DISTRIBUTION OF TROPHIC GROUPS OF EPIFAUNAL ECHINODERMS AND MOLLUSCS IN THE SOFT SEDIMENT AREAS OF THE CENTRAL GREAT BARRIER REEF SHELF

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ABSTRACT

Echinoderms (103 species, 2235 individuals) were the most abundant, and molluscs (196 species, 1992 individuals) the most diverse epifaunal taxa at four intensively sampled sites located on a transect across the soft sediment areas of the GBR shelf off Townsville. An inner site (depth 22 m) separated clearly from more offshore sites (depth 26-41 m) based on species of both molluscs and echinoderms. Community structure was similar with highest species richness and species diversity at offshore sites.

Proportional species richness and abundance in trophic categories showed substantial differences between sites for both echinoderms and molluscs, although the separation between inner and middle shelf sites was not always consistent between the two taxa. The same sharply defined pattern was evident for both taxa in a general browser category. High diversity and abundance were correlated with the abundance of coarse biogenic rubble and algae which provided the primary feeding focus of many browsers. This material, especially abundant on the inner middle shelf, also supported a suite of hard-substrate dependent, suspension feeding taxa (crinoids, dendrochirote holothurians, siliquariid gastropods and various bivalves) amongst whom acrophilic behaviour was common. Suspension feeders from both phyla were generally abundant on the middle shelf and dominated the echinoderms at the deepest site. The inner shelf molluscs were dominated by infaunal suspension feeding bivalves. Carnivorous echinoderms dominated the inner shelf due to the abundance of a single asteroid whereas highest numbers of carnivorous molluscs occurred on the middle shelf due to several, widely distributed gastropods. Deposit feeders of both groups were abundant at all sites. Differences between phyla at sites across the shelf may reflect patchiness in space and time of a few abundant deposit feeders.

INTRODUCTION

Knowledge of the trophic relationships of benthic organisms is important to an understanding of the processes which might structure communities and the functional role of trophic groups has been the focus of increasing interest (e.g. reviews by Woodin and Jackson 1979, Posey 1987). In this study, we examine the variation in trophic groups of two major epifaunal taxa, echinoderms and molluscs, across a broad tropical continental shelf, in relation to environmental variation.

METHODS

Four sites were sampled along transect C (figure 1). Each site was a square with sides of one nautical mile (1.9 km). The centres of adjacent sites were separated by eight nautical miles (14.9 km) in a north-south direction. Samples were collected with a modified Ockelmann sledge (Ockelmann 1964) and sieved to a 2 mm mesh sieve. Sampling and other field procedures were as given in Birtles and Arnold (1983), except that at sites on transect C, eight samples were taken in a north-south direction within the one nautical mile square in addition to the four samples taken along the sides of the square.

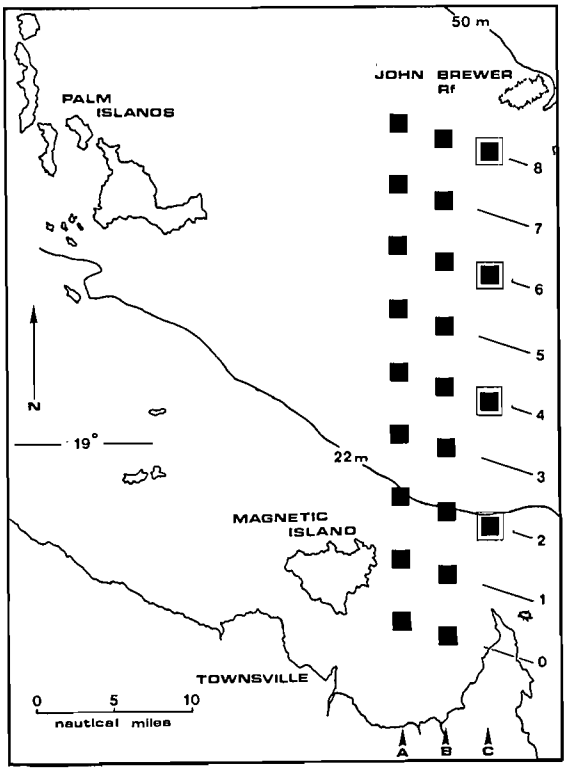


Figure 1. Map of the study area off Townsville.

Sediment was collected from the south-east corner of each site with an 0.06 m^2 Smith-McIntyre grab. Samples of about 150 g were wet sieved after disaggregation with sodium hexametaphosphate after the method outlined in Carver (1971). Major visual components of the sediment and their relative abundance on a three point scale (present, common and very common) were recorded during sorting, as were the more dominant seagrasses and algae.

