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ORIGINAL PAPER

Baseline diversity and host relationships of symbiotic caridean shrimps on the coast of northern Taiwan, southern East China Sea, prior to the establishment of a conservation area

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Abstract

Symbiotic caridean shrimps were collected from diverse host invertebrates in a coral reef habitat of the southern East China Sea during the summer from April to August in 2014. Regular weekly sampling was conducted by scuba diving in the zone above 25 m depth at the Wang-Hai-Xiang Bay (also called as Fan-Zai-Aou Bay) in northeastern Taiwan. This region is influenced by the China Coast Current and the Kuroshio Current. In total, 27 species of shrimp in 20 genera and 3 families were identified, being taxonomically dominated by Palaemonidae (70.4% of species) and followed by Alpheidae (22.2%) and Hippolytidae (7.4%). The shrimp species were apportioned among hosts of various groups, as follows: scleractinians (45.2%), gorgonians (16.1%), echinoids (12.9%), crinoids (9.7%), actiniarians (6.5%), alcyonarians (3.2%), hydroids (3.2%), and sponges (3.2%). Six species are reported for the first time from the waters of Taiwan: *Synalpheus neomeris* (de Man, 1897); *Cristimenes zanzibaricus* (Bruce, 1967); *Manipontonia paeneglabra* Bruce, 2012; *Miopontonia yongei* Bruce, 1985; *Palaemonella spinulata* Yokoya, 1936; and *Thaumastocaris streptopus* Kemp, 1922. Of these, *C. zanzibaricus* also represents a northern range extension for the species. Five species, *Arete indicus* Coutière, 1903; *Cuapetes amymone* (de Man, 1902); *Jocaste lucina* (Nobili, 1901); *Palaemonella pottsi* (Borradaile, 1915); and *Pontoniopsis comanthi* Borradaile, 1915, showed higher than 60% prevalence on their hosts. These results provide useful baseline information on symbiotic shrimps prior to the establishment of a conservation area at this site in 2016, and also fill in faunal distribution gaps in the coral reef region between the southern Ryukyu arc and the Coral Triangle.

Keywords Alpheidae · Hippolytidae · Palaemonidae · Symbiosis · Conservation area · Taiwan

Introduction

Tropical coral reefs of the Indo-West Pacific region are the most biologically diverse marine ecosystems in coastal areas (Paulay 1997; Stella et al. 2011; Veron 2000). Reefs are dominated by invertebrates (Stella et al. 2011), presumably because the complex morphology of corals provides an excellent refuge against predators (Austin et al. 1980; McCoy and Bell 1991; Patton 1994; Stella et al. 2010; Vytopil and Willis 2001). Shrimps of the infraorder Caridea, comprising approximately 3438 species (De Grave and Fransen 2011), are presently known as the second most species-rich group among the decapods. Many kinds of caridean shrimp can be found concealing themselves within the interstices of live macro-invertebrates.

In the Indo-West Pacific, caridean shrimps of the three families Hippolytidae, Alpheidae, and Palaemonidae are particularly common (Bruce 1972, 1976a; Glynn and Enochs 2011). Members of these families are known to have developed commensal habits in many cases (Bruce 1976a) and are

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associated with a variety of hosts, including species in the following phyla: Porifera, Cnidaria, Annelida, Mollusca, Arthropoda (crustaceans), Echinodermata, and Chordata (ascidians, fish) (Anker et al. 2005; Bruce 1972, 1976a, 1982; De Grave 1999; Fautin et al. 1995; Fransen 2006; Glynn and Enochs 2011; Guo et al. 1996; Marin 2007; Wei et al. 2005).

Obligate symbiotic species rely on the presence of their hosts for survival (Stella et al. 2011). Conversely, several caridean symbionts play a crucial role in increasing the survival rate of their hosts. They defend the hosts against predators (Glynn 1987; McKeon et al. 2012; Nakano and Fujii 2014), assist in clearing sediment away from their coral hosts (Stier et al. 2012), and enhance their host by providing nitrogenous nutrients (Spotte 1996). Some host species are reliant on these services and are unable to survive without their symbionts (Nakano and Fujii 2014; Stella et al. 2011; Stier et al. 2012).

Taiwan, formerly called Formosa, is an island located in the Western Pacific Ocean, with its northern part connected to the southern Ryukyu arc in the southernmost part of the East China Sea, and its southern side facing the South China Sea and the Coral Triangle through the Luzon Strait (Fig. 1). Taxonomy of caridean shrimps in Taiwan has been considerably studied since the early 1900s. First, two species of *Palaemon* were collected and described from Taiwan (Parisi 1919). Then, Maki and Tsuchiya (1923) published the first monograph on Taiwanese decapods, which provided excellent illustrations of caridean shrimps of genera such as *Macrobrachium* and *Palaemon* and still contributes to decapod studies in Taiwan. An early report on the symbiotic marine carideans (Holthuis 1952) of Taiwan recorded *Anchistus custos* (Forskål, 1775); *Conchodytes biunguiculatus* (Paul'son, 1875); and *Conchodytes monodactylus* Holthuis, 1952, all of which were associated with pen shells when collected from southern Taiwan in 1907. Later on, various symbiotic caridean shrimps in coral reef zones were studied by Taiwanese scientists, mainly by Chan and Yu (2002), Chang (2010), Chang et al. (2010), Jeng (1997, 1998, 2000), Jeng and Chang (1985), and Kou et al. (2013). Most symbiotic shrimps are small in size and cryptic in color (Bruce 1976a). Many of them might have been overlooked, still awaiting discovery to reveal their actual diversity.

