A review of Caribbean Copepoda associated with reef-dwelling cnidarians, echinoderms and sponges

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Abstract

This review of copepod crustaceans associated with reef-dwelling cnidarians, sponges and echinoderms of the Greater Caribbean is based on published records, systematically arranged by the classification of symbiotic copepods and their hosts, sampling sites, coordinates, depth and date of sampling, literature sources, and three recent surveys (Cuba, St. Eustatius in the Eastern Caribbean and Curaçao in the Southern Caribbean). This resulted in totals of 532 records of 115 species of symbiotic copepods (47 genera, 17 families, three orders) hosted by 80 species of invertebrates, representing scleractinians (47%), octocorals (9%), echinoderms (3%), and sponges (1%). Among ten Caribbean ecoregions, the Greater Antilles (with 64 species of symbiotic copepods) as well as the Southern and Eastern Caribbean (with 46 and 17 species of copepods, respectively) are the most studied and best represented, whereas only six species of copepods are known from Bermuda, one from Southwestern Caribbean and none from the Gulf of Mexico. The absence of poecilostomatoid copepods (Anchimolgidae, Rhynchomolgidae and Xarifidae) on Caribbean stony corals as noted by Stock (1988) is confirmed. The results indicate that the diversity and ecology of Caribbean symbiotic copepods are still poorly investigated.
Introduction

Symbiotic copepods are a widespread, numerous and diverse group of crustaceans living in association (parasitism, commensalism, mutualism) with other marine animals (Gotto, 1979, 1993; Humes, 1985a, 1994; Ho, 2001). At least one third of all known copepods are symbionts of marine fish and invertebrates. Symbiotic copepods are the most diverse in the tropics, and only a small number of their potential marine invertebrate hosts has been explored so far (1.14% according to Humes, 1994). A high degree of endemism as well as a remarkable difference in taxonomic composition of copepods living in a poorly studied symbiosis with Caribbean stony corals is noticed in comparison with the Indo-Pacific (Stock, 1988). The paucity of knowledge of symbiotic copepods of the Greater Caribbean region has repeatedly been noted (Stock, 1973, 1975a, 1987, 1988; Humes & Hendler, 1972; Herriott & Immermann, 1979; Grygier, 1980; Ivanenko et al., 2017).

The first study of symbiotic copepods living on cnidarians, echinoderms and sponges of the Greater Caribbean was conducted by Edwards (1891), who discovered Diogenidium nasutum (fig. 1c), living on the sea cucumber Holothuria scabra, in the Bahamas (species authorities in tables 1–2). Taxonomic studies of the Caribbean symbiotic copepods were continued by a number of researchers, who described large numbers of new species, as reviewed by Gotto (1993). A number of copepods representing two families (the ectosymbiotic Asterocheridae and the endoparasitic Corallovexiidae) have been found living on and in stony corals (Hoeksema et al., 2017b). Very few are reports have been published about the Asterocheridae living and usually abundant on sponges (Stock & Kleeton, 1964; Stock, 1967; Boxshall & Huys, 1994; Kim, 2010; Varela et al., 2005b, 2007a, b, 2008; Varela, 2010a, b, 2012). Twelve families of copepods have been reported on diverse Caribbean echinoderms (Edwards, 1891; Emson & Madenov, 1987; Emson et al., 1985; Hendler & Kim, 2010; Humes & Hendler, 1972, 1999; Humes & Ho, 1970, 1971; Humes & Stock, 1973; Humes, 1969a, 1998, 2000; Kim, 2009, 2010; Stock & Gooding, 1986; Stock & Humes, 1995; Stock et al., 1962, 1963a, b; Stock, 1968; Varela et al., 2003, 2005b, 2008; Varela, 2010a, 2011a). Most of these studies on Caribbean invertebrate-associated copepods are from the last century and only 19 of them have been published since 2000 (Humes, 2000; Varela et al., 2003, 2005a, b, 2008; Varela & Lalana, 2007; Kim, 2009, 2010; Hendler & Kim, 2010; Varela, 2010a, b, 2011a, b, 2012; Ivanenko et al., 2017; Shelyakin et al., 2018; Garcia-Hernandez et al., 2019).

Caribbean reef corals are under threat from climate change and local impacts (Carpenter et al., 2008; Hughes et al., 2017) and some symbiotic (including parasitic) copepods potentially may have an impact on the state of corals and other invertebrate hosts (Stock, 1975a; Butter, 1979; Herriott & Immermann, 1979; Burke & Maidens, 2004; Ivanenko et al., 2017; Shelyakin et al., 2018). Despite a long history of marine biodiversity research in the Caribbean, our knowledge of microscopic symbiotic copepods does not satisfy the needs for defining priorities in conservation and the development of management plans (Miloslavich et al., 2010; Zeppilli et al., 2015, 2018). The goal of our review is to analyze all published data on copepods living in symbiosis with the Caribbean reef-dwelling anthozoans, echinoderms and sponges as important structural...
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FIGURE 1  Poecilostomatoid Cyclopoida, dorsal view. a – *Hemicyclops columnaris* (Clausidiidae), b – *Corallovexia similis* (Corallovexiidae), c – *Diogenidium nasutum* (Lichomolgidae), d – *Macrochiron echinicolum* (Macrochironidae), e – *Pseudanthessius deficiens* (Pseudanthessiidae), f – *Doridicola astrophyticus* (Rhynchomolgidae), g – *Eupolymniphilus occidentalis* Kim, 2009 (Sabelliphilidae), h – *Meomicola amplectans*, i – *Presynaptiphilus amphioplus* (Synapticolidae). After Stock et al. (1963b), Humes & Ho (1969), Humes & Hendler (1972), Stock (1973, 1975a), Humes & Stock (1975), Kim (2009).
and functional components of Caribbean coral reefs in order to identify the least-studied ecoregions and groups of hosts as well as to identify directions for further research.

**Characteristics of the Greater Caribbean**

The Greater Caribbean (The Caribbean s.l.) in the present review consists of the Caribbean Sea plus the Gulf of Mexico and Bermuda (Spalding et al., 2007; Hoeksema et al., 2017a). The Caribbean Sea (Caribbean s.s.) is a large semi-enclosed sea of the western Atlantic Ocean with clear and warm water (22–29°C) and low tidal amplitude (0.4 m) (Kinder et al., 1985). The Caribbean is enclosed by the land masses of Central and South America (Brazil) from the west and south. It is separated by island arcs of the Great and Lesser Antilles in the north and east (Bayer, 1961; Spalding et al., 2004; Alvarado, 2011). The Caribbean is a unique biogeographic region with a number of endemic species (Rivera-Monroy et al., 2004; Alvarado, 2011). It is recognized as a global marine biodiversity hot spot and an important biogeographic coral reef province (Spalding et al., 2001; Roberts et al., 2002; Milo-slavich et al., 2010; Alvarado, 2011). The Greater Caribbean includes ten marine ecoregions: Northern Gulf of Mexico, Southern Gulf of Mexico, Floridian, Western Caribbean, Greater Antillean, Southwestern Caribbean, Southern Caribbean, Eastern Caribbean, Bahamian, and Bermudian (Burke & Maidens, 2004; Spalding et al., 2007; Hoeksema et al., 2017a). The Bahamian and Bermudian are adjacent to the temperate northwestern Atlantic. The marine ecoregions of the Southern and Eastern Caribbean are affected by biota from adjacent Brazilian waters (Alvarado, 2011). The Gulf of Mexico has colder and more isolated water, which is relatively poor in species (Felder & Camp, 2009).

**Material**

The data are combined in the originally designed Database on Caribbean copepod crustaceans associated with reef-dwelling corals, echinoderms and sponges. This database includes five main tables: Hosts, Symbionts, Samples, Sites, and Publications linked with each other and two combined tables Literature Records and Sample Records; each record contains data on the taxonomy of the host and its symbiont, the references to unique records in the World of Copepods (Walter & Boxshall, 2019), the number of associates per host, the nature of the association, the name and coordinates of the collection site, the depth and the date of collection, as well as their reference (Korzhavina & Ivanenko, 2019). In addition, data on samples of symbiotic copepods and their hosts collected at St. Eustatius (in 2015, with 104 samples), Curaçao (in 2017, with 77 samples) and Cuba (in 2019, with 56 samples) preserved in 96% ethanol and including underwater photographs have been added to the table Sample Records.

**Results and discussion**

The database includes 532 records from 154 localities and 54 references published since 1891 (Edwards, 1891). There are 115 species of copepods (47 genera, 17 families, 3 orders) found in symbiosis with 80 invertebrate host species representing 58 genera, 39 families, 22 orders and 7 classes of corals, sponges and echinoderms (figs. 1–7, tables 1–7). Only one species of copepods, the poecilostomatoid cyclopoid *Hemicyclops columnaris* (syn *Hemicyclops geminatus*) was found in the area under consideration (Bahamas, Barbados, Curaçao, and Jamaica, associated with a burrowing ghost shrimp, a sponge, an ophiuroid, hermit crabs) and on the Pacific coast of Panama (on a stony
| Copepod | Host species: valid name (and as in original record) | Site abbreviation* | Reference |
|---------|------------------------------------------------------|---------------------|-----------|
| Copepoda | *Clathrina lutea* Azevedo et al., 2017 | Po PR | Garcia-Hernandez et al., 2017 |
| Calanoida | *Bartholomea annulata* (Le Sueur, 1817) | Act Pan | Humes & Smith, 1974 |
| Pseudocyclopidae | ... | ... | ... |
| *Ridgewayia foshageni* Humes & Smith, 1974 | ... | ... | ... |
| Cyclopoida | ... | ... | ... |
| *Hemicyclops columnaris* Humes, 1984 | *Ophiocoma wendtii* Müller & Troschel, 1842 (as *Ophiocoma riisei* Lütken, 1856) | Op Bah | Kim, 2009 |
| *Hemicyclops columnaris* Humes, 1984 | Porifera | Po Bah | Kim, 2009 |
| *Corallovexia* | ... | ... | ... |
| *Corallonoxia baki* Stock, 1975 | *Dendrogyra cylindrus* Ehrenberg, 1834 | Sc Cur | Stock, 1975a |
| *Corallonoxia baki* Stock, 1975 | *Eusmilia fastigiata* (Pallas, 1766) | Sc Cur | Stock, 1975a |
| *Corallonoxia longicauda* Stock, 1975 | *Dendrogyra cylindrus* Ehrenberg, 1834 | Sc Cur | Stock, 1975a; Butter, 1979 |
| *Corallonoxia longicauda* Stock, 1975 | *Meandrina meandrites* (Linnaeus, 1758) | Sc Cur | Stock, 1975a |
| *Corallonoxia sp.* | *Dichocoenia stokesii* Milne Edwards & Haime, 1848 | Sc Cur | Stock, 1975a |
| *Corallovexia brevibrachium* Stock, 1975 | *Pseudodiploria strigosa* (Dana, 1846) (as *Diploria strigosa* (Dana, 1846)) | Sc VI | Herriott & Immermann, 1979 |
| *Corallovexia brevibrachium* Stock, 1975 | *Diploria labyrinthiformis* (Linnaeus, 1758) | Sc Cur | Stock, 1975a |
| *Corallovexia dorsospinosa minor* Stock, 1975 | *Montastraea cavernosa* (Linnaeus, 1767) (as *Montastraea brasiliana* (Verrill, 1901)) | Sc Cur | Stock, 1975a |
| *Corallovexia dorsospinosa* Stock, 1975 | *Montastraea cavernosa* (Linnaeus, 1767) | Sc Cur | Stock, 1975a |
| Copepod                  | Host species: valid name (and as in original record) | Host abbreviation* | Site abbreviation** | Reference                        |
|-------------------------|-------------------------------------------------------|---------------------|---------------------|-----------------------------------|
| Corallovexia kristensis Stock, 1975 | *Colpophyllia natans* (Houttuyn, 1772) (as *Colpophyllia natans* (Müller)) | Sc                   | Cur                   | Stock, 1975a                      |
| Corallovexia longibrachium Stock, 1975 | *Pseudodiploria strigosa* (Dana, 1846) | Sc                   | Cur                   | Stock, 1975a                      |
| Corallovexia longibrachium Stock, 1975 | *Colpophyllia natans* (Houttuyn, 1772) | Sc                   | Cur                   | Stock, 1975a                      |
| Corallovexia longibrachium Stock, 1975 | *Manicina areolata* (Linnaeus, 1758) (as *Manicina areolata* f. mayori Wells, 1936) | Sc                   | Cur                   | Stock, 1975a                      |
| Corallovexia mediobrachium Stock, 1975 | *Colpophyllia natans* (Houttuyn, 1772) | Sc                   | VI                    | Herriott & Immermann, 1979        |
| Corallovexia mediobrachium Stock, 1975 | *Manicina areolata* (Linnaeus, 1758) | Sc                   | Cur                   | Stock, 1975a                      |
| Corallovexia mediobrachium Stock, 1975 | *Pseudodiploria clivosa* (Ellis & Solander, 1786) (as *Diploria clivosa* (Ellis & Solander, 1786)) | Sc                   | Cur, VI               | Stock, 1975a; Herriott & Immermann, 1979 |
| Corallovexia mediobrachium Stock, 1975 | *Pseudodiploria strigosa* (Dana, 1846) (as *Diploria strigosa* (Dana, 1846)) | Sc                   | Cur, VI               | Stock, 1975a; Herriott & Immermann, 1979 |
| Corallovexia mixtibrachium Stock, 1975 | *Colpophyllia natans* (Houttuyn, 1772) | Sc                   | Cur, VI               | Stock, 1975a; Herriott & Immermann, 1979 |
| Corallovexia similis Stock, 1975 | *Acropora palmata* (Lamarck, 1816) | Sc                   | Cur, VI               | Stock, 1975a; Herriott & Immermann, 1979 |
| Corallovexia similis Stock, 1975 | *Pseudodiploria strigosa* (Dana, 1846) | Sc                   | VI                    | Herriott & Immermann, 1979        |
| Corallovexia sp. | *Acropora palmata* (Lamarck, 1816) | Sc                   | VI                    | Herriott & Immermann, 1979        |
| Corallovexia sp. | *Meandrina meandrites* (Linnaeus, 1758) | Sc                   | VI                    | Herriott & Immermann, 1979        |
| Species                                | Host                          | Author       | Year       |
|----------------------------------------|-------------------------------|--------------|------------|
| Coralloexia sp.                         | *Montastraea cavernosa* (Linnaeus, 1767) | Sc           | VI         | Herriott & Immermann, 1979 |
| Coralloexia sp.                         | *Mycetophyllia lamarckiana* Milne Edwards & Haime, 1849 | Sc           | VI         | Herriott & Immermann, 1979 |
| Coralloexia sp.                         | *Orbicella annularis* (Ellis & Solander, 1786) (as *Montastraea annularis* (Ellis & Solander, 1786)) | Sc           | Cur        | Stock, 1975a               |
| Coralloexia sp.                         | *Pseudodiploria strigosa* (Dana, 1846) | Sc           | VI         | Herriott & Immermann, 1979 |
| Coralloexia ventrospinosa Stock, 1975  | *Montastraea cavernosa* (Linnaeus, 1767) | Sc           | Cur        | Stock, 1975a               |
| Lamippidae                              |                               |              |            |
| *Enalcyonium* sp.                       |                               |              |            |
| *Enalcyonium euniceae* Stock, 1973      | *Eunicea mammosa* Lamouroux, 1816 | Oc           | PR         | Stock, 1973               |
| *Enalcyonium nudum* Stock, 1973         | *Plexaura homomalla* (Esper, 1794) (as *Plexaura homomalla f. homomalla* Esper, 1794) | Oc           | PR         | Stock, 1973               |
| *Enalcyonium ramosum* Stock, 1973       | *Plexaura homomalla* (Esper, 1794) | Oc           | PR         | Stock, 1973               |
| *Enalcyonium varicauda* Stock, 1973     | *Briareum asbestinum* (Pallas, 1766) | Oc           | PR         | Stock, 1973               |
| *Lamippina aequalis* Stock, 1973        | *Antillogorgia* Bayer, 1951 (as *Pseudopterogorgia* Kükenthal, 1919) | Oc           | Cur        | Stock, 1973               |
| *Lamippina aequalis* Stock, 1973        | *Antillogorgia acerosa* (Pallas, 1766) (as *Pseudopterogorgia acerosa* (Pallas, 1766)) | Oc           | Cur        | Stock, 1973               |
| *Linaresia bouligandi* Stock, 1979      | *Placogorgia* sp.              | Oc           | Flo        | Stock, 1979               |
| *Magnippe caputmedusae* Stock, 1978     | *Thesea* sp.                   | Oc           | Flo        | Stock, 1978               |
| *Sphaerippe caligicola* Grygier, 1980   |                               | Oc           | Bah        | Grygier, 1980             |
| *Sphaerippe* sp.                        |                               | Oc           | SE         | Ivanenko et al., 2017     |
| Lichomolgidae                            |                               |              |            |
| *Diogenella deichmannae* Humes & Ho, 1970 | *Holothuria (Thymiosycia) arenicola* Semper, 1868 | Hol         | Bar        | Humes & Ho, 1970          |
| *Diogenella impar* Humes & Ho, 1970     | *Holothuria (Thymiosycia) arenicola* Semper, 1868 (as *Brandothuria arenicola* (Semper)) | Hol         | Bar        | Humes & Ho, 1970          |
**TABLE 1** Copepod crustaceans recorded as associated with Caribbean reef-dwelling anthozoans, echinoderms and sponges (cont.)