The 103 species of echinoderms and 196 species of molluscs were classified as carnivores (C), deposit feeders (D), suspension feeders (S), browsers (B) and parasites (P). Species were assigned to particular trophic categories based on our diving observations and gut content analyses of the numerical dominants, extensively augmented

by recent compilations (e.g. Taylor, Morris and Taylor 1980; Jangoux and Lawrence 1982). Although the term browser is most commonly applied to herbivores (Walker & Bambach 1974), many marine predators also browse upon their prey (Woodin 1982). Many of the asteroids, echinoids and gastropod molluscs in this study, could not be satisfactorily separated into either browsers on plant material or browsers on colonial encrusting animals (bryozoans, ascidians, cnidarians, sponges, etc.), due to their polytrophic and opportunistic feeding behaviour and the dearth of accurate, and especially quantitative dietary information. They were therefore all included in the same generalised "browser" category even though animals at either end of the dietary spectrum would be at quite different trophic levels.

Hierarchical cluster analysis, using the package CLUSTAN 1C, was based on log10(n+1) transformed values of species abundances at the sites. Dissimilarity was calculated using the Bray-Curtis index and the dendrogram constructed using the flexible sorting strategy, with B=-0.25.

RESULTS

Environment

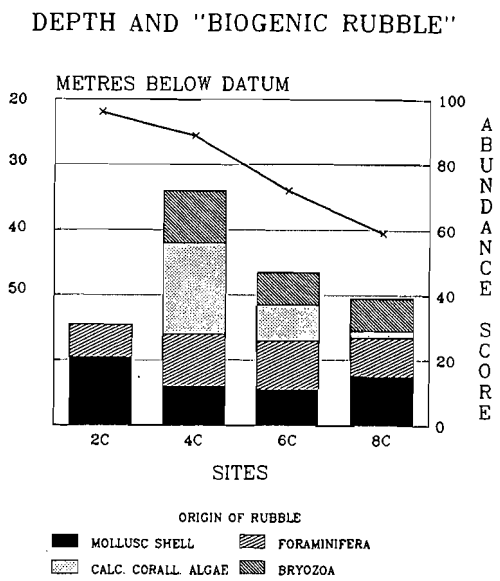
The depth gradient was least between the inner site 2C (mean depth below datum 21.9 m) and 4C (depth 25.6 m); the latter, and the two more offshore sites 6C and 8C (depths 34 m and 40.5 m), were more evenly spaced by depth (figure 2). The sediment at 2C was dominated by mud (28%) and medium to very fine sand (59%); fine gravel and pebble particles (>2.00 mm), collectively termed "rubble", comprised only 2.5%. Sites 4C, 6C and 8C had 10% or less mud and were dominated by coarse and very coarse sand (45%, 53% and 57%, respectively) and rubble (33%, 23% and 9%, respectively). The three offshore sites consistently varied from 2C in having a greater diversity and abundance of large rubble of biological origin (foraminifera, calcareous red algae, bryozoa, mollusc) as well as of seagrasses and algae (figure 2).

Faunal Patterns

The major separation of sites in the classification analysis, for both echinoderms and molluscs, occurred between the inner site 2C and the more offshore, middle shelf sites 4C-8C. Within the offshore site grouping, the outer two sites (6C, 8C) separated from the inner middle shelf site 4C for both echinoderms and molluscs (figure 3).

Echinoderm abundances at the offshore sites were 1.2-1.6 times that at site 2C, the number of species at each of the offshore sites was more than double (2.3-2.5) that at 2C (figure 3A). Low species richness combined with low evenness J, so that species diversity H' at 2C was about half to two-thirds that of offshore sites. Although abundances were lower at 4C than at the other offshore sites, species richness, species diversity and evenness were comparable (figure 3A).

At 6C and 8C, mollusc abundance and species richness were about double that at 2C and evenness was similar at these three sites. However, while abundances were similar at 2C and 4C, species richness was almost twice as high at the latter site, and species diversity and evenness were higher at 4C than at any other site (figure 3B).



