

## **Spatial and Seasonal Variation in Demersal Trawl Fauna Associated with a Prawn Fishery on the Central Great Barrier Reef, Australia**

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### *Abstract*

Regular monthly sampling at eight trawl sites in Great Barrier Reef waters identified variations in both species composition and the relative abundance of the more common species over a 2-year period. Faunal composition was affected more by the location of sample sites than by the time when samples were taken. Ordination analysis differentiated a 'nearshore' group of sites from a 'midshelf' and an 'inter-reef' group. The composition of 'inter-reef' fauna remained strikingly uniform below the 40 m depth contour regardless of proximity to coral reef formations. Classification of the samples also revealed weakly separated 'wet' and 'dry' season temporal groupings, with the former characterized by higher abundances of several 'nearshore' species.

### **Introduction**

Extensive commercial demersal trawling has continued within areas of the Great Barrier Reef Marine Park despite increasing concern over its effects on fish and invertebrate communities (Sainsbury and Poiner, personal communication). The great diversity of taxa and marine habitats within the Park has made it difficult to create comprehensive checklists for all areas. The scale of seasonal and annual variation in species abundance and community associations is, for the most part, unknown. An understanding of the natural spatial and temporal variability of benthic communities is a basic pre-requisite for deductions on man-induced changes (which include the effects of fishing), the duration of their effects, and the subsequent recovery of the communities (Flint and Younk 1983). To date, this lack of knowledge has made it all but impossible to predict or substantiate the effects of prawn trawling in the Marine Park. Management authorities have therefore zoned the Marine Park for use primarily according to socio-economic considerations that assume an underlying faunal homogeneity and stability.

Previous work on the Central Great Barrier Reef has established that demersal, soft-bottom faunal assemblages are correlated with sediment type, water depth and distance offshore (Watson and Goeden 1989) but not with the distribution of trawling effort. These site assemblages or zones lie parallel to the coastline, though their boundaries appear to be transitional in nature (Cannon *et al.* 1987; Watson and Goeden 1989). Similar transitions have been described for other taxa of the Central Great Barrier Reef region. These include hard corals (Done 1982), soft corals (Dinesen 1983), echinoderms and molluscs (Birtles and Arnold 1989), and fishes (Williams 1982). The absence of sample replication and short duration of most of these studies has meant that seasonal or year-to-year effects could not be examined.

This paper reports fine-scale spatial changes in faunal communities on the Central Great Barrier Reef, as well as variations in species abundance at fixed sites through a consecutive 24-month period. These findings can serve as a basis for comparison with future studies which specifically examine the effects of fishing on the Marine Park.

## Materials and Methods

### Study Area

Trawl sites were chosen in conjunction with a 1985 study (Courtney and Dredge 1988) of an existing prawn fishery on Queensland's continental shelf between 18°30'S and 20°S (Fig. 1). The initial arrangement of 20 sites sampled during 1985 produced data on the composition of trawlable fauna in a range of water depths, distances from shore and coral reefs, levels of fishing effort and sediment types (Watson and Goeden 1989). In 1986, many of the more southerly sites were eliminated and several northern sites were added (Fig. 1). Seven sites were sampled throughout both years; these represented an inshore to near-reef transect (sites 1-6 and 20). The new sites (21-24) added in 1986 gave a transect with finer spatial resolution from the reef to the midshelf Great Barrier Reef lagoonal environment (sites 21-22-23-6-24-20).

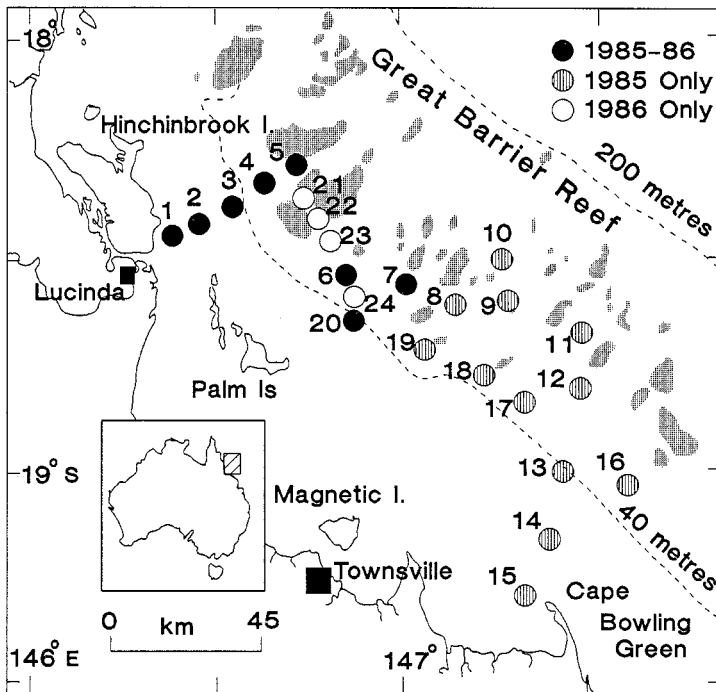


Fig. 1. Location of trawling sample sites.

