

Distribution and Ecology of Shallow-Water Crinoids at Enewetak Atoll, Marshall Islands, with an Annotated Checklist of Their Symbionts¹

D. L. ZMARZLY²

ABSTRACT: Six species of comatulid crinoids were found to inhabit coral reefs between depths of 3 and 36 m at Enewetak Atoll, Marshall Islands. These species were *Eudiocrinus tenuissimus*, *Dorometra nana*, *Comaster gracilis*, *Comanthus bennetti*, *Comanthus parvicirrus*, and *Comanthina schlegeli*. The first four species were previously recorded from other atolls in the Marshall Islands, but *Comanthus bennetti* was the only species reported from Enewetak. *Comanthus parvicirrus* and *Comanthina schlegeli* have not been previously recorded for the area. Nine shallow-water species are now known from the Marshall Islands, compared to 21 species from the Palau Archipelago and 7 from Guam. At Enewetak, abundance and diversity of crinoids were greatest at sites with exposure to regular current flow, and depth zonation of species was apparent. Three of the species at Enewetak were polychromatic; color varieties found at Enewetak are compared to those documented for conspecifics at other Indo-Pacific locations. Spatial distribution patterns and relative abundances of the noncryptic crinoids at three sites remained nearly constant over a half-year period. No mortality or recruitment was observed in the monitored populations. Eighteen species of macro-invertebrates were found in association with the crinoids: 3 species of gastropod mollusks, 3 species of myzostomid worms, 1 species of scaleworm, 1 species of copepod, and 10 species of decapod crustaceans.

STUDIES OF THE BATHYMETRIC and zoogeographic distribution of crinoids, initiated nearly a century ago, relied on specimens obtained by large-scale dredging (e.g., Bell 1884; Carpenter 1888; A. H. Clark 1909, 1911a, 1911b; H. L. Clark 1921; Hartlaub 1895, 1912). More recently, our knowledge of species composition, bathymetry, and ecology of shallow-water crinoid faunas has been greatly increased by the use of skin- and SCUBA-diving. Extensive field studies on the ecology and distribution of Caribbean crinoids were reported by Meyer (1971, 1973a, 1973b), Macurda (1973, 1975), and Meyer and Macurda (1974). Magnus (1967), Rutman and

Fishelson (1969), and Fishelson (1974) conducted in situ studies on crinoids in the Red Sea, but comparatively little work has focused on Indo-West Pacific comatulids except for that of H. L. Clark (1915), Macurda and Meyer (1975, 1976), Meyer and Macurda (1980), and Zmarzly and Holland (1981). These in situ studies are mainly of short duration, involving observations over periods of days to weeks.

Longer term observations of crinoid populations inhabiting shallow tropical seas are lacking. In Palau, Meyer and Macurda (1980) found the number of *Cenometra bella* (Hartlaub) in a small area to be nearly constant during visits in two consecutive years. From this observation, they suggested that *C. bella*, although capable of active swimming, maintains stable populations in favorable areas. Clearly, continuous monitoring is needed to assess parameters such as individual longevity, frequency of migration

¹ This field research was made possible by the support and facilities of the Mid-Pacific Research Laboratory. Manuscript accepted 30 December 1983.

² University of California, San Diego, Scripps Institution of Oceanography, A-008, La Jolla, California 92093.

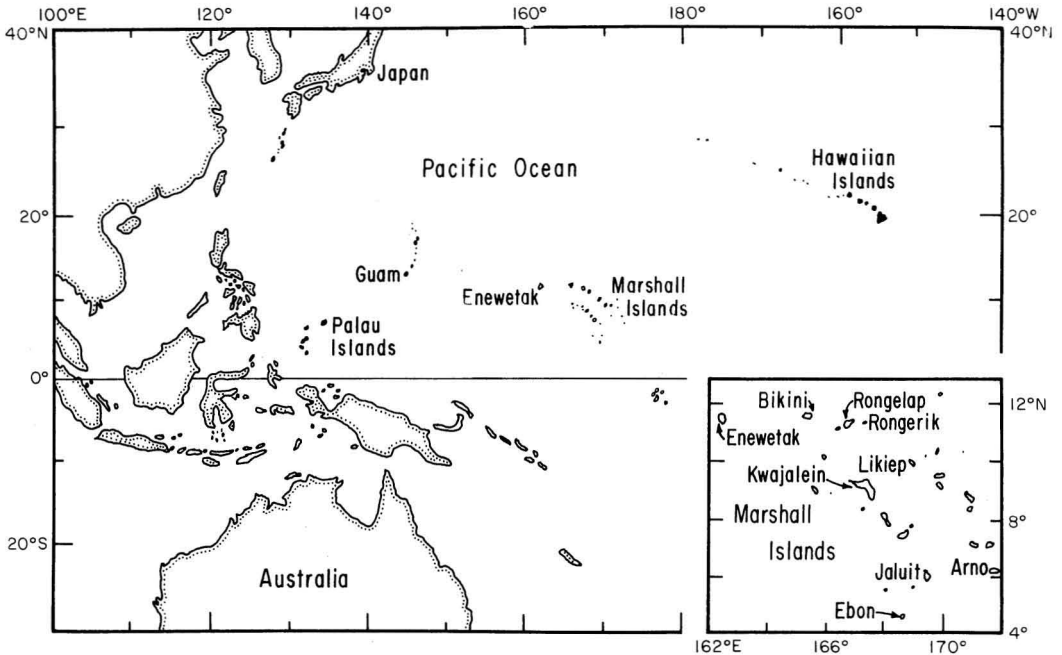


FIGURE 1. Map of Pacific Ocean showing location of Enewetak Atoll, Marshall Islands, with inset showing distribution of atolls in the Marshall Islands where crinoids have previously been collected.

within and between sites, and frequency of recruitment.

This paper synthesizes crinoid records previously published for the Marshall Islands with new data on the species composition and distribution patterns of the crinoid fauna inhabiting reefs to 36 m at Enewetak Atoll ($11^{\circ}30'N$, $162^{\circ}10'E$, Figure 1). Observations on crinoid populations monitored in situ at intervals over a 6 month period are also presented.

In the course of this study, the taxonomy and ecology of symbiotic organisms living on the crinoids were also investigated. Potts (1915) presented observations on the associates of northern Australian crinoids, with reference to their color resemblance to their host. Fishelson (1974) reported 27 associate species from 14 crinoid species in the northern Red Sea. Preliminary observations on species composition and other structural aspects of the community of invertebrates living in association with crinoids at Enewetak Atoll are reported herein.

MATERIALS AND METHODS

This investigation was carried out over a 6 month period from June through November 1980. Abundance and distribution of crinoids at seven sites about the atoll, which differed in topography, currents, and depth range, were determined by diving with SCUBA. All SCUBA surveys were conducted during the day. Site locations are shown in Figure 2; habitat descriptions are given in Table 1.

All sites, except site 3, where crinoid density was extremely high, were surveyed by swimming over the study area and recording the species, color variety, and depth of all fully or partially visible crinoids. No effort was made to reveal cryptic species. For logistical reasons, sites 1, 5, 6, and 7 were surveyed only once for species present. Sites 2, 3, and 4 were resurveyed on a biweekly basis to monitor changes in the crinoid populations over time.

