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Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. I. Agile shrimps

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ABSTRACT: In a 4 yr study, the agile shrimp fauna associated with live and dead *Pocillopora verrucosa* was sampled systematically from isolated coral heads placed at leeward and windward zones of 1 inner shelf reef, 3 mid-shelf reefs and 1 outer shelf reef in the central region of the Great Barrier Reef. A total of 165 pairs of live coral heads and 720 pairs of dead coral heads were sampled. There were pronounced cross-shelf patterns in species abundances and distributions and consistent patterns of habitat association. Live and dead corals from each of the mid-shelf reefs yielded significantly greater numbers of agile shrimps than similar sized corals from the inner shelf reef or the outer shelf reef. On all reefs the shrimp fauna on live corals was dominated by a single species. However, there was regional variation in the response of live coral associates to disturbance. By contrast, the shrimp fauna associated with dead corals showed a more even distribution of individuals among species and a more regular pattern of regional species replenishment. The dead coral fauna from the inner shelf reef was distinctly different from that found on the other reefs. Within reefs, differences in exposure of sites generally had little effect on species composition or abundance. Abiotic and biotic factors that may sustain the observed cross-shelf patterns in species abundances and distributions are discussed.

INTRODUCTION

Ecological studies of the fauna on tropical coral reefs have focussed on the larger, more conspicuous organisms such as frame-building corals and fishes. Most coral reefs, however, support a rich fauna of smaller organisms which may be equally important in the functioning of these ecosystems (McCloskey 1970, Patton 1976, Austin et al. 1980). One group, the benthic Crustacea, is particularly abundant in most coral habitats and may comprise the most abundant associates of living coral (Patton 1974, Abele & Patton 1976, Austin et al. 1980, Black & Prince 1983). These associations range from obligate dependancy in which the crustaceans obtain food from coral mucus (Knudsen 1967, Patton 1974) to facultative arrangements in detritivorous species where the coral host is one of a range of habitats providing temporary shelter (Patton 1974, Bruce 1976a, Coles 1980). Despite their small size, benthic crustaceans may transform substantial amounts of energy from detrital sources to higher trophic levels such as the reef fishes (Hiatt & Strasburg 1960, Randall 1967). However, our quantitative understanding of these communities is poor.

Most previous ecological studies of benthic reef crustaceans have been restricted to examining the decapod macrofauna found on randomly collected live corals (e.g. Patton 1974, Abele & Patton 1976) with few studies conducted on other habitats within the general reef environment (e.g. Coles 1980). Collections from live corals have shown that the species composition of the decapod community responds to the size of the host coral (Abele & Patton 1976, Austin et al. 1980), the habitat of the coral (Abele 1976, Edwards & Emberton 1980, Kropp & Birkeland 1981, Black & Prince 1983, Gotelli & Abele 1983) and behavioural interactions among species (Lassig 1977). Defaunated living corals are rapidly colonised by juvenile and small adult decapod associates (Abele 1984). The death of host corals results in a shift from a predominance of relatively large symbiotic species to minute, facultatively associated non-symbionts (Coles 1980). Although these

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studies have revealed local and regional variations in species composition and relative abundance, there have been few attempts to quantify distributions, abundances and species replenishment systematically at any scale.

The present study was the result of the incidental collection of benthic crustaceans during a 4 yr project studying the recruitment of juvenile coral reef fishes (Doherty unpubl.). In this study isolated heads of *Pocillopora verrucosa* coral, both living and dead, were used as recruitment traps for settling reef fishes. A large number of these coral isolates were positioned on reefs across a transect spanning the width of the continental shelf in the central region of the Great Barrier Reef. At regular intervals these corals were brought to the surface and washed to remove fishes, resulting also in the systematic collections of the crustacean associates. Subsequent destructive sampling of the corals showed that the washing had effectively removed almost all the crustacean microfauna and agile shrimps (as defined by Patton 1974) but very few of the resident crabs, alpheids and stomatopods. This paper is one of 2 describing the spatial and temporal patterns in the community structure and relative abundance of the former groups. This paper focuses on the agile shrimps; the second on the microfauna (Preston & Doherty unpubl.). A third paper based on the destructive sampling will examine the cross-shelf distribution and relative abundance of the sedentary macrofauna (Preston et al. unpubl.).

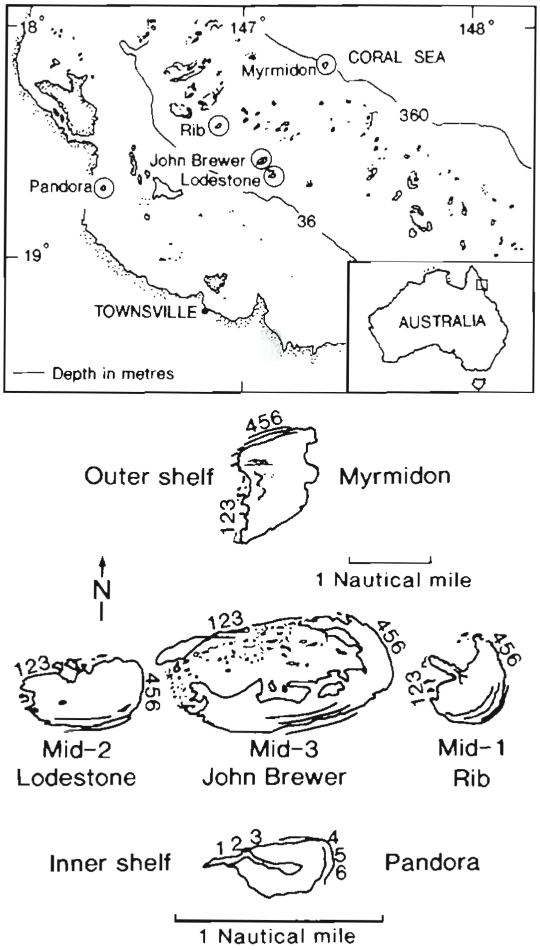

Fig. 1. Location of reefs and collection sites. Sites 1, 2 and 3: leeward (back reef); Sites 4, 5 and 6: windward (front reef). Lower scale bar refers to Pandora reef only

MATERIALS AND METHODS

Sampling procedures. During 1982, 240 heads of *Pocillopora verrucosa* were placed on 5 coral reefs spanning the width of the continental shelf off Townsville, Australia (Fig. 1). On each of the 5 coral reefs, there were 6 major sampling sites: 3 sites on the back reef (leeward) and 3 sites on the front reef (windward). Adjacent sites within each exposure were separated by at least 100 m. Within each site, there were 4 pairs of corals. Adjacent pairs were separated by 5 to 10 m, and individual coral isolates within pairs were separated by 1 m. All corals were deployed on star pickets driven into the sand about 5 m beyond the edge of the outer reef slope in depths of 8 to 12 m.

Of the 4 pairs of corals constituting each site, 3 pairs were made of dead coral and 1 of living coral. All coral units were as similar as possible in size and other characteristics, with an approximate volume of 15 000 cm^3. All were made of coral collected from a single locality in the mid-shelf and transplanted to the other reefs.

The fish and crustacean fauna associated with these corals were collected by placing a cage and plankton net over the coral head. The cage consisted of a wooden top and bottom joined with metal bars to form a cylinder. The cage was hinged so that it completely enclosed the coral head and base with minimum disturbance. The plankton net had a mesh size of 250 µm and surrounded the cage during transport to the surface. At the surface the netted corals were washed vigorously with a stream of water from an electric bilge pump and the dislodged fauna was collected in the cod-end of the net. Live corals were replaced at the same site but not on the same stakes. Dead corals were returned to the ship and replaced with others in order to prevent the accumulation of fouling algae. Recently washed dead corals were kept in the sun for at least 48 h before being swapped with dead corals collected from the next reef.

All the crustaceans washed off the corals were preserved in 10 % buffered formalin. In the laboratory, adult and juvenile shrimps were sorted to species.

Specimens smaller than the smallest male with well-developed appendix masculina or the smallest egg-bearing female of a species were recorded as juveniles.

