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The Role of Isopod Crustaceans in the Reef Crest Community at Carrie Bow Cay, Belize

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With 7 figures and 4 tables

Key words: *Isopoda, Crustacea,* coral reef crest ecology, Caribbean.

Abstract. The species composition and numbers of specimens of isopod crustaceans from the rubble of a Belizean reef crest were obtained. Four sets of 30 samples were taken from three rubble zones (rubble with algal turf, rubble between *Thalassia* plants, and pure rubble), in four different collecting periods. Twenty-four species of isopods were identified, sexed and counted. By means of a Likelihood Ratio Chi-square Contingency Table Analysis the presence of 13 species was shown to be positively correlated with habitat, 15 species with season, and nine species with habitat and season combined. From the spread of total numbers and of ovigerous females it is proposed that the isopods may be grouped into three patterns: a) those present and breeding in the reef crest rubble throughout the year, *i. e.* stress-tolerant species; b) those showing a breeding peak in summer and a population decrease in winter-spring, *i. e.* opportunist species; and c) those showing a breeding peak in the fall, and a second peak in spring, and a decrease or complete avoidance of the habitat, especially by ovigerous females, in the summer. The diversity of the Belizean reef crest isopod fauna is compared with the published report of the isopod fauna of a coral reef in Madagascar. Several similarities in composition are noted. The multiplicity of microhabitats is invoked as a possible explanation for the relatively high diversity of anthuridean isopods in coral reefs.

Problem

After several visits to Carrie Bow Cay, Belize, field station for the Smithsonian Institution's IMSWE (Investigations into Marine Shallow Water Ecosystems) project, with the purpose of collecting reef crustaceans for taxonomic studies, it became clear that the shallowest part of the reef system, the intertidal reef crest, was inhabited by an extremely diverse and abundant fauna. Further collecting also indicated that peracaridan crustaceans were a major component of this fauna, with isopods being particularly abundant. Perusal of ecological literature on the Caribbean revealed no in-depth reef crustacean studies.

What few ecological data exist on the isopods are to be found in scattered taxonomic papers (*e. g.* Menzies & Glynn, 1968).

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It was decided to examine this habitat at Carrie Bow Cay more carefully, in an attempt to answer the following basic questions: What specific organisms constitute the fauna of the reef crest (it was soon found to be necessary to restrict the answer to the *Isopoda*, most of the other groups either requiring a taxonomic expertise beyond the author, or being taxonomically too poorly documented to yield anything but superficial results); what are the relative proportions of the isopod species in the reef crest habitat; to what extent is variation in the structure and stability of the substrate of the reef crest reflected in the isopodan fauna; do these isopods exhibit feeding or reproductive adaptations for life in the reef crest; and finally, what is the role of the isopods in the reef crest habitat.

Material and Methods

1. Description of the study area (Figs. 1 and 2)

The area sampled lies at the south-east end of the fringing reef of Carrie Bow Cay (16°48'N, 88°05'W) and is separated from the island by a 70–80 m band of sand and rubble interspersed with *Thalassia* seagrass. The area is part of the shallowest reef crest zone, characterized by RÜTZLER & MACINTYRE (1982) as a rubble and pavement zone. This area would correspond, in PICARD's (1967; p. 5) Tulear reef classification, with his "zone de transfert et dêpot des graviers et sables plus ou moins grossiers (retenue d'eaux epirecifale, platier friable et couloirs de sable coraliens").

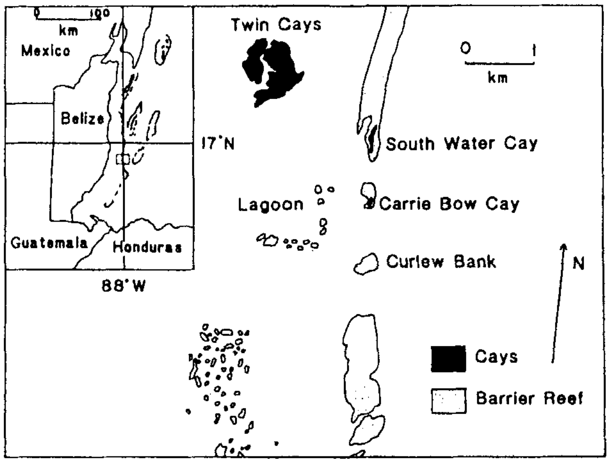

Fig. 1. Location of Carrie Bow Cay, Belize.

Between the *Thalassia* reef flat and the reef crest is a sand channel about 1 m deep, followed by the steeply rising ledge of pavement rock, which at the crest is often exposed at low tide. The pavement rock is overlain by a layer of packed well-sorted rubble, having a maximum depth of 0.3 m. The interstices of the rubble contain very coarse sand, composed mostly of molluscan shell, calcareous algal and echinoderm shell fragments. The rubble of the entire area tends to form a fairly compact 'pavement'. Much of the rubble pieces come from *Acropora palmata* and *A. cervicornis*, and the fragments (usually not more than 10 cm in greatest diameter) of the former come to lie horizontally oriented, while the latter species forms cylindrical fragments seldom more than 10–15 cm in length. The rubble area itself is not uniform, but may be divided into three zones.

