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Three way symbiosis between a goby, a shrimp, and a crab

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Abstract A unique case of triple symbiosis between a goby, a pistol shrimp, and a porcellanid crab sharing the same burrow close to reef patches in Lembeh Strait, Indonesia, is described from direct observations for the first time. The burrow, typically occupied by shrimps and gobies, is shared with the porcellanid *Enosteoides lobatus*. In the goby–shrimp association, the fish inhabits the burrow, which is constructed and kept clean by the shrimp, and the fish warns the shrimp of potential dangers approaching their refuge. The porcellanid lives in the burrow and also benefits from living in a habitat where it could not survive without the two sentinel species. Because the limiting resource for the suspension-feeding porcellanid is protected space, this liaison is an adaptation by *E. lobatus* to a symbiotic life in a habitat that protects it from predation, and is optimal for filter feeding.

Keywords Goby–shrimp association · Gobiidae · Alpheidae · Porcellanidae · Symbiosis · Indo-West Pacific

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Introduction

Symbiotic associations between gobies and burrowing pistol shrimps have captured the attention of biologists for decades (Karplus 1979, 1992; Longley and Hildebrand 1941; Polunin and Lubbock 1977; Randall et al. 2005; Wirtz 2008) because of their complex behavioral interactions that evolved into cooperation between species from distant phyla. Observations of the association between gobies and burrowing pistol shrimps have been described from numerous localities in tropical and subtropical waters, and in different kinds of habitats, such as coral reefs, mud flats, and sea-grass beds, ranging from the intertidal zone to a depth of more than 50 m. In the Indo-West Pacific, over one hundred species of gobiid fish representing 20 genera live symbiotically with pistol shrimps of the genus *Alpheus*. More than 30 species of this shrimp genus live in such an alliance, and in most cases the shrimp lives in pairs. The alpheid excavates in the sediment to construct a burrow that is kept clean by constantly removing settling material. To prevent the cave's collapse, the shrimp reinforces the roof and sides of the opening with coral and shell fragments. The goby uses the burrow as a refuge, and in turn, through an elaborate warning behavior, it keeps both the constructor and burrow safe from potential danger, mainly posed by predatory fish and crustaceans, and by other gobies searching for a new burrow. In many cases, the shrimp follows the fish out of the burrow and senses the fish's warning movements by touching it constantly with its second antennae. The goby–shrimp association varies from being species-specific to involving the same goby species occupying the burrow of different shrimp species, and from being obligatory in most cases to facultative in others (reviewed by Karplus 1987; Wirtz 2008).

Here, we report on a porcellanid crab as a third partner in shrimp–goby burrows located in the vicinity of scattered reef patches in the area of Lembeh Strait, North Sulawesi,

Indonesia. Although symbiosis is not infrequent in Porcellanidae, no species of this family has yet been observed to live symbiotically with fish. The only known symbiosis of a porcellanid crab with a shrimp is that of *Pachycheles rudis* Stimpson with the shrimp *Betaeus setosus* Hart, 1964 in the northeastern Pacific. In this association, the minute shrimp seeks out protection by the thick-clawed porcellanid (Jensen 1986). Most porcellanid species live on hard-substrates, some are involved in symbiotic associations with invertebrate hosts like anemones, sea urchins and stars, and polychaetes (Viviani 1969; Werding and Haig 1982; Werding 1983; Viviani et al. 2010), and a few are found in muddy burrows in mangrove swamps and estuaries (Werding and Hiller 2004). Porcellanids feed by filtering water-borne detritus with their large, feather-like, third maxillipeds, and are thus located at the base of the marine food web. A consequence of this feeding habit is that the main resource limitation they encounter is not food per se, but available substrate, which may account for the specialization of different species for different habitats (Hiller et al. 2006, 2010).

Material and methods

Field observations of goby–shrimp burrows were made in September 2013 and 2015 by SCUBA diving in the area of Lembeh Strait (1°26′N 125°14′E). Dives were made at 5–25-meter depths in silty, sandy habitats surrounding reef patches and coral rubble. Burrows were photographed while each being observed for approximately 15 minutes.

