CORAL ASSEMBLAGES OF MORETON BAY, QUEENSLAND, AUSTRALIA, BEFORE AND AFTER A MAJOR FLOOD

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The scleractinian coral assemblages of coral reefs inside and outside a bay on the east coast of temperate Australia were examined before, immediately after, and seven years after a major flood. Of the 25 fringing reefs flourishing inside the bay, 15 were killed by flood water. Seven years later, recolonization on a single reef reflects aspects of its original nature. The reef outside the bay was not damaged by the flood and provides insights into factors conditioning the bay's coral assemblages. Comparison between the recent and subfossil reefs gives evidence for a long term change in the Bay environment.
□ *Scleractinia, corals, fringing reefs, coral reefs, coral death.*

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The diversity of genera and species of scleractinian corals attenuates with increasing latitude along the east Australian coast (Wells, 1955b; Veron, 1974; Veron, 1986). Moreton Bay is an area of particular interest because of its extra-tropical location and the simultaneous presence of two assemblages. One assembalge comprises the subfossil remnants within the bay and as a living reef outside the bay at Flinders Reef. The other comprises the living bay corals which represent a reduction in species number and change in dominance from a period of greater richness and abundance (Wells, 1955a).

The dominant species in the subfossil and modern assemblages differ at the subordinal level. The subfossil assemblage is characterized by the suborder Astrocoeniina, containing the genera common to the Indo-Pacific province, e.g. *Stylophora, Pocillopora and Acropora* (Stehli and Wells, 1971). The present assemblage is characterized by the suborder Faviina with overwhelming dominance by Favia speciosa. Though components of the Indo-Pacific subprovince presently exist, the composition conforms to the proposed 'southwestern subprovince' of Stehli and Wells (1971). Subsequent work at the species level has questioned the validity of this distinction on a regional basis (Veron, 1986).

This paper investigates the change in the coral assemblages of Moreton Bay by examination of those inside the bay and by comparing them with Flinders Reef outside the bay. Re-examination of the assemblages after a major flood in 1974 and assessment of recolonization seven years later has lead to speculation about their nature, both past and present.

PRESENT REEFS

The reef structures formed in Moreton Bay are fringing reefs. They differ from their consolidated tropical offshore counterparts by being composed of unconsolidated coral rubble mixed with terrigenous sediments. This rubble is predominantly subfossil in composition and is overlain by the recent living assemblages (Fig. 1). These recent reefs therefore may be defined more appropriately as 'coral communities' after Wainwright (1965) whose definition described coral assemblages growing on a substrate other than that of its own production.

EARLY HISTORY

Throughout the late Quaternary (7×10^5 years B.P.) sea level fluctuated between present MSL and -150 m (Chappell, 1981). Moreton Bay was drained and filled repeatedly. Little evidence remains of the effects this may have had on earlier Pleistocene reef development. A late Pleistocene coral fauna (1.2×10^5 years B.P.) from tidal level at Evans Head (Pickett, 1981) and similar material from North Stradbroke Island (Pickett *et al.*, 1985) provide evidence of local coral occurrence prior to the development of the Holocene reefs (< 8,000 years B.P.).

Information on sea-level changes and radiocarbon dates provide some reasonable estimates of the age of Holocene reefs. It is accepted that Moreton Bay lies on the margin of the stable Maryborough Basin (Hill and Denmead, 1960) and that tectonic movement has not greatly biased the evidence in support of eustatic flux.

The reefal thickness of Mud Island reef extends to a depth of 6 m (Richards, 1931) and 5–7 m depth

