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Original Article

Comparison of the ecology of pelagic copepods as basibionts and suctorian ciliates as epibionts in the subarctic Pacific

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ABSTRACT

Suctorian ciliates are widely distributed in both freshwater and marine environments. In the open ocean, they attach to crustacean zooplankton, specifically copepods, as epibiont hosts. However, criteria for host preference in oceanic areas remain unclear. In this study, we conducted a molecular analysis, examined copepod community relationships and performed laboratory-rearing experiments on suctorian ciliates in the subarctic Pacific. Suctorians belonging to five genera and species were observed on the exoskeletons of 20 copepod species across 10 genera. Additionally, species-specific host preferences were observed. Molecular analyses revealed intraspecific variations and haplotypes in suctorian ciliates, with no correlation between the haplotypes and host copepods or geographical location. Suctorians did not prefer numerically dominant or large-sized copepod species but favored deep-sea or diel vertical migration (DVM) species, specifically carnivorous copepods. A high suctorian prevalence was observed during the late copepodite stages, specifically among adult females and in regions with cold waters. These characteristics indicate that suctorians rely on prey or host molting events. Laboratory experiments confirmed novel suctorian attachments and growth from swarmer to trophont within 24 h. This study indicates that suctorian epibionts prefer late copepodite stages in deep-sea habitats, exhibiting DVM, prolonged stage duration and low predation risk.

KEYWORDS: haplotypes; host preference; laboratory-rearing experiments; ZooScan; *Acineta euchaetae*; *Copterus tyloloricatus*; *Ephelota coronata*; *Paracineta gaetani*; *Rhabdophrya truncata*

INTRODUCTION

It has been reported that the body surfaces of pelagic copepods are often host to suctorian ciliates as epibionts (Sewell, 1951; Sherman and Schaner, 1965; Dovgal, 2002). Suctorian ciliates possess a unique morphology and life cycle among protozoan ciliates. They lose their swimming ability when in the trophont stage and become sessile, adhering to substrates while using tentacles to attach to unicellular organisms in the surrounding water to obtain nutrition (Sundermann *et al.,* 1986; Dovgal, 2002; Savage *et al.,* 2023). The suctorian ciliate species that are typically epibiont on copepods include *Ephelota* spp. and *Acineta* spp. These species exhibit specific differences in their attachment modes, host preferences and attachment cell densities (Fernández-Leborans and Tato-Porto, 2000; Ohtsuka *et al.,* 2011; Endo *et al.,* 2022). However, information regarding the species composition and prevalence of suctorian ciliates in oceanic areas is limited, as is knowledge about how these parameters relate to the species of host copepods and their developmental stages (Yamaguchi and Ikeda, 2001; Yamaguchi, 2006; Endo *et al.,* 2022).

Studies have shown that the attachment of suctorian ciliates to host copepods can lead to reduced swimming abilities and decreased feeding efficiency in the copepods (Sherman and Schaner, 1965; Fernández-Leborans and Tato-Porto, 2000; Gregori *et al.,* 2016). For the suctorian ciliates, attachment to the planktonic copepods may allow them to adapt to life in the oceanic pelagic zone. In this context, the ciliates can release swarmers that swim freely to locate new attachment sites, as well as access prey cells or organic matter. This indicates that the relationship between epibiont suctorian ciliates and their basibiont host copepods may be more complex than previously thought (Wahl *et al.,* 1997; Ohtsuka *et al.,* 2000, 2011). To better understand the interactions between these two groups, it is essential to investigate how suctorian ciliates select their host copepod species based on various ecological characteristics, including species composition, abundance, biomass, body size, feeding modes, developmental stages and life cycle patterns (Endo *et al.,* 2022).

In this study, we examined the occurrence and species composition of suctorian ciliates attached to the body surface of

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pelagic copepods collected from the sea surface down to a depth of 3000 meters in the broader subarctic Pacific. Our goal was to evaluate the community structure of the sympatric pelagic copepods in order to clarify the criteria that suctorian ciliates use to select their host species. We analyzed the copepods from various perspectives, including species, abundance, biomass, body size, feeding modes, developmental stages, sex differences (female or male) and life cycle strategies. This comprehensive evaluation aims to better understand the criteria by which suctorian ciliates select their host copepods. Additionally, we conducted molecular genetic analyses of the suctorian ciliates and carried out onboard rearing experiments with the ciliates attached as epibionts to the copepods. Through these studies, we hope to shed light on how suctorian ciliates select their host species by analyzing the ecological characteristics of the copepods. Ultimately, this research may contribute to a better understanding of microsymbiotic systems within the less-studied oceanic ecosystem, covering a broader area and extending into bathypelagic depths.

METHODS

Field sampling

Zooplankton net sampling was conducted at 32 stations along east–west longitudinal transect along 47°N in the subarctic Pacific carried out from 16 July to 17 August 2021 during the MR21-04 cruise by R/V *Mirai* of Japan Agency for Marine-Earth Science and Technology (JAMSTEC) (Fig. 1). At each station, a Quad-NORPAC net (mouth diameter 45 cm) (Hama *et al.,* 2019) was towed vertically from a depth of 0 to 150 m at night. This net was equipped with a flowmeter and a 335 μm mesh to collect preserved samples, as well as a 63 μm mesh net with a bucket cod end for collecting laboratory-reared specimens and sorting onboard. The samples collected using the 335 μm mesh nets were immediately preserved in a 5% formalin-seawater solution after collection.

Additionally, at each station, an 80 cm ring net with 335 μm mesh and a bucket cod end was vertically towed from either 150 or 500 m depth at night. These samples were reared in the laboratory and sorted onboard. Details of the sample collection are presented in Supplementary Table 1. At three stations (located in the western, central and eastern areas) along the 47°N line, vertically stratified zooplankton net samplings were also conducted during the daytime using the vertical multiple plankton sampler (VMPS) (Tsurumi Seiki Co. Ltd, Terazaki and Tomatsu, 1997). This device has a mouth opening area of 0.25 m^2 and uses 63 μm mesh nets. These samplings covered 12 discrete depths, ranging from 0 to 3000 m. At most sampling stations, temperature, salinity and dissolved oxygen (DO) were measured using a conductivity, temperature and depth (CTD) profiler (SBE 911plus, Sea-Bird Electronics). Additionally, chlorophyll *a* (Chl. *a*) was measured for the water samples collected at various depths down to 250 m. These hydrographic data are publicly available on websites, including the JAMSTEC Voyage and Dive Data Sample Search System at https://www.godac.jamstec.go.jp/darwin_tmp/explain/81/j/.

Live specimens collected using bucket-cod end nets (NORPAC and 80-cm ring net) and calanoid copepods with exoskeleton-attached suctorian ciliates were immediately assessed and sorted onboard under a stereomicroscope. Sorted specimens were identified and photographed, and a few were selected for laboratory rearing. The remaining specimens were preserved in ethanol (99.5%), refrigerated and used for molecular analyses in the laboratory. Additionally, the samples collected using the VMPS were assessed onboard under a stereomicroscope, and calanoid copepods with attached suctorian ciliates were sorted and preserved in ethanol (99.5%), refrigerated and used for molecular analysis in the laboratory.

Additional zooplankton sampling was conducted at six stations in the Chukchi Sea during the MR21-04C cruise of the R/V *Mirai* from 16–20 September 2021 (Fig. 1). During the cruise, zooplankton samples were collected using vertical hauls of the same Quad-NORPAC net and 80-cm ring net from depths of either 500 m or 5 m above the seafloor (for stations with depths shallower than 500 m). Copepod specimens attached to suctorian ciliates were assessed, sorted and preserved in 99.5% ethanol for refrigeration. These samples were later used for molecular analysis in the land laboratory.

Molecular analysis

DNA was extracted from suctorian ciliate cells using a 5% Chelex solution (200–400 Na$^+$, BIO-RAD, California). Ethanol-preserved suctorian ciliate samples were dissected from the copepods. The cells were washed with filtered sterile seawater and placed in a 0.2 mL Eppendorf tube (96.09852.9.01, Treff Lab Inc.) containing 15 μL of 5% Chelex solution. The tube was then heated at 90°C for 20 minutes using a thermal cycler (Veriti 96 Well, Applied Biosystems, California, USA). Finally, the sample was vortexed for 5 seconds to ensure the DNA was fully extracted (Richlen and Barber, 2005).

Single-cell PCR was performed using DNA extracted, from the D1/D2 region of nuclear 28S rDNA. The primers D1R (ACCCGCTGAATTTAAGCATA) and D2C (CCTTGGTCCGTGTTTCAAGA) (Scholin and Anderson, 1994), similar to dinoflagellates, were used to amplify a fragment of ~700 bp using PCR. The PCR mixture composition matched the reagent's manual, and reaction conditions involved 40 cycles of denaturation at 98°C (10 s), annealing at 58°C (30 s), and extension at 68°C (40 s), following an initial denaturation at 94°C for 2 min. Enzymes from KOD Plus (ver. 2) (Toyobo, Osaka, Japan) were used. The obtained products were confirmed using 1.5% tris-acetate-EDTA (TAE) agarose gel electrophoresis. Following purification with ExoSAP (78 200; Affymetrix, California, USA), direct sequencing was performed to determine the sequence.

