

THE MACROBENTHOS OF THE  
MIDDLE BANKS AREA  
OF MORETON BAY\*

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ABSTRACT

This study was undertaken to quantify certain aspects of the benthic biota of the Middle Banks area, with a view to predicting the effects of sand removal for use as 'fill' in enlarging Brisbane Airport. Fifty-seven sites lying roughly in a rectangle 9 km  $\times$  1.5 km were sampled at 3 month intervals from September 1972 to June 1974. Each sample comprised duplicate catches with an 0.1m<sup>2</sup> Smith-McIntyre grab. The northern sites lie in the area of the proposed excavation and the southern ones (in deeper water) in a prawn fishing area. There is a sharp division between coarser northern and finer southern sediments, and suggestions of a progressive coarsening of sediments during the study.

A total of 468 'species' were originally sorted from the collections, a noticeably richer and more diverse biota than Bramble Bay (on the western side of Moreton Bay). To reduce the size of the data matrix to analyse, the first classifications were undertaken with successive lots of 50 taxa  $\times$  57 sites  $\times$  8 times. Sites were clearly separable into northern and southern subareas and the same broad area pattern was generated by abundant and less abundant species. Subsequent analyses involved separate consideration of the two sub-areas, and eventually 12 site-groups were recognised with their characterising species. Effects on the biota of current dredging of a navigational channel are detectable.

There were problems in separating microtopographical changes, due to inaccurate relocation of sites, from chronological changes. It appears that of the species investigated about 10% have recurrent seasonal patterns, about 40% have sequential patterns, and about 45% have obscure patterns, possibly influenced by microtopography. The sequential patterns are akin to those obtained in preflood data from Bramble Bay, with occupancy of appropriate areas for tolerably brief periods (e.g. 6 months) and then giving way to other species. Few of the sequential breaks appear related to abiotic conditions.

It is suggested that almost the entire biota is in a continual state of flux, with most species either annuals or 'subannuals', with few attaining sexual maturity in the area, with the population dependent upon recurrent recruitment, and with intermittent but severe predation by fish as an important possibility. The consequences of temporary human disturbance to the area are discussed.

A proposal to enlarge Brisbane Airport would involve 'filling' a considerable area with fine sand from the Middle Banks portion of Moreton Bay. The present work was requested by the (then) Commonwealth Department of Housing and Construction and by the Queensland Department of the Co-ordinator General hopefully to predict

the effects of removal of the sand on the benthos.

There is already human interference in the Middle Banks area, with the south-western portion kept dredged to 12 m for shipping purposes. This breaks an otherwise W shaped area of banks shallower than 10 m and allows the considerable

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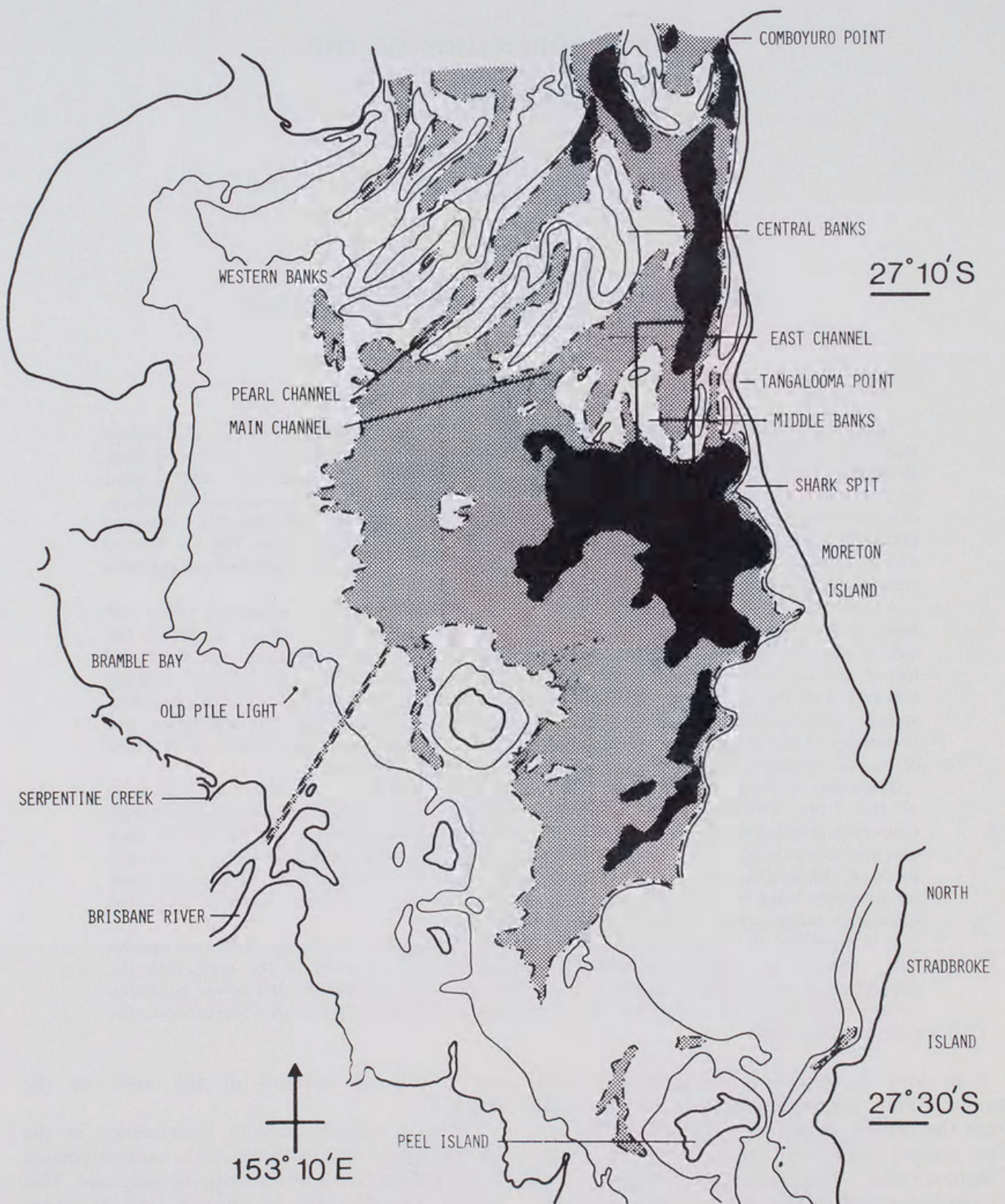


FIG. 1: Moreton Bay showing localities mentioned in the text, sampling area enclosed in rectangle. Depths from Admiralty chart 236 of 1973: > 20 m dark stipple, 10-20 m pale stipple, 5 m thin contin. line, high water mark thick contin. line.



tidal currents in the area more easy access to the deeper waters to the south.

The area initially selected for dredging lay on the eastern edge of the Middle Banks, abutting on the East Channel (see Fig. 1). The effects of dredging this area are likely to be numerous. First, benthic organisms and their environment would be removed from a relatively small area, and there would be an interval before this was recolonised. Secondly, the local topography would alter as sediments filled the excavated area. Thirdly, if the

excavation led to generally increased current velocities in the area as a whole, it could lead to general erosion. While such erosion could facilitate navigation it could affect the benthos more widely, and possibly could affect the adjacent shores of Moreton Island. Fourthly, material suspended in the water during dredging would be distributed by the tides. The most important effects could well be due to the slower flood tide which would carry material into the deeper waters to the south. Here there is known to be a rich benthos (Stephenson, Williams and

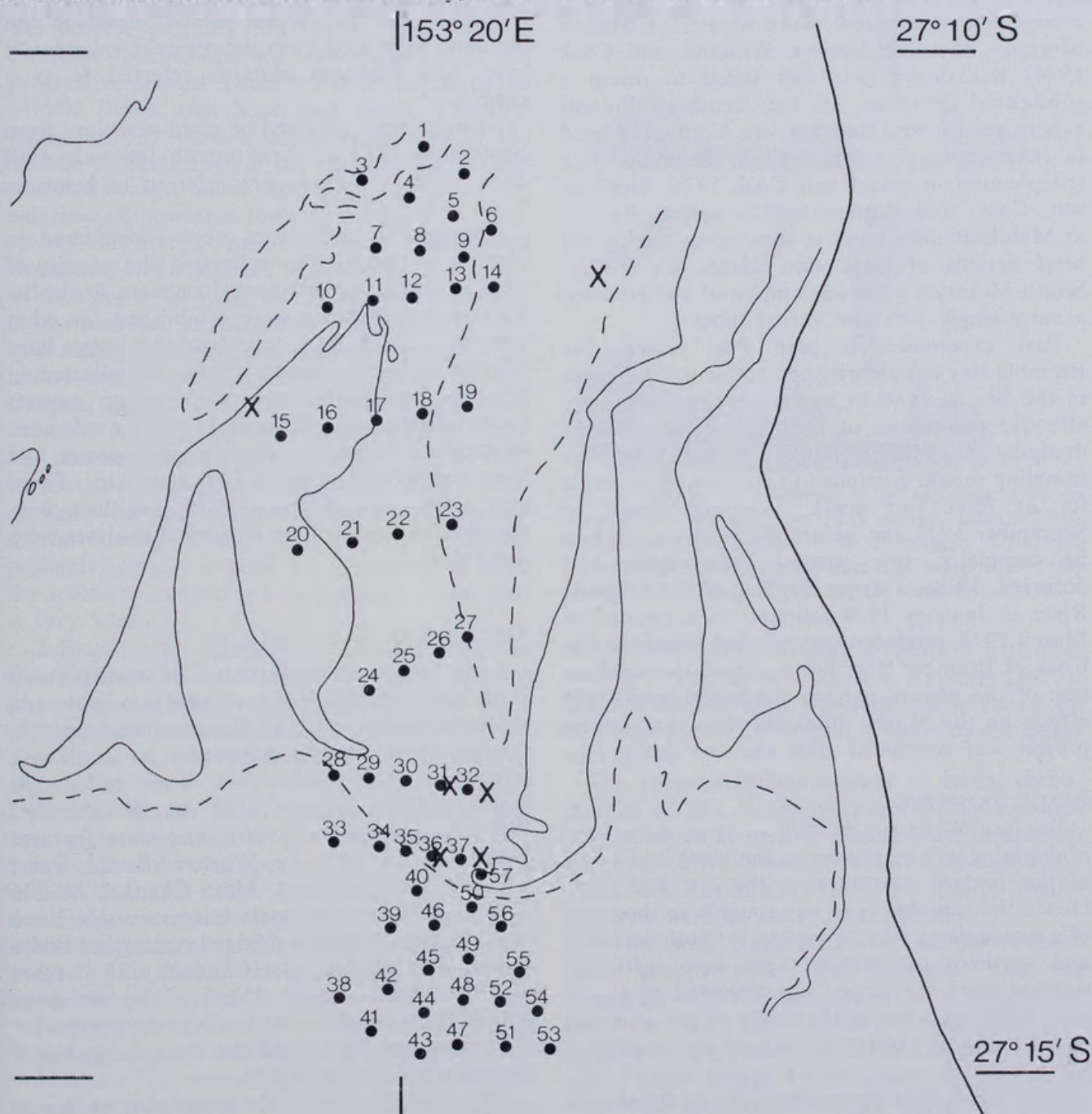


FIG. 2: Location of sites within sampling area. Depths from 1972 survey by Queensland Dept. of Harbours and Marine: 10 fm broken line, 5 fm thin contin. line, high water mark thick contin. line. Sites as solid circles, beacons or buoys as crosses.



Lance 1970) and there is also a seasonal fishery for penaeid prawns.

After considering the above, we advised against dredging near the existing dredged break in the banks because it was felt this would give maximal erosion and most widespread biotic effects and it is gratifying to record that this advice was accepted. The position tentatively selected was in the vicinity of our sampling sites 22, 25, and 26, (see Fig. 2).

A past survey of the area (Stephenson, Williams and Lance 1970) was made with a naturalists dredge and subsequent work at Peel Island in Moreton Bay (Stephenson, Williams and Cook 1974) has shown that this failed to reveal a substantial fraction of the benthos. Present experience showed that the van Veen grab used in near-concurrent studies in Bramble Bay (Stephenson, Raphael and Cook 1976, Stephenson, Cook, and Raphael 1977) was ineffective at Middle Banks except in some areas during the brief periods of slack tide. Hence an 0.1 m<sup>2</sup> Smith-McIntyre grab was employed and revealed a surprisingly rich and varied biota.

Past experience at both Peel Island and Bramble Bay has shown appreciable time changes in the benthos and to make even approximately effective predictions of the likely effect of sand dredging at Middle Banks, it was felt that sampling should continue at three month intervals for at least two years. Sampling began in September 1972 and before the work was due to be completed two natural catastrophes had occurred. These, a major flooding of the Brisbane River in January 1974 followed by a cyclone in March 1974, produced very marked effects on the biota of Bramble Bay, but preliminary examination of the present catches suggested only slight effects on the Middle Banks benthos, and so the project was concluded after the two years.

#### BIOTIC SAMPLING

Because of the rapid tidal currents, the effects of dredging will be greater to the north and south of the dredged area than to the east and west. Hence the sampled area was roughly in the form of a rectangle ca 9 km × 1.5 km. At both northern and southern extremities there were sufficient sighting marks for sites to be arranged on a grid ca 0.4 km apart but in the centre of the area due to a paucity of marks they lay on traverses ca 1 km apart.

Fifty-eight sites were originally sampled but because one (site 39) was overlooked on one occasion, for present purposes we consider 57 sites, with original sites 40–58 renumbered 39–57.

(Labelled specimens to be deposited in the Queensland Museum carry the original numbering.) The positions of the final sites are shown in Fig. 2.

Locations of sites were by horizontal sextant angles on conspicuous objects in the vicinity (landmarks or beacons) and inaccuracy in relocating sites is believed to be not greater than 50 m.