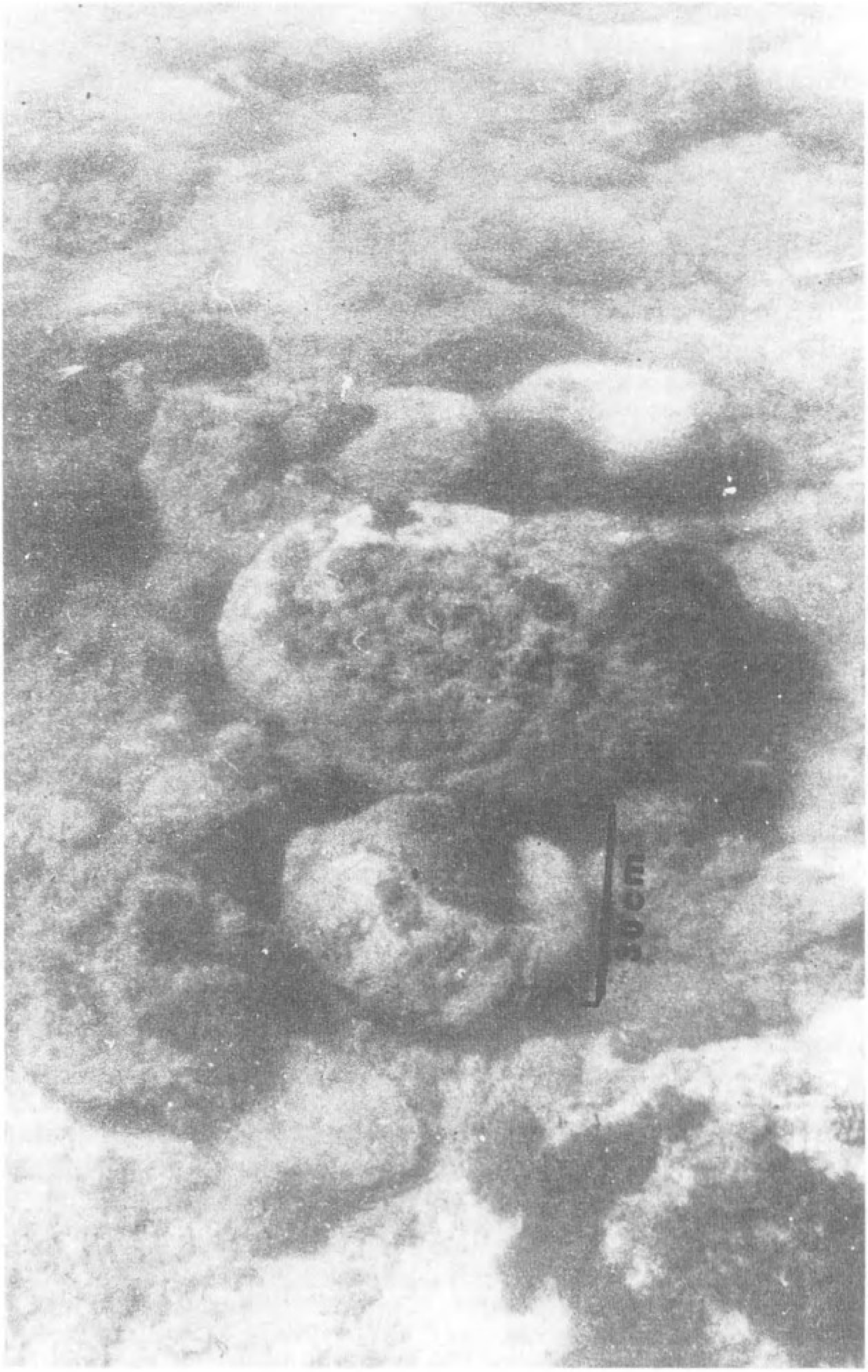

FIG 1. Present coral assemblage on the northern margin of Peel Island.

was ascertained for Moreton Bay's southwestern short deposits (Flood, 1978). Most of the bay's coral facies appear to begin at 3-4 m (Andrew, 1964; Smith, 1973). This level has been related to a Holocene shoreline dated 7,500 years B.P. (Wood, 1972). This date agrees with the eustatic curve of Thom and Chappell (1975) showing initial colonization at 7 m below the present mean sea level.

The oldest direct evidence of post glacial transgression is a radiocarbon date of 6,250 ± 135 years B.P. (SUA 857) from an *in situ* colony of *Favia* sp. from eastern Peel Island (Hekel *et al.*, 1979). Other evidence of reef development from an earlier period comes from samples dated between 6,000 ± 3,710 years B.P. (Rubin and Alexander, 1958; Marshall, 1975). Additional evidence for a Holocene eustatic high are the occurrences of *in situ* coralla in the intertidal zone near Cassim Island (Friederich, 1978) and the subfossil deposits in the southern and mainland margins of Moreton Bay (Andrew, 1964) where recent coral is now scarce or absent (e.g. Coochiemudlo, Macleay, Perulpa/Lamb Islands and the Pelican Banks).

Evidence from a Moreton Bay site dated 4,600 years B.P. suggests that an eustatic high of 1 m above present MSL existed (Jones *et al.*, 1978). The most convincing estimate of a late postglacial high sea level of +2 m was from mollusc shells in a stand of beachrock dated at 2,540 ± 85 years B.P. (Lovell, 1975b).

Subfossil Reefs

Massive coral banks around Mud Island attest to the dominance by the genus *Acropora* and to the degree of reef development (Fig. 2). Subfossil coralla exist on all of the present reef areas with recent species often growing on them.

Estimates of reefal deposits by the Queensland Cement and Lime Co. provide a measure of their former extent: 3×10^{10} kg of reefal limestone occur on the western perimeter of the bay (e.g. Raby Bay, Cleveland Bay and Wellington Point), 2.4×10^{8} kg are estimated for the southern bay areas (e.g. Coochiemudlo, Macleay, Perulpa Island and the Pelican Banks). Quantities extracted from Mud Island in the central bay region were 6×10^{6} kg in a 6 year period (approximation from Queensland Cement and Lime Co., 1971). None of these areas now exhibit substantial reef development.

Comparing the information on reefal deposits with that of the present survey two points become clear: 1, the subfossil reefs developed unequally, forming the basis of recent reef areas; 2, the subfossil reefs were more extensive throughout the bay and occurred in areas where there is no present development (e.g. southern bay areas).

METHODS

Sites

Moreton Bay is a wedge shaped body of water, bordered by the Australian mainland to the west and the islands of Moreton and Stradbroke to the east. Open communication with the oceanic waters of the north Tasman Sea is mainly through the northern 13 km wide passage. The southern end terminates in a complex network of channels. The reefs studied are present around the islands of Mud, St Helena, Green, King, Peel, Bird and Goat, Cassim, Coochiemudlo, and the western mainland at Raby Bay and Myora on Stradbroke Island (Fig. 3). Flinders Reef is located 1.5 km NE of Cape Moreton on Moreton Island. It is principally a sandstone outcrop exposed at low tide and surrounded by a diverse coral assemblage.

Assessment of the Present Assemblage

Species composition was assessed by placing four m^2 quadrats every 10 m along transect lines, oriented perpendicular to the shore and extending to the bayward limit for each assemblage. The number of colonies of each species was recorded. An individual colony was defined as any specimen growing independently of its neighbour and having more than half of its area inside the quadrat. The species diversity measure used was that after Brillouin (1962). The percentage of living coverage was determined by the use of the line transect method of Loya (1972) where the presence of a colony under the transect line was measured and noted as a proportion of the whole line. Selection of the sample areas was made in areas of maximum reef development. The survey was carried out during 1972 and 1973.

Assessment of the Post Flood Assemblage

In January-February 1974 the greatest flood of this century in Queensland occurred in the Brisbane Basin (Beattie, 1980). The survey sites were revisited in April. Mortality following flooding was determined by visual inspection of the original transect areas. The complete or minimal nature of the flooding mortality in most areas allows confidence in this method. Initial line transects were run to verify the subjective estimations.

FIG 2. Subfossil coralla, mostly *Acropora* spp., comprise the reefal material around the islands in Moreton Bay (Photo: Mud I.).

FIG 3. Chart of Moreton Bay, Queensland.

ASESSMENT OF RECOLONIZATION

In May 1981, seven years after the flood, a site was chosen which had experienced total flood mortality. The site was surveyed in the original manner. Eighteen quadrats (72 m^2) were sampled. Comparison was made with the original transects in terms of species number, diversity (H), evenness (J) and the percentage of living cover.

The *Favia speciosa* in the sample were measured. From the colony diameters, the age class distribution was determined and the periods of recruitment assessed.