To elucidate the phylogenetic relationships among the 28S rDNA sequences of each sample, an alignment (ClustalW) was performed using GENETYX (ver. 1.2). Subsequently, a phylogenetic tree was constructed using the maximum likelihood (ML) method with the general time reversible (GTR) model using the molecular evolutionary genetics analysis (MEGA) software (ver. 7.0) (Kumar *et al.,* 2016). A bootstrap analysis comprising 1000 iterations was conducted to determine the support values for each branch. Sequences obtained in this study were deposited in the DNA Data Bank of Japan/European Molecular Biology

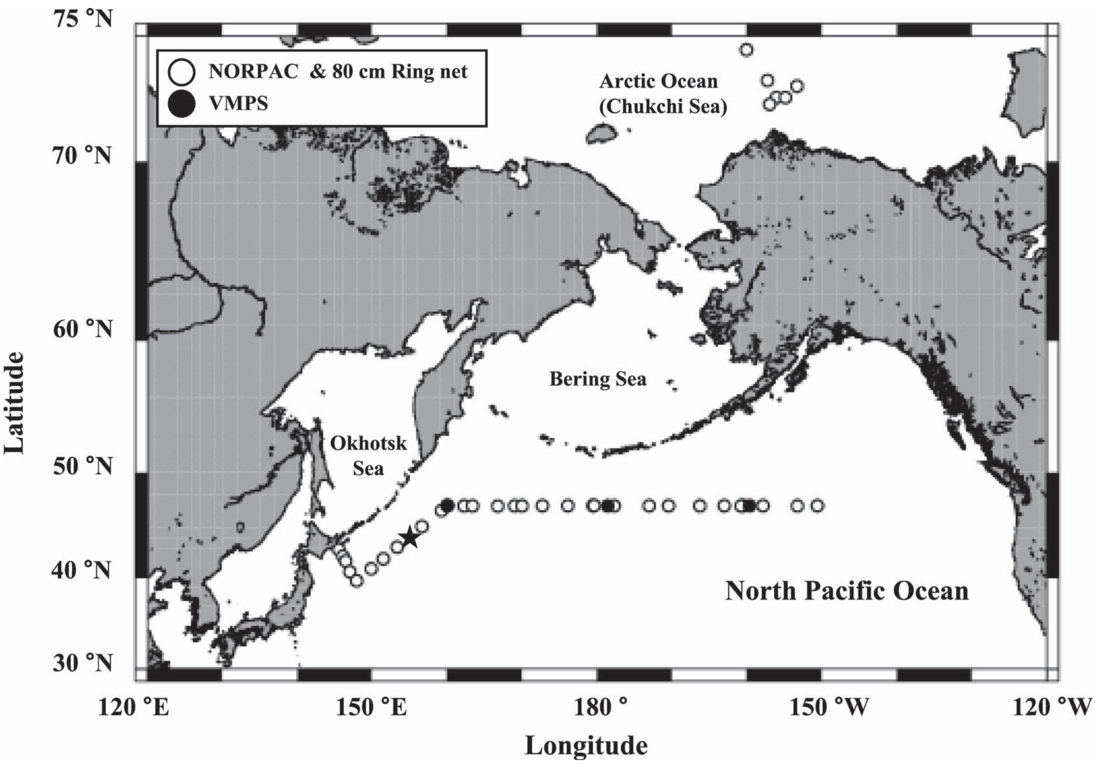


Fig. 1. Location of the sampling stations in the subarctic Pacific from 16 July to 17 August 2021 and those in the western Arctic Ocean (Chukchi Sea) from 16–20 September 2021. Vertical hauls of the NORPAC net and 80-cm ring net were made for the sample collections at the open circled stations, and the vertically stratified samplings from discrete depths were made from the VMPS at the stations shown by the solid circles. For details of the sampling/examined items at each station, see Supplemental Table 1. Solid star represents St. KNOT (44°N, 155°E), where copepod abundance and biomass were quantified by Yamaguchi *et al.* (2002) and utilized for constructing Fig. 10.

Laboratory (DDBJ/EMBL/GenBank) databases, each accompanied by a unique accession number (LC794525-LC794534).

Copepod community analysis

To evaluate the copepod community structure, we conducted imaging analysis using ZooScan on formalin-preserved zooplankton samples collected with a 335 μm mesh net. We quantified the abundance and biovolume of copepods at the genus or species level. The ZooScan measurements followed the methods outlined by Gorsky *et al.* (2010). Background images were recorded using a scanning cell filled with deionized water. We then scanned zooplankton subsamples, which ranged from 1/10 to 1/20 of the total volume, capturing images with ZooScan. Before the measurements, the floating specimens sank to the bottom, and the overlapping samples were separated using needles. The obtained images were divided into individual images using the ZooProcess software and saved. The sample images were digitized at a resolution of 2 400 dpi. Lastly, we uploaded the saved images to the EcoTaxa website (http://ecotaxa.obs-vlfr.fr/) for manual taxonomic identification and counting of copepods.

We calculated the area excluded in square millimeters (mm^2) from the area excluded data in pixels, using a conversion factor of 10.58 μm per pixel. The equivalent spherical diameter (ESD) was then determined using the formula:

$$ESD\ (mm) = 2 \times \sqrt{\frac{Area\ excluded\ \left(mm^2\right)}{\pi}}$$

The biovolume (mm^3) for each image was calculated using the following formula:

$$Biovolume\ \left(mm^3\right) = \frac{4}{3}\pi\left(\frac{ESD\ (mm)}{2}\right)^3$$

The samples were also examined microscopically. For specifically abundant samples, a 1/10 subsample was generated using a large-bore pipette. The subsamples were assessed under a stereomicroscope. We counted the copepod genera *Metridia*, *Pleuromamma*, *Gaetanus*, *Paraeuchaeta* and *Candacia*, which were found in the hosts of suctorian ciliates, noting their species and copepodite stages. Additionally, we recorded the presence or absence of suctorian ciliate attachments. The identification of suctorian ciliate species was conducted using the following references: Sewell (1951), Fernández-Leborans and Tato-Porto (2000), Dovgal (2002) and Dovgal *et al.* (2023).

The preference of suctorian ciliates for the adult females of each copepod species as attaching host was assessed using Ivlev's electivity index (Ei) formulated as follows:

$$Ei = \left(\frac{ri - pi}{ri + pi}\right)$$

In this equation, r_i represents the proportion of species i among the suctorian ciliate-attached to adult females, while p_i denotes the proportion of species i in the overall copepod community.

Onboard experiments

During the *Mirai* cruise, two laboratory-rearing experiments were conducted using fresh copepods (both individuals with and without attachment to suctorian ciliates). The first experiment aimed to determine whether suctorian ciliates increased in number or attached to the same individuals. Copepods (*Metridia pacifica* adult females, stage C6F) with fewer than ten attached ciliate cells were reared in 6-well microplates containing 20 mL of seawater at varying temperatures (3, 7 and 11°C) and under two feeding conditions (with food and without food). LED lighting with an intensity of 3.75 μmol m^{-2} s^{-1} was provided in the incubator to simulate a light and dark cycle of 15 hours of light (L) and 9 hours of dark (D), corresponding to conditions at a water depth of ~50 m. One 6-well microplate was set up for each temperature condition, with three wells designated for feeding and three wells for no-food conditions (water filtered using a glass microfiber (GF/F) filter). One copepod was placed in each well. Phytoplankton, primarily consisting of diatoms, were collected using a 63 μm NORPAC net and concentrated through sedimentation to serve as food. Copepods were assessed every 24 hours under a stereomicroscope, and changes in the number of attached ciliate cells were recorded. For microscopic observations, the copepods were anesthetized using a small amount of soda water, and rapid observation and counting were performed using photography. Observations continued until the host copepods died. The experiments were repeated throughout the cruise until fresh copepods with attached ciliates were collected.

To observe the attachment of novel suctorian ciliates to individual copepods, two *M. pacifica* C6F were reared in glass bottles (100 mL). One bottle contained copepods with attached ciliates, while the other had copepods without any attachment. The water temperature was maintained at 3°C, and the light conditions were set to 3.75 μmol m^{-2} s^{-1} for a photoperiod of 15 hours of light (L) and 9 hours of darkness (D). Each bottle included a chamber with a 200 μm mesh at the bottom, which served to isolate copepods with attached ciliates from those without. Additionally, feeding conditions were established with some bottles offering food while others did not. Each condition (mesh isolation and food availability) was replicated in triplicate (A–C). Every 24 hours, the individual copepods were examined using a stereomicroscope. If a novel suctorian ciliate attachment was detected on an unattached copepod, it was recorded and photographed. For microscopic observation, the copepods were anesthetized using a small amount of soda water.

RESULTS

Hydrography

For the hydrography at 0–1000 m in the subarctic Pacific during the study period, the temperature ranged from 1.4–22.0°C, with warmer temperatures at 0–10 m depth of west of 150°E near Hokkaido (Fig. 2a). Additionally, the water mass termed cold intermediate water (CIW), from the Okhotsk Sea (<4°C) (Anma *et al.,* 1990), was observed at a depth of ~100 m on the western side, extending 170°E along the observation line. Salinity ranged from 32.4–34.6, with higher values observed at the southernmost sampling station near Hokkaido and lower values at the eastern stations east of 160°W (Fig. 2b). The DO was high at depths of 10–100 m at most stations (Fig. 2c). Chl. *a* concentration was high above 50 m at most stations (Fig. 2d).

Suctorian ciliates

During our examination of the samples, we confirmed the attachment of five species of suctorian ciliates to the exoskeletons of 20 copepod species (Table I, Fig. 3). We observed species-specific interactions among the suctorian ciliates. Notably, *Paracineta gaetani* and *Acineta euchaetae* were frequently found on various host copepods. The former and latter had host copepods of 17 and 8 species, respectively. In contrast, *Rhabdophyra truncata* and *Copterus tyloloricatus* were only observed on three carnivorous copepod species each. Additionally, *Ephelota coronata* was only found on *M. pacifica* as a host.

Of the 20 host copepod species observed, 11 were suspension feeders, 8 were carnivores and only 1 was a detritivore. Each suspension-feeding copepod hosted one or two suctorian ciliate species, while the carnivorous copepod species hosted between one and four suctorian ciliates. The total length of adult females of the host copepods ranged from 2.4 to 11.0 mm, which is much larger than that of other copepod species in this region. Among the 20 different species of host copepods, only 9 were found in the NORPAC net samples collected from depths of 0 to 150 m. The remaining 11 species were identified in the VMPS samples collected from depths up to 3000 m. In the shallower 0 to 150 m depths, the dominant host copepods found throughout the region were *M. pacifica*, *Pleuromamma scutullata*, *Gaetanus simplex* and *Paraeuchaeta elongata*, all of which are known for their diel vertical migration (DVM) behavior.