At site 3, abundance and bathymetric distribution of noncryptic crinoids were studied by census of a transect area established on the

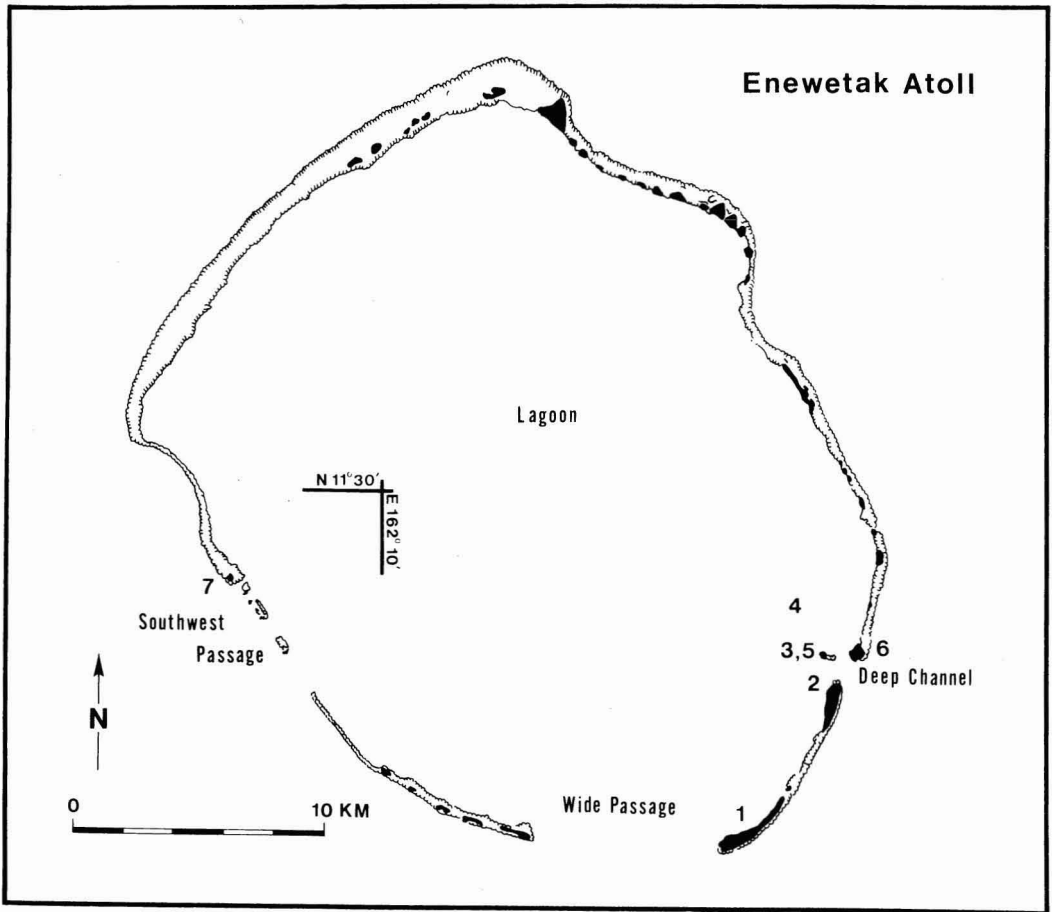


FIGURE 2. Map showing locations of sites surveyed for crinoids at Enewetak Atoll.

reef slope between 9 and 36 m depth. The transect area was 50 m long; horizontal lines were spaced along the reef slope 4 m apart, which represented approximately 3 m depth intervals. The total area censused covered 2000 m². The area was mapped on an underwater slate, and crinoids were counted by making a single pass up one side of the transect line and down the other side. The species, color variety, and location of all individuals within 2 m perpendicular to each transect line were recorded. Crinoids on the border between two transects were assigned to one of the transects by the flip of a coin. The map was used during subsequent resurveys to monitor changes in distribution of noncryptic

crinoids. Color pattern, coupled with location, was used to identify individual crinoids during resurveys so that disturbance by physical tagging was avoided. The perches of 10 crinoids were marked with surveyor's tape for additional reference points. Photographs were taken in situ to record living position, substrate, and color varieties of each species.

For analysis of symbiotic organisms, single crinoids were isolated in plastic bags in the field. Species, location, depth, and color variety were recorded for each individual. The specimens were then transported to the laboratory, where they were transferred to individual containers with fresh seawater.

Symbiotic organisms were removed from

TABLE 1
HABITAT DESCRIPTIONS OF STUDY SITES SURVEYED FOR CRINOIDS AT ENEWETAK ATOLL

STUDY SITE	HABITAT TYPE	CURRENT	DEPTHS SURVEYED (m)
1	Patch reefs on gradually sloping sand bottom within lagoon	Generally slack	3-10.5
2	Patch reefs on sand bottom within lagoon; bottom steeply sloping to Deep Channel entrance	Weak and variable	6-21
3	Steep reef slope on east side of wedge protruding into Deep Channel	Strong daily flows	9-36
4	Isolated coral pinnacle inside lagoon	Downstream from flow at site 3; current channeled by local reef formations	6-36
5	Steep reef slope on west side of wedge protruding into Deep Channel	Strong daily flows	9-36
6	Windward seaward reef	Weak and variable	9-36
7	Leeward seaward reef	Generally slack	9-30

crinoids by sealing the container, bubbling nitrogen gas through the water for 10-15 minutes to narcotize the symbionts, then agitating the host slightly to dislodge clinging organisms. Symbionts and hosts could be revived, if desired, by transferring them to fresh seawater. To check the thoroughness of symbiont removal by the nitrogen narcotization procedure, seven randomly selected crinoids (approximately 10 percent of the sample group) were fixed in 70 percent ethanol, and their arms were individually examined under a microscope for any remaining symbionts. A total of two small scaleworms were found during this procedure. The cross-check was performed on only one of the host species but was considered representative of the effectiveness of the nitrogen procedure in defaunating other crinoid species.

Following removal of epizoic organisms, the digestive tract of each crinoid was examined for endoparasites. Some symbiotic organisms were immediately fixed in 70 percent ethanol for later analyses; others were kept alive in flow-through containers for behavioral observation.

RESULTS

Six species of comatulid crinoids in three families were found in shallow-water environ-

ments at Enewetak Atoll: *Comanthus bennetti* (J. Müller), *Comanthus parvicirrus* (J. Müller), *Comanthina schlegeli* (P. H. Carpenter), and *Comaster gracilis* (Hartlaub), family Comasteridae; *Eudiocrinus tenuissimus* Gislén, family Eudiocrinidae; and *Dorometra nana* (Hartlaub), family Antendonidae. The first four species were common, while *E. tenuissimus* was collected only once under a ledge on a seaward reef. *Dorometra nana* was not encountered by the author but was collected at Enewetak on two occasions by other workers (D. M. Devaney, pers. comm.). Any strictly nocturnal species were probably missed since no night dives were made.

The crinoid species encountered at Enewetak were readily distinguished during the daytime in the field by differences in color patterns, form, and habits. *Comanthus bennetti* and *Comanthina schlegeli* are relatively large, robust, extremely multibrachiate species. In adult *Comanthus bennetti* the average number of arms was 100 ($n = 37$), with arm length about 18 cm. Adult *Comanthina schlegeli* averaged 130 arms ($n = 5$) about 15 cm in length. Both were non-cryptic by habit. *Comanthus bennetti* was found perching on live coral heads (mainly *Pocillopora* spp.) or dead coral outcrops elevated well above the reef, with its arms ex-



FIGURE 3a. *Comanthus bennetti*, showing arcuate filtration fan assumed when feeding. Arm length about 18 cm; depth 12 m.



FIGURE 3b. *Comanthus bennetti*, showing arm posture of nonfeeding individual; depth 3 m.

tended into an arcuate filtration fan (Meyer and Macurda 1980) when feeding. When the animals were not feeding, the arms were curled inward over the oral disk (Figures 3a, 3b). Small *Comanthina schlegeli* often had their oral disk wedged in a crevice or beneath a soft coral, but adults were found perching underneath or on the side of ledges or outcrops or wedged between the branches of the coral *Millepora tenera* (according to Wells' 1954 classification) (Figure 3c). The arms of *Comanthina schlegeli* were typically held in a meridional arrangement over the oral disk.