Results

In some of the goby-shrimp burrows a little crab was observed sitting in the vicinity of the opening of the hole, apparently hiding in this refuge when disturbed. Repeated observations confirmed that the crab consistently lives in association with the fish and shrimp, which did not behave agonistically towards the crab. The photographs (Fig. 1) were used to identify the species of fish, shrimp, and crab. The gobies and the shrimp belong to complexes of species that can only be accurately identified by sampling specimens. The fish specimens in some associations belong to the Indo-Pacific genus *Amblyeleotris* (Fig. 1d, e), and in others to the West Pacific yellow goby *Cryptocentrus* cf *cinctus* (Herre, 1936) (dark color morph; Fig. 1f; I. Karplus, pers. comm). The shrimp was most probably the Indo-West Pacific tiger pistol shrimp *Alpheus bellulus* (Miya and Miyake, 1969) (Fig. 1c, d, f; A. Anker, pers. comm.), which is widely distributed, and comprises a species complex as well. The crab was the porcellanid *Enosteoides lobatus* Osawa, 2009 (Decapoda, Anomura, Porcellanidae) (Fig.1a-f), first described from Japan as living underneath coral blocks near the outer reef edge, and later identified by us from a collection of the Muséum National d'Histoire Naturelle (MNHN), Paris, from Papua New Guinea. The porcelain crab is apparently uncommon in the shrimp–fish association, although its presence can be easily overlooked, as the crab is small, shy, moves close to the refuge's opening, and resembles a piece of rubble. A total of six porcellanid individuals were found in different goby–shrimp burrows at different depths (7–20 meters). The crab sits near the burrow's opening on the hard habitat offered by the coral and shell fragments that the shrimp uses to reinforce the cave and avoid its collapse. When the goby and alpheid recede into the cave because of an approaching potential danger, so does the porcellanid by moving toward the roof of the burrow's entrance. When the shrimp moves out of the cave, the porcellanid's claw comes in contact with it, and the crab exits as well (Fig. 1c, d). The efficiency of filter-feeding by the crab is higher outside the burrow, as water movement becomes stronger, and detritus is suspended through the movement of the other partners. However, predation risk, mainly posed by fish and other crustaceans, also increases as the crab moves farther from the burrow.

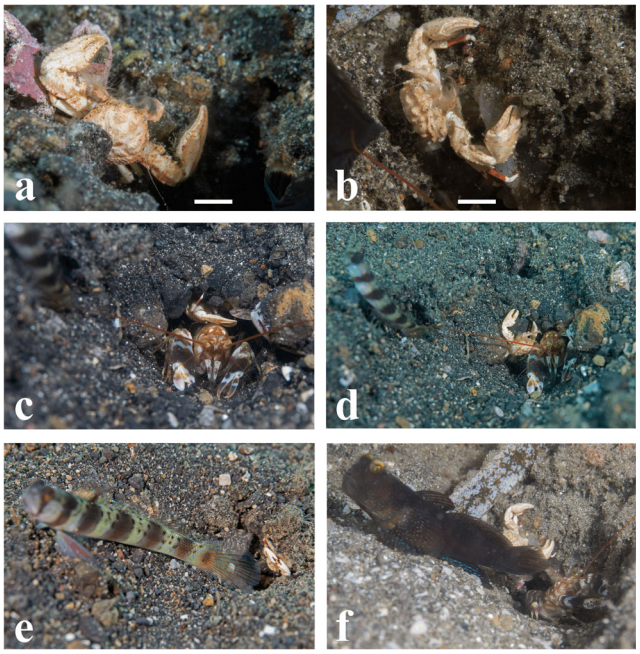

Fig. 1 Photographs of burrows shared by gobies, shrimp, and porcellanids in the coral reef area of Lembeh Strait, Indonesia. (**a**, **b**) *Enosteoides lobatus* lying close to the burrow's opening. Scale = 0.5 cm. (**c**) *E. lobatus* in its typical position in the burrow, sitting on the roof of the opening, and touching with its chelipeds a pistol-shrimp individual, most probably of the species *Alpheus bellulus*. (**d**) *E. lobatus* at the opening of the burrow while *Amblyeleotris* sp. and *Alpheus* cf *bellulus* are moving in and out of their refuge. (**e**) *E. lobatus* close to *Amblyeleotris* sp. (**f**) *E. lobatus* in the same situation as in (**c**), but sharing the burrow with *Cryptocentrus* cf *cinctus*

