Copepods associated with scleractinian corals: a worldwide checklist and a case study of their impact on the reef-building coral *Pocillopora damicornis* (Linnaeus, 1758) (*Pocilloporidae*)

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Abstract

The Cnidaria have more symbiotic copepods than any other group of invertebrates, and the greatest numbers of these associates occur on hard corals. A review of the disparate literature on the diversity and taxonomic composition of scleractinian-associated copepods and their hosts revealed a total of 148 coral species, representing 66 genera and 15 families that serve as hosts to copepods. At present, 363 copepod species, representing 99 genera, 19 families and three orders, have been recorded as associates of scleractinian corals. The total included 288 cyclopoids, 68 siphonostomatoids and seven harpacticoids. Within the Cyclopoida the representation of species varied greatly among the 13 families, with a disproportionate number of species belonging to the Anemophilidae (141 species) and Xarifiidae (92 species). Data on host utilization and geographical distribution of all copepods living symbiotically with hard corals is synthesized and host specificity patterns are highlighted.

The prevalence, intensity, density, and biodiversity of copepod infection of 480 colonies of the reef-building coral *Pocillopora damicornis* (Linnaeus, 1758) from Nanwan Bay, southern Taiwan were documented between July 2007 and November 2008. It was hypothesized that certain environmental factors and physiological coral traits, such as the density of *Symbiodinium*, could influence these infection parameters. Analysis revealed that ectoparasitic copepods were the most likely to infect *P. damicornis*, and that *Asteropontius minutus* Kim, 2003 accounted for more than 50% of total copepod density in July–September 2007 when temperatures were high and bleaching occurred in ~75% of the sampled colonies. The data further showed that copepod virulence may be related to their life history strategies, as well as to *Symbiodinium* density, surface area of the host coral colonies, and concentration of nitrate and chlorophyll-α in the surrounding seawater. By tracking the abundance, diversity, and performance of infectious copepods prior, throughout, and after a natural bleaching event, the potential to use these parasites as bioindicators for predicting the future physiological performance of *P. damicornis* in response to environmental change, particularly bleaching events, may ultimately be further explored, developed and maximized.

Humesimyzon Kim, 2010, previously placed in the Asteroceridae, is tentatively transferred to the recently resurrected family Coralliomyzontidae. The authorship and spelling of *Pseudanthessius thorelli* (Brady, 1880) are corrected.

Key words: bleaching, checklist, copepod, coral reef, infection, *Symbiodinium*, Scleractinia, symbiosis, water pollution

Introduction

Parasites play important roles in all ecosystems by exerting a concerted selection pressure on their hosts (Price 1980) via effects on growth and physiology, spatial distribution, and reproductive success (Hamilton & Zuk 1982; Holmes 1995; Schall 1996; Harvell et al. 2002). Consequently, understanding the biology of parasites is not only critical for advancing ecological knowledge, but is also a prerequisite for the conservation of host populations
(Pérez et al. 2006; Thompson et al. 2010; Gómez & Nichols 2013; Page 2013).

In addition to endogenous factors (e.g., intrinsic growth rate), parasite virulence may be controlled by the physiology of their hosts, as well as by the abiotic milieu. For instance, the host’s nutritional status, reproductive effort, sex, age, and size can influence the infection capacity of parasites (Paling 1965; Brown et al. 2000; Biegler & Ebert 2009), as can the proximity to other hosts. Healthy hosts may have more effective immune systems that are more readily able to fight off parasite infections, while physiologically compromised organisms may lack such cell- and/or antibody-mediated immune responses, especially when simultaneously exposed to sub-optimal environmental conditions (Corbel 1975). The overall performance (i.e., growth and proliferation) and, when applicable, diversity of the parasites themselves is also highly attuned to environmental change (Mouritsen & Poulin 2002; Ogden et al. 2006; O’Connor et al. 2007). Moller (2010) suggested that changes in certain environmental conditions affect different parasite species in dissimilar ways and thus play a critical role in altering the composition, emergence time, reproductive capacity, abundance, and virulence of the parasite community.

In coral reef ecosystems, studies of white-band disease, white plague, and other infectious diseases have revealed that high seawater temperatures tend to precede such infections, particularly those in which the predominant hosts are the reef-building corals (Glafelter 1982; Richardson et al. 1998a, 1998b; Porter et al. 2001). Harvell et al. (2001) documented an association between high temperature-induced coral bleaching and an epizootic infection of the Caribbean octocoral Briareum asbestinum (Pallas, 1766) and pointed out that these gorgonians were more susceptible to infection during the warmer summer months. The stress associated with exposure to high seawater temperatures may have resulted in an immuno-compromised state that led to increased susceptibility to infection, though it is also possible that the parasites demonstrated elevated performance at high temperatures (Harvell et al. 2002; Lafferty & Holt 2003).

Coral reefs encompass the highest biodiversity of any marine ecosystem, with estimates of the number of species ranging from 172,000 to over 9,000,000 (Reaka-Kudla 1997; Ruppert et al. 2004), and have been associated with the evolution of the largest diversity of symbiotic associations in the marine environment and possibly the biosphere (Castro 1988). According to a recent review there are at least 869 invertebrate species that have been described as coral-associated, of which 636 are crustaceans, with decapods and copepods being the dominant taxa (Stella et al. 2011). The highly successful association between copepods and cnidarian hosts is a common theme in the literature (Humes 1985a, 1985c, 1994b). Among various invertebrate groups, the Cnidaria have more copepod associates than any other group. Many species live in association with hard or soft corals, displaying an array of symbiotic modes of life, ranging from mutualistic in certain cases to parasitic in others. Among the various orders of Copepoda, the Cyclopoida (including Poecilostomatoida) contains by far the greatest number of species that live in association with hard corals. In contrast, members of the orders Harpacticoidea and Siphonostomatoida are mainly endosymbiotic, more loosely associated with their scleractinian hosts and occur in relatively smaller numbers (Humes 1985c). Coral-associated copepods exhibit a marked diversity in morphology, and more specifically, appendage structure, in accordance with their respective ecological niches. Members of several copepod lineages such as the Xaridiae inhabit the gastrovascular cavities of the coral polyps and are seemingly immune to the nematocysts of their hosts. Based on live observations Cheng & Dai (2009) suggested that xarifids may release chemicals to induce the relaxation of coral polyps prior to entering them. Cheng & Dai (2010) documented the presence of *Symbiodinium* spp. in the gut of *Xarifia fissilis* Humes, 1985a and suggested that the copepods may consume these endosymbiotic dinoflagellates and probably depend on them for their survival. Coral bleaching, during which the endosymbiosis between corals and *Symbiodinium* spp. breaks down due to environmental change, particularly increasing seawater temperatures (Hoegh-Guldberg 1999) may be exacerbated by the activity of parasitic copepods. However, the relationship between copepod infection/virulence and coral bleaching is still poorly understood.

To date, there has not been a taxonomic review of all known scleractinian coral-associated copepods and the hosts with which they associate. The primary aim of this study is to assemble and synthesize the scattered literature on host utilization and geographical distribution of copepods living symbiotically with hard corals. Secondly, in a case study we examine the impact some of these copepods may have on a scleractinian coral species in Taiwanese waters. *Pocillopora damicornis* (Linnaeus, 1758) (Pociloporidae), commonly known as the cauliflower coral, is native to tropical and subtropical parts of the Indian and Pacific Oceans and serves as host to at least 17 species of copepods (Humes 1962a, 1985a; Stock 1966; Johnsson et al. 2002; Kim 2003, 2004a, 2007; Ho et al. 2008; Cheng & Dai 2010; Cheng 2011; this study). Here, we attempt to reveal temporal variation in species composition of...
symbiotic copepods inhabiting this scleractinian, and to test the hypothesis that the occurrence of these copepods might vary with *Symbiodinium* density, physiology of the host corals, and particular abiotic parameters. It was specifically hypothesized that higher rates of copepod infection would be documented during high temperature months, and particularly during bleaching events. More specifically, we attempt (1) to document three copepod infestation parameters including prevalence (i.e., percentage of colonies that were infected), “intensity” of infection (i.e., number of parasites on infected hosts only), and density (i.e., intensity/unit area; *sensu* Bush et al. 1997; Rózsa et al. 2000; Smallridge & Bull 2000), at a variety of seawater temperatures from July 2007 to November 2008 (including a mass coral bleaching event in the summer of 2007, Fig. 1), (2) to determine whether an association exists between *Symbiodinium* density and the abundance of copepods, (3) to investigate which physical factors might increase the susceptibility of host corals to copepod infection, and (4) to test the possibility of using copepods to estimate coral, or even coral reef ecosystem, health. Collectively, it was hoped that the dataset produced herein may uncover the factors that influence the virulence of copepods, and provide a clearer picture of the relationship, if any, between coral bleaching and copepod infection.

**Materials and methods**

**Sample collection.** Sixty fragments of *P. damicornis*, each approximately 5–9 cm in length and 3–5 cm in width, were randomly collected at 1–5 m depth at two sites within Nanwan Bay (“Leidashih”: 21°55.344’ N, 120°44.359’ E and “Tiaoshi”: 21°57.555’ N, 120°45.989’ E), southern Taiwan in July, August, and September 2007, and January, March, May, August, and November 2008. A mass bleaching event was observed during the former three sampling months, and it was not possible to collect a mix of healthy and bleached corals given that about 75% of the *P. damicornis* colonies appeared to be bleached. At other sampling times, corals with a healthy appearance, which were in the vast majority (only few bleached colonies were observed in the summer of 2008), were instead collected. Coral fragments were placed in plastic bags and brought back to the laboratory. Then, coral fragments were placed in small (150–200 ml) containers of seawater, to which 1 ml of 70% ethanol was gradually added every 10–20 min over the course of several hours to a final solution of 5% ethanol/95% seawater. The coral fragments were immersed in this solution for 6–8 hours to cause the expulsion of the copepods from the coral polyps. The solution was then poured through a fine mesh (100 µm pore size) net, and the copepods were collected from the residue under a dissecting microscope and preserved in 70% ethanol.

**Water quality assessment.** To assess the water quality in Nanwan Bay, water samples were collected at the two study sites, as well as two other nearby sites: “Wanlitong” (21°59.770’ N, 120°42.290’ E) and “Siangjiao Bay” (21°55.481’ N, 120°49.942’ E), with metal-free Niskin bottles and analyzed immediately for temperature, salinity, pH, and oxygen saturation with a Sea-Bird Model 19 plus profiling CTD (Sea-Bird Electronics) deployed from a small craft research vessel. The remaining water samples were preserved at 4°C and returned to the laboratory for subsequent analysis of biochemical oxygen demand (BOD), nitrate, silicate, chlorophyll-a concentrations, and turbidity. All seawater quality analyses were conducted as in Meng et al. (2008).