### Sample Collection

Full details of the sampling methodology are given in Watson and Goeden (1989). Monthly samples of trawlable fauna were obtained between January 1985 and December 1986. All samples were collected within 5 days of the new moon except the May 1985 set, which was delayed by 8 days because of adverse weather. A 19-m vessel was used to trawl along the depth contour for 30 min at  $6 \text{ km h}^{-1}$  using two 'Florida Flyer' demersal trawl nets, each with a 11-m headline. Samples were taken from the starboard net which was made to standard commercial design (50-mm stretched mesh throughout). The port net, which was made from 40-mm stretched mesh, was used only when the starboard net failed to fish (a total of 12 samples). These samples contributed to the derivation of a checklist of taxa present.

Sponges, corals, sea snakes, and specimens longer than 1 m such as stingrays and sharks (which were uncommon in the samples) were noted and discarded. The total catch from the starboard net was weighed and a random subsample of approximately 10 kg was retained and frozen. In the laboratory, all specimens of Mollusca, Crustacea, Echinodermata, Elasmobranchii and Osteichthyes were identified to species level where possible, or forwarded to the Queensland Museum for identification. Taxa have been listed in Jones and Derbyshire (1988).

Substrate samples were obtained at all sample sites in November 1985 and July 1986, using a small bucket dredge. Sediment size composition was measured and documented after Folk (1974).

#### Data Analysis

Species frequencies were calculated, and those present in fewer than 5% of samples taken in 1985 were omitted from subsequent analysis. To facilitate comparison between trawl samples, the numbers of individuals for the species remaining were standardized as the natural log of the number caught in the starboard net per hour of trawling.

The PATN programme package (Belbin 1988) was used for cluster analysis. Quasi-metric Bray-Curtis measures were calculated (Bray and Curtis 1957) and a hierarchic fusion of the matrix was performed using unweighted pair-group arithmetic averages with beta set at  $-0.1$  (Belbin, personal communication) to produce cluster groups. Ordination via multidimensional scaling was used to assist interpretation of temporal and spatial relationships (Faith *et al.* 1987; Belbin 1988, pp. 194-8). Cramer measures (Lance and Williams 1977) were used to identify species which contributed most significantly to the classification.

Table 1. Position and characteristics of sites sampled in 1986, Great Barrier Reef

Site No.	Position	Depth (m)	Distance from shore (km)	Proximity to nearest reef (km)	Mean particle size ( $\phi$ )	Organic carbon (%) <sup>A</sup>
1	18°27.5'S, 146°22.5'E	17	4.5	31.5	6.70	8.83
2	18°27'S, 146°25.5'E	23	9	26	2.78	4.40
3	18°23'S, 146°32.5'E	35	20	13	0.93	3.51
4	18°20.5'S, 146°38'E	42	31.5	4.5	2.36	4.81
5	18°17.5'S, 146°42'E	56	40	1	2.63	4.97
6	18°28.5'S, 146°48'E	53	50	4	2.63	4.90
7	18°33.5'S, 146°58.5'E	49	70	4.5	1.35	5.22
20	18°40.5'S, 146°52.5'E	44	53.5	17.5	1.88	4.09
21	18°19.5'S, 146°40'E	44	35	3	1.69	3.79
22	18°22.5'S, 146°43'E	49	40.5	0.5	1.97	5.32
23	18°26'S, 146°47'E	53	48	2.5	2.85	4.19
24	18°33'S, 146°48'E	43	50	10	1.71	4.76

<sup>A</sup> After J. W. A. Robertson (unpublished data).

## Results

### Sample Site Data

Details of sample site position, depth, distance from shore and nearest coral reef, mean substrate particle size and organic carbon content are given in Table 1. Sediments from inshore sites were characterized by fine particle size and high organic content, possibly of terrigenous origin. Sample sites in the midshelf and near-reef areas had substrates with larger grain size and lower organic carbon content; these may have been of biogenic origin. Depth, distance from shore and mean particle size of sediments were confounded characteristics of the sample sites (Table 1).

### Fauna

Specimens collected from January 1985 to December 1986 represented nine phyla, 18 classes, 158 families and 477 species or species complexes (Jones and Derbyshire 1988). The majority of species were represented by only a few individuals. Fewer than 15 species represented over 80% of all individuals collected (Fig. 2).

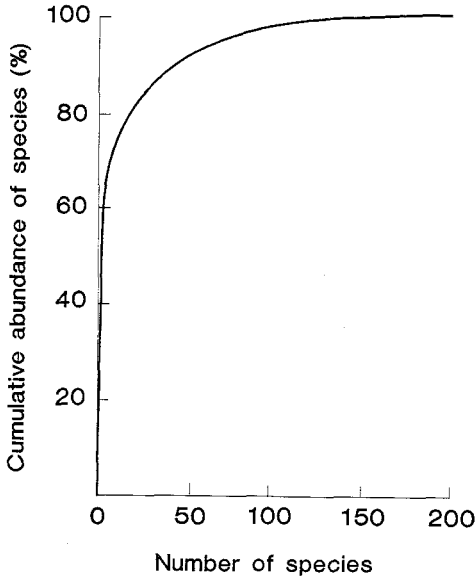


Fig. 2. Relationship between the cumulative abundance of all animals sampled (%) and the number of species.

