

The Natural Recruitment and Recovery Process of Corals at Green Island

V.J. Harriott and D.A. Fisk



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THE NATURAL RECRUITMENT AND RECOVERY PROCESS OF CORALS AT GREEN ISLAND

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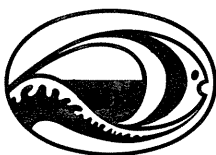
KEYWORDS: Hard corals, Green Island, Great Barrier Reef, coral regeneration, coral recruitment, coral juveniles, Acanthaster planci

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EXECUTIVE SUMMARY

The hard coral community at Green Island Reef is in the early stages of recovery following major damage caused from predation by Acanthaster planci between 1979 and 1981. Five years after the outbreak, in 1985, the coral community was dominated by juvenile corals mainly of the family Acroporidae. Of 20 sites surveyed by line transect, only 5 had a hard coral cover greater than 10%. Some Pocillopora damicornis was apparently undamaged by A. planci, and some staghorn Acropora thickets were regenerating from small parts of colonies which had escaped predation.

There was no significant change in hard coral cover at any of 12 sites resurveyed one year later in 1986. The absence of an increase in hard coral cover over the one year period is probably partly due to the early successional stage of the coral community, but it might also be partly attributable to the effects of Cyclone Winifred which passed through the area in February 1986.

While soft corals are abundant in some areas, they have not dominated the reef at most sites following destruction of the hard corals. Soft coral cover did not change at 10 of the 12 sites between 1985 and 1986; it was greater at one site and less at another.

Racks of settlement plates were placed on forereef and backreef sites at Green Island, Upolu and Michaelmas Reefs, during winter 1985, summer 1985/86, and winter 1986. Settlement was higher in summer than in winter (2200, cf. 61 and 220). Acroporids generally dominated summer plates while pocilloporids dominated winter plates. Settlement was significantly higher on the backreef than on the forereef during summer.

Recruitment was highest at Green Island Reef, despite its relatively depauperate adult fauna. Inter-reef dispersal is probably the dominant factor in determining the number of recruits. This indicates that badly damaged reefs should be able to recover quickly provided that there is a source of larval coral recruits 'upstream' from them.

Juvenile coral populations were mapped and measured in square metre quadrats at Green Island Reef. The abundance, recruitment rate, mortality rate, and growth rate of the juvenile corals over a 10-month period are presented. Acroporid corals were the most abundant family of juvenile corals, they recruited most rapidly and grew fastest during the study period. Juvenile corals were more abundant and recruitment was more rapid on the backreef site, but corals grew faster on the forereef site.

There were similarities in the patterns of abundance of coral spat on recruitment plates, recruitment of juveniles in marked quadrats in the field, and the pre-existing coral fauna on the quadrats. This suggests that recruitment patterns of corals at the family level have been consistent at Green Island Reef for at least seven years.

Juvenile coral dynamics indicate a clear recovery process following predation by A. planci, and the early stages of the recovering coral community are dominated by Acropora, the preferred prey species of the starfish. In the next few years there should be a rapid increase in hard coral cover on this reef.

Green Island Reef currently supports a small population of juvenile A. planci. It is impossible to predict at this time whether the starfish population will reach an equilibrium with the recovering corals, or whether as the coral population increases, we might see the resurgence of a large starfish population on a reef dominated by the preferred prey species, Acropora.

Recommendations:

Because outbreaks were first observed on Green Island Reef in both episodes of A. planci on the Great Barrier Reef, and because of its importance as a tourist destination, we recommend that a comprehensive monitoring program be undertaken on this reef. It is also important that the monitoring commenced in these studies be continued to establish long-term trends.

The following should be monitored:

- . coral recruitment on settlement plates to examine the interconnectivity of reefs;
- . regeneration of the coral community;
- . recruitment and dynamics of A. planci (as an 'early warning' of possible future outbreaks on the GBR);
- . environmental parameters (e.g. rainfall, nutrient levels) in an attempt to establish those factors causing, or contributing to outbreaks.

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1 RECOVERY OF THE CORAL COMMUNITY AT GREEN ISLAND

1.1 INTRODUCTION

Green Island lies at 16°45'S, 145°57'E, approximately 20 km from the coastline near Cairns. Apart from being the most heavily visited coral cay on the Great Barrier Reef, Green Island Reef has the distinction of twice having carried very large populations of Acanthaster planci. It is the site where large numbers of starfish were first reported in 1964, when damage to the coral community was considerable (Pearson and Endean 1969). The coral community was in the process of re-establishing itself when large numbers of starfish were again present from 1979 to 1981. After the second starfish outbreak, coral cover was reportedly less than 1% over large areas of the reef (Kenchington and Pearson 1982). Manta tow surveys in late 1983 assessed the cover of hard corals as being very low with little visible sign of coral recovery apart from the presence of some juvenile corals (Harriott, unpub.).