In northeastern Taiwan, a number of recent studies on marine communities have focused on copepods (Chou et al. 2012), jellyfish (Tseng et al. 2015), symbiotic crabs (Limviriyakul et al. 2016a), and macro-algae (Lin et al. 2018). Baseline knowledge of marine carideans in Taiwan is quite sparse and relies on just a few publications. In contrast, knowledge about the diversity of anomuran and brachyuran crabs in Taiwan has become almost complete during recent decades, as shown in Baba et al. (2009), Chan et al. (2009), Chan et al. (2010), Chan and Yu (2002), McLaughlin et al. (2007), and Ng et al. (2001). Therefore, the unknown diversity of caridean shrimps still presents a challenge to biologists. In the present study, we collected specimens in the reef zone of northeastern Taiwan to evaluate the diversity of symbiotic caridean shrimp and thereby provide baseline taxonomic and distributional information for these animals in the coastal areas of the southern East China Sea.

Materials and methods

Study area description

Wang-Hai-Xiang Bay, with an area of about 2.4 km^2, is a semi-enclosed body of water in the vicinity of Keelung City in the northeastern coast of Taiwan in the southern East China Sea. The Wang-Hai-Xiang Chao-Jing Bay Resource Protected

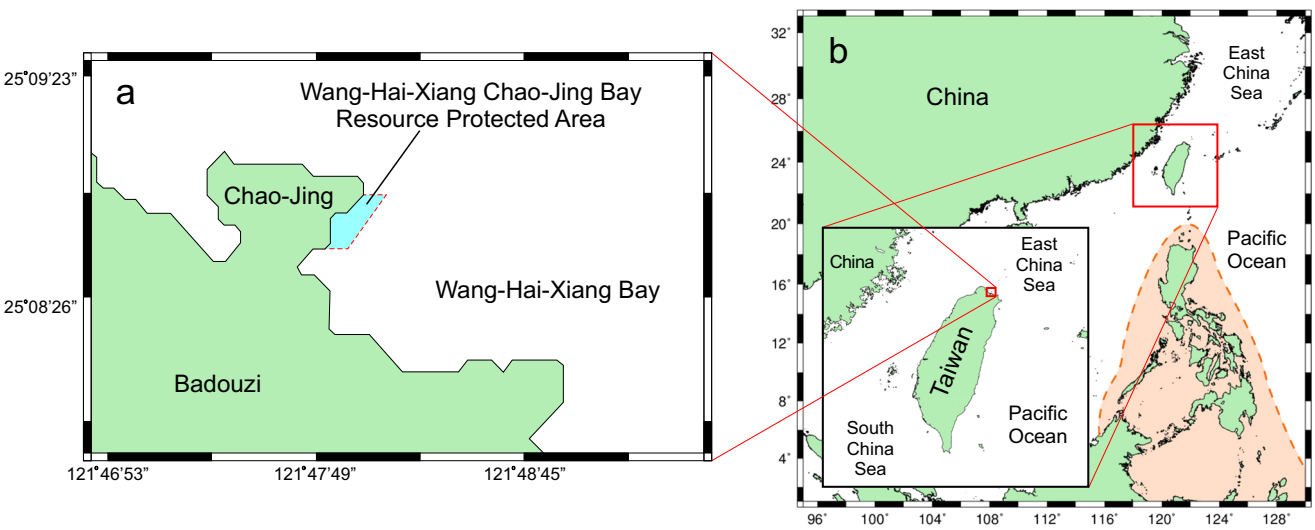


Fig. 1 **a** Map of the sampling area and **b** location in northeastern Taiwan during the sampling period of April to August in 2014. Orange dashed lines indicate the boundaries of the Coral Triangle

Table 1 Species, occurrence rate (%), depth of collection (m), symbiotic host, and recording month in 2014 of caridean shrimps collected from northeastern Taiwan. Occurrence: ++++ = > 90%, +++ = > 60%, ++ = 20–60%, + = < 20%. Asterisk indicates first report of the species in Taiwan

Scientific name	Occurrence	Depth	Host(s) on the coast of northern of Taiwan	Apr	May	Jun	Jul	Aug
Order Decapoda Latreille, 1802								
Suborder Pleocyemata Burkenroad, 1963								
Infraorder Caridea Dana, 1852								
Superfamily Alpheoidea Rafinesque, 1815								
Family Alpheidae Rafinesque, 1815								
Alpheus lottini Guérin-Méneville, 1838	+	2–4	Scleractinia: *Pocillopora*, *Seriatopora*	+			+	
Arete indicus Coutière, 1903	+++	0–3	Echinoidea: *Echinometra mathaei*		+	+	+	
Synalpheus charon (Heller, 1861)	+	3	Scleractinia: *Pocillopora damicornis*		+			
Synalpheus neomeris (de Man, 1897)*	+	2–21	Alcyonaria: *Dendronephthya*			+		
Synalpheus streptodactylus Coutière, 1905	+	4	Scleractinia: *Acropora*	+				
Synalpheus tumidomanus tumidomanus (Paulson, 1875)	+	3	Scleractinia: *Pocillopora damicornis*				+	
Family Hippolytidae Bate, 1888								
Saron marmoratus (Olivier, 1811)	+	3–5	Scleractinia: *Acropora*, *Seriatopora*				+	
Thor amboinensis (De Man, 1888)	+	3	Scleractinia: *Stylophora*; Actiniaria: *Entacmaea quadricolor*				+	+
Superfamily Palaemonoidea Rafinesque, 1815								
Family Palaemonidae Rafinesque, 1815								
Ancylocaris brevicarpalis Schenkel, 1902	++	1–5	Actiniaria: *Entacmaea quadricolor*			+	+	
Coralliocaris graminea (Dana, 1852)	+	2	Scleractinia: *Acropora*			+		
Coralliocaris superba (Dana, 1852)	++	3–5	Scleractinia: *Acropora*			+		+
Coralliocaris viridis Bruce, 1974	+	3	Scleractinia: *Acropora*					+
Cristimenes zanzibaricus (Bruce, 1967)*	+	5–10	Echinoidea: *Diadema setosum*, *Echinothrix*			+		
Cuapetes amymone (de Man, 1902)	+++	2–7	Scleractinia: *Acropora*, *Pocillopora*, *Stylophora*		+	+	+	+
Cuapetes elegans (Paulson, 1875)	+	4–12	Scleractinia: *Pocillopora*; Gorgonacea	+			+	
Hamodactylus boschmai Holthuis, 1952	++	15–25	Gorgonacea: *Melithaea*, *Ellisella*			+	+	+
Hamopontonia corallicola Bruce, 1970	+	3	Scleractinia: *Goniopora*			+		
Jocaste lucina (Nobili, 1901)	+++	2–10	Scleractinia: *Acropora*	+	+	+	+	+
Laomenes ceratophthalmus (Borradaile, 1915)	+	20	Crinoidea			+		
Manipontonia paeneglabra Bruce, 2012*	+	18–22	Hydroida; Gorgonacea: *Melithaea*			+		
Miopontonia yongei Bruce, 1985*	+	20	Gorgonacea: *Ellisella*				+	
Palaemonella pottsi (Borradaile, 1915)	+++	3–24	Crinoidea		+	+	+	
Palaemonella spinulata Yokoya, 1936*	+	5–20	Scleractinia: *Acropora*; Gorgonacea			+	+	
Pontoniopsis comanthi Borradaile, 1915	+++	4–24	Crinoidea		+	+	+	
Stegopontonia commensalis Nobili, 1906	+	5–10	Echinoidea: *Diadema*		+			
Thaumastocaris streptopus Kemp, 1922*	++	14–25	Porifera: *Callyspongia*, *Xestospongia*			+	+	
Tuleariocaris zanzibarica Bruce, 1967	+	5	Echinoidea: *Diadema*			+		

