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Multispecies associations of macrosymbionts on the comatulid crinoid *Comanthina schlegeli* (Carpenter) in southern Taiwan

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Abstract
Macrosymbionts on comatulid crinoids *Comanthina schlegeli* (n=41) were surveyed at Kenting National Park, southern Taiwan. Symbionts were found on 40 of 41 of *C. schlegeli*. The 135 adults and one juvenile found included 10 species of decapod crustaceans in four families (97% of the total). The clingfish, *Discotrema crinophila*, accounted for the remaining 3%. Up to nine individuals and five species were associated with a single host. Synalpheid snapping shrimps and clingfish were mutually exclusive and found alone or in heterosexual pairs on the oral disk. Five species of palaemonid shrimps were found usually as pairs on arms. A galatheid anomuran *Allogalathea elegans* and a brachyuran *Permanotus purpureus* occupied the base of the cirri. Co-occurring symbionts partitioned host space.

Keywords: Symbiosis, crinoid, crustacean, *Comanthina schlegeli*, snapping shrimp, clingfish

1. Introduction

Tropical crinoids are colonized by a wide variety of taxonomic groups, ranging from non-obligates to parasites (Potts, 1915; Clark, 1921). Ordovician fossils indicate gastropod and worm symbionts on crinoids (Morris and Felton, 1993). Gastropods, annelids, copepods, amphipods, decapods and gobiesocid fish are obligate associates of extant comatulid crinoids (Fishelson, 1974; Zmarzly, 1984; Fabricius and Dale, 1993).

The comatulid crinoid *Comanthina schlegeli* is a large, robust, variably colored species that ranges across the Indo-Pacific, north to Japan, and west to the Maldives and Western Australia (Chen et al., 1988). A mature *C. schlegeli* has approximately 130 arms (Zmarzly, 1984). Snapping shrimps, palaemonid shrimps, and galatheid anomuran symbionts have been documented in Japan (Fujita and Baba, 1999), the Marshall Islands (Zmarzly, 1984), Papua New Guinea (VandenSpiegel et al., 1998), and the central Great Barrier Reef (Fabricius and Dale, 1993). Based on morphology and behavior, most symbionts are commensal or parasitic (Fishelson, 1974; Fabricius and Dale, 1993). Here we report on symbionts of *C. schlegeli* off southern Taiwan, with preliminary analysis on symbiont assemblage structure.

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2. Materials and Methods

Collections were conducted on a patch reef, Gudanshr Reef, in Nanwan Bay, Kenting National Park (Fig. 1). On 13 August 2000, 18 and 19 July 2001, 24 June 2002, 19 July 2002, 41 *C. schlegeli* with arm lengths >15 cm and their symbionts were collected by SCUBA. Each collection covered the same 4 ha area at depths from 10 to 20 m.