The most easily detected difference between *Comanthus bennetti* and *Comanthina schlegeli* was the number and length of cirri. *Comanthus bennetti* typically possessed 30 to 35 clawlike cirri, 4.0 to 4.5 cm in length, which were used in anchoring the animal firmly to its perch, especially during the strong current

flows which were characteristic of its environment. *Comanthina schlegeli* typically had 5 to 20 short (1.8 to 2.0 cm) cirri, and several of the lower arms were used in addition to the cirri for tethering animals to their perch. In other areas of the Indo-West Pacific, the cirri of *Comanthina schlegeli* are reported as highly variable in number or altogether lacking (Clark and Rowe 1971: pl. 1, fig. 6; Meyer and Macurda 1980).

Comaster gracilis and *Comanthus parvicirrus*, with fewer arms, were only partially visible by day. Their oral disks and the basal parts of their arms were generally buried within the reef, with only the tips of the arms emerging. The arms of *Comaster gracilis* were long and slender, with the tips often curled into tendrils (Figure 3d). The pinnules on the arms were thin and more widely spaced than those of *Comanthus parvicirrus*, which were

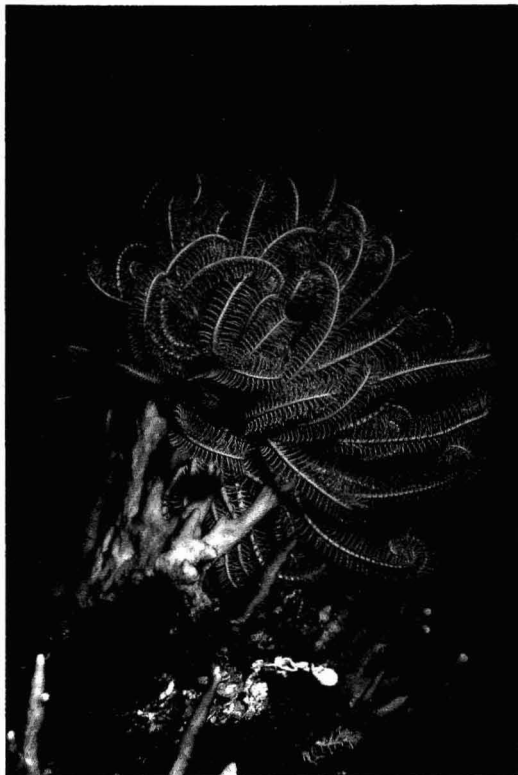


FIGURE 3c. *Comanthina schlegeli*, showing large adult clinging to branches of a milleporid coral; depth 24 m.



FIGURE 3d. *Comaster gracilis*, showing daytime emergence of arms from reef; depth 15 m.

longer, thicker, and more closely aligned. *Comanthus parvicirrus* was sometimes found wedged between the branches of the large shrub coral, *Pocillopora eydouxi* (Milne-Edwards and Haime). *Comaster gracilis* had no cirri; the cirri of *Comanthus parvicirrus* were short (1.0 to 1.3 cm) and few in number (see Meyer and Macurda 1980, fig. 6g and h).

Eudiocrinus tenuissimus was encountered only once, under a ledge on the leeward seaward reef. This small species had five arms of approximately 45 mm length. The cirri were well developed, about 4 mm in length, 12 to 15 in number, and had a distinct beaded appearance.

The ten-armed *Dorometra nana* is of cryptic habit and was collected under coral rubble both on the windward reef and in the lagoon (D. M. Devaney, pers. comm.).

Polychromatism

With the exception of *Comanthus parvicirrus* and *Eudiocrinus tenuissimus*, the crinoid species at Enewetak were polychromatic. *Comanthina schlegeli* had five recurring color varieties (Table 2). Varieties CS1, CS3, and CS4 were common, while CS2 and CS5 were comparatively rare.

Four recurring color varieties, listed in Table 3, as well as several nonrecurring types were noted for *Comanthus bennetti*. CB1 was the variety most frequently encountered, encompassing 69.5 percent of the individuals in the transect area (site 3). CB3 was found exclusively at depths exceeding 21 m.

The partially cryptic *Comaster gracilis* had only three color varieties. Most commonly the arms and pinnules were golden orange, but

TABLE 2
 COLOR VARIETIES OF *Comanthina schlegeli* AT ENEWETAK ATOLL

DESIGNATION	ORAL DISK	CIRRI	DIVISION SERIES & ARMS	PINNULES
CS1	Brown, often with white spots	White with brown or orange bands	Orange or orange-brown; random white variegations encompassing brachials and pinnules	Brown with yellow tips except for variegations where pinnules are white with yellow tips
CS2	Orange-brown with white spots	White with orange tips	Orange-brown with random white variegations	Orange-brown with white tips except for variegations where pinnules are all white
CS3	Black with white spots	White	Orange or orange-brown with random white variegations	Black with yellow tips except for variegations where pinnules are white with yellow tips
CS4	Bright yellow	Bright yellow	Bright yellow	Bright yellow
CS5	Bright yellow	Bright yellow	Bright yellow	Black or brown with yellow tips; random yellow variegations

TABLE 3
 COLOR VARIETIES OF *Comanthus bennetti* AT ENEWETAK ATOLL

DESIGNATION	ORAL DISK	CIRRI	DIVISION SERIES & ARMS	PINNULES
CB1	Black with bright green speckling	Same or black	Black with bright green speckling	Black; with yellow tips in some individuals, orange tips in others
CB2	Yellow, often dusted with black or green	Black	Yellow	Proximally yellow, then black; with yellow tips in some individuals, orange tips in others
CB3	Light orange; some with white markings on perimeter of disk	Light orange	Light orange	Orange darkening to brown distally; individuals either with yellow, orange, or no tip color; sporadic white frosting on pinnules; oral pinnules white
CB4	Orange-brown	Orange-brown	Orange, orange-brown, or brown	Orange darkening to brown distally or brown turning to orange distally; individuals either with yellow, orange, or no tip color

some individuals were dark brown or reddish brown.

Although *Comanthus parvicirrus* is reported to be highly variable in color at Palau (Meyer and Macurda 1980), all individuals of this species at Enewetak were black.

A single color pattern was also noted for

Eudiocrinus tenuissimus. The arms were variegated brown and tan. Narrow maroon lines flanked each side of the ambulacrum, breaking up into stippling on the pinnules. The anal cone was tan, with brown and white spots.

No color data were available for *Dorometra nana*.

Distribution of Crinoids

The lagoon at Enewetak reaches a maximum depth of 62 m. There are three passages into the lagoon, all in the southern half of the atoll: the Southwest Passage, which is less than 2 m in depth; the Deep Channel, which is less than 2 km wide but reaches a depth of 58 m; and the Wide Passage, which is nearly 10 km in width and 11 to 22 m deep. One major current stream moves through these latter two passes, affecting less than a quarter of the lagoon area. Maximal tidal flow has been measured at 2 kn in the Deep Channel and 1 kn in the Wide Passage. Inside the lagoon, a wedge-shaped reef (sites 3 and 5) protrudes into the Deep Channel from the north and receives good exposure to these tidal currents (Emery, Tracey, and Ladd 1954). Elsewhere, the lagoon bottom is predominantly sandy and is dotted by patch reefs of variable size (sites 1 and 2) and coral pinnacles (site 4) which rise to within 10 m of the surface (see Figure 2 for site locations). While *Comanthus bennetti* was the most common crinoid at Enewetak, different species dominated the crinoid fauna at different sites.