Area, covering an area of about 0.15 km^2 in the eastern part of the Wang-Hai-Xiang Bay (25° 8′ 40.45″ N, 121° 48′ 17.16″ E; Fig. 1), was established on 12 May 2016. It serves as a multi-function fishery resource protection area and also supports travel, leisure, and diving activities. Animal collection, fishing, and all forms of habitat change and destruction are prohibited there except for proposes of academic research. Economic seaweeds, mainly Gelidiaceae spp. (Lin et al. 2018), however, could be harvested from November to June with a permit granted by the governmental management department.

Field sampling and sample treatment

Weekly collections were made under permit from April to August 2014, within the boundaries of what is now the

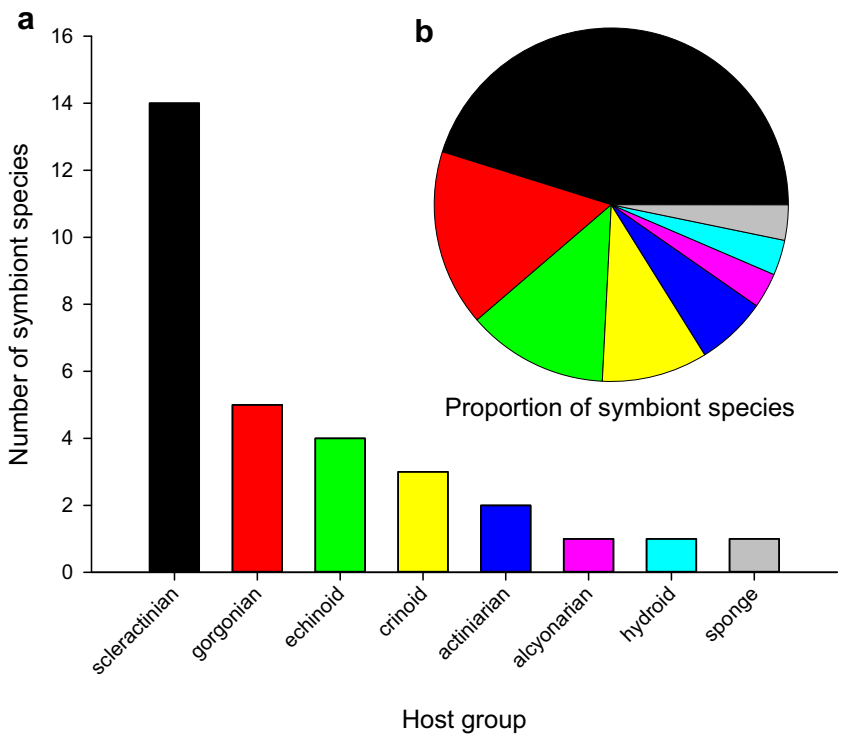


Fig. 2 **a** Numbers and **b** proportions of symbiotic shrimps identified from different host groups in the investigation area

Wang-Hai-Xiang Chao-Jing Bay Resource Protected Area. Symbiotic shrimp specimens were collected by scuba diving in the reef zone down to 24 meters (m) depth. Potential host animals (sponges, hydroids, actiniarians, scleractinians, gorgonians, alcyonarians, crinoids, and echinoids) were investigated. For each kind of potential host, the frequency of encounter, prevalence of symbiotic shrimps, and depth were recorded. Each host, along with its symbionts, was placed separately in a plastic zip-lock bag or box and taken to the Chao-Jing Ocean Center (National Museum of Marine Science and Technology) for identification. There, the specimens were photographed, preserved in 70% ethyl alcohol, and deposited in the center's collection. The prevalence of each symbiont was calculated by dividing the number of host species individuals bearing the symbiont by the total number of host individuals checked.

Shrimp identification

In the laboratory, the caridean shrimps were identified under a dissecting microscope (Olympus SZX16) using the following keys: for Alpheidae, Anker and Jeng (2007), Chace Jr. (1988), Suzuki (1970), and Wang and Sha (2015); for Hippolytidae, Chace Jr. (1997) and Xu and Li (2015); for Palaemonidae, Bruce (1982), Chace Jr. and Bruce (1993), Berggren (1994), Bruce (2004), Mitsuhashi and Takeda (2008), Marin (2009, 2014), Bruce (2010), Marin and Anker (2011), and Fransen and Rauch (2013).