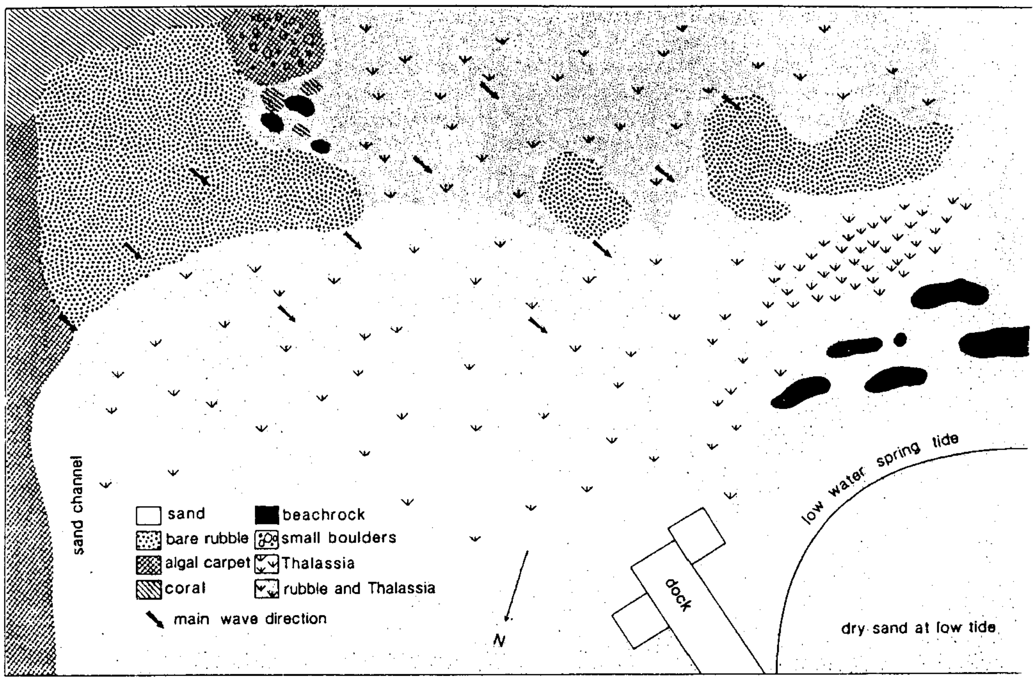

Fig. 2. Semi-diagrammatic plan of study area at Carrie Bow Cay, Belize.

2. Sample sites

1. Pure rubble, *i. e.* not having interspersed *Thalassia* plants. The exposed surfaces of rubble pieces are generally well covered by encrusting coralline algae (*Mesophyllum* sp., *Hydrolithon* sp., and *Neogoniolithon* sp.) and dotted with the red foraminiferan *Homotrema* sp.; this zone is probably the least stable crest rubble area. Occasional clumps of *Halimeda* sp. occur in this area but these were avoided in the sampling, as examination of this alga indicated the presence of larger and different animals than those occurring in the rubble.

2. Rubble pieces almost covered with encrusting coralline algae and *Homotrema*, packed around fairly dense (40–60 plants · m^{-2}) *Thalassia*. The presence of the *Thalassia* probably confers a stability to the rubble, as bare circles from previously sampled areas remain visible for at least six months. With direct observations in the pure rubble area, pieces of rubble were seen to move with wave action, the smallest pieces rolling along the bottom. Rubble movement was never observed in the *Thalassia* area, or in the algal turf area, although undoubtedly, storms would produce major rearrangements and transport in all the areas.

3. Coral rubble with the exposed surfaces and part of the undersides covered by yellow-brown coloured algal turf seldom more than 3 cm in height. This turf is a complex of species including *Laurencia papillosa, Centroceras clavulatum, Gelidium pusillum,* and *Gelidium* sp. The underside of these rubble pieces frequently bear dense clusters of *Homotrema.* The algal turf, often spreading between pieces of rubble also makes the entire area more stable.

3. Treatment of samples

Ten replicates were taken in each of the three rubble areas at low tide. Sets of 30 samples were taken on four separate occasions, *i. e.* at the beginning (March 1980) and end (August 1980) of summer, in the fall (October/November 1981), and in winter (December 1981 / January 1982).

Each replicate consisted of all the rubble within a circle of 25 cm diameter to a depth of 8 cm. An open cylinder of 25 cm diameter and 40 cm length was placed randomly over the rubble, keeping the water inside quiet enough to see and collect. The collected rubble was placed in a bucket, covered with sea water and allowed to stand in sunlight. After one hour, a few drops of 5 % formalin were added and the water swirled around. This procedure was repeated every few hours for a total of 12 hours, with the amount of formalin gradually being increased. The rubble was then vigorously washed in the bucket, large pieces were broken up, and the washings screened through a 1 mm sieve and preserved in 5 % buffered formalin. Microscopic examination of the rubble pieces showed that almost all the animals (with the exception of burrowing sipunculans) were removed by this method, including those cryptic forms in crevices or holes in the rubble.

The displacement volume of each sample was measured after the animals were removed. The rubble remnants were sun-dried and volume measured to the nearest 5 cm^3. The average volume of the samples was 1400 cm^3 (range 1100–1800 cm^3).

Daily consecutive records of 8–16 days of sea temperature over the crest were made with permanently submerged max.-min. thermometers during the four sampling periods (Fig. 3).

The temperature of the rubble exposed at low tide was read directly in all three rubble areas on several occasions during the four sampling periods. These temperatures were always several degrees higher than that of the surrounding sea water, with 40 °C being recorded several times during the August sampling period.

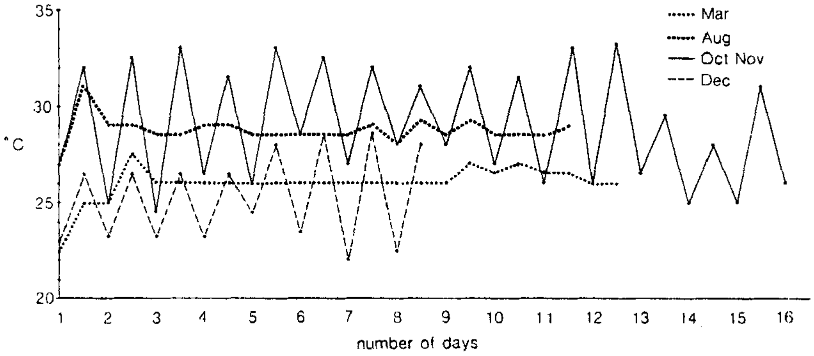

Fig. 3. Daily sea-water temperatures on the reef crest at Carrie Bow Cay, Belize, during four collecting seasons.

