Parasite diversity of *Nyctiphanes simplex* and *Nematoscelis difficilis* (Crustacea: Euphausiacea) along the northwestern coast of Mexico

Jaime Gómez-Gutiérrez[1,3,*]**, Carlos J. Robinson**[2]**, So Kawaguchi**[3]**, Stephen Nicol**[3]

[1]**Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas, A.P. 592, C.P. 23096, La Paz, Baja California Sur, México**

[2]**Laboratorio de Ecología de Pesquerías, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, A.P. 70-305, México D.F. C.P. 04510, México**

[3]**Australian Antarctic Division, Department of Environment, Water, Heritage and Arts, 203 Channel Highway, Kingston, Tasmania 7050, Australia**

ABSTRACT: The diversity of parasites found on *Nyctiphanes simplex* and *Nematoscelis difficilis* (Order Euphausiacea) was compared during 10 oceanographic cruises made off both coasts of the Baja California peninsula, Mexico. We tested the hypothesis that *N. simplex* has a more diverse parasitic assemblage than *N. difficilis* because it is a neritic species, has larger population abundance, and tends to form denser and more compact swarms than *N. difficilis*. These biological and behavioral features may enhance parasite transmission within swarms. We detected 6 types of ectoparasites: (1) epibiotic diatoms *Licmophora* sp.; (2) Ephelotidae suctorian ciliates; (3) Foettingeriidae exuviotrophic apostome ciliates; (4) an unidentified epicaridean cryptoniscus larvae (isopoda); and 2 castrators: (5) the ectoparasitic Dajidae isopod *Notophryxus lateralis* and (6) the ellobiopsid mesoparasite *Thalassomyces fagei*. We also detected 7 types of endoparasites: (1) an undescribed *Collinia* ciliate (Apostomatida); 3 types of Cestoda: (2) a *Tetrarhynchobothruium* sp. (Trypanorhyncha), (3) *Echinobothrium* sp. (Diphyllidea: Echinobothyriidae), and (4) unidentified metacestode; (5) a Trematoda *Paronatrema*-like metacercaria (Syncoeliidae); (6) the nematode *Anisakis simplex* (L3); and (7) Polymorphidae acantocephalan larvae (acanthor, acanthella, and cystacanth larval stages). *N. simplex* is affected by all types of parasites, except the isopod *N. lateralis*, having a considerably larger parasitic diversity and prevalence rates than *N. difficilis*, which is only infested with 3 types of ectoparasites and *T. fagei*. Euphausiid swarming is an adaptive behavior for reproduction, protection against predators, and increased efficiency in food searching, but has a negative effect due to parasitism. Although the advantages of aggregation must overcome the reduction of population and individual fitness induced by parasites, we demonstrated that all types of parasites can affect ~14% of *N. simplex* individuals. *Collinia* spp. endoparasitoids must occasionally have a significant influence on population mortality with potential epizootic events.

KEY WORDS: Parasites · Parasitoids · Euphausiids · *Nyctiphanes simplex* · *Nematoscelis difficilis* · Bahía Magdalena · Gulf of California

INTRODUCTION

Several euphausiid (krill) species are able to attain massive biomasses and can form vast, dense swarms or schools playing a significant role in pelagic food webs in several ecosystems. Numerous macropredators take advantage of these krill aggregations, but the role of parasites in krill health condition and mortality is only fragmentarily known, particularly in tropical and subtropical ecosystems. Since several landmark reviews discussed the parasites of euphausiids (Mauchline & Fisher 1969, Komaki 1970, Mauchline 1980), an

increasing number of parasites and parasitoids have been discovered. The parasites of euphausiids include an array of interspecific associations that ranges from almost innocuous parenthetic epibiotic organisms such as diatoms (McClatchie et al. 1990), suctorians (Nicol 1984, Tarling & Cuzin-Roudy 2008), and apostome exuviotrophic ciliates (Lindley 1978, Rakusa-Suszczewski & Filcek 1988, Landers et al. 2006), to castrators (Field 1969) and parasitoids (Capriulo & Small 1986, Gómez-Gutiérrez et al. 2003, 2006, 2009). It is now apparent that each euphausiid species has a complex interspecific parasite–host association that depends on its life cycle, feeding habits, reproductive strategy, zoogeographic affinity, daily vertical migration, and swarming/schooling behavior (Shimazu 1975a,b, 2006, Théodoridès 1989, Ohtsuka et al. 2000, Gómez-Gutiérrez et al. 2003, 2006, 2009).

The aggregating behavior of euphausiids can develop in early larval stages, as young as furcilia IV (Hamner et al. 1989), possibly enhancing parasitic transmission after the ontogenetic formation of dense swarms and/or schools. The high density and swarming behavior characteristic of most numerically dominant euphausiid species may facilitate ecto-, meso-, and endoparasitic transmission within individuals of the same swarm (Hamner 1984, Nicol 1984, O'Brien 1988). This inherent disadvantage of social behavior of euphausiids has not been specifically tested by comparing congeneric species that overlap in their distribution range but have distinctly different lifestyles and swarming behaviors. We compared the parasite diversity and prevalence rates of the 2 numerically dominant euphausiids from the northwestern coast of Mexico: *Nyctiphanes simplex*, which comprises between 85 and 95 % of total euphausiid abundance, and *Nematoscelis difficilis*, with between 4 and 14 % of the total euphausiid abundance (see Table 1) (Brinton & Townsend 1980, Gómez 1995, Gómez-Gutiérrez et al. 2009).

Nyctiphanes simplex is a small (19 mm max. length), neritic, and omnivorous species that frequently forms dense daytime surface (Gendron 1992, Ladrón de Guevara et al. 2008) and epibenthic swarms (Robinson & Gómez-Gutiérrez 1998, Gómez-Gutiérrez & Robinson 2006). Theoretically, *N. simplex* has small nearest neighbor distances (NND) among individuals deducted from high density swarms observed with underwater video cameras and hydroacoustic observations (~1 to 15 cm) (Gómez-Gutiérrez & Robinson 2006). *Nematoscelis difficilis* is a larger (25 mm max. length), mostly carnivorous species that performs extensive daily vertical migrations and is mostly distributed in oceanic regions across the North Pacific Ocean (Brinton 1962, Brinton & Townsend 1980). However, they show a strong preference for the neritic zone

in the California Current System (Bucklin et al. 2002). *N. difficilis* has occasionally been observed aggregating near surface during the day, but in low densities, supposedly having large NND (>50 cm to meters) (D. L. Gendron pers. comm.). Indirect evidence of these interspecific swarming behavior differences is that several predators that require high densities of prey, like the mobulid rays (*Mobula thurstoni* and *M. japonica*) and the blue whale *Balaenoptera musculus*, prey significantly more on *N. simplex* than on *N. difficilis* in the Gulf of California (Notarbartolo-di-Sciara 1988, Gendron 1992, Del Ángel-Rodríguez 1997).

The only previous report of parasites of these 2 euphausiid species is the ellobiopsid *Thalassomyces fagei* infesting *Nyctiphanes simplex* in the Galapagos and Humboldt Current regions (Cornejo-De Gonzalez & Antezana 1980), and *Nematoscelis difficilis* infestation by the dajidae isopod *Notophryxus lateralis* off California (Field 1969) and exuviotrophic ciliates of the genus *Gymnodinoides* off the Oregon coast (Landers et al. 2006). The Dajidae isopod *Notophryxus lateralis* has been shown to infest *N. difficilis* during a shore stranding event in Bahía de La Paz (De Silva-Dávila et al. 2004). Additionally, the ectoparasitic Dajidae isopod *Oculophryxus bicaulis* was discovered infesting the euphausiids *Stylocheiron affine* and *S. longicorne* along the west coast of the Baja California peninsula (Shields & Gómez-Gutiérrez 1996).

The present study is the first comprehensive description of the diversity, prevalence rates (number of individuals of a host species infected with a particular parasite species divided by the number of hosts examined), and intensity (number of individuals of a particular parasite species in each infected host) of the parasite assemblages of euphausiids from Mexican waters. Our main aims are first to identify the multispecific ecto-, meso-, and endoparasitic assemblages to the lowest possible taxonomical level and to compare the parasitic diversity and prevalence rates of *Nyctiphanes simplex* and *Nematoscelis difficilis*, 2 numerically dominant euphausiid species in northwestern Mexico, as a function of their different life styles, and second to explore the possible role of swarming behavior in parasite diversity, prevalence, infection, and infestation rate.

MATERIALS AND METHODS

An extensive study of vertical distribution, swarming behavior, and reproductive biology of *Nyctiphanes simplex* and *Nematoscelis difficilis* was conducted on 3 oceanographic cruises off the continental shelf and mouth of Bahía Magdalena (24° 30′ N, 112° 30′ W; 16 March to 2 April, 28 June to 16 July, and 1–18 Decem-

ber 2004) and on 3 oceanographic cruises off the northern and central Gulf of California (16 November to 3 December 2005, 12–31 January 2007, and 17 July to 3 August 2007) (Gómez-Gutiérrez & Robinson 2006, Gómez-Gutiérrez et al. 2009). The 6 oceanographic cruises were carried out on-board the RV 'El Puma' (Fig. 1). To study euphausiid aggregation behavior, we obtained hydroacoustic records along the ship track of the sound scattering layer using a Simrad EY-60 split-beam echosounder (120 kHz). Two underwater video cameras were used to identify the acoustic scatterers as described in Gómez-Gutiérrez & Robinson (2006).

Euphausiids were collected using 4 types of gear: (1) 4 manually operated opening–closing nets towed obliquely (0.5 m mouth diameter with 300 μm mesh) to study vertical distribution patterns; (2) standard oblique Bongo net trawls (300 and 500 μm mesh) to estimate column-integrated euphausiid abundance (see Table 1); (3) non-quantitative samples with a 1 m diameter, 5 m-long net (300 μm black mesh) to obtain live euphausiids for shipboard observations; and (4) occasionally euphausiids were collected with an Isaac-Kidd mid-water trawl (2 × 2 m mouth, Kalhsico) (Gómez-Gutiérrez et al. 2009).

From these samples, live juvenile and adult euphausiids were sorted out on-board immediately after collection and observed using a Carl Zeiss (SV11) stereoscope fitted with a calibrated micrometer to identify species, sex, and gonad development and measure total length (TL, from behind the eye to the tip of the telson). Other simultaneous krill studies included: identification of digestive tract bacterial load, estimation of lipid content, and oxidative stress analyses (Aguilar-Méndez 2008, Tremblay 2008). Additionally, numerous specimens were incubated shipboard for 48 h at 16°C in dark conditions and observed every 12 h to estimate body growth, molt, and egg production rates (Gómez-Gutiérrez et al. 2009).

