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Research

Host-epibiont relationship between calanoid copepods and suctorian ciliates in the northern North Pacific Ocean

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Abstract: This study investigated the host-epibiont relationship between calanoid copepods and suctorian ciliates collected widely from the northern North Pacific Ocean. Mid- and deep-water adult female calanoids without dormant stages were found to be infested with suctorians, probably because of their larger size, longer intermolt duration and longevity in comparison to males and surface water species. A total of 259 calanoids belonging to sixteen species were infested with five suctorian species. Among them, *Candacia columbiae*, *Gaetanus minutus*, *Lucicutia bicornuta*, *Metridia similis*, *Pleuromamma scutullata*, and *Racovitzanus antarcticus* were reported to be infested with suctorians for the first time in the present study. *Ephelota coronata* infested only *Metridia pacifica* and displayed a strong host preference, whereas the other suctorians displayed a weaker host preference. Any suctorian species that infested *Metridia pacifica* and *M. similis* attached almost exclusively to their urosome. Suctorians might avoid or could not stay attached to the anterior parts of these fast-swimming copepods. The attachment sites of *Actinocyathula pleuromammae* and *Paracineta gaetani* extended to the anterior part of the copepod body as the number of attached suctorians increased, suggesting they were obliged to attach to suboptimal parts that were exposed to faster flow speed.

Key words: calanoid copepods, epibiosis, North Pacific, suctorian ciliates

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Introduction

Epibiotic relationships involving planktonic crustaceans as basibionts (i.e. hosts) are widespread in marine environments and include a variety of organisms as epibionts, including bacteria, algae, and ciliates (Utz & Coats 2005). The body surface of the crustaceans is one of the few hard surfaces available for these small and soft-bodied organisms to colonize. Copepods are probably the most numerous multicellular organisms on Earth and have a major influence in the design and functioning of marine ecosystems (Mauchline 1998). Suctorian ciliates are one of the most species-rich groups among Ciliophora and are known to infest various marine organisms, including plants and animals (Dovgal 2002). Their life cycle consists of a free-swimming larval stage (swarmers) that possesses locomotor ciliature, crawling swarmers that lack ciliature [e.g., genus *Rhabdophrya* (Chatton & Collin, 1910)] (Dovgal 2002), or even crawling swarmers that possess ciliature (*Ephelota gigantea* Noble, 1929) (Noble 1929, Kobayashi et al. 2011). The swarmer attaches to a substrate suitable for settlement and undergoes metamorphosis, which involves the resorption of the ciliature and development of the stalk, lorica (if present) and tentacles (Dovgal 2002). Fernandez-Leborans & Tato-Port (2000) examined previous reports and showed that 46 copepod species have been found to be infested with 39 species of suctorian ciliates. A study on copepods in the coastal waters of the Gulf of Maine revealed that adult female *Metridia lucens* Boeck, 1864 was found to be heavily infested with suctorians (Sherman & Schaner 1965). Additionally, the seasonal

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change in infestation rate and attachment sites of suctorians on copepods in the North Pacific Ocean were also studied (cf. Yamaguchi & Ikeda 2001, Yamaguchi 2006).

However, extensive studies on the epibiotic relationship between suctorians and a taxonomic group of host organisms with different behavioral and ecological characteristics are quite limited. A good example of such studies is nematodes, which are the most abundant, ubiquitous and diverse meiofaunal group and serve as ideal basibionts for many suctorians (cf. Baldrighi et al. 2020). Baldrighi et al. (2020) compiled reports from various parts of the world that covered 33 species of nematodes that host 20 suctorian species. They explored the effects of epibiosis on nematodes and suctorians, and host-epibiont species specificity and found that most nematodes were basibiont only for one epibiont species. Addintionally, half of the studied nematodes were colonized on the posterior body part, and the majority of basibionts were adult nematodes which do not molt anymore. Such studies may provide us with important information on the host and attachment-site preferences of suctorians, which may be determined by the mutual relationship between them.

We sampled calanoid copepods widely from the northern North Pacific Ocean and the Bering Sea, including as many as 16 calanoid species infested with suctorians. The biological characteristics of these copepods, such as their vertical distribution, diel vertical migration, feeding habits, and body size, were examined in relation to suctorian infestation. Additionally, the attachment sites of suctorians on these copepods were investigated for each copepod and suctorian species. Based on these examinations, the characteristics of copepods that are conducive for suctorian infestation and the host- and attachment-site preference of suctorian species were outlined. The attachment site of newly settling suctorians may be restricted by the existence of pre-attached suctorians. Therefore, we investigated how attachment sites extended with an increase in the number of attached suctorians.

Materials and Methods

Zooplankton samples were collected using a ring net with a mouth diameter of 80 cm and mesh width of 335 μm during the T.S. *Oshoro Maru* cruise to the northern North Pacific Ocean and the Bering Sea from June to August 2012 (Fig. 1). The net was vertically hauled from either 150 m or 1000 m to the surface. Calanoid copepods were checked for infestation with suctorians under a dissecting microscope on board ship and the infested copepods were picked up from 22 stations and fixed with 99.5% ethanol or 5% formalin seawater together with attached suctorians.

At the land laboratory, these copepods were observed under a light microscope (Olympus BX53) or an inverted microscope (Olympus IX70) to ascertain the number of attached suctorians on each of the 7 body parts of the copepods, namely, the antennules, cephalosome, mouth appendages, metasome, swimming legs, urosome, and caudal rami. The prosome length of the copepods and body size of suctorians were measured with an eye-piece micrometer under a light microscope. The measurements were made at least six months after these copepods and suctorians were fixed.

The shape of the macronucleus of an unknown suctorian that attached to *Paraeuchaeta birostrata* Brodsky, 1950 and *Paraeuchaeta elongata* (Esterly, 1913) and bore a resemblance to the genus *Acineta* Ehrenberg, 1834 or *Pelagacineta* Jankowski, 1978 was determined by staining it with Mayer's hematoxylin.

