

THE EFFECT OF A MAJOR FLOOD ON THE MACROBENTHOS OF BRAMBLE BAY QUEENSLAND

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ABSTRACT

The macrobenthos of Bramble Bay, which may be affected by proposed extensions to Brisbane Airport, was influenced by a severe flood in Jan. 1974. The benthic study involved two study periods—preflood (June 1972 to Dec. 1973) and postflood (Mar. 1974 to Mar. 1975), with the former already published (Stephenson, Raphael and Cook 1976). Hence the present work evaluates effects of the flood upon a known biota.

Salinities were reduced to at least 24‰ in the area of sampling, and the affected period was prolonged by rainfall associated with a cyclone in Mar. 1974. A transient cover of soft silt occurred after the flood. Sites were grouped by their sedimentary compositions in separate analysis of preflood and postflood data, using clustering technique previously applied to sites/species. Sediment site-groups after the flood showed a complex mosaic of areas and there was an overall increase in muddiness.

The biotic data (preflood and postflood) form a 3D matrix with the main interest in the time axis. Data were derived on the average number of individuals per site (n), average number of species per site (s), and average standardised Shannon diversities per site (d), in each of the times. Diversities were lower after the flood but not significantly so, s values were significantly lower almost throughout, n values were originally significantly lower and finally significantly higher.

Flood effects on separate sites were evaluated by comparing n and s values in various times. In one or another postflood period significant changes occurred in 26/27 sites for n data and 25/27 sites for s data. Overall population effects were greater, with many sites showing higher populations in late postflood than in preflood times.

Flood effects on the 74 most abundant species, were evaluated species by species in terms of populations and areas of distribution. Thirty-six of these species, mostly low in the abundance hierarchy, showed no 'significant' effects. The others showed effects variously categorised for example as v. transient decreases (5 spp.), and 'permanent' decreases (7 spp.), transient increases (5 spp.), and 'permanent' increases (2 spp.). Increases were mostly in areas occupied, rather than site populations, with the commonest species (*Spisula*) increasing from 6-9 to 25 sites.

Investigations were made of changed site-species patterns, and involved hierarchical classifications of species \times sites matrices over selected times viz. preflood, early postflood and late postflood. The technique followed Stephenson, Raphael and Cook (1976) except that the Manhattan metric dissimilarity measure was now used. Preflood there is an inshore site-group characterised by *Spisula*, *Xenophthalmus*, *Terebellides*, *Pupa* etc.; an intermediate depth grouping with *Anadara*, tunicates and an oyster, and an offshore group with *Placamen*, two species of *Amphioplus*, *Theora lata* etc.

In early postflood four sites formed a 'near-rivers' group with *Spisula* markedly dominant, followed by *Pupa* and *Parcanassa*; three sites formed an offshore group with two species of *Amphioplus* and *Theora lata*, and 20 sites with an impoverished biota were weakly characterised by *Anadara*.

In late postflood 22 sites formed a *Spisula-Parcanassa* community, reflecting the spread of these species into the previously 'scarified' area. Two small offshore site-groups were characterised by more species than in early postflood.

A tentative conceptual model of benthic changes in the area is proposed based on the assumption of occasional severe flooding. The effects of the present natural events are likely to be much more obvious than those caused by the proposed airport enlargement.

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Extensions of Brisbane Airport if effected will involve extensive filling of Serpentine Creek and increased drainage through Jackson's Creek. It is possible that these may affect the biota of the adjacent area of Moreton Bay, viz. Bramble Bay (see Fig. 1). Two studies of the macrobenthos of Bramble Bay were planned, the first being before the construction and in the nature of a 'base-line' study. From this it was hoped that predictions could be made of the effects of airport extension. The second proposed study, after construction, would evaluate the actual effects.

Twenty-seven sites, *c.* 1 km apart, were selected in Bramble Bay, and these were sampled for macrobenthos every three months beginning June

1972 (see Fig. 2). Duplicate catches were made by an 0.1 m² van Veen grab and sieved through 1 mm apertures; the two catches were pooled to give a 'sample'.

Heavy rainfall in the catchment of the Brisbane River caused extremely heavy flooding in Jan. 1974 (see Ward 1974). Samples from seven pre-flood times were available and when the eighth set was obtained, *c.* two months after the flood, it was evident that the benthic biota had suffered a marked decline. Just after this collection was made there was further heavy rainfall associated with a cyclone and as shown later, this may have prolonged the adverse effects due to the flood. Sampling continued (from *t*8 Mar. 1974 to *t*12

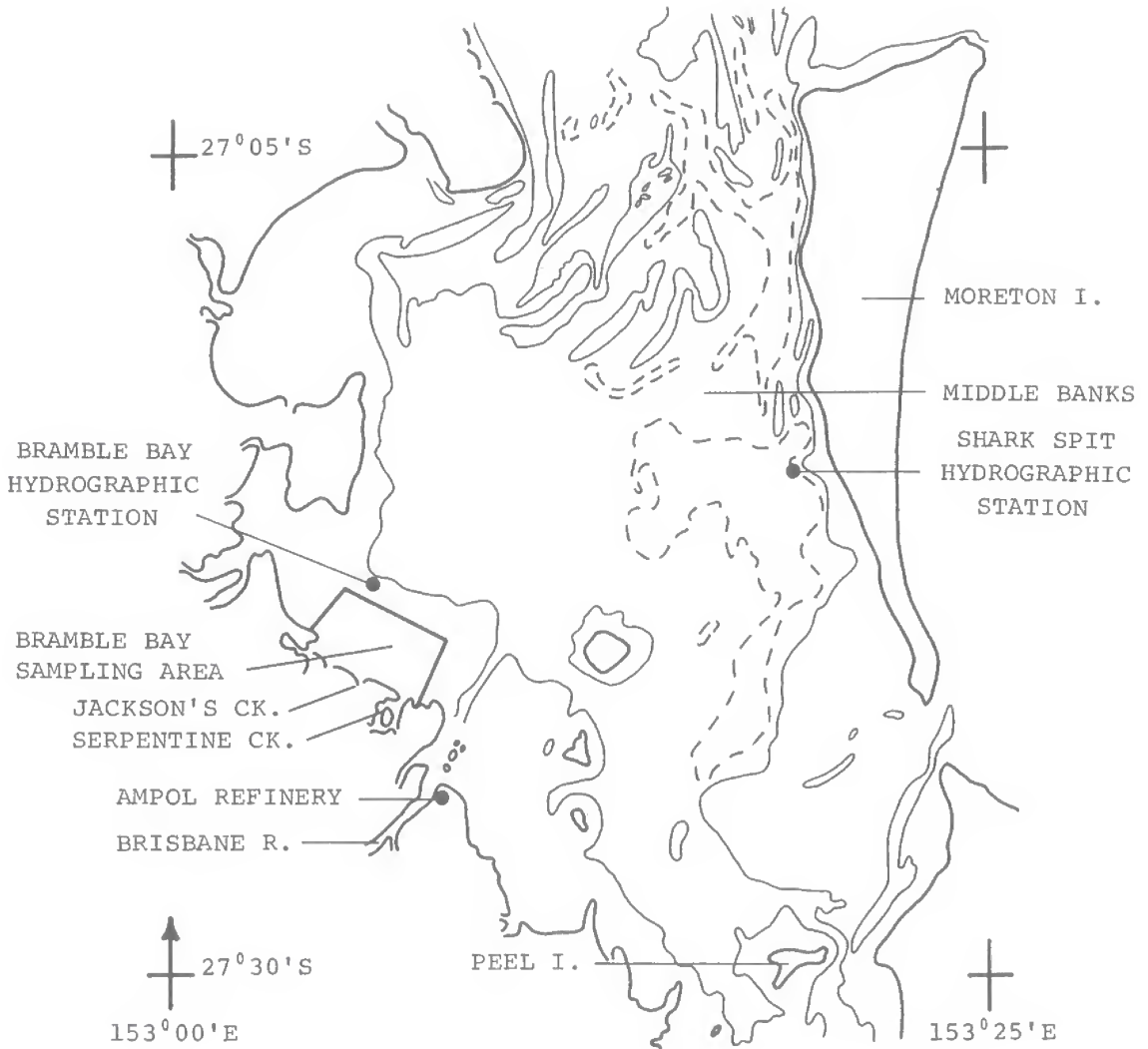


FIG. 1: Map of Moreton Bay showing sampling area and locations mentioned in the text.

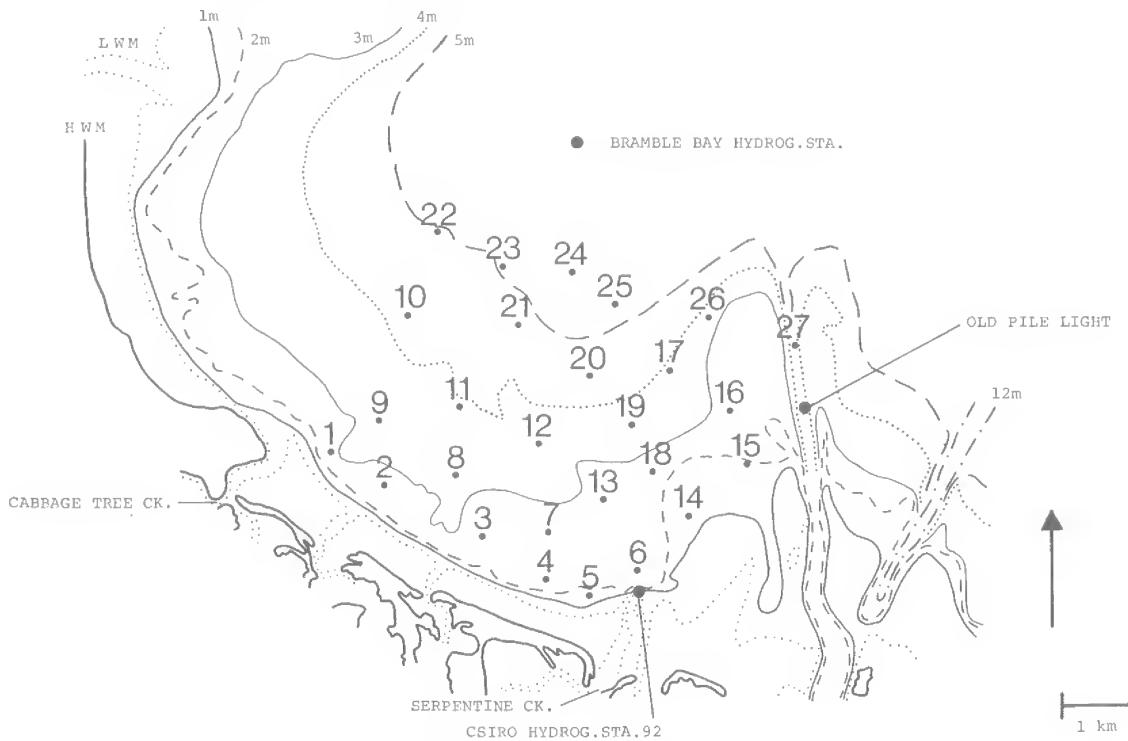


FIG. 2: Positions of sampling sites, CSIRO hydrographic stations, etc. in the Bramble Bay region.

Mar. 1975) until there was clear evidence of biotic recovery. The preflood situation has been documented by Stephenson, Raphael and Cook (1976), and we now consider the postflood situation and relate it to the reasonably normal preflood 'base-line'.

The extensive preflood data permits an unrivalled opportunity to quantify the effects of the flood and cyclone. The analyses of these data are also of applied value and raise the possibility of a later comparison between the effects of a man-made disturbance (airport construction) with natural ones.

Abiotic and biotic data are treated in separate sections in the account which follows, with methods in their relevant sections.

ABIOTIC DATA

DEPTHS: Preflood depth data are given by Raphael (1974) and Stephenson, Raphael and Cook (1976). These data are repeated here on Fig. 2. During the first postflood collection of biotic data (March 1974) it was noted that on the eastern side of the study area (sites 15, 16) depths had decreased by as much as 1.5 m. This was attributed to settlement of material scoured by the flood from

the Brisbane R. At the time of writing there has been no official resurvey of depths in the area.

SALINITY: Two hydrographic studies were undertaken by the CSIRO Division of Fisheries and Oceanography, one at roughly fortnightly intervals over the period Apr. 28th 1972 to May 4th 1973, and another at monthly intervals from Aug. 1972 with data available up to Feb. 1975. One locality in the first study (CSIRO No. 92), near the mouth of Serpentine Ck, is close to our site 6 and monthly averages of salinity at that locality are plotted on Fig. 3A.