At each site on each occasion, duplicate catches were made with the 0.1 m<sup>2</sup> Smith-McIntyre grab. Catches were sieved through a final aperture of 1 mm and the two catches pooled, preserved and the biota separated from the residual sediment at base. The resultant biota is referred to as a sample.

Samples were obtained on eight occasions from September 1972 at three month intervals until June 1974, and these are referred to below as times 1–8.

Considerable difficulties were encountered in identifying species, this reflecting the paucity of work in similar environments in eastern Australia. Reference collections were established for what were adjudged to be species, and these were later referred either to named specimens collected in previous benthic surveys or to group experts (acknowledge later). In several cases the reference specimens belonged to more than one species, and these polyspecific taxa are indicated later. There were a few cases of 'oversplitting' and these were not apparent until all the numerical analyses were completed.

#### THE AREA OF SAMPLING

1. GENERAL DESCRIPTION: The northern exit from Moreton Bay consists of alternate banks and channels which, south of the narrowest portion, run generally from a north-east to south-west direction. This portion has been called the 'north-eastern corrugations' by Stephenson, Williams and Lance (1970). The main features from west to east are Western Banks, Pearl Channel, Central Banks, Main Channel, Middle Banks, and East Channel. Larger vessels leave Moreton Bay through a dredged cutting in Middle Banks, then via the East Channel until it fuses with the Main Channel. North of the narrowest portion there are extensive banks to the north-west of Comboyuro Point, and the main navigational channel runs to the NNW.

The southern part of the sampled area lies in the deepest portion of Moreton Bay, earlier called the 'basin' by Stephenson, Williams and Lance (1970). Depths are almost 30 m and here the tidal



current on the sea floor is likely to be negligible. The substratum contains obvious silt.

The general topography of the northern exit from Moreton Bay is suggestive of a basin c. 30 m deep which has been partially filled by sand. Maxwell (1970) states that wind and stream erosion as well as undercutting of the shore line have been responsible for large quantities of sand being carried westwards into Moreton Bay. Presumably Moreton Island has supplied the sand for the north-eastern corrugations.

While over a long period the Middle Banks area has become partially filled with sand, there is evidence that this has not been a continuous and progressive process. Three sets of soundings of the Middle Banks area have been made. The first made in 1865 show a considerable area of the Middle Banks shallower than 10 fm. The second soundings were made in 1946 and show an enlarged shallow area towards the south. A third set of soundings made by the Queensland Department of Harbours and Marine in relation to the Airport Scheme in 1972 show a reduction of the southern shallow area. This must be due to dredging the navigational channel. However the later soundings show that the portion of the East Channel deeper than 10 fm has become more extensive (see Fig. 3), and it seems likely that sand has been removed to the north. Throughout tidal currents are strong and underwater observations showed sand ripples c. 0.5 m high on the bottom in the vicinity of site 12 and these conditions probably apply to most of the northern sites. Here the sediment surface will be partially mobile and is very 'clean'.

2. SEDIMENTS: These were collected using the 0.1 m<sup>2</sup> Smith-McIntyre grab, with hand selection of an aliquot. (It was not appreciated at the times of collection that hand selection causes error, see Stephenson, Cook and Raphael 1977.) Samples were obtained in September 1972, September 1973 and March 1974. Analyses were by wet sieving as described in previous papers, using sieves of the following apertures in mm: 2.00, 1.00, 0.50, 0.25, 0.125, 0.063. The retained grades are described respectively as gravel = shell grit, very coarse sand, coarse sand, medium sand, fine sand, and very fine sand, with the material passing the finest sieve described as mud.

The data comprise a three-dimensional matrix of percentages of 7 sediments grades  $\times$  57 sites  $\times$  3 times. This was classified by a hierarchical agglomerative method (Bray-Curtis, group average) differing from the methodology for biotic data (see later) only in that sedimentary data were not transformed (they are already standardised by



FIG. 3: Depths of southern  $\frac{1}{3}$  of sampling area on successive surveys; top 1865 survey, middle 1946, bottom 1972. Depths: > 10 fm, stipple; 6 fm, thin contin. line; 3 fm, dotted line; high water mark, thin contin. line. Arrow, true north; scale line 1 km.

sample total). The method is identical with that used by Stephenson, Cook and Raphael (1977). Classification of sites by sediments is shown by dendrogram on Fig. 4a, and of times by sediments on Fig. 4b.

The sites-classification gives an initial dichotomy at ca 70% dissimilarity and the main groups were accepted at 10-25% dissimilarity. In contrast the times-classification gives an initial dichotomy at ca 6% dissimilarity and the groups finally accepted were at ca 4% dissimilarity.

In the sites classification of sediments three main groups were first accepted, and the subgroups of two of these explored for topographic coherence. Only one showed this and hence four sediment site-groups were finally accepted, and on Fig. 5 these groups are map-plotted. They form a general sequence from site-group 1 in the south-west, through site-group 2 as a transverse southern band to site-group 4 in the north. Site-group 3 consists of flanking sites mostly



forming a western wedge between site-groups 2 and 4.

Mean compositions of the sediments in the four site-groups are given in Table 1. In site-group 1 the modal grade of sediment is fine sand, followed by mud; in site-group 2 it is fine sand followed distantly by medium sand while in site-group 3 it is again fine sand but more closely followed by medium sand. The northern sediment site-group (4) differs markedly from the remainder in having medium sand as the modal group.

The mean composition of sediments in the three times are given in Table 1. This shows a progressive change towards coarseness over the period of investigation. It had been anticipated, following analyses on sediments in Bramble Bay, that the floods of January 1974 would have caused increased mudiness. By the time post-flood Middle Banks sediments could be collected there had been a cyclone. Wave action due to the latter could have been responsible for removal of mud and increased coarseness. Against this there is a distinct suggestion of progressive change.

TABLE 1: MEAN PERCENTAGES OF GRADES OF SEDIMENT IN SEDIMENT SITE-GROUPS AND SEDIMENT TIMES-GROUPS.

Sediment grade	Sediment Site-groups				Times		
	1	2	3	4	1 (Sept 72)	5 (Sept 73)	7 (March 74)
Mud	15.7	8.4	6.9	1.4	5.2	5.0	4.4
Very fine sand	4.4	1.9	1.7	0.1	1.0	1.2	1.0
Fine sand	76.0	78.7	59.8	13.4	40.6	36.9	33.8
Medium sand	3.6	12.9	31.7	83.6	52.0	56.1	59.6
Coarse sand	0.1	0.2	0.3	0.7	0.5	0.6	0.5
Very coarse sand	0.1	0.1	0.1	0.3	0.2	0.2	0.3
Gravel/shell grit	0.1	0.2	0.2	0.6	0.5	0.3	0.4

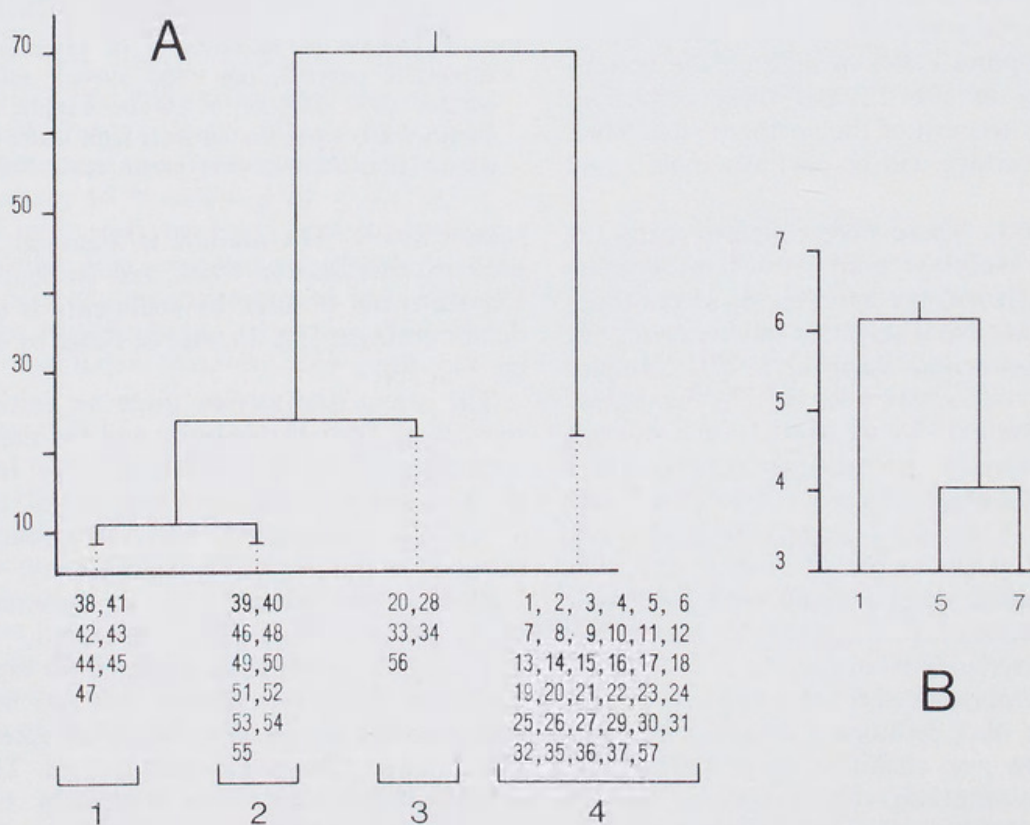


FIG. 4: Dendrograms showing classifications using sediment compositions as attributes: A of 57 sites, B of 3 times.



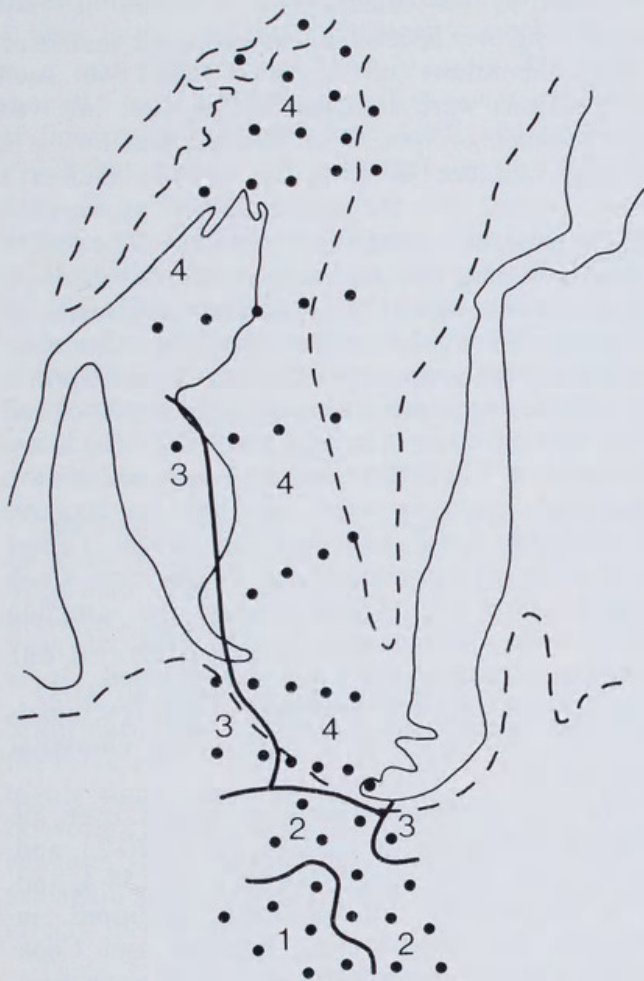


FIG. 5: Topographic distribution of the four sediment site-groups.

Further analyses were conducted, to determine in which sediment site-group the chronological changes were greatest. First, grades of sediments were reduced to five by fusion of coarse sand, very coarse sand and gravel. Next, in each sediment site-group the variance due to the three times in each sediment grade was obtained, and variances were then summated over grades. Results for sediment site-groups 1–4 were sequentially as follows: 10.08, 8.58, 220.52 and 42.06. There is greater variation in the two northern sediment site-groups (3 and 4) than in the two southern ones (1 and 2) with extremely high variance in sediment site-group 3.

3. HYDROGRAPHY: (a) Currents. No precise data are available on the extent of penetration of Pacific Ocean water into Moreton Bay and its mixation with the waters of the Bay. General observation suggests that surface water from outside the Bay penetrates to well beyond the sampled area on each tidal cycle.

Also no precise data are available on tidal currents. It is known that they flood from and ebb to the north and that surface currents are generally in excess of 1 km/hr apart from periods of slack water.

(b) Salinities. Data are available for Shark Spit ( $27^{\circ}17'S$ ,  $153^{\circ}22'E$ .) from a survey made by the CSIRO Division of Fisheries and Oceanography. The data from the deepest samples (*c.* 29 m) taken at Shark Spit have been reviewed by Stephenson, Cook and Raphael (1977). From August 1972 to July 1973 the salinity averaged  $34.5^{\circ}/_{\infty}$  and ranged from  $33.1^{\circ}/_{\infty}$  to  $35.3^{\circ}/_{\infty}$ . The variations showed a marked inverse relationship to rainfall in the catchment of the Brisbane River in the previous month.

From October 1973 to September 1974 the average salinity was  $33.7^{\circ}/_{\infty}$  and the range of  $32.0^{\circ}/_{\infty}$  to  $35.1^{\circ}/_{\infty}$ . There was a period of relatively low salinity (*c.*  $32.1^{\circ}/_{\infty}$ ) from February 1974 to August 1974 evidently due to the effects of the excessive runoff from the flood of January 1974 being prolonged by the rainfall associated with the cyclone of March 1974.

It is clear that the effects of the extreme climatic disturbances on the salinities were prolonged but relatively minor.