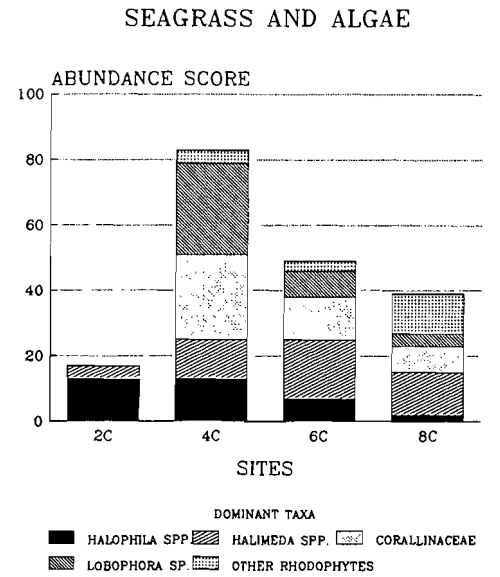
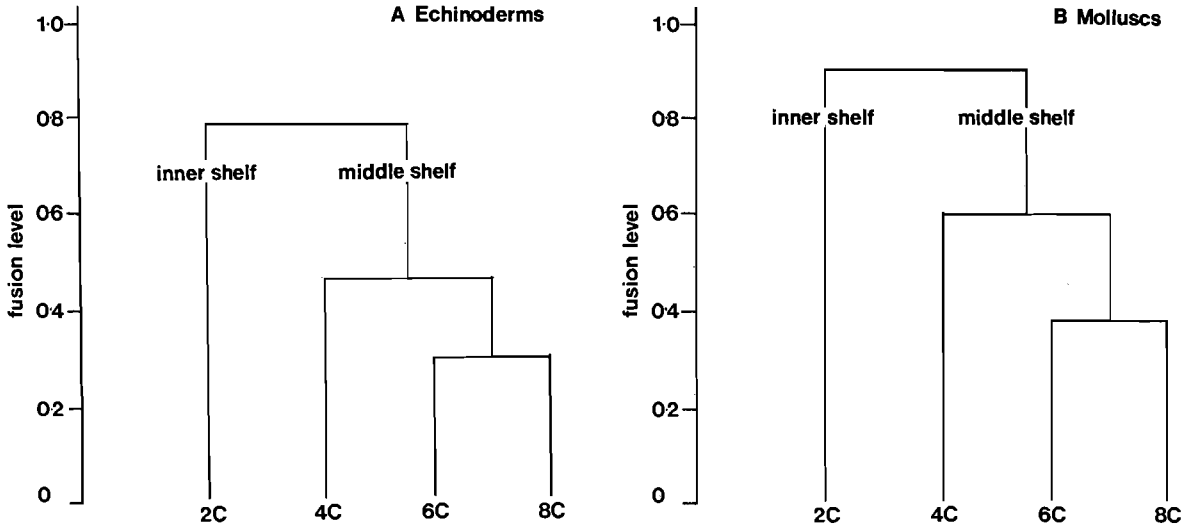


Figure 2. Environmental features of transect C. Abundance scores based on categories recorded in the field; present=1, common=2, and v. common=3. Scores are summed over all 12 sites to give site total.

Echinoderm trophic groups

A systematic breakdown of feeding types is given in Appendix I and a breakdown by class of species and abundance in the trophic groups is given in table 1. The overall proportion occupied by each of the trophic categories (summed over all sites) was similar whether species richness or total abundance was considered. Suspension feeders dominated (44.7% of species, 40.8% of individuals), followed by deposit feeders and browsers (table 1). The major discrepancy was with carnivores which accounted for only 8.7% of species but 19.4% of individuals.



SITE	TOTAL ABUND.	NO. OF SPP.	H'	J	H(MAX)
2C	424	28	0.8787	0.6072	1.4472
4C	497	69	1.5560	0.8462	1.8389
6C	628	65	1.4022	0.7734	1.8129
8C	686	67	1.5608	0.8547	1.8261

SITE	TOTAL ABUND.	NO. OF SPP.	H'	J	H(MAX)
2C	270	47	1.2512	0.7483	1.6721
4C	327	89	1.6837	0.8637	1.9494
6C	619	107	1.5724	0.7748	2.0294
8C	778	89	1.5280	0.7838	1.9494

Figure 3. Cluster analysis of sites, based on distribution and abundance of species. See text for details of transformations, similarity index and sorting strategy. Abundance, species richness, species diversity and evenness are given for each site. **A.** Echinoderms. **B.** Molluscs.

Table 1. Echinoderm trophic groups. Breakdown by class of the number of species and abundance (percentage species and abundance in parentheses) in five trophic categories.

