exclusively on *Tubastraea coccinea*. Fifteen species were found associated with Antipatharia. The two species associated with *Antipathes* sp. were also found in *Myriopathes panamensis*. Only one associated deep-water decapod, *Coralaxius galapagensis*, was found on *Lillipathes ritamariae*. In Octocorallia, 22 associated species were found. *Eugorgia mutabilis* was the host with the greatest diversity of decapods, six. The two most common decapods in octocorals were *Neopontonides henryvonprahli* and *Pseudoveleronia laevifrons*; four crustaceans could not be identified to species. In the hydrozoans, symbionts have only been collected from *Stylaster marenzelleri*, where *Munida* sp. and *Pseudocoutierea elegans* were found.

Mollusca

Four species of decapods, distributed in two orders, two families and three genera, were found associated with four species of molluks. Symbionts have been found primarily in bivalves. In specimens of the pearl oyster *Pinctada mazatlanica,* pairs of the shrimp *Pontonia margarita* have been found living inside the oyster on numerous occasions; *P. simplex* was found in *Pinna rugose*. In the oyster, *Saccostrea palmula,* the pinnotherid crab *Austinotheres angelicus* has been reported as a guest with a prevalence of 38% (Mena et al. 2014). Only pairs of *Calyptraeotheres pepeluisi* were found living in the interior of the gastropod *Crepidula* sp. on the mangrove roots at Punta Morales.

Annelida

Four species of decapods, distributed two orders, two families and four genera, were found associated with three species of polychaetes. The tubes of one species of Onuphidae, one species of Terebellidae and the tube of an unidentified family were inspected in the intertidal zone of Punta Morales, Gulf of Nicoya. The Pinnotheridae crab, *Glassella costaricana* was found associated with the polychaete *Lanicola* sp. The species *Pinnixa longipes* and *Polyonyx quadriungulatus* were found in the tube of the onuphids.

Echinodermata

Nine species of decapods, distributed in two orders, four families and nine genera, were found associated with 12 species of echinoderms. These species were observed living as epibionts in four species of echinoids and five species of asteroids (Table 1). On the sea star *Asteropsis carinifera*, three species were found: *Pachycheles biocellatus*, *Zenopontonia soror* and *Calyptraeotheres* sp., while in the sea star *Pentaceraster cumingi* and the sea urchin *Diadema mexicanum,* several individual symbionts of both sexes and in different stages of development were found in a single host individual. Symbiotic decapods were found both in solitary and in aggregated echinoderms, such as *Astropyga pulvinata* and *D. mexicanum* in reef sites in Bahía Culebra, the sea star *Nidorellia armata* in rocky reefs close to Playa Rajada, Bahía Salinas, the sea star *Pentaceraster cumingi* on soft bottoms near reefs in Golfo Dulce. Aggregates of *P. cumingi* are common in the rhodolith beds of Isla del Coco, however, no decapods were found associated.

The shrimp *Z. soror* was found in the five sea star species collected, which belong to the families Oreasteridae (*N. armata* and *P. cumingi*), Ophidiasteridae (*Pharia pyramidata* and *Phataria unifascialis*) and Asteropsidae (*A. carinifera*). The shrimp *Tuleariocaris holthuisi* was found associated with two species of sea urchins of the family Diadematidae (*A. pulvinata* and *D. mexicanum*) in Bahía Culebra. Finally, a female of *Gnathophylloides mineri* was found associated with *Tripneustes depressus* in Bahía Wafer, Isla del Coco, at a depth of 8 m.

Chordata

Only one species of decapod, *A. pusilla,* was found associated with two species of ascideans. In 1970, *Ascidonia pusilla* was collected from specimens of the recently described ascidian *Rhopalaea birkelandi* from Playas del Coco, Bahía Culebra (Fujino 1972), and was described as *Pontonia spighti*. A specimen of *A. pusilla* was found in association with an unidentified sea squirt (Ascidiacea) from Isla Bolaños, northern Pacific Costa Rica.

Symbiotic decapods in Isla del Coco

In total, 28 associations of 24 species of decapods, in five ordens and 17 families, were found at Isla del Coco. Of the species found, 10 belong to the infraorder Brachyura and 10 to the infraorder Caridea, associated with nine orders distributed among four phyla (Tables 1 and 2).

Discussion

In Costa Rica, few studies have focused on symbiotic decapods, with the majority carried out in the Pacific and only one in the Caribbean (Azofeifa-Solano et al. 2014). Most of these studies were focused on reproductive aspects of decapod guests. Fifty percent of the studies deal with pea crabs (Pinnotheridae), 35% are about the shrimp family Palaemoniidae, and the remaining 15% are derived from studies of the diversity of organisms associated with the coral *P. damicornis* (Cabrera-Peña and Solano-López 1996; Cabrera-Peña et al. 2001; Alvarado and Vargas-Castillo 2012; Azofeifa-Solano et al. 2014; Mena et al. 2014; Salas-Moya et al. 2014). There is a need for more detailed studies of decapod crustaceans associated with macroinvertebrates.