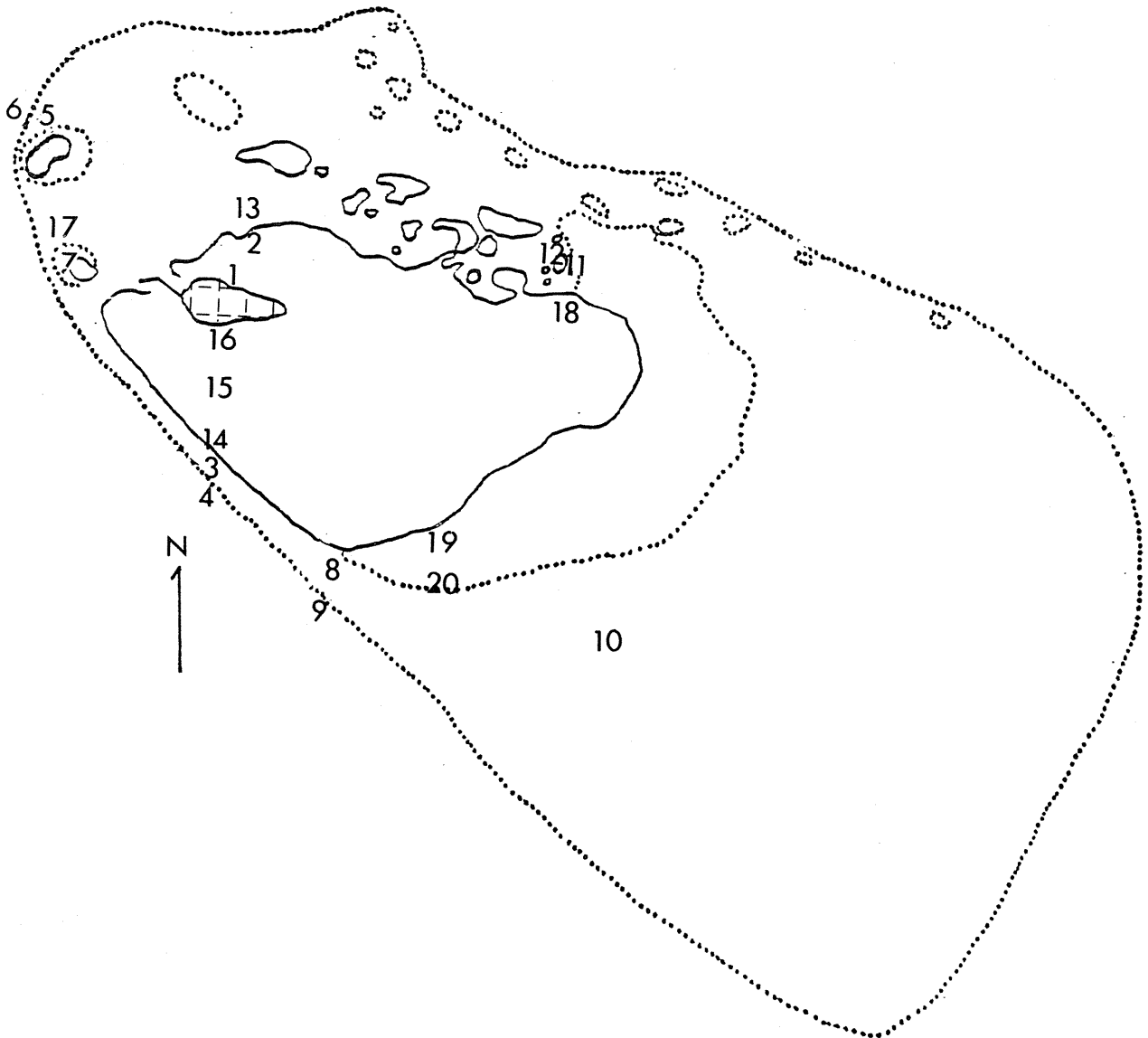
Aspects of the recovery process of corals following predation by A. planci are well documented (Pearson 1974, 1981; Done 1985; Endean 1976; Colgan 1981). The time estimated for recovery of the corals following damage depends on the extent of the damage, the size of the patch affected, and the availability of a source of larval recruits. The recovery process of Green Island Reef is of particular interest because of the value of the reef as a recreational resource.

We describe here the results of quantitative surveys of a number of sites on Green Island Reef in 1985, approximately five years after the starfish population had declined to very low levels. The nature of the recovering community is described, and predictions of the recovery pathway in the absence of further major predation episodes are made. We also present results of a resurvey of a subset of sites in 1986 and determine whether coral cover changed significantly in the one year period.

1.2 METHODS

Between 22 July and 20 September 1985, we surveyed 20 sites around Green Island (figure 1), using line transect surveys similar to those developed at the Australian Institute of Marine Science (Marsh et al. 1984; DeVantier et al. 1985). At each site a series of four 30m lines was used. A 30m tape measure was attached to the substrate at random, and the tape was extended over the substrate along the depth contour (+/- 1m), following the surface relief where possible. The length under the tape (=interval) for the target groups was measured. Hard corals were identified to the taxonomic level where identifications were almost certainly correct; for most corals this was to genus, but some groups were readily identifiable to species, and others, particularly small faviids, could only be recorded to family. The growth form of the coral i.e. encrusting, branching, tabulate, massive etc. was also noted.

Figure 1. Line transect survey sites at Green Island.



Between 8 August and 17 September 1986, a set of 12 of the original 20 sites was resurveyed using the same technique, but only cover of hard and soft corals was recorded.

1.3 RESULTS

1.3.1 Coral cover in 1985

Results of the line transects are given in the appendix and are summarised in table 1. Of the 20 sites surveyed, coral cover was less than 12% at 17 sites. Of the other sites with higher coral cover, two (sites 15 and 16) were on the reef flat in an area dominated by Montipora digitata (=ramosa), and one was an isolated patch dominated by Pocillopora damicornis apparently undamaged by A. planci predation (site 8).

Table 1. Summary of line transect data for Green Island Reef for 1985 and 1986. (%H.C.=%hard corals, %S.C.=%soft coral, No. Cols.=number of colonies, mean Int.=mean interval, Acr.=acroporids, Poc.=pocilloporids, Por.=poritids, Fav.=faviids)

Site (year)	Depth (m)	%H.C.	%S.C.	No. Cols.	Mean Int.	Number of Colonies			
						Acr.	Poc.	Por.	Fav.
1	(85) 0.5	5.6	17.8	60	11.2	23	1	10	11
	(86)	3.7	16.8	49	9.0	20	3	5	15
2	(85) 2.0	7.4	4.5	24	37.0	17	1	0	0
	(86)	8.9	6.0	28	38.1	20	1	2	1
3	(85) 3.0	5.5	4.9	92	7.2	50	3	14	16
	(86)	3.9	7.2	56	8.3	38	3	4	6
4	(85) 6.0	4.0	0.8	107	4.5	45	2	12	37
	(86)	2.7	0.7	76	4.3	30	0	8	27
5	(85) 2.0	2.4	3.6	59	4.9	25	6	15	8
	(86)	1.8	7.2	32	6.7	14	3	6	3
6	(85) 5.0	5.6	6.9	95	7.1	40	14	8	21
	(86)	3.9	6.6	68	6.9	30	7	12	14
7	(85) 3.0	11.3	17.2	78	17.4	48	3	14	9
	(86)	11.2	10.1	98	13.5	66	2	19	6
8	(85) 3.0	16.1	2.9	137	14.1	38	81	4	11
	(86)	5.4	9.9	66	9.7	43	11	1	5
9	(85) 5.0	10.9	13.7	81	16.1	28	7	27	10
	(86)	10.2	7.6	51	18.0	20	2	20	4
10	(85) 5.0	6.8	20.8	80	10.2	17	26	21	3
	(86)	5.7	10.7	65	10.6	24	16	8	2
11	(85) 3.0	9.2	18.5	95	11.6	25	43	15	8
	(86)	6.7	15.3	52	15.4	13	30	2	6
12	(85) 5.0	5.4	25.2	42	15.4	7	23	9	2
	(86)	1.6	13.0	15	13.0	0	6	4	1
13	(85) 5.0	2.6	15.4	40	7.8	8	3	10	8
14	(85) 0.0	1.8	0.0	32	6.8	12	0	1	17
15	(85) 0.0	28.5	0.0	130	26.3	92	4	25	9
16	(85) 0.0	20.3	0.0	127	19.2	63	16	32	12
17	(85) 3.0	8.6	19.5	60	17.2	9	42	2	2
18	(85) 0.0	2.8	24.9	55	6.1	10	6	18	18
19	(85) 2.0	3.6	35.2	37	11.7	18	15	0	1
20	(85) 6.0	1.0	46.7	13	9.2	3	2	3	0