Results

Twenty-seven species of symbiotic shrimp, representing 20 genera and 3 families, were identified from the study area (Table 1). The following 5 species showed a particularly high prevalence of occurrence (more than 60%) on their hosts: *Arete indicus* Coutière, 1903; *Cuapetes amymone* de Man, 1902; *Jocaste lucina* Nobili, 1901; *Palaemonella pottsi* Borradaile, 1915; and *Pontoniopsis comanthi* Borradaile, 1915. Furthermore, 6 species, *Synalpheus neomeris* (de Man, 1897); *Cristimenes zanzibaricus* Bruce, 1967; *Manipontonia paeneglabra* Bruce, 2012; *Miopontonia yongei* Bruce, 1985; *Palaemonella spinulata* Yokoya, 1936; and *Thaumastocaris streptopus* Kemp, 1992, were recorded for the first time in the waters of Taiwan.

Symbiotic carideans were not distributed evenly among the host taxa. Among the shrimp species found by us, 3.2% were on sponges, 3.2% on hydroids, 6.5% on actiniarians, 45.2% on scleractinians, 16.1% on gorgonians, 3.2% on alcyonarians, 9.7% on crinoids, and 12.9% on echinoids (Fig. 2). Fourteen species, nearly half of the total (45.2%), were associated with scleractinian hosts, especially with branching corals. The proportions of symbiotic shrimps belonging to the three families were as follows: Alpheidae, 22.2% (6 species; Fig. 3); Hippolytidae, 7.4% (2 species; Fig. 4); and Palaemonidae, 70.4% (19 species; Fig. 5). Among these shrimps, the genus *Synalpheus* was dominant in species number, represented by 4 species in all. All of the species in the family Palaemonidae were so-called pontoniine shrimps, a

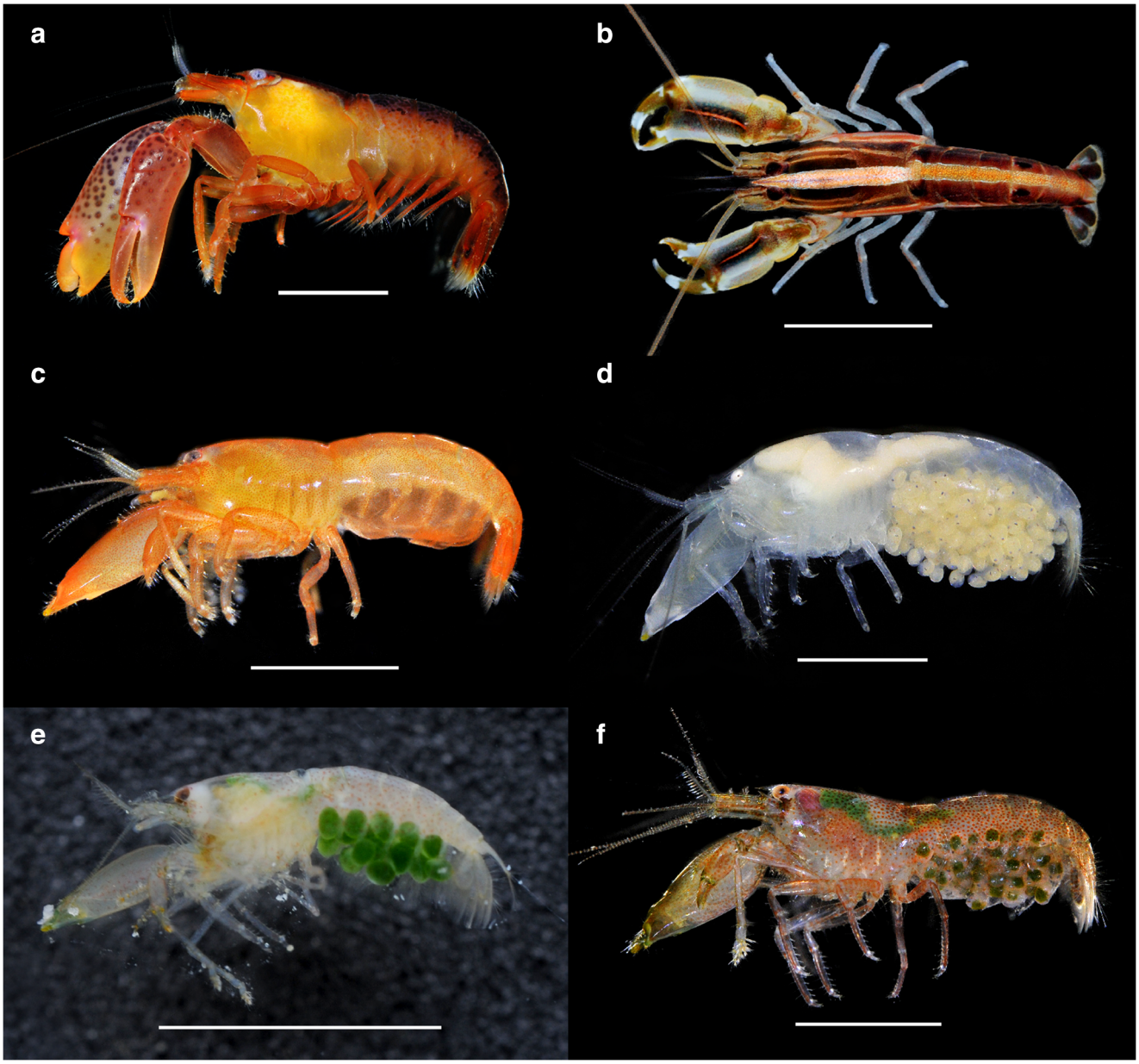


Fig. 3 Family Alpheidae. **a** *Alpheus lottini*; **b** *Arete indicus*; **c** *Synalpheus charon*; **d** *Synalpheus neomeris*; **e** *Synalpheus streptodactylus*; **f** *Synalpheus tumidomanus tumidomanus*. Scale bars each represent 5 mm

