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Parasitic copepods (Crustacea, Hexanauplia) on fishes from the lagoon flats of Palmyra Atoll, Central Pacific

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Abstract

We surveyed copepods parasitic on the fishes at Palmyra, a remote atoll in the Central Indo-Pacific faunal region. In total, we collected 849 individual fish, representing 44 species, from the intertidal lagoon flats at Palmyra and recovered 17 parasitic copepod species. The parasitic copepods were: *Orbitacolax williamsi* on *Mulloidichthys flavolineatus*; *Anuretes serratus* on *Acanthurus xanthopterus*; *Caligus confusus* on *Carangoides ferdau*, *Carangoides orthogrammus*, *Caranx ignobilis*, *Caranx melampygus*, and *Caranx papuensis*; *Caligus kapuhili* on *Chaetodon auriga* and *Chaetodon lunula*; *Caligus laticaudus* on *Rhinecanthus aculeatus*, *Pseudobalistes flavimarginatus*, *M. flavolineatus*, *Upeneus taeniopterus*, *Chrysiptera glauca,* and *Epinephalus merra*;

Caligus mutabilis on *Lutjanus fulvus* and *Lutjanus monostigma*; *Caligus randalli* on *C. ignobilis*; *Caligus* sp. on *L. fulvus*; *Caritus serratus* on *Chanos chanos*; *Lepeophtheirus lewisi* on *A. xanthopterus*; *Lepeophtheirus uluus* on *C. ignobilis*; *Dissonus similis* on *Arothron hispidus*; *Nemesis* sp. on *Carcharhinus melanopterus*; *Hatschekia longiabdominalis* on *A. hispidus*; *Hatschekia bicaudata* on *Chaetodon auriga* and *Chaetodon lunula*; *Kroyeria longicauda* on *C. melanopterus* and *Lernanthropus* sp. on *Kyphosus cinerascens*. All copepod species reported here have been previously reported from the Indo-Pacific but represent new geographical records for Palmyra, demonstrating large-scale parasite dispersion strategies.

Keywords
Parasitic copepods, fish, geographical isolation, islands, Indo-Pacific, atoll

Introduction

Although there have been several surveys of copepods parasitic on Indo-Pacific fishes, including the Great Barrier Reef (Australia), New Caledonia, New Guinea, India, Taiwan and the Hawaiian Islands (Yamaguti 1963, Kabata 1966, Lewis 1968, Pillai 1968, 1985, Cressey and Boyle 1973, Cressey and Cressey 1979, Ho and Dojiri 1977, Deets and Dojiri 1990, Ogawa 1991, Ho and Lin 2004, Boxshall and Justine 2005, Tang and Kalman 2005, Palm and Bray 2014), the East Indo-Pacific has received little sampling effort. Lafferty et al. (2008) compared parasite communities, including parasitic copepods, at two coral atolls in the Line Islands chain of the central Pacific (Kiritimati Island and Palmyra Atoll). However, their analysis was limited to broad patterns of richness and abundance of morphospecies, conservatively grouped into broad taxonomic categories. Palm and Bray (2014) listed parasites from Hawaiian fishes, reporting 64 copepod species (13 families) from 298 identified fish species.

Palmyra Atoll is one of the northern Line Islands located in the Indo-Pacific (IP) marine ecoregion (Spalding et al. 2007), 1680 km SSW of Hawaii. It is presently a marine protected area and has not supported regular human settlement since World War II. Palmyra Atoll has a relatively long history with little to no exploitation (DeMartini et al. 2008, Sandin et al. 2008). All fishing has been prohibited at Palmyra since it became a US National Wildlife Refuge in 2000 (before that, its remoteness kept fishing pressure low).

As part of a larger project assembling food webs at Palmyra Atoll, we have been cataloging the parasites found in the system. This paper is a companion to two others examining different fish parasite taxa (Vidal-Martínez et al. 2012, 2017). We recovered a considerable number of parasitic copepods from 44 fish species. As such, our tabulation adds to the few published species descriptions or host records from the Central Indo-Pacific region (Cressey and Boyle 1973, 1979, Cressey 1977, Ho and Lin 2004, Palm and Bray 2014), with an emphasis on describing diversity of the copepod supracommunity (Bush et al. 1997) at this site. The goal of this study is two-

fold. First, we list the copepod species recovered, and note, for each, taxonomic issues and report their prevalence, mean intensity and host species. Second, we then discuss this diversity survey with respect to previously published records for the region.

Material and methods

We collected fish by seine, spear, and hook and line from the intertidal sand flats bordering the lagoon of Palmyra Atoll between October 2009 and July 2012. To avoid loss or mixing of parasites among fishes, immediately after capture, we placed fish in individual plastic bags with lagoon water and transported them to the laboratory facility of the Palmyra Atoll Research Consortium (PARC). We examined only freshly killed fish (and the bag water). Observations were under a stereomicroscope. Skin and fins of each host were carefully examined. The gill arches were removed and examined under a stereomicroscope. The copepods obtained were counted, preliminarily identified, fixed in 95 % EtOH, labelled and stored in vials for later evaluation. Then, in the Laboratory of Aquatic Pathology of CINVESTAV-Mérida, specimens were mounted and cleared with lactophenol to identify species based on morphology using an Olympus BX-53 microscope (Olympus Corporation, Shinjuku, Tokyo, Japan). Prevalence and mean intensity concepts were applied following Bush et al. (1997). Synonyms for each host species and copepod species were obtained from FishBase (Froese and Pauly 2018) and World of Copepods (Walter and Boxshall 2018), respectively. Voucher specimens were deposited in the United States National Parasite Collection, Washington, DC (USNPC), and the Helminthological Collection of the Laboratory of Parasitology, at the Centre for Research and Advanced Studies, National Polytechnic Institute, Mérida, Yucatán, México (CHCM).