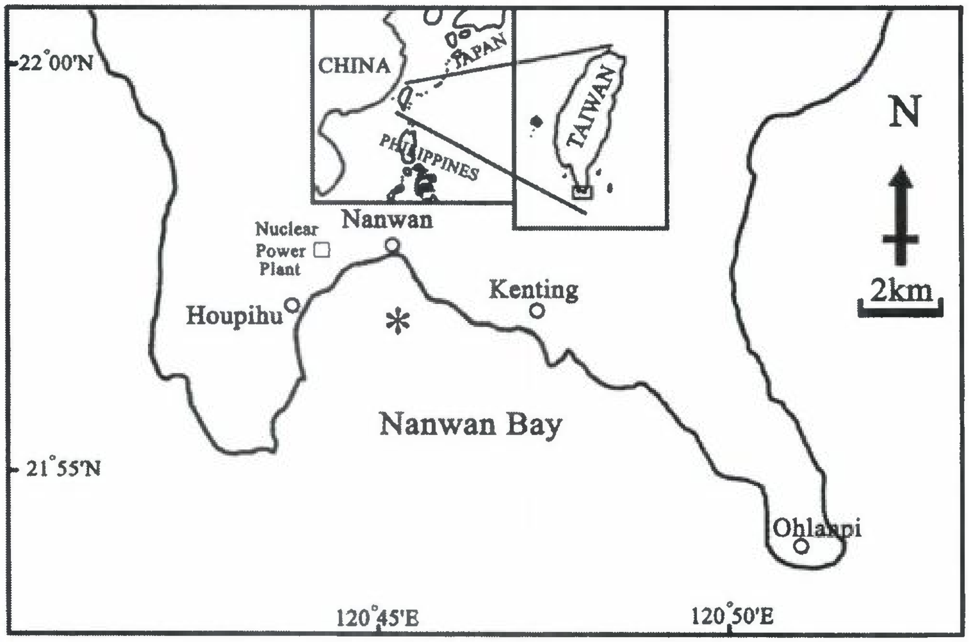

Figure 1. Map of the study area, Nanwan Bay of southern Taiwan. Asterisk indicates the collection site, the Gudanshr Reef.

Each crinoid was placed immediately into a 38×50 cm ziplock bag and taken to the dive boat. On the boat, each crinoid was placed in a rectangular 30×40 cm white plastic pan filled with seawater to a depth of approximately 5 cm. When the crinoid extended its arms after a few minutes, symbiont locations and numbers were recorded. Symbionts were collected by gently shaking the crinoid in the water. The number of arms was counted and range in size measured with a caliper on six *C. schlegeli*.

Data from the collections were pooled and analyzed for the frequency of symbiont co-occurrence. Expected frequencies of co-occurrence for any two symbiont species assumed random assortment and were computed by multiplying the frequencies of individual crinoids that each species occupied. Expected and observed frequencies were compared by chi-square test (Wirtz, 1997).

3. Results

General observations

Smaller adults (maximum arm length <15 cm) were often wedged between the branches of *Acropora* corals or in crevices. Larger adults (arm length >15 cm) were found perched on ledges or outcrops. As reported by Zmarzly (1984), five to twenty cirri of approximately 2 cm, and several lower arms were used for perching. The average arm number was 137.5±10.7 (mean±SD, n=6). Arm lengths ranged from 5 to 24 cm. When feeding, the outer arms were extended in a meridional arrangement with the inner arms curled protectively over the oral disk and providing shelter for symbionts.

Forty of 41 *C. schlegeli* (98%) hosted at least one symbiont. Thirty-four crinoids (83%) harbored more than two individuals. Up to nine individuals occurred on a single crinoid (Fig. 2). The frequencies of occupation were not significantly different from random assortment (χ^2=5.90, df=8, P=0.66).

Location of symbionts

Symbionts occurred in predictable locations (Fig. 3). Synalpheid snapping shrimps were found as individuals or heterosexual pairs on the oral disk. Palaemonid shrimps were found on arms, where they blended with pinnules. The anomuran *Allogalathea elegans* and the brachyuran *Permanotus purpureus* were at the base of the arms and among the cirri. Clingfish *Discotrema crinophila* was on the oral disk.

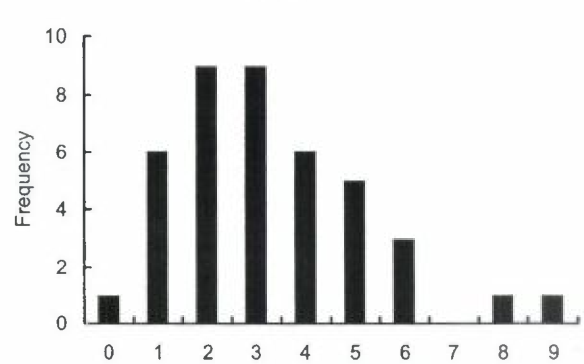

Figure 2. Frequency of crustacean and fish symbiont on *Comanthina schlegeli* (41 crinoids, 136 symbionts).