Molecular analysis

We obtained 28S rRNA sequences for three species: *P. gaetani*, *R. truncata* and *E. coronata*. The phylogenetic tree constructed in this study revealed that *Paracineta* and *Rhabdophrya*, which belong to Endogenina and Exogenina, respectively, formed sister groups with *Acineta*, also belonging to Endogenina (Fig. 4). However, these relationships exhibited low bootstrap support values of 52% and 34%, respectively.

Within the analyzed species, we observed branches with high bootstrap values (>80%) for both *P. gaetani* and *R. truncata.* We also identified four haplotypes within *P. gaetani*. Although haplotypes were present in each species, we did not find any correlations between the morphotypes (such as stalk length, as shown in Fig. 3), the associated host copepods (Table I) and regional variations.

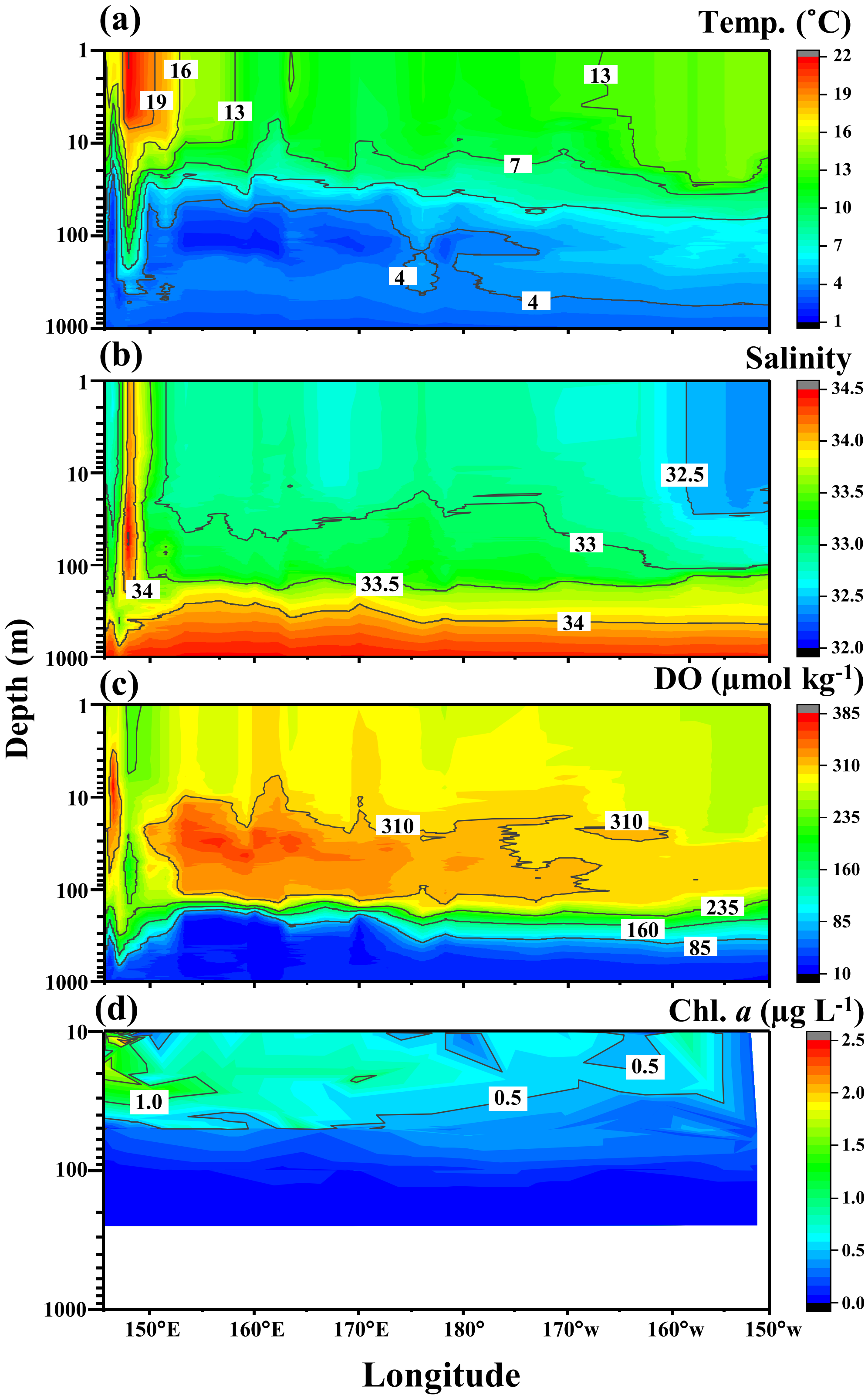


Fig. 2. Longitudinal changes in the vertical section of hydrography: (**a**) temperature, (**b**) salinity, (**c**) DO, and (**d**) chlorophyll *a* (chl. *a*) at 0–1000 m depths in the subarctic Pacific from 16 July to 17 August 2021. Note that vertical scales are on a log scale.

Table I: *Host specification of the suctorian ciliate species on the host copepod species observed in this study. The mean abundance of host species is derived from NORPAC net tow samples at 0–150 m depth in the subarctic Pacific. Circles indicate the four dominant host copepod species in this study. Asterisks represent reported as the suctorian host copepods by* Endo et al. (2022)*. Hyphens detected only for the VMPS samples and the samples in the western Arctic Ocean. Information on the total length of adult females (*Brodskii, 1950*), vertical distribution (*Yamaguchi et al., 2002, 2004*), and feeding modes (*Ohtsuka and Nishida, 1997*) is shown for the copepod species. DVM: species known to perform diel vertical migration, S: suspension feeders, C: Carnivores, D: detritivores*

Host copepod species	**Mean abundance of host species (ind m^{-3}: 0–150 m)**	**Suctorian ciliate species**						**Copepod ecology**		
		Paracineta gaetani***	***Acineta euchaetae***	***Rhabdophrya truncata******	***Copterus tyloloricatus***	***Ephelota coronata******	**Total species number**	**Total length (mm)**	**Vertical distribution (m)**	**Feeding mode**
• *M. pacifica* *	83.4	●				●	2	2.6–3.1	0–900 m (DVM)	S
• *Pleuromamma scutullata**	2.7	●					1	3.6–4.0	0–900 m (DVM)	S
• *Gaetanus simplex**	1.1	●					1	3.1–3.2	0–900 m (DVM)	S
• *Paraeuchaeta elongata**	1.7	●	●	●	●		4	6.3–6.5	0–1000 m (DVM)	C
*Heterorhabdus tanneri**	0.25	●	●		●		3	4.0–4.1	250–500 m	C
*Candacia columbiae**	0.20	●	●	●			3	3.7–4.1	0–500 m	C
*Gaetanus minutus**	0.10	●					1	3.2–3.6	100–1400 m	S
Pleuromamma xiphias	0.05	●					1	3.5–5.8	-	S
Pleuromamma abdominalis	0.003	●					1	2.4–4.3	-	S
Euchirella messinensis	-	●					1	4.5–5.4	-	S
Euchirella rostrata	-	●	●				2	2.9–3.1	700 m	S
Gaetanus brevispinus	-	●					1	4.0–4.8	400–1000 m	S
Gaetanus tenuispinus	-	●					1	3.5–3.8	270–750 m	S
Lucicutia grandis	-	●	●				2	6.5–8.2	2250–2750 m	S
*Heterostylites major**	-	●	●	●			3	4.7–5.2	-	C
Paraeuchaeta barbata	-		●				1	8.0–8.4	2250–2750 m	C
*Paraeuchaeta birostrata**	-				●		1	7.2–8.0	250–1900 m	C
Paraeuchaeta glacialis	-	●					1	10.0–11.0	-	C
Paraeuchaeta rubra	-		●				1	7.3–7.5	250–3000 m	C
*Scaphocalanus magnus**	-	●					1	4.5–5.2	400–1500 m	D
Total		17	8	3	3	1				