| Copepod               | Host species: valid name (and as in original record) | Host abbreviation* | Site abbreviation** | Reference                     |
|-----------------------|------------------------------------------------------|---------------------|---------------------|-------------------------------|
| Diogenella seticauda  Stock, 1968 | Holothuria (Thymiosycia) arenicola Semper, 1868 | Hol | MI | Humes & Ho, 1970 |
| Diogenella seticauda  Stock, 1968 | Holothuria (Thymiosycia) impatiens (Forsskål, 1775) (as Holothuria impatiens (Forsskål, 1775)) | Hol | PR | Stock, 1968 |
| Diogenella seticauda  Stock, 1968 | Holothuria (Semperothuria) surinamensis Ludwig, 1875 (as Halodeima surinamensis (Ludwig)) | Hol | MI, PR | Stock, 1968; Humes & Ho, 1970 |
| Diogenella spinicauda Stock, 1968 | Holothuria (Halodeima) mexicana Ludwig, 1875 (as Ludwigothuria mexicana (Ludwig)) | Hol | Bah, Cur, Jam, MI, PR | Stock, 1968; Humes & Ho, 1970 |
| Diogenidium deformae Stock, 1968 | Holothuria (Selenkothuria) glaberrima Selenka, 1867 | Hol | PR | Stock, 1968 |
| Diogenidium deformae Stock, 1968 | Holothuria (Halodeima) mexicana Ludwig, 1875 | Hol | Bah, PR | Hendler & Kim, 2010 |
| Diogenidium deformae Stock, 1968 | Holothuria (Thymiosycia) arenicola Semper, 1868 | Hol | Bar | Hendler & Kim, 2010 |
| Diogenidium nasutum Edwards, 1891 | Actinopyga agassizii (Selenka, 1867) (as Muelleria agassizii Selenka, 1867) | Hol | Bah | Hendler & Kim, 2010 |
| Diogenidium nasutum Edwards, 1891 | Holothuria (Halodeima) grisea Selenka, 1867 | Hol | Jam | Hendler & Kim, 2010 |
| Diogenidium nasutum Edwards, 1891 | Holothuria (Halodeima) mexicana Ludwig, 1875 | Hol | Cur, Jam, MI, PR | Stock, 1968; Hendler & Kim, 2010 |
| Diogenidium nasutum Edwards, 1891 | Holothuria (Metriatyla) scabra Jaeger, 1833 | Hol | Bah | Edwards, 1891 |
| Diogenidium spinulosum Stock, 1968 | Isostichopus badionotus (Selenka, 1867) | Hol | Jam, PR | Stock, 1968; Hendler & Kim, 2010 |
| Diogenidium tectum Humes & Ho, 1971 | Actinopyga agassizii (Selenka, 1867) | Hol | Bah, Jam | Hendler & Kim, 2010 |
| **Macrochironidae** | | | | |
| **Macrochiron echinicolium** Humes & Stock, 1973 | Echinometra viridis A. Agassiz, 1863 | Ec | Cur | Humes & Stock, 1973 |
| Common Name | Scientific Name | Authors | Family | Location(s) | Notes |
|-------------|-----------------|---------|--------|-------------|-------|
| **Macrochiron echinicolum** Humes & Stock, 1973 | *Lytechinus variegatus* (Lamarck, 1816) | | Ec | | Bah, Bar, Bon, Cur, Jam, MI, PR |
| **Macrochiron sargassi** Sars, 1916 | *Renilla reniformis* (Pallas, 1766) | | Oc | | Humes & Stock, 1973 |
| **Pseudanthessiidae** | | | | | |
| *Pseudanthessius acutus* Kim, 2009 | | | Po | | Jam, Kim, 2009 |
| *Pseudanthessius deficiens* Stock, Humes & Gooding, 1963 | *Holothuria (Halodeima) mexicana* Ludwig, 1875 | Humes & Stock, 1973 | Hol | Cur | Stock et al., 1963b |
| *Pseudanthessius deficiens* Stock, Humes & Gooding, 1963 | *Ophiderma brevispina* (Say, 1825) (as *Ophiderma brevispinum* (Say, 1825)) | Stock et al., 1963b | Op | Bel | Humes & Hendler, 1999 |
| *Pseudanthessius deficiens* Stock, Humes & Gooding, 1963 | *Ophiderma cinerea* Müller & Troschel, 1842 (as *Ophiderma cinereum* Müller & Troschel, 1842) | Stock et al., 1963b | Op | Bel, Cur, MI, SM | Humes & Hendler, 1999 |
| *Pseudanthessius exilicornis* Stock & Humes, 1995 | *Meoma ventricosa* (Lamarck, 1816) | | Ec | | Cur, Stock & Humes, 1995 |
| *Pseudanthessius pectinifer* Stock, Humes & Gooding, 1964 | *Clypeaster rosaceus* (Linnaeus, 1758) | | Ec | | Bah, Jam, MI |
| **Rhynchomolgidae** | | | | | |
| *Acanthomolgus aequiseta* Stock, 1975 | *Muricea laxa* Verrill, 1864 | | Oc | | Cur, Stock, 1975c |
| *Acanthomolgus affinis* Stock, 1975 | *Eunicea flexuosa* (Lamouroux, 1821) | | Oc | | Cur, Stock, 1975c |
| *Acanthomolgus affinis* Stock, 1975 | *Plexaura sp.* | | Oc | | Cur, Varela, 2011a |
| *Acanthomolgus affinis* Stock, 1975 | *Plexaura homomalla* (Esper, 1794) | | Oc | | Cur, Stock, 1975c |
| *Acanthomolgus bayeri* Humes, 1973 | *Gorgonia ventalina* Linnaeus, 1758 | | Oc | | Ber, Humes, 1973 |
| *Acanthomolgus bayeri* Humes, 1973 | *Pseudoplexaura sp.* | | Oc | | Cub, Varela et al., 2003 |
| *Acanthomolgus bayeri* Humes, 1973 | *Pseudoplexaura porosa* (Houttuyn, 1772) | | Oc | | Ber, Humes, 1973 |
| *Acanthomolgus bilobipes* Humes & Stock, 1973 | *Antillogorgia acerosa* (Pallas, 1766) | | Oc | | Bar, Cur, Jam, Humes & Stock; 1973; Stock, 1975c |
| *Acanthomolgus bilobipes* Humes & Stock, 1973 | *Antillogorgia elastica* Bieschowsky | | Oc | | PR, Humes & Stock, 1973 |
| Copepod                     | Host species: valid name (and as in original record)                                                                 | Host abbreviation* | Site abbreviation** | Reference                  |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------|--------------------|---------------------|---------------------------|
| *Acanthomolgus dionyx* Stock, 1975 | Antílógorgia americana (Gmelin, 1791) (as Pseudopterogorgia americana (Gmelin, 1791))                           | Oc                 | Cur                 | Stock, 1975c              |
| *Acanthomolgus gorgoniae* Humes, 1973 | Gorgonia ventalina Linnaeus, 1758                                                                                   | Oc                 | Ber, Cur, SE        | Humes, 1973; Stock, 1975c |
| *Acanthomolgus intermedius* Stock, 1975 | Eunicea laciniata Duchassaing & Michelotti, 1860                                                                       | Oc                 | Cur                 | Stock, 1975c              |
| *Acanthomolgus intermedius* Stock, 1975 | Muricea sp.                                                                                                          | Oc                 | Cub                 | Varela et al., 2003       |
| *Acanthomolgus longidactylus* Stock, 1975 | Eunicea flexosa (Lamouroux, 1821)                                                                                   | Oc                 | Cur                 | Stock, 1975c              |
| *Acanthomolgus longifurca* Stock, 1975 | Eunicea tourneforti Milne Edwards & Haime, 1857                                                                    | Oc                 | Cur                 | Stock, 1975c              |
| *Acanthomolgus monononyx* Stock, 1975 | Eunicea clavigera Bayer, 1961                                                                                       | Oc                 | Cur                 | Stock, 1975c              |
| *Acanthomolgus muriceanus* Humes, 1973 | Muricea atlantica (Kükenthal, 1911)                                                                                    | Oc                 | Ber                 | Humes, 1973; Stock, 1975c |
| *Acanthomolgus seticornis* Stock, 1975 | Plexaurella dichotoma (Esper, 1791)                                                                                    | Oc                 | SM                  | Stock, 1975c              |
| *Acanthomolgus triangulipes* Stock, 1975 | Gorgonia ventalina Linnaeus, 1758                                                                                   | Oc                 | Cur, SE, SM         | Stock, 1975c              |
| *Acanthomolgus triangulipes* Stock, 1975 | Gorgonia mariae Bayer, 1961                                                                                         | Oc                 | Cub                 | Varela et al., 2003       |
| *Acanthomolgus verrucipes* Humes, 1973 | Eunicea calyculata (Ellis & Solander, 1786)                                                                          | Oc                 | Ber                 | Humes, 1973               |
| *Aspidomolgus stoichactinus* Humes, 1969 | Corynactis denticulosa (Le Sueur, 1817) (as Homostichanthes denticulosus (Le Sueur, 1817))                       | Act                | Barad, PR, SM       | Stock, 1975b              |
| *Aspidomolgus stoichactinus* Humes, 1969 | Stichodactyla helianthus (Ellis, 1768) (as Stoichactis anemone (Ellis), Stoichactis helianthus (Ellis, 1768))     | Act                | Bah, Bar, Bon,      | Humes, 1969a; Stock, 1975b; Ortiz et al., 1998 |
|                              | Stichopathes sp.                                                                                                     | Anti               | Cub, Cur, Bon,      | Humes & Goenaga, 1978     |
| *Calonastes imparipes* Humes & Goenaga, 1978 | Stichopathes lutkeni Brook, 1889                                                                                    | Anti               | PR                  | Humes & Goenaga, 1978     |
| *Calonastes imparipes* Humes & Goenaga, 1978 | Stichopathes lutkeni Brook, 1889                                                                                    | Anti               | PR                  | Humes & Goenaga, 1978     |
| *Critomolgus* Humes & Stock, 1983 | Astrephyton muricatum (Lamarck, 1816)                                                                                 | Op                 | Cub                 | Varela et al., 2008       |
| Genus and Species                                      | Associated with                          | Location(s)       | Author(s) and Year(s) |
|-------------------------------------------------------|------------------------------------------|-------------------|-----------------------|
| *Critomolgus astrophyticus* (Humes & Stock, 1973)     | *Astrophyton muricatum* (Lamarck, 1816)  | Op                | Bar, Jam, MI, PR      | Humes & Stock, 1973 |
| (as *Doridicola astrophyticus* Humes & Stock, 1973)   |                                          |                   |                       |                      |
| *Critomolgus titillans* (Humes, 1982) (as *Doridicola*  | *Condylactis gigantea* (Weinland, 1860)  | Act               | PR                    | Humes, 1982          |
| *titillans* Humes, 1982)                               |                                          |                   |                       |                      |
| *Paramolgus antillianus* Stock, 1975                  | *Ricordea florida* Duchassaing & Michelotti, 1860 | Cor               | PR                    | Stock, 1975c         |
| *Sabelliphilidae*                                      |                                          |                   |                       |                      |
| *Eupolymniphilus occidentalis* Kim, 2009              |                                          | Po                | Jam                   | Kim, 2009            |
| *Synapticolidae*                                       |                                          |                   |                       |                      |
| *Caribulus* sp                                        | *Actinopyga agassizii* (Selenka, 1867)   | Hol               | Bah, Cur, Jam         | Humes, 1969b         |
| *Caribulus* sp                                        | *Isostichopus badionotus* (Selenka, 1867) | Hol               | Bar, Jam              | Humes, 1969b         |
| *Caribulus sculptus* (Humes, 1969) (as *Actinopyga*    | *Isostichopus badionotus* (Selenka, 1867) | Hol               | Bah, Bon, Cur, Jam    | Humes, 1969b         |
| *agassizii* (Humes, 1867)                             |                                           |                   |                       |                      |
| *Scambicornus sculptus* Humes, 1969)                  |                                          |                   |                       |                      |
| *Caribulus sculptus* (Humes, 1969)                    | *Holothuria mexicana* Ludwig, 1875       | Hol               | Bah, Bar, Jam, MI, PR | Humes, 1969b         |
| *Caribulus sculptus* (Humes, 1969)                    |                                           |                   |                       |                      |
| *Meomicola amplectans* Stock, Humes & Gooding, 1963    | *Meoma ventricosa* (Lamarck, 1816)       | Ec                | Cur, Jam              | Stock et al., 1963b  |
| *Meomicola amplectans* Stock, Humes & Gooding, 1963    |                                           |                   |                       |                      |
| *Synaptiphilidae*                                      |                                          |                   |                       |                      |
| *Presynaptiphilus amphipli* Humes & Hendler, 1972      | *Amphiplus sp.*                          | Op                | FK                    | Humes & Hendler, 1972 |
| *Thaumatopsyllidae*                                    |                                          |                   |                       |                      |
| *Caribeopsyllus chawayi* Suárez-Morales in             | *Ophiothrix angulata* (Say, 1825)        | Op                | Bel                   | Hendler & Kim, 2010  |
| Suárez-Morales & Castellanos, 1998                    |                                           |                   |                       |                      |
| *Caribeopsyllus chawayi* Suárez-Morales in             | *Ophiothrix oerstedii* Lütken, 1856      | Op                | Bel                   | Hendler & Kim, 2010  |
| Suárez-Morales & Castellanos, 1998                    |                                           |                   |                       |                      |
| *Caribeopsyllus* sp.A                                  |                                          | Op                | SE                    | Ivanenko, unpublished |
| *Ophiuroida*                                           |                                          |                   |                       |                      |
### TABLE 1  
Copepod crustaceans recorded as associated with Caribbean reef-dwelling anthozoans, echinoderms and sponges (cont.)