Results

Copepods of fishes from Palmyra lagoon flats

During this study, 849 individual fish from 44 species were collected. Fourteen of the 44 fish species examined were parasitized by at least one parasitic copepod species. *Caranx ignobilis* (Forsskål) was host to three copepod species, the most of any fish. *Acanthurus xanthopterus* Valenciennes, *Carcharhinus melanopterus* (Quoy & Gaimard), *Chaetodon auriga* Forsskål, *Chaetodon lunula* (Lacépède), *Lutjanus fulvus* (Forster), *Mulloidichthys flavolineatus* (Lacépède) and *Arothron hispidus* (Linnaeus) served as host for two copepod species. All other infected species hosted a single copepod species. Thirty fish species were found free of any copepod parasite (Table 1). Ten of the 17 copepod species recovered belong to the Caligidae family (Table 2).

Table 1. Fish species examined from the lagoon flats from the Palmyra Atoll. N = number of fish examined; Max = maximum length reported for that fish species in FishBase (http://www.fishbase.se); Range = total length range of the fish examined.

Host examined	Fish common name	N	Infected hosts	Max (cm)	Range (cm)
Acanthuridae					
Acanthurus triostegus (Linnaeus, 1758)	Convict surgeonfish	50	0	27	10–18
Acanthurus xanthopterus Valenciennes, 1835	Yellowfin surgeonfish	20	2	70	20–40
Albulidae					
Albula glossodonta (Forsskål, 1775)	Roundjaw bonefish	24	0	90	37–58
Apogonidae					
Cheilodipterus quinquelineatus Cuvier, 1828	Five-lined cardinalfish	5	0	13	5–6
Balistidae					
Pseudobalistes flavimarginatus (Rüppell, 1829)	Yellowmargin triggerfish	4	0	60	17–53
Rhinecanthus aculeatus (Linnaeus, 1758)	Blackbar triggerfish	18	0	30	8–24
Belonidae					
Platybelone argalus (Lesueur, 1821)	Keeltail needlefish	2	0	50	9–36
Carangidae					
Carangoides ferdau (Forsskål, 1775)	Blue trevally	5	0	75	33–38
Carangoides orthogrammus (Jordan & Gilbert, 1882)	Island trevally	3	0	75	25–35
Caranx ignobilis (Forsskål, 1775)	Giant trevally	4	3	170	56–79
Caranx melampygus Cuvier, 1833	Bluefin trevally	6	2	117	31–66
Caranx papuensis Alleyne & MacLeay, 1877	Brassy trevally	5	2	88	12–41
Carcharhinidae					
Carcharhinus melanopterus (Quoy & Gaimard, 1824)	Blacktip reef shark	5	3	200	46–219
Chaetodontidae					
Chaetodon auriga Forsskål, 1775	Threadfin butterflyfish	13	4	23	12–19
Chaetodon lunula (Lacepède, 1802)	Raccoon butterflyfish	14	6	20	11–16
Chanidae					
Chanos chanos (Forsskål, 1775)	Milkfish	5	1	180	31–57
Gobiidae					
Amblygobius phalaena (Valenciennes, 1837)	Whitebarred goby	18	0	15	1.3–7
Asterropteryx semipunctata Rüppell, 1830	Starry goby	12	0	6	2–4
Gnatholepis anjerensis (Bleeker, 1851)	Eye-bar goby	2	0	8	2–3
Istigobius decoratus (Herre, 1927)	Decorated goby	5	0	13	7–11
Istigobius ornatus (Rüppell, 1830)	Ornate goby	26	0	11	3–6
Istigobius rigilius (Herre, 1953)	Rigilius goby	1	0	11	4
Oplopomus oplopomus (Valenciennes, 1837)	Spinecheek goby	26	0	10	2–7
Psilogobius prolatus Watson & Lachner, 1985	Longjaw shrimpgoby	11	0	6	2–4
Valenciennea sexguttata (Valenciennes, 1837)	Sixspot goby	14	0	14	2–9
Hemiramphidae					
Hemiramphus depauperatus Lay & Bennett, 1839	Tropical half-beak fish	20	0	40	20–34
Kiphosidae					
Kyphosus cinerascens (Forsskål, 1775)	Blue sea chub	2	1	50	35–38
Lutjanidae					
Lutjanus fulvus (Forster, 1801)	Blacktail snapper	26	5	40	7–26
Lutjanus monostigma (Cuvier, 1828)	One spot snapper	6	1	60	17–37
Mugilidae					
Crenimugil crenilabis (Forsskål, 1775)	Fringelip mullet	42	0	60	8–45
Liza vaigiensis (Quoy & Gaimard, 1825)	Squaretail mullet	54	0	63	3–32
Valamugil engeli (Bleeker, 1858)	Kanda	63	0	30	1–20
Mullidae					
Mulloidichthys flavolineatus (Lacepède, 1801)	Yellowstripe goatfish	52	8	43	8–37
Upeneus taeniopterus Cuvier, 1829	Finstripe goatfish	5	3	33	1–30
Muraenidae					
Gymnothorax pictus (Ahl, 1789)	Paintspotted moray	7	0	140	41–70

Host examined	Fish common name	N	Infected hosts	Max (cm)	Range (cm)
Ophichthidae					
Myrichthys colubrinus (Boddaert, 1781)	Harlequin snake eel	3	0	97	33–65
Pinguipedidae					
Parapercis lata Randall & McCosker, 2002	Y-Barred Sandperch	13	0	21	2–3
Pomacentridae					
Abudefduf septemfasciatus (Cuvier, 1830)	Banded sergeant	12	0	23	14–20
Abudefduf sordidus (Forsskål, 1775)	Blackspot sergeant	18	0	24	14–19
Chrysiptera glauca (Cuvier, 1830)	Grey demoiselle	3	0	12	8–10
Stegastes nigricans (Lacepède, 1802)	Dusky farmerfish	10	0	14	8–10
Serranidae					
Epinephelus merra Bloch, 1793	Honeycomb grouper	2	0	32	13–24
Sphyraenidae					
Sphyraena barracuda (Edwards, 1771)	Great barracuda	2	0	200	65–76
Tetraodontidae					
Arothron hispidus (Linnaeus, 1758)	White-spotted puffer	15	9	50	17–49

Table 2. Parasitic copepods of fishes from the lagoon flats of Palmyra Atoll; N = number of fish examined. The authorities for parasites were included in the text.