The sampling strategy for collecting agile shrimps varied according to time available during the fish study A summary of the sampling scheme is given in Table 1. In the first summer, the 240 stations were each sampled 3 times; December 1982, January 1983 and February 1983. In December, separate collections of crustaceans were taken from live and dead corals but samples were pooled into single collections for each substrate representing leeward (back reef) and windward (front reef) exposures on each reef. Subsequently, crustaceans collected from coral isolates in the first summer were pooled into live coral and dead coral samples representing individual sites.

A full complement of live corals was maintained during the first summer. At the end of this summer, these corals were left in position while the dead corals were removed to prevent algal fouling. By the start of the second summer (December 1983), some live corals had been killed by *Acanthaster planci* on most reefs. Consequently, the surviving live corals were transplanted to make a full complement on the back reef sites and sampling of live corals on the front reef sites was abandoned. Crustaceans collected from live corals in 1983/84 were pooled into single monthly collections. Dead corals were re-established on both sides of the reef and a full complement of these corals was sampled on the 5 reefs during the second summer. Crustaceans collected from dead corals in 1983/84 were pooled within sites each month.

At the end of the second summer, all corals were left in position. These corals were then sampled twice more: once in February 1985 and once in February 1986. In both these surveys, crustaceans taken from individual coral heads were maintained separately with no pooling.

To determine the extent to which cleared corals were recolonised immediately after clearance, 3 pairs of live corals from each reef (except John Brewer) were resampled after 24 h of immersion. A similar survey was carried out on dead corals but only on the 3 mid-shelf reefs. This experiment was done once in February 1986. After the final survey, subsets of dead corals (12 pairs from each reef) and all live corals were removed to the ship and sampled destructively to collect Crustacea not dislodged by the washing technique.

Data analysis. Because of the variable numbers of live corals and the pooling procedures, tests for significant variation in the abundance of shrimps among reefs, within reefs and through time could only be done for samples from live corals collected in January and February 1983. The same analysis was feasible for dead corals based on samples collected in January and February 1983 and 1984. Spatial variation in numbers of shrimps was examined in relation to 2 factors: reefs and zones (back reef and front reef). These factors were considered as fixed and analysed by ANOVA (Underwood 1981). The temporal stability of abundance patterns was also analysed by ANOVA. Cochran's test was used to determine the homogeneity of variances in such analyses. Where significant interaction terms were detected, further analysis was done using the Student-Newman-Keuls (SNK) procedure (Winer 1971).

Table 1. Summary of the number of corals sampled on each reef and the pooling procedures used. Each exposure (back reef and front reef) had 3 sites, with a total of 3 pairs of dead (D) and 1 pair of live (L) corals per site. After February 1983 there were no live corals from front reef sites (*). Boxes enclosing corals within arrays denote pooling (no pooling in 1985 and 1986)

Date	Back reef sites	Coral array		Front reef sites	Coral array	
Dec 1982	1	DD DD DD	LL	4	DD DD DD	LL
	2	DD DD DD	LL	5	DD DD DD	LL
	3	DD DD DD	LL	6	DD DD DD	LL
Jan 1983, Feb 1983	1	DD DD DD	LL	4	DD DD DD	LL
	2	DD DD DD	LL	5	DD DD DD	LL
	3	DD DD DD	LL	6	DD DD DD	LL
Dec 1983, Jan 1984, Feb 1984	1	DD DD DD	LL	4	DD DD DD	*
	2	DD DD DD	LL	5	DD DD DD	*
	3	DD DD DD	LL	6	DD DD DD	*
Feb 1985, Feb 1986	1	DD DD DD	LL	4	DD DD DD	*
	2	DD DD DD	LL	5	DD DD DD	*
	3	DD DD DD	LL	6	DD DD DD	*

The stability of species composition was examined by estimating dissimilarity coefficients (Bray & Curtis 1957) among reefs for each monthly collection.

RESULTS

On completion of the project, destructive sampling of live corals, after vigorous washing, yielded 4 adult and 12 juvenile agile shrimps representing less than 1 % of the total yield from 24 corals. Destructive sampling of 24 dead corals also yielded less than 1 % of the total yield. Thus the technique provided an effective method for obtaining systematic quantitative comparisons of the distribution and abundance of agile shrimps from standard sized units of habitat.

Spatial patterns in distribution, abundance and diversity

The total collection from live corals (270 corals) sampled in the first 2 summers yielded 6467 adults and 21 species. Dead corals (1080 corals) yielded 25 324 adults and 28 species. The identification of juveniles was restricted to relatively few common species (*Periclimenes amymone, P. toloensis, Thor paschalis* and *Chlorocurtis jactans*) and was based on definitive characters in each species.

The species collected from live and dead corals are listed in Tables 2 and 3 together with their relative abundances on back and front reef sites within each reef. The species lists are arranged to emphasise the cross-shelf pattern of distribution. Although sampling

Table 2. List of species collected from live *Pocillopora verrucosa* coral heads from 5 reefs in the central region of the Great Barrier Reef during summers of 1982/83 and 1983/84. Cross-shelf distribution of each species is shown as a percentage of the total number of shrimps from leeward (back) and windward (front) sites within each reef. Front reef sites were not sampled in 1983/84

	Inner-shelf				Mid shelf				Outer shelf	
	(Pandora)		Mid 1 (Rib)		Mid 2 (Lodestone)		Mid 3 (Brewer)		(Myrmidon)	
	Back	Front	Back	Front	Back	Front	Back	Front	Back	Front
HIPPOLYTIDAE										
Thor paschalis	6.9	7.6	9.3	3.6	3.3	4.2	4.9	10.0	9.9	7.3
Thor amboinensis	2.9	–	0.1	–	0.2	–	0.4	–	–	–
Latreutes mucronatus	1.0	0.7	–	–	0.1	–	–	–	–	–
Saron marmoratus	–	–	0.2	0.2	0.1	0.3	0.7	0.3	1.7	2.4
Hippolysmata vittata	–	–	–	–	0.05	–	–	–	–	–
Hippolyte ventricosus	–	–	0.1	5.8	–	–	–	–	–	–
Phycocaris simulans	–	–	0.2	–	–	–	0.3	0.5	–	–
PANDALIDAE										
Chlorocurtis jactans	–	–	6.6	4.5	4.5	10.5	5.4	14.6	6.1	9.7
Chlorotocella gracilis	–	–	0.2	–	0.1	–	–	–	–	–
PALAEMONIDAE										
Periclimenes amymone *	65.1	57.6	82.1	85.0	90.3	79.9	80.7	69.5	60.6	68.3
Palaemonella rotumana	3.6	1.5	0.3	0.5	0.5	–	0.7	–	–	–
Harpiliopsis depressa *	1.1	1.5	–	–	0.05	0.3	0.3	–	6.2	4.9
Periclimenes elegans	1.8	–	0.05	–	–	–	0.05	0.3	–	–
Periclimenes longirostris	–	–	0.05	0.2	0.1	0.3	0.9	–	5.0	2.4
Periclimenes madreporae *	–	–	0.5	–	0.6	4.5	1.2	2.4	8.4	4.9
Periclimenes seychellensis	–	–	–	0.2	–	–	0.6	0.5	2.1	–
Periclimenes spiniferus	–	–	0.1	0.1	–	–	2.9	1.1	–	–
Periclimenes holthuisi	–	–	0.2	–	–	–	–	–	–	–
Periclimenes andamanensis	11.9	18.9	–	–	–	–	–	–	–	–
Periclimenes toloensis	4.8	12.1	–	–	–	–	–	–	–	–
PROCESSIDAE										
Processa australiensis	0.8	–	–	–	–	–	1.0	0.8	–	–
No. of corals sampled	36	18	36	18	36	18	36	18	36	18
No. of shrimps ×100	2.1	1.3	19.5	4.5	15.7	3.5	11.9	3.7	1.6	0.8
Mean no. per coral	6	7	54	25	44	19	33	21	4	4
Total species	10	7	14	8	12	7	14	10	8	7

* Live coral specialists (Bruce 1983)

effort was not equal for live and dead corals, values for the mean number of individuals per coral head, estimated from pooled samples, provides a comparison of relative abundance on these different substrates.