The feeding habits and distributional characteristics of infested calanoids were checked to ascertain whether these factors bore a relationship with suctorian infestation. The feeding pattern of copepods was classified into three types based on Arashkevich's (1969) and Ohtsuka & Nishida's

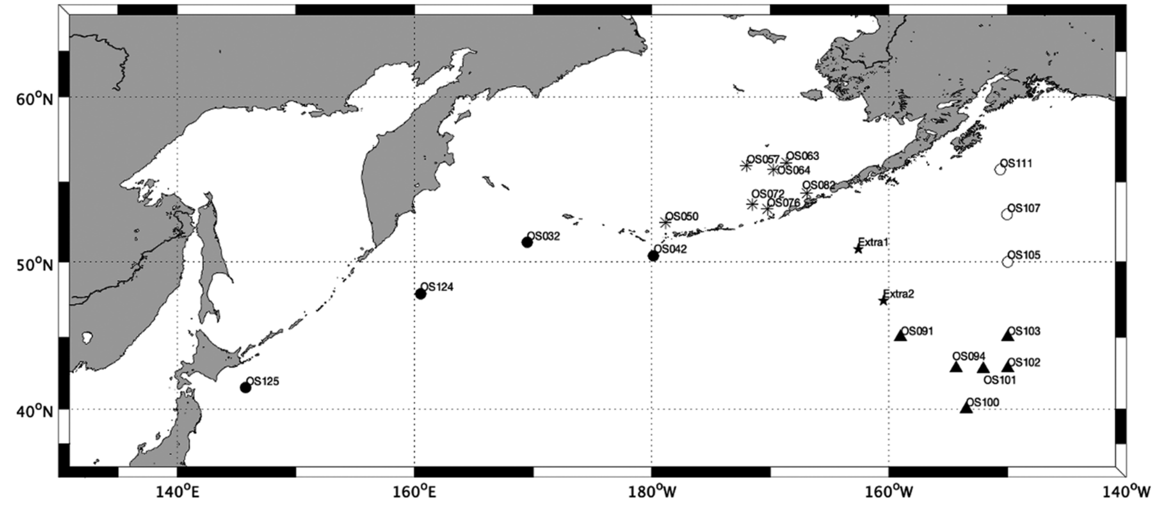

Fig. 1. Station map of the present study during the cruise of the T.S. *Oshoro Maru* to the northern North Pacific Ocean. Stations were classified into 4 sea areas according to temperature-salinity profiles based on Favorite et al. (1976). *: Bering Current System, ●: Subarctic Current System, ▲: Transition Domain, ○: Alaska Current System, ★: unknown area (lack of CTD casts).

(1997) classifications: i.e., suspension feeders, detritivores and carnivores. For information on the distributional depth we referred to Brodskii (1967), Deevey & Brooks (1977) and Haury et al. (2000), and for performance of vertical migration by copepods we referred to Vervoort (1965), Minoda (1971), Madhupratap & Haridas (1990) and Yamaguchi et al. (2002, 2004, 2020).

CTD casts were performed at 19 stations out of the 22 stations in this study, and these stations were divided into four oceanographic areas, as defined by Favorite et al. (1976) based on their temperature-salinity relationship.

We performed ANOVA to compare the effect of preservatives on the body size of copepods and suctorians.

Results

Effect of preservatives on sizes of copepods and suctorians

We used two preservatives to fix copepods, namely, 5% formalin-seawater and 99.5% ethanol. The body shrinkage of copepods and suctorians may differ based on the preservatives used on them. Therefore, we compared the prosome length of three abundant copepod species, *Gaetanus simplex* Brodsky, 1950, *Metridia pacifica* Brodsky, 1950 and *Paraeuchaeta elongata*, fixed with both preservatives. The ANOVA showed no significant difference in the prosome length of these three copepod species between the two preservatives (Table 1). However, significant preservative-induced differences were observed in the total length (body length + stalk length) of *Actinocyathula pleuromammae* (Steuer, 1928) which infested *M. pacifica*, and *Paracineta gaetani* Sewell, 1951 which infested *G. simplex* (Table 1). The shrinkage was more pronounced in ethanol-preserved suctorians than in formalin-preserved ones. Specifically, when preserved with 99.5% ethanol as opposed to 5% formalin-seawater, the total length of *A. pleuromammae*, which attached to *M. pacifica*, was 14.5% shorter, and that of *P. gaetani*, which attached to *G. simplex*, was 15.0% shorter. In the present study, most of the infested copepods were preserved with 99.5% ethanol and the body size of suctorians was used only when they were compared with the length of the host copepod.

Hydrography of the study area

Four sea areas were identified using Favorite et al.'s (1976) temperature-salinity relations framework. These included: Transition Domain (6 stations), Subarctic Current System (4 stations), Alaska Current System (3 stations), and Bering Current System (7 stations, Fig. 1). At two stations, Extra-1 and Extra-2, CTD casts were not performed. Therefore, the sea areas could not be determined for these stations.

Symbioses between calanoids and suctorians

A total of 259 calanoid individuals belonging to 16 species were found to be infested with suctorians (Table 2). Almost all of them were adult females: C6F (256 ind), C6M (2 ind), and C5M (1 ind). Four species of suctorian ciliates were identified, *Actinocyathula pleuromammae*, *Paracineta gaetani*, *Ephelota coronata* Kent, 1881, and *Rhabdophrya truncata* (Dons, 1915) (Fig. 2). One unknown species that attached to *Paraeuchaeta birostrata* and *P. elongata* and showed a resemblance to the genera *Acineta* or *Pelagacineta* proved to have a spherical, not ramified, macronucleus by hematoxylin staining (Fig. 2f). Therefore, it does not belong to the genus *Pelagacineta* according to Dovgal (2002), and we treated this species as *Acineta* sp.

The demographic and ecological features of these 16 calanoid copepods infested with suctorian ciliates are listed in Table 3. They are large-sized copepods, the smallest of which is *Racovitzanus antarcticus* Giesbrecht, 1902, which has a female prosome length of 1.75 mm. These 16 species are mid- or deep-water species. Nine out of 16 species perform vertical migration. The feeding habits of these copepods also vary. Eight of them are suspension feeders, whereas two are detritivores and six are carnivores.

Among the suctorian ciliates, *E. coronata* infested only *Metridia pacifica* (Table 2). *Rhabdophrya truncata* infested three species, *Candacia columbiae* Campbell, 1929, *Lucicutia pacifica* Brodsky, 1950 and *Paraeuchaeta*

Table 1. ANOVA to test the difference in copepod prosome length and suctorian total length between the two preservatives, 5% formalin-seawater and 99.5% ethanol. Number of individuals measured are shown in parentheses.

	Mean body size (μm)		F	P
	99% Ethanol	5% Formalin		
Copepods				
Gaetanus simplex	2895.5 (33)	2925.0 (10)	1.11	0.299
Metridia pacifica	2128.2 (63)	2122.7 (22)	0.03	0.855
Paraeuchaeta elongata	4896.0 (25)	5066.7 (6)	2.66	0.114
Suctorians				
Actinocyathula pleuromammae that infested *Metridia pacifica*	113.1 (40)	132.3 (24)	4.49	0.038
Paracineta gaetani that infested *Gaetanus simplex*	95.7 (78)	112.6 (14)	9.4	0.003

Table 2. Species and developmental stages of copepods infested with suctorian ciliates. Occurrence areas of suctorians are also shown. For the two suctorian species that attached to a copepod species and had different occurrence areas, the areas are shown separately for each suctorian species by attaching * or **. C: copepodite stage, F: female, M: male.