The more extensive study involved measurements at different water depths at several localities in Moreton Bay. Those of interest are: Bramble Bay, $27^{\circ}18'S$, $153^{\circ}06'E$, ca 3 km NW. of our site 22, the most NW. of our sites; near Ampol Refinery (mouth of the Brisbane R.), $27^{\circ}25'S$, $153^{\circ}09'E$, ca 6 km from our site 15, and Shark Spit $27^{\circ}17'S$, $153^{\circ}22'E$. Initially we considered salinities in the deepest water sample at each locality (c. 5 m, 11 m and 29 m respectively) as being those most relevant to the benthos. The Brisbane R. samples were less variable than those at Bramble Bay, and because the shallower water at the Brisbane R. would be in more direct communication with Bramble Bay, an intermediate depth (c. 6 m) was also considered.

There were some gaps in the data (see Fig. 3A) but two continuous periods each of a year were available for study viz. Aug. 1972 to July 1973 and Oct. 1973 to Sept. 1974.

The benthic sampling area lies between two of the hydrographic stations and by taking intermediate values from Table I we can assume an average salinity in the preflood year of *c.* 32.5‰.

TABLE I: SALINITIES (PARTS PER 1000) MONTHLY SAMPLES AT FOUR HYDROGRAPHIC STATIONS

Station	Preflood year (Aug. 72–July 73)			Postflood year (Oct. 73–Sept. 74)		
	mean	range	variance	mean	range	variance
Bramble Bay ca 5 m	32.76	27.9–34.94	5.23	30.27	24.3–33.5	10.21
Nr. Ampol Refinery ca 6 m	32.34*	30.1–34.76*	2.79*	29.69	24.8–33.8	5.91
Nr. Ampol Refinery ca 11 m	32.94	30.5–35.14	2.42	30.16	26.2–33.8	4.36
Shark Spit ca 29 m	34.50	33.13–35.33	0.55	33.70	32.0–35.08	1.32

*Values for Nov. 1972, Feb. 1973 not available.

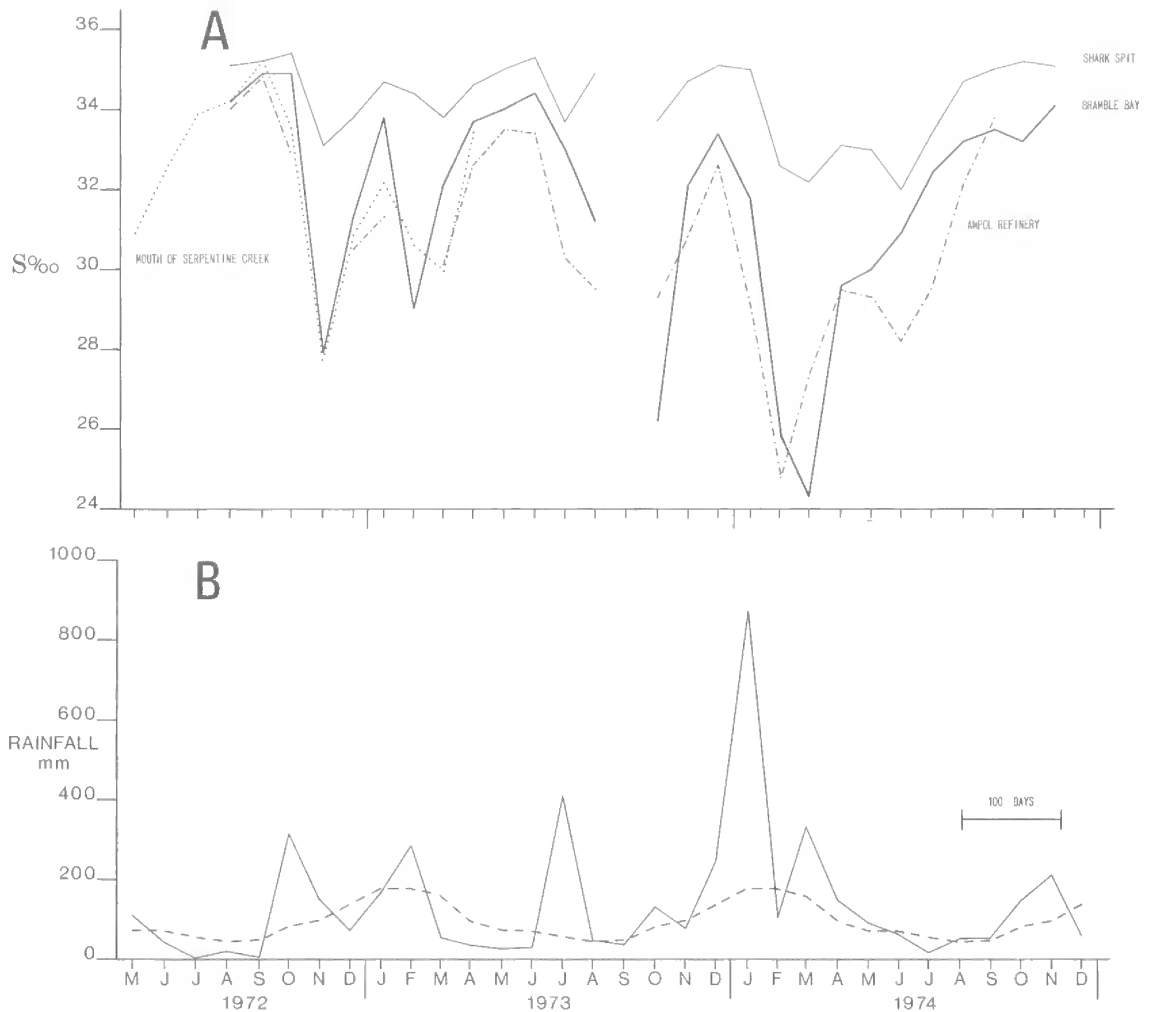


FIG. 3A: Salinities over the period Mar. 1972 to Dec. 1974, monthly means plotted at Middle of each month. Original data from CSIRO Division of Fisheries and Oceanography at localities mentioned.

FIG. 3B: Rainfall data from catchment of Brisbane R. (see text). Monthly values from Mar. 1972 to Dec. 1974 (continuous line) compared with monthly averages over years 1915–1972 (dotted line).

(about $2^{\circ}/\text{‰}$ below Shark Spit) and an annual range of *c.* $28^{\circ}/\text{‰}$ to $35^{\circ}/\text{‰}$. These assumptions are supported by the monthly means from the shorter hydrographic study near our site 6 (Fig. 3A, dotted line). In the flood year the average would be *c.* $30^{\circ}/\text{‰}$, (about $3.5^{\circ}/\text{‰}$ below that of Shark Spit) with a range from *c.* $24^{\circ}/\text{‰}$ to $34^{\circ}/\text{‰}$, and with approximately twice the variance of the pre-flood year.

In both years, salinity variability measured as variance was, somewhat surprisingly, greatest at the Bramble Bay station, followed by the mouth of the Brisbane R., 6 m, 11 m, and Shark Spit in that order.

Fig. 3A shows four occasions of salinity reduction, with three in the pre-flood period (Nov. 1972, Feb. 1973 and July 1973 possibly until Oct. 1973). In Jan. 1974 even before the flood, salinities were reduced in Bramble Bay and near the mouth of the Brisbane R. The greatest reduction at the mouth of the Brisbane R. was in February 1974 but at Bramble Bay and at Shark Spit was in Mar. 1974. High salinities returned about Aug. 1974. A further reduction occurred at Shark Spit and the mouth of the Brisbane R. (but not at Bramble Bay) in June 1974, and this is attributed to the rainfall accompanying the cyclone of Mar. 1974.

It is clear that the flood of Jan. 1974 followed by the Mar. cyclone produced severe, widespread and

prolonged reductions in salinities in Bramble Bay and elsewhere in Moreton Bay.

RAINFALL: In a recent study of the pre-flood benthos of Serpentine Ck., Stephenson and Campbell (1976) showed a close inverse relationship between salinity at the mouth of the Creek and rainfall at the Brisbane Weather Station. In the present case, with a main interest in the flood, rainfall from a much wider area is considered, and a variable time-lag between rainfall and reduction of salinities is to be expected.

Following Raphael (1974) rainfall data were obtained for four weather stations considered representative of the catchment of the Brisbane R. These were: Maleny, one of the higher rainfall areas in the region of the Stanley R.; Kalbar, in the region of the Bremer R.; Crow's Nest, in the region of Lockyer Ck; and Brisbane City. Values for these stations were averaged on a monthly basis covering the period of direct interest, and mean values for the years 1915 to 1972 were also obtained. These data are given in Fig. 3B.

Between Mar. 1972 and Nov. 1973 there were three periods in which rainfall was distinctly above average: (i) Oct. 1972, (ii) Feb. 1973, and (iii) more markedly, July 1973. These correspond to salinity reductions with about a month's delay in (i) and (ii), and with a more prolonged effect in (iii).

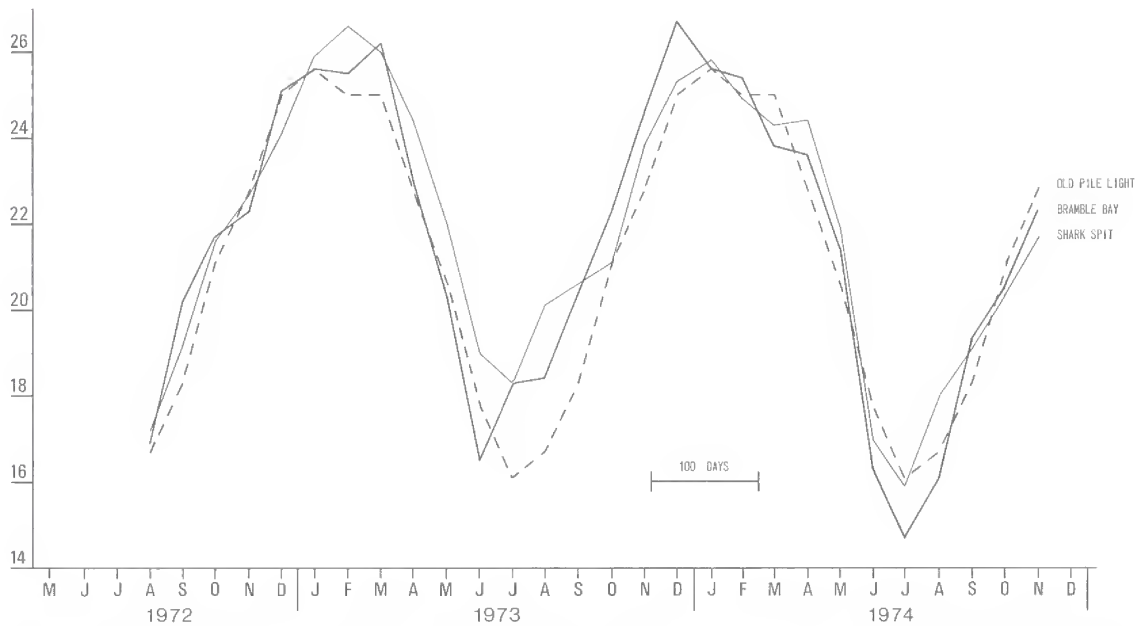


FIG. 4: Water temperatures in $^{\circ}\text{C}$, data plotted at middle of each month. Continuous lines, CSIRO hydrographic stations, Apr. 1972 to Nov. 1974. Dashed line—Ole Pile Light monthly averages over years 1931–1950.

TABLE 2: TEMPERATURE IN °C AT FOUR HYDROGRAPHIC STATIONS; MONTHLY SAMPLES OVER TWO YEARS

Station	Preflood year (Aug. 72–July 73)			Postflood year (Oct. 73–Sept. 74)		
	mean	range	variance	mean	range	variance
Bramble Bay ca 5 m	21.66	16.2–25.5	11.06	21.41	14.6–27.0	13.80
Nr. Ampol Refinery ca 6 m	21.54*	16.3–27.0*	14.23*	21.85	14.8–27.4	18.88
Nr. Ampol Refinery ca 11 m	21.49	16.3–25.8	13.80	21.73	14.8–26.7	18.13
Shark Spit ca 29 m	22.25	17.2–26.6	10.55	21.79	15.9–25.8	12.25

*Values for Nov. 1972, Feb. 1973 not available.

Rainfall increased from Dec. 1973 to an exceptionally high value (873 mm) in Jan. 1974, and after a normally wet Feb. (105 mm) again became higher than normal in Mar. (334 mm). The Dec.–Jan. rains produced minimal salinities in Mar. (except at the mouth of the Brisbane R.) while the Mar. rains produced a second salinity reduction in June 1974 (except at Bramble Bay). As stated earlier the combined effects of the two wet periods had not disappeared until Aug. 1974.