Some of the sites surveyed are illustrated in figure 2. At many sites, living corals are not immediately obvious, and even the very large Porites colonies have been completely killed in many parts of the reef. In other parts, small areas of tissue survived, and these are now regrowing to form a number of smaller colonies on a large otherwise dead colony (figure 2 a,b). In many sites, juvenile corals are the most distinctive element of the coral fauna, especially on dead Acropora plates in the areas where the plates were formerly dominant (figure 2 h). Heliopora and an encrusting soft coral are abundant on the eastern sides of the reef (figure 2 h,k). Several relatively large patches of Pocillopora damicornis have survived as virtually monotypic stands. On the leeward bommie site, staghorn Acropora patches have small areas of living corals that have regenerated from surviving sections of the now mostly dead thickets (figure 2 d).

Taxonomically, Acropora species dominate the recovering community (table 1), with pocilloporids, faviids and poritids all present but not abundant.

1.3.2 Size frequency distribution

The frequency distribution of intervals on the line transects shows that the hard coral fauna is dominated by small corals, indicating the abundance of juveniles in the coral fauna. Forereef and backreef sites, deep and shallow sites, all showed a similar size frequency distribution. The size distribution of the Pocillopora patches and glass-bottom boat patch are different from the damaged reef slope sites in having a greater proportion of larger corals (figure 3).

We examined the taxonomic composition of the smaller (<10cm interval) versus the larger (>25cm interval) corals. If we can assume that most corals which have a minimum diameter of 25cm grow at 1cm to 5cm in diameter/year (Buddemeier and Kinzie 1976), then these corals were almost certainly present before the most recent A. planci outbreak. The smaller corals are more likely to have recruited since the last outbreak. Both large and small corals are dominated by the family Acroporidae (figure 4), and this family forms over 50% of the larger corals. Some of these colonies have regenerated from fragments of living tissue that remained when the rest of the colony was eaten.

Pocilloporidae are not well represented among the smaller corals but they are the second most abundant amongst the larger corals, reflecting their apparent ability to escape A. planci predation. This lack of juvenile pocilloporids is discussed in later sections. Poritids form about 20% of both large and small corals, while faviids are represented amongst the small corals but not at all amongst the larger ones. This absence may be partly explained by the fact the faviids grow relatively slowly, but certainly large faviids are rare on the reef, and faviids are a favoured food of A. planci.

Figure 2. Illustrations of sites around Green Island showing typical features of each area.

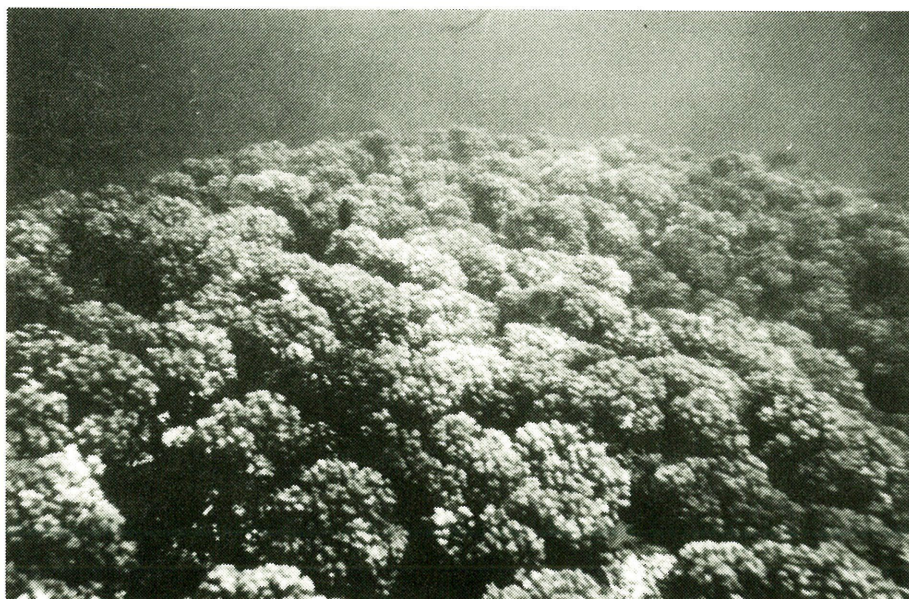
- a,b. Regeneration of corals from small remnant areas, site 11.
- c. Patches of surviving Pocillopora, site 17.
- d. Regeneration of staghorn Acropora from remnant patches, site 2.
- e. Site for shallow transplants, site 5.
- f. Reef flat sites, 15 and 16.
- g,h. South-east slope sites showing dead Acropora plates and some new recruits.
- i. Heliopora colonies are abundant at site 19.
- j. Glass bottom boat patch, site 7.
- k. Encrusting soft corals dominate large areas at sites 10 and 20.
- l. Soft corals and macroalgae dominate at site 11.



