Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Blooms of shrimp-algae symbiotic colonies on artificial substrates in the subtropical shallow waters of the northwestern Pacific

Tomoya Hanaoka

hanatomo141205@gmail.com

Kyoto University

Ryuichiro Aoki

Kindai University

Yoshiki Katsuda

Kindai University

Masayuki Fukuoka

Nagoya City Institute For Environmental Sciences

Ryutaro Goto

Kyoto University

Short Report

Keywords: cultivation mutualism, Alpheidae, Alpheus frontalis, Alpheus pachychirus, Moorena bouillonii, aquaculture

Posted Date: November 18th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11476503/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Blooms of shrimp-algae symbiotic colonies on artificial substrates in the subtropical shallow waters of the northwestern Pacific

Tomoya Hanaoka[1, 2*] (https://orcid.org/0009-0002-4339-4794)·**Ryuichiro Aoki**[3] (https://orcid.org/0000-0001-5553-7305)·**Yoshiki Katsuda**[4]·**Masayuki Fukuoka**[5] (https://orcid.org/0009-0007-0101-4227)·**Ryutaro Goto**[2] (https://orcid.org/0000-0002-5425-9603)

[1] Graduate School of Science, Kyoto University, Kitashirakawa-Oiwake, Kyoto, Kyoto 606-8502, Japan

[2] Seto Marine Biological Laboratory, Field Science Education and Research Center, Kyoto University, 459, Shirahama, Nishimuro, Wakayama 649-2211, Japan

[3] Aquaculture Research Institute, Amami experiment station, Kindai University, 137, Katen, Setouchi, Oshima, Kagoshima 894-1853, Japan

[4] Aquaculture Technology and Production Center, Kindai University, 137, Katen, Setouchi, Oshima, Kagoshima 894-1853, Japan

[5] Nagoya City Institute for Environmental Sciences, 5-16-8, Toyoda, Minami-ku, Nagoya, Aichi 457-0841, Japan

*Corresponding author. E-mail: hanatomo141205@gmail.com

Abstract

Snapping shrimp *Alpheus frontalis* and *Alpheus pachychirus* (Alpheidae) are symbiotically associated with filamentous benthic cyanobacterial algae, mainly *Moorena bouillonii* (Coleofasciculaceae). These species dwell in tubes of symbiotic algae on various natural benthic substrates (e.g., stones and corals) in subtropical and tropical shallow waters. While shrimp-algae colonies have been reported from natural substrates, they have never been recorded from artificial ones. Here, we report the blooms of the shrimp-algae colonies over the floating fish cages in coastal waters of Amami-Oshima Island, Ryukyu Archipelago, southern Japan. Samples were collected from quadrats (1×1 m) in three cages. The population density of *A. frontalis* on the fish cages was 12 to 26 individuals m^{-2}. In contrast, the population density of *A. pachychirus* was 4 individuals m^{-2} and restricted to the shallowest quadrat. The colonization of this shrimp on fish cages suggests that such artificial substrates offer favorable conditions for colony expansion and provide opportunities to study this interesting shrimp-algae symbiotic association in detail (e.g., seasonal monitoring).

Key words: cultivation mutualism, Alpheidae, *Alpheus frontalis*, *Alpheus pachychirus*, *Moorena bouillonii*, aquaculture

1. Introduction

The snapping shrimp, *Alpheus frontalis* H. Milne Edwards, 1837 and *Alpheus pachychirus* Stimpson, 1860, are known to be symbiotically associated with filamentous benthic cyanobacteria such as *Moorena bouillonii* (L. Hoffmann & Demoulin) Engene & Tronholm, 2019. These shrimp weave cyanobacterial filaments to construct dwelling tubes (Fig. 1). They inhabit an algal tube either as a solitary individual or as a mating pair (Cowles 1913; Fishelson 1966; Banner and Banner 1982; Nomura 2003; Leber 2020; Leber et al. 2021). Both *A. frontalis* and *A. pachychirus* occur in subtropical and tropical shallow waters of the Indo-Pacific and the Red Sea (e.g., Richters 1880; Coutière 1899, 1905; Fishelson 1966; Banner and Banner 1982). In Japan, they have been recorded from the Ryukyu Archipelago (Stimpson 1860; Ortmann 1890; Nakazawa 1927; Miya 1974; Kamezaki et al. 1988; Nomura 2003).

