

Larval trematodes *Paronatrema mantae* and *Copiatestes* sp. parasitize Gulf of California krill (*Nyctiphanes simplex*, *Nematoscelis difficilis*)

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ABSTRACT: During 4 quantitative-systematic oceanographic cruises at 99 sampling stations in the Gulf of California (January and July 2007, August 2012, and June 2013), we found 2 trematode species (non-encysted mesocercaria stage) parasitizing the hemocoel of 2 krill species at near-shore locations. *Copiatestes* sp. parasitized *Nematoscelis difficilis* in January 2007, and *Paronatrema mantae* parasitized *Nyctiphanes simplex* in July 2007. Both trematode species had an intensity of 1 parasite per host. This is the first endoparasite known for *N. difficilis*, the first record of *P. mantae* infecting zooplankton, and the first confirmed trematode parasitizing krill species in the Gulf of California. We provide quantitative evidence that these 2 trematode species infect krill with considerably low station prevalence (0.03–0.16%) and low population abundances (<1.2 trematodes 1000 m⁻³). A review of trematodes parasitizing krill indicates that syncoeliid trematodes also have (with few exceptions) low population densities and prevalence and lower species diversity than previously thought (suggesting a broader zoogeographic distribution range of these parasites). Due to the low host specificity of syncoeliid trematodes that typically infect more than 1 secondary intermediate host species in their complex life cycle, we propose that *N. simplex* and *N. difficilis* are intermediate hosts (although non-conspicuous) for the transmission of syncoeliid trematodes in the Gulf of California.

KEY WORDS: Digenean trematoda · Endoparasite · Mesocercaria · Metacercaria · Syncoeliidae · *Paronatrema mantae* · *Copiatestes* · Krill · Gulf of California

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INTRODUCTION

Nyctiphanes simplex Hansen, 1911 and *Nematoscelis difficilis* Hansen, 1911 (Crustacea: Euphausiacea) are the 2 most abundant euphausiid (krill) species distributed in the northwest coastal waters of Mexico (Brinton & Townsend 1980, Brinton 1981, Lavaniegos-Espejo et al. 1989, Gómez-Gutiérrez et al. 2010, 2012a,b). Although the 2 krill species coexist in the Gulf of California, they show several

biological and ecological differences: *N. simplex* is omnivorous, <19 mm in total length, has a subtropical and neritic zoogeographic pattern, is highly abundant throughout the year, and forms large and dense aggregations and schools. *N. difficilis* is omnivorous with large body size (<22 mm total length), large bi-lobulated eyes, and strong periopods, suggesting voracious predator activity. This species is distributed in a transoceanic belt pattern at mid-latitudes in the northeastern Pacific Ocean and Gulf

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of California (with subarctic and oceanic zoogeographic patterns), and it is moderately abundant, forming small and relatively low density aggregations (Kanaeva & Pavlov 1976, Brinton & Townsend 1980, Gómez-Gutiérrez et al. 2010). Because krill attain high population abundance and form dense social aggregations, they are a dominant component in the epipelagic food web as a major biomass link among primary producers and multiple zooplanktonic and nektonic predators (Kanaeva & Pavlov 1976, Brinton & Townsend 1980, Notarbartolo-di-Sciara 1988, Gendron 1992, Sampson et al. 2010). Their high abundance and biomass also make them potentially significant vectors of trophically transmitted helminth parasites (Trematoda, Cestoda, Acanthocephala, and Nematoda). Although krill are parasitized by all types of helminths (Shimazu & Oshima 1972, Shimazu 1975, 2006, Shimazu & Kagei 1978, Gómez-Gutiérrez et al. 2010, Gregori et al. 2012, 2013), in Mexico there are only 2 previous records of helminths infecting krill, namely *N. simplex* in the Gulf of California (Gómez-Gutiérrez et al. 2010) and *Euphausia americana* Hansen, 1911 in the Caribbean Sea (González-Solís et al. 2013).

To date, only 15 studies have reported infections of krill by trematodes (most of them accidentally discovered), for a total of 42 trematode records (8 genera, 10 species, and multiple non-identified species) parasitizing 12 of the 86 extant krill species known worldwide (Table 1). Systematic and quantitative studies focusing on parasites of krill, rather than opportunistic or sporadic discoveries, will increase our knowledge of parasite diversity, biology, and ecology, and particularly our understanding of parasite distribution, densities, and prevalence patterns, and how krill interact with their prey and predators as a vector of parasites in the pelagic food web.

Here, we report on 2 trematode species of the family Syncoeliidae that parasitize 2 numerically abundant krill species, *N. simplex* and *N. difficilis*, that were systematically collected during 4 oceanographic cruises carried out in the Gulf of California under contrasting seasonal conditions. We discuss the ecological relevance of krill as intermediate planktonic hosts for trematodes to complete their complex life cycle based on trematode developmental stages previously recorded, parasite-host population densities, and prevalences. Finally, we compare the occurrence of these 2 trematodes to other records of helminths parasitizing krill species in the Gulf of California and worldwide to provide an integrated quantitative perspective about the frequency of such infections in krill populations in nature.

MATERIALS AND METHODS

Field sampling and laboratory analysis

Krill were collected at 99 zooplankton-sampling stations during 4 oceanographic cruises (January and July 2007, August 2012, and June 2013) carried out aboard the RV 'El Puma' (Universidad Nacional Autónoma de México, UNAM) in the central Gulf of California (Fig. 1). Zooplankton was quantitatively sampled with oblique tows of a standard Bongo net (equipped with 333 and 500 μm mesh net, 3 m long, and 0.6 m mouth diameter). Each net was equipped with a digital flowmeter (General Oceanics) to estimate volume of filtered seawater (Smith & Richardson 1979). We analyzed the 500 μm mesh net samples, which were fixed with non-denatured 96% ethanol. All developmental phases of krill (calyptopis, furcilia, juvenile, and adult) were sorted from the zooplankton samples and were cleared with a 5% dilution of 70% glycerin-ethanol to identify them (Baker et al. 1990, Brinton et al. 2000) under a stereoscope (Stemi SV11, Carl Zeiss) equipped with a calibrated micrometer. Krill specimens were counted and classified by species, sex, and development phase. Each krill specimen was dissected with entomological needles to record the presence/absence of helminths. We recorded the intensity (number of individuals of a particular parasite species observed parasitizing each krill host) (Bush et al. 1997). Krill and endoparasite trematode abundances were standardized to ind. 1000 m^{-3} to estimate population abundance (PA) of the hosts and the parasites in the sampled water column (Smith & Richardson 1979):

