

Assessment of hidden diversity of crinoids and their symbionts in the Bay of Nhatrang, Vietnam

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Abstract Crinoid associates represent an abundant and diverse, but poorly explored, component of the hidden biodiversity of coral-reef ecosystems. We studied data from 5 years of collecting in the Bay of Nhatrang (BN), Vietnam, to assess the diversity of crinoids and their symbionts, to compare it with other areas of the Indo-West Pacific, and to elucidate the extent to which the observed diversity of crinoids and their symbionts corresponds to their true diversity. In total, about 2,287 specimens of symbionts belonging to 70 species were found on 203 specimens of crinoids belonging to 33 species. Among the crinoids, the most numerous species were *Himerometra robustipinna* (36 specimens) and *Cenometra bella* (29 specimens), among the symbionts the polychaete *Paradyte crinoidicola* (c. 850 specimens) and the galatheid crustacean *Allogalatea elegans* (180 specimens). Species accumulation curves suggest that we have sampled most of the crinoid diversity in the BN, whereas the diversity of their symbionts remained undersampled. Estimated species richness of crinoids was higher than previously observed richness, and varied from 39 (estimated by bootstrap) to 46 (jackknife 2). Estimated species richness of symbionts was higher than observed richness, and varied from 71 (bootstrap) to 93 (jackknife 2). We suggest a slight increase in the number of crinoid species to result from more detailed studies of nocturnal species, and an increase in the number of symbiotic species when studies of nocturnal crinoid associates and sibling species among decapods are included. Our study revealed a rather rich crinoid fauna in

the bay compared to other areas of the Indo-West Pacific, and the highest species richness of crinoid associates known from anywhere in the World Ocean.

Keywords Biodiversity · Species richness · Crinoids · Symbionts · Vietnam

Introduction

Symbiotic associations between marine animals and large sessile invertebrates are a hallmark of coral-reef ecosystems, where their biodiversity is comparable to, or even higher than, the diversity of free-living species. For instance, Naumov et al. (1980) reported that diversity of coral associates in the lagoon of the Gilbert Islands (Micronesia) was twice as high as diversity of benthic organisms inhabiting the substrate between coral colonies. In fact, this ratio should be even higher, since the authors did not estimate parasites of invertebrates and fishes. Bouchet (2006, p. 49) considered symbionts as one of the two “black boxes that are seen as immense reservoirs of unknown biodiversity, but where our ignorance is greatest.” In general, it seems likely that the diversity of symbionts exceeds that of free-living species. In spite of this, biodiversity studies are usually focused on the free-living organisms, which are easier to collect and identify, while symbiotic animals are usually overlooked or underestimated due to their small size, cryptic mode of life, and wide distribution of sibling/cryptic species specialized to their particular host species (Knowlton 1993; MacDonald et al. 2006; Martin et al. 2003).

There are several biodiversity studies of symbiotic animals in coral-reef ecosystems that focused mainly on selected groups of scleractinian and sponge hosts and

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demonstrate surprising diversity of the associated fauna (Abele and Patton 1976; MacDonald et al. 2006; Patton 1966). For instance, 55 species of crustaceans were found in the colonies of only one coral species, *Pocillopora damicornis*, in the Gulf of Panama (Abele and Patton 1976). Recently, 36 species of *Synalpheus* shrimps were discovered to be associated with sponges on the coast of Belize (MacDonald et al. 2006). Among echinoderms, the most diverse symbiotic fauna was found associated with crinoids (Deheyn et al. 2006). High diversity of crinoid dwellers is likely related to their host morphology and tissue content (Deheyn et al. 2006; Rideout et al. 1979). Crinoids have complex external morphology that protects their symbionts from predators and provides various microhabitats, which allows co-occurrence of several symbiotic species on the same host (Deheyn et al. 2006). They are filter-feeders transporting the captured particles to the mouth in ambulacral grooves, whereby concentrated food becomes easily accessible to symbionts (Deheyn et al. 2006). Finally, polyketide sulphates produced by crinoids defend them from fish attacks (Rideout et al. 1979).

Symbiotic fauna associated with crinoids has been studied by scientists for nearly a century. The first report on this subject was published by Potts (1915). Data on crinoid-associated fauna have been obtained for various areas of the World Ocean, though chiefly in the Indo-West Pacific: for the Red Sea (Fishelson 1974), for the coast of South Africa (Hempson and Griffiths 2008), for the Maldives Islands (Tchesunov et al. 1989), for the Bay of Bengal (Rao and Sowbhagyavathi 1972), for Hong Kong (Morton and Mladenov 1992), for Taiwan Island (Huang et al. 2005), for New Guinea (Deheyn et al. 2006), for the Great Barrier Reef (Fabricius and Dale 1993), and for the Marshall Islands (Zmarzly 1984). These reports provide general information on symbiotic fauna and the wide distribution of specialized assemblages associated with crinoids. However, the number of studied host and symbiont species varies significantly, as does the accuracy of their identification, which impedes comparisons of the data. Moreover, crinoid associates have not been studied or poorly studied in many areas, including the South China Sea, one of the centers of marine biodiversity.

Our report assesses the diversity of crinoids and their symbionts in the Bay of Nhatrang (BN), Vietnam, and compares it to that in other areas of the Indo-West Pacific. Previously, the crinoid-associated fauna of Vietnam was poorly studied, with only 13 species of crinoid-associated shrimps described (Anker and Marin 2007; Marin 2006, 2009; Marin and Chan 2006), while the known number of their crinoid hosts was rather high, about 57 species (Dao Tan Ho 1994; Mekhova and Britayev in press). In addition, we tried to determine to what extent the observed diversity of crinoids and their symbionts reflects their true diversity.