TEMPERATURES: Relevant temperature data, obtained by the CSIRO Division of Fisheries and Oceanography are plotted in Fig. 4, with summarising data in Table 2. Although there is greater variability in the flood year there are no obvious or immediate relationships to the flood.

SEDIMENTS: Maxwell (1970) investigated the sediments of Moreton Bay and showed in Bramble Bay there was an inshore area of medium sand (modal type) and an offshore area of fine sand. Raphael (1974) noted that sediments were muddier than Maxwell's results indicated, and undertook sediment collection and analyses. The results showed considerable and apparent random variation and Stephenson, Raphael and Cook (1976) were only able to derive meaningful topographical patterns by considering the finest and coarsest sediment fractions.

Grab samples made in Mar. 1974, (one month after the flood) showed that a layer of soft oozy mud had settled over the entire sampling area. The layer ranged in thickness from 1–5 cm without any obvious topographical pattern in thickness. It was suggested earlier that sediments scoured from the Brisbane R. had settled in the eastern part of the sampled area and reduced depths, and the widespread layer of soft mud had clearly originated in the same way, no doubt as the last sediment fraction to settle. Recently dead bivalves were buried beneath the mud. Four months after the flood, the fine soft layer was doubtfully recognisable. It was suspected that some had been dispersed by water movements and some had consolidated.

In the hopes of quantifying the sediment settlement, and showing that the grounds had become 'permanently' more muddy, sediment samples were collected at the end of the period of biotic sampling—in Mar. 1975. Meanwhile the heterogeneity in the preflood sediment data had become apparent, and this was attributed to hand selection of aliquots from within 0.1 m² van Veen samples. At this stage the preflood data were regarded as unreliable and the collecting methods were revised, however further analyses showed that the preflood data were of value.

Raphael's (1974) data on the present 27 sites were considered, involving triplicate analyses (at 6 month intervals); we neglected her additional data on 21 further sites (involving duplicate annual analyses). Time changes in the data, obtained in June 1972, Dec. 1972, and June 1973 are not apparent, and only area patterns were sought.

Sites were classified using as attributes the mean of the percentages of sediment grades in the three samples. As a preliminary the variability in the data was assessed as the average probable error in the means of the mud percentages of the three samples; this was *c.* 2.75% in an average of *c.* 50%. It is felt that only a negligible fraction of this would be due to seasonal variation. The data we quote are given to the nearest 1%, but are clearly less accurate than this except in the rarer fractions.

Raphael's analyses and the present ones, were by wet sieving with sieve sizes (in mm): 2.00, 1.00, 0.50, 0.25, 0.125, and 0.63. The grades retained are referred to as gravel (=shell), very coarse sand, coarse sand, medium sand, fine sand, and very fine sand respectively. The fraction passing the finest sieve is referred to as mud.

In classification the Bray-Curtis dissimilarity measure and group-average sorting were used—see Clifford and Stephenson (1975) for explanation of these terms.

The dendrogram of the preflood sediment site-groups is given in Fig. 5 and originally the seven groups marked X on this figure were chosen. Three groups are small, comprising sites 16, 17+23, and

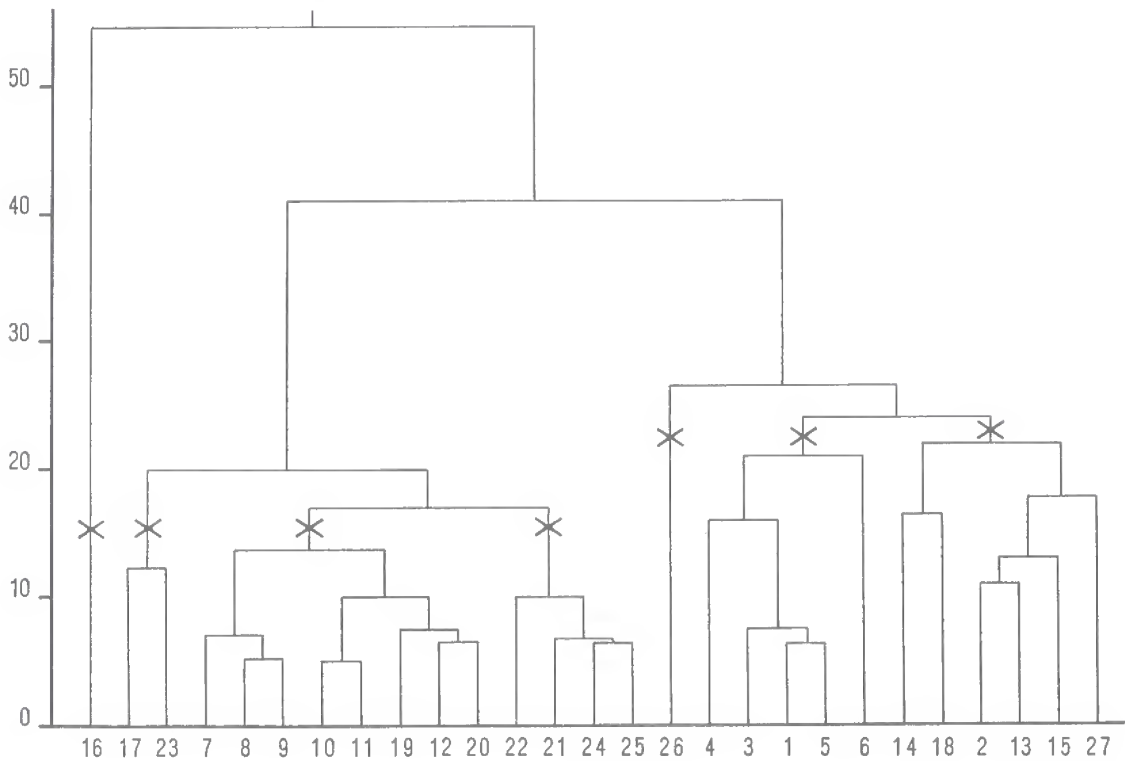


FIG. 5: Dendrogram of sites classification using pre-flood sediments. Vertical scale percentage 'Bray-Curtis' dissimilarity, X indicates site-groups originally accepted.

26, and of these the second and third were readily reallocated. Mean percentages of sediment fractions in the five resultant site-groups are shown in Table 3A and the site-groups are map plotted on Fig. 6.

Fig. 6 shows that a topographically coherent pattern is obtained and in conjunction with Table 3A the overall situation is:

Group 1, site 16, low mud percentage, and high percentages of coarse grades.

Group 2, sites 2, 13, 14, 15, 18, 26, 27,—inshore and mostly adjacent to the Brisbane R., with an isolate (site 2) off the mouth of Cabbage Tree Ck, broad spectrum of sediment fractions.

Group 3, sites 1, 3, 4, 5, 6,—most inshore sites, sediments mostly mud and very fine sand.

Group 4, sites 7, 8, 9, 10, 11, 12, 17, 19, 20, 23,—the bulk of the sampled area and at intermediate depths, sediments predominantly (c. 2/3) mud.

Group 5, sites 21, 22, 24, 25,—the deepest and most offshore sites, sediments very predominantly (c. 4/5) mud.

Overall, the western part of the sampled area gives groups with increasing muddiness in deeper water. The eastern part has less muddy sediments, and presumably is under influence from the Brisbane R. The coarse sediments at site 16 probably have a biotic origin (dead shell material).

In the post-flood sediment sampling, we used a Smith McIntyre grab covering half the surface of a normal 0.1 m² grab, but penetrating to the same depth, and took entire grab samples back to base. Here they were homogenised by vigorous stirring in a larger container, adding water if necessary. After settling and if necessary partially evaporating in air, three subsamples were taken simultaneously with separate 5 cm corers and each closed at base by a hand-manipulated metal disc. Sediment analyses were carried out separately on each core, and the means of the three determinations were used. The average probable error of the means of the most variable fraction, the mud, was now c. 0.4% in values averaging 58%, and the results are hence about 7 times more accurate than the pre-flood data.



FIG. 6: Topography of site-groups from pre-flood sediments.

Data were processed as before and the dendrogram of the sediment site classification is given in Fig. 7. Initially we accepted the seven site-groups marked X on that figure, and then reallocated the group consisting of a single site (12). The six resultant groups are map plotted on Fig. 8. Average percentages of each grade of sediment in each site group are given in Table 3B.

Comparison of pre-flood and post-flood sediments on a gross basis indicates an average increase in the mud percentage from 51% to 58%. It was suspected that, in the post-flood sampling, the snapping of the jaws of the Smith McIntyre grab caused the loss of some softer material on the surface of the samples. If so the difference in mud percentages between post-flood and pre-flood samplings would have appeared greater.

Comparison of Figs. 6 and 8 shows considerable changes, with the western side of the sampled area the least changed and with inshore (group 3), middle (group 5) and offshore (group 6) groups still apparent. However the mud percentages of the inshore and middle groups have increased by *c.* 10%, while the offshore group (with a mud percentage unchanged at *c.* 82%) has moved its boundary inshore. The eastern side of the sampled area is markedly changed into a mosaic pattern. The area with coarsest sediments (group 1) now includes site 27 as well as site 16, suggesting a scouring effect. The next coarsest (group 2) has the same broad spectrum of sediment fractions as in the pre-flood group 2 and appears relatively unaltered by the flood.

BIOTIC DATA

GENERAL CONSIDERATIONS

Methods of collection of biotic data are as described in the pre-flood paper (Stephenson,

TABLE 3: MEAN PERCENTAGES OF SEDIMENT FRACTIONS PER SITE IN THE SEDIMENT SITE-GROUPS. A—PRE-FLOOD, B—POST-FLOOD

Sed. site-grp.	Sites in Site-group	Mean percentages of sediment fractions						
		V.F. Mud	F sand	M sand	C sand	V.C. sand	Gravel (= shell)	
A								
1	16	5	2	13	23	24	9	25
2	2, 13-15, 18, 26, 27	30	15	16	20	6	2	12
3	1, 3-6	39	31	16	6	1	1	7
4	7-12, 17	66	10	4	5	3	1	10
5	19, 20, 23, 21, 22, 24, 25	81	6	3	3	1	1	6
B								
1	16, 27	13	3	11	30	24	5	15
2	13, 14, 18	25	22	29	14	5	1	3
3	1-6, 15, 17	50	29	9	5	2	1	5
4	12, 19, 24, 25	70	9	8	5	4	1	3
5	7, 8, 9, 11	77	12	3	1	1	1	6
6	10, 20-23, 26	83	6	4	1	1	1	4

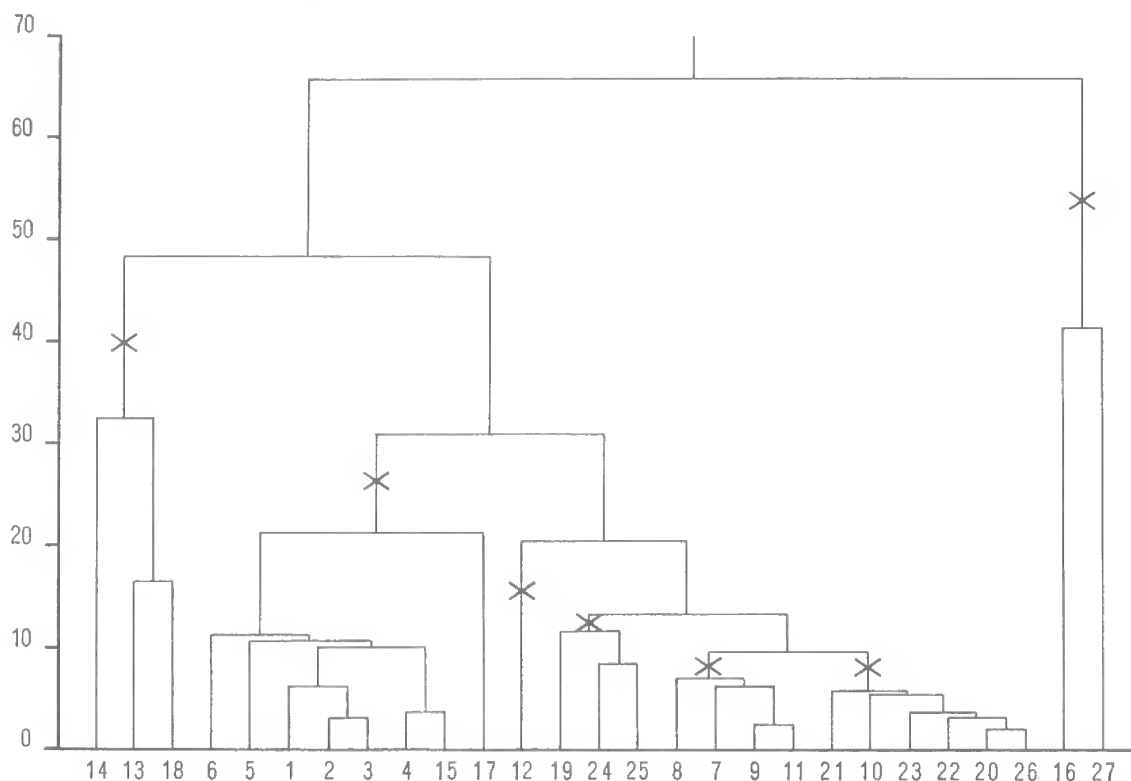


FIG. 7: Dendrogram of sites classification using postflood sediments. Vertical scale percentage 'Bray-Curtis' dissimilarity, X indicates site-groups originally accepted.