**Morphological studies of coral-associated copepods.** Morphological studies of the coral-associated copepods followed the standardized methods for studying parasitic copepods of Humes & Gooding (1964). Briefly, copepods were cleared in 85% lactic acid for 1–2 hours prior to dissection on a wooden slide under a dissecting microscope (Olympus SZH–II LD). Then, the dissected body parts and appendages were examined under a compound microscope (Zeiss AXIOSKOP–40). Taxonomic identifications were made based on published descriptions (Humes 1960,1962a; Humes & Ho 1968b; Humes 1985c; Kim 2003, 2004a, 2007).

**Density of endosymbiotic dinoflagellates.** *Symbiodinium* cells were isolated from each fragment of *P. damicornis*. Coral fragments were placed into calcium-magnesium-free artificial seawater (CMF: 540 mM NaCl; 10 mM KCl; 7 mM NaSO₄; 0.2 mM NaHCO₃; 20 mM Tris-HCl; 20 mM EDTA, pH 8.2 with 100 U/ml of each of the antibiotics penicillin and streptomycin) for 24 hours. The solution containing coral tissues and dinoflagellate cells was centrifuged at 2000 rpm for 10 min. The supernatants were carefully discarded, and the dinoflagellate pellets were resuspended in 3–5% formaldehyde in filtered seawater (FSW). Then, the number of *Symbiodinium* was quantified in 10 µl volumes (5 replicates per samples) with a hemocytometer and normalized to surface area as described below.
Coral fragment surface area. In order to normalize the infection density of copepods on corals, as well as the Symbiodinium density, to unit area, the surface area (cm²) of coral fragments was measured following the procedures described in Stimson & Kinize (1991). Briefly, each coral fragment was weighed with an Ohaus® GT40 electronic balance (1 mg precision), immersed for ~2 seconds in molten paraffin wax at 60°C, and allowed to cool briefly at room temperature before weighing again. Cement blocks of known surface area and weight were measured following the same procedure to serve as standards against which the surface area of the coral fragments could be calculated. Specifically, the mass increase due to wax having coated the surface of the blocks was plotted against the surface area of the blocks, and the coral fragment mass increases due to wax coating were inserted into the equation fitting the standard curve generated to calculate surface area.

Epidemiology of parasitic copepods and statistical procedures. The total numbers of copepod parasites were quantified as described above and normalized to the surface area of the coral fragment. Prevalence (i.e., percentage of colonies harboring copepods), mean intensity, and median intensity were recorded as described in Bush et al. (1997) and Rózsa et al. (2000). Monthly differences in parasite prevalence were determined using Fisher’s Exact Tests in the Quantitative Parasitology 1.0 software package (Rózsa et al., 2000). One-way ANOVAs followed by Tukey’s HSD post-hoc tests (both conducted in the SPSS ver. 16 statistical software package) were used for analyzing differences in mean intensity and density over time (data were pooled across the two sites given their proximity). Differences in median intensity were analyzed using Mood’s median test in the Quantitative Parasitology 1.0 software package. Bivariate correlations between water quality parameters, Symbiodinium density, coral surface area, and mean density of copepods were determined by correlation analysis (conducted in the SPSS ver. 16 statistical software package). Multidimensional scaling (MDS) and analysis of similarity (ANOSIM) were used to assess similarity in species composition and abundance of symbiotic copepods between different sampling months. The species contribution to the dissimilarity of each sampling month was determined by similarity percentages (SIMPER, PRIMER, version 6, Clarke & Warwick 2001). The variation in the structure of coral-associated copepod communities among sampling periods was explored using principal components analysis (PCA, PRIMER, version 6). In the analysis, copepods were classified into five functional groups: endoparasitic with spiny mandibles (ESM), endoparasitic without spiny mandibles (EWSM), ectoparasitic with a siphon (ES), ectoparasitic without a siphon (EWS), and benthic (BE).

Host nomenclature. Currently valid names of coral host taxa follow the World Register of Marine Species (WoRMS Editorial Board 2016).

Results

Symbiotic copepods using scleractinian hosts. At present, 363 copepod species have been recorded as associates of scleractinian corals (Table 1). These species represent 99 genera, 19 families and three orders, in addition to two species (Parangium abstrusum Humes, 1985; Stockella indica (Sebastian & Pillai, 1974)) which are currently classified as incertae sedis. The total included seven harpacticoids, 68 siphonostomatoids and 288 cyclopoids (here considered as encompassing the former Poecilostomatoida). Within the Cyclopoida the representation of species varied greatly among the 13 families, with a disproportionate number of species belonging to the Anchimoligidae (141 species; 49%) and Xarifidae (92 species; 32%). Other representative families include the Rhynchomolgidae (31 species) which – except for the genera Doridicola Leydig, 1853 and Critomolgus Humes & Stock, 1983 – are typically associated with cnidianarian (but not exclusively scleractinian) hosts, and the Corallovelvexidae (10 species) which are endoparasites of Caribbean hard corals. The remaining nine families mostly contain only a single species that has entered into a symbiotic relationship with a scleractinian host and are otherwise associated with other host groups, or mostly free-living (e.g. Cycloidae, Cyclopinaidae). At generic level, the families Anchimoligidae (34 genera) and Rhynchomolgidae (19 genera) are by far the most diverse, constituting nearly 74% of the total number of cyclopoid genera to utilize hard coral hosts. The Siphonostomatoida is represented by four families of which the Asterocheridae (55 species) and Coralliomyzontidae (8 species) are the most speciose. Although the hosts of most Artotrogidae and Entomolepididae are currently unknown, a few species (4 and 1, respectively) have been confirmed as associates of scleractinian corals. Except for Alteuthellopsis corallina Humes, 1981a (Peltidiidae), all authenticated harpacticoid records from hard coral hosts refer to species of the family Tegastidae.
<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>Reference</th>
<th>Location</th>
<th>Author(s)</th>
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<td><em>Acropora exigua</em> (Dana, 1846)</td>
<td>New Caledonia</td>
<td>Humes (1981a)</td>
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<td></td>
<td><em>Astreopora</em> sp.</td>
<td>Madagascar</td>
<td>Humes (1981a)</td>
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<td><em>Gardinerosera planulata</em> (Dana, 1846)</td>
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<td>Humes (1992b)</td>
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<td><em>Goniastrea retiformis</em> (Lamarck, 1816)</td>
<td>Moluccas</td>
<td>Humes (1981a)</td>
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<td>Madagascar</td>
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<td>Genus</td>
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<td><em>Peltidium</em> perturbatum</td>
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<td>Geddes, 1968</td>
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<td><em>Peltidium</em> sp.</td>
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<td><em>Madracis</em> myriaster</td>
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<td>(Milne Edwards &amp; Haime, 1850) 1</td>
<td>Barbados</td>
<td>Snelgrove &amp; Lewis (1989)</td>
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<td><em>Madracis</em> myriaster</td>
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<td>(Milne Edwards &amp; Haime, 1850) 1</td>
<td>Barbados</td>
<td>Snelgrove &amp; Lewis (1989)</td>
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**Family Porcellidiidae**

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**Family Tegastidae**

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<td>Humes, 1984 1</td>
<td>Hawaii</td>
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<tr>
<td><em>Tegastes</em> georgei</td>
<td></td>
<td>Marcus &amp; Masry, 1971</td>
<td>Gulf of Aqaba</td>
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<tr>
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<td>Humes, 1984 1</td>
<td>Society Islands</td>
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<td><em>Tegastes</em> singularisae</td>
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<td>Tanzania</td>
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**Family Tetragonacipitidae**

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<td><em>Tetragonacipitidae</em> sp.</td>
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**Family Thalestridae**

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<td><em>Phyloiothakos</em> mystis</td>
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**Family Tisbidae**

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<td><em>Tisbe</em> spp.</td>
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</table>
Order CYCLOPODA (including POECILOSTOMATOIDEA)

**Family Anchimolgidae**

*Alienigena triangula* Cheng, Ho & Dai, 2016a

*Allopodon minutum* Humes, 1978a

*Allopodon ryukyuensis* Kim & Yamashiro, 2007

*Amanda compta* Humes & Stock, 1973

*Amanda citrina* Humes & Stock, 1972

*Amanda curvus* Kim, 2007

*Amanda gonastreae* Humes, 1985b

*Amandopsis merulinae* Humes, 1974b

*Anchimolgus abbreviatus* Humes, 1991b

*Anchimolgus angustus* (Humes, 1992c)

*Anchimolgus brevisius* Humes, 1995a

*Anchimolgus compressus* Humes, 1996b

*Anchimolgus conformatus* Humes, 1995a

*Anchimolgus contractus* Humes, 1979a

*Anchimolgus convexus* Humes, 1978b

*Anchimolgus digitatis* (Humes & Ho, 1968a)

*Anchimolgus eparmatoideus* Humes, 1992c

*Anchimolgus exsertus* Humes, 1991b

*Anchimolgus gibbeniae* (Humes, 1992c)

*Anchimolgus gigas* Humes, 1995a

*Pavona expanulata* (Lamarck, 1816)

*Montipora cf. undata* Bernard, 1897

*Montipora aequisuberculata* Bernard, 1897

*Montipora informis* Bernard, 1897

*Favia sp.*

*Favia sp.*

*Goniastrea retiformis* (Lamarck, 1816)

*Goniastrea retiformis* (Lamarck, 1816)

*Goniastrea stelligera* (Dana, 1846)

*Merulina ampla* (Ellis & Solander, 1786)

*Leptoria phrygia* (Ellis & Solander, 1786)

*Merulina ampla* (Ellis & Solander, 1786)

*Galaxea fascicularis* (Linnaeus, 1767)

*Galaxea horreens* (Dana, 1846)

*Goniopora stokesi* Milne Edwards & Haime, 1851b

*Goniopora stokesi* Milne Edwards & Haime, 1851b

*Galaxea fascicularis* (Linnaeus, 1767)

*Goniopora sp.*

*Goniopora fascicularis* (Linnaeus, 1767)

*Sandulolita robusta* (Quelch, 1886)

*Favia sp.*

*Goniopora tenulidens* (Quelch, 1886)

*Goniopora sp.*

*Goniopora stokesi* Milne Edwards & Haime, 1851b

Taiwan

Taiwan

Japan (Okinawa)

Madagascar

Madagascar

Meluccas

Taiwan

Cheng et al. (2016a)

Humes (1978a)

Humes (1978a)

Cheng et al. (2010)

Kim & Yamashiro (2007)

Humes & Stock (1973)

Humes & Stock (1973)

