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Original article

Bacterial communities in *Branchinella thailandensis* and *Streptocephalus sirindhornae*

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Abstract

The fairy shrimp is a freshwater crustacean found in both temporary and permanent freshwaters. In Thailand, fairy shrimp are farmed as live food for ornamental fish. This study aimed to investigate the bacterial compositions in two fairy shrimp species, *Branchinella thailandensis* and *Streptocephalus sirindhornae*. Both species were cultured, and total DNA was extracted. The V3-V4 region of the 16S rRNA gene was amplified and sequenced using Illumina Miseq. All data were analyzed by Illumina 16S Metagenomics (version 1.0.1) workflow in Base Space-Illumina. Each read was blasted against the Illumina-curated version of the Greengenes database to determine the operational taxonomic units (OTUs) corresponding to the 16S rRNA gene sequence. The results showed that the Shanon-Weiner diversity index of bacterial compositions in *B. thailandensis* and *S. sirindhornae* were 2.135 and 3.122, respectively. The evenness and genus-level richness of the bacterial composition in *B. thailandensis* were 0.364 and 354 genera, respectively. The dominant bacterium found in *B. thailandensis* was *Nevskia.* In *S. sirindhornae*, the evenness and genus-level richness of the bacterial composition were 0.521 and 400 genera, respectively. *Azohydromonas* was the dominant bacterium. Our results showed that the compositions and proportions of bacterial communities were specific to each species of fairy shrimp. This study will be useful for further experiments in aquaculture and ecological studies related to symbiotic interaction.

Key words: bacteria, fairy shrimp, *Branchinella thailandensis*, *Streptocephalus sirindhornae*

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Introduction

The fairy shrimp is a freshwater crustacean which is found in both permanent and temporary freshwater habitats. The adult male fairy shrimp has a body length of approximately 16-28 mm, while the female has a body length of 18-30 mm. In Thailand, three species of fairy shrimp have been described: *Streptocephalus sirindhornae*, *Branchinella thailandensis* and *Streptocephalus siamensis* (Sanoamuang et al. 2000, 2002, Sanoamuang and Saengphan 2006). Currently, *S. sirindhornae*, and *B. thailandensis* are popular in aquaculture in Thailand, and both species are farmed as live food for ornamental fish because fairy shrimps have high nutritional values and produce huge numbers of cysts (Sanoamuang et al. 2000, Dararat et al. 2011). Nauplii of fairy shrimps comprise 54.6% protein, 25.5% lipid, 3.0% carbohydrate, 5.4% moisture, 4.6% fiber, and 6.9% ash. Fairy shrimps are also a source of canthaxanthin (Murugan et al. 1995, Sornsupharp et al. 2013). A previous study revealed that dried *S. sirindhornae* increased carotenoid deposition in flowerhorn cichlids (*Amphilophus citrinellus* x *Cichlasoma trimaculatum*) (Sornsupharp et al. 2015). The cysts of fairy shrimps are widely used instead of *Artemia* cysts (Saengphan et al. 2005, Sornsupharp et al. 2015). A study of the life history of fairy shrimp showed that the adult female *B. thailandensis* can produce 14.20±4.60 cysts/batch every 1.14±0.04 days, while the adult female *S. sirindhornae* can produce 37.62±2.29 cysts/batch at a frequency of 1.27±0.07 days (Boonmak et al. 2007). However, the hatching rate of *S. sirindhornae* was lower than that of *B. thailandensis* (Dararat et al. 2011). Increasing the production of fairy shrimp cysts is necessary to improve the supply of this live food for aquaculture.