Table 2. Percentage breakdown of demersal trawl fauna by class, based on numbers of individuals

Phylum	Class	1985	1986
Chordata	Asciacea	1	<1
	Osteichthyes	41	34
Arthropoda	Crustacea	39	54
Echinodermata	Crinoidea	<1	<1
	Asteroidea	1	<1
	Ophiuroidea	<1	<1
	Echinoidea	16	7
	Holothuroidea	<1	<1
Mollusca	Gastropoda	<1	<1
	Bivalvia	3	3
	Cephalopoda	1	1

The gross composition of trawl by-catch from common sites sampled in 1985 and 1986 varied considerably. The percentage of individuals in Crustacea increased in 1986 while the percentage in Osteichthyes and Echinoidea decreased (Table 2). Other classes of trawl fauna were essentially unchanged.

The twelve most abundant species have been ranked by abundance in the 1985 and 1986 samples (Table 3). There were some differences in these rankings between years. Numbers in both years were dominated by crustaceans, particularly the non-commercial prawns (*Metapenaeopsis* spp. and *Trachypenaeus* spp.); however, in 1985 the flatfish

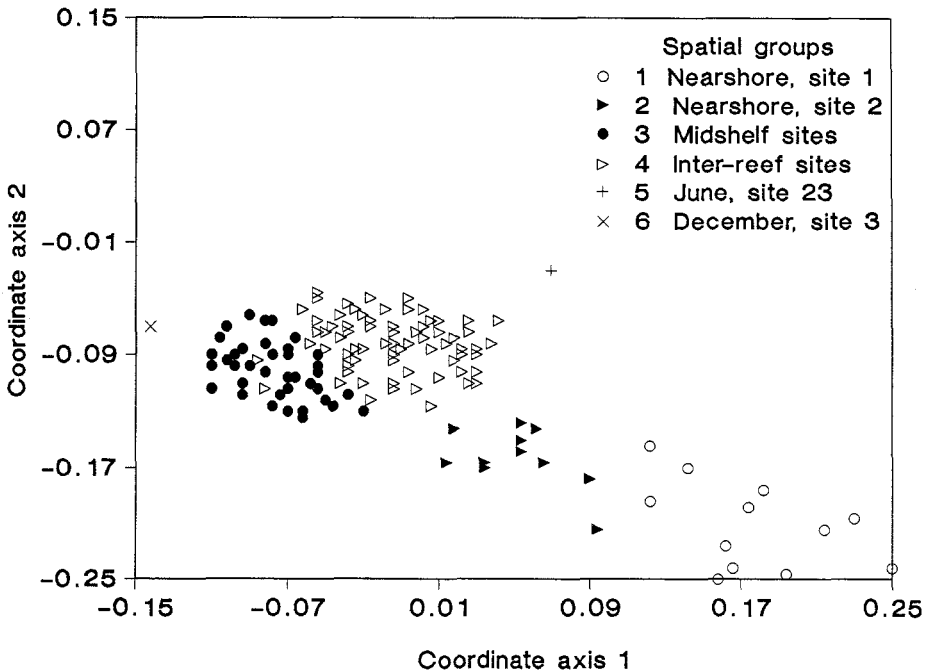
**Table 3. Twelve most numerous species in demersal trawl fauna (ranked by numerical order in 1985)**

Species	Rank	
	1985	1986
<i>Metapenaeopsis</i> spp. (Crustacea)	1	1
<i>Maretia planulata</i> (Echinodermata)	2	4
<i>Engyprosopon grandisquama</i> (Osteichthyes)	3	7
<i>Trachypenaeus</i> spp. (Crustacea)	4	3
<i>Portunus tenuipes</i> (Crustacea)	5	2
<i>Paramonacanthus japonicus</i> (Osteichthyes)	6	6
<i>Upeneus</i> sp. 1 (Osteichthyes)	7	9
<i>Amusium balloti</i> (Mollusca)	8	10
<i>Portunus rubromarginatus</i> (Crustacea)	9	13
<i>Lepidotrigla calodactyla</i> (Osteichthyes)	10	16
<i>Portunus argentatus</i> (Crustacea)	11	8
<i>Nemipterus celebicus</i> (Osteichthyes)	12	5

*Engyprosopon grandisquama* and the urchin *Maretia planulata* were amongst the three highest ranking species. These species were ranked 4th and 7th in abundance in 1986.

*Temporal v. Spatial Effects*

Ordination of all samples taken during 1986 revealed three major cluster groups (Fig. 3). These groups were: all samples taken at nearshore site 1 (group 1), those taken at site 2 (group 2), and those taken elsewhere. Spatial effects were therefore far more important than temporal effects in the formation of cluster groups. The classification of sites was, on the