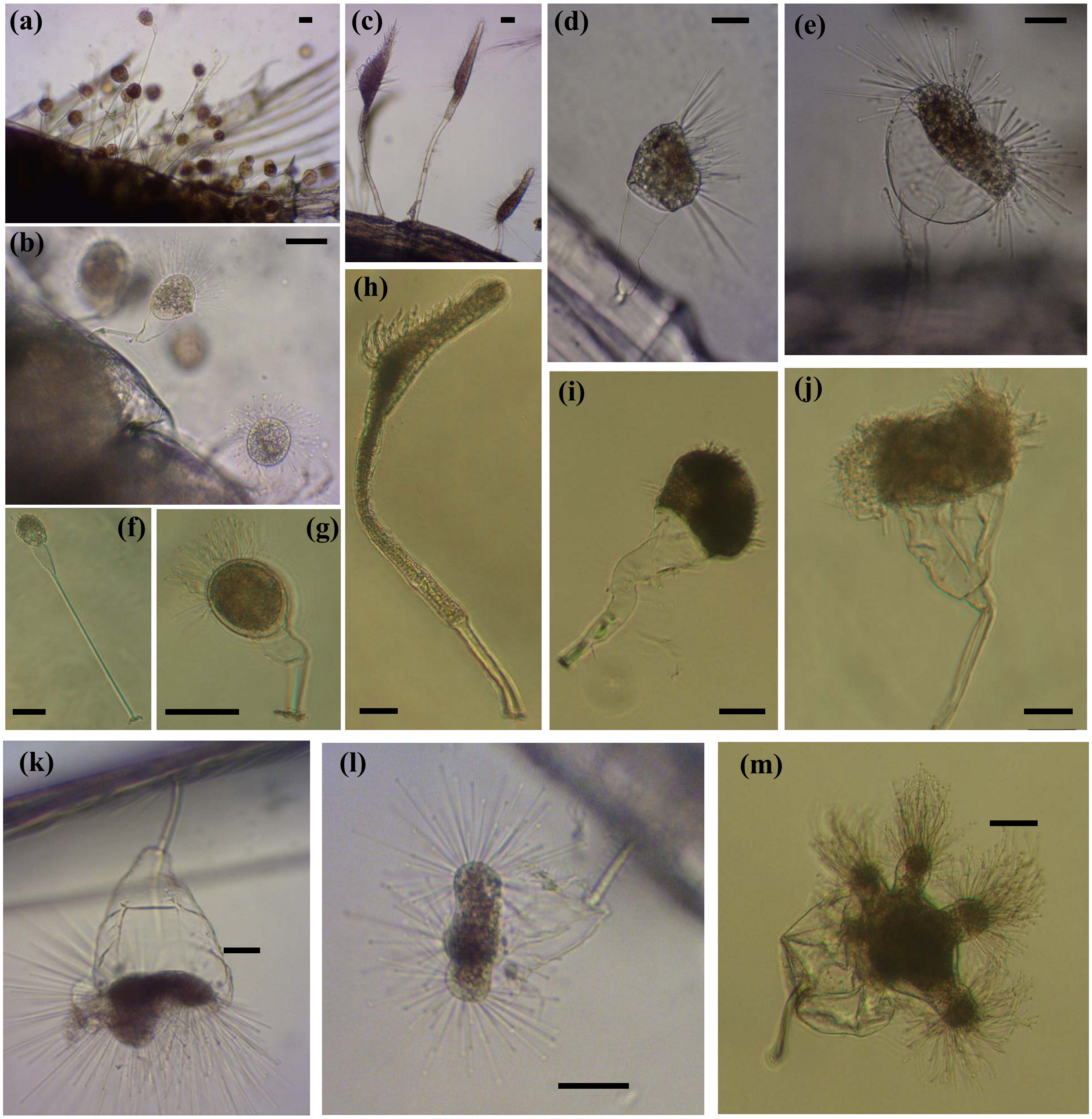


Fig. 3. Diagrams of suctorian ciliate species attached on the calanoid copepod species observed in this study: (**a**) *Paracineta gaetani* with long stalk, (**b**) *P. gaetani* with short stalk, (**c**) *Rhabdophrya truncata*, (**d**) *Ephelota coronata*, (**e**) *Acineta euchaetae*. For pictures taken under the biological microscope on ethanol preserved conditions: (**f**) *P. gaetani* with long stalk, (**g**) *P. gaetani* with short stalk, (**h**) *R. truncata*, (**i**) *E. coronata*, (**j**) *A. euchaetae*. *C. tyloloricatus*: (**k, l**) pictures taken under the biological microscope at living conditions, (**m**) ethanol preserved condition. Scale bars = 50 μm.

Copepod community

The abundance of copepods at depths of 0–150 m along the east–west transect varied between 58 and 1346 ind. m^{-3} (Fig. 5a). Taxonomically, *Metridia* spp. were dominant in the western region, while *Calanus* spp. were more abundant in the east. Throughout the entire region, *Pseudocalanus* spp. and *Oithona* spp. were also found to be abundant.

The copepod biovolume ranged from 58 to 1 051 mm^3 m^{-3} (Fig. 5b). Biovolume analysis indicated that larger body-sized species, such as *Neocalanus* spp. and *Eucalanus bungii*, made significant contributions to the overall biovolume across the region.

The proportion of the suctorian ciliate host copepod species within the entire copepod community was low, typically comprising <10% of for most of both abundance and biovolume at most sampling stations (Fig. 5). In terms of geographical distribution, the occurrence of host copepod species was notably higher in the western region, primarily due to the dominance of *M. pacifica* in that area.

Suctorian ciliates on the four dominant host copepods

Among the four dominant host copepods, *M. pacifica* showed a high abundance west of 170°E (Fig. 6a). The prevalence of

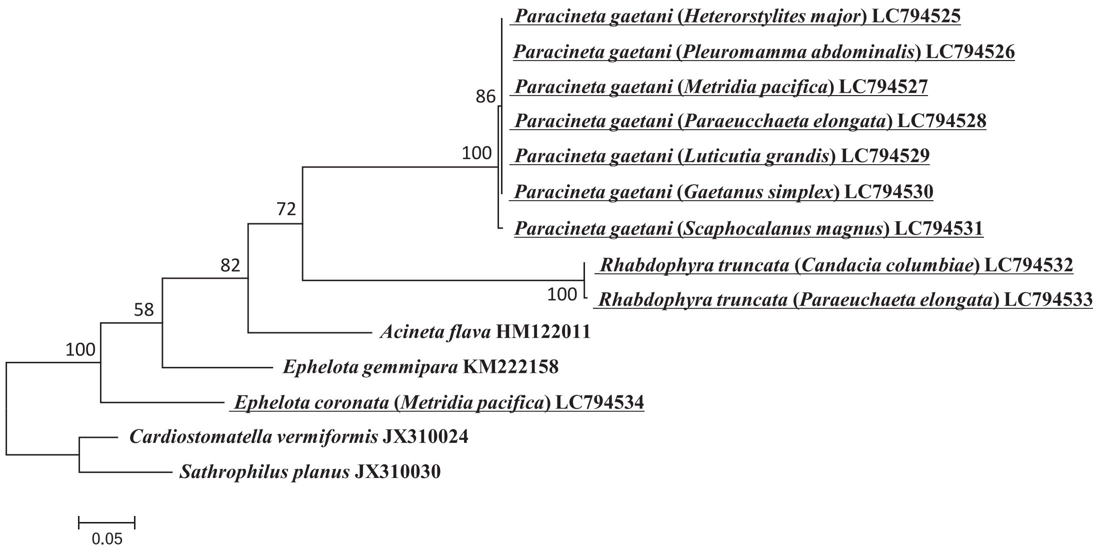


Fig. 4. An ML tree constructed from 28S ribosomal RNA (28S rRNA) gene nucleotide sequences for the suctorian ciliates. Numbers at the nodes represent the bootstrap percentages (%) based on the 1000 replicates. The horizontal scale bar corresponds to 10 substitutions per 100 nucleotide positions. Novel sequences added by this study are underlined. The species name in the parentheses indicates the host copepods.

Table II: *Mean abundance of adult females in the major host copepod species (Metridia pacifica, Pleuromamma scutullata, Gaetanus simplex, Paraeuchaeta elongata, and Candacia columbiae), mean infected specimens of each species, mean infection rates of each species and Ivlev's* E_i. *SE: standard error*

	Host copepod species				
	M. pacifica	***P. scutullata***	***G. simplex***	***P. elongata***	***C. columbiae***
Mean abundance of adult female (inds m^{-3})	10.2	1.60	0.45	0.07	0.042
Mean abundance of infected specimens (inds m^{-3})	4.9	0.03	0.19	0.05	0.003
Mean prevalence (% ± SE)	28.8 ± 5.4	1.08 ± 0.40	43.9 ± 7.0	58.8 ± 11.2	10.0 ± 9.5
Ivlev's E_i	0.426	−0.351	0.846	0.100	−0.094

suctorian ciliates, primarily *P. gaetani*, was also notably high in this region, peaking at 89.8%. *P. scutullata*, which belongs to the same metridinid family, also showed high abundance in the western area (Fig. 6b), but its prevalence was relatively low, reaching a maximum of 9.1% for C6F. In contrast, *G. simplex*, did not display a clear east–west pattern regarding abundance or the prevalence of suctorian ciliates (Fig. 6c); in fact, its prevalence reached 100% at certain stations. Lastly, *P. elongata* hosted four different suctorian ciliates, marking a distinction from the three previously mentioned copepod species, and no east–west variations were observed in either copepod abundance or suctorian ciliate prevalence (Fig. 6d).

In terms of the host preferences of suctorian ciliates, *G. simplex* displayed the highest Ivlev's *Ei* by suctorian ciliates at 0.846, followed by *M. pacifica*, which had an index of 0.426 (Table II). On the other hand, *P. scutullata* showed an avoidance tendency by the suctorian ciliates with an index of −0.351. The mean prevalence of suctorian ciliates among the three preferred copepod species was notably high, ranging from 28.8% to 58.8%. In contrast, the two avoided copepod species showed a much lower mean prevalence of suctorian ciliates, ranging from 1.1% to 10.0%.

For the ontogenetic changes in prevalence, suctorian attachment was only observed in copepodite stages older than C4 across all copepod species (Fig. 7). Consequently, no infections by suctorian ciliates were found in the younger stages (C1–C3) of any copepod species. The highest prevalence of suctorian ciliates was observed in C6F for most copepod species.

There was no significant relationship between the prevalence of suctorian ciliates and the abundance of host copepods (Fig. 8). However, a high prevalence was observed in the dominant region of CIW within the water column. This pattern was consistent among the four dominant host copepod species. Based on the temperature–salinity (T–S) diagram derived from the mean T–S values in the 0–150 m water column, a high prevalence of suctorian ciliates was identified at high latitudes in the subarctic domain, particularly in temperatures below 6°C.