Some studies have indicated that symbiotic bacteria enhance the reproduction of arthropods, such as the water flea (*Daphnia magna*), the fruit fly (*Drosophila melanogaster*), the blue bottle fly (*Calliphora vomitoria*) and other insects (Douglas 1992, Dedeine et al. 2001, Kikuchi et al. 2007, Ben-Yosef et al. 2008, Rosengaus et al. 2011, Erkosar et al. 2013, Kikuchi and Fukatsu 2014, Peerakietkhajorn et al. 2015, 2016). A study of microbiota in the freshwater crustacean *D. magna* revealed that Betaproteobacteria was the dominant class of symbiotic bacteria (Freese and Schink, 2011), and *Limnohabitans* was the dominant bacterium. Betaproteobacteria and *Limnohabitans* were reported to be important factors in reproduction and increased the number of viable juveniles (Peerakietkhajorn et al. 2015, 2016). However, the symbiotic bacteria of fairy shrimps have not been widely studied. Therefore, in this study, we aimed to investigate the bacterial compositions in *B. thailandensis* and *S. sirindhornae* to gain useful information for further studies to improve the cyst production of fairy shrimps.

Materials and Methods

Branchinella thailandensis and *Streptocephalus sirindhornae*

B. thailandensis was collected from temporary aquatic habitats in central and northeastern Thailand (Sanoamuang et al. 2002). *S. sirindhornae* was originally collected from a temporary pond, approximately 2 km north of Khon Kaen University in Ban Non Muang subdistrict, Khon Kaen Province, Thailand. Subsequently, both species were cultured in a laboratory at the Applied Taxonomic Research Center, Khon Kaen University, Thailand (Sanoamuang et al. 2000). Cysts of both species were bought from a local shop which received the cysts from the Applied Taxonomic Research Center. The resting eggs were hatched according to a procedure described previously (Saengphan et al. 2005), and the 1-day-old nauplii were collected for use in the experiments. The experimental protocol was approved by the Institutional Animal Care and Use Committee of Prince of Songkla University (project license number: MHESI 6800.11/827 Ref. 37/2020).

Chlorella culture fed to *S. sirindhornae* and *B. thailandensis*

In 1 L of sterilized COMBO medium (Kilham et al. 1998), $7.5x10^7$ cells of *Chlorella* were inoculated and incubated under a 16-h light and 8-h dark photoperiod at 23°C with continuous aeration for 7 days. The *Chlorella* cells were then collected and centrifuged at 3,000 rpm for 5 min. The cell pellet was washed twice with filtered COMBO medium, resuspended in filtered COMBO medium and stored at 4°C until used (Sanpradit et al. 2020).

Experimental design and sample collection

Ten nauplii of each species were cultured in 750 ml of sterilized COMBO medium at 28 ± 1°C under a 16-h light and 8-h dark photoperiod for 10 days. They were fed daily with $1x10^6$ cells of *Chlorella* for 6 days and then with double amount of *Chlorella* cells from day 7 onwards. On day 10, ten individuals of each species were collected and kept at -80°C.

DNA extraction, PCR, and Sequencing

To extract total DNA, the 10 individuals were homogenized in 200 µl of buffer A solution containing

Table 1. Diversity, evenness and OTU richness (genus-based) of bacterialcommunities in *Branchinella thailandensis* and *Streptocephalus sirindhornae.*

Indices	*B. thailandensis*	*S. sirindhornae*
Shannon - Wiener Diversity Index	2.135	3.122
Evenness	0.364	0.521
OTU richness	354	400

100 mM Tris-HCl (Fisher Scientific), 100 mM ethylenediaminetetraacetic acid [EDTA] (Ajax Finechem), 100 mM NaCl (Ajax Finechem), and 0.5% sodium dodecyl sulfate [SDS] (Ajax Finechem), at pH 7.5. The homogenate was incubated at 65°C for 30 min. The incubated homogenate was then mixed with 400 µL of a mixture of 5 M potassium acetate (Ajax Finechem) and 6 M lithium chloride (Ajax Finechem) (both mixed at a ratio of 1:2.5), further incubated on ice for 10 min, and centrifuged for 15 min at 15,000 rpm. After centrifugation, 500 µL of the supernatant was transferred to a new tube, mixed with 300 µL of isopropanol, and centrifuged for 15 min at 15,000 rpm. Lastly, the supernatant was removed, and the precipitate was washed with 70% ethanol, dried and resuspended in 100 uL of MilliQ (Sangkuanun et al. 2020). All DNA samples were kept at -30˚C until the 16S rRNA gene was amplified.