Discussion

Triple symbiosis among metazoa

Symbioses between gobiid fish and burrowing pistol shrimps have been widely described from different habitats and localities, mostly in the Indo-West Pacific. However, a third metazoan joining this symbiosis has been rarely reported, either because this complex association is hard to document from field observations, or because it does not occur so frequently in the evolution of the shrimp-goby cooperation. Species of gobies (genera *Amblyeleotris* and *Ctenogobiops*) associated with burrowing shrimps seem to be temporary hosts of the West Pacific nudibranch *Gymnodoris nigricolor* Baba 1960, which attaches to the fish fin membrane with its buccal apparatus (Karplus 2014; Williams and Williams 1986). The mollusk seems to be a facultative parasite rather than a symbiont, as it seasonally attaches to the fish to feed on the fin membranes (Karplus 2014; Osumi and Yamasu 2000). The dark color of the nudibranch probably affects the fish also by making it more conspicuous to predators in a sandy habitat (Karplus 1979, 2014). Another interesting example of a triple symbiosis among Metazoa is posed by the shrimp *Alpheus rapacida* De Man, 1908 and the gobiid *Vanderhorstia* sp., which seem to share the same burrow with a second species of shrimp, *Orygmalpheus polites* De Grave and Anker, 2000. The present observation comprises a further novel discovery of a third metazoan joining the shrimp-goby association. To our knowledge, porcellanid crabs have not been previously observed living in burrows shared by gobiids and burrowing shrimps.

Evolutionary pathways of porcellanid symbiosis and the genus *Enosteoides*

Although porcellanids are generally free-living and adapted to hard substrates, there is a marked tendency to commensalism. Out of roughly 300 known species, 40 are known to live in association with other invertebrates, which are used by the porcellanid as a protected substratum on which to live, feed, and mate. Porcellanids are filter-feeders adapted to moving in shallow waters that transport plankton and detritus. In this situation, the crabs need a stable and sheltered substratum in which to filter-feed with minimum exposure to predators. Finding a host and evolving a commensal lifestyle opens an opportunity to alternative substrates and additional protection. This strategy is especially attractive in the rocky intertidal, where substrates are highly competed for, and in soft bottoms, where porcellanids otherwise would not be able to survive. Commensalism in porcellanids has developed independently in various lineages and to different grades of morphological and behavioral adaptation (Hiller et al. 2010). Some commensal species do not show evident morphological adaptations regarding their free-living congeneric species (e.g. *Clastotoechus* Haig, 1960), with three species associated with sea urchins, and three free-living species). Other commensals, like most members of the *Polyonyx sinensis* group (Johnson 1958), live in pairs in the tubes of sand-dwelling annelids (Werding 2001), and are morphologically extremely adapted to moving sideways within the tubes of their host.

Enosteoides lobatus seems to have evolved an elegant strategy of efficient feeding while enjoying lower predation risk by specializing to a pre-established fish-shrimp symbiosis. Most probably the crab senses tactile and visual cues from the shrimp and the goby (mostly from the shrimp) as warning signals.

The genus currently contains five species distributed in the Indo-West Pacific. All species, except *E. lobatus*, are apparently free-living with a marked affinity for bottoms covered by fine debris, most frequently occurring under stones or among coral fragments deposited on fine sediment. *E. lobatus* and *E. philippinensis* Dolorosa and Werding, 2014 are known only from the original descriptions, the first from Japan, and the second from the Philippines. *E. ornatus* (Stimpson, 1858) and *E. melissa* (Miyake, 1942) are known from a wide geographic range in the Indo-West Pacific. *E. palauensis* (Nakasone and Miyake, 1968) is restricted to the West Pacific (Osawa 2009).