Copepod species	Stage: number	Suctorian species	Occurrence area of suctorians
Arietellus giesbrechti	C6F: 1	*Paracineta gaetani*	Transition
Candacia columbiae	C6F: 3	*Paracineta gaetani, Rhabdophrya truncata*	Subarctic
Gaetanus simplex	C6F: 114, C5M: 1	*Actinocyathula pleuromammae**, *Paracineta gaetani***	Bering*,**, Subarctic*,**, Alaska*, Transition*, Unknown*,**
Gaetanus minutus	C6F: 2	*Actinocyathula pleuromammae*	Subarctic
Heterorhabdus tanneri	C6F: 1, C6M: 1	*Paracineta gaetani*	Subarctic
Heterostylites major	C6F: 1	*Paracineta gaetani*	Subarctic
Lucicutia bicornuta	C6F: 1	*Paracineta gaetani*	Transition
Lucicutia pacifica	C6M: 1	*Rhabdophrya truncata*	Transition
Metridia pacifica	C6F: 84	*Actinocyathula pleuromammae**, *Ephelota coronata***	Bering*,**, Subarctic*,**, Transition**, Unknown*
Metridia similis	C6F: 1	*Paracineta gaetani*	Transition
Paraeuchaeta birostrata	C6F: 13	*Acineta* sp.	Subarctic, Alaska, Transition
Paraeuchaeta elongata	C6F: 30	*Acineta* sp.*, *Rhabdophrya truncata***	Bering**, Subarctic*,**, Alaska*,**, Transition**, Unknown*,**
Pleuromamma abdominalis abdominalis	C6F: 2	*Actinocyathula pleuromammae*	Transition
Pleuromamma scutullata	C6F: 1	*Actinocyathula pleuromammae*	Alaska
Racovitzanus antarcticus	C6F: 1	*Paracineta gaetani*	Subarctic
Scaphocalanus magnus	C6F: 1	*Paracineta gaetani*	Alaska

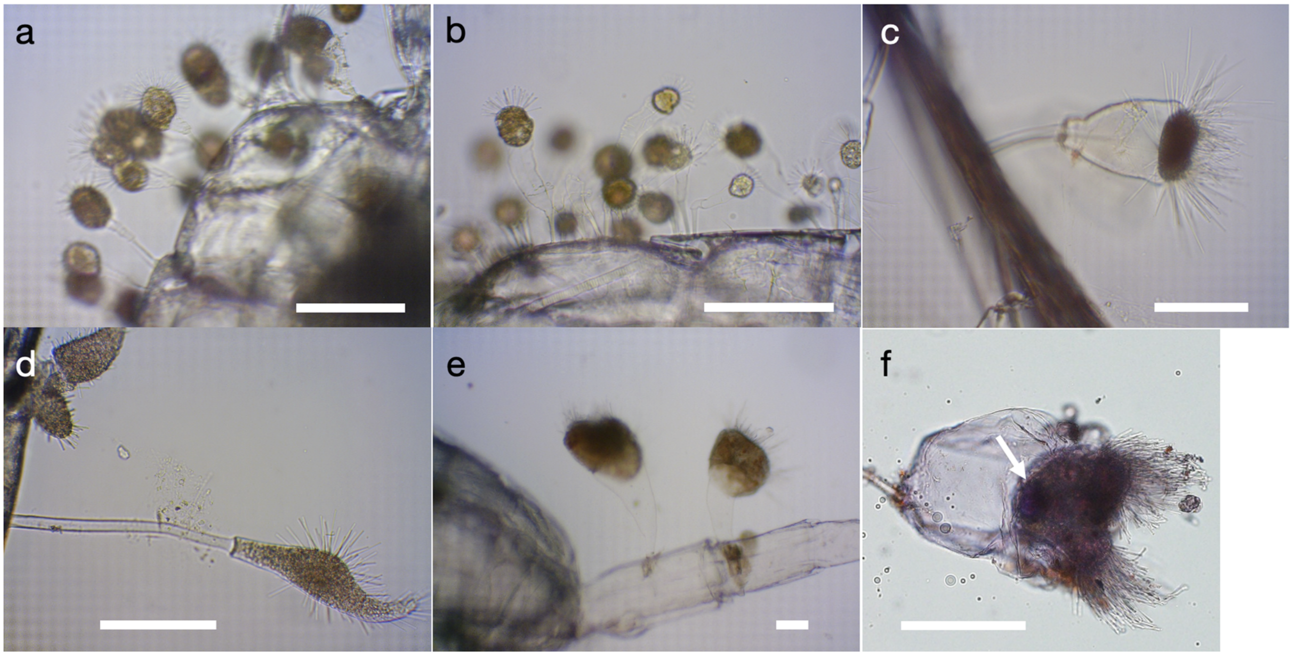

Fig. 2. Photographs of 5 suctorian species found to have infested calanoid copepods in the present study. a: *Paracineta gaetani*, b: *Actinocyathula pleuromammae*, c: *Acineta* sp., d: *Rhabdophrya truncata*, e: *Ephelota coronata*, f: *Acineta* sp. stained with hematoxylin. Arrow shows macronucleus. White scale bar shows 100 μm.

elongata. *Acineta* sp. infested only two species of the genus *Paraeuchaeta*, namely, *P. birostrata* and *P. elongata*; both of these species are carnivores but only the latter species is a migrator (Table 3). *Paracineta gaetani* infested as many as nine species of calanoids with widely ranging feeding habits and with/without vertical migration. Lastly,

Table 3. Size, distribution depth, performance of diel vertical migration (DVM) and food habit of the copepods infested with suctorian ciliates. ○: presence DVM, ×: absence DVM.

Species	Prosome length (mm)	Distribution depth (m)	DVM	Food habit
Arietellus giesbrechti	4.70–5.70[1]	500–1,000[2]	○[5]	carnivore[11]
Candacia columbiae	3.30–3.65	200–1,000[3]	○[6]	carnivore[11,12]
Gaetanus simplex	2.70–3.05	> 400[3]	○[7]	suspension feeder[11]
Gaetanus minutus	2.75–2.95	> 200[3]	×[7]	suspension feeder[11]
Heterorhabdus tanneri	2.60–2.85	500–2,000[3]	○[6]	carnivore[11,12]
Heterostylites major	2.90	1,000–4,000[3]	×[8]	carnivore[11,12]
Lucicutia bicornuta	4.25	> 1,500[3]	○[9]	suspension feeder[12]
Lucicutia pacifica	2.28	1,000–4,000[3]	×[8]	suspension feeder[12]
Metridia pacifica	1.75–2.38	> 50[3]	○[7]	suspension feeder[11,12]
Metridia similis	2.30	1,000–4,000[3]	×[8]	suspension feeder[11,12]
Paraeuchaeta birostrata	5.45–6.00	200–1,000[3]	×[7]	carnivore[11,12]
Paraeuchaeta elongata	4.50–5.35	200–500[3]	○[7]	carnivore[11,12]
Pleuromamma abdominalis abdominalis	2.70–2.75	0–600[4]	○[4]	suspension feeder[11,12]
Pleuromamma scutullata	2.55	1,000–4,000[3]	○[7]	suspension feeder[11,12]
Racovitzanus antarcticus	1.75	400–500[3]	×[8]	detritivore[11]
Scaphocalanus magnus	4.30	100–4,000[3]	×[8]	detritivore[11]