(c) Temperatures. Data equivalent to the above on water temperatures are: August 1972 to July 1973, mean  $22.25^{\circ}C$ , range  $17.2$ – $26.6^{\circ}C$ ; October 1973 to September 1974, mean  $21.79^{\circ}C$ , range  $15.9$ – $25.8^{\circ}C$ . Comparison with data average over the period 1931–50 at the Old Pile Light near the mouth of the Brisbane River suggests that from December 1972 until about December 1973 temperatures at Shark Spit were consistently about half a degree warmer than average.

#### BIOTIC DATA — ANALYSES INVOLVING ALL SPECIES

Many species were present in so few samples and in such small numbers that they are excluded from later analyses. These rarer species are important in aspects such as faunistics, species richness and diversity, and these and similar topics are dealt with in the present section.

FAUNISTIC COMPOSITION OF THE SAMPLES: A total of 468 taxa were obtained originally, and this reduced to 463 because of 'oversplitting'. Fifteen of the listed taxa are known to be polyspecific. All but the rare species are listed in the Appendix, together with the code numbers used throughout.



The number 463 compares with 420 taxa (excluding amphipods) from grab sampling an area of c. 3 km<sup>2</sup> near Peel Island (Stephenson, Williams and Cook 1974), 182 from an area of 30 km<sup>2</sup> in Bramble Bay (Raphael 1974) and 98 from Serpentine Creek (Stephenson and Campbell 1977).

Of the 463 taxa 31.8% were polychaetes, 27.9% crustaceans (10.6% decapods and 7.2% amphipods), 23.5% molluscs (10.8% gastropods and 12.5% bivalves) and 6.3% echinoderms. The recording of 18 species of cumaceans and 14 species of fish was noteworthy. Amongst the latter were small specimens of dubiously benthic species, and several crustaceans (e.g. *Lucifer*) were also doubtfully benthic. Unless clearly non-benthic (e.g. some crustacean larvae, and some planktonic molluscs) all taxa which were caught are listed.

**DISTRIBUTION PATTERNS OF RARER SPECIES:** Rarer species are here taken as those in which only one or two individuals were recorded in the survey. By taking recordings of each individual and summing over times we can determine whether the rare species were concentrated in any patterns of sites, and conversely by summing over sites we can search for patterns in times.

The number of rarer recordings in sites ranged from zero to 10, and map plotting suggested a pattern in the data somewhat comparable to that obtained in the sediment site-groupings. Mean numbers in sediment site-groups were: site-group 1 (South-west) 3.57, group 2 (southern transverse band) 4.00, group 3 (flanking middle) 8.20 and group 4 (northern) 2.35. Overall the northern area has few rare recordings, the southern area an intermediate number, and the middle flanking portion (with the most unstable sediments) has the largest number.

The number of rare recordings in times ranged from 18 to 29 with September values (mean 28.5) noticeably greater than the remainder.

**SITES  $\times$  TIMES ANALYSES:** The total data which were available for analysis formed a three dimensional matrix of 468 taxa ( $s$  for species)  $\times$

57 sites ( $q$  for quadrats)  $\times$  8 times ( $t$ ). By summing over species we derived  $q \times t$  matrices with dimensions of 57  $\times$  8 and two such summations were considered. The first involved the number of species ( $s$ ) per sample; this is a simple measure of diversity and in Hulbert's (1971) terms it is the species density appropriate to the particular sampling parameters. The second summation was the total number of individuals ( $n$ ) of all species, and is the numerical equivalent of biomass. Numerous sample measures other than direct summations are available provided species become anonymous, and we used the standardized Shannon diversity (to log base 10) which we designate  $d$ . These three measures  $s$ ,  $n$ , and  $d$  were previously used in work on Bramble Bay by Stephenson, Cook and Raphael (1976) (albeit with different symbolism) and Stephenson, Cook and Raphael (1977) and because the sampling procedures differed only in the type of grab employed comparisons can be effected. It is appreciated that with polyspecific and fractionated taxa, the value of  $s$  and  $d$  are somewhat inaccurate.

We are interested firstly in means over all samples. These are for  $s$  32.14, for  $n$  170.23, and for  $d$  1.143. They compare with 12.2, 158.4, and 0.74 respectively for preflood conditions in Bramble Bay (Stephenson, Raphael and Cook 1976). Clearly the Middle Banks grounds as a whole carried a richer and more diverse biota than did Bramble Bay in the preflood sampling.

Secondly we are interested in the variation of  $s$ ,  $n$  and  $d$  values between sites and between times. This requires first averaging by rows and by columns in each of the  $q \times t$  tables, and secondly assessing the variability in row means and in column means. Variation was expressed as ranges and variances and results are given in Table 2.

These results show there is greater heterogeneity in sites than in times, with the ratios of variances being 4.72 for  $s$ , 2.94 for  $n$  and 8.67 for  $d$ . While a fraction of the differences may be due to greater 'random' variation in the sites data which are meaned over eight times compared with

TABLE 2: RANGES AND VARIANCES OF MEAN VALUES OF  $s$ ,  $n$  AND  $d$  IN SITES AND IN TIMES.

	Sites Means		Times Means	
	Range	Variance	Range	Variance
$s$	20.10-57.13	82.30	24.67-38.30	17.42
$n$	67.75-392.88	8393.4	85.44-217.65	2854.6
$d$	0.978-1.394	0.00702	1.104-1.186	0.00081



times data over 57 sites, the greater importance of sites in the overall heterogeneity is believed to be a real phenomenon. The Bramble Bay work showed a most marked time effect due to the flood of January 1974 (Stephenson, Cook and Raphael 1977) but this is not apparent in the present data.

Table 2 shows reasonable constancy in diversities ( $d$ ) from place to place and from time to time. This suggests that changes in numbers of species and number of individuals 'balance out' in the diversity formulation as noted previously in the postflood data from Bramble Bay and also in work on the Serpentine Creek benthos by Stephenson and Campbell (1977).

Significant positive correlations were obtained between  $s$ ,  $n$  and  $d$  for the different sites. Spearman rank correlation coefficients were: between  $s$  and  $n$  +0.83, between  $s$  and  $d$  +0.68 and between  $n$  and  $d$  +0.33.

Data on time trends are given in Table 3. Spearman rank correlation coefficients between the three sets of values were:  $s$  and  $n$  +0.98 (very highly significant), between  $s$  and  $d$  +0.24 and between  $n$  and  $d$  +0.13 (neither significant). This suggests that chronological changes in  $s$  and  $n$  are again sufficiently parallel almost to cancel out effects in diversity.

Table 3 shows high values of  $n$  in each of the two Septembers, and this follows the pattern obtained in an earlier study at Peel Island (Stephenson, Williams and Cook 1974). The results are also similar in that lowest values occur in March of a non-flood year. Values of  $s$  follow the same tendency, but no general tendency is apparent in the diversity data.

## CLASSIFICATORY TECHNIQUES

**GENERAL TECHNIQUES:** The general approach is classificatory, beginning with a three dimensional matrix of  $s$  (species)  $\times q$  (sites or quadrats)  $\times t$  (times). By summation over times we derive an  $s \times q$  matrix and by classification obtain site-groups and their related species-groups;

similarly by summation over sites we derive an  $s \times t$  matrix and hence times-groups and their related species-groups. The classification of the two derived matrices (viz.  $s \times q$  and  $s \times t$ ) followed the methods used by Stephenson, Raphael and Cook (1976) and this involved: transformation of data using  $\log_{10} (n+1)$ , Bray-Curtis dissimilarity measure, group average sorting. For entity (i.e. site or time) classification data were not standardised; for species classification the transformed data were standardised by totals prior to deriving inter-species dissimilarities.

Past experience has shown that the main objection to this method lies in the species classification where rarer species form isolated and 'dominating' species-groups. It was hoped that by operating in the first instance within narrow ranges of species abundances that this objection would be less serious (see later). In fact the species groupings which were obtained throughout still left much to be desired.

Following earlier work (Stephenson, Raphael and Cook 1976; Stephenson and Campbell 1977; Stephenson, Cook and Raphael 1977) we take the view that species should be placed in the same species-group if they characterise groups of entities (sites or times) in a similar way. A satisfactory entity classification then becomes a necessary pre-requisite to a satisfactory species classification. Because of occasional misclassifications, some re-allocation of entities may be necessary, involving either the occasional and obvious cases (e.g. Stephenson and Williams 1971) or by procedures such as REMUL (Lance and Williams 1975). In the present cases there were no obvious misclassifications and re-allocations have not been made.

If the entities are sites then the next step is to replace the species  $\times$  sites matrix by the much smaller species  $\times$  site-group matrix—this contains the mean recordings of the species. By inspection we can immediately see which species may positively characterise a given site-group by occurring there in proportionally the largest numbers.

TABLE 3: MEAN VALUES OF  $s$ ,  $n$  AND  $d$  AT DIFFERENT TIMES.

	1 (Sept 72)	2 (Dec 72)	3 (March 73)	Times 4 (June 73)	5 (Sept 73)	6 (Dec 73)	7 (March 74)	8 (June 74)
$s$	32.88	28.23	24.67	32.65	38.30	35.32	33.54	32.53
$n$	185.21	128.54	85.44	171.05	271.65	191.61	162.25	165.09
$d$	1.115	1.144	1.104	1.127	1.139	1.186	1.172	1.163



However the variability of recordings within the site-groups may be such that differences between means are misleading. To locate such cases, as in work of the recent past, we use a 'pseudo- $F$  test' and employ such terms as 'conformity' and 'noticeably different' instead of 'significant', using the 0.05 probability appropriate to the  $F$  test as a cut-off point.

For a given array of species recordings arranged in site-groups there are many possibilities for testing, for example each site-group set against all the remainder, each pair of site-group sets against the remainder etc. It has been found more economical to perform pseudo- $F$  testing by a programmable hand calculator on those sets suggested by perusal of the data, than to test all by a computer-based programme.

Pseudo- $F$  testing reveals species which do not conform to the entity-groupings. When species with a range of abundances are considered we may expect non-conformers to include common species which are evenly distributed amongst the entity-groups and which must not be lost sight of. We may also expect them to include rarer species insufficiently concentrated in any entity group for the results to be meaningful.

**DATA REDUCTION:** In benthic work there are typically many rare species which add little to the ecological understanding of an area beyond the contributions they make to analyses like those of the previous section. There is a more pragmatic reason for their exclusion: they greatly increase computing costs and their inclusion may result in the computer being unable to accept the total data. In the present case, to achieve the limiting matrix of  $199 \times 57 \times 8$  would mean excluding species occurring 12 times or less, and it was felt this might be too severe. Because there are objections to most of the methods of data reduction previously employed we here attempted alternative approaches. The first consisted of dealing with the species in successive lots of 50 and compared the classifications obtained. This showed, *inter al*, that the sites were divisible into two markedly dissimilar groups. We then considered the two groups of sites separately — by reducing the  $q$  dimension in the matrix the critical  $s$  dimension becomes automatically reduced.

#### ANALYSES ON LOTS OF FIFTY SPECIES

The potential advantages of this method are first that the 'stopping rule' as regards species is indicated by the data themselves. It occurs at that point in the successive analyses when either no

patterns or 'nonsensical' patterns emerge. This involves only a minimum of subjectivity. Secondly it shows whether the patterns revealed by the abundant and less abundant species are similar, and thirdly the results should be less dependent on the data transformation which is employed. This is because there is a narrower range of abundances in a matrix; in practice this relative independence increased as we moved to the less abundant group of species. It was anticipated that the main disadvantage of the method would be in comparing the results of the different analyses but in the event this was only a minor problem.

We deal first with all  $s \times q$  analyses, then all  $s \times t$  analyses.

**SPECIES  $\times$  SITES ANALYSES:** We first consider the site classifications, then the conforming species.

(a) Sites — first 50 species: The dendrogram of the classification (Fig. 6A) shows remarkably clear separation into two site-groups which consist of southern and northern sites. Apart from a single site (29) the boundary follows the topography of the area, and coincides with the 10 fm depth contour on the 'lip' of the Middle Banks. Three subordinate groupings are evident within the southern subarea, and although these have topographic coherence we do not discuss them further at this stage.

(b) Sites — second 50 species: The dendrogram (Fig. 6B) again shows clear separation into northern and southern site-groups, although less clearly than in the previous dendrogram. The two main site-groupings are identical with the previous ones. Three subordinate groupings are again evident in the southern subarea but their constituent sites are not identical with the previous ones.

(c) Sites — third 50 species: The northern and southern site-groups were identical with those above.