RESULTS

CORAL COMPOSITION BEFORE THE 1974 FLOOD

Of the 27 species of hermatypic scleractinia in the bay, 26 occur in the subfossil and 18 in the current assemblage (94% co-occurrence) (Appendix). Twelve species were recorded in the quadrat analysis and five noted only as site records. *Favia speciosa* occurred in 93% of transects, representing in terms of absolute numbers, 6391 colonies or 89.4% of the bay samples. *Goniopora lobata*, comprising 296 colonies or 4.1%, was second in abundance. It occurred in 68% of the transects. Next most abundant and present in 35.2% of the transects were *Favites halicora, Favites abdita* and *Turbinaria peltata*. They represent 1.8%, 1.4% and 0.9% of the bay samples, respectively. Table 1 summarizes the species presence at the bay sites with the localities ranked with respect to number of species present. Site species diversity (H), evenness (J) and the percentage of coral cover are noted.

Species rich areas are found at Peel, Bird and Goat Islands and prior to the 1974 flood the eastern reef of Green Island (Table 1). Peel Island had the most species (16), three of which are unique to this location. All other bay sites comprise a reduced component of this assemblage. *Favia speciosa, Goniopora lobata, Favites abdita, Turbinaria peltata* and *Cyphastrea serailia* were the principle elements of the near mainland and northern island sites.

112 species were found at Flinders Reef. As with the subfossil assemblage this was dominated by *Acropora*. Only two species, *Acropora digitifera* and *Favia stelligera*, occurred in the bay's past and present corals but 4 were absent from Flinders Reef.

CORAL ASSEMBLAGES AFTER THE 1974 FLOOD

All coral assemblages on the mainland side of the bay experienced 100% mortality (Fig. 4). The islands of Mud, St Helena and Green also had extensive mortality with the exception of the deep reef on the eastern side of Green Island. Partial or no mortality occurred in the eastern bay in areas of relic water (Stephenson, 1968) and in those sites buffered by depth.

In areas of partial mortality, coral deaths were confined to particular genera. Portions of colonies were often killed. Death was characterized by a fleshless, silt covered corallum. Coral mortality was not confined to the species *Favia speciosa* (cf. Slack-Smith, 1959). On the contrary, the species *Turbinaria peltata, T. frondens* and *Goniopora lobata* were most affected by the flooding influence. This was unexpected as these genera are some of the most abundant in the bay, often occurring in the western sites. Mortality on the deep reef on the eastern margin of Green Island was partial. The hardiest species in terms of survival was *Psammocora contigua* which averaged 50%. *Favia speciosa* in this area was more greatly affected with a mortality estimated at 70%.

The extent of coral mortality correlated highly with species diversity and percentage of living cover. Areas of low diversity (0.15) generally experienced total mortality. They comprised one

TABLE 1. Species occurrence and diversity indices at the sites within Moreton Bay. The sites and species listing are ranked by species and site presence, respectively.

REEF SITES

Species	Specimen Records	E Green I	NE Peel I	NW Peel I	SW Peel I	E Bird and Goat I	SE Peel I	Sub Peel I	W Peel I	SE Green I	NE St Helena I	E Peel I	W Bird and Goat I	Myora	SW Peel I	Cassim I	King I	N Green I	N Coochiemudlo I	N St Helena I	Raby Bay	SE St Helena I	SW Mud I	W Peel I	W Green I	NE Coochiemudlo I	SW St Helena I	Site Records
Diversity H		0.26	0.20	0.17	0.17	0.36	0.29	0.25	0.18	0.31	0.33	0.09	0.25	0.06	0.15	0.07	0.07	0.03	0.06	0.05	0.02	0.13	0.12	0.07	0	0	0	
Evenness J		0.42	0.28	0.25	0.30	0.38	0.50	0.39	0.22	0.56	0.66	0.20	0.40	0	0.24	0.20	0.09	0.10	0.16	0.33	0.09	0.67	0.50	0.17	0.27	0	0.09	
% Cover %		36.2	11.0	31.0	36.9	5.0	1.0	37.1	13.7	5.0	2.8	1.0	15.6	1.0	20.9	1.4	1.4	30.6	1.0	1.0	2.8	1.0	1.0	1.0	1.0	1.0	1.70	
Favia speciosa	6391	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	26
Goniopora lobata	286	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				23
Favites halicora	148	×	×	×	×	×	×	×	×	×	×	×	×				×											13
Favites abdita	99	×	×	×	×	×	×	×	×	×			×		×	×			×	×	×			×				16
Turbinaria peltata	64	×	×	×	×	×	×	×	×	×	×	×			×		×	×					×					15
Cyphastrea serailia	57	×	×	×	×	×	×	×	×		×		×		×	×	×	×	×		×	×						17
Psammocora contigua	47	×	×	×		×	×	×	×			×								×								9
Platygyra lamellina	36	×	×	×		×		×	×	×				×														8
Plesiastrea versipora	16	×			×									×														3
Goniopora stutchburyi	8	×							×	×	×						×											6
Favia stelligera	5				×	×			×	×					×													4
Turbinaria frondens	2	×	×		×			×				×																5
Acropora digitifera	P*	×	×		×	×	×						×	×														7
Hydnophora exesa	P	×	×	×										×														4
Lobophyllia corymbosa	P		×		×	×																						3
Mycedium elephantotus	P	×																										1
Coscinaraea columna	P			×																								1
Species presence		**14**	**12**	**10**	**11**	**11**	**8**	**9**	**10**	**8**	**6**	**6**	**6**	**6**	**6**	**4**	**6**	**4**	**4**	**4**	**4**	**3**	**3**	**3**	**1**	**1**	**1**	

ISLAND SITES

Species	Peel I	Green I	Bird and Goat I	St Helena I	Myora	King I	Cassim I	Coochiemudlo I	Raby Bay	Mud I	Site Records
Favia speciosa	×	×	×	×	×	×	×	×	×	×	10
Goniopora lobata	×	×	×	×	×	×	×	×	×	×	10
Favites halicora	×	×	×	×		×					5
Favites abdita	×	×	×	×			×	×	×		7
Turbinaria peltata	×	×	×	×	×	×				×	7
Cyphastrea serailia	×	×	×	×		×		×	×		7
Psammocora contigua	×	×	×	×			×				5
Platygyra lamellina	×	×	×				×				4
Plesiastrea versipora	×	×	×	×	×						5
Goniopora stutchburyi	×	×		×							3
Favia stelligera	×	×		×							3
Turbinaria frondens	×	×									2
Acropora digitifera	×	×	×								3
Hydnophora exesa	×	×									2
Lobophyllia corymbosa	×										1
Mycedium elephantotus		×									1
Coscinaraea columna	×										1
Species presence	**16**	**15**	**10**	**10**	**4**	**5**	**5**	**4**	**4**	**3**	