$$PA = \left(\frac{a}{fv} \right) \times 1000 \quad (1)$$

where a is total number of healthy krill specimens (without trematode infection) in each sample to estimate total krill abundance (excluding calyptopis stage) or is the total number of trematodes parasitizing krill specimens in each zooplankton sample to estimate total trematode abundance, and fv is the net-filtered seawater volume expressed in cubic meters (m^3), calculated according the method described by Smith & Richardson (1979). These abundance estimates allowed us to calculate the absolute prevalence (AP, scaled to percentage) recorded at each sampling station:

$$AP = \left(\frac{D_p}{D_h} \right) \times 100 \quad (2)$$

where D_p is the density of the parasite (ind. 1000 m^{-3}) and D_h is the density of the krill host (ind. 1000 m^{-3}).

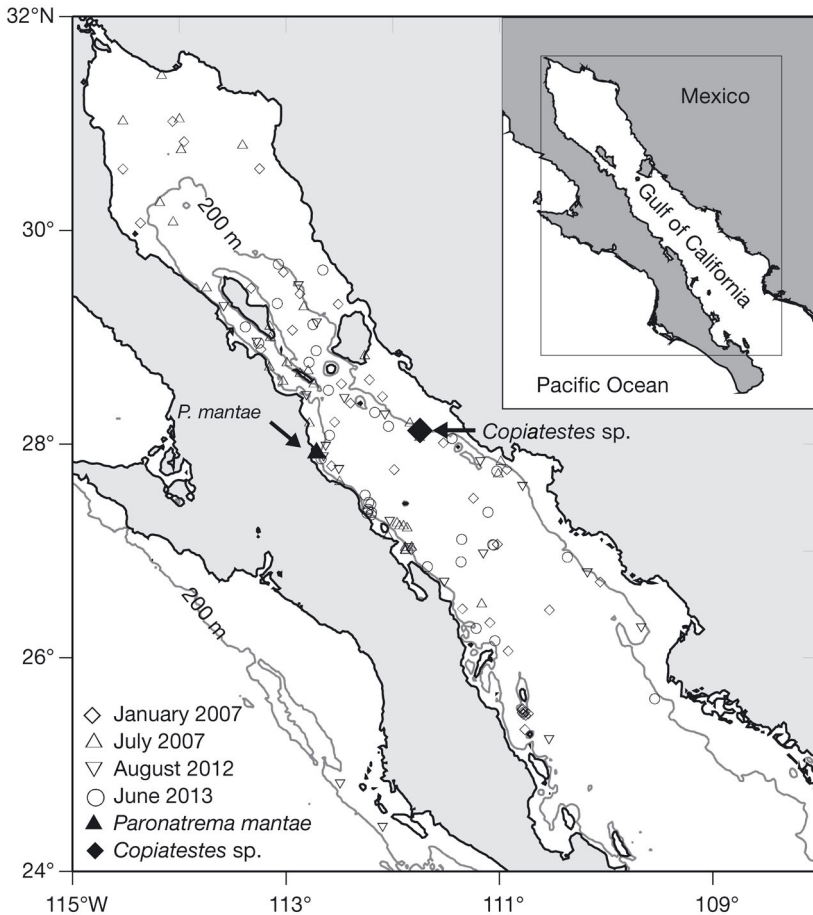


Fig. 1. Area of study. Open symbols indicate the location of the zooplankton samples collected during 4 oceanographic cruises (January and July 2007, August 2012, and June 2013) in the Gulf of California. Black symbols indicate the near-shore locations of krill parasitized by trematodes

The absolute prevalence is distinct from the relative prevalence estimate that counts the number of hosts parasitized with each parasite species divided by the number of host specimens examined in the sample expressed in percent (Bush et al. 1997). Because we examined all krill specimens collected in the samples, both methods provided the same percent value; however, it would be different if we had used subsamples.

Identification of parasites

Specimens of parasites were stained with Harris hematoxylin, dehydrated through a series of graded ethanol concentrations (70–96%), cleared in methyl salicylate, and mounted in synthetic resin for permanent preparations. Observations of fixed and later stained specimens were viewed with an optical mi-

croscope (Axiostar, Carl Zeiss) equipped with a digital camera (Hyper HAD, Sony). The schematic drawings were made with a microscope equipped with a lucid camera. The morphological measurements were expressed in μm for trematodes and in mm for krill. Identification of trematode species was done using several taxonomic references (Manter 1940, Dollfus 1966, Overstreet 1970, Shimazu 1975, 2006, Curran & Overstreet 2000, Gibson et al. 2002, Shvetsova 2004, Eduardo 2010).

RESULTS

We dissected 26751 *Nyctiphanes simplex* specimens and 5885 *Nematocelis difficilis* specimens collected from 99 plankton samples. Only 3 trematode specimens belonging to 2 species of the family Syncoeliidae Looss, 1899 were detected parasitizing the krill. All of them showed morphology intermediate between cercaria and metacercaria (without tail) stages that we interpreted to be a mesocercaria stage (an unencysted larva with bifurcated tail and an incipient reproductive system). A trematode larva of *Copiasteses* sp. Crowcroft, 1948 was found parasitizing a juvenile female

N. difficilis (8.1 mm total length) during winter (January 2007). Two specimens of *Paronatrema mantae* Manter, 1940 were found, with the forebody laterally bent, compressing the ventral sucker. One trematode was found parasitizing a juvenile *N. simplex* (6.8 mm total length) from the Bongo net and another one was found parasitizing an adult *N. simplex* male (10 mm total length) collected at the same station but with the non-quantitative zooplankton net during summer (July 2007). We did not find trematodes parasitizing krill in samples collected during August 2012 and June 2013 cruises at 44 oceanographic stations. In addition to these trematodes, we found other helminth species during the same cruises ($N = 530$ parasitizing *N. simplex* specimens), where Cestoda were the numerically dominant helminth endoparasites (98.8%). Acanthocephala (0.56%), Nematoda (0.18%), and Trematoda (0.37%) were present in considerably low proportions. This information provides a quantitative