(d) Sites — fourth to sixth lots of 50 species: In the fourth lot the results were only broadly similar to the above with one subgroup mostly of topographically northern sites (7, 20, 23, 24, 29, 35) in the main southern group which also included site 36. In the fifth lot excluding two vacant sites (9, 27), the original groups were revealed excepting that site 31 was in the southern group. In the sixth lot of species the south and north pattern was not evident. There were eight isolated sites and three groups at a 98%



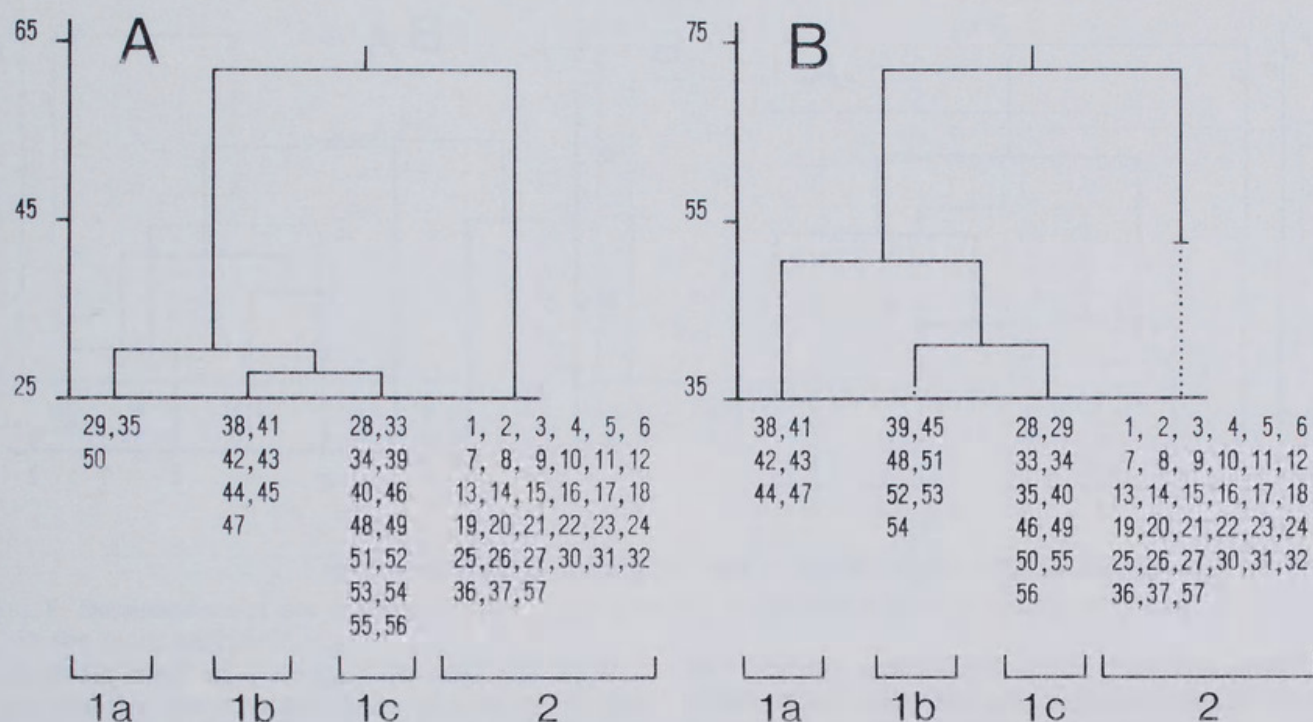


FIG. 6: Dendrograms of site classifications using species recordings as attributes: A first 50 species, B second 50 species.

dissimilarity level with only one group showing approximate topographic coherence. The stopping point is clearly at or about the fifth lot of species (species occurrence >6).

The distinctiveness of the northern and southern subgroups decreased progressively from the first to the fifth lots of species. This is indicated in Table 4.

TABLE 4: LEVELS OF DENDROGRAM FUSIONS FOR SPECIES LOTS WITH DECLINING ABUNDANCES

Species lot	Approx level of lowest fusions	Approx level of highest dichotomy
First 50	10	60
Second 50	20	70
Third 50	30	85
Fourth 50	40	90
Fifth 50	50	100

(e) Conformity of species to main site-groupings: For species in the first to third lots, the main site-groups are identical. For species in the fourth to sixth lots of 50 it seems more appropriate to test conformity to the general pattern than to the fragmenting remnants of it.

In these cases the rationale of testing for conformity is altered. We obtain groups from elsewhere and test on the lines of a 'construction

set' of data and a 'validation set'. Instead of 'noticeable differences' of species distributions we might now approximate more closely to 'significant differences' excepting that the problems of non-normal distribution with series of zero recordings became more acute.

The sixth lot of 50 species takes in only some of the species in which three specimens were recorded and omits others so the present testing was extended to all occurring three times. Below three recordings there can be no conformity in the sense we have used the term.

Results of conformity tests to the southern and northern groups of sites covering all species except the less abundant ones are given in the Appendix. It will be noted that more species positively characterise the southern site-group than the northern one. With decreasing abundance of species there are increasing proportions which fail to conform. Thus for 6 and 7 recordings the percentage not conforming is 29, for 5 recordings 36, for 4 it is 56 and for 3 it is 65.

(f) The main 'communities': If we view a benthic community as an area and the species which characterise it positively, then we have two main communities. It is of interest that identical areas show up in analyses on the first, second and third sets of species and an almost identical one in the fifth set. Clearly the abundant and less abundant species follow the same broad area pattern.



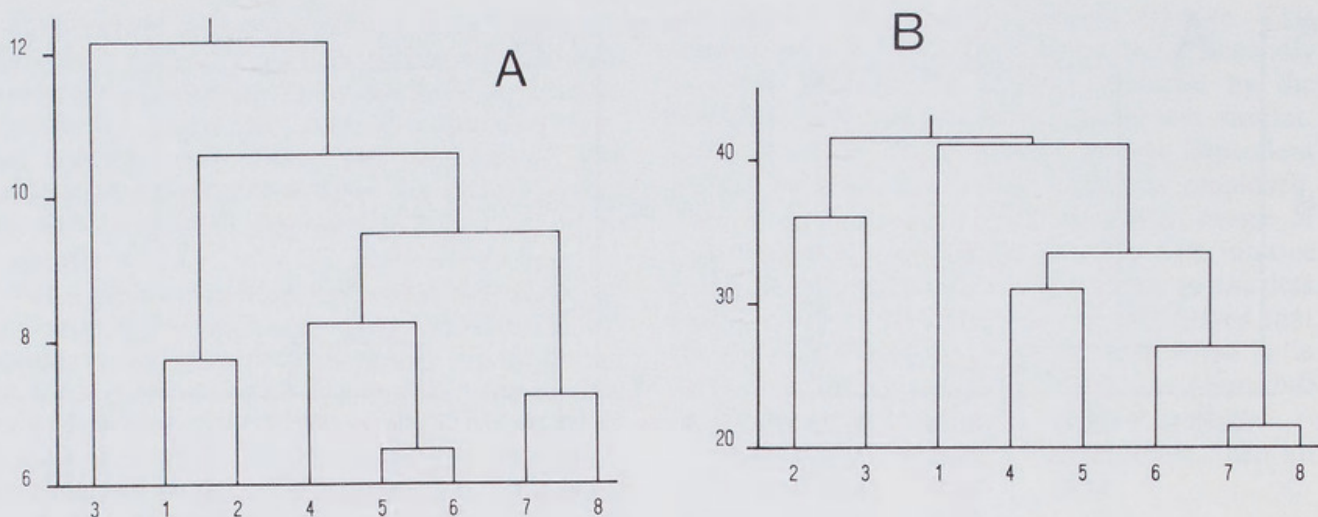


FIG. 7: Dendrograms of time classifications: A first 50 species, B third 50 species.

There are very many conforming species, 158 in the southern community and 80 in the northern one, and to assist comprehension these data must be compressed. If we list only the five commoner species which conform to each of the areas we arrive at a southern community of *Prionospio*, tanaid 1, *Solemya*, *Callianassa* and *Poecilochaetus* and a northern community of *Urohaustorius*, *Amphiura octacantha*, *Concholestes*, mysid 4 and amphipod 3. Four of the northern species are small crustaceans which are possibly mobile; mobility could be an advantage in this generally turbulent area.

Conforming species are possibly different from numerically dominant species — a conforming and dominant species in the southern area may well be a dominant species (but clearly not a positively conforming one) in the northern area. Purely on a dominance basis the southern area is a community of *Prionospio*, tanaid 1, *Solemya*, *Poecilochaetus* and *Discobotellina* while the northern area is a *Urohaustorius*, *Prionospio*, *Amphiura octacantha*, *Concholestes* and mysid 4 community.

**SPECIES × TIMES ANALYSES:** Time classifications of the first and third lots of 50 species are shown as dendrograms on Fig. 7, and these are representative of the remainder. No two classifications were identical and the only common grouping was of times 7 and 8. The times were grouped in a sequential or near-sequential order throughout, and there were never close groupings of the equivalent seasons of the two years.

By comparing Figs. 6 and 7 it is evident that dissimilarities between times are much less than between sites.

With the lack of constancy in time patterns, tests of conformity of species to these patterns are on a somewhat shifting basis. Taking three times-groups in each case gave only 75 conforming species compared with 238 conforming to two site-groups. Further consideration of times-groupings is deferred until the next section.

#### BIOTIC DATA — SEPARATE ANALYSES OF NORTHERN AND SOUTHERN AREAS

**GENERAL:** For reasons given earlier it was decided to subdivide the study area into southern and northern subareas and to analyse each separately. Additional reasons are (a) by working within these respective communities heterogeneity is greatly reduced, (b) special attention can be given to the northern area which would be most immediately involved in human interference, (c) it is possible that time changes differ in the two areas.

The problem about subdivision is that three different criteria can be used and each gives slightly different results. Using sediments site 20 is included in the southern group, but its biotic and topographic affinities are with the northern group. Using topography site 29 is in the northern group, but using biotic affinities it is in the southern. Site 36 alters affinities between one biotic classification and another. Eventually an overlapping division was decided upon with sites 29 and 36 in both groups. The northern group then consists of sites 1–27, 29–32, 36, 37 and 57 (34 in all) while the southern group consists of sites 28, 29, 33–36, 38–56 (25 in all).



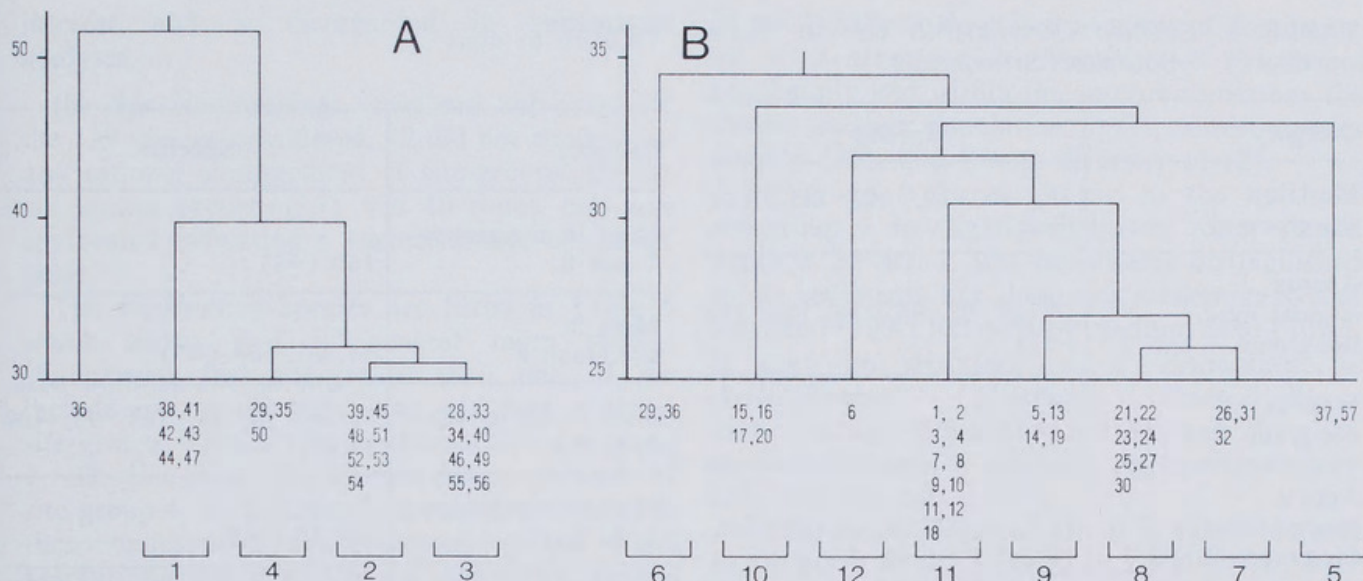


FIG. 8: Dendrograms of site classifications in A southern and B northern sub-areas. (Site-group 12 is disregarded in the main analysis.)



FIG. 9: Topographic distribution of the 11 main site-groups. Site-groups 4 and 6 overlap and their individual sites are shown by the symbols indicated.

**SPECIES CONSIDERED:** An arbitrary cut-off level was adopted, and species occurring less than 10 times in the reduced data were excluded. Because we now look for finer patterns and hence more site-groups, a higher cut-off level than previously was thought desirable. It was confirmed later as being approximately correct. The southern analyses involved 159 species and the northern ones 115.

**SPECIES  $\times$  SITES ANALYSES:** (a) Sites classifications. The dendrograms of site-classifications are given in Figure 8. We first consider the marginal sites 29 and 36 common to the two analyses. Site 36 joins the southern area dendrogram at a much higher dissimilarity level than for the northern area and is henceforth considered as a northern site. Site 29 is ambiguous in its affinities and is treated as both a northern and southern site.

In Figure 8A four site-groups are readily recognisable at a dissimilarity level of *c.* 30% and these show topographical coherence. They are map plotted in Figure 9 and numbered 1–4 in a S–N direction. In Figure 8B at just over 30% dissimilarity there are five groups of very dissimilar sizes. The largest group divides at a slightly lower level to give groups of 11 and 14 sites and of these the former gives a chained series and is retained as a unit. The latter spans the area of greatest interest where excavation may occur, and divides into three topographically coherent sub groups at about 25% level. These subgroups were retained. In all eight northern groups were tentatively accepted and are map plotted as groups 5–12 (see Fig. 9). Site-group 12 consists of the single site 6 which is marginal to the area of



TABLE 5: SPECIES CONFORMING TO THE FOUR SOUTHERN SITE-GROUPS.

Category	Species
Most in site-group 1	25, 16, 19, 90, 111, 134, (=6)
Approx coequal most site-groups 1 and 2	14, 29, 98, 96, 118, 124, 170 (=7)
Most in site-group 2	156, 176 (=2)
Approx coequal most site-groups 2 and 3	1, 9, 15, 37, 66, 75, 139, 146, 181, 212 (=10)
Most in site-group 3	3, 4, 45, 65, 94, 108, 93, 172, 137, 173, 175, 219 (=12)
Approx coequal most site-groups 3 and 4	52, 48, 68, 63, 64, 32, 61, 53, 34, 20, 84, 83, 88, 103, 22, 85, 126, 135, 128, 151, 113, 131, 49, 143, 147, 161, 168 (=27)
Most in site-group 4	51, 8, 2, 7, 23, 21, 81, 46, 18, 43, 106, 58, 56, 150, 129, 6, 44, 57, 70 (=19)
Most in site-groups 1, 2, 3 (least in 4)	24, 27, 33, 36, 38, 60, 95, 127, 159 (=9)
Most in site-groups 2, 3, 4 (least in 1)	26, 30, 39, 35, 97, 74, 107, 117, 77, 144, 141 (=11)

Species are ranked from those with highest to those with lowest recordings in each group.