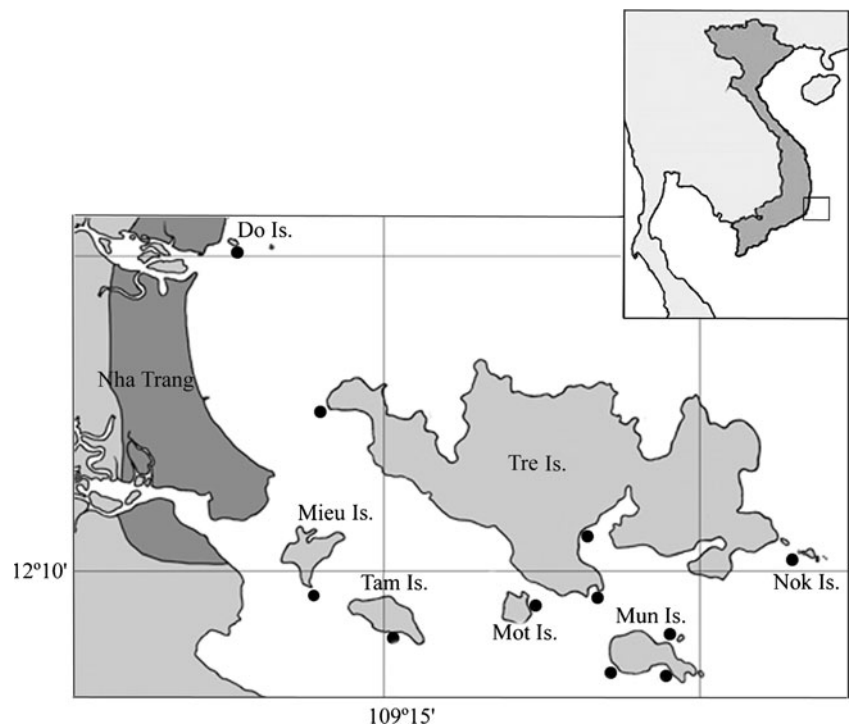
Material and methods

Crinoids and their symbionts were hand-collected by SCUBA diving between 2004 and 2008 in the BN, Central Vietnam, and the South China Sea. Our studies were relied on the facilities and logistics of the Coastal Branch of the Russian-Vietnamese Tropical Centre. Sampling was performed at depths of 2–35 m, largely during the day but with a few crinoid specimens collected at night. Eleven sites throughout the bay were studied (Fig. 1). Crinoids were gently pulled away from the substrate, immediately placed in individual zip-lock plastic bags, and transported to the laboratory for analyses. A total of 203 specimens of crinoids were collected.

Crinoids were carefully checked for symbionts with unaided eyes and under a binocular microscope. Additional symbiotic fauna was extracted by washing the crinoids in a 20% solution of alcohol in marine water, and sieving the solution through 100 μm mesh. Crinoids and macro-symbionts were preserved in 70% alcohol and identified. Decapods were identified by I.N. Marin. Symbiotic copepods and cysticolous myzostomids were numerous in our samples but were not included in this study due to the difficulties with their identification.

To test whether crinoid species and their symbionts were sampled adequately, accumulation curves were calculated for crinoid species as a function of the number of samples (crinoid specimens) collected, and for all symbiotic species as a function of the number of individual crinoids collected. Samples were ordered according to collection date. Accumulation curves were also calculated for each ‘numerous’ crinoid species (with ten or more individuals sampled). The true total number of species was estimated with four methods: jackknife 1, jackknife 2, bootstrap and Chao 2 (program packages PAST v. 2.01). The first-order jackknife estimate of species richness (S_1) is based on the number of species that occur in only one sample (L), $S_1 = S_{\text{obs}} + L((n - 1)/n)$, where n is the number of samples, and S_{obs} is the observed number of species. The second-order jackknife estimate (S_2) is based on the number of species that occur in only one sample (L) and the number that occur in exactly two samples (M): $S_2 = S_{\text{obs}} + [L(2n - 3)/n - M(n - 2)^2/n(n - 1)]$. The bootstrap estimate of species richness (S_3) is based on p_j , the proportion of quadrats containing each species j : $S_3 = S_{\text{obs}} + \sum (1 - p_j)^n$. The ‘Chao 2’ estimator can be applied to the distribution of species among samples, which requires only presence-absence data: $S_4 = S_{\text{obs}} + (L^2/2M)$ (Colwell and Coddington 1994). We applied the terms ‘point species richness’ for the number of symbiotic species in the single host (sampling unit), ‘habitat species richness’ for the number of symbiotic species associated with particular host species, and ‘large area species richness’ or ‘ γ -diversity’ for the area studied, which includes a variety of studied hosts (crinoids) (modified after Gray 2000).

Fig. 1 Locations of sampling sites (circles) in the Bay of Nha Trang, Vietnam



Results

Crinoid species richness

The sampling efforts yielded a total of 203 specimens of crinoids belonging to 33 species in five families (Table 1). The most diverse family of crinoids was Comasteridae with 19 species (59% of all species found); other families were less abundant, with five species of Mariametridae (16%), four species of Himerometridae (13%), and two species (6%) each in Colobometridae and Zygometridae (Fig. 2a). The two most numerous species in our samples, *Himerometra robustipinna* (Carpenter, 1881) with 36 specimens, and *Cenometra bella* (Hartlaub, 1890) with 29 specimens, belong to Himerometridae and Colobometridae, respectively (Fig. 3a, b).

The number of crinoid species increased approximately linearly with the first 60 specimens sampled, and approached an asymptote of 30 species after about 90 crinoids had been sampled. Increasing the number of samples to 180 added only three more crinoid species (Fig. 4a). Estimated species richness was higher than observed richness and varied from 39 (bootstrap method) to 46 (jackknife 2) (Table 2).