Table 1. Worldwide parasitic diversity of digenetic trematodes reported parasitizing krill (Order Euphausiacea). Larval stage given as 'reported (corrected)'; current taxonomy given where different from first column. Ad: adult; Juv: juvenile; Int.: intensity; Prev.: prevalence; (—) not reported in original reference

Trematode Species and authority	Larval stage	Host Species and authority
Family unidentified		
(Monogenea)	—	<i>Euphausia pacifica</i> Hansen, 1911
(Digenea)	—	<i>Thysanoessa inermis</i> (Krøyer, 1846)
Unidentified	—	<i>Euphausia</i> sp.
Unidentified	—	<i>Thysanopoda tricuspidata</i> Milne-Edwards, 1837
Lepocreadiidae		
<i>Opisthogonoporus</i> spp.	—	<i>Euphausia similis</i>
Opecoelidae		
<i>Pseudopecoelus japonicus</i> (Yamaguti, 1938) von Wicklen, 1946	Metacercaria (Metacercaria)	<i>Euphausia similis</i>
<i>Pseudopecoelus japonicus</i>	—	<i>Thysanopoda</i> sp.
<i>Neonotoporus trachuri</i> (Yamaguti, 1938) Srivastava, 1942	Metacercaria (Metacercaria)	<i>Euphausia similis</i>
<i>Pseudopecoelus japonicus</i>	Metacercaria (Metacercaria)	<i>Euphausia similis</i>
Syncoeliidae		
<i>Distomum filiferum</i> (Leukard in G.O. Sars, 1885)	Metacercaria (Mesocercaria)	<i>Nematoscelis megalops</i> G.O. Sars, 1883
<i>Distomum filiferum</i>	Metacercaria (Mesocercaria)	<i>Thysanoessa gregaria</i> G.O. Sars, 1883
<i>Paronatrema</i> sp.	Metacercaria (Metacercaria)	<i>Nyctiphanes couchii</i> (Bell, 1853)
(<i>Metacercaria theomonodi</i>) (genus and species not valid)	(Metacercaria)	<i>Nyctiphanes couchii</i>
(Metacercaria type B)	—	<i>Euphausia similis</i> G.O. Sars, 1885
<i>Paronatrema</i> spp.	Mesocercaria (Metacercaria)	<i>Euphausia similis</i>
<i>Paronatrema</i> sp. (1)	Mesocercaria (Metacercaria)	<i>Euphausia similis</i>
<i>Paronatrema</i> sp.	—	<i>Euphausia similis</i>
<i>Syncoelium</i> sp.	Metacercaria (Mesocercaria)	<i>Euphausia similis</i>
<i>Syncoelium</i> spp.	Metacercaria (Mesocercaria)	<i>Euphausia similis</i>
<i>Paronatrema</i> sp.	(Metacercaria)	<i>Euphausia diomedea</i> Ortmann, 1894
<i>Distomum filiferum</i> (Leukard in G.O. Sars, 1885)	Metacercaria (Mesocercaria–Metacercaria)	<i>Nematoscelis megalops</i>
<i>Paronatrema</i> sp.	Metacercaria (Mesocercaria)	<i>Euphausia pacifica</i>
<i>Paronatrema</i> spp.	Metacercaria (Mesocercaria)	<i>Euphausia pacifica</i>
<i>Syncoelium</i> spp.	Metacercaria (Mesocercaria)	<i>Euphausia pacifica</i>
<i>Syncoelium thyrssitae</i>	Metacercaria (Metacercaria)	<i>Nematoscelis</i> sp.
<i>Syncoelium</i> spp.	Metacercaria (Metacercaria)	<i>Nematoscelis</i> sp.
<i>Syncoelium filiferum</i>	Metacercaria (Mesocercaria)	<i>Euphausia diomedea</i> , <i>E. recurva</i> and <i>T. gregaria</i>
<i>Syncoelium filiferum</i>	Metacercaria (Mesocercaria)	<i>Euphausia diomedea</i> , <i>E. recurva</i> , and <i>T. gregaria</i>
<i>Syncoelium filiferum</i>	Metacercaria (Mesocercaria)	<i>Euphausia diomedea</i>
<i>Syncoelium filiferum</i>	Metacercaria (Mesocercaria)	<i>Euphausia diomedea</i>
<i>Paronatrema</i> sp. 1	Metacercaria (Mesocercaria)	<i>Euphausia diomedea</i>
<i>Syncoelium filiferum</i>	Metacercaria (Mesocercaria)	<i>Euphausia diomedea</i>
<i>Syncoelium ragazzii</i> (Setti, 1897)	—	<i>Euphausia diomedea</i>
<i>Paronatrema</i> sp. A,B	Metacercaria (Mesocercaria)	<i>Euphausia recurva</i> Hansen, 1905
<i>Syncoelium</i> spp.	Metacercaria (Mesocercaria)	<i>Euphausia vallentini</i> Stebbing, 1900
<i>Paronatrema</i> sp. (2)	Metacercaria (Mesocercaria)	Not identified
<i>Copiatestes filiferus</i> (Leuckart in G.O. Sars, 1885) Gibson & Bray, 1977	—	<i>Euphausia diomedea</i>
<i>Syncoelium</i> spp.	Metacercaria (Mesocercaria)	<i>Euphausia similis</i>
<i>Copiatestes filiferus</i>	—	<i>Nematoscelis megalops</i>
<i>Copiatestes thyrssitae</i>	(Metacercaria)	<i>Nematoscelis</i> sp.
<i>Copiatestes filiferus</i>	—	<i>Thysanoessa gregaria</i> G.O. Sars, 1883
<i>Paronatrema</i> sp.	—	<i>Nyctiphanes simplex</i> Hansen, 1911
<i>Copiatestes</i> sp.	(Mesocercaria)	<i>Nematoscelis difficilis</i> Hansen, 1911
<i>Paronatrema mantae</i> Manter, 1940	(Mesocercaria)	<i>Nyctiphanes simplex</i>