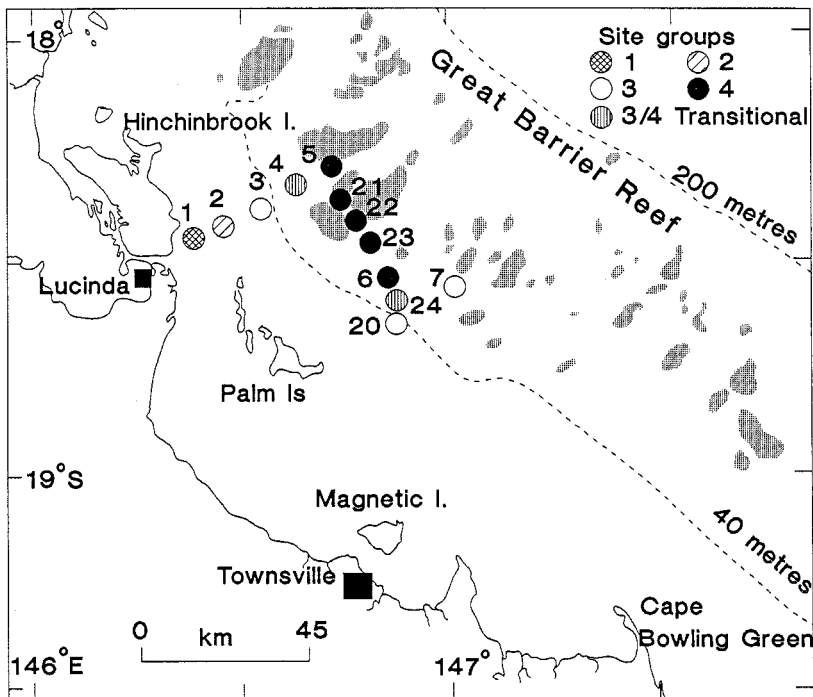


**Fig. 3.** Ordination of 1986 samples showing spatial and temporal relationships.

**Table 4. Summary of results of temporal/spatial analysis of 1986 samples at trawl sites**  
 Cluster groups represented by their group number (1-4), singleton groups represented by x, missing samples by blanks

Month	Site											
	1	2	3	4	5	6	7	20	21	22	23	24
Jan.	1	2	3	3	4	4		3	3	4	4	3
Feb.	1	2	3	3	4	4		3	4	4	4	4
Mar.	1	2	3	4	4	4		3	4	4	4	4
Apr.	1	2	3	4	4	4		3	4	4	4	4
May	1	2	3	4	4	4		3	4	4	4	4
June	1	2	3	3	4	4	3	3	4		x	4
July	1	2	3	4	4	4	3	3	4	4	4	4
Aug.	1	2	3	4	4	4	3	3	4	4	4	3
Sept.	1	2	3	3	4	4		3	4	4	4	4
Oct.	1	2	3	4	4	4	3	3	4	4	4	3
Nov.	1	2	3	3	4	4	3	3	3		4	3
Dec.	1	2	x	4	4	4			4	4	4	4

whole, consistent throughout the year of study (Table 4). Removal of the nearshore sites 1 and 2, which dominated the analysis, revealed two other major groupings. Sites 3, 7 and 20, all midshelf sites, consistently grouped together (group 3). The inter-reef sites 5, 6 and 21-23 formed a second group (group 4; Figs 3 and 4). Two sites (4 and 24) did not group consistently throughout the year. In some months these sites were associated with the midshelf group, and in others with the inter-reef group. After the manner of Watson



**Fig. 4.** Classification of trawling sites into site groups.

**Table 5. Species characteristic of temporal/spatial groups in demersal trawl fauna**  
(C) Crustacea, (O) Osteichthyes and (M) Mollusca

Species	Cramer value	F value	Log of mean catch rate in each group					
			1	2	3	4	5	6
(O) <i>Nemipterus celebicus</i>	0.91	123.30	—	0.76	4.34	4.99	—	6.04
(O) <i>Epinephelus sexfasciatus</i>	0.88	84.96	1.52	2.38	—	—	—	—
(O) <i>Pomadasys trifasciata</i>	0.85	65.58	2.10	0.10	—	—	—	—
(C) <i>Portunus tenuipes</i>	0.85	65.40	—	1.30	4.30	5.69	3.61	5.09
(C) <i>Metapenaeopsis</i> spp.	0.84	63.33	1.52	1.55	6.00	6.39	3.66	—
(O) <i>Saurida tumbil</i>	0.84	62.32	2.73	0.45	—	0.09	—	—
(O) <i>Upeneus sundiacus</i>	0.82	53.13	—	1.96	—	—	—	—
(C) <i>Penaeus semisulcatus</i>	0.82	52.39	1.85	1.94	—	—	—	—
(O) <i>Apogon quadrifasciatus</i>	0.82	51.46	4.22	2.03	0.38	0.17	—	—
(O) <i>Pseudorhombus elevatus</i>	0.81	47.53	2.03	3.45	0.18	0.11	1.61	—
(O) <i>Apogon poecilopterus</i>	0.80	45.61	3.76	2.16	0.15	0.25	—	—
(O) <i>Portunus argentatus</i>	0.78	40.69	0.13	—	0.78	4.26	3.22	—
(C) <i>Penaeus longistylus</i>	0.77	37.85	—	—	4.06	3.51	—	4.17
(O) <i>Parapercis nebulosa</i>	0.76	34.83	—	—	3.73	2.17	—	—
(O) <i>Repomuscenus belcheri</i>	0.75	33.50	1.25	3.91	0.50	0.11	—	—
(O) <i>Minous versicolor</i>	0.75	33.45	—	—	—	0.09	—	4.17
(O) <i>Scolopsis taeniopterus</i>	0.74	31.36	—	2.28	—	0.03	—	—
(O) <i>Euristhmus nudiceps</i>	0.74	30.58	0.09	3.05	—	0.43	—	—
(O) <i>Terapon theraps</i>	0.73	28.17	1.76	1.31	0.06	—	—	—
(O) <i>Paramonacanthus japonicus</i>	0.72	27.42	0.13	1.60	4.54	3.87	1.10	7.21
(C) <i>Charybdis truncata</i>	0.72	27.28	5.16	4.03	0.62	1.37	—	—
(O) <i>Nemipterus hexodon</i>	0.72	26.61	2.70	2.13	0.34	0.13	—	3.50
(M) <i>Amusium pleuronectes</i>	0.71	26.53	1.47	3.12	0.05	0.17	—	—
(O) <i>Torquigener whitelyi</i>	0.71	25.23	0.83	2.13	—	—	—	—
(O) <i>Orbonymus rameus</i>	0.70	24.61	—	—	2.71	0.32	—	—