Raphael and Cook 1976). Species identifications were almost exclusively by comparison with the earlier reference collections. Individuals of each species in each sample were counted and recorded.

Analyses of data were similar to those of the earlier paper, but included different derivatives of the data.

The original data comprise a 3D matrix of 182 species (s) \times 27 sites (q for quadrats) \times 12 times (t) containing meristic values (whole numbers). We declare a main interest in the times dimension of the matrix, with this divisible into *preflood* comprising $t1$ to $t7$ (June 1972 to Dec. 1973) and *postflood* comprising $t8$ to $t12$ (Mar. 1974 to Mar. 1975). One set of derived data are in binary form (i.e. recording the presence or not recording the presence of species), but otherwise the matrix is identical with the original.

The easiest way to handle either of the 3D matrices is to summate (and then possibly to average) across a specified axis. The various summations are considered later.

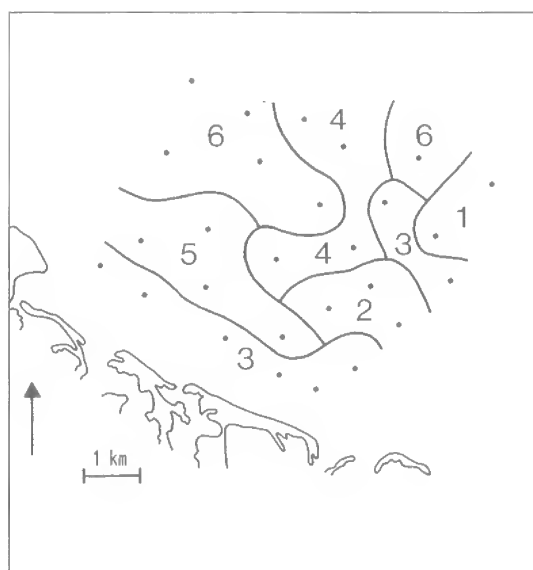


FIG. 8: Topography of site-groups from postflood sediments.

EFFECT OF THE FLOOD ON ALL SPECIES IN ALL SITES

To investigate this we first summated across the species axis in the two previous matrices and derived two $t \times q$ matrices with dimensions 12×27 in each case. The values in the meristic matrix are the sample populations of all species, which are the numerical equivalent of biomass which we designate n , while the values in the summated binary matrix are the number of species in each sample which we designate s . The latter are the species densities per sample (Hurlbert, 1971) and are a simple measure of diversity. A great number of other diversity (and evenness and equitability) measures are also available, and we used the standardised Shannon diversity to base 10 which we designate d . It is the diversity per individual in a given sample. As a result we have three 2D matrices of $t \times q$, containing values of n , s , and d respectively.

We are more interested in t than q , and particularly in how sample parameters change after the flood. This is most easily approached by a further summation and averaging over sites. The matrices are each now collapsed into a one-dimensional array. The n values give a mean n or \bar{n} array, these being the population per sample at a given time averaged over all sites. The s matrix gives an \bar{s} array, values being species densities per sample at a given time, again averaged over sites. Similarly from d we get \bar{d} values. Because occasional very high values of n bias \bar{n} we also used mean $\log(n+1)$ data which approximate to geometric means of n .

Values of the above (see Table 4) suggest that, with all four sample parameters, there are immediate decreases after the flood (in $t8$, Mar. 1974). To show significant differences necessitates parametric tests and these require that the data be 'at random', and have normal distributions or can be transformed to normality. These constraints apply only to the pre-flood data and previous analyses data have shown negligible seasonal trends (Stephenson, Raphael and Cook 1976) so they can be taken as approximating to random samples.

TABLE 5: MOMENT COEFFICIENTS OF SKEWNESS (ζ_1) AND OF KURTOSIS (ζ_2) OF DIFFERENT FORMS OF MEANS DATA AFTER VARIOUS TRANSFORMATIONS, (DATA FROM TABLE 4)

Mean data on sites	Transformation	ζ_1	ζ_2
s	none	0.17	1.68
	square root	0.09	1.59
	\log_{10} *	0.02	1.52
n	\log_{10}	0.16	2.67
Mean $\log(n+1)$	none	-0.31	1.94
	squaring	-0.21	1.81
	antilog minus 1*	0.02	1.55
d	none	-0.74	2.34
	squaring	-0.63	2.20
	antilog	-0.59	2.12
	5th power	-0.38	1.88
	10th power*	0.01	1.65

*Optimal transformations (ζ_1 and ζ_2 nearest to zero).

Various transformations were applied to the rows of pre-flood data and normality was judged by the moment coefficient of skewness (ζ_1) approximating to zero (see Table 5).

For s values a log transformation is acceptable and for n values detransformation of mean $\log(n+1)$ values is acceptable. The d values are negatively skewed and require the 'ridiculous' 10th power transformation to remove this skewness. In Table 5 moment coefficients of kurtosis (ζ_2) are also tabulated, and it will be noted that transformations removing skewness leave considerable positive kurtosis. Using the above transformations, and accepting that data are still not normal, we felt justified in using parametric tests. The test selected, the F test, is identical with the t test as applied below.

The seven pre-flood values were compared with a single post-flood value viz. $t8$, $t10$, $t11$, and $t12$ respectively, and results are given in Table 6.

Based on Tables 4 and 6 we can tentatively group the five post-flood times into (a) early post-flood with

TABLE 4: MEAN NUMBER OF SPECIES PER SITE (s), MEAN NUMBER OF INDIVIDUALS PER SITE (n), MEAN $\log_{10}(n+1)$ VALUES AND MEAN INDIVIDUAL SHANNON DIVERSITY (d) IN THE DIFFERENT TIMES

	Pre-flood Times							Post-flood Times				
	1	2	3	4	5	6	7	8	9	10	11	12
s	13.56	13.74	15.89	9.41	10.22	12.74	9.81	2.26	4.15	7.30	6.96	6.48
n	130.1	102.0	107.3	53.0	199.1	367.6	150.2	22.2	90.6	303.7	292.0	412.55
mean $\log_{10}(n+1)$	1.87	1.67	1.86	1.65	1.48	1.82	1.64	0.74	1.02	2.06	2.11	2.21
d	0.69	0.77	0.80	0.63	0.80	0.76	0.73	0.24	0.38	0.36	0.25	0.23

TABLE 6: RESULTS OF SIGNIFICANT TESTS OF PREFLOOD VALUES COMPARED WITH SINGLE POSTFLOOD VALUES INDICATED BELOW. DATA TRANSFORMED FROM TABLE 1

	t8	t9	t10	t11	t12
\bar{s}	lower**	lower**	lower	lower*	lower*
mean $\log(n+1)$	lower*	lower	higher*	higher*	higher*
\bar{d}	lower	lower	lower	lower	lower

** indicates 0.01 significance or better, * indicates 0.05 significance, no star indicates difference not significant.

devastation and early recovery—times 8 and 9; (b) intermediate—time 10. By two measures recovery is still proceeding (mean $\log(n+1)$ and s), by the third d it is at or past the postflood peak; (c) late postflood—times 11 and 12. It is of interest to note that diversities immediately after the flood are identical with those in the later period. However the values of s and n are quite different in the two; to this extent the d values conceal useful information.

EFFECTS OF THE FLOODS UPON ALL SPECIES IN SEPARATE SITES

The above analyses have shown effects averaged over all sites, and involve taking the entire sampled area and the entire biota as the unit of measure. In the present analyses we treat the sites separately. We again consider the $t \times g$ matrices involving summation over species, but omit the final averaging over sites. Only two such matrices were considered involving s values (species densities per sample) and n values (populations per sample).

For each site the seven preflood values of a sample parameter were compared in the first instance with each postflood value taken singly. As before the F test was used following an appropriate transformation of the preflood data.

In some cases where a 7:1 comparison failed to show a significant difference it was suspected that a 7:2 or 7:3 comparison, involving additional postflood values, would show the effect. However the

basis of the F test is now further eroded; while the preflood samples can still be regarded as being at random there are trends and not randomness in the postflood period. We decided to retain the parametric testing but to interpret results with caution.

Another reason for caution is that prior to the analyses, (and unfortunately) species reduction had been effected (see later). Only 74 species are used in the present analyses and this will particularly effect s , although n will be negligibly affected.

Effects of transformations upon normality of preflood values were essayed by computation of moment coefficients of skewness (γ_1) as before. It appeared that, for a given form of data, there was a different optimal transformation for each site and this is yet a further reason for caution in interpretation. The mean coefficient of skewness over all 27 sites was used, and the transformation which reduced this closest to zero was accepted. For the s data \sqrt{s} was used (mean $\gamma_1 + 0.10$) and for n data $\log(n+1)$ (mean $\gamma_1 + 0.36$).

Tabulating the numbers of sites with 'significant' changes in (s) and in (n) (see Table 7) shows that s and n data give comparable results, with effects apparently least in roughly the middle of the postflood periods of sampling. The high numbers of affected sites will be noted.

Considering the data on a site by site basis, and considering each postflood time separately revealed that all sites showed 'significant' changes in

TABLE 7: NUMBER OF SITES WITH SIGNIFICANT CHANGES IN NUMBERS OF SPECIES PRESENT (s) AND IN TOTAL POPULATIONS OF ALL SPECIES (n) POSTFLOOD TIMES (BELOW) COMPARED WITH PREFLOOD TIMES

	t8	t9	t10	t11	t12	t8 + 9	t9 + 10	t8 + 9 + 10	t11 + 12	Summation over all comparisons
s	20	14	4	4	8	22	15	21	9	25
n	19	16	10	10	13	23	6	11	14	26

either *s* or *n* values on one or another occasion. Four sites showed no 'significant' changes in *s* viz. sites 8, 9, 10, 11 and two no 'significant' changes in *n* viz. 1, 14. Cases of 'significant' changes are given in Table 8A and B, with sites arranged in groups.

Comparison of Table 8A (*s*) and 8B (*n*) shows that the populations data (*n*) show much more change than species numbers (*s*), mainly due to 'significant' increases in populations of sites from time 10 onwards—there were no 'significant' increases in numbers of species in any of the sites at any time; and that the groupings of sites show scant resemblance between the two sets of data, the only obvious resemblances being that transient decreases form the largest group in both cases and contain some sites in common (3, 12, 20 and 27).

Two topographical patterns are revealed by these data. Sites with very transient increases in the number of species (*s*) are generally distant from the

TABLE 8: SITES SHOWING 'SIGNIFICANT' CHANGES IN NUMBER OF SPECIES (A) OF INDIVIDUALS OF ALL SPECIES (B) WHEN SINGLE POSTFLOOD SAMPLINGS (AS LISTED) ARE COMPARED WITH PREFLOOD SAMPLINGS (TIMES 1-7)

A. NUMBERS OF SPECIES (ALL DECREASES)

Designation of sites	Site nos.	t8	t9	t10	t11	t12
Very transient decrease	4	*				
	21	*				
	22	*				
	23	*				
Transient decrease	1	*	*			
	3	**	*			
	6	**	**	*	*	
	7	*	*			
	12	**	*	*		
	13	*	**			
	20	*	**			
	26	*	*			
	27	**	*			
Delayed onset decrease	2		**			
	14					**
	25					*
Permanent decrease	18	**	**		**	**
	19	**	**	*	*	**
Decreases of uncertain pattern	5	**				*
	15	**		*		
	16	**	**			**
	17	**				*
24	**	**			*	

B. NUMBER OF INDIVIDUALS (DECREASES AND INCREASES)

Designation of sites	Site nos.	t8	t9	t10	t11	t12	
Very transient decrease	5	*					
	17	**					
	21	*					
	22	**					
	23	**					
	Transient decrease	2	**	**			
		3	**	**			
		4	**	**			
		11	*	**			
		12	**	*			
15		*	**				
20		*	**				
25		*	*				
27	**	*					
Delayed onset decrease	6		*				
	8					*	
	9		*				
	19		**				
	26		*				
Permanent decrease	7	**	**	**		**	
	13	**	*	**	**	*	
Decreases of uncertain pattern	16					*	
	18	**	**		**		
Transient increase	24	**		*			
	11				**		
Delayed onset increase	16	*					
	19					*	
Permanent increase	21					**	
	10			**	**	**	
	15			**	**	**	
	17			**	**	**	
	20			*	*	*	
	22				**	**	
Increases of uncertain pattern	26			**	**	**	
	12			**		**	
	27			**		*	
	12			**		**	
	27			**		*	

*0.05 probability **0.01 probability

Brisbane R. Sites with increases in population at one time or another form a band at intermediate depths (see Fig. 9).