In this study, *T. holthuisi* is reported from Bahía Culebra, where 24 individuals (juvenile, adult, egg bearing females, females without eggs and males) were associated with *D. mexicanum* and *A. pulvinata* collected in 2013 and 2014. This species is distributed from the east coast of Africa (Hipeau-Jacquotte 1965; Bruce 1982), the north east of Australia (Bruce 1990) and in Tahiti (J. Poupin pers. comm. in Marín and Anker 2009). It has also been found in Baja California, Mexico, where two individuals were collected (Wicksten and Hernández 2000) and in Isla Coiba, Panama, where an egg-bearing female was captured (Marín and Anker 2009). Bruce (1982) reported that *T. holthuisi* was found in different species of sea urchins in the Indo-Pacific, for example *Astropyga radiata*, *Echinothrix diadema*, *Stomopneustes variolaris* and *Echinometra mathaei*. However, in the eastern tropical Pacific, *T. holthuisi* has only been found associated with the black sea urchin, *D. mexicanum* (Wicksten and Hernández 2000; Marín and Anker 2009). We have continued surveying and collecting the sea urchins *D. mexicanum* and *A. pulvinata*, but *T. holthuisi* has not been observed again. These results may be due to the fact that the sea urchins in Bahía Culebra displayed the highest population density levels of the eastern tropical Pacific after serious degradation of the reefs and a series of harmful algal proliferations of phytoplankton between 2005 and 2006 (Alvarado et al. 2012, 2016b). But in recent years the populations of sea urchins have declined, possibly due to the continual degradation of the reefs (Alvarado et al. 2018), which might explain the absence of *T. holthuisi.*

Knowledge on *Psedocoutierea elegans* in the region is scarce. It has been reported for the Gulf of California and in the Galapagos Islands (Holthuis 1951). Because the collection method in this case was with the submarine *DeepSee*, which uses an arm and single specimen container that does not permit the separation of collection events, the authors consider that it is possibly associated with the sea urchin *Centrocidaris doederleini*, since it has been found associated with this species on three occasions (2009, 2013, 2016). New collection surveys of *C. doederleini* are recommended to confirm this association at Isla del Coco. It could be assumed that *P. elegans* tends to be more of a generalist in its host selection due to the low availability of hosts in the deep locations where it has been found (greater than 60 m).

The shrimp *Gnathophylloides mineri* is the decapod that is most frequently found associated with the sea urchin *T. depressus*, but we found only one female. It has been reported to represent up to 94% of the decapods associated with *Tripneustes ventricosus* in Isla Borracha, Venezuela (Vera-Caripe et al. 2017). In Australia, the association of *G. mineri* with sea urchins of the genus *Tripneustes* has also been reported (Bruce 1988).

The anomuran (false crab or porcelain crab) *Pachycheles biocellatus* was found to be associated with the seastar *A. carinifera.* However, it is known that this crab associates primarily with corals (García-Madrigal 1999), and there are reports of the species in rocky reefs or in sites near small coral colonies (García-Madrigal 2009). Another species that was found associated with *A. carinifera* is the pea crab from the family Pinnotheridae, *Calyptraeotheres* sp. This genus has already been reported by Campos (1990) to be associated with seastars, but it is more common to find it associated with

mollusks of the genus *Crepidula* (Campos and Hernández-Ávila 2010).

The cnidarians were the group where the most symbiont organisms were found. This result was influenced by the study done by Alvarado and Vargas-Castillo (2012), which focused on symbionts of the coral *P. damicornis*. Additionally, in the case of soft corals, collection of associated organisms has been carried out for many years, although not systematically. Possibly, a greater diversity of associated decapod species may be found by increasing research efforts in a systematic way.

Of the 21 species found, 14 are new reports for Isla del Coco, according to the compilation done by Cortés (2012). The host in which the greatest number of symbiotic species at Isla del Coco was the black coral, *Myriopathes panamensis*. Host information was recorded for some of the decapod specimens of Isla del Coco in the collection of the MZUCR but not for others, as they were not collected in targeted surveys.

A small fraction of Pacific Costa Rica was surveyed. Even so, 14 new records of decapods associated with macroinvertebrates were found in the very well-studied Isla del Coco and four new records were discovered for Costa Rica. These results highlight the need to conduct more detailed studies in which time of year, depth, physico-chemical characteristics of the water, type of environment, the abundance of symbionts and hosts, and location in the hosts. This information will help to determine the real diversity and ecological importance of the associations between marine organisms.

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Authors' contributions
All authors contributed to the study conception and design. Material collection, preparation, data collection and analysis were performed by all authors, especially CSM and RVC. The first draft of the manuscript was written by CSM and checked by all authors. JC prepared the English version and final manuscript that was submitted and the revised darft. JCAS prepared the map. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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