Six crinoids were encountered on the small patch reefs within site 1. Five of these were *Comanthus bennetti*, with the shallowest occurrence at 3 m. The other was a large *Comanthina schlegeli*, also at 3 m.

At site 2, which ranged in depth from 6 to 21 m, *Comanthina schlegeli* was more abundant than *Comanthus bennetti*, but the *Comanthina schlegeli* individuals were much smaller than those encountered elsewhere. Currents at this site were weak and unpredictable. On two occasions, large particles of flocculent material were observed both in the water column and clinging to the benthic fauna.

At site 4, which ranged in depth from 6 to 36 m, 10 *Comanthus bennetti* were found in a wedge between 10 and 18 m where local reef formations concentrated current flow. Two *Comaster gracilis* were also present at this site, but *Comanthina schlegeli* and *Comanthus parvicirrus* were absent.

Comanthus bennetti, *C. parvicirrus*, *Comanthina schlegeli*, and *Comaster gracilis*

all co-occurred and reached peak abundance at sites 3 and 5, where regular, strong currents flowed. Under these favorable conditions, an average density of 0.129 crinoids per m² was measured. Because the two sites were very similar, a quantitative survey was carried out only at site 3.

At site 3, *Comaster gracilis* and *Comanthus parvicirrus*, of semicryptic habit by day, were the only species present on the reef flat at depths of 9 m and less where the water was often turbulent. *Comaster gracilis* was present at all transect depths, but reached peak abundance at 21 m. *Comanthus parvicirrus* was most abundant at 24 m, its lower limit of distribution at site 3 (Figure 4). Densities of *Comaster gracilis* and *Comanthus parvicirrus* in the transect area (2000 m²) were low, 0.017 and 0.011 per m², respectively.

Mixed aggregations of *Comanthus bennetti* and *Comanthina schlegeli* covered promontories which projected into current channels at this site, especially at depths exceeding 18 m. Otherwise, crinoids typically occurred as isolated individuals, with the minimum distance between individuals determined by the presence of suitable substrate. *Comanthus bennetti* first occurred at 12 m and *Comanthina schlegeli* first occurred at 15 m. Both species were observed deeper than the last transect line at 36 m. *Comanthus bennetti* was more abundant than *Comanthina schlegeli* at all transect depths where they occurred, but depth zonation of the two species was evident (Figure 5). Peak abundance was reached by *Comanthus bennetti* between 18 and 24 m, while the abundance of *Comanthina schlegeli* was greatest between 27 and 33 m.

Densities of *Comanthus bennetti* and *Comanthina schlegeli* in the transect area were 0.086 and 0.015 per m², respectively. Maximum densities can be calculated by considering only the number of crinoids in the zone of peak abundance, an area of 600 m² in both cases. These maximum densities are approximately two times the overall densities, or 0.203 per m² for *Comanthus bennetti* and 0.028 per m² for *Comanthina schlegeli*.

On the windward seaward reef (site 6), the reef sloped gradually to depth, and stony corals were not very well developed.

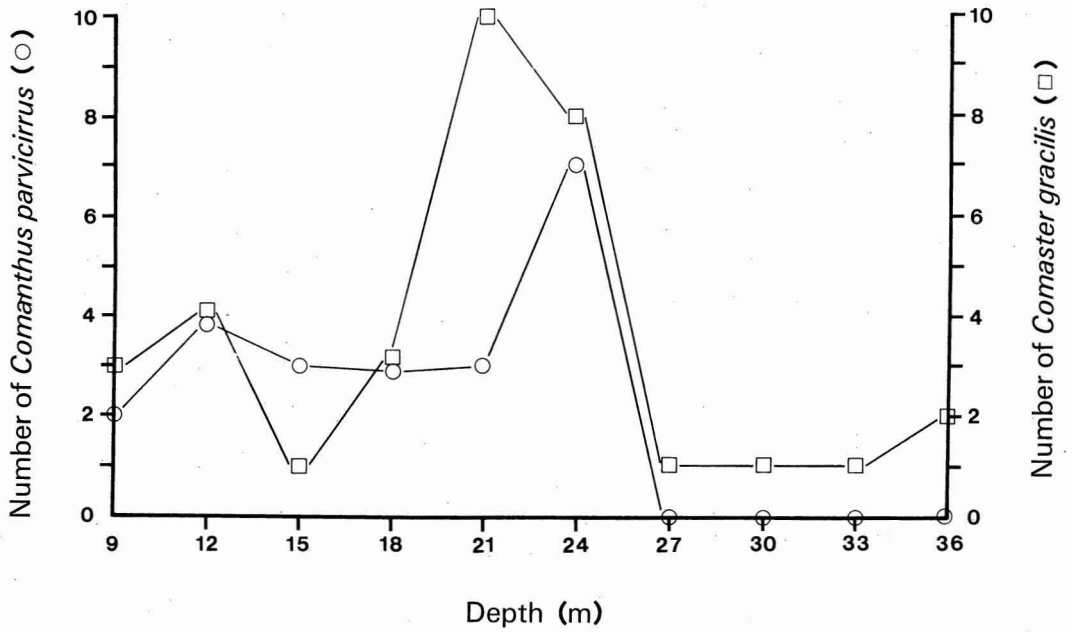


FIGURE 4. Depth distribution of *Comanthus parvicirrus* and *Comaster gracilis* in transect area, site 3, Enewetak lagoon.

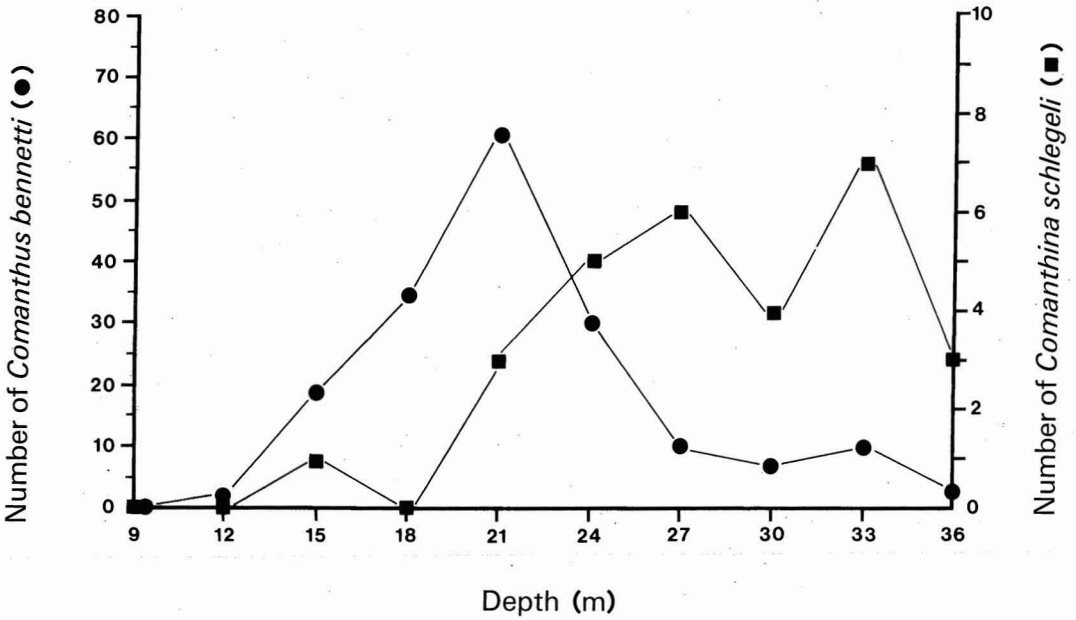


FIGURE 5. Depth distribution of *Comanthus bennetti* and *Comanthina schlegeli* in transect area, site 3, Enewetak lagoon.