Copepod species	Hosts	N	Infected hosts	Prevalence (%)	Mean intensity (± SD)
Bomolochidae					
Orbitacolax williamsi	*Mulloidichthys flavolineatus*	52	1	1.9	1
Caligidae					
Anuretes serratus	*Acanthurus xanthopterus*	20	1	5	6
Caligus confusus	*Carangoides ferdau*	5	2	40	2 ± 0.0
	Carangoides orthogrammus	3	1	33.3	6
	Caranx ignobilis	4	3	75	12.7 ± 12.2
	Caranx melampygus	6	2	40	4 ± 0.0
	Caranx papuensis	5	2	33.3	2 ± 0.0
Caligus kapuhili	*Chaetodon auriga*	13	1	7.7	8
	Chaetodon lunula	14	4	28.6	2.5 ± 1.7
Caligus laticaudus	*Rhinecanthus aculeatus*	18		5.6	1
	Pseudobalistes flavimarginatus	4	2	50	21 ± 26.9
	Mulloidichthys flavolineatus	52	7	13.5	1.5 ± 0.5
	Upeneus taeniopterus	5	3	60	2.7 ± 2.1
	Chrysiptera glauca	3	1	3.33	2
	Epinephalus merra	2	1	50	1
Caligus aff. mutabilis	*Lutjanus fulvus*	26	4	15.4	1.75 ± 1.5
	Lutjanus monostigma	6	1	16.6	2
Caligus randalli	*Caranx ignobilis*	4	1	25	1
Caligus sp.	*Lutjanus fulvus*	26	1	3.8	1
Caritus serratus	*Chanos chanos*	5	1	20	4
Lepeophtheirus lewisi	*Acanthurus xanthopterus*	20	1	5	1
Lepeophtheirus uluus	*Caranx ignobilis*	4	1	25	4
Dissonidae					
Dissonus similis	*Arothron hispidus*	15	2	13.3	2 ± 0.0
Eudactylinidae					
Nemesis sp.	*Carcharhinus melanopterus*	5	2	40	2 ± 0.0
Hatschekiidae					
Hatschekia longiabdominalis	*Arothron hispidus*	15	8	53.3	100 ± 329.2
Hatschekia bicaudata	*Chaetodon auriga*	13	3	23.1	7.3 ± 3.1
	Chaetodon lunula	14	2	14.3	5 ± 1.4
Kroyeriidae					
Kroyeria longicauda	*Carcharhinus melanopterus*	5	2	40	16 ± 2.8
Lernanthropidae					
Lernanthropus sp.	*Kyphosus cinerascens*	2	1	50	2

Order Cyclopoida Milne Edwards, 1840
Bomolochidae Claus, 1875
***Orbitacolax* Shen, 1957**

***Orbitacolax williamsi* Cressey & Cressey, 1989**

Type host. *Scolopsis taenioptera* (as *S. dubiosus*) (Cuvier) (Nemipteridae).

Other host and localities. *Scolopsis taenioptera* (as *S. dubiosus*) from Okinawa, Japan (Cressey and Cressey 1989). *Coris batuensis* (Bleeker) (Labridae) from Lizard Island, Australia (Muñoz and Cribb 2006). *Thamnaconus degeni* (Regan) (Monacanthidae) from South Australia (Hayward et al. 2011).

Current host. *Mulloidichthys flavolineatus* (Mullidae).

Site of infection. Gills.

Prevalence and mean intensity. 1.9 and 1 (n = 52).

Specimens deposited. CHCM No. 560 (voucher) (1 vial, 1 specimen ♀).

Remarks. To date, the genus *Orbitacolax* includes 10 valid species, which form two clusters (Venmathi Maran et al. 2014), the *hapalogenyos*-group with four species (*O. hapalogenyos*, *O. pteragogi*, *O. trichiuri*, and *O. unguifer*) and *analogus*-group with six species (*O. analogus*, *O. dactylopterusi*, *O. aculeatus*, *O. leptoscari*, *O. uniunquis*, and *O. williamsi*). This second group is based on the second endopodal segment of leg 2 either no inner seta or having 1 inner seta. Particularly, *O. williamsi* lacks seta on the second endopodal segment of leg 2, as seen in our specimen and the original description provided by Cressey and Cressey (1989). However, Venmathi-Maran et al. (2014) pointed out that *O. williamsi* carries 1 inner seta in that segment, but this is likely inaccurate. *Orbitacolax williamsi* has been found on western Pacific fishes from four families, suggesting that this parasite may have a low host specificity.

Order Siphonostomatoida Burmeister, 1835
Caligidae Burmeister, 1834
***Anuretes* Heller, 1865**

***Anuretes serratus* Shiino, 1954**

Type host. *Prionurus scalprum* (as *Xesurus scalprum*) Valenciennes (Acanthuridae).

Other host and localities. *Prionurus scalprum* (as *Xesurus scalprum*) (Acanthuridae) from Seto, Wakayama Prefecture, Japan (Shiino 1954). *Naso hexacanthus* (Bleeker) (Acanthuridae) from Oahu, Hawaii (Lewis 1964a, Palm and Bray 2014); from Japan and India (Prabha and Pillai 1986). *Prionurus microlepidotus* Lacepède (Acanthuridae) from Australia (Boxshall 2018).

Current host. *Acanthurus xanthopterus* (Acanthuridae).

Site of infection. Gills.

Prevalence and mean intensity. 5 and 6 (n = 20).

Specimens deposited. CHCM No. 561 (voucher) (1 vial, 1 specimen ♀).

Remarks. The validity of the genus *Anuretes* is questionable given the considerable morphological overlap with the members of *Lepeophtheirus* (Dojiri and Ho 2013). Currently, *Anuretes* includes 21 valid species (Boxshall 2018, Walter and Boxshall 2018); of which *A. serratus* may be distinguished by stout spines on distal exopodal segment of leg 1, and a branched spine on first exopodal segment of leg 2 (Shiino 1954, Lewis 1964a), which were clearly observed in our specimens. In addition, *A. serratus* lacks sternal furca. According to Dojiri and Ho (2013), a sternal furca is rarely absent in species of *Anuretes*.