TABLE 6: SPECIES IN THE SEVEN NORTHERN SITE-GROUPS.

Category	Species
Approx coequal most site-groups 5 and 6	31, 3 (=2)
Most in site-group 6	1, 10, 4, 52, 9, 30, 15, 63, 26, 13, 11, 40, 83, 37, 41, 91, 17 (=17)
Most in site-groups 5, 6, 7	138 (=1)
Most in site-groups 6 and 7	5 (=1)
Most in site-group 7	49, 199 (=2)

TABLE 6: cont

Category	Species
Most in site-groups 7 and 8	160 (=1)
Most in site-group 8	54, 86, 104 (=3)
Most in site-groups 7, 8, 9	7, 57, 70, 91, 163, 93, 109 (=7)
Most in site-groups 7, 8, 9, 11	20, 59 (=2)
Most in site-groups 6, 7, 8, 9	23, 77 (=2)
Most in site-group 9	6, 8, 102, 89, 116, 203 (=6)
Most in site-group 10	21, 47, 55, 155, 182 (=5)
Most in site-group 11	43, 99, 136, 140 (=4)
Most in site-groups 10 and 11	2 (=1)
Most in site-groups 9, 10, 11	32 (=1)
Most in site-groups 9 and 11	105 (=1)
Most in site-groups 5, 6, 7, 8 (least in 9, 10, 11)	39 (=1)
Most in site-groups 5, 6, 7, 8, 9 (least in 10, 11)	34 (=1)
Most in site-groups 5, 6, 7, 8, 9, 10 (least in 11)	113 (=1)
Most in site-groups 6, 7, 8, 9, 10, 11 (least in 5)	18 (=1)
Most in site-groups 5, 7, 8, 9, 10, 11 (least in 6)	22 (=1)

Species are ranked from those with highest to those with lowest recordings in each group.



interest and is disregarded in subsequent analyses.

(b) Species-groupings, southern sub-area. Of the 159 species considered, 42 did not conform to any rational arrangement of site-groups. Of the six species occurring 11 and 10 times, only one conformed indicating a correct choice of cut-off point.

The conforming species are listed in Table 5 which shows that in general more species characterise two site-groups than one. If we include species characterising one, two or three, site-groups, then 22 species characterise site-group 1, 39 site-group 2, 69 site-group 3 and 57 site-group 4. To describe communities in terms of these numbers of characterising species is not helpful. As stated earlier an alternative method is not to consider conforming species but instead a few of the numerically dominant species in each site-group and this we follow.

(c) Species-groupings, northern sub-area. Of the 115 species considered, 54 did not conform to any rational arrangement of site-groups. Of the four species occurring less than 12 times, only one conformed, again confirming the choice of cut-off level.

The conforming species are listed in Table 6, which shows that site-group 6 has the largest number of uniquely characterising species (17); this agrees with the isolated position of site-group 6 on the dendrogram (Fig. 8B).

Many of the species conform to combinations of site-groups, with the largest number (17) involving site-groups 7 and 8 followed by site-groups 7, 8 and 9 (16 spp.). This confirms the similarity of these site-groups, again as shown in the dendrogram.

Counting species which characterise more than one site-group, then 7 characterise site-group 5, 27 site-group 6, 21 site-group 7, 20 site-group 8, 23 site-group 9, 10 site-group 10 and 11 site-group 11.

(d) Overall view of site-groups. Table 7 shows the site composition of each of the eleven main site-groups considered, and their more abundant characterising species. Data from the previous  $q \times t$  analyses are added to this table. They comprise the mean number of individuals of all species per site in a site-group per time ( $\bar{n}$ ), the mean number of species ( $\bar{s}$ ) and mean standardised Shannon diversity (to log base 10) ( $\bar{d}$ ).

Site-group 1 occupies the extreme SW. of the sampled area where sediments are predominantly fine sand (76%) with the highest percentage of mud (ca 16%), and in relatively deep water (ca

31 m). It may be described in terms of dominants as a *Schizaster* — *Nucula* — *Prionospio* community and within the southern area has the lowest average population (197), lowest species density (36), and lowest diversity (1.12).

Site-group 2 forms an arc to the north of site-group 1 in slightly shallower water (mean depth c. 30 m). It was not clearly distinguished by its sediments but these are predominantly of fine sand (79%) followed by medium sand (10%). It may be described as a *Prionospio* — *Aglaophamus* — *Callianassa* community, has a high average population (278) and for the southern sub-area a relatively low species density (38) and diversity (1.17).

Site-group 3 (depth c. 22 m) is parallel to and to the north of site-group 2. It does not precisely follow the topography of the area, lying at a slight angle to the 20 m contour and is mostly deeper than this. It is not clearly distinguished by its sediments. These are predominantly fine sand (69%) followed by medium sand (24%). It may be described as a *Prionospio* — tanaid — *Solemya* community. It has the highest recorded population (320) and number of species (48), and the average of the diversity in the total area (1.20).

Site-group 4 (depth ca 16 m) consists of three sites straddling and somewhat askew to the 20 m contour just south of the southern 'lip' of the sampled area. Its sediments are highly variable, site 50 having predominantly fine sand (78%), and both sites 29 and 35 having predominantly medium sand (76% and 66% respectively). It could be described as a *Rhizammia* — *Discobotellina* — *Prionospio* — *Solemya* community but for the fact that the first named species is markedly seasonal. The population (215) is below the average for the southern site-groups but much in excess of any northern groups. The species density (46) is almost that of site-group 3, and the diversity (1.29) is the highest of the southern site-groups. Almost identically high diversity also occurs in site-group 6 (depth c. 9 m) which again contains site-group 29. It can be described as a *Prionospio* — *Urohaustorius* community, has the lowest population (79) of any site-group, the lowest species density (24) but the highest diversity (1.56). Site-group 5 is at the western edge of the Middle Banks lip, with a modal sediment of medium sand (82%). It is a *Prionospio* — *Urohaustorius* — tanaid community and if reckoned as within the northern sub-area has its highest population (143), and species density (38), and has a high diversity (1.30), second only to site-group 6 (depth c. 11 m).



TABLE 7: DETAILS OF SITE-GROUPS.

Site-group	1	2	3	4	5
Constituent sites	38, 41, 42 43, 44, 47	39, 45, 48, 51, 52, 53, 54	28, 33, 34, 40, 46, 49, 55, 56	29, 35, 50	37, 57
Most abundant species (occurrences*)	25(22), 12(22), 1(21), 10(18), 16(17), 19(14), 14(14), 11(11)	1(72), 11(17), 5(14), 9(14), 3(13), 4(12), 3(11)	1(77), 3(32), 4(30), 9(16), 13(13), 15(12)	28(27), 10(20), 1(16), 4(14), 3(10)	1(11), 2(9)
$\bar{n}^*$	197	278	320	215	79
$\bar{s}^*$	36	38	48	46	24
$\bar{d}^*$	1.12	1.17	1.20	1.29	1.56
Main sed. grades	76% fine sand 16% mud	79% fine sand 10% med. sand	69% fine sand 24% med. sand	Variable	87% med. sand
Mean depth (m)	30.5	29.9	22.3	16.2	11.0

\* Rounded

None of the remaining site-groups appear to be distinguished by their sediments, all having predominantly medium sand present as in the two previous cases.

Site-group 7 (depth c. 15 m) includes two sites (31, 32) in or close to the northern end of the dredged navigational channel. It can be described as a *Concholestes* — *Callianassa* — *Prionospio* community, and has almost the lowest population of any site-group (81), and also low species richness (25) and diversity (1.11).

Site-group 8 (depth c. 14 m) lies on the eastern slopes of the Middle Banks in the area from which sand might be dredged and may be described as a *Concholestes* — *Urohaustorius* — mysid 4 community. It has a relatively low population density (91) but somewhat higher species richness (30) and diversity (1.18) than adjacent site-groups.

Site-group 9 lies in the NE. of the sampled area, in generally deeper water than adjacent sites (depth c. 19 m) and may be described as a *Concholestes* — *Amphiura octacantha* — mysid 4 community. It has a higher population than adjacent site-groups (125); species richness is low (25) as is diversity (1.09).

Site-group 10 lies in the W. of the sampled area in a generally shallow and turbulent area (depth c. 8 m). It forms a *Urohaustorius* — *Platyschnopus* — *Prionospio* community with low population (113), species density (25) and diversity (1.03).

Site-group 11 is the northernmost area sampled. It lies in a turbulent area adjacent to but deeper than that of site-group 10 (depth c. 14 m). It forms a *Urohaustorius* — *Amphiura octacantha* — *Prionospio* community, again with low population (96), species richness (25) and diversity (1.11).

**SPECIES  $\times$  TIMES ANALYSES:** The dendrograms of time classification for the southern sub-area (Fig. 10A) and northern sub-area (Fig. 10B) are alike in showing groupings which are predominantly of sequential times and in not following seasonal patterns. The sequential pattern is slightly better developed in the northern sub-area and also the inter-time dissimilarities are generally lower.

By dealing with sub-areas the dissimilarity levels in the times dendrograms have become roughly equated to those of the sites dendrograms and hence times now become relatively more important. Perusal of the two-way coincidence table of time-groups with species showed that less than a third of the species conformed noticeably to the time-groups of the dendrograms.

As an alternative to the dendrogram groupings of times, these were dissected into chronologically meaningful groupings and the conformity of species to these groupings was investigated. Approximately half the species analysed conformed to these groupings. Some of the remaining species occurred at random (see later) and it was concluded here there were no chronological



TABLE 7: Cont.

6	7	8	9	10	11
29, 36	26, 31, 32	21, 22, 23 24, 25, 27, 30	5, 13, 14, 19	15, 16, 17, 20	1, 2, 3, 4, 7, 8, 10, 11, 12, 18
1(24), 2(6), 3(5)	7(10), 5(10), 1(8), 6(6),	7(19), 2(8), 8(8), 6(6), 20(6), 1(6)	7(27), 6(21), 8(14), 1(7), 23(6)	2(34), 21(12), 1(10), 18(7), 8(5)	2(16), 6(14), 1(10), 8(9)
143	81	91	125	113	96
38	25	30	25	25	25
1.30	1.11	1.18	1.09	1.03	1.11
82% med. sand	—	—	> 80% med. sand	—	—
9.1	14.6	14.0	19.2	7.6	14.0

changes. For the residue while recordings were too heterogeneous to be statistically at random, the groupings of times to which the species conformed did not make obvious chronological sense.

Finally the species were divided into four broad categories, and each of these further subdivided. Throughout the categories were non-overlapping and sometimes this involved difficult decisions regarding allocation. The categories were: *A* — those occurring at random, and hence showing no chronological pattern. For the commoner species randomness was tested by  $\chi^2$  using summed recordings in each of the eight times. For species occurring with fewer than 16 individuals, the limit of formal use of  $\chi^2$  is exceeded. We have still applied the mechanics of the  $\chi^2$  test, which might now be designated a 'pseudo- $\chi^2$  test' and describe the species as 'pseudo-random'; *B* — those with

sequential patterns of various types. One sequence of times was dissected from the remainder and the pseudo *F* test applied to the  $\log_{10} (n + 1)$  transformations of the two sets of recordings. The first dissection point separated times 1–6 from 7 and 8, and we thus determine the species with noticeably decreased numbers after the flood and those with noticeably increased numbers. The second point was between times 1–4 and 5–8, separating the two years of study, and we thus derive species occurring in high numbers in the second year and in the first year respectively. The remaining sequential species followed a variety of time combinations and we first separated those with three sequential noticeably high recordings ('9 month species') from those with two in sequence ('6 month species'). Finally we listed species with a sequence of two noticeably low

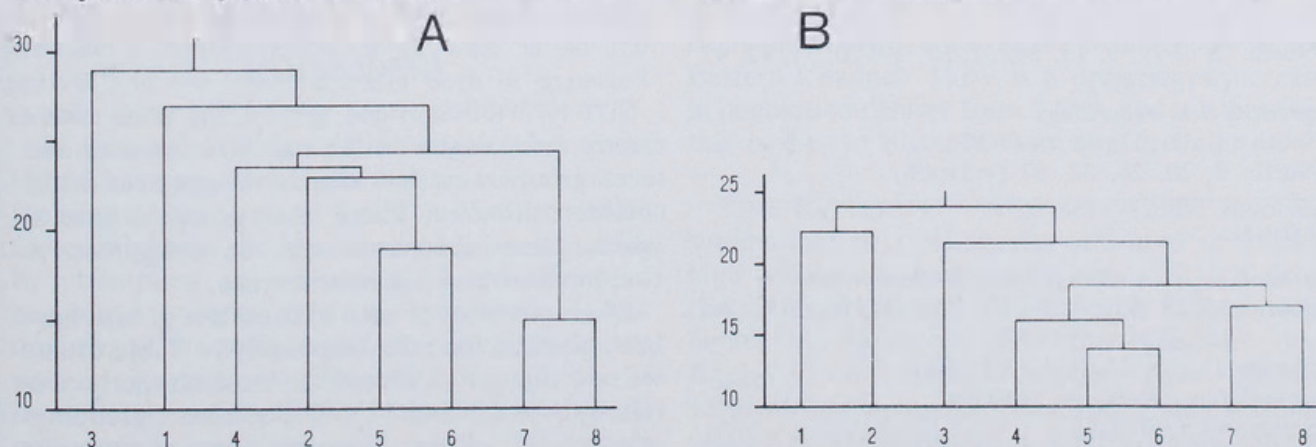


FIG. 10: Dendrograms of time classifications within A southern and B northern sub-areas.



recordings; *C* — those with seasonal patterns with noticeably high recordings in the same season of both years (mostly in September) and those with noticeably low recordings; *D* — non-random species giving apparently 'nonsense' chronological patterns; these are presented in order of decreasing likelihood that they give conceptual sense. The first group contains species with a single outstandingly low value, the second species

TABLE 8: CONFORMITY OF SPECIES TO PRESCRIBED TIME-GROUPS.