Results

Examination of the 120 samples revealed extremely dense concentrations of several of the higher taxa. The majority of organisms were of small size, *i. e.* less than 10 mm total length (with the exception of some polychaetes, sipunculans, and decapod and stomatopod crustaceans). While most samples contained polychaetes, amphipods, isopods, tanaids, harpactacoid copepods, myodocopid ostracods, and nematodes, the following groups were encountered in lesser numbers: *Porifera, Anthozoa, Hydrozoa, Turbellaria, Bryozoa,* gastropod, bivalve, and amphineuran *Mollusca,* podocopid *Ostracoda, Pycnogonida,* marine *Acari,* dipteran larvae, crinoid, ophiuroid, and holothurian *Echinodermata.*

Twenty-four species of isopods were recorded from the reef crest (Table 1). Ten of these were found to have ovigerous females during one or several of the

Table 1. Distribution of twenty-four species of isopods plus unidentified amphipods and tanaidaceans, occurring in the Carrie Bow Cay reef crest. Note – Depth distribution applies only to Carrie Bow Cay. Categories identified only to generic level represent new species to be described in a separate publication.

Taxon	% Presence at 120 stations	Depth (m)
Accalathura crenulata (RICHARDSON)	23	Intertidal - 30
**Accalathura* sp.	22	Intertidal
Apanthura geminsula KENSLEY	51	Intertidal - 1.5
Apanthura sp.	21	Intertidal
Apanthuroides millae MENZIES & GLYNN	18	Intertidal - 30
Belizanthura sp.	10	Intertidal
**Eisothistos* sp.	12	Intertidal
Mesanthura fasciata KENSLEY	58	Intertidal - 24
**Mesanthura paucidens* MENZIES & GLYNN	53	Intertidal - 1.5
Mesanthura pulchra BARNARD	18	Intertidal - 1.5
Mesanthura punctillata KENSLEY	3	Intertidal - 12
Paranthura caribbiensis KENSLEY	2	Intertidal - 1.5
Paranthura infundibulata RICHARDSON	6	Intertidal
**Pendanthura tanaiformis* MENZIES & GLYNN	75	Intertidal
**Excorallana tricornis* (HANSEN)	41	Intertidal - 50
**Cirolana parva* HANSEN	78	Intertidal - 30
**Metacirolana* sp.	41	Intertidal - 15
Gnathia puertoricensis MENZIES & GLYNN	2	Intertidal - 30
Cymodoce sp.	4	Intertidal - 30
**Bagatus algicola* (MILLER)	79	Intertidal - 30
Jaeropsis sp.	2	Intertidal - 15
**Stenetrium minocule* MENZIES & GLYNN	3	Intertidal - 30
Stenetrium sp.	5	Intertidal - 30
**Stenetrium serratum* HANSEN	29	Intertidal - 50
Amphipoda	93	
Tanaidacea	72	

* = ovigerous females present

collecting seasons; as these are the species which remain in the reef crest habitat while the young develop in the brood pouch, they may be regarded as truly well adapted reef crest inhabitants. The remaining fourteen species may be either casual visitors to the habitat, or may move to a different habitat when gravid. Either way, these species may be less well adapted to the habitat.

The number of specimens for each species was plotted by habitat within the crest, against the station number for the four collecting seasons. For several of the species too few specimens were collected to discern any pattern of distribution or allow any comments of meaning. Several species, however, appear to fit into three general patterns, which are discussed further below (Figs. 4–6). The three patterns are: 1. a uniform spread throughout the seasons, with varying numbers within the three habitats. This pattern is exhibited by *Stenetrium serratum, Accalathura crenulata, Pendanthura tanaiformis* (Fig. 4 a), *Cirolana* *parva* (Fig. 4 b), and *Apanthuroides millae;* 2. a marked drop in numbers in all the habitats during the August (summer) collecting season. This pattern is demonstrated by the following species: *Mesanthura fasciata* (Fig. 5 b), *Excoral-*