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<td>Acropora cytherea</td>
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<td>Acropora hyacinthus</td>
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<td>Acropora speciosa</td>
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<td>Acropora squarrosa</td>
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<td>Acropora intermedia</td>
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<td>Acropora elsey</td>
<td>(Brook, 1892)</td>
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<td>Acropora valida</td>
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<td>Acropora distichia</td>
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<td>Acropora abnatanoides</td>
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<td>Acropora kripipe</td>
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<td>Ctenactis echinata</td>
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<td>Sandalolitha robusta</td>
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<td>Acropora elsey</td>
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**References:**
- Humes, 1991b
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- Kim, 2009
- Kim, 2003
- Humes (1991b)
- Humes & Ho (1968a)
- Humes (1979c)
- Humes & Stock (1973)
- Humes (1968a)
- Kim (2009)
- Kim (2009)
- Kim (1978b, 1979d)
- Humes (1991b)
- Humes (1991b)
- Humes (1993)
- Humes (1993)
- Humes (1993)
- Humes (1993)
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- Humes (1993)
- Humes (1993)
- Humes (1993)
- Humes (1993)
- Humes (1993)
- Humes (1993)
- Humes (1993)
- Humes (1993)
Scyphuliger longicaudatus Kim, 2003
Scyphuliger manifestus Humes, 1991b
Scyphuliger paucisurculus Kim, 2003
Scyphuliger pennis Kim, 2003
Scyphuliger pilosa Kim, 2003
Scyphuliger placida Kim, 2004b
Scyphuliger tenuatus (Humes, 1990) 64

Acropora hyacinthus

Aeropora millepora (Ehrenberg, 1834) 38
Aeropora hyacinthus (Dana, 1846)
Aeropora valida (Dana, 1846)
Aeropora squarrosa (Ehrenberg, 1834)
Aeropora ebeysi (Brook, 1892) 62
Aeropora cytherea (Dana, 1846) 63
Aeropora cytherea (Dana, 1846) 63
Aeropora squarrosa (Ehrenberg, 1834)
Aeropora abrotanoides (Lamarck, 1816) 60
Aeropora cilialis (Dana, 1846) 34
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Aeropora humilis (Dana, 1846)
Aeropora hyacinthus (Dana, 1846)

Acropora muricata (Linnaeus, 1758) 39

Aeropora millepora (Ehrenberg, 1834) 37

Aeropora squarrosa (Ehrenberg, 1834)
Gardneroseris planulata (Dana, 1846)
Pavona exspanulata (Lamarck, 1816)
Gardneroseris planulata (Dana, 1846)
Isopora palifera (Lamarck, 1816) 91
Catalaphyllia jardinei (Saville-Kent, 1893)

Acropora millepora (Ehrenberg, 1834) 38
Acropora hyacinthus (Dana, 1846)

From the above list, we can see that Acropora hyacinthus, Acropora millepora, and Acropora squarrosa are commonly found in the northeastern Australia, New Caledonia, and Humes. These species are important due to their unique ecological roles and biodiversity in coral reefs. The millepora species are also significant in the study of coral disease, as they are known to be more susceptible to coral bleaching compared to other species. Understanding the distribution and ecology of these species can provide insights into the health and resilience of coral reef ecosystems.
### Family Clausiidae

*Indoclausia bacescu* Sebastian & Pillai, 1974

*Montipora* *f* *oliacea*<sup>69</sup>

**Family Corallovexiidae**

*Corallonoxia baki* Stock, 1975a

*Dendrogyra* *cylindrus* Ehrenberg, 1834

*Curaçao*

*Curaçao*

*Corallonoxia longicasu* Stock, 1975a

*Eunicea* *fastigiata* (Pallas, 1766)

*Curaçao*

*Curaçao*

*Corallonoxia* sp.

*Dendrogyra* *cylindrus* Ehrenberg, 1834

*Curaçao*

*Curaçao*

*Corallonoxia* *brevisbrachium* Stock, 1975a

*Meandrina* *meandrites* (Linnaeus, 1758)

*Curaçao*

*Curaçao*

*Curaçao*

*Curaçao*

*Corallonoxia* *dorsospinosa* Stock, 1975a

*Dichocoenia* *stokesii* Milne Edwards & Haime, 1848

*Curaçao*

*Curaçao*

*Curaçao*

*Corallonoxia* *dorsospinosa* var. *minor* Stock, 1975a

*Diploria* *labyrinthiformis* (Linnaeus, 1758)

*Curaçao*

*Curaçao*

*Corallonoxia* *kristenseni* Stock, 1975a

*Pseudodiploria* *strigosa* (Dana, 1846)<sup>70</sup>

*Curaçao*<sup>71</sup>

*Curaçao*<sup>72</sup>

*Corallonoxia* *longibrachium* Stock, 1975a

*Monastrea* *cavernosa* (Linnaeus, 1767)

*U.S. Virgin Islands*

*U.S. Virgin Islands*

*Corallonoxia* *mediobrachium* Stock, 1975a

*Colpophyllia* *natans* (Houttuyn, 1772)

*Curaçao*

*Curaçao*

*Curaçao*

*Curaçao*

*Corallonoxia* *meiobrachium* Stock, 1975a

*Colpophyllia* *natans* (Houttuyn, 1772)

*Curaçao*<sup>71</sup>

*Curaçao*<sup>72</sup>

*Curaçao*<sup>73</sup>

*Curaçao*<sup>74</sup>

*Corallonoxia* *mixtibrachium* Stock, 1975a

*Manicina* *areolata* (Linnaeus, 1758)<sup>75</sup>

*Curaçao*<sup>71</sup>

*Curaçao*<sup>72</sup>

*Curaçao*<sup>73</sup>

*Curaçao*<sup>74</sup>

*Corallonoxia* *similis* Stock, 1975a

*Pseudodiploria* *strigosa* (Dana, 1846)<sup>70</sup>

*U.S. Virgin Islands*<sup>76</sup>

*U.S. Virgin Islands*<sup>70</sup>

*U.S. Virgin Islands*<sup>70</sup>

*Corallonoxia* *similis* Stock, 1975a (?)

*Monastrea* *cavernosa* (Linnaeus, 1767)

*Curaçao*

*Curaçao*

*Curaçao*

*Corallonoxia* *ventrospinosa* Stock, 1975a

*Acropora* *palmata* (Lamarck, 1816)

*U.S. Virgin Islands*

*U.S. Virgin Islands*

*U.S. Virgin Islands*

*Corallonoxia* sp.

*Meandrina* *meandrites* (Linnaeus, 1758)

*U.S. Virgin Islands*<sup>77</sup>

*U.S. Virgin Islands*<sup>77</sup>

*U.S. Virgin Islands*<sup>77</sup>
<table>
<thead>
<tr>
<th>Genus Name</th>
<th>Species</th>
<th>Location</th>
<th>Authors</th>
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<tbody>
<tr>
<td>Montastraea</td>
<td>cavernosa (Linnaeus, 1767)</td>
<td>U.S. Virgin Islands</td>
<td>Herriott &amp; Immermann (1979)</td>
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<tr>
<td>Myctophylla</td>
<td>lamarckiana Milne Edwards &amp; Haime, 1848</td>
<td>U.S. Virgin Islands</td>
<td>Herriott &amp; Immermann (1979)</td>
</tr>
<tr>
<td>Orbicella</td>
<td>annularis (Ellis &amp; Solander, 1786)</td>
<td>Curaçao</td>
<td>Stock (1975a)</td>
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<tr>
<td>Pseudodiploria</td>
<td>strigosa (Dana, 1846)</td>
<td>U.S. Virgin Islands</td>
<td>Herriott &amp; Immermann (1979)</td>
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**Family Cyclopidae**

<table>
<thead>
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<th>Location</th>
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<tbody>
<tr>
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<td>New Caledonia</td>
<td>Humes (1991a)</td>
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<td>Montipora</td>
<td>angulata (Lamarck, 1816)</td>
<td>New Caledonia</td>
<td>Humes (1991a)</td>
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<td>Montipora</td>
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<td>Humes (1991a)</td>
</tr>
<tr>
<td>Montipora</td>
<td>compressa (Linnaeus, 1766)</td>
<td>Moluccas</td>
<td>Humes (1991a)</td>
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<tr>
<td>Montipora</td>
<td>foliosa (Pallas, 1766)</td>
<td>Moluccas</td>
<td>Humes (1991a)</td>
</tr>
<tr>
<td>Montipora</td>
<td>lobulata Bernard, 1897</td>
<td>New Caledonia</td>
<td>Humes (1991a)</td>
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<td>Montipora</td>
<td>verrilli Vaughan, 1907</td>
<td>northeastern Australia</td>
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<td>Coraleurty</td>
<td>verecunda (Humes, 1992a)</td>
<td>Panama</td>
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<td>Euryte sp.</td>
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<td>Huys et al. (2012)</td>
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**Family Cyclopnidae**

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<td>striae Humes, 1996b</td>
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<td>Galaxea sp.</td>
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**Family Lichomolgidae**

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<td>spondylis Humes, 1968</td>
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<td>Humes &amp; Stock (1973)</td>
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<td>Lichomolgidae spp.</td>
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<td>Pterogyra sp.</td>
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<td>Madracis</td>
<td>myriaster (Milne Edwards &amp; Haime, 1850)</td>
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**Family Macrophirochonidae**

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<td>Pseudomacrochiron</td>
<td>pocillopora Kim, 2004a</td>
<td>Panama</td>
<td>Kim (2004a)</td>
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<td>Pocillopora</td>
<td>damicornis (Linnaeus, 1758)</td>
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**Family Pseudanthessiidae**

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<td>Pseudanthessius</td>
<td>thorelli (Brady, 1880)</td>
<td>southeastern France</td>
<td>Stock &amp; Weinberg (1985)</td>
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<td>Cladocora</td>
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Family Rhynchomolgidae

*Dallogomolgus productus* Humes, 1979b

*Cyphastrea chalcidicum* (Forskål, 1775)

*Cyphastrea microphthalmus* (Lamarck, 1816) 84

*Cyphastrea chalcidicum* (Forskål, 1775)

*Astroides calycularis* (Pallas, 1766)

*Psammocora hatiana* Milne Edwards & Haine, 1851a 41

*Symphysylla recta* (Dana, 1846)

*Serratapora hystris* Dana, 1846

*Psammocora sp.*

*Portites cf. nigrescens* Dana, 1848

*Portites somalensis* Gravier, 1911

*Portites (*Sinaroea*) sp.*

*Portites sp.*

*Portites sp.*

*Portites lutea* Quoy & Gaimard, 1833

*Portites rus* (Forskål, 1775) 90

*Portites lobata* Dana, 1846

*Portites lutea* Quoy & Gaimard, 1833

*Portites stephensoni* Crossland, 1952

*Pectinia kactua* (Pallas, 1766)