| Copepod                        | Host species: valid name (and as in original record) | Host abbreviation* | Site abbreviation** | Reference                                      |
|--------------------------------|--------------------------------------------------------|---------------------|---------------------|------------------------------------------------|
| Caribeopsyllus sp.A            | *Ophiothrix angulata* (Say, 1825)                      | Op                  | Bel                 | Hendler & Kim, 2010                             |
| **Siphonostomatoida**          |                                                        |                     |                     |                                                |
| **Asterocheridae**             |                                                        |                     |                     |                                                |
| Asterocheres sp.               | *Callyspongia vaginalis* (Lamarck, 1814)               | Po                  | Cub                 | Varela et al., 2005b                           |
| Asterocheres antillensis Varela, 2010 | *Callyspongia sp.*                                        | Po                  | Cub                 | Varela, 2010                                   |
| Asterocheres bahamensis Kim, 2010 | *Porifera*                                                | Po                  | Bah                 | Kim, 2010                                      |
| Asterocheres crinoidicola Varela, 2000 | Crinoidea                                                 | Cr                  | Jam                 | Kim, 2010                                      |
| Asterocheres crinoidicola Varela, 2000 | *Davidaster rubiginosus* (Pourtalès, 1869)               | Cr                  | Bel, Cub            | Humes, 2000; Varela, 2010                       |
| Asterocheres crinoidicola Varela, 2000 | *Nemaster grandis* AH Clark, 1909                      | Cr                  | Bel                 | Humes, 2000                                   |
| Asterocheres cubensis Varela, 2010 | *Agelas dilata* Duchassaing & Michelotti, 1864           | Po                  | Cub                 | Varela, 2010                                   |
| Asterocheres espinosai Varela, Ortiz & Lalana, 2007 | *Callyspongia vaginalis* (Lamarck, 1814)               | Po                  | Cub                 | Varela et al., 2007a                           |
| Asterocheres fernandezmilerai Varela, 2010 | *Agelas wiedenmayeri* Alcolado, 1984                    | Po                  | Cub                 | Varela, 2010                                   |
| Asterocheres garrioi Varela, Ortiz & Lalana, 2007 | *Ptilocaulis walpersii* (Duchassaing & Michelotti, 1864) | Po                  | Cub                 | Varela et al., 2007                           |
| Asterocheres kimi Varela, 2012  | *Niphates digitalis* (Lamarck, 1814)                    | Po                  | Cub                 | Varela, 2012                                   |
| Asterocheres lalanai Varela, 2013 | *Niphates digitalis* (Lamarck, 1814)                    | Po                  | Cub                 | Varela, 2012                                   |
| Asterocheres maxillatus Stock, 1987 | *Manicina areolata* (Linnaeus, 1758)                   | Sc                  | Cur                 | Stock, 1987                                    |
| Asterocheres maxillatus Stock, 1987 | *Orcicella annularis* (Ellis & Solander, 1786)          | Sc                  | Cur                 | Stock, 1987, 1989                              |
| Asterocheres oricurvis Kim, 2010 | *Porifera*                                               | Po                  | Jam                 | Kim, 2010                                      |
| Asterocheres peniculatus Kim, 2010 | *Porifera*                                               | Po                  | Bah                 | Kim, 2010                                      |
| Asterocheres plumosus Kim, 2010  | *Porifera*                                               | Po                  | Bah                 | Kim, 2010                                      |
| Asterocheres reginae Boxshall & Huys, 1994 | *Agelas sp.*                                            | Po                  | Cub                 | Varela et al., 2008                            |
| Asterocheres reginae Boxshall & Huys, 1994 | *Agelas clathrodes* (Schmidt, 1870)               | Po                  | Bel                 | Boxshall & Huys, 1994                           |
| COPEPODS ASSOCIATED WITH CARIBBEAN INVERTEBRATES |
|--------------------------------------------------|
| *Asterocheres simulans* (T. Scott, 1898) (as *Asco-
myzon simulans* T. Scott, 1898) | *Lythechinus variegatus* (Lamarck, 1816) | Ec | Cur | Stock & Humes, 1995 |
| *Asterocheres trisetatus* Kim, 2010 | Porifera | Po | Bah | Kim, 2010 |
| *Asterocheres unioviger* Kim, 2010 | *Eucidaris tribuloides* (Lamarck, 1816) | Ec | Bah, PR | Kim, 2010 |
| *Asterocheres unioviger* Kim, 2010 | Echinidea | Ec | Jam | Kim, 2010 |
| *Asteropontella foliata* Stock, 1989 | *Oribicella annularis* (Ellis & Solander, 1786) | Sc | Cur | Stock, 1989 |
| *Asteropontius capillatus* Kim, 2010 | *Meandrina* sp. | Sc | Bar | Kim, 2010 |
| *Asteropontius iuxtus* Stock, 1989 | *Meandrina meandrites* (Linnaeus, 1758) | Sc | Cur | Stock, 1989 |
| *Asteropontius longipalpus* Stock, 1975 | *Ricordea florida* Duchassaing & Michelotti, 1860 | Cor | PR | Stock, 1975b |
| *Asteropontius mycetophylliae* Varela, Ortiz & Lalana, 2005 | *Mycetophyllia lamarckiana* Milne Edwards & Haime, 1849 | Sc | Cub | Varela et al., 2005 |
| *Asteropontius parvipalpus* Stock, 1975 | *Condylactis gigantea* (Weinland, 1860) | Act | Bah, Cur, Jam, MI, PR | Stock, 1975b; Humes, 1982 |
| *Asteropontius proximus* Stock, 1987 | *Colphophylla natans* (Müller)) | Sc | Cur | Stock, 1987 |
| *Asteropontius ungelatus* Stock, 1975 | *Phymanthus crucifer* (Le Sueur, 1817) | Act | MI | Stock, 1975b |
| *Asteropontius ungelatus* Stock, 1975 | *Stichodactyla helianthus* (Ellis, 1768) | Act | Jam, PR | Stock, 1975b; Kim, 2010 |
| *Asteropontopsis faviae* Stock, 1987 | *Favia fragum* (Esper, 1795) | Sc | Cur | Stock, 1987 |
| *Chelacheres longipalpus* Stock & Humes, 1995 | *Echinometra lucunter* (Linnaeus, 1758) | Ec | Bah, Cub, Cur, Jam, PR, SM | Stock & Humes, 1995; Varela, 2011 |
| *Chelacheres longipalpus* Stock & Humes, 1995 | *Tripneustes ventricosus* (Lamarck, 1816) | Ec | Cur | Stock & Humes, 1995 |
| *Chelacheres optans* Stock & Humes, 1995 | *Echinometra lucunter* (Linnaeus, 1758) | Ec | PR | Stock & Humes, 1995 |
| *Collocheres lunulifer* Humes, 1998 | *Ophiothrix (Ophiothrix) angulata* (Say, 1825) | Op | Bar | Humes, 1998 |
| *Collocheres lunulifer* Humes, 1998 | *Ophiothrix (Acanthophiothrix) suensonii* Lütken, 1856 | Op | Bar | Humes, 1998 |
| *Hermacheres diploriae* Stock, 1987 | *Pseudodiploria clivosa* (Ellis & Solander, 1786) | Sc | Cur | Stock, 1987 |
| *Hermacheres montastreae* Stock, 1987 | *Montastrea cavernosa* (Linnaeus, 1767) | Sc | Cur | Stock, 1987 |
| Copepod                      | Host species: valid name (and as in original record) | Host abbreviation* | Site abbreviation** | Reference                          |
|-----------------------------|-----------------------------------------------------|--------------------|---------------------|------------------------------------|
| *Hetairosynella aculeata* Kim, 2010 | *Porifera*                                          | Po                 | Bah                 | Kim, 2010                          |
| *Hetairosynella angulata* Kim, 2010 | *Porifera*                                          | Po                 | Jam                 | Kim, 2010                          |
| *Hetairosynella bifurcata* Kim, 2010 | *Porifera*                                          | Po                 | Jam                 | Kim, 2010                          |
| *Kimcheres fastigatus* (Kim, 2010) (as *Asterocheres fastigatus* Kim, 2010) | *Porifera*                                          | Po                 | Bar                 | Kim, 2010                          |
| *Meandromyzon coronatum* Stock, 1989 | *Meandrina meandrites* (Linnaeus, 1758)             | Sc                 | Cur                 | Stock, 1989                        |
| *Neoasterocheres humesi* (Varela, 2012) | *Callyspongia vaginalis* (Lamarck, 1814)            | Po                 | Cub                 | Varela, 2012                       |
| *Onychocheres alatus* Stock & Gooding, 1986 | *Diodia antillarum* Philippi, 1845                 | Ec                 | Cub, Cur            | Stock & Gooding, 1986; Varela et al., 2005b |
| *Orecturus antillensis* Varela, 2011 | *Eunicea mammosa* Lamouroux, 1816                   | Oc                 | Cub                 | Varela, 2011b                      |
| *Orecturus ortizi* Varela & Lalana, 2007 | *Briareum asbestinum* (Pallas, 1766)               | Oc                 | Cub                 | Varela & Lalana, 2007              |
| *Ophiurocheres bellulus* Humes, 1998 | *Ophiomyxa flaccida* (Say, 1825)                   | Op                 | MI                  | Humes, 1998                        |
| *Peltomyzon rostratum* Stock, 1975 | *Montastrea cavernosa* (Linnaeus, 1767)            | Sc                 | Cur                 | Stock, 1975d                       |
| *Scottocheres elongatus* (Scott T. & Scott A., 1894) | *Iotrochota birotulata* (Higgin, 1877)             | Po                 | Cub                 | Varela et al., 2008                |
| *Setacheres parabolus* (Johnson, 1998) | *Callyspongia vaginalis* (Lamarck, 1814)            | Po                 | Cub                 | Varela, 2012                       |
| *Stenomyzon edentatum* Kim, 2010 | *Porifera*                                          | Po                 | PR                  | Kim, 2010                          |

**Cancerillidae**

| Copepod                      | Host species: valid name (and as in original record) | Host abbreviation* | Site abbreviation** | Reference                          |
|-----------------------------|-----------------------------------------------------|--------------------|---------------------|------------------------------------|
| *Ophiopsyllus latus* Humes & Hendler, 1999 | *Ophiocomella ophiactoides* (Clark, 1900)          | Op                 | Bel                 | Humes & Hendler, 1999              |
| *Ophiopsyllus latus* Humes & Hendler, 1999 | *Ophiocomella pumila* Lütken, 1856                 | Op                 | Bel, FK             | Humes & Hendler, 1999              |
| *Ophiopsyllus latus* Humes & Hendler, 1999 | *Ophiocomella ophiactoides* (Clark, 1900)          | Op                 | Bel                 | Humes & Hendler, 1999              |
**Copepods Associated with Caribbean Invertebrates**

*Ophiopsyllus reductus* Stock, Humes & Gooding, 1963

*Ophiocoma echinata* (Lamarck, 1816)

Op Bel, Cur Stock et al., 1963a; Humes & Hendler, 1999

*Ophiopsyllus reductus* Stock, Humes & Gooding, 1963

*Ophiocomella ophiactoides* (Clark, 1900)