Laboratory experiments

During laboratory rearing, the majority of specimens showed a decrease in the number of suctorian ciliate cells throughout the experiments (Fig. 9a). However, in some specimens, the number

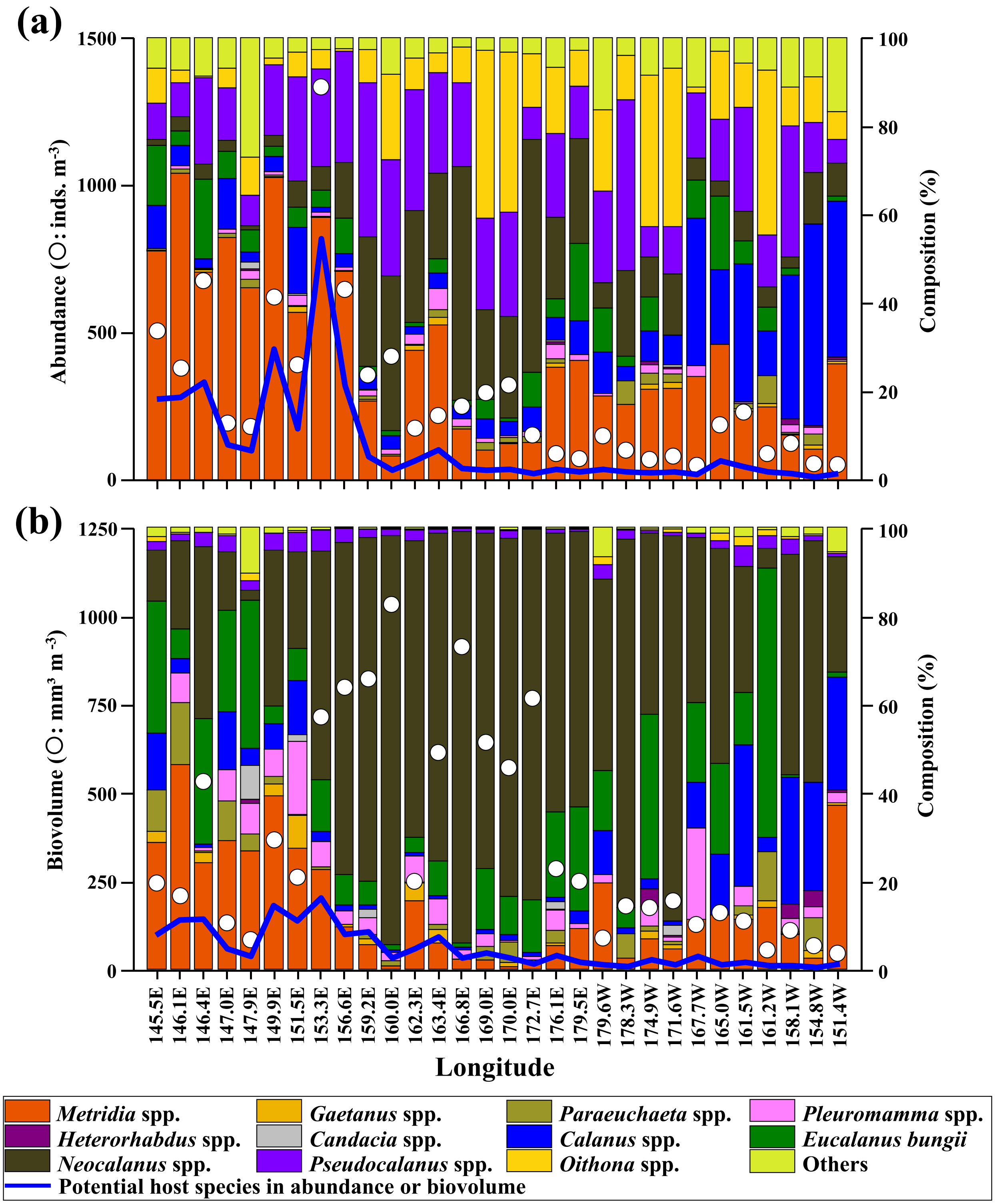


Fig. 5. Longitudinal alterations in copepod abundance (**a**) and biovolume (**b**) and their taxonomic compositions along the east–west transect in the subarctic Pacific from 16 June to 17 August 2021. Blue lines indicate the total abundance or biovolume of the potential host species for suctorian ciliates.

of suctorian cells increased regardless of the food-rearing conditions. Additionally, budding was observed several times, with one or two buds per instance (Fig. 9b).

In the laboratory experiments evaluating the attachment of suctorian ciliates to a novel specimen, attachment was noted on the 7th day, both when mesh separation was present and no food was available, as well as on the 7th and 8th days when there was no mesh separation and food was available (Table II). Thus, attachment to the novel copepod specimen occurred regardless of the mesh separation and food availability.

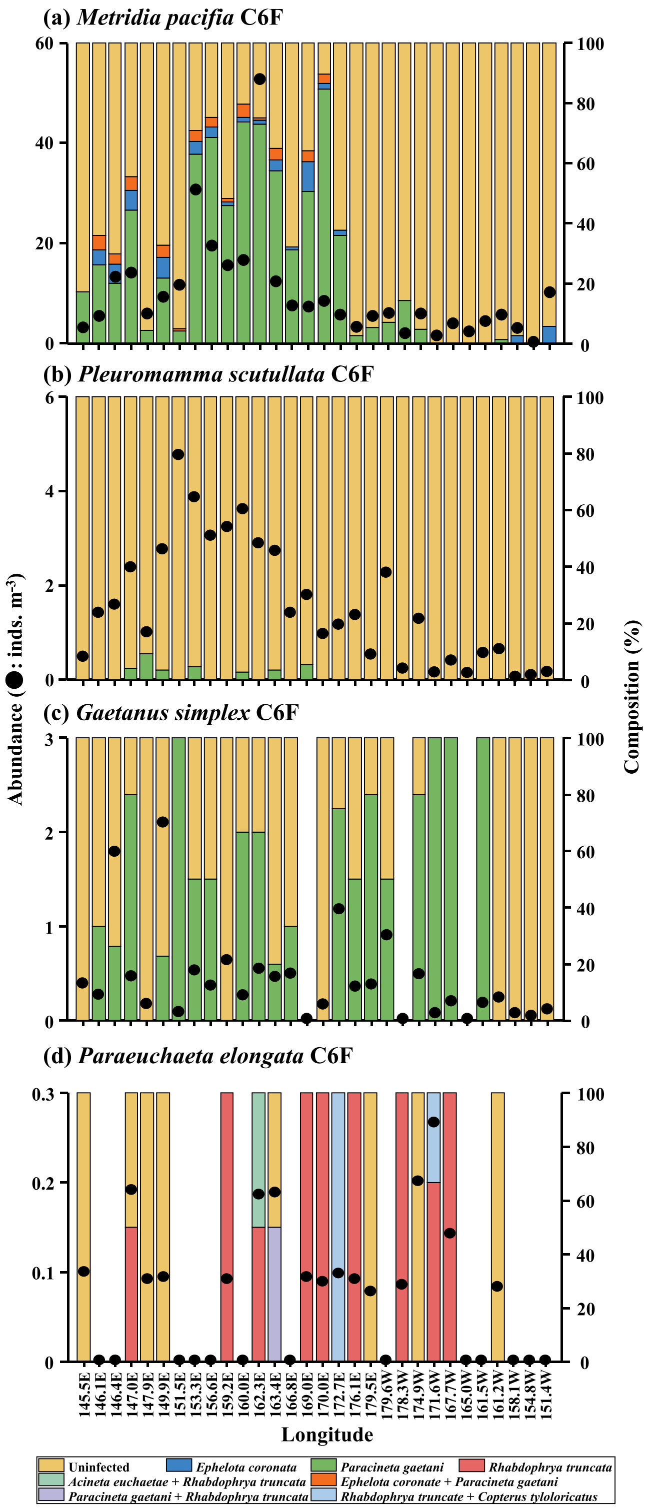


Fig. 6. Longitudinal changes in abundance (black dots) and composition (bars) of suctorial ciliates on the adult females of the major host copepod species: (**a**) *Metridia pacifica*, (**b**) *Pleuromamma scutullata*, (**c**) *Gaetanus simplex* and (**d**) *Paraeuchaeta elongata* along the east–west transect in the subarctic Pacific. Differences in the color columns indicate differences in the suctorian ciliate species.

DISCUSSION

This study clarifies six key points regarding the ecology of epibiont suctorian ciliates on pelagic copepods in the oceanic region of the subarctic Pacific: (i) In this area, 20 copepod species serve as basibiont hosts, while five species of epibiont suctorian ciliates were identified, each showing specific preferences for particular copepod species. (ii) The prevalence of suctorian ciliates was higher in regions characterized by cold water temperatures. (iii) Suctorian ciliates were more frequently found on late copepodite stages, particularly on stage C6F, while they were rare on stage C6M. (iv) Large-bodied carnivorous copepods were the most preferred host species for these ciliates. (v) Although genetic haplotypes were found in suctorian ciliates, no relationships were observed between haplotypes and morphotypes, host copepod species or geographic areas. (vi) Laboratory rearing experiments were successful, but improvements are needed in the experimental conditions for rearing. In the following sections, we will discuss each of these points in detail.

The host copepod species for suctorian ciliates is rare

The basibiont host copepod species of suctorian ciliates are minimal in both abundance and biomass. In terms of abundance, the dominant species are small-sized copepods, such as *Oithona* spp. from the Cyclopoida order, *Oncaea* spp. from the Poecilostomatoida order, and *Pseudocalanus* spp. from the Calanoida order (Yamaguchi *et al.,* 2002). In terms of biomass, the dominant species are larger copepods, like *Neocalanus* spp. and *E. bungii*, which belong to the Calanoida order and have a diapause phase in the deep layer (Ikeda *et al.,* 2008). Interestingly, these dominant species, whether in abundance or biomass, are not selected as hosts for suctorian ciliates, and no suctorian cells have been observed on their body surfaces (Table I).

It is believed that the numerically dominant small-sized species are not suitable hosts for suctorian ciliates due to their limited surface area for attachment and their short life spans. Conversely, larger Calanoida species such as *Neocalanus* spp. and *E. bungii*, which are all suspension feeders, undergo a diapause period at greater depths, during which they stop feeding and remain in that layer throughout the day (Kobari and Ikeda, 1999, 2001a, 2001b; Shoden *et al.,* 2005). Research indicates that suctorian ciliates primarily feed on flagellates as part of their dietary habits (Ohtsuka *et al.,* 2011). Therefore, it is thought that they do not attach to larger copepod species like *Neocalanus* spp. and *E. bungii* because their deep-sea diapause period is disadvantageous for the ciliates' nutritional needs.

The host copepods of suctorian ciliates were not dominant species within the copepod community, accounting for <10% of the total copepods at most sampling stations (Fig. 5). Interestingly, the host copepods were limited to certain families, including Aetideidae, Candaciidae, Euchaetidae, Heterorhabditidae, Lucicutiidae, Metridinidae and Scolecitrichidae (Table I). These findings suggest that when searching for a suitable host specimen, the swarmer cells of suctorian ciliates may rely on chemical signals or chemosensory secretions from their target species or taxa.

