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, Tuleariocaris 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 temporally 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.
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-
| 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   | Islas Pelones, Bahía Culebra, Guanacaste | Abundant  | 6         | 1992       |
|            |                | Pavona gigantea    | Opecarcinus crescentus   | Playa Pochote, Guanacaste               | Abundant  | NI        | 1994       |
|            |                | Pocillopora damicornis | Aa coromuta              | 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 | Amphithrix tuberculatus  | Playa Blanca, Bahía Culebra, Guanacaste  | Rare      | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Cyclaxonthops vitratus   | Playa Blanca, Bahía Culebra, Guanacaste  | Rare      | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Femera chacei            | Playa Blanca, Bahía Culebra, Guanacaste  | Abundant  | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Hapalocarcinus manusiplai | Islas Palmitas, Bahía Huevo, Guanacaste  | Rare      | 6         | 1991       |
|            |                | Pocillopora damicornis | Horpilopsis 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 | Pachychele 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 | Petroelites haigae       | Playa Blanca, Bahía Culebra, Guanacaste  | Abundant  | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Teleophys cristulipes    | Playa Blanca, Bahía Culebra, Guanacaste  | Abundant  | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Tropezia bidentata       | Playa Blanca, Bahía Culebra, Guanacaste  | Abundant  | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Tropezia cornallina      | Playa Blanca, Bahía Culebra, Guanacaste  | Abundant  | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Trizopagus magnificus    | Playa Blanca, Bahía Culebra, Guanacaste  | Rare      | 3         | 2003–2004  |
|            |                | Pocillopora damicornis | Williamsstimpsonia stimpsoni | Playa Blanca, Bahía Culebra, Guanacaste  | Rare      | 3         | 2003–2004  |
|            |                | Pocillopora sp.     | Alpheus lottini          | Bahía Thomas, Cuajiniquil, Guanacaste    | Abundant  | 2         | 2016       |
|            |                | Pocillopora sp.     | Brachycarps bungulaculatus | Bahía Thomas, Cuajiniquil, Guanacaste    | Abundant  | 2         | 2016       |
|            |                | Pocillopora sp.     | Domencia hispida         | Bahía Santa Elena, Guanacaste            | Rare      | NI        | 1994       |
|            |                | Pocillopora sp.     | Hapalocarcinus manusiplai | Isla del Caño, Puntarenas                | Rare      | 8–10      | 1986       |
|            |                | Pocillopora sp.     | Horpilopsis depressa     | Bahía Santa Elena, Guanacaste            | Abundant  | NI        | 1994       |
|            |                | Pocillopora sp.     | Hemus finneganae         | Playa Matapalo, Guanacaste               | Very abundant | 6–14      | 2008       |
|            |                | Pocillopora sp.     | Lepethesites leersus     | Playa Matapalo, Guanacaste               | Rare      | 6–14      | 2008       |
|            |                | Pocillopora sp.     | Stenorhynchus debilis    | Playa Matapalo, Guanacaste               | Very abundant | 6–14      | 2008       |
|            |                | Pocillopora sp.     | Tropezia bidentata       | Bahía Thomas, Cuajiniquil, Guanacaste    | Abundant  | 2         | 2016       |
|            |                | Pocillopora sp.     | Tropezia cymodoce        | Bahía Santa Elena, Guanacaste            | Abundant  | NI        | 1994       |
| Porites    |                | Aphides floridanus  |                           | Parque Nacional Isla del Coco            | Rare      | NI        | 2004       |
| Lobata     |                | Pachygraps 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 Petrosthes antifons | 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 |
|             | Tubastrea coccinea Patrypodella rotundata | Isla San José, Islas Murieléago, Guanacaste | Abundant | 30 | 2010      |
|             | Antipatharia Antipathes sp. | Penicillines murcielagensis | San Pedrito, Islas Murieléago, Guanacaste | Rare | 25 | 1996      |
|             |            | Waldola schmitti | San Pedrito, Islas Murieléago, Guanacaste | Rare | 25 | 1996      |
|             |            | Corallaxius galapagensis | Parrita, Puntarenas | Rare | 1000 | 2009      |
|             |            | Euplikumum xantuarii | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Gnathophyllum panamensis | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Irriapusurus occidentalis | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Lipkenemaus spinulifer | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Pachycheles velanea | Everest, Parque Nacional Isla del Coco | Abundant | 70–80 | 2009      |
|             |            | Penicillines murcielagensis | Peñon Abrazo de la Muerte, Islas Murieléago, Guanacaste | Rare | 30 | 1999      |
|             |            | Plluminus stimpsonii | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Quadrella nitida | Peñon Abrazo de la Muerte, Islas Murieléago, Guanacaste | Rare | 30 | 1999      |
|             |            | Stenorhynchus debilis | Everest, Parque Nacional Isla del Coco | Abundant | 70–80 | 2009      |
|             |            | Synalpheus sp. | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Veleronia sympathec | Everest, Parque Nacional Isla del Coco | Abundant | 70–80 | 2009      |
|             |            | Waldola schmitti | Peñon Abrazo de la Muerte, Islas Murieléago, Guanacaste | Rare | 30 | 1999      |
|             | Octocorallia Eugorgia mutabilis | Megalobrachium tuberculipes | Los Poteros, Puerto Jiménez, Puntarenas | Abundant | Intertidal | 2013      |
|             |            | Neoprontonisides hennyonprahli | Los Poteros, Puerto Jiménez, Puntarenas | Rare | 11 | 2013      |
|             |            | Orthocelia purnilla | Los Poteros, Puerto Jiménez, Puntarenas | Rare | Intertidal | 2013      |
|             |            | Pseudotolmerina kawaiifrons | Los Poteros, Puerto Jiménez, Puntarenas | Rare | Intertidal | 2013      |
|             |            | Typton sp. | Los Poteros, Puerto Jiménez, Puntarenas | Rare | 11 | 2013      |
|             |            | Hippolyte sp. | Punta Islotes, Golfo Dulce, Puntarenas | Rare | NI | 1997      |
|             |            | Penicillines infrasinis | Punta Islotes, Golfo Dulce, Puntarenas | Rare | NI | 1997      |
|             |            | Penicillines sp. | Punta Islotes, Golfo Dulce, Puntarenas | Rare | NI | 1997      |
|             |            | Raytheres clavapedathus | San Pedrito, Islas Murieléago, Guanacaste | Rare | NI | 1994      |
|             |            | Pseudocteniaria elegans | Everest, Parque Nacional Isla del Coco | Abundant | 70–80 | 2009      |
|             |            | Quadrella noida | Everest, Parque Nacional Isla del Coco | Rare | 70–80 | 2009      |
|             |            | Quadrella nitida | Rodolitos, Parque Nacional Isla del Coco | Rare | 50 | 2009      |
|             |            | Megalobrachium | Playa Matapalo, Península de Osa, Puntarenas | Rare | 11 | 2013      |