TROPHIC GROUPS	CRINOIDS		ASTEROIDS		OPHIUROIDS		ECHINOIDS		HOLOTHURIAN		TOTALS	
	# SPP	ABUND	# SPP	ABUND	# SPP	ABUND	# SPP	ABUND	# SPP	ABUND	# SPP	ABUND
CARNIVORES			5	276	4	157					9	433
			(29)	(42)	(15)	(40)					(9)	(19)
DEPOSIT			1	169	5	7	8	297	13	72	27	545
			(6)	(26)	(19)	(2)	(47)	(74)	(45)	(20)	(26)	(24)
SUSPENSION	14	419			16	201			16	291	46	911
	(100)	(100)			(62)	(51)			(55)	(80)	(45)	(41)
BROWSERS			11	215			9	105			20	320
			(65)	(33)			(53)	(26)			(19)	(14)
PARASITES					1	26					1	26
					(4)	(7)					(1)	(1)
TOTALS	14	419	17	660	26	391	17	402	29	363	103	2235
	(14)	(19)	(17)	(30)	(25)	(17)	(17)	(18)	(28)	(16)		

When the classes of echinoderms are treated separately, there were substantial differences in the representation of trophic groups, according to whether species richness or abundance was considered. The majority of asteroids (11) were browsers, but they represented only 33% of individuals. The five species of carnivorous asteroids contributed 42% of individuals, while the only deposit-feeding asteroid, Stellaster equestris, accounted for 26% (table 1). Within the ophiuroids, the majority of species and individuals were suspension feeders. Although 19% of species were deposit feeders, they represented only 2% of individuals. In contrast, four carnivorous species contributed 40% of the ophiuroid individuals. Ophiomaza cacaotica was the sole parasitic echinoderm. The echinoid species were about evenly divided between deposit feeders (eight species of sand dollars and heart urchins) and browsers (nine regular urchins), but the former category contained about three-quarters of echinoid individuals (table 1). The holothurian species were also about equally divided into two groups, with suspension feeders

(order Dendrochirotida) slightly more diverse than deposit feeders (orders Aspidochirotida, Molpadida and Apodida). However, suspension feeders were about four times as abundant as deposit feeders.

The differences in the proportion of species in each of the five main trophic groups at the four sites were not great, with the three middle shelf sites in particular showing considerable similarity (figure 4). There were greater proportions of carnivores (18%) and especially deposit feeders (39%) and fewer of browsers (11%) and suspension feeders (32%) at 2C. In contrast, there were some very marked differences in the percentage abundance of each trophic group at the four sites (figure 4). The most striking difference was the very high abundance of carnivores at 2C in contrast to offshore, where they formed 10% or less of the site totals. The same site had a greatly reduced number of suspension feeders and browsers. At 4C, the proportion of browsers was almost double the total percentage for all sites, while at 6C the number of deposit feeders was raised to 42% of site total. The deepest site 8C, showed a marked increase in the number of suspension feeders totalling 63% of the individuals at the site.

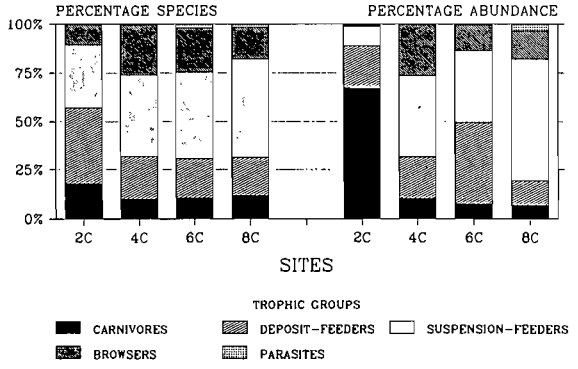


Figure 4. Proportions of echinoderm trophic groups at each site: nos. of species (l.), abundance (r.)

Figure 5 illustrates the inter-site differences in trophic group abundances in greater detail. Carnivores dominated site 2C, forming 68% of the site total (figure 5A). Asteroids comprised 50% of the echinoderms at the site, with Astropecten velitaris contributing 47.4% of the site total. The remaining 18% was contributed mostly by two ophiuroids Ophiopsammus yoldii and Ophiochasma stellatum. Deposit feeders formed 21.5% of the site total; over half of them consisted of the asteroid Stellaster equestris. Suspension feeders contributed less than 10% to the site total and the number of browsers was negligible.

Site 4C (figure 5B) was very different to 2C except for deposit feeders, which again formed just over 21% of the site total. At 26% of the site total, the browsers were abundant; 84% of this was asteroids. Ten of the total of 11 browsing asteroids occurred at 4C but over a third (35%) of all asteroids at this site were Pentaceraster regulus. Although browsing echinoids were not abundant, all but one of the nine species found on transect C were also obtained at this site. Apart from the raised browser numbers, the 4C abundance pattern was similar to that of the other middle shelf sites. Carnivores (10%) were reduced to a typically low offshore value; suspension feeders had substantial contributions from three taxa although there were more holothurians than crinoids and ophiuroids combined. This was due, at least partly to the abundance of the dendrochirote Pentacta australis which was the most abundant echinoderm at the site (11% of site total).