and Goeden (1989), these sites could be described as transitional in nature. They were geographically positioned between those which grouped consistently with the midshelf group, and those in the inter-reef group (Fig. 4). There were also two samples collected in 1986, one in June (site 23, group 5; Fig. 3) and the other in December (site 3, group 6; Fig. 3), which formed singleton groups. The June 1986 sample at site 23 was exceptionally small (2 kg); hence, the entire catch formed the sample for that month. The small catch could have resulted from partial failure of the trawl gear. The weight of the total catch of the December 1986 sample from site 3 was unusually high at 153 kg.

These largely spatial groups have been characterized by those species most important in their formation on the basis of Cramer measures (Table 5). Group 1 (site 1) had large numbers of *Pomadasys trifasciata* and *Saurida tumbil* which were rare elsewhere, whereas group 2 (site 2) samples had large numbers of several species including: *Upeneus sundiacus*, *Repomuscenus belcheri*, *Scolopsis taeniopterus*, *Euristhmus nudiceps*, *Amusium pleuronectes* and *Torquigener whitelyi* (Table 5).

In addition to these species, the two nearshore groups also had much higher numbers of *Epinephelus sexfasciatus*, *Penaeus semisulcatus* (grooved tiger prawn), *Terapon theraps*, and *Charybdis truncata* than those groups which represented offshore sites (Table 5).

Compared with the nearshore sites, the offshore sites (groups 3 and 4; Table 5) had high numbers of the fish *Nemipterus celebicus*, *Parapercis nebulosa* and *Paramonacanthus japonicus*. The crustaceans *Metapenaeopsis* spp. (coral prawns), *Penaeus longistylus* (red spot king prawn) and *Portunus tenuipes* were also relatively more abundant at the offshore sites than at the inshore sites. The inter-reef group had characteristically high numbers of the crab *Portunus argentatus* compared with the nearshore sites.

The singleton groups 5 and 6 came from trawl samples dominated by high numbers of relatively few species such as *N. celebicus* and *P. japonicus* (Table 5).

### Temporal Effects

Temporal effects were examined by classification. Data from the seven sites which were sampled throughout 1985 and 1986 were grouped from each month's samples to give 24 entities. This process revealed cluster groups of sample months (Fig. 5) that demonstrated

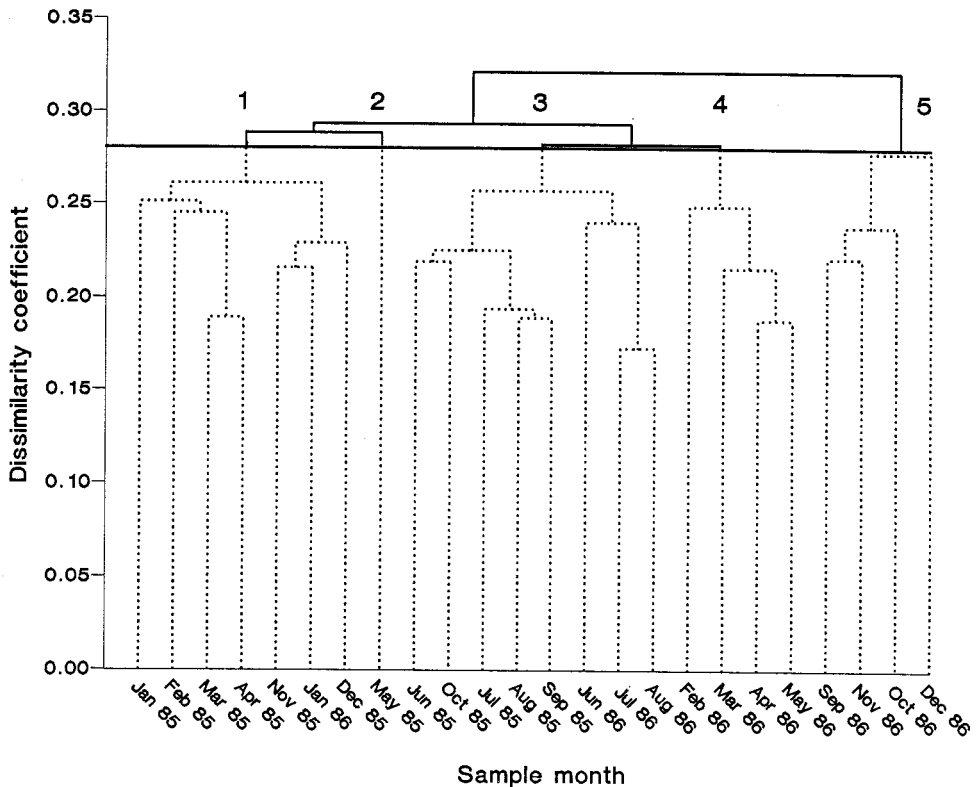


Fig. 5. Temporal relationships from summation of fauna from all sites sampled over 24 months.