Op Bel, Ber, Jam Emson et al., 1985; Emson & Mladenov, 1987

*Paraphiopsyllus ligatus* Humes & Hendler, 1972

*Amphioplus sp.*

Op FK Humes & Hendler, 1972

**Entomolepididae**

*Parmulodes verrucosa* Wilson C.B., 1944

*Chondrilla nucula* Schmidt, 1862

Po PR Stock, 1992b

*Parmulella emarginata* Stock, 1992

*Chondrilla nucula* Schmidt, 1862

Po Cur Stock, 1992b

*Parmulodes verrucosa* Wilson C.B., 1944 (as *Parmulodes verrucosus* Wilson C.B., 1944)

*Chondrilla nucula* Schmidt, 1862

Po Aru, Cub, Cur, PR Stock, 1992b; Variela et al., 2008

**Micropontiidae**

*Microponius glaber* Stock, Humes & Gooding, 1963

*Meoma ventricosa* (Lamarck, 1816)

Ec Jam Stock et al., 1963a

**Nanaspidae**

*Nanaspis exigua* Stock, Humes & Gooding, 1962

*Isostichopus badionotus* (Selenka, 1867)

Hol Jam Stock et al., 1962

*Nanaspis media* Stock, Humes & Gooding, 1962

*Isostichopus badionotus* (Selenka, 1867)

Hol MI, PR Stock et al., 1962

*Nanaspis pollens* Stock, Humes & Gooding, 1962

*Holothuria (Thymiosycia) arenicola* Semper, 1868

Hol Jam Stock et al., 1962

*Nanaspis pollens* Stock, Humes & Gooding, 1962

*Holothuria (Semperothuria) surinamensis* Ludwig, 1875

Hol MI Stock et al., 1962

*Nanaspis pollens* Stock, Humes & Gooding, 1962

*Holothuria (Thymiosycia) arenicola* Semper, 1868 (as *Brandtothuria arenicola*) and *Holothuria (Semperothuria) surinamensis* Ludwig, 1875 (as *Semperothuria surinamensis*) (mixed)

Hol PR Stock et al., 1962

*Nanaspis pollens* Stock, Humes & Gooding, 1962

*Isostichopus badionotus* (Selenka, 1867)

Hol Bah, Jam Stock et al., 1962

*Nanaspis pollens* Stock, Humes & Gooding, 1962

*Meoma ventricosa* (Lamarck, 1816)

Ec Jam Stock et al., 1962
TABLE 1  Copepod crustaceans recorded as associated with Caribbean reef-dwelling anthozoans, echinoderms and sponges (cont.)

| Copepod           | Host species: valid name (and as in original record) | Host abbreviation | Site abbreviation | Reference          |
|-------------------|------------------------------------------------------|-------------------|-------------------|--------------------|
| *Nanaspis truncata* Stock, Humes & Gooding, 1962 | *Holothuria (Platyperona) parvula* (Selenka, 1867) | Hol               | MI, PR            | Stock et al., 1962 |
| *Nanaspis truncata* Stock, Humes & Gooding, 1962 | *Holothuria (Thymiosycia) arenicola* Semper, 1868 | Hol               | MI                | Stock et al., 1962 |

* Host Abbreviations: Act – Actiniaria, Anti – Antipatharia, Cor – Corallimorpharia, Cr – Crinoidea, Ec – Echinoidea, Hol – Holothuroidea, Oc – Octocorallia, Op – Ophiuroidea, Po – Porifera, Sc – Scleractinia.

** Site Abbreviations: Aru – Aruba, Bah – Bahamas, Bar – Barbados, Barad – Baradal, Bel – Belize, Ber – Bermuda, Bon – Bonaire, Cub – Cuba, Cur – Curacao, Flo – Florida, Jam – Jamaica, MI – Magueyes Island, LK – Loggerhead Key, Pan – Panama, PR – Puerto Rico, SE – St. Eustatius, SM – St. Martin, VI – Virgin Islands.
COPEPODS ASSOCIATED WITH CARIBBEAN INVERTEBRATES

FIGURE 2  Cyclopoida. Lamippidae (a–d): a – *Enalcyonium nudum*, dorsal view; b – *Linaresia bouligandi*, dorsal view; c – *Magnippe caputmedusae*, ventral view; d – *Sphaerippe caligicola*, lateral view. Thaumatopsyl-lidae (e): nauplius (N1), metanauplius (MN), copepodid stages 1–5 (CI–CV) of *Caribeopsyllus amphiodae*, dorsal view. After Stock (1973, 1978, 1979), Grygier (1980), Dojiri et al. (2008).
| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|---|---|---|---|---|
| **Cnidaria** | | | | |
| **Anthozoa** | | | | |
| **Hexacorallia** | | | | |
| **Actinia** | | | | |
| *Condylactis gigantea* (Weinland, 1860) | *Asteropontius parvipalpus* Stock, 1975 | Ast | Bah, Cur, Jam, MI, PR | Stock, 1975b; Humes, 1982 |
| *Condylactis gigantea* (Weinland, 1860) | *Critomolgus titillans* (Humes, 1982) (as *Doridicola titillans* Humes, 1982) | Rhy | PR | Humes, 1982 |
| *Corynactis denticulosa* (Le Sueur, 1817) (as *Homostichanthus denticulosus* (Le Sueur, 1817)) | *Aspidomolgus stoichactinus* Humes, 1969 | Rhy | Barad, PR, SM | Stock, 1975b |
| *Phymanthus crucifer* (Le Sueur, 1817) | *Asteropontius ungelatus* Stock, 1975 | Ast | MI | Stock, 1975b |
| *Stichodactyla helianthus* (Ellis, 1768) (as *Stoichactis anemone* (Ellis, 1768) and *Stoichactis helianthus* (Ellis, 1768)) | *Aspidomolgus stoichactinus* Humes, 1969 | Rhy | Bah, Bar, Bon, Cub, Cur, FK, Jam, MI, PR | Humes, 1969a; Stock, 1975b; Ortiz et al., 1998 |
| *Stichodactyla helianthus* (Ellis, 1768) | *Asteropontius ungelatus* Stock, 1975 | Ast | Jam, PR | Stock, 1975b; Kim, 2010 |
| **Antipatharia** | | | | |
| *Bartholomea annulata* (Le Sueur, 1817) | *Ridgewayia fossaHageni* Humes & Smith, 1974 | Psec | Pan | Humes & Smith, 1974 |
| *Stichopathes* sp. | | | | |
| *Stichopathes lutkeni* Brook, 1889 | *Calonastes imparipes* Humes & Goenaga, 1978 | Rhy | PR | Humes & Goenaga, 1978 |
| | *Calonastes imparipes* Humes & Goenaga, 1978 | Rhy | PR | Humes & Goenaga, 1978 |
**Corallimorpharia**

*Ricordea florida* Duchassaing & Michelotti, 1860

- *Asteropontius longipalpus* Stock, 1975

*Ricordea florida* Duchassaing & Michelotti, 1860

- *Paramolgus antillianus* Stock, 1975

**Scleractinia**

*Acropora palmata* (Lamarck, 1816)

- *Corallovexia mediobrachium* Stock, 1975

*Acropora palmata* (Lamarck, 1816)

- *Corallovexia similis* Stock, 1975

*Colpophyllia natans* (Houttuyn, 1772)

- *Asteropontius proximus* Stock, 1987

*Colpophyllia natans* (Houttuyn, 1772)

- *Asteropontius kristensi* Stock, 1975

*Colpophyllia natans* (Houttuyn, 1772)

- *Asteropontius longibrachium* Stock, 1975

*Colpophyllia natans* (Houttuyn, 1772)

- *Corallovexia mediobrachium* Stock, 1975

*Colpophyllia natans* (Houttuyn, 1772)

- *Corallovexia mixtibrachium* Stock, 1975

*Dendrogyra cylindrus* Ehrenberg, 1834

- *Corallonoxia baki* Stock, 1975

*Dendrogyra cylindrus* Ehrenberg, 1834

- *Corallonoxia longicauda* Stock, 1975

*Dichocoenia stokesii* Milne Edwards & Haime, 1848

- *Corallonoxia sp.*

*Diploria labyrinthiformis* (Linnaeus, 1758)

- *Corallovexia brevibrachium* Stock, 1975

*Eusmilia fastigiata* (Pallas, 1766)

- *Corallonoxia baki* Stock, 1975

*Favia fragum* (Esper, 1795)

- *Asteropontis faviae* Stock, 1987

*Manicina areolata* (Linnaeus, 1758)