a



b



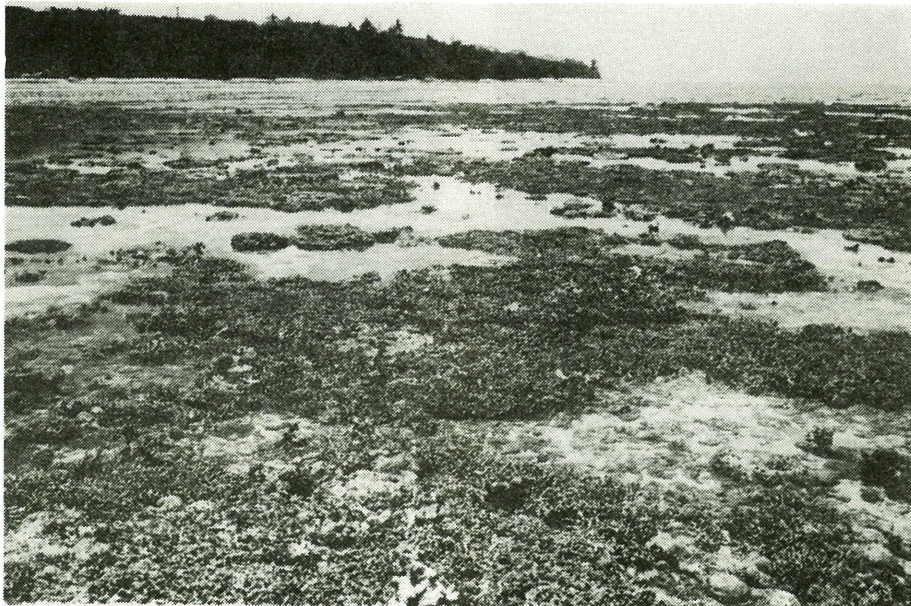
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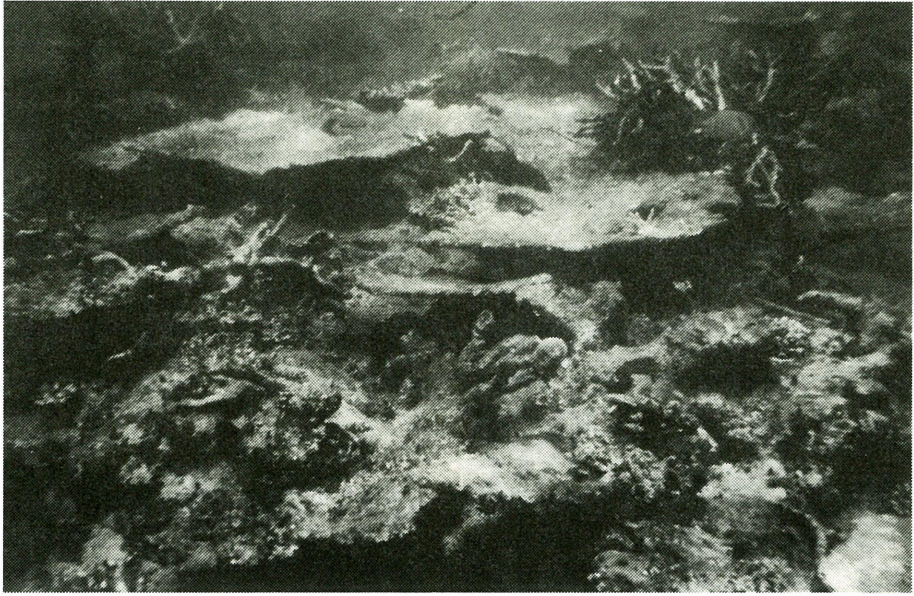
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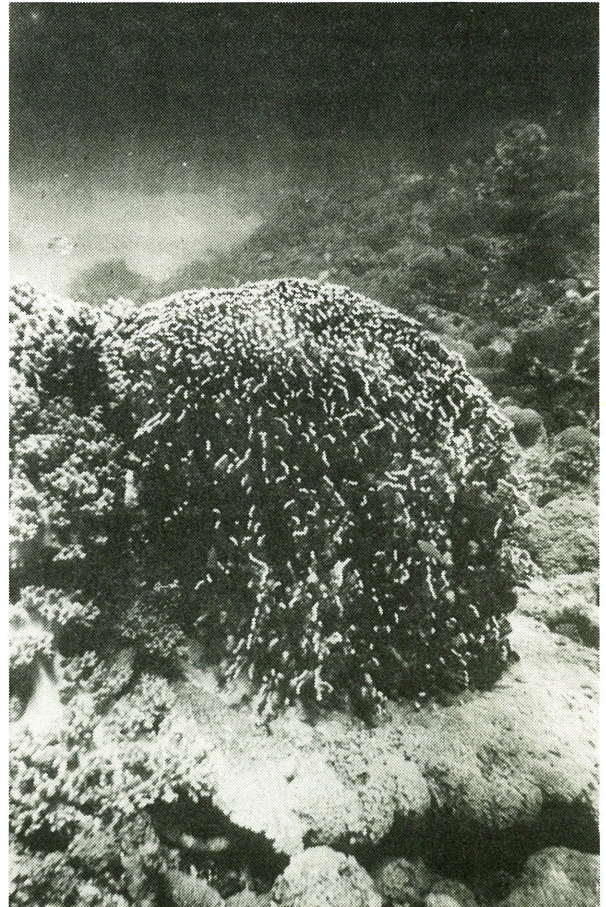
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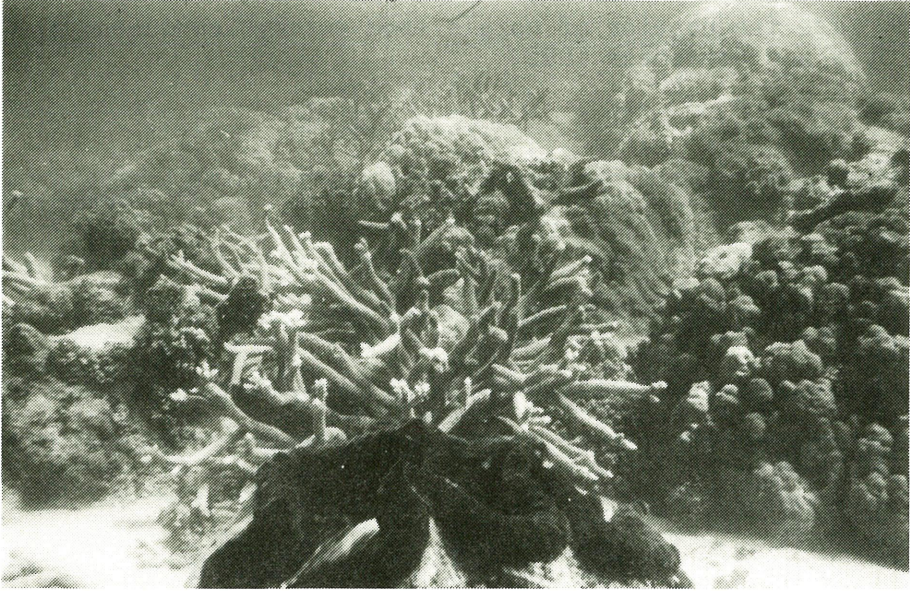
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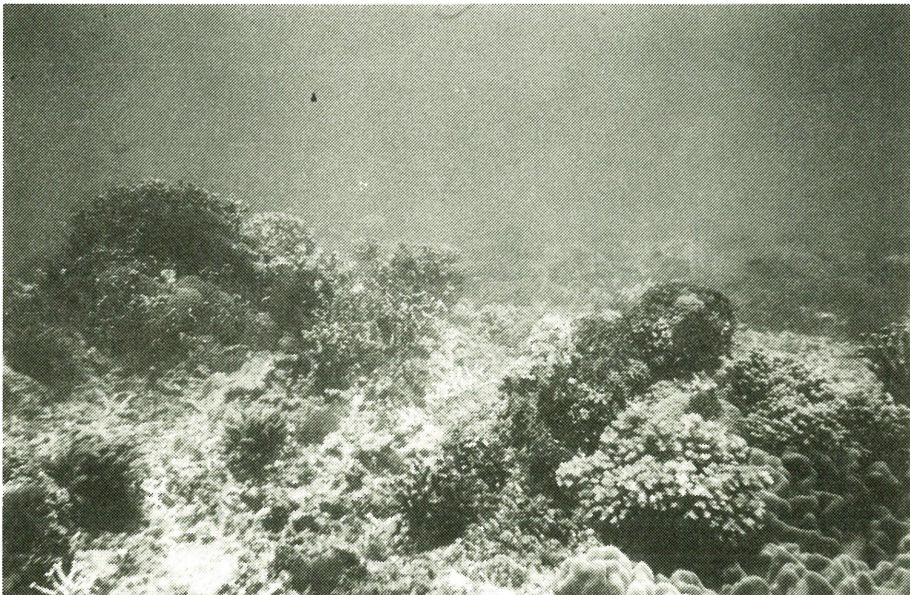
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k