The main contributors to the higher proportion of deposit feeders at 6C were echinoids, especially the sand dollar Peronella orbicularis which formed 19% of the site total (figure 5C). If this species were removed however, the proportion of deposit feeders was reduced to below that of the transect overall (22% cf. 24%).

Site 8C was dominated by high abundances of suspension feeders which formed 63% of the site total; 57% of this category were crinoids. Suspension feeders occupied seven of the first eight positions, when echinoderms at the site were ranked by abundance. Five of the top six were crinoids, four of these in the genus Comatula (figure 5D). Ophiactis luteomaculata, the second most abundant echinoderm at the site, formed 65% of the suspension-feeding ophiuroid total. The remaining 23% of the suspension feeders were dendrochirote holothurians. Both the browser and carnivore abundance were similar to that of 6C, and these were fairly evenly divided between asteroid and echinoids, in the former case, and between asteroids and ophiuroids in the latter. The ninth ranked echinoderm at the site was Ophiomaza cacaotica, the only echinoderm in the transect C samples regarded as parasitic (Clark 1976). Its abundance at 8C reflected the distribution of its crinoid hosts (Comatula cratera, C. rotalaria, C. solaris).

Mollusc feeding groups

For carnivorous and suspension feeding molluscs summed over all sites, there were generally similar patterns whether species richness or abundance were considered. The major discrepancies were with deposit feeders, with 9.7% of species but 26.4% of individuals, and the browsers, with 14.3% of species but only 4.9% of individuals (table 2). Molluscs were dominated both in numbers of species and individuals by carnivores (41.8% and 38.5% respectively).

Table 2. Mollusc trophic group totals.

TROPHIC GROUPS	SPECIES NO.	SPECIES PERC.	ABUNDANCE NO.	ABUNDANCE PERC.
CARNIVORES	83	42.3	769	38.6
DEPOSIT	19	9.7	519	26.0
SUSPENSION	63	32.1	597	30.0
BROWSERS	29	14.8	101	5.1
PARASITES	2	1.0	6	0.3
TOTALS	196		1992	

When classes of molluscs are treated separately, there were substantial differences in representation of trophic groups. Scaphopods and cephalopods were exclusively carnivorous, while chitons browse on both animal and plant material. None of these classes were abundant, although cephalopods were moderately diverse, with 10 species.