^aPrevalence and location reported by Claugher (1976)

Table 1 (continued)

Phase	Infection		Sampling region	Original reference	Trematode current taxonomy (reference)
	Int.	Prev. (%)			
—	—	0.003526	East China Sea, 31.16° N, 126.52° E	Kagei (1974)	<i>Paronatrema</i> sp. (Shimazu & Kagei 1978)
—	—	0.565	East China Sea, 49°40' N, 151°11' E	Kagei (1974)	
—	—	—	Tropical western Pacific Ocean, 5° N–15° S, 160° W–180° W		Slankis & Shevchenko (1974)
—	—	—	Tropical western Pacific Ocean, 5° N–15° S, 160° W–180° W		Slankis & Shevchenko (1974)
—	—	—	Suruga Bay, Japan	Shimazu (1972)	
Juv-Ad	—	1.7–38.3	Suruga Bay, Japan	Komaki (1970)	
—	—	—	Russia	Reimer et al. (1971)	
—	—	—	Suruga Bay, Japan	Shimazu (1972)	
Juv-Ad	1	0.08–1.28	Suruga Bay, Japan	Shimazu (1982)	
Ad	1–2	90 ^a	South Atlantic, 37°29' S, 27°31' W ^a	Sars (1885)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
Ad	1–2	—	South Atlantic	Sars (1885)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
Ad	1	—	Mediterranean Sea	Dollfus (1937)	<i>Paronatrema</i> sp.
Ad	—	—	Mediterranean Sea	Dollfus (1966)	<i>Paronatrema</i> sp. Manter & Pritchard in Dollfus (1966)
—	—	—	Suruga Bay, Japan	Komaki (1970)	
—	—	0.00004	Tosa Bay, North Pacific	Shimazu (1971)	
—	—	0.000005	Suruga Bay, Japan	Shimazu (1972)	
—	—	—	Suruga Bay, Japan	Shimazu (1972)	
—	—	—	Suruga Bay, Japan	Shimazu (1972)	
—	—	0.000030	Suruga Bay, Japan	Shimazu (1972)	
—	1	—	Tropical western Pacific Ocean, 5° N–15° S, 160° W–180° W	Slankis & Shevchenko (1974)	
Ad	1–2	—	South Atlantic, 36°55' S, 12°12' W	Claugher (1976)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
Ad	1	—	East China Sea, 31°16' N, 126°52' E	Shimazu & Kagei (1978)	
Ad	1	0.000035	East China Sea, 31°16' N, 126°52' E	Shimazu & Kagei (1978)	
—	—	0.007	No data	Kagei (1979)	<i>Syncoelium</i> sp.
—	1	0.91	North of Possession Island, 44°29' S, 55°58' E	Kagei (1979)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	0.45	North of Possession Island, 44°29' S, 55°58' E	Kagei (1979)	<i>Syncoelium</i> sp.
—	—	0.88	Eastern New Caledonia, 24°49' S, 177°24' E	Kagei (1979)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	0.85	Eastern New Caledonia, 24°49' S, 177°25' E	Kagei (1979)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	0.101	Solomon Sea, 10°17' S, 157°56' E	Kagei (1979)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	0.056	Solomon Sea, 10°17' S, 157°56' E	Kagei (1979)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	0.155	Eastern New Caledonia, 25°15' S, 177°49' E	Kagei (1979)	
—	—	1.01	10°17' S, 157°56' E	Kagei (1979)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	0.056	Eastern New Caledonia, 10°07' S, 157°51' E	Kagei (1979), Shimazu (2006)	
—	—	0.012	Eastern New Caledonia, 24°42' S, 177°17' E	Kagei (1979)	
—	—	0.009	North of Port Aux Francais, 45°53' S, 65°08' E	Kagei (1979), Shimazu (2006)	
—	—	—	East China Sea	Shimazu (1982)	
—	—	—	Suruga Bay, Japan	Shimazu (2006)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	—	—	Shimazu (2006)	
—	—	—	—	Shimazu (2006)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
—	—	—	—	Shimazu (2006)	
—	—	—	—	Shimazu (2006)	<i>Copiatestes thyrsitae</i> (Shvetsova 2004)
Ad	1	0.0285	Gulf of California, Mexico	Gómez-Gutiérrez et al. (2010)	Cestoda mis-identified as a trematode (present study)
Juv	1	0.16	Gulf of California, Mexico, 28°08.47' N, 111°44.65' W	Present study	
Juv	1	0.03	Gulf of California, Mexico, 27°56.77' N, 112°42.86' W	Present study	

perspective about the low frequency and relative abundance of trematodes that parasitize krill in the Gulf of California.

The 3 specimens of krill parasitized with trematodes had normal external appearance (without swollen cephalothorax or body deformation), and the parasites were discovered only after the cephalothorax was dissected. The parasitized *N. simplex* male had an extruded spermatophore but no evident gonad development in the cephalothorax. The *N. difficilis* juvenile female had an immature gonad (Stage I) and without spermatophore attached to the thelycum that would indicate recent reproductive activity.