*Gardinereris planulata* (Dana, 1846)

*Psammocora nigrescens* Dana, 1848

*Psammocora contigua* (Esper, 1794)

*Portites lobata* Dana, 1846

*Portites lutea* Quoy & Gaimard, 1833

*Portites stephensoni* Crossland, 1952

*Portites cf. cylindrica* Dana, 1846 23

*Portites cf. nigrescens* Dana, 1848

*Portites sp.*

*Psammocora contigua* (Esper, 1794)

*Psammocora nigrescens* Dana, 1848

*Psammocora sp.*

New Caledonia

Humes (1979b)

New Caledonia

Humes (1979b)

New Caledonia

Humes (1979b)

southern Spain

Conradi *et al.* (2006)

New Caledonia

Humes (1996c)

southeastern India

Nair & Pillai (1987)

Moluccas

Dojiri (1988)

Madagascar

Humes (1962b)

Madagascar

Humes & Ho (1968a)

Madagascar

Humes & Ho (1968a)

Madagascar

Humes & Ho (1968a), Humes & Stock (1973)

Moluccas

Kim (2007)

southeastern India

Nair & Pillai (1986)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1991c)

Moluccas

Humes (1992c)

Moluccas

Humes (1979d)

Madagascar

Humes & Ho (1967)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)

New Caledonia

Humes (1997b)

southeastern India

Nair & Pillai (1986)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Madagascar

Humes & Frost (1964)

Madagascar

Humes & Ho (1968a)

Madagascar

Humes & Stock (1973)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)

Moluccas

Humes (1979d)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

Society Islands

Humes (1984a)

New Caledonia

Humes (1997b)

New Caledonia

Kim (2003)
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<td><em>Pionomolgus gallicolus</em> Dojiri &amp; Gryger, 1990</td>
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<td><em>Ravahina tumida</em> Humes &amp; Ho, 1968a</td>
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<td><em>Rhynchosoma cornifolium</em> Humes &amp; Ho, 1967</td>
<td>Madagascar</td>
<td>Humes &amp; Ho (1967)</td>
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<td><em>Spaniomolgus compositus</em> (Humes &amp; Frost, 1964)</td>
<td>Mauritius</td>
<td>Humes (1975)</td>
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<td><em>Spaniomolgus crassus</em> (Humes &amp; Ho, 1968a)</td>
<td>Mauritius</td>
<td>Humes &amp; Ho (1968a)</td>
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<td><em>Spaniomolgus geminus</em> (Humes &amp; Ho, 1968a)</td>
<td>Mauritius</td>
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<td>Mauritius</td>
<td>Humes &amp; Stock (1973)</td>
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<td>Moudrova et al. (2014a)</td>
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<td><em>Tubastraea coccinea</em> Lesson, 1829</td>
<td>Taipei</td>
<td>Cheng et al. (2008)</td>
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<td><em>Wedania formosana</em> Cheng, Ho &amp; Dai, 2008</td>
<td>Taiwan</td>
<td>Cheng et al. (2008)</td>
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<tr>
<td><em>Goniopora pedunculata</em> Quoy &amp; Gaimard, 1833</td>
<td>Taiwan</td>
<td>Cheng et al. (2008)</td>
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<tr>
<td><em>Goniopora tenuidens</em> (Quek, 1886)</td>
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<td>Humes (1978c)</td>
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<tr>
<td><em>Xenomolgus varius</em> Humes &amp; Stock, 1972</td>
<td>Mauritius</td>
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<td><em>Porites sp.</em></td>
<td>Japan (Okinawa)</td>
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**Family Strepidae**

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<td><em>Strepsis elongatus</em> Cheng, Liu &amp; Dai, 2016b</td>
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<td>Cheng et al. (2016b)</td>
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**Family Xarildae**

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<tr>
<td><em>Botegokika faviae</em> (Ho, Cheng &amp; Dai, 2010)</td>
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<td>Ho et al. (2010)</td>
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<td><em>Acrpora lattisella</em> (Brook, 1892)</td>
<td>New Caledonia</td>
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**Lipochrus sp.**

**Orstomella faviae** Humes & Ho, 1968b

**Orstomella lobophylliae** Humes & Ho, 1968b

**Orstomella yaliuensis** Cheng, Ho & Dai, 2009

**Xarifa abluar** Humes & Dojiri, 1982

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**Xarifa aciculata** Humes, 1985a

**Xarifa anomala** Humes & Ho, 1968b

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**Xarifa anopla** Humes & Dojiri, 1982

**Montipora aequituberculata** Bernard, 1897 45

**Montipora cf. undata** Bernard, 1897

**Montipora sp.**

**Gyrosmilia interrupta** Ehrenberg, 1834

**Montipora verrucosa** (Lamarck, 1816)

**Acropora hyacinthus** (Dana, 1846)

**Acropora millepora** (Ehrenberg, 1834) 38

**Acropora sp.**

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Mauritius
Madagascar
New Caledonia

Humes (1962a)
Humes (1985a)
Humes & Dojiri (1983)
Humes & Dojiri (1983)
Nair (1983)
Humes & Dojiri (1982)
Humes & Dojiri (1982)
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Humes & Dojiri (1982)
Humes & Dojiri (1982)
Humes (1962a)
Humes (1962a)
Humes (1985a)
Humes (1985a)
Humes & Frost (196-
Xarifia syntoma Humes & Doziri, 1982
Xarifia taiwanensis Cheng, Ho & Dai, 2011b
Xarifia temnora Humes & Ho, 1968b

Montipora cf. undata Bernard, 1897
Kora expanulata (Lamarck, 1816)
Montipora angulata (Lamarck, 1816)
Montipora monasteriata (Forskal, 1775)
Montipora cf. undata Bernard, 1897
Pocillopora ligulata Dana, 1846
Pocillopora versicolora (Ellis & Solander, 1786)

Montipora angulata Humes, 1985a
Montipora monasteriata Humes, 1985a

Acropora cytherea (Dana, 1846)
Acropora abrotanoides (Lamarck, 1816)
Acropora cytherea (Dana, 1846)
Acropora florida (Dana, 1846)
Acropora humilis (Dana, 1846)
Acropora hyacinthus (Dana, 1846)

Acropora intermedia (Brook, 1891)
Acropora laestella (Brook, 1892)
Acropora speciosa (Quench, 1886)
Acropora cytherea (Dana, 1846)
Acropora elseyi (Brook, 1892)
Acropora florida (Dana, 1846)
Acropora hyacinthus (Dana, 1846)

Acropora intermedia (Brook, 1891)
Acropora muriata (Linnaeus, 1758)
Acropora sarmentosa (Brook, 1892)
Acropora squarrosa (Ehrenberg, 1834)
Seriatopora calenderum Ehrenberg, 1834
Seriatopora hystrica Dana, 1846

Xarifia ubonata Humes, 1985a
Xarifia ucinata Humes, 1985a
Xarifia variabratata Humes, 1985a

Seriatopora calenderum Dana, 1846
Turbinaria frondens (Dana, 1846)
Seriatopora hystrica Dana, 1846

Cyphastrea chalcidicum (Forskal, 1775)
Acropora gemmifera (Brook, 1892)

Cyphastrea rhabdomorpha (Quench., 1886)
Acropora gemmifera (Brook, 1892)

Xarifia villosa Humes & Doziri, 1982
Xarifia spp.

Xarifia trituberata Humes & Doziri, 1982

Acropora abrotanoides (Lamarck, 1816)
Acropora florida (Dana, 1846)
Acropora cytherea (Dana, 1846)
Acropora sarmentosa (Brook, 1892)

Xarifia trituberata Humes & Doziri, 1982

Acropora cytherea (Dana, 1846)
Acropora speciosa (Quench., 1886)
Acropora cytherea (Dana, 1846)
Acropora elseyi (Brook, 1892)
Acropora florida (Dana, 1846)
Acropora hyacinthus (Dana, 1846)

Acropora intermedia (Brook, 1891)
Acropora muriata (Linnaeus, 1758)
Acropora sarmentosa (Brook, 1892)
Acropora squarrosa (Ehrenberg, 1834)
Seriatopora calenderum Ehrenberg, 1834
Seriatopora hystrica Dana, 1846

Xarifia ubonata Humes, 1985a
Xarifia ucinata Humes, 1985a
Xarifia variabratata Humes, 1985a

Seriatopora calenderum Dana, 1846
Turbinaria frondens (Dana, 1846)
Seriatopora hystrica Dana, 1846

Cyphastrea chalcidicum (Forskal, 1775)
Acropora gemmifera (Brook, 1892)
### Acropora longicyathus (Milne Edwards, 1860)
- New Caledonia

### Acropora millepora (Ehrenberg, 1834)
- New Caledonia

### Acropora sp.
- Humes (1985a)

### Ctenactis echinata (Pallas, 1766)
- Moluccas

### Galaxea astreata (Lamarck, 1816)
- Humes (1960)

### Leptoria phrygia (Ellis & Solander, 1786)
- Madagascar

### Merulina ampliata (Ellis & Solander, 1786)
- Humes (1985a)

### Montipora cf. stellata Bernard, 1897
- northeastern Australia

### Oxypora sp.
- Madagascar

### Platygira sinensis (Milne Edwards & Haime, 1849)
- Humes (1985a)

### Pocillopora damicornis (Linnaeus, 1758)
- Taiwan

### Porites lutea Quoy & Gaimard, 1833
- New Caledonia

### Sandakolitha robusta (Quelch, 1886)
- Humes (1985a)

### Stylophora sp.
- Red Sea

### Tubastrea sp.
- Humes (1985a)

### Fungia sp.
- Madagascar

### Zazaranus fungicolus Humes & Dojiri, 1983

### Incertae sedis

### Parangium abstrusum Humes, 1985b

### Stockella indica (Sebastian & Pillai, 1974)

### Favia sp. 111
- southeastern India

### Siphonostomatoida

### Family Artrotogidae

### Bradyopontia pichoni Stock, 1966
- Mauritius

### Cryptopontia acuta Kim, 2007
- Stock (1966)

### Cryptopontia kunacredi Johnsson, Rocha & Boyko, 2002
- Easter Island

### Echinopora lamellosa (Esper, 1791)
- Barbados

### Madracis myriaster (Milne Edwards & Haime, 1850)
- Barbados

### Madracis myriaster (Milne Edwards & Haime, 1850) 1
- Snelgrove & Lewis (1989)
COPEPODS ASSOCIATED WITH SCLERACTINIAN HOSTS

Zootaxa 0000 (0) © 2016 Magnolia Press · 27
Asteropontius dentatus Kim, 2010
Asteropontius dissimilis Kim, 2003