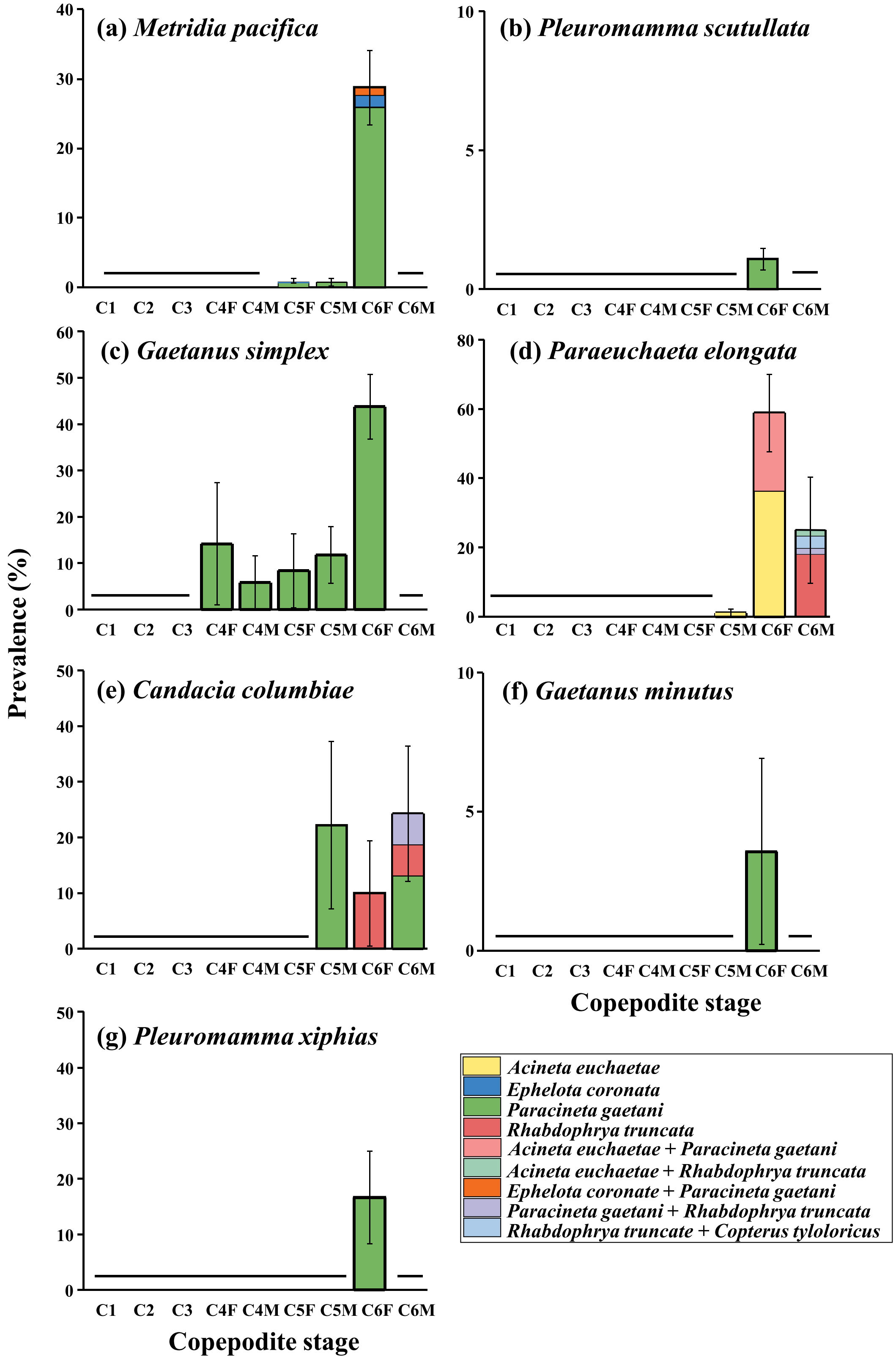
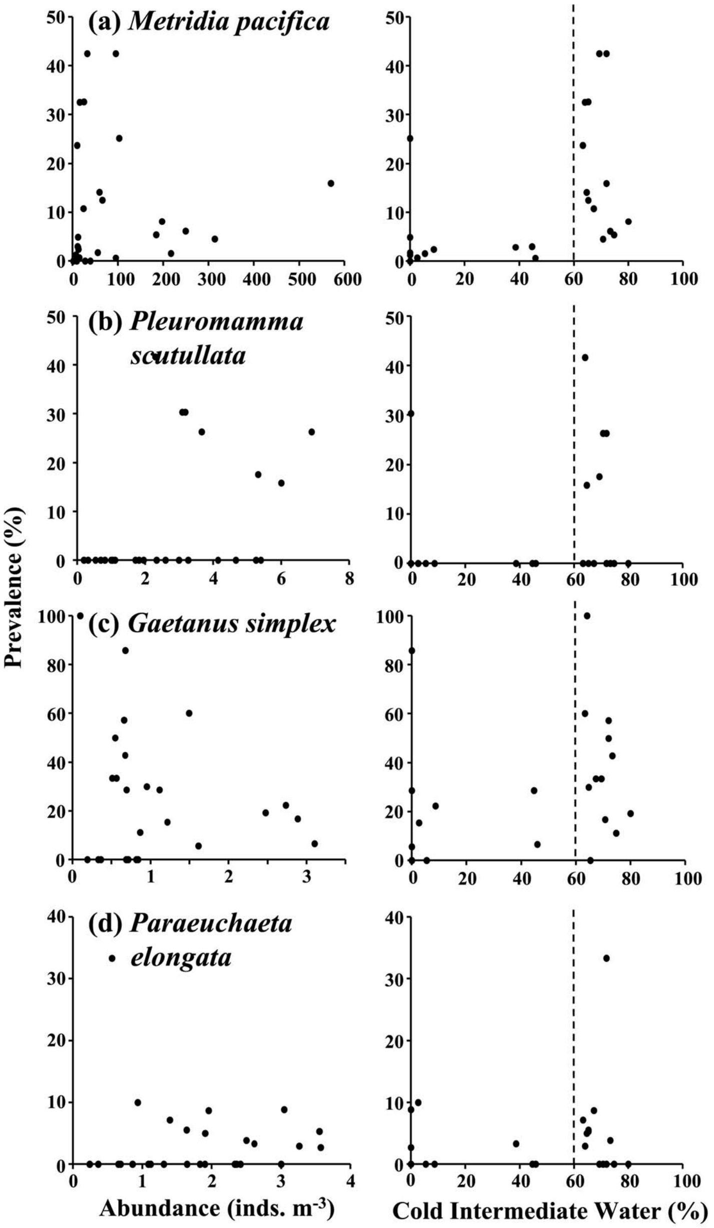


Fig. 7. Summary of the mean prevalence for each copepodite stage of the host copepod species observed in this study for the subarctic Pacific. Vertical bars represent standard errors of the prevalence. Stages marked by the horizontal lines indicate no occurrence of the suctorian ciliates. F: females, M: males.



(e) T-S diagram

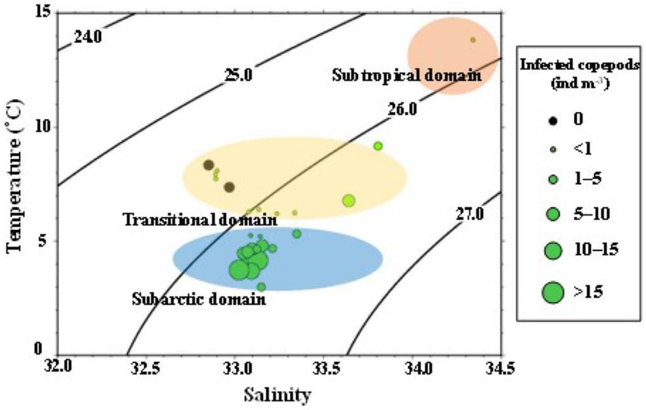


Fig. 8. Scatter plots between the prevalence of the suctorial ciliates (%) and abundance of the host copepods (left panels) and between the prevalence of the suctorian ciliates (%) and proportion of the CIW (<4°C, CIW) at the 0–150 m water column (right panels) of (**a**) *Metridia pacifica*, (**b**) *Pleuromamma scutullata*, (**c**) *Gaetanus simplex*, and (**d**) *Paraeuchaeta elongata*. Dashed lines in the right panels show that the position at 0.6 (=60%) of CIW was present at 0–150 m water column volume at each station. (**e**) Scatter plots of the suctorian ciliate infected copepods at 0–150 m depths plotted on the T–S diagram observed in the subarctic Pacific. Plotted points in the panel represent mean values of 0–150 m data at each station. Separating the three regions: subtropical, transitional, and subarctic regions was also made.