#### RANDOM

##### *Random*

South: 29, 53, 125, 137, 156 (=5=3%)

North: 15, 72, 73, 83, 87, 116, 130, 134, 136, 142 (=10=9%)

##### *Pseudo-random*

South: 110, 171, 180, 190, 191, 192, 219, 224 (=8=5%)

North: 17, 38, 109, 117, 149, 169, 189 (=7=6%)

#### SEQUENTIAL

##### *Fewer after flood*

South: 25, 30, 41 (=3=2%)

North: 22, 42, 110 (=3=3%)

##### *More after flood*

South: 4, 56, 58, 66, 105, 127, 146, 149, 161, 184 (=10=6%)

North: 31, 59, 86, 146, 203 (=5=4%)

##### *More in 1st year*

South: 96, 131 (=2=1%)

North: 89, 199 (=2=2%)

##### *More in 2nd year*

South: 9, 15, 19, 20, 23, 26, 38, 49, 55, 65, 75, 109, 111, 133, 147, 212 (=6=12%)

North: 49, 66, 125, 162, 182 (=5=4%)

##### *9-month species*

South: 6, 59, 83, 95, 128 (=5=3%)

North: 18, 23, 54, 55, 74 (=5=4%)

##### *6-month species*

South: 1, 2, 7, 8, 10, 13, 14, 16, 21, 24, 27, 33, 39, 44, 50, 64, 71, 74, 106, 107, 120, 154, 166, 197 (=24=15%)

North: 2, 6, 7, 11, 13, 24, 37, 67, 69, 70, 71, 82, 92 (=13=11%)

##### *Sequential low recordings*

South: 3, 31, 32, 48 (=4=3%)

North: 9, 20, 26, 32, 57 (=5=4%)

#### SEASONAL

##### *Seasonal high recordings (mostly Septembers)*

South: 12, 28, 45, 54, 61, 81, 97, 101, 108, 118, 126, 129, 135 (=13=8%)

North: 21, 63, 77, 121 (=4=3%)

##### *Seasonal low recordings (various)*

South: nil (=0=0%)

North: 5, 8, 56, 58 (=4=3%)

#### OBSCURE

##### *Single outstanding low*

South: 36, 37, 40, 69 (=4)

North: 20, 35, 39, 43, 44, 46, 50 (=7)

##### *Oscillating*

South: 11, 18, 35, 42, 43, 46, 47, 52, 57, 60, 62, 67, 70, 76, 80, 84, 85, 88, 90, 91, 92, 93, 94, 98, 104, 113, 115, 117, 122, 132, 139, 141, 143, 152, 153, 168, 170, 172, 176, 204, 209, 216 (=42)

North: 1, 4, 10, 12, 19, 40, 41, 45, 47, 48, 53, 62, 65, 75, 78, 79, 85, 91, 93, 99, 102, 104, 105, 112, 113, 114, 132, 140, 141, 147, 155, 158, 160, 163, 185, 187 (=36)

##### *Single outstanding high*

South: 5, 17, 22, 34, 51, 68, 77, 87, 103, 124, 138, 144, 145, 150, 151, 159, 173, 175, 178, 181, 186, 196, 211 (=23)

North: 3, 27, 43, 52, 100, 119, 138, 148, 164 (=9)

with oscillating values and typically with alternate high and low recordings, while the last group contains species with a single outstandingly high value.

Details of the species in each of these categories in southern and northern sub-areas are given in Table 8. Summated percentages of random and pseudorandom species are 8% S., 15% N.; of sequential species 40% S., 33% N.; of seasonal species 8% S., 7% N., and of obscure time patterns 43% S., and 45% N. None of the differences between the two sub-areas were significant.

The flood of 1974 produced noteworthy changes in less than 10% of the species, in marked contradistinction to Bramble Bay (Stephenson, Cook and Raphael 1977). More species occurred in noticeably high numbers after the flood (15) than in noticeably low numbers. Apart from flood-affected species, 21 species occurred in higher numbers in the second year of study compared with four in the first year.

#### DISCUSSION

**SITE-PATTERNS:** Four groups of sites were clearly recognisable in the southern sub-area and seven groups were less clearly recognisable in the northern sub-area. There is no accepted level at which these site-groups can be designated as communities and subcommunities.

Characteristics of each of these site-groups have been given in the text (especially in Table 6) and we now discuss all except the most northerly ones (site-groups 10 and 11). The southern groupings (site-group 1-4) are in deeper areas of fine sand furthest from oceanic water and have relatively



high populations, species densities and diversities. The individual groups within the southern area do not precisely follow either the topography or sedimentology of the area and one can only assume that a combination of hydrographic parameters is responsible for their delineation. A likely combination would be distance from oceanic water and current velocity. The highest populations and species densities occur on the relatively steep slopes just south of the Middle Banks, and further south populations and species densities are reduced and other 'communities' can be recognised. Within the confines of our study area the areas of highest populations and species densities do not form an ecotone between south and north; there is no doubt the populous area belongs to a southern site-group. One suspects on the basis of a study of the dredged biota of Moreton Bay by Stephenson, Williams and Lance (1970), that our most south-western site-group 1 may extend considerably beyond our study area, in which case the populous area of site-group 3 (and to a lesser extent site-group 2) become something of especial local interest.

Taking site-groups 2 and 3 together, in terms of population density we have an average of *c.* 1500 animals per square metre contrasting with *c.* 1000 further south and *c.* 600 further north. These are not high values within either a Moreton Bay or a more global context. For example inshore at Bramble Bay, Stephenson, Raphael and Cook (1976) give preflood mean values of up to and 3000 organisms per square metre, and quote both higher and lower figures from the literature. On the other hand both species density (*c.* 43) and diversity (*c.* 1.2) are much higher than were obtained with a van Veen grab at Bramble Bay (*c.* 12 and 0.8 respectively). The dense macrobenthos in site-groups 2 and 3 corresponds with an area in which prawn trawling is concentrated. Presumably the factors responsible for the dense benthos, plus the benthos itself, produce a concentration of prawns. If so the prawns and the trawling could both be expected to take their toll of the benthos.

It is undesirable that future engineering works should have any permanent deleterious effects on the areas of site-groups 2 and 3. We can obtain some insight on the likelihood of these occurring by attempting an evaluation of the effects of engineering works now in operation — viz. dredging of the navigational channel (between the beacons in Fig. 2). Sites 40, 50 and 56 lie immediately south of this channel, and they do not appear to show any biotic differences compared with neighbouring sites. In fact two of

these sites (40 and 56) are in the area of greatest population density (site-group 3).

Site-group 5 is of especial interest because the two sites lie in (site 37) and in immediate proximity with (site 57) the southern end of the dredged channel. They are characterised by the lowest population density (79) and species density (24) obtained in the entire survey, and it is difficult to believe other than that dredging has been responsible. It is of interest to note that this site-group has the highest standardised Shannon diversity (mean value 1.56), and this provides a good example of how misleading diversity measures can be.

Site-groups 4 and 6 lie respectively just south of the topographic boundary between southern and northern areas, and on or just north of the sedimentary boundary. They are intermediate as regards population density (ranging from *c.* 1050 to *c.* 750 individuals per square metre) but have higher species densities and diversities than northern sites. Site-group 4 is of especial interest because two of its characterising species (*Rhizammina* and *Discobotellina*) are arenaceous Foramenifera, although one of these (*Rhizammina*) is markedly seasonal. *Discobotellina* is widespread in Moreton Bay (Stephenson, Williams and Lance 1970) and in different areas is in association with a great variety of other species. There is a reasonably close parallel with dominance of other species of arenaceous Foramenifera off the W. African coast (Buchanan 1960).

In site-group 7 one site (32) lies in the northern end of the dredged navigational channel, one lies very near this end (31) and the third (26) *c.* 1½ km away. Populations densities and species densities are approximately as low as those of site-group 5, and again it seems that dredging is responsible.

Site-groups 7, 8 and 9 show considerable biotic similarity and form a series running northwards from the dredged area on the western side of the Eastern Channel. There is a progressive increase in population density from 7 to 9, and it is possible this is due to distance from the dredging.

**TIME-PATTERNS:** Analyses which involved summations over all species indicated seasonally high populations and species densities in each of the Septembers and further that values were higher in the second year than the first one. Analyses on separate species gave obscure sequential groupings of times rather than seasonal groupings, and suggested a progressive shift in the biota.



The latter analyses, while generally more informative, run into a major problem in interpretation which has been raised in an earlier study (Stephenson, Raphael and Cook 1976). Because of inaccurate relocation of sites on successive samplings different local concentrations of species are likely to be sampled on different occasions. It could be argued that because the values considered involve summated recordings at many sites (25 and 34 in the main analyses) 'random' microtopographical variations should cancel out. Against this species may be concentrated in certain areas, and a single exceptional patch within these areas could bias the results. The importance of microtopographical patterns has been demonstrated by Poiner (1977) working north of Peel Island. In the present study we can only estimate the relative importance of chronology and microtopography. We assume that when species conform to apparently meaningful chronological changes these changes are real, and that when the chronological picture is decreasingly meaningful there is an increasing possibility of a microtopographical effect.

Almost 10% of the species considered conformed to seasonal patterns and in most cases showed noticeably high populations in the two Septembers. High September values have been noted in two previous local studies — near Peel Island (Stephenson, Williams and Cook 1974) and at Bramble Bay before the 1974 flood (Stephenson, Raphael and Cook 1976) and can now be regarded as an established feature in the benthic calendar. Sequential patterns of one sort or another occurred in about 40% of the species analysed. Because there is a growing interest in non-seasonal changes in benthos (e.g. Stephenson, Williams and Cook 1974; Buchanan, Kingston and Shearer 1974; Eagle 1975; Stephenson, Raphael and Cook 1976; and Stephenson, Cook and Raphael 1977) and because this was the largest category of species with recognisable patterns, special attention was devoted to it.

The general approach we followed was to look for changes in biota which are paralleled by abiotic changes and to assume in the first instance that the former are due to the latter. Where no such parallels occur we must fall back upon biotic interactions either between benthic species (Rhoads and Young 1970; Eagle 1975) or between benthic organisms and nektonic predators (Stephenson and Searles 1960; Levings 1972, 1974; Mills 1975). In the present case the most severe abiotic changes for nearly a century were probably the floods of January 1974 and resultant prolonged dilution of the Middle Banks area

(Stephenson, Cook and Raphael 1977). Almost 10% of the species showed noticeable changes between the preflood times (times 1–6) and the postflood ones (times 7–8). While this is more than for any other sequential period, it is a miniscule effect compared with that on Bramble Bay (Stephenson, Cook and Raphael 1977). Moreover at Middle Banks the floods had a 'beneficial' effect with 15 species occurring in noticeably higher numbers after the flood and only six before. The effect was most noticeable in the southern area, where ten species increased in number after the flood. The simplest explanation, that this is due to a supply of sedimentary food material, as MacGinitie (1939) suggested after a Californian flood, appears unlikely. There was less small particulate sediment in the area after the flood than before.

The remaining sequentially occurring species mostly involved noticeably high numbers for only two consecutive sampling periods i.e. for 6 months or slightly longer. It appears that a sequence of species occupied (in quantity) the different areas of sampling each for tolerably brief periods and were then replaced by others. This is suggestive of rapid recruitment and rapid replacement, as Stephenson, Raphael and Cook (1976) suggested at Bramble Bay. It implies that biotic interactions, whose nature is as yet unknown, are an underlying phenomenon. Superimposed on the transitory aspects of the data there is an underlying trend from time 1 to time 8 (as shown by the dendrograms) suggesting an overall biotic shift. The somewhat scanty sedimentary data suggest a parallel shift towards coarser sediments and it is tempting to interrelate the two.

The largest single category of species revealed by the times analyses (40–45% of the species considered) fail to give immediate chronological sense. There are two possible explanations, microtopographical patchiness or real chronological changes on a 3 monthly time bases. For example species with a single outstandingly low value could reflect a single occasion of severe predation followed by replacement during the next three months; species with oscillating values could reflect irregular and repeated recruitment; while species with a single outstandingly high value would be showing settlement in 3 months and disappearance during the next three months. Present data do not permit an easy choice between the alternative microtopographic or rapid chronological changes; current work suggests both are about equally applicable on an 8 week time basis.



**CONTINUAL BIOTIC FLUX:** We have noted the likelihood of tolerably rapid changes in at least 40% of the species — the sequential ones. We have suggested that rapid changes may be a feature of a greater proportion of the species.

If the bulk of the biota consisted of perennial species we would not expect the biota to show rapid changes, and what might appear as such would be due to topographical patchiness. If the bulk of the species were annuals, rapid changes would be inevitable. Thus in theory we could argue from life-spans to the reality of the chronological changes. Unfortunately we have no direct information upon the life-spans of species from the area apart from some data on *Discobotellina* (Stephenson and Rees 1965a, b) which suggests that larger specimens may be three years old. In general we can only assume that relatively large size equates to an age exceeding one year, and amongst the 100 most abundant species the only cases of relatively large sized species are: spp. 5, 10, 12, 14, 24, 25, 29, 39, 41, 42, 49, 69, 87, 95 and 98 (i.e. 15 in all). Amongst the less abundant species the proportion of large species is much lower, and that of annuals or subannuals must be very high. As Eagle (1975) has noted when populations consist of single year classes we can expect instability. He relates this to low diversity, but as indicated by Stephenson, Williams and Cook (1974) it could go a long way to explaining high diversity in a time context.