both seasonal and inter-annual trends (Fig. 6). Five groups were identified: January–April 1985 and December 1985–January 1986 (group 1); May 1985 (group 2); June–October 1985 and July–August 1986 (group 3); February–May 1986 (group 4); and September–December 1986 (group 5). These could be further characterized as two ‘wet’ season groups (groups 1 and 4; Fig. 6) that occurred approximately from late December to April, and two ‘dry’ season groups (groups 3 and 5; Fig. 6). Samples from similar monthly periods from the two sample years formed similar, yet separate, groups. Temporal group 2 consisted only of May 1985.

These temporal groups are again characterized by their contributing species according to their derived Cramer values (Table 6). Samples taken during May 1985 (group 2) had greater abundances of *Upeneus sulphureus* and *Tetrosomus gibbosus* than at other times (Table 6). Three scorpaenid species: *Tetraroge leucogaster*, *Minous trachycephalus* and *Inimicus caledonicus* were not present in these samples, while present at all other sampling occasions. *Metapenaeopsis* spp. were relatively less abundant in group 2 than in all other temporal groups.



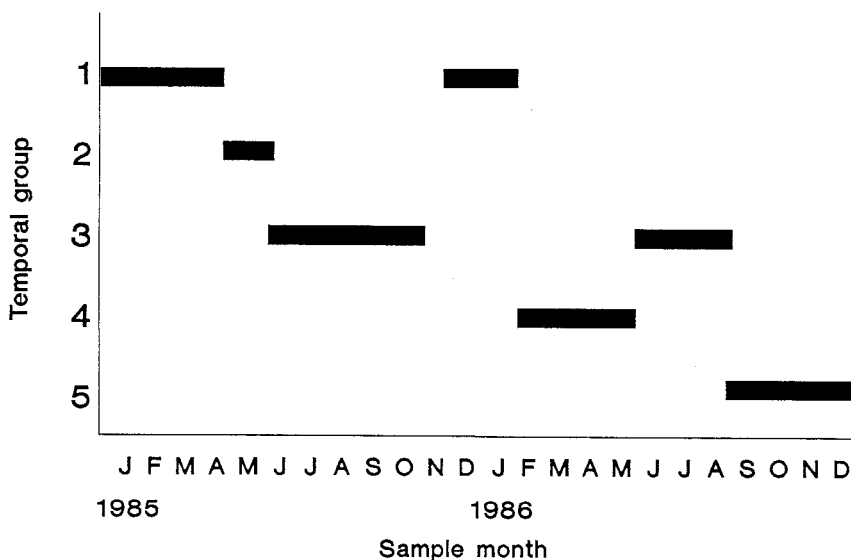


Fig. 6. Time chart showing temporal relationships for the 24-month period 1985-86.

Table 6. Species characteristic of temporal groups in demersal trawl fauna  
(C) Crustacea, (E) Echinodermata, (O) Osteichthyes and (M) Mollusca

Species	Cramer value	F Value	Log of mean catch rate in each group				
			1	2	3	4	5
(O) <i>Samaris cristatus</i>	0.87	14.28	0.23	—	0.17	0.51	0.95
(C) <i>Portunus rubromarginatus</i>	0.86	14.04	1.64	2.60	2.86	3.10	2.04
(O) <i>Nemipterus tolu</i>	0.81	9.15	0.40	0.64	0.52	1.80	0.14
(O) <i>Upeneus tragula</i>	0.79	8.04	0.32	0.57	1.51	0.51	0.98
(C) <i>Portunus gracilimanus</i>	0.79	8.00	0.64	1.41	0.47	1.11	—
(C) <i>Metapenaeopsis</i> spp.	0.78	7.40	4.79	2.85	4.47	4.16	5.07
(C) <i>Portunus pelagicus</i>	0.77	7.11	0.85	0.26	0.44	1.46	0.19
(O) <i>Parapercis nebulosa</i>	0.76	6.31	1.17	1.62	1.86	2.54	1.65
(O) <i>Tetrosomus gibbosus</i>	0.75	6.16	—	0.34	—	0.09	—
(E) <i>Stellaster equestris</i>	0.75	6.12	0.28	1.54	0.18	0.30	0.53
(O) <i>Pseudorhombus spinosus</i>	0.75	6.02	2.22	1.78	1.74	2.48	1.34
(C) <i>Trachypenaeus</i> spp.	0.74	5.78	4.15	1.90	4.53	4.87	3.89
(O) <i>Tetraroge leucogaster</i>	0.74	5.69	0.04	—	0.75	0.47	0.37
(O) <i>Dactyloptena papilo</i>	0.74	5.64	1.72	2.95	1.76	0.90	0.44
(M) <i>Amusium pleuronectes</i>	0.73	5.35	1.18	0.26	0.59	1.29	0.72
(O) <i>Engyproson grandisquama</i>	0.72	5.24	3.35	3.11	3.83	4.02	2.95
(C) <i>Charybdis truncata</i>	0.72	5.00	1.95	2.46	1.43	2.83	1.49
(O) <i>Minous trachycephalus</i>	0.71	4.94	0.22	—	1.08	0.66	0.85
(O) <i>Inimicus caledonicus</i>	0.70	4.61	0.73	—	1.28	0.57	0.64
(O) <i>Upeneus sulphureus</i>	0.70	4.58	0.68	2.20	0.76	0.48	0.18
(O) <i>Euristhmus nudiceps</i>	0.70	4.55	0.29	0.26	0.60	0.92	0.56
(O) <i>Terapon theraps</i>	0.70	4.48	0.89	1.89	0.43	0.76	0.26