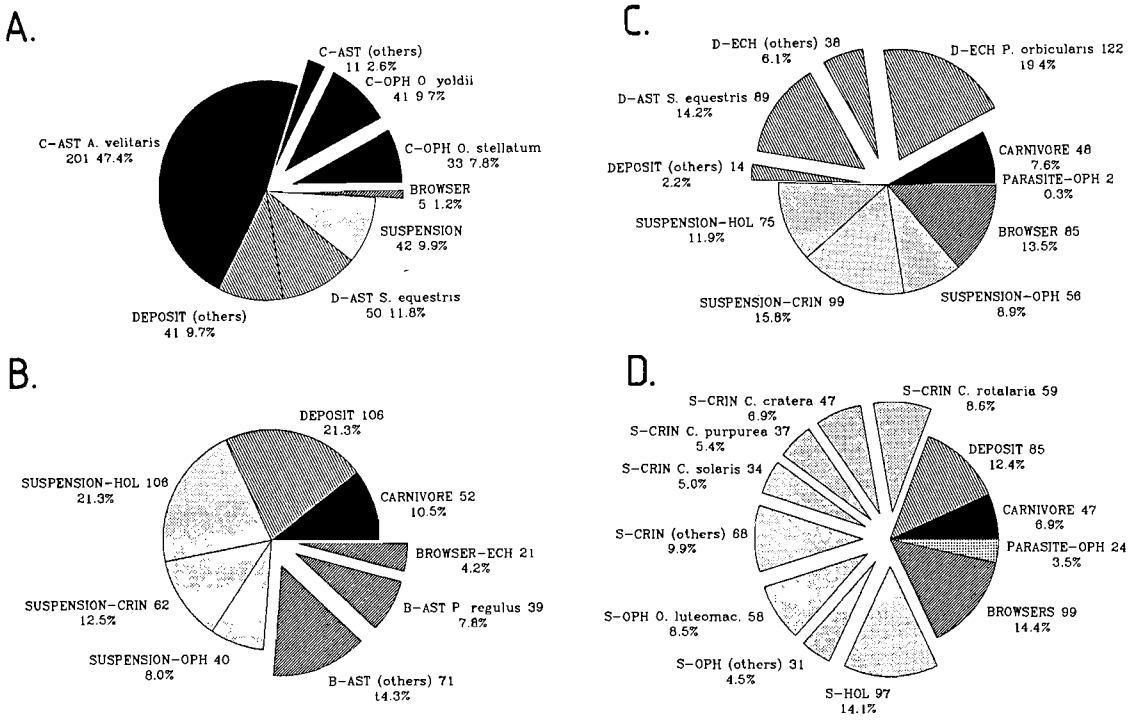


Figure 5. Proportional abundance of echinoderm trophic groups at each site. The five categories (see shading) are subdivided to show class contributions and those of numerically dominant species (abundance & percent. of site total). C=Carnivore, D=Deposit, S=Suspension, B=Browser. **A.** Site 2C **B.** 4C **C.** 6C **D.** 8C.

Bivalves were almost exclusively suspension feeders (57 species, 547 individuals). Only the tellinaceans (2 species, 2 individuals) were considered deposit feeders. Gastropods had the widest range of feeding types (Appendix I), but were dominated by carnivores (72 species, 744 individuals). Although there were only 17 species of deposit feeding gastropods, these included 517 individuals and represented the next most important feeding category in the class.

When sites are considered separately, there was a major distinction between abundances of the various trophic categories at site 2C and those at the middle shelf sites (figure 6). The degree of dominance within deposit feeders at site 2C was especially obvious, with only 13.6% of species but 45.6% of individuals. This was due to the abundance of three species: Strombus vittatus, Xenophora solarioides and Philine sp. The last is generally considered a carnivore, but the small specimens collected had guts full of foraminiferans and appeared to be selective deposit feeders (pers. obs.).

There was a general similarity in the proportions of individuals in each trophic category at the three middle shelf sites. Carnivores were especially abundant at the middle shelf sites (35.8-44.6%). Five species (Tudicula armigera, Chicoreus banksii, Fusinus colus, Phos senticosus and Latirus paetelianus) accounted for 55.5-61.4% of the numbers of carnivores at these middle shelf sites. Of these, only C. banksii was associated with patches of biogenic rubble, the others being sand-dwelling carnivores of infauna, especially polychaetes (pers. obs.).

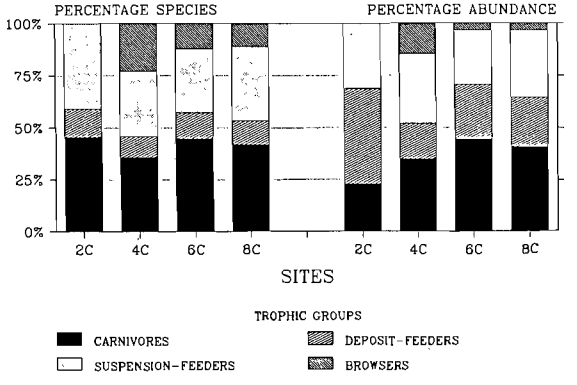


Figure 6. Proportions of mollusc trophic groups at each site: nos. of species (l.), abundance (r.).

Deposit feeders were especially abundant at the outer sites 6C and 8C (figure 6). Five species (in order of abundance: Strombus dilatatus, Xenophora solarioides, X. cerea, Monilea lentiginosa and S. vittatus) accounted for 89% of the individuals at these sites.

Suspension feeders were uniformly distributed along the transect but the species varied from site to site. At site 2C, the numerical dominants were the infaunal glycymeridid Melaxinea labryntha and an epifaunal pteriid. At site 4C, the

numerical dominant was a siliquariid gastropod, associated with sponges. Sites 6C and 8C had a diverse fauna of suspension feeding bivalves, the most abundant being an unidentified ostreid, epizoic on Strombus species. Other families, both infaunal (glycymeridids, cardiids) and epifaunal (arcids, chamids and anomiids) were also well represented at these sites.

No browsers were recorded from the inner shelf site 2C, but they occurred at all middle shelf sites. However there were about twice as many species and about four times as many individuals at site 4C, compared with the outer sites 6C and 8C.

DISCUSSION

The major separation of sites in both echinoderms and molluscs occurred between 2C (21.9 m) and 4C (25.6 m) (figure 3). More extensive sampling along transects A and B (figure 1), as summarised in Birtles & Arnold (1983), indicated a clear separation of echinoderms, molluscs, crustaceans, bryozoans, demersal fishes, ascidians and algae at about 22-23 metres. This major faunal discontinuity corresponded closely to the separation of an inner shelf and middle shelf zone by Belperio (1983), based on sediment characteristics. We also indicated that these overall patterns of distribution and abundance had remained stable for the previous six years (1977-1982).