Live corals

Overall, live corals from the mid-shelf reefs yielded more species and greater numbers of individuals than either the inner shelf reef or the outer shelf reef (Table 2). On all reefs the palaemonid *Periclimenes amymone*, was the dominant species contributing between 58 and 90 % of the total number of individuals. This species is common on live acroporid and pocilloporid corals (Bruce 1983) and is thought to feed on coral mucus (Patton 1976). Only 2 of the other 20 species collected from live corals are thought to be live coral specialists (Bruce 1983).

Table 3. List of species collected from dead *Pocillopora verrucosa* coral heads from 5 reefs in the central region of the Great Barrier Reef during summer of 1982/83 and 1983/84. Cross-shelf distribution of each species is shown as a percentage of the total number of shrimps from leeward (back) or windward (front) sites within each reef

	Inner-shelf		Mid shelf						Outer shelf	
	(Pandora)		Mid 1 (Rib)		Mid 2 (Lodestone)		Mid 3 (Brewer)		(Myrmidon)	
	Back	Front	Back	Front	Back	Front	Back	Front	Back	Front
HIPPOLYTIDAE										
Thor paschalis	25.8	25.6	48.1	42.8	42.3	46.4	44.8	35.3	18.8	11.6
Phycocaris simulans	1.1	0.05	0.3	0.2	0.6	0.9	0.3	0.6	2.5	1.6
Hippolyte varians	0.9	0.6	0.7	0.4	0.3	0.9	–	–	0.3	10.6
Latreutes mucronatus	13.3	3.2	0.05	–	0.05	–	–	–	–	0.2
Saron marmoratus	–	0.05	0.6	0.4	0.8	0.2	0.3	0.5	6.8	12.8
Hippolysmata vittata	–	–	–	–	–	–	–	–	0.1	–
Thor amboinensis	–	–	–	–	–	–	–	0.05	–	–
Thor maldivensis	–	–	–	–	–	–	–	–	–	1.5
PANDALIDAE										
Chlorocurtis jactans	–	–	25.6	47.2	31.0	40.4	30.6	49.2	55.2	49.7
Chlorotocella gracilis	7.4	1.3	0.3	0.1	0.2	0.4	0.1	0.3	0.3	–
PALAEMONIDAE										
Palaemonella rotumana	12.8	2.4	0.7	0.5	1.4	0.4	0.2	0.4	0.4	0.1
Periclimenes amymone•	1.2	1.7	0.3	0.3	1.1	0.2	1.4	1.0	0.3	0.1
Periclimenes elegans	2.1	0.9	0.4	0.2	0.6	0.4	0.2	0.1	0.5	0.7
Periclimenes spiniferus•	0.2	0.4	5.7	1.9	1.1	–	3.4	0.3	0.3	–
Periclimenes seychellensis•	0.2	–	3.0	0.7	3.8	2.3	1.5	0.8	1.7	0.5
Periclimenes andamanensis	16.8	10.3	0.2	–	–	–	0.05	0.1	–	–
Periclimenes longirostris	–	–	11.2	3.4	15.5	6.4	6.9	6.3	11.3	9.7
Periclimenes suvadivensis	–	–	0.8	0.6	0.5	0.5	1.0	0.2	0.1	–
Periclimenes madreporae•	–	–	0.2	1.1	0.2	0.5	7.9	4.4	0.3	0.5
Harpiliopsis depressa•	–	–	–	–	–	–	0.5	0.05	1.0	0.4
Periclimenes holthuisi	–	–	1.5	0.05	–	–	–	–	–	–
Periclimenes grandis	–	–	–	0.1	–	–	–	–	–	–
Periclimenes toloensis	16.4	53.0	–	–	–	–	–	–	–	–
Palaemonella spinulata	0.7	0.2	–	–	–	–	–	–	–	–
Thaumatocaris streptopus	0.4	–	–	–	–	–	–	–	–	–
Philocheras sp.	0.3	–	–	–	–	–	–	–	–	–
SICYONIIDAE										
Sicyonia sp.	–	–	–	–	0.4	–	–	–	–	–
PROCESSIDAE										
Processa australiensis	0.4	0.2	0.3	0.1	0.1	20.05	0.8	0.3	0.1	–
No. of corals sampled	108	108	108	108	108	108	108	108	108	108
No. of shrimps ×100	4.6	16.5	49.3	33.5	32.3	37.7	35.5	30.4	6.5	7.2
Mean no. per coral	4	15	46	31	30	35	33	28	6	7
Total species	16	14	19	18	16	14	16	17	16	14

• Species known to occur in seagrass beds (Ledoyer 1968, 1984)

Analysis of variance of the spatial pattern in abundance demonstrated significantly greater numbers of total adults and both adult and juvenile *Periclimenes amymone* on the mid-shelf reefs than on the inner or outer shelf reefs (Table 4). Analysis of the temporal pattern in abundance showed that there was significant within-reef variation in monthly abundance which was not consistent among reefs (Table 4, Fig. 2). Back reef sites on the mid-shelf reefs consistently yielded significantly greater numbers of total adults than front reef sites but no significant differences were detected between zones on the inner or outer shelf reefs. Back reef sites on 2 of the mid-shelf reefs yielded significantly greater total numbers of adult *P. amymone* than front reef sites. However, analysis of the monthly abundances of adult *P. amymone* in January and February 1983 showed no significant differences between zones. In January 1983 back reef sites on Rib Reef yielded significantly greater numbers of juvenile *P. amymone* than any other sites (SNK tests). Otherwise there was no consistent cross-shelf pattern in the abundance of juveniles among reefs or within zones (Fig. 2). Although pooling of samples collected in 1984 precluded analysis, mean monthly abundances showed a more consistent cross-shelf pattern with greater numbers of both adults and juveniles on the mid-shelf reefs.

Dead corals

On dead corals, the pattern of total abundance among localities was similar to that on live corals, with mid-shelf reefs yielding more species and greater numbers of individuals than the inner shelf reef or the outer shelf reef (Table 3). At all locations there were 2 or 3 dominant species which collectively contributed between 75 and 87 % of the total number of individuals. Many of the species found on dead coral were also found on live coral and 9 of the more common species found on dead coral are known to occur also in seagrass beds (Ledoyer 1968, 1984).

A summary of the patterns of distribution of the 8 most abundant species found on live or dead corals shows that the degree of habitat association varied among species but was generally consistent across locations (Fig. 3). The hippolytid *Thor paschalis* was common at all locations and always more abundant on dead corals. The palaemonid *Palaemonella rotumana* had a more restricted distribution but was more evenly distributed among live and dead corals. Both species have previously been found on live *Pocillopora*

Table 4. Summary of analyses of variance in the number of total adult shrimps and *Periclimenes amymone* adults and juveniles collected from 6 pairs of live *Pocillopora verrucosa* coral heads in each zone (windward and leeward) of 5 reefs in the central region of the Great Barrier Reef in January and February 1983

Source of variation	Degrees of freedom of F-ratio	Taxon Total adults	*P. amymone* Adults	*P. amymone* Juveniles
Spatial pattern				
Reefs	4,50	***	***	***
Zones	1,50	*	***	***
Reefs × Zones	4,50	NS	**	**
Temporal pattern				
Reefs (R)	4,4	*	***	NS
Zones (Z)	4,1	*	NS	NS
Months (M)	1,40	***	*	*
R × Z	4,4	NS	NS	*
R × M	4,40	***	NS	***
Z × M	1,40	NS	NS	NS
R × Z × M	4,40	NS	NS	NS

