Journal of Helminthology (2012) **86**, 493–509 doi:10.1017/S0022149X11000526

Digenean metacercariae of fishes from the lagoon flats of Palmyra Atoll, Eastern Indo-Pacific

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(Received 12 January 2011; Accepted 23 August 2011; First Published Online 5 January 2012)

Abstract

Although many studies on the taxonomy of digenean trematodes of marine fishes have been completed in the Eastern Indo-Pacific (EIP) marine ecoregion, only a few have considered metacercarial stages. Here, the results are presented of a taxonomic survey of the digenean metacercariae of fishes from Palmyra Atoll, a remote and relatively pristine US National Wildlife Refuge located 1680 km SSW of Hawaii. Up to 425 individual fish were collected, comprising 42 fish species, from the sand flats bordering the lagoon of the atoll. Quantitative parasitological examinations of each fish were performed. Morphological descriptions of the encountered digenean metacercariae are provided, together with their prevalence, mean intensities, host and tissue-use. Up to 33,964 individuals were recovered representing 19 digenean metacercaria species from eight families. The species composition of digeneans in lagoon fishes at Palmyra Atoll is a subset of what has previously been reported for the EIP. Further, the large diversity and abundance of metacercariae reported in this study highlight the utility of including this group in future ecological research in the EIP marine ecoregion.

Introduction

Digenean trematode species richness appears to be particularly high in the Eastern Indo-Pacific (EIP) and Central Indo-Pacific (CIP) marine ecoregions (Yamaguti, 1970; Cribb *et al.*, 1994). Several studies have examined adult digenean trematodes of marine fishes in these ecoregions, including Australia, the South Pacific regions of French Polynesia, New Caledonia and Hawaii (see, for example, Cribb *et al.*, 1994, 2002; Nolan & Cribb, 2005). However, only a few such studies have considered digenean metacercariae (e.g. Yamaguti, 1970; Køie & Lester, 1985; Cribb, 1998 and references therein), perhaps partly because metacercariae are more difficult to locate, recognize and identify than adult worms. However, knowledge of metacercariae is obviously necessary for understanding the population dynamics of both digeneans and hosts, the ecological impacts on hosts and the broader role of digeneans in ecosystems. For example,

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metacercariae, being trophically transmitted, require their host to be eaten by a final host and they therefore have an inherently different relationship with their hosts than do adult trematodes (which die if their host is eaten). Metacercariae can dominate the parasite community of fishes in both numbers of individuals and species (Salgado-Maldonado & Kennedy, 1997; Rodríguez-González & Vidal-Martínez, 2008). More generally, trophically transmitted parasites, including abundant metacercariae, had substantially greater biomass than did adult parasites in a study in three estuarine ecosystems (Kuris *et al.*, 2008).

Palmyra Atoll is one of the northern Line Islands, located in the East Indo-Pacific marine ecoregion (*sensu* Spalding *et al.*, 2007), 1680 km SSW of Hawaii (5°52′55.54′N; 162°04′59.05″W). During the Second World War, Palmyra supported a few thousand military personnel. The atoll has otherwise never had a permanent human population. 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 a part of a larger research project on the role of parasites in EIP atoll food webs (Lafferty *et al.*, 2008), a survey of the parasites of the fishes from the lagoon flats of Palmyra Atoll was conducted. A substantial diversity and abundance of digenean metacercariae infecting fish as second intermediate hosts was found. The lack of comprehensive taxonomic studies of digenean metacercariae in the EIP prompted us to provide morphological descriptions of these parasites, and to summarize their prevalence, mean intensity and host and tissue use. The primary aim of this paper is to provide a document that can facilitate ecological, taxonomic and other biological research involving these trematodes at Palmyra Atoll, and perhaps more broadly throughout the EIP.

Materials and methods

Between 13 October–10 November 2009 and 22 June–28 July 2010, fish were collected by seine, spear, and hook and line from the intertidal sand flats bordering the Palmyra Atoll lagoon (see Fig. 1 in Papastamatiou *et al.*, 2009). Fish were individually bagged and examined fresh within 24 h (except for four bonefish, which were frozen for 4 months at −60°C before examination).

Parasitological examinations were conducted using stereomicroscopes, using 0.7% saline solution as necessary. Metacercaria abundance was quantified by squashing tissues, organs and body parts between two glass plates. For most body parts with clear bilateral symmetry (i.e. body surface, muscles, pectoral and pelvic fins, eyes and gills), metacercariae were enumerated in the left half and multiplied by two to estimate the expected intensity for both sides. Brain, liver, gall bladder, spleen, kidney, intestine, stomach, heart and swim bladder were squashed in their entirety. For body parts > 25 g (primarily large jack muscle fillets and shark livers), tissue interspersed throughout the body part area was excised to squash a maximum of 25 g. The observed intensities were multiplied by the appropriate weight proportion to estimate intensity in the whole body part. Both prevalence and mean intensity values were calculated using ‘expected’ data, while reported total number of individuals recovered reflect only directly ‘observed’ metacercariae.

Metacercariae generally lack diagnostic adult structures that characterize most species descriptions. Thus, it is generally not possible to identify metacercariae to the species level without previous life cycle or molecular work linking them to adults. However, metacercariae do have a suite of morphological characters. This makes it possible frequently to place them into the appropriate family and genus, and to designate them as different morphospecies. Even if morphospecies designations are somewhat provisional, they provide a clear, working hypothesis of specific identity that can immediately facilitate research. To identify metacercariae, up to 10–20 cysts of a putative species were removed from host tissues and individually isolated on a slide with a drop of saline solution. The site of infection, shape, movements, colour and number of metacercarial cysts were recorded. The metacercarial cyst dimensions were measured for those that withstood coverslip pressure. Surgical needles were used to free metacercariae from cysts that did not excyst with coverslip pressure. A coverslip was added to flatten the worm, and the corners of the coverslip were fixed to the slide with Du-Noyer sealant (1 part dehydrated lanolin and 4 parts melted resin) that was melted to the slide using an alcohol lamp. Then, a small amount of ammonium picrate fixative (1:1 saturated ammonium picrate and glycerin) was added to one side of, and drawn under, the coverslip using a Kimwipe® on the opposite side. Although metacercariae suffer some deformation by flattening, fixation with ammonium picrate works well for fieldwork because of its simplicity, rapid staining and its ability to clarify internal morphology and external sclerotized structures. This technique produces semi-permanent slides which can be preserved for 1–2 years by adding small amounts of fixative after monthly inspection (for further details see Scholz & Aguirre-Macedo, 2000). Sketches or high-quality digital photographs were used to document morphological details. Measurements of metacercariae were based on flattened specimens fixed with ammonium picrate, unless otherwise indicated. In some cases, which are indicated, we acquired morphometrics from excysted specimens that were killed in hot water, fixed in 4% formalin, stained with carmine and mounted in Canada balsam. Images of the metacercariae were captured using a digital camera and drawn on a digitizing tablet using Adobe Illustrator software. All other helminthological methods followed were those recommended by Vidal-Martinez *et al.* (2001). Synonyms for each host species were obtained from FishBase (http://www.fishbase.com) and helminth records for each of the possible host synonyms were researched using Web of Science (ISI Web of Knowledge℠; http://wok.mimas.co.uk), Google Scholar (http://scholar.google.com), and the Host–Parasite Database of the Natural History Museum, London (Gibson *et al.*, 2005). In the tables, fish species are arranged by family, in taxonomic order following Randall *et al.* (1997). Voucher specimens of the metacercariae have been deposited in the United States Parasitological collection (USNPC), Beltsville, Maryland. All measurements below are in micrometres (range, mean ± standard deviation), unless otherwise stated. For each taxon, the prevalence and mean intensity were calculated following Bush *et al.* (1997). Observations of other parasite taxa and stages will be reported elsewhere.

Results

Table 1 presents the species and numbers of host fishes examined, and the prevalence and mean intensity (± SD) of digenean metacercariae. Up to 425 individual fish were dissected, belonging to 42 species and 21 families. Three hundred and sixty-four (86%) of the 425 dissected fish were infected by one or more digenean species. The following species were not infected by metacercariae: *Carcharhinus melanopterus* (Quoy & Gaimard, 1824) (number of fish examined = 4), *Albula glossodonta* (Forsskål, 1775) (12), *Gymnothorax pictus* (Ahl, 1789) (2), *G. rueppelliae* (McClelland, 1844) (1), *Chanos chanos* (Forsskål, 1775) (3), *Epinephelus merra* Bloch, 1793 (1), *Caranx melampygus* Cuvier, 1833 (2), *Parapercis* sp. (16), *Oplopomus oplopomus* (Valenciennes, 1837) (19), *Istigobius rigilius* (Herre, 1953) (1), *Psilogobius prolatus* Watson & Lachner, 1985 (4) and *Asterropterix semipunctata* Ruppell, 1830 (8).

Of the 33,964 metacercariae counted, 19 digenean species were recognized comprising 8 families. The digenean families recovered, in decreasing order of number of species and individuals, were Bucephalidae Poche 1907 (8 species with 29,480 individuals), Cyathocotylidae Mühling 1898 (2 and 2209), Cryptogonimidae Ward, 1917 (2 and 1923), Strigeidae Railliet, 1919 (1 and 270), Didymozoidae Monticelli, 1888 (2 and 42), Acanthocolpidae Lühe, 1906 (2 and 38), Heterophyidae Leiper, 1909 (1 and 1) and Zoogonidae Odhner, 1902 (1 and 1).

In general, the most prevalent taxon was *Bucephalus* sp. 2 with prevalence values between 15% in *Valenciennea sexguttata* (Valenciennes, 1837) and 91% in *Arothron hispidus* (Linnaeus, 1758), followed by other bucephalids such as *Rhipidocotyle* spp. 1–3 (table 1). This range does not include the 100% prevalence of *Bucephalus* sp. 2 observed in three *Stegastes nigricans* (Lacepède, 1802). In this case, and others with low host sample size, there is substantial error around prevalence estimates. The species with the highest mean intensity in our samples was also *Bucephalus* sp. 2 with 1053 ± 1365 individuals in *A. hispidus*, followed by Cyathocotylidae with 714 ± 732 individuals in *Hyporhamphus affinis* (Günther, 1866) and *Rhipidocotyle* sp. 1 with 147 ± 187 in *A. hispidus*.

Table 1 presents 167 host records for the 19 digenean species, none of which have been recorded from Palmyra Atoll. The following section presents morphological descriptions for each of the recovered species, including host information and site(s) of infection.