FIG. 9: Sites with increased populations (at one time or another) after the flood—vertical lines, and with very transient decreases in numbers of species—horizontal lines.

EFFECTS OF THE FLOODS UPON SPECIES

Here we consider species for the first time, and operate with $t \times s$ matrices, derived from the 3D matrices by summation across sites.

Data were reduced by elimination of the rarer species—those with <12 individuals in the pre-flood sampling of the wider area of original study (27 + 21 sites). This insured that species were numbered as in Stephenson, Raphael and Cook (1976). The choice of cut-off level followed preliminary analyses which showed that rarer species never gave noticeable differences between pre-flood and postflood data. The 74 species retained for these analyses are listed in the Appendix together with their code numbers. Subsequently species are generally referred to by code number, when names

are cited generic names are used except when more than one species of a genus was considered.

Two $t \times s$ matrices were considered. By summation of meristic data we obtain the total population in all sites of a species at a given time and this we designate p (for population). Similar summation of binary data gives the number of sites (out of 27) occupied by a species at a given time and this we designate q (for quadrats). It measures the ubiquity of a species in space at a given time.

To determine whether a species shows changes in population or ubiquity by the first period after the flood we compare seven pre-flood values with the first postflood value. Additional 7:1 comparisons were made using later postflood times, and further comparisons with 7:2 and 7:3 arrays. Transformations were applied to the pre-flood values (only) and as before to reduce skewness to minimal values, different transformations were required in each case; following Taylor (1961, 1971) this is entirely expected. For present purposes we worked with 12 hopefully representative species and chose the transformations which gave the mean of the moment coefficients of skewness closest to zero. For q values this involved no transformation (mean $\gamma_1 + 0.07$) and for p values the $\log(p+1)$ transformation (mean $\gamma_1 + 0.18$). The F test was used with the transformed data.

The numbers of species showing 'significant' changes in ubiquity and in populations in the different postflood times were roughly comparable (see Table 9). Effects are least near the middle of the postflood observations because early decreases and later increases are balancing.

Data were next considered on a species by species basis. Using data from each postflood time separately showed that 36 of the 74 species did not show any 'significant' differences. These species were: 2, 4, 8, 23, 24, 30, 31, 32, 35, 37, 38, 40, 42, 43, 46, 47, 48, 49, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 63, 65, 66, 67, 69, 70, 71 and 74. Twenty-six of these are from the 37 species in the lower half of the abundance hierarchy and here the pre-flood values are generally too low and too variable for 'significance' to show. However apart from three cases

TABLE 9: NUMBER OF SPECIES WITH 'SIGNIFICANT' CHANGES IN NUMBER OF SITES OCCUPIED (q) AND IN TOTAL POPULATIONS IN POSTFLOOD TIMES (p) COMPARED WITH PREFLOOD TIMES 1-7

	t8	t9	t10	t11	t12	t8 + 9	t9 + 10	t8 + 9 + 10	t11 + 12	All comparisons
q	10	6	7	11	16	14	13	17	16	27
p	16	11	6	9	11	27	19	22	19	34

(spp. 32, 40, 46) the mean preflood recordings were at least four times those of times 8+9.

Sixteen of the remaining species showed 'significant' differences only when a pair of postflood values was compared with the preflood data: in each case the postflood values were the lower. The species were 7, 21, 22, 25, 26, 28, 29, 33, 36, 41, 44, 50, 61, 68, 72 and 73.

The remaining species showed 'significant' effects by one measure or another. They form two (overlapping) groups, the first showing decreases

(17 spp.) and the second showing eventual increases (7 spp.). These groups with further groupings within them, are given in Table 10.

Table 10 shows that five species show a very transient decrease (only 'significant' in time 8) viz. spp. 12, 13, 20, 27 and 39, while two more show a transient decrease viz. spp. 5 and 19. Two show a delayed onset of decrease (spp. 16 and 64) but one of these is a weak case (sp. 16). The largest group is of seven species showing a permanent decrease viz. spp. 2, 6, 10, 14, 17, 18 and 45.

TABLE 10: SPECIES SHOWING 'SIGNIFICANT' CHANGES IN NUMBER OF SITES OCCUPIED AND/OR IN POPULATION IN ALL SITES WHEN COMPARING SINGLE POSTFLOOD SAMPLINGS (AS LISTED) AND PREFLOOD SAMPLINGS (TIMES 1-7)

Designation of species	Spp. no.	Sites occupied (<i>q</i>)					Populations all sites (<i>p</i>)				
		t8	t9	t10	t11	t12	t8	t9	t10	t11	t12
Very transient decreases ¹	12	*					**				*
	13						*				
	20						*				
	27	*					**	*			
	39	*					*				
Transient decreases ²	5	*	*	*			*	*			
	19	*	*	*	*		*	*	**	**	
Delayed onset decreases ³	16							*			
	64				*	*				**	*
'Permanent' decreases ⁴	2	*	*		*		**	**	**	*	**
	6	**	**	**	**	**	**	*	*	**	*
	10						*	*	*	*	*
	14	**			*		**	*		*	*
	17	*	*	*		*	**	**	**	*	**
	18						*		*	*	*
	45						*	*			*
Decreases of uncertain pattern ⁵	9	**	**		*	**	**	*			
Transient increases ⁶	11							*			
	12				**						
	15			**							
	34			**	**						
	62				*						
'Permanent' increases ⁷	1			**	**	**					
	13				*	**			*	**	

*0.05 probability **0.01 probability

¹significance only or mostly in first postflood period, t8.

²significance in first four postflood periods t8-t11.

³not significant in early postflood period.

⁴significance essentially unchanged throughout the first five post-flood periods.

⁵elements of two of the above.

⁶not significant at the end of sampling.

⁷significant at the end of sampling.

Five species show a transient increase, mostly shown in times 9 and 10 viz. spp. 11, 12, 15, 34 and 62, while two showed a permanent increase (spp. 1 and 13). The majority of cases of increase are in number of sites (i.e. area) occupied rather than in populations and a noteworthy case is the most abundant species of all, sp. 1 *Spisula*. Here populations show no significant change but number of sites occupied changes from a pre-flood mean of 6.86 to the following values in the last three post-flood samplings: 23, 25 and 25 respectively. With only 27 sites available, these are spectacular increases.

EFFECTS ON SPECIES \times SITES AT SELECTED TIMES

ANALYTICAL METHODS: There is a final way of handling a 3D matrix of $s \times q \times t$ and this is to make t separate analyses of $s \times q$. This has been attempted by Hailstone (1972) but encounters problems due first to the considerable computing which is required and secondly because results may be difficult to interpret.

In the present case groupings of times were used. The main chronological discontinuity in the data is between pre-flood times ($t1-7$) and post-flood ($t8-12$). Earlier we have dissected the latter into times 8+9 designated 'early post-flood' and times 11+12 designated 'late post-flood'. (Time 10 shows intermediate tendencies and was omitted in the present context).

By summation over these periods we derive three 74 species \times 27 sites matrices; actually the post-flood sets had fewer species. Each matrix was classified to obtain site-groups characterized by species-groups in the hope of elucidating changes in site-species patterns caused by the flood.

The pre-flood data have already been classified by Stephenson, Raphael and Cook (1976). For grouping sites we previously used: data transformed by $\log_{10}(n+1)$, Bray-Curtis dissimilarity measure, and group-average sorting. Whereas this technique gave meaningful site-groups in the earlier work (and various other analyses) when applied to post-flood data the outcomes verged on the meaningless. As an illustrative example in times 8+9 one site had no species present (site 27) while one (site 20) had one species represented by one individual; these sites are completely dissimilar when using the Bray-Curtis measure. We require a dissimilarity measure in which almost equally impoverished sites show only a small dissimilarity, and the Manhattan metric was chosen. For two sites and recordings of a given species n_1 and n_2 , then for s species the formulation is $\sum_1^s |n_1 - n_2|$. This measure is the numerator of the Bray-Curtis measure, without its standardizing denominator. The method

used for sites in the post-flood was then: data transformed by $\log_{10}(n+1)$, Manhattan metric dissimilarity measure, group-average sorting. To ensure comparability it was necessary to reanalyse the pre-flood data with the same technique.

Site-groups were selected from the dendrograms on two bases: to derive the maximum number of major groups with topographical coherence, and by perusal of the two-way table to ensure that there were the maximum number of conforming species (see later). In each case this resulted in three main site-groups. For the few sites which appeared to have been misclassified reallocations were effected and these increased the topographical coherence of the groups.

For species-groupings we used the Manhattan metric equivalent of the technique used by Stephenson, Raphael and Cook (1976). This involved an extra stage, standardization by total of transformed values prior to obtaining Manhattan dissimilarities. As indicated elsewhere (Stephenson and Campbell 1976) there are several problems concerning species-groupings. If we declare an interest in species as characterizing groups of sites rather than individual sites, species classifications often fail to group together like species.

A species may characterize a site-group in one of two ways. A positive characterization means that the recordings in a given site-group are higher than in the other site-groups, while a negative characterization means that the recordings are lower than in the other site-groups. Of the two, positive characterizations are conceptually more satisfying. Such species can be selected visually, in which case a series of high recordings in the sites of a given site-group 'stand out' from the remainder. There are obvious objections to such a visual method, and an objective technique is desirable. The alternatives are tests based upon the usual tests of significance. Here again objections can be raised. Tests of significance require that the arrays of data which are compared are random samples, and clearly this does not apply in cases like the present in which data have been clustered to optimise dissimilarities. It can be argued that, if after this optimisation, the recordings of a species are not significantly different in the different site-groups, then the data are really at random; this argument we do not pursue. Instead we use the mechanics of a standard test of significance of difference because this closely parallels the results of visual scanning. We avoid the use of the word 'significant' and refer to differences as 'noticeable' or 'outstanding'. The test used is referred to as the 'pseudo-F-test' and was employed using $\log(n+1)$ transformed values. It

identifies species in which variability within site-groups was such as to render differences between means 'non-noticeable', and in the terms of Stephenson, Williams and Cook (1974) it picks out non-conforming species. A level, equating to a probability level of 0.05 in the *F* test was chosen as cut-off point. It should be noted that the present method involves post-classificatory removal of species.

In the pre-flood data relatively few species did not conform to the site-groups and the species-groups of the original classification which remained after their removal required only minor re-allocations to give the optimal species-groupings in site-groups. In the two post-flood data sets, the species-groupings as illustrated by the dendrograms showed excessive chaining and hence virtually no species-groupings. Most of the species were non-conforming (reflecting the paucity of data) and the small residue of conformers were readily classified by visual inspection of the data.

RESULTS: (i) *Pre-flood data (summed over times 1-7)*. On the dendrogram of the site-classification (Fig. 10) at just over 20 units of dissimilarity there

are four groups, one containing a single site. This site was reallocated and we accepted the following site-groups:

- A. (inshore): Sites 1-6, 8, 9, 14, 15
- B. (middle): Sites 7, 10-13, 16-20, 26, 27
- C. (offshore): Sites 21-25.

These groupings are map-plotted on Fig. 11 with the equivalent groupings when the Bray-Curtis dissimilarity measure was used shown on Fig. 12. The two plottings are similar in showing inshore, middle and offshore site-groups, with those of the present analyses possibly showing greater correspondence with the distribution of pre-flood sediments (see Fig. 6).

The dendrogram of the species classification gave nine unequal groups at a dissimilarity level of ca. 1.20. When species not conforming to the site-groups were excluded 47 species remained in three main groups with 6 other species in four other groups. After reallocation of the 6 species, four groups were obtained, the three largest being essentially the original groups. The final groups are given in Table 11, together with the mean number of individuals per site in the site-groups, reduced to the equivalent of a single sampling time.