Numerous large tables of *Acropora* sp. were broken and turned over as a result of storm damage in 1979 (M. V. DeGruy, pers. comm.). No crinoids were found during a survey between 9 and 36 m.

In contrast, the seaward reef on the leeward side of the atoll showed a sharp break in slope at 12 m. Corals and other sessile benthic invertebrates were well developed at site 7. Four crinoid species occurred at the site investigated to depths of 30 m: *Comanthus bennetti*, *C. parvicirrus*, *Comanthina schlegeli*, and *Eudiocrinus tenuissimus*.

Persistence of Observed Crinoid Distribution Patterns

The distribution of *Comanthus bennetti* and *Comanthina schlegeli* at three lagoonal sites (2, 3, and 4) monitored at biweekly intervals remained nearly constant throughout the 6 month period. No recruitment, mortality, or emigration out of the area was observed. At site 3, two *Comanthus bennetti* moved into the 18 m transect zone in November from some point outside of the transect area itself. This was considered to be a case of immigration rather than recruitment since the animals were of adult size. The other crinoids remained on their original perches over the 6 months. Random removal of individuals from monitored populations did not affect the established distribution patterns.

Another instance of migration was observed at site 1, which was not mapped or resurveyed. During one dive, a single *Comanthus bennetti* was encountered in transit. Its imprint in the sand could be followed to a small patch reef about 3 m away. This individual, recognizable by its distinct coloration, was found stationary on a nearby patch reef the next day. The following day, the same crinoid was again observed actively crawling over the sand, approximately 8 m from its previous site.

Fauna Associated with Crinoids at Enewetak Atoll

A total of 18 species of macro-invertebrates, representing Mollusca (Gastropoda), Poly-

chaeta (Polynoidae and Myzostomidae), and Crustacea (Copepoda and Decapoda, Caridea and Anomura), were found in association with four crinoid species at Enewetak Atoll. Symbiont species, along with the host species on which they were found, are listed in Table 4. *Eudiocrinus tenuissimus* was excluded from symbiont studies due to its small size and infrequent occurrence. Over half of the symbiont species were associated with a single host species. Only the scaleworm, *Paradyte crinoidicola*, utilized all four host species.

ASSOCIATES OF *Comanthus bennetti*: Specimens of *Comanthus bennetti* were collected from a variety of lagoonal habitats between 3.5 and 36 m depth, in order to make as broad a survey as possible.

The anomuran crab, *Allogalatea* (formerly *Galatea*) *elegans*, is thought to be extremely common on crinoids across the Indo-Pacific to Japan and South Africa and into the Red Sea (Baba 1969, Haig 1973, Lewinsohn 1969). However, the taxonomy of this species is currently in question (see Baba 1969), and any zoogeographic data reported for *A. (Galatea) elegans* may have to be reconsidered. At Enewetak, only 23 percent of the *Comanthus bennetti* sampled were occupied by the crab, although crabs occurred over a wide depth range from 8 to 36 m. On 50 percent of hosts, *A. elegans* occurred as a heterosexual pair. In the remainder of cases, hosts were occupied by single individuals, generally males. As figured by Fishelson (1974), these crabs were typically found clinging to the aboral side of the bases of the host's arms, with their large chelae pointing outward. *Allogalatea elegans* was also found on an alternate host, *Comanthina schlegeli*, with greater frequency (54 percent).

Periclimenes amboinensis and *Araiopontonia odontorhyncha* were the largest of the pontonine shrimps associated with *Comanthus bennetti*. The two species were similar in size and shape, had robust chelae, and were found exclusively on *C. bennetti*. In both species, a single heterosexual pair of shrimp occupied a host. In addition to their morphological similarity and association with the same host species, both species occupied the oral disk

TABLE 4

PERCENT OCCURRENCE OF SYMBIOTIC ORGANISMS ON FOUR CRINOID HOST SPECIES AT ENEWETAK ATOLL

SYMBIONT SPECIES	HOST CRINOIDS			
	<i>Comanthina schlegeli</i> n = 13	<i>Comanthus bennetti</i> n = 73	<i>Comanthus parvicirrus</i> n = 7	<i>Comaster gracilis</i> n = 4
Crustacea, Decapoda				
Galatheidae				
<i>Allogalatea elegans</i> (Adams & White)	54	23		
Palaemonidae, Pontoniinae				
<i>Araiopontonia odontorhyncha</i> Fujino & Miyake		14		
<i>Palaemonella pottsi</i> (Borradaile)	46	*	43	50
<i>Periclimenes amboinensis</i> (DeMan)		49		
<i>P. commensalis</i> Borradaile	54	70		
<i>P. pilipes</i> Bruce & Zmarzly	46			
<i>P. tenuis</i> Bruce		18		
<i>Pontoniopsis comanthi</i> Borradaile		†	71	
Alpheidae				
<i>Synalpheus carinatus</i> (DeMan)	92		29	
<i>S. stimpsoni</i> (DeMan)			71	100
Crustacea, Copepoda				
<i>Pseudanthessius comanthi</i> Humes		‡		
Annelida, Polychaeta				
Polynoidae				
<i>Paradyte crinoidicola</i> (Potts)	46	48	14	25
Myzostomidae				
<i>Myzostoma</i> Leuckart sp. 1		31		
<i>M.</i> sp. 2		‡		
<i>M.</i> sp. 3	15			
Mollusca, Gastropoda				
Unidentified sp.	08	03		
<i>Calliostoma</i> Swainson sp.	08	07	14	
<i>Clanculus atropurpureus</i> Gould	15			

* Only one juvenile *P. pottsi* was encountered on *Comanthus bennetti*.† *P. comanthi* was found on *Comanthus bennetti* only once, on a host with no other symbiotic organisms.

‡ Specimens were collected from several hosts for taxonomic analysis but presence was not quantitatively assessed.

of the crinoid. The two species were never found to co-occur, except in a single case where a juvenile *A. odontorhyncha* was found on a host already occupied by a pair of *P. amboinensis*.

Araiopontonia odontorhyncha, a rare species, was encountered on only 14 percent of the *Comanthus bennetti* examined and was restricted in its occurrence to depths between 7 and 27 m. *Periclimenes amboinensis*, which was found over the entire depth range sampled, occurred 3.5 times more often than *A. odontorhyncha*.

Periclimenes amboinensis, of which the type material from Ambon, Indonesia (DeMan 1888), is no longer extant, has since been reported from Heron Island, Australia (Bruce

1983). *Araiopontonia odontorhyncha* was previously known only from its type locality in the Ryukyu Islands, Japan (Fujino and Miyake 1970), until its discovery at Enewetak Atoll.

The small *Periclimenes commensalis* was found on 70 percent of the hosts examined, from 3.5 to 36 m depth. *P. commensalis* is commonly reported on crinoids throughout the Indo-Pacific, from the east coast of Africa to Hong Kong, New Caledonia, and Australia (Bruce 1971, 1980, 1982). Typically at Enewetak, two to three pairs of adults in addition to several juveniles occurred together on a host. These shrimp appeared to occupy the distal parts of the arms of the crinoid and were frequently observed darting between

arms. *P. commensalis* also occurred frequently on another host, *Comanthina schlegeli*.

Periclimenes tenuis, a small and slender species, often co-occurred on *Comanthus bennetti* with *P. commensalis*, with which it shared the distal parts of the arms of the host. Twelve to 15 *P. tenuis* per host was common, with up to half being juveniles. This species was comparatively rare, occurring on only 18 percent of the hosts examined. While *P. tenuis* was found between 12 and 36 m, its incidence of occurrence markedly increased to 43 percent on hosts from depths exceeding 18 m. In addition, *P. tenuis* occurred on 100 percent of the hosts of color variety CB3, found only at depths exceeding 21 m. *Periclimenes tenuis* was first described from East Africa (Bruce 1969) and has since been reported from the northern Red Sea (Fishelson 1974) and Heron Island, Australia (Bruce 1983).