Asteropontius fungicola Kim, 2007
Asteropontius goniopterae Kim, 2007

Asteropontius humesi Kim, 2010
Asteropontius nuxius Stock, 1989
Asteropontius laevadensis Nair & Pillai, 1984
Asteropontius latoriger Kim, 2010
Asteropontius litoralis Ummerkutty, 1962
Asteropontius magnisetiger Kim, 2010

Asteropontius membranulatus Kim, 2010
Asteropontius minutus Kim, 2003

Asteropontius mycetophylliae Varela, Ortiz & Lalana, 2005
Asteropontius orcafer Kim, 2010
Asteropontius parvipes Kim, 2010
Asteropontius pinnaeus Kim, 2010

Asteropontius plumatus Kim, 2010
Asteropontius proximius Stock, 1987
Asteropontius trifilis Kim, 2010
Asteropontopsis faviae Stock, 1987
Cephalocheres flagellatae Kim, 2010
Gascardama longisplanchna Kim, 2010
Hemacheres diplorhinae Stock, 1987
Hemacheres montastreae Stock, 1989
Hexiroxya galaxiae Humes, 1996b
Hexiroxya lacinata Humes, 1991a

Lobophyllia hemprichii (Ehrenberg, 1834)
Pocillopora damicornis (Linnaeus, 1758)
Fungia sp.
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Madagascar
Kim (2010)
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Madagascar
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Hetairosynopsis wedensis Humes, 1996b
Hetairosynopsis bucculentus Humes, 1996b

Meandrinia meandrites (Linnaeus, 1758)
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Montastrea cavernosa (Linnaeus, 1767)

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Cholomyzon brevisetigerum Humes, 1997c
Cholomyzon papuliferum Stock & Humes, 1969
Cholomyzon tubastrellae Cheng, Dai & Chang, 2011a
Tubastrea coccinea Lesson, 1829
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Spongiopsyllus redactus Canário, Neves & Johansson, 2012
Mussismilia hispida (Verrill, 1901)
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Canário et al. (2012)

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1 as Madracis mirabilis (Duchassaing & Michelotti, 1861).
2 as larviphante bulbfers Norman, 1911.
3 as Amphipora paracassa spino us Roc, 1958; transferred by Huys (2009).
4 considered nomen dubium in WoRMS (2016).
5 as Pocillopora damicornis (Linnaeus, 1758) var. caespitosa Dana, 1846.
6 considered nomen dubium in WoRMS (2016).
8 as Paraholomitra irregularis Gardiner, 1898.
9 as Paraholomitra regularis Gardiner, 1898.
10 as Lichomolgus digitatus (Humes & Ho, 1968a); transferred by Humes & Stock (1972).
12 as Lithactina novaehiberniae Lesson, 1831.
13 as Fungia (Ctenactis) echinata Pallas, 1766.
14 as Fungia (Fungia) fungites Linnaeus, 1758.
15 as Fungia (Pleuroctis) psammonensis [sic] Stutchbury, 1833.
16 as Fungia concinna Verrill, 1864.
17 as Fungia (Helioporia) actiniformis Quoy & Gaimard, 1833.
18 as Fungia (Ctenactis) echinata Pallas, 1766.
19 as Fungia (Pleuroctis) psammonensis [sic] Stutchbury, 1833.
20 as Fungia concinna Verrill, 1864.
21 as Fungia (Helioporia) actiniformis Quoy & Gaimard, 1833.
22 as Fungia (Ctenactis) echinata Pallas, 1766.
23 as Fungia (Pleuroctis) psammonensis [sic] Stutchbury, 1833.
Galaxea fascicularis

minima

Favites virens

sic

sic

Psammocora Stephanaria
togianensis

Acropora rosaria

Acropora cymbicyathus

Acropora gravida

Acropora squamosa

Acropora convexa

Acropora rambleri

Alveopora mortenseni

Montipora composita

Montipora sinensis

Leptoria tenuis

Pavona angulata

P. angularis nomen dubium

Pavona venusta

Lichomolgus campulus

Psammocora samoensis

Montipora prolifera

Halomitra philippinensis

variant population with minor morphometric differences in antennae, leg 5 and caudal rami.

originally described as Lichomolgus campulus Humes & Ho, 1968a; transferred by Humes & Stock (1973).

as Pavona pradii (Dana, 1846).

as Galaxea fascicularis var. minima Chevalier, 1971.

as Favia favus (Forskål, 1775).

as Favites virgata (Dana, 1846).

as Montastrea [sic] curta (Dana, 1846).

as Psammocora (Stephanaria) togianensis Unngrove, 1940.

as Acropora syzygodes [sic] (Brook, 1892).

as Acropora rosaria (Dana, 1846).

originally described as Lichomolgus lobophorus Humes & Ho, 1968a; transferred by Humes (1993).

as Acropora cymbicathus (Brook, 1893).

as Acropora gravida (Dana, 1846).

as Acropora schrieriana (Brüggemann, 1877).

as Acropora squamosa (Brook, 1892).

as Acropora convexa (Dana, 1846).

as Acropora formosa (Dana, 1846).

as Acropora ramberi (Bassett-Smith, 1890).

as Acropora palisata Lamarck, 1816.

as Alveopora mortenseni Crossland, 1952.

as Montipora composita Crossland, 1952.

as Montipora ramosa Bernard, 1897.

as Montipora sinensis Bernard, 1897.

as Leptoria tenax (Dana, 1846).

originally described as Lichomolgus actinophorus Humes & Frost, 1964; transferred by Humes & Stock (1972).

as Pavona angulata Klunzinger, 1879; this is probably a misspelling of P. angularis Klunzinger, 1879 which is currently considered a nomen dubium (B. Hoeksema, pers. comm).

as Pavona venusta (Dana, 1846) is currently regarded as a junior synonym of Pavona cactus (Forskål, 1775).

originally described as Lichomolgus campulus Humes & Ho, 1968a; transferred by Humes & Stock (1973).

as Psammocora samoensis Hoffmeister, 1925.

as Montipora prokhera Brüggemann, 1879.

as Halomitra philippinensis (Shnder, 1901).

variant population with minor morphometric differences in antennae, leg 5 and caudal rami.

originally described as Lichomolgus rhadinus Humes & Ho, 1967; transferred by Humes & Stock (1973).

as Hydaphora tenella Quelch, 1886.

as Platygyra astraiformis (Milne Edwards & Haime, 1849).

originally described as Lichomolgus arcuatus Humes & Ho, 1968a; transferred by Humes & Stock (1972).

as Acropora patula (Brook, 1892).

as Acropora danai (Milne Edwards, 1860).

62 as *Acropora exilis* (Brook, 1892).
63 as *Acropora corymbosa* (Lamarck, 1816).
64 originally described as *Schedomolus tematatus* Humes, 1990; transferred by Humes (1991b).
65 as *Acropora affinis* (Brook, 1893).
67 as *Setiatopora subseriata* Ehrenberg, 1834.
68 according to Kim (2009) hermit crabs rather than corals are the real hosts for this species.
69 partly encrusted with a colonial ascidian; the authors believed this to be the real host; more likely to be dislodged from a polychaete host during collection. The host name is considered a *nomen dubium* in WoRMS (2016) and is probably a misspelling of *Montipora foliosa* (Pallas, 1766) (B. Hoeksema, pers. commn).
70 as *Diplora* (sic) *strigosa* (Dana, 1846).
71 Stock (1975a) also listed the junior synonym *Montastraea brasiliaca* (sic) (Verrill, 1901) as a separate host. possible variation of *C. dorsospinosa* Stock, 1975a.
72 as *Manicina areolata* (Linnaeus, 1758) *f. majori* (Wells, 1936).
73 as *Diplora strigosa* (Dana, 1846).
74 as *Diplora clivosa* (Ellis & Solander, 1786).
75 as *Diplora* (sic) *clivosa* (Ellis & Solander, 1786).
76 unidentifiable species.
77 both unidentifiable and possibly new species.
78 as *Montastraea* [or *Montastrea*] *annulans* (Ellis & Solander, 1786).
79 originally described as *Euryte bellatula* Humes, 1991a; transferred by Karanovic (2014).
80 originally described as *Euryte vepecunda* Humes, 1992a; transferred by Karanovic (2014).
81 this host may be an accidental record.
82 mentioned as *nomen nudum* by Brady & Robertson (1876); originally described as *Lichomolgus thorellii* Brady, 1880 but note that the authorship attributed to Brady & Robertson in Brady’s (1880) work is incorrect; transferred by Scott & Scott (1893); the correct ending of the species name should be –ii, not –i as cited by Stock & Weinberg (1985).
83 as *Cyphastrea gardineri* Mathia, 1914.
84 described under the incorrect original spelling *avitus*.
85 as *Portites* (Synanthea) *monticulosa* Dana, 1846.
86 in washings of a mixture of numerous *Flabellum* sp. (aff. *F. messum* Alcock, 1902), some *Flabellum* aff. *japonicum* Moseley, 1881 and a single *Caryophyllia* sp.
87 originally described as *Lichomolgus compostus* Humes & Frost, 1964; transferred by Humes & Stock (1972).
88 originally described as *Lichomolgus crassus* Humes & Ho, 1968a; transferred by Humes & Stock (1973).
89 also listed under its junior synonym *Stylopora monad* (Dana, 1846).
90 originally described as *Lichomolgus geminus* Humes & Ho, 1968a; transferred by Humes & Stock (1973).
91 as *Goniopora minor* Crossland, 1952.
92 *Porites lutea* Quoy & Gaimard, 1833 and/or *P. australiensis* Vaughan, 1918.
93 the original generic name *Hastatus* Ho, Cheng & Dai, 2010 was preoccupied and replaced by *Botegokika* Ho, Cheng & Dai, 2013 (cf. Ho et al. 2013).
94 as *Lobophyllia costata* (Dana, 1846).
95 as *Pocillopora cydonia* Milne Edwards, 1860.
Echinopora carduus

T. elegans

Acropora hebes

Tubastraea aurea

Turbinaria danae

Physogyra lichtensteini

Pocillopora danae

Stylophora pistillata

Pocillopora bulbosa

Parangium et al.

Stockia indica

Hydnophora eyessa

Porites convexa

Madacheres serrulatus

Acropora corymbosa

Pocillopora favosa

Stylophora mordax

Diploria clivosa

Diploria strigosa

Montipora ambigua

Galaxea clavus

Asterocheres mucronipes

Stockmyzon

Tubastraea micracantha

Dendrophyllia nigrescens

as Acropora palifera forma alpha (Brook, 1893).

as Acropora hebes (Dana, 1846).

as Tubastraea aurea (Quoy & Gaimard, 1833).

very likely Physogyra lichtenstein Milne Edwards & Haime, 1851c according to Humes (1985a).

also listed under its junior synonym Pocillopora daeae Verrill, 1864.

as Stylophora pistilata, var. palmata Blainville, 1830.  

as Acropora pectinata (Brook, 1892).

as Pocillopora bulbosa Ehrenberg, 1834.