*Site records only

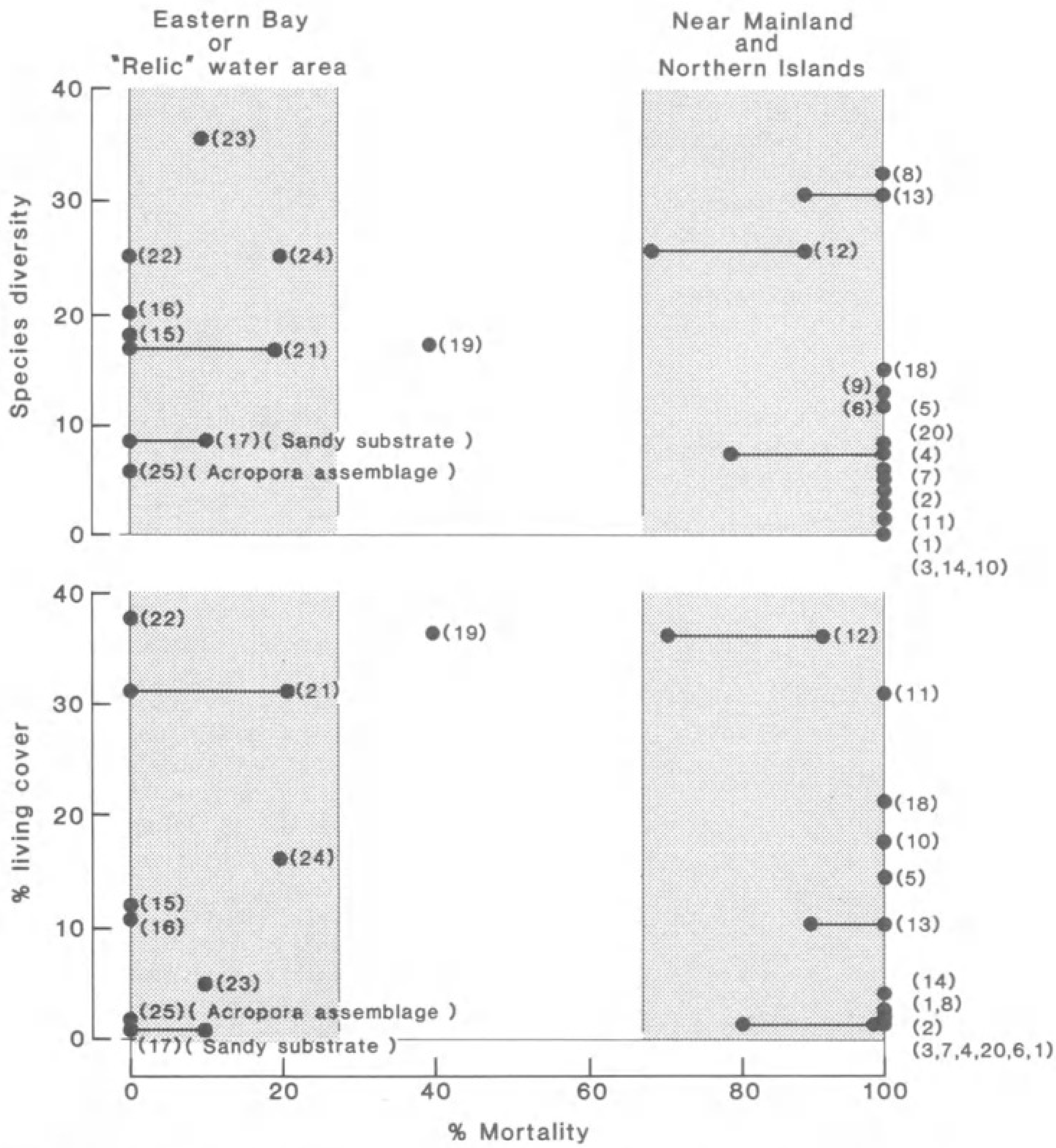

FIG 4. Post-flood mortality related to species diversity and percentage of living cover. Shaded areas contrast the marked flood effect in near mainland areas with those sites buffered by distance or circulation patterns. The bracketed numbers refer to the sites in the legend. Site legend: Western Bay Sites: 1. Raby Bay, 2. King Island; Southern Islands: 3. NE Coochiemudlo Island, 4. N Coochiemudlo Island, 5. Cassim Island; Northern Bay Islands: 6. SW Mud island, 7. N St Helena Island, 8. NE St Helena Island, 9. SE St Helena Island, 10. SW St Helena Island, 11. N Green Island, 12. E Green Island, 13. SW Green Island, 14. W Green Island; Central Bay: 15. N Peel Island, 16. NE Peel Island, 17. E Peel Island, 18. SW Peel Island, 19. SW Peel Island, 20. W Peel Island, 21. NW Peel Island, 22. 'Submerged Reef'; Peel Island: 23. Bird and Goat Island, 24. Bird and Goat Island, 25. Myora 'coral patch'.

to six species and generally had a low percentage of living cover. Exceptions to these trends were: 1, Low diversity assemblages at Myora (0.064) and at the eastern side of Peel Island (0.090) which experienced no mortality; 2, High diversity areas with a low percentage of living cover such as southeast Green Island and northeast St Helena Island where a high degree of mortality was experienced; 3, High mortality occurring in areas of high living cover having low diversity.

CORAL RECOLONIZATION TO 1981

343 specimens were sampled from SW Peel Island. Seven species were found, two more than the pre-flood condition (Table 2). The species diversity (H) is 0.12 (0.15 pre-flood). Evenness is 0.16 (0.24 pre-flood) (Table 2).