## Discussion

The faunal assemblage sampled in this study was tropical western Pacific in affinity and dominated by small fishes (Jones and Derbyshire 1988). Few studies of the Great Barrier Reef region have included all the faunal groups included in Table 2 but it appears

that this breakdown may be typical of the tropical north-eastern Australian coastal waters. Some crustacean species were the most numerous taxa in the trawl catch. Species of *Metapenaeopsis* and *Portunus* were also found to be abundant on the tropical continental shelf of north-western Australia (Ward and Rainer 1988).

The major change in the breakdown of taxa by class between 1985 and 1986 was the proportionate increase of crustacean abundance, and corresponding decrease in bony fishes and echinoderms (Table 2). The crustacean species which were relatively more abundant in 1986 included the portunid *P. tenuipes*, and prawns in the genus *Trachypenaeus* (Table 3). The echinoderm *M. planulata* and the flatfish *E. grandisquama* were relatively less abundant in the by-catch between 1985 and 1986. Catches of *M. planulata* were erratic and our samples showed that it was clumped in distribution. Jones and Derbyshire (1988) found that it was discontinuously very numerous and sometimes dominated the trawl catch. They did not believe that its occurrence represented a static '*M. planulata*' community.

There was some evidence of interannual faunal variation (Tables 2 and 3). Unfortunately, two years' data are not likely to characterize the normal extent of interannual variation. We concur with Flint and Younk (1983) who found that the literature included few long-term data sets with which to evaluate the normal dynamics of benthic communities over extended periods. Williams (1986) found that the largest interannual variation in reef fish communities was no greater than the observed inter-reef variability at a particular time. He suggested that some species may be inherently more variable than others and that this was in part due to a year-to-year variability in recruitment (Williams 1982). Riesen and Reise (1982) found that substantial changes had occurred in the faunal composition at sites revisited after 55 years, and attributed these to human interference. Rainer (1984) reported that the relative abundances of dominant species varied substantially over seasons and suggested that this probably occurred over longer periods as well. In general, benthic faunal distributions may vary considerably in time and space. This may be a consequence of variation in recruitment, of patchy species occurrence related to the overall heterogeneity of the benthic habitat such as variability in bottom sediment and man-induced effects (Flint and Younk 1983), or of chance occurrences, as has been suggested by Sale (1978) for some reef-dwelling fish.

In the present study, spatial variation was much more pronounced than seasonal variation. Flint and Younk (1983) also concluded that spatial variability was much greater than temporal variability for benthic communities. Williams *et al.* (1988) found that almost all taxa of larval fish showed significant station  $\times$  cruise interactions. Spatially dependent physical factors such as water depth and topographical complexity had more effect on coral reef fish communities than did temporal effects such as variability in their recruitment (Williams 1982). Williams (1986) reported that differences in fish species abundances between reefs within a shelf location (localized spatial effects) were similar to, or greater than, temporal variation within reefs but were much less than differences across the continental shelf (large-scale spatial effects).

This study showed clear differences between the two nearshore sites (sites 1 and 2, Fig. 4). These were, however, grouped together in the 'coastal' site assemblage in a previous study (Watson and Goeden 1989). Watson and Goeden's study, based on sites samples in 1985 (Fig. 1), covered greater geographical range but spatial resolution in the proximity of the reef was poorer. The use of a range of sites (21-23, 6, 24 and 20; Fig. 4) that grade away from the reef was intended to determine whether an assemblage more closely related to that of the reef itself existed in close proximity to the reef. Instead, this series of sites demonstrated how similar the inter-reef fauna remains, regardless of proximity to the reef, in the depth range of 40-55 m and an off-reef distance of 0.5 to 10 km (Fig. 4).

The spatial segregation of faunal groups corresponded closely with clines in depth, distance from shore, and substrate composition. As these parameters were closely linked, a single determinant of the faunal associations could not be identified. The species which made up each faunal association may have adapted to the environmental conditions which

prevailed at those sample sites. Therefore, there must have been sufficient environmental variation in the 70-km transect from the shore to the reef to support the segregated faunal groups identified.

Dredge (1989) examined the trawl fauna from the same inter-reef sites and found very little similarity with the true reefal community described by Russell (1983), despite sampling stations being as close as 0.5 km to reefs. This suggests that other physical features such as sediment type, and not simply proximity to the reef, are the key determinants of the distribution of these benthic fauna. This contention is supported by the work of Somers (1987) who showed that the distribution of penaeid prawns was influenced by both sediment composition and depth in the Gulf of Carpentaria. Macrobenthos community composition correlated well with sediment data in New Caledonia (Chardy *et al.* 1988).