Relative to site 2C, the middle shelf sites had a higher diversity and greater abundance of large calcareous rubble elements, which were of biological origin (figure 2). Such biogenic rubble, often several centimetres across, acts as a settlement site for solitary and clonal organisms. Where these organisms themselves secrete calcareous skeletons, there is often a build-up of calcareous material to provide quite a large, stable surface, suitable for the settlement of numerous other organisms. This process can lead to the development of multi-species clumps (as defined by Fedra 1977). Other large settlement surfaces are provided by single taxa such as stolidobranch ascidians (Herdmania, Polycarpa) and sponges (Ircinia). We refer collectively to all these hard substrate elements (biogenic rubble, multi-species clumps and single taxa) as "natural isolates". Seagrasses and algae, which were a diverse and abundant feature of the middle shelf sites (figure 2), also act as settlement surfaces. Living corallinaceans were especially abundant at 4C and their dead skeletons were of particular importance in the development of the large biogenic rubble elements which were abundant at the site.

Within both the echinoderms and the molluscs, browser abundance corresponded closely with that of biogenic rubble. As outlined in Methods, this generalised browsing category included both herbivores and animals feeding primarily on clonal animals (sponges, cnidarians, bryozoans). The latter trophic group corresponds to the Group II carnivore category used to characterise feeding types of asteroids (Jangoux 1982). Browsers were absent (molluscs) or in greatly reduced numbers (echinoderms) at 2C, but occurred at all the middle shelf sites. However, it was at 4C, with the maximum concentration of biogenic rubble and algae (figure 2), that the browsers were most strongly represented. Proportional abundance of browsers at 4C was twice and four times that at other middle shelf sites for the echinoderms and molluscs respectively.

While the relative abundance of suspension feeding molluscs was similar across the shelf, suspension feeding echinoderms were clearly best represented on the middle shelf, and especially at site 8C. In situ observations while diving have shown that the dendrochirote holothurians and crinoids are rheophilic and acrophilic behaviour is frequent. Most species are largely restricted to the natural isolates (discussed above) which form islands of hard substrate in a "sea" of otherwise unstable soft-sediment. The elevation provided by such substrate can substantially increase the resources available to passive suspension feeders (Fedra 1977). However, this association with hard substrate clearly did not control crinoid abundance at 8C, which had the highest numbers of crinoids but the smallest amount of biogenic rubble of the middle shelf sites (figure 2). The explanation lay in the fact that the two most abundant crinoids at the site (Comatula rotalaria, C. cratera), at least as adults, do not require hard substrate, supporting themselves on their arms on the surface of the sediment. Why should the environment at 8C be favourable to large, epifaunal suspension feeding echinoderms? Several possibilities can be advanced, including increased bottom stability at the greater depths and hence also lower turbidity, greater availability of suspended food either through currents or because of the effects of pulses of upwelled, nutrient rich water, as suggested by Andrews and Gentien (1982).

The greater abundance of suspension feeding molluscs at 2C is partly explained by the numerical dominance of juvenile pteriid bivalves epizoic on plumulariid hydroids; this flexible substrate is not used by any echinoderm. The majority however, were infaunal suspension feeding bivalves which may be functionally different from the larger epifaunal echinoderms and are often put in a distinct trophic category (Walker & Bambach 1974).

The distribution of carnivorous molluscs was also different from that of carnivorous echinoderms, with the former dominant at middle shelf sites and the latter inshore. This may reflect the difficulty of placing a species unambiguously in a single trophic category. Many of the middle shelf asteroids in our generalised browser category have been classified as carnivores by Jangoux (1982). Philine, a numerically dominant mollusc at 2C, although usually carnivorous (Kohn 1983), was classified as a deposit feeder based on gut content analyses of specimens at that site.

All but one of the numerically dominant echinoderm and mollusc carnivores were infaunal feeders. The inner shelf site was dominated by Astropecten velitaris which feeds primarily on bivalve and gastropod molluscs and small crustaceans (Lemmens 1986). Its high numbers at 2C may be due to the ease of feeding in soft mud compared with the more compact sediment of the middle shelf, rather than simply prey availability; large specimens are confined to offshore sites. The middle shelf molluscan carnivores were dominated by gastropods feeding primarily on sedentary polychaetes. This also does not simply reflect availability of prey

items as there is a rich polychaete fauna within the inner shelf zone (Arnold 1979).