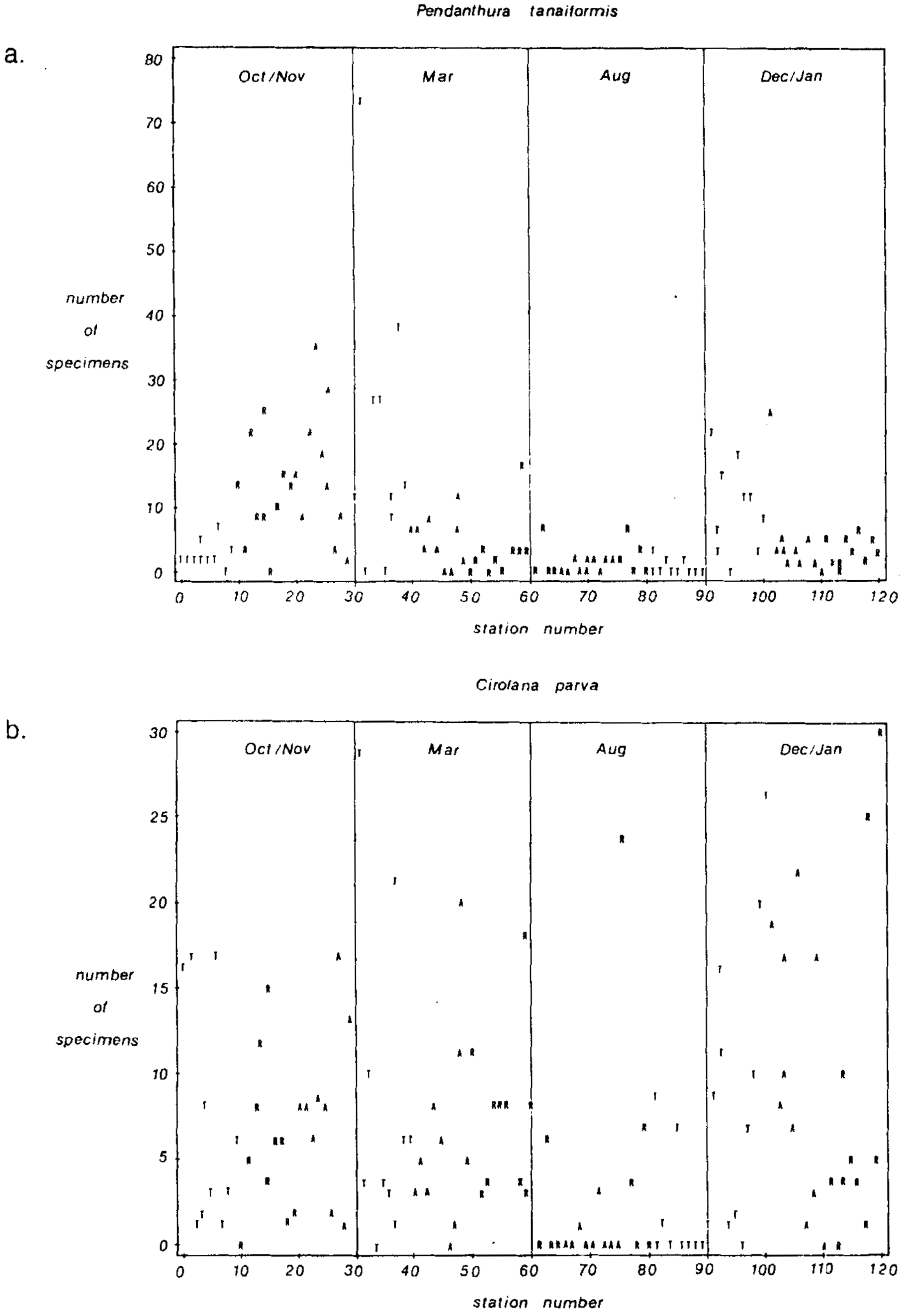

Fig. 4. Numbers of specimens from three rubble zones, during four collecting periods: a. *Pendanthura tanaiformis;* b. *Cirolana parva.* A – algal turf rubble; R – Pure rubble; T – *Thalassia* rubble.

lana tricornis, *Metacirolana* sp., *Mesanthura pulchra*, *Apanthura geminsula* (Fig. 5 a), *Apanthura* sp., *Belizanthura* sp., *Eisothistos* sp.; 3. a marked drop in numbers during the March collecting season, shown in *Bagatus algicola* (Fig. 6 a) and *Accalathura* sp. (Fig. 6 b).

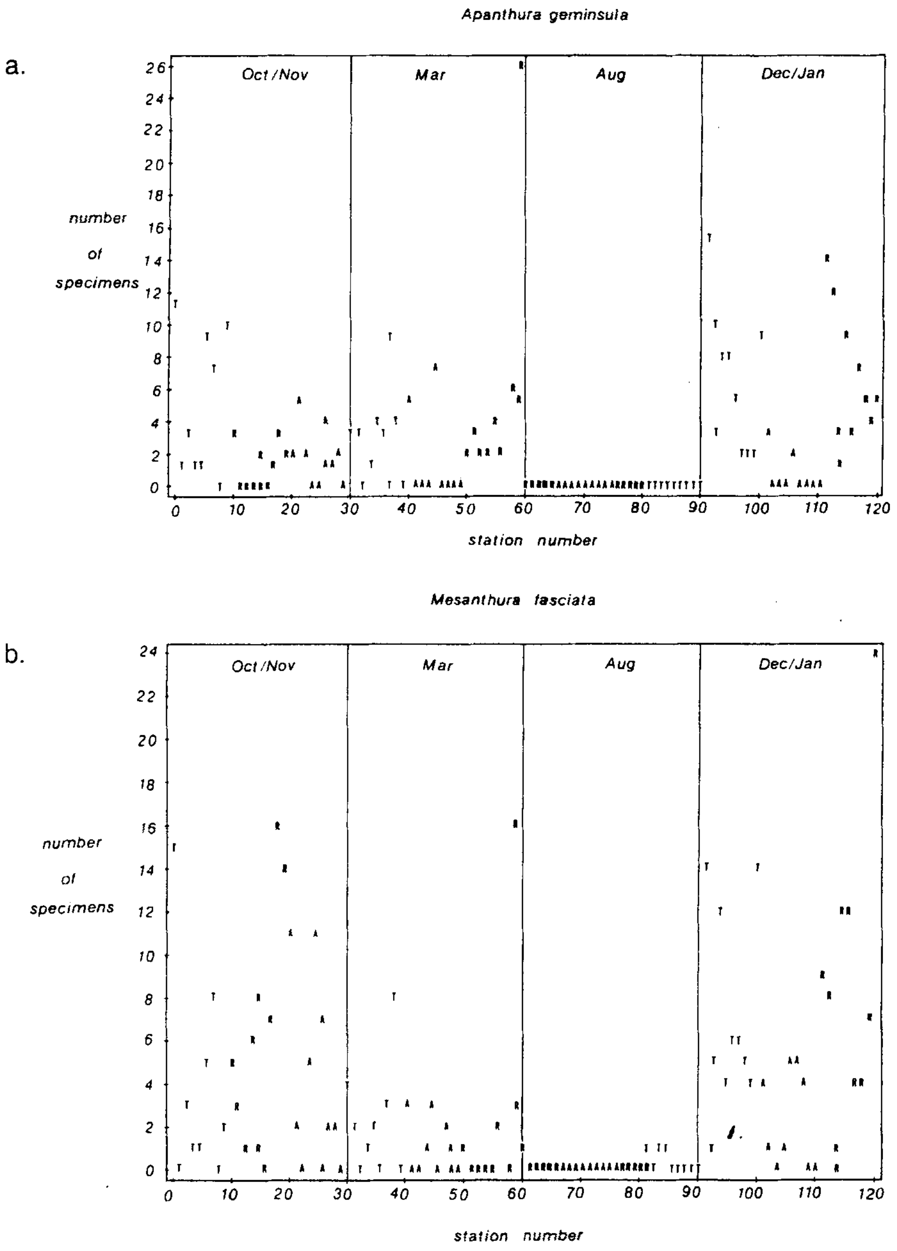

Fig. 5. Numbers of specimens from three rubble zones, during four collecting periods: a. *Apanthura geminsula*; b. *Mesanthura fasciata*. A – algal turf rubble; R – pure rubble; T – *Thalassia* rubble.