Family Acanthocolpidae

Stephanostomum sp. (fig. 1a)

Description. Based on three flattened individuals, one from *Arothron hispidus* (USNPC No. 104843) and two from *Acanthurus triostegus*. Body length 810–2050 (1230 ± 710), maximum width 220–350 (264 ± 74) towards posterior end of the body, tegument densely covered with spines at anterior half. Eye-spot pigment present scattered in anterior part of the body. Oral sucker 92–210 (132 ± 68) long and 117–320 (187 ± 115) wide, with double row of 30 spines and without ventral hiatus. Acetabulum equatorial, 90–200 (134 ± 58) long and 85–190 (121 ± 60) wide. Prepharynx 132–250 (207 ± 64) long. Oesophagus short, 20–62 (44 ± 22) long. Caeca bifurcating immediately preacetabularly, extending to anterior excretory vesicle. Developing testes median, tandem. Anterior (right) testis 55–150 (102 ± 67) long, 50–125 (87 ± 53) wide. Posterior (left) testis 70 ($n = 1$) long, 55 ($n = 1$) wide. Ovary not distinguishable. Excretory vesicle V-shape, excretory pore terminal.

Hosts. Carangidae: *Caranx papuensis* Alleyne & MacLeay, 1877 (encysted in intestine wall); Pomacentridae: *Abudefduf septemfasciatus* (Cuvier, 1830) (muscle); Mugilidae: *Valamugil engeli* (Bleeker, 1858–59) (fins); Acanthuridae: *Acanthurus triostegus* (Linnaeus, 1758) (fins); Tetraodontidae: *A. hispidus* (fins).

Comments. *Stephanostomum* Looss, 1899 is a large genus comprising 118 species (Bray & Cribb, 2003, 2006, 2008). However, due to the number of spines around the oral sucker (30) and the lack of a ventral hiatus, only two species previously described in the Indo-Pacific region could be the potential adult stages: *S. madhaviae* Bray et Cribb, 2003 (30–34 spines) from *Caranx ignobilis* (Forsskål, 1775) from Queensland and *S. rachycentronis* Shen, 1990 (30–34 spines) from *Rachycentron canadum* (Linnaeus, 1766) from Hainan Island, China (Bray & Cribb, 2003).

Acanthocolpidae gen. sp. (fig. 1b)

Description. Based on two flattened individuals; one from *Mulloidichthys vanicolensis* (Valenciennes, 1831) (USNPC No. 104844) and one from *Valamugil engeli*. Body length 510–715, maximum width 75–82 at posterior part of body, tegument densely covered with fine spines, especially at anterior half. Eye-spot pigment present at prepharyx level. Oral sucker subterminal 75–82 long and 80–87 width. Acetabulum postequatorial, 67 long and 72 width. Prepharynx 267 long, pharynx 34 long and 33 wide, nearly equatorial. Oesophagus and caeca not distinguishable. Genitalia non-developed. Excretory vesicle clavate, occupying last quarter of body.

Hosts. Mullidae: *Mulloidichthys vanicolensis* (fins); Mugilidae: *Valamugil engeli* (brain, heart, muscle).

Comments. This metacercaria is likely an acanthocolpid, based on the tegument covered with fine spines, lack of circumoral spines, neck region enlarged, pharynx present and small acetabulum close to midbody. This species may be one of the several acanthocolpid genera that lack oral spines, e.g. *Acanthocolpus* Luhe, 1906; *Lepidauchen* Nicoll, 1913; *Neophasis* Stafford, 1904; *Spinoplagioporus* Skrjabin et Koval, 1958; and *Ningalooia* Bray et Cribb, 2007 (Bray & Cribb, 2007).

Table 1. Prevalence (above, in percentage) and mean intensity (below ± SD) of digenean metacercariae of marine fishes from Palmyra Atoll. All fish species are in phylogenetic order following Randall *et al.* (1997), and digeneans following Olson *et al.* (2003). Acronyms are as follows: *n*, number of fish sampled; St, *Stephanostomum* sp., Ac, Acanthocolpidae gen. sp.; C1–C2, Cryptogonimidae gen. spp. 1–2; Sl, *Stellantchasmus* sp.; Zo, Zoogonidae gen. sp.; B1–B3, *Bucephalus* spp. 1–3; Do, *Dollfustrema* sp.; R1–R3, *Rhipidocotyle* spp. 1–3; Pr, *Prosorhynchus* sp.; Me, *Mesostephanus* sp.; Cy, Cyathocotylidae gen. sp.; Ca, *Cardiocephaloides* sp.; Mo, Monolicaecum-type; To, Torticaecum-type.

	n	St	Ac	C1	C2	Sl	Zo	B1	B2	B3	Do	R1	R2	R3	Pr	Me	Cy	Ca	Mo	To
Hemiramphidae																				
Hemiramphus	5	–	–	–	20	–	–	–	–	–	–	40	60	–	–	–	40	–	–	20
lutkei		–	–	–	1	–	–	–	–	–	–	4 ± 2	13 ± 23	–	–	–	59 ± 32	–	–	1
Hyporhamphus	5	–	–	–	80	–	–	–	20	–	–	60	40	20	–	–	100	–	–	–
affinis		–	–	–	21 ± 39	–	–	–	98	–	–	17 ± 27	3 ± 9	1	–	–	714 ± 732	–	–	–
Belonidae																				
Platybelone	1	–	–		–	–	–	–	–	–	–	100	100	–	–	100	100	–	–	–
argalus		–	–		–	–	–	–	–	–	–	1	4	–	–	268	76	–	–	–
Apogonidae																				
Cheilodipterus	5	–	–	–	–	–	–	20	80	–	–	–	20	–	–	–	–	–	–	–
quinquelineatus		–	–	–	–	–	–	1	41 ± 62	–	–	–	2	–	–	–	–	–	–	–
Carangidae																				
Carangoides ferdau	1	–	–	–	–	–	–	–	100	–	–	–	–	–		–	–	–	–	–
		–	–	–	–	–	–	–	40	–	–	–	–	–		–	–	–	–	–
Caranx ignobilis	2	–	–	–	–	–	–	50	50	–	–	50	50	–		–	–	–	–	–
		–	–	–	–	–	–	1	3	–	–	3	2	–		–	–	–	–	–
Carangoides	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100
orthogrammus		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
Caranx papuensis	5	20	–	–	–	–	–	40	20	20	–	20	20	20		–	–	–	–	–
		4	–	–	–	–	–	8 ± 25	39	1	–	15	27	1		–	–	–	–	–
Lutjanidae																				
Lutjanus fulvus	19	–	–	–	–	–	–	10	–	–	–	10	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	1 ± 14	–	–	–	1	–	–	–	–	–	–	–	–
Lutjanus	5	–	–	–	–	–	–	–	40	–	–	–	20	–		–	–	–	–	20
monostigma		–	–	–	–	–	–	–	2 ± 6	–	–	–	1	–		–	–	–	–	8
Mullidae																				
Mulloidichthys	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100	–
flavolineatus		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Mulloidichthys	28	–	14	7	7	–	–	11	53	–	29	57	71	18	4	–	–	11	–	–
vanicolensis		–	1 ± 2	1 ± 6	1 ± 1	–	–	1	15 ± 22	–	2 ± 6	92 ± 240	17 ± 23	3 ± 18	1	–	–	1 ± 1	–	–
Upeneus arge	1	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	100
		–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	5
Kyphosidae																				
Kyphosus	3	–	–	–	–	–	–	–	33	33	–	33	–	–		–	–	33	–	–
cinerascens		–	–	–	–	–	–	–	3	1	–	11	–	–		–	–	1	–	–
Chaetodontidae																				
Chaetodon auriga	3	–	–	–	–	–	–	67	33	–	–	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	1	4	–	–	–	–	–	–	–	–	–	–	–
Chaetodon lunula	5	–	–	20	–	–	–	40	60	–	40	–	–	–	40	–	–	40	–	–
		–	–	5	–	–	–	3 ± 5	8 ± 9	–	12 ± 10	–	–	–	14 ± 38	–	–	1 ± 1	–	–
Pomacentridae																				
Abudefduf	11	9	–	–	9	–	–	82	64	–	27	–	18	–	9	–	–	–	–	–
septemfasciatus		2	–	–	3	–	–	60 ± 101	84 ± 148	–	84 ± 10	–	2	–	1	–	–	–	–	–
Abudefduf sordidus	12	–	–	17	8	–	–	42	92	17	8	8	33	–	–	–	–	8	–	–
		–	–	6 ± 4	3	–	–	6 ± 5	27 ± 32	10 ± 9	2	2	5 ± 1	–	–	–	–	1	–	–
Pomacentrus adelus	3	–	–	–	–	–	–	67	67	33	67	–	–	–	–	–	–	–	–	–
		–	–	–	–	–	–	17 ± 27	8 ± 16	9 ± 18	5 ± 6	–	–	–	–	–	–	–	–	–
Stegastes nigricans	3	–	–	–	–	–	–	33	100	67		–		–		–	–	–	–	–
		–	–	–	–	–	–	1	9 ± 8	7 ± 6		–		–		–	–	–	–	–
Mugilidae																				

Table 1 – *continued*

	n	St	Ac	C1	C2	Sl	Zo	B1	B2	B3	Do	R1	R2	R3	Pr	Me	Cy	Ca	Mo	To
Crenimugil	40	–	–	5	–	–	–	65	50	7	2	57	50	2	–	12	7	47	–	–
crenilabris		–	–	1 ± 1	–	–	–	38 ± 75	31 ± 57	1 ± 3	1	12 ± 27	6 ± 62	1	–	1 ± 9	1 ± 7	13 ± 29	–	–
Liza vaigiensis	44	–	–	–	6	–	2	34	23	–	–	20	68	–	–	–	–	4	2	–
		–	–	–	1 ± 3	–	1	7 ± 38	6 ± 21	–	–	1 ± 3	6 ± 8	–	–	–	–	1	1	–
Valamugil engeli	50	2	6	18	38	3	–	38	36	38	–	–	24	3	4	14	26	–	–	–
		1	1 ± 1	1 ± 2	2 ± 3	1	–	35 ± 165	11 ± 23	11 ± 23	–	–	2 ± 9	1	1 ± 1	1 ± 4	1 ± 3	–	–	–
Sphyraenidae																				
Sphyraena	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50	–	–	–	–
barracuda		–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Gobiidae																				
Amblygobius	12	–	–	–	–	–	–	8	33	17	8	–	8	–	–	–	–	–	8	–
phalaena		–	–	–	–	–	–	1	2 ± 5	3 ± 21	1	–	1	–	–	–	–	–	1	–
Istigobius ornatus	9	–	–	–	–	–	–	–	33	–	–	–	–	–	–	–	–	–	–	–
Valenciennea	13	–	–	–	–	–	–	–	15	8	8	–	–	8	–	–	–	–	–	–
sexguttata		–	–	–	–	–	–	–	1 ± 10	1	1	–	–	1	–	–	–	–	–	–
Acanthuridae																				
Acanthurus	23	5	–	5	41	–	–	61	85	15	61	–	39	24	12	2	24	2	–	–
triostegus		1 ± 1	–	2	102 ± 85	–	–	65 ± 169	76 ± 68	11 ± 8	52 ± 69	–	6 ± 8	17 ± 11	22 ± 4	1	2	26	–	–
Acanthurus	10	–	–	20	–	–	–	70	60	10	60	10	70	20	10	–	–	10	–	–
xanthopterus		–	–	2	–	–	–	81 ± 123	133 ± 121	236	135 ± 23	2	78 ± 11	5 ± 2	46 ± 32	–	–	1	–	–
Balistidae																				
Rhinecanthus	7	–	–	–	–	–	–	43	86	–	–	14	29	14	–	–	–	14	–	–
aculeatus		–	–	–	–	–	–	30 ± 53	206 ± 163	–	–	1	3 ± 11	1	–	–	–	1	–	–
Tetraodontidae																				
Arothron hispidus	11	9	–	18	9	–	–	–	91	54	64	9	45	54	–	–	–	–	–	–
		1	–	1 ± 2	1	–	–	–	1053 ± 1365	10 ± 12	147 ± 187	3	21 ± 36	12 ± 33	–	–	–	–	–	–