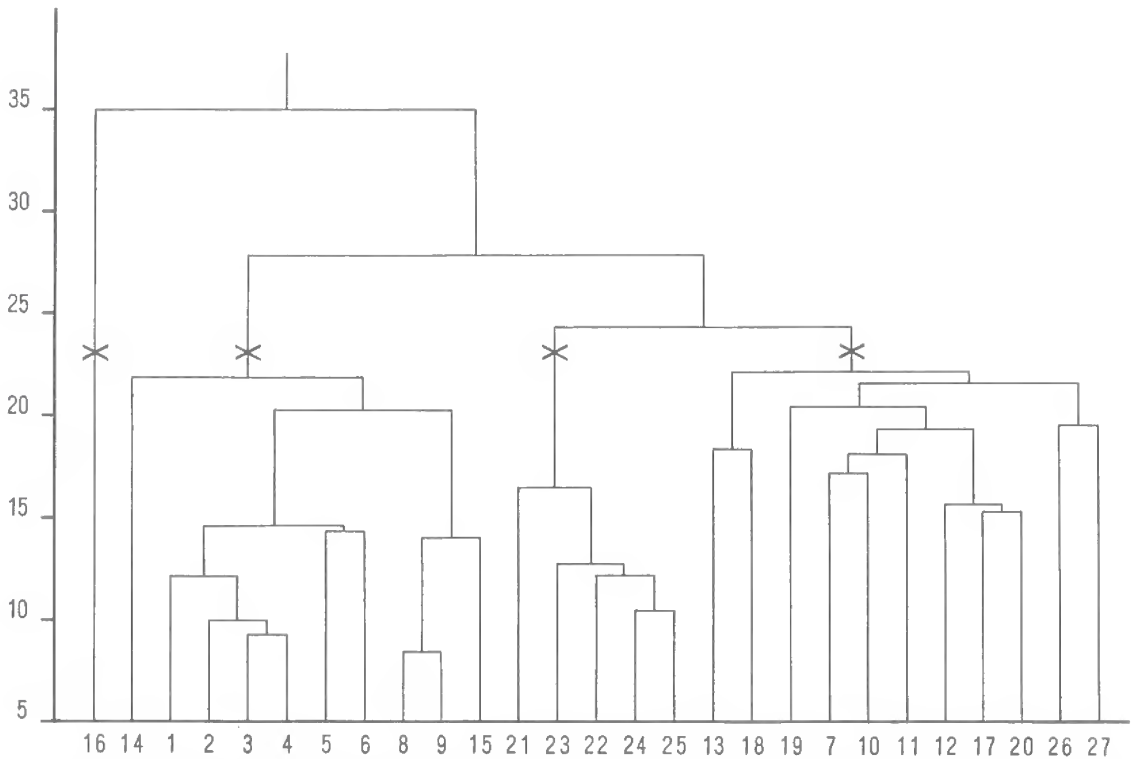


FIG. 10: Dendrogram of sites classification using 74 species, pre-flood data (times 1-7). Vertical scale Manhattan metric dissimilarity, X indicates site-groups accepted.

TABLE 11: PREFLOOD DATA (TIMES 1-7). MEAN NUMBER OF INDIVIDUALS OF CONFORMING SPECIES PER SITE IN EACH SITE-GROUP, REDUCED TO A SINGLE TIME

Species group	Species no.	Site-groups†		
		A (inshore)	B (intermediate)	C (offshore)
I (inshore spp.)	1	230.2	0.1	0
	3	25.7	5.7	1.1
	9	3.7	0.5	0.3
	11	2.6	0	0
	15	2.2	0.3	0
	16	1.5	0.1	0
	24	0.7	0.3	0.1
	26	1.4	0	0
	40	0.3	0.1	0
	50*	0.2	0.1	0
	54	0.2	0.1	0
70*	0.2	0	0	
II (middle spp.)	5	0.5	5.3	0
	18	0.3	0.9	0
	22	0	0.5	0
	28	0.2	0.4	0
	38*	0	0.2	0
	49	0.1	0.3	0
	59	0	0.2	0
	60	0	0.2	0
	63	0	0.1	0
	68	0	0.1	0
	69*	0	0.2	0
III (offshore spp.)	4	0.3	7.2	39.5
	6	0	0.9	5.5
	7	0	1.5	7.6
	8	0	0.7	1.8
	10	0.9	1.2	2.0
	12	0.6	1.0	2.1
	13	0.1	0.4	4.2
	14	0.5	0.9	1.8
	17	0.4	0.5	0.6
	19	0	0.1	1.1
	20	0.1	0.4	1.5
	21	0.2	0.3	1.3
	23	0.1	0.5	1.1
	25	0.1	0.3	1.0
	29	0	0.2	1.6
	30	0.1	0.4	0.7
	33	0	0.2	0.8
	37	0.1	0.1	0.8
	42	0	0.3	0.5
	45	0	0.1	0.8
47	0	0.1	0.4	
48	0	0.1	0.5	
53	0	0.1	0.4	
57	0	0	0.5	
58	0.1	0.1	0.4	
62	0	0.1	0.3	
66	0	0	0.3	
72*	0	0	0.3	

Species group	Species no.	Site-groups†		
		A (inshore)	B (intermediate)	C (offshore)
IV	41*	0.1	0.3	0.2
(avoiding inshore)	46	0	0.3	0.3

*reallocated species.

†see text.

Referring to Table 11, the 12 species of species-group I positively characterize the inshore sites, and these sites can be given a 'community' name by as many species as are desired: *Spisula* (1), *Xenopthalmus* (3), *Terebellides* (9), *Pupa* (11) etc. The 11 species of species-group II positively characterize the intermediate depth sites which can be described as a 'community' of: *Anadara* (5), tunicate 1 (18), oyster 1 (22) etc. The 28 species of species-group III positively characterize the offshore sites as a *Paratapes* (4), *Amphioplus* sp. (6), *Amphioplus lobatus* (7), *Theora lata* (8), *Amphitrite* (10) etc., 'community'. The two species of group IV viz. *Placamen* (41) and *Trichomya* (46) negatively characterize the inshore sites. It will be noted that, of the three main species-groups, the third group has the most cases of 'overlap' from one site-group to another, and mostly from offshore to middle sites. A few species (10, 12, 14 and 17) also extend appreciably into the inshore site-group.

(ii) *Early postflood (times 8 and 9)*. From the dendrogram of the site classification (Fig. 13) three site-groups were accepted in the present data at a dissimilarity level of ca 4 compared with ca 20 for

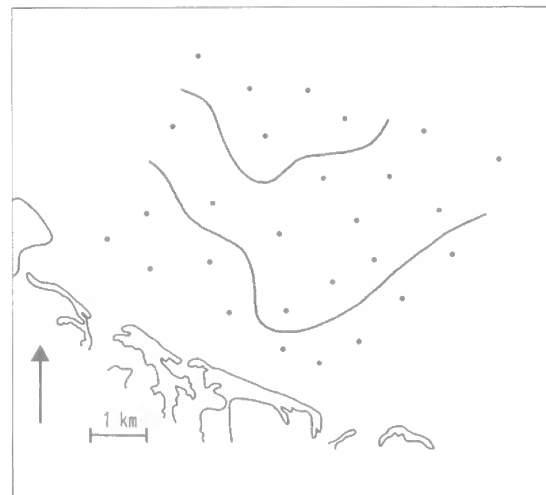


FIG. 11: Inshore, middle and offshore site-groups from pre-flood biotic data using Manhattan metric dissimilarity.

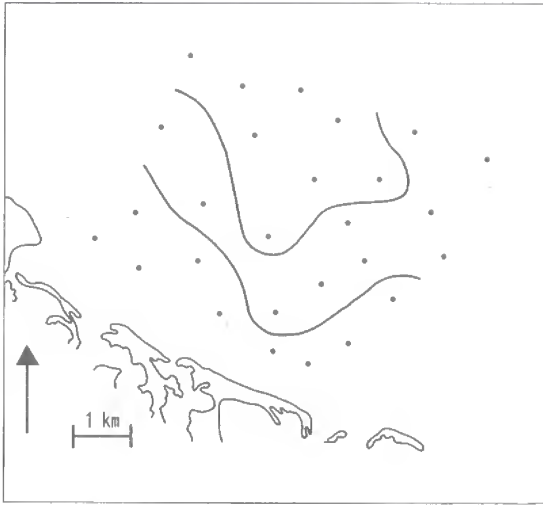


FIG. 12: Inshore, middle and offshore site-groups from preflood biotic data using 'Bray-Curtis' dissimilarity measure.

TABLE 12: EARLY POSTFLOOD DATA (TIMES 8 AND 9). MEAN NUMBER OF INDIVIDUALS OF CONFORMING SPECIES PER SITE IN EACH SITE-GROUP

Species group	Species	Site-groups		
		A (near rivers)	B (offshore)	C (majority)
I (near rivers)	1	321.2	0	0.1
	11	1.3	0	0
	15	1.8	0	0.2
	24	0.4	0	0
II (offshore)	7	0	5.0	0.3
	8	0.1	1.9	0.1
	13	0	8.4	0.5
	14	0	0.5	0.1
	30	0	0.5	0
	33	0	0.8	0
	42	0	0.3	0
	66	0	0.3	0
III (majority of sites)	5	0	0	0.2

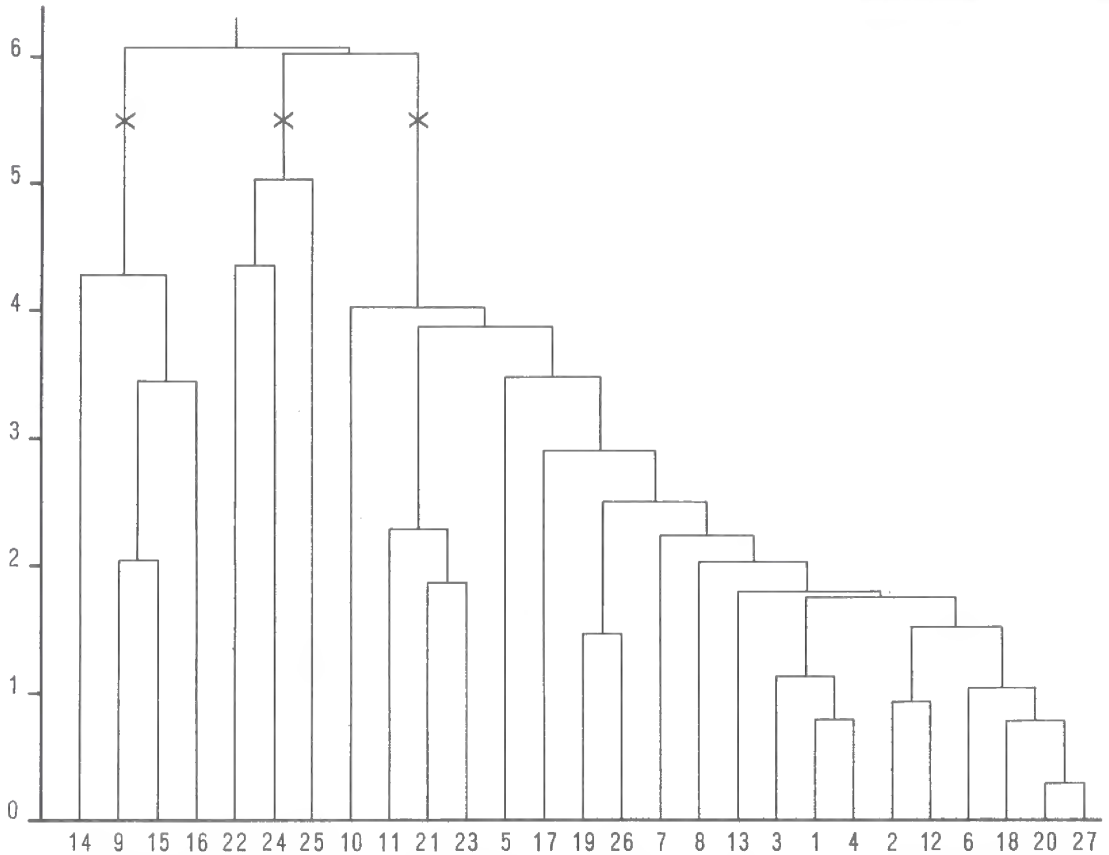


FIG. 13: Dendrogram of sites classification using 74 species, early postflood data (times 8, 9). Vertical scale Manhattan metric dissimilarity, X indicates site-groups accepted.

preflood data. Some of the differences will be due to the reduced sampling intensity (over two times instead of seven) but most of it reflects biotic impoverishment.