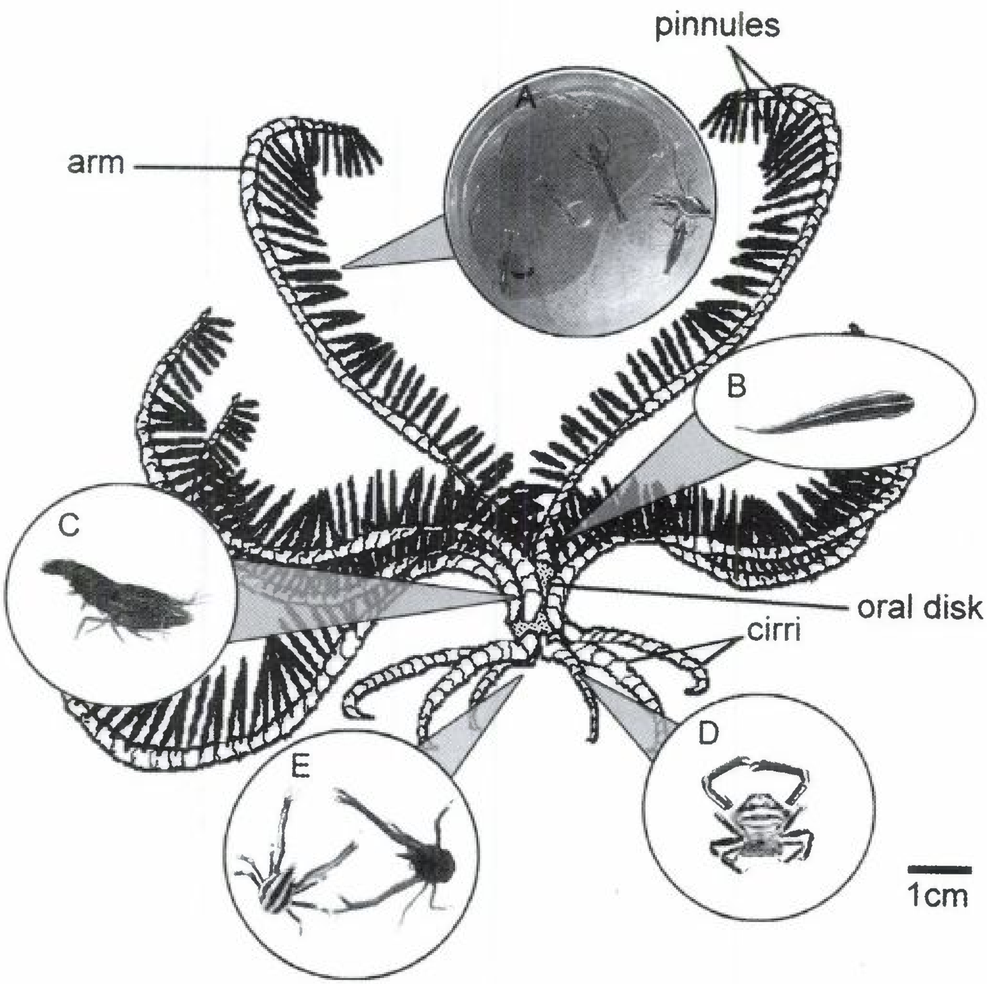

Figure 3. Schematic illustration of physical location of symbionts on crinoid host. A. Palaemonid shrimps live among host arms. B. The clingfish *Discotrema crinophila* rest upon oral disks of crinoids. C. Synalpheid snapping shrimps live on host oral disk. D. The brachyuran *Permanotus purpureus* (adapted from Ng and Jeng, 1999), and E. the galatheid anomuran *Allogalathea elegans* hide under cirri and arm bases of the host.

Symbiont occurrence

In total 136 symbionts, 135 adults and one late stage juvenile were collected. Five families were represented: Galatheidae (the anomuran *Allogalathea elegans*), Palaemonidae (*Araiopontonia odontorhyncha, Periclimenes amboinensis, Periclimenes commensalis, Periclimenes cornutus, Periclimenes tenuis*), Alpheidae (*Synalpheus carinatus, Synalpheus demani, Synalpheus stimpsoni*), Eumedonidae (the brachyuran crab *Permanotus purpureus*), and Gobiesocidae (the clingfish *Discotrema crinophila*). With the exception of a heterosexual pair and a juvenile *Synalpheus carinatus*, all symbionts found were individuals or pairs (Table 1).