***Paronatrema mantae* Manter, 1940**

The 2 specimens of *P. mantae* (Fig. 2A–H) were detected in the mesocercaria stage, collected from 1 of 16 zooplankton samples collected in July 2007 (27°56.77'N, 112°42.86'W). At this location, *N. simplex* had a total abundance of 4077 ind. 1000 m⁻³ and the trematodes had an abundance of 1.2 trematodes 1000 m⁻³, with an absolute station prevalence of 0.03%. This is the first report of *P. mantae* in the larval phase; thus, we describe its morphology from one of our specimens available for further comparative morphological studies. *P. mantae* was 3160 µm long and 800 µm wide (just posterior to the acetabulum); body dorso-ventrally flattened; forebody narrow, 1550 µm long; hindbody 1000 µm long, with a bifurcated tail with granular appearance, 390 µm long and 860 µm wide (Fig. 2A). Oral sucker terminal, 450 µm long and 520 µm wide, with an internal ring armed with about 40 small accessory suckers. Ventral sucker 930 µm long with 36 small accessory suckers, protruding 590 µm on a muscular base; oral/ventral sucker with a length ratio of 1:2. Mouth without prepharynx, pharynx 240 µm long and 130 µm wide. Ceca bending anteriorly to mid-pharynx level (apparently a cecal pouch is present). It is not clear whether the sinuous intestinal cecum opens into the excretory vesicle. The uterus is well-developed in many narrow transverse coils filling most of hindbody (covering other organs) and extending to the near posterior end of the body; the genital pore is located opposite the pharynx. The general morphology of the adult stage of *P. mantae* is shown in Fig. 2H (obtained from Manter 1940). A comparison of the morphological and biometric measurements and proportions among the *P. mantae* mesocercaria (present study) and metacercaria larval stages (Dollfus 1966) and the adult stage (Manter 1940) is shown in Table 2.

Mesocercaria and metacercaria larval stages of *Paronatrema* described from krill bear slight differences between them and compared to adults. One of the most noticeable ontogenetic changes from larval stage to adult is the forebody:hindbody ratio. In larval stages, the forebody is larger than the hindbody, and this is reversed in the adult stage, suggesting an allometric growth pattern (Table 2).

Remarks

Dollfus (1966) reported the trematode *Metacercaria teomondi* as a parasite of *Nyctiphanes couchii* (Bell, 1853). Kagei (1974) reported a 'monogenean trematode' parasitizing *Euphausia pacifica* Hansen, 1911. Later, both specimens were referred to as *Paronatrema* spp. (Syncoeliidae) (Manter & Pritchard pers. comm. in Dollfus 1966, Shimazu & Kagei 1978). More recently, Gómez-Gutiérrez et al. (2010) reported '*Paronatrema*-like metacercaria (Syncoeliidae)' parasitizing *N. simplex* in the Gulf of California. However, analyzing their published photographs, they actually showed photographs of a Eutetrarhynchidae cestode rather than a trematode (see their Figs. 5c,d). *Paronatrema* sp. parasitizing *E. pacifica* (Shimazu & Kagei 1978) differs from our *P. mantae* specimen because their specimen has an oral sucker that lacks accessory suckers and has fewer accessory suckers (n = 26) on the acetabulum (Fig. 2D–G). Our tailed *P. mantae* mesocercaria had a total length (3160 µm long) similar to that of the untailed metacercaria specimen (1500–3000 µm) reported by Dollfus (1966). However, the specimens described by Dollfus (1966) are slender, have a variable number of accessory suckers (sometimes absent), and have a relatively smaller ventral sucker (700 µm diameter) than *P. mantae* (930 µm diameter). The type species in the adult stage of *P. vaginicola* Dollfus, 1937 and *P. boholanum* Eduardo, 2010 (larval stages unknown) have accessory suckers only in the ventral sucker (Table 2). The genus *Paronatrema* currently includes 3 extant species (*P. mantae*, *P. vaginicola*, and *P. boholanum*) (World Register of Marine Species [WoRMS], www.marinespecies.org).

***Copiatestes* sp. Crowcroft, 1948**

Copiatestes sp. was found in the mesocercaria stage, parasitizing *N. difficilis* at 1 of the 30 sampling stations in January 2007 (28°08.47'N, 111°44.65'W). At this location, *N. difficilis* had an abundance of