The overall impression was of a biota dominated by small individuals, of which very few species would attain sexual maturity within the study area. This was particularly so in the northern sub-area; of the 15 larger species listed only one characterised the northern sub-area. If species disappear from within the area before attaining sexual maturity, predation by fish seems a likely cause. Levings (1972, 1974) has shown how seasonal variations in predation by a single species of fish can produce complex changes in a relatively simple benthic biota off the Atlantic coast of Canada. In the present study area there are probably some 20 species of benthic feeding fish (personal communication from Professor J. M. Thomson) and their predation could account for the various and sometimes rapid quasi-seasonal declines in population which were observed.

Non-seasonal increases in population are more difficult to explain. One possibility is that many species have prolonged breeding seasons (which is not unlikely in a subtropical situation) and can occupy vacant space at any period within a prolonged settlement period. A balance between

prolonged settlement and variable predation could well explain the cases of oscillation noted above. It is clear that much more data are required before this suggestion can be confirmed.

Meanwhile the evidence that the benthic population is in an overall state of flux seems tolerably strong. It carries some important consequences as regards a temporary human disturbance of the area. Excavation in the proposed area is unlikely to cause major destruction of breeding populations because few species remain there long enough under natural circumstances to breed. Also, if the normal method of maintenance of the biota is by settlement of one of a great variety of species, it seems probable that this process will only be briefly interrupted, and that a biota roughly comparable with the original should soon be re-established. We might postulate that the settling biota will be more simplified than originally because a larger area and a more vacant area than that provided after fish predation will be available. After some predator-prey oscillations possibly of a few months duration a situation very comparable with the original could be expected.

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## APPENDIX

Species from Middle Banks benthos with indications of their systematic positions. Code numbers are in hierarchical order of abundance.

Code No.	Species	Systematic position	Number Collected	Main site group
1	<i>Prionospio</i> sp.1	Polychaeta: Spionidae	12802	S
2	<i>Urohaustorius</i> sp. — polyspecific	Amphipoda: Haustoriidae	3394	N
3	tanoid 1	Tanaidacea	3094	S
4	<i>Solemya terraereginae</i> (Iredale)	Bivalvia: Solemyidae	3075	S
5	<i>Callianassa arenosa</i> Poore	Crustacea: Callianassidae	2776	S
6	<i>Amphiura octacantha</i> H. L. Clark	Ophiuroidea: Amphiuridae	2741	N
7	<i>Concholestes</i> sp. — polyspecific	Amphipoda: Corophiidae	2674	N
8	mysid 4	Mysidacea	2390	N
9	<i>Poecilochaetus</i> sp.	Polychaeta: Trochochaetidae	2258	S
10	<i>Discobotellina biperforata</i> Collins	Foraminifera: Astrorhizidae	2131	S
11	<i>Aglaophamus verrilli</i> McIntosh	Polychaeta: Nephtyidae	2040	S
12	<i>Nucula</i> spp. — polyspecific	Bivalvia: Nuculidae	1922	S
13	<i>Prionospio</i> sp.4	Polychaeta: Spionidae	1837	S
14	<i>Brissopsis luzonica</i> Gray	Echinoidea: Spatangidae	1343	S
15	<i>Magelona</i> sp.2 ('cincta')	Polychaeta: Magelonidae	1341	S
16	aloidid	Bivalvia: Aloididae	1274	S
17	<i>Magelona</i> sp.3 ('capensis')	Polychaeta: Magelonidae	1217	S
18	amphipod 3	Amphipoda	993	N
19	<i>Golfingia trichocephala</i> (Sluiter)	Sipuncula: Golfingiidae	927	S
20	<i>Eunice</i> cf. <i>indica</i> Kinberg	Polychaeta: Eunicidae	886	N
21	<i>Platyischnopus</i> sp. — polyspecific	Amphipoda: Haustoriidae	852	N
22	gastropod (red and white)	Gastropoda	819	N
23	amphipod 4	Amphipoda	792	N
24	bivalve 1	Bivalvia	775	S
25	<i>Schizaster lacunosus</i> (Linnaeus)	Echinoidea: Hemiasteridae	703	S
26	<i>Goniada emerita</i> Audouin and Milne Edwards	Polychaeta: Glyceridae	688	S
27	<i>Leptomya pura</i> Angas	Bivalvia: Semelidae	673	S
28	<i>Rhizammina</i> cf. <i>algaeformis</i> H. B. Brady	Foraminifera: Astrorhizidae	668	N
29	<i>Xenophthalmoides dolichophallus</i> Tesch	Decapoda: Goneplacidae	654	S
30	carid 2	Decapoda: Caridae	648	S
31	<i>Dispio</i> sp.2	Polychaeta: Spionidae	643	N
32	juv. fibularid	Echinoidea: Fibularidae	632	N
33	' <i>Dentalium</i> ' sp.	Scaphopoda	564	S
34	<i>Tharyx</i> sp.A (undescri.)	Polychaeta: Cirratulidae	466	N
35	amphipod 6	Amphipoda	433	S
36	<i>Paralacydonia paradoxa</i> Fauvel	Polychaeta: Lacydoniidae	432	S
37	<i>Terebellides stroemi</i> Sars	Polychaeta: Terebellidae	428	S
38	<i>Haploscoloplos bifurcatus</i> Hartman	Polychaeta: Orbiniidae	423	S
39	<i>Branchiostoma moretonensis</i> Kelly	Cephalochordata	412	S
40	<i>Sthenelais</i> sp.	Polychaeta: Aphroditidae	409	S
41	<i>Echinocardium cordatum</i> (Pennant)	Echinoidea: Spatangidae	405	S
42	<i>Neosolen vaginoides</i> (Lamarck)	Bivalvia: Cultellidae	403	N
43	<i>Mesanthura</i> sp.1	Isopoda: Anthuridae	396	N
44	amphipod 5	Amphipoda	380	N
45	orbiniid spp. — polyspecific	Polychaeta: Orbiniidae	360	S
46	<i>Caulleriella</i> sp.A + <i>Tharyx</i> sp.B — polyspecific (both undescri.)	Polychaeta: Cirratulidae	349	N
47	<i>Lucifer hansenii</i> Nobili	Decapoda: Sergestidae	344	N
48	lumbrinerid 1	Polychaeta: Lumbrineridae	322	N
49	<i>Epigonichthys cultellus</i> Peters	Cephalochordata	298	N
50	<i>Glycera prashadi</i> Fauvel	Polychaeta: Glyceridae	293	N
51	<i>Ophiura kinbergi</i> Ljungman	Ophiuroidea: Ophiolopidae	290	S
52	<i>Amphipholis loripes</i> Koehler	Ophiuroidea: Amphiuridae	269	S



Code No.	Species	Systematic position	Number Collected	Main site group
53	nemertean (pink) — polyspecific	Nemertea	264	S
54	<i>Micronephthys sphaerocirrata</i> Wesenberg-Lund	Polychaeta: Nephtyidae	262	
55	nemertean (pale) — polyspecific	Nemertea	256	
56	<i>Marphysa</i> sp.	Polychaeta: Eunicidae	227	N
57	<i>Mesanthura</i> sp.2	Isopoda: Anthuridae	219	N
58	<i>Magelona</i> cf. <i>papillicornis</i> Muller	Polychaeta: Magelonidae	212	N
59	polycirrinae — polyspecific	Polychaeta: Terebellidae	208	S
60	bivalve 2	Bivalvia	188	S
61	<i>Amphioplus depressus</i> (Ljungman)	Ophiuroidea: Amphiuridae	184	S
62	anthurid (undescr. genus 2, sp.2)	Isopoda: Anthuridae	180	N
63	amphipod 15 — polyspecific	Amphipoda	179	S
64	bivalve 8	Bivalvia	171	S
65	? <i>Notomastus</i> cf. <i>aberans</i> Day	Polychaeta: Capitellidae	168	S
66	= species 34 ( <i>Tharyx</i> sp.A)	Polychaeta: Cirratulidae	165	S
67	? <i>Notomastus latericeus</i> Sars	Polychaeta: Capitellidae	162	S
68	polyzoan 1	Polyzoa	161	S
69	<i>Sipunculus aequabilis</i> Sluiter	Sipuncula: Sipunculidae	157	S
70	terebellid (undescr. genus)	Polychaeta: Terebellidae	151	N
71	amphipod 14	Amphipoda	137	S
72	anthurid (undescr. genus 2, sp.1)	Isopoda: Anthuridae	134	N
73	<i>Thalenessa</i> sp.	Polychaeta: Aphroditidae	133	N
74	<i>Polydora</i> sp.1	Polychaeta: Spionidae	129	
75	<i>Owenia fusiformis</i> Delle Chiaje	Polychaeta: Oweniidae	117	S
76	<i>Sthenolepis</i> cf. <i>japonica</i> (McIntosh)	Polychaeta: Aphroditidae	109	S
77	<i>Aricidea</i> sp.	Polychaeta: Paraonidae	109	S
78	bivalve 4	Bivalvia	106	N
79	bivalve 12	Bivalvia	102	N
80	bivalve 14	Bivalvia	95	S
81	bivalve 6	Bivalvia	94	S
82	<i>Chaetozone</i> sp.A (undescr.)	Polychaeta: Cirratulidae	93	N
83	<i>Scalibregma inflatum</i> Rathke	Polychaeta: Scalibregmidae	90	S
84	amphipod 8	Amphipoda	90	S
85	nemertean (orange banded) — ?polyspecific	Nemertea	85	S
86	<i>Eunice</i> sp.2	Polychaeta: Eunicidae	84	N
87	<i>Polycarpa tinctor</i> (Quoy and Gaimard)	Tunicata: Styelidae	84	S
88	<i>Chaetozone</i> sp.B (undescr.)	Polychaeta: Cirratulidae	82	S
89	<i>Paraonides</i> sp.	Polychaeta: Paraonidae	80	N
90	<i>Paphia</i> sp.	Bivalvia: Veneridae	80	S
91	phoronid — ?polyspecific	Phoronidae	80	S
92	amphipod 9	Amphipoda	78	
93	<i>Cyclaspis tribulis</i> (Hale) complex	Cumacea: Bodotriidae	78	S
94	<i>Euclymene</i> sp.	Polychaeta: Maldanidae	75	S
95	<i>Pectinaria antipoda</i> Schmarda	Polychaeta: Pectinariidae	75	S
96	<i>Alpheus distinguendus</i> de Man	Decapoda: Alpheidae	75	S
97	<i>Natica</i> cf. <i>collieri</i> Recluz	Gastropoda: Naticidae	74	S
98	<i>Raphidopus ciliatus</i> Stimpson	Decapoda: Porcellanidae	73	S
99	<i>Lumbrineris</i> sp.1	Polychaeta: Eunicidae	71	N
100	gastropod 10	Mollusca: Gastropoda	70	
101	<i>Eocuma agrion</i> (Zimmer)	Cumacea: Bodotriidae	69	S
102	bivalve 7	Bivalvia	69	N
103	gastropod 5	Gastropoda	68	S
104	<i>Loimia medusa</i> (Savigny)	Polychaeta: Terebellidae	66	S
105	<i>Apseudes</i> sp.	Tanaidacea	66	
106	<i>Aspidosiphon inquilinus</i> Sluiter	Sipuncula: Aspidosiphonidae	66	S
107	<i>Fulvia</i> sp.	Bivalvia: Cardiidae	65	S
108	amphipod 20	Amphipoda	64	S
109	nereid 1	Polychaeta: Nereidae	63	S
110	isopod 5 — polyspecific	Crustacea: Isopoda	63	N



Code No.	Species	Systematic position	Number Collected	Main site group
111	bivalve 29	Bivalvia	63	S
112	<i>Scoloplos johnstonei</i> Day	Polychaeta: Orbiniidae	57	N
113	<i>Leptanthura</i> cf. <i>australis</i> Haswell	Isopoda: Anthuridae	56	
114	<i>Matuta inermis</i> Miers	Crustacea: Calappidae	56	N
115	amphipod 28	Amphipoda	51	S
116	<i>Thermiste</i> sp.	Sipuncula: Golfingiidae	51	N
117	<i>Conuber conica</i> (Lamarck)	Gastropoda: Naticidae	50	S
118	<i>Tellina</i> sp.1	Bivalvia: Tellinidae	50	S
119	<i>Diogenes</i> cf. <i>rectimanus</i> Miers	Decapoda: Paguridae	49	N
120	<i>Natica</i> sp.1	Gastropoda: Naticidae	49	S
121	bivalve 16	Bivalvia	49	N
122	amphipod 13	Amphipoda	48	S
123	gastropod 8	Gastropoda	47	
124	<i>Protankyra</i> sp.	Holothuriidae: Synaptidae	47	S
125	<i>Sigalion</i> sp.	Polychaeta: Aphroditidae	46	
126	<i>Dimorphostylis australis</i> (Foxon)	Cumacea	46	S
127	aphroditid 3	Polychaeta: Aphroditidae	44	S
128	<i>Harmothoe</i> sp.	Polychaeta: Aphroditidae	44	S
129	mysid 1	Mysidacea	44	S
130	<i>Drilonereis</i> sp.	Polychaeta: Eunicidae	43	N
131	capitellid spp. (juv) — polyspecific	Polychaeta: Capitellidae	40	S
132	carid 4	Decapoda: Caridae	40	
133	bivalve 22	Bivalvia	40	S
134	<i>Lumbrineris</i> sp.2	Polychaeta: Eunicidae	39	N
135	amphipod 18	Amphipoda	39	S
136	<i>Syllidia</i> sp.	Polychaeta: Hesionidae	36	N
137	<i>Nereis jacksoni</i> Kinberg	Polychaeta: Nereidae	36	S
138	amphipod 17	Amphipoda	36	
139	<i>Chloeia flava</i> (Pallas)	Polychaeta: Amphinomidae	35	S
140	onuphid 1	Polychaeta: Eunicidae	35	N
141	carid 3	Decapoda: Caridae	35	
142	<i>Veletuceta hedleyi</i> (Lamy)	Bivalvia: Glycymeridae	35	N
143	amphipod 21	Amphipoda	34	S
144	gastropod 3	Gastropoda	34	S
145	bivalve 3	Bivalvia	34	S
146	phyllodocid 3	Polychaeta: Phyllodocidae	33	
147	sabellid 2	Polychaeta: Sabellidae	33	S
148	isopod 3	Isopoda	33	N
149	amphipod 11	Amphipoda	33	
150	amphipod 16	Amphipoda	33	S
151	gastropod 2	Gastropoda	33	S
152	<i>Leonnates stephensoni</i> Ruillier	Polychaeta: Nereidae	32	S
153	<i>Muraenichthys godeffroyi</i> Regan	Pisces: Myridae	32	S
154	isopod 2	Isopoda	31	S
155	bivalve 5	Bivalvia	31	N
156	<i>Tellina texturata</i> Sowerby.	Bivalvia: Tellinidae	29	S
157	<i>Theora lata</i> Hinds	Bivalvia: Semelidae	29	
158	bivalve 17	Bivalvia	29	N
159	<i>Spiochaetopterus</i> sp.	Polychaeta: Chaetopteridae	28	S
160	<i>Pomacuma cognata</i> (Hale)	Cumacea: Bodotriidae	26	N
161	nereid 2	Polychaeta: Nereidae	25	S
162	cumacean 6	Cumacea	25	N
163	<i>Austrolepidoda schmitti</i> Efford and Haig	Decapoda: Albuncidae	25	N
164	platyhelminth 1	Platyhelminthes: Polycladida	24	N
165	amphipod 10	Amphipoda	24	
166	isopod 1	Isopoda	23	S
167	anemone 1	Actiniaria	22	
168	bivalve 9	Bivalvia	22	