[1] Ohtsuka (1997), body length, [2] Deevey & Brooks (1977), [3] Brodskii (1967), [4] Haury et al. (2000), [5] Vervoort (1965), [6] Minoda (1971), [7] Yamaguchi et al. (2004), [8] Yamaguchi et al. (2002), [9] Madhupratap & Haridas (1990), [10] Yamaguchi et al. (2020), [11] Ohtsuka & Nishida (1997), [12] Arashkevich (1969)

A. pleuromammae infested five species of copepods that are all suspension feeders.

The number of each suctorian species per copepod varied widely from 1 ind of *E. coronata* that infested *M. pacifica* to 513 ind of *P. gaetani* that infested *Gaetanus simplex* (Table 4). The mean numbers of *Acineta* sp. and *R. truncata* per copepod were relatively small; 6.3–22.8 ind for the former and 1.0–20.1 ind for the latter. Compared to these suctorians, the number of *P. gaetani* and *A. pleuromammae* per copepod were larger; 16.0–102.0 ind for the former and 15.0–76.9 ind for the latter.

The relationship between the mean total length of the suctorian species and mean prosome length of the copepods infested with suctorians is presented in Fig. 3. Since most of the copepods were preserved with 99.5% ethanol, only ethanol-preserved samples were used, except for *A. pleuromammae* infesting *Gaetanus minutus* (Brodsky, 1950), which was preserved with formalin. Excluding *E. coronata*, which infested *M. pacifica* and is disproportionately large for the host copepod, there was a statistically significant correlation between copepod length and suctorian length ($r = 0.782$, $p = 0.002$). Even when the total length of *A. pleuromammae* that infested *G. minutus* was calibrated to ethanol-preserved values (16.9% shorter), a statistically significant correlation was obtained ($r = 0.781$, $p = 0.002$). *Actinocyathula pleuromammae* and *P. gaetani* infested five or more species, but there was no significant correlation between the length of these two suctorians and copepod length ($r = 0.057$, $p = 0.927$ for *A. pleuromammae*, $r = 0.323$, $p = 0.677$ for *P. gaetani*), which indicates that the size of *A. pleuromammae* and *P. gaetani* did not differ among their host copepod species. *Actinocyathula pleuromammae* infested smaller copepods in comparison to *P. gaetani*. The exception was *R. truncata*; it was larger when attached to *P. elongata* (prosome length was 4.50–5.35 mm) than when attached to *L. pacifica* (prosome length was 2.28 mm) and *C. columbiae* (prosome length was 3.45 mm). *Acineta* sp. infested only large copepod species with prosome length ≧4.93 mm.

Attachment site of suctorians

The body part to which suctorian ciliates attached themselves differed based on copepod species as well as suctorian species (Fig. 4). *Ephelota coronata* attached almost exclusively to the dorsal side of the urosome of *Metridia pacifica*. *Rhabdophrya truncata* infested three species of copepods, *Candacia columbiae*, *Lucicutia pacifica* and *Paraeuchaeta elongata*; its attachment site was more restricted than that of other suctorian species, as it only attached to the urosome of *Lucicutia pacifica* (only one copepod, therefore not shown) and *P. elongata* and only to the dorsal part of the metasome of *C. columbiae*. *Acineta* sp. attached to all three parts of *Paraeuchaeta birostrata*, namely, cephalosome, metasome and urosome. A higher percentage of its population attached to the metasome and mouth appendages of *P. elongata*.

Paracineta gaetani and *Actinocyathula pleuromammae* attached to a similar site on *Gaetanus simplex*, which was the most heavily infested copepod in the present study. The metasome was the most common attachment site of these two suctorians, followed by swimming legs and urosome. There seemed to be no difference in the attachment

Table 4. Attached number (mean and range) of each suctorian ciliate to copepod species.

Suctorians	Copepods	Mean	Range	*N*
Paracineta gaetani	*Candacia columbiae*	92.7	64–130	3
	Gaetanus simplex	83.0	8–513	45
	Heterorhabdus tanneri	34.0	34	1
	Heterostylites major	50.0	50	1
	Lucicutia bicornuta	102.0	102	1
	Metridia similis	26.0	26	1
	Racovitzanus antarcticus	16.0	16	1
	Scaphocalanus magnus	16.0	16	1
Actinocyathula pleuromammae	*Gaetanus simplex*	76.1	1–339	69
	Gaetanus minutus	20.5	16–25	2
	Metridia pacifica	76.9	3–268	79
	Pleuromamma abdominalis abdominalis	48.0	23–73	2
	Pleuromamma scutullata	15.0	15	1
Acineta sp.	*Paraeuchaeta birostrata*	22.8	3–46	13
	Paraeuchaeta elongata	6.3	1–19	7
Rhabdophrya truncata	*Candacia columbiae*	2.0	2	2
	Lucicutia pacifica	1.0	1	1
	Paraeuchaeta elongata	20.1	1–45	30
Ephelota coronata	*Metridia pacifica*	1.1	1–2	8

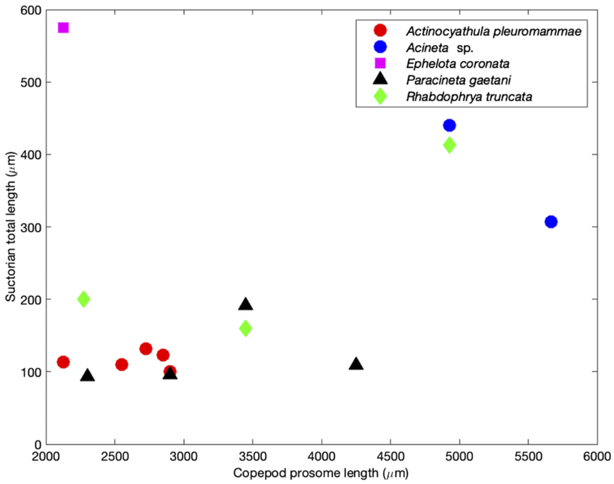

Fig. 3. Mean total length of suctorian species (μm) plotted against prosome length (μm) of the calanoid species to which each suctorian species was attached.

sites based on sea areas.