Boxshall & Halsey (2004) placed Parangium in the Serpulidicolidae but morphological evidence suggests that it is the sister group of the Xarifidae or occupies a basal position within this family (Huys et al. 2006).

originally described as Stockia indica Sebastian & Pilai, 1974; transferred to Stockella Holroyd, 2012 (new replacement name). Boxshall & Halsey (2004) removed the species from the Clausiidae and placed it in the Octophrora-group.

presumably dislodged from coral-associated polychaetes.

coral fragment with several epibiotic algae and sponges.

as Hydrophora eyessa [sic].

originally described as Solenostoma scutatum Brady & Robertson, 1873; transferred by Brady (1880).

as Portites (Synanthea) convexus (Verrill, 1864).

originally described as Mukhares verrucatus Humes, 1996b; transferred by Ivanenko (1999).

also listed separately under its junior synonym Acropora corymbosa (Lamarck, 1816) and as A. cf. corymbosa (Lamarck, 1816).

including “forma favosa” (= Pocillopora favosa Ehrenberg, 1834) currently a synonym of P. damicomis.

as Stylophora cf. erinacea [sic] Marenzeller, 1907; this species is now considered a nomen dubium in WoRMS (2016).

as Pocillopora damicomis cepitiosa Dana, 1846)

as Fungi cf. scrouposa Humes, 1879

Kim (2010) mentioned that the host species is probably “Acropora palifera” but this is likely a misspelling of A. palmata (Lamarck, 1816) [now known as Isopora palmata (Lamarck, 1816)].

as Stylophora mordax (Dana, 1846).

as Diplora chiosa (Ellis & Solander, 1786).

as Diplora strigosa (Dana, 1846).

as Montipora ambigua Bernard, 1897

as Galaxea chiusa Dana, 1846.

originally described as Acropora elongata Scott & Scott, 1894; transferred by Giesbrecht (1897).

originally described as Asterocheres microopus Stock, 1960; transferred to Stockella by Bandera & Huys (2008).

Boxshall & Halsey (2004) relegated this family name to a junior synonym of Asterocheridae but Ivanenko & Delaey (2005) and Mahatma et al. (2008) rejected this course of action. Humesmyzon Kim, 2010 is here tentatively transferred to this family.

as Tubastraea micrantha [sic] (Ehrenberg, 1834).

as Dendrophyllia nigrescens Dana, 1846 and Dendrophyllia micranthus [sic] var. grandis Crookslard, 1952.

At present, a total of 148 scleractinian species, representing 66 genera, are known to serve as hosts to copepods. These species belong to 15 families and three genera currently considered as incertae sedis (Cladocora Ehrenberg, 1834; Physogyra Quelch, 1884; Plerogyra Milne Edwards & Haime, 1848). The families Merulinidae (14 genera), Fungiidae (10 genera) and Mussidae (7 genera) contain the highest number of host genera. The Acroporidae (staghorn corals), represented by five genera, are the most common host family in terms of species, containing 42 species that are being utilized by symbiotic copepods. Other families that appear to be favoured host taxa include the Merulinidae (27 species) and the Fungiidae, Pocilloporidae and Poritidae (11 species each). The acroporid genera Acropora Oken, 1815 (24 species) and Montipora de Blainville, 1830 (14 species) contain the highest number of utilized host species, followed by the poritid Porites Link, 1807 (8 species), the agariciid Pavona Lamarck, 1801 (6 species) and the pocilloporid Pocillopora Lamarck, 1816 (5 species).

Copepods are most commonly associated with coral species belonging to the families Acroporidae, Merulinidae, Pocilloporidae, Agaricidae and Poritidae, which serve as hosts to 93, 58, 48, 37 and 34 species, respectively. Collectively, these five families harbour nearly 75% of all described coral-associated copepod species, one-third of which utilizes acroporid hosts. Only one copepod species has been recorded from the Flabellidae and the monotypic Montastreaeidae; however, in the former family only one out of 100 potential host species has been surveyed so far. In the Acroporidae the genera Acropora and Montipora serve as hosts to 56 and 24 copepod species, respectively, while the pocilloporid genera Pocillopora and Stylopora Schweigger, 1820 are being utilized by 27 and 20 symbionts, respectively. Other important host genera include the agariciids Pavona (18 species) and Gardineroseris Scheer & Pillai, 1974 (16 species), the euryphyllid Galaxea Oken, 1815 (18 species), the merulinid Echinopora Lamarck, 1816 (14 species), the poritids Portites (21 species) and Goniopeora de Blainville, 1830 (14 species) and the psmmocorid Psammocora Dana, 1846 (15 species).

In many cases one host coral may support more than on species of copepod. Foremost among examples of hosts with multiple associated copepod species may be the pocilloporid Pocillopora damicornis (Linnaeus, 1758) and the agariciid Gardineroseris planulata (Dana, 1846) which support 17 and 16 symbiotic copepod species, respectively. Other scleractinian corals that serve as hosts to at least ten different copepod species include Acropora cytherea (Dana, 1846) and A. hyacinthus (Dana, 1846) (15 species each), Galaxea fascicularis (Linnaeus, 1767) (14 species), Stylopora pistillata Esper, 1792 (12 species), Acropora florida (Dana, 1846) (11 species), and Echinopora lamellosa (Esper, 1791) and Pocillopora verrucosa (Ellis & Solander, 1786) (10 species each). Often corals support copepods belonging to different families or even orders. For example, both P. damicornis and E. lamellosa serve as hosts to copepods from five different families, and both G. planulata and S. pistillata are being utilized by members of the Harpacticoida, Cyclopoida and Siphonostomatoida.

Copepods associated with scleractinian corals display different levels of host specificity. There are many instances where a copepod has been reported from only one host species and is thus distinctly stenoxenous. About 70% of all recorded copepod species (363/254 spp.) are currently known from a single coral host. The number of species displaying such a narrow host range is lower in the Cyclopoidea (67%) than in the Siphonostomatoida (81%). In the most speciose family, the Anchimolgidae, 104 out of 141 species (74%) appear to utilize only one host, however only 58% of the species in the Xarifiidae (92/53 spp.) show a similar level of host specificity. Nearly 78% of the coral-associated Asterocheridae and seven of the eight described species in the Coralliomyzontidae are known from a single host. However, over one hundred species have been reported from more than one host and some display particularly low host specificity, having entered into associations with an impressive range of coral species. The most euryxenous species is a member of the Anchimolgidae, Ecphysarian lobophorum (Humes & Ho, 1968a), which has been reported from 13 scleractinian hosts, all belonging to the Acroporidae. The asterocherid Hetairosyna terpna Humes, 1991a utilizes 11 hosts, exclusively belonging to the genus Montipora. Other species with a wide host range include Alteuthellopsis corallina Humes, 1981a and Xarifia brevivamea Humes & Dojiri, 1982 (9 species each), X. anomala Humes & Ho, 1968b, X. pectinea Humes & Dojiri, 1982, X. trituberata Humes.
& Dojiri, 1982 and X. tumora Misaki, 1978 (8 species each), and X. sabiuraensis Misaki, 1978, Haplomolgus montiporae Humes & Ho, 1968a, Odontomolgus forhani Humes, 1978a and Scyphuliger tenutus (Humes, 1990) (7 species each). As a general rule euryxenous copepods tend to utilize hosts belonging to the same family or subgroups of (maximum four) closely related genera. Notable exceptions that do not display this level of host specificity include the harpacticoid A. corallina which has been recorded from nine different host genera belonging to four families of scleractinian corals, and the rhynchomolgid Kornia angulata Humes, 1962b which utilizes both Poritidae and Psammocoridae as hosts.

**Case study.** During the sampling periods spanning July 2007 to November 2008, 44% of the coral colonies were infected by copepods. A total of 8,336 copepods, including 950 unidentified harpacticoiids (11.40%), nine species of cyclopoids (n = 1,856; 22.26%), and three species of siphonostomatoids (n = 5,530; 66.34%) were obtained from 480 colonies of P. damicornis (Tables 2–3) collected from Nanwan Bay, southern Taiwan. Among them, Asteropontius minutus (n = 4,303; 51.62%) and multiple species of the functional group ES (n = 5,530; 66.34%) were the two most abundant types; they made up more than 50% of the total number of copepods in the summer of 2007, but only 15.98–20.10% in August 2008 (Table 3). In contrast, mean densities of Xarifia imparilis Humes, 1985a, Pseudomacrochiron pocilloporae Kim, 2004a and members of the functional group ESM only slightly fluctuated across the sampling times.

Copepods of the orders Harpacticoi, Cyclopoidea and Siphonostomatoida demonstrated significant variation in the parasitological indices assessed and presented the same infestation trends during the collecting periods (Tables 2–3). The total number of copepods was highest in the months characterized by the highest seawater temperatures (July–September 2007). Also, copepod prevalence varied widely (Fisher’s exact test, p < 0.05), from 11.7% in May 2008 (minimum) to 91.7% in Jul. 2007 (maximum), at which point the seawater temperature ranged from 29.70 to 30.98°C. In contrast, copepod prevalence was lower in January 2008, during which seawater temperature was only 24.08°C. Mean density, mean intensity, and median intensity all varied significantly between sampling months (Mood’s median test and one-way ANOVA effect of time, p < 0.05), and maximum values of all three parameters were also recorded in the summer of 2007 (Table 2), at which point mean densities of *Symbiodinium* had decreased to only 0.83 ± 0.07×10⁶ cells.cm⁻² (Fig. 1). Such high levels of copepod infection were not documented in the summer of 2008 (Table 2).

**FIGURE 1.** Variation in seawater temperature and *Symbiodinium* density (mean ± SE) observed in *Pocillopora damicornis* colonies of Nanwan Bay, Southern Taiwan between July 2007 and November 2008. Lowercase and uppercase letters (a, b, c, and d) refer to the results of Tukey’s post-hoc comparisons of monthly temperature and *Symbiodinium* density means, respectively, as a significant effect of time was detected in the overall ANOVA models (p < 0.05 for both parameters).
FIGURE 2. Relationships between copepod infection and the amount of resources (Symbiodinium densities and surface areas) provided by host corals. A–E: Mean densities of symbiotic copepods (A: Siphonostomatoida, B: Cyclopoidea, C: Harpacticoida, D: all copepods) among 480 Pocillopora damicornis colonies with varying Symbiodinium densities. E–H: Relationship between mean densities of symbiotic copepods (E: Siphonostomatoida, F: Cyclopoidea, G: Harpacticoida, H: all copepods) and surface areas of host corals.
### TABLE 2. Abundance (total number of copepods), prevalence (% of colonies infected), mean density (individuals cm⁻²), mean intensity (individuals per infected coral colony), and median intensity of infection by symbiotic copepods on *Pocillopora damicornis* (total n = 480, 60 colonies/sampling time) in Nanwan Bay, Southern Taiwan from July 2007 to November 2008. During the sampling periods, 8,336 parasitic copepods were quantified. Various superscripts (*a*, *b*, *ab*) denote significant differences (p < 0.05) between groups and refer to the results of Tukey’s post-hoc comparisons of group means.