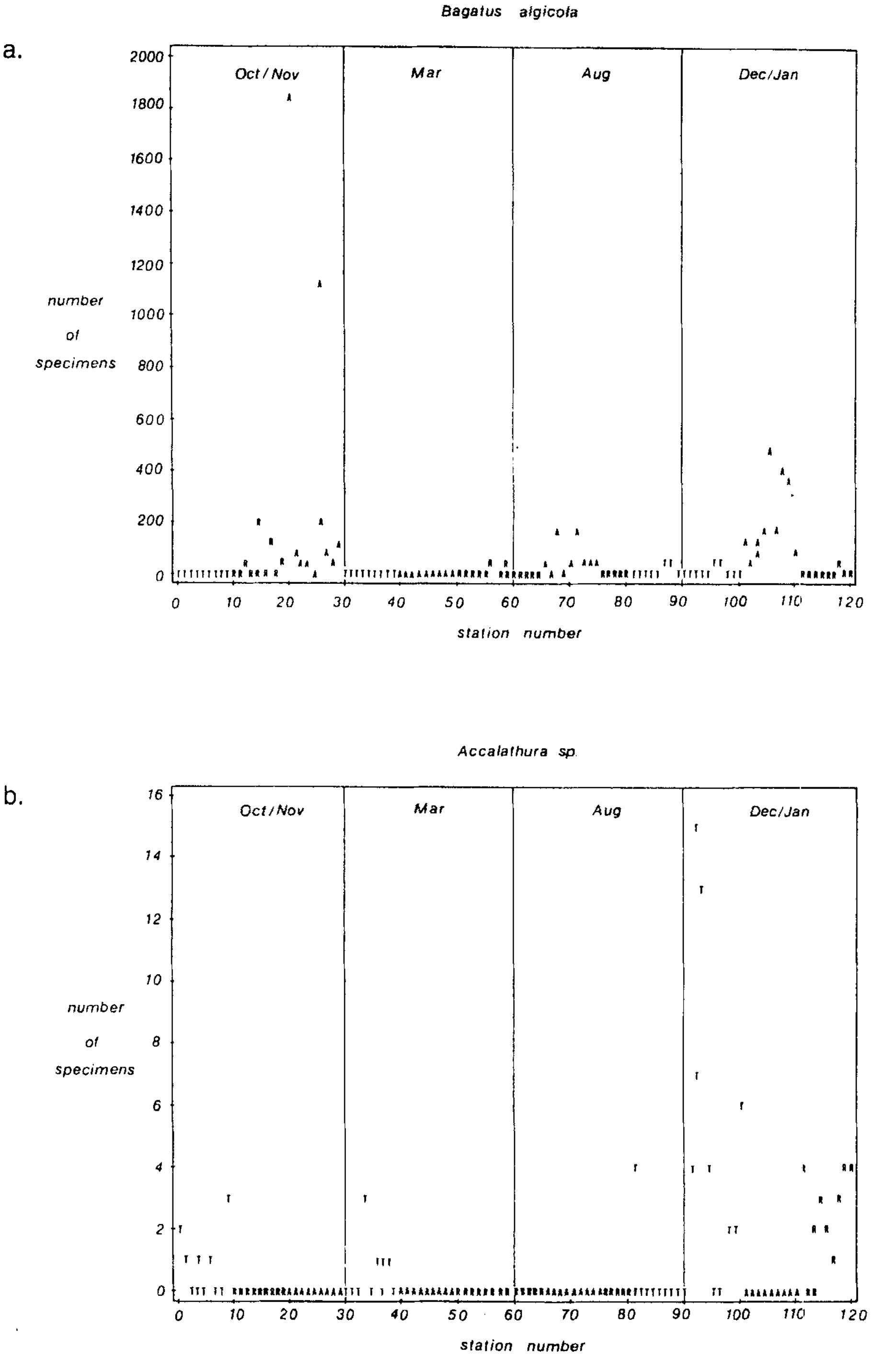

Fig. 6. Numbers of specimens from three rubble zones, during four collecting periods: a. *Bagatus algicola;* b. *Accalathura* sp. A – algal turf rubble; R – Pure rubble; T – *Thalassia* rubble.

From the graphs of these three generalized patterns it is difficult to detect correlations with any of the three rubble distribution patterns by visual examination. However, statistical testing of the correlations between isopod species presence and habitat, species presence and season, and species presence and habitat and season combined, by a Likelihood Ratio Chi-square Contingency Table Analysis (Brown, 1976) (see Table 2) shows that 13 of the 24 species are correlated with habitat type ($p \leq 0.01$), 15 species with season ($p \leq 0.01$), nine species with habitat and season (≤ 0.01), and one species with habitat and season ($p \leq 0.05$). For eight species there are too many absences to test for significance.

Bearing in mind the abovementioned three seasonal distribution patterns, it was decided to examine the three species for which there were sufficient numbers to extract significant information. Feeding and habitat preferences were invoked to explain how these species have solved the problems of living in what appears to be an unstable fluctuating habitat. The three species are an anthuridean *(Pendanthura tanaiformis)*, an asellote *(Bagatus algicola)*, and a flabelliferan *(Cirolana parva)*.