Colonization of suctorians on copepod bodies

In order to estimate to which part of copepod body suctorians attach first before spreading to other parts, the attached number of suctorians were checked across various parts of the host copepod body at several infestation levels. For this purpose, we selected two heavily infested copepod species, namely, *Gaetanus simplex*, which was infested with *Actinocyathula pleuromammae* and *Paracineta gaetani*, and *Metridia pacifica*, which was infested with *A. pleuromammae*. Copepods were grouped separately based on the total number of suctorians attached to them, namely, less than 25, from 25 to 50, from 50 to 100, and over 100 ind per copepod (Fig. 5).

Most of *A. pleuromammae* attached to the urosome of *M. pacifica*. When the total number of *A. pleuromammae* was small (less than 50 ind), nearly 80% of them attached to the urosome, but when the total number exceeded 100 ind, slightly more than 60% of them attached to the urosome and the rest attached to the metasome and cephalosome (Fig. 5). On the other hand, *A. pleuromammae* mainly attached to the metasome of *G. simplex*. When the attached number of *A. pleuromammae* was small (less than 25 ind), about 56% of this suctorian attached to the metasome and the rest attached to the urosome and swimming legs. However, when the total attached number was larger, the percentage that were attached to the metasome slightly decreased and the percentage that attached to the cephalosome increased.

Paracineta gaetani mainly attached to the metasome of *G. simplex*. About 50% of *P. gaetani* attached to the metasome when their total number was less than 100 ind, while the rest attached to the swimming legs and urosome, but when the total number exceeded 100 ind, the percentage that attached to the metasome decreased to 42%, and the percentage that attached to the cephalosome increased. Therefore, in all these three cases, the percentage of suctorians that attached to the anterior part of the copepod body rather than their peak attachment site increased as the total number of attached suctorians increased.

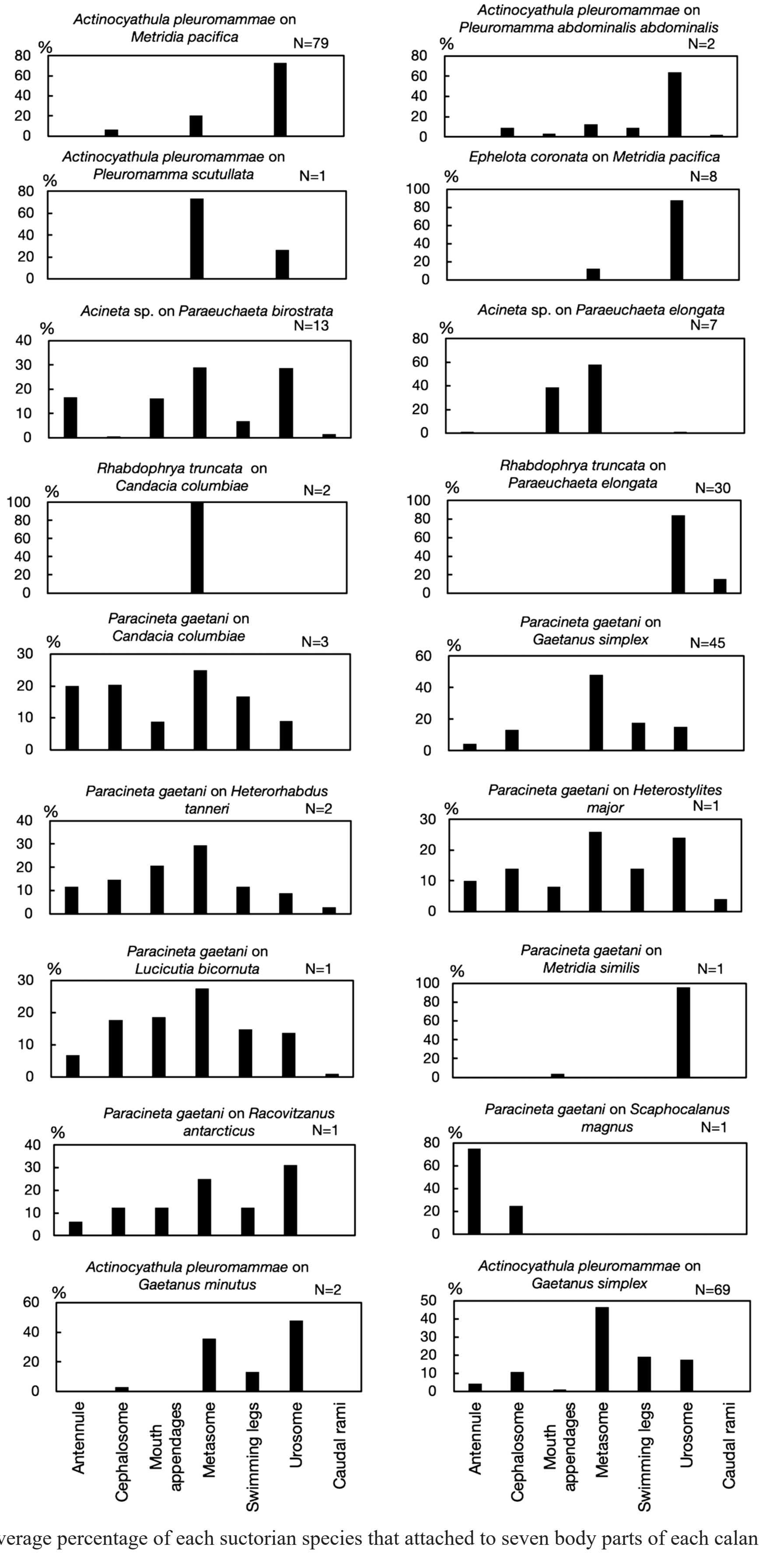

Fig. 4. Average percentage of each suctorian species that attached to seven body parts of each calanoid species.