Caligus Müller, 1785

Caligus confusus Pillai, 1961

Type host. *Caranx ignobilis* (as *C. sansun*) (Carangidae).

Other host and localities. *Alepes djedaba* (Forsskål) from Durban; *Caranx caballus* (Günther) and *Caranx caninus* (Günther) from Mexican Pacific and Ecuador; *Caranx djedaba* (Forsskål) from Durban, South Africa and Sri Lanka; *Caranx hippos* (Linnaeus) from Galapagos Islands and Panama; *Caranx ignobilis* from Taiwan, Indian and Australia; *Caranx melampygus* Cuvier from Eniwetok Atoll and Taiwan; *Caranx sexfasciatus* Quoy & Gaimard from South Africa, Taiwan, Indonesia and Australia; *Caranx* sp. from Celebes and New Caledonia (all Carangidae); *Coryphaena hippurus* Linnaeus (Coryphaenidae) from Galapagos Islands and Panama; *Decapterus* sp. (Carangidae) from Tonkin Gulf, Vietnam; *Elagatis bipinnulata* (Quoy & Gaimard) (Carangidae) from Galapagos Islands, Panama, India and Taiwan; *Elagatis* sp. from Celebes; *Epinephelus tauvina* (Forsskål) (Serranidae) from Kuwait; *Rhabdosargus holubi* (Steindachner) (Sparidae) from South Africa; *Seriola dumerili* (Risso) (Carangidae) from Taiwan; *Seriola* sp. (Carangidae) from Colombia (Kabata 1968, Grobler et al. 2003, Ho and Lin 2004, Yuniar et al. 2007, Kazachenko et al. 2014, Morales-Serna et al. 2014, 2015, Boxshall 2018).

Current host. *Carangoides ferdau* (Forsskål), *Carangoides orthogrammus* (Jordan & Gilbert), *Caranx ignobilis*, *Caranx melampygus* and *Caranx papuensis* Alleyne & MacLeay (all Carangidae).

Site of infection. Gills.

Prevalence and mean intensity. 40 and 2 (n = 5) to *Carangoides ferdau*, 33.3 and 6 (n = 3) to *Carangoides orthogrammus*, 75 and 12.7 ± 12.2 (n = 4) to *Caranx ignobilis*; 33.3 and 2 (n = 6) to *Caranx melampygus*; 40 and 4 (n = 5) to *Caranx papuensis*.

Specimens deposited. CHCM No. 562 (voucher) (1 vial, 1 specimen ♀) (from *Caranx ignobilis*), CHCM No. 563 (voucher) (1 vial, 2 specimens ♂ ♀) (from *Caranx papuensis*), USNM No. 1550598 (voucher) (1 vial, 1 specimen ♀) (from *Caranx ignobilis*).

Remarks. The genus *Caligus* contains approximately 250 species. According to Ho and Lin (2004), before the establishment of *C. confusus*, specimens of this species were confused with *Caligus productus* (as *Caligus alalongae*) Dana, 1852 and *Caligus constrictus* Heller, 1865. However, these authors pointed out nine characteristics known only for *C. confusus*. The morphology of our specimens (♂ and ♀) fits with the description of Ho and Lin (2004). Additionally, based on the examination of the present material and also that from previous surveys in the Eastern Pacific (Morales-Serna et al. 2014, 2015), we suggest that the shape of the first segment of the antenna and sternal furca may be useful in identifying *C. confusus*. Clearly, *C. confusus* has high affinity for carangid fish; nonetheless, this parasite can also be found on fish from different families. To date, it is distributed in tropical waters of the Eastern Pacific and Indo-Pacific, with no records for the Atlantic Ocean.

Caligus kapuhili Lewis, 1967

Type host. *Chaetodon miliaris* Quoy & Gaimard (Chaetodontidae).

Other host and localities. *Chaetodon miliaris* Quoy & Gaimard, *Chaetodon fremblii* Bennett from Hawaii (Lewis 1967, Palm and Bray 2014). *Chaetodon auripes* Jordan & Snyder and *Chaetodon vagabundus* Linnaeus from Taiwan (all Chaetodontidae) (Ho and Lin 2007).

Current host. *Chaetodon auriga* and *Chaetodon lunula* (Chaetodontidae).

Site of infection. Gills.

Prevalence and mean intensity. 7.7 and 8 (n = 13) to *Chaetodon auriga*; 28.6 and 2.5 ± 1.7 (n = 14) to *Chaetodon lunula*.

Specimens deposited. CHCM No. 564 (voucher) (1 vial, 1 specimen ♂) (from *C. auriga*). CHCM No. 565 (voucher) (1 vial, 1 specimen ♂) (from *C. lunula*). USNM No. 1550599 (voucher) (1 vial, 1 specimen ♂) (from *C. lunula*).

Remarks. According to Lewis (1967) and Lin and Ho (2007), *C. kapuhili* is morphologically close to *Caligus laticaudus* Shiino, 1960. However, the abdomen is 1-segmented in *C. kapuhili* and 2-segmented in *C. laticaudus*. We found specimens of *C. laticaudus* (see below), which facilitated our morphological analysis. Likewise, we identified *C. kapuhili* based on host preference, since this species has only been found on fish of the genus *Chaetodon* from the North-West Pacific.

Caligus laticaudus Shiino, 1960

Type host. *Pagrus major* (as *Pagrosomus major*) (Temminck & Schlegel) (Sparidae).