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS: not significant

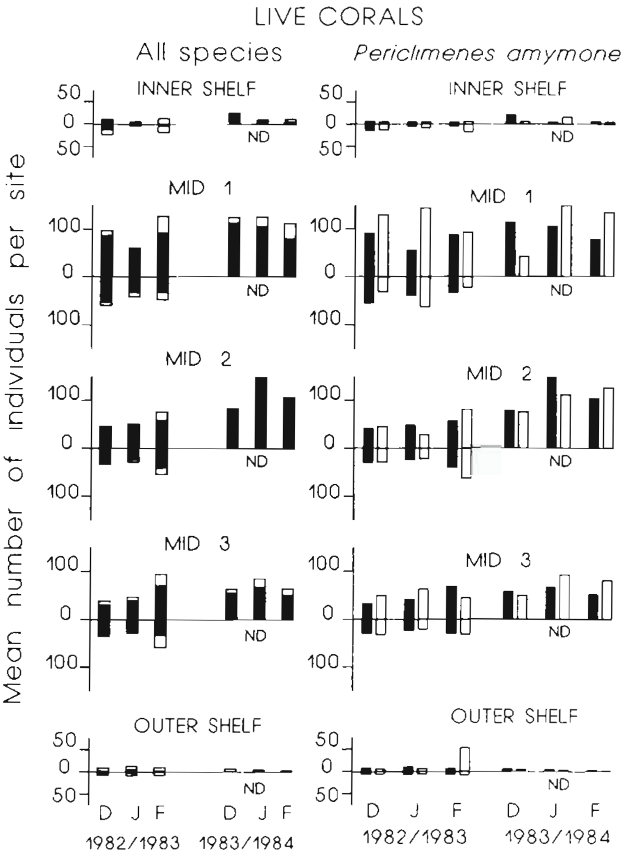

Fig. 2. Cross-shelf pattern in mean monthly abundance of shrimps collected from 3 pairs of live *Pocillopora verrucosa* coral in back reef (upper bars) and front reef (lower bars) zones of 5 reefs in 1982/83 and 1983/84. For total adults unshaded portion shows proportion of live coral specialists. For *Periclimenes amymone* shaded bars show adults, unshaded bars show juveniles. ND: no data

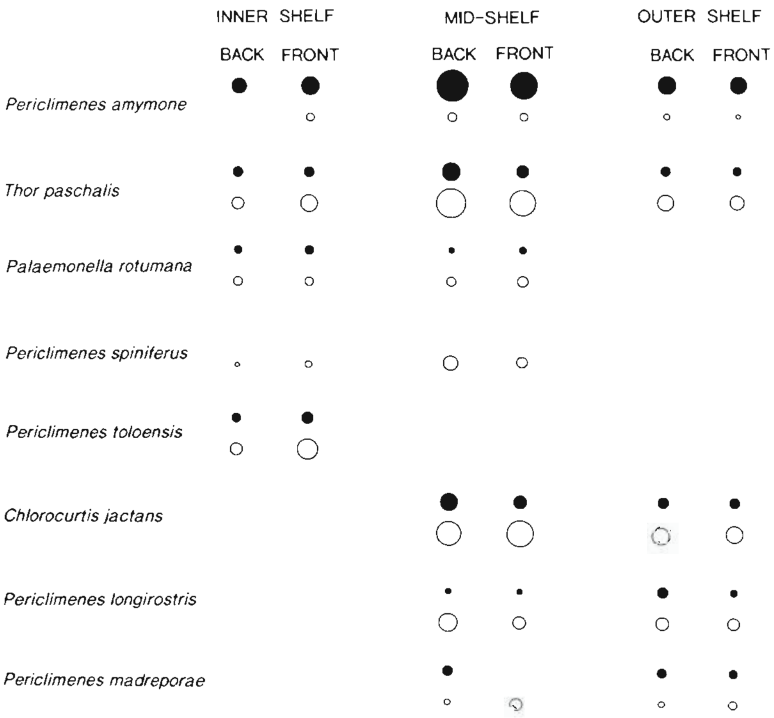

Fig. 3. Summary of the distribution of the 8 most common species of agile shrimps collected during summer 1982/83. Area of each circle is proportional to mean abundance per pair of live corals (filled circles) or dead corals (open circles)

damicornis (Black & Prince 1983) and in other habitats (Bruce 1976b). All other species that were common on dead corals showed pronounced variation in abundance among localities. For example the pandalid *Chlorocurtis jactans* was absent from the inner shelf reef but abundant on all other reefs. The palaemonid *Periclimenes toloensis* which was restricted to the inner shelf reef, has previously only been recorded on the Great Barrier Reef in association with a hydroid (Bruce 1983).

Table 5. Summary of analyses of variance in abundance of total adult shrimps and adults and juveniles of *Thor paschalis, Chlorocurtis jactans* and *Periclimenes toloensis* on 9 pairs of dead *Pocillopora verrucosa* coral heads in each zone (leeward and windward) of 5 reefs in the central region of the Great Barrier Reef in January and February 1983 and 1984

Source of variation	Degrees of freedom of F-ratio	Total adults	*T paschalis* Adults	*T paschalis* Juv.	df	Taxon *C. jactans* Adults	*C. jactans* Juv.	df	*P. toloensis* Adults	*P. toloensis* Juv.
Spatial pattern										
Reefs	4,110	•••	•••	••	3,88	•••	•••	–	–	–
Zones	1,110	NS	NS	NS	1,88	•••	NS	1,23	•••	•••
Reefs × Zones	4,110	•••	••	•••	3,88	NS	NS	–	–	–
Temporal pattern										
Reefs	4,8	•••	•••	••	3,6	••	•	–	–	–
Zones	1,2	NS	NS	NS	1,2	•	NS	1,2	•	•
Years	1,2	NS	NS	NS	1,2	NS	NS	1,2	NS	NS
Months (Y)	2,80	NS	•••	•••	2,64	NS	•	2,16	NS	NS
R × Z	4,8	•	NS	•	3,6	NS	NS	–	–	–
R × Y	4,8	•	•••	NS	3,6	•	NS	–	–	–
R × M (Y)	8,80	NS	NS	•••	6,64	NS	•	–	–	–
Z × Y	1,2	•	NS	NS	1,2	•	NS	1,2	NS	NS
Z × M (Y)	2,80	NS	NS	NS	2,64	NS	NS	2,16	•	•
R × Z × M	4,8	NS	NS	NS	3,6	NS	NS	–	–	–
R × Z × M (Y)	8,80	•	NS	NS	6,64	NS	NS	–	–	–

• $p < 0.05$, •• $p < 0.01$, ••• $p < 0.001$; NS: not significant

The results of analysis of variance demonstrated significant cross-shelf variation in abundance of total adults but, as indicated by the reef by zone interaction, differences in abundance between back reef and front reef sites were not consistent among reefs (Table 5). The dominant species showed regular, within-reef, patterns of abundance and consistent patterns of cross-shelf distribution. There were always significantly fewer adult *Thor paschalis* on sites at the inner and outer shelf reefs than at those on mid-shelf reefs (Table 5, Fig. 4).

However, the abundance of juvenile *Thor paschalis* on the inner and outer shelf reefs was not always significantly less than that on the mid-shelf reefs. The cross-shelf pattern for *Chlorocurtis jactans* was more distinct with no adults or juveniles ever found on the inner shelf reef (Fig. 4). Although the general trend in distribution was for greater numbers on mid-shelf reefs compared with the outer shelf reef, there were no significant differences in abundances of either adults or juveniles among reefs in 2 of the 4 monthly collections (SNK tests). Adult and juveniles of *Periclimenes toloensis* were restricted to Pandora Reef and were consistently more abundant on front reef sites than on the back reef (Table 5).

Community structure

The cross-shelf pattern in the dominance of *Periclimenes amymone* on live corals is shown in dominance diversity plots based on the total shrimp collection taken in the summer of 1982/83 (Fig. 5). The relative abundance of *P. amymone* was greater on the mid-shelf reefs than on the inner shelf (Pandora) or outer shelf (Myrmidon) reefs where individuals were more evenly distributed among species. There was no pronounced difference in dominance diversity between collections of shrimps from front reef and back reef sites. In contrast to the live coral shrimp fauna, there was no distinct cross-shelf pattern in the community structure of shrimps found on dead corals. Comparison of back reef and front sites showed little difference in the structure of the shrimp communities found in these zones.