Symbiont species richness

A total of 70 species of symbionts were found on these hosts (Table 3). The most diverse groups were myzostomids with 37 species (52.9% of all symbiotic species found) and

decapods with 23 species (32.9%). The other groups, gastropods (five species, 7.1%), polychaetes (three species, 4.3%), ophiuroids and fishes (one species and 1.4% each) were substantially less diverse (Fig. 2b). The most numerous symbiotic species in our samples were the polynoid scaleworm *Paradyte crinoidicola* (Potts, 1910) with about 850 specimens, and the galatheid *Allogalatea elegans* (Adams and White, 1848) with 180 specimens (Fig. 3c, d). All species found were obligatory associates of crinoids, except for the scaleworm *Hololepidella laingensis* Britayev et al., 1999, found also on starfishes (Antokhina and Britayev *in press*).

The number of symbiotic species increased approximately linearly with an increase in the number of crinoid specimens, and approached an asymptote of 70 species after c. 190 crinoids had been sampled (Fig. 4b). Estimated species richness was higher than observed richness and varied from 71 (bootstrap) to 93 (jackknife 2) (Table 2). All crinoid species examined harbored symbionts; however, the number of symbiotic species associated with each crinoid host species (habitat species richness) varied significantly from 2 to 20 (Table 1). In general these figures were positively correlated to sampling effort; the richest symbiotic fauna was found on the crinoid species most numerous in our collection (Fig. 5). However, the number of symbionts was maximal (20 species) in the assemblage associated with *Comaster nobilis* (Carpenter, 1884) (24 specimens), while the best-represented crinoid, *Himerometra robustipinna* (36 specimens), harbored 16 symbiotic species only (Table 1).

Table 1 List of crinoid species from the Bay of Nhatrang (Vietnam), with numbers of specimens and of associated symbiont species

Crinoid species	Number of samples	Number of symbiont species
Comasteridae		
<i>Capillaster multiradiatus</i> (Linnaeus, 1758)	2	2
<i>Comanthus briareus</i> (Bell, 1882)	2	5
<i>Comaster nobilis</i> (Carpenter, 1884)	24	20
<i>Comaster schlegelii</i> (Carpenter, 1881)	4	7
<i>Comanthus alternans</i> (Carpenter, 1881)	7	9
<i>Comanthus gisleni</i> Rowe et al., 1896	10	9
<i>Comanthus parvicirrus</i> (Müller, 1841)	22	12
<i>Comanthus wahlbergii</i> (Müller, 1843)	2	6
<i>Phanogenia gracilis</i> (Hartlaub, 1890)	6	14
<i>Phanogenia multibrachiatus</i> (Carpenter, 1888)	1	5
<i>Comaster multifidus</i> (Müller, 1841)	6	8
<i>Comatella nigra</i> (Carpenter, 1888)	4	9
<i>Comatella stelligera</i> (Carpenter, 1880)	8	13
<i>Comatula (Comatula) pectinata</i> (Linnaeus, 1758)	1	1
<i>Oxycomanthus bennetti</i> (Müller, 1841)	18	11
<i>Oxycomanthus imbricatus</i> (A.H. Clark, 1908)	2	2
<i>Oxycomanthus cf. japonicus</i> (Müller, 1841)	3	5
<i>Oxycomanthus pinguis</i> (A.H. Clark, 1909)	8	7
Mariametridae		
<i>Dichrometra flagellata</i> (Müller, 1841)	4	9
<i>Lamprometra palmata</i> (Müller, 1841)	10	13
<i>Liparometra regalis</i> (Carpenter, 1888)	5	6
<i>Stephanometra indica</i> (Smith, 1876)	10	11
<i>Stephanometra tenuipinna</i> (Hartlaub, 1890)	4	9
<i>Oxymetra cf. finschii</i> (Hartlaub, 1890)	1	2
Himerometridae		
<i>Amphimetra ensifera</i> (A.H. Clark, 1909)	2	5
<i>Amphimetra tessellata</i> (Müller, 1841)	3	5
<i>Himerometra robustipinna</i> (Carpenter, 1881)	36	16
Zygommetridae		
<i>Zygometra comata</i> A.H. Clark, 1911	1	6
<i>Zygometra elegans</i> (Bell, 1882)	3	3
<i>Zygometra microdiscus</i> (Bell, 1882)	1	2
Colobometridae		
<i>Cenometra bella</i> (Hartlaub, 1890)	29	11
<i>Colobometra perspinosa</i> (Carpenter, 1881)	5	7
Totals	203	70

To study the relationship between crinoid species, sampling effort and number of symbiotic species, we considered

accumulation curves of symbiotic species as a function of the number of crinoid specimens collected for the six most numerous crinoid species in our collection (10–36 specimens; Fig. 6). The accumulation curves approached an asymptote in three species of crinoids, *Cenometra bella*, *Himerometra robustipinna*, and *Comanthus gisleni* Rowe et al., 1986, but did not approach an asymptote in the other three species, *Comaster nobilis*, *Comanthus parvicirrus* (Müller, 1841), and *Lamprometra palmata* (Müller, 1841) (Fig. 6). It is interesting to note that in some species, e.g. in *Comanthus gisleni*, the accumulation curve already approached an asymptote after only seven crinoids had been sampled (Fig. 6e), while in other species such as *Himerometra robustipinna* and *Cenometra bella*, it approached an asymptote when the sample size was 2–3 times higher (Fig. 6a, c).