The three site-groups are of dissimilar sizes, A comprising sites 9, 14, 15 and 16; next B with 22, 24 and 25; and last C a 'chained' succession of the remainder. Most of site-group A are near the outflows of the Brisbane River or Cabbage Tree Creek, and site-group B are the deepest sites most distant from the Brisbane River. Site-group B corresponds to the offshore site-group of the previous analyses but contains fewer sites.

The species dendrogram showed considerable chaining with only minor groupings and was discarded. Only 13 species conformed to the site-groupings compared with 54 in the preflood situation, and the 13 were grouped visually. Results are given in Table 12 which shows mean recordings per site in a site-group reduced to a single sampling time.

The species form three unequal groups with only one species *Anadara* (5) weakly characterizing the largest site-group (c). Four species characterize the near-rivers site-group which can be described as a *Spisula* (1), *Pupa* (11), *Parcanassa* (15) 'community' in which *Spisula* is markedly dominant. Eight species characterize the offshore sites, which can be described as an *Amphipholis loripes* (13),

Amphioplus lobatus (7), *Theora lata* (8) 'community'.

It is surprising that the near-river site-group (A) which one might have expected to be most affected by the flood, is least affected. The most obvious explanation, that they were recovering at a more rapid rate than the remainder, is supported by the fact that all specimens in sites 14, 15 and 16 at time 8 were extremely small. On this basis sites 9, 14, 15 and 16 are a focus of recolonisation by *Spisula* and possibly the two other species in the group. These are predatory gastropods no doubt feeding on juvenile *Spisula*.

The offshore site-group was previously characterized by 28 species, and now in the immediate postflood samplings is characterized only by eight species. The population of the dominant species *Amphipholis loripes* is higher than before; previously *Paratapes* (4) was the commonest offshore species.

(iii) *Late postflood (times 11 and 12)*. From the sites dendrogram (Fig. 14) three unequal groups were accepted at a dissimilarity level of 8; this compares with the previous one of ca 4 and reflects the fuller data now available for analysis. The two small site-groups, A (sites 24 and 25) and B (sites 20, 21 and 23), are both in the deeper more muddy area most distant from the Brisbane R. The third site-group, C, comprises the 22 remaining sites.

Compared with the early postflood groups the largest group now includes two of the previous groups (majority and near-river) while the previous offshore group has now become enlarged and divided into two groups; collectively these are essentially the same area as the offshore group in the pre-flood data.

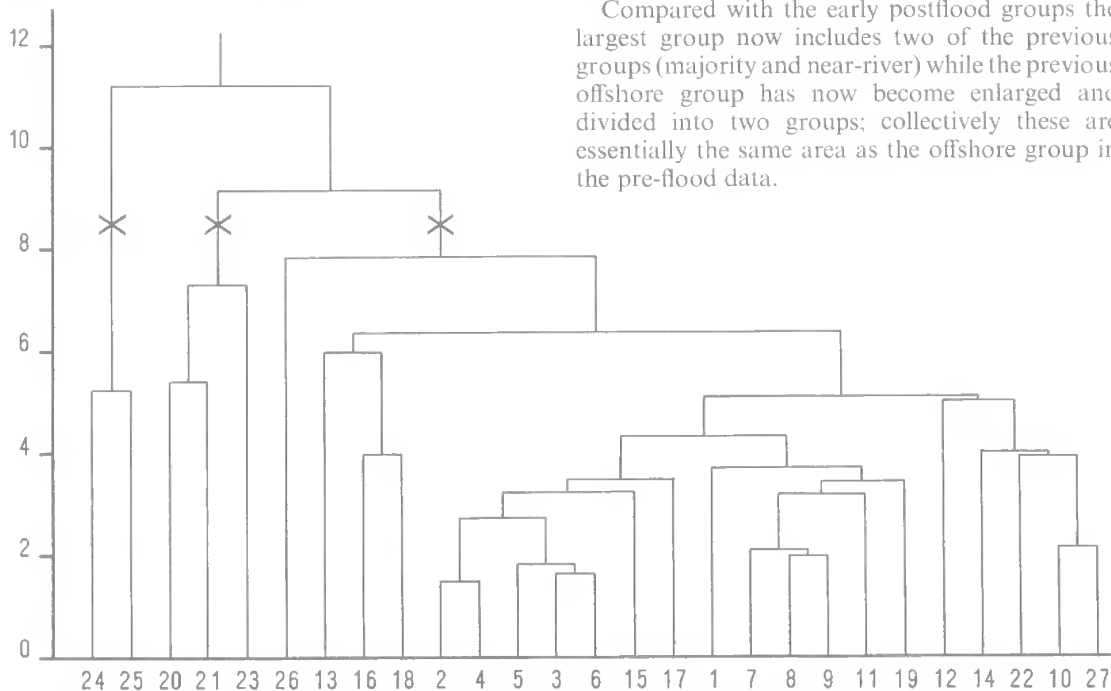


FIG. 14: Dendrogram of sites classification using 74 species, late postflood data (times 11, 12). Vertical scale Manhattan metric dissimilarity, X indicates site-groups accepted.

Only 14 species conformed to the late postflood site-groupings and these species were grouped visually. Results, with mean recordings of species per site per time are given in Table 13. The majority of sites now form a *Spisula* (1), *Parcanassa* (15) 'community'. Clearly the area of dominance of *Spisula* has spread rapidly since the early preflood period, although its population per site is much as before. Both area and population density have increased with *Parcanassa*.

Most of the commoner species which characterized the offshore area in the early preflood again characterize the larger offshore area, but whereas previously eight species were involved there are now twelve. One is less abundant than in early preflood (*Amphipholis loripes* 13) but additional and common species are *Paratapes* (4) and *Amphioplus* sp. (6). Of these the former is now approximately to its preflood density at least within a small area (sites 24, 25).

There are considerable differences between the two offshore site-groups A and B. Site-group B lies within the area of dominance of *Spisula*, and the species is actually commoner here than elsewhere, and also commoner than in its areas of pre-flood dominance. This site-group can be described as a *Spisula* (1), *Paratapes* (4), *Parcanassa* (15), and *Amphioplus* sp. (6) area. Site-group A is without

Spisula and *Parcanassa* and can be described as a *Paratapes* (4), *Amphioplus* sp. (6), and *Theora lata* (8) 'community'.

DISCUSSION

This concerns numerical methodology, the general picture of flood effects, and a possible beginning of a conceptual model of long term changes in the biota of Bramble Bay.

NUMERICAL METHODOLOGY: The only important change from the methods used in the analyses of the biota in the previous paper (Stephenson, Raphael and Cook 1976) has been the use of the Manhattan metric dissimilarity measure instead of the Bray-Curtis. This was because while the Bray-Curtis measure is sensitive to abundance it 'breaks down' in the extreme case of comparing a vacant site with one containing a minimal species recording.

The Manhattan metric extends from zero to an undetermined upper value, and dendrograms must be 'scaled to fit'. (We are grateful to Mr C. Andrews for this routine and for writing all our present programmes).

In the present paper methods of numerical analyses developed for handling biotic data have been applied successfully to sedimentary data. The technique employed the Bray-Curtis measure of dissimilarity (because 'impoverishment' is here not relevant) and classified sites by the group-average method, using percentages of sediment grades as attributes.

EFFECTS OF THE PRESENT FLOODS: All 27 sites were biotically affected one way or another by the flood. Effects on sites were an early reduction in number of individuals present, and throughout reductions in number of species and in (standardized) Shannon diversities. By the end of the study in many sites the populations recovered and then exceeded those of the preflood period. These sites were concentrated in the intermediate sampling depths.

With few exceptions all species which were present in sufficient numbers in the preflood collections to show 'significant' differences were 'significantly' affected. Most of these species declined in areas of occupancy and in overall populations and in most of these cases the declines persisted until the end of the present study i.e. for 14 months.

The main exception was the bivalve *Spisula*. Soon after the flood its area of dominance was changed and restricted but then followed rapid, extensive and dense colonization of the previously depauperate area. By the later postflood periods,

TABLE 13: LATE POSTFLOOD DATE (TIMES 11 AND 12). MEAN NUMBER OF INDIVIDUALS OF CONFORMING SPECIES PER SITE IN EACH SITE-GROUP

Species group	Species no.	Site-groups		
		A (Sites 24, 25)	B (Sites 20, 21, 23)	C (remaining sites)
I (not in A)	1	0	387.1	252.5
	15	0	4.3	5.2
II (A only)	30	0.5	0	0
III (B only)	13	0	1.3	0
IV (mostly A, also in B)	4	35.7	12.8	0.3
	6	2.3	2.2	0
	8	1.6	1.4	0.2
	12	0.5	0.3	0
	20	0.8	0.2	0
V (mostly in B, also in A)	33	0.5	0.3	0
	7	2.1	2.8	0
V (mostly in B, also in A)	9	0.2	0.5	0
	14	0.7	1.4	0
	25	0.2	0.9	0

(times 11 and 12) the area of dominance of *Spisula* had extended to cover all but two of the 27 sites and there had been comparable spread of a predatory gastropod *Parcanassa*. Whereas the population per site of *Spisula* in the pre-flood and late post-flood 'communities' was very similar (1150 cf. 1284 per m²), the population of *Parcanassa* more than doubled (11 cf. 26). It is possible that the predator population in the late post-flood period was such as to begin reducing the *Spisula* numbers to below their pre-flood values. It should be noted that other potential predators of *Spisula* are present in low numbers in times 11 and 12.

In a few offshore sites (those most distant from the Brisbane R.) immediately after the flood there remained a small but noticeable remnant of an originally diverse biota with *Paratapes* originally the commonest species. In the later samplings the offshore biota occupied a somewhat larger area and was characterized by more individuals of more species. The area approximated to that of the offshore site-group in the pre-flood samplings, but the characterizing biota comprised many fewer species.

We now consider changes in environmental conditions during and after the floods, to elucidate possible relationships between biota and abiotic factors. As shown earlier we can neglect for present purposes any abnormalities in water temperatures, and hence concentrate on salinities and sediments. Salinities in that part of Bramble Bay sampled for benthos seem to average about 32.5‰ in a non-flood year. During the pre-flood year the greatest reduction in salinity from average, due to rainfall, was ca 5‰ and the equivalent value in the flood year was ca 8.5‰. This difference alone would not lead one to expect biotic impoverishment on the scale which was observed.

There is a more impressive difference in the duration of dilution effects during 1974 compared with the previous year. Salinities were already being reduced before the Jan. 1974 floods by rainfall in Dec. 1973 and did not return to 'normal' until about July 1974. Some of this prolonged effect must have been directly due to the flood, in terms of continued drainage from the surrounding country and in terms of slow dissipation. A second period of higher than usual rainfall in March 1974 accompanying a cyclone is believed to have played an important part in prolonging the period of reduced salinity.

The flood produced early effects on the sediments of the area, and caused a 'blanketing' of the surface by a layer of soft mud several cm thick. It is unfortunate that pressure of work precluded adequate investigation of this phenomenon. Its

very existence suggests that while the earliest flood effects would involve dilution, before a month had elapsed both dilution and siltation would be involved.

Fourteen months after the flood there was evidence of a 'permanent' change in the sediments of the area, with an overall increase in the muddiness, and a complex pattern of sediment distribution of the eastern side of the sampled area, nearest to the Brisbane R.

One of the biotic effects which became detectable in late post-flood was an increase in the population (of all species summated) in the area as a whole. It is tempting to relate this to the increased muddiness, and hence increased supply of mud-associated nutriment, to the area. The main species involved in the population increase was *Spisula*, which in our pre-flood investigations was not associated with the muddier grounds, but which is known to occupy muddy areas within the estuary of the Brisbane R. (Hailstone 1972). Whether, with the muddiness remaining in the area, populations will remain high is uncertain (see below).

COMPARISON WITH THE LITERATURE OF FLOOD EFFECTS ON BENTHOS: While there have been several autecological and physiological reviews of the effects of sudden dilution on benthid organisms (e.g. Pearse and Gunter 1957, Gunter *et al* 1973) the literature on 'community' effects does not appear to have been consolidated and the present account is likely to be incomplete.

Most of the Queensland literature has been concerned with the effects of dilution and sediment suspension upon coral biotas. It includes Hedley (1925), Rainford (1925), Fairbridge and Teichert (1947, 1948), Stephenson (1956), Endean, Kenny and Stephenson (1956), Stephenson, Endean and Bennett (1958), Slack Smith (1960), and Lovell (1976). In general there is slow recovery from flood damage, in some cases taking years and in other cases it is doubtful if recovery to the pre-flood situation will ever occur (Rainford 1925). It appears that where flooding occurs only at very infrequent intervals a complex biota of species which lack flood tolerance develops, and that this takes a long period to redevelop after a flood. An interesting example of coral effects was reported by Hedley (1925) and apparently has generally been overlooked in the literature. It involved a layer of freshwater floating for several days on the surface of the sea, and a probability that putrefaction and deoxygenation contributed to the devastation.