Nomura (2003) has suggested that *A. frontalis* actively manages its symbiotic algae (as *Microcoleus lyngbyaceus*). This shrimp weeds out damaged portions of algae and debris from its algal tubes and reweaves the algal filaments using its chelate legs (second pereopod).

This active management is defined as caring behavior (Nomura 2003). In addition, a previous study suggested that nutrients derived from the shrimp improved the growth conditions of the algae (Leber et al. 2021).

Furthermore, several studies have pointed out that shrimp also use the algal tube as a food resource (Fishelson 1966; Leber 2020). Therefore, the relationship between *A. frontalis* and *M. bouillonii* suggests a mutualistic association (Nomura 2003). For *A. pachychirus*, however, it remains unclear whether it maintains and nourishes its algal tubes, as *A. frontalis* does.

Shrimp-algae colonies have been recorded across a wide range of natural hard substrates. *Alpheus frontalis*-algae colonies have been collected from rocks and corals (Fishelson 1966; Nomura 2003; ; Leber 2020). *Alpheus pachychirus*-algae colonies have been collected in algal tubes under rocks or in coral crevices (Nomura 2003; Hurt et al. 2021). Notably, the corals used by *A. frontalis* are taxonomically well documented. These included octocorals such as *Annella reticulata* (Yamashiro et al. 2014) and scleractinian corals such as *Porites rus*, *Porites cylindrica* and *Porites* cf. *deformis* (Miya 1974). Shrimp-algae colonies have been frequently recorded from natural substrates, but they have never been recorded from artificial substrates.

In this study, we report blooms of shrimp-algae colonies on floating fish cages at the Amami Station, Aquaculture Research Institute, Kindai University, Amami-Oshima Island, Ryukyu Archipelago, southern Japan. Specifically, we measured the size of the blooms on these cages and determined shrimp density using a 1×1 m quadrat.

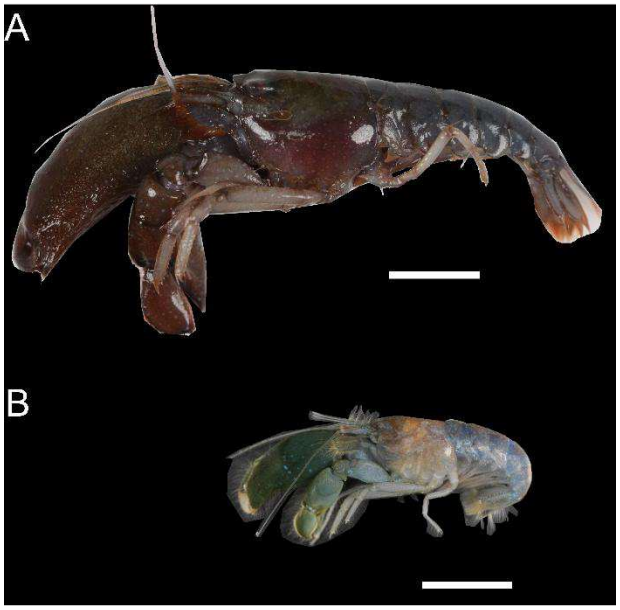


Fig. 1 A, *Alpheus frontalis* (male, cl. 14.7 mm, tl. 46.8 mm); B, *Alpheus pachychirus* (male, cl. 8.3 mm, tl. 28.8 mm); Scale bars: 10 mm. Photographs: by T. Hanaoka

2. Materials and methods

2.1 Field observations

Observations and sampling were conducted on December 5, 2025 (winter). Shrimp and algae were collected by SCUBA diving in front of Amami Station, Aquaculture Research Institute, Kindai University, located in the southern part of Amami-Oshima Island (28° 13′ 35.02″ N, 129° 12′ 50.90″ E), facing Oshima strait, opposite Kakeroma Island (Figs. 2, 3A).

A total of 14 net cages were installed at the site: 12 cages measuring 30 m in diameter and 15 m in depth, one cage measuring 20 m in diameter and 15 m in depth, and one cage measuring 30 m in diameter and 10 m in depth. Of the 14 net cages, Pacific bluefin tuna (*Thunnus orientalis*) were stocked in 12 cages, while the remaining two cages were unstocked (no fish present).