A number of questions on the ecology, behavior, and reproductive biology of *E. lobatus* still need to be answered through more quantitative sampling and observations in the field and in aquaria. It is unclear whether the crab lives in pairs, as other symbiotic porcellanid species do [e.g. *Clastotoechus vanderhorsti* (Schmitt, 1924) living under the sea urchin *Echinometra lucunter* (Linnaeus, 1758); (Schoppe and Werding 1995)], or whether the structure of the burrow [one or more openings (see (Karplus 1987))] and distance between occupied burrows allows the porcellanid to move within and among them in search of mates in the neighborhood of its domicile. Another question is whether the association of the porcellanid with its hosts is obligatory, and whether the crab is able to colonize any goby-shrimp burrow independently of the inhabiting species.

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References

Baba K (1960) The genera *Gymnodoris* and *Nembrotha* from Japan (Nudibranchia-Polyceridae). Publications of the Seto Marine Biological Laboratory 8:71–74

De Grave S, Anker A (2000) A new genus and new species of alpheid shrimp (Crustacea: Decapoda) from Papua New Guinea. Raffles Bull Zool 48:249–256

De Man JG (1908) Diagnoses of new species of macrurous decapod Crustacea from the" Siboga-Expedition". Notes Leyden Mus 30: 98–112

Dolorosa R, Werding B (2014) A new mangrove-inhabiting porcellanid crab of the genus *Enosteoides* (Crustacea: Decapoda: Anomura) from Puerto Princesa Bay, Palawan, the Philippines. Bull Mar Sci 90:865–872

Haig J (1960) The Porcellanidae (Crustacea Anomura) of the eastern Pacific. Allan Hancock Pacific Expeditions 24, pp 1–440

Hart JFL (1964) Shrimps of the genus *Betaeus* on the Pacific Coast of North America with descriptions of three new species. Proc U S Natl Mus 115:431–466

Herre AWCT (1936) Eleven new fishes from the Malay Peninsula. Bull Raffles Mus 12:5–16

Hiller A, Kraus H, Almon M, Werding B (2006) The *Petrolisthes galathinus* complex: Species boundaries based on color pattern, morphology and molecules, and evolutionary interrelationships between this complex and other Porcellanidae (Crustacea: Decapoda: Anomura). Mol Phylogenet Evol 40:547–569

Hiller A, Viviani CA, Werding B (2010) Hypercarcinisation: An evolutionary novelty in the commensal porcellanid *Allopetrolisthes spinifrons* (Crustacea: Decapoda: Porcellanidae). Nauplius 18:95–102

Jensen GC (1986) Some observations of the alpheid shrimp *Betaeus setosus* Hart with its host, *Pachycheles rudis* Stimpson. Bull South Calif Acad Sci 85:180–18

Johnson DS (1958) The Indo-West Pacific species of the genus *Polyonyx* (Crustacea, Decapoda, Porcellanidae). Ann Zool 11(8):95–119

Karplus I (1979) The tactile communication between *Cryptocentrus steinitzi* (Pisces, Gobiidae) and *Alpheus purpurilenticularis* (Crustacea, Alpheidae). Z Tierpsychol 49:173–196

Karplus I (1987) The association between gobiid fishes and burrowing alpheid shrimps. Oceanogr Mar Biol Annu Rev 25:507–562

Karplus I (1992) Obligatory and facultative goby shrimp partnerships in the western tropical Atlantic. Symbiosis 12:275–291

Karplus I (2014) Symbiosis in fishes: The biology of interspecific partnerships. Wiley Blackwell, Oxford, pp 1–449

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius, Holmiae ii, 824 pp

Longley WH, Hildebrand SF (1941) Systematic Catalogue of the Fishes of Tortugas, Florida. Carnegie Institute of Washington, Publication 535, 331 pp