The overall proportion of deposit feeders was similar for the echinoderms and molluscs (24% and 26% of total abundance, respectively) and they formed a substantial proportion at all sites. However, there was a condiderable discrepancy between numbers of deposit feeding echinoderms and molluscs, especially at 2C and 6C. This may largely reflect patchiness in space and/or time of numerically dominant deposit feeders such as Peronella orbicularis on the middle shelf (pers. obs.) and Laganum depressum which, while rare at 2C, could occur in large numbers at other sites on the inner shelf (Birtles & Arnold 1983).

The clearest pattern in the data was the separation of the inner site 2C from the outer sites. It differed not only in taxonomic composition, but in the proportional abundance of some of the feeding types represented. This is especially well shown by the browsers. In the middle shelf zone, sites with higher concentrations of biogenic rubble and natural isolates (e.g. site 4C) provided both food resources (as evident from distribution of browsers) as well as hard substrate for acrophilic and rheophilic suspension feeders, especially crinoids and dendrochirote holothurians. These suspension feeders and the predominantly suspension feeding species which comprise the isolates, may represent an important pathway along which energy is passed from the water column to the benthos (Fedra 1977). Especially where such natural isolates are formed from relatively long-lived organisms (e.g. large stolidobranch ascidians, sponges), they may be vulnerable to short-term but frequent disturbances such as trawling concentrated in particular areas. This is in contrast to the inner shelf zone where the bottom appears to be more unstable and there is less biogenic hard substrate.

Our demonstration of substantial variation in epibenthic taxa and functional groups over the scale of tens of kilometres, and at least partially linked to variability in substrate across the shelf, indicates that caution is necessary in making generalisations. It belies the recent attempt to include the whole central Great Barrier Reef shelf benthos into a single "super-community" (Goeden and Watson 1987). We suggest that an important implication of this is that the distinct zones across the shelf which we have demonstrated will probably require different management strategies. At a different level, such small-scale variability may confuse attempts to make broad-scale inter-regional comparisons. We thus question the validity of the attempt by Petersen and Curtis (1980) to contrast latitudinal patterns of energy flow, given that they used only a single location in Thailand to represent all tropical marine shelf soft sediment habitats.

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Appendix I. Trophic categories of echinoderms (103 species) and gastropod molluscs (124 species). Values are the number of species per family within the trophic category.

TROPHIC GROUP	ECHINODERMS				GASTROPOD MOLLUSCS			
CARNIVORES	Asterinidae	1			Acteonidae	1	Muricidae	14
	Astropectinidae	2			Atyidae	2	Nassariidae	3
	Luidiidae	2			Buccinidae	2	Naticidae	1
	Ophiodermatidae	3			Bursidae	2	Pleurobranchidae	1
	Ophiuridae	1			Conidae	8	Ranellidae	7
					Coralliophilidae	1	Terebridae	2
					Costellariidae	6	Turbinellidae	1
					Fasciolariidae	3	Turridae	13
					Melongenidae	1	Volutidae	3
					Mitridae	1		
DEPOSIT FEEDERS	Amphiuridae	3	Laganidae	5	Cerithiidae	3	Trochidae	2
	Brissidae	1	Lovenidae	1	Eulimidae	2	*Euchelus atra*	
	Caudinidae	1	Ophiotrichidae	2	Philinidae	1	*Monilia lentiginosa*	
	Clypeasteridae	1	Stichopodidae	2	Pyramidellidae	1	Xenophoridae	3
	Goniasteridae	1	Synaptidae	2	Strombidae	5		
	Holothuriidae	8						
SUSPENSION FEEDERS	Antedonidae	1	Ophiacanthidae	1	Siliquariidae	3		
	Colobometridae	1	Ophiactidae	2	Trochidae	2		
	Comasteridae	8	Ophiocomidae	1	*Umbonium* spp.			
	Cucumariidae	11	Ophionereidae	1	Vermetidae	1		
	Euryalidae	1	Ophiotrichidae	10				
	Himerometridae	1	Phyllophoridae	5				
	Mariametridae	1	Zygometridae	2				
BROWSERS	Cidaridae	1	Pterasteridae	1	Aplysiidae	1	Ovulidae	1
	Echinasteridae	1	Temnopleuridae	6	Architectonicidae	2	Polyceridae	1
	Goniasteridae	3	Toxopneustidae	2	Cypraeidae	2	Triphoridae	2
	Metrodiridae	1			Doridiidae	7	Trochidae	3
	Ophidiasteridae	2			Fissurellidae	5	Turbinidae	2
	Oreasteridae	3			Lamellariidae	1		
PARASITES	Ophiotrichidae	1			Hipponycidae	2		