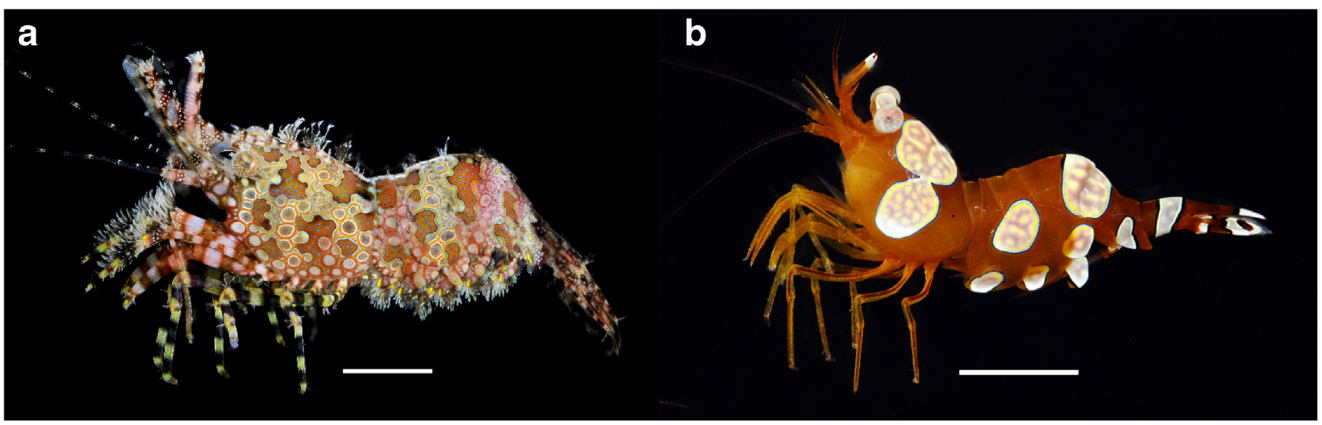


Fig. 4 Family Hippolytidae. **a** *Saron marmoratus*; **b** *Thor amboinensis*. Scale bars each represent 5 mm

name used for members of the former but no longer recognized as subfamily Pontoniinae (De Grave et al. 2015), which are almost exclusively tropical and subtropical marine symbionts. Such shrimps are rarely found in temperate or fresh waters (Bruce 1983).

Discussion

The dominant hosts of symbiotic shrimps

The present results indicate that branching corals are not only important to the reef ecosystem on their own account but also contribute to the biodiversity of decapod crustaceans. Nearly half of the symbiotic shrimp species in the area were associated with scleractinian corals. Among these, 90% were found to live on branching species of *Acropora* and Pocilloporidae, while the remainder was associated with massive corals. Similarly, a study of symbiotic crabs in northeastern Taiwan found most of them to be associated with branching corals (Limviriyakul et al. 2016a). A substantial predilection for decapod symbionts to live on branching corals has also been reported elsewhere in the Indo-Pacific (Bruce 1972, 1976a, 1998; Fransen 2008, 2010, 2012; Limviriyakul et al. 2016b; Patton 1966; Stella et al. 2010; Stella et al. 2011; Vytopil and Willis 2001).

The growth form of scleractinian corals is a factor affecting the diversity of coral-associated organisms (Pratchett et al. 2009; Stella et al. 2010; Vytopil and Willis 2001). A branching morphology benefits symbionts by providing more surface area on which to live, greater protection against predators, and more food in the form of coral tissue and mucus (Castro 1988; Vytopil and Willis 2001). Furthermore, more complex branching is correlated with a higher diversity of associated organisms (Stella et al. 2010).

Non-branching corals, including massive, encrusting and mushroom corals, harbor fewer species of symbiotic carideans (Bruce 1976a, 1998). Many species of these corals that do harbor associated shrimp, such as *Euphyllia glabrescens* (Chamisso & Eysenhardt, 1821), *Fungia* spp., *Galaxea fascicularis* (Linnaeus, 1767), *Goniopora* spp., *Heliofungia actiniformis* (Quoy & Gaimard, 1833), and *Physogyra lichtensteini* (Milne Edwards & Haime, 1851), have long-extended or swollen polyps (Bruce 1976a; De Grave 1998; Hoeksema et al. 2012; Marin 2014). In the present study, we found *Hamopontonia corallicola* Bruce, 1970, is associated with massive corals of the genus *Goniopora*.