Two species of gastropods were occasionally found in association with *Comanthus bennetti*. An unidentified parasitic species (sp. 1) was attached to the host. Snails tentatively identified as *Calliostoma* sp. were generally found in groups of three to six individuals, clustered on the substrate under the cirri of the crinoid. When the crinoid was removed, the snails quickly scattered to the nearest cover. This species appeared to be a facultative associate at best, but it was frequently encountered. It was also found to shelter under *Comanthina schlegeli* and *Comanthus parvicirrus*.

The polynoid scaleworm, *Paradyte crinoidicola*, was found to inhabit *Comanthus bennetti*, in addition to the other three host species examined. These scaleworms roamed the arms of their host, generally orienting longitudinally in the ambulacrum. Of the *C. bennetti* examined, 50 percent had at least one to a maximum of four scaleworms.

Two species of myzostomid worms, specialized parasites of crinoids and a few other echinoderms, occurred on *Comanthus bennetti*, one endozoic and the other epizoic. *Myzostoma* sp. 1 typically occurred as a pair, just inside the mouth of its host. Occasionally one or two juveniles would also be found. An epizoic species in the same genus (sp. 2) was ubiquitous on the host specimens examined, with up to 30 individuals on a single host.

SYMBIONT SPECIES ON OTHER HOSTS: A pair of alpheid shrimp was generally found on the oral disk of crinoids other than *Comanthus bennetti*. *Comanthina schlegeli* was exclusively occupied by *Synalpheus carinatus*, with 92 percent of the hosts examined inhabited by this shrimp. A closely related species, *S. stimpsoni*, was the only alpheid found on *Comaster gracilis*. Although only a small number of this host species could be examined, all were found to carry a pair of *S. stimpsoni*. *Comanthus parvicirrus* was an alternate host for both alpheid species, although they were never found to co-occur on a single host. *Synalpheus stimpsoni* occurred more frequently than *S. carinatus* in the *C. parvicirrus* samples. A third species, *S. demani*, was reported from crinoids at Enewetak by Banner and Banner (1968), but the host determination as *Comanthus bennetti* is believed to be in error. *S. demani* was not collected during the present study and is a comparatively rare species.

Several other pontonine shrimps were collected from Enewetak crinoids. The recently described *Periclimenes pilipes* (Bruce and Zmarzly 1983) was specific to *Comanthina schlegeli*. *Pontoniopsis comanthi* was found once in association with *Comanthus bennetti*, on a host with no other symbionts, but more commonly occurred on *Comanthus parvicirrus*. Similarly, a juvenile *Palaemonella pottsii* was obtained once from *C. bennetti*, but mated pairs of this shrimp were routinely encountered on *C. parvicirrus*, *Comaster gracilis*, and *Comanthina schlegeli*. Neither *P. comanthi* nor *P. pottsii* is felt to be a significant associate of *Comanthus bennetti* at Enewetak.

A comparatively rare myzostomid species, *Myzostoma* sp. 3, was epizoic on *Comanthina schlegeli*. It was found wrapped around individual pinnules, which it mimicked in coloration, on the arms of its host.

The gastropod *Clanculus atropurpureus* was found to shelter under the cirri of *Comanthina schlegeli* in a manner similar to that described for *Calliostoma* sp. in the previous section.

DISCUSSION

Table 5 gives all records of crinoid species from atolls in the Marshall Islands. Although

TABLE 5
RECORDS OF MARSHALL ISLAND CRINOIDEA

CRINOID SPECIES	ATOLLS AND COORDINATES WHERE COLLECTED									
	ENEWETAK 11°30' N 162°10' E	BIKINI 11°40' N 165°25' E	RONGELAP 11°10' N 166°30' E	RONGERIK 11°15' N 167°40' E	LIKIEP 10°00' N 169°10' E	KWAJALEIN 9°00' N 167°40' E	ARNO 7°05' N 171°45' E	JALUIT 6°00' N 169°30' E	EBON 4°35' N 168°45' E	
Comasteridae										
<i>Comanthus bennetti</i> (J. Müller)	+ , 1, 8, 9, 10		4			5, 7	6			
<i>Comanthus parvicirrus</i> (J. Müller)	+									
<i>Comanthina schlegeli</i> (P. H. Carpenter)	+									
<i>Comaster gracilis</i> (Hartlaub)	+ , 1	4								
Mariametridae										
<i>Lamprometra palmata</i> (J. Müller)					3			3	2*, 3	
<i>Stephanometra indica protectus</i> (Lütken)/ <i>S. indica indica</i> (Smith)		1	4	4				3	2†, 3, 4*	
Eudiocrinidae										
<i>Eudiocrinus tenuissimus</i> Gislén	+							3		
Colobometridae										
<i>Cenometra bella</i> (Hartlaub) as <i>C. bella</i> var. <i>magnifica</i>								3		
Antedonidae										
<i>Dorometra nana</i> (Hartlaub)	+							3	3	

KEY:

1 = Specimens housed in the reference collection of the Mid-Pacific Research Laboratory.

2 = Hartlaub 1912.

* (as *Antedon brevicuneata*; see A. H. Clark 1952:303).

† (as *Antedon monacantha*; synonymized by Gislén 1940:11).

3 = Gislén 1940.

4 = A. H. Clark 1952.

* (as *Himerometra heliaster* in A. H. Clark 1908; see Clark 1952:303)

5 = Holthuis 1953.

6 = A. H. Clark 1954 (additional records on p. 263 for Arno Atoll not tabulated here; see text for explanation).

7 = Banner 1959.

8 = Banner and Banner 1968 (the crinoid host listed as *Comanthus bennetti* may have been incorrectly identified).

9 = Humes 1972.

10 = Bartolini, Erdman, and Scheuer 1973.

+ = Present collection.

only one species, *Comanthus bennetti*, was previously reported from Enewetak (Banner and Banner 1968, Bartolini, Erdman, and Scheuer 1973, Humes 1972), seven species of comatulid crinoids in five families had been recorded for the Marshall Islands, excluding the record of *Antedon* sp. from Arno Atoll (Banner 1957) which is most likely incorrect. Specimens of *Comanthus parvicirrus* and *Comanthus samoanus* are erroneously listed by Clark (1954: 263) from Arno Atoll, M. I. but are confirmed to have been collected at Onotoa Atoll, Gilbert Islands (as indicated in Clark 1954: 249) in the records of the U.S. National Museum (Smithsonian Institution), where the specimens were deposited (M. E. Downey, pers. comm.). Two species, *Comanthus bennetti* and *Comaster gracilis*, were present in the reference collection of the Mid-Pacific Research Laboratory (MPRL) at the time of this work. *Comanthina schlegeli* and *Comanthus parvicirrus* were not known from the Marshall Islands, the closest previous records being the Mortlock Islands in the eastern Caroline group (Meyer and Macurda 1980) and Onotoa Atoll, Gilbert Islands (Clark 1954), respectively. However, a specimen of *Comanthina schlegeli* was present in the MPRL reference collection, incorrectly determined as *Comanthus bennetti*. Six species in three families are now known from Enewetak, and a total of nine species, representing five families, is now recorded for the Marshall Islands (see also short review on this subject by Devaney, in press).