- *Asterocheres maxillatus* Stock, 1987

*(as Manicina areolata f. mayori* Wells, 1936)*
| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|---|---|---|---|---|
| Manicina areolata (Linnaeus, 1758) | Corallovexia mediobrachium Stock, 1975 | Cor | Cur | Stock, 1975a |
| Manicina areolata (Linnaeus, 1758) | Corallovexia longibrachium Stock, 1975 | Cor | Cur | Stock, 1975a |
| Meandrina sp. | Asteropontius capillatus Kim, 2010 | Ast | Bar | Kim, 2010 |
| Meandrina meandrites (Linnaeus, 1758) | Asteropontius iuxitus Stock, 1989 | Ast | Cur | Stock, 1989 |
| Meandrina meandrites (Linnaeus, 1758) | Corallonoxia longicauda Stock, 1975 | Cor | Cur | Butter, 1979 |
| Meandrina meandrites (Linnaeus, 1758) | Corallovexia sp. | Cor | VI | Herriott & Immermann, 1979 |
| Meandrina meandrites (Linnaeus, 1758) | Meandromyzon coronatum Stock, 1989 | Ast | Cur | Stock, 1989 |
| Montastraea cavernosa (Linnaeus, 1767) (as Montastraea brasiliensis (Verrill, 1901)) | Corallovexia dorsospinosa minor Stock, 1975 | Cor | Cur | Stock, 1975a |
| Montastraea cavernosa (Linnaeus, 1767) | Corallovexia dorsospinosa Stock, 1975 | Cor | VI | Stock, 1975a |
| Montastraea cavernosa (Linnaeus, 1767) | Corallovexia sp. | Cor | VI | Herriott & Immermann, 1979 |
| Montastraea cavernosa (Linnaeus, 1767) | Corallovexia ventrospinosa Stock, 1975 | Cor | Cur | Stock, 1975a |
| Montastraea cavernosa (Linnaeus, 1767) | Hermacheres montastreae Stock, 1987 | Ast | Cur | Stock, 1989 |
| Montastraea cavernosa (Linnaeus, 1767) | Pelomyzon rostratum Stock, 1975 | Ast | Cur | Stock, 1975b |
| Mycetophyllia lamarckiana Milne Edwards & Haime, 1849 | Asteropontius mycetophylliae Varela, Ortiz & Lalana, 2005 | Ast | Cub | Varela et al., 2005 |
| Mycetophyllia lamarckiana Milne Edwards & Haime, 1849 | Corallovexia sp. | Cor | VI | Herriott & Immermann, 1979 |
| Orbicella annularis (Ellis & Solander, 1786) (as Montastraea annularis (Ellis & Solander, 1786)) | Asterocheres maxillatus Stock, 1987 | Ast | Cur | Stock, 1989 |
| Orbicella annularis (Ellis & Solander, 1786) | Asteropontella foliata Stock, 1989 | Ast | Cur | Stock, 1989 |
| Taxon                  | Species                                      | Order | Family | Genus | Reference                  |
|-----------------------|----------------------------------------------|-------|--------|-------|----------------------------|
| **Octocorallia**      | **Alcyonacea**                               |       |        |       |                            |
| *Antillogorgia acerosa* (Pallas, 1766) | *Acanthomolgus bilobipes* Humes & Stock, 1973 |       |        |       |                            |
| *Antillogorgia acerosa* (Pallas, 1766) | *Lamippina aequalis* Stock, 1973              |       |        |       |                            |
| *Antillogorgia americana* (Gmelin, 1791) | *Acanthomolgus dionyx* Stock, 1975           |       |        |       |                            |
| *Antillogorgia sp.* (as *Pseudopterogorgia acerosa* (Pallas, 1766)) | *Lamippina aequalis* Stock, 1973              |       |        |       |                            |
| *Antillogorgia acerosa var. elastica* Bielschowsky, 1929 (as *Antillogorgia elastica* Bielschowsky, 1929) | *Acanthomolgus bilobipes* Humes & Stock, 1973 |       |        |       |                            |
| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|---|---|---|---|---|
| *Briareum asbestinum* (Pallas, 1766) | *Enalcyonium variicauca* Stock, 1973 | Lam | PR | Stock, 1973 |
| *Briareum asbestinum* (Pallas, 1766) | *Orecturus ortiz* Varela & Lalana, 2007 | Ast | Cub | Varela & Lalana, 2007 |
| Callogorgia sp. | *Sphaerippe caligicola* Grygier, 1980 | Lam | Bah | Grygier, 1980 |
| *Eunicea calyculata* (Ellis & Solander, 1786) | *Acanthomolgus verrucipes* Humes, 1973 | Rhy | Ber | Humes, 1973 |
| *Eunicea clavigera* Bayer, 1961 | *Acanthomolgus mononyx* Stock, 1975 | Rhy | Cur | Stock, 1975c |
| *Eunicea clavigera* (Lamouroux, 1821) (as *Plexaura flexuosa* Lamouroux, 1821) | *Acanthomolgus affinis* Stock, 1975 | Rhy | Cur | Stock, 1975c |
| *Eunicea flexuosa* (Lamouroux, 1821) | *Acanthomolgus longidactylus* Stock, 1975 | Rhy | Cur | Stock, 1975c |
| *Eunicea flexuosa* Lamouroux, 1821 | *Acanthomolgus intermedius* Stock, 1975 | Rhy | Cur | Stock, 1975c |
| *Eunicea laciniata* Duchassaing & Michelotti, 1860 | *Acanthomolgus longidactylus* Stock, 1975 | Rhy | Cur | Stock, 1975c |
| *Eunicea mammosa* Lamouroux, 1816 | *Enalcyonium euniceae* Stock, 1973 | Lam | PR | Stock, 1973 |
| *Eunicea mammosa* Lamouroux, 1816 | *Orecturus antillensis* Varela, 2011 | Ast | Cub | Varela, 2011b |
| *Eunicea tourneforti* Milne Edwards & Haime, 1857 | *Acanthomolgus longifurca* Stock, 1975 | Rhy | Cur | Stock, 1975c |
| *Gorgonia mariae* Bayer, 1961 | *Acanthomolgus triangulipes* Stock, 1975 | Rhy | Cub | Varela et al., 2008 |
| *Gorgonia ventalina* Linnaeus, 1758 | *Acanthomolgus bayeri* Humes, 1973 | Rhy | Ber | Humes, 1973 |
| *Gorgonia ventalina* Linnaeus, 1758 | *Acanthomolgus gorgoniae* Humes, 1973 | Rhy | Ber, Cur, SE | Stock, 1973; Stock, 1975c |
| *Gorgonia ventalina* Linnaeus, 1758 | *Acanthomolgus triangulipes* Stock, 1975 | Rhy | Cur, SE, SM | Stock, 1975c |
| *Gorgonia ventalina* Linnaeus, 1758 | *Sphaerippe sp.* | Lam | SE | Ivanenko et al., 2017 |
| *Muricea* sp. | *Acanthomolgus intermedius* Stock, 1975 | Rhy | Cub | Varela et al., 2008 |
| Species                          | Copepod Species     | Host                  | Author     | Reference          |
|---------------------------------|---------------------|-----------------------|------------|--------------------|
| *Muricea atlantica* (Kukenthal, 1911) | *Acanthomolgus muriceanus* | Humes, 1973          | Ber        | Humes, 1973; Stock, 1975c |
| *Muricea laxa* Verrill, 1864     | *Acanthomolgus aequiseta* Stock, 1975 | Rhy               | Cur        | Stock, 1975c       |
| *Placogorgia* sp.                | *Linaresia bouligandi* Stock, 1979 | Lam                | Flo        | Stock, 1979        |
| *Plexaura* sp.                   | *Acanthomolgus affinis* Stock, 1975 | Rhy                | Cub        | Varela, 2011a      |
| *Plexaura homomalla* (Esper, 1794) (as *Plexaura homomalla f. homomalla* Esper, 1794) | *Acanthomolgus affinis* Stock, 1975 | Rhy          | Cur        | Stock, 1975c       |
| *Plexaura homomalla* (Esper, 1794) | *Enalcyonium nudum* Stock, 1973 | Lam                | PR         | Stock, 1973        |
| *Plexaura homomalla* (Esper, 1794) | *Enalcyonium ramosum* Stock, 1973 | Lam                | PR         | Stock, 1973        |
| *Plax Aurella dichotoma* (Esper, 1791) | *Acanthomolgus seticornis* Stock, 1975 | Rhy          | SM         | Stock, 1975c       |
| *Plax Aurella nutans* (Duchassaing & Michelotti, 1860) | *Enalcyonium sp.* | Lam                | Cub        | Varela et al., 2005b |
| *Pseudoplexaura porosa* (Houttuyn, 1772) | *Acanthomolgus bayeri* Humes, 1973 | Rhy          | Ber        | Humes, 1973        |
| *Pseudoplexaura* Wright & Studer, 1889 | *Acanthomolgus bayeri* Humes, 1973 | Rhy          | Cub        | Varela et al., 2003 |
| *Thesea*                          | *Magnippe caputmedusae* Stock, 1978 | Lam                | Flo        | Stock, 1978        |
| *Pennatulacea*                    | *Macrochiron sargass* Sars, 1916 | Mac                | SM         | Humes & Stock, 1973 |
| *Echinodermata*                  |                      |                      |            |                    |
| *Crinoidea*                      |                      |                      |            |                    |
| *Comatulida*                     |                      |                      |            |                    |
| *Davidaster rubiginosus* (Pourtales, 1869) | *Asterocheres crinoidicola* Humes, 2000 | Ast          | Jam        | Kim, 2010          |
| *Nemaster grandis* Clark, 1909   | *Asterocheres crinoidicola* Humes, 2000 | Ast          | Bel, Cub   | Humes, 2000; Varela, 2010 |
| *Echinoidea*                     |                      |                      |            |                    |
| *Echinoidea*                     |                      |                      |            |                    |
| *Camarodonta*                    |                      |                      |            |                    |
| *Echinometra lucunter* (Linnaeus, 1758) | *Chelaches longipalpus* Stock & Humes, 1995 | Ast          | Bah, Cub, Cur, Jam, MI, SM, PR | Stock & Humes, 1995; Varela, 2011a |
| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|-------------------------------------------------|----------------------|-----------------------------|---------------------|-----------|
| *Echinometra lucunter* (Linnaeus, 1758)       | *Chelacheres optans* Stock & Humes, 1995 | Ast | PR | Stock & Humes, 1995 |
| *Echinometra viridis* A. Agassiz, 1863       | *Macrochiron echinicolum* Humes & Stock, 1973 | Mac | Cur | Humes & Stock, 1973 |
| *Lytechinus variegatus* (Lamarck, 1816)      | *Asterocheres simulans* (T. Scott, 1898) (as *Ascomyzon simulans* T. Scott, 1898) | Ast | Cur | Stock & Humes, 1995 |
| *Lytechinus variégatus* (Lamarck, 1816)      | *Macrochiron echinicolum* Humes & Stock, 1973 | Mac | Bon, Cur, Jam, MI, PR | Humes & Stock, 1973 |
| *Tripneustes ventricosus* (Lamarck, 1816)    | *Chelacheres longipalpus* Stock & Humes, Ast 1995 | Cur | Stock & Humes, 1995 |
| *Tripneustes ventricosus* (Lamarck, 1816)    | *Macrochiron echinicolum* Humes & Stock, 1973 | Mac | Bah, Bar, Cur, Jam, MI | Humes & Stock, 1973 |
| **Cidaroida**                                |                      |                             |            |           |
| *Eucidaris tribuloides* (Lamarck, 1816)      | *Asterocheres unioviger* Kim, 2010 | Ast | Bah, PR | Kim, 2010 |
| **Clypeasteroida**                           |                      |                             |            |           |
| *Clypeaster rosaceus* (Linnaeus, 1758)       | *Pseudanthessius pectinifer* Stock, Humes Pse & Gooding, 1964 | Pse | Bah, Jam, MI | Stock et al., 1963b |
| **Diadematoida**                             |                      |                             |            |           |
| *Diadema antillarum* Philippi, 1845          | *Onychocherces alatus* Stock & Gooding, 1986 | Ast | Cub, Cur | Stock & Gooding, 1986; Varela et al., 2005b |
| **Spatangoida**                              |                      |                             |            |           |
| *Meoma ventricosa* (Lamarck, 1816)           | *Meomicola amplexans* Stock, Humes & Gooding, 1963 | Sync | Cur, Jam | Stock et al., 1963b |
| *Meoma ventricosa* (Lamarck, 1816)           | *Micropontius glaber* Stock, Humes & Gooding, 1963 | Mic | Jam | Stock et al., 1963a |
| Meoma ventricosa (Lamarck, 1816) | Nanaspis pollens Stock, Humes & Gooding, 1962 | Nan | Jam | Stock et al., 1962 |
|---------------------------------|-----------------------------------------------|-----|-----|-------------------|
| Meoma ventricosa (Lamarck, 1816) | Pseudanthessius exilicornis Stock & Humes, 1995 | Pse | Cur | Stock & Humes, 1995 |
| **Holothuroidea**                |                                               |     |     |                   |
| Actinopyga agassizii (Selenka, 1867) (as Muelleria agassizii Selenka, 1867) | Caribulus sp. | Sync | Bah, Jam | Humes, 1969b |
| Actinopyga agassizii (Selenka, 1867) | Caribulus sculptus (Humes, 1969) | Sync | Bah, Jam | Humes, 1969b |
| Actinopyga agassizii (Selenka, 1867) | Diogenidium nasutum Edwards, 1891 | Lic | Bah | Hendler & Kim, 2010 |
| Actinopyga agassizii (Selenka, 1867) | Diogenidium tectum Humes & Ho, 1971 | Lic | Bah, Jam | Hendler & Kim, 2010 |
| Holothuria (Halodeima) grisea Selenka, 1867 | Caribulus sculptus (Humes, 1969) | Sync | Jam | Humes, 1969b |
| Holothuria (Halodeima) grisea Selenka, 1867 | Diogenidium nasutum Edwards, 1891 | Lic | Jam | Hendler & Kim, 2010 |
| Holothuria (Halodeima) mexicana Ludwig, 1875 | Caribulus sp. | Sync | Bah, Cur, Jam | Humes, 1969b |
| Holothuria (Halodeima) mexicana Ludwig, 1875 | Caribulus sculptus (Humes, 1969) (as Scambicornus sculptus Humes, 1969) | Sync | Bah, Bon, Cub, Cur, Jam | Humes, 1969b; Varela et al., 2003 |
| Holothuria (Halodeima) mexicana Ludwig, 1875 | Diogenella spinicauda Stock, 1968 | Lic | Bah, Cur, Jam, MI, PR | Stock, 1968; Humes & Ho, 1970 |
| Holothuria (Halodeima) mexicana Ludwig, 1875 | Diogenidium deforme Stock, 1968 | Lic | Bah, PR | Hendler & Kim, 2010 |
| Holothuria (Halodeima) mexicana Ludwig, 1875 | Diogenidium nasutum Edwards, 1891 | Lic | Cur, Jam, MI, PR | Stock, 1968; Hendler & Kim, 2010 |
| Holothuria (Halodeima) mexicana Ludwig, 1875 | Pseudanthessius deficiens Stock, Humes & Gooding, 1963 | Pse | Cur | Stock et al., 1963b |
| Holothuria (Metriatyla) scabra Jaeger, 1833 | Diogenidium nasutum Edwards, 1891 | Lic | Bah | Edwards, 1891 |
| Holothuria (Platyperona) parvula (Selenka, 1867) (as Microethele parvula (Selenka)) | Diogenidium nasutum Edwards, 1891 | Lic | MI, PR | Stock et al., 1962 |
| Holothuria (Selenothuria) glaberrima Selenka, 1867 | Diogenidium deforme Stock, 1968 | Lic | PR | Stock, 1968 |
### Table 2
Caribbean reef-dwelling anthozoans, echinoderms and sponges as hosts of copepod crustaceans (cont.)

| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|---|---|---|---|---|
| *Holothuria (Semperothuria) surinamensis* Ludwig, 1875 | *Diogenella seticauda* Stock, 1968 | Lic | MI, PR | Stock, 1968; Humes & Ho, 1970 |
| *Holothuria (Semperothuria) surinamensis* Ludwig, 1875 (as *Halodeima surinamensis* (Ludwig)) | *Nanaspis pollens* Stock, Humes & Gooding, 1962 | Nan | MI | Stock et al., 1962 |
| *Holothuria (Thymiosycia) arenicola* Semper, 1868 | *Diogenella deichmannae* Humes & Ho, 1970 | Lic | Bar | Humes & Ho, 1970 |
| *Holothuria (Thymiosycia) arenicola* Semper, 1868 (as *Brandtothuria arenicola* (Semper, 1868)) | *Diogenella impar* Humes & Ho, 1970 | Lic | Bar | Humes & Ho, 1970 |
| *Holothuria (Thymiosycia) arenicola* Semper, 1868 | *Diogenidium deformae* Stock, 1968 | Lic | Bar | Hendler & Kim, 2010 |
| *Holothuria (Thymiosycia) arenicola* Semper, 1868 | *Diogenella seticauda* Stock, 1968 | Lic | MI | Humes & Ho, 1970 |
| *Holothuria (Thymiosycia) arenicola* Semper, 1868 | *Nanaspis pollens* Stock, Humes & Gooding, 1962 | Nan | Jam | Stock et al., 1962 |
| *Holothuria (Thymiosycia) arenicola* Semper, 1868 | *Nanaspis truncata* Stock, Humes & Gooding, 1962 | Nan | MI | Stock et al., 1962 |
| *Holothuria (Thymiosycia) impatiens* (Forsskal, 1775) | *Diogenella seticauda* Stock, 1968 | Lic | PR | Stock, 1968 |