Depth-delineated community zonation has been identified for Central Great Barrier Reef waters (e.g. Done 1982; Williams 1982). Birtles and Arnold (1989) found that a major separation of mollusc and echinoderm communities occurred between 22 and 26 m depth. They also reported this depth delineation for crustaceans, bryozoans, demersal fishes, ascidians and algae (Birtles and Arnold 1983). Our nearshore sites (1 and 2) were delineated from offshore site groups in a similar way. Birtles and Arnold (1983) found, as we did, that their offshore sites further differentiated into two groups. Birtles and Arnold (1989) believed that abundant coral rubble and algae at their middle-shelf sites (inshore zone) supported a higher diversity and abundance of echinoderms and molluscs than elsewhere. Their faunal spatial zones corresponded with zones based on sediment characteristics (Belperio 1983) and when reported had remained stable for at least 6 years.

Maxwell's (1968) sediment studies of the Great Barrier Reef described a 'nearshore' (0–9 m depth) and an inner-shelf zone (9–37 m depth). Watson and Goeden (1989) found a correspondence between depth, sediment particle size and carbonate content (after Maxwell 1968) with zones or site assemblages. Rainer and Munro (1982) found three cluster site groups: nearshore (2–5 m depth), shallow offshore (6–14 m depth) and deep offshore (15–35 m depth) when they observed abundances of demersal fish and cephalopods in the Gulf of Carpentaria. They related these zones to physical factors such as depth and salinity, and found, as our study confirms, that such zones tended to grade into one another, often shared many species, and did not always remain constant through time.

Analysis of spatial differences was dominated by the strong differences between site 1 and site 2, and between these sites and all others. Differences between the midshelf and inter-reef site groups were minor by comparison.

Analysis of temporal patterns in the fauna demonstrated both seasonal patterns ('wet' and 'dry' season faunal associations) and year-to-year variation between 1985 and 1986. Apparent separation in these groupings between the two study years can be explained by substantial variation in the catch of some faunal groups between years as described above.

Significant temporal variation has been reported in the structure of reef fish assemblages at the local scale (Williams 1986). Watson (1984) reported that significant changes occurred in the abundance and relative dominance of some families of tropical demersal fishes through a period of several months. These authors have suggested that the constancy of spatial community patterns cannot be assumed.

Rainer (1984) reported seasonal patterns in catch rate and species richness per site in Gulf of Carpentaria trawl fauna, with highest values found nearshore in summer, and offshore in autumn and winter. He believed that these changes were associated with the movements of inshore species to deeper water at times of high temperature and reduced salinities. Many species caught in benthic trawl gear are, however, small and slow-moving, otherwise they would not be caught. They appear to be distributed along, and perhaps constrained by, such physical gradients as depth, sediment particle size and carbonate content (Watson and Goeden 1989). The largest source of seasonal variability in community structure is likely to be recruitment variability rather than mass migrations of the relatively immobile adult forms. It is possible that smaller species, presumed to be slower moving, are

most affected by seasonal variability in habitat. Ward and Rainer (1988) found that most decapods that exhibited seasonal variability were smaller than those whose numbers remained relatively stable over time.

Rainer (1984) reported that seasonal changes in abundance were greatest in the estuarine species. Nearshore coral communities also showed greater seasonal variation than those offshore. These nearshore coral communities were also the most affected by periods of reduced salinity, increased siltation and possibly nutrient enrichment, all resulting from the outflows of nearby large rivers (Done 1982). Well-defined onshore-offshore salinity gradients have been described for the Central Great Barrier Reef region which correspond to the two distinctive 'wet' and 'dry' seasons (Brandon 1973).

We expected to find seasonal variation corresponding to the tropical 'wet' and 'dry' seasons in nearshore communities, with offshore communities remaining comparatively unaffected. Offshore communities might, however, be affected by other seasonal events such as the cross-shelf intrusion of nutrient-rich water from adjacent deeper areas. Williams *et al.* (1988) observed the latter effect primarily in summer when blooms of diatoms were associated with this upwelling season. Watson and Goeden (1989) found that changes in species abundances between the 'wet' and 'dry' seasons caused 'transitional' sites to change their affiliation between the 'inshore' and 'inter-reef' site groups.

In the present study there was little clear pattern in the abundance of species between the 'wet' and 'dry' seasons (Table 6). There were, however, higher abundances in the 'wet' season than in the 'dry' season for some species characterizing the nearshore groups (Table 5). Examples of this were *A. pleuronectes*, *C. truncata*, and *T. theraps*. Though the effect of summer rains may influence the abundance of some inshore species, a causal relationship cannot be assumed in the absence of confirmatory data.

In May 1985, trawl sampling occurred more than 8 days after the new moon because of adverse weather. Night-time illumination from the moon at this time was considerably brighter than in the other 23 months of samples. This could explain why these samples formed a separate temporal group (Fig. 6).

An insight into the spatial and temporal variability of benthic communities is a prerequisite in the interpretation of research on the effects of trawling in the Great Barrier Reef Marine Park. In addition to socio-economic factors, management zonation of the Park must consider the underlying spatial structure of the benthic community. Only with continued investigation into the natural range of variability in these communities can we hope to differentiate the effects of man's activities.

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