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Figure 3. Size frequencies of corals from surveys conducted at Green Island between July and September 1985.

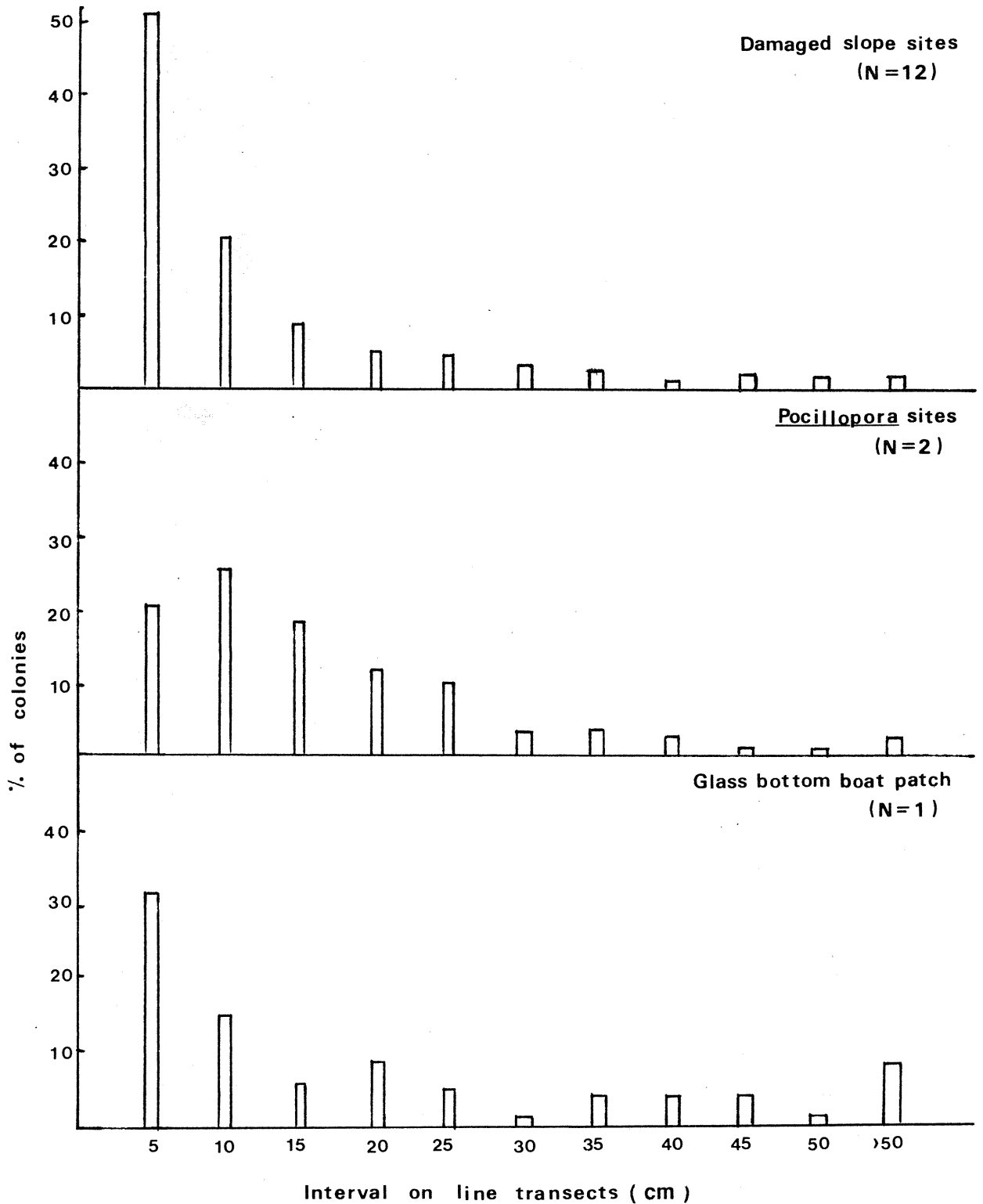
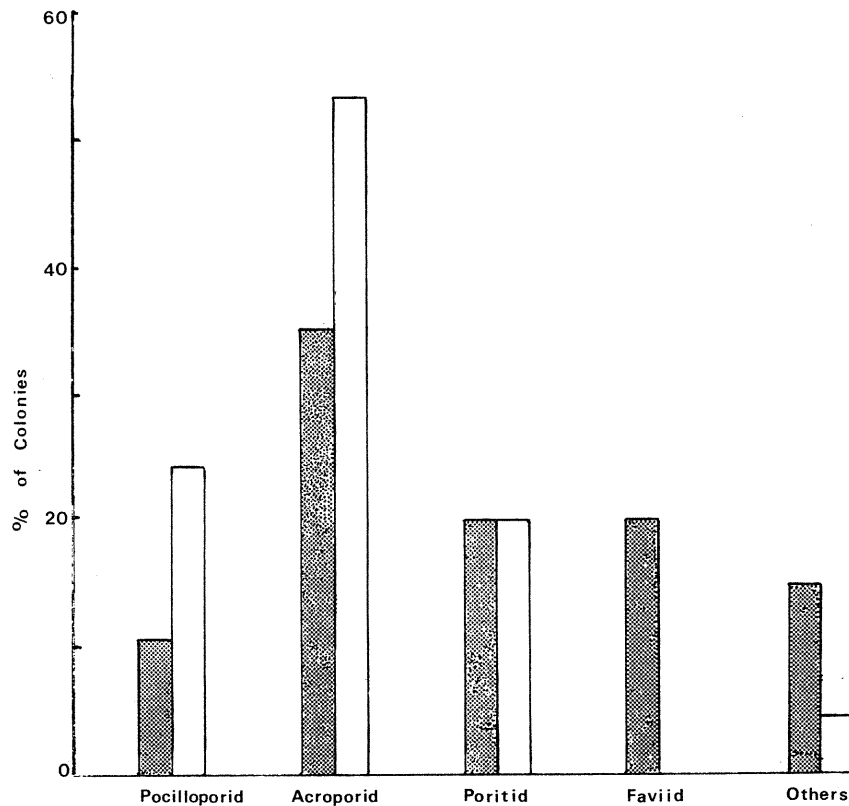