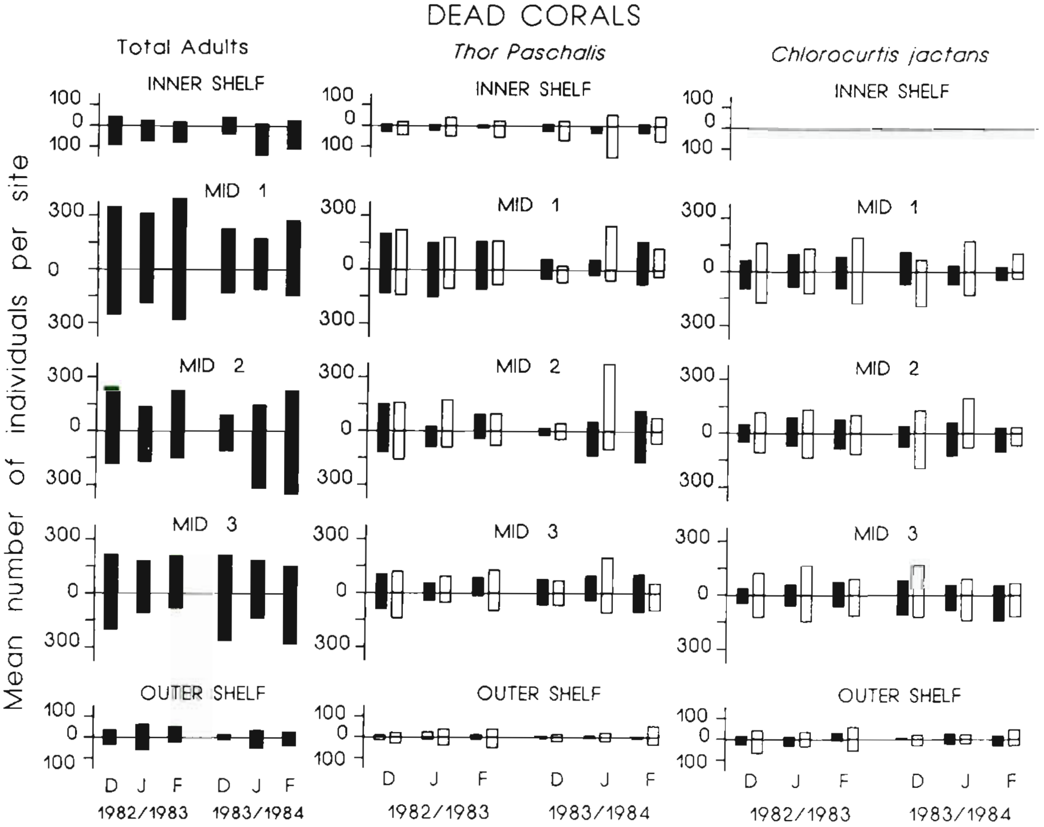

Fig. 4. Cross-shelf pattern in mean monthly abundance of total adult shrimps, *Thor paschalis* adults and juveniles, and *Chlorocurtis jactans* adults and juveniles collected from 9 pairs of dead *Pocillopora verrucosa* corals in each zone (back reef and front reef) of 5 reefs during the summers of 1982/83 and 1983/84 (convention follows Fig. 2)

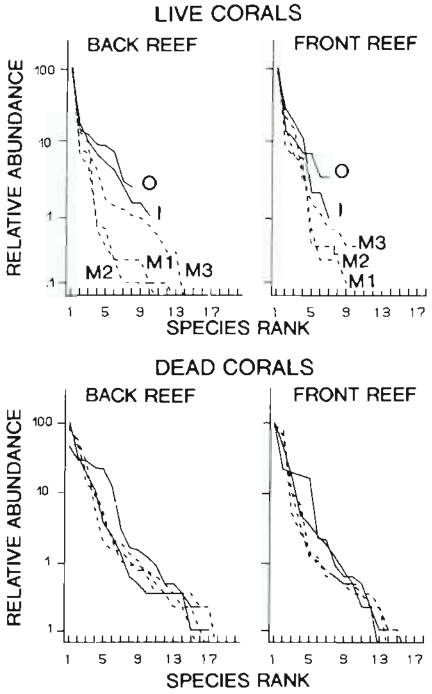

Fig. 5. Cross-shelf pattern in dominance diversity of agile shrimps collected from 5 reefs during summer 1982/83. Upper: collections from 9 pairs of live *Pocillopora verrucosa* coral heads in each zone (back reef and front reef) within reefs. Lower: collections from 27 pairs of dead coral heads in each zone. I: inner shelf reef; M1, M2, M3: mid-shelf reefs; O: outer shelf reef

Temporal stability in patterns of species composition

Live corals

Monthly comparisons of community structure and faunal similarity revealed regional variation in species replenishment following defaunation of live corals (Fig. 6). In the first month of sampling (December 1982), there was a high degree of faunal similarity among all reefs, particularly on front reef sites. In subsequent collections, there was a decrease in the level of faunal similarity between the inshore reef, the outer shelf reef and the group of 3 mid-shelf reefs. The general cross-shelf pattern of faunal replenishment was similar on back reef and front reef sites.

In the second summer, when only back reef sites were sampled, the trend was similar but the pattern was more variable. The shrimp fauna from the corals that had been left undisturbed for 9 mo (December 1983) showed a high level of similarity among all reefs and a single species was dominant at all locations. In subsequent sampling, the pattern observed was similar to that of the previous year, with the mid-shelf reefs retaining a high degree of faunal similarity. In the last month the mid-shelf group and the inshore reef shared a similar fauna which was markedly different in species composition to that from the outer shelf reef.

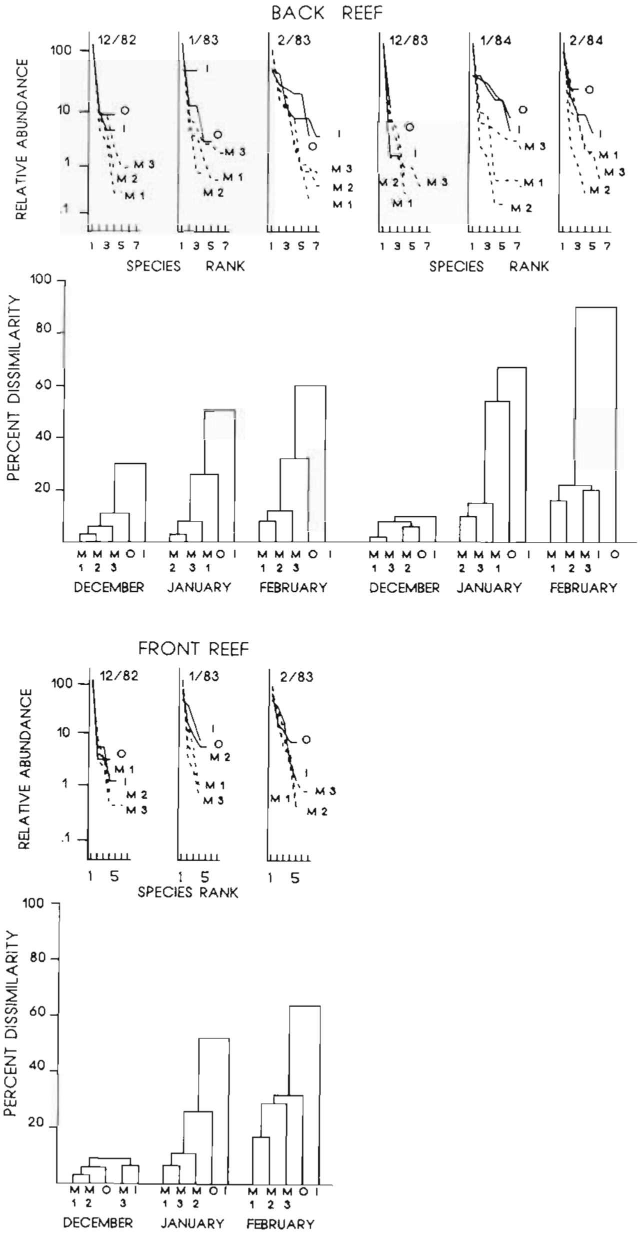

Fig. 6. Cross-shelf pattern of monthly variation in dominance diversity and faunal similarity of agile shrimps collected from 3 pairs of live *Pocillopora verrucosa* coral heads in each zone (back reef and front reef) of 5 reefs. Front reef sites were sampled in 1982/83 only

The temporal variations in the pattern of faunal similarity among reefs were due to changes in the relative abundance of live coral specialists and generalist species (Fig. 2). Species replenishment on the mid-shelf reefs was characterised by a high proportion of specialists (mainly *Periclimenes amymone*) whereas at the inner shelf and the outer shelf reefs there was generally a marked temporal decline in the relative abundance of such species. In February 1984 no adult coral specialists were found on Myrmidon Reef, hence the lack of species overlap with the fauna from the other reefs.