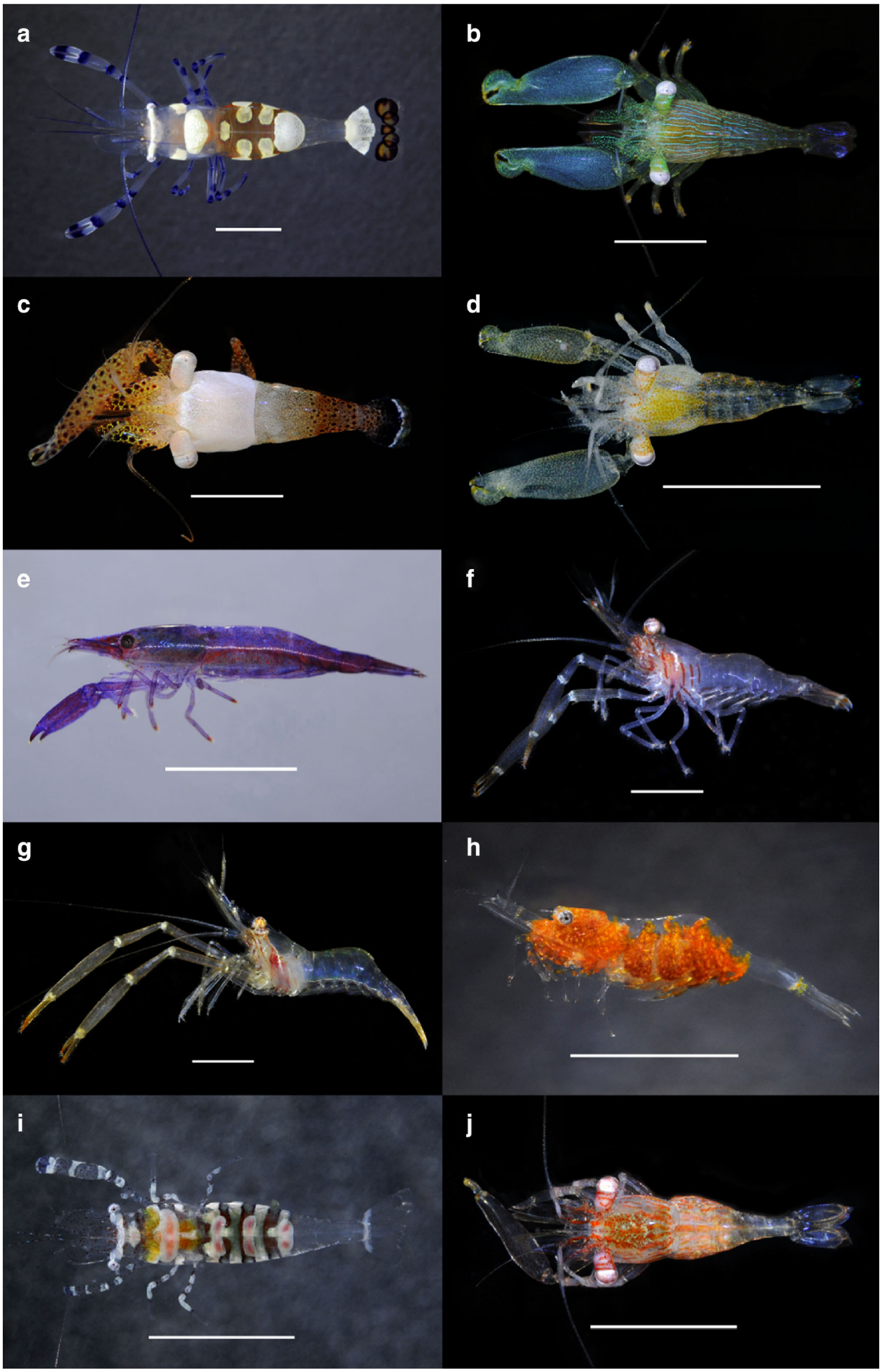
The dominant species of symbiotic shrimps

The five species of symbiotic shrimp with particularly high prevalence in the investigated area have varied distribution records worldwide. The alpheid shrimp *Arete indicus* (Fig. 3b) is common throughout the Indian Ocean and Western Pacific Ocean. It inhabits intertidal rocky shores (Suzuki 1970), which is consistent with our record of *A. indicus* in the 0–3-m-depth zone. This cryptically colored shrimp is most commonly associated with *Echinometra mathaei* (Blainville, 1825) (Banner and Banner 1973), but it also occurs on various other genera of echinoids, including *Centrostephanus*, *Diadema*, and *Heliocidaris* (Banner and Banner 1973; Bruce 1982). All of the specimens in the present study were found beneath the rock-boring sea urchin, *E. mathaei*, and most of the sea urchins were giving shelter to a couple of shrimps. The prevalence of *A. indicus* in the area was extraordinary; approximately 90% of *E. mathaei* specimens harbored the shrimp species, and the echinoid was also abundant in the intertidal zone of the study area, attaining densities of 60 individuals per square meter or more. In addition, *A. indicus* was usually observed together with an anomuran crab, *Petrolisthes virgatus* Paulson, 1875, which lives in the cavities excavated in the substrate by the urchin (Limviriyakul et al. 2016a).

The pontoniine shrimps *Cuapetes amymone* (Fig. 5f) and *Jocaste lucina* (Fig. 5j) are obligatory symbionts of scleractinian branching corals and both species have been widely recorded sympatrically across the Indo-West Pacific (Electronic Supplementary Material, Table S1). *C. amymone* has been found from the shallows to a depth of 23 m (Bruce 2004) whereas the maximum recovered depth for *J. lucina* is 54 m (Li 2008). *C. amymone* is usually associated with the genera *Acropora*, *Pocillopora*, *Seriatopora*, and *Stylophora* (Bruce 1972, 2004; Stella et al. 2011) whereas *J. lucina* is mainly associated with *Acropora*, and only rarely with *Pocillopora* (Bruce 1972), *Stylopora* (Bruce 1998), *Porites* (Bruce 1981a), hydroids of the genus *Millepora* (Bruce 1981a), and dead coral heads (Head et al. 2015). In the present study, we collected *C. amymone* from various genera of branching corals, and *J. lucina* from *Acropora* spp. As has been noted before (Limviriyakul et al. 2016a), we found these two species occurring together on the same host colony, and also with *Tetralia* crabs, *Cymo* crabs, *Coralliocaris* shrimps, and coral gobies.

The symbiotic shrimps *Palaemonella pottsi* (Fig. 5n) and *Pontoniopsis comanthi* (Fig. 5p) occur on crinoids and are broadly distributed throughout the Indo-West Pacific (ESM, Table S1), most commonly associated with genera such as *Anneissia*, *Comanthus*, *Comaster*, *Comatella*, *Comatula*, *Heterometra*, *Lamprometra*, and *Phanogenia* (Bruce 1970,