Discussion

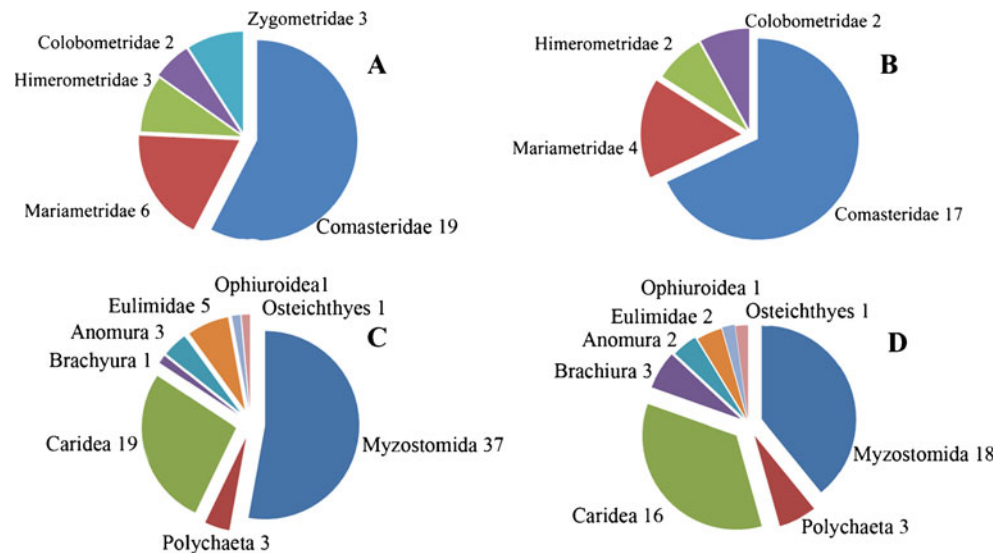
Diversity assessment

Our data provide quantitative assessments of the diversity of coral reef macroinvertebrates and their symbionts. Thus, an important question in interpreting our data involves the completeness of sampling: Have we sampled the crinoids and the associated fauna diversity in the BN in its entirety?

The species accumulation curves suggest that we have sampled most of the crinoid diversity in the BN. The list consisting of 33 crinoids can be considered as complete for the diurnal species. However, as has been demonstrated for Kwajalein Atoll, Marshall Islands (Zmarzly 1985), a significant proportion of crinoids are nocturnal, hiding during the day under coral rubble or within coral formations and rocks. Since our sampling efforts were significantly higher during the day than at night, it is possible that the number of crinoids known from the bay will increase if more detailed studies of nocturnal species are conducted. The estimated species richness did not vary significantly among the four estimates (39–46 species). We suggest that the estimated range of the species number is close to the true total number of diurnal crinoids in the bay.

In contrast to the accumulation curve for the crinoid species, the overall curve for symbiotic species (Fig. 2b) did not reach an asymptote, which suggests that the sampled number of symbiotic species does not reflect the total number of symbiont species. In some symbiotic assemblages associated with target species of crinoids, species accumulation curves approached an asymptote after a relatively small number of crinoids had been sampled (7–17), whereas in others an asymptote was not approached at the same sample size (Fig. 6). This appears to indicate that both the latter group of crinoids and the poorly represented crinoids (most of the species in our collection) likely harbor greater

Fig. 2 Comparison of taxonomic structure of crinoids and their symbionts in the Bay of Nha-trang, Vietnam (our data), and in the Hansa Bay, PNG (from Deheyn et al. 2006). **a** Crinoids from the BN. **b** Crinoids from PNG. **c** Symbionts from BN. **d** Symbionts from PNG



symbiont species richness. One can expect an increase of symbiotic species diversity in the bay with further studies of myzostomids, since these animals have aggregated distribution patterns and high levels of specificity (Deheyn et al. 2006). The number of crinoid associates may well increase with further taxonomic study of the undescribed species. Also, complexes of cryptic species have been found recently among *Laomenes* shrimps (Marin 2009). Detailed morphological studies of *Laomenes amboinensis* (De Man, 1888) and *L. jackhintoni* (Bruce, 2006) revealed the existence of two cryptic species complexes, and included four and two species, respectively (Marin 2009). It is likely that the alpheid shrimp *Synalpheus stimpsoni* (De Man, 1888) and the galatheid *Allogalthea elegans* represent cryptic species

complexes consisting of 4–5 species each (Marin and Macpherson, personal communications). Finally, symbiotic biodiversity will increase with studies of copepods and cisticulous myzostomids, which are a very abundant and diverse group of crinoid associates (Fishelson 1974; Grygier 2000) not included in the present study. Therefore, the expected species richness of crinoid-associated symbiotic animals in the BN should exceed 93 species, the maximum estimated true total number of species (bootstrap 2).

Comparison of the BN fauna with other regions

The next question in interpreting our data concerns the assessment of the biodiversity of crinoids and their

Fig. 3 The most numerous crinoids (**a**, **b**) and their symbionts (**c**, **d**). **a** *Himerometra robustipinna* (Himerometridae). **b** *Cenometra bella* (Colobometridae). **c** *Allogalthea elegans* (Crustacea, Galatheidae). **d** *Paradyte crinoidicola* (Polychaeta, Polynoidae)