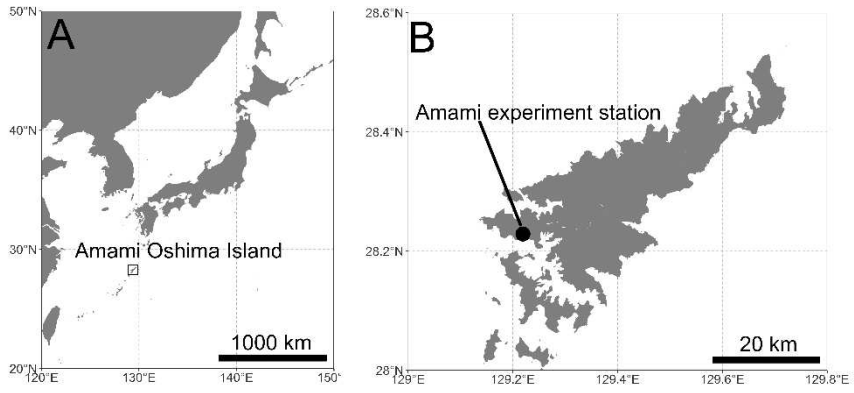


Fig. 2 Geographic location of the sampling site. A, Japan; B, Amami-Oshima Island.

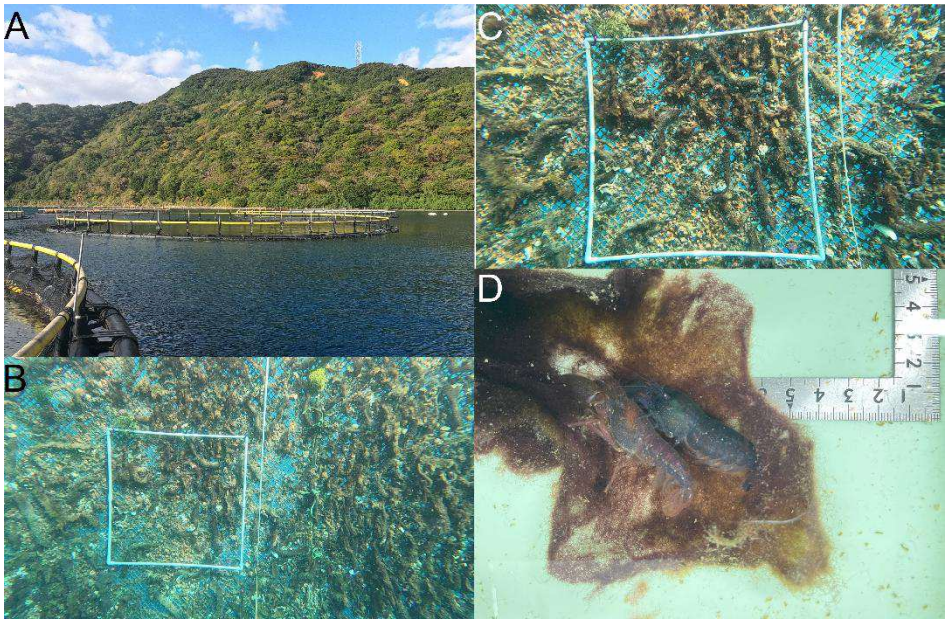


Fig. 3 A, Fish cage in Amami Station; B, exterior view of the fish cage; C, overview of the fish cage; D, a male-female pair in an algal tube . Photographs: A, by R. Aoki; B–D, by Y. Katsuda

2.2 Species identification

The identification of alpheid shrimp was based on morphological characters, following Miya (1974) and Banner and Banner (1982). Images of the shrimp were taken with digital cameras (Tough TG-5, Olympus, Japan; EOS Kiss X6i, Canon, Japan) and a binocular stereomicroscope (SMZ18, Nikon, Japan).

Cyanobacterial specimens from the dwelling tubes were transported to the Nagoya City Institute for Environmental Sciences and identified based on morphological identification of Hoffmann and Demoulin (1991) and Engene et al. (2012).