The V3-V4 hypervariable region of the bacterial 16S rRNA gene was amplified using 2x KAPA HiFi-HotStart Ready mix DNA polymerase (Kapa Biosystems Ltd., London, UK) and primers with overhang adapter sequences (forward primer: 5'-TCGTCGG CAGCGTCAGATGTGTATAAGAGACAGCCTACG GGNGGCWGCAG-3', and reverse primer: 5'-GTCTC GTGGGCTCGGAGATGTGTATAAGAGACAG GACTACHVGGGTATCTAATCC-3') (Johnston et al. 2017). Cycle conditions were 3 min at 95°C followed by 25 three-temperature cycles (30s at 95°C, 30s at 55°C, and 3 min at 72°C), then a final extension of 72°C for 5 min. Libraries were purified using AMPure XP beads (LABPLAN; Naas, Ireland) in accordance with the Illumina 16S metagenomics sequencing library protocol. Dual Indices from the Illumina Nextera XT index kit (Illumina, San Diego, USA) were added to the target amplicons in the second PCR using 2x KAPA HiFi HotStart Ready mix DNA polymerase (Kapa Biosystems Ltd., London, UK) under the following conditions: 3 min at 95°C followed by 9 three-temperature cycles (30 s at 95°C, 30 s at 55°C and 3 min at 72°C), then a final extension of 72°C for 5 min. Libraries were purified using AMPure XP beads (LABPLAN; Naas, Ireland).

The barcoded amplicon libraries were combined into a single pool. The library pool was diluted and denatured according to the Illumina Miseq library preparation guide. Sequencing was conducted on the Illumina Miseq using the 600 cycle Miseq reagent kit (version 3), to produce paired 301-bp reads. All sequencing data produced in this study were deposited in the NCBI SRA repository and are available via series accession number PRJNA792302.

Metagenomic analysis

Paired-end read sequences generated from Illumina Miseq were processed using the Illumina 16S Metagenomics (version 1.0.1) workflow in Base Space-Illumina (https://basespace.illumina.com/). Each read was blasted against the Illumina-curated version of the Greengenes database (greengenes.secondgenome.com/ /downloads/database/13_5) to determine the operational taxonomic units (OTUs) which corresponded to the 16S rRNA gene sequences. Taxa which did not conform to the necessary classification, such as "unclassified at Kingdom level" and "Viruses", were excluded from the subsequent diversity analysis. OTU richness, Shannon-Weiner diversity index and evenness based on genera of bacteria were calculated.

Results

The bacterial communities of *B. thailandensis* and *S. sirindhornae* were investigated by performing 16S amplicon sequencing using Illumina Miseq. We received 271,747 and 352,234 reads from the respective samples of *B. thailandensis* and *S. sirindhornae*, and 243,277 and 318,300 reads, respectively were classified as bacteria. The results showed that the genus-based bacterial diversity of *B. thailandensis* and *S. sirindhornae* were 2.135 and 3.122, respectively (Table 1). The evenness of *S. sirindhornae* (0.521) was higher than the evenness of *B. thailandensis* (0.364)

Proteobacteria (93.46%), Verrucomicrobia (1.84%), Bacteroidetes (1.68%), Planctomycetes (0.52%), and Firmicutes (0.42%) were the five most predominant phyla in *B. thailandensis* (Fig. 1A). Proteobacteria (80.48%), Bacteroidetes (15.95%), Cyanobacteria (1.30%), Firmicutes (0.56%), and Chlamydiae (0.21%) were the five most predominant phyla in *S. sirindhornae* (Fig. 1B).