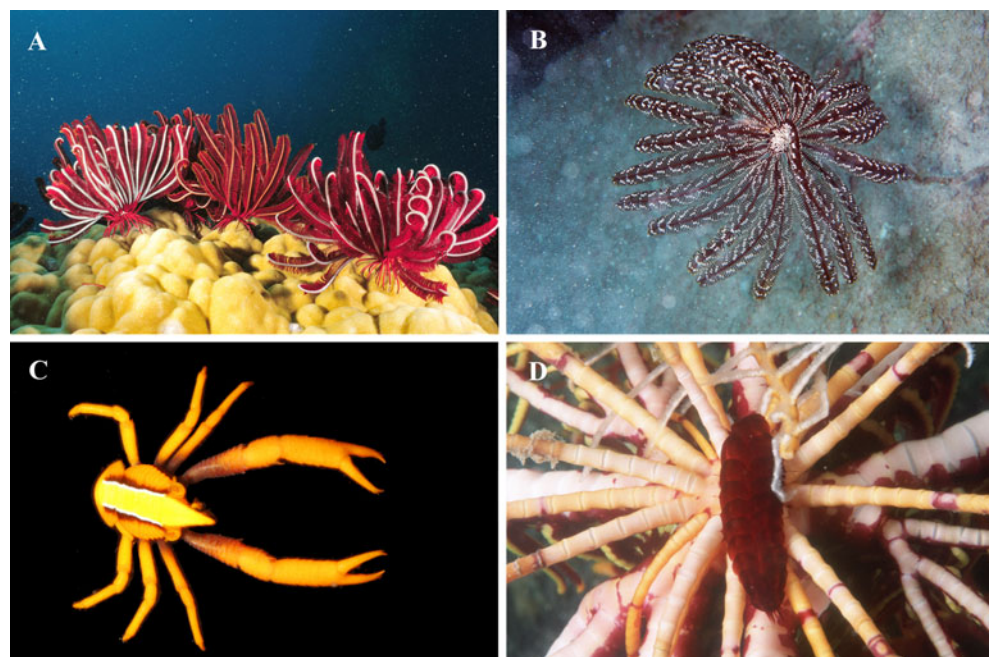
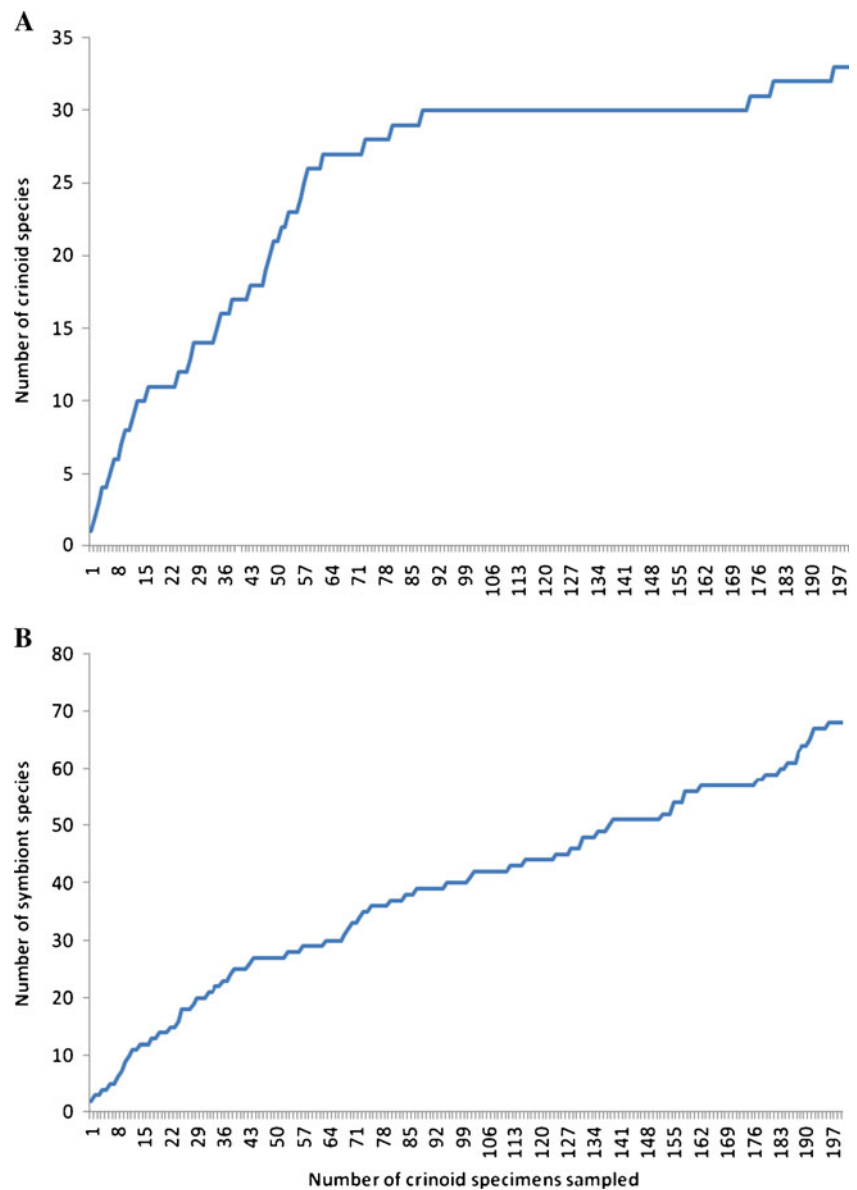


Fig. 4 Species accumulation curves. **a** Accumulation of crinoid species as a function of collecting effort (number of crinoid specimens collected). **b** Accumulation of symbiont species as a function of collecting effort (number of crinoid specimens collected)



associates: Are the figures of species richness obtained high or low for the regional fauna?

Our data revealed a relatively rich crinoid fauna in the bay even in comparison to some larger areas. For instance, 15 crinoid species were reported for the northern Red Sea (Fishelson 1974), 21 species for the Guam and North Marian Islands (Kirkendale and Messing 2003), 14 species for the

Table 2 Observed and estimated species richness of crinoids and their symbionts in the Bay of Nhatrang (Vietnam)

Organisms	Species richness				
	Observed	Jackknife 1	Jackknife 2	Bootstrap	Chao 2
Crinoids	33	43	46	39	40
Symbionts	70	84	93	71	78

Marshall Islands (Zmarzly 1984, 1985), 14 species for Kerama Island (Okinawa) (Pilcher and Messing 2001), and 25 species for Hansa Bay (comparable in area to the Bay of Nhatrang) north-east of Papua New Guinea (PNG) (Deheyn et al. 2006). However, the crinoid diversity reported from some other areas is higher than in NB: 39 species on the coast of Thailand (Putchakarn and Sonchaeng 2004), 38 species in the northern and central Sulu Sea, 58 species in the Jolo Archipelago, and 43 and 54 species, respectively, in the Banda Sea (Messing 1998) and the central part of the Great Barrier Reef and Lizard Island (GBR) (Fabricius and Dale 1993; Messing 1998).