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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       |
|-------------|------------|---------------------------------------|--------------------|------------------------------------------------|-----------|-----------|------------|
|             |            | tberculipes                           |                    | Playa Matapalo, Península de Osa, Puntarenas    | Rare      | 11        | 2013       |
|             |            | Pacifigorgia irene                    | Neopontonides henryvongrahi | Playa Matapalo, Península de Osa, Puntarenas    | Rare      | 11        | 2013       |
|             |            | Pacifigorgia irene                    | Orthochela purnilla  | Playa Matapalo, Península de Osa, Puntarenas    | Rare      | 11        | 2013       |
|             |            | Pennatulacea                          | Euceramus transversilineatus | Punta Sortija, Bahía Santa Elena, Guanacaste | Rare      | NI        | 2013       |
| Hydrozoa    | Stylaster  | Munida sp.                            |                    | Everest, Parque Nacional Isla del Coco          | Rare      | 86        | 2014       |
| Mollusca    | Gastrozoa  | Crepidula sp.                          | Calyptraeotheres pelopis | Punta Morales, Golfo de Nicoya, Puntarenas      | Rare      | Intertidal | 2014–2016  |
|             | Bivalvia   | Pinctada mazatamica                   | Pontonia marganta  | Isla Tortuga, Golfo de Nicoya, Puntarenas       | Rare      | 2–18      | 1993–2018  |
|             |            | Pinctada mazatamica                   | Pontonia marganta  | Parque Nacional Isla del Coco                    | Rare      | 8         | 2014       |
|             |            | Pinna rugosa                           | Pontonia simplex    | Playa Iguanita, Bahía Culebra, Guanacaste       | Very rare | NI        | 1995       |
|             |            | Sacostrea palmula                      | Austerotheres angelicus | Punta Morales, Golfo de Nicoya, Puntarenas      | Very abundant | Intertidal | 2012–2014  |
|             | Polychaeta | Lanicola sp.                           | Glossella costaricana | Punta Morales, Golfo de Nicoya, Puntarenas      | Abundant  | Intertidal | 1992       |
|             |            | Ni                                     | Tetras scabripes    | Bajo Manuela, Parque Nacional Isla del Coco     | Rare      | 66        | 2009       |
|             |            | Onuphidae                             | Pinxia longipes     | Punta Isletos, Golfo Dulce, Puntarenas          | Rare      | 10        | 2014       |
|             |            | Onuphidae                             | Polyonyx nitidus    | Punta Isletos, 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                      | Absent    | 12        | 2014–2016  |
|             |            | Astropecten regalis                   | Myriococcus kiki    | Manglar de Térraba-Sierpe, Puntarenas          | Rare      | 8         | 2013       |
|             |            | Nidorella armata                      | Zenopontonia soror  | Bahía Salinas, Guanacaste                      | Absent    | 3–8       | 2014–2016  |
|             |            | Nidorella armata                      | Zenopontonia soror  | Bahía Culebra, Guanacaste                      | Absent    | 3         | 2014–2018  |
|             |            | Pentaceraster cumingi                 | Zenopontonia soror  | Isla Tortuga, Golfo de Nicoya, Puntarenas      | Absent    | 6         | 2013       |
|             |            | Pentaceraster cumingi                 | Zenopontonia soror  | Golfo Dulce, Puntarenas                        | Absent    | 2–16      | 2014       |
|             |            | Pentaceraster cumingi                 | Zenopontonia soror  | Bahía Culebra, Guanacaste                      | Abundant  | 25        | 2014–2016  |
|             |            | Pentaceraster cumingi                 | Zenopontonia soror  | Bahía Cuajiniquil, Golfo de Santa Elena        | Abundant  | 2–12      | 2014–2018  |
|             |            | Astropyga pulvinata                   | Tuleariocaris halithusi | Bahía Culebra, Guanacaste                | Abundant* | 6–8       | 2013–2014  |
|             |            | Centroidea                           | Pseudocoutierea elegans | Parque Nacional Isla del Coco               | Abundant  | 85–103    | 2009, 2013,
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.