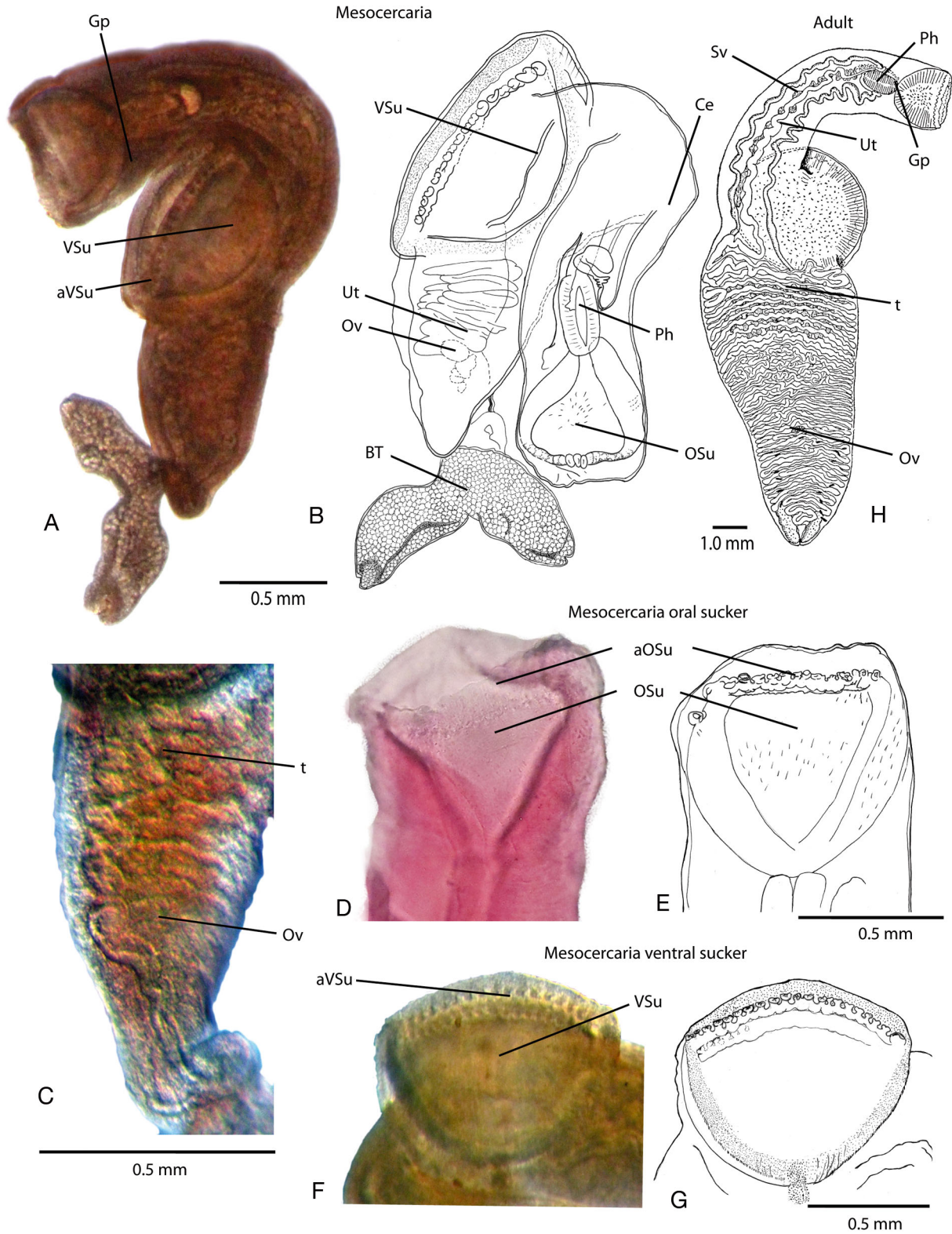


Fig. 2. *Paronatrema mantae* Manter 1940. (A–H) Trematode mesocercaria (unencysted) parasitizing the krill *Nyctiphanes simplex* in the Gulf of California. (A,C,D,F) Photograph with optical microscope and (B,E,G) drawings of mesocercaria. Detail of (C) coiled uterus, (D,E) accessory suckers of oral sucker, (F,G) accessory suckers of acetabulum, and (H) drawing of an adult taken from Manter (1940). VSu: ventral sucker; aVSu: accessory ventral sucker; OSu: oral sucker; Ce: ceca; Ph: pharynx; Ut: uterus; Ov: ovary; Gp: genital pore; Te: testes; Sv: seminal vesicle; BT: bifurcate tail

Table 2. Comparison of *Paronatrema mantae* morphological and biometrical measurements and proportions among larval-stage mesocercariae (with tail, present study), metacercariae (no tail), and adults (Manter 1940). TL: total length; BW: body width; Os: oral sucker; Vs: ventral sucker; Pp: prepharynx; PL: pharynx length; PW: pharynx width; Fb: forebody; Hb; hindbody

Species Stage (n) (Reference)	Body			Suckers			Pharynx		
	TL (μm)	BW (μm)	TL:BW	Os (μm)	Vs (μm)	Os:Vs	Pp	PL (μm)	PW (μm)
<i>Paronatrema</i> sp. Mesocercaria (n = 1) (Shimazu & Kagei 1978)	3710	730	5.1:1	430	950	1:2	Absent	240	210
<i>P. mantae</i> Mesocercaria (n = 1) (Present study)	3160	800	4.0:1 ^a	450	930	1:2 ^a	Absent ^a	240	130
<i>Paronatrema</i> sp. Metacercaria (n = 12) (Dollfus 1966)	3000	1000	3:1	190	700	1:3.6	Absent	111	85
<i>P. vaginicola</i> Adult (n = 7) (Dollfus 1937)	8000– 20500	2000– 3500	4.0–5.9:1	932– 1179	1824– 2807	1:1.7–2.1	Absent	494– 870	371– 477
<i>P. mantae</i> Adult (n = 3) (Manter 1940)	17500	4180– 4610	3.8–4.2:1	1809– 1971	3064– 3591	1:2 ^a	Absent ^a	1147– 1200	634– 815
<i>P. boholanum</i> Adult (n = 20) (Eduardo 2010)	6349	1725– 6125	1.0– 3.7:1	437– 625	1050– 3950	1:3.3– 4.8	Absent	390– 570	200– 400

^aMorphological features that overlap between *P. mantae* mesocercaria and adult stages
^bCecal pouches observed in drawing reported by Dollfus (1966) but not explicitly mentioned in his text

745 ind. 1000 m⁻³, and the abundance of the trematode was 1.2 ind. 1000 m⁻³, with an absolute prevalence of 0.16 %.

We describe the larval morphology for further comparative studies. Body cylindrical and elongated; 2970 μm long and 360 μm wide (at mid-posterior body); cuticle smooth and thick (difficult to observe internal organs); forebody 1490 μm long (about 50 % of the total body length), with small papillae easily detected at pharynx that spreads out from the oral sucker to the acetabulum; hindbody 1140 μm long; bifurcated tail located at the posterior part of the body, 300 μm long and 820 μm wide. Oral sucker and acetabulum without accessory suckers; oral sucker 330 μm long and 390 μm wide; acetabulum 560 μm long and 360 μm wide; acetabulum with a stalk 170 μm long, located near the middle part of the body and with extrinsic well-developed musculature; oral/ventral sucker length ratio 1:1.6. Mouth without prepharynx; pharynx located immediately behind the oral sucker, 120 μm long and 100 μm wide; esophagus extremely short and divides almost immediately into 2 ceca that follow a sinuous shape to the area of the ventral sucker, where they diverge toward the sides of the hindbody; >35 oval testes (23 μm mean diame-

ter) aligned roughly along 5 rows; small projecting genital papilla in a posterior-lateral position of the oral sucker (Fig. 3), seminal vesicle showed a sinuous shape to a point near the pharynx where it joins with the uterus to form a common genital sinus opening at the tip of the small genital papilla; ovary 60 μm long located posterior from the testes in the first third of the hindbody (600 μm from the proximal tail).