Table 2. Tests of Effect of Habitat (H), Season (S), and Habitat/Season (H/S) for 24 species of reef-crest isopods, using Likelihood Ratio Chi-square Contingency Table Analysis.

Species	Effect			No. of 0 Cells
	H	S	H/S	
Accalathura crenulata	**	**	**	3
Accalathura sp.	**	**	ns	7
Apanthura geminsula	**	**	**	3
Apanthura sp.	ns	**	ns	4
Apanthuroides millae	**	**	ns	4
Belizanthura sp.				8
Eisothistos sp.	**	**	ns	6
Mesanthura fasciata	**	**	**	1
Mesanthura paucidens	**	**	**	0
Mesanthura pulchra	**	**	ns	4
Mesanthura punctillata				10
Paranthura caribbiensis				10
Paranthura infundibulata				9
Pendanthura tanaiformis	**	**	**	0
Excorallana tricornis	**	**	*	3
Cirolana parva	ns	**	**	0
Metacirolana sp.	**	**	**	3
Gnathia puertoricensis				10
Cymodoce sp.				7
Bagatus algicola	**	**	**	0
Jaeropsis sp.				10
Stenetrium minocule				10
Stenetrium sp.	ns	ns	ns	7
Stenetrium serratum	**	**	**	0

** – $p \leq 0.01$
* – ≤ 0.05
ns – not significant

Pendanthura tanaiformis

This squat species of anthurid, has a body about 6.5 times longer than wide. An ovigerous female has a body length of 3.0 mm, the mature male 2.6–2.8 mm. Whether the species is protogynous has not been established. The animal seems incapable of swimming, but has a propensity for crawling into hollows and crevices.

The species was present in 75 % of the 120 samples (see Table 3), with adult males or ovigerous females in 69 % of the samples. From the four seasons of sampling, plus many additional records, the species would seem to breed throughout the year, having eggs or manca in the brood pouch in all months of the year. The highest numbers of specimens were taken in November and March, the highest percentage of ovigerous females (9.4 %) occurring in March, the lowest percentage (2.9 %) in August. The lowest numbers of individuals occurred in rubble in August (the end of summer, with possible heat-stress/desiccation damage being incurred in the algal turf area), in the algal turf in November, and in the *Thalassia* rubble in December and March. The August record, with only 34 specimens from all three zones, would indicate a drop-off in the population at the end of summer. As *Pendanthura* occurs (direct observation) in crevices or burrows of other organisms in the rubble, it would be vulnerable to the combination of high temperatures and desiccation occurring for short periods of exposure at low tide. (Water temperatures over the reef crest in August fluctuated daily between a minimum of 28.5 °C and a maximum of 33.5 °C, with substrate temperatures on exposure at low tide reaching 40 °C). S. LEWIS (personal communication) notes that at the vernal equinox of 1982, the low spring tide left the reef crest exposed for two hours, with a resulting marked

Table 3. Three commonest isopod species in the reef crest, showing distribution of ovigery with month and habitat

Species	Month	Habitat with Highest No. Animals	Total No. Animals	Ovig. ♀ % of Total No. Animals	Ovig. ♀ % of Total No. ♀
Pendanthura tanaiformis	Aug	Rubble	34	2.9	6
	Oct/Nov	Algae	294	5.7	27
	Dec/Jan	*Thalassia*	181	4.4	24
	Mar	*Thalassia*	286	9.4	26
Bagatus algicola	Aug	Algae	1340	8.6	63
	Oct/Nov	Algae	4050	3.2	30
	Dec/Jan	Algae	2237	2.3	14
	Mar	Rubble	118	0	0
Cirolana parva	Aug	Rubble	71	0	0
	Oct/Nov	Algae	207	5.3	68
	Dec/Jan	Algae	294	0.6	40
	Mar	*Thalassia*	213	3.2	70

damage to the algal turf. Possibly, as postulated by SEAPY & LITTLER (1982), this type of unpredictable event could reduce maximal species diversity by exceeding an optimal intermediate level of disturbance. Just what effect this type of event would have on the contained cryptofauna of the algal turf is unknown.

For the remaining three collecting seasons (October/November, December/January, and March), the highest number of individuals were taken once in the algal turf, and twice in the *Thalassia* rubble. The rubble in the *Thalassia* area is almost always encrusted with lavender-pink coralline algae, closely matching the dorsal pigmentation of *Pendanthura*. In these three seasons also, the percentage of ovigerous females was higher (5.7 %, 4.4 %, 9.4 %) than in August.

While no attempt was made to establish protogyny by direct observation and by the finding of an intermediate submale stage, total numbers of males from the three rubble habitats were consistently lower than numbers of females, which is often an indication of protogyny (Table 4).

Table 4. Distribution of sexes in the three rubble habitats

	Total No. Females	Total No. Males	% Male/Female
Thalassia	108	76	70
Algal turf	59	50	84
Pure rubble	54	46	85

In the 39 ovigerous females examined, the number of eggs in the marsupium varied from one to four. The 15 larvigerous females carried 1–3 manca larvae per marsupium (see Fig. 7).

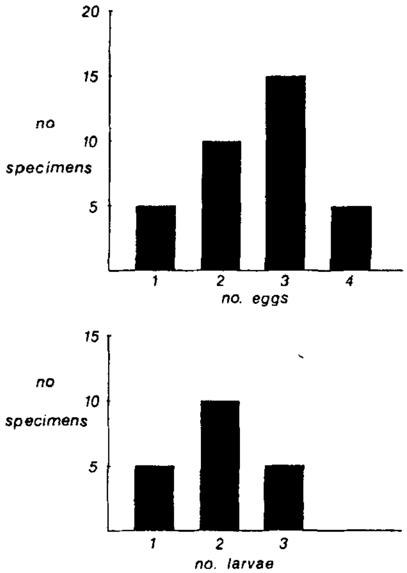

Fig. 7. Number of eggs and manca larvae in marsupia of *Pendanthura tanaiformis*.