Figure 4. Taxa of large colonies (>25cm intervals)(open bars) and small colonies (<10cm intervals)(solid bars), taken from line transect data in 1985.



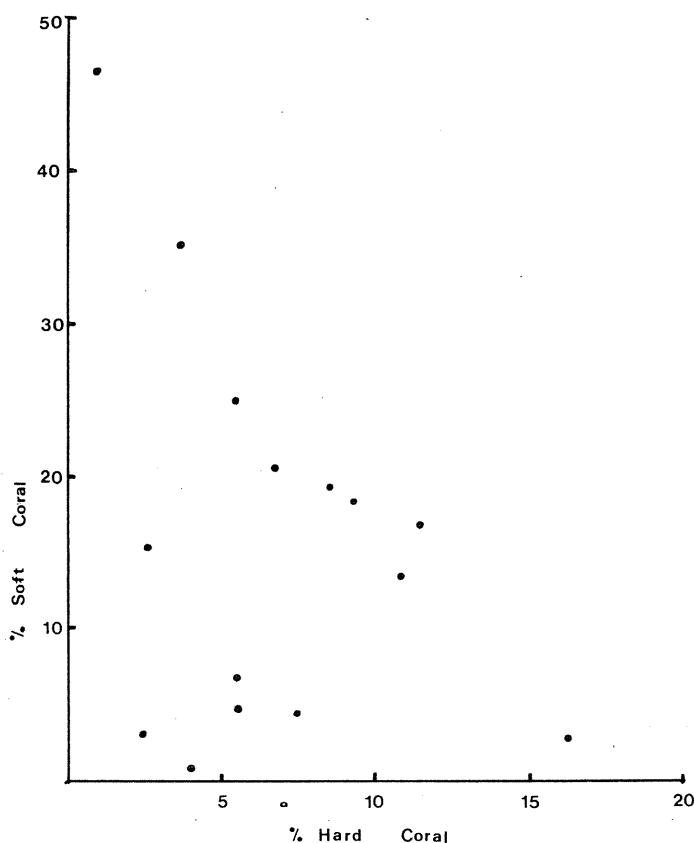
1.3.3 Hard versus soft corals

It has been suggested by some authors (e.g. Endean 1976), that soft corals are able to increase rapidly in abundance following death of the hard coral population and take over large areas of reef. If this has occurred, most of Green Island Reef should currently be dominated by soft corals. The relationship between the cover of hard and soft coral is shown in figure 5. For the 12 sites where hard coral cover was low (less than 10%), soft coral cover ranged from 1% to 47%. The relationship between hard and soft corals is not clear-cut, and at many sites of low hard coral cover, soft corals remain an insignificant element of the fauna.

1.3.4 Changes in the coral community over 1 year

The percentage cover of hard and soft corals for the sites re-surveyed in 1986 are given in table 1. Results were tested using paired t-tests to determine whether coral cover had changed significantly between 1985 and 1986. None of the 12 sites tested showed a significant difference in hard coral cover between the two samples ($P(t) > 0.05$). At two sites, soft coral cover was significantly different from the previous year; at the 3m south-east slope site (site 8) soft coral cover was higher in 1986, and at the eastern bommie field site (site 10) it was lower in 1986.

Figure 5. Relationship between the cover of hard and soft corals from line transect data collected in 1985.



1.4 DISCUSSION

In several studies of recovery of reefs following predation by *A. planci* (Randall 1973; Colgan 1981; Pearson 1981; Moran et al. 1985), some common features emerge. The first phase of the recovery process is a lag phase in which coral cover is very low, visible new recruits are uncommon, and the diversity of the coral community is dependent on the number and type of surviving and partly eaten corals. Done (1985) has discussed in detail the importance of these corals in the recovery process. Wallace et al. (1986) observed coral recruitment during an outbreak of *A. planci* on a central Great Barrier Reef mid-shelf reef and found that *in situ* recruitment of microscopic sized corals had begun while the outbreak was still in progress.

The second phase includes the establishment of juvenile corals at a visible size, often up to 5 years after predation. The third phase shows a rapid increase in coral cover of the fast-growing acroporid corals until cover is high, diversity is relatively low and corals have occupied much of the available space. This phase may be completed 8 to 15 years after the initial predation.

The final hypothesised phase is where the slower growing or sporadically recruiting corals increase in abundance as the more opportunistic corals are out-competed or are physically damaged by storms etc. This phase has not been reached in the post-*A. planci*

recovering reefs on the Great Barrier Reef because the interval between the last two outbreaks of the starfish has been less than 15 years.

Green Island Reef, five years after the conclusion of the last A. planci outbreak, is in the second stage of the recovery process. Hard coral cover remains low at the majority of sites. The size distribution demonstrates that the majority of corals present are juveniles, and these are abundant in most areas of the reef.