Other host and localities. *Pagrus major* (as *Pagrosomus major*) (Sparidae) from Japan (Shiino 1960). *Acanthurus olivaceus* Bloch & Schneider (Acanthuridae) from Eniwetok Atoll; *Dentex tumifrons* (Temminck & Schlegel) (Sparidae) from Korea; *Liza haematocheila* (Temminck & Schlegel) (Mugilidae) from China; *Caranx melampygus*

(Carangidae), *Lutjanus vitta* (Quoy & Gaimard), *Lutjanus russellii* (Bleeker) (Lutjanidae) and *Parapristipoma trilineatum* (Thunberg) (Haemulidae), *Polydactylus plebeius* (Broussonet) and *Polydactylus sextarius* (Bloch & Schneider) (Polynemidae) from Taiwan; *Parastomateus niger* (Bloch) (Carangidae) from Malaysia; *Filimanus heptadactyla* (Cuvier) (Polynemidae) and *Rhabdosargus sarba* (Forsskål) (Sparidae) from India (Ho and Lin 2004, Moon and Kim 2012). *Gnathanodon speciosus* (Forsskål), *Caranx sexfasciatus* Quoy & Gaimard (Carangidae), *Heniochus acuminatus* (Linnaeus) (Chaetodontidae), *Kyphosus bigibbus* Lacepède (Kiphosidae), *Pseudolabrus guentheri* Bleeker (Labridae), *Pagrus auratus* (Forster) (Sparidae) from Australia (Boxshall 2018).

Current host. *Rhinecanthus aculeatus* (Linnaeus), *Pseudobalistes flavimarginatus* (Rüppell) (Balistidae), *Mulloidichthys flavolineatus*, *Upeneus taeniopterus* Cuvier (Mullidae), *Chrysiptera glauca* (Cuvier) (Pomacentridae) and *Epinephalus merra* Bloch (Serranidae).

Site of infection. Gills..

Prevalence and mean intensity. 5.6 and 1 (n = 18) to *Rhinecanthus aculeatus*; 50 and 21 ± 26.9 (n = 4) to *Pseudobalistes flavimarginatus*; 13.5 and 1.5 ± 0.5 (n = 52) to *Mulloidichthys flavolineatus*; 60 and 2.7 ± 2.1 (n = 5) to *Upeneus taeniopterus*; 3.33 and 2 (n = 3) to *Chrysiptera* glauca; 50 and 1 (n = 2) to *Epinephalus merra*.

Specimens deposited. CHCM No. 566 (voucher) (1 vial, 2 specimens ♂ ♀) (from *M. flavolineatus*). USNM No. 1550600 (voucher) (1 vial, 1 specimen ♂) (from *M. flavolineatus*).

Remarks. Ho and Lin (2004) indicated that the female of *C. laticaudus* may be identified by a combination of five characteristics (the corpus of the maxilliped with a large, conical protrusion in the myxal region; the terminal elements on last segment of exopod of leg 1 lack accessory processes; outermost element 1 of the four terminal elements of leg 1 exopod about one third of the length of other three elements which are subequal in length; formula of the 3-segmented exopod of leg 4 as I-0; I-0; III; and the terminal three spines on leg 4 subequal in length). Our results support the view that *C. laticaudus* infects fishes only from the Indo-West Pacific.

Caligus aff. *mutabilis* Wilson, 1905

Type host. *Centropristis striata* (as *Centropristes striatus*) (Linnaeus) (Serranidae).

Other host and localities. *Centropristis striata* (as *Centropristes striatus*) (Serranidae) from North American waters (Wilson 1905). *Acanthocybium* sp., *Euthynnus* sp., *Sarda* sp., *Scomberomorus* sp., and *Thunnus* sp. (all Scombridae) from Colombia; *Archosargus rhomboidalis* (Linnaeus) (Sparidae), *Chaetodipterus faber* (Broussonet) (Ephippidae), *Mycteroperca microlepis* (Goode & Bean), *Scomberomorus brasiliensis* Collette, Russo & Zavala-Camin, *Scomberomorus maculatus* (Mitchill) (Scombridae) and *Trachinotus goodei* Jordan & Evermann (Carangidae) from Brazil; *Balistes* sp. (Balistidae), *Calamus brachysomus* (Lockington) (Sparidae), *Centropomus* sp. (Centropomidae), *Chaetodipterus zonatus* (Girard) (Ephippidae), *Epinephelus labriformis* (Jenyns) (Serranidae),

Hoplopagrus guentherii Gill (Lutjanidae), *Katsuwonus pelamis* (Linnaeus) (Scombridae), *Kyphosus elegans* (Peters) (Kyphosidae), *Lutjanus guttatus* (Steindachner), *Lutjanus peru* (Nichols & Murphy) (Lutjanidae), *Menticirrhus undulatus* (Girard) (Sciaenidae), *Microlepidotus brevipinnis* (Steindachner) (Haemulidae), *Mugil cephalus* (Linnaeus) (Mugilidae), *Paralabrax clathratus* (Girard), *Paralabrax maculatofasciatus* (Steindachner), *Paralabrax nebulifer* (Girard) (all Serranidae), *Sarda chiliensis* (Cuvier), *Scomberomorus sierra* Jordan & Starks (Scombridae) and *Selene orstedii* Lütken (Carangidae) from Mexican Pacific; *S. brasiliensis* from Costa Rica; *Scomberomorus cavalla* (Cuvier) (Scombridae) from Surinam; *S. maculatus* from Florida; *Scomberomorus japonicus* from Campeche (Gulf of Mexico); *E. labriformis*, *Eucinostomus entomelas* Zahuranec (Gerreidae), *Haemulopsis axillaris* (Steindachner) (Haemulidae), *Paralabrax callaensis* Starks (Serranidae), *Chromis cyanea* (Poey) and *Chromis multilineata* (Guichenot) (Pomacentridae) from Ecuador (Cressey and Cressey 1980, Luque and Tavares 2007, Gomes-Sanches et al. 2012, Morales-Serna et al. 2016).

Current hosts. *Lutjanus fulvus* and *Lutjanus monostigma* (Cuvier) (Lutjanidae).

Site of infection. Gills..

Prevalence and mean intensity. 15.4 and 1.75 ± 1.5 (n = 26) to *L. fulvus*; 16.6 and 2 (n = 6) to *L. monostigma*.

Specimens deposited. CHCM No. 567 (voucher) (1 vial, 1 specimen ♂) (from *L. fulvus*), CHCM No. 568 (voucher) (1 vial, 1 specimen ♂) (from *L. monostigma*). USNM No. 1550601 (voucher) (1 vial, 1 specimen ♂) (from *L. monostigma*).