Bagatus algicola

A small asellote (total length of ovigerous female 1.8 mm), this species is very abundant, occurring in 78 % of the samples. The species occurs in a wide range of habitats, nearly always associated with some form of vegetation. It occurs on algae (red turfs, corallines, *Halimeda, Turbinaria, Dictyota),* from the reef crest to depths of 40 m, and on the reef flat and in the lagoon on *Thalassia, Syringodium, Amphiroa, Ceramium,* and *Acanthophora.* From Table 3, it would seem to have its peak breeding season in summer, with 63 % of all adult females being ovigerous (8.6 % of the total August sample). The number of eggs per marsupium ranged from 16 to 27 (average for 10 specimens = 21), while the number of larvae per marsupium ranged from 8 to 14. While high numbers of specimens per sample were recorded for October/November, and December/January (4050 and 2237 resp.) the percentage of ovigerous females dropped (3.2 and 2.3 resp.). In August, October/November, and December/January, the highest number of animals occurred in the algal turf rubble. In March, the highest numbers of specimens were recorded from coralline-encrusted rubble, but numbers showed a significant reduction compared with the three other collecting seasons. No ovigerous females were found in March, indicating that perhaps for a short period at the end of winter, the species does not breed. This period would coincide with the vernal equinox and the exposure of large areas of the reef. Examination of the gut of ten specimens showed almost the entire alimentary canal to be packed with fine particulate matter – possibly very fine pieces of sediment and detritus. When kept alive in the laboratory, *Bagatus* was seen to manipulate individual algal fronds with the maxillipeds, perhaps removing adhering bacteria, diatoms, and protozoans.

Cirolana parva

This large (ovigerous female 5.8–6.0 mm total length) actively swimming flabelliferan occurred in 78 % of the 120 samples, and has been found in a variety of habitats, including coarse and fine sediments in the lagoon (both relatively open sand and seagrass sediments), in rubble from the reef flat, and in several species of algae in the spur and groove zone, in depths from the intertidal reef crest to 40 m.

The highest numbers of specimens were found in the coralline encrusted rubble in August, in the algal turf rubble in October/November and December/January, and in *Thalassia* rubble in March. In August, no ovigerous females were found, indicating either that the species does not breed at the end of summer, or that gravid females avoid the physically stressed shallow areas sampled. Ovigerous females were encountered in the remaining three sampling seasons: 5.3 % of the population, with 68 % of females ovigerous in October/November, 0.6 % in December/January, and 3.2 % in March, with 70 % of females ovigerous. Being an active swimmer, the species is capable of avoiding the high shallow-water temperatures of summer, as well as the exposure of very low spring tides. The number of eggs per marsupium ranged from 11–28 (average = 15 for 10 specimens). Examination of gut-contents revealed that the species is probably a carnivore, several specimens containing the remnants of small crustaceans.

Discussion

The fauna of coral reefs has long occupied the attention of biologists, and one of the faunal groupings frequently dealt with is the cryptofauna. What exactly constitutes cryptofauna varies from one investigator to the next. For example, HUTCHINGS & WEATE (1977) regard cryptofauna as the animals living in crevices or burrows inside live or dead coral, while JACKSON & BUSS (1975) write of cryptofauna as living under ledges or plates of coral, *i. e.* hidden communities. The concept of cryptofauna has since become more narrowly defined, and the groupings 'true endocryptolithic' fauna, 'opportunistic cryptolithic' fauna (HUTCHINGS & WEATE, 1979), 'motile' cryptofauna (PEYROT-CLAUSADE, 1980), and 'boring' cryptofauna (HUTCHINGS & WEATE, 1977) have been recognized.

While the associated fauna of the reef crest rubble habitat may be composed of all or several of the above components, in this paper the term cryptofauna is used in the sense of those motile animals sheltering in the rubble, whether in hollows or crevices, under rubble pieces, in abandoned burrows, or in algae or other epibionts associated with the rubble. Thus from the 120 samples taken, all the fauna was kept. However, only the isopod component is dealt with, this artificial taxonomically restricted group being regarded as part of the motile cryptofauna.

By far the greater number of studies on coral reef cryptofauna has been carried out in the Indo-Pacific region, especially Madagascar and Australia. While some cryptofaunal groups have received considerable attention (for example, polychaetes by HUTCHINGS & WEATE, 1977, 1979; sipunculans by RICE & MACINTYRE, 1982) other components have been neglected. General statements, for example CLAUSADE's (1970) recording the presence of motile invertebrates in every 'organic tract' across the coral reef flat, are frequently made. A few of these papers deal with crustaceans. PEYROT-CLAUSADE (1980) investigated several biota at Tulear, Madagascar, including the upper spur platform, reef glacies, boulder tract, gravel tails, compact reef flat, and scattered coral. Not surprisingly, many species were found to be eurytopic, while some were linked to specific microhabitats on the reef. From the use of artificial habitats, PEYROT-CLAUSADE (1980) found that amphipods, isopods, and tanaids form over 50 % of the motile cryptofauna, with isopods being the major group. This would agree with the present study, in which isopods were found to be present in all 120 samples, amphipods in 112 samples, and tanaids in 86. Analysis of the latter two groups could not be attempted, the taxonomy of both being too poorly known.