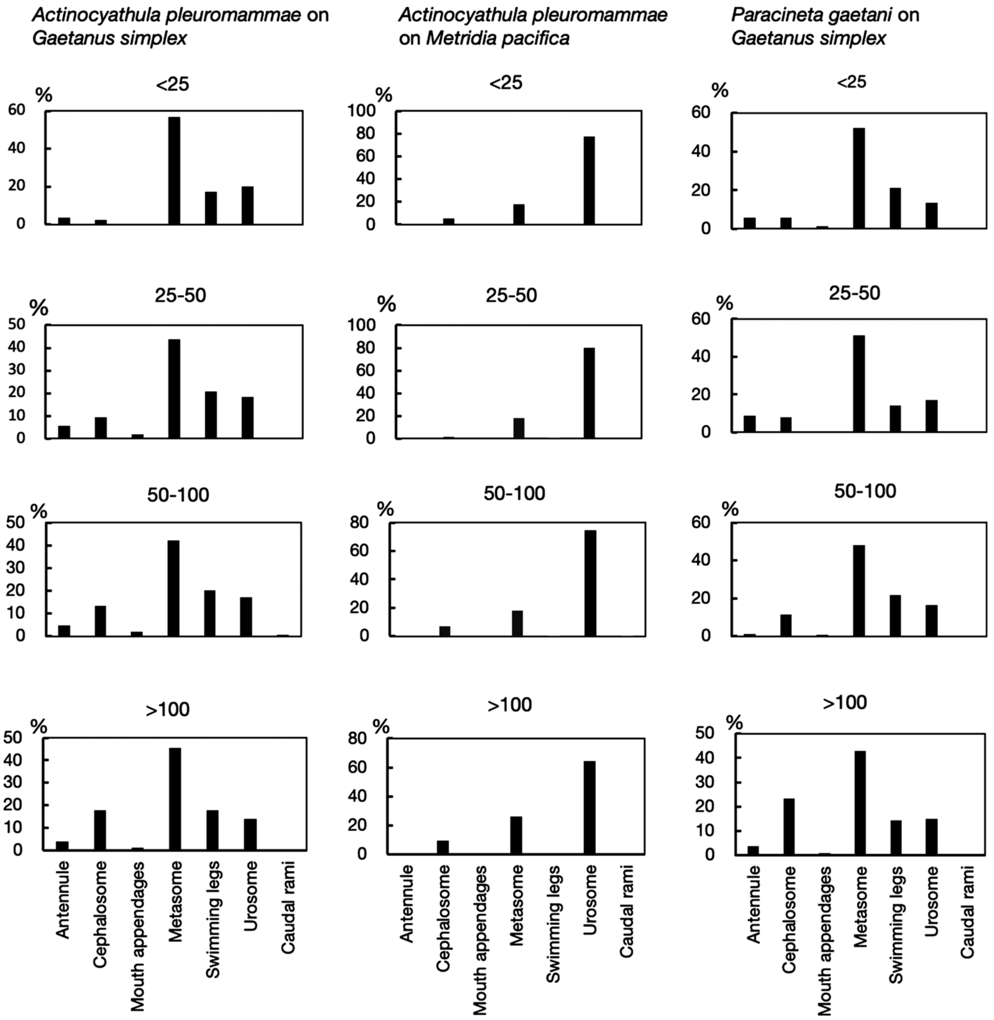

Fig. 5. Average percentage of attached suctorians to seven body parts of a calanoid copepod at four infestation levels (<25, 25–50, 50–100, >100 per copepod) for *Actinocyathula pleuromammae* that attached to *Gaetanus simplex* and *Metridia pacifica*, and *Paracineta gaetani* that attached to *Gaetanus simplex*.

Discussion

Calanoids and infested suctorians

A total of 16 calanoid species were found to be infested with suctorians in the present study. Among them, six species were reported to be infested with suctorians for the first time in the present study: *Candacia columbiae*, *Gaetanus minutus*, *Lucicutia bicornuta* Wolfenden, 1911, *Metridia similis* Brodsky, 1950, *Pleuromamma scutullata* Brodsky, 1950, and *Racovitzanus antarcticus*. On the other hand, many suctorian ciliates found in the present study have already been reported to infest copepods. Namely, *Paracineta gaetani* has been reported to infest *Gaetanus antarcticus* Wolfenden, 1905, and *G. curvicornis* Sars, 1905 (Fernandez-Leborans & Tato-Port 2000), *Metridia longa* (Lubbock, 1854) and *M. lucens* Boeck, 1864 (Sherman & Schaner 1965). Type A of Yamaguchi (2006), which is thought to be *Paracineta gaetani*, was reported to have infested *Gaetanus armiger* Giesbrecht, 1888, *G. simplex*, *G. minutus*, *Heterorhabdus tanneri* (Giesbrecht, 1895), *Heterostylites major* (Dahl, 1894), *Metridia pacifica*, *Paraeuchaeta birostrata*, *P. elongata*, *P. rubra* Brodsky, 1950, and *Scaphocalanus magnus* (T.Scott, 1894). *Actinocyathula pleuromammae* (=*Paracineta pleuromammae*) has been reported to infest *Pleuromamma abdominalis abdominalis* and *P. xiphias* (Giesbrecht, 1889) by Steuer (1928), *Metridia longa* and *M. lucens* by Sherman & Schaner (1965). Yamaguchi's (2006) type B, which is thought to be *Ephelota coronata*, was reported to have infested *Metridia pacifica*. Yamaguchi & Ikeda's (2001) "shooting star," which is thought to be *Rhabdophrya truncata*, was reported to have infested *Paraeuchaeta elongata*.

Calanoids infested with suctorians

Almost all copepods (98.8%, 256/259) infested with suctorians in the present study were adult females (Table 2). These copepods are relatively large, and the smallest of them is *Racovitzanus antarcticus*, which has a prosome length of 1.75 mm. Sedlacek et al. (2013) also reported that epibionts including suctorians are found significantly more frequently on female deep-sea harpacticoid copepods than males. Adult female calanoids are generally larger than males. A larger size may be necessary for suctorian infestation, as suggested in the case of deep-sea isopods (Ólafsdóttir & Svavarsson 2002). Furthermore, copepods show strongly female-skewed sex ratios both naturally and in the rearing condition, probably because of the higher longevity in females in comparison to males, and the sex change induced by environmental conditions (Gusmão et al. 2013). In the case of *Scaphocalanus magnus*, adult males do not feed and have shorter life spans than females, skewing the adult sex ratio towards females (Yamaguchi et al. 2020). These may be the reasons why adult female copepods were the main target of suctorians.

All the calanoids infested with suctorians in the present study were mid- or deep-water species. This may be because surface water species are generally small (Grice & Hulsemann 1965, Mauchline 1972). For instance, in descending order of abundance, the surface water copepods whose distributional depth is limited to the surface 200 m of the western subarctic Pacific Ocean include Cyclopoida, *Paracalanus parvus* (Claus, 1863), *Calanus pacificus* Brodsky, 1948, *Scolecithricella minor* (Brady, 1883), *Pseudocalanus newmani* Frost, 1989, *Acartia longiremis* (Lilljeborg, 1853), *Candacia bipinnata* Giesbrecht, 1889, and *Mesocalanus tenuicornis* (Dana, 1849)(Yamaguchi et al. 2002). In descending order of abundance, the surface water copepods in the Bering Sea include Cyclopoida, *Metridia pacifica*, *Eucalanus bungii* Giesbrecht, 1892, *Pseudocalanus newmani*, *P. minutus* (Krøyer, 1845), *P. mimus* Frost, 1989, *Neocalanus plumchrus* (Marukawa, 1921), *Pseudocalanus moultoni* Frost, 1989, *Calanus pacificus*, and *Acartia longiremis* (Homma & Yamaguchi 2010). Among these surface water species, those larger than 2 mm in body length are as follows: *Aetideus pacificus* Brodsky, 1950, *Candacia bipinnata*, *C. columbiae*, *Eucalanus bungii*, *Neocalanus plumchrus*, *Neocalanus flemingeri* Miller, 1988, *Neocalanus cristatus* (Kröyer, 1848), and *Calanus pacificus* (Brodskii 1967, Toda 1997). Besides *Aetideus pacificus*, *Candacia bipinnata* and *C. columbiae*, these larger species have dormant stages (Mauchline 1998). Specifically, their C5 stage is characterized by the cessation of feeding, reduced metabolic rates, high lipid reserves and inactivity (Hirche 1996). Therefore, these copepods can be ruled out as hosts for suctorians, because they cannot provide a good condition for suctorians to get nutrition. The abundance of *A. pacificus* and *C. bipinnata* may be too low and their size may be not large enough for suctorians to infest, which may be why these two species did not appear as basibionts in the present study. *C. columbiae* was found to be infested in the present study. Therefore, suctorians may have infested larger mid- or deep-water calanoids. The deep ocean is generally characterized by its lower water temperatures, which makes the intermolt periods and longevity of copepods longer than in the surface waters.