The taxonomic structure of the crinoid fauna (relative species richness in crinoid families) of central Vietnam is similar to that in other areas of the West and Central tropical Pacific, due to the prevalence of Comasteridae species (44–

Table 3 Numbers of individuals (n) of symbiont species sampled in association with crinoids from the Bay of Nhatrang (Vietnam)

Species	n
Decapoda: Anomura	
<i>Allogalatea elegans</i> (Adams and White, 1848)	180
<i>Galathea amboinensis</i> De Man, 1888	2
<i>Galathea</i> sp.	3
Decapoda: Brachyura	
<i>Harrovia</i> sp.	32
Decapoda: Caridea	
<i>Atanas anaitidactilus</i> Anker & Marin, 2006	1
<i>Brucecaris tenuis</i> (Bruce, 1969)	24
<i>Crinotonia anastasiae</i> Marin 2006	1
<i>Crinotonia attenuatus</i> (Bruce, 1971)	2
<i>Araipontonia odontorhynchus</i> Fujino and Miyake, 1970	2
<i>Palaemonella pottsii</i> (Borradaile, 1915)	41
<i>Laomenes amboinensis</i> (De Man, 1888)	10
<i>Laomenes nudirostris</i> (Bruce, 1968)	8
<i>Laomenes clarki</i> Marin 2009	4
<i>Laomenes pardus</i> Marin 2009	4
<i>Laomenes tigris</i> Marin 2009	2
<i>Laomenes ceratophthalmus</i> (Borradaile, 1915)	13
<i>Parapontonia nudirostris</i> Bruce, 1968	3
<i>Periclimenes afinis</i> (Zehntner, 1894)	23
<i>Periclimenes commensalis</i> Borradaile, 1915	72
<i>Pontoniopsis comanthi</i> Borradaile, 1915	83
<i>Synalpheus stimpsoni</i> (De Man, 1888)	4
<i>Synalpheus tropidodactylus</i> Banner and Banner, 1975	8
<i>Synalpheus</i> sp.	15
Myzostomida	
<i>Myzostoma abundans</i> Graff, 1883	1
<i>Myzostoma agassizii</i> Graff, 1883	5
<i>Myzostoma alatum</i> Graff, 1884	1
<i>Myzostoma ambigum</i> Graff, 1887	7
<i>Myzostoma antennatum</i> Graff, 1884	143
<i>Myzostoma areolatum</i> Graff, 1883	9
<i>Myzostoma attenuatum</i> Grygier, 1989	6
<i>Myzostoma brevicirrum</i> Graff, 1884	1
<i>Myzostoma capitocutis</i> Eeckhaut et al., 1994	8
<i>Myzostoma carinatum</i> Graff, 1883	3
<i>Myzostoma coronatum</i> Graff, 1884	12
<i>Myzostoma fissum</i> Graff, 1884	27
<i>Myzostoma polycyclus</i> Atkins, 1927	80
<i>Myzostoma labatum</i> Graff, 1877	1
<i>Myzostoma marginatum</i> Graff, 1883	15
<i>Myzostoma radiatum</i> Graff in Clark, 1921	6
<i>Myzostoma rubrofasciatum</i> Graff, 1884	1
<i>Myzostoma vastum</i> Graff, 1883	2
<i>Myzostoma echinus</i> Graff, 1884	27
<i>Myzostomida</i> gen. sp. 1	7
<i>Myzostomida</i> gen. sp. 2	10

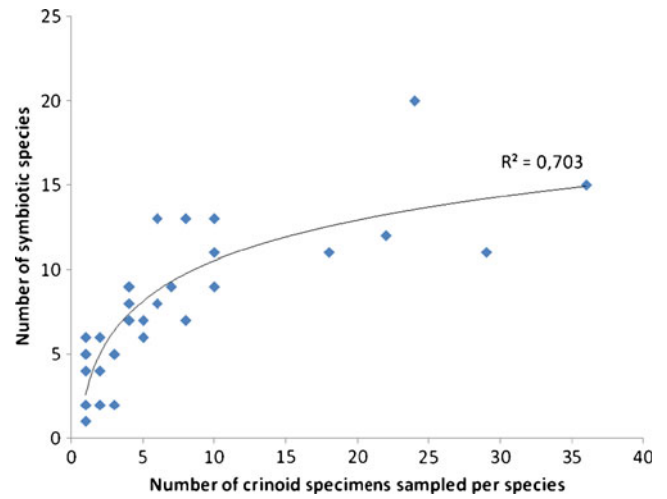
Table 3 (continued)