**Synallactida**

| *Isostichopus badionotus* (Selenka, 1867) | *Caribulus* sp. | Sync | Bah, Bar, Jam | Humes, 1969b |
| *Isostichopus badionotus* (Selenka, 1867) | *Caribulus sculptus* (Humes, 1969) | Sync | Bah, Bar, Jam, MI, PR | Humes, 1969b |
| *Isostichopus badionotus* (Selenka, 1867) | *Diogenidium spinulosum* Stock, 1968 | Lic | Jam, PR | Stock, 1968; Hendler & Kim, 2010 |
| Species                                      | Host                | Location | Reference                     |
|---------------------------------------------|---------------------|----------|-------------------------------|
| *Isostichopus badionotus* (Selenka, 1867)    | *Nanaspis exigua*   | Nan      | Jam                          | Stock et al., 1962 |
|                                             | Stock, Humes &      |          |                               |                    |
|                                             | Gooding, 1962       |          |                               |                    |
| *Isostichopus badionotus* (Selenka, 1867)    | *Nanaspis media*    | Nan      | MI, PR                        | Stock et al., 1962 |
|                                             | Stock, Humes &      |          |                               |                    |
|                                             | Gooding, 1962       |          |                               |                    |
| *Isostichopus badionotus* (Selenka, 1867)    | *Nanaspis pollens*  | Nan      | Bah, Jam                      | Stock et al., 1962 |
|                                             | Stock, Humes &      |          |                               |                    |
|                                             | Gooding, 1962       |          |                               |                    |
| **Ophiuroidea**                             |                     |          |                               |                    |
| **Euryalida**                               |                     |          |                               |                    |
| *Astrophyton muricatum* (Lamarck, 1816)      | *Critomolgus*       | Rhy      | Cub                          | Varela et al., 2008 |
|                                             | Stock, Humes &      |          |                               |                    |
|                                             | Gooding, 1983       |          |                               |                    |
| *Astrophyton muricatum* (Lamarck, 1816)      | *Critomolgus*       | Rhy      | Bar, Jam, MI, PR              | Humes & Stock, 1973 |
|                                             | *astrophyticus*     |          |                               |                    |
|                                             | (Humes & Stock, 1973) |         |                               |                    |
|                                             | (as *Doridicola*    |          |                               |                    |
|                                             | *astrophyticus*     |          |                               |                    |
|                                             | Humes & Stock, 1973 |          |                               |                    |
| **Ophiurida**                               |                     |          |                               |                    |
| **Ophiuroidea**                             |                     |          |                               |                    |
| *Amphioplus* sp.                            | *Caribeopsyllus*    | Tha      | SE                           | Ivanenko, unpublished |
|                                             | sp. A               |          |                               |                    |
| *Amphioplus* sp.                            | *Parophiopsyllus*   | Can      | FK                           | Humes & Hendler,  |
|                                             | *ligatus*           |          |                               | 1972               |
|                                             | Humes & Hendler,    |          |                               |                    |
|                                             | 1972                |          |                               |                    |
|                                             | *Presynaptiphilus*  | Synp     | FK                           | Humes & Hendler,  |
|                                             | *amphioplī*        |          |                               | 1972               |
|                                             | Humes & Hendler,    |          |                               |                    |
|                                             | 1972                |          |                               |                    |
| *Ophiocoma echinata* (Lamarck, 1816)         | *Ophiopsyllus*      | Can      | Bel, Cur                      | Humes & Hendler,  |
|                                             | *reductus*          |          |                               | 1999; Stock et al., |
|                                             | Stock, Humes &      |          |                               | 1963a              |
|                                             | Gooding, 1963       |          |                               |                    |
| *Ophiocoma pumila* Lutken, 1856              | *Ophiopsyllus*      | Can      | Bel, FK                       | Humes & Hendler,  |
|                                             | *latus*             |          |                               | 1999               |
|                                             | Humes & Hendler,    |          |                               |                    |
|                                             | 1999                |          |                               |                    |
| *Ophiocoma wendtii* Muller & Troschel, 1842  | *Hemicyclops*       | Cla      | Bah                          | Kim, 2009          |
| (as *Ophiocoma riisei* Lutken, 1856)         | *columnarīs*        |          |                               |                    |
|                                             | Humes, 1984         |          |                               |                    |
| *Ophiocomella ophiactoides* (Clark, 1900)    | *Ophiopsyllus*      | Can      | Bel                           | Humes & Hendler,  |
|                                             | *latus*             |          |                               | 1999               |
|                                             | Humes & Hendler,    |          |                               |                    |
|                                             | 1999                |          |                               |                    |
| *Ophiocomella ophiactoides* (Clark, 1900)    | *Ophiopsyllus*      | Can      | Bel, Jam                      | Emson & Mladenov, |
|                                             | *reductus*          |          |                               | 1987; Emson et al., |
|                                             | Stock, Humes &      |          |                               | 1985               |
|                                             | Gooding, 1963       |          |                               |                    |
| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|---|---|---|---|---|
| *Ophioderma brevispina* (Say, 1825) (as *Ophioderma brevispinum* (Say, 1825)) | *Pseudanthessius deficiens* Stock, Humes & Gooding, 1963 | Pse | Bel | Humes & Hendler, 1999 |
| *Ophioderma cinerea* Muller & Troschel, 1842 (as *Ophioderma cinereum* Muller & Troschel, 1842) | *Pseudanthessius deficiens* Stock, Humes & Gooding, 1963 | Pse | Bel, Cur, MI, SM | Stock et al., 1963b; Humes & Hendler, 1999 |
| *Ophiomyxa flaccida* (Say, 1825) | *Ophiurocheres bellulus* Humes, 1998 | Ast | MI | Humes, 1998 |
| *Ophiothrix (Acanthophiothrix) suensonii* Lutken, 1856 | *Collocheres lunulifer* Humes, 1998 | Ast | Bar | Humes, 1998 |
| *Ophiothrix (Ophiothrix) angulata* (Say, 1825) | *Caribeopsyllus* sp. A | Tha | Bel | Hendler & Kim, 2010 |
| *Ophiothrix (Ophiothrix) angulata* (Say, 1825) | *Caribeopsyllus chawayi* Suarez-Morales, In: Suarez-Morales & Castellanos, 1998 | Tha | Bel | Hendler & Kim, 2010 |
| *Ophiothrix (Ophiothrix) oerstedii* Lutken, 1856 | *Collocheres lunulifer* Humes, 1998 | Ast | Bar | Humes, 1998 |
| *Porifera* | *Caribeopsyllus chawayi* Suarez-Morales, In: Suarez-Morales & Castellanos, 1998 | Tha | Bel | Hendler & Kim, 2010 |
| *Porifera* | *Asterocheres bahamensis* Kim, 2010 | Ast | Bah | Kim, 2010 |
| *Porifera* | *Asterocheres oricurvus* Kim, 2010 | Ast | Jam | Kim, 2010 |
| *Porifera* | *Asterocheres peniculatus* Kim, 2010 | Ast | Bah | Kim, 2010 |
| *Porifera* | *Asterocheres plumosus* Kim, 2010 | Ast | Bah | Kim, 2010 |
| *Porifera* | *Asterocheres trisetatus* Kim, 2010 | Ast | Bah | Kim, 2010 |
| *Porifera* | *Eupolymniphilus occidentalis* Kim, 2009 | Sab | Jam | Kim, 2009 |
| *Porifera* | *Hemicyclops columnaris* Humes, 1984 | Cla | Bah | Kim, 2009 |
| *Porifera* | *Hetairosynella aculeata* Kim, 2010 | Ast | Bah | Kim, 2010 |
| *Porifera* | *Hetairosynella angulata* Kim, 2010 | Ast | Jam | Kim, 2010 |
| *Porifera* | *Hetairosynella bifurcata* Kim, 2010 | Ast | Jam | Kim, 2010 |
| Porifera | *Kimcheres fastigatus* (Kim, 2010) (as *Asterocheres fastigatus* Kim, 2010) | Ast | Bar | Kim, 2010 |
|----------|---------------------------------------------------------------|-----|-----|-----------|
| Porifera | *Pseudanthessius acutus* Kim, 2009 | Pse | Jam | Kim, 2009 |
| Porifera | *Stenomyzon edentatum* Kim, 2010 | Ast | PR | Kim, 2010 |
| Calcarea | Calcinea | Clathrinida | *Clathrina lutea* Azevedo, Padua, Moraes, Rossi, Muricy & Klautau, 2017 | Copepoda | PR | García-Hernández et al., 2019 |
| Demospongiae | Heteroscleromorpha | Agelasida | *Agelas sp.* | *Asterocheres reginae* Boxshall & Huys, 1994 | Ast | Cub | Varela et al., 2008 |
| | | | *Agelas clathrodes* (Schmidt, 1870) | *Asterocheres reginae* Boxshall & Huys, 1994 | Ast | Bel | Boxshall & Huys, 1994 |
| | | | *Agelas dilatata* Duchassaing & Michelotti, 1864 | *Asterocheres cubensis* Varela, 2010 | Ast | Cub | Varela, 2010b |
| | | | *Agelas wiedenmayeri* Alcolado, 1984 | *Asterocheres fernandezmilerai* Varela, 2010 | Ast | Cub | Varela, 2010b |
| Axinellida | Haplosclerida | *Ptilocalcis walpersii* (Duchassaing & Michelotti, 1864) | *Asterocheres garridoi* Varela, Ortiz & Lalana, 2007 | Ast | Cub | Varela et al., 2007 |
| Calyxpongia sp. | *Asterocheres antillensis* Varela, 2010 | Ast | Cub | Varela, 2010 |
| Calyxpongia vaginalis (Lamarck, 1814) | *Asterocheres Boeck, 1859* | Ast | Cub | Varela et al., 2005b |
| Calyxpongia vaginalis (Lamarck, 1814) | *Asterocheres espinosai* Varela, Ortiz & Lalana, 2007 | Ast | Cub | Varela et al., 2007a |
| Calyxpongia vaginalis (Lamarck, 1814) | *Neoasterocheres humesi* (Varela, 2012) | Ast | Cub | Varela, 2012 |
### TABLE 2  Caribbean reef-dwelling anthozoans, echinoderms and sponges as hosts of copepod crustaceans (cont.)

| Invertebrate Host (valid name and as indicated in the original record) | Copepod species name | Copepod family abbreviation* | Site abbreviation** | Reference |
|---|---|---|---|---|
| *Callyspongia vaginalis* (Lamarck, 1814) | *Setachera paraboeki* (Johnsson, 1998) | Ast | Cub | Varela, 2012 |
| *Niphates digitalis* (Lamarck, 1814) | *Asterocheres kimi* Varela, 2012 | Ast | Cub | Varela, 2012 |
| *Niphates digitalis* (Lamarck, 1814) | *Asterocheres ialanai* Varela, 2013 | Ast | Cub | Varela, 2012 |
| **Poecilosclerida** | | | | |
| *Iotrochota birotulata* (Higgin, 1877) | *Scottocheres elongatus* (Scott T. & Scott A., 1894) | Ast | Cub | Varela et al., 2008 |
| **Verongimorpha** | | | | |
| **Chondrillida** | | | | |
| *Chondrilla nucula* Schmidt, 1862 | *Parmulella emarginata* Stock, 1992 | Ent | Cur | Stock, 1992b |
| *Chondrilla nucula* Schmidt, 1862 | *Parmulodes verrucosa* Wilson C.B., 1944 (as *Parmulodes verrucosus*) | Ent | Aru, Cub, Cur, PR | Stock, 1992b; Varela et al., 2008 |

* Copepod family Abbreviation: Ast – Asterocheridae, Can – Cancerillidae, Cla – Clausidiidae, Cor – Corallovexiidae, Ent – Entomolepididae, Lam – Lamippidae, Lic – Licchomolgidae, Mac – Macrochironidae, Mic – Micropontiidae, Nan – Nanaspidae, Pse – Pseudanthessiidae, Psec – Pseudocyclopidae, Rhy – Rhynchomolgidae, Sab – Sabellichilidae, Sync – Synapticolidae, Synp – Synaptiphilidae, Tha – Thaumatopsyllidae.

** Site Abbreviation: Aru – Aruba, Bah – Bahamas, Bar – Barbados, Barad – Baradal, Bel – Belize, Ber – Bermuda, Bon – Bonaire, Cub – Cuba, Cur – Curacao, Flo – Florida, Jam – Jamaica, MI – Magueyes Island, LK – Loggerhead Key, Pan – Panama, PR – Puerto Rico, SE – St. Eustatius, SM – St. Martin, VI – Virgin Islands.
COPEPODS ASSOCIATED WITH CARIBBEAN INVERTEBRATES

Coral (fig. 1a) (Humes, 1984; Stock, 1992a; Kim, 2009). All other species of symbiotic copepods are found in the Caribbean only, which may be the result of high endemism of their host species (Miloslavich et al., 2010; Soest et al., 2012; Zea et al., 2014; Ivanenko, 2016).

The copepods were collected by washing of the hosts in seawater or tap water (Butter, 1979; Garcia-Hernandez et al., 2017), a solution of formalin (Varela & Lalana, 2007; Varela et al., 2003, 2005a, b, 2007a, b, 2008; Varela, 2010a, b, 2011a, b, 2012), a solution of ethanol (Stock et al., 1962, 1963a, b, Humes, 1969a, 1998, 2000; Humes & Stock, 1973; Stock, 1975a, b, d; Herriott & Immermann, 1979; Stock & Humes, 1995) or a solution of magnesium-chloride (Stock & Humes, 1995), dissecting of the host's tissues or galls (see Stock et al., 1962; Humes & Hendler, 1972, 1999; Humes & Goenaga, 1978; Stock, 1978; Grygier, 1980; Emson et al., 1985; Emson & Mladenov, 1987; Hendler & Kim, 2010; Ivanenko et al., 2017), by a suction device (Humes & Stock, 1973) or by dissolving soft tissues of host corals with bleach (Stock 1975a, 1989). Most of the host invertebrates were collected by SCUBA living down to 41 m depth. The only exceptions are the three of eight species of the Caribbean copepods of the family Lamippidae tentatively included in the database found in galls or tissue of octocorals collected by a submersible away from reefs at depths of 55–330 m (fig. 2 a–d) (Stock, 1978, 1979; Grygier, 1980). It is noteworthy that there are no data on symbiotic copepods associated with reef-dwelling sponges, echinoderms and corals living at mesophotic depths; studies on reef communities and coral-associated fauna from mesophotic depths seems to be an important task that has just started (Bongaerts et al. 2010, 2015; van der Meij et al., 2015; Hoeksema et al., 2017c; Garcia-Hernández et al., 2018; Veglia et al., 2018).

Symbiotic copepods are reported from eight out of ten ecoregions of the Greater Caribbean, but none from the Northern and Southern Gulf of Mexico (table 6, figs. 4–7; Spalding et al., 2007; Hoeksema et al., 2017a). Eight records are known for Bermuda: four species of poecilostomatoid cyclopoids representing genus Acanthomolgus and the siphonostomatoid Ophiopsyllus reductus were found associated with alcyonaceans and an ophiuroid, respectively (Stock et al., 1963a; Humes, 1973). Only one record is reported for the Southwestern Caribbean: the calanoid Ridgewayia fossiiageni aggregating on the actinarian Bartholomea annulata. Only Aspidomolgus stoichactinus living on the actinarian Stichodactyla helianthus and the corallimorpharian Corynactis denticulosa, recorded as Homostichanthus denticulosus, is found in five ecoregions (Humes, 1969a; Stock, 1975b). Five species of copepods are found in four ecoregions, viz. Caribulus sculptus living on holothurians, Chelaches longipalpus and Macrochiron echinicolum (fig. 1d) found on sea urchins, Ophiopsyllus reductus living on ophiuroids. Seventeen and 87 species of copepods are recorded found in only two and one ecoregions, respectively (table 6).

The data show that the three most intensively explored ecoregions are the Bahamian, Greater Antilles and Southern Caribbean, with studies centered at Curacao (123 records, 36 species of hosts, 49 species of copepods), Puerto Rico (105, 22, 27) and the Bahamas (57, 11, 19). The mosaic data show poor knowledge of most ecoregions as well as and many host taxa. This current state of the knowledge limits analysis of the distribution of symbiotic copepods in the whole Caribbean. Well planned studies of different Caribbean regions and the application of modern methods of integrative taxonomy are needed to carry out such analyses (DeBiasse et al., 2016; Jossart et al., 2017; Ivanenko et al., 2018).