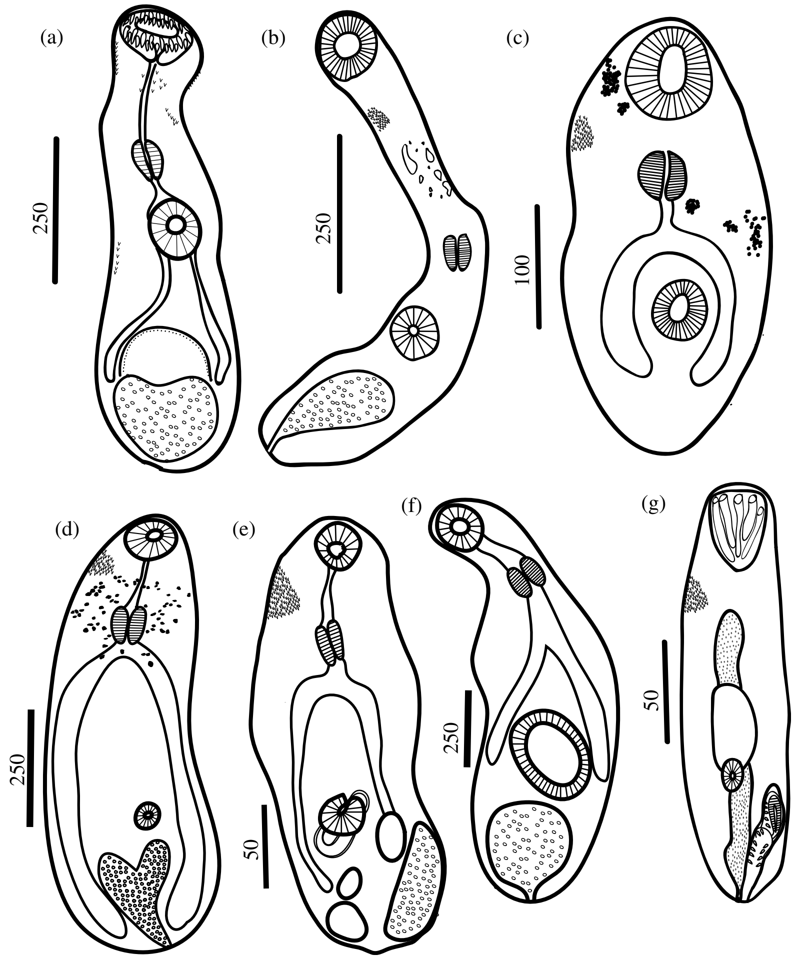

Fig. 1. Excysted metacercariae from lagoon-flat fishes of Palmyra Atoll (all worms in ventral view). (a) *Stephanostomum* sp.; (b) Acanthocolpidae gen. sp.; (c) Cryptogonimidae gen. sp. 1; (d) Cryptogonimidae gen. sp. 2; (e) *Stellantchasmus* sp.; (f) Zoogonidae gen. sp.; (g) *Bucephalus* sp. 1. All scale bars are in micrometres.

Family Cryptogonimidae

Cryptogonimidae gen. sp. 1 (fig. 1c)

Description. Based on two excysted specimens; one flattened (USNPC No. 104845) from *Arothron hispidus* and one unflattened from *Valamugil engeli*. Body oval, 260–350 long, 150–200 wide, tegument covered with spines. Eye spots scattered in anterior third. Oral sucker 20–82 by 35–77; acetabulum postequatorial, 25–35 in diameter. Sucker ratio 1:0.45–0.71. Prepharynx 37–45 long, pharynx 30–42 by 42; oesophagus short, 5 long; caeca bifurcation at equatorial level, caeca extending near to posterior end; excretory vesicle V-shaped, observed in fresh material but not apparent in fixed individuals.

Hosts. Mullidae: *Mulloidichthys vanicolensis* (eye, intestine, kidney); Chaetodontidae: *Chaetodon lunula* (Lacepède, 1802) (fins), *Abudefduf sordidus* (Forsskål, 1775) (fins); Mugilidae: *Crenimugil crenilabris* (Forsskål, 1775) (kidney, spleen), *Valamugil engeli* (intestine); Acanthuridae: *Acanthurus triostegus* (fins), *Acanthurus xanthopterus* Valenciennes, 1835 (fins); Tetraodontidae: *Arothron hispidus* (fins).

Comments. This metacercaria has key characteristics of the family Cryptogonimidae, such as a spiny body with eye spots, a well-developed oral sucker and pharynx and an acetabulum smaller than oral sucker (Miller & Cribb, 2008). Unfortunately, a V-shaped excretory vesicle was observed only in fresh material but was not apparent in fixed individuals.

Cryptogonimidae gen. sp. 2 (fig. 1d)

Description. Based on two flattened specimens; one (USNPC Nos 104846 and 104847) from *Hemiramphus lutkei* Valenciennes, 1847, and one from *Hyporhamphus affinis*. Body elongated, slightly clavate without spined tegument, maximum length 490–820, maximum width 147–155 at equatorial level. Eye-spot pigment scattered in the anterior third of the body. Oral sucker subterminal, 70–97 long and 80–82 wide. Acetabulum postequatorial, 70–80 in diameter. Sucker ratio 1:0.87–0.97. Prepharynx absent or very short, pharynx 32–35 by 22–25; oesophagus short or absent; caeca long, reaching posterior end of body; excretory vesicle Y-shaped and excretory pore subterminal.

Hosts. Hemiramphidae: *Hemiramphus lutkei* (liver), *Hyporhamphus affinis* (liver); Mullidae: *Mulloidichthys vanicolensis* (intestine, stomach); Pomacentridae: *Abudefduf septemfasciatus* (liver), *Abudefduf sordidus* (liver); Mugilidae: *Liza vaigiensis* (Quoy & Gaimard, 1825) (intestine), *Valamugil engeli* (liver); Acanthuridae: *Acanthurus triostegus* (fins, muscle); Tetraodontidae: *Arothron hispidus* (fins).

Comments. This metacercaria has key characteristics of the family Cryptogonimidae, such as a spiny body with eye spots, a well-developed oral sucker and pharynx, acetabulum smaller than oral sucker, and excretory vesicle Y-shaped (Miller & Cribb, 2008).

Family Heterophyidae

Stellantchasmus *sp. (fig. 1e)*

Description. Based on two flattened specimens (one sent to USNPC, No. 104848) from *Valamugil engeli*. Cyst 220 long and 120 wide. Thickness of cyst wall 5. Body elliptical 250–530 long and 122–217 wide. Tegument highly spined. Oral sucker rounded, 25–50 long and 35–47 wide, mouth subterminal. Ventral sucker, post-equatorial, rounded to oval, 24–43 long and 34–40 wide, slightly smaller than oral sucker, without visible spines. Seminal vesicle provided with a thick muscular wall and transformed in an expulsor, 40 long and 12 wide. Prepharynx 29–57 long, pharynx 27–35 long and 20–37 wide. Intestinal bifurcation in first third of body. Caeca long, narrow, terminate blindly, unequal, reaching anterior margin of testis anlagen. Testis slightly diagonal, 26–32 long and 20–32 wide. Ovary anlagen oval, 36 long and 23 wide. Excretory vesicle saccular and intertesticular, 74 long and 30 wide.

Hosts. Mugilidae: *Valamugil engeli* (kidney).

Comments. This metacercaria was identified based on the presence of nearly symmetrical testes, the seminal vesicle modified as a muscular expulsor and the caeca reaching the testis anlagen. The lowest values of the range for each one of the measurements obtained are well in the range of those reported by Yamaguti (1970) and Scholz *et al.* (1991). In contrast, the largest values for each measurement are, in general, out of ranges reported by these authors, which is possibly explained by our specimens being slightly flattened. Yamaguti (1970) reported the metacercariae of *Stellantchasmus falcatus* Onji et Nishio, 1915 from *Mugil cephalus* Linnaeus, 1758 from Hawaii. There are several reports of *Stellantchasmus* for the CIP region because it is zoonotic (Rekharani & Madhavi, 1985; Hong, 2000).

Family Zoogonidae (Odhner, 1902)

Zoogonidae gen. sp. (fig. 1f)

Description. Based on one specimen from water in the holding bag of *Liza vaigiensis*. Cyst oval, 328 long, 304 wide. Body pear-shaped, 550 long, 209 wide; tegument with spines extending to up to ventral sucker, and sparse posteriorly. Eye-spot pigment absent. Oral sucker small, 71 long, 70 wide; ventral sucker very large, 117 long, 111 wide. Sucker ratio 1:1.58. Prepharynx 56 long; pharynx 54 long, 37 wide; oesophagus short, 51 long; caeca short, extending to about midlevel of ventral sucker. Excretory vesicle saccular. Excretory pore terminal.

Hosts. Mugilidae: *Liza vaigiensis* (water in the holding bag).

Comments. The morphological characteristics of this metacercaria, such as the absence of a prepharynx, the small size of the pharynx, the short caeca and sucker ratio (1:1.58), are similar to those of the members of Zoogonidae. This is a cosmopolitan family, also widely distributed in the Indo-Pacific region (see Bray, 1987). The metacercariae of a member of this family have been recorded encysted on plants (Bray, 1987), which could have been eaten by the mullet and regurgitated after capture. Unfortunately, the specimen was lost during processing.