Miya Y, Miyake S (1969) Description of *Alpheus bellulus* sp. nov. associated with gobies from Japan (Crustacea, Decapoda, Alpheidae). Publ Seto Mar Biol Lab 16:307–314

Miyake S (1942) Studies on the decapod crustaceans of Micronsia. III. Porcellanidae. Palau Trop Biol Station Stud 2:329–379

Nakasone Y, Miyake S (1968) A new species of *Porcellana* (Anomura: Porcellanidae) from the Palau Islands, with description of its related forms. Occasional Paper of Zoological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan 1: 165–171

Osawa M (2009) New records of three species of the genus *Enosteoides* Johnson, 1970 (Decapoda: Anomura: Porcellanidae) from Japan, with description of a new species. Bull Natl Mus Nat Sci Ser A Zool Supplement 3:157–166

Osumi D, Yamasu T (2000) Feeding behavior and early development of *Gymnodoris nigricolor* Baba, 1960 (Mollusca: Nudibranchia) associated with the fins of marine gobies. Jpn J Benthol 55:9–14

Polunin NVC, Lubbock R (1977) Prawn-associated gobies (Teleostei: Gobiidae) from the Seychelles, western Indian Ocean: Systematics and ecology. J Zool 183:63–101

Randall JE, Lobel PS, Kennedy CW (2005) Comparative ecology of the gobies *Nes longus* and *Ctenogobius saepepallens*, both symbiotic with the snapping shrimp *Alpheus floridanus*. Environ Biol Fishes 74:119–127

Schmitt WL (1924) The macruran, anomuran and stomatopod Crustacea. Bijdragen tot de kennis der fauna von Curaçao. Resultaten eener reis van Dr. C. J. van der Horst, in 1920. Bijdragen tot de Dierkunde 23: 61–81

Schoppe S, Werding B (1995) The boreholes of the sea urchin genus *Echinometra*: (Echinodermata: Echinoidea: Echinometridae) as a microhabitat in tropical South America. Mar Ecol 17:181–186

Stimpson W (1858) Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VII. Crustacea Anomura. Proc Acad Nat Sci Phila 1858:225–252

Viviani CA (1969) Los Porcellanidae (Crustacea Anomura) chilenos: Distribución geográfica, y algunas observaciones biocenóticas sobre los porcelánidos en la bahía de Mehuín. Stud. Neotrop. Fauna Environ 6:40–56

Viviani CA, Hiller A, Werding B (2010) Swarming in open space in the rocky intertidal: A new population-settlement strategy in the eastern Pacific porcellanid crab *Allopetrolisthes punctatus* (Decapoda, Anomura, Porcellanidae). Crustaceana 83:435–442

Werding B (1983) Kommensalische Porzellaniden aus der Karibik (Decapoda, Anomura). Crustaceana 45:1–14

Werding B (2001) Description of two new species of *Polyonyx* Stimpson, 1858 from the Indo-West Pacific, with a key to the species of the *Polyonyx sinensis* group (Crustacea: Decapoda: Porcellanidae). Proc Biol Soc Wash 114:109–119

Werding B, Haig J (1982) The porcellanid crabs of the Isla Gorgona, Pacific coast of Colombia, with a description of *Clastotoechus grogonensis* sp. nov. (Crustacea: Anomura). Anales del Instituto de Investigaciones Marinas de Punta de Betín 12:57–70

Werding B, Hiller A (2004) Description of a new species of *Petrolisthes* from the Western Pacific (Decapoda, Anomura, Porcellanidae). Crustaceana 77:257–264

Williams EH, Williams LB (1986) The first association of an adult mollusk (Nudibranch: Doridae) and a fish (Perciformes: Gobiidae). Venus 45:210–212

Wirtz P (2008) The Gulf of Guinea goby-shrimp symbiosis and a review of goby-thalassinidean associations. Arquipélago. Life Mar Sci 25: 71–76