Fig. 5 Family Palaemonidae. **a** *Ancylocaris brevicarpalis*; **b** *Coralliocaris graminea*; **c** *Coralliocaris superba*; **d** *Coralliocaris viridis*; **e** *Cristimenes zanzibaricus*; **f** *Cuapetes amymone*; **g** *Cuapetes elegans*; **h** *Hamodactylus boschmai*; **i** *Hamopontonia corallicola*; **j** *Jocaste lucina*; **k** *Laomenes ceratophthalmus*; **l** *Manipontonia paeneglabra*; **m** *Miopontonia yongei*; **n** *Palaemonella pottsi*; **o** *Palaemonella spinulata*; **p** *Pontoniopsis comanthi*; **q** *Stegopontonia commensalis*; **r** *Thaumastocaris streptopus*; **s** *Tuleariocaris zanzibarica*. Scale bars each represent 5 mm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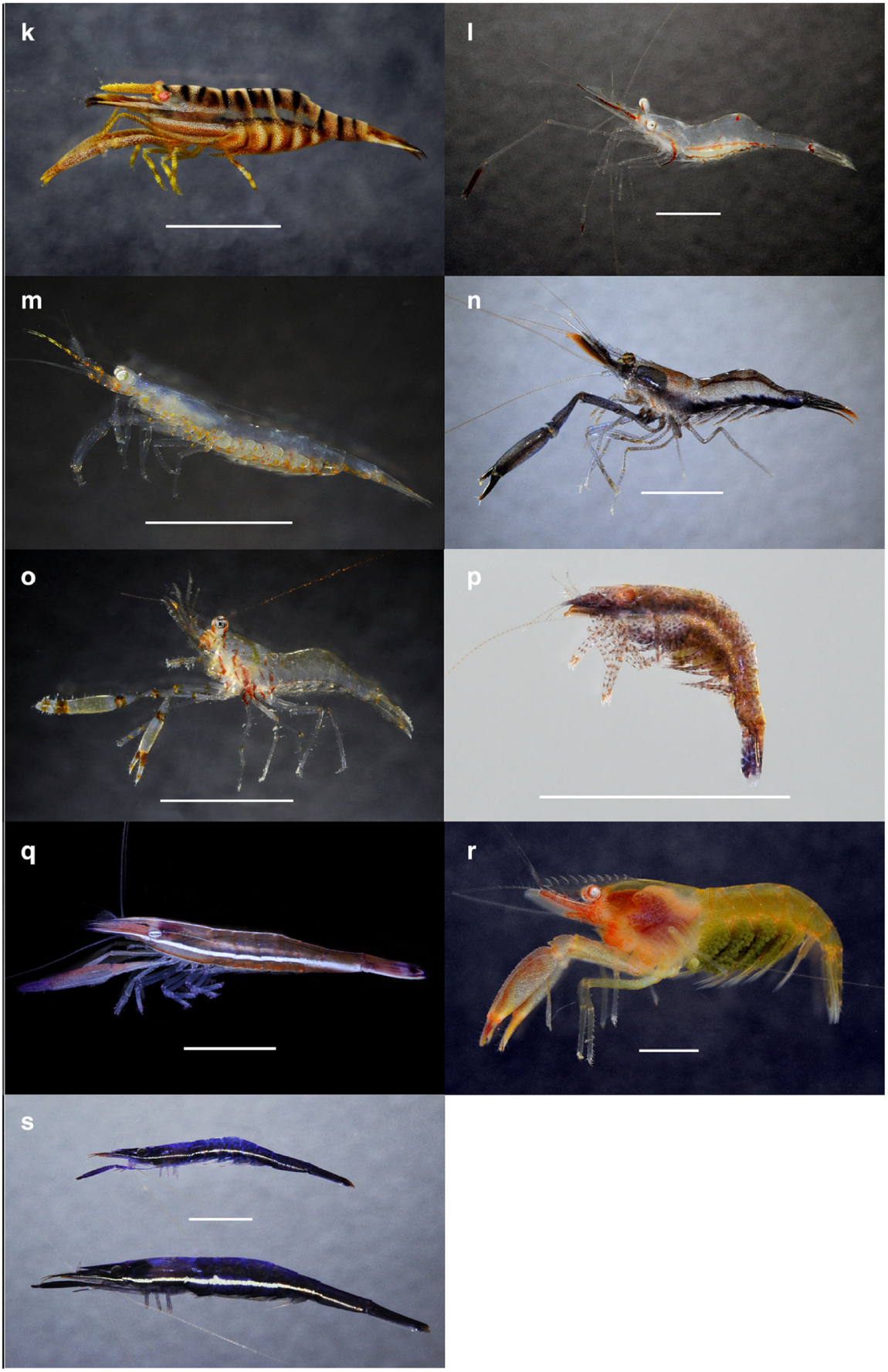
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1982, 1994; Li and Bruce 2006). Both species have been reported from shallow water to 25–30 m depth (De Grave 2000). All of our specimens of *Pa. pottsi* and *Po. comanthi* were collected from crinoids, with the prevalence of more than 60% and 85%, respectively. Studies from Vietnam also report that the number of *Pa. pottsi* specimens collected per host is much lower than those of *Po. comanthi* (Britayev and Mekhova 2011; Dgebuadze et al. 2012). Both shrimps have their own particular niche on the host. In this study, *Pa. pottsi* were approximately 2.0–4.2 mm in carapace length and lived in the center near the tegmen and mouth of the host. In contrast, *Po. comanthi* were relatively small, with a carapace length of approximately 0.9–1.6 mm, and inhabited the arms of crinoids. The aggregation habits of both shrimps were also dissimilar: *Pa. pottsi* usually lived in a heterosexual pair on a crinoid while *Po. comanthi* lived in large groups of adults and juveniles of both sexes. Most of the crinoids in the study area harbored at least 1 individual of *Po. comanthi*, but none was found on small crinoids with an arm length of less than 7 cm. These two species were commonly found to live together and with another symbiotic shrimp, *Synalpheus stimpsonii* (de Man, 1888), and also with the symbiotic anomuran and brachyuran crabs *Allogalathea elegans* (Adams and White, 1848) and *Permanotus purpureus* (Gordon, 1934).

Newly recorded species in Taiwan

One species of Alpheidae and 5 species of Palaemonidae represent new records for Taiwan. The alpheid shrimp *Synalpheus neomeris* (Fig. 3d) has been found on soft corals from East Africa to Australia. Typically found in pairs, it is usually associated with *Dendronephthya* spp. and *Xenia* spp. (Chace Jr. 1988) but has also been recorded in association with sponges, bryozoans, and dead coral heads (Banner and Banner 1975; Chace Jr. 1988). It ranges from the shallow subtidal to 250 m depth (Banner and Banner 1983; Chace Jr. 1988). In the present study, specimens were found on alcyonarians of the genus *Dendronephthya*.