When live parasites of *Nyctiphanes simplex* and *Nematoscelis difficilis* were detected, they were photographed and/or videotaped with an Olympus digital camera (Camedia 3040, 3.3×10^6 pixel resolution) fixed on the stereoscope. Because parasites were clearly visible in transparent live euphausiids, shipboard observations gave us the opportunity to measure and describe the parasite's external morphology, coloration, behavior, prevalence, and intensity rates (without the need for dissection). This is advantageous
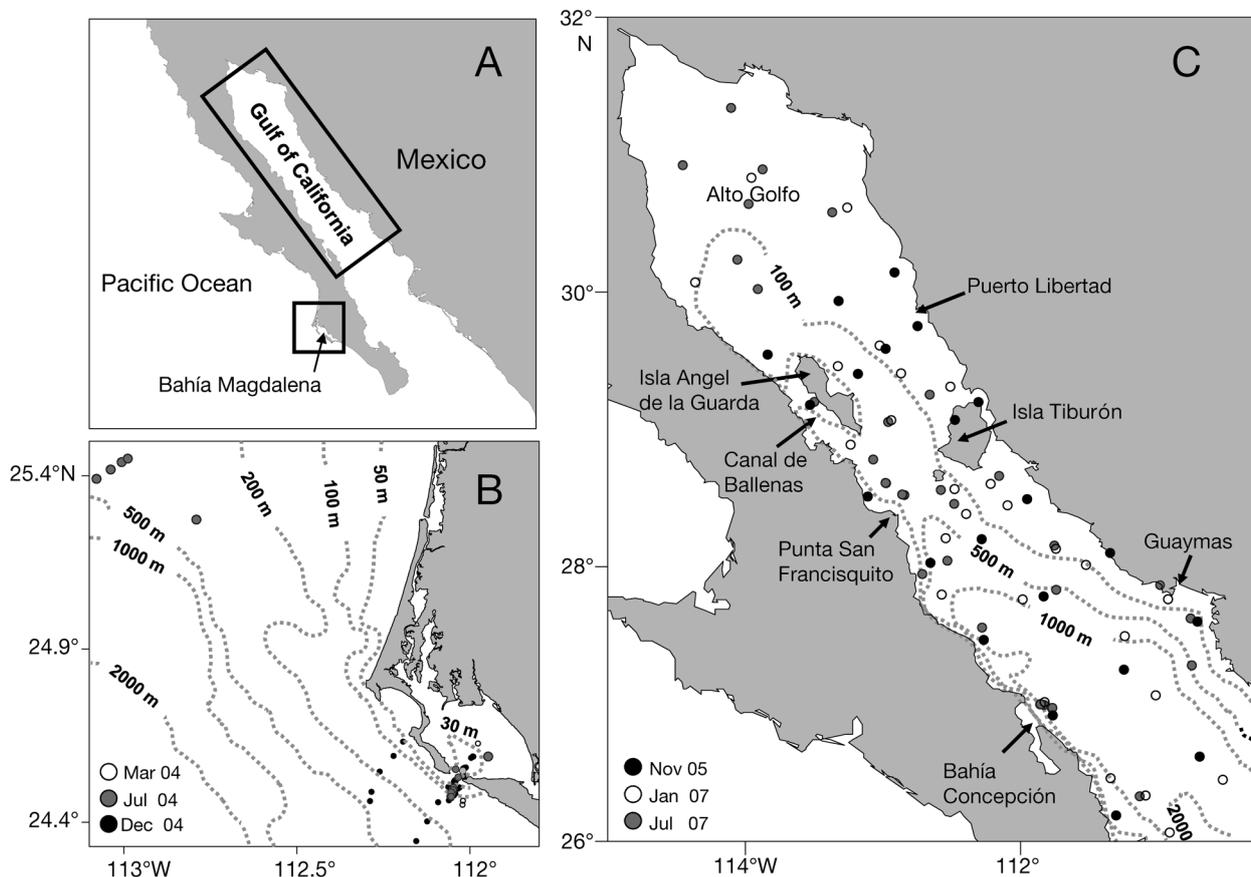

Fig. 1. (A) Study area showing sampling effort during (B) March, July, and December, 2004 along the continental shelf and mouth of Bahía Magdalena and (C) November 2005 and January and July 2007 in the Gulf of California

because euphausiids rapidly lose transparency after death or through chemical preservation, making it difficult to detect endoparasites. Several preserved euphausiids were cleared with pure lactic acid to observe them after preservation for taxonomic identification. We were able to detect ecto-, meso-, and endoparasites as small as 30 μm in length (apostome ciliates). We calculated prevalence rates from the proportion of euphausiids with parasites from the total number of live specimens observed at each sampling station at Bahía Magdalena (n = 2212 euphausiids observed), but this was not systematically conducted in the Gulf of California cruises. Several *N. simplex* (n = 24) and *N. difficilis* (n = 3) specimens collected along the west coast of the Baja California peninsula (29 to 23°N) during July 1987, December 1993, October 1994, and March 1996 were detected parasitized mostly with the ellobiopsids *Thalassomyces fagei* and the nematode *Anisakis simplex*. Additional parasite records of *N. difficilis* from the Oregon–California coast (2002–2003) are also included here for interspecific comparative purposes (J. Gómez-Gutiérrez unpubl. data). Our intention was not to identify and describe new species, but to distinguish distinct types of ecto-, meso-, and endoparasites from well-defined taxonomic groups that have considerable differences in morphology, life-stage, feeding, life cycle, and pathological patterns.

RESULTS

Nyctiphanes simplex was the numerically dominant euphausiid off both coasts of the Baja California peninsula, with between 6 and 22 times greater abundance than *Nematoscelis difficilis* in the Gulf of California (Table 1). Selection of 2 dusk–nighttime echograms (during ascent migration), where submarine video cameras and zooplankton net samples showed almost monospecific aggregations of *N. simplex* and *N. diffi-*

cilis, showed *N. simplex* had considerably more dense and spatially larger aggregations than *N. difficilis* (Fig. 2). *N. difficilis* was collected almost exclusively in the Gulf of California because this species has an oceanic affinity and our sampling grid along the southwest coast of the Baja California peninsula was exclusively over the continental shelf. Thus, except for the apostome exuviotrophic ciliates that seem to be ubiquitous in euphausiids, all of the parasites reported for *N. difficilis* were encountered in the Gulf of California. Combining data from Oregon (J. Gómez-Gutiérrez unpubl. data) and from both sides of the Baja California peninsula, we detected 13 distinct taxonomic types of parasites, 5 ectoparasites, 1 mesoparasite, and 7 endoparasites (Table 2). Some of them await formal taxonomic description because they appear to be new species.

Nyctiphanes simplex epibiotic organisms, ectoparasites, and mesoparasites

Epibiotic diatoms

Epibiotic stalked, triangular, pennate diatoms (*Licmophora* sp.) infested *Nyctiphanes simplex* at 8 oceanographic stations located over the continental shelf of Bahía Magdalena. Intensity varied from a few cells per appendage, or per animal, to many thousands, covering most of the thoracic appendages, antennae, gills, ovigerous sacs, and the eyes (Fig. 3A,B). Heavy infestations had considerable negative effects on swimming and respiration and gave the animals a fuzzy appearance that made them more visible to predators. Infested *N. simplex* ranged between 7.6 and 17.2 mm TL, but higher prevalences (average 8%, range 1 to 17%) and intensity rates were observed in larger individuals (>12 mm) (Fig. 4A). Epibiotic diatoms were present on euphausiids over the conti-

Table 1. *Nyctiphanes simplex*, *Nematoscelis difficilis* and *Euphausia eximia*. Average, maximum and SE of the abundance (ind. 1000 m^{-3}) of juveniles and adults (larvae not included) of the 3 most abundant euphausiids (*N. simplex*, *N. difficilis* and *E. eximia*) along the Gulf of California during November 2005 and January and July 2007. Sta+: number of stations with presence of juveniles and adults as an indicator of widespread horizontal distribution; *Ns/Nd* and *Ns/Ee*: abundance ratio of *N. simplex*/*N. difficilis* and *N. simplex*/*E. eximia*

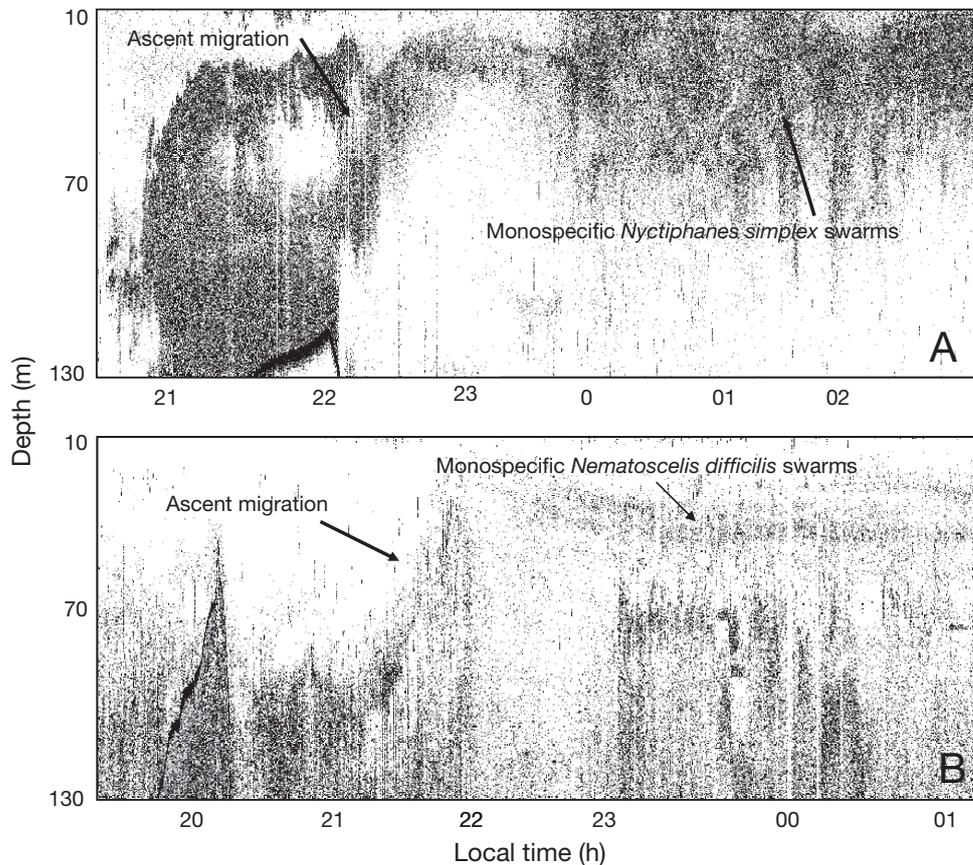| Species	November 2005 (n = 24 stn)			January 2007 (n = 35 stn)			July 2007 (n = 36 stn)		
	Average (max.)	SE	Sta+	Average (max.)	SE	Sta+	Average (max.)	SE	Sta+
N. simplex	4690.5 (66113.3)	2699.6	23	6155.6 (75400.8)	2175.0	34	314.8 (2956.8)	97.2	26
N. difficilis	216.3 (1189.5)	66.7	17	885.6 (6371.3)	234.2	33	49.26 (369.9)	15.9	17
E. eximia	5.0 (77.1)	3.5	4	16.6 (245.7)	8.2	9	4.3 (41.5)	1.6	7
Ns/Nd	21.7			7.0			6.4		
Ns/Ee	938.1			370.8			49.1		

Fig. 2. *Nyctiphanes simplex* and *Nematoscelis difficilis*. Hydroacoustic echograms (target strength threshold = –65 dB) showing almost monospecific aggregations of *N. simplex* (26 July 2007, near Bahía Concepción, 27° 53.67′ N, 112° 40.20 W) and *N. difficilis* (23 July 2007, Canal de Ballenas, 29° 07.81′ N, 113° 25.89′ W) in the Gulf of California. For comparative purposes of interspecific swarming behavior both echograms were recorded during dusk–nighttime when the pelagic organisms responsible for the sound scattering layer ascend. Numerically dominant euphausiid species were determined using underwater video cameras and zooplankton nets. Six fin whales *Balaenoptera physalus* were feeding in the *N. simplex* swarm location

nental shelf in March (15.8 to 18.2°C, mesotropic conditions) and July (15.6 to 20.4°C, oligotrophic conditions), but were absent in December (21.3 to 22.4°C, oligotrophic conditions) (Table 3, Gómez-Gutiérrez & Robinson 2006). Thus *Licmophora* sp. infestation is seasonally restricted to periods with high water column phytoplankton biomass. In the Gulf of California, we detected *Licmophora* sp. infestations at considerably lower intensities than in the Bahía Magdalena region. We did not observe epibiotic diatoms infesting the oceanic euphausiids *Nematoscelis difficilis* or *Euphausia eximia*.