Dead corals

Comparison of the samples collected from dead corals during the summers of 1982/83 and 1983/84 revealed a uniform pattern in the structure of agile shrimp communities among localities (Fig. 7). Community structure showed little variation in response to regular removal of the shrimps. Comparison of faunal similarity revealed a generally consistent cross-shelf pattern with orderly species replenishment among locations. The species collected from the 3 mid-shelf reefs and the outer shelf reef consisted of a group that varied in relative abundance through time and was consistently different from the distinct inner shelf reef fauna.

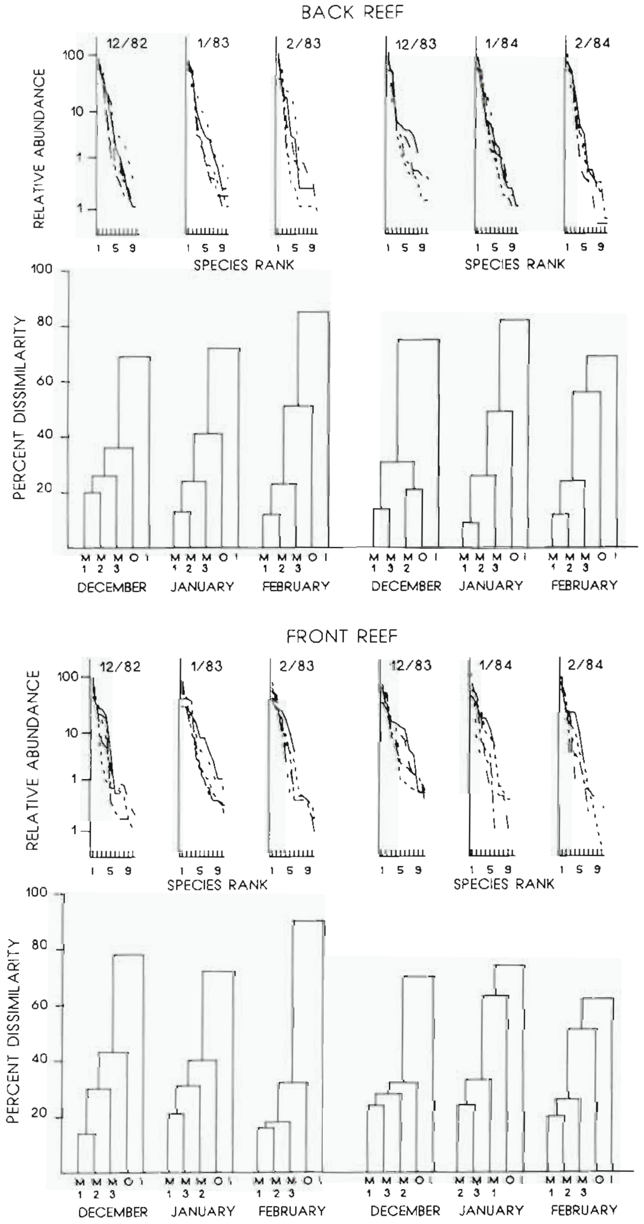

Fig. 7 Cross-shelf pattern of monthly variation in dominance diversity and faunal similarity of agile shrimps collected from 9 pairs of dead *Pocillopora verrucosa* corals in each zone (back reef and front reef) of 5 reefs in 1982/83 and 1983/84

Longer-term trends

Live corals

In the last 2 summers (February 1985 and February 1986), during which single surveys were done, no new species were found on either live or dead corals. At all locations at least some of the live corals survived and continued to grow until the end of the survey. On 2 of the mid-shelf reefs, Rib (M 1) and Lodestone (M 2), all the transplanted live corals survived and sustained high but variable numbers of shrimps (Fig. 8). As in previous years, *Periclimenes amymone* was the domi-

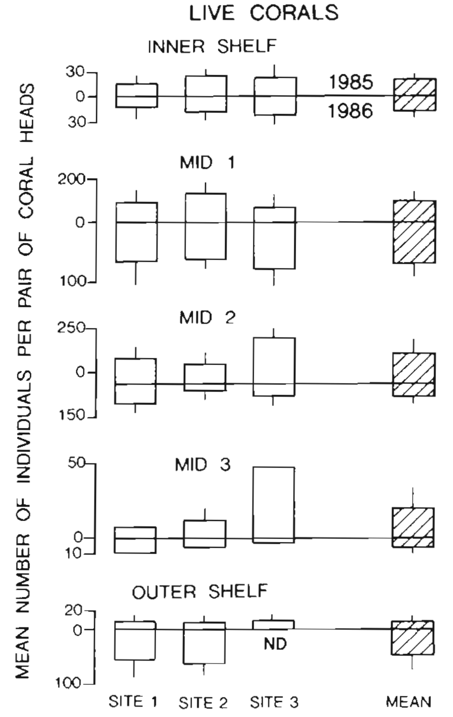

Fig. 8. Cross-shelf pattern in mean abundance (+ SE) of total adult shrimps on each of 3 pairs of live *Pocillopora verrucosa* coral heads at 3 back reef sites on 5 reefs in February 1985 (upper bars) and February 1986 (lower bars). Absence of error bars denotes loss of coral. Shaded bars show site means. Note changes in y-axis scale

nant species. On the third mid-shelf reef, John Brewer, all live corals showed a marked reduction in size and some were completely destroyed by *Acanthaster planci* in 1985 or Cyclone Winifred in 1986. By February 1985, the mean abundance of shrimps on the remaining live corals was as low as those on the inshore and outer shelf reefs. Moreover, the pattern of relative abundance of species at John Brewer (M 3) differed from that on all other reefs (Fig. 9). In 1986, the remaining live corals yielded very few shrimps but the species composition was similar to that of the other mid-shelf reefs.

On the inner shelf reef all the live corals survived in a healthy state. As in previous years, the total abundance of shrimps in these corals was low. Likewise the agile shrimp community from undisturbed corals on this reef had a species composition similar to that found on healthy corals from mid-shelf reefs.

Some of the corals on the outer shelf reef were destroyed but the remainder were healthy. In 1986, the remaining corals on this reef had significantly greater numbers of shrimps than in previous years with comparable yields to healthy corals on the mid-shelf reefs and a similar composition of species.

Dead corals

At all locations the dead corals were eroded during the lengthy intervals between the final sampling periods. By February 1985, the size of dead corals at all locations was reduced by 10 to 15 % and many of the corals were fouled with luxuriant algal growths. By the time of the final survey in February 1986, some of the dead corals on front reef sites at each location had been destroyed, particularly on the outer shelf reef where all were destroyed (Fig. 10). Reduction in the size of corals was accompanied by a substantial reduction in the yield of shrimps compared to previous years. Although the cross-shelf pattern in faunal similarity observed in the previous summers was retained, differences in species composition among reefs were less pronounced (Fig. 9).