Frequency distribution of diameters provides evidence that recruitment commenced during the reproductive period following the flood (November, 1974). The range in growth indicates that recruitment has occurred in each year (Fig. 5).

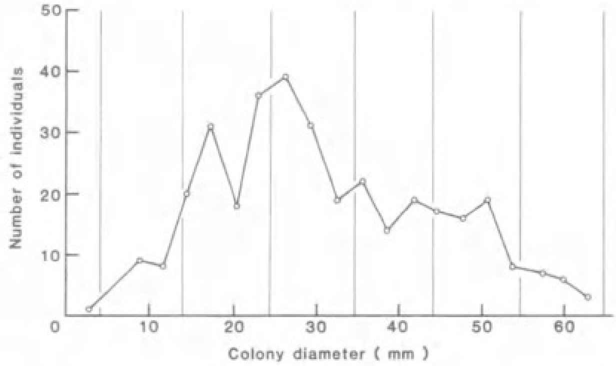

FIG 5. Size frequency distribution of *Favia speciosa* recruitment. Vertical lines show expected year class growth at 10 mm diameter per year. The period between the annual spawning and the sample date is 0.42 year. The vertical lines are positioned accordingly.

TABLE 2. Pre- and Post-flood composition of the coral assemblage at Southwest Peel Island.

	Pre-flood	After flood	1981 Survey
Species number:	5	0	7
diversity (H)	0.15	0	0.12
evenness (J)	0.24	0	0.16
cover (%)	20.9	0	1.6
	Pre-flood		1981 survey
Species component:			
Favia speciosa	×		×
Goniopora lobata	×		×
Favites abdita	×		×
Turbinaria peltata	×		×
Cyphastrea serailia	×		×
Acanthastrea sp.			×
Favites halicora			×

DISCUSSION

The results clearly show that the fringing reefs in Moreton Bay are highly modified by their bay environment but that their present nature is self-sustaining. The present distribution is best appreciated within four principle considerations: the bay's history; the range of coral assemblages; the flood effect; and evidence for recolonization.

HISTORY

A late Pleistocene fauna near the bay provides a basis for speculation as to an earlier coral presence. During the last glaciation (Wurm: *c.* 1.0 $\times 10^5$ to 1.0 $\times$ 1.0^4 years B.P.) the bay existed as a landscape with the first direct evidence of reef development occurring in the Holocene. The distinctive reefs of that period developed to relatively recent times. A change in that fauna occurred in the form of a reduction of that assemblage. As assemblage similar to the subfossil is extant at Flinders Reef, providing insight into the nature of the bay's paleoenvironment. The present distribution comprises those species tolerant to sedimentation and periodic dilution through flooding. The pre-flood description of this fauna and the subsequent differential flood mortality illustrate the most potent factors influencing the present distribution.

PRESENT REEF ASSEMBLAGES

The north side of Peel Island represents the diversity centre in the bay. Diversity is generally lower in the mainland sites and northern islands. Exceptions exist in those areas buffered by depth. The monospecific *Acropora* assemblage at Myora is unique and considered either a relic or the result of recent fortuitous immigration.

Comparing the sites' parameters of species diversity (H), evenness (J), species number and the percentage of living cover provides a fine scale description of the reefs and allows insight into the influences conditioning them (Table 3). Sites with a high diversity (H) are also characterized by high evenness (r_s = 0.77, Table 3a). They share similarities in the nature of their habitats. These are areas least affected by mainland influences. Those characterised by low index values are areas around the northern islands and the near mainland sites. A third group is represented by E Peel Island, the Myora 'coral patch' and E Bird and Goat Islands. They are thought to be principally limited by an unstable substrate.

The independence of sites from mainland influences is due to their distance (e.g. Peel, Bird and Goat Islands) or locations bayward of near

TABLE 3. Comparison of site diversity (H) with respect to, **a**, evenness ($J = H/H_{max}$), **b**, species number and, **c**, percentage of living cover; **d**, comparison of number of species to the percentage of living cover. 'H' and 'L' denote high and low categories. The bracketed values quantify these categories. The Spearman Rank Correlation coefficient (r_s) compares the significance of the parameters considered. Comparisons of species number with evenness, and evenness with the percentage of living cover, were not significant.

a)

Evenness	Diversity (H): H (> 0.15)	Diversity (H): L
H (> 10%)	NE St Helena I. SE Green I. E Green I. SW' Peel I. SW Peel I. SE Peel I. NE Peel I. N Peel I. Submerged Peel I. NW Peel I. W Bird and Goat I. E Bird and Goat I.	SW Mud I. SE St Helena I. N St Helena I. W Green I. Cassim I. N Coochiemudlo I. W Peel I. E Peel I.
L		SW St Helena I. N Green I. King I. Raby Bay NE Coochiemudlo I. Myora

$r_s = 0.77$ Highly significant

b)

Species Numbers	Diversity (H): H (> 0.15)	Diversity (H): L
H (> 5)	NE St Helena I. E Green I. SW' Peel I. SW Peel I. SE Peel I. NE Peel I. N Peel I. Submerged Peel I. NW Peel I. E Bird and Goat I. W Bird and Goat I.	Myora E Peel I.
L	SE Green I. SE Peel I.	SW Mud I. SW St Helena I. SE St Helena I. N St Helena I. W Green I. N Green I. King I. Raby Bay Cassim I. N Coochiemudlo I. NE Coochiemudlo I. W Peel I.

$r_s = 0.69$ highly significant

c)

% Living Cover	Diversity (H): H (> 0.15)	Diversity (H): L
H (> 10%)	E Green I. SW' Peel I. SW Peel I. NE Peel I. N Peel I. Submerged Peel I. NW Peel I. W Bird and Goat I.	Cassim I. N Green I. SW St Helena I.
L	E Bird and Goat I. SE Peel I. NE St Helena I. SE Green I.	SW Mud I. SW St Helena I. N St Helena I. W Green I. King I. Raby Bay N Coochiemudlo I. NW Coochiemudlo I. W Peel I. E Peel I. Myora

$r_s = 0.35$ significant

d)

% Living Cover	Species Numbers: H (> 5)	Species Numbers: L
H (> 10%)	E Green I. SW' Peel I. SW Peel I. NE Peel I. N Peel I. Submerged Peel I. NW Peel I. W Bird and Goat I.	SW St Helena I. N Green I. Cassim I.
L	NE St Helena I. E Peel I. SE Peel I. E Bird and Goat I. Myoroa SE Green I.	SW Mud I. SE St Helena I. N St Helena I. W Green I. King I. Raby Bay N Coochiemudlo I. NE Coochiemudlo I. W Peel I.