Bucephalidae

Bucephalus *sp. 1 (fig. 1g)*

Description. Based on ten individuals flattened: three from *Cheilodipterus quinquelineatus* Cuvier, 1828, three from *Lutjanus fulvus*, one from *Abudefduf sordidus* (USNPC No. 104849), and three from *Liza vaigiensis*. Cyst spherical, 110–180 (148 ± 17) long, 70–150 (105 ± 23) wide. Body shape ellipsoid, total length 166–285 (228 ± 41), maximum width 49–135 (85 ± 25). Width represents 26–56% (38 ± 10) of body length. Tegument with fine spines. Rhynchus sucker-like, 31–70 (50 ± 13) long, 31–70 (48 ± 13) wide, with seven tentacular appendages. Rhynchus length as % of body length: 17–25 (22 ± 3). Mouth 117–225 (174 ± 37) from anterior end, or 68–87% (76 ± 6%). Pharynx 14–31 (21 ± 6) in diameter. Intestine sac-like, 40–90 (63 ± 18) long, oriented anteriorly. Testis primordia smooth. Post-testicular distance 60–92 (77 ± 16). Post-testicular distance as % of body length: 27–38 (33 ± 5). Cirrus sac 41–88 (55 ± 15) long, 9–21 (13 ± 4) wide, opens terminally at posterior. Anterior-most reach of cirrus sac as % of body length: 15–32% (24 ± 6%). Excretory vesicle simple, elongate saccular, 132–206 (169 ± 25) long, empties terminally at posterior body.

Hosts. Apogonidae: *Cheilodipterus quinquelineatus* (heart); Carangidae: *Caranx ignobilis* (intestine), *Caranx papuensis* (heart, intestine); Lutjanidae: *Lutjanus fulvus* (Forster, 1801) (heart); Mullidae: *Mulloidichthys vanicolensis* (heart, eye); Chaetodontidae: *Chaetodon auriga* Forsskål, 1775 (heart), *Chaetodon lunula* (heart); Pomacentridae: *Abudefduf septemfasciatus* (gills, heart, kidney), *Abudefduf sordidus* (heart, kidney, tissue surrounding eye), *Pomacentrus adelus* Allen, 1991 (fins), *Stegastes nigricans* (heart); Mugilidae: *Crenimugil crenilabris* (fins, heart, kidney, spleen), *Liza vaigiensis* (heart, kidney), *Valamugil engeli* (heart, kidney); Gobiidae: *Amblygobius phalaena* (Valenciennes, 1837) (eye); Acanthuridae: *Acanthurus triostegus* (fins, muscle), *Acanthurus xanthopterus* (fins, heart); Balistidae: *Rhinecanthus aculeatus* (Linnaeus, 1758) (kidney, tissue surrounding eye).

Comments. These metacercariae were identified as belonging to the genus *Bucephalus* Baer, 1827 because the rhynchus was a simple sucker with tentacles around the anterodorsal rim, the mouth was between middle- and hind-body, the caecum was sac-like and variably directed from pharynx, the pars prostatica was straight (not figured), and the excretory vesicle was variable in length. This metacercaria mainly infected host hearts. It is 0.58 times smaller in length than *Bucephalus* sp. 2 (Student's $t_{0.05,21}$ test: 8.34, $P < 0.05$), which also infected the heart. The only way to distinguish these species without excystation is by cyst length, *Bucephalus* sp. 1 being 0.55 smaller than that of *Bucephalus* sp. 2 (Student's $t_{0.05,18}$ test: -6.22, $P < 0.01$ for length; $t_{0.05,18}$ test: -3.87, $P = 0.001$ for width). *Bucephalus* sp. 1 was not found as an adult in the predatory fishes examined at Palmyra (see table 1).

Although it was possible to distinguish *Bucephalus* spp. 1–3 as separate species, it was not possible to assign specific species names without adults. However, these metacercariae could belong to one of the species already described in the Central Indo-Pacific (CIP) or East Indo-Pacific (EIP) marine ecoregions. *Bucephalus* species recorded for these marine ecoregions are: *B. fragilis* Velasquez, 1959 for *Megalaspis cordyla* (Linnaeus, 1758); *B. leognathi* Velasquez, 1959 for *Leognathus* sp.; *B. pseudovaricus* Velasquez, 1959 for *Caranx* sp. and *B. paraheterotentaculatus* Velasquez, 1959 for *Seriolina nigrofasciata* (Rüppell, 1829); all of them from the Philippines (Velasquez, 1959). Other species described in these ecoregions are: *B. varicus* Manter, 1940 from *Caranx* sp. from Fiji Islands (Manter, 1963); *B. sphyraenae* Yamaguti, 1952 for *Sphyraena* sp., and *B. retractilis* Yamaguti, 1952 for *Caranx* sp. from Celebes Islands (Yamaguti, 1952); *B. carangis* Yamaguti, 1970 for *Caranx lugubris* Poey, 1860, *B. carangoides* Yamaguti, 1970 for *Carangoides* sp., *B. kaku* Yamaguti, 1970 for *Sphyraena barracuda* (Edwards, 1771), *B. sextentaculatus* Yamaguti, 1970 for *Caranx sexfasciatus* Quoy & Gaimard, 1825, *B. ulua* Yamaguti, 1970 for *Carangoides ferdau* (Forsskål, 1775), all from Hawaii (Yamaguti, 1970); and *B. gorgon* (Linton, 1905) Eckmann, 1932 for *Seriola lalandi* Valenciennes, 1833 from New South Wales, Australia (Hutson *et al.*, 2007). It is also possible that not enough predatory fish were examined to find adult bucephalids. Adult bucephalids have been recorded previously from jacks (*C. sexfasciatus* and *C. ignobilis*) in Japan (Sakaguchi, 1966).

Bucephalus *sp. 2 (fig. 2a)*

Description. Based on 13 individuals: five from *Abudefduf septemfasciatus*, five from *Abudefduf sordidus* (one sent to USNPC, Nos 104850, 104851 and 104852) and three from *Acanthurus triostegus*. Cyst oval, 190–290 (215 ± 29) long, 120–200 (146 ± 25) wide. Body shape ellipsoid, total length 300–445 (385 ± 47), maximum width 90–152 (118 ± 23). Width as % of body length: 24–39% (31 ± 5%). Tegument with fine spines. Rhynchus sucker-like, 55–100 long, 47–80 width (69 ± 11 long, 68 ± 9 width) with 7–10 tentacular appendages. Rhynchus length as % of body length: 14–23 (18 ± 2%). Mouth 155–345 (271 ± 54) from anterior end. Pre-mouth distance as % of body length: 40–81% (71 ± 12%). Pharynx 20–37 (28 ± 5) in diameter. Intestine saccular, 25–208 long (98 ± 61 long), oriented anteriorly. Testis primordia smooth. Post-testicular distance 0–34 (11 ± 30). Post-testicular distance as % of body length: 0–28% (2 ± 8%). Cirrus sac 55–107 (74 ± 15) long, 10–25 (16 ± 5) width. Anterior-most reach of cirrus sac as % of body length: 15–26% (18 ± 7%). Excretory vesicle elongate, saccular, with undulating margins, 195–342 (267 ± 64 long).

Hosts. Hemiramphidae: *Hyporhamphus affinis* (muscle); Apogonidae: *Cheilodipterus quinquelineatus* (heart, muscle); Carangidae: *Carangoides ferdau* (Forsskål, 1775) (fins), *Caranx ignobilis* (intestine), *Caranx papuensis* (heart, intestine); Lutjanidae: *Lutjanus monostigma* (Cuvier, 1828) (heart, fins); Mullidae: *Mulloidichthys vanicolensis* (heart, eye); Kyphosidae: *Kyphosus cinerascens* (Forsskål, 1775) (fins); Chaetodontidae: *Chaetodon auriga* (heart), *Chaetodon lunula* (heart); Pomacentridae: *Abudefduf septemfasciatus* (heart), *Abudefduf sordidus* (heart, gills), *Pomacentrus adelus* (heart, kidney), *Stegastes nigricans* (eye, fins, gills, heart, kidney); Mugilidae: *Crenimugil crenilabris* (heart), *Liza vaigiensis* (eye, fins, gills, heart, intestine, muscle, stomach), *Valamugil engeli* (body cavity, brain, heart, muscle, kidney); Gobiidae: *Amblygobius phalaena* (tissue surrounding eye), *Istigobius ornatus* (Rüppell, 1830) (eye, gills, muscle), *Valenciennea sexgutatta* (gills, muscle); Acanthuridae: *Acanthurus triostegus* (fins, gills, heart, kidney, liver), *Acanthurus xanthopterus* (fins); Balistidae: *Rhinecanthus aculeatus* (fins, tissue surrounding eye); Tetraodontidae: *Arothron hispidus* (fins, heart).

Comments. See comments for *Bucephalus* sp. 1.

Bucephalus *sp. 3 (fig. 2b)*

Description. Based on five individuals (one sent to USNPC, No. 104853) from *Acanthurus triostegus*. Cyst fragile, oval, 217 long, 110 wide (*n* = 2). Body shape ellipsoid, total length 325–680 (498 ± 176), maximum width 117–190 (145 ± 33). Width as % of body length: 17–49% (33 ± 14). Tegument with fine spines. Rhynchus funnel-shape, 62–95 (74 ± 13) long, 65–77 (70 ± 5) width, with seven tentacular appendages. Rhynchus length as % of body length: 10–21% (16 ± 5). Mouth in last fifth of body, 240–558 (446 ± 132) from anterior end. Pre-mouth distance as % of body length: 69–87% (77 ± 7). Pharynx 27–42 (34 ± 7) in diameter. Intestine saccular, 108–150 (129 ± 24) long, oriented anteriorly. Excretory vesicle elongate, sac-like, 198 long.