Remarks. Wilson (1905) observed that the genital complex of *C. mutabilis* varies according to the age of the individuals as well as the developmental stage of the eggs. Also, this author described *C. mutabilis* as having a short, 2-segmented abdomen. Later, Cressey and Cressey (1980) redescribed this species based on material collected from scombrid fish. These authors noted an incomplete 2-segmented abdomen and at least two other differences from the type specimens; however, such differences were not considered sufficient to propose a new species. Recently, Morales-Serna et al. (2014, 2015) reported *C. mutabilis* from different host species in the Eastern Pacific, but a molecular analysis revealed relatively high intraspecific genetic divergence among the *C. mutabilis* isolates. Our specimens share the morphological characteristics described by Cressey and Cressey (1980).

Caligus randalli Lewis, 1964

Type host. *Acanthurus triostegus* (Linnaeus) (Acanthuridae).

Other host and localities. To our knowledge, *C. randalli* has not been recorded since its original description (Lewis 1964a). *Acanthurus triostegus* (Acanthuridae) from Hawaii (Lewis 1964a, Palm and Bray 2014).

Current host. *Caranx ignobilis* (Carangidae).

Site of infection. Gills.

Prevalence and mean intensity. 25 and 1 (n = 4).

Specimens deposited. CHCM No. 569 (voucher) (1 vial, 2 specimens ♂♀). USNM No. 1550602 (voucher) (1 vial, 1 specimen ♂).

Remarks. Lewis (1964a) observed that *Caligus randalli* is morphologically close to *C. constrictus* Heller, 1865. According to this author, one of the main differences between both species is the length of the urosome. The urosome of *C. randalli* is one and a half times the length of the urosome of *C. constrictus*. In the present study, we noted that *C. randalli* resembles *Caligus aesopus* Wilson, 1921. However, the urosome in *C. aesopus* is shorter than in *C. randalli*. Hayes et al. (2012) included *C. aesopus* and another nine species of *Caligus* (*C. chorinemy* Kroyer, 1863, *C. tenax* Heller, 1865, *C. spinosurculus* Pearse, 1951, *C. germoi* Pearse, 1951, *C. rectus* Pearse, 1952, *C. confusus*, *C. cordyla* Pillai, 1963, *C. zylanica* Hameed & Pillai, 1986 and *C. equulae* Ho & Lin, 2003) within a cluster of caligid species sharing the following characteristics in the female: bifid postantennal process; bifid posterior process on the maxillule; heavily ornamented apron of the third leg; an inner rosette of large spinules and prominent rib-like structure with a bifid apex, arising near the border with the intercoxal sclerite of leg 3: a massive and strongly incurved spine on the first exopodal segment of leg 3; and a 3-segmented exopod on leg 4 armed with I,I,III spines. *Caligus randalli* also shares these characteristics, and after a detailed examination. We confirmed that the morphological characteristic of our specimens fit with the description Lewis (1964a) for *C. randalli*. This is also supported by records of *C. randalli* in the Central Pacific.

Caligus sp.

Current host. *Lutjanus fulvus* (Lutjanidae).

Site of infection. Gills.

Prevalence and mean intensity. 3.8 and 1 (n = 26).

Specimens deposited. CHCM No. 570 (voucher) (1 vial, 1 specimen ♂).

Remarks. *Caligus* sp. is morphologically close to *Caligus laticaudus*, mainly by the shape and armature of cephalothoracic appendages and legs. However, our specimen differs from *C. laticaudus* in the shape and size of the urosome. Unfortunately, the single specimen of *Caligus* sp. in our collection is not sufficient for a more detailed taxonomic study.

Caritus Cressey, 1967

Caritus serratus Cressey, 1967

Type host:. *Chanos chanos* (Forsskål) (Chanidae).

Other host and localities. *Chanos chanos* (Chanidae) from Nosy Bé, Madagascar (Cressey 1967). Reported as *Caritus tolii* from *Tenualosa toli* (as *Hilsa toli*) (Valenciennes) (Clupeidae) from Sassoon Docks, Bombay (Rangnekar 1984).

Current host. *Chanos chanos* (Chanidae).

Site of infection. Gills.

Prevalence and mean intensity. 20 and 4 (n = 5).

Specimens deposited. CHCM No. 571 (voucher) (1 vial, 1 specimen ♀).

Remarks. Currently, *C. serratus* is the unique valid species included in the genus *Caritus*. Morphological characteristics of our specimens agree well with the redescription provided by Dojiri and Ho (2013).

Lepeophtheirus von Nordmann, 1832

Lepeophtheirus lewisi Hewitt, 1971

Type host. *Acanthurus olivaceus* (Acanthuridae).

Other host and localities. *Acanthurus olivaceus* (Acanthuridae) from Hawaii (Hewitt 1971). *Naso hexacanthus* (Bleeker), *Acanthurus triostegus* (Acanthuridae), *Myripristis* sp., *Fistularia petimba* Lacepède (Fistulariidae) (Lewis 1964a, 1964b, Palm and Bray 2014).

Current host. *Acanthurus xanthopterus* (Acanthuridae).

Site of infection. Gills.

Prevalence and mean intensity. 5 and 1 (n = 20).

Specimens deposited. CHCM No. 572 (voucher) (1 vial, 1 specimen ♂). USNM No. 1550603 (voucher) (1 vial, 1 specimen ♂).

Remarks. *Lepeophtheirus lewisi* was originally described as *Dentigryps bifurcatus* by Lewis (1964a). However, Hewitt (1971) stated that there is not a useful character to separate *Dentigryps* Wilson, 1913 from *Lepeophtheirus* and, therefore, reassigned species of *Dentigryps* to *Lepeophtheirus*. As the name *L. bifurcatus* was preoccupied by *L. bifurcatus* Wilson 1905, Hewitt (1971) renamed Lewis' species as *L. lewisi*. The material of the present study corresponds to a male of *L. lewisi*. The identification of this species was difficult without female specimens; nonetheless, the morphology of our material fits the description provided by Lewis (1964a) for the male of *L. lewisi*. In addition, this copepod has been mainly found in acanthurid fish from the Central Pacific as in the present work.