$r_s = 0.57$ highly significant

mainland islands (e.g. NE St Helena, E Green Islands). The eastern reef area on Green Island is relatively deep (3-4 m below MSL) and was the only northern island site to escape total destruction in the 1974 flood. The nearby NE assemblage at St Helena Island extends to this depth and has been characterized by its ocean-like environment on the basis of plankton samples (Greenwood, 1973). The buffering by depth in these areas during times of flood is inferred from the observed stratifications of freshwater during the 1974 flood and during the 1968 flood (Stephenson, 1968). Squires (1962) observed stratified runoff in Fiji where species presence was related to the distance from the Rewa River mouth.

With some exceptions, areas of low diversity are the result of an environment physically controlled by sporadic flood runoff. Distance from the mainland or occurrence in areas buffered by depth allow relatively more time for development towards a more diverse situation. In addition to the historical component, low index values reflect near mainland conditions where the immediate and persistent effects of silt make the area inhospitable to the development of coral assemblages. Bull (1982) in comparing two bays on Magnetic Island, North Queensland, found a marked reduction in species complement with the near absence of *Acropora* in the site most affected by siltation. Roy and Smith (1971) found a 50% lower coverage in turbid areas of the Fanning Island lagoon. Porter (1972a,b) attributed diversity reduction in back shelf regions of Caribbean reefs to sedimentation. Loya (1972) concluded that heavy sedimentation may be a very significant factor in determining scleractinian community structure. He attributed a reduction in species abundance and percentage cover in areas on Eilat Reefs to this agent. He points out that the few massive species found in this zone have probably evolved cleaning mechanisms. Marshall and Orr (1931), in studying the effects of sedimentation at Low Isles, Queensland found the predominant bay genus of *Favia* to be a very efficient sediment remover.

It is speculated that low diversity in areas unaffected by runoff (e.g. E and W Peel, E Bird and Goat Islands, Myora 'coral patch') are due to the unstable sandy substrate which is unsuitable for coral colonization. Motoda (1940) explained the paucity of reef corals in certain areas in Palau as due to favourable substances. Kissling (1965) found substrate to be the prime factor in regulating coral distributions in the shallow water environment at Spanish Harbour.

The high measure of evenness in low diversity situations relates to the overwhelming predominance of *Favia* speciosa. Sites grouped on the basis of evenness do not separate areas with any observed variable. Its independence of other parameters such as species number and percentage of living cover, indicates that the apportionment of the individuals among the species is not related to the physical factors presumed operative in conditioning the other measures.

In most sites an increase in species number represents a proportional increase in their relative abundances making the species number the best indication of diversity ($r_s = 0.69$, Table 3b). Areas of low diversity but high species number reflect a lack of physical stresses which prevent intolerant species from occurring. These sites are discussed with respect to unsuitable substrates. Areas of high diversity but low species number describe the situation where the species contribution to the index is low but their abundances are relatively equal. The sites do not share a common physical habitat but are characterized by low densities. It is uncertain as to the combination of factors which cause this. Areas of low diversity and species number invariably describe near mainland habitats where the species have been sorted by environmental stresses to those which are tolerant. The rarity of such species as *Coscinarea columna, Hydnophora exesa* and *Mycedium elephantotus* indicate that, to a very limited extent, recruitment of the bay corals may rely on communication with Flinders Reef where these corals are more abundant.

The relationship of diversity and species number to the percentage of living coverage are correlated with high significance ($r_s = 0.35, 0.57$, Table 3c,d respectively). Generally, relatively high diversity and species number were accompanied by appreciable coverage or were low with sparse coral occurrences. The groupings again separate the ocean-like sites from the near mainland areas. An exception to this relationship is the substrate limitation at W Peel Island. It is speculated that areas of limited coverage and high species numbers are due to a more predictable environment. Abundances here are reduced by unsuitable substrates.

Areas of low diversity, low species numbers and high coverage are typified by the predominance of *F. speciosa*. This species has utilized substrates unavailable to species intolerant of the flood-prone environment. Colonization here approaches the coverage characteristic of the more diverse areas. The 1974 flood caused complete mortality in these areas.

EFFECTS OF THE MAJOR FLOOD OF 1974

Between January 25 and February 1, 1974, torrential rainfall in the Brisbane Basin resulted in the greatest flood of this century. The influence of this condition on the bay coral was catastrophic.

Coral death was caused by intense rain during a cyclone coincident with a low tide that occurred on the Queensland coast in 1918 (Hedley, 1925a; Rainford, 1925). Slack-Smith (1959) recorded coral deaths at Peel Island in Moreton Bay due to rainfall. From Stoddart (1969), 'excessive water has killed shallow water biota by stream flooding in Jamaica' (Goodbody, 1961) and on the reefs in Tahiti (Crossland, 1928) and Samoa (Major, 1924). Endean *et al.* (1956) recorded similar destruction at Coral Point near Mackay, Queensland in 1951. Coral death at Low Isles following the flooding of the Daintree River in 1945 was investigated by Fairbridge and Teichert (1947, 1948).

The flood influence was principally confined to the western portion of the bay and islands. No mortality was observed on the northern margin of Peel Island or at the Myora 'coral patch'. The mechanism by which these areas escape destruction is due to bay circulation patterns. During times of flooding, there is pooling of undiluted seawater which remains as 'relic' or backwater on the northern side of the island (Stephenson, 1968).

Comparative salinities recorded by Kelley (unpublished) in the final two days of the 5-day flood period, allow comparison of the differential conditions experienced by the bay coral. In the northern area characterized by low diversities, he observed stratification of the freshwater, noting 10°/₀₀ salinity in the first metre near Mud Island. This increased to 15.5°/₀₀ in the second metre. St. Helena Island had salinities of 7.1°/₀₀ in the first metre, increasing to 13–15°/₀₀ in the second. In contrast, salinities on the north Peel Island reefs decreased to 21°/₀₀ in the first two metres and 24.6°/₀₀ by the sixth. The surface temperature at all sites and depths was relatively constant 23.6–26°C.