The hypothesised recovery pathway will vary depending on the relative contributions of the various sources of coral regrowth. These are:

1. Growth of colonies unaffected by A. planci. At Green Island, this includes mainly P. damicornis, a few massive species e.g. Diploastrea and a few isolated outcrops, which are located particularly towards the eastern end of the reef where starfish were first reported.
2. Growth of fragments of corals otherwise eaten by A. planci. This includes largely staghorn corals and large Porites colonies where small uneaten portions have started new colonies.
3. Growth of corals which were new recruits during the outbreak period and hence escaped predation by being small and cryptic.
4. New recruits since the last outbreak.

The extent of the contributions by the different forms of regrowth depends on the extent of the damage. At the pocilloporid patches (sites 8 and 17) and the leeward bommie (site 2), the dominant regrowth of new recruits is from categories 1. and 2. above respectively. The most obvious growth of new recruits is on the south-east slope sites. Dead Acropora plates that once dominated the site and most likely were killed in the last A. planci outbreak, now support up to 10 or sometimes more new recruits. Frequently these are new Acropora recruits with diameters from 1 to 15cm. The importance of dead Acropora plates for post-A. planci coral recruitment has been emphasised by Wallace et al. (1986). The recruitment rate and growth of juvenile corals are described in more detail in section 3.

The reef at present supports large numbers of established (1 to 5 year old) juvenile corals, mainly acroporids. Because most corals recruit only annually (Wallace and Bull 1982; Harriott 1985), and growth in the early stages is extremely slow (Harriott 1985; Wallace 1985a, 1985b; Babcock 1985), the time required for a denuded reef to contain significant numbers of visible corals (e.g. >5cm diameter) is in the order of 5 years. Green Island has reached this stage. From this point, the more rapid potential growth rate of the currently established corals means that there is the possibility of a rapid increase in coral cover in the next 3 to 5 years. It is likely that this will result in a significant change in the appearance of the reef, but the reef will be dominated by rapidly-recruiting, fast-growing species for many years.

There was no significant increase in coral cover between 1985 and 1986. This may be because the reef had not yet reached the rapid growth phase, but it may also be attributable to the effects of Cyclone Winifred, which passed by Green Island in February 1986 (Harriott and Fisk 1987a). While the cyclone did not cause a significant decline in coral cover, the peripheral damage it caused to colonies may have delayed the recovery growth to some extent.

It has been proposed that soft coral may take over large areas of reef denuded of hard corals by A. planci (Endean 1976). At Green Island, soft corals are abundant in some areas of low hard coral cover, but not others. There was no increase in soft coral cover between 1985 and 1986 in 11 of the 12 sites surveyed, despite the low hard coral cover. There are areas of the reef where soft coral cover is so high that the availability of suitable settlement space for coral recruits may well limit the potential for a future increase in the hard corals. In the absence of data on the community composition of Green Island Reef prior to the A. planci outbreaks, it is difficult to determine whether such areas have always been dominated by soft corals, or whether the previous community structure made the site susceptible to an expansion of the soft coral population. Skeletal evidence of long-term occupancy of soft corals can be seen at a few sites. Certainly an inevitable takeover by soft corals is not supported by the data from Green Island.

While the reef at Green Island seems poised to proceed to a rapid growth of hard corals, whereby coral cover within a few years may not differ greatly from the pre-A. planci levels, there are several other factors to consider. Firstly, during the last major predation episode, coral colonies perhaps hundreds of years old were killed and the population structure of the reef totally altered (Cameron and Endean 1981; Endean and Cameron 1985). The recovering community will be dominated by fast-growing Acropora species. Other species will undoubtedly recruit and feature more prominently in the community over time. Secondly, the recovering community is dominated by acroporid corals, and many small starfish (recruited from summer 84/85 spawnings) have been found in surveys on Green Island Reef (Fisk and Harriott, unpublished data), which could indicate that the reef may be entering a stage of chronic starfish infestation (e.g. Bradbury et al. 1985). That is, the starfish population will continue to keep the coral population in the early successional stages with a dominance of their favoured coral food.

2 RECRUITMENT AND DISPERSAL OF SCLERACTINIAN CORALS AT GREEN, MICHAELMAS AND UPOLU REEFS

2.1 INTRODUCTION

The Great Barrier Reef is comprised of a series of more than 2900 individual reefs, covering a distance of 2300 km from north to south, with variable but relatively narrow width across the continental shelf (Hopley and Davies 1986). In recent years one aspect of the ecology of the Great Barrier Reef that has particularly interested biologists is the contribution of dispersal processes to the recruitment patterns of reef organisms (e.g. Williams et al. 1984; Leis and Goldman 1984, 1987; Bull 1986). In particular, the degree of dispersal of the larval stages of both fish and corals has received detailed attention, and there is much work in progress that attempts to elucidate the process.

Green Island, near Cairns on the north-central region of the Great Barrier Reef, was badly affected by the crown of thorns starfish, first in the 1960s and again in 1979/80. Following the second outbreak, the surviving cover of hard coral was estimated to be less than 10% by independent observers (Cameron and Endean 1981; Nash and Zell 1981). Even in 1985, about 5 years after the passing of the starfish, line transect surveys at sites around the reef slope showed only 3 of 15 sites with coral cover greater than 10%, and at many sites the cover was still less than 5% (section 1).

The situation at Green Island provides the opportunity for a natural experiment to test the source of coral recruitment to the reef, by comparing the rate of recruitment at Green Island Reef with that at nearby reefs. Since there are few adult corals at Green Island, we hypothesise that the rate of coral recruitment would be less than at nearby flourishing reefs if recruitment was predominantly local (i.e. if reefs were self-seeding).

The aims of this section of the study were three-fold: to examine the natural variation in hard coral recruitment by comparing a number of reefs and reef sites simultaneously; to determine if the recovery of the hard coral community at Green Island Reef following severe predation by the crown of thorns starfish was likely to be limited by a reduction in the reproductive output of the reef; and to look at the dispersal patterns of coral recruits which might give clues to dispersal paths and the degree of interconnectedness of these reef systems.

2.2 METHODS

Racks of settlement plates were placed at depths of 3 to 5m at low tide on the forereef and backreef areas of Green, Upolu and Michaelmas Reefs (figure 6). There were racks at two sites in each forereef and backreef, separated by a distance of 20 to 40m. Each rack contained 8 plates cut from *Platygyra* colonies, 4 with relatively smooth cut surfaces, and 4 with one surface from the outer part of the colony. Plates were bolted in pairs above and below the rack forming a narrow space between the plates (figure 7). This space is referred to as the 'gap' habitat.