Heterospecific coexistence of symbionts on crinoids was common. Among the 40 *C. schlegeli* with symbionts, 29 (73%) hosted two or more species and four (10%) hosted four or more species (Fig. 4). Coexistence of symbionts

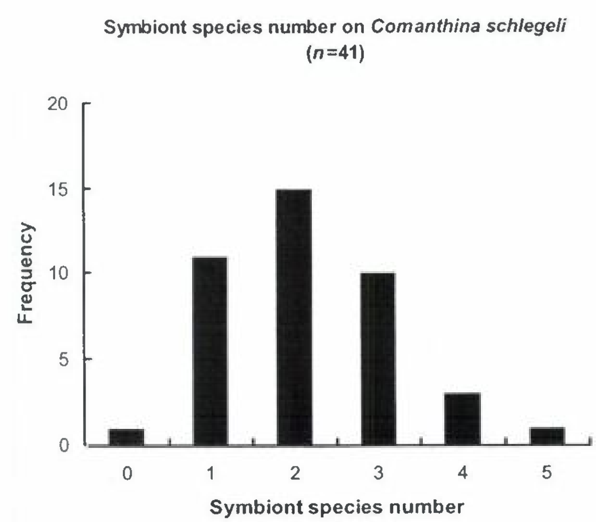

Figure 4. Numbers of symbiont species found on individual crinoids (41 crinoids, 136 symbionts).

Table 1. Associated macrosymbiont species on the crinoid *Comanthina schlegeli* (n=41), the abundance, and the percentage of inhabited crinoids.

Symbiont species	Specimens collected	Crinoids inhabited (%)
Class Malacostraca		
Order Decapoda		
Family Galatheidae		
Allogalathea elegans (Adams and White)	5	10
Family Palaemonidae		
Araiopontonia odontorhyncha Fujino and Miyake	2	44
Periclimenes amboinensis (DeMan)	3	5
Periclimenes commensalis Borradaile	12	22
Periclimenes cornutus Borradaile	2	2
Periclimenes tenuis Bruce	30	44
Family Alpheidae		
Synalpheus carinatus (DeMan)	5	5
Synalpheus demani Borradaile	51	71
Synalpheus stimpsoni (DeMan)	2	2
Family Eumedonidae		
Permanotus purpureus (Gordon)	1	2
Class Actinopterygii		
Order Gobiesociformes		
Family Gobiesocidae		
Discotrema crinophila Briggs	4	7

Table 2. Observed and expected frequencies of co-occurrence of the four most common symbionts.

Co-occurrences	Obs.	Exp.	χ^2	P
Synalpheus demani-Periclimenes commensalis	6	6.31	0.015	P=0.90
Synalpheus demani-Periclimenes tenuis	13	12.73	0.006	P=0.94
Synalpheus demani-Araiopontonia odontoryncha	13	12.73	0.006	P=0.94
Periclimenes commensalis-Periclimenes tenuis	4	3.95	0.001	P=0.98
Periclimenes commensalis-Araiopontonia odontoryncha	3	3.95	0.228	P=0.63
Periclimenes tenuis-Araiopontonia odontoryncha	11	7.9	1.216	P=0.27

was dependent upon location. Species occupying the oral disk (three species of snapping shrimps and a clingfish) were not found coexisting. Multiple species of palaemonid shrimps occupied arms. Fifteen (38%) of the 40 crinoids hosted two to four palaemonid shrimp species. Each species was found on different arms. Snapping shrimps shared hosts with palaemonid shrimp in 25 cases (63%). One clingfish *D. crinophila* was found on a host with a palaemonid shrimp. The cirri dwellers, the brachyuran *P. purpureus* and the galatheid anomuran *A. elegans*, were found on crinoids with symbionts on the oral disk and arms.