The results of laboratory work of Edmondson (1929) agree at the generic level with the 1974 post-flood observations. Of 23 species of Hawaiian corals introduced into seawater diluted by 50% with distilled water two bay genera *Favia* and *Psammocora* proved most hardy. They survived six days. These are the only corals which survived on the eastern reef of Green Island. All species died within a half hour of submergence in freshwater with the exception of *Favia hawaiiensis* which died after four hours. Of additional interest is that two genera, *Pocillopora* and *Montipora* which occurred only in the subfossil as well as at Flinders Reefs, proved very intolerant to dilution, dying in 23 to 26 hours respectively, after dilution in the 50% solutions.

Comparison of reef diversities and percentage of living cover with the percentages of the 1974 flood mortality (Fig. 4), served to validate the hypothesis that diversity in Moreton Bay is physically controlled. Diversity is generally thbe result of the degree of immunity from periodic flooding. As large floods are relatively rare, the potential for higher diversity and percentage cover exists in reef areas more removed from the effects of river discharge.

RECOLONIZATION

Recruitment on a reef flat which experienced total flood mortality seven years previous, shows development consistent with aspects of its previous nature. The species complement is two species in excess of the pre-flood situation. The lower diversity and evenness are due to the predominance of *Favia speciosa* in the sample. Lower coral coverage reflects the juvenile nature of the assemblage.

Growth rate studies (Lovell, 1975a; Moore and Krishnaswami, 1973) enable the assessment of colony age from its diameter. A size frequency plot for *Favia speciosa* (Fig. 3) reveals a range of colony sizes indicating growth, beginning the season following the flood (November, 1974). Subsequent recruitment occurred every year until 1981. Variability in growth rate ($\bar{X}$ = 5 mm; range 1.2 to 8.7 mm) makes it impossible to discern age classes and thus permits only a general appreciation of recruitment over the post-flood period. From the reproductive biology of similar faviids, it is assumed that the species has an annual spring spawning season (Kojis and Quinn, 1982; Babcock, 1984).

CHANGES IN THE NATURE OF THE BAY REEFS

Several hypotheses have been proposed to explain the change in the assemblage. Saville-Kent (1893) considered a general climatic change in temperature or in local elevation to be important. He believed that the islands of Stradbroke and Moreton were closing off the bay circulation, intensifying the effects of flooding from the Brisbane, Logan and Albert River systems. Wells (1955b) attributed the decline in development to a worsening of general conditions through a recent lowering of temperature (Hedley, 1925b; Howchin, 1924) and depth. A descrease in depth of 2–4 m was deduced from species present in the subfossil which are found in deeper water in the Great Barrier Reef areas.

The proposition that circulation with oceanic waters has been reduced due to the passages north of Moreton Island and that north of Stradbroke Island has not been substantiated by comparative aerial photos (e.g. 40 yr time span) or present observations (Stephenson, pers. comm.). Shorelines at the culmination of the post-glacial trangression 6,000 years B.P., show slightly greater communication. Subsequent build-up of land about the bay and island perimeters has decreased the bay volume (Hekel *et al.*, 1979; Flood, 1978).

The lowering of sea temperature does not appear to be a principal factor in the reduction in the number of species. This conclusion is based on the large number of species present (112 spp) at Flinders Reef near Moreton Bay. With the exception of two species, all of the subfossil species are living in Flinders Reef. From the Solitary Islands off the New South Wales coast (30°S) there are 47 species representing a 59% co-occurrence with the subfossil record. Veron *et al.* (1974) note a temperature regime which is generally similar to Moreton Bay (Hedley, 1925b; Crohamhurst Conservatory, 1936; Greenwood, 1973). Information on sea temperature around Flinders Reef (CSIRO unpublished) indicates a similar regime to that of Moreton Bay and the Solitary Islands. Though temperatures between 14°C to 15°C have been recorded several times during detailed bay observations it is the author's opinion that deeper areas are immune to these extremes which represent surface records. Substantial tidal exchange between bay and oceanic waters aids in modifying the shallow water extremes resulting from local weather.

The differences between the environments and coral assemblages of the bay and Flinders Reef are evident today. The question remains, 'how similar was the Moreton Bay environment to that of Flinders Reef when a similar coral assemblage developed'? Species presence does not necessarily reflect the luxuriance or species abundance of the coral community. It is difficult to say whether the subfossil fauna living in the bay occurred as it now does at Flinders Reef. In terms of mass, the subfossil reefs would suggest this. Distinct from the recent, the subfossil and Flinders Reef assemblages are principally represented by elements of the Indo-Pacific province (Stehli and Wells, 1971).

With the transgression, reef development began occurring in shallow water. Why such development was unaffected by terrestrial runoff and other mainland influences as siltation remains speculative. A change in climate from one with an equable rainfall to that of the present seasonal climate would affect the bay environment by increasing the potential sediment yield (Hekel *et al.*, 1979) and increase the runoff during the wet season.

The most evident temporal change in the bay environment was eustacy. Prior to 10,000 yrs B.P. the bay was a landscape. Subsequent filling with water allowed the Holocene reefal structures to begin development approximately 7,500 yrs B.P. (Flood, 1978). At 6,000 yrs B.P., the present mean sea level was reached (Thom and Chappell, 1975). Dated coral and beach rock indicates a high sea level between 1–2 m above present MSL (Jones *et al.*, 1978; Lovell, 1975b). It was during this eustatic high that the subfossil reefs developed. Such a substantial reef accretion could have only occurred in an environment of a more oceanic nature.

With eustatic decline, the reef assemblage became more vulnerable to the influences of the mainland on the bay environment. The effect of periodic flooding became more pronounced as the volume of the bay decreased. A change in direction of the Brisbane River outflow from a northerly to easterly direction gave the northern islands of Mud, St. Helena and Green, a nearshore nature with the encroachment of the river delta (Hekel *et al.*, 1979). This event does not constitute the principal reason for the change in the nature of the entire bay assemblage as Peel Island, representing a diversity centre, is relatively immune to this effect.