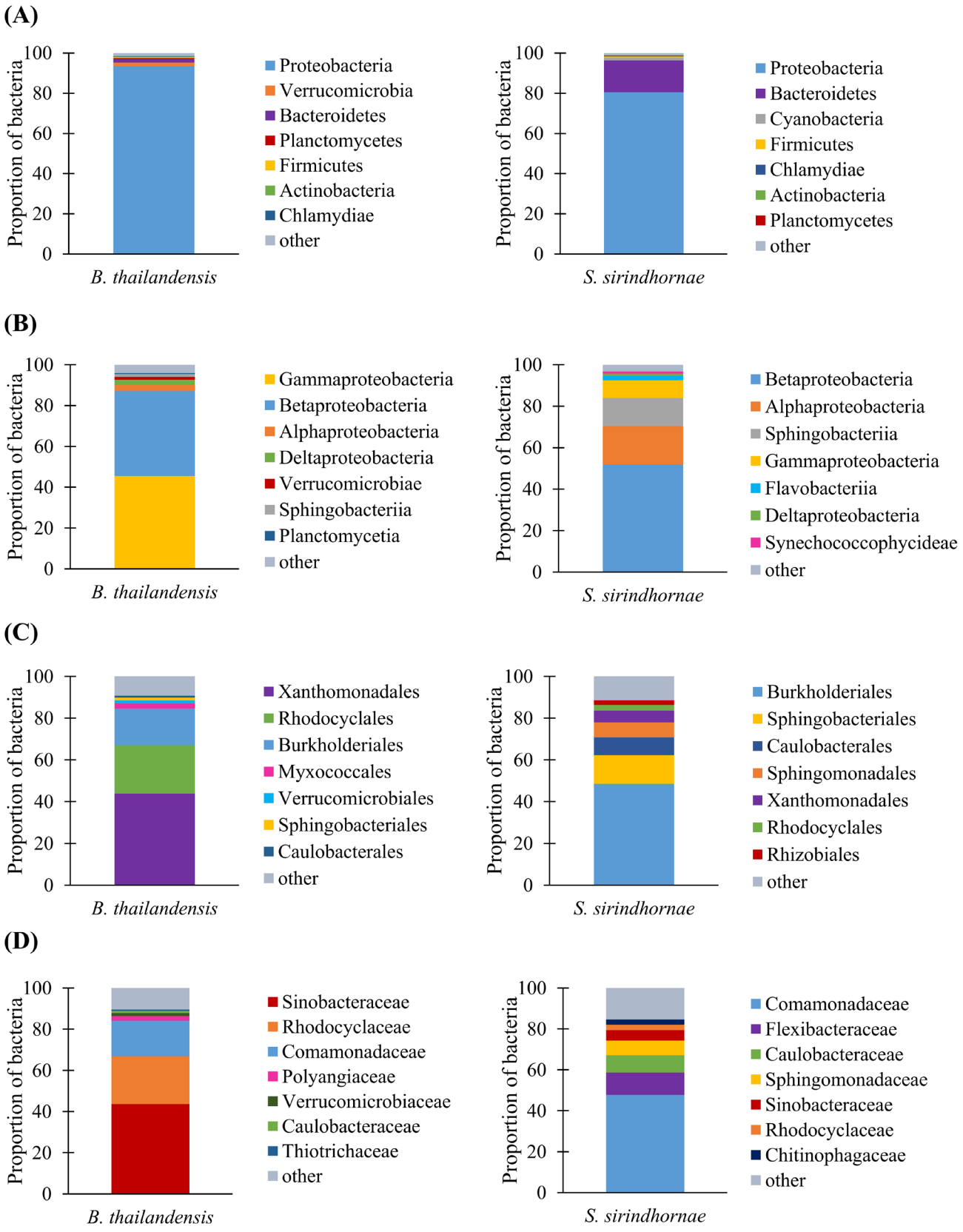

Fig. 1. Bacterial compositions in *Branchinella thailandensis* and *Streptocephalus sirindhornae* at the levels of (A) Phylum, (B) Class, (C) Order, and (D) Family.