Lepeophtheirus uluus Lewis, 1964

Type host. *Caranx melampygus* (Carangidae).

Other host and localities. *Caranx melampygus* (Carangidae) from Oahu, Hawaii (Lewis 1964b, Palm and Bray 2014). Reported as *Dentigryps ulua* on *Caranx ignobilis* from Heron Island, Australia (Ho and Dojiri 1977).

Current host. *Caranx ignobilis* (Carangidae).

Site of infection. Gills.

Prevalence and mean intensity. 25 and 4 (n = 4).

Specimens deposited. CHCM No. 573 (voucher) (1 vial, 2 specimens ♂♀).

Remarks. *Lepeophtheirus uluus* was originally described as *Dentigryps ulua* by Lewis (1964b) and then transferred to *Lepeophtheirus* by Hewitt (1971). The morphology of our specimens corresponds to the original description.

Dissonidae Kurtz, 1924
***Dissonus* Wilson, 1906**

***Dissonus similis* Kabata, 1966**

Type host. *Tetractenos hamiltoni* (Richardson) (as *Spheroides hamiltoni*) (Tetraodontidae).

Other host and localities. *Tetractenos hamiltoni* (as *Spheroides hamiltoni*) (Tetraodontidae) from Queensland, Australia (Kabata 1966). *Arothron hispidus* from Philippines; *Arothron meleagris* (Anonymous) from Guam; *Arothron nigropunctatus* (Bloch & Schneider) from Australia, Philippines and New Guinea; and *Arothron stellatus* (Anonymous) (all Tetraodontidae) from New Guinea (Tang and Kalman 2005).

Current host. *Arothron hispidus* (Tetraodontidae).

Site of infection. Gills.

Prevalence and mean intensity. 13.3 and 2 ± 0.5 (n = 15).

Specimens deposited. CHCM No. 574 (voucher) (1 vial, 1 specimen ♀). USNM No. 1550604 (voucher) (1 vial, 1 specimen ♀).

Remarks. The family Dissonidae comprises only two genera, *Innaprokofevnas* Kazatchenko, 2001 with a single species (*I. orientcolae* Kazatchenko, 2001) and *Dissonus* with 12 species (*D. excavatus* Boxshall, Lin, Ho, Ohtsuka, Venmathi Maran & Justine, 2008; D. furcatus Kirtisinghe, 1950; *D. glaber* Kurtz, 1950; *D. heronensis* Kabata, 1966; *D. hoi* Tang & Kalman, 2005; *D. inaequalis* Boxshall, Lin, Ho, Ohtsuka, Venmathi Maran & Justine, 2008; *D. kapuri* (Ummerkutty, 1976); *D. manteri* Kabata, 1966; *D. nudiventris* Kabata, 1965; *D. ruvetti* Nuñes-Ruivo & Fourmanoir, 1956; *D. similis*; and *D. spinifer* Wilson, 1906).

According to Kabata (1966), *D. similis* is morphologically closer to *D. furcatus*. However, *D. similis* may be separated from *D. furcatus* and other congeners by the lack of a sternal furca or stylet and the presence of a genital spinulation extending over the anterior half to two thirds of ventral surface of genital complex (Tang and Kalman 2005, Boxshall et al. 2008). As indicated by Tang and Kalman (2005), *D. similis* is restricted to the tropical western Pacific and is highly host specific to tetraodontid fishes.

Eudactylinidae Wilson C.B., 1932

***Nemesis* sp. Risso, 1826**

Current host. *Carcharhinus melanopterus* (Carcharhinidae).

Site of infection. Gills.

Prevalence and mean intensity. 40 and 2 ± 0.1 (n = 5).

Specimens deposited. CHCM No. 575 (voucher) (1 vial, 1 specimen ♀).

Remarks. *Nemesis* is one of 12 genera in the family Eudactylinidae and includes about nine species (Mangena et al. 2014). *Nemesis* species can be divided into two groups by the relative width of the cephalothorax, free thoracic segments and genital segments (Dippenaar et al. 2008). One group (consisting of most of the species) has a fourth free thoracic segment that is much narrower than the preceding three, whereas the other (consisting of *N. lamna* only) has all four segments of about the same width (Kabata 1979). The identification and comparison of *Nemesis* species belonging to the first group is difficult because of morphological variation among individuals and the inconsistencies in the literature (Hewitt 1969, Kabata 1979).

Hatschekiidae Kabata, 1979
Hatschekia Poche, 1902

Hatschekia longiabdominalis Uyeno & Nagasawa, 2013

Type host. *Arothron hispidus* (Tetraodontidae).

Other host and localities. *Arothron hispidus* (Tetraodontidae) from Japan (Uyeno and Nagasawa 2013). To date, *H. longiabdominalis* has not been recorded from others host and locality.

Current host. *Arothron hispidus* (Tetraodontidae).

Site of infection. Gills.

Prevalence and mean intensity. 53.3 and 100 ± 329.2 (n = 15).

Specimens deposited. CHCM No. 576 (voucher) (1 vial, 1 specimen ♀). USNM No. 1550605 (voucher) (1 vial, 1 specimen ♀).

Remarks. Of the nine genera included in the Hatschekiidae, the most speciose genus is *Hatschekia*, with approximately 140 valid species so far. According to Uyeno and Nagasawa (2013), *H. longiabdominalis* may be separated from other congeners by having a fusiform trunk with posterior lobes, the urosome markedly projecting beyond posterior lobes of the trunk, and unique intercoxal sclerites of legs 1 and 2, which strongly project from the middle of the anterior margin and bear four blunt processes on the posterior margin. We observed all of these characters in our specimens.

Hatschekia bicaudata Kabata, 1991

Type host. *Chaetodon aureofasciatus* Macleay (Chaetodontidae).

Other host and localities. *Chaetodon aureofasciatus* (Chaetodontidae) from Australia (Kabata 1991). *Chaetodon auripes* Jordan & Snyder (Chaetodontidae) from Seto, Wakayama Prefecture, Japan (Izawa 2016).