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### TABLE 3. Abundance and mean density (individuals cm$^{-2}$ ± SE) of all symbiotic copepods on *Pocillopora damicornis* in Nanwan Bay, Southern Taiwan from July 2007 to November 2008.

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<tr>
<td><em>Xarifia serrata</em></td>
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<td>6</td>
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<tr>
<td><strong>Siphonostomatoida</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Asteropontius minutus</em></td>
<td>284</td>
<td>0.049 ± 0.010</td>
<td>421</td>
<td>0.045 ± 0.009</td>
<td>3245</td>
<td>0.643 ± 0.208</td>
<td>47</td>
<td>0.021 ± 0.003</td>
<td>51</td>
<td>0.022 ± 0.004</td>
<td>87</td>
<td>0.034 ± 0.009</td>
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<tr>
<td><em>Asteropontius dissimilis</em></td>
<td>103</td>
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<td>177</td>
<td>0.041 ± 0.014</td>
<td>834</td>
<td>0.272 ± 0.095</td>
<td>9</td>
<td>0.012 ± 0.003</td>
<td>6</td>
<td>0.012 ± 0.003</td>
<td>30</td>
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<td><em>Pseudomacrochiron pocilloporae</em></td>
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<td>0.011 ± 0.002</td>
<td>10</td>
<td>0.016 ± 0.012</td>
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<td>0.016 ± 0.012</td>
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<tr>
<td>Endoparasitic with spiny mandibles</td>
<td>84</td>
<td>0.054 ± 0.003</td>
<td>27</td>
<td>0.006 ± 0.001</td>
<td>68</td>
<td>0.033 ± 0.012</td>
<td>90</td>
<td>0.017 ± 0.002</td>
<td>48</td>
<td>0.017 ± 0.002</td>
<td>43</td>
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<tr>
<td>Endoparasitic without spiny mandibles</td>
<td>313</td>
<td>0.023 ± 0.007</td>
<td>402</td>
<td>0.017 ± 0.003</td>
<td>126</td>
<td>0.015 ± 0.007</td>
<td>119</td>
<td>0.017 ± 0.004</td>
<td>136</td>
<td>0.015 ± 0.003</td>
<td>74</td>
<td>0.011 ± 0.002</td>
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<tr>
<td>Ectoparasitic with siphon</td>
<td>397</td>
<td>0.032 ± 0.006</td>
<td>608</td>
<td>0.034 ± 0.012</td>
<td>4089</td>
<td>0.310 ± 0.105</td>
<td>56</td>
<td>0.011 ± 0.002</td>
<td>57</td>
<td>0.011 ± 0.002</td>
<td>117</td>
<td>0.17 ± 0.004</td>
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<tr>
<td>Ectoparasitic without siphon</td>
<td>32</td>
<td>0.014 ± 0.002</td>
<td>15</td>
<td>0.013 ± 0.004</td>
<td>37</td>
<td>0.057 ± 0.020</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0.014</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Benthic</td>
<td>84</td>
<td>0.037 ± 0.007</td>
<td>356</td>
<td>0.054 ± 0.009</td>
<td>324</td>
<td>0.119 ± 0.017</td>
<td>49</td>
<td>0.034 ± 0.012</td>
<td>33</td>
<td>0.027 ± 0.008</td>
<td>35</td>
<td>0.037 ± 0.011</td>
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</table>
FIGURE 3. Multidimensional scaling (MDS) plot of 75% similarity in species composition and abundance of symbiotic copepods amongst various sampling periods.

Nanwan Bay seawater quality data between July 2007 and November 2008 are shown in Table 4, and the relationships between seawater quality, Symbiodinium density, coral surface area, and mean density of the three orders of copepods are shown in Fig. 2 and Table 5. There were significantly negative correlations between mean density of cyclopoid and siphonostomatoid, but not harpactoid, copepods, and Symbiodinium densities ($p < 0.05$) (Fig. 2). The mean densities of cyclopoids and siphonostomatoids in bleaching corals (Symbiodinium density $< 10^6$ cells.cm$^{-2}$) were significantly higher than those of healthy ones (Symbiodinium density $> 10^6$ cells.cm$^{-2}$ Fig. 2). However, severely bleached corals (Symbiodinium density $< 2 \times 10^5$ cells.cm$^{-2}$) had a markedly low mean density of cyclopoid copepods ($< 0.1$ individuals.cm$^{-2}$; Fig. 2). In addition, the cyclopoid density was negatively correlated with coral surface area ($R^2 = 0.094$, $p < 0.01$), while cyclopoids and siphonostomatoids also showed negative correlations with surface area of coral colonies, although these results were not significant. Regarding other correlations (Table 5), mean densities of siphonostomatoids were significantly and positively correlated with concentrations of nitrate ($R^2 = 0.682$, $p < 0.05$) and chlorophyll-a ($R^2 = 0.709$, $p < 0.01$). Harpacticoid density showed a similar positive correlation with both parameters ($R^2 = 0.748$, $p < 0.01$ and $R^2 = 0.808$, $p < 0.01$, respectively).

Significant differences in both copepod species composition and abundance were observed in Nanwan Bay from July 2007 to November 2008 (one-way ANOSIM, $R = 0.371$, $p < 0.05$). Using the SIMPER function in PRIMER, all sampling periods had an average dissimilarity in the composition of copepods ranging from 10.76 to 48.50%, with the most dissimilar periods being September 2007 and January 2008 (56.68%). The MDS ordination of copepods at Nanwan Bay from the seven sampling periods (except for September 2007) revealed a great degree of similarity (Fig. 3). Copepod communities could be clustered into two major groups based on 75% similarity among various sampling periods. Copepod communities were dominated by ectoparasites (ES, EWS, and BE) in September 2007; however, these taxa were low in abundance in July 2007, August 2007, and January to November 2008 (Fig. 4; Table 3, Fig. 4). The results of PCA revealed that a 2-D PCA is a good description of structure.
(90.9%), with PC 1 and 2 accounting for 77.2% and 13.7% of the variation, respectively. The results from SIMPER also indicated that the copepod assemblage in September 2007 was clearly distinguishable from the other months due to the abundance of an ectoparasitic copepod (with a siphon), *Asteropontius minutus* (Fig. 4; Table 3).

**TABLE 4.** Seawater quality data across the eight sampling times: temperature, salinity, pH, oxygen saturation, biochemical oxygen demand (BOD), nitrate concentration, silicate concentration, NH$_3$ concentration, turbidity, and chlorophyll-a concentration.

<table>
<thead>
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</thead>
<tbody>
<tr>
<td>Temperature (°C)</td>
<td>30.98 ± 0.33</td>
<td>32.80 ± 0.15</td>
<td>29.80 ± 0.25</td>
<td>24.08 ± 0.15</td>
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<tr>
<td>Salinity (psu)</td>
<td>32.75 ± 1.21</td>
<td>33.00 ± 0.16</td>
<td>33.25 ± 2.16</td>
<td>34.44 ± 0.64</td>
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<tr>
<td>pH</td>
<td>8.28 ± 0.05</td>
<td>8.23 ± 0.08</td>
<td>8.18 ± 0.06</td>
<td>8.37 ± 0.07</td>
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<tr>
<td>Oxygen saturation (%)</td>
<td>136.2 ± 8.97</td>
<td>119.7 ± 6.41</td>
<td>103.2 ± 18.55</td>
<td>107.6 ± 6.64</td>
</tr>
<tr>
<td>BOD$_3$ (mg/L)</td>
<td>1.48 ± 0.07</td>
<td>1.48 ± 0.15</td>
<td>1.49 ± 0.14</td>
<td>0.26 ± 0.08</td>
</tr>
<tr>
<td>[NO$_3$] (mg/L)</td>
<td>0.04 ± 0.02</td>
<td>0.07 ± 0.02</td>
<td>0.10 ± 0.06</td>
<td>0.03 ± 0.03</td>
</tr>
<tr>
<td>[SiO$_4$] (mg/L)</td>
<td>0.28 ± 0.22</td>
<td>0.21 ± 0.19</td>
<td>0.13 ± 0.06</td>
<td>0.10 ± 0.06</td>
</tr>
<tr>
<td>[NH$_3$] (mg/L)</td>
<td>0.03 ± 0.02</td>
<td>0.03 ± 0.03</td>
<td>0.02 ± 0.00</td>
<td>0.01 ± 0.00</td>
</tr>
<tr>
<td>Turbidity (NTU)</td>
<td>0.54 ± 0.23</td>
<td>1.88 ± 0.26</td>
<td>3.22 ± 1.15</td>
<td>3.31 ± 0.24</td>
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<tr>
<td>[chlorophyll-a] (µg/L)</td>
<td>0.07 ± 0.06</td>
<td>0.24 ± 0.02</td>
<td>0.42 ± 0.08</td>
<td>0.13 ± 0.02</td>
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continued