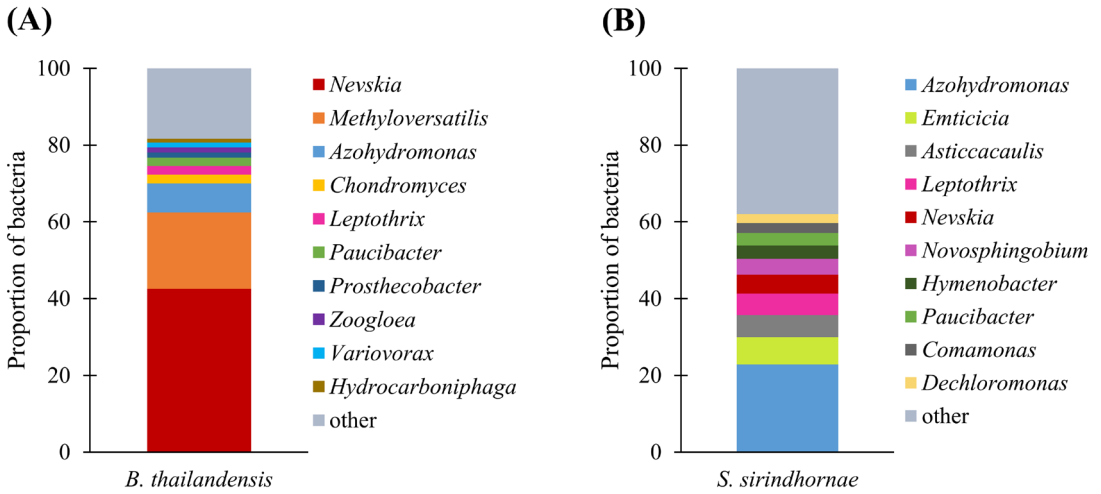

Fig. 2. The ten most predominant species of bacteria in (A) *Branchinella thailandensis* and (B) *Streptocephalus sirindhornae*.

Gammaproteobacteria (45.47%), Betaproteobacteria (41.60%), Alphaproteobacteria (3.09%), Deltaproteobacteria (2.47%), and Verrucomicrobiae (1.42%) were the five most predominant classes in *B. thailandensis* (Fig. 1C). Betaproteobacteria (51.85%), Alphaproteobacteria (18.49%), Sphingobacteriia (13.67%), Gammaproteobacteria (8.45%), and Flavobacteriia (2.18%) were the five most predominant classes in *S. sirindhornae* (Fig. 1D).

Xanthomonadiales (43.79%), Rhodocyclales (23.19%), Burkholderiales (17.64%), Myxococcales (2.37%), and Verrucomicrobiales (1.42%) were the five most predominant orders in *B. thailandensis* (Fig. 1E). Burkholderiales (48.60%), Sphingobacteriales (13.67%), Caulobacterales (8.54%), Sphingomonadales (7.11%), and Xanthomonadales (5.63%) were the five most predominant orders in *S. sirindhornae* (Fig. 1F).

Sinobacteraceae (43.67%), Rhodocyclaceae (23.19%), Comamonadaceae (17.24%), Polyangiaceae (2.33%), and Verrucomicrobiaceae (1.43%) were the five most predominant families in *B. thailandensis* (Fig. 1G). Comamonadaceae (47.77%), Flexibacteraceae (10.85%), Caulobacteraceae (8.54%), Sphingomonadaceae (7.11%), and Sinobacteraceae (5.12 %) were the five most predominant families in *S. sirindhornae* (Fig. 1H).

Altogether, 354 and 400 bacterial genera were identified in *B. thailandensis* and *S. sirindhornae*, respectively (Table 1). *Nevskia* (42.56%), *Methyloversatilis* (19.87%), *Azohydromonas* (7.54%), *Chondromyces* (2.32%), and *Leptothrix* (2.61%) were the five most predominant genera in *B. thailandensis* (Figure 2A). *Axohydromonas* (22.89%), *Emticicia* (7.09%) *Asticcacaulis* (5.75%), *Leptothrix* (5.58%), and *Nevskia* (4.90%) were the five most predominant genera in *S. sirindhornae* (Fig. 2B).

Discussion

This study revealed that compositions of symbiotic bacteria were different in *B. thailandensis* and *S. sirindhornae*. *Nevskia* and *Azohydromonas* were found in both species but *Nevskia* was the dominant bacterium of *B. thailandensis,* while *Azohydromonas* was the dominant bacterium of *S. sirindhornae.* A previous study revealed that *Nevskia* was a sulfur-oxidizing bacteria which could express the *mddA* gene and encode a methyltransferase to methylate methanethiol and generate dimethylsulphide (DMS) (Carrión et al. 2015). DMS acts as a chemo-attractant for zooplankton and plays a key role in the global sulfur cycle (Dey 2017). Therefore, the generation of DMS might promote the ingestion of this bacteria, zooplankton leading to increase growth and reproduction of zooplankton (Procter et al. 2019, Shemi et al. 2021). *Azohydromonas*, a nitrogen fixing bacteria, plays an important role in shrimp metabolism and acts as an essential pollutant degrader (Dahal et al. 2021, Prathiviraj et al. 2021).