Remarks

The first known digenetic trematode *Distomum filiferum* parasitizing *Nematoscelis megalops* G.O. Sars, 1883 and *Thysanoessa gregaria* G.O. Sars, 1883 reported by Sars (1885) (= *Copiatestes filiferus* (Leuckart in G.O. Sars, 1885) Gibson & Bray, 1977 was recognized as junior synonyms of the monotypic genus *Copiatestes thyrstiae* Crowcroft, 1948 (Shvetsova 2004). However, we cautiously did not assign it to this species because our specimen had slight morphological differences that cannot be easily attributed to ontogenetic or interspecific features: (1) a well-developed bifurcated tail, (2) no long filaments located at the extreme of the hindbody (shown

Table 2 (continued)

Os:PL	Cecal pouch	No. of accessory suckers at:		Fb (μm)	Hb (μm)	Fb:Hb ^a	Ovary position	Tail	Genital pore position
		Os	Vs						
1:0.55	Present ^b	Absent	26	1550	1500	1.3:1	Near middle of Hb	Present	Anterior, bordering pharynx
1:0.53 ^a	Present ^a	~40 ^a	36 ^a	1558	1006	1.5:1	~1/3 TL from anterior end ^a	Present	Anterior, opposite pharynx
1:0.58	Present ^b	Present	Present	2000	1000	2:1	~1/3 TL from anterior end		Anterior, opposite pharynx
1: 0.41–0.73		Absent	35–38	3004–6512	4800–6961	0.4–1.3:1	Ventral portion of Hb		Anterior to pharynx
1:0.6–0.66 ^a	Present ^a	41–47 ^a	29–37 ^a	6680–7000	6300–8400	1.1:1	~1/3 TL from anterior end ^a		Anterior, opposite pharynx
1:0.62–0.91		Absent	Present	2500	3000	0.8:1	~1/4 TL from posterior end		Ventral, level with pharynx

in Sars 1885 and Claugher 1976), (3) a lobulated ovary located in the last third of the hindbody (in other *Copiatestes* descriptions, it is located in the middle part of the hindbody), and (4) arguably, the considerably high number of testes (up to 35) in the specimen collected in the Gulf of California while other specimens had only 11–18 testes. Because we have only 1 available specimen, we cannot conclude anything about intraspecific variability of such taxonomic characters. Therefore, we cannot determine whether our single specimen is a new species or whether it can be identified, without doubt, as *C. thyrstitae*. However, Gibson (2015), contrary to the point of view of Shvetsova (2004), reported in WoRMS (www.marinespecies.org) that the genus *Copiatestes* is not monotypic and includes 2 extant species: *C. thyrstitae* and *C. filiferus*.

Worldwide records of trematodes infecting krill

Assembling all published information highlights the enormous taxonomic problem posed by the originally reported 8 genera (10 species) and multiple unidentified trematode specimens. If synonymy of

Copiatestes species is valid (see Shvetsova 2004), the number of taxa infecting krill would decrease considerably. *C. thyrstitae*, *P. mantae*, and *P. japonicus* are the most frequent digenetic trematodes parasitizing krill (Table 1). This implies that these species should have broader zoogeographic patterns than previously thought and low specificity infecting different krill species (Table 1). Although our samples came from cruises collecting quantitative data, the prevalences were remarkably similar to previous reports involving non-quantitative trawls (Table 1).

DISCUSSION

Most investigations of trematodes parasitizing krill have been carried out from accidental findings or from non-quantitative sampling trawls (Table 1). This situation prevents estimating abundance of parasites and host populations that could lead to better understanding of the role of krill in the syncoeliid trematode life cycle. We estimated considerably low trematode population abundances (<1.2 ind. 1000 m⁻³) and prevalences (0.03 and 0.16%) from quantitative zooplankton sampling. Comparing occurrence

(our observations, 0.37%) and prevalence of trematodes worldwide (Table 1), and those detected for other helminths in the Gulf of California (Cestoda [$>98.8\%$], Acanthocephala [0.56%], and Nematoda [0.18%]; with $n = 530$ parasitizing *Nyctiphanes simplex* specimens from the same cruises (J. R. Morales-Ávila et al. unpubl. data) quantitatively confirms that *N. simplex* and *Nematoscelis difficilis* are not conspicuous intermediate hosts for these trematodes. This is partly explained by the low host specificity known for syncoeliid trematodes that frequently infect more than one secondary intermediate host species in their complex life cycle (Slankis & Shevchenko 1974). This has been observed in other regions, where digenetic trematodes parasitize krill with low prevalences ($<1\%$) and typically with an intensity of 1, rarely 2 (Table 1). For example, *Euphausia similis* shows very low prevalence (0.00004%) at Tosa Bay, Japan (Shimazu 1971, 1982). There are only 2 reports of trematodes infecting krill at relatively high densities and prevalences (Table 1): *Pseudopocoelus japonicus* parasitizes *E. similis* G.O. Sars, 1883 with a prevalence of up to 38% at Suruga, Japan (Komaki 1970), and from the re-examination of the specimens from the Challenger Expedition 1872–1876, Claugher (1976) reported the highest (90%) digenetic trematode (*Copiatestes thyrstiae*) prevalence documented so far in krill (120 specimens of *Nematoscelis megalops*), from the South Atlantic. From summarized information in Table 1 emerged a pattern that trematodes have distinct infection success and spreading strategies in different krill species and even in the same species in different areas. Most importantly, the diversity of trematodes infecting krill is not as high as previously thought (based on the synonymies), and these trematode species may have broad zoogeographic patterns infecting different krill species (low specificity). Our study is the first report of an endoparasite of *N. difficilis* (Table 1), which was previously known to be infected only with epibionts, ectoparasites, and mesoparasites (Field 1969, De Silva-Dávila et al. 2004, Landers et al. 2006, Gómez-Gutiérrez et al. 2010).