Species	n
<i>Myzostomida</i> gen. sp. 3	1
<i>Myzostomida</i> gen. sp. 4	4
<i>Myzostomida</i> gen. sp. 5	5
<i>Myzostomida</i> gen. sp. 6	1
<i>Myzostomida</i> gen. sp. 7	9
<i>Myzostomida</i> gen. sp. 8	10
<i>Myzostomida</i> gen. sp. 9	36
<i>Myzostomida</i> gen. sp. 10	2
<i>Myzostomida</i> gen. sp. 11	14
<i>Myzostomida</i> gen. sp. 12	11
<i>Myzostomida</i> gen. sp. 13	18
<i>Myzostomida</i> gen. sp. 14	2
<i>Myzostomida</i> gen. sp. 15	5
<i>Myzostomida</i> gen. sp. 16	6
<i>Myzostomida</i> gen. sp. 17	11
<i>Myzostomida</i> gen. sp. 18	2
Cysticolous myzostomids	200
Polychaeta	
<i>Paradite crinoidicola</i> (Potts, 1910)	850
<i>Hololepidella laingensis</i> Britayev et al., 1999	5
Ophiuroidea	
<i>Gymnolophus obscura</i> (Ljungman, 1867)	47
Gastropoda: Eulimidae	
<i>Annulobalcis</i> sp1	45
<i>Annulobalcis</i> sp2	60
<i>Fusceulima jacksonensis</i> Laseron, 1955	5
<i>Goodingia varicose</i> (Schepman and Nierstrasz, 1909)	2
<i>Curveulima cornuta</i> Laseron, 1955	4
Osteichthyes	
<i>Discotrema crinophilum</i> Briggs, 1976	20

71% of the total species number; Fig. 2a, b), and quite differs from the Red Sea fauna with its prevalence of Colobometridae (29%).

Our results confirm that the assemblage of crinoid-dwelling animals in the BN is the most diverse in comparison with other areas of the tropical Indo-Pacific (Table 4). The data from the BN are comparable to the previously most comprehensive data sets from the Hansa Bay (PNG) (Deheyn et al. 2006) and the central part of GBR (Fabricius and Dale 1993), where 47 and 46 species of crinoid dwellers were found (Table 4). In general, the taxonomic structure of the symbiotic fauna was similar in the Nhatrang and the Hansa Bays, with myzostomids and decapods predominant in terms of species richness, and relatively low diversity of other groups, such as gastropods, polychaetes, ophiuroids and fishes (Fig. 2c, d). Yet in the BN the relative quantities of myzostomids and gastropods

Fig. 5 Symbiotic species richness as a function of the number of specimens sampled per crinoid species



were higher, while the quantity of crabs was lower. The crinoid-associated fauna of the GBR is similar to that of BN

in the high diversity of decapods (22 species), while the diversity of gastropods is lower in the BN, and specialized

Fig. 6 Accumulation of symbiont species as a function of collecting effort for six of the most numerous crinoid species. **a** *Cenometra bella*. **b** *Himrometra robustipinna*. **c** *Comanthus gisleni*. **d** *Comaster nobilis*. **e** *Comanthus parvicirrus*. **f** *Lamprometra palmata*