Ellobiopsidae

The ellobiopsid *Thalassomyces fagei* (Boschma), which could be considered a mesoparasite because it penetrates the external exoskeleton of euphausiids, was observed infesting *Nyctiphanes simplex* in Bahía

Magdalena with low prevalence rates (<1.5%) and invariably with an intensity of 1 parasite per host (Tables 3 & 4). A total of 24 specimens of *N. simplex* (furcilia I, 2.2 mm TL, to adult, 12.0 mm TL) collected along the west coast of the Baja California peninsula (29 to 23°N) during July 1987 (n = 4), December 1993 (n = 1), October 1994 (n = 8), and March 1996 (n = 11) were also infected with *T. fagei*. *T. fagei* is the only ellobiopsid species reported in euphausiids worldwide and is characteristically attached to the mid-dorsal part of the carapace, inserted deeply into the host nervous system above the gonad region and, in some cases, in the first third of the carapace not connected to the gonad region (Fig. 3C,D, Tables 2 & 3) (Boschma 1948). The observed *T. fagei* had brown holdfasts and transparent basal stems with up to 28 branches (average 1.2 mm length) with 6 cells of distinct size per basal stem (trophomeres, 0.1 to 0.44 mm length) bearing dark terminal gonomere spheres. Euphausiids are the definitive hosts of ellobiopsids

Table 2. *Nyctiphanes simplex* and *Nematoscelis difficilis*. List of parasites of krill *N. simplex* (*Ns*) and *N. difficilis* (*Nd*) and main characters at both coasts of the Baja California peninsula, Mexico. BM: continental shelf and mouth of Bahía Magdalena; GC: Gulf of California

| Parasite	Host	Location	Description	Average prevalence (%) per station (intensity)
Chlorophytas Pennate diatoms				
Licmophora spp.	*Ns*	BM, GC	Epibiotic diatoms, average size 30 µm (cell without stalk), triangular cells	8 (1–10 000)
Ellobiopsidea				
Thalassomyces fagei	*Ns*, *Nd*	BM, GC	Mesoparasitic castrator, 1.2 mm, early stage 0.62 mm	1.5 (1)
Ciliophora Suctoria				
Ephelota sp.	*Nd*	Oregon	Average length of stalk with head 0.79 mm (range 0.22–1.77 mm), head diameter 250 µm	0.1 (1–80)
Apostomatida Foettingeriidae	*Ns*, *Nd*	BM, GC	Ectoparasite phoront and trophont exuviotrophic ciliates, average size 40 µm length × 20 µm width, with distinct color (transparent, black, orange) that indicates a diverse assemblage of species	29 (1–300)
Collinidae				
Collinia sp.	*Ns*	BM, GC	Endoparasitic parasitoid average 36 µm length (range 20–40 µm depending on life stage), number of kinety rows varies between 12 and 18	1–40 (<100 000)
Animalia Helmintha Trematoda				
Paronatrema sp.	*Ns*	GC	Endoparasite trophically transmitted, cluster 1080 µm length	0.001 (1)[a]
Cestoda Trypanorhyncha *Tetrarhyncho-bothrium* sp.	*Ns*	BM	Endoparasite trophically transmitted, Cestoda plerocercoid with a blastocyst, 1340 × 860 µm blastocyst, light brown embryo, embryo total length 1140 µm, head 440 µm and body 300 µm in width	<0.001 (1)
Unidentified metacestode		GC	Endoparasite trophically transmitted, cluster 680 µm diameter, each larvae 55 µm	0.001 (1)[a]
Diphyllidea Echinobothyriidae				
Echinobothrium sp.	*Ns*	GC	Endoparasite trophically transmitted, 2.6 mm total length, body slender, scolex proper 289 µm wide, very energetic movements	<0.001 (1)
Anisakis simplex	*Ns*		L3 stage can be larger than the host (12.1 mm, host total length of 11.8 mm, 9.4 mm, host total length of 10 mm), prominent larval tooth and large mucron (20 µm length), width 0.4 mm, body width/length ratio 3.3%, distance anus to tip of the tail 100 µm	0.0001 (1)
Acanthocephala Polymorphidae	*Ns*	BM, GC	Endoparasite trophically transmitted; 3 larval stages: acanthor (elongated pear-shaped), acanthella (pear-shaped), and cystocanth (oval); acanthocephalan size and development stage was positively associated with the total length of the krill host	3.1 (1)
Crustacea Isopoda Epicaridea	*Ns*	BM	Ectoparasite, unidentified Epicaridea cryptoniscus larval stage, 1.3 mm total length, brown, with eyes and 14 segments infesting *N. simplex* female 9.8 mm total length	<0.1 (1)
Dajidae *Notophryxus lateralis*	*Nd*	GC	Ectoparasitic castrator, large female 2.1 mm length × 1 mm width, and small female 1.8 mm length × 0.9 mm width (found in different individual hosts), ovoid body highly modified by parasitic mode life, orange-brown color, male 400 µm	<1 (1)

[a]Estimated prevalence
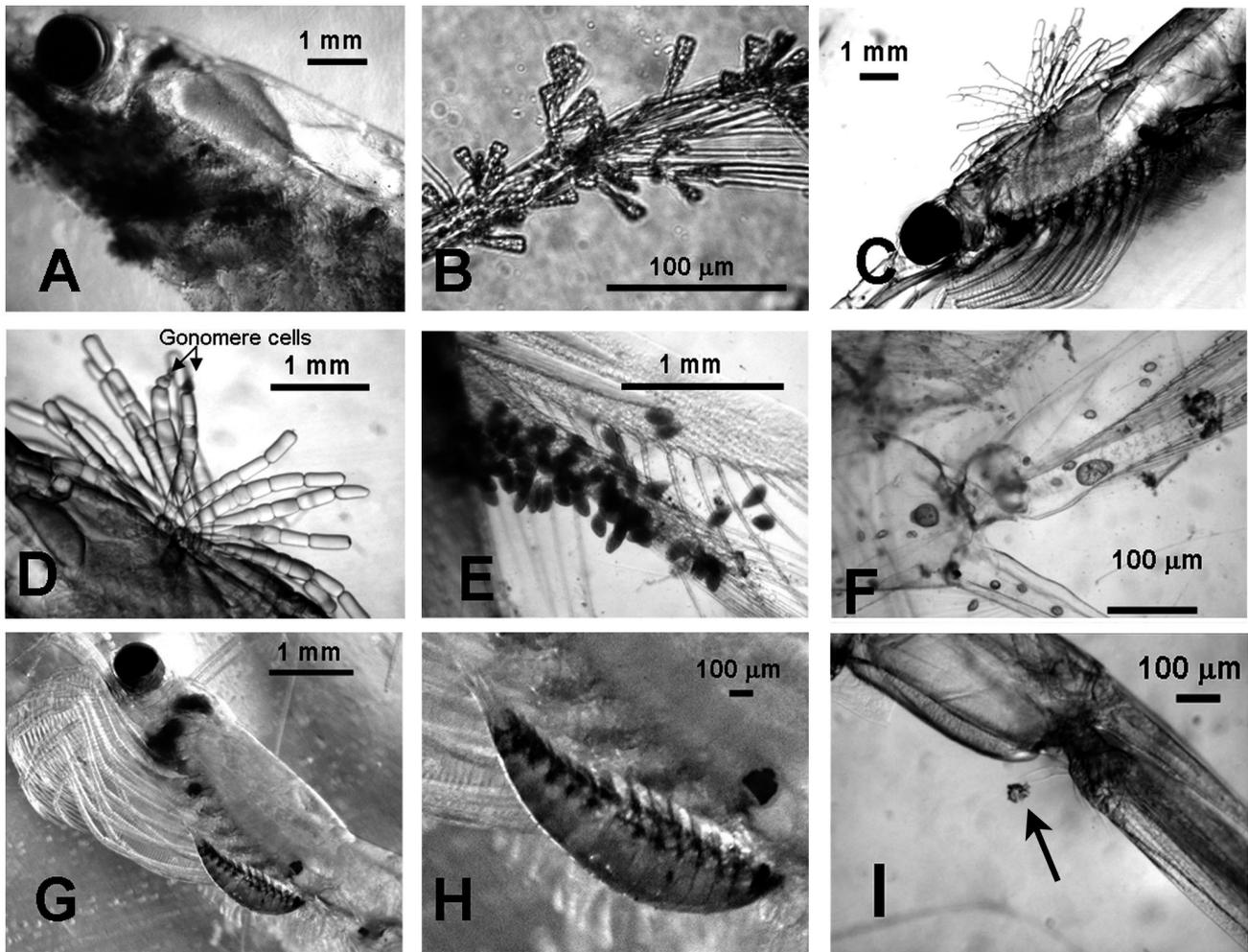
Fig. 3. *Nyctiphanes simplex* ectoparasites and mesoparasites collected off Bahía Magdalena and along the Gulf of California. (A,B) Epibiotic diatom *Licmophora* sp. (C,D) Ellobiopsidae *Thalassomyces fagei* (mesoparasite). (E,F) Multispecific assemblage of apostome ciliates of the family Foettingeriidae, (E) phoront stages attached to the setae of the appendages, antennae, telson, and uropods and (F) trophont stage swimming and feeding inside the molt, confirming its exuviotrophic nature. (G,H) unidentified Epicaridea cryptoniscus stage. (I) Epibiotic suctorian ciliate Ephelotidae attached to uropod (arrow)

because it is frequently observed that the parasite reaches sexual maturity (gonomere cells) in euphausiids. Infested *N. simplex* molted with a 4 d intermoult period, maintaining the parasite attached after the molt; we also observed additional infested euphausiids in the post-molt stage. We detected ellobiopsid infestation even in furcilia stages. This evidence suggests that *T. fagei* infestation does not inhibit the euphausiid's molting process and that once infested they maintain this parasite–host association for the rest of the host's life. The intensity of *T. fagei* infestation was usually 1 parasite per host, except an *N. simplex* specimen infested with 2 individuals of distinct sizes (750 and 400 μm). Observation of the host cleared with lactic acid showed that these were indeed 2 separate *T. fagei* parasites.

Exuviotrophic apostome ciliates

Unidentified encysted phoront ciliates were frequently observed attached to *Nyctiphanes simplex* and *Nematoscelis difficilis.* During multiple 48 h shipboard incubations, we observed how, after the euphausiid molted, the phoront ciliates excysted, transforming into a trophont stage that actively swam and fed inside the molt. Thus we experimentally confirmed that phoront cells are apostome exuviotrophic ciliates. They were the most frequent (higher prevalence rates) and widespread epibiotic organisms infesting *N. simplex* and *N. difficilis* (Table 2). In Bahía Magdalena, considerably higher prevalence rates were recorded in March and July than in December 2004 (Table 3). Phoront cells (40 × 20 μm) were mostly attached to
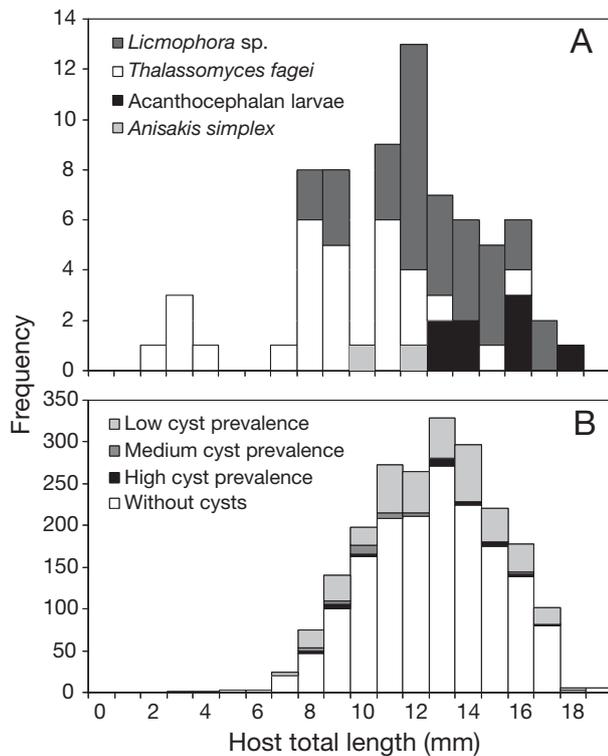
Fig. 4. *Nyctiphanes simplex*. Total length frequency distribution of *N. simplex* in Bahía Magdalena (March, July, December 2004) and along the west coast of Baja California (1987, 1993, 1994, and 1996). (A) *N. simplex* infested by epibiotic *Licmophora* sp., the ellobiopsid *Thalassomyces fagei*, an unidentified acanthocephalan larvae (acanthor, acantella, and cystacanth stages), and the nematode *Anisakis simplex*. (B) *N. simplex* without external apostome cysts and infested with low (<10 cysts pleopod^{-1}), medium (10–20 cysts pleopod^{-1}), and high (>20 cysts pleopod^{-1}) prevalence of apostome cysts of the family Foettingeriidae