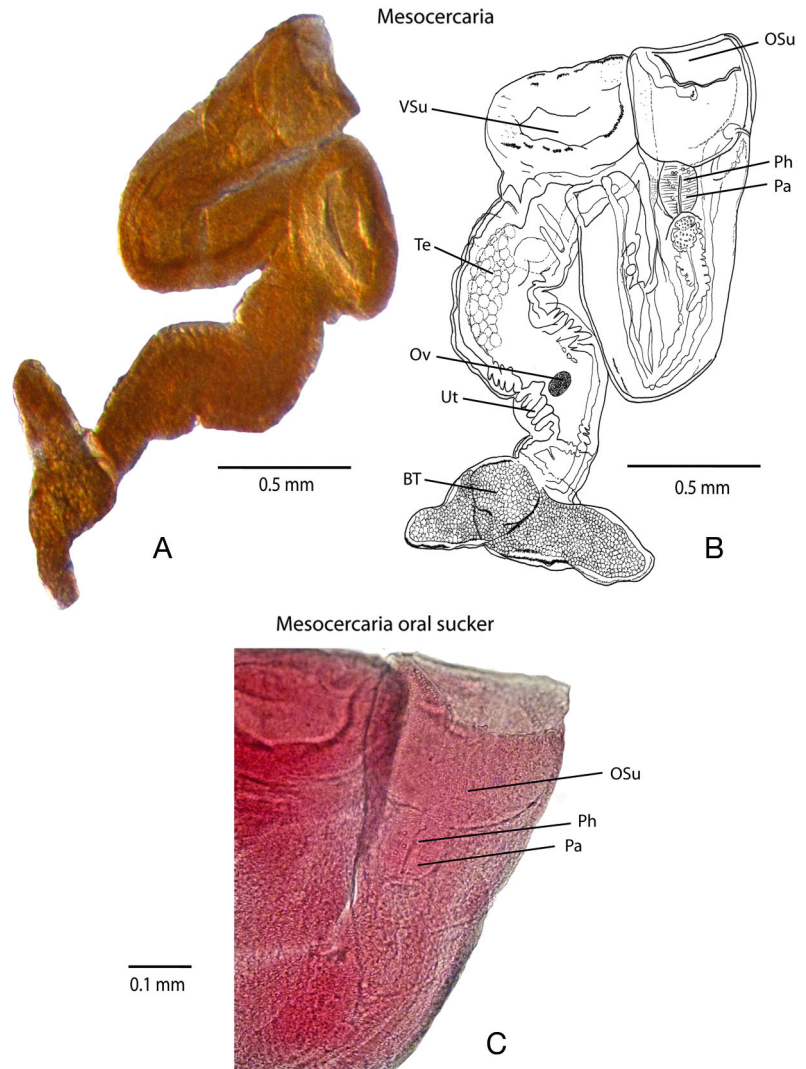


Fig. 3. *Copiatestes* sp. Crowcroft 1947. Trematode mesocercaria (unencysted) parasitizing the krill *Nematoscelis difficilis* in the Gulf of California. (A) Photograph with optical microscope, (B) drawing of mesocercaria, and (C) oral sucker. VSu: ventral sucker; OSu: oral sucker; Ce: ceca; Pa: papilla; Ph: pharynx; Te: testes; Ut: uterus; BT: bifurcate tail

Syncoeliidae life cycle

The life cycle of syncoeliid species is partly known, but nothing is known about the egg–cercaria stages of syncoeliid parasites, nor their first intermediate hosts (Gibson & Bray 1977), although copepods and krill are considered their second intermediary hosts (Overstreet 1970, Marcogliese 1995, Busch et al. 2012). Syncoeliid trematodes show low host specificity because they have been previously found as: (1) mesocercaria stage in the krill hemocoel (unencysted with tail, present study), (2) free-living metacercariae (without host) (Odhner 1911, Dollfus 1966, Shimazu 1982, 2006), (3) metacercariae externally attached on

zooplankton (trematodes without tail), such as on *Nyctiphanes couchii* (Dollfus 1966), and copepods (Overstreet 1970, Schell 1985), and (4) metacercaria stage in krill hemocoel (presumably with tail) (Kagei 1979). Syncoeliid trematodes are most frequently observed as non-encysted tailed larvae (inappropriately named 'unencysted metacercariae,' but we think it is actually a mesocercaria stage with immature reproductive organs, defined as an intermediate form between cercaria and metacercaria; Galaktionov & Dobrovolskij 2003) occurring in the hemocoel of *N. megalops* and *Thysanoessa gregaria* (Sars 1885, Claugher 1976), *E. pacifica* (Shimazu & Kagei 1978, Shimazu 2006), and *N. simplex* and *N. difficilis* (present study). In nektonic final hosts, syncoeliids are found attached to skin, and buccal and gill cavities of teleosteans (Shvetsova 2004), zooplanktophagous Chondrichthyes fish (*Manta birostris* (Walbaum, 1792) and *Rhincodon typus* Smith, 1828 parasitized by *Paronatrema mantae* and *P. boholanum*; Dyer et al. 1988, Villareal & Dailey 1993, Curran & Overstreet 2000, Eduardo 2010), and carnivorous shark species (*Prionace glauca* (Linnaeus, 1758) parasitized by *P. vaginicola*; Curran & Overstreet 2000), and syncoeliid trematodes were reported attached to the legs of seabirds (Claugher 1976). Because trematodes have been detected inside krill hemocoel as mesocercariae (unencysted with tail) and metacercariae (Claugher 1976, Kagei 1979), we propose that trematodes can develop in this kind of host; thus, krill should be considered an intermediate host rather than a paratenic or an accidental host (Table 1).

The neritic krill *N. simplex* migrates and forms dense swarms close the seafloor (unlikely for *N. difficilis* because this is an oceanic species; Robinson & Gómez-Gutiérrez 1998, Gómez-Gutiérrez & Robinson 2006). This transient epibenthic *N. simplex* behavior may facilitate transmission of parasites from benthic to nektonic prey and predators in the pelagic habitat. Future studies may determine whether syncoeliid trematodes actively search for the next host or passively infect krill and their predators through trophic prey-predator interactions.

CONCLUSIONS

This is the first confirmed record of trematodes infecting krill in the Gulf of California. The occurrence of *Paronatrema* infecting *Nyctiphanes simplex* represents the first record of *P. mantae* in the larval phase (mesocercaria) parasitizing a zooplankton host. Additionally, *Copiatestes* trematodes infecting *Nemato-*

scelis difficilis is the first known endoparasite recorded in this species. Although these 2 numerically dominant krill species tend to form relatively dense aggregations available to predators and parasites, we present quantitative evidence that trematodes in the Gulf of California typically have considerably low population abundance and low prevalences. From a worldwide review of the literature on trematodes parasitizing krill emerges the perspective that syncoeliid trematodes also have (with few exceptions) low population densities and prevalences and lower species diversities than previously thought (suggesting a broader zoogeographic distribution range of these parasites). The finding of syncoeliid trematodes as mesocercariae (a transitional developmental stage between cercaria and metacercariae stages) inside the host suggests that krill species in the Gulf of California function as intermediate hosts.

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