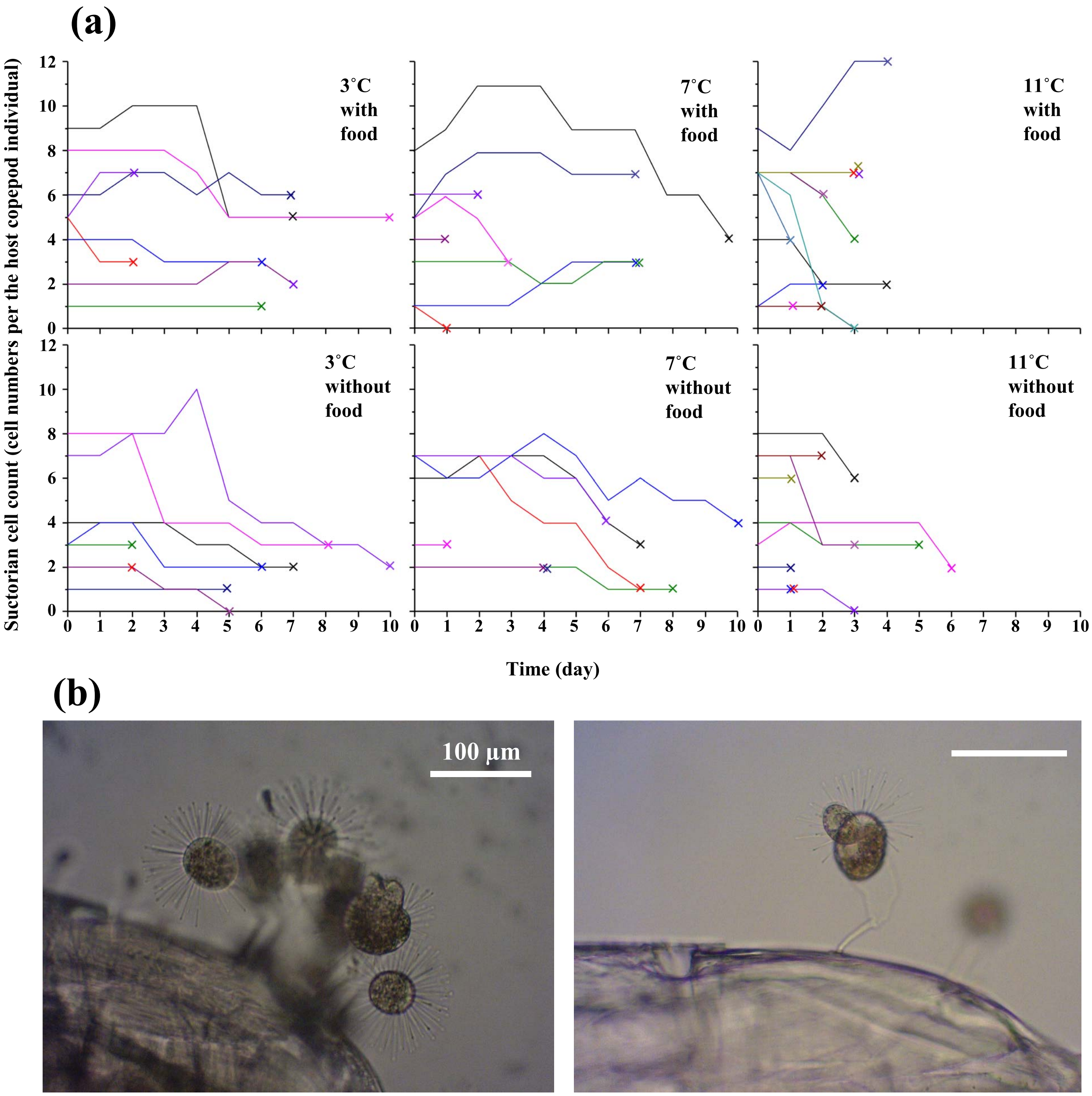


Fig. 9. (**a**) Results of temporal changes in the infected cell numbers of suctorian ciliates attached on the host copepods (*Metridia pacifica* C6F) reared at six different conditions (3, 7, 11°C and with food or without food) for 10 days. Line breaks indicate the death of the host copepods. (**b**) Budding of *Paracineta gaetani* observed during the laboratory rearing. Scale bars = 100 μm.

Among the two host species within the same family (Metridinidae), *M. pacifica* was found to be more prevalent, while *P. scutullata* had a lower prevalence (Fig. 6). Additionally, *M. pacifica* showed a high selectivity index, whereas *P. scutullata*'s index was negative (Table II). Both Metridinidae species exhibit DVM, spending the day at deeper depths and migrating upwards at night. The only notable difference is that *P. scutullata* is slightly larger in size (Yamaguchi and Ikeda, 2000a; Padmavati *et al.*, 2004). While both species share similar ecological behaviors, the differences in prevalence and selectivity indicate that suctorian ciliates may have a preference for certain hosts; however, the underlying mechanism remains unknown.

Long intermolt durations of copepods under low water temperature conditions lead to a high prevalence of suctorian ciliates

All suctorian ciliate basibionts are associated with deep-sea copepods. The abundant species that serve as hosts for these ciliates exhibit DVM, remaining in deeper waters during the day and migrating upward at night (Yamaguchi *et al.*, 2004; Abe *et al.*, 2012). The reason these copepods are selected as hosts for suctorian ciliates is their long intermolt duration, which is caused by the cold temperatures found in deep water. Observations of euphausiids indicate that since suctorian ciliates attach to the host's body surface, they may detach during the host's molting process (Nicol, 1984; Endo *et al.*, 2017). To minimize the detachment of suctorian ciliates, host copepods require a prolonged intermolt duration in cold water conditions. For instance, research on *M. pacifica*, reared at 3, 5 and 8°C in the laboratory, found that the development time from egg to adult was 183, 167 and 112 days, respectively (Padmavati and Ikeda, 2002). It is well known that there is a negative relationship between the development time of copepods and water temperature (Mauchline, 1998). The prevalence of deep-sea copepods among the hosts of suctorian ciliates likely results from their preference for species with long intermolt durations and extended generation times, which are associated with low water temperatures. Consequently, suctorian ciliates can remain attached to the host specimens for prolonged intermolt periods in cold water conditions.

In the study area, cold water temperature conditions were observed primarily on the western side, where a water mass known as the CIW is predominant (Fig. 2a). This water mass originates from the Okhotsk Sea, the southernmost ice-covered ocean in the Northern Hemisphere (Anma *et al.,* 1990). For all four dominant host copepod species, the prevalence of suctorian ciliates was notably high in regions where the CIW accounted for over 60%, as well as in areas with low water temperatures, as illustrated in the T–S diagram (Fig. 8).

Regarding the latitudinal variation in the prevalence of *P. gaetani* on *M. pacifica* C6F, it has been observed to be high (67%) at higher latitudes (50°N), gradually decreasing in warmer, lower latitudes until it reached 0% south of 45°30'N. This decline is believed to be linked to changes in intermolt duration due to temperature gradients along latitude, with colder conditions at higher latitudes (Ohtsuka *et al.,* 2011). The extended intermolt duration of copepods under low-temperature conditions results in a higher prevalence of suctorian ciliates. This phenomenon may lead to both vertical changes in prevalence in the cold deep layers and spatial (geographical) changes in the prevalence of suctorian ciliates. Consequently, high prevalence is associated with cold water mass conditions and cold high-latitude regions, highlighting the relationship between geographical water mass distribution and north–south variations.

Suctorian ciliates preferentially choose adult female copepods as hosts because they do not molt and long stage duration

When a host molts, the epibiont suctorian ciliates detach from it (Nicol, 1984; Endo *et al.,* 2017). In this study, we did not observe any occurrence of suctorian ciliates in younger copepodite stages C1–C3 (Fig. 7). The younger developmental stages are small, have short stage durations (Padmavati and Ikeda, 2002) and frequently molt, making them less suitable as attachment substrates for suctorian ciliates. Conversely, the highest prevalence of suctorian ciliates was found on adult females (C6F). Because C6F represents the final developmental stage, these individuals do not molt and have the longest duration and longevity within the species. As a stable substrate, C6F may provide an ideal environment for suctorian ciliates. In fact, Endo *et al.* (2022) found that among 259 individuals observed for the suctorian ciliate host copepods in the subarctic Pacific, 256 were identified as C6F. In our study, among the seven species examined, six showed the highest prevalence of suctorian ciliates at the C6F stage (Fig. 7).

The difference in the prevalence of suctorian ciliates between C6F and C6M is noteworthy. While C6F shows a high prevalence of suctorian ciliates in both *M. pacifica* and *G. simplex*, no attachment to C6M has been observed. These sexual differences in prevalence are believed to be linked to the distinct ecologies of C6F and C6M. In Aetideidae and Euchaetidae, which host suctorian ciliates, the feeding appendages of C6M have degenerated (Hiragi and Yamaguchi, 2019). C6F undergoes diel vertical migration (DVM), while C6M stays in the deep layer throughout the day, exhibits a smaller body size, ceases feeding and has a shorter lifespan (Yamaguchi and Ikeda, 2000b, 2002a, 2002b). In contrast, the feeding appendages of C6M in *M. pacifica* do not degenerate (Hiragi and Yamaguchi, 2019). It is well documented that C6F of *M. pacifica* performs DVM, whereas C6M remains in the deep layer during the day (Batchelder, 1985; Padmavati *et al.,* 2004).

The food sources for suctorian ciliates primarily include small unicellular organisms, such as flagellates (Ohtsuka *et al.,* 2011). Given these circumstances, if suctorian ciliates attach to C6F, which performs DVM, they would benefit from a good attachment substrate due to C6F's larger body size. This migration to the surface layer, where flagellates are abundant, could provide nutritionally favorable conditions. In contrast, the small body size of C6M makes it an unsuitable substrate for attachment. Its short lifespan and tendency to inhabit deeper layers—where food sources like flagellates are likely to be scarce—explain why C6M is not considered a suitable attachment organism for suctorian ciliates.

Carnivorous large-sized copepods are preferred as hosts

In this study, we conducted a quantitative analysis of the copepod community based on NORPAC net samples collected from depths of 0 to 150 m. Additionally, we analyzed samples collected by VMPS, which took stratified samples from depths of 0 to 3000 m at three stations across the western, central and eastern regions of the longitudinal line. However, we lacked data on the abundance or biomass from the VMPS samples. Therefore, we referenced the abundance and biomass data of copepods found at depths of 0 to 4000 m in the same subarctic Pacific (Yamaguchi *et al.,* 2002) as well as body size data (Brodskii, 1950). Using this published information, we organized the copepods according to their abundance, biomass and body size, and subsequently assessed the characteristics of the suctorian ciliate-hosting copepods (Fig. 10).

In the study conducted by Yamaguchi *et al.* (2002), three feeding modes were examined: suspension feeders, detritivores and carnivores. The proportion of host copepods for suctorian ciliates varied significantly among these categories. Specifically, suspension feeders comprised 8 out of 59 species (13.6%), detritivores accounted for one out of 18 species (5.6%), and carnivores included 7 out of 24 species (29.2%) as hosts for suctorian ciliates. Carnivorous copepod species hosted 3 to 4 species of suctorian ciliates, whereas suspension feeders and detritivores hosted only 1 to 2 species each (Table I). Based on abundance and biomass, the top five carnivorous copepod species were identified as hosts for the suctorian ciliate species (Fig. 10). Additionally, it was found that larger carnivorous species were more likely to be selected as hosts.