Hosts. Carangidae: *Caranx papuensis*, (stomach); Kyphosidae: *Kyphosus cinerascens* (heart); Pomacentridae: *Abudefduf sordidus* (heart, kidney), *Pomacentrus adelus* (eye, muscle), *Stegastes nigricans* (eye, kidney, liver, muscle); Mugilidae: *Crenimugil crenilabris* (fins, heart, kidney, muscle), *Valamugil engeli* (muscle); Gobiidae: *Amblygobius*

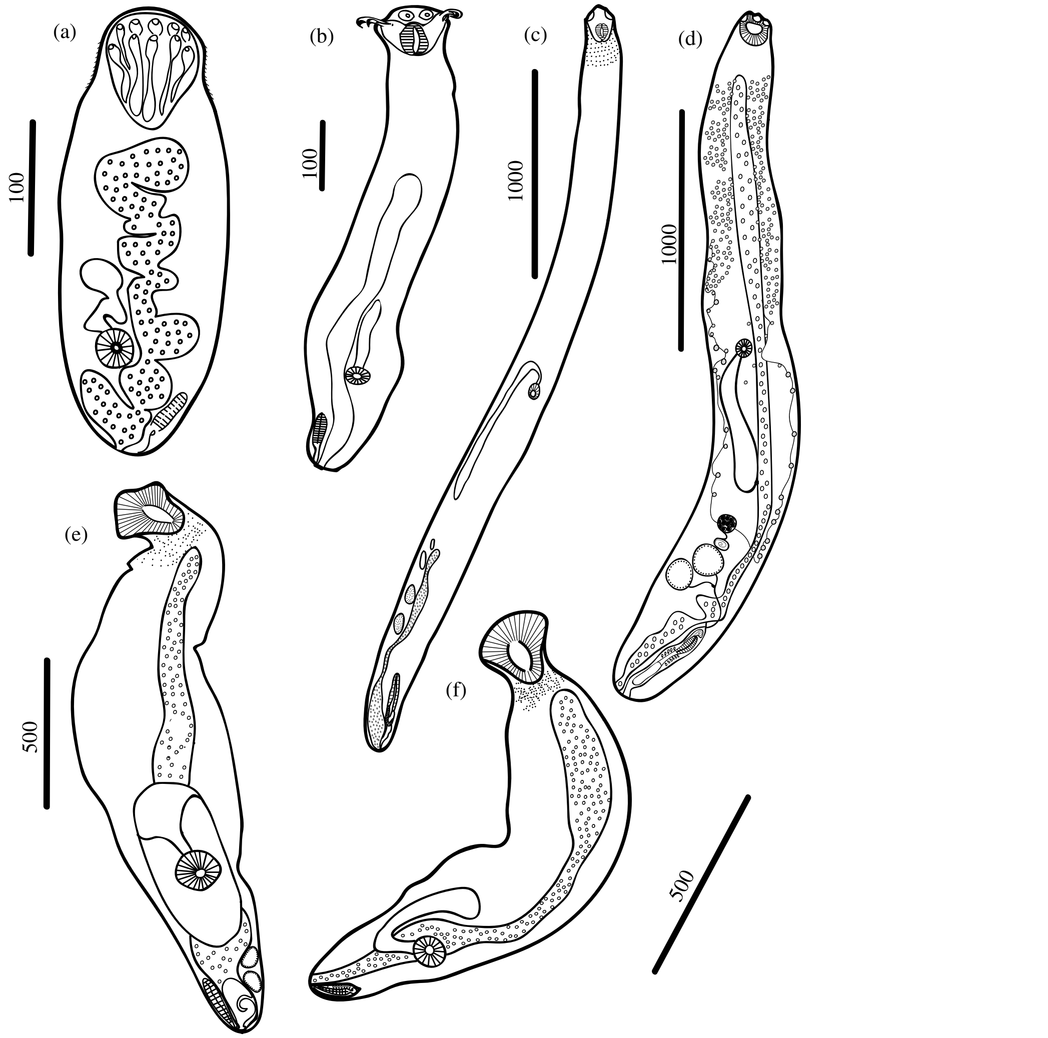

Fig. 2. Excysted metacercariae from lagoon-flat fishes of Palmyra Atoll (all worms in ventral view). (a) *Bucephalus* sp. 2; (b) *Bucephalus* sp. 3; (c) *Rhipidocotyle* sp. 1; (d) *Rhipidocotyle* sp. 2; (e) *Rhipidocotyle* sp. 3; (f) *Prosorhynchus* sp. All scale bars are in micrometres.

phalaena (eye, muscle), *Valenciennea sexguttata* (muscle); Acanthuridae: *Acanthurus triostegus* (gills), *Acanthurus xanthopterus* (fins); Tetraodontidae: *Arothron hispidus* (fins).

Comments. This is the largest metacercaria of the three members of *Bucephalus* in the present study. However, only a few specimens were recovered. Additional comments as for *Bucephalus* sp. 1.

Rhipidocotyle *sp. 1 (fig. 2c)*

Description. Based on ten individuals; three from *Hyporhamphus affinis,* one from *Crenimugil crenilabris* (USNPC, No. 104854) and six from *Liza vaigiensis*. Cyst elliptical, 400–625 long, 175–273 wide. Body shape cylindrical, total length 2380–3630 (2843 ± 387), maximum width 210–510 (320 ± 83). Width as % of body length: 6–18% (11 ± 3%). Tegument with fine spines. Rhynchus funnel shaped, 90–160 long (133 ± 24), 100–170 width (130 ± 26) with a crown of five lobes. Rhynchus length as % of body length: 4–6% (5 ± 1%). Mouth opening 890–1890 (1275 ± 291) from anterior end. Pre-mouth distance as % of body length: 33–52% (45 ± 7%). Pharynx 40–80 (57 ± 12) in diameter. Intestine tubular 240–810 (571 ± 176), oriented posteriorly. Pars prostatica slightly bent. Post-testicular distance 270–530 (412 ± 85). Post-testicular distance as % of body length: 10–19% (15 ± 3%). Cirrus sac 190–370 long (283 ± 53), 40–80 width (55 ± 13). Anterior-most reach of cirrus sac as % of body length: 7–13% (10 ± 2%). Ovary pretesticular (not measured). Vitelline glands two bands along the body sides anterior to ovary.

Hosts. Hemiramphidae: *Hemiramphus lutkei* (body cavity, brain, kidney, muscle, tissue surrounding brain), *Hyporhamphus affinis* (fins, spleen, tissue surrounding eye and intestine); Belonidae: *Platybelone argalus* (Lesueur, 1821) (kidney); Carangidae: *Caranx ignobilis* (intestine), *Caranx papuensis* (fins, intestine); Lutjanidae: *Lutjanus* *fulvus* (spleen, body cavity); Mullidae: *Mulloidichthys vanicolensis* (heart, kidney); Kyphosidae: *Kyphosus cinerascens* (fins, heart, kidney); Pomacentridae: *Abudefduf sordidus* (fins); Mugilidae: *Crenimugil crenilabris* (fins, gills, muscle, heart, kidney, tissue surrounding brain and eye), *Liza vaigiensis* (heart, kidney, tissue surrounding brain and intestine, liver, body cavity); Acanthuridae: *Acanthurus xanthopterus* (fins); Balistidae: *Rhinecanthus aculeatus* (tissue surrounding eye); Tetraodontidae: *Arothron hispidus* (fins).

Comments. These metacercariae belong to the genus *Rhipidocotyle* Diesing, 1858 because they had a rhynchus with a crown of five lobes, a pars prostatica slightly bent, and a pre-testicular ovary, following the generic definition of Overstreet & Curran (2002). This metacercaria is different than *Riphidocotyle* sp. 2 in being significantly larger in total body length (Student's $t_{0.05,16}$ test: 8.54, $P < 0.001$), by having a rhynchus with a pentagonal hood and by having a smaller rhynchus length to body length ratio (Student's $t_{0.05,16}$ test: -3.65, $P < 0.002$). These metacercariae could belong to one of the species of *Rhipidocotyle* already described in the CIP or EIP marine ecoregions and include: *Rhipidocotyle khalili* Nagaty, 1937 from *Sphyraena* sp. from Makassar, India (Yamaguti, 1953); *R. eggletoni* Velasquez, 1959 in *Sillago sihama* (Forsskål, 1775) and *R. laruei* Velasquez, 1959 from *Psettodes erumei* (Bloch & Schneider, 1801) from the Philippines (Velasquez, 1959); *R. labrodei* Jones, Grutter & Cribb, 2003 from *Labroides dimidiatus* (Valenciennes, 1839) from Lizard Island, Australia (Jones *et al*., 2003); *R. danai* Bray & Palm, 2009 from *Thyrsitoides marleyi* Fowler, 1929 and *R. jayai* Bray & Palm, 2009 from *Johnius macropterus* (Bleeker, 1853) from Java, Indonesia (Bray & Palm, 2009).

Rhipidocotyle *sp. 2 (fig. 2d)*

Description. Based on seven individuals; five from *Hemiramphus lutkei*, one from *Crenimugil crenilabris* and one from *Liza vaigiensis* (USNPC No. 104855). Cyst oval, 520–680 length (617 ± 85), 150–420 width (313 ± 144). Body shape cylindrical, total length 890–1860 (1410 ± 305), maximum width 170–490 (281 ± 107). Width as % of body length: 10–30% (20 ± 7%). Tegument with fine spines. Rhynchus sucker-like, 60–200 long (116 ± 51 long), 70–240 wide (124 ± 59) with 3–4 rounded lobes on the anterior end. Rhynchus length as % of body length: 5–12% (8 ± 3%). Mouth opening 410–1370 (737 ± 247) from anterior end. Pre-mouth distance as % of body length: 43–87% (57 ± 17%). Pharynx 40–120 (59 ± 28) in diameter. Intestine tubular, 150–880 long (313 ± 263), oriented posteriorly. Vitelline glands two bands along body sides anterior to ovary. Post-testicular distance 40–370 (196 ± 113). Post–testicular distance as % of body length: 2–24% (14 ± 7%). Cirrus sac 60–190 long (139 ± 45), 30–90 width (47 ± 21). Anterior-most reach of cirrus sac as % of body length: 5–14% (10 ± 4%). Excretory vesicle 1170–1350 ($n = 2$) length.

Hosts. Hemiramphidae: *Hemiramphus lutkei* (fins), *Hyporhamphus affinis* (gills, heart, liver); Belonidae: *Platybelone argalus* (kidney, water); Apogonidae: *Cheilodipterus quinquelineatus* (eye); Carangidae: *Caranx ignobilis* (intestine), *Caranx papuensis* (intestine, stomach); Lutjanidae: *Lutjanus monostigma* (fins); Mullidae: *Mulloidichthys vanicolensis* (heart, eye); Pomacentridae: *Abudefduf septemfasciatus* (gills), *Abudefduf sordidus* (fins, kidney, muscle); Mugilidae: *Crenimugil crenilabris* (fins, heart, kidney, muscle), *Liza vaigiensis* (muscle, heart, kidney, tissue surrounding brain, body cavity, intestine), *Valamugil engeli* (tissue surrounding brain, heart); Gobiidae: *Amblygobius phalaena* (muscle); Acanthuridae: *Acanthurus triostegus* (fins, gills), *Acanthurus xanthopterus* (fins); Balistidae: *Rhinecanthus aculeatus* (heart); Tetraodontidae: *Arothron hispidus* (fins).

Comments. See comments for *Rhipidocotyle* sp. 1.

Rhipidocotyle *sp. 3 (fig. 2e)*

Description. Based on four individuals; one from *Mulloidichthys vanicolensis* (USNPC No. 104856) and three from *Acanthurus xanthopterus*. Cyst oval, 480–600 length, 187–320 width. Body shape cylindrical, total length 610–820 (712 ± 87), maximum width 215–325 (295 ± 53). Width as % of body length: 35–47% (41 ± 5%). Tegument with fine spines. Rhynchus sucker-like, 127–182 long (152 ± 23), 132–160 wide (151 ± 13), with a long tranverse bump on anterior end. Rhynchus length as % of body length: 21–22 (21 ± 1%). Mouth 497–652 (563 ± 65) from anterior end. Pre-mouth distance as % of body length: 75–81% (79 ± 3%). Pharynx 62–77 (69 ± 7) in diameter. Intestine tubular, 277–545 (422 ± 114), oriented posteriorly. Ovary pre-testicular, 10–25 long ($n = 2$), 5–12 wide ($n = 2$). Testis smooth, 25–37 long (32 ± 7), 12–22 (15 ± 3) wide. Post-testicular distance 57–62 (60 ± 3). Post-testicular distance as % of body length: 7–9% (8 ± 1%). Cirrus sac 95–120 long (105 ± 13), 27–35 (32 ± 4) width. Anterior-most reach of cirrus sac as % of body length: 12–20 (15 ± 4%). Excretory vesicle 477–615 long (532 ± 72).