Although only six of the nine species now known to occur in the Marshalls were found at Enewetak, this is the maximum number so far recorded for any of the individual atolls. Because it is reasonable to expect that the total number of species present in a local area will be less than that recorded for the region defined by a set of islands, it is possible that the three species not found during the survey at Enewetak do not occur there. However, two of the three missing species are reported to be highly cryptic within the reef infrastructure by day and perhaps are only nocturnally active (Meyer and Macurda 1980). Since no night collections were made during this survey, it is also possible that these species do

occur at Enewetak but were overlooked. The third species, *Cenometra bella*, is reported to perch on certain antipatharians and gorgonians (Meyer and Macurda 1980), which were uncommon at the sites investigated; therefore *C. bella* may be restricted in occurrence by substrate requirements.

The decrease in diversity from 21 shallow-water species in four families in the Palau Islands to 9 species in five families in the Marshall Islands is consistent with the general attenuation of species which occurs with distance from the Indo-Pacific center of distribution (Clark and Rowe 1971). With the exception of *Eudiocrinus tenuissimus*, a small and cryptic species which may easily be overlooked, the crinoid fauna of the Marshall Islands is a subset of that in Palauan waters. The seven comatulid species found in Guam are also a subset of the Palauan fauna, yet Guam and the Marshall Islands have only four species in common (see Meyer and Macurda 1980 for species lists from Palau and Guam). With some minor variations, the species found at Enewetak conform well to the species descriptions, based on specimens from other areas of the Indo-Pacific, in A. H. Clark's (1931) monograph.

The three most abundant crinoid species at Enewetak were polychromatic. The pigments of Indo-Pacific comatulids have been studied in detail (Sutherland and Wells 1967, Powell, Sutherland, and Wells 1967, Smith and Sutherland 1971, Bartolini, Erdman, and Scheuer 1973), but the functional significance, if any, of crinoid polychromism is unknown. While polychromism is prevalent among shallow-water crinoids, it is lacking below 100 m, where illumination ceases (D. B. Macurda, pers. comm.) At Enewetak, the trend appeared to be for individuals of the more exposed species to be the most variable in color, while individuals of the more cryptic species showed little or no variation in color. This trend requires further testing on both larger numbers of conspecific individuals and larger numbers of species grouped by living position and behavior. The results of this study, compared with other published accounts of crinoid coloration, confirm that there are intraspecific differences in color pat-

terns between regional populations. Some varieties, like CB1, are conserved between regions. Meyer and Macurda (1980) reported a color variety of *Comanthus bennetti* found exclusively at depths exceeding 15 m, similar to CB3 at Enewetak.

The distribution and abundance of shallow-water crinoids around Enewetak Atoll were highly variable. As indicated by their increase in abundance at sites with daily current flow, *Comanthus bennetti*, *C. parvicirrus*, *Comanthina schlegeli*, and *Comaster gracilis* are rheophilic species. These species all exhibit mechanical or behavioral adaptations which enable them to inhabit environments with strong currents. *Comanthus bennetti* has extremely robust clawlike cirri which grasp coral substrates; *Comanthina schlegeli* has reduced cirri and occurs on coral substrates with smaller diameter branches which the cirri can grasp firmly. This species does not perch high above the substrate like *Comanthus bennetti*, but lowers itself between the coral branches on which it is perching or sits on the protected side of the substrate, tethered by several arms. *Comanthus parvicirrus* has similarly reduced cirri but fewer arms and occurs in protected crevices or well within the protection of a coral head. *Comaster gracilis*, with no cirri and long, slender arms, occurs exclusively within the reef with only its arms emerging. Perhaps because of their cryptic habits, the latter 2 species can invade shallow turbulent areas from which *Comanthus bennetti* and *Comanthina schlegeli* are excluded.

The results of the present study suggest that over this half-year period, migration, recruitment, and mortality were not significant factors in population regulation. Individual longevity may figure prominently in the persistence of crinoid populations over time, but data on longevity, reproductive periodicity, and juvenile settling are needed before such constancy can be assessed.

Our knowledge of structural and functional aspects of crinoid symbiotic associations is still extremely limited, but the following points regarding structure are stated in summary: (1) a pool of potential colonizers, based on host specificities, was identified for each

crinoid species; (2) occurrence of some symbiont species appeared to be correlated with host depth; (3) occurrence and organization of symbionts on individual hosts seemed to be related to partitioning of host space and perhaps, although not directly assessable, to interspecific competition for preferred sites. This idea is supported by the mutually exclusive occurrence of species which inhabit the same site on a host (for example, *Periclimenes amboinensis* and *Araiopontonia odontorhyncha*). The occurrence, in several species, of a single pair of individuals per host is probably indicative of active defense of host space against invasion by conspecifics. Predator-prey relationships between symbiont species, although possible, were not observed but may also play an important role in the structure of these symbiont microcommunities.

ACKNOWLEDGMENTS

I am extremely grateful to D. M. Devaney for his enthusiastic encouragement of this work and for his critical reading of an earlier draft of the manuscript; this paper is dedicated to his memory. Thanks are due A. Fielding for sharing her field knowledge of the problem and for providing invaluable advice, and C. Arneson for his infinite patience underwater. I would also like to thank the following experts for confirming or providing species identifications: D. M. Banner, A. J. Bruce, R. Hanley, E. A. Kay, and D. L. Meyer. The manuscript was improved by comments from D. B. Macurda, Jr. and from members of my doctoral committee, especially W. A. Newman and P. K. Dayton.

REFERENCES CITED

- BABA, K. 1969. Four new genera with their representatives and six new species of the Galatheidæ in the collection of the Zoological Laboratory, Kyushu University, with the redefinition of the genus *Galathea*. OHMU, Kyushu University 2(1):1-32.

- BANNER, A. H. 1957. Contributions to the knowledge of the alpheid shrimp of the Pacific Ocean. II. Collection from Arno Atoll, Marshall Islands. *Pac. Sci.* 11(2):190-206.
- . 1959. Contributions to the knowledge of the alpheid shrimp of the Pacific Ocean. IV. Various small collections from the central Pacific area, including supplementary notes on alpheids from Hawaii. *Pac. Sci.* 13(2):130-155.
- BANNER, A. H., and D. M. BANNER. 1968. Contributions to the knowledge of the alpheid shrimp of the Pacific Ocean. XII. Collections from the Marshall and Caroline Islands. *Micronesica* 4(2):261-294.
- BARTOLINI, G. L., T. R. ERDMAN, and P. J. SCHEUER. 1973. Anthraquinone pigments from the crinoid *Comanthus bennetti*. *Tetrahedron* 29:3699-3702.
- BELL, F. J. 1884. Echinodermata. Pages 117-177 and 509-512, plates 8-17 and 45 in R. W. Coppinger, ed. Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert," 1881-2. London.
- BRUCE, A. J. 1969. Preliminary descriptions of sixteen new species of the genus *Periclimenes* Costa, 1844 (Crustacea, Decapoda, Natantia, Pontoniinae). *Zool. Meded., Leiden* 43(20):253-278.
- . 1971. Records of some rare pontoniid shrimps from Australian waters, with remarks upon the mouthparts of some species of the genus *Periclimenes* Costa, 1844. *Zool. Verh., Leiden* 114:1-32.
- . 1980. Some pontoniine shrimps from the Solomon Islands. *Micronesica* 16(2):261-269.
- . 1982. The shrimps associated with Indo-West Pacific echinoderms, with the description of a new species in the genus *Periclimenes* Costa, 1844 (Crustacea: Pontoniinae). *Aust. Mus. Mem.* 16:191-216.
- . 1983. The pontoniine shrimp fauna of Australia. *Aust. Mus. Mem.* 18:195-218.
- BRUCE, A. J., and D. L. ZMARZLY. 1983. *Periclimenes pilipes*, new species, a crinoid associate from Enewetak Atoll, Marshall Islands (Crustacea: Decapoda: Pontoniinae). *J. Crust. Biol.* 3(4):644-654.
- CARPENTER, P. H. 1888. Report on the Crinoidea collected during the voyage of H.M.S. "Challenger" during the years 1874-1876. II. The Comatulæ. Report Sci. Results Voyage "Challenger," *Zool.* 26:1-399.
- CLARK, A. H. 1908. Notice of some crinoids in the collection of the Museum of Comparative Zoology. *Bull. Mus. Comp. Zool., Harvard* 51(8):233-248 + 2 pls.
- . 1909. On a collection of recent crinoids from the Philippine Islands. *Proc. U.S. Natl. Mus.* 36:391-410.
- . 1911a. The recent crinoids of the coasts of Africa. *Proc. U.S. Natl. Mus.* 40:1-51.
- . 1911b. On a collection of unstalked crinoids made by the United States Fisheries steamer "Albatross" in the vicinity of the Philippine Islands. *Proc. U.S. Natl. Mus.* 39:529-563.
- . 1931. A monograph of the existing crinoids. I. The comatulids. Part 3. Superfamily Comasterida. *Bull. U.S. Natl. Mus.* 82(3). 816 pp., + 82 pls.
- . 1952. Echinoderms from the Marshall Islands. *Proc. U.S. Natl. Mus.* 102:265-303.
- . 1954. Records of Indo-Pacific echinoderms. *Pac. Sci.* 8:243-263.
- CLARK, A. M., and F. W. E. ROWE. 1971. Monograph of shallow-water Indo-West Pacific echinoderms. British Museum (Nat. Hist.) Publ. No. 690. 238 pp.
- CLARK, H. L. 1915. The comatulids of Torres Strait: with special reference to their habits and reactions. *Pap. Dept. Mar. Biol. Carnegie Inst. Wash.* 8:97-125.
- . 1921. The echinoderm fauna of Torres Strait: Its composition and its origin. *Pap. Dept. Mar. Biol. Carnegie Inst. Wash.* 10:1-223 + 38 pls.
- DEVANEY, D. M. (in press). Echinoderms (other than Holothuroidea). In D. M. Devaney, E. S. Reese, P. Helfrich, and P. Colin eds. Natural history of Enewetak Atoll. U.S. Dept. of Energy Publ.
- DEMAN, J. G. 1888. Bericht über die von Herrn Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte* 53(1):215-600, pls. 7-22a.