setae of the pleopods, the site of highest intensities, but they were also observed attached to setae of periopods, antennae, uropods, and telsons. After the host molted, the phoront excysted and increased in size, transforming into a trophont cell changing from transparent to orange or yellow coloration (Fig. 3F). We detected several distinct phoront and trophont forms (morphology, coloration, and size), likely indicating that both euphausiids posses a multispecific assemblage of apostome exuviotrophic ciliates. Light microscopy unequivocally demonstrated the metamorphosis from an apostome tomite stage through transformation and metamorphosis to the pre-feeding stage (with 9 spiraling kineties) that, following criteria described by Landers et al. (2006), allowed us tentatively to identify them as exuviotrophic apostome ciliates of the family Foettingeriidae (Fig. 3E,F). Along the continental shelf of Bahía Magdalena, infested *N. simplex* ranged from 3 to 18 mm TL with an overall average prevalence per station of 29% (max. 88%) (Tables 2 & 3). Because *N.*

simplex molts every 5 to 7 d (Jerde & Lasker 1966, J. Gómez-Gutierrez unpubl. data), the average prevalence rate suggests a close association of infestation of phoronts with the intermolt period. The intensity of the phoront infestation from samples collected from Bahía Magdalena did not have any clear, positive association with *N. simplex* length (Fig. 4B, Table 3) or sex (data not shown), but a close association was found with the molt stage. Animals in post-molt stage were free of epibiotic ciliates, while euphausiids at intermolt and pre-molt stages had phoront ciliates.

Epicaridea isopoda larvae

At Bahía Magdalena (December 2004), we discovered an epicaridean ectoparasite in cryptoniscus stage larvae (1.3 mm length, Isopoda) attached to the ventral part of a *Nyctiphanes simplex* female (9.76 mm TL). This euphausiid was simultaneously infected with the endoparasitoid ciliate *Collinia* sp. apostome (with an orange and swollen cephalothorax) (Fig 3G,H). When *Collinia* ciliates killed the euphausiid, the isopod detached and abandoned the carcass. Another identical cryptoniscus stage larva was observed attached to the head of an *N. simplex* individual (Puerto Libertad, Gulf of California, 16 January 2007). The cryptoniscus isopods had 14 segments (typical of Epicaridea larvae), brown pigmented bodies, black eyes, oral sucking disks, and were larger (1.3 mm, Fig. 3H) than cryptoniscus (0.58 mm) and microniscus (0.26 mm) larvae of *Notophyxus lateralis* (Dajidae) that infest *Nematoscelis difficilis* (Field 1969). *N. lateralis* cryptoniscan larvae are transparent and without eyes (Field 1969, his Fig. 9a). Thus we do not think this was a *N. lateralis* cryptoniscus larval stage. Although their prevalence rates were low, it is clear that these isopods can easily detach during sampling and fixation processes, which could potentially underestimate their actual prevalence rates. Isopod larvae seem to be opportunistic rather than obligate euphausiid ectoparasites. These are the first observations of cryptoniscus larvae infesting euphausiids (previously known to infest only copepods and cephalopods).

Suctorida ciliates

We observed a *Nyctiphanes simplex* specimen infested with one epibiotic suctorian ciliate of the family Ephelotidae attached to the lower and anterior part of the uropod (27 July 2007) (Table 4, Fig. 3I). Because systematic observations of epibiotic protists attached in the external body was not carried out during the Gulf of California cruises, it is likely they were overlooked.

Table 3. Parasites of *Nyctiphanes simplex* (*Ns*) and *Nematoscelis difficilis* (*Nd*) detected over the continental shelf of Bahía Magdalena, Baja California Sur, Mexico, during March (19 stations, 1330 individuals), July (10 stations, 548 individuals), and December 2004 (12 stations, 322 individuals). The number of positive stations and number of individuals parasitized in relation to the total number of stations and number of euphausiids collected and observed per month, respectively, are shown in parentheses. Apostome ciliates were present in 31 out of 39 oceanographic stations; therefore, integrated prevalence per month is shown. nd: no data; F: female; M: male

Parasite	Host	Date	Positive/ total stations	No. of euphausiids Observed	No. of euphausiids Parasitized	Parasitized sex ratio (F:M)	Prevalence Per station	Prevalence Per month
Licmophora sp.	*Ns*	19 Mar	0.105 (2/19)	38	5	0.25	0.132	0.007 (9/1330)
		24 Mar		176	4	0.33	0.027	
		06 Jul	0.800 (6/10)	86	1	F	0.012	0.044 (24/548)
		06 Jul		30	1	M	0.033	
		06 Jul		38	2	1.00	0.056	
		06 Jul		13	2	F	0.154	
		09 Jul		116	20	4.00	0.172	
		13 Jul		39	2	1.00	0.051	
Thalassomyces fagei	*Ns*	22 Mar	0.263 (5/19)	107	2	M	0.019	0.005 (6/1330)
		24 Mar		176	1	M	0.006	
		28 Mar		230	1	M	0.004	
		29 Mar		109	1	F	0.009	
		31 Mar		26	1	F	0.038	
Foettingeriidae apostome ciliates	*Ns*	19–31 Mar	0.882 (15/17)	1336	304	0.86	0.00 to 0.88	0.307 (average)
		01–13 Jul	1.000 (10/10)	531	125	1.36	0.07 to 0.79	0.343 (average)
		05–15 Dec	0.545 (6/11)	317	63	1.95	0.00 to 0.55	0.165 (average)
	Nd	06 Jul	1.000 (1/1)	10	8	3.5	0.088	0.800 (1/10)
Collinia sp.	*Ns*	25–30 Mar	0.158 (3/19)	100	4	F	0.03 to 0.07	0.003 (4/1330)
		6–12 Jul	0.200 (2/10)	73	4	F	0.03 to 0.07	0.007 (4/548)
		5–15 Dec	0.545 (6/11)	172	39	F	0.01 to 0.40	0.123 (39/317)
Anisakis simplex	*Ns*	20 Mar	0.105 (2/19)	196	4	1.00	0.094	0.005 (6/1330)
		24 Mar		176	2	M	0.011	
		13 Jul	0.100 (1/10)	39	2	M	0.051	0.004 (2/548)
Tetrarhynchobothrium	*Ns*	14 Jul	0.100 (1/10)	39	1	M	0.05	0.001 (1/548)
Epicaridea cryptoniscus larval stage (Isopoda)	*Ns*	12 Dec	0.091 (1/11)	Unknown[a]	1	F	Unknown[a]	Unknown[a]
Total				4151	602		Average 14%	

[a]This oceanographic station had a massive collection of *N. simplex*; thus, the Epicaridea isopod dajid prevalence is presumed very low

However, our data suggest that suctorian prevalence and intensities rates of *N. simplex* are extremely low.

Nyctiphanes simplex endoparasites

We detected an endoparasitoid protist with moderate prevalence and high intensity rates, an acanthocephalan, and at least 5 distinct types of helminth endoparasites with usually low prevalence rates. In some cases, the helminth attained a total length comparable to their euphausiid hosts.

Apostomatida ciliates

Endoparasitoid apostome ciliates of the genus *Collinia* exclusively infected *Nyctiphanes simplex* off both coasts of the Baja California peninsula (Fig. 5A,B, Tables 2 & 3). The taxonomic description, life cycle, and ecophysiological aspects of this parasitoid infection will be published elsewhere (J. Gómez-Gutiérrez et al. unpubl. data). In Bahía Magdalena, *Collinia* infections were observed at 15 to 50% of the oceanographic stations sampled, with average prevalence rates per station ranging from 1 to 40% (average 10%). At Bahía Magdalena, higher infection rates were detected during the warmer season (December) when the North Equatorial Current advances northward, but no seasonal trend was detected in the Gulf of California (Table 3). Infected, live *N. simplex* were recognized by the beige (early infection) or intense orange (late infection phase) swollen cephalothorax (Fig. 5A). We observed all life stages known for the *Collinia* genus (phoront, trophont, tomont, and tomite); all had between 12 and 16 kineties, being morphologically distinct from any known *Collinia* species that infect euphausiids (Fig. 5B), such as *C. beringensis* (Capriulo & Small 1986) or *C. oregonensis* (Gómez-Gutiérrez et al. 2006). Shipboard observations showed that the host

Table 4. Parasites detected in *Nyctiphanes simplex* (*Ns*) and *Nematoscelis difficilis* (*Nd*) in the Gulf of California, Mexico, during November 2005 (24 stations), and January (35 stations) and July 2007 (36 stations). Number of positive stations and total number of samples collected per month are shown in parentheses. Parasites that were likely overlooked (small size or too abundant) are only mentioned at how many stations were actually observed. Stratified samples show depth of collection. nd: no data; F: female; M: male

Parasite	Host	Date	Positive/ total stations	No. of euphausiids parasitized	Parasitized sex ratio (F:M)
Thalassomyces fagei	*Ns*	25 Nov 05	0.083 (2/24)	3	F
		26 Jul 07	0.056 (2/36)	1	F
		1 Aug 07		1	M
	Nd	26 Jul 07	0.056 (2/36)	1	nd
	Nd	27 Jul 07	0.056 (2/36)	1	F
Suctoria Ephelotidae	*Ns*	27 Jul 07	1 positive station	1	nd
Foettingeriidae exuviotropic ciliates	*Ns*	25–27 Nov 05	3 positive stations	>100 per ind.	nd
		21–28 Jan 07	3 positive stations	Several	nd
	Nd	27 Jul 07	1 positive station	Several	nd
Collinidae sp.	*Ns*	24 Nov 05	0.042 (1/24)	2	F
		17 Jan 07	0.086 (3/35)	3	F
		19 Jan 07		1	F
		25 Jan 07		1	F
		19 Jul 07	0.083 (3/36)	1	F
		27 Jul 07		3	F
		29 Jul 07		1	F
Trematoda *Panoratrema* sp.	*Ns*	19 Jan 07	0.029 (1/35)	1	Unknown
Unidentified cestode (larvae) (Diphyllidea)	*Ns* (100 m)	27 Jul 07	0.028 (1/36)	1	F
Cestode *Echinobothrium* sp.	*Ns*	24 Jul 07	1 positive station	1	F
Nematoda *Anisakis simplex*		22 Dec 05	0.083 (2/24)	2	F
		19 Jul 07		1	M
Polymorphidae acanthocephala larvae	*Ns*	17 Jan 07	0.086 (3/35)	1	nd
		19 Jan 07		1	nd
		26 Jan 07		6	F
		31 Jul 07	0.308 (8/26)	6	nd
		19 Jul 07		2	F
		26 Jul 07		3 (100 m), 1 (75 m), 1 (surface)	F
		27 Jul 07		1 (100 m), 1 (150 m)	1.00
		28 Jul 07		2	1.00
		29 Jul 07		1 (25 m), 2 (75 m)	F
		1 Aug 07		1	nd
		2 Aug 07		2	F
Epicaridea cryptoniscus larval stage (Isopoda)	*Ns*	16 Jan 07	0.029 (1/35)	1	F (juvenile)
Notophyxus lateralis	*Nd*	22 Nov 05	0.042 (1/24)	4	F

euphausiid dies <3 d after infection, bursting and releasing a large number of transmission cells (tomites) confirming its parasitoid life cycle strategy (Fig. 5A). *Collinia* sp. is, without doubt, the most widespread parasitoid of the *N. simplex* population off both coasts of the Baja California peninsula.