Ninety-five percent of the symbionts were shrimps. Over half (five species, 68 individuals) were palaemonid shrimps and the rest (three species, 58 individuals) were snapping shrimps. Co-occurrence of snapping shrimps and palaemonid shrimps was 49% of total. Sole occupations by snapping shrimps or palaemonid shrimps were nine (22%) and three (7%) cases, respectively. Co-occurrence frequencies of the four most common associates were not significantly different from random indicating no preference or exclusion among these species (Table 2). The only vertebrate symbiont, the clingfish *D. crinophila*, was found on three crinoids. Two individuals and one heterosexual pair of clingfish were observed on the oral disk. In one case, a palaemonid shrimp *P. commensalis* was found on a criniod hosting a single clingfish.

The symbionts on oral disk of the *C. schlegeli* did not associate randomly. Of the 40 crinoids with symbionts, 35 (88%) were inhabited by oral disk dwellers. Snapping shrimps occupied 32 crinoids and the clingfish three hosts. None of the *C. schlegeli* oral disk was shared by symbionts of different species. Disk symbionts were mutually exclusive (χ^2=5.21, df=1, P<0.05).

4. Discussion

In Taiwan *C. schlegeli* hosts ten decapods and one fish. Heterosexual pairs of snapping shrimps are on the oral disk with palaemonid shrimps on the arms and the galatheid anomuran *A. elegans* and the rare brachyuran *P. purpureus* live among the cirri. Although the species are often different, similar crustacean assemblages in similar locations were found on the *C. schlegeli* in other regions of the Indo-Pacific (Zmarzly, 1984; Fabricius and Dale, 1993). However, the other assemblages were more diverse: in the Marshall Islands, they included two polychaetes (*Paradyte crinodicola* and one unidentified myzostome worm), and three gastropods (*Clanculus atropurpureus*, *Calliostoma* sp., and one unidentified sp.) (Zmarzly, 1984); on the central Great Barrier Reef, the communities included several species of isopods, ophiuriods, and polychaete worms (Fabricius and Dale, 1993). *Comanthina schlegeli* assemblages of Taiwan lacked non-crustacean invertebrates. These symbionts may associate with other hosts or Taiwan is possibly near the end of the range of these species.

Although heterosexual pairs or small groups suggest territoriality, the relatively large size and complex crinoid morphology make it difficult for a symbiont to monopolize the host (Thiel and Baeza, 2001). Most symbionts occupy specific locations which serve to partition space and enable coexistence and high assemblage diversity (Figs. 3 and 4).

The relatively large size of the crinoid combined with low symbiont density suggests that, with the exception of the oral disk, there is little competition for space.

The oral disk was the only location where symbionts were mutually exclusive. The oral disk is the optimal location on the host because it provides food (Hyman, 1955) and shelter. Thus, this small area has all the conditions necessary for competition to occur.

Across the Indo-Pacific one of the snapping shrimp species, *S. carinatus*, *S. demani*, or *S. stimpsoni* usually dominate in abundance (Zmarzly, 1984; Fabricius and Dale, 1993). Dominance by synalpheid shrimps suggests that they are efficient competitors.

Of the symbionts collected, all except one late stage juvenile were adults. Similar observations were made by Fishelson (1974), Zmarzly (1984), and Fabricius and Dale (1993). The absence of juvenile and larval stages on adult crinoids supports the hypothesis that the symbionts have complex life cycles that includes an interval of larval and juvenile development that is associated either with juvenile crinoids or with an entirely different habitat. Recruitment to crinoids as late stage juveniles or as adults is likely. Symbionts such as snapping shrimps can use visual and chemical cues to locate a host (VandenSpiegel et al., 1998). As crinoids are found in relatively stable aggregations on the reef (Chen et al., 1988), there is potential for the relatively mobile decapods and fish to move between hosts and resulting in a fluid assemblage structure.

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