Cristimenes zanzibaricus (Fig. 5e) was collected from the echinoids *Diadema setosum* and *Echinothrix* sp. at 5–10 m depth. This report represents the first record of this shrimp in the northern hemisphere and the second locality for it in the Pacific Ocean. In East Africa (Tanzania, Kenya, and Seychelles) and Australia (Bruce 1967, 1976b, 1983; Fransen 1994), *C. zanzibaricus* has been found to live with the echinoid hosts *Astropyga radiata* (Leske, 1778); *Centrostephanus tenuispinus* H.L. Clark, 1914; *Diadema savignyi* (Audouin, 1829); *Diadema setosum* (Leske, 1778); and *Echinothrix calamaris* (Pallas, 1774) (Bruce 1967, 1976b, 1982) from the subtidal to 12 m depth (Fransen 1994).

Manipontonia paeneglabra (Fig. 5l) was found on the gorgonian *Mopsella* sp. and on a hydroid from relatively shallow depths of 18–22 m. The present record is just the fourth report and the northernmost record of this species, and the first for which the hosts are known. It was first described by Bruce (2012) in Indo-West Pacific waters, and it is distributed in the South China Sea (Paracel Islands), Singapore, Australia, and Papua New Guinea (Anker and De Grave 2016; Bruce 2012; Muséum national d'Histoire naturelle 2013). The previously known depth range was 82.3–105 m, and nothing was known about the shrimp's habitat or host (Bruce 2012).

Miopontonia yongei (Fig. 5m) was sampled from a gorgonian host, *Ellisella* sp., at 20 m depth. This rare species of Palaemonidae has previously been found associated with *Ellisella plexauroides* (Toeplitz, 1919) and with an antipatharian, *Cirrhipathes anguina* (Dana, 1846) (Okuno 1998; Wagner et al. 2012). It has been reported at 40–80 m depth from just a few localities: Indonesia (Bali and Raja Ampat), Philippines, Japan, and Australia (Bruce 1985; Fransen 2008; Gan et al. 2015; Okuno 1998; Williams and Boyko 2012).

The pontoniine shrimp *Palaemonella spinulata* (Fig. 5o) is distributed in East Africa and the West Pacific Ocean (ESM, Table S1) from the intertidal to 60 m depth (Bruce 1994; Poupin 2003), often living among coral heads, algae, dead coral, and coral rubble (Li and Bruce 2006; Stella et al. 2011). It is probably a free-living micro-predator in coral reefs (Bruce 1981b). In the present study, specimens were collected from gorgonians and from branching scleractinian corals of the genera *Acropora* and *Seriatopora*.

Thaumastocaris streptopus (Fig. 5r), a widespread shrimp species, has been reported from most areas of the Indo-West Pacific as well as the Gulf of Mexico (ESM, Table S1). It is usually found living in pairs within the spongocoel of several genera of Porifera, such as *Acarnus*, *Callyspongia*, *Haliclona*, *Leucetta*, *Mycale*, *Oceanapia*, *Petrosia*, *Siphonochalina*, and *Xestospongia* (Bruce 1981b, 2005; De Grave 2000), but it is occasionally associated with scleractinian corals of the genera *Pocillopora* and *Stylophora* (Preston and Doherty 1990). In our study, all specimens of this shrimp were found inside *Callyspongia* sponges except for one specimen from a small barrel sponge, *Xestospongia testudinaria* Lamarck, 1815. Barrel sponges are well-known for their large size and have a relatively wide spongocoel radius compared with the other known hosts of this shrimp. It may be that *T. streptopus* can live in any sponge with a narrow exhaust tube, including small barrel sponges.

Diversity of pontoniine shrimps in Taiwan

The world species richness of marine caridean shrimps is dominated by the family Palaemonidae (981 species), followed by Alpheidae (663) and Hippolytidae (338) (De Grave and Fransen 2011). So-called pontoniine shrimps, members of the family Palaemonidae, are among the most diverse

invertebrate-associated taxa on tropical reefs in the Indo-Pacific (Bruce 1972, 1976a; De Grave 2001), with more than 602 species known (De Grave and Fransen 2011). Approximately 60–70% of them are involved in some form of symbiotic association (De Grave 2001). The present study identified 19 pontoniine shrimps, with 5 species recorded from Taiwan for the first time, thereby raising the total number of pontoniine shrimp species from Taiwan to 83 (ESM, Table S1). These represent approximately 14% of the known species of pontoniine shrimps, more than a previous estimate by Shao (1998) that the marine "pontoniine" species around Taiwan represent one tenth of those worldwide.

Conclusion

The present study revealed 27 species of symbiotic caridean shrimps at the study site in northeastern Taiwan; among them, 6 species were reported from Taiwan for the first time. The high species richness of these shrimps in this part of the southern East China Sea shows that this region holds great promise for advanced studies on caridean shrimps. It also provides a hint of the state of health of the diverse benthic fauna in the investigated areas, because some of these symbiotic shrimps, which have the ability to mitigate environmental stresses and enhance nutrient flow to their hosts, are considered to increase the persistence and resilience of their hosts. Currently, coral reef fauna are threatened by various anthropogenic impacts and climate change. Subtropical reefs in Taiwan have the valuable potential to serve as climate change refuges for vulnerable tropical coral reef species. To effectively maintain and manage these coral reefs, more complete knowledge of the reef fauna biodiversity is essential. Our present data have established which species of symbiotic caridean shrimp were dominant before the establishment of the Wang-Hai-Xiang Chao-Jing Bay Resource Protected Area in northeastern Taiwan, thereby, providing baseline information to enable future monitoring of the effectiveness of the Protected Area.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities. The study is compliant with CBD and Nagoya protocols.

Data availability statement All relevant data pertaining to this study are included in this published article and its supplementary information files.

Author contribution statement TWS and JSH wrote the proposal and designed the study. Specimens collected by PL, LCT, and YHT. PL completed the taxonomic work of shrimp species identification and took photographs of shrimps. PL and LCT analyzed the data and drafted the manuscript. TWS and JSH finalized the manuscript. All authors read and approved the final manuscript.

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