2.3 Quantitative survey

Shrimp-algae colonies were confirmed in 8 of the 14 fish cages. Of these, three cages were randomly selected for the quantitative survey. In total, we placed five 1 × 1 m quadrats inside the cages (Cage I–III) (Fig. 3B, C; Table 1). In Cage I, a single line transect was laid out from the water surface to a depth of 13 m. Samples were collected from one quadrat placed at each of three depths (A: 3 m, B: 8 m, C: 13 m), at vertical intervals of 5 m starting from 3 m, to compare the extent of blooming among the depths (Table 1).

In addition, to confirm that blooming on the net cages was not an incidental occurrence, samples were collected from both Cage II (D) and Cage III (E). In each of these cages, a single line transect was laid out from the water surface to a depth of 3 m, and one quadrat was placed at the end of the transect (Table 1). Samples were frozen for preservation and subsequently shipped to the Seto Marine Biological

Laboratory, Kyoto University, for analysis. The number of individuals in each quadrat was expressed as density (individuals m^{-2}). The mean and standard error (SE) were calculated from the five quadrats.

depth	3m	8m	13m
Fish cage I	A	B	C
Fish cageII	D		
Fish cageIII	E		

Table 1 List of fish cage locations of surveyed quadrats

3 Results

3.1 Field observation

Shrimp-algae colonies were observed in eight of the 14 cages at Amami Station (Fig. 3A). Of these eight cages, six were 30 m in diameter and 15 m in depth, one was 20 m in diameter and 15 m in depth, and one was 30 m in diameter and 10 m in depth. All of these cages had been maintained for more than two years since they were installed in the sea at the time of the survey.

Shrimp-algae colonies were observed regardless of the presence of Pacific bluefin tuna. Of the eight cages, six were stocked with Pacific bluefin tuna, while the remaining two contained no fish.

The algal tubes were constructed by weaving filamentous cyanobacteria to the cage netting (Fig. 3C). Qualitative observations indicated that colony abundance was greater on the inner surface of the cages than on the outer surface.

3.2 Species Identification

In total, 94 alpheid shrimp were collected from the algal tubes in the quadrats of the fish cages I–III (Figs. 4, 5), comprising 90 specimens of *A. frontalis* and 4 specimens of *A. pachychirus. Alpheus frontalis* was identified based on the following diagnostic characters: (i) anterior margin of carapace without rostrum, and (ii) merus of third pereopod without tooth. *Alpheus pachychirus* was identified based on the following diagnostic characters: (i) anterior margin of carapace bearing a minute rostrum, and (ii) merus of third pereopod with an acute tooth.

Based on morphological observations, all algae symbiotic with the shrimp were identified as the genus *Moorena.* Within the genus, the algae were identified as *Moorena bouillonii.*

3.3 Population Structure

3.3.1 Shrimp Density

Alpheus frontalis was collected from all five quadrats, whereas *A. pachychirus* was collected only from Quadrat A in Cage I. The average densities of alpheid shrimp, *A. frontalis*, and *A. pachychirus* were 18.8 ± 3.4 (SE), 18.0 ± 3.0 (SE), and 0.8 ± 0.8 (SE) individuals m^{-2}, respectively (Table 2). The sex ratio

was approximately 1:1 (male:female) in all quadrats (Figs. 4, 5; Table 2). Some shrimps formed monogamous (one male–one female) pairs and inhabited the same tube (Fig. 3D). However, algal tubes were entangled with one another, so the exact number of tubes and the proportion of paired individuals could not be determined.

3.3.2 Vertical distribution

In Cage I, the population density of shrimp was higher in shallow areas (Fig. 4; Table 2). Quadrat A (3 m depth) showed the highest density of shrimp in Cage I, with 28 individuals m^{-2}. Of these, *A. frontalis* (24 individuals m^{-2}) and *A. pachychirus* (4 individuals m^{-2}) were collected. Twelve individuals m^{-2} of *A. frontalis* and no *A. pachychirus* were collected from each of Quadrat B (8 m depth) and Quadrat C (13 m depth) (Fig. 4, Table 2).