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**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* | *Diadema mexicanum* | Stenorhynchus debilis | Isla Tortuga, Golfo de Nicoya, Puntarenas | Abundant | 2–15 | 2014–2019 |
| *Diadema mexicanum* | *Tulacoriocaris holthuvi* | Bahía Culebra, Guanacaste | Abundant* | 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 | Asciidea | *Rhopaloeola birkelandi* | Ascidia pusilla | Playas del Coco, Bahía Culebra, Guanacaste | Rare | Shallow | 1970 |
| | | *Ascidaia pusilla* | Isla Bolaños, Bahía Salinas, Guanacaste | Rare | NI | 2012 |

*NI* No information  
*Seasonally abundant, otherwise rare*
| #  | 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 kepidus* (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 veleae* Haig, 1960                     | Porcellanidae |                       | 2746  |
| 10 | *Pachycheles biocellatus* (Lockington, 1878)        | Porcellanidae |                       | 3709–03 |
| 11 | *Petrolithes antifrons* a Haig, 1960                | Porcellanidae |                       | 2552  |
| 12 | *Petrolithes haigae* Chace, 1962                     | Porcellanidae |                       | NC    |
| 13 | *Polyonyx nitidus* Lockington, 1878                 | Porcellanidae |                       | 3413  |
| 14 | *Coralaxius galapagensis* Kensley, 1994             | Axiidea    |                       | 2733, 2738 |
| 15 | *Paracallianidea laevicauda* (Gill, 1859)           | Callianideida |                    | 2552  |
| 16 | *Hapalocarcinus marsupialis* Stimpson, 1859         | Brachyura  | Criptochiroidae       | 1652, 1924 |
| 17 | *Opecarcinus crescentus* (Edmondson, 1925)         | Criptochiroidae |                  | 1646, 1801, 1957 |
| 18 | *Domecia hilda* Eydoux & Souleyet, 1842            | Domeciidae |                       | 1929  |
| 19 | *Pachygrapsus transversus* (Gibbes, 1850)          | Grapsidae  |                       | 2552  |
| 20 | *Stenorhynchus debilis* (Smith, 1871)               | Inachidiidae |                    | 3461  |
| 21 | *Ala cornuta* (Stimpson, 1860)                      | Mithracidae |                       | NC    |
| 22 | *Amphithrax tuberculatus* (Stimpson, 1860)         | Mithracidae |                       | 2364  |
| 23 | *Hemus finneganeae* Garth, 1958                    | Mithracidae |                       | 2607  |
| 24 | *Nemausa sinensis* a (Rathbun, 1892)                | Mithracidae |                       | 2413  |
| 25 | *Teleophys cristipes* Stimpson, 1860               | Mithracidae |                       | NC    |
| 26 | *Uca (Petruca) panamensis* (Stimpson, 1859)         | Ocypodiidae |                       | 2552  |
| 27 | *Eupilumnus xantusi* a (Stimpson, 1860)            | Oziidae    |                       | 2744  |
| 28 | *Panopeus chilensis* H. Milne Edwards & Lucas, 1843| Panopeidae |                       | 3272  |
| 29 | *Plumrus stimpsoni* b Miers, 1886                   | Plumriniidae |                    | 3466  |
| 30 | *Austinotheres angelicus* (Lockington, 1877)        | Pinnotheridae |                   | 1627, 2831, 2832, 2833, 3068, 3069 |
| 31 | *Calyptraeotheres pepeluisi* b E. Campos and Hernández-Avila, 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* Rathburn, 1898                  | Pinnotheridae |                   | 2821  |
| 39 | *Quadrella nitida* Smith, 1869                     | Trapezidae  |                       | 1963, 2309, 2730, 2737 |
| 40 | *Trapezia bidentata* (Forskål, 1775)                | Trapezidae  |                       | 2294, 2852, 3565 |
| 41 | *Trapezia corallina* Gerstaecker, 1856              | Trapezidae  |                       | 2851  |
| 42 | *Trapezia cymodoce* (Herbst, 1801)                 | Trapezidae  |                       | 1929  |
| 43 | *Trapezia digitalis* Latreille, 1828               | Trapezidae  |                       | 1010  |
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.