Trematoda: Digenea (flatworms)

In January 2007, we detected a single *Nyctiphanes simplex* infected by a syncoeliid unencysted metacercaria (without the tail) tentatively identified as a member of the genus *Paronatrema*, particularly similar to *Paronatrema* sp. 2 (Shimazu & Kagei 1978, Shimazu 2006). Its specific identification cannot be established until its adult stage is obtained. The infection site of this *Paronatrema*-like endoparasite was in the posterior part of the mid-gut gland, apparently suspended in the krill hemocoel. The parasite had a characteristic trematode broad body and a relatively small excretory vesicle in the middle part of the body (Fig. 5C,D).

Cestodes

We identified 3 distinct types of Cestoda larvae. The first was a brown, bean-shaped, plerocercoid cestode with a blastocyst (1.34 × 0.86 mm) in the back of the mid-gland of a *Nyctiphanes simplex* male (16.36 mm
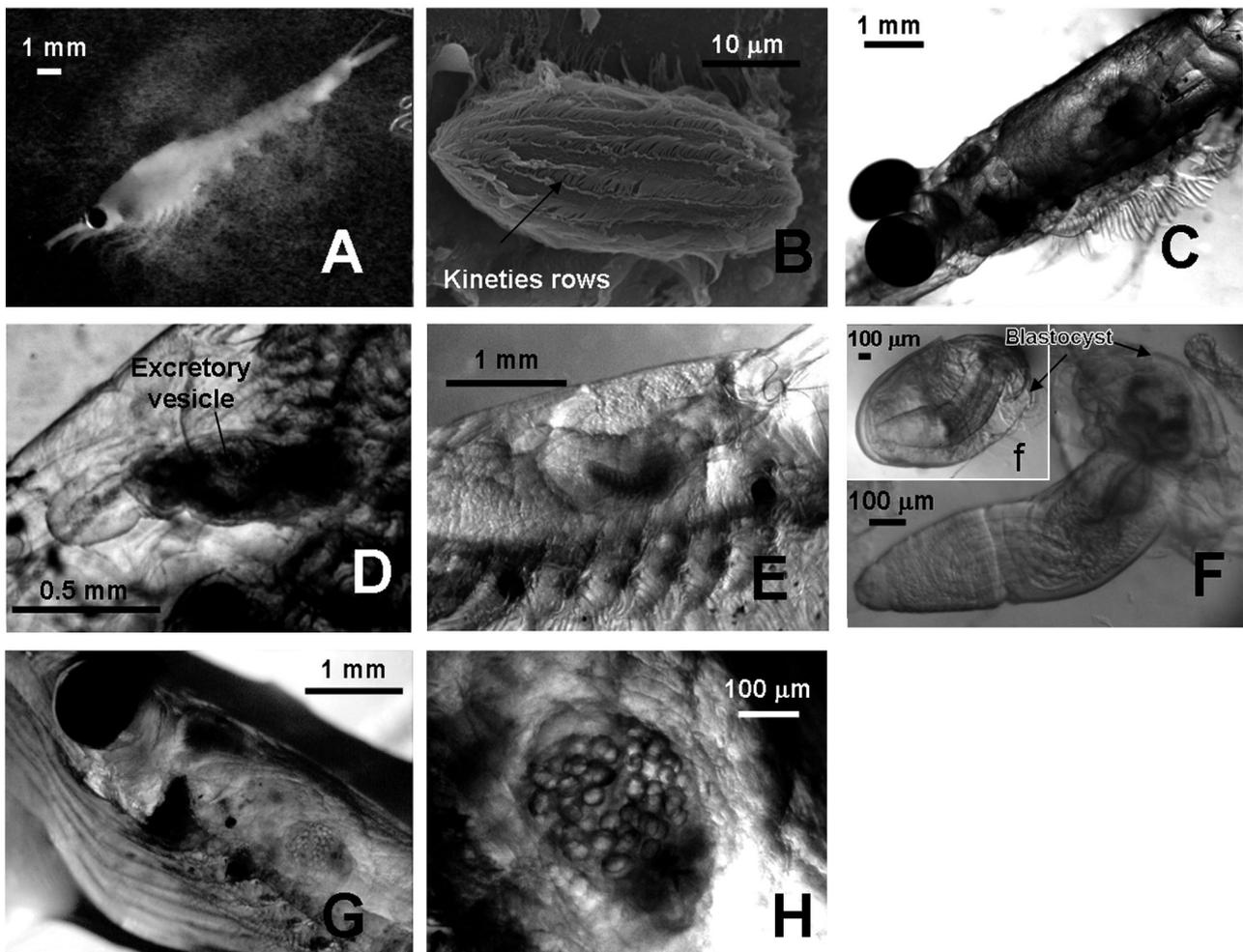
Fig. 5. (continued overleaf) *Nyctiphanes simplex* endoparasites collected off Bahía Magdalena and along the Gulf of California. (A,B) Apostomatida parasitoid ciliate of the genus *Collinia*. (C,D) Trematoda, likely *Paranotrema* sp. (E,F) *Tetrarhynchobothrium* sp. cestode plerocercoid with a blastocyst, (F,f) dissected blastocyst cleared with pure lactic acid. (G,H) Unidentified metacestode. (I,J) *Echinobothrium* sp. (Diphyllidea: Echinobothyriidae) cestode. (K,L) Third larval stage of *Anisakis* sp. (M) *Anisakis* anterior end showing prominent larval tooth (bt: boring tooth; ed: excretory duct; ep: excretory pore); and (N) Posterior end showing mucron (m). (O,P) Polymorphidae acanthocephalan larvae showing (O) the apical pole (ap) of the acanthor stage (ac) and the (P) cystocanth infective stage with the proboscis armed with hooks

TL) collected over the continental shelf of Bahía Magdalena (14 July 2004). Suspended inside the blastocyst was an embryo (1.14 × 0.3 mm) (Fig. 5E). The dissected specimen (immersed in pure lactic acid) showed the alveoli having a proboscis bulb that we identified as a plerocercoid of the genus *Tetrarhynchobothrium* (Order Trypanorhyncha, suborder Cystoidea) (Shimazu 1975a, 2006) (Fig. 5F, Tables 2 & 3).

The second cestode was an unidentified metacestode detected in the posterior part of the hepatopancreas having a spherical cluster (680 µm diameter) of cells with an external membrane (Fig. 5G,H, Table 2). The cells were transparent and it was not possible to identify this metacestode without further research (Fig. 5H).

The third type of cestode larvae was detected inside the posterior part of the cephalothorax of a *Nyctiphanes simplex* adult. This plerocercoid cestode was tentatively assigned to the genus *Echinobothrium* (Order Diphyllidea, Family Echinobothriidae), due to its slender and relatively short body and typical scolex bipartite, consisting of scolex proper and cephalic peduncle (Fig. 5I,J). The external morphology of the cestode resembled the 4 *Echinobothrium* species discovered from elasmobranchs in the Gulf of California (Tyler & Caira 1999, Tyler 2001). Because the specimen was not preserved, we were unable to observe the cephalic peduncle and apical hooks; therefore it was identified only to genus level. During shipboard incubations, the plerocercoid was discovered attached to
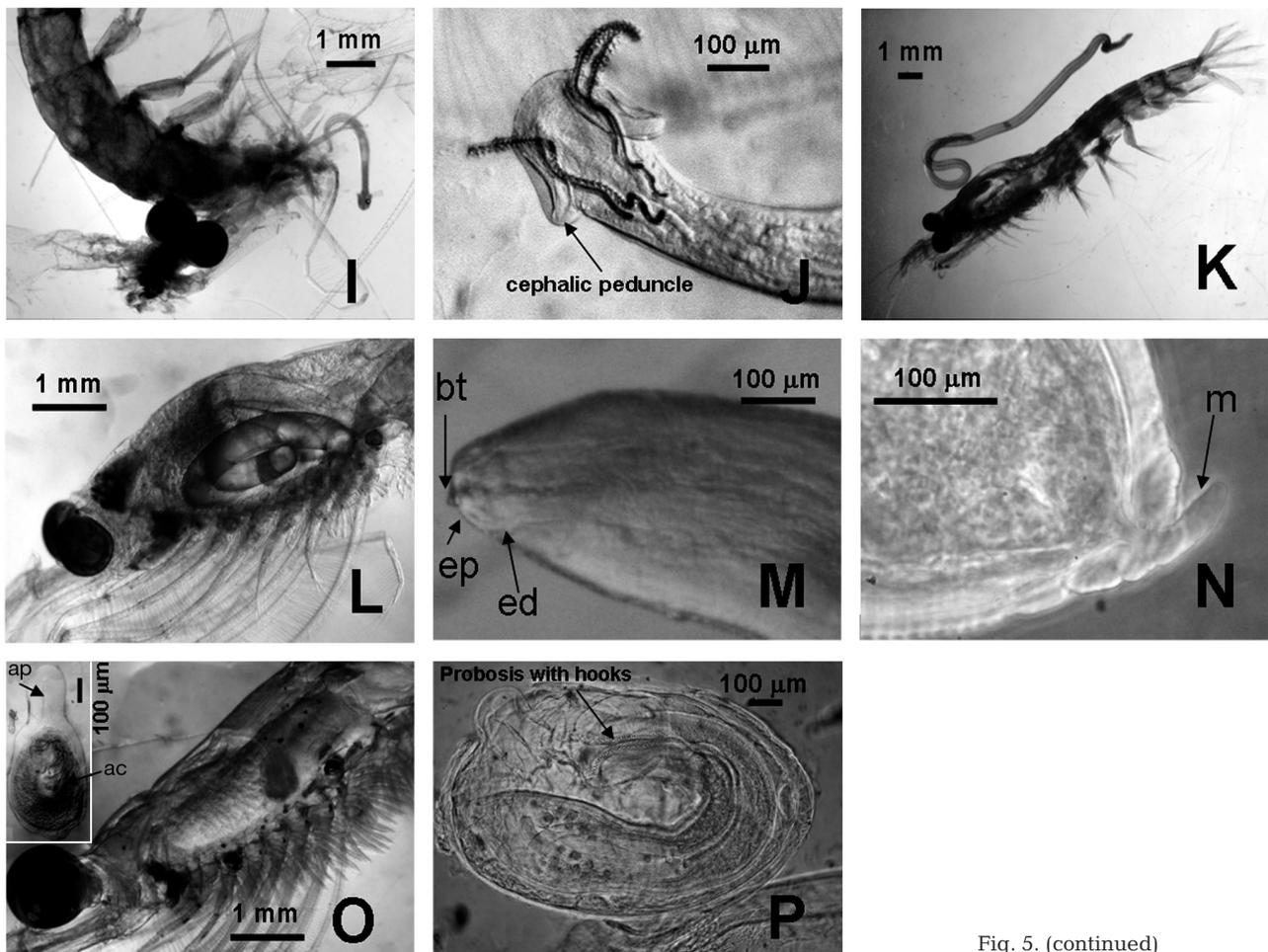
Fig. 5. (continued)

the anterior and central part of the cephalothorax of a dead krill, moving energetically in lateral whiplashes (Fig. 5I). Considering its slender and relatively small body size, it is likely that this type of cestode was overlooked in other *N. simplex* specimens (Table 3).

Nematoda: Ascariodea (round worms)

In the Gulf of California, a large ascaridoid larva (third larval stage, 12.1 × 0.4 mm) was detected coiled inside the cephalothorax and part of the abdomen of a single *Nyctiphanes simplex* exceeding the total length of the host (11.8 mm) (Fig. 5K,L). The specimen had a prominent boring tooth on the tip of the head, the excretory pore opened before the nervous ring (Fig. 5M), which had a distinct mucron (20 μm), and the distance from the anus to the tail was 100 μm (Fig. 5N). These morphological features, together with the observation that the specimen had neither intestinal caecum nor ventricular appendix, indicate that this is *Anisakis simplex* (Hurst 1984a,b, Smith 1983a,b). However, its body

width:length ratio was 3.3%, which is within the range of the genus *Pseudoterranova* sp. (Hurst 1984a) and considerably larger than that reported for *A. simplex* (2.14%, Hurst 1984a; and 1.72 to 1.78%, Shimazu & Oshima 1972). Due to the high *A. simplex*:euphausiid length ratio, this parasite must represent a considerable proportion of the host's biomass and energy. The dissection of the *N. simplex* hosts showed a reduced hepatopancreas and absence of gonads. The infected *N. simplex* was in pre-molt stage (D), but never molted onboard. Another *A. simplex* third larval stage specimen (9.4 mm TL) was collected along the west coast of the Baja California peninsula (February 1994), infecting an *N. simplex* of 10 mm TL.