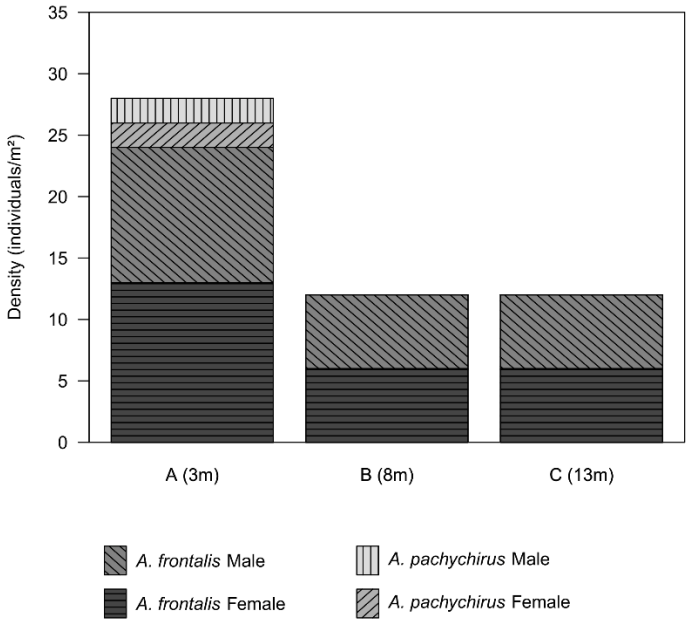


Fig. 4 Density of shrimp individuals per square meter at each water depth in Cage I. A–C indicate the respective quadrats, with water depth shown in parentheses. Patterns indicate species and sex: Right-diagonal lines represent male *A. frontalis*; horizontal lines represent female *A. frontalis*; vertical lines represent male *A. pachychirus*; left-diagonal lines represent female *A. pachychirus*

3.3.3 Comparison among cages

High densities were also observed at 3 m in Cages II and III (Fig. 5, Table 2). Quadrat D (3 m depth of Cage II) showed 16 individuals m^{-2} (all *A. frontalis*) and Quadrat E (3 m depth of Cage III) showed 26 individuals m^{-2} (all *A. frontalis*).

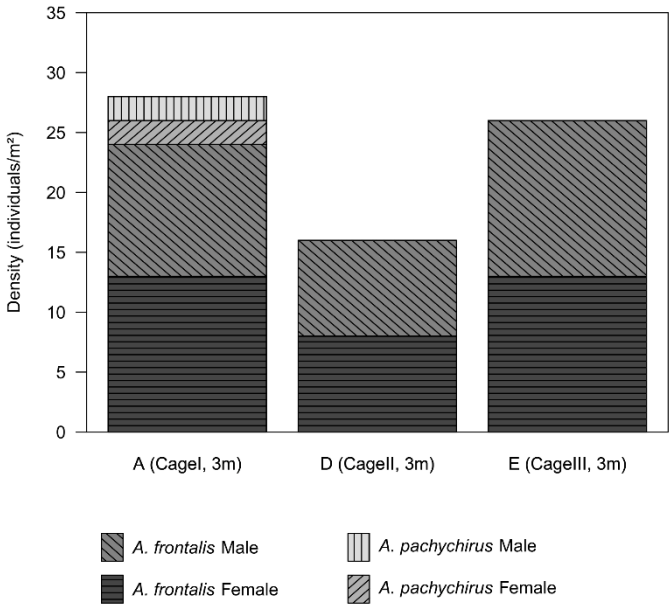


Fig. 5 Comparison of the density of shrimp individuals per square meter among cages. A, D, E indicate the respective quadrats, with the number of the cage and water depth shown in parentheses. Patterns indicate species and sex: Right-diagonal lines represent male *A. frontalis*; horizontal lines represent female *A. frontalis*; vertical lines represent male *A. pachychirus*; left-diagonal lines represent female *A. pachychirus*

Quadrat	*A. frontalis*			*A. pachychirus*			Total
	Male	Female	Total	Male	Female	Total	
A	11	13	24	2	2	4	28
B	6	6	12	0	0	0	12
C	6	6	12	0	0	0	12
D	8	8	16	0	0	0	16
E	13	13	26	0	0	0	26
Average	8.8	9.2	18.0	0.4	0.4	0.8	18.8
Standard error	1.4	1.6	3.0	0.4	0.6	4.9	3.4

Table 2 Number of shrimp individuals (ind. m^{-2}) of *A. frontalis* and *A. pachychirus* recorded in each quadrat, categorized by sex. Total values represent the combined number of both species, and average and standard error were calculated across Quadrats A–E

4. Discussion

4.1 Blooming of shrimp-algae colonies on fish cages

In previous studies, both *A. frontalis* and *A. pachychirus* were frequently recorded on natural substrates (e.g., Banner and Banner 1982; Yamashiro et al. 2014; Leber et al. 2021). In contrast, neither

species has been collected from artificial one. Thus, this is the first record of shrimp-algae colonies on artificial substrates.