The performance of vertical migration and feeding habits of copepods do not seem to be related to the infestation of suctorians.

Host preference of suctorians

Paracineta gaetani attached to as many as nine species of calanoids and appeared in all five sea areas (including the unknown area, Table 2). *Actinocyathula pleuromammae* infested five species of copepods and appeared in all five sea areas. Therefore, these two suctorian species do not seem to have any host preferences. On the other hand, *Ephelota coronata* infested only *Metridia pacifica* and appeared in the four sea areas where *M. pacifica* were infested with a suctorian species (except the Alaska Current System). This suggests that this suctorian has a strong host preference. *Rhabdophrya truncata* appeared in all five sea areas and attached to three calanoid species, *Candacia columbiae*, *Lucicutia pacifica* and *Paraeuchaeta elongata*; therefore, it displayed some host preference. Yamaguchi & Ikeda (2001) also reported the infestation of this suctorian (as "shooting star") to *P. elongata*. *R. truncata* was originally reported in brown algae *Desmarestia viridis* (O.F. Müller), the hydroid *Abietinaria abietina* (Linnaeus, 1758) (reported as *Diphasia abietina*) and red algae by Dons (1915). Other species of the genus *Rhabdophrya* have been reported to infest various organisms: *Rhabdophrya trimorpha* Chatton & Collin, 1910 infested a burrowing harpacticoid copepod *Cletodes longicaudatus* Boeck, 1872 (Chatton & Collin 1910), *Rhabdophrya populiformis* (Gassovsky, 1916) infested the bryozoan *Caberea ellisii* (Fleming, 1814), the hydrozoan *Halecium* sp. and an isopod *Idothea* (Gassovsky 1916), and *Rhabdophrya nymphonis* (Gassovsky, 1916) infested a Pantopoda (sea spider) *Nymphon* sp. (Gassovsky 1916). Considering these facts, *R. truncata* does not seem to have attached to host species with particular biological characteristics. *Acineta* sp. attached to only one genus *Paraeuchaeta*, the species being *P. birostrata* and *P. elongata*. *Acineta* sp. did not appear in the Bering Current System, even though *P. elongata* infested with other suctorians were found there. Therefore, this suctorian shows some host preference but may have a limited geographical distribution.

Host specificity is fairly well established for peritrich ciliates (Nenninger 1948, Lust 1950), but not for suctorians. Baldrighi et al. (2020) reported that most of their suctorian species were found only on nematodes, and most nematodes were found to be basibiont only for one epibiont species; only a few nematodes could recruit different epibionts in different environments. Most species of suctorians colonize a broad range of substrates, both inert and living (Cook et al. 1998). In the present study, large-sized suctorian species tended to show some host preference. However, size alone cannot explain the epibiotic relation because *Ephelota coronata* infested only the relatively small *Metridia pacifica*. Further research is needed to clarify the host preference/specificity of suctorian ciliates.

Attachment site of suctorians

Ephelota coronata mainly attached to the urosome of *Metridia pacifica*. Yamaguchi (2006) also noted that this suctorian (as Type B suctorian) mainly attached to the urosome and metasome of *M. pacifica*. Holt (1891) showed that *E. coronata* (as *Hemiophrya dalyelli*) attached mainly to the urosome and egg strings of a Caligidae copepod, *Caligus rapax* Milne Edwards, 1840, which is parasitic on marine fishes and adult females possess two egg strings. Therefore, the posterior part of the copepod body seems to be a preferred attachment site for *E. coronata*. *Rhabdophrya truncata* attached only to the dorsal part of the metasome of *Candacia columbiae*, and only to the urosome of *Paraeuchaeta elongata.* Yamaguchi & Ikeda (2001) reported that *R. truncata* attached mainly to the last somite of the metasome and the urosome of *P. elongata*. There are two other studies that reported that *Rhabdophrya* species attached to copepods but the attachment site was not mentioned (Chatton & Collin 1910, Wailes 1932). For large suctorians such as *E. coronata* and *R. truncata*, which might be prone to receive greater impact from the water flow around the host body, the attachment site might be restricted to the posterior part of copepod body where water flow is slower.

Acineta sp. in the present study attached to all three parts of *Paraeuchaeta birostata*, but a higher percentage of its population was attached to the cephalosome (mainly mouth appendages) and metasome of *P. elongata.* Therefore, this species may be able to attach to various parts of a copepod's body. The "Bell"-shaped and "Flask"-shaped suctorians of Yamaguchi & Ikeda (2001) are thought to be *Acineta euchaetae* Sewell, 1951 and were reported to have attached mainly to the last somite of the metasome and the urosome of *P. birostarata* and *P. rubra*. Kahl (1934) reported that *Acineta schulzi* Kahl, 1934 attached to the urosome of copepods.

Actinocyathula pleuromammae attached mainly to the metasome of *Gaetanus simplex* and *Pleuromamma scutullata* but to the urosome of *Metridia pacifica* and *Pleuromamma abdominalis abdominalis* in the present study. Steuer (1928) and Sewell (1951) also reported that *A. pleuromammae* attached to the last somite of the metasome and the urosome of copepods of the genus *Pleuromamma*.

Paracineta gaetani attached mainly to the metasome of *G. simplex*, urosome of *Metridia similis*, and antennule of *Scaphocalanus magnus*. On the other hand, this species attached rather evenly to various body parts of *C. columbiae*, *Heterorhabdus tanneri*, *Heterostylites major*, *Lucicutia bicornuta* and *Racovitzanus antarcticus*. Sewell (1951) reported that *P. gaetani* attached mainly to the anterior appendages of two *Gaetanus* species. Therefore, *P. gaetani* may be able to attach to various parts of a copepod's body.

It is interesting that all suctorian species attached themselves mainly to the urosome of *Metridia* species. *M. pacifica* has been reported to have a fairly high swimming speed of 8–25 mm s^{-1} (Enright 1977). It is probable that suctorians cannot endure larger flow speeds when attached to the anterior body part of this copepod.