Acanthocephala larvae

Brown Acanthocephala larvae (Family Polymorphidae) were frequently observed infecting exclusively *Nyctiphanes simplex,*, with intensities of 1 parasite per host, in different larval stages: acanthor (with long and

narrow apical pole, 955 × 450 µm, Fig. 5O) infecting a female of 9.3 mm TL; acanthella (moderate and broad apical pole, pear-shaped, 1155 × 645 µm) infecting females of 8.9 and 10.7 mm TL; and cystacanth (oval infective stage, 1125 × 705 µm) infecting a male of 11.2 mm TL. All larvae were detected in the posterior part of the hepatopancreas (mid-gland) surrounded by a thin acellular envelope that likely protects the developing larva from cellular responses of the euphausiid (Fig. 5O,P), resembling acanthocephalan larvae described by Shimazu (1975b). All the infected *N. simplex* females had gonads in oogonia (stage I). In the oceanographic station where we detected several fin whales feeding on a dense *N. simplex* swarm (Fig. 2A), we collected 6 krill specimens infected with acanthocephalan larvae in 3 distinct stages. Lactic acid-cleared larvae showed that all the specimens had progressive proboscis development (intruded), armed with 3 rows of hooks at each side that eventually will become the characteristic acanthocephalan proboscis. Acanthocephalan larvae were the most frequent and widespread endoparasite in *N. simplex* from the Gulf of California, particularly in July 2007 (Table 4). The larvae were coiled inside 3 membranes exhibiting slow movements, but sometimes actively migrating inside the carapace. They were never observed in the digestive tract.

Nematoscelis difficilis mesoparasites and ectoparasites

Ellobiopsidea

The mesoparasite *Thalassomyces fagei* was also observed infesting juvenile and adult *Nematoscelis difficilis* in the Gulf of California (July 2007) (Fig. 6A,B) and furcilia larvae along the west coast of the Baja California peninsula (October 1994, n = 3, 2 to 4 mm total length). A juvenile *N. difficilis* was infested with *T. fagei* in early development (budding) stage with dichotomous branching (Fig. 6B). This suggests that the ellobiopsids infest early in the euphausiid's life cycle and grow and reproduce as the euphausiids age. Thus *T. fagei* has a long-life parasitic association, castrating its host but not inhibiting the molting process. We observed *N. difficilis* at 2 stations with an unusual double infestation of adult *T. fagei* (attached to the first third of the cephalothorax, instead of the most common insertion site at the dorsal mid-part of the cephalothorax) and a mature Dajidae isopod female *Notophryxus lateralis* attached to the thoracic appendages and gills (Fig. 6A). This demonstrates that macroparasite castrators may change infestation patterns when on the same host.
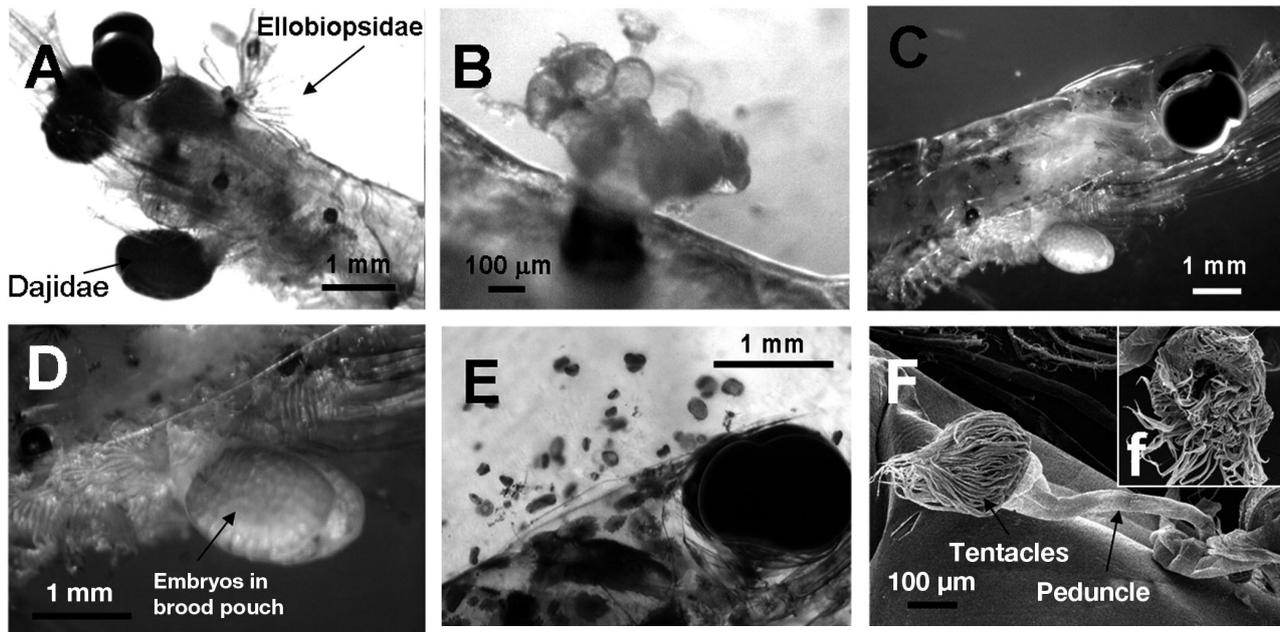

Fig. 6. *Nematoscelis difficilis* ectoparasites and mesoparasites collected along the (A–D) Gulf of California and (E,F) Oregon coast, USA. (A) Unusual double infestation of *N. difficilis* by ecto- and mesoparasitic host castrators: the Dajidae isopod *Notophryxus lateralis* attached to the periopods and gills and the ellobiopsid *Thalassomyces fagei* attached to the cephalothorax (mesoparasite). (B) Ellobiopsidae *T. fagei* in early infestation life stage on a juvenile *N. difficilis*. (C,D) Dajidae female castrator isopod *Notophryxus lateralis* attached to periopods and gills. (E,F) Epibiotic suctorian ciliate *Ephelota* sp.

Dajidae isopods

The Dajidae isopod *Notophryxus lateralis* was discovered infesting *Nematoscelis difficilis* at one station of each oceanographic cruise made in the Gulf of California. The average female isopod length was 2.1 mm and they infested large adult female *N. difficilis* with immature gonads (castration) with low prevalence rates per station (<1%) (Tables 2 & 4). This is the first record of *N. lateralis* in the central and northern part of the Gulf of California. Dissection of the females, embryos, and neotenic males confirmed the species identification (Field 1969). Live females have a pale orange coloration and the eggs in their brood pouch (80 μm diameter) were whitish. The posterior ventral part of the brood pouch has a small bright green spot (Fig. 6C,D). Each female had one male (400 μm) in their pouch. One ovigerous *N. lateralis* female had 661 embryos (average 160×90 μm).

Apostome ciliates

We observed exuviotrophic apostome ciliates of the family Foettingeriidae (40 μm length) infesting *Nematoscelis difficilis* off both coasts of Baja California with a prevalence of 80% at Bahía Magdalena (n = 10).

DISCUSSION

Without doubt no euphausiid species is invulnerable to parasitism. However, for parasites and, particularly, parasitoids, not all euphausiid species are suitable as hosts to facilitate parasite transmission, complete their life cycle, and/or sustain stable parasite populations due to restrictions in host body size, feeding habits, population density, daily vertical migration, and social behavior. According to Kuris et al. (1980, p. 571), 'individual host organisms are unequivocal 'islands' for parasites, where infection (or infestation) is equivalent to immigration of the parasite population and extinction represent the loss of a parasite population either from natural death of the parasites with short life spans, competition from other parasite populations, and/or host defensive responses'. Thus euphausiids may be regarded as islands for parasites at several levels of organization: (1) individuals, (2) swarms or schools, (3) populations, (4) euphausiid species, and perhaps (5) species assemblages with similar zoogeographic affinity. Here we addressed interspecific differences between 2 species with distinct swarming densities and behavior patterns.

Nyctiphanes simplex interacted with virtually all types of ectoparasites, mesoparasites, and endopara-

sites observed in the present study, except the ectoparasitic Dajidae *Notophryxus lateralis*, which to date has been detected exclusively in *Nematoscelis difficilis*. However, an unidentified epicaridean cryptoniscus stage isopoda infested *N. simplex*. Thus, *N. simplex* is exposed to all types of parasites discovered off both coasts of the Baja California peninsula. Even combining parasites of *N. difficilis* observed in Oregon (suctorian and Foettingeriidae ciliates) (Fig. 6E,F) (Field 1969, Landers et al. 2006) and the west coast of the Baja California peninsula (Foettingeriidae ciliates, ellobiopsiids, and Dajidae isopods), *N. simplex* has about 3 times the parasite diversity of *N. difficilis* (Tables 3 & 4). *N. simplex* was vulnerable to lethal *Collinia* sp. infections and usually had higher prevalence rates than *N. difficilis* of non-lethal parasites (Tables 2 to 4). For the coevolution of a stable parasite–host association, parasites require relatively accessible hosts with high replacement rates. We conclude that the considerably higher densities of *N. simplex* facilitate parasite transmission and, in the long term, endoparasites can complete their life cycle infecting preferentially, if not exclusively, euphausiid species that form dense swarms and have a wide distribution range and a high abundance throughout the year (Table 1).

Although individual parasite species generally have low prevalence rates, the cumulative rates of the entire parasite assemblage indicate that, on average, about 14% of the *Nyctiphanes simplex* population was infested or infected. This implies that parasites have a considerable effect on *N. simplex* populations (Tables 3 & 4). There is no evidence that *N. difficilis* (a species with oceanic affinity) temporally inhabit the epibenthic ecosystem during their daily vertical migrations. Conversely, because juveniles and adults of *N. simplex* typically spend <6 h near the benthos over the continental shelf during their daily vertical migrations (Robinson & Gómez-Gutiérrez 1998) and at the mouth of shallow bays (Gómez-Gutiérrez & Robinson 2006), this species is also vulnerable to epibiotic infestation of *Licmophora* diatoms, similar to *Nyctiphanes australis* (McClatchie et al. 1990), and trematode infections, which typically infect benthic mollusks as primary hosts (Shimazu 2006). These parasites likely associated with the benthic environment were not detected in the more oceanic *Nematoscelis difficilis*.

Several euphausiid species are known to form daytime surface swarms with densities of up to 7.7×10^6 ind. m^{-3} for *Meganyctiphanes norvegica* (Nicol 1986), 1.5×10^6 ind. m^{-3} for *Euphausia lucens* (Nicol et al. 1987), 2×10^4 to 6×10^4 ind. m^{-3} for *E. superba* (Hamner 1984, Hamner et al. 1983), and 100 to 1.5×10^6 ind. m^{-3} for *Nyctiphanes australis* (O'Brien 1988). This social behavior may significantly decrease the

NND and increase interaction between individuals that will facilitate parasite transmission. For example, *M. norvegica* in surface swarms exhibit a higher infestation rate (8 to 82%) by epibiotic suctorians in comparison with samples taken at depth offshore (2%) (Nicol 1984). About 70% of daytime surface *N. australis* swarms were infested with *Thalassomyces fagei* (prevalence rates <1 to 6%) (O'Brien 1988). Hamner (1984) observed that *E. superba* sometimes have whitish individuals (presumably parasitized) positioned behind the school unable to swim as fast as healthy individuals. Strand & Hamner (1990) reported *E. superba* exclusively forming schools, and the few solitary individuals they captured were almost always damaged and/or parasitized.