Furthermore, on these fish cages, population densities of alpheid shrimp reached 28 individuals m^{-2} (Quadrat A) and colonies were widely observed across multiple fish cages (Fig. 4, 5; Table 2). These high-density settlements are defined as blooming, following the case of Yamashiro et al. (2014). Yamashiro et al. (2014) observed high-density settlements of *A. frontalis–M. bouillonii* colonies on a coral reef at Aka Island, Okinawa, Japan.

Field observations suggested that the fish cage environment may be favorable for the expanding of colonies under certain conditions. First, the colonies tended to be more abundant on the inner side of the cage than on the outer side of the cage. This may suggest that the mesh structure of these cages prevents large predators from entering the inner area, thereby reducing predation pressure. Within the cage, predation pressure caused by bluefin tuna may also be a factor; however, in this observation, the colonies remained abundant regardless of the presence or absence of tuna. This suggests that predation pressure from tuna may have been low compared to that from external predators.

In addition, additional nutrients from aquaculture operations, such as excess tuna feed, are likely to flow into this area. This nutrient-enriched environment may promote blooms of shrimp-algae colonies. Moreover, the density of shrimp differs among water depths. In this survey, population density of shrimp was higher at 3 m (Quadrat A) than at 8 m (Quadrat B) and at 13 m (Quadrat C) in Cage I. The algal growth may be limited by light reduction with increasing depth. Further studies need to clarify the conditions under which blooms of shrimp-algae colonies occur.

4.2 Comparison of population density with previous studies

In this survey, the maximum population densities of *A. frontalis* were 26 individuals m^{-2} (Quadrat E) and that of *A. pachychirus* were 4 individuals m^{-2} (Quadrat A). This is the first survey to measure population density per unit area for both *A. frontalis* and *A. pachychirus*.

However, algal tube densities have been examined in previous studies. Leber et al. (2021) surveyed *A. frontalis-M. bouillonii* colonies on coral reefs and calculated algal tube density per square meter by establishing two line transects at each of two sites (Laulau Bay, Saipan, and Finger Reef, Guam) and placing quadrats along each transect to calculate algal tube density per square meter. The maximum density was 5.8 and 3.5 tubes m^{-2} (transect 1 and 2) at Laulau Bay and 1.5 and 3.8 tubes m^{-2} (transect 1 and 2) at Finger Reef. The average densities were 4.7 and 3.1 tubes m^{-2} (transect 1 and 2) at Laulau Bay and 0.5 and 1.3 tubes m^{-2} (transect 1 and 2) at Finger Reef.

Nomura (2003) reported average algal tube densities for both *A. frontalis* and *A. pachychirus* on the coral reef of Kuroshima Island in the Yaeyama Islands, Japan; that of *A. frontalis* was 15 tubes m^{-2}, and that of *A. pachychirus* was 33 tubes m^{-2}. For both species, however, the maximum algal tube density was not described.

Algal tubes were entangled with one another, so the exact number of tubes could not be calculated in this study. Instead, tube density could be estimated from the population density of shrimps per square meter.

In this study, shrimp occupied tubes either solitarily or in pairs. Assuming that all individuals occupied tubes solitarily, the maximum tube densities were estimated as follows: 26 tubes m^{-2} for *A. frontalis* and 4 tubes m^{-2} for *A. pachychirus*. The average tube densities were estimated at 18.0 tubes m^{-2} and at 0.8 tubes m^{-2}, respectively. Assuming that all individuals formed pairs, the maximum tube densities were estimated to be half of those in the solitary case: 13 tubes m^{-2} for *A. frontalis* and 2 tubes m^{-2} for *A. pachychirus*. The average tube density for *A. pachychirus* was estimated at 0.4 tubes m^{-2} as expected from the half-density assumption, whereas that for *A. frontalis* was estimated at 9.2 tubes m^{-2} rather than 9.0 tubes m^{-2}. This is because at least two females in Quadrat A were estimated to have occupied tubes solitarily (Table 2).