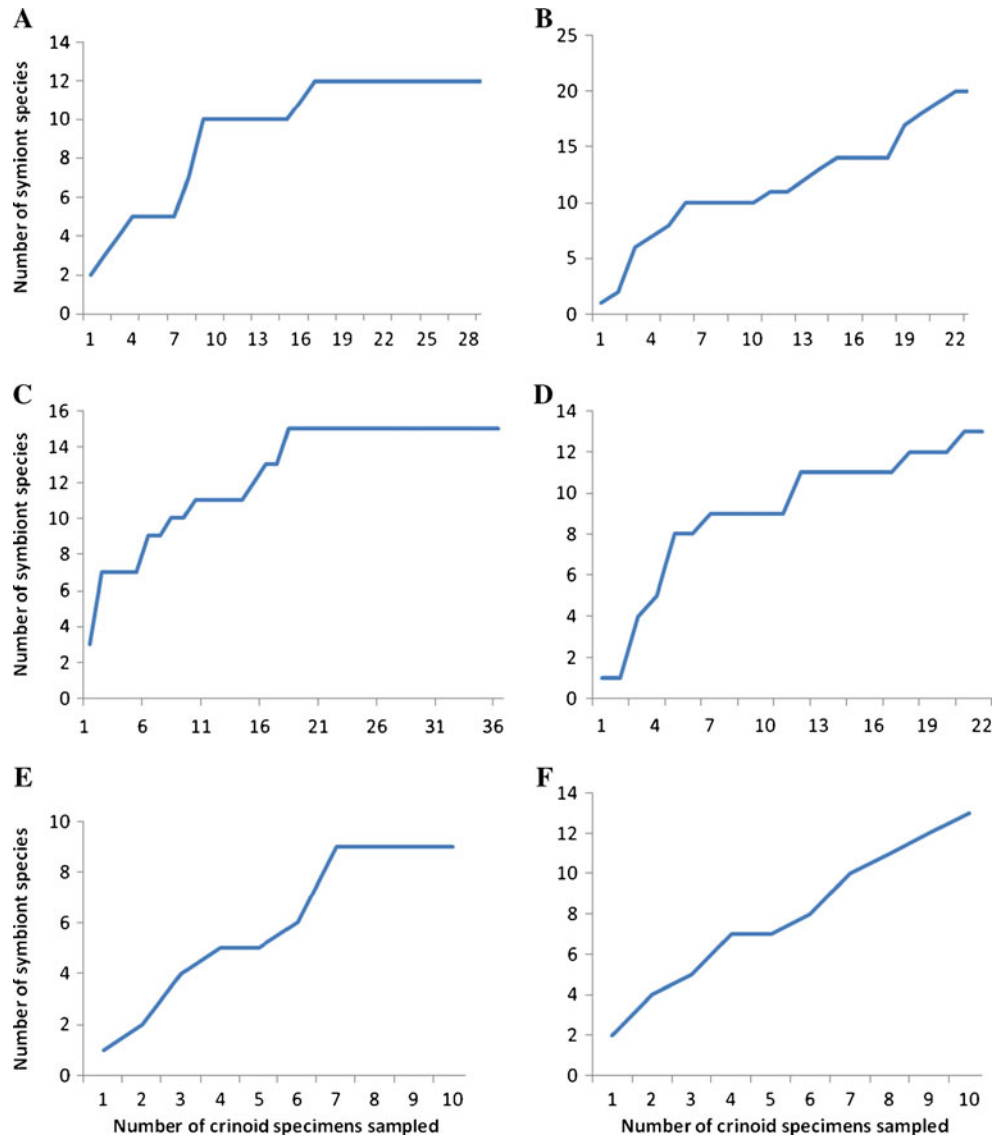


Table 4 Geographic comparison of crinoids and associated symbiont species

Study area	Number of crinoid species	Sample size	Number of symbiont species	Reference
Great Barrier Reef (central part between 18°50' and 15°10' S)	43	1114	46	Fabricius and Dale (1993)
Vietnam (Nhatrang Bay)	33	203	70	present study
New Guinea (Hansa Bay)	25	141	47	Deheyn et al. (2006)
Red Sea (northern part, especially Gulf of Aqaba)	14	no data	27	Fishelson (1974)
Marshall Islands (Enewetak Atoll)	9	97	18	Zmarzly (1984)
Maldives Islands (Fiartu and Genego Islands, North Nilandu Atoll)	2	25	14	Tchesunov et al. (1989)
Torres Strait and Murray Island	2	no data	13	Potts (1915)
Hong Kong (Breakers Reef, New Territories)	2	23	5	Morton and Mladenov (1992)
Taiwan (Gudanshr Reef, Nanwan Bay, Kenting National Park)	1	42	11	Huang et al. (2005)

symbiotic species of amphipods and isopods were not found there. A similar taxonomic structure of the symbiotic fauna, with prevalence of decapods and myzostomids, is characteristic also for the Red Sea (Fishelson 1974), Hong Kong (Morton and Mladenov 1992), and likely for the other areas of the tropical Indo-Pacific.

BN symbiotic fauna: high diversity or sampling efforts?

Our results confirm that the diversity of crinoid-dwellers in the BN is the highest of all crinoid-associated faunas in the World Ocean known to date. Does this described diversity really reflect extremely high diversity of the BN fauna, or is it the result of sampling efforts and other subjective factors?

One may assume that the observed diversity of symbionts depends on the location, taxonomic expertise of researchers, coverage of the host species (habitats), adequate distribution of sampled specimens of hosts among species of hosts, and sampling efforts (number of sampled hosts).

Fishelson (1974) gave no exact data on the sampling effort concerning Red Sea crinoids and their symbionts; however, the number of crinoid species reported (15) and rather long period of observations (over 8 years) suggest a substantial effort. Moreover, all host species and all main taxa of symbiotic animals, including copepods, were treated. These circumstances indicate that the crinoid-associated fauna of the northern part of the Red Sea likely is rather well studied, that the figures reported are close to the real diversity of the fauna, and that the diversity of the regional fauna is relatively low.

The largest reported numbers of crinoid species and specimens sampled (43 species and 1,114 specimens) were collected at the GBR (Fabricius and Dale 1993). The number of symbiotic species collected was very close to that of Hansa Bay and much lower than for the BN (Table 4). This can be explained by the fact that several important groups of symbionts, like polychaetes, mizosto-

mids and copepods, were not studied (Fabricius and Dale 1993). In addition, sampling efforts were distributed randomly among crinoid hosts, and samples required for the habitat species richness assessment were obtained for less than half of the crinoid species.

The symbiotic faunas of Taiwan and the Marshall Islands were also underestimated, but in these cases the sample sizes for the studied crinoids were rather large (from 4 to 73 specimens), while only small parts of their hosts' diversity was explored (Chen et al. 1988; Zmarzly 1984, 1985).

The most comprehensive data on the symbiotic fauna have been obtained for Hansa Bay (Deheyn et al. 2006) and the BN (our data). In both studies the main taxonomic groups of symbionts excluding copepods were explored, the diversity of host species was rather well studied, and sampling efforts were distributed randomly among crinoid hosts. However, sampling effort in the BN was higher than in Hansa Bay (Table 4).

This brief comparison suggests that we currently have only a rough assessment of the γ -diversity of crinoid associates in most of the studied areas, and that new symbiotic species can be found in any area of the Indo-West Pacific. Precisely, the true diversity of the symbiotic fauna in the BN is higher than in the Red Sea or Marshall Islands, areas with relatively low species richness of crinoids. However, studies of the BN symbiotic fauna were done with significant effort concerning sampling and identification of the main taxonomic groups of symbionts. This means that we should expect finding comparable or even more diverse symbiotic faunas upon increasing the sampling efforts in other areas with diverse crinoids fauna, such as GBR or PNG.

Symbiont/host species ratio

The important index of the diversity of symbionts is the ratio of symbiotic species number to host species number

(Rohde 1982). Our calculation based on the published data demonstrates that this index was about 2 and was similar for those areas of the Indo-Pacific in which the fauna of crinoids and their associates was well studied, i.e. the Red Sea, the Marshall Islands, and PNG. The index was lower, about 1, at the GBR, although this points to underestimation of the symbiotic fauna rather than to low actual diversity. It was about 2 in the BN also, but taking into consideration the minimal expected number of crinoid symbionts in the bay (93 species), we may expect the index value to increase up to 3. This figure is comparable to or even higher than for the monogeneans parasitizing tropical fishes (Rohde 1982), a case that has been used to illustrate high diversity of symbiotic animals (Bouchet 2006). So, we may conclude that the crinoid-associated fauna of BN so far represents the most diverse regional fauna of crinoid-associated animals, and likely one of the most diverse regional faunas of symbiotic coral-reef animals associated with particular groups of macroinvertebrates like scleractinians, octocorals, sponges, bivalves, holothurians, starfishes, etc.

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