### 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 | *Lipaesthes luminarius* Rathbun, 1898     | Xanthidae  | 2607            |             |
| 47 | *Lipkemedaes spinulifer* (Rathbun, 1898) | Xanthidae  | 3461            |             |
| 48 | *Platypodia ratundata* (Stimpson, 1860)  | Xanthidae  | 2813            |             |
| 49 | *Williamstimpsonia stimpsoni* (A. Milne-Edwards, 1879) | Xanthidae  | 2853–05         |             |
| 50 | *Alpheus floridanus* a Kingsley, 1878    | Caridea    | 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 | 2744            |             |
| 59 | *Gnathophyllum panamense* a Faxon, 1893  | Palaemonidae | 2234, 3312, 3408, 3434 |             |
| 60 | *Neopontonides hervynorprihli* Ramos, 1995 | Palaemonidae | 3187            |             |
| 61 | *Periclimenes infrasinus* (Rathbun, 1902) | Palaemonidae | 2247, 2308, 2309, 3526 |             |
| 62 | *Periclimenes muciagensis* Vargas, 2000  | Palaemonidae | 3187            |             |
| 63 | *Periclimenes* sp. O.G. Costa, 1844      | Palaemonidae | 1572, 1682, 3186, 3188 |             |
| 64 | *Pontonia margarita* a Smith in Verrill, 1869 | Palaemonidae | 2202            |             |
| 65 | *Pontonia simplex* Holthuis, 1951        | Palaemonidae | 2731, 3521, 3350 |             |
| 66 | *Pseudocoutierea elegans* a Holthuis, 1951 | Palaemonidae | 2233, 2413, 3312, 3408, 3434 |             |
| 67 | *Pseudoveleronia laevifrons* a Holthuis, 1951 | Palaemonidae | 3443, 3444, 3446 |             |
| 68 | *Tuleariocaris holthuisi* b Hipeau-Jacquotte, 1965 | Palaemonidae | 3443            |             |
| 69 | *Typton* sp. O.G. Costa, 1844            | Palaemonidae | 2233            |             |
| 70 | *Veleronia serratifrons* Holthuis, 1951  | Palaemonidae | 2727            |             |
| 71 | *Veleronia sympathes* a (De Ridder & Holthuis, 1979) | Palaemonidae | 2247, 2309     |             |
| 72 | *Waldola schmitti* Holthuis, 1951        | Palaemonidae | 3445, 3449, 3709–02 |             |
| 73 | *Zenopontonia soror* Nobili, 1904        | Palaemonidae | 1770, 1925      |             |
| 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

*Note:* The table continues on the next page.
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 xiiids, 34 brachyurans, 24 carideans, and one gebiodid (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 pepeluissi* 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 *Panopecus 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 *Tubastrea coccinea*. Fifteen species were found associated with Antipatharia. The two species associated with *Antipathes* sp. were also found in *Myriopathes panamensis*. Only one additional deep-water decapod, *Coralaxius galapagensis*, was found on *Lillipathes rita-mariae*. 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 henyvonprahl* 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 margarita*, pairs of the shrimp *Pontonia* 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 *Lanciola* 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: *Pachyteles biocellatus*, *Zenopontonia soror* and *Calyptraeotheres* sp., while in the sea star *Pentaceraster cuningi* 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 cuningi* on soft bottoms near reefs in Golfo Dulce. Aggregates of *P. cuningi* 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 Asteropsidea (*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 spigoti*. A specimen of *A. pusilla* was found in association with an unidentified sea squirt (*Ascidacea*) from Isla Bolaños, northern Pacific Costa Rica.

**Symbiotic decapods in Isla del Coco**

In total, 28 associations of 24 species of decapods, in five orders 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 *Palaemonidae*, 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 *Astrophyga radiata*, *Echinothrix diadema*, *Stomopneustes variolarius* 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 *Pseudocoulliera 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 *Centroechidaris 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 symbiotic 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 draft. 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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