Overall, both the average and maximum tube densities of *A. frontalis* estimated in this study were substantially higher than those reported by Leber et al. (2021).
Furthermore, the average density was also higher than that reported by Nomura (2003) only if all individuals were assumed to occupy tubes solitarily. These results indicate that fish cage substrates may provide a favorable habitat for *A. frontalis*-algae colonies, comparable to or better than those of natural substrates.

In contrast, the situation was different for *A. pachychirus*. Its average density was substantially lower than that reported by Nomura (2003), even when all individuals were assumed to occupy tubes solitarily. These results suggest that fish cage substrates may not be a favorable environment for *A. pachychirus*. Further studies are needed to clarify the factors underlying such interspecific differences in density.

4.3 Is this cultivation mutualism?

In marine ecosystems, algae-herbivore interactions are much rarer than plant-herbivore interactions in terrestrial ecosystems (Hata and Kato 2006). Notably, the damselfish *Stegastes nigricans* has evolved an obligate mutualistic relationship with the red alga *Polysiphonia* sp. 1, a relationship that has been identified as cultivation mutualism (Hata and Kato 2006). *Stegastes nigricans* maintains algal farms dominated by *Polysiphonia* sp. 1. The fish actively excludes other herbivores from around their farms and selectively weed out unpalatable algae (Hata and Kato 2002, 2004, 2006).

Nomura (2003) reported that *A. frontalis* show caring behavior, including the removal of other algae and debris. This behavior is similar to the weeding behavior of *S. nigricans*. This suggests that *A. frontalis*, at least, may be in a mutualistic relationship with its associated cyanobacteria. Such a relationship would be similar to the cultivation mutualism between damselfish and red algae. It remains to be determined whether *A. pachychirus* is also in such a relationship.

The fish cages examined in this study provide an environment in which quantitative sampling of shrimp-algae associations can be conducted repeatedly over time, making them a suitable setting for testing the cultivation mutualism hypothesis.

Acknowledgements

We thank Mariko Kawamura (Kyoto University) and Sho Shirakashi (Kindai University) for providing an opportunity to study the shrimp-algae blooms on fish cages at Kindai University. We thank Keiichi Nomura (Kushimoto) for advice on this study. We thank the staff of the Aquaculture Research Institute, Kindai University Amami Experiment Station, for permission to collect samples. We thank Takahiro Koshiba (Kyoto University), Mio Takezawa (Kyoto University), and Maho Taniguchi (Kyoto University) for their help in collecting samples.

Author contributions

TH designed the study, collected data, and drafted the manuscript. RA and YK conducted field sampling. MF identified cyanobacteria. RG designed and supervised the study, collected data, and drafted the manuscript. All authors read and approved the final version of the manuscript.

Funding

This study was financially supported by KAKENHI grant (25K02033) and FY2025 MUSUBIME of Kyoto University to RG.

Data availability

All data generated or analyzed during this study are included in this published article.

Declarations

Ethical Declaration

The authors declare that this study involved no experiments on vertebrates or humans. Study was conducted in accordance with local regulations and following accepted ethical standards. The authors declare no conflicts of interest.

Competing interests

The authors declare no competing interests.

References

Banner DM, Banner AH (1982) The alpheid shrimp of Australia Part III: The remaining alpheids, principally the genus *Alpheus*, and the family Ogyrididae. Rec Aust Mus 34:1–357. https://doi.org/10.3853/j.0067-1975.34.1982.434

Coutière H (1899) Les Alpheidae: morphologie externe et interne, formes larvaires, bionomie. Masson et Cie, Paris

Coutière H (1905) Les Alpheidae. In: Gardiner JS (ed) The fauna and geography of the Maldive and Laccadive Archipelagoes, vol 2(4). University Press, Cambridge, pp 852–921

Cowles RP (1913) The habits of some tropical Crustacea. Philipp J Sci 8:119–124

Engene N, Rottacker EC, Kaštovský J, Byrum T, Choi H, Ellisman MH, Komárek J, Gerwick WH (2012) *Moorea producens* gen. nov., sp. nov. and *Moorea bouillonii* comb. nov., tropical marine cyanobacteria rich in bioactive secondary metabolites. Int J Syst Evol Microbiol 62:1171–1178. https://doi.org/10.1099/ijs.0.033761-0

Fishelson L (1966) Observations on the littoral fauna of Israel. V. On the habitat and behavior of *Alpheus frontalis* H. Milne Edwards (Decapoda, Alpheidae). Crustaceana 11:98–104. https://doi.org/10.1163/156854066X00496.