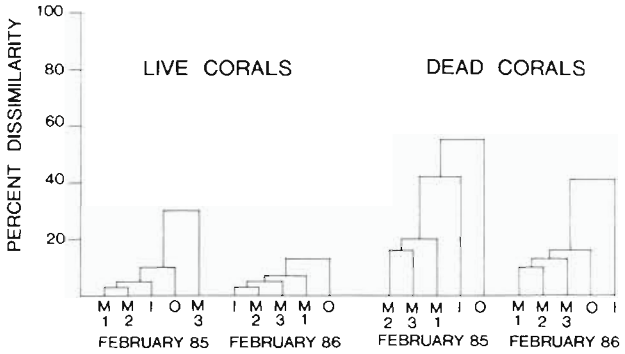

Fig. 9. Cross-shelf pattern of faunal similarity of agile shrimps from live and dead *Pocillopora verrucosa* corals in February 1985 and February 1986

Despite the substantial reduction in total yield, the data obtained from individual coral heads provided useful information about the small-scale variation in abundance of shrimps. Analysis of variance demonstrated significant variation in abundance between members of pairs of coral heads, among sites and among reefs but little variation between zones within reefs (Table 6). Partitioning of this variation revealed that individual coral heads contributed a greater proportion of the overall variation than reefs, sites or zones.

24 h re-sampling

Live corals that were cleared and resampled 24 h later yielded few species and relatively low numbers compared to the monthly samples (Table 7). The cross-shelf pattern was consistent with previous observations, with fewer species and individuals collected from the inner or outer shelf reefs compared with the mid-shelf reefs. The dead corals that were re-sampled on the mid-shelf reefs also yielded few species and individuals compared to the monthly samples but the mean numbers of adults and juveniles per coral pair was approximately double that on live corals of a similar size.

DISCUSSION

During the past decade there have been a number of quantitative surveys of corals and coral reef fauna from the same cross-shelf transect surveyed in the present study. Studies of hard corals (Done 1982), soft corals (Dinesen 1983) and fish (Williams 1982, Williams & Hatcher 1983, Russ 1984) revealed major variations in the structure of these communities across the narrow zone of latitude encompassed in the transect. Moreover, Williams (1986) found that temporal variation had little effect on the magnitude of cross-shelf differences in the community structure of the fishes.

Present results demonstrate that agile shrimp communities also show pronounced cross-shelf variation in species abundance and distribution which persisted throughout the 4 yr study. The patterns of habitat association among species also persisted through time.

Previous comparative studies of the crustacean communities on live corals have been restricted to the associates of naturally occurring coral heads. Much of the discussion arising from these studies concerned variations in species composition among locations due to the influence of the abiotic (Abele 1976, Austin et al.

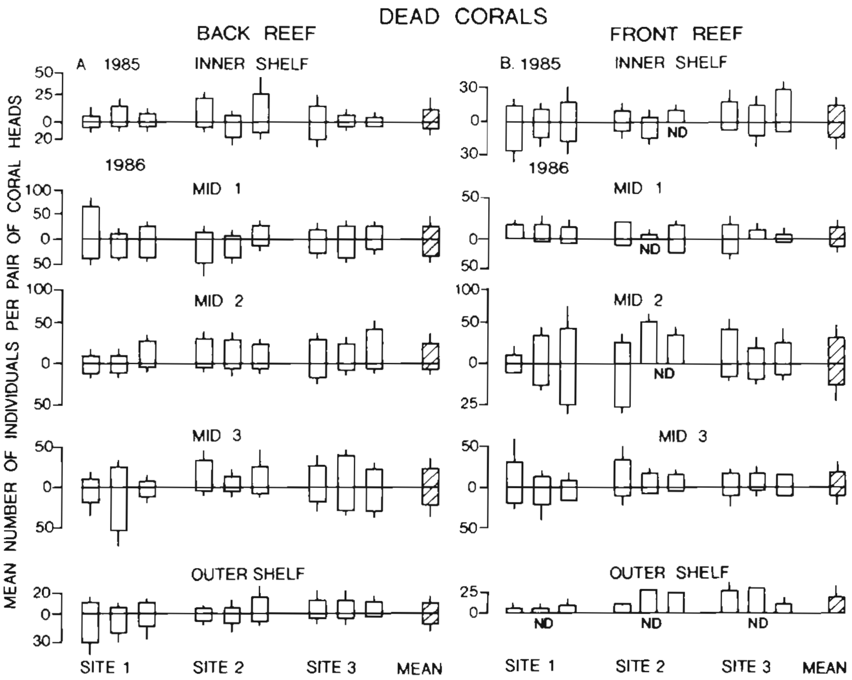

Fig. 10. Cross-shelf pattern of mean abundance (+ SE) of total adult shrimps on each of 9 pairs of dead *Pocillopora verrucosa* coral heads at 6 sites on each of 5 reefs. (A) Back reef sites in February 1985 (upper bars) and 1986 (lower bars). (B) Front reef sites. Absence of error bars denotes loss of corals. Shaded bars show site means. Note changes in y-axis scale. ND: no data

Table 6. Nested analysis of variance in the abundance of total adult shrimps on isolated heads of dead *Pocillopora verrucosa* coral from leeward and windward zones on 5 reefs in the central region of the Great Barrier Reef in February 1985. N = 18 in each zone. Data transformed to log (x + 1)

Source	SS	df	MS	F	p	% Var.
Reefs (R)	5.15	4	1.29	5.2	***	23.0
Zones (Z)	0.77	5	0.15	0.6	NS	3.6
Sites (S)	5.02	20	0.25	1.9	**	14.4
Coral heads (R, Z, S)	7.76	60	0.13	2.8	***	26.0
Residual	4.19	90	0.05	–	–	33.0

1980) or biotic (Kropp & Birkland 1981, Black & Prince 1983) environment external to the live coral. The results of the present study, in which live corals were transplanted to different reefs, have provided an experimental test of previous observations concerning regional variations in the species composition of crustacean associates in relation to the location of the host coral.

Periclimenes amymone, the dominant species on live corals on all the reefs surveyed in this study, showed significant regional variation in distribution and abundance among standard sized units of live coral.

Table 7. Mean number (+ SE) of each species of agile shrimp collected from 3 pairs of *Pocillopora verrucosa* coral heads at each reef after 24 h immersion. Dead corals were only sampled from mid-shelf reefs

	Inner shelf (Pandora)		Mid-shelf (Rib (M 1))		Mid-shelf (Lodestone (M 2))		Outer shelf (Myrmidon)	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Live corals								
Periclimenes amymone	–	–	6 (0.3)	14 (4.4)	5 (0.6)	8 (1.5)	–	–
Chlorocurtis jactans	–	–	4 (0.7)	9 (9.4)	2 (0.6)	3 (1.5)	1 (0.3)	–
Thor paschalis	2 (0.6)	3 (0.6)	3 (1.2)	9 (4.6)	< 1	2 (0.6)	–	–
Unidentified	–	–	– –	6 (1.5)	– –	3 (0.6)	–	2 (1)
Mean total	2	3	13	38	7	16	1	2
Dead corals								
Thor paschalis	Not sampled		15 (2.1)	56 (20.1)	13 (2.9)	19 (3.9)	Not sampled	
Chlorocurtis jactans	Not sampled		6 (1.2)	11 (5.1)	5 (1.5)	7 (2.3)	Not sampled	
Periclimenes longirostris	Not sampled		8 (4.3)	4 (0.3)	2 (0.3)	2 (0.6)	Not sampled	
Unidentified	Not sampled		– –	16 (2.1)	– –	4 (1.8)	Not sampled	
Mean total	Not sampled		29	87	20	32	Not sampled	

Although larvae of this species have not been described, most species of agile shrimp found in shallow tropical waters have dispersive larvae. Only one species of Pontoniid shrimp is known to have abbreviated larval development (Bruce 1972). Replenishment of vacant live corals with adults and juveniles, as demonstrated in this study, suggests that both migration and recruitment provided significant input at all locations. However, the mid-shelf reefs apparently sustained greater population densities of this species than the inner or outer shelf reefs where both migration and recruitment rates were comparatively low. In a survey of coral communities across the same transect surveyed in this study, Done (1982) found a paucity of acroporid and pocilloporid corals on inner shelf reefs, greater abundance on the mid-shelf reefs and relatively low abundance on the outer shelf reefs. Thus the cross-shelf pattern of abundance of *P. amymone* was consistent with the cross-shelf patterns of its host acroporid and pocilloporid corals.