Current host. *Chaetodon auriga* and *Chaetodon lunula* (Chaetodontidae).

Site of infection. Gills.

Prevalence and mean intensity. 23.1 and 7.3 ± 3.1 (n = 13) to *Chaetodon auriga*; 14.3 and 5 ± 1.4 (n = 14) to *Chaetodon lunula*.

Specimens deposited. CHCM No. 577 (voucher) (1 vial, 1 specimen ♀) (from *Chaetodon auriga*). CHCM No. 578 (voucher) (1 vial, 1 specimen ♀) (from *Chaetodon lunula*). USNM No. 1550606 (voucher) (1 vial, 1 specimen ♀) (from *Chaetodon lunula*).

Remarks. Our samples corresponded to a single mature female from each host, which were not dissected for morphological analysis. Nonetheless, these parasitic copepods resemble *H. bicaudata* in its habitus, antenna, maxilla, and armature of legs 1 and 2, as well as in its preferred hosts, which are butterfly fishes distributed in warm waters from Australia to Japan (see Izawa 2016).

Kroyeriidae Kabata, 1979
Kroyeria van Beneden, 1853

Kroyeria longicauda Cressey, 1970

Type host. *Carcharhinus limbatus* (Müller & Henle) (Carcharhinidae).

Other host and localities. *Carcharhinus limbatus* (Carcharhinidae) from Florida. *Carcharhinus brevipinna* (Müller & Henle) (Carcharhinidae) from Madagascar (Deets 1994).

Current host. *Carcharhinus melanopterus* (Carcharhinidae).

Site of infection. Gills.

Prevalence and mean intensity. 40 and 16 ± 2.8 (n = 5).

Specimens deposited. CHCM No. 579 (voucher) (1 vial, 1 specimen ♀). USNM No. 155607 (voucher) (1 vial, 1 specimen ♀).

Remarks. The family Kroyeriidae comprises three genera, *Kroeyerina* Wilson, 1932 with nine species, *Kroyeria* with 15 species, and *Prokroyeria* Deets, 1987 with a single species (Walter and Boxshall 2018). Within *Kroyeria*, *K. longicauda* can be identified by the lateral tine on the deeply incised, bifid dorsal stylet, the lateral cuticular flange on the caudal rami, and the small number of unusually large endopodal denticulations of legs 1 to 4 that are unique to this species (Deets 1994).

Lernanthropidae Kabata, 1979
Lernanthropus de Blainville, 1822

Lernanthropus sp.

Current host. *Kyphosus cinerascens* (Forsskål) (Kyphosidae).

Site of infection. Gills.

Prevalence and mean intensity. 50 and 2 (n = 2).

Specimens deposited. CHCM No. 580 (voucher) (1 vial, 1 specimen ♀).

Remarks. The genus *Lernanthropus* includes about 120 species and it is one of the commonest genera of parasitic copepods on marine fishes. In this study, a single female of *Lernanthropus* sp. was collected. We were unable to proceed with the species identification because of the lack of specimens for dissection, which is necessary to observe appendages of the cephalothorax as well as legs 1 and 2. Even with enough material, the identification of *Lernanthropus* sp. is quite difficult because many species have not been described with sufficient detail (Koyuncu et al. 2012).

Discussion

The present study is the first detailed survey of the diversity and ecological attributes of the parasitic copepods infecting fishes at Palmyra Atoll. All records we report here are new geographical records. Most copepods (10 of 17) belonged to the family Caligidae. Of these ten caligid species, six were in the genus *Caligus* and two in the genus *Lepeophtheirus*. These finding are in agreement with the fact that *Caligus* copepods are mostly found on warm water fishes, while *Lepeophtheirus* copepod diversity is low in the tropics (Ho and Lin 2004, Suárez-Morales and Gasca 2012, Morales-Serna et al. 2016). However, as far as we know, specific evolutionary or ecological mechanisms underlying this greater diversification *Caligus* species in the tropics are not well understood. On the other hand, in experiments carried out by Bravo et al. 2010, they suggest that species of *Caligus* are more active swimmers than species of *Lepeophtheirus*, which in turns increase transmission between hosts. Clearly, such swimming ability could be contributing to dispersal of *Caligus* and host switching. Several copepods species can parasitize multiple fish species (Dojiri and Ho 2013). This is the case of *C. mutabilis* found on *Lutjanus monostigma* and *L. fulvus* in the present study however, this species has been reported in at least 13 families of marine fishes from the Atlantic and Pacific oceans (Morales-Serna et al. 2015).

Consistent with observations of the monogenean fauna of Palmyra Atoll fishes (Vidal-Martínez et al. 2017), parasitic copepod richness at Palmyra Atoll qualitatively appears low relative to other localities in the Indo-Pacific region. Most of the fish species we examined (30 of 44) were not parasitized by copepods, even with large sample sizes for some fish species (e.g. *Acanthurus triostegus*, n = 50). Several fishes that were unparasitized at Palmyra have copepod records at other sites. For example, *Acanthurus triostegus, Gymnothorax pictus, Epinephelus merra* and *Sphyraena barracuda* have been reported as hosts of at least one species of parasitic copepod in other localities of the Indo-Pacific (Boxshall and Huys 2007, Palm and Bray 2014). Because ectoparasite species richness, host size and age are positively related (Rhode 1993, Muñoz and Cribb 2005), the lack of copepods in some host species could be due to our sampling of only young (*Chanos chanos*) or small individuals (*Sphyraena barracuda*). Furthermore, the intertidal habitat sampled at Palmyra differs from the more often sampled fore-reef and reef flat habitats, making a direct comparison among studies difficult. More generally, Palmyra's remoteness may contribute to its depauperate copepod parasite fauna. The

Line Islands are far from the Austro-Malayan-Philippine region, the presumed center of origin of Indo-West Pacific (IWP) fishes and their parasites. Because we found fewer copepod species than described from Hawaii, which is still further from the presumed center of origin, we suggest that the remote location of the Line Islands and the particularly small size of Palmyra Atoll also contribute to the depauperate nature of the parasitic copepod fauna.

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