Hata H, Kato M (2002) Weeding by the herbivorous damselfish *Stegastes nigricans* in nearly monocultural algae farms. Mar Ecol Prog Ser 237:227–231. https://doi.org/10.3354/meps237227

Hata H, Kato M (2004) Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. J Exp Mar Biol Ecol 313:285–296. https://doi.org/10.1016/j.jembe.2004.08.009

Hata H, Kato M (2006) A novel obligate cultivation mutualism between damselfish and Polysiphonia algae. Biol Lett 2:593–596. https://doi.org/10.1098/rsbl.2006.0528

Hoffmann L, Demoulin V (1991) Marine cyanophyceae of Papua New Guinea. II. *Lyngbya bouillonii* sp. nov., a remarkable tropical reef-inhabiting blue-green alga. Belg J Bot 124 (1):82–88

Hurt C, Hultgren K, Anker A, Lemmon AR, Lemmon EM, Bracken-Grissom H (2021) First worldwide molecular phylogeny of the morphologically and ecologically hyperdiversified snapping shrimp genus *Alpheus* (Malacostraca: Decapoda). Mol Phylogenet Evol 158:107080. https://doi.org/10.1016/j.ympev.2021.107080

Kamezaki N, Nomura K, Hamano T, Omae H (1988) Okinawa Kaichu Seibutsu Zukan Vol. 8. Crustacea (Shrimps and Hermit Crabs). Shinsei Toho Shuppan, Okinawa

Leber CA (2020) The *Moorea bouillonii* and *Alpheus frontalis* symbiosis: Patterns in chemical ecology, chemogeography, and genomics. Dissertation, University of California, San Diego

Leber CA, Reyes AJ, Biggs JS, Gerwick WH (2021) Cyanobacteria-shrimp colonies in the Mariana Islands. Aquat Ecol 55:453–465. https://doi.org/10.1007/s10452-021-09837-6

Milne Edwards H (1837) Histoire Naturelle des Crustacés, Comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux, vol 3. Librairie Encyclopédique de Roret, Paris

Miya Y (1974) The Alpheidae (Crustacea, Decapoda) of Japan and its adjacent waters. Part II. Publ Amakusa Mar Biol Lab 3:103–195

Nakazawa K (1927) Crustacea Decapoda. In: Uchida S (ed) Nippon Dobutsu Zukan. Hokuryukwan, p 1017

Nomura K (2003) Umi no ganman: Teppouebi-rui no tayousei. In: Asakura A (ed) Koukakuruigaku: ebi, kani to sono nakama no sekai. Tokai University Press, Kanagawa, pp 54–74

Ortmann AE (1890) Die Unterordnung Natantia Boas. Theil I. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. Zool Jahrb Abt Syst Geogr Biol Tiere 5:437–542

Richters F (1880) Decapoda. In: Möbius K (ed) Beriträge zur Meeresfauna der Insel Mauritius und der Seychellen bearbeitet von K Mobius, F Richters und E von Martens nach Sammlungen, angelegt auf einer Reise nach Mauritius. Gutmann, Berlin, pp 164–165

Stimpson W (1860) Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republic Federata missa, Cadwaladore Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII, Crustacea Macrura. Proceedings of the Academy of Natural Sciences of Philadelphia 12:24–47

Tronholm A, Engene N (2019) *Moorena* gen. nov., a valid name for "*Moorea* Engene & al." nom. inval. (Oscillatoriaceae, Cyanobacteria). Notul Algarum 122:1–2

Yamashiro H, Isomura N, Sakai K (2014) Bloom of the cyanobacterium *Moorea bouillonii* on the gorgonian coral *Annella reticulata* in Japan. Sci Rep 4:6032. https://doi.org/10.1038/srep06032