Abele (1976) has suggested that regional differences in the population density of coral mucus-feeding species might be due to differences in the environmental conditions that affect the growth and survival of the host coral. In the present study the live coral heads that were transplanted from the mid-shelf reefs to the inner shelf or the outer shelf reefs survived for 4 yr. Given sufficient time, the agile shrimps attracted to these corals were dominated by *Periclimenes amymone* resulting in a community very similar to that found on the mid-shelf reefs. Although the total abundance of shrimps on the inner and outer shelf reefs was characteristically low, occasionally live coral heads from these reefs yielded as many juvenile *P. amymone* as did those mid-shelf reefs. Moreover the final survey showed that corals transplanted to the outer shelf reef attracted as many adult *P. amymone* as similar sized corals on the mid-shelf reefs. Nevertheless, the recruitment or migration of *P. amymone* to vacant live corals at the inner or the outer shelf reefs was less predictable than to live corals on the mid-shelf reefs. Consequently there was regional variation in the response of the associated shrimp communities to regular clearing of the corals. These results support Abele's (1976) observation that low regional population density of coral mucus-feeding specialists increases the chances of local extinction following an environmental disturbance of the host coral.

Previous studies have shown that regional differences in the environmental conditions of the host coral may affect the species composition of the fauna associated with pocilloporid corals (Abele 1976, Kropp & Birkland 1981). However, Austin et al. (1980) found that differences in the physical environment at 4 sites on 2 reefs in the Capricorn group of the Great Barrier Reef did not affect species diversity of the fauna associated with *Pocillopora damicornis*. They suggested that small spatial scale (zones within reefs) variations in the degree of environmental disturbance could be swamped out due to the dispersal of larvae. In support of this observation we found that the pattern of distribution of the juveniles of the dominant live-coral shrimp, *Periclimenes amymone*, was highly variable within and among the reefs surveyed. We also found that, within reefs, differences in exposure between back reef and front reef sites did not appear to greatly affect the species composition or abundances of shrimp associates of *Pocillopora verrucosa*.

Apart from *Periclimenes amymone*, live corals at all locations also yielded significant numbers of other species. These were predominantly the same species as those found on the adjacent dead corals within each locality. As suggested by Black & Prince (1983), species composition on live corals reflects, in part, the species composition in surrounding habitats. In the present study, resampling live and dead corals after 24 h indicated that, other than *P. amymone*, all of the species that rapidly colonised vacant corals preferentially settled on dead coral. On those reefs that apparently supported low population densities of *P. amymone* opportunistic, free-living species were the first arrivals on vacant live corals. Although these species may only represent transient communities on live coral, their presence contributed to the pronounced cross-shelf differences in community structure following short-time (daily or monthly) replenishment of vacant live corals.

Whereas the association between the mucus-feeding species and live coral is well established, little is known about the connection between the free-living species and dead coral habitats. The majority of the shrimps collected from dead corals in this study are known to be free-living species that are commonly found throughout the Indo-West Pacific (Bruce 1976, 1983). Their abundance on dead corals could provide a measure of their regional population density across a number of habitats, although it could also indicate a preference for this particular habitat. Coles (1980) has suggested that species which can exist independently of live coral use coral skeletons principally for habitat and protection. Although agile shrimps may leave corals at night and enter new corals in new combinations by day (Patton 1974) the greater yields from monthly samples than from 24 h samples suggest that dead coral colonists are not entirely transitory. Until more is known about the feeding behaviour and food preferences of the free-living species, it remains to be seen whether they derive any significant nutritional benefits from their association with dead corals.

In the first 2 summers of this study it was clearly established that standard sized units of dead coral located at the inner shelf reef or the outer shelf reef consistently yielded far fewer agile shrimps than those in the mid-shelf region. Even the most productive sites on the inner shelf reef only yielded about half the total number of adults as the least productive sites on the mid-shelf reefs. In general the community of shrimps found on dead coral was similar to that found in subtropical seagrass beds (Ledoyer 1968, 1984). The exception to this was at the inner shelf reef where the dead coral community was dominated by *Periclimenes toloensis*, a species that has not been recorded from seagrass beds. Similarity to shrimp fauna from seagrasses was particularly evident for those species with the greatest abundance and/or the most cosmopolitan distribution among the reefs surveyed in the present study. Although one such species, *Chlorocurtis jactans*, has previously only been recorded from seagrasses (Ledoyer 1968, 1984, Bruce 1976b), others, such as *Thor paschalis* and *Palaemonella rotumana*, has previously been found in other habitats including live coral (Black & Prince 1983). Cross-shelf variations in the distributions and abundances of free-living species that inhabit dead corals may reflect concurrent patterns of distributions and abundances of particular habitats, such as seagrass beds. However the task of establishing whether such a link exists will need to accommodate the heterogeneous distribution of these species as demonstrated by the use of standard sized units of habitat in this study. The results of partitioning variation in the abundance of shrimps at different spatial scales demonstrated that the smallest scale, in this case individual coral heads, accounted for the greatest proportion of the overall variation.

The results of this study do not support the concept that amount of space available is necessarily a limiting resource for benthic crustaceans that have formed an association with a live coral (Abele 1976), nor is this the case for the free-living species that inhabit dead corals (Coles 1980). Consistently lower yields of agile shrimps from standard sized units of live and dead coral at the inner and outer shelf reefs compared with the mid-shelf reefs suggests that the former reefs sustain a relatively depauperate agile shrimp fauna. Relatively low rates of replenishment by recruitment or migration apparently maintain this cross-shelf pattern.

Williams & Hatcher (1983) considered that differential availability of larvae, patterns of settlement and habitat selection by postlarvae or differential survivorship after settlement could cause or maintain cross-shelf differences in the community structure of coral reef fishes. These factors could also apply to benthic coral reef crustaceans. Present results indicate that, for common species with a cosmopolitan distribution of adults, inner shelf and outer shelf reefs receive fewer juveniles than the mid-shelf reefs. However, in the absence of quantitative information on larval distribution, differential survivorship after settlement cannot be discounted. Consistent patterns of habitat associations among species suggest that cross-shelf patterns in species distributions and abundances do reflect distributions and abundances of particular habitats.

Interactions among or between species may have influenced the patterns of distribution observed in this study particularly on live corals which maintained their resident, non-agile, fauna when transplanted. Although agonistic interactions between resident and foreign crabs and sedentary shrimps have been observed (Glynn 1983) the nature of any interactions between agile shrimps and other fauna has not been determined. In any case, since individual residents may migrate often (Castro 1978), it is unlikely that any residents persisted on their original host coral throughout the 4 yr study.

For those species of agile shrimps that occupy a variety of habitats it might be expected that variations in abundances on standard sized units of habitat would reflect the areal amount of adjacent habitat that could provide a source of migrants. However, comparisons among mid-shelf reefs surveyed in this study showed that abundances of agile shrimps on coral isolates did not reflect the size of individual reefs. John Brewer Reef is about twice the size of Lodestone or Rib, yet the mean yield of shrimps from live or dead corals on John Brewer was less than that from either of the smaller reefs. The results also showed that the proximity of John Brewer to Lodestone did not ensure a higher level of faunal similarity between these reefs than with the more distant Rib Reef. In comparison with the mid-shelf reefs Pandora Reef on the inner shelf and Myrmidon Reef on the outer shelf are relatively isolated from other reefs which could provide a source of migrants or recruits. This factor alone could account for the relatively depauperate fauna of agile shrimps on these reefs.

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