Methyloversatilis, *Chondromyces*, *Leptothrix*, *Paucibacter*, *Prosthecobacter*, *Zoogloea*, *Variovorax* and *Hydrocarboniphaga* were also in the top ten of symbiotic bacteria found in *B. thailandensis*. *Methyloversatilis* is a methane-oxidizing bacteria (Kumaresan et al. 2018). It is also a symbiotic bacterium of copepods (*Pleuromamma* spp.) (Sadaiappan et al. 2021). *Chondromyces* is a Deltaproteobacteria that protects against pathogens (Diez et al. 2012). *Leptothrix* and *Paucibacter* were in the top ten symbiotic bacteria in both of *B. thailandensis* and *S. sirindhornae*. *Leptothrix* is an iron-oxidizing bacteria (Otte et al. 2018) which symbioses with *Daphnia magna* and *Danio rerio* (Freese and Schink 2011, Hirt and Body-Malapel 2020). *Paucibacter* is a symbiont of the

cherry shrimp *Neocaridina denticulata* (Cheung et al. 2015) that can degrade cyclic cyanobacterial hepatotoxin, microcystins and nodularin (Rapala et al. 2005). *Prosthecobacter* has also been found in *D. magna* (Sullam et al. 2018) and is involved in carbon cycling to degrade zooplankton carcasses (Kolmakova et al. 2018). *Zoogloea* is a denitrifier, changing nitrite to nitrogen gas (Gwin et al. 2018), and can uptake copper and produce polysaccharide (Moppert et al. 2009). *Variovorax* is a polyphosphate-accumulating bacterium involved in the regeneration of cuticle during molting and is also found in copepods and *Moina* (Niswati et al. 2005, Kostanjšek et al. 2017). Finally, *Hydrocarboniphaga* can degrade alkanes and aromatic hydrocarbons (Palleroni et al. 2004).

The top ten bacteria found in *S. sirindhornae* included *Azohydromonas*, *Emticicia*, *Asticcacaulis*, *Leptothrix*, *Novosphingobium*, *Nevskia*, *Hymenobacter*, *Paucibacter*, *Comamonas*, and *Dechloromonas*. *Emticicia* and *Hymenobacter* are reported symbionts of *D. magna* and coral reef fish (*Lutjanus kasmira*), respectively (Cooper and Cressler 2020, Gao et al. 2020). *Asticcacaulis* is an Alphaproteobacteria that could degrade lignocellulose (Alessi et al. 2018). *Novosphingobium* has been found as a symbiont in *Macrobrachium rosenbergii* and *Penaeus monodon* (Rungrassamee et al. 2014, Liu et al. 2020), and contains unsaturated fatty acid (Ngo et al. 2016). Unsaturated fatty acids enhance the growth and reproduction of zooplankton (Demott and Muller-Navarra 1997, Martin-Creuzburg et al. 2011). Moreover, *Novosphingobium* has been reported to degrade ibuprofen, eliminating this organic contaminant of aquatic ecosystems (Rutere et al. 2020). *Comamonas* was a denitrifier in freshwater ecosystems (Baskaran et al. 2020), and also played a role in poly-β-hydroxybutyrate degradation in *Artemia* sp. and *Litopenaeus vannamei* (Ludevese-Pascual et al. 2021, 2020). *Dechloromonas* is a Betaproteobacteria that can degrade organic compounds (Chang et al. 2014) and denitrify aquatic ecosystems (Otte et al. 2018).

In conclusion, the compositions and proportions of the bacterial communities were specific to each host, and the different bacterial communities may be related to the physiological functions and life history traits of the hosts. Therefore, our study will help further investigations to improve the reproduction of both these species of fairy shrimp in commercial aquaculture.

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