The low prevalence rates of parasites, castrators, and parasitoids detected in euphausiids in the present study (excepting epibiotic organisms with an apparently negligible effect on the host) indicate how several parasites have to deal with many intermediate and paratenic hosts to infest or infect their definitive hosts and complete their complex life cycles. In other words, population density and swarming behavior of the hosts may control parasite population dynamics. We propose that most parasites, particularly endoparasites, depend on and must be closely associated with highly abundant and widely distributed euphausiid host species that are available throughout the year to maintain long-term, stable populations. We demonstrated that *Nyctiphanes simplex*, which has considerably higher densities (6 to 22 times greater) and a more compact, dense, swarming behavior than *Nematoscelis difficilis* (Table 1, Fig. 2A,B), facilitates a coevolutionary association with a more diverse assemblage of ecto-, meso-, and endoparasites. This does not mean parasites cannot infest or infect *N. difficilis* (or other euphausiid species with low abundance); however, the likelihood of *N. difficilis* becoming parasitized must be considerably lower. For example, Sporozoa gregarines and Dajidae isopods have been detected in *Nematoscelis megalops*, *N. difficilis*, and *Nematoscelis* spp. (Field 1969, Théodoridès & Desportes 1975), and trematodes and cestodes also infect several *Nematoscelis* species (Sars 1885, Shimazu 2006).

Although several of the parasites in the present study were not identified to species level, each type of ectoparasite, mesoparasite, and endoparasite likely represents distinct taxonomic groups that have their own morphological, biological, pathological, and life cycles pattern, and the actual diversity reported here is probably underestimated. A multispecific Foettingeriidae apostome ciliate assemblage was discovered in 6 euphausiid species from the Oregon coast (Landers et al. 2006), and a similar assemblage likely occurs in our area of study. We report the first observation of an Epi-

caridea isopod (cryptoniscus stage larvae) attached to a euphausiid, confirming Field's (1969) hypothesis that cryptoniscus stage isopods can infest euphausiids during their life cycle.

Our main conclusion is that euphausiid species that attain considerably large biomasses and tend to form compacted swarms are exposed to higher infestation and infection rates and may have a resultant low body condition or high mortality rates due to parasitism. *Euphausia pacifica*, an abundant, densely swarming, North Pacific euphausiid, is also associated with a diverse ecto-, meso-, and endoparasite assemblage (Shimazu & Oshima 1972, Mooney & Shirley 2000, Gómez-Gutiérrez et al. 2003, 2006, 2009, Smith & Snyder 2005, Landers et al. 2006, Shimazu 2006). Species with relatively small biomass and/or with a tendency to form diffuse swarms off both coasts of the Baja California peninsula simply do not produce the host density threshold required for many parasites to successfully transmit, reproduce, and complete their life cycles. In our area of study we did not detect parasites or parasitoids in the relatively few specimens collected of tropical euphausiids (*Euphausia eximia*, *E. distinguenda*, and *E. tenera*), but they must be studied in the near future, particularly in the mouth of the Gulf of California and Eastern Tropical Pacific, where such species dominate the euphausiid's community structure. Host density seems to be particularly critical for endoparasites like the parasitoid *Collinia* spp. ciliates and Platyhelminthes, so far exclusively observed in *Nyctiphanes simplex*. One remarkable ecological and evolutionary trend is that the parasitoid ciliates *Collinia* spp. infect only highly abundant euphausiids (definitive hosts) in the Bering Sea (*Thysanoessa inermis*) (Capriulo & Small 1986) and off the Oregon–California coast (*E. pacifica*, *T. spinifera*, and *T. gregaria*) (Gómez-Gutiérrez et al. 2003, 2006). *N. simplex* is apparently the only euphausiid species from the northwest of Mexico that has the biological capabilities to attain a sufficiently large population, biomass, and aggregation density to enhance and sustain *Collinia* spp. parasitoid populations.

To our knowledge, this is the first observation of cestode, tramatode, nematode, and acanthocephalan larvae infecting euphausiids in the northeast Pacific Ocean. We detected at least 3 distinct types of cestodes. In general, cestode taxonomy, life cycle, and biology is highly fragmented, but it is better studied in euphausiid species from the Northwest Pacific (Shimazu 1975a, 2006, Shimazu & Amano 2001). We found a trematode, tentatively identified as *Paronatrema* sp., infecting *Nyctiphanes simplex*, previously reported as unidentified metacercaria infecting *Euphausia pacifica* in the East China Sea (Shimazu & Kagei 1978). The life cycle of tetrarhynchobothriids is not known, but

Shimazu (1975a) reported a plerocercoid *Tetrarhyncho-bothrium* sp. from *E. similis*. We detected *Tetrarhyn-chobothrium* and *Echinobothryum* cestode larvae infecting *N. simplex*. Trematodes of these genera are known to infect elasmobranch fishes in the Gulf of California (Tyler & Caira 1999, Tyler 2001). It is likely that small pelagic fish could be intermediate or paratenic hosts to these trematodes which eventually infect elasmobranchs. The mobulid ray *Mobula japonica*, which feeds exclusively on *N. simplex* in the Gulf of California, is occasionally infected with unidentified try-panorhynch cestodes within their pleurperitoneal cavity (Notarbartolo-di-Sciara 1988).

Laboratory observations of live *Anisakis* sp. first and second larval stages indicate that molt inside the egg and newly hatched third-stage larvae apparently are not infective to adult euphausiids (Shimazu & Amano 2001). Shimazu & Amano (2001) suggested that L3 may be infective for younger euphausiids and/or the eu-phausiids become infected via copepods as paratenic hosts. In the Gulf of California, *Nyctiphanes simplex* may be a significant vector of helminth transmission of third larval stage but abundant copepods and am-phipods from the Gulf of California may also be impor-tant as they have been detected as relevant intermedi-ate hosts of nematodes (Klimpel et al. 2004). *A. simplex*, like most gut parasites, has a very low level of host specificity and has been reported in at least 200 fish species, 25 cephalopods, 53 mammals (Klimpel et al. 2004), and at least 14 euphausiid species (Smith & Sny-der 2005) because they enter a host via predation. This lack of specificity has been interpreted as spreading out the risk of failure to complete their life cycles (Marcogliese 1995). Both parasitoids and castrators have the ability to decrease host fitness to zero (Kuris 1974), imposing considerably pressure in a population level if they have elevated prevalence rates. Adult helminthes and acanthocephalids spawn and release their eggs in whale feces, and copepods and euphausi-ids may act as true intermediate hosts. The prevalence rates of helminth castrators of euphausiids are typically too low (typically <1/4000) to be considered a threat at the euphausiid population level. However, because most predators ingest large quantities of euphausiids, krill are relevant vectors (intermediate or paratenic hosts) that promote high prevalence rates and intensi-ties in higher trophic level organisms (final parasite's hosts) (Marcogliese 1995). For example, the blue whale *Balaenoptera musculus* is a species that feeds almost exclusively on swarms of *N. simplex* and *Nematoscelis difficilis* during their winter–spring incursion on the Gulf of California, and the fin whale *B. physalus* feeds on euphausiids and small pelagic fish schools through-out the year (Gendron 1992, Del Ángel-Rodríguez 1997, Ladrón de Guevara et al. 2008). Analysis of blue whale and fin whale feces provides evidence of infec-tions with adult acanthocephala (9 to 17 mm, family Polymorphidae, likely of the genera *Bolbosoma* or *Corynosoma*) and their eggs with prevalence rates of 22% (n = 27) for blue whales and 29% (n = 7) for fin whales and eggs of Ascariodea helminths (Nematoda: Anisakidae) and cestodes *Diphyllobothrium* spp. (Ces-toda, Diphyllobothriidae) (Gendron & Urban 1993, Rocha-Gosselin 2009). We detected the 3 acantho-cephalan larval stages (acanthor, acanthella, and cysto-canth) infecting *N. simplex*, providing strong evidence that *N. simplex* is a significant krill species vector for whale acanthocephalan infection in the Gulf of Califor-nia. Helminth eggs were found in 57% of blue whale feces, compared to 29% for fin whales, suggesting that the exclusively krill-based blue whale diet may pro-mote higher endoparasitic prevalence rates (Rocha-Gosselin 2009). Acantocephalan and helminth infec-tions in euphausiids occur at extremely low prevalence rates (Sars 1885, Lindley 1977, Shimazu 1975b, Smith 1983a,b, Marcogliese 1995). However, *N. simplex* are consumed in massive quantities by baleen whales in the Gulf of California (630 to 960 kg d^{-1}, equivalent to 3–4 × 10^8 individuals) (Tamura & Ohsumi 1998, J. Del Ángel-Rodríguez unpubl. data). Thus, even with extremely low prevalence rates, *N. simplex* may represent a relevant infection vector that explains the relatively high pre-valence rates in cetacean definitive hosts.

The links between intermediate and definitive hosts throughout the parasite life cycles in the Gulf of Cali-fornia need to be investigated. The parasite assem-blage of the euphausiid population may act as primary intermediate hosts of helminth and acanthocephalan endoparasites, significant infection vectors to higher trophic levels (intermediate and/or definitive hosts), with potential health effects for humans that feed on other intermediate hosts (e.g. Anisakiasis). Addition-ally, *Collinia* spp. ciliates may represent a relevant predator that can consume euphausiids at rates similar to other predators (e.g. *Mobula* or *Balaenoptera*), and epibiotic exuviotrophic apostome ciliates may have a role in nutrient cycling as the discarded molts sink to deeper waters. All this indicates how parasites of abundant pelagic species can play multiple ecological roles in the trophic web of the northwestern coast of Mexico. Because of their high prevalence rates, histophagous behavior, and short life cycles (Gómez-Gutiérrez et al. 2003, 2006), *Collinia* spp. have the most potential to cause epizootic events in *Nyctiphanes sim-plex*. Although typically each type of parasite affects a small fraction of the euphausiid population (typically <1%) on both coasts of the Baja California peninsula, they can pose a considerable threat to the health, spe-cies diversity, and population dynamics of resident euphausiid species.

LITERATURE CITED

Aguilar-Méndez MJ (2008) Diversidad bacteriana asociada al parasitoidismo de ciliados *Collinia* spp., en eufáusidos del Golfo de California. MS thesis. Centro de Investigaciones Biológicas del Noroeste, La Paz (with English abstract)

Boschma H (1948) Sur les organelles d'absorption chez une espèce d'*Amallocystis* (Protozoa, Ellobiopsidae). Proc Kon Ned Akad Wetensch Amst 51:446–449

Brinton E (1962) The distribution of Pacific euphausiids. Bull Scripps Inst Oceanogr 8:51–269

Brinton E, Townsend AW (1980) Euphausiids in the Gulf of California — the 1957 cruises. Calif Coop Ocean Fish Invest Rep 21:211–236

Bucklin A, Wiebe PH, Smolenack SB, Copley NJ, Clarke ME (2002) Integrated biochemical, molecular, genetic, and bioacoustical analysis of mesoscale variability of the euphausiid *Nematoscelis difficilis* in the California Current. Deep-Sea Res II 49:437–462

Capriulo GM, Small EB (1986) Discovery of an apostome ciliate (*Collinia beringensis* n. sp.) endoparasitic in the Bering Sea euphausiid *Thysanoessa inermis*. Dis Aquat Org 1:141–146

Cornejo-De Gonzalez M, Antezana TJ (1980) Nuevas localidades y huéspedes para *Thalassomyces fagei* (Bochma) [(Ellobiopsidae, Protista, (Insertae sedis))]. Acta Oceanogr Pacífico 1:74–81

De Silva-Dávila R, Palomares-García R, González-Rodríguez E, Maldonado-López V (2004) Varamiento de *Nematoscelis difficilis* en la Bahía de La Paz, Baja California Sur, México. In: Hendricks ME (ed) Contributions to the study of East Pacific crustaceans. Universidad Nacional Autónoma de México 3:89–97