Faunal change may have been abrupt as the recent coral is observed growing on the subfossil facies. These facies, dated to recent times (Hekel *et al.*, 1979; Marshall, 1975) indicate that they have never been subjected to erosion from a marine regression. Reefal facies comprising only recent material are uncommon. The age of the recent assemblage has been estimated at 1,000–2,000 yrs B.P. (Hekel *et al.*, 1979). The possibility remains that the faunal change was much later.

Assessment of subsequent recolonization reflects the nature of the surviving species, in both complement and relative abundance. The attenuation of the subfossil species to those of the present is expected on the basis of species tolerance, given the presumed alteration of the bay environs. In areas of high diversity, lack of disturbance has resulted in longer periods for development. When local extinction occurs through flooding, the less flood prone areas represent a component which will bias the composition of recolonization. The bay species differ in their physiological tolerances to this stress which serves as the mechanism in determining the assemblage.

The second factor is the presence of unsuitable substrate or the effect of silt suspension. The importance of silt as an inhibiting factor is uncertain. Observed were the limitation of reef areas by the presence of silt at the northern islands and near mainland sites, and the unconsolidated sandy areas on the eastern side of the bay.

CONCLUSIONS

1. The subfossil reefs occur more widely throughout the bay than the present living ones do. This older assemblage most likely occurred during a period when the bay was more oceanic in nature.
2. The reduction in the number of species in the bay has occurred during the period of eustatic decline. It is uncertain whether this was gradual or relatively abrupt.
3. This reduction is mainly the result of two circumstances:
   a) The increased susceptibility of reef areas to the periodic effects of flooding.
   b) The effects of siltation, turbidity and unsuitable substrate from terrestrial sedimentation.
4. The present day assemblage in the longer term, can survive a major flood. Circulation patterns allow the more diverse areas to remain relatively unaffected, providing a source of recruitment.
5. Recolonization of a flood devastated reef indicates that species number and, to a lesser extent, diversity are maintained.

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APPENDIX

Hermatypic Scleractinia of Moreton Bay (recent and subfossil)[1] and Flinders Reef[2].

	Moreton Bay 27.5°S		Flinders Reef 27.5°S
	Recent 18 species	Subfossil 26 species	112 species
Thamnasteriidae			
Psammocora contigua	+	+	+
P. digitata			+
P. haimeana			+
Pocilloporidae			
Pocillopora damicornis		+	+
Seriatopora hystrix			+
Stylophora pistillata		+	+
Faviidae			
Favia favus		+	
F. pallida			+
F. maritima			+
F. speciosa	+	+	+
F. stelligera	+	+	
Favites abdita	+	+	+
F. chinensis			+
F. flexuosa			+
F. halicora	+	+	+
F. pentagona			+
F. russelli			+
Goniastrea australiensis			+
G. favulus			+
G. pectinata			+
Platygyra daedalea		+	+
P. lamellina	+	+	+
P. sinensis			+
Leptoria phrygia			+
Hydnophora exesa	+	+	+
H. microconos			+
Montastrea annuligera			+
M. curta			+
M. magnistellata			+
Plesiastrea versipora	+	+	+
Leptastrea bewickensis			+
L. transversa			+
Cyphastrea serialia	+	+	+
Agariciidae			
Pavona explanulata			+
P. maldivensis			+
P. minuta			+
P. varians			+
Siderastreidae			
Coscinaraea columna	+	+	+
Fungiidae			
Cycloseris costulata	+		+
Mussidae			
Acanthastrea bowerbanki			+
A. echinata			+
A. hillae		+	+
A. lordhowensis			+
Lobophyllia corymbosa	+	+	+
L. hemprichii			+
Scolymia australis			+
S. cf. *vitiensis*			+
Pectiniidae			
Echinophyllia aspera			+
Mycedium elephantotus	+	+	+
Caryophylliidae			
Euphyllia ancora			+
Dendrophylliidae			
Heteropsammia cochlea			+
Turbinaria bifrons			+
T. frondens	+	+	+
T. mesenterina			+
T. patula			+
T. peltata	+	+	+
T. radicalis			+
T. stellulata			+
Poritidae			
Alveopora allingi			+
A. marionensis			+
A. spongiosa			+
Goniopora djiboutensis			+
G. lobata	+	+	+
G. somaliensis			+
G. stutchburyi	+	+	+
Porites australiensis			+
P. lobata			+
P. lutea			+
P. murrayensis			+
Acroporidae			
Acropora austera			+
A. clathrata			+
A. cytherea			+
A. danai			+
A. divaricata			+
A. digitifera	+	+	
A. donei			+
A. florida			+
A. gemmifera			+
A. glauca			+
A. grandis			+
A. humilis			+
A. hyacinthus		+	+
A. latistella			+
A. lutkeni			+
A. microclados			+
A. millepora			+
A. nana			+
A. nasuta		+	+
A. nobilis			+
A. palifera			+

APPENDIX cont.

	Moreton Bay 27.5°S		Flinders Reef 27.5°S		Moreton Bay 27.5°S		Flinders Reef 27.5°S
	Recent 18 species	Subfossil 26 species	112 species		Recent 18 species	Subfossil 26 species	112 species
A. palmerae			+	*A. moretonensis*		+	+
A. robusta			+	*A. myriopthalma*			+
A. samoensis			+	*Montipoia caliculata*			+
A. sarmentosa			+	*M. danae*			+
A. secale			+	*M. foveolata*			+
A. solitaryensis			+	*M. mollis*		+	+
A. subulata			+	*M. peltiformis*			+
A. valida		+	+	*M. spongodes*			+
A. verweyi			+	*M. spumosa*			+
A. yongei			+	*M. tuberculosa*			+
Astreopora cucullata			+	*M. turtlensis*			+
A. listeri			+	*M. venosa*			+

[1]An early version of this was published in Lovell (1975b). The taxonomy now conforms to Veron *et al.* (1976–1984); Flinders Reef species list was compiled jointly with Dr Veron.
[2]Wells (1955a). The taxonomy now conforms to Veron *et al.* (1976–1984).