A comparison of taxonomic names from literature sources with their current nomenclature revealed name changes for 29 (of 80) species and 12 (of 58) genera of the hosts
FIGURE 3  Siphonostomatoida, dorsal view. a – *Asterocheres unioviger*, b – *Cyclocheres sensilis* (Asterocheridae), c – *Parophiopsyllus ligatus* (Cancerillidae), d – *Micropontius glaber* (Micropontiidae), e – *Nanaspis pol-lens* (Nanaspididae). After Stock et al. (1962, 1963a), Humes & Hendler (1972), Kim (2010).
| Host family          | Number of copepod records | Number of copepod species |
|----------------------|---------------------------|---------------------------|
| **Echinodermata**    |                           |                           |
| Holothuriidae        | 75                        | 12                        |
| Stichopodidae        | 35                        | 5                         |
| Ophiocomidae         | 29                        | 3                         |
| Ophiotrichidae       | 19                        | 2                         |
| Toxopneustidae       | 18                        | 3                         |
| Echinometridae       | 17                        | 3                         |
| Gorgonocephalidae    | 13                        | 1                         |
| Ophiodermatidae      | 10                        | 1                         |
| Amphiuridae          | 9                         | 2                         |
| Brissidae            | 9                         | 4                         |
| Clypeasteridae       | 6                         | 1                         |
| Diadematidae         | 4                         | 1                         |
| Comatulidae          | 3                         | 1                         |
| Cidaridae            | 2                         | 1                         |
| Ophiomyxidae         | 1                         | 1                         |
| **Cnidaria**         |                           |                           |
| Faviidae             | 47                        | 12                        |
| Plexauridae          | 29                        | 16                        |
| Stichodactylidae     | 22                        | 2                         |
| Gorgoniidae          | 21                        | 6                         |
| Meandrinidae         | 20                        | 5                         |
| Actiniidae           | 16                        | 3                         |
| Montastraedae        | 13                        | 6                         |
| Merulinidae          | 7                         | 2                         |
| Acroporidae          | 5                         | 2                         |
| Corallimorphidae     | 4                         | 2                         |
| Briareidae           | 4                         | 2                         |
| Aiptasiidae          | 2                         | 1                         |
| Antipathidae         | 2                         | 1                         |
| Ricordeidae          | 2                         | 1                         |
| Renillidae           | 1                         | 1                         |
| Phymanthidae         | 1                         | 1                         |
| Primnoidae           | 1                         | 1                         |
| **Porifera**         |                           |                           |
| Clathrinidae         | 42                        | 1                         |
| Chondrillidae        | 12                        | 2                         |
(WoRMS, 2019). The taxonomic names are changed for nine (of 115) species and six (of 47) genera of the copepods. There are six records of symbiotic copepods identified to genus (Asterocheres, Corallovexia, Corallonoxia, Critomolgus, Enalcyonium, Sphaerippe). These taxa are included in; among 16 hosts (for 18 records) that have no identification at species level; of these one is assigned to a phylum, three to a class and 12 to a genus. There are 41 records for which the hosts are identified only to taxonomic categories such as phylum, order or subclass. There are 81 records of copepods found on sponges, but hosts of 14 of them are defined only to phylum (Kim, 2009, 2010). The absence of precise identifications and the necessity of linking outdated host names with valid ones show the need for specimen collections of not only copepods but also of their invertebrate hosts, as well as

| Host family     | Number of copepod records | Number of copepod species |
|-----------------|---------------------------|---------------------------|
| Callyspongiidae | 5                         | 4                         |
| Agelasidiae     | 4                         | 3                         |
| Niphatidae      | 2                         | 2                         |
| Iotrochotidae   | 1                         | 1                         |
| Axinellidae     | 1                         | 1                         |

| Copepod family       | Number of records | Number of species |
|----------------------|-------------------|------------------|
| Asterocheridae       | 103               | 45               |
| Rhynchomolgidae      | 78                | 19               |
| Corallovexiidae      | 66                | 11               |
| Synapticolidae       | 53                | 3                |
| Lichomolgidae        | 43                | 8                |
| Cancerillidae        | 34                | 3                |
| Pseudanthessiidae    | 21                | 4                |
| Nanaspidae           | 19                | 4                |
| Macrophironidae      | 18                | 2                |
| Thaumatopsyllidae    | 17                | 1                |
| Lamippidae           | 16                | 8                |
| Entomolepididae      | 12                | 2                |
| Synaptiphilidae      | 3                 | 1                |
| Clausidiidae         | 2                 | 1                |
| Micropontiidae       | 2                 | 1                |
| Pseudocyclopidae     | 2                 | 1                |
| Sabelliphilidae      | 1                 | 1                |
TABLE 5  Families of reef-dwelling Caribbean symbiotic copepods and their host families (anthozoans, echinoderms and sponges)*

| Copepod family     | Host family       | Host class or type |
|--------------------|-------------------|--------------------|
| Asterocheridae     | Actiniidae        | Ant                |
|                    | Agelasidae        | Dem                |
|                    | Axinellidae       | Dem                |
|                    | Briareidae        | Ant                |
|                    | Callymenopodidae  | Dem                |
|                    | Cidaridae         | Ech                |
|                    | Comatalidae       | Cri                |
|                    | Diademataidae     | Ech                |
|                    | Echinometridae    | Ech                |
|                    | Iotrochotidae     | Dem                |
|                    | Meandrinidae      | Ant                |
|                    | Merulinidae       | Ant                |
|                    | Montastraeidae    | Ant                |
|                    | Niphidae          | Dem                |
|                    | Ophiomyxidae      | Oph                |
|                    | Ophiotrichidae    | Oph                |
|                    | Phymanthidae      | Ant                |
|                    | Plexauridae       | Ant                |
|                    | Ricordeidae       | Ant                |
|                    | Stichodactylidae  | Ant                |
|                    | Toxopneustidae    | Ech                |
| Cancerillidae      | Amphiuridae       | Oph                |
|                    | Ophiocomidae      | Oph                |
| Clausidiidae       | Ophiocomidae      | Oph                |
| Corallovexiidae    | Acroporidae       | Ant                |
|                    | Meandrinidae      | Ant                |
|                    | Merulinidae       | Ant                |
|                    | Montastraeidae    | Ant                |
|                    | Faviidae          | Ant                |
|                    | Chondrillidae     | Dem                |
| Lamippidae         | Briareidae        | Ant                |
|                    | Gorgonidae        | Ant                |
|                    | Plexauridae       | Ant                |
|                    | Primnoidae        | Ant                |
| Lichomolgidae      | Holothuriidae     | Hol                |
|                    | Stichopodidae     | Hol                |
| Macrochironidae    | Echinometridae    | Ech                |
|                    | Renillidae        | Ant                |
|                    | Toxopneustidae    | Ech                |
| Micropontiidae     | Brissidae         | Ech                |
morphological and molecular studies of this material (Rocha et al., 2014). The DNA-barcoding of the hosts, photographing of hosts alive underwater, and photographing of host skeletons along with basic locality data are important for both identification and maintaining information about each copepod host and the establishment of base line information about their distributions (Hoeksema et al., 2011).

In total, there are 253, 197 and 81 records of copepods found associated with echinoderms, cnidarians and sponges, respectively (figs. 1–3). Forty-seven and 20 records of copepods are linked to the scleractinian coral families Faviidae and Meandrinidae (updated classification in Hoeksema & Cairns, 2019), respectively; 36 and 16 of these records pertain to the endoparasitic copepod symbionts belonging to the family Corallovexiidae. Most records from holothurians from the families Holothuriidae and Stichopodidae (75 and 35 records), from ophiuroids the families Ophiocomidae and Ophiotrichidae (29 and 19 records) are most common, from sea cucumbers the family Stichopodidae (35 records) is well represented, alcyonaceans the family Plexauridae (29), and corallimorpharians (four records) also are represented (table 3). Many
Figure 4  Caribbean copepods found on sponges (x; x = number of records and number of copepod species, respectively).

Figure 5  Caribbean copepods found on octocorals (Anthozoa: Octocorallia) (x; x – number of records and number of copepod species, respectively).
Figure 6  Caribbean copepods found on hexacorallians (Anthozoa: Hexacorallia) (x; x – number of records and number of copepod species, respectively).

Figure 7  Caribbean copepods found on echinoderms (x; x – number of records and number of copepod species, respectively).
| Copepod species / Ecoregion                                      | Bahamian | Bermuda | Eastern Caribbean | Floridian | Greater Antilles | Southern Caribbean | Southwestern Caribbean | Western Caribbean |
|---------------------------------------------------------------|----------|---------|-------------------|-----------|------------------|--------------------|-----------------------|------------------|
| *Acanthomolgus aequiseta* Stock, 1975                         |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus affinis* Stock, 1975                           |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus bayeri* Humes, 1973                            | x        |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus bilobipes* Humes & Stock, 1973                 |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus dionyx* Stock, 1975                            |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus gorgoniae* Humes, 1973                         |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus intermedius* Stock, 1975                       |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus longidactylus* Stock, 1975                     |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus longifurca* Stock, 1975                        |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus mononyx* Stock, 1975                           |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus muriceanus* Humes, 1973                        |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus seticornis* Stock, 1975                        |          |         |                   |           |                  |                    |                       | x                |
| *Acanthomolgus triangulipes* Stock, 1975                      |          |         |                   |           |                  |                    |                       |                  |
| *Acanthomolgus verrucipes* Humes, 1973                        |          |         |                   |           |                  |                    |                       |                  |
| *Aspidomolgus stoichactinus* Humes, 1969                      | x        |         |                   | x         |                  |                    |                       | x                |
| Asterocheres sp.                                               |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres antillensis* Varela, 2010                       |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres bahamensis* Kim, 2010                           |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres crinoidica* Humes, 2000                         |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres cubensis* Varela, 2010                          |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres espinosai* Varela, Ortiz & Lalana, 2007          |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres fernandezmilerai* Varela, 2010                  |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres garridoi* Varela et al., 2007                   |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres kimi* Varela, 2012                              |          |         |                   |           |                  |                    |                       |                  |
| *Asterocheres lalanai* Varela, 2013                           |          |         |                   |           |                  |                    |                       |                  |
**Table 6** Symbiotic copepods recorded on reef-dwelling anthozoans, echinoderms and sponges of the Greater Caribbean. The Gulf of Mexico has no records and is not included (cont.)

| Copepod species / Ecoregion | Bahamian | Bermuda | Eastern Caribbean | Floridian | Greater Antilles | Southern Caribbean | Southwestern Caribbean | Western Caribbean |
|----------------------------|----------|---------|--------------------|-----------|------------------|--------------------|------------------------|------------------|
| *Asterocheres maxillatus* Stock, 1987 | | | | | | | | x |
| *Asterocheres reginae* Boxshall & Huys, 1994 | | | | | | | | x |
| *Asterocheres oricurvus* Kim, 2010 | | | | | | | | x |
| *Asterocheres peniculatus* Kim, 2010 | | | | | | | | x |
| *Asterocheres plumosus* Kim, 2010 | | | | | | | | x |
| *Asterocheres reginae* Boxshall & Huys, 1994 | | | | | | | | x |
| *Asterocheres simulans* (T. Scott, 1898) | | | | | | | | x |
| *Asterocheres trisetatus* Kim, 2010 | | | | | | | | x |
| *Asterocheres unioviger* Kim, 2010 | | | | | | | | x |
| *Asteropontella f oliata* Stock, 1989 | | | | | | | | x |
| *Asteropontius capillatus* Kim, 2010 | | | | | | | | x |
| *Asteropontius iuxtus* Stock, 1989 | | | | | | | | x |
| *Asteropontius longipalpus* Stock, 1975 | | | | | | | | x |
| *Asteropontius mycetophylliae* Varela, Ortiz & Lalana, 2005, 2005 | | | | | | | | x |
| *Asteropontius parvipalpus* Stock, 1975 | | | | | | | | x |
| *Asteropontius proximus* Stock, 1987 | | | | | | | | x |
| *Asteropontius ungellatus* Stock, 1975 | | | | | | | | x |
| *Asteropontopsis faviae* Stock, 1987 | | | | | | | | x |
| *Calonastes imparipes* Humes & Goenaga, 1978 | | | | | | | | x |
| *Caribeopsyllus* sp. A | | | | | | | | x |
| *Caribeopsyllus chawayi* Suárez-Morales, 1998 | | | | | | | | x |
| *Caribulus sculp tus* (Humes, 1969) | | | | | | | | x |
| *Chelacheres longipalpus* Stock & Humes, 1995 | | | | | | | | x |
| *Chelacheres optans* Stock & Humes, 1995 | | | | | | | | x |
| Species                                              | Status |
|------------------------------------------------------|--------|
| *Collocheres lunulifer* Humes, 1998                  | x      |
| *Corallonoxia baki* Stock, 1975                      | x      |
| *Corallonoxia longicauda* Stock, 1975                | x      |
| *Coralloxenia brevibrachium* Stock, 1975             | x      |
| *Coralloxenia dorsospinosa minor* Stock, 1975        | x      |
| *Coralloxenia dorsospinosa* Stock, 1975              | x      |
| *Coralloxenia kristensenii* Stock, 1975              | x      |
| *Coralloxenia longibrachium* Stock, 1975             | x      |
| *Coralloxenia mediobrachium* Stock, 1975             | x      |
| *Coralloxenia mixtibrachium* Stock, 1975             | x      |
| *Coralloxenia similis* Stock, 1975                   | x      |
| *Coralloxenia ventrospinosa* Stock, 1975             | x      |
| *Critomolgus* sp.                                    | x      |
| *Critomolgus astrophyticus* (Humes & Stock, 1973)   | x      |
| *Critomolgus titillans* (Humes, 1982)                | x      |
| *Diogenella deichmannae* Humes & Ho, 1970           | x      |
| *Diogenella impar* Humes & Ho, 1970                 | x      |
| *Diogenella seticauda* Stock, 1968                   | x      |
| *Diogenella spinicauda* Stock, 1968                  | x      |
| *Diogenidium deforme* Stock, 1968                    | x      |
| *Diogenidium nasatum* Edwards, 1891                  | x      |
| *Diogenidium spinulosum* Stock, 1968                 | x      |
| *Diogenidium tectum* Humes & Ho, 1971                | x      |
| *Enalcyonium* sp.                                    | x      |
| *Enalcyonium euniceae* Stock, 1973                   | x      |
| *Enalcyonium nudum* Stock, 1973                      | x      |
| *Enalcyonium ramosum* Stock, 1973                    | x      |
| *Enalcyonium varicauda* Stock, 1973                  | x      |
| *Eupolymniphilus occidentalis* Kim, 2009             | x      |
TABLE 6  Symbiotic copepods recorded on reef-dwelling anthozoans, echinoderms and sponges of the Greater Caribbean. The Gulf of Mexico has no records and is not included (cont.)