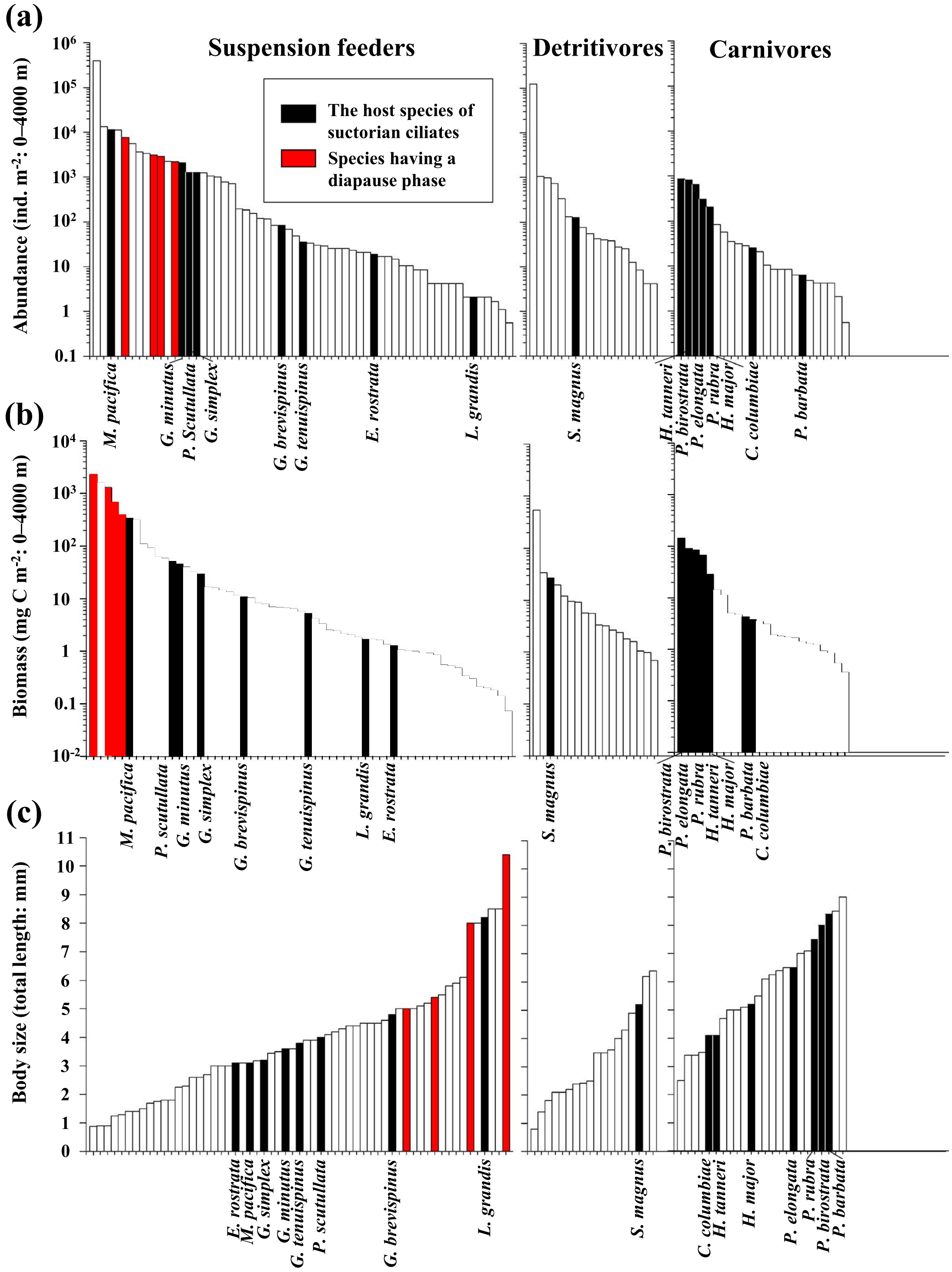


Fig. 10. The pelagic copepod species in order of (**a**) abundance, (**b**) biomass and (**c**) body size of suspension feeders (left), detritivores (middle), and carnivores (right) in the subarctic Pacific. The black and red filled bars indicate that the host species of the suctorian ciliates and species having a diapause phase, respectively. Data on abundance and biomass are derived from Yamaguchi *et al.* (2002), and on body size (total length of adult females) are from Brodskii (1950).

The characteristics of host species for suctorian ciliates in carnivorous copepods include high abundance, significant biomass and large body size. In contrast, for suspension feeders, the relevant characteristics are large copepod species, such as *Neocalanus* spp. and *E. bungii*, which enter a diapause phase in deeper layers (Kobari and Ikeda, 1999, 2001a, 2001b; Shoden *et al.,* 2005). However, these copepod species are not selected as hosts for suctorian ciliates because of their deep-sea diapause period in their life cycle, as previously mentioned.

In contrast, detritivorous copepods, such as those from the Scolecitrichidae family, could serve as potential hosts; however, only *Scaphocalanus magnus* has been selected as a host, and the proportion of suctorian ciliates found on it is extremely low. This indicates that detritivorous species, which primarily inhabit deeper waters and possess chemoreceptors or specialized feeding mechanisms, are not favored as hosts for suctorian ciliates.

Consequently, suctorian ciliates prefer carnivorous copepods that exhibit large body size, high abundance and significant biomass as host species. Since many suctorian ciliates utilize carnivores as hosts, this suggests a preference for these types of copepods. One possible explanation for this preference is that larger carnivorous copepods are less likely to be preyed upon, resulting in a lower predation risk.

The ecology of suctorian ciliates revealed by molecular analysis and laboratory experiments

In this study, we successfully conducted a molecular analysis of *P. gaetani*, which infected the highest number of copepod species, totaling 17. The analysis of suctorian ciliates included cells from the most abundant species, *M. pacifica*, as well as the deep-sea species *Lucicutia grandis*, which appears in smaller quantities. Although multiple haplotypes were identified, there was no correlation found with morphotypes, host copepod species or geographic distribution (Fig. 4). This indicates that the suctorian ciliate *P. gaetani* can move among the 17 copepod species, spanning from epipelagic to deep-sea environments.

Notably, deep-sea species like *L. grandis* are known to inhabit depths of 2250–2750 m throughout the day without engaging DVM (Yamaguchi *et al.,* 2002). This suggests that swarmer cells may attach to new hosts in these deep layers. Indeed, the infection of suctorian ciliates in *P. elongata* C6M, which remains in the deep layer throughout the day, demonstrates the attachment of suctorian ciliates (Fig. 7d). This supports the notion that swarmer cell attachment to new individuals occurs in the deeper layers. However, due to the low population density of deep-sea copepods, it is believed that the formation of localized hotspots, where organisms are concentrated at higher densities, is essential for successful attachment in the deep layer.

Through laboratory experiments, it was observed that the cell number of suctorian ciliates increased, with instances of budding occurring (Fig. 9). The newly attached cells can grow into trophonts within 24 hours. Kobayashi *et al.* (2011) reported that in laboratory experiments with the larger species *Ephelota gigantea*, the suctorian ciliates reached their maximum size in one day, and each cycle from settlement to the next settlement took about five days. The findings of this study indicate that the growth from settlement to trophont is also completed within 24 hours in *P. gaetani*.

Table III: *Results of laboratory rearing on infection transmission from infected to non-infected specimens of Metridia pacifica C6F under 3°C conditions. This study was tested under different conditions: with or without food and with or without mesh separation. Laboratory rearings were conducted in triplicate (A, B, and C). The symbol "×" indicates that no infection was observed during the 10-day observation period. In the three rearing conditions, new attachment of suctorians was noted after 7 or 8 days*

	Separation with 200 μm mesh			**No separation with mesh**		
Condition	**A**	**B**	**C**	**A**	**B**	**C**
With food	×	×	×	8 days	×	7 days
Without food	7 days	×	×	×	×	×

The attachment to new individuals is carried out by swarmers, which may have the ability to swim short distances. This suggests that they can search for new hosts not only through simple contact (Kent, 1981; Fernández-Leborans and Cárdenas, 2009; Kobayashi *et al.,* 2011). However, the prolonged time it takes for the swarmers to attach to new individuals, ranging from 7 to 8 days (Table III), suggests that their swimming ability is limited. While it has been demonstrated that rearing experiments are feasible, further research is needed to ascertain whether these observations reflect the species' natural ecology.

CONCLUSION

This study found that the host copepods of suctorian ciliates in the oceanic region of the subarctic Pacific belong to seven specific families. However, these copepods are not dominant species in terms of either abundance or biomass. At most sampling stations, the copepods hosting suctorian ciliates accounted for <10% of the total copepod population in terms of abundance and biomass. Suctorian ciliates prefer to attach to carnivorous and larger-bodied copepod individuals, likely due to the lower predation risk associated with these hosts. Since suctorian ciliates attach to the body surface of copepods, they detach from their hosts during each molting event. Consequently, the prevalence of suctorian ciliates is higher in conditions that promote longer intermolt durations, such as cooler water temperatures. The highest prevalence of suctorian ciliates is observed in adult female copepods, as they do not undergo molting. In contrast, the prevalence in adult male copepods is low. This is thought to be related to males typically residing in deeper water layers where food availability is limited, as well as their smaller body sizes, which provide less surface area for attachment, and shorter life spans. Molecular analysis indicated that suctorian ciliates share haplotypes across multiple copepod hosts, demonstrating their ability to move between different copepod species. Although it is possible to rear suctorian ciliates in the laboratory while attached to copepods, there is a need to improve the experimental conditions. This study is unique as it examines the factors influencing the host preferences of suctorian ciliates from the perspective of the ecology of their copepod hosts.

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SUPPLEMENTARY DATA

Supplementary Data can be found at Journal of Plankton Research online.

DATA AVAILABILITY

Data are available from the corresponding author upon request.

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