Hosts. Hemiramphidae: *Hyporhamphus affinis* (gills); Carangidae: *Caranx papuensis* (fins); Mullidae: *Mulloidichthys vanicolensis* (fins, heart, kidney, muscle); Mugilidae: *Crenimugil crenilabris* (kidney), *Valamugil engeli* (heart, kidney); Gobiidae: *Valenciennea sexgutatta* (muscle); Acanthuridae: *Acanthurus triostegus* (body cavity, fins, heart, kidney, muscle), *Acanthurus xanthopterus* (fins); Balistidae: *Rhinecanthus aculeatus* (muscle); Tetraodontidae: *Arothron hispidus* (fins, heart).

Comments. This species is smaller than *Rhipidocotyle* spp. 1 and 2. Additional comments as for *Rhipidocotyle* sp. 1.

Prosorhynchus *sp. (fig. 2f)*

Description. Based on four individuals from *Acanthurus xanthopterus* (one sent to USNPC , No. 104857). Cysts oval to elliptical, 270–500 (378 ± 105; $n = 5$) long, 190–200 (197 ± 6; $n = 3$) wide. Total body length 800–1475 (1184 ± 317), maximum width 210–300 (271 ± 42). Width as % of body length: 20–29% (24 ± 4). Tegument with fine spines. Rhynchus funnel-shaped, 100–180 (144 ± 33) long, 150–185 (174 ± 16) wide. Rhynchus length as % of body length: 7–19% (13 ± 5%). Mouth 620–1063 (883 ± 217) from anterior end. Pre-mouth distance as % of body length:

72–77% (75 ± 2%). Pharynx 68–103 (80 ± 16) in diameter. Intestine tubular, 270–490 (380 ± 156) long, oriented posteriorly. Testes smooth, 40–82 (61 ± 30) long, 30–52 (41 ± 16) wide. Post-testicular distance 50–112 ($n = 2$). Post-testicular distance as % of body length: 3–8% ($n = 2$). Cirrus sac 110–122 ($n = 2$) long, 20–40 ($n = 2$) wide. Seminal duct coiled. Pars prostatica straight. Anterior-most reach of cirrus sac as % of body length: 8% ($n = 2$). Excretory vesicle 1287–1340 long.

Host. Mullidae: *Mulloidichthys vanicolensis* (muscle); Chaetodontidae: *Chaetodon lunula* (heart); Pomacentridae: *Abudefduf septemfasciatus* (heart); Mugilidae: *Valamugil engeli* (kidney, muscle); Acanthuridae: *Acanthurus triostegus* (eye, fins), *Acanthurus xanthopterus* (fins).

Comments. These metacercariae were considered to belong to the genus *Prosorhynchus* because the rhynchus is not in the form of a sucker and the testes are diagonal rather than in tandem. These generic characteristics agree with those described by Overstreet & Curran (2002). This metacercaria could belong to one of the several species described for the CIP or EIP marine ecoregions: *Prosorhynchus freitasi* Nagaty, 1937 of *Epinephelus* sp. and *Plectropomus maculatus* (Bloch, 1790) from Heron Island and New Caledonia (Manter, 1953); *P. thapari* Manter, 1953 of *Plectropomus maculatus* (Bloch, 1790) from Fiji Island (Manter, 1953); *P. crucibulus* (Rudolphi, 1819) Odhner, 1905 of *Acanthopagrus berda* (Forsskål, 1775), *P. paracrucibulus* Velasquez, 1959 of *Ambassis buruensis* Bleeker, 1856, *P. luzonicus* Velasquez, 1959 of *Lates calcarifer* (Bloch, 1790), *P. longus* Velasquez, 1959 of *Psettodes erumei*, (Bloch et Schneider, 1801), all from the Philippines (Velasquez, 1959); *P. longissacatus* Durio et Manter, 1968 of an unidentified serranid known locally as 'leche' from New Caledonia (Durio & Manter, 1968); *P. serrani* Durio et Manter, 1968 of *Variola louti* (Forsskål, 1775) from New Caledonia (Durio & Manter, 1968); *P. maternus* Bray et Justine, 2006 of *E. malabaricus* (Bloch & Schneider, 1801) from New Caledonia (Bray & Justine, 2006); *P. robertsthomsoni* Bott et Cribb, 2009 from *Cephalopholis argus* Schneider, 1801, *C. cyanostigma* (Valenciennes, 1828) and *C. miniata* (Forsskål, 1775), *P. lafii* Bott et Cribb, 2009 of *Epinephelus fuscoguttatus* (Forsskål, 1775), *P. conorjonesi* Bott et Cribb, 2009 of *Cromileptes altivelis* (Valenciennes, 1828), *P. jexi* Bott et Cribb, 2009 of *E. quoyanus* (Valenciennes, 1830), *P. milleri* Bott et Cribb, 2009 of *V. louti*, all from Great Barrier Reef, Australia (Bott & Cribb, 2009).

Dollfustrema *sp. (fig. 3a)*

Description. Based on seven individuals; three from *Mulloidichthys vanicolensis*, and four (one sent to USNPC, No. 104858) *Acanthurus xanthopterus*. Body ellipsoidal, 188–450 (288 ± 96) long, 63–130 (106 ± 30) wide. Width as % of body length: 29–45% (38 ± 6%). Tegument with fine spines. Rhynchus a shallow funnel topped with two circlets of short spines 30–57 (48 ± 10) long, 40–95 (70 ± 19) wide. Rhynchus length as % of body length: 12–24 (17 ± 4). Mouth 138–310 (218 ± 67) from anterior end. Pre-mouth distance as % of body length: 67–75% (72 ± 3%). Pharynx 25–42 (31 ± 6) in diameter. Intestine sac-like, 55–155 (101 ± 49), oriented anteriorly. Cirrus sac 128 long ($n = 1$), 23 width ($n = 1$). Anterior-most reach of cirrus sac as % of body length: 9%. Excretory vesicle 73–233 (169 ± 62) long.

Hosts. Mullidae: *Mulloidichthys vanicolensis* (fins); Chaetodontidae: *Chaetodon lunula* (fins); Pomacentridae: *Abudefduf septemfasciatus* (eye, fins), *Abudefduf sordidus* (fins), *Pomacentrus adelus* (fins); Mugilidae: *Crenimugil crenilabris* (kidney); Gobiidae: *Amblygobius phalaena* (liver), *Valenciennea sexguttata* (muscle); Acanthuridae: *Acanthurus triostegus* (fins, gills, tissue surrounding eye), *Acanthurus xanthopterus* (fins); Tetraodontidae: *Arothron hispidus* (fins).

Comments. The recovered material of *Dollfustrema* had two circlets of spines around the rhynchus. This characteristic and those of the terminal genitalia correspond well with the generic description provided by Overstreet & Curran (2002). Two species of *Dollfustrema* Eckmann, 1934 (*Dollfustrema bipapillosum* Manter et Pritchard, 1961 of *Gymnothorax petelli* (Bleeker, 1856) and *D. strombyrhynchum* Manter et Pritchard, 1961 of *G. petelli*) have been described from Hawaii by Manter & Pritchard (1961). Recently, Nolan & Cribb (2010) described *Dollfustrema gibsoni* from *Gymnothorax woodwardi* McCulloch, 1912 from southwest Western Australia. Due to the geographical proximity, any of the species mentioned above could be the adult of the *Dollfustrema* sp.

Family Cyathocotylidae

Mesostephanus *sp. (fig. 3b)*

Description. Based on five flattened individuals (one sent to USNPC, No. 104859) from *Crenimugil crenilabris*. Body pyriform 290–540 (433 ± 127) long and 170–340 (233 ± 65) wide. Tegumental spines not observed. 'Handle' of hind-body completely undifferentiated. Oral sucker 35–52 (44 ± 7) long and 40–52 (46 ± 7) wide. Ventral sucker probably non-functional, 27–37 (33 ± 4) long and 14–39 (28 ± 12) wide. Pharynx 17–32 (26 ± 6) long and 17–25 (21 ± 3) wide. Prepharynx absent; oesophagus narrow, 35–70 (47 ± 17) long. Caeca narrow, extends into hind-body. Tribocytic organ fully developed, 70–113 (93 ± 21) long, 67–113 (84 ± 21) wide. Genital rudiment a prominent mass of cells dorso-posterior to tribocytic organ. Excretory system ascending parallel to caeca, forming an extracaecal ring. Excretory pore subterminal.

Hosts. Belonidae: *Platybelone argalus* (muscle); Mugilidae: *Crenimugil crenilabris* (brain, heart, muscle), *Valamugil engeli*, (muscle); Sphyraenidae: *Sphyraena barracuda* (Edwards, 1771) (gills); Acanthuridae: *Acanthurus triostegus* (fins).