| Copepod species / Ecoregion | Bahamian | Bermuda | Eastern Caribbean | Floridian | Greater Antilles | Southern Caribbean | Southwestern Caribbean | Western Caribbean |
|----------------------------|----------|---------|-------------------|-----------|------------------|---------------------|------------------------|-------------------|
| *Hemicyclops columnaris* Humes, 1984 | × | × | | | | | | |
| *Hermacheres diploriae* Stock, 1987 | | | | | | | | |
| *Hermacheres montastreae* Stock, 1987 | | | | | | | | |
| *Hetairosynella aculeata* Kim, 2010 | × | | | | | | | |
| *Hetairosynella angulata* Kim, 2010 | | | | | | | | |
| *Hetairosynella bifurcata* Kim, 2010 | | | | | | | | |
| *Kimcheres fastigatus* (Kim, 2010) | × | | | | | | | |
| *Lamippina aequalis* Stock, 1973 | | | | | | | | |
| *Linaresia bouligandi* Stock, 1979 | | | | | | | | |
| *Macrochiron echinicolum* Humes & Stock, 1973 | × | | | | | | | |
| *Macrochiron sargassi* Sars, 1916 | × | | | | | | | |
| *Magnippe caputmedusae* Stock, 1978 | × | | | | | | | |
| *Meandromyzon coronatum* Stock, 1989 | | | | | | | | |
| *Meomicola amplectans* Stock, Humes & Gooding, 1963 | × | | | | | | | |
| *Micropontius glaber* Stock, Humes & Gooding, 1963 | | | | | | | | |
| *Nanaspis exigua* Stock, Humes & Gooding, 1962 | × | | | | | | | |
| *Nanaspis media* Stock, Humes & Gooding, 1962 | | | | | | | | |
| *Nanaspis pollens* Stock, Humes & Gooding, 1962 | | | | | | | | |
| *Nanaspis truncata* Stock, Humes & Gooding, 1962 | | | | | | | | |
| *Neoasterocheres humesi* (Varela, 2012) | × | | | | | | | |
| *Onychocheres alatus* Stock & Gooding, 1986 | | | | | | | | |
| *Ophiopsyllus latus* Humes & Hendler, 1999 | × | | | | | | | |
| *Ophiopsyllus reductus* Stock, Humes & Gooding, 1963 | × | | | | | | | |
| Species | Authors and Year |
|---------|-----------------|
| *Ophiurocheres bellulus* | Humes, 1998 |
| *Orecturus antillensis* | Varela, 2011 |
| *Orecturus ortizi* | Varela & Lalana, 2007 |
| *Paramolgus antillianus* | Stock, 1975 |
| *Parmulella emarginata* | Stock, 1992 |
| *Parmulodes verrucosa* | Wilson C.B., 1944 |
| *Parophiopsyllus ligatus* | Humes & Hendler, 1972 |
| *Peltomyzon rostratum* | Stock, 1975 |
| *Presynaptiphilus amphioplus* | Humes & Hendler, 1972 |
| *Pseudanthessius acutus* | Kim, 2009 |
| *Pseudanthessius deficiens* | Stock, Humes & Gooding, 1963 |
| *Pseudanthessius exilicornis* | Stock & Humes, 1995 |
| *Pseudanthessius pectinifer* | Stock, Humes & Gooding, 1964 |
| *Pseudanthessius pectinifer* | Stock, Humes & Gooding, 1964 |
| *Ridgewayia fosshageni* | Humes & Smith, 1974 |
| *Scottocheres elongatus* | (Scott T. & Scott A., 1894) |
| *Setacheres paraboecki* | (Johnsson, 1998) |
| *Sphaerippe caligicola* | Grygier, 1980 |
| *Sphaerippe sp.* | |
| *Stenomyzon edentatum* | Kim, 2010 |
(25 of 81) records of copepods found on unidentified sponges.

Cyclopoida, representing mainly poecilo-stomatoids, with 317 records for 59 species is the most diverse order of copepods found in symbiosis with corals, sponges and echinoderms; Siphonostomatoida with 170 records of 55 species is the next (figs. 1–3, table 4). The order Calanoida is represented by the only known symbiotic calanoid copepod *Ridgewayia fosshageni* found associated with an actinian at the Atlantic coast of Panama (Humes & Smith, 1974). The absence in the literature of any records of symbiotic harpacticoids is contradicted by the results recently obtained from samples of undescribed harpacticoids representing the family Laophontidae (see Yeom et al., 2018). Siphonostomatoid copepods of the diverse but poorly investigated family Asterocheridae and poecilostomatoid cyclopoids representing endoparasitic Corallovexiidae have the greatest diversity of associations and the highest number of host families (table 5). Asterocheridae are found living on invertebrates belonging to 22 families of cnidarians, echinoderms and sponges; Rhynchomolgidae are recorded from eight families of anthozoans and echinoderms; Corallovexiidae from five families of stony corals only. Three families (Lamippidae, Pseudanthesiidae, and Synaptiphilidae) are found associated with four host families; Macrochironidae and Nanaspidiidae are found with three host families; Cancerillidae and Lichomolgidae are found with two host families; seven families (Clausidiidae, Entomolepididae, Micropontiidae, Pseudocyclopidae, Sabelliphilidae, Synaptiphilidae, and Thaumatopsyllidae) are restricted to only one family of invertebrate hosts (table 5). The remarkable absence on Caribbean host corals for copepods of the families Anchimolgidae (124 species in 32 genera) and Xarifidae (96 species in 6 genera) so far only found on Indo-Pacific scleractinians (Stock, 1988), is confirmed by literature data and results of our recent sampling (Cheng et al., 2016; Hoeksema et al., 2017b; table 1). To explain this distribution a study of phylogenetic relationships of Corallovexiidae with other families of the order and the additional search for endoparasitic copepods living in Indo-Pacific stony corals is needed. This proposed study should includemethodsthatenablealldissolutiononlyof soft coral tissue while the chitinous exoskeletons of microscopic crustaceans to remain intact.

### Table 7

Numbers of reef-dwelling species of Caribbean anthozoans, sponges, and echinoderms recorded as host for copepods

| Taxa                           | Estimated number of invertebrate host species | Number of species associated with copepods | Percent of total species |
|--------------------------------|-----------------------------------------------|-------------------------------------------|-------------------------|
| Subclass Hexacorallia (1)      | 45                                            | 21                                        | 47%                     |
| Subclass Octocorallia (2)      | 195                                           | 18                                        | 9%                      |
| Phylum Echinodermata (3, 4)    | 955                                           | 31                                        | 3%                      |
| Phylum Porifera (5)            | 760                                           | 9                                         | 1%                      |
| Total number                   | 1955                                          | 79                                        | 4%                      |

1 – Ivanenko, 2016, 2 – Bayer, 1961, 3 – Alvarado, 2011, 4 – Pawson et al., 2009, 5 – Perez et al., 2017
Fifty of 115 species of symbiotic copepods are mentioned in literature only once; 83 of 115 species of copepods are reported from only one species or one genus of the host. Only 13 species are reported in symbiosis with representatives of different families. Four species of copepods, the poecilostomatoids *Eupolymniphilus occidentalis* (fig. 1g), *Hemicyclops columnaris*, *Pseudanthessius deficiens* (fig. 1e) and the siphonostomatoid *Nanaspis pollens* (fig. 3e) are found in symbiosis with representatives of different classes. Of these species only *Hemicyclops columnaris* is found associated with invertebrates representing different phyla: echinoderms, corals, sponges and arthropods. The finding on sponge and on a compound ascidian of the copepod *Eupolymniphilus occidentalis* (family Sabelliphilidae) typically living on tubicolous polychaetes requires additional confirmation (Kim, 2009). Only two species of copepods are reported living on different classes: *Pseudanthessius deficiens* is found on three species of echinoderms to holothurians and echinoids; *Nanaspis pollens* is found on holothurians and ophiuroids. Thus, most species of symbiotic copepods are found associated with invertebrate hosts belonging to a single genus or only one family. These finding suggest the need to study the effect of host specificity more extensively. Similar studies of host switching events may show that this phenomenon has occurred several times during in the evolution of symbiotic copepods, as it has among decapod crustacean taxa (Fransen & Hoeksema, 2014; Brinkmann & Fransen, 2016; García-Hernández et al., 2016; Horká et al., 2016; Hoeksema & Fransen, 2017; Hoeksema et al., 2018). The very nature of the specificity of copepods to the host or to the group of hosts requires a thorough sampling program as well as the use of molecular methods (Ivanenko et al., 2018).

The number of copepod species found on a single host species varies from one to six. The sea cucumber *Holothuria arenicola* hosts six species of copepods (table 2). Three scleractinian and two holoturian species host five copepod species. The sea urchin *Meoma ventricosa* and the sea cucumber *Actinopyga agassizii* host four copepod species; three corals and one sponge host three species each; 18 host species have been recorded with two associated species of symbiotic copepods. Numerous findings of different species of symbiotic copepods on the same hosts as well as the presence on these hosts of other symbionts (shrimps, polychaetes, decapods, amphipods, fish etc.) shows little knowledge of species relationships in the symbiotic complexes (Stella et al., 2011; Hoeksema et al., 2012).

Copepod crustaceans living in symbiosis with the Caribbean reef invertebrates express diverse body shapes (cyclopiform, spherical, flattened etc.), remarkably different body sizes ranging from 0.25 mm (such as *Collocheres lunulifer*) to 4.75 mm (such as *Corallovelaxia ventrospinosa*), and various types of feeding apparatuses as well as host utilizations. Analysis of literature and sorting of samples shows a different, and sometimes very large number of individual copepods living on a single host. The most numerous are the poorly studied asterocherid copepods living on and in diverse sponges: in one sample on one sponge thousands of individual copepods belonging to several species (*Schirl, 1973; Ivanenko & Smurov, 1997; Ivanenko, 1998; Klinger et al., 2019; present study). The diversity, host specificity and phylogenetic relationships of these copepods with other siphonostomatoid copepods, especially species found in association with Caribbean stony corals are among the most interesting unexplored topics in coral reef ecology.

The symbiotic copepods are characterized by different ways of attachment to their host (loosely associated with or aggregating on the host's surface, tightly attached to the host
by claw-like appendages, inducing a gall-like structure, or residing inside of intestine, body cavity, or the host tissues). They also show marked variation in the number of embryos present in the egg-sacs (from one embryo, as in *Peltomyzon rostratum*, to 50 embryos, as in *Caribulus sculptus*) or numerous embryos laid in copepod-induced galls. The symbiotic copepods have different types of lecithotrophic and planktotrophic naupliar stages, some of which, like Thaumatopsyllidae, are parasitic in the stomach of its host brittle star (fig. 2e; Hendler & Kim, 2010).

Most of the ecological observations of the Caribbean symbiotic copepods are short comments added to the taxonomic descriptions and describe behavioral features and/or location on the host. Exceptions are the study of *Ophiopsyllus reductus* parasitizing on shallow-water ophiuroids (Emson & Mladenov, 1987; Emson et al., 1985), the ecological observations of the endoparasitic copepods of the family Corallocoxidae living in stony corals (Butter, 1979; Herriott & Immermann, 1979), the studies of the life cycle and ecology of copepods of the family Thaumatopsyllidae parasitizing living in the ophiuroids at naupliar stages and having non-feeding adult and subadult copepodid stages (Suarez-Morales & Castellanos, 1998; Suarez-Morales & Tovar, 2004; Hendler & Kim, 2010; Ferrari et al., 2010; Ferrari & von Vaupel Klein, 2019), and the experiments on calanoid copepods that were discovered in a host-specific association with only one species of actinarian (Humes & Smith, 1974). Recent field trips to sample Caribbean symbiotic copepods lead to the discovery of new species of octocorals, 3% of echinoderms and of less than 1% species of sponges (table 7). They are found on 4% of potential hosts of the Caribbean invertebrates which corresponds with previous data on symbiotic copepods (Humes, 1994). The literature and samples analyses indicate a poor knowledge of the diversity and distribution of symbiotic copepods living on different hosts in various ecoregions, and a particularly poor knowledge of copepods living on corals and sponges (Boxshall & Huys, 1994; García-Hernández et al., 2019; present study) with unknown but potentially high impact on their host and reef community (Ho, 2001; Berkenbusch & Rowden, 2003; Hatcher et al., 2012; Shelyakin et al., 2018; Zeppilli et al., 2015, 2018).

**Acknowledgements**

The preparation of the database, sampling in Cuba and processing of the paper were supported by the Russian Foundation for Basic Research (grant 18-54-34007). The data on samples from St. Eustatius (2015) and Curacao (2017) were obtained with support of a Temminck-Fellowships to VNI by Naturalis Biodiversity Center. BWH and VNI want to thank staffs of the Caribbean Netherlands Science Institute (CNSI) at St. Eustatius and the Carmabi Research Station at Curacao for hospitality and assistance. Sorting of samples and identification of copepods were conducted with partial support of the Russian Foundation for Basic Research (grant 18-04-01192). Jaaziel Emmanuel Garcia-Hernandez (University of Puerto Rico at Mayagüez) provided identification of sponges collected during the field trips; Frank Ferrari commented on a draft of the manuscript; Maickel Armenteros (University of Havana) hosted VNI and OAK during the field trip to Cuba.
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RECEIVED: 29 APRIL 2019 | REVISED AND ACCEPTED: 2 JULY 2019

EDITOR: R.W.M. VAN SOEST