Code No.	Species	Systematic position	Number Collected	Main site group
169	amphipod 24	Amphipoda	21	
170	bivalve 11	Bivalvia	21	S
171	<i>Spiochaetopterus</i> cf. <i>vittrarius</i> (Ehlers)	Polychaeta: Chaetopteridae	20	S
172	<i>Glyphocuma</i> sp.	Cumacea	20	S
173	<i>Penaeus plebejus</i> (Hesse)	Decapoda: Peneidae	20	S
174	<i>Polyonyx transversus</i> (Haswell)	Decapoda: Porcellanidae	20	
175	phyllodocid 7	Polychaeta: Phyllodocidae	19	
176	<i>Sternaspis scutata</i> (Renier)	Polychaeta: Sternaspidae	19	S
177	<i>Metapenaeus bennettiae</i> Racek and Dall	Decapoda: Peneidae	19	
178	gastropod 16	Gastropoda	19	S
179	phyllodocid 1	Polychaeta: Phyllodocidae	17	
180	<i>Glyphocuma halei</i> Greenwood and Johnston	Cumacea: Bodotriidae	17	S
181	<i>Chaetopterus variopedatus</i> Renier	Polychaeta: Chaetopteridae	16	S
182	<i>Moiria lethe</i> Lutken	Echinoidea: Hemiasteridae	16	N
183	capitellid 1	Polychaeta: Capitellidae	15	
184	tanaid 6	Tanaidacea	15	S
185	<i>Trachypenaeus fulvus</i> Dall	Decapoda: Peneidae	15	
186	<i>Philine angasi</i> Crosse and Fisher	Gastropoda: Philinidae	15	S
187	gastropod 27	Gastropoda	15	N
188	<i>Cyclaspis mawsonae</i> (Hale)	Cumacea: Bodotriidae	14	
189	isopod 4	Isopoda	14	N
190	<i>Dosinia</i> cf. <i>sculpta</i> Hanley	Bivalvia: Veneridae	14	S
191	bivalve 10	Bivalvia	14	S
192	<i>Ophiocentrus</i> sp.	Ophiuroidea: Amphiuridae	14	
193	phyllodocid 2	Phyllodocidae	13	
194	amphipod 26	Amphipoda	13	
195	juv. carid 1	Decapoda: Caridae	13	
196	bivalve 13	Bivalvia	13	S
197	bivalve 18	Bivalvia	13	S
198	gastropod 20	Gastropoda	13	N
199	gastropod 21	Gastropoda	13	N
200	<i>Ophiodromus</i> sp.	Polychaeta: Hesionidae	12	
201	<i>Dorvillea</i> sp.	Polychaeta: Eunicidae	12	
202	<i>Travisia</i> cf. <i>forbesii</i> Johnston	Polychaeta: Opheliidae	12	
203	maldanid 1	Polychaeta: Maldanidae	12	N
204	maldanid 2	Polychaeta: Maldanidae	12	S
205	tanaid 5	Tanaidacea	12	S
206	<i>Apanthura</i> sp.	Isopoda: Anthuridae	12	N
207	amphipod 29	Amphipoda	12	N
208	<i>Hexapus granuliferus</i> Campbell and Stephenson	Decapoda: Goneplacidae	12	S
209	<i>Modiolus</i> sp.	Bivalvia: Mytilidae	12	S
210	bivalve 21	Bivalvia	12	
211	bivalve 30	Bivalvia	12	S
212	<i>Natica</i> sp. 4	Gastropoda: Naticidae	12	S
213	gastropod 25	Gastropoda	12	
214	<i>Pista</i> spp. — polyspecific	Polychaeta: Terebellidae	11	S
215	<i>Laonice</i> sp.	Polychaeta: Spionidae	11	S
216	<i>Nerinides</i> sp.	Polychaeta: Spionidae	11	S
217	<i>Cyclaspis</i> ? <i>cretata</i> (Hale)	Cumacea: Bodotriidae	11	N
	? <i>granulos</i> (Hale)			
218	anthurid (undescr. genus 1 sp.1)	Isopoda: Anthuridae	11	
219	<i>Doxander vittatus</i> Linnaeus	Gastropoda: Strombidae	11	S
220	nemertean (green)	Nemertea	10	
221	aphroditid 1	Polychaeta: Aphroditidae	10	S
222	<i>Diplocirrus</i> sp.	Polychaeta: Flabelligeridae	10	S
223	? <i>Pontophilus</i> sp.1 (doubtfully benthic)	Crustacea: Crangonidae	9	N
224	<i>Phos sculptilis</i> Watson	Gastropoda: Photidae	10	S
225	phyllodocid 6	Polychaeta: Phyllodocidae	9	N



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226	= species 216 ( <i>Nerinides</i> sp.)	Polychaeta: Spionidae	9	S
227	<i>Matuta</i> spp. juv. not <i>M. inermis</i> ) — polyspecific	Decapoda: Calappidae	9	N
228	bivalve 15	Bivalvia	9	N
229	bivalve 24	Bivalvia	9	S
230	<i>Sthenolepis</i> sp.	Polychaeta: Aphroditidae	8	S
231	<i>Pseudeurythoe microcephala</i> (Fauvel)	Polychaeta: Amphinomidae	8	S
232	nereid 4	Polychaeta: Nereidae	8	S
233	eunicid 1	Polychaeta: Eunicidae	8	N
234	<i>Travisia</i> sp.2	Polychaeta: Opheliidae	8	N
235	bivalve 19	Bivalvia	8	N
236	<i>Luidia</i> sp.	Asteroidea: Luididae	8	S
237	<i>Rhynobrissus pyramidalis</i> Agassiz	Echinoidea: Spatangidae	8	N
238	<i>Glossobalanus</i> sp.	Balanoglossidae	8	S
239	polyzoa 2	Bryozoa	7	
240	nemertean (brown)	Nemertea	7	S
241	<i>Eupanthalis</i> sp.	Polychaeta: Aphroditidae	7	S
242	<i>Etenone</i> sp.	Polychaeta: Phyllodocidae	7	
243	<i>Nephtys vikingensis</i> Paxton	Polychaeta: Nephtyidae	7	N
244	spionid 7 — polyspecific	Polychaeta: Spionidae	7	S
245	<i>Ophelina</i> cf. <i>acuminata</i> Oersted	Polychaeta: Opheliidae	7	
246	tanaid 3	Tanaidacea	7	S
247	amphipod 22	Amphipoda	7	
248	amphipod 27	Amphipoda	7	S
249	<i>Betaeus</i> spp. — polyspecific	Decapoda: Alpheidae	7	S
250	oyster 1	Bivalvia: Ostreidae	7	
251	<i>Amphiura catephes</i> H. L. Clark	Ophiuroidea: Amphiuridae	7	S
252	<i>Nematonereis</i> sp.	Polychaeta: Eunicidae	6	S
253	<i>Polydora</i> sp.2	Polychaeta: Spionidae	6	S
254	bivalve 20	Bivalvia	6	S
255	blenny 1 (doubtfully benthic)	Pisces: Blenniidae	7	N
256	phyllodocid 15	Polychaeta: Phyllodocidae	5	N
257	<i>Arabella</i> sp.	Polychaeta: Eunicidae	5	
258	maldanid 3	Polychaeta: Maldanidae	5	S
259	sabellid 3	Polychaeta: Sabellidae	5	
260	amphipod 19	Amphipoda	5	S
261	<i>Eucrassatella cumingii</i> (Adams)	Bivalvia: Eucrassatellidae	5	N
262	<i>Mactra</i> sp.	Bivalvia: Mactridae	5	N
263	<i>Tellina</i> sp.2	Bivalvia: Tellinidae	5	N
264	<i>Natica</i> sp.3	Gastropoda: Naticidae	5	S
265	gastropod 33	Gastropoda	5	
266	<i>Mogula mollis</i> Herdmann	Tunicata: Molgulidae	5	
267	<i>Euleanira</i> sp.	Polychaeta: Aphroditidae	4	S
268	phyllodocid 5	Polychaeta: Phyllodocidae	4	
269	phyllodocid 8	Polychaeta: Phyllodocidae	4	S
270	phyllodocid 10	Polychaeta: Phyllodocidae	4	S
271	nereid 3	Polychaeta: Nereidae	4	
272	<i>Prionospio</i> sp.3	Polychaeta: Spionidae	4	
273	amphipod 25	Amphipoda	4	
274	<i>Alpheus</i> spp. (larva) — polyspecific	Decapoda: Alpheidae	4	S
275	<i>Albunea</i> cf. <i>microps</i> Miers	Decapoda: Albuneidae	4	
276	<i>Limaria</i> sp.	Bivalvia: Limidae	4	S
277	bivalve 25	Bivalvia	4	S
278	bivalve 26	Bivalvia	4	S
279	bivalve 31	Bivalvia	4	
280	gastropod 13	Gastropoda	4	
281	gastropod 15	Gastropoda	4	
282	<i>Pentaceraster australis</i> (Luther)	Asteroidea: Oreasteridae	4	
283	enteropneust	Enteropneusta	4	



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284	<i>Paraplagusia unicolor</i> (Macleay)	Pisces: Cynoglossidae	4	S
285	<i>Leanira yhleni</i> Malmgren	Polychaeta: Aphroditidae	3	S
286	aphroditid 7	Polychaeta: Aphroditidae	3	
287	phyllodocid 4	Polychaeta: Phyllodocidae	3	
288	phyllodocid 12	Polychaeta: Phyllodocidae	3	
289	phyllodocid 14	Polychaeta: Phyllodocidae	3	
290	phyllodocid 19	Polychaeta: Phyllodocidae	3	S
291	syllid 1	Polychaeta: Syllidae	3	
292	spionid 6 — polyspecific	Polychaeta: Spionidae	3	N
293	= species 216 ( <i>Nerinides</i> sp.)	Polychaeta: Spionidae	3	
294	<i>Ophelina gigantea</i> Rullier	Polychaeta: Opheliidae	3	
295	capitellid 2	Polychaeta: Capitellidae	3	
296	sabellid 6	Polychaeta: Sabellidae	3	S
297	unknown polychaete	Polychaeta	3	
298	<i>Gynodiastylis</i> sp.	Cumacea: Diastylidae	3	
299	tanaid 7	Tanaidacea	3	S
300	mysid 2	Mysidacea	3	
301	mysid 3	Mysidacea	3	
302	<i>Squilla laevis</i> Hess	Crustacea: Stomatopoda	3	S
303	<i>Lysiosquilla perpasta</i> (Hale)	Crustacea: Stomatopoda	3	
304	? <i>Pontophilus</i> sp.3	Decapoda: Crangonidae	3	N
305	<i>Conchocetes artificiosus</i> (Fabricius)	Decapoda: Dromiidae	3	
306	<i>Dorippe australiensis</i> Miers	Decapoda: Dorippidae	3	
307	<i>Actumnus squamosus</i> de Haan	Decapoda: Xanthidae	3	S
308	<i>Achaeus lacertosus</i> Stimpson	Decapoda: Majidae	3	S
309	<i>Sanguinolaria</i> sp.	Bivalvia: Sanguinolariidae	3	
310	gastropod 1	Gastropoda	3	
311	gastropod 7	Gastropoda	3	
312	gastropod 19	Gastropoda	3	N
313	gastropod 22	Gastropoda	3	N
314	gastropod 26	Gastropoda	3	
315	gastropod 29	Gastropoda	3	
316	<i>Amphipholis squamata</i> (Delle Chiaje)	Ophiuroidea: Amphipruridae	3	S
317	<i>Lovenia camorata</i> H. L. Clark	Echinoidea: Spatangidae	3	
318	holothurian 5	Holothuroidea	3	





Stephenson, William., Cook, S. D., and Newlands, S.J. 1978. "The macrobenthos of the Middle Banks area of Moreton Bay." *Memoirs of the Queensland Museum* 18, 185–212.

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