Studies involving a mixture of hard-bottom epibiota, soft-bottom epibiota and soft-bottom infauna have been carried out by Fischer-Piette (1931) in France, MacGinitie (1939) in Southern

California, Sandison and Hill (1959) in Lagos, and Goodbody (1961) in Jamaica. In each case the hard-bottom epibiota was the most affected, especially the tunicates. MacGinitie (1939) suspected that most of the soft-bottom biota, especially the infauna, escaped the effects of the brief dilution he considered.

The floods described in the literature involve different periodicities, different degrees of salinity reduction and of putrefaction and also different durations. Regular annual flooding occurs at Lagos in East Africa (Hill and Webb 1958) and the original biota returns in 1–2 months without any succession (Sandison and Hill 1959). In Queensland there is something approaching a wet summer season but this occurs irregularly and the present floods lie somewhere between the augmentation of a normal seasonal flood as described by Fischer-Piette (1931) and by Goodbody (1961) and the very occasional catastrophe described by MacGinitie (1939).

In several of the literature cases, as with Hedley (1925), a distinct layer of freshwater remained on the surface after flooding, and the biotic effects were virtually restricted to the shallower organisms (MacGinitie 1939, Sandison and Hill 1959 and Goodbody 1961). In the present case the entire area was affected, involving depths to 5 m and no doubt beyond. It is true that the deepest water furthest from the Brisbane R. was somewhat less affected than the remainder.

The duration of flood effects as reported in the literature ranges from a matter of days (MacGinitie 1939) to more than a month (Goodbody 1961). Goodbody noticed that prolonged dilution of Kingston Harbour, Jamaica caused the greatest effect, and in the present case it appears that the duration of dilution has been a major factor contributing to the biotic effects.

Flood recolonisation does not appear to have been closely studied. Goodbody (1961) described recolonisation as starting after two months, and this would agree with our observations. MacGinitie (1939) noted that recolonisation was complete after nine months but added that many species had by then established themselves in larger numbers than were present before the flood. This 'over-response' has only applied to a limited number of species in the present data, and specifically to the bivalve *Spisula*. MacGinitie (1939) considered the over-response as being due to a deposition of sediment improving the food supply. This could apply in the case of *Spisula*, but additional factors could well include an elimination of competitors and reduction of predation levels. The present data suggest that the immediate effect

of sediment deposition might have been harmful to the biota.

None of the overseas surveys, apart from that of Stone and Reisch (1965) considered numerical data, and their study involved only three species. The only past study involving numerical data on many species appears to be that of Stephenson, Williams and Cook (1974) at Peel Island in Moreton Bay. During the Peel Island study a flood occurred and this by present standards would be described as 'minor'. Flood effects were postulated to cause an overall increase in complexity and the authors stated (p. 110): 'gross instability is likely to lead to reduction in complexity, whereas instability within acceptable limits may well increase it'. The present floods are an example of the former.

POSSIBLE LONG TERM CHANGES: Flood data summarised by Ward (1974) show that the 1974 flood was not, by hydrographic standards, the most severe one which has affected the Brisbane R. since records have been kept. The worst recorded floods were in the 1840's followed by two severe floods in the 1890's and then by the 1974 flood. In addition there have been concentrations of floods of somewhat lesser intensity roughly 25 years ago, and roughly 50 years ago.

We now make two assumptions. The first is that floods will affect the biota of Bramble Bay at roughly 25 year intervals. The second is that effects will be roughly comparable with those described for the 1974 flood. On these bases within about a year of the flooding there will be recovery to the point of Bramble Bay being occupied by a *Spisula-Parcanassa* community with high populations but low diversity. At this stage there will also be a recovering offshore population in which *Paratapes* will be dominant, accompanied by ophiuroids. This offshore population will be more diverse than that over the remainder of the area.

As time proceeds one would expect the area of dominance of *Spisula* to decrease. One likely cause of this restriction will be predation by the gastropod *Parcanassa* whose populations about a year after the flood were roughly double those before the flood. It is possible that there will be 'Gaussian' oscillations in the populations of these two species with predator overeating its food supply and hence declining, and with resultant secondary increases in *Spisula*. Oscillations of this nature could well explain some of the chronological changes in the biota in the pre-flood period as investigated by Stephenson, Raphael and Cook (1976).

The long term rate of recovery to a broad *Spisula-Anadara-Paratapes* situation is not known

except that presumably it takes less than 25 years. Equally unknown is whether the chronological changes at such a time are oscillations about a state of pseudo-equilibrium triggered by environmental changes (e.g. annual wet season) or whether they are progressive stages towards a climax situation which was still not attained in 1973.

It is clear that further investigations of the area are required and these are in train. It is equally clear that any detailed predictions of the effects of enlargement of Brisbane Airport should be linked to a given stage of recovery from flood effects. It is suggested that the effects of airport enlargement are likely to be much less obvious than those caused by the natural 'catastrophes' of early 1974.

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We are also grateful to the CSIRO Division of Fisheries and Oceanography for access to their currently unpublished hydrographic data, and to the Bureau of Meteorology, Brisbane for weather information.

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APPENDIX

Code numbers and species in order of abundance in pre-flood samples (27 × 7 + 21 × 2); only species occurring > 11 times listed. For systematic groups see Stephenson Raphael and Cook 1976, pp. 445–6.

1	<i>Spisula trigonella</i> (Lamarck)	38	balanid 1
2	<i>Mesochaetopterus minutus</i> Potts	39	<i>Edwardsia</i> sp.
3	<i>Xenophthalmus pinnotheroides</i> White	40	<i>Onuphis</i> sp.
4	<i>Paratapes scordalus</i> Iredale	41	<i>Placamen sydneyense</i> Menke
5	<i>Anadara trapezia</i> Deshayes	42	<i>Dasybranchus caducus</i> (Grube)*
6	<i>Amphioplus</i> sp.	43	<i>Arca</i> sp. 1
7	<i>Amphioplus lobatus</i> (Ljungman)	44	oyster 3
8	<i>Theora lata</i> Hinds	45	<i>Amphioplus depressus</i> Ljungman
9	<i>Terebellides stroemi</i> Sars	46	<i>Trichomya hirsuta</i> (Lamarck)
10	<i>Amphitrite rubra</i> (Risso)	47	<i>Leptomya pura</i> Angus
11	<i>Pupa fumata</i> (Reeve)	48	<i>Mesochaetopterus</i> sp.
12	<i>Theora</i> sp.	49	aphroditid 1
13	<i>Anphipholis loripes</i> Koehler	50	<i>Leonnates stephensoni</i> Rullier
14	<i>Leanira yhleni</i> Malmgren	51	<i>Clorida granti</i> (Stephenson)
15	<i>Parcanassa mangeloides</i> Reeve	52	<i>Marphysa sanguinea</i> (Montague)
16	<i>Lumbrineris latreille</i> Audouin and Milne Edwards	53	<i>Glossobalanus hedleyi</i> Hill
17	<i>Loimia medusa</i> (Savigny)	54	<i>Reticumassa paupera</i> Gould
18	tunicate 1	55	nemertean 'pink'
19	tunicate 3	56	whip coral
20	bivalve 1	57	<i>Venus</i> sp.
21	<i>Nucula astricta</i> Iredale	58	<i>Macoma donaciformis</i> Deshayes
22	oyster 1	59	<i>Ophiactis perplexa</i> Koehler
23	<i>Pectinaria antipoda</i> Schmarda	60	<i>Anomia</i> sp.
24	<i>Nereis jacksoni</i> Kinberg	61	amphipod 4
25	<i>Mesochaetopterus capensis</i> (McIntosh)	62	<i>Elamenopsis lineata</i> A. Milne Edwards
26	<i>Ophelina gigantea</i> Rullier	63	<i>Pista</i> sp.
27	sea anemone 1	64	amphipod 2
28	<i>Isolda pulchella</i> Müller	65	<i>Amaeana trilobata</i> (Sars)*
29	bivalve 2	66	<i>Hexapus granuliferus</i> Campbell and Stephenson
30	<i>Tellina texturata</i> Sowerby	67	tunicate 2
31	<i>Glycera prashadi</i> Fauvel	68	<i>Chaetopterus variopedatus</i> Renier
32	<i>Cirriformia</i> sp.	69	Sabellid 1
33	<i>Protankyra</i> sp.	70	<i>Natica</i> sp.
34	<i>Petaloproctus terricola</i> Quatrefages*	71	amphipod 6
35	bivalve 3	72	<i>Tapes wailingi</i> Iredale
36	<i>Chama fibula</i> Reeve	73	amphipod 1
37	<i>Cycladicama</i> sp.	74	<i>Bedeve hanleyi</i> Angus

*Possibly misidentified.

PENAROSA NETENTA, A NEW MIDDLE CAMBRIAN TRILOBITE
FROM NORTHWESTERN QUEENSLAND

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ABSTRACT

A new species, *P. netenta*, is described and assigned to the nepeid genus *Penarosa* Öpik, 1970. The pygidium of *Penarosa* is correctly identified from this new species and, as the same pygidial type is known to occur in *Nepea*, it is taken to be typical of the family.

The only previous knowledge of the Nepeidae comprises the original description of *Nepea narinosa* Whitehouse, 1939, with a considerable discussion of its possible relationships (Whitehouse 1939, pp. 210–11); a reinterpretation of *N. narinosa* with clarification of all cephalic structures (Öpik 1963); description of two Upper Cambrian genera (Öpik 1967); and a monograph of Middle Cambrian species in 4 genera (Öpik 1970). This paper proposes a new specific name, provides a detailed description in modern terms of every aspect of the morphology of a nepeid species, and correctly identifies its pygidium pointing out Öpik's (1970) probable error in assignment of a pygidium to *Penarosa retifera* Öpik, 1970.

The material is deposited and catalogued (QM) in the Queensland Museum, Brisbane.

I am thankful to Dr J. B. Jago, South Australian Institute of Technology, Adelaide, for providing me with a latex cast of an uncatalogued, undescribed species of *Nepea* from Tasmania.

Family NEPEIDAE Whitehouse, 1939

Genus *Penarosa* Öpik, 1970

Penarosa Öpik, 1970, p. 24. (*Type species: P. retifera* Öpik, 1970, p. 25, figs. 9–10, pl. 8, figs. 1, 2; pl. 9, figs. 1, 2, 4; pl. 17, figs. 7–9 from the Age Creek Formation and Current Bush Limestone, north-western Queensland and Northern Territory, *Euagnostus opimus* Zone, late Middle Cambrian; by original designation.)

Trinepea Palmer and Gatehouse, 1972, p. 25. (*Type species: T. trinodus* Palmer and Gatehouse, 1972, p. 25, pl. 4, figs. 1, 2 from the Nelson Limestone in the Neptune Range, Antarctica, *Amphoton oatesi* faunule, late Middle Cambrian; by original designation.)

DIAGNOSIS: Öpik's (1970, p. 24) diagnosis of the genus stands.

REMARKS: When Palmer and Gatehouse (1972) described *Trinepea*, they did not refer to Öpik's paper in which *Penarosa* was described. The size of the three bosses on the brim, the unpaired ocular ridges and the short (sag.) anterior border furrow are the only characters quoted as distinguishing *Trinepea*. In fact the lateral bosses on the brim are of similar size to those of several species of *Penarosa* (cf. Öpik 1970, pl. 9, fig. 5a; pl. 12, fig. 2b; pl. 13, fig. 1b); in several specimens figured by Öpik the ocular ridges are not clearly bifurcate (1970, pl. 9, fig. 1; pl. 12, fig. 2a) and in others the bifurcation only appears distally, a position where Palmer and Gatehouse's single figured specimen is damaged; and the short border furrow is only of specific value. *Trinepea* is thus clearly synonymous with *Penarosa*.

Penarosa netenta sp. nov.

Figure 1; Plate 21, figs. 1–8

Etymology: An anagram from my wife's name—Annette.
MATERIAL EXAMINED

HOLOTYPE: QMF7059, a cranidium from locality QML152.

PARATYPES: QMF7060–70, a cranidium, two free cheeks, an incomplete thorax and a thorax plus pygidium from locality QML152; and four cranidia and two free cheeks from locality QML136.

Queensland Museum locality L152 is 1.7 km south of Chummy Bore which is 6 km west of Thornton Homestead on the road to Camooweal at 19°31.5'S., 138°52'E. and QML136 is at Chummy Bore. The material occurs in weathered red, white or yellow siliceous shales of the Chummy Bore Formation (De Keyser and