Del Ángel-Rodríguez J (1997) Hábitos alimentarios y distribución espacio-temporal de los rorcuales común (*Balaenoptera physalus*) y azul (*Balaenoptera musculus*) en la Bahía de La Paz, B.C.S., México. MS thesis, Centro Interdisciplinario de Ciencias Marinas, La Paz (with English abstract)

Field LH (1969) The biology of *Notophryxus lateralis* (Isopoda: Epicaridea) parasitic on the euphausiid *Nematoscelis difficilis*. J Parasitol 55:1271–1277

Gendron D (1992) Population structure of daytime surface swarms of *Nyctiphanes simplex* (Crustacea: Euphausiacea) in the Gulf of California, Mexico. Mar Ecol Prog Ser 87:1–6

Gendron DL, Urban JR (1993) Evidence of feeding by humpback whales (*Megaptera novaeangliae*) in the Baja California breeding ground, México. Mar Mamm Sci 9:76–81

Gómez JG (1995) Distribution patterns, abundance and population dynamics of the euphausiids *Nyctiphanes simplex* and *Euphausia eximia* in the west coast of Baja California, México. Mar Ecol Prog Ser 119:63–76

Gómez-Gutiérrez J, Robinson CJ (2006) Tidal current transport of epibenthic swarms of the euphausiid *Nyctiphanes simplex* in a shallow subtropical bay on Baja California peninsula, México. Mar Ecol Prog Ser 320:215–231

Gómez-Gutiérrez J, Peterson WT, De-Robertis A, Brodeur R (2003) Mass mortality of krill caused by parasitoid ciliates. Science 301:339

Gómez-Gutiérrez J, Peterson WT, Morado JF (2006) Discovery of a ciliate parasitoid of euphausiids off Oregon, USA: *Collinia oregonensis* n. sp. (Apostomatida: Colliniidae). Dis Aquat Org 71:33–49

Gómez-Gutiérrez J, Kawaguchi S, Nicol S (2009) Ectobiotic suctorians and enigmatic ecto- and endoparasitoid dinoflagellates of euphausiid eggs (Euphausiacea) off Oregon, USA. J Plankton Res 31:777–786

Gómez-Gutiérrez J, Tremblay N, Martínez-Gómez S, Robinson CJ, Del Ángel-Rodríguez J, Rodríguez-Jaramillo C, Zavala-Hernández C (2009) Biology of the subtropical sacspawning euphausiid *Nyctiphanes simplex* in the northwestern seas of Mexico: vertical and horizontal distribution patterns and seasonal variability of brood size. Deep-Sea Res II (in press), doi: 10.1016/j.dsr2.2009.10.010

Hamner WM (1984) Aspects of schooling of *Euphausia superba*. J Crustac Biol 4:67–74

Hamner WM, Hamner PP, Strand SW, Gilmer RW (1983) Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. Science 220:433–435

Hamner WM, Hamner PP, Obst BS (1989) Field observations on the ontogeny of shooling of *Euphausia superba* furciliae and its relationship to ice in Antarctic waters. Limnol Oceanogr 34:451–456

Hurst RJ (1984a) Identification and description of larval *Anisakis simplex* and *Pseudoterranova decipiens* (Anisakidae: Nematoda) from New Zealand waters. NZ J Mar Freshw Res 18:177–186

Hurst RJ (1984b) Marine invertebrate hosts of New Zealand Anisakidae (Nematoda). NZ J Mar Freshw Res 18:187–196

Jerde CW, Lasker R (1966) Molting of euphausiid shrimps: shipboard observations. Limnol Oceanogr 11:120–124

Klimpel S, Palm HW, Ruckert S, Piatkowski U (2004) The life cycle of *Anisakis simplex* in the Norwegian Deep (northern North Sea). Parasitol Res 94:1–9

Komaki Y (1970) On the parasitic organisms in a krill, *Euphausia similis*, from Suruga Bay. J Oceanogr Soc Jpn 26:283–295

Kuris AM (1974) Trophic interactions: similarity of parasitic castrators to parasitoids. Q Rev Biol 49:129–148

Kuris AM, Blaustein AR, Alió JJ (1980) Hosts as islands. Am Nat 116:570–586

Ladrón de Guevara PP, Lavaniegos BE, Heckel G (2008) Fin whales (*Balaenoptera physalus*) foraging on daytime surface swarms of the euphausiid *Nyctiphanes simplex* in Ballenas Channel, Gulf of California, Mexico. J Mammal 89:559–566

Landers SC, Gómez-Gutiérrez J, Peterson WT (2006) *Gymnodinioides pacifica*, n. sp., an exuviotrophic ciliated protozoan (Ciliophora, Apostomatida) from euphausiids of the Northeastern Pacific. Eur J Protistol 42:97–106

Lindley JA (1977) Continuous plankton records: the distribution of the Euphausiacea (Crustacea: Malacostraca) in the North Atlantic and the North Sea, 1966–1967. J Biogeogr 4:121–133

Lindley JA (1978) Continuous plankton records: the occurrence of apostome ciliates (Protozoa) on Euphausiacea in the North Atlantic Ocean and North Sea. Mar Biol 46:131–136

Marcogliese DJ (1995) The role of zooplankton in the transmission of helminth parasites to fish. Rev Fish Biol Fish 5:336–371

Mauchline J (1980) The biology of mysids and euphausiids. In: Blaxter JHS, Russell FS, Younge M (eds) Advances in marine biology, Book 18. Academic Press, San Diego, CA, p 373–681

Mauchline J, Fisher LR (1969) The biology of the euphausiids. In: Russell, FS, Younge M (eds) Advances in marine biology, Book 7. Academic Press, San Diego, CA

McClatchie S, Kawachi R, Dalley DE (1990) Epizoic diatoms on the euphausiid *Nyctiphanes australis*: consequences for gut-pigment analyses of whole krill. Mar Biol 104: 227–232

Mooney JR, Shirley TC (2000) New hosts, prevalence, and density of the ellobiopsid parasite *Thalassomyces fagei* on euphausiids in Prince William Sound. Alaska. J Crustac Biol 20:320–325

Nicol S (1984) *Ephelota* sp. a suctorian found on the euphausiids *Meganyctiphanes norvegica*. Can J Zool 62:744–746

Nicol S (1986) Shape, size and density of daytime surface swarms of the euphausiid *Meganyctiphanes norvegica* in the Bay of Fundy. J Plankton Res 8:29–39

Nicol S, James A, Pitcher G (1987) A first record of daytime surface swarming by *Euphausia lucens* in the Southern Benguela region. Mar Biol 94:7–10

Notarbartolo-di-Sciara G (1988) Natural history of the rays of the genus *Mobula* in the Gulf of California. Fish Bull 86:45–66

O'Brien DP (1988) Surface schooling behaviour of the coastal krill *Nyctiphanes australis* (Crustacea: Euphausiacea) off Tasmania, Australia. Mar Ecol Prog Ser 42:219–233

Ohtsuka S, Nagasawa K, Gejima K (2000) Review of parasites of marine zooplankton. Bull Plankton Soc Jpn 47:1–16 (in Japanese with English abstract)

Rakusa-Suszczewski S, Filcek K (1988) Protozoa on the body of *Euphausia superba* Dana from Admiralty Bay (the South Shetland Island). Acta Protozool 27:21–30

Robinson CJ, Gómez-Gutiérrez J (1998) Daily vertical migration of dense scattering layers related to shelf-break area in the northwest coast of Baja California, México. J Plankton Res 20:1679–1697

Rocha-Gosselin A (2009) Caracterización de la carga microbiana y parasitaria de tres especies de misticetos en las costas de la península de Baja California, México. MS thesis, Centro Interdisciplinario de Ciencias Marinas (IPN), La Paz (with English Abstract)

Sars GO (1885) Report on the Schizopoda collected by H.M.S. Challenger, during the years 1873–1876. In: Thomson CW, Murray J (eds) Report on the scientific results of the voyage of H.M.S. Challenger, during the years 1873–76. Zoology 37. 13:1–228

Shields JD, Gómez-Gutiérrez J (1996) *Oculophryxus bicaulis* a new genus and species of Dajid isopod parasitic on the euphausiid *Stylocheiron affine* Hansen. Int J Parasitol 26:261–268

Shimazu T (1975a) On the parasitic organisms in a krill, *Euphausia similis*, from Suruga Bay. V. Larval cestodes. Jpn J Parasitol 24:122–128 (in Japanese with English Abstract)

Shimazu T (1975b) Some cestode and acanthocephalan larvae from euphausiid crustaceans collected in the northern North Pacific Ocean. Bull Jpn Soc Sci Fish 41:813–821 (in Japanese with English Abstract)

Shimazu T (2006) Trematodes and cestodes parasitic in euphausiids. Bull Plankton Soc Jpn 53:45–53 (in Japanese with English Abstract)

Shimazu T, Amano M (2001) *Anisakis simplex* (Nematoda:Anisakidae): Newly hatched third-stage larvae are not infective to adults of the euphausiid crustacean *Euphausia pacifica*. Otsuchi Mar Sci 26:40–45

Shimazu T, Kagei N (1978) A metacercaria of the genus *Paronatrema* (Trematoda; Syncoelliidae) parasitic in *Euphausia pacifica* (Crustacea; Euphausiidae) from the East China Sea. Zool Mag 87:158–161

Shimazu T, Oshima T (1972) Some larval nematodes from euphausiid crustaceans. In: Takenouti AY (ed) Biological oceanography of the Northern North Pacific Ocean. Idemitsu Shoten, Tokyo, p 403–409

Smith JW (1983a) Larval *Anisakis simplex* (Rudolphi, 1809, det. Krabbe, 1878) and larval *Hysterothylacium* sp. (Nematoda: Ascaridoidea) in euphausiids (Crustacea: Malacostraca) in the North-East Atlantic and northern North Sea. J Helminthol 57:167–177

Smith JW (1983b) *Anisakis simplex* (Rudolphi, 1809, det. Krabbe, 1878) (Nematoda: Ascaridoidea): morphology and morphometry of larvae from euphausiids and fish, and a review of the life-history and ecology. J Helminthol 57:205–224

Smith JW, Snyder JM (2005) New locality records for third-stage larvae of *Anisakis simplex* (*sensu lato*) (Nematoda: Ascaridoidea) in euphausiids *Euphausia pacifica* and *Thysanoessa raschii* from Prince William Sound, Alaska. Parasitol Res 97:539–542

Strand SW, Hamner WM (1990) Schooling behavior of Antarctic krill (*Euphausia superba*) in laboratory aquaria: reactions to chemical and visual stimuli. Mar Biol 106:355–359

Tamura T, Ohsumi S (1998) Increasing competition between fisheries and whales. Japan's whale research in the Western North Pacific (JARPN II). Fisheries Agency, Tokyo, p 130–171

Tarling GA, Cuzin-Roudy J (2008) External parasite infestation depends on moult-frequency and age in Antarctic krill (*Euphausia superba*). Polar Biol 31:121–130

Théodoridès J (1989) Parasitology of marine zooplankton. Adv Mar Biol 25:118–159

Théodoridès J, Desportes O (1975) Sporozoaires d'Invertébrés pélagiques de Villefrenche-sur-mer (étude descriptive et faunistique). Protistologica 11:205–220

Tremblay N (2008) Variación estacional de los indicadores de estrés oxidativo asociada a la migración vertical de los eufáusidos subtropicales del Golfo de California. Tesis de Maestría. Centro Interdisciplinario de Ciencias Marinas, La Paz, BCS (with English Abstract)

Tyler GA (2001) Diphyllidean cestodes of the Gulf of California, México with descriptions of two new species of *Echinobothrium* (Cestoda: Diphyllidea). J Parasitol 87:173–184

Tyler GA, Caira JN (1999) Two new species of *Echinobothrium* (Cestoidea: Diphyllidea) from myliobatiform elasmobranchs in the Gulf of California, México. J Parasitol 85:327–335