Comments. These metacercariae were identified as *Mesostephanus* Lutz, 1935 due to the presence of a spherical oral sucker, a ventral sucker slightly pre-equatorial and smaller than the oral sucker, the voluminous tribocytic organ and the genital primordial excretory vesicle I-shaped. Four species of *Mesostephanus* have been described for the region: *M. haliasturis*

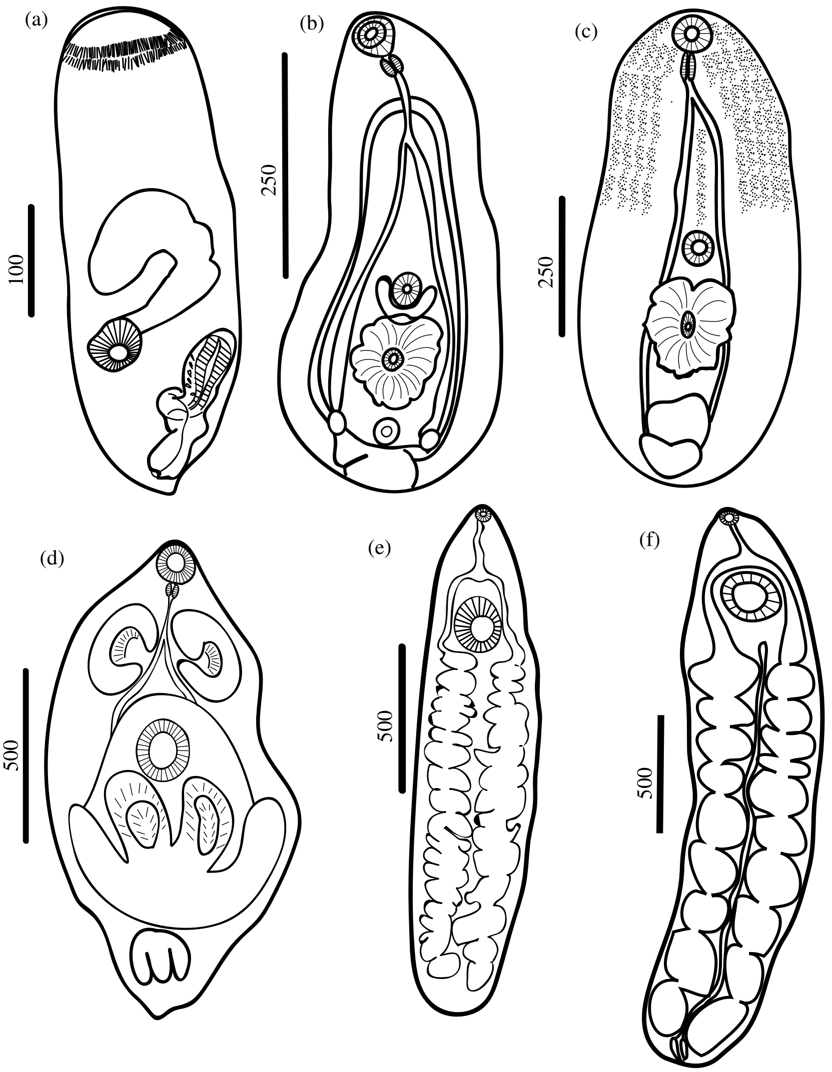

Fig. 3. Excysted metacercariae recovered from lagoon-flat fishes of Palmyra Atoll (all worms in ventral view). (a) *Dollfustrema* sp.; (b), *Mesostephanus* sp.; (c) Cyathocotylidae gen. sp.; (d) *Cardiocephaloides* sp.; (e) Monolicaecum-type; (f) Torticaecum-type. All scale bars are in micrometres.

Tubangui et Masilungan, 1941 for *Haliastur indus intermedius* Blyth, 1865 from the Philippines (Tubangui & Masilungan, 1941); *M. neophocae* Dubois et Angel, 1976 for *Neophoca cinerea* (Péron, 1816) and *Mirounga leonina* (Linnaeus, 1758) from Australia (Dubois & Angel, 1976); *M. haliasturis* and *M. scottae* Cribb, Barker et Beuret, 1995 for *Phalacrocorax sulcirostris* (Brandt, 1837) and *P. varius* (Gmelin, 1789), and *M. pelecani* Cribb, Barker et Beuret, 1995 for *Pelecanus conspicillatus* Temminck, 1824 from Queensland, Australia (Cribb *et al.*, 1995). The metacercariae recovered from *C. crenilabris* could belong to any of these species. Lutz (1935) reported the presence of *Mesostephanus* from the booby *Sula brasiliensis* Spix, 1825 from Brazil. Several species of boobies, such as the brown boobies (*Sula leucogaster* (Boddaert, 1783)), nest at Palmyra Atoll and could serve as potential definitive hosts.

Cyathocotylidae gen. sp. (fig. 3c)

Description. Based on seven slightly flattened individuals; one (USNPC No. 104860) from *Hemiramphus lutkei* and six from *Hyporhamphus affinis*. Body foliaceous to elliptical, slightly folded dorsally at its anterior end; length 680–1080 (877 ± 147), maximum width 320–525 (425 ± 71) at posterior quarter of body. Tegument smooth with granular pigments on anterior part of body, pre-acetabularly. Oral sucker subterminal, long 49–72 (65 ± 8), width 52–72 (62 ± 8). Acetabulum postequatorial, 46–65 long (58 ± 6) and 42–74 width (59 ± 10). Prepharynx absent; pharynx small, elliptical 35–47 long (41 ± 5) and 25–35 (30 ± 4) wide. Oesophagus 50–122 long (76 ± 30). Caeca narrow, close to middle ventral line of body, extending to posterior end. Tribocytic organ fully developed. Developing testes median, in tandem at posterior end, overlapping one to each other, globular. Anterior testis 67–125 long (92 ± 24) and 110–185 (149 ± 28). Posterior testis 52–110 long (84 ± 24) and 112–180 (143 ± 34) wide. Excretory pore subterminal.

Hosts. Hemiramphidae: *Hemiramphus lutkei* (muscle), *Hyporhamphus affinis* (eye, fins, muscle); Belonidae: *Platybelone argalus* (eye, muscle); Mugilidae: *Crenimugil crenilabris* (muscle), *Valamugil engeli* (body cavity, heart, kidney, intestine, muscle); Acanthuridae: *Acanthurus triostegus* (eye, fins, muscle).

Comments. These metacercariae were morphologically different from *Mesostephanus* due to the foliaceous body shape, granular pigment on anterior part of body, very narrow caeca, and primordia of testes in tandem posterior to tribocytic organ. Based on its general morphology, it might be a cyathocotylid such as *Cyathocotyle* Mühling, 1896 *Holostephanus* Szidat, 1936 or *Paracoenogonimus* Katsurada, 1914. The first intermediate and definitive hosts may be similar to those of *Mesostephanus* sp.

Family Strigeidae Railliet, 1919

Cardiocephaloides *sp. (fig. 3d)*

Description. Based on two flattened individuals (one sent to USNPC, No. 104861) from *Crenimugil crenilabris*. Body oval, 925–1038 long, maximum width at middle 850–1025. Short anterior part of body 140–150 long and 210–240 wide, bearing oral sucker separated by transverse tegumental fold from rest of body. Middle part of body 810–980 long and 1010–1200 wide, with broad longitudinal lateral fields of darker tissue on each side. Posterior part of body 190–270 long and 330–420 wide. Oral sucker subterminal, measuring 110 long and 100–140 wide. Acetabulum situated approximately at middle body, 110–180 long by 160–180 wide. Two well-developed pseudosuckers present about one-quarter into the body, each lateral to gut, centred at level of oesophagus bifurcation. Pharynx 60–80 in diameter. Oesophagus 140–160 long, bifurcating at middle level of pseudosuckers into two caeca ending near caudal end of body. Large, transverse holdfast situated at end of middle part of body, measuring 270–460 long and 510–760 wide. Posterior part of body provided with anlagen of sexual glands and subterminal excretory pore.

Hosts. Mullidae: *Mulloidichthys vanicolensis* (brain); Kyphosidae: *Kyphosus cinerascens* (brain); Chaetodontidae: *Chaetodon lunula* (brain); Pomacentridae: *Abudefduf sordidus* (brain); Mugilidae: *Crenimugil crenilabris* (brain, eye, fins, muscle, kidney), *Liza vaigiensis* (brain); Acanthuridae: *Acanthurus triostegus* (muscle), *Acanthurus xanthopterus* (brain); Balistidae: *Rhinecanthus aculeatus* (brain).

Comments. These metacercariae were originally described in the genus *Cardiocephalus* Szidat, 1928, and later transferred to the genus *Cardiocephaloides* Sudarikov, 1959 (Niewiadomska, 2002). These metacercariae were assigned to *Cardiocephaloides* due to the presence of two pseudosuckers posterolateral to the small pharynx and the large bilobed tribocytic organ posterior to the acetabulum. As metacercariae, these digeneans infect marine fishes from the Sparidae and Scombresocidae families (Niewiadomska, 2002). Several other families of fish at Palmyra Atoll were infected with these metacercariae. The adults of *Cardiocephaloides* infect marine birds (Lariidae, Spheniscidae and Procellaridae) all over the world (Díaz *et al.*, 2010), and the cercariae develop in molluscs (Prosobranchia: Nassidae) (Niewiadomska, 2002). *Cardiocephaloides musculosus* (Johnston, 1904) is the only species that has been recorded as an adult from the crested tern (*Thalasseus bergii* (Lichtenstein, 1823)) from Australia (Johnston, 1942) and the EIP.

Family Didymozoidae

'Monolicaecum-type' (fig. 3e)

Description. Based on one specimen (USNPC 104862) from *Amblygobius phalaena*. Body unarmed, elongate, 1712 by 440. Parenchyma vesicular. No eye spots or eye-spot pigment. Mouth terminal. Oral sucker 42–62, within body. Acetabulum 182–185, muscular, embedded in body parenchyma, at level of anterior body fourth. Sucker length ratio 1:2.9. Pharynx absent. Oesophagus 155 long, narrow, bifurcation posterior to mid-forebody, 205 from the anterior end. 'Stomach' just perceptible. Caeca with narrow and inflated areas, descending in undulating fashion, terminating 77 from posterior extremity. Parenchymal glands fill entire body in zone beneath thin subcuticular longitudinal muscle layer. No reproductive structures. Excretory vesicle postcaecal.

Hosts. Mullidae: *Mulloidichthys flavolineatus* (fins, muscle); Mugilidae: *Liza vaigiensis* (intestinal wall); Gobiidae: *Amblygobius phalaena* (tissue surrounding eye).

Comments. 'Metacercariae' of Didymozoidae are commonly found in marine fishes as third intermediate or paratenic hosts from the Indo-Pacific region (Køie & Lester, 1985; Cribb *et al.*, 2000). Due to the fact that this metacercaria apparently has a stomach and lacks gland-cells around the oesophagus, it was tentatively recognized as a 'Monolicaecum-type' juvenile (Yamaguti, 1970; Pozdnyakov & Gibson, 2008). However, due to the lack of development, it was not possible to identify this larva at the genus or species level. In fact, due to the strong morphological changes undergone by didymozoids from juvenile to adult stages, molecular tools or experimental infections are needed for identification. Potential definitive hosts for these metacercariae are marine fishes such *Thunnus albacares* (Bonnaterre, 1788) and *T. obesus* (Lowe, 1839) from which Yamaguti (1970) described 14 species of didymozoids from Hawaii. Cribb *et al.* (2000) also described adult stages of didymozoids from pelagic fishes of the subfamily Thunninae (Scombridae) for the CIP marine ecoregion. The life cycles of didymozoids in the CIP and EIP are not known. However, Cribb *et al.* (2000) presume that most of these life cycles should be pelagic, including molluscs such as heteropods and pteropods, and coral reef fishes such as Lethrinidae and Serranidae as third intermediate hosts.