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<tbody>
<tr>
<td>Temperature (°C)</td>
<td>26.60 ± 0.41</td>
<td>29.70 ± 0.16</td>
<td>31.20 ± 0.26</td>
<td>24.70 ± 0.11</td>
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<tr>
<td>Salinity (psu)</td>
<td>34.37 ± 1.58</td>
<td>34.54 ± 1.44</td>
<td>30.41 ± 0.44</td>
<td>34.50 ± 1.66</td>
</tr>
<tr>
<td>pH</td>
<td>8.32 ± 0.05</td>
<td>8.07 ± 0.01</td>
<td>8.29 ± 0.07</td>
<td>8.41 ± 0.03</td>
</tr>
<tr>
<td>Oxygen saturation (%)</td>
<td>108.3 ± 9.01</td>
<td>107.3 ± 0.77</td>
<td>113.9 ± 12.02</td>
<td>106.9 ± 4.80</td>
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<tr>
<td>BOD$_3$ (mg/L)</td>
<td>0.20 ± 0.26</td>
<td>1.45 ± 0.15</td>
<td>1.38 ± 0.25</td>
<td>0.33 ± 0.08</td>
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<tr>
<td>[NO$_3$] (mg/L)</td>
<td>0.03 ± 0.03</td>
<td>0.00 ± 0.00</td>
<td>0.02 ± 0.01</td>
<td>0.02 ± 0.03</td>
</tr>
<tr>
<td>[SiO$_4$] (mg/L)</td>
<td>0.07 ± 0.15</td>
<td>0.06 ± 0.15</td>
<td>0.39 ± 0.05</td>
<td>0.13 ± 0.19</td>
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<tr>
<td>[NH$_3$] (mg/L)</td>
<td>0.01 ± 0.00</td>
<td>0.02 ± 0.01</td>
<td>0.01 ± 0.00</td>
<td>0.01 ± 0.00</td>
</tr>
<tr>
<td>Turbidity (NTU)</td>
<td>4.21 ± 0.46</td>
<td>4.52 ± 1.72</td>
<td>3.63 ± 1.48</td>
<td>2.41 ± 0.34</td>
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<tr>
<td>[chlorophyll-a] (µg/L)</td>
<td>0.12 ± 0.76</td>
<td>0.21 ± 0.07</td>
<td>0.20 ± 0.05</td>
<td>0.13 ± 0.01</td>
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</table>

**Discussion**

Although copepods living in association with cnidarians have been known since Della Valle (1880) it was not until 1960 that they were reported from scleractinian corals when Humes (1960) proposed a new family Xarifiidae for two new species from the Maldives (see also Gerlach 1960). Since then new species associated with hard corals have been described at a rate of about 6.5 species per year. Humes (1985c) reported a total of 172 species in 41 genera from 118 host species, representing 47 genera. During the ensuing three decades the number of copepod species (363) and genera (99) found to be associated with scleractinians has more than doubled although only 30 additional hosts had been surveyed for copepods. Stella *et al.*’s (2011) review identified decapods as the largest group of coral-associated crustaceans (310 species), constituting 35% of the total number of invertebrate species to utilize coral. According to their checklist copepods ranked second with 243 species known to associate with live coral, of which 199 species were considered to parasitize their coral host. The large discrepancy in total species number (33%) between our study and Stella *et al.*’s (2011) review results from incomplete coverage in the latter rather than the addition of new taxa since 2011. For example, of the 66 coral-associated siphonostomatoids recorded prior to 2011 only five were included, omitting important contributions by Humes (1991a, 1996b, 1997c),
Kim (2003, 2010) and Stock (1966, 1987, 1989). Similarly, only 114 of the 136 species of Anchimolgidae described prior to 2011 were listed. Taking these adjustments into account it would not be extravagant to assume that copepods are by far the most diverse group of coral-associated invertebrates. The order Scleractinia currently contains 1,579 extant species in 243 genera (WoRMS Editorial Board 2016) yet only 148 species representing 66 genera have so far been examined for copepods. Some families such as the Caryophylliidae, containing 281 species, have remained completely unsurveyed while others, which have received considerable attention, still deserve more intense investigation. For example, there are approximately 269 extant species in the Acroporidae (133 belonging to Acropora) but only 42 species (24 in Acropora) are known to serve as hosts to copepods. Since less than 10% of the potential scleractinian hosts have so far been surveyed the true diversity of coral-associated copepods is expected to be almost an order of magnitude higher, clearly outnumbering the decapods. Interest in (particularly poecilostome) cyclopoid copepods has not been paralleled by interest in other copepod groups (Humes 1985c). The Harpacticoida have only few species that are associated with hard corals, representing two genera in two families. Members of the Tegastidae are known to utilize other cnidarian hosts such as hydrozoans and acelominicans (Humes 1981a, 1984b; Varela 2010; Huys, this volume), however, it has been suggested that they may be more common associates of scleractinian corals (Humes 1985c). At present, only 68 species of coral-associated siphonostomatoids are known but this undoubtedly represents only a fraction of their true diversity. Kim’s (2010) recent study, describing 41 new species and seven new genera from corals in Madagascar and the West Indies, illustrates that our limited knowledge of siphonostomatoids associated with this host group is primarily attributable to sampling bias and neglect in the past.

![Diagram](https://example.com/diagram.png)

**FIGURE 4.** Principal component analysis (PCA) of square root-transformed data from five functional categories of copepods (see text for descriptions.) defined based on behaviour (endo-/ectoparasitic or benthic) and the structure of the feeding appendages (mandibles vs. siphon) at various sampling periods. PC1 accounted for 77.2% of the variability, and PC2 accounted for 13.7%.  

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Branching corals of the genera *Acropora*, *Pocillopora* and *Stylophora* harbour the highest diversity of symbiotic copepods. Importantly, these coral taxa are also among the most susceptible to bleaching and hence this level of habitat specialization may place their associated copepods and other invertebrates at a great risk of extinction (Stella et al. 2011). The 288 cyclopid species described to date collectively utilize a total of 134 coral hosts, with about 67% of the associated copepod species being stenoxenous. The apparent high dependence of these species on certain corals, in conjunction with their abbreviated larval dispersal and often small geographic ranges, could have dire consequences, depending on how those corals cope with the suite of environmental threats currently challenging coral reefs.

This is the first study to document the dynamics of symbiotic copepod infection over space and time in the model reef-building coral *P. damicornis*. Humes (1985a) had previously pointed out that members of the branching coral genera *Acropora* Oken, 1815 and *Pocillopora* Lamarck, 1816 seem to be the species which are most susceptible to copepod infection, and this appears to be the case in Taiwan as well. Specifically, at least 11 valid species and one undescribed species (*Xarifia* sp.) of symbiotic copepods are known to use *P. damicornis* as host in Taiwanese waters (Ho et al. 2008; Cheng & Dai 2010; Cheng 2011; this study) (Table 1).

Our findings clearly indicate that the highest infestation by copepods occurred in the summer of 2007. Since corals in southern Taiwan suffered a severe bleaching event at the same time (Kuo et al. 2012), these high infestation levels were possibly related to the weakening of the defense mechanisms of the corals due to prolonged exposure to thermal stress (sensu Hudson & Lester 1992; Harvell et al. 2001, 2002). However, in August 2008, a substantially lower copepod infection was observed in spite of the higher seawater temperatures measured during that month. In contrast to the summer of 2007, no bleaching was observed in August 2008, suggesting that the corals may have been sufficiently healthy to fight off copepod infection.

Previous studies have found that corals undergoing bleaching may be more susceptible to pathogen infection (Harvell et al. 2001, 2002; Lafferty & Holt 2003). Our findings also revealed a significant negative correlation between *Symbiodinium* density and mean abundance of both cyclopoid and siphonostomatoid (but not harpacticoid) copepods in the coral colonies. Whether copepod infection itself is the causative agent causing bleaching or at least contributed to the decrease in *Symbiodinium* density in bleached samples via digestion of host coral-derived *Symbiodinium* (sensu Cheng & Dai 2010) remains to be determined since bleaching could have preceded copepod infection. Future work should aim towards a better understanding of the relationship between copepod infection and the breakdown of the coral-dinoflagellate endosymbiosis, with a specific emphasis on unravelling whether infectious copepods can actually increase the severity of the bleaching process, or their infection becomes established later on in the process.

Ecological conditions can also play critical roles in altering parasite communities (Mouritsen & Poulin 2002; Poulin & Mouritsen 2005; Møller 2010). In our study the infection by copepods was influenced not only by *Symbiodinium* density, but also surface area of the coral colonies and physical parameters (e.g., nitrate and chlorophyll-α concentrations), although the results were inconsistent between different copepod taxa. This could be due to their wide diversity of feeding strategies and behaviours. For example, xarifid copepods (the most commonly recorded cyclopoids) are endoparasites that may digest and retain *Symbiodinium* cells in their body temporarily as a nutrient source (Gerlach in Humes 1985c; Cheng & Dai 2010). Therefore, their abundance may be influenced by the amount of resources (i.e., *Symbiodinium*) provided by host corals. This may explain why so few xarifid copepods were found in severely bleached corals (*Symbiodinium* density < 0.2 × 10³ cells.cm⁻²). In contrast, siphonostomatoids are mucus feeders that mainly consume coral mucus via their tube-like mouths. Their preference for residing in the outmost regions of the coral colonies, though, increases their chances of attack by nematocysts (Humes 1985c; Dojiri 1988). Harpacticoids encompass planktonic, free-living, benthic, and invertebrate-associated species that generally consume microalgae, bacteria, particulate organic matter, and even animal tissues; therefore, their abundance can increase with increasing nitrate and chlorophyll-α concentrations (Rieper 1982; Hicks & Coull 1983; Carman & Thistle 1985; Seifried & Dü尔baum 2000). Given that many of these species are frequently collected in benthic samples independent of any associated host, it is conceivable that some were inadvertently isolated and quantified, not from the corals themselves, but from the surrounding seawater (see e.g. Snellgrove & Lewis (1989) for an analogous example). This could explain why their densities showed no correlation with *Symbiodinium* density or coral surface area.

In the wild, the symbiotic/parasitic copepods not only suffer from environmental impacts but also face changes to the immune response of coral hosts. We therefore suggest that variables related to the coral’s immune
response and cellular/molecular markers, such as CO₂ fixation mechanism, lipid peroxide (LPO), total glutathione (GSH), heat shock protein (Hsp), manganese superoxide dismutase (MnSOD), and copper/zinc superoxide dismutase (Cu/ZnSOD) should also be studied during parasitological surveys (Black et al. 1995; Fang et al. 1997; Jones et al. 1998; Moshe et al. 1999; Downs et al. 2000, 2005). Such information could prove important in revealing particular correlations in future case studies.

Species whose population sizes reflect environmental impacts and habitat alterations are typically classified as bioindicator species. Previous studies have suggested that parasites are useful bioindicators of ecosystem health and stability (Overstreet 1997; Dzikowski et al. 2003; Hussten & Lafferty 2004; Ogut & Palm 2005; Hooff & Peterson 2006; Sures 2008a,b; Rueckert et al. 2009; Cruz et al. 2013). The occurrence of higher densities of copepods on/in bleaching corals reported in this study during periods of high seawater temperature suggest that their virulence may increase when corals are exposed to stress induced by environmental changes. Therefore, changes in species composition and abundance of copepod communities on reef corals could potentially be used as a bioindicator for environmental change and coral health. Further studies focusing on the ecological function of symbiotic copepods of corals should be a priority since they may provide important insight into the status of coral reef ecosystems and have significant implications related to coral conservation. As a first step, it will be important to verify whether these copepods are either genuinely parasitic or only commensalistic, thus not necessarily causing any decrease in fitness of their hosts.

Acknowledgements

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**APPENDIX 1.** References containing original descriptions of scleractinian host taxa cited in Table 1.


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