As the number of attached suctorians increases, the at-

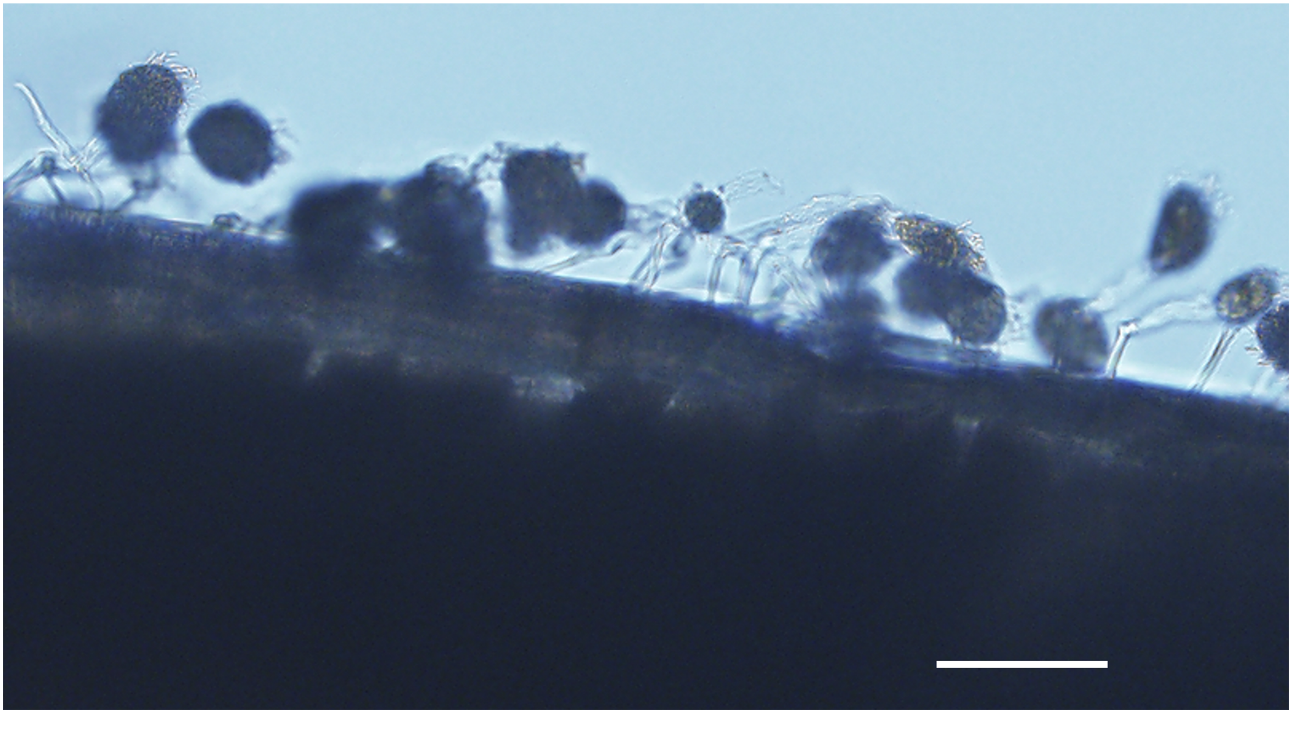

Fig. 6. Photograph of *Actinocyathula pleuromammae* with posteriorly-bent stalks that attached to the dorsal surface of the cephalosome and metasome of *Metridia pacifica*. White scale bar shows 100 μm.

tachment site may extend to other body parts of copepods. In all three cases examined in the present study, the attachment was confined to the metasome (*G. simplex*) or urosome (*M. pacifica*) when the number of suctorians was small (Fig. 5). When the number of attached suctorians was large, more suctorians were found to have attached themselves to the anterior part of the copepod's body; the percentage attached to the cephalosome increased in the case of *G. simplex*, whereas those attached to the metasome increased in the case of *M. pacifica*. A similar extension of attachment sites to the anterior part of the copepod body with an increase in suctorians was suggested for *Metridia lucens* collected from the Gulf of Maine (Sherman & Schaner 1965). The movement of suctorians from one copepod individual to another would take place when swarmers are formed and copepods make close contact (such as during copulation (Dovgal 2002)). The common contact location during copepod copulation is the urosome (Gauld 1957, Blades & Youngbluth 1980). Swarmers would move to another copepod individual and settle at these contact locations. When a suitable attachment site had been already occupied by other individuals, the late-coming swarmers had to attach to neighboring suboptimal sites on the copepod's body. A similar situation would occur when the attached suctorians reproduce and release swarmers on the same copepod individual. It has been shown that the flow speed is slower at the urosome than the anterior part both when feeding (Yen & Strickler 1996) and when free swimming (Gemmell et al. 2014). The anterior part of the copepod body is thus susceptible to faster flow speed. Suctorians with a posteriorly bent stalk were found when many suctorians attached to these parts (Fig. 6). At posterior parts such as the urosome, however, such suctorians with a uniformly posteriorly bent stalk were not found. The stalk development of suctorians has not been observed in detail, but may take a short time, say, less than a day as observed in the case of *Ephelota gigantea* (Kobayashi et al. 2011), and the bent stalks found in the present study may be formed during their development.

Attached suctorians should be feeding and when they attain maturation they may reproduce. Dovgal (2013) compiled observations on suctorian feeding: eight suctorian species have been observed to feed on free-swimming ciliates and in some cases flagellates (e.g., Hickson & Wadsworth 1909), and three species were even cultured using ciliates as a prey (e.g., Nerad & Daggett 1992, Evans et al. 1995). Those suctorians, however, are all freshwater species that attached to immotile basibionts. To our knowledge, there is no such observation on the feeding of marine suctorians, or the suctorians that attach to motile basibionts. The processes of migratory stage formation and detachment of ciliates from hosts are known for peritrich ciliates (Bickel et al. 2012), but have hardly ever been observed in the case of suctorian ciliates. Budding and swarmer formation processes were observed in *Ephelota gemmipara* (Hertwig, 1875) that attached to a hydroid *Eudendrium racemosum* (Cavolini, 1785) (Tazioli & Di Camillo 2013). Processes of budding, swarmer formation and development after settlement of *Ephelota gigantea* that attached to a seaweed *Undaria pinnatifida* (Harvey) Suringar were described by Kobayashi et al. (2011). A steady increase of body width of *Ehelota plana* Wailes, 1925 was observed with the molt stage development of its basibiont, the North Pacific krill *Euphausia pacifica* Hansen, 1911 (Endo et al. 2017). Budding individuals first appeared at the early premolt stage and increased toward the late premolt stage, suggesting that the life cycle of *E. plana* is adapted to the molt cycle of *E. pacifica*. Life history studies on other species of suctorians are necessary to characterise their settlement and growth on host copepods.

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