With regard to the isopods, the most detailed work is that of ROMAN (1970, 1979), a study of the autecology of isopods and tanaids and associated sediments at Tulear. Her observations may be summarized in the following way (taken from ROMAN, 1979; Table 45):

Outer Reef Slope	– up to 36 species (incl. 9 species of anthurids)
External Reef Flat	– up to 30 species (incl. 13 species of anthurids)
Rubble Flat	– up to 21 species (incl. 7 species of anthurids)
Internal Reef Flat	– up to 11 species (incl. 1 anthurid)

While the Indo-West-Pacific crustacean fauna is undoubtedly more diverse than that of the Caribbean (BRIGGS, 1974; p. 13), a similar pattern may be discerned, with 24 species of isopods including 14 species of anthurids, recorded from the Carrie Bow Cay reef flat. ROMAN (1979) sampled several biotopes for peracaridan crustaceans, and while several species were obviously eurytopic, a similarity with the Belize study site can be seen. For example, dealing with the reef crest rubble area at Tulear (23°25′S, 43°42′E), ROMAN found several anthurids including *Mesanthura* species, asellotes, *Paracilicaea, Cirolana, Gnathia,* and *Paranthura* in soft algae; *Gnathia, Paracilicaea, Exosphaeroma, Synidotea, Cilicaea, Eisothistos, Dynamenella, Mesanthura, Dynoides,* asellotes, and tanaids in encrusting coralline algae. At Carrie Bow Cay (16°48′N, 88°05′W), the reef crest algal turf, which included soft as well as calcareous encrusting coralline algae, yielded *Gnathia, Paracerceis, Cirolana, Metacirolana, Mesanthura* spp., several asellotes, *Dynamenella, Exosphaeroma, Eisothistos* (associated with fine serpulid and spirorbid polychaete tubes), *Paranthura, Apanthura,* and *Accalathura.* Valviferans appear to be absent in the Carrie Bow reef habitats.

Given the reservations due to paucity of data resulting from only four sampling seasons, it would seem that the above three species could represent three possible life-modes which illustrate varying degrees of adaptation to the reef crest habitat.

Pendanthura tanaiformis breeds throughout the year, with a drop in summer and a peak in the spring. This species would correspond with VERMEIJ's category 'stress tolerant' (VERMEIJ, 1978; p. 182), being both able to withstand physiological stress and a relatively slow reproducer.

Bagatus algicola shows a breeding peak in summer, a complete drop-off in winter-spring. Given the high reproductive rate and probable short life-span, this species might be regarded as an 'opportunist' (VERMEIJ, 1978). *Bagatus algicola,* however, does not have high dispersibility, lacking as it does a planktonic stage, and judging from its broad depth distribution, does not have the reduced long-term competitive ability characteristic of opportunists.

Cirolana parva shows a breeding peak in the fall, with a possible drop in the winter, a second peak in spring, and a complete drop-off or avoidance of the habitat by gravid females in the summer.

The high percentage (58 %) of anthurideans in the Belize reef crest isopod fauna deserves further examination (see KENSLEY, 1982, for Belize anthuridean taxonomy). While many isopod infraorders appear to reach their maximum diversity either in temperate oceans (for example, the sphaeromatid *Flabellifera,* HURLEY & JANSEN, 1977) or in the deep oceans (for example, the ilyarachnid and eurycopid *Asellota,* WILSON & HESSLER, 1981), the anthurideans appear to be especially well represented in tropical areas, with coral reefs having the highest percentage of species. (KENSLEY, unpublished data, has 20 species of anthurideans from a single reef in Belize). This high diversity may be a function of collecting effort, as careful sampling of discrete habitats has seldom been carried out. Nevertheless, ROMAN (1979) has recorded 31 species of anthurideans from reefs and associated habitats at Tulear. Why this group of isopods should be so well represented is difficult to explain. Possibly the slender cylindrical body characteristic of all members of the group is especially well adapted to the multiplicity of nooks and crannies found in coral reefs. Until more is known of the modes of feeding and reproduction of this group, and thereby giving greater insight into their ecological role, further speculation would be fruitless. While members of the *Anthuridae* generally possess unspecialized mouthparts, which could conceivably allow generalized detritus/omnivorous feeding, some species display considerable specialization. *Apanthuroides millae,* for example, has a finely ridged spiciform molar in one mandible and lacks a molar on the opposing mandible. *Eisothistos* spp. have been observed to prey on tiny serpulid polychaetes in the reef crest habitat (see WÄGELE, 1979; KENSLEY, personal observation). Of the *Paranthuridae,* with their elongate mouthparts apparently adapted for piercing, little has been reported on feeding. WÄGELE (1982) records two Mediterranean species of *Paranthura* feeding on small arthropods including amphipods, tanaids, and dipteran larvae. A similar lack of knowledge exists for the *Hyssuridae,* represented by *Belizanthura* sp. in the Belize study.

Summary

Examination of the rubble-inhabiting isopod crustacean cryptofauna from a Belizean reef crest reveals that of the 24 species found, 13 species show a positive correlation with the habitat (either pure rubble, rubble interspersed with *Thalassia* plants, or rubble with algal turf), 15 species show a positive correlation with season, and nine species show a positive correlation with habitat and season combined. These correlations were demonstrated by a Likelihood Ratio Chi-square Contingency Table Analysis.

Three patterns of distribution were demonstrated amongst these isopods. One group, best illustrated by *Pendanthura tanaiformis,* appears to be fairly evenly present in the rubble habitat throughout the year. These species breed throughout the year, but show a drop in the number of ovigerous females in summer, and are considered well adapted to the environmentally fluctuating reef crest habitat. A second group, illustrated by *Apanthura geminsula* and *Mesanthura fasciata,* shows a marked drop in numbers during the summer, in all rubble habitats. It is possible that in these species, the ovigerous females somehow avoid the harsh summer conditions in the reef crest. The third group, best illustrated by *Bagatus algicola,* shows a marked drop in numbers at the end of winter, and a breeding peak in summer.

There is no obvious explanation for the high diversity of the anthuridean species found in the samples, although it can be assumed that diversity is promoted by the multitude of cryptic microhabitats available in the reef.

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