- EMERY, K. O., J. I. TRACEY, Jr., and H. S. LADD. 1954. Geology of Bikini and nearby atolls. U.S. Geol. Surv. Prof. Pap. 260-A:1-265 + 64 pls.
- FISHELSON, L. 1974. Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. *Mar. Biol.* 26:183-192.
- FUJINO, T., and S. MIYAKE. 1970. *Araio-pontonia odontorhyncha* gen. et sp. nov., a new shrimp from the Ryukyu Islands, Japan (Decapoda, Palaemonidae, Pontoninae). OHMU, Kyushu University 3(1):1-10.
- GISLÉN, T. 1940. A collection of crinoids from the South Sea Islands. *K. svenska Vetenskakad. Handl., ser. 3*, 18(10):1-16 + 3 pls.
- HAIG, J. 1973. Galatheidea (Crustacea, Decapoda, Anomura) collected by the F.I.S. "Endeavour." *Rec. Aust. Mus.* 28(14):269-289.
- HARTLAUB, C. 1895. Reports on the dredging operations... carried on by the "Albatross" during 1881. XVIII. Die Comatuliden. *Bull. Mus. Comp. Zool., Harvard* 27(4):127-152 + 4 pls.
- . 1912. Report on the results of dredging... by the U.S. Coast Survey Steamer "Blake". XLV. Die Comatuliden. *Mem. Mus. Comp. Zool., Harvard* 27(4):275-491 + 18 pls.
- HOLTHUIS, L. B. 1953. Enumeration of the decapod and stomatopod Crustacea from Pacific coral islands. *Atoll Res. Bull.* 24:1-66.
- HUMES, A. G. 1972. *Pseudanthessius comanthi* n. sp. (Copepoda, Cyclopoida) associated with a crinoid at Eniwetok Atoll. *Pac. Sci.* 26:373-380.
- LEWINSOHN, C. 1969. Die Anomuren Des Roten Meeres (Crustacea Decapoda: Paguridea, Galatheidea, Hippidea). *Zool. Verh., Leiden* 104:1-213 + 2 pls.
- MACURDA, D. B., Jr. 1973. Ecology of comatulid crinoids at Grand Bahama Island. *Hydro-Lab Jour.* 2:9-24.
- . 1975. The bathymetry and zoogeography of shallow-water crinoids in the Bahama Islands. *Hydro-Lab Jour.* 3:5-24.
- MACURDA, D. B., Jr., and D. L. MEYER. 1975. The behavior and ecology of the crinoids of the East Indies. *Geol. Soc. Amer. Abstracts with Prog.* 7(7):1184.
- . 1976. The ecology and zoogeography of the crinoids of the Indian Ocean. *Geol. Soc. Amer. Abstracts with Prog.* 8(6):992.
- MAGNUS, D. B. E. 1967. Ecological and ethological studies and experiments on the echinoderms of the Red Sea. *Stud. Trop. Oceanogr., Miami* 5:635-664.
- MEYER, D. L. 1971. Functional morphology and autecology of the shallow-water unstalked crinoids (Echinodermata) of the Caribbean Sea. Doctoral Dissertation, Yale University.
- . 1973a. Distribution and living habits of comatulid crinoids near Discovery Bay, Jamaica. *Bull. Mar. Sci.* 23:244-259.
- . 1973b. Feeding behavior and ecology of shallow-water unstalked crinoids (Echinodermata) in the Caribbean Sea. *Mar. Biol.* 22:105-129.
- MEYER, D. L., and D. B. MACURDA, Jr. 1974. The zoogeography of Caribbean crinoids: A model for paleontological interpretation. *Geol. Soc. Amer. Abstracts with Prog.* 6(7):868.
- . 1980. Ecology and distribution of the shallow-water crinoids of Palau and Guam. *Micronesica* 16:59-99.
- POTTS, F. A. 1915. The fauna associated with the crinoids of a tropical coral reef: with especial reference to its color variations. *Pap. Dept. Mar. Biol. Carnegie Inst. Wash.* 8:71-96 + 1 pl.
- POWELL, V. H., M. D. SUTHERLAND, and J. W. WELLS. 1967. Pigments of marine animals. V. Rubrocomatulid monomethyl ether, an anthraquinoid pigment of the *Comatula* genus of crinoids. *Aust. J. Chem.* 20(3):535-540.
- RUTMAN, J., and L. FISHELSON. 1969. Food composition and feeding behavior of shallow-water crinoids at Eilat (Red Sea). *Mar. Biol.* 3:46-57.
- SMITH, I. R., and M. D. SUTHERLAND. 1971. Pigments of marine animals. XI. Angular naphthopyrones from the crinoid *Comanthus parvicirrus timorensis*. *Aust. J. Chem.* 24:1487-1499.
- SUTHERLAND, M. D., and J. W. WELLS. 1967. Pigments of marine animals. IV. The anthraquinoid pigments of the crinoids,

- Comatula pectinata* L. and *C. cratera* A. H. Clark. Aust. J. Chem. 20(3):515-533.
- WELLS, J. W. 1954. Recent corals of the Marshall Islands: Bikini and nearby atolls. Part 2. Oceanography (Biologic). Geol. Surv. Prof. Papers 260-I:385-486 + pls. 94-185.
- ZMARZLY, D. L., and N. D. HOLLAND. 1981. Rates of food transport down the ambulacral grooves and through the gut of *Comanthus bennetti* (Echinodermata: Crinoidea) observed *in situ*. Mar. Ecol. Prog. Ser. 6(2):229-230.