'Torticaecum-type' (fig. 3f)

Description. Based on two broken specimens (one sent to USNPC, No. 104863) from *Hemiramphus lutkei*). Body unarmed, filiform, 2850–3450 long by 150–180 wide. No eye spots or eye-spot pigment. Mouth terminal. Oral sucker 40–42 by 32–37, within body. Acetabulum 40–76 by 41–67, muscular, embedded in body parenchyma, at level of anterior body fourth. Sucker length ratio 1:1.28–1.81. Pharynx absent. Oesophagus long, narrow, bifurcation posterior to mid-forebody 205 from the anterior end. 'Stomach' absent. Caeca with narrow and inflated areas, descending in undulating fashion, terminating 67–132 from posterior extremity. Parenchymal glands fill entire body in zone beneath thin subcuticular longitudinal muscle layer. No reproductive structures. Excretory vesicle postcaecal.

Host. Hemiramphidae: *Hemiramphus lutkei* (fins); Carangidae: *Carangoides orthogrammus* (Jordan & Gilbert, 1882) (muscle, water in holding bag); Lutjanidae: *Lutjanus monostigma* (fins); Mullidae: *Upeneus arge* Cuvier, 1829 (water in holding bag, scales).

Comments. This 'metacercaria' was tentatively recognized as belonging to the 'Torticaecum-type' given the absence of stomach, absence of pharynx and lack of gland-cells around oesophagus. See additional comments for 'Monolicaecum-type' sp.

Discussion

Up to 425 individual host fish were surveyed belonging to 42 species and 33,964 metacercariae of 19 digenean species of 8 families were recovered. Three digenean families were particularly common in the metacercaria assemblage: Bucephalidae, Cryptogonimidae and Cyathocotylidae (table 1). Bucephalid species appear to have the broadest specificity, infecting up to 13 host families, 26 host species, and 14 sites within hosts (tables 1 and 2). Four other digenean families appeared less frequently (Acanthocolpidae, Heterophyidae, Strigeidae and Didymozoidae). All these families are a subset of those previously detected as adults or metacercariae throughout the CIP or EIP marine ecoregions (e.g. Yamaguti, 1970; Cribb *et al.*, 1994). Metacercariae in the abundant and less-abundant families originate from first intermediate host infections in bivalves or snails (Yamaguti, 1975), both of which are common on Palmyra's lagoon flats (unpublished observations). Trematode species in the common and rarer families use fishes and birds as final hosts (Yamaguti, 1975), indicating the role of both fishes and birds as predators on fish at Palmyra.

A few surveys have examined metacercariae infecting marine fishes in the Central and East Indo-Pacific ecoregions (Yamaguti, 1970; Køie & Lester, 1985; Cribb, 1998 and references therein). Our study differed from these previous surveys in several respects, and this perspective frames the rest of our discussion.

First, the fish assemblage was broadly surveyed, aiming to examine all the potential host species of the lagoon flats. Most other studies have focused on particular host taxa, or have obtained hosts haphazardly (e.g. via sporadic sampling at fish markets). We have thus far sampled 42 of 47 recorded fish species (unpublished data) from Palmyra's lagoon flats. Sampling a major portion of the local fish diversity helps to establish an accurate baseline expectation for the diversity and composition of the parasite community occurring in the entire ecosystem. In fact, a randomized species accumulation curve suggests that we have encountered most of the metacercaria species of the Palmyra Lagoon flats (fig. 4).

Second, each individual fish was thoroughly and systematically processed, squashing different tissues to count and identify individual metacercariae. This processing facilitated the detection of rare trematode

Table 2. Metacercaria species generality in terms of number of host families, species and sites within hosts used.

Metacercaria family	Metacercaria species	Number of fish families	Number of fish species	Number of sites within hosts[a]
Acanthocolpidae	*Stephanostomum* sp.	5	5	3
	Acanthocolpidae gen. sp.	2	2	5
Cryptogonimidae	Cryptogonomidae gen. sp. 1	5	6	6
	Cryptogonomidae gen. sp. 2	5	9	12
Heterophyidae	*Stellantchasmus* sp.	1	1	2
Zoogonidae	Zoogonidae gen. sp.	1	1	1
Bucephalidae	*Bucephalus* sp. 1	10	18	10
	Bucephalus sp. 2	13	26	13
	Bucephalus sp. 3	8	14	7
	Rhipidocotyle sp. 1	10	13	14
	Rhipidocotyle sp. 2	12	18	14
	Rhipidocotyle sp. 3	9	10	5
	Prosorhynchus sp.	5	6	5
	Dollfustrema sp.	7	11	6
Cyathocotylidae	*Mesostephanus* sp.	4	5	4
	Cyathocotylidae gen. sp.	4	6	6
Strigeidae	*Cardiocephaloides* sp.	7	9	4
Didymozoidae	Monolicaecum-type	1	1	2
	Torticaecum-type	5	6	4

[a] 'Sites within hosts' provides a crude indication of variability in tissue/organ site use, which may vary within or among host species. See metacercaria species descriptions for detailed information.

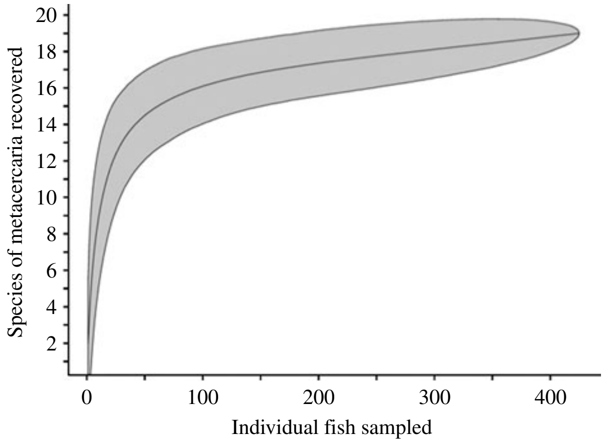

Fig. 4. A randomized species-accumulation curve (Gotelli & Colwell, 2001) for the metacercaria species detected with varying number of individual hosts processed. The curve represents the average of 10,000 randomizations of the 425 fish in our data set, counting for each randomization the number of encountered metacercaria species for each number of dissected host individuals. The shaded region represents the 95% confidence region, calculated using the standard error and *t*-distribution. The initial rapid approach to the asymptote indicates that our sampling has captured most of the lagoon-flat metacercaria diversity.

species within individual hosts. This intensive, within-host effort combined with our broad sampling of the fish community to further help to capture adequately the metacercaria diversity of the lagoon flats.

Third, the parasitological survey was conducted on fishes from a largely unexplored habitat: the lagoon flats. Previous efforts in the CIP and EIP marine ecoregions have been restricted to fore-reef habitats. To our knowledge only one of these fore-reef surveys (Lafferty *et al.*, 2008) processed individual fish in a manner similar to our own. Lafferty *et al.* (2008) sampled five fish species from the fore-reef at Palmyra Atoll. From the 110 individuals they processed, they recovered only a single morphospecies of metacercaria. If this represents fore-reef metacercaria diversity, then it is low compared to the 19 species that we documented on the sand flats. Although Lafferty *et al.* did not broadly sample the fore-reef fish assemblage, data from the present study were re-sampled to make sampling efforts more comparable. Ten thousand random draws (without replacement) of 110 individual fish (matching the number of individuals from Lafferty *et al.*) from our lagoon-flat data set recovered a minimum of 13 metacercaria species, with a mean ± SD of 16.0 ± 0.9. Additionally, controlling for the number of species examined by randomly sampling 11 individuals (Lafferty *et al.*'s minimum per species sample size) from 5 of the 14 fish species in our data set with adequate sample sizes, we recovered a minimum of four metacercaria species, with a mean ± SD of 13.0 ± 1.7. Further supporting the hypothesis that fore-reef fish may harbour lower metacercaria diversity, Lafferty *et al.* (2008) also only encountered a single metacercaria species during their sampling of the fore reef of a nearby Atoll (Christmas Island).

Why might lagoon flats have relatively high diversity and abundance of metacercariae? Compared to the fore reef, the lagoon flats are characterized by shallow, relatively still waters and high densities of probable first intermediate host bivalves and snails (unpublished data). These factors may contribute to greater infectious cercaria densities and higher transmission rates to second intermediate host fishes on the lagoon flats compared to the fore reef.

Another unique attribute of the present study is that it took place in a remote, small, relatively undisturbed atoll. As a trophically intact system, Palmyra Atoll may help establish baseline expectations for undisturbed community structure of both hosts and parasites. This may be particularly useful for efforts to develop parasites as ecological indicators of free-living diversity. For instance, trematode parasites in easily sampled first intermediate hosts can indicate more difficult to sample free-living invertebrates, fishes, birds and mammals (Huspeni *et al.*, 2005; Lafferty & Dunham, 2005; Hechinger *et al.*, 2007). The host specificity documented herein can inform future efforts to use trematode assemblages in first intermediate hosts to indicate surrounding free-living diversity in the CIP and EIP marine ecoregions.

The low variability of the morphological measures used to differentiate metacercariae suggests that each taxon identified is a discrete species. However, cryptic species may, of course, occur within any of our delineated species. This may be most likely for those metacercariae with few developed morphological characters (e.g. the two didymozoids). Further cryptic diversity may be associated with those species characterized by very discrete and disjunct tissue or host use. The descriptions of morphology, and tissue and host use for these metacercariae should help guide future taxonomic research on these trematodes.

In conclusion, metacercariae appear to be abundant and diverse in Palmyra lagoon-flat fishes. The descriptions provided here will facilitate future ecological work by providing names and descriptions. The descriptions and information on host use may also help guide future life cycle and taxonomic research focused on EIP trematodes. Additionally, we hope that the diversity and abundance of metacercariae documented here highlight their importance and the need to include them in future studies of fish–helminth interactions or of the role of parasites in ecosystems.

Acknowledgements

The authors thank The Nature Conservancy staff for their support of research and are particularly indebted to Amanda Meyer (United States Fish and Wildlife Service), Franklin Viola, Brad Kintz, Aaron Kierzek, Jan Eber, Anthony Wilson and Lynette Williams. Gareth Williams and Ingrid Knapp shared their field knowledge. Dr Tomáš Scholz and Dr William Cole made valuable comments on an earlier version of this paper. University of California, Santa Barbara (UCSB), and the US Geological Survey funded travel and accommodation. This study was supported financially by the grant Secretaria de Educación Pública-Programa de Mejoramiento del Profesorado (SEP-PROMEP) 'Propuesta sobre Calentamiento Global y Cambio Climático de la Red Académica de Instituciones SEP-PROMEP del Sureste: área Sensibilidad Marina', Fondos Mixtos Conacyt-Gobierno de Yucatán (FOMIX Yucatán) Grant 108929 'Sensibilidad y vulnerabilidad de los ecosistemas costeros del sureste de México ante el Cambio Climático Global' to V.M.V-M. This document is an output from the British Council Mexico Research Links Project funded by the British Council for the benefit of the Mexican Higher Education Sector and the UK Higher Education Sector. The UC-Mexus-CONACyT program provided funds for a sabbatical research fellowship to M.L.A-M. and V.M.V-M. at UCSB during the academic year 2009–10. Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

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