Figure 6. The location of reefs used in the larval recruitment study.

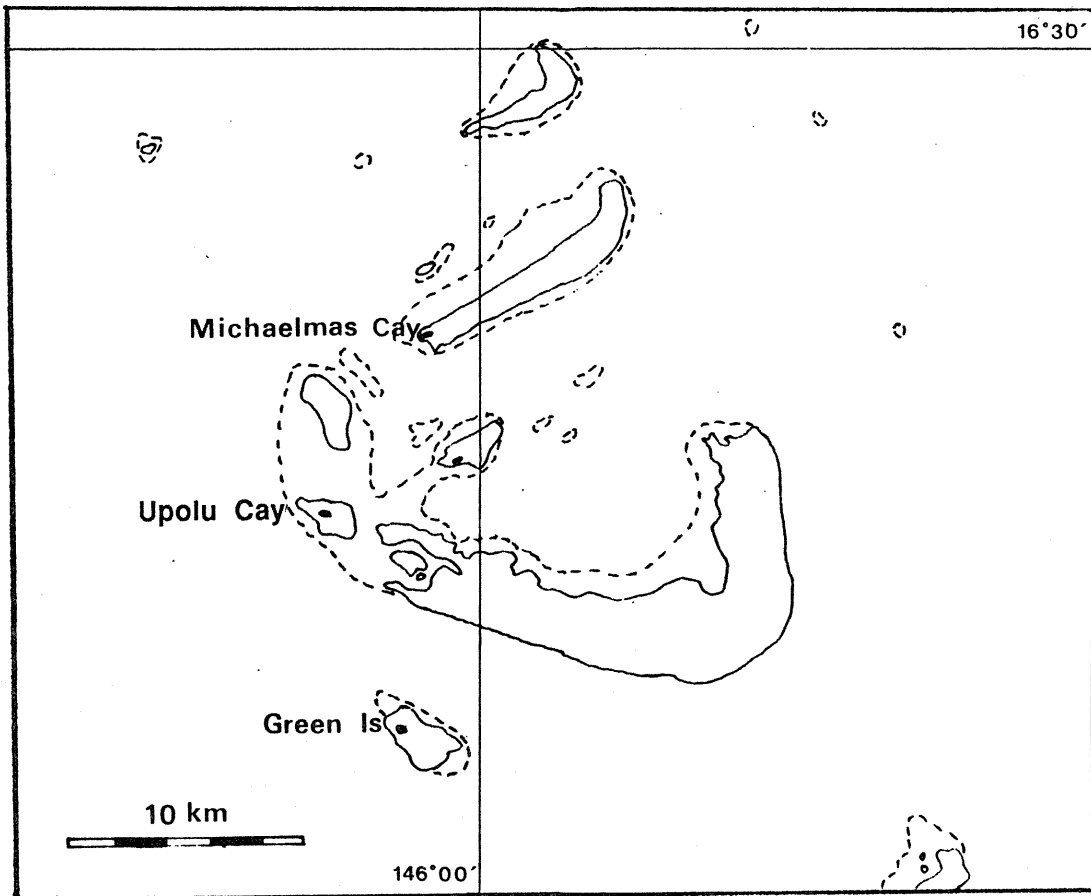
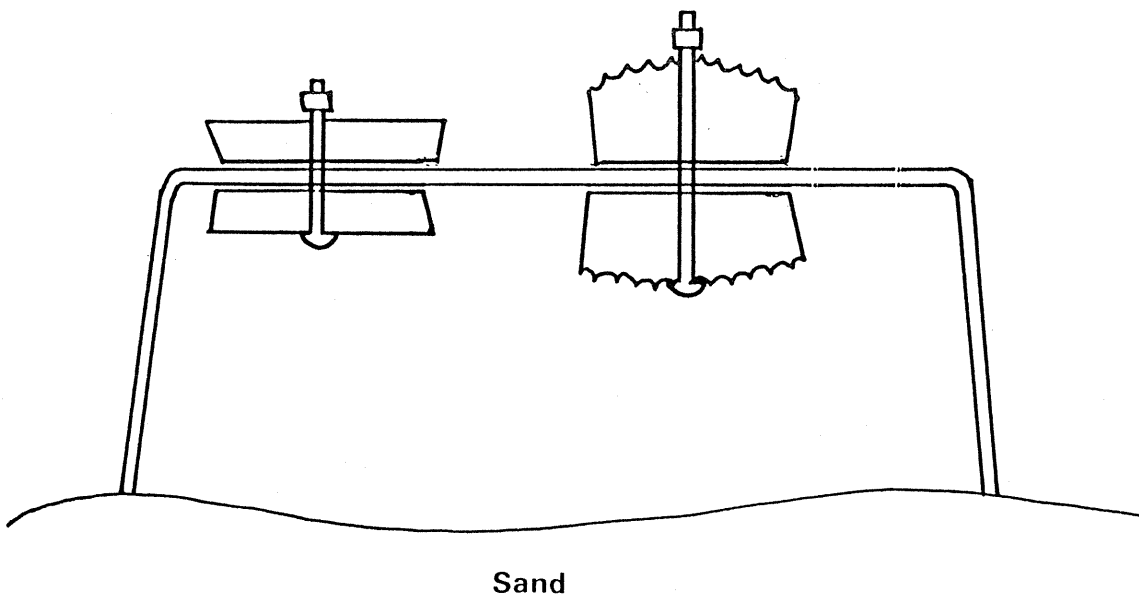


Figure 7. The attachment of settlement plates showing the 'gap' habitat.



Plates were collected and replaced at approximately 6-monthly intervals, in October 1985, March and September 1986. After collection, plates were bleached in a chlorine solution, dried and examined under a dissecting microscope. The number of spat on the top and bottom of each plate was counted. Spat were identified to family level where possible.

2.3 RESULTS

Over 2500 spat were found on all the plates. Of these, only one was found on the uppermost surface of the plates. 52% of spat were found on the lowermost surface of a pair of plates bolted together, and 48% were found in the narrow gap between the two plates. This is consistent with the results reported by Harriott and Fisk (1987b) on settlement preferences of coral spat for different plate types.

The number and identification of spat recruiting over the 18-month period are shown in figure 8. There is a summer/winter variation in the number of spat recruiting at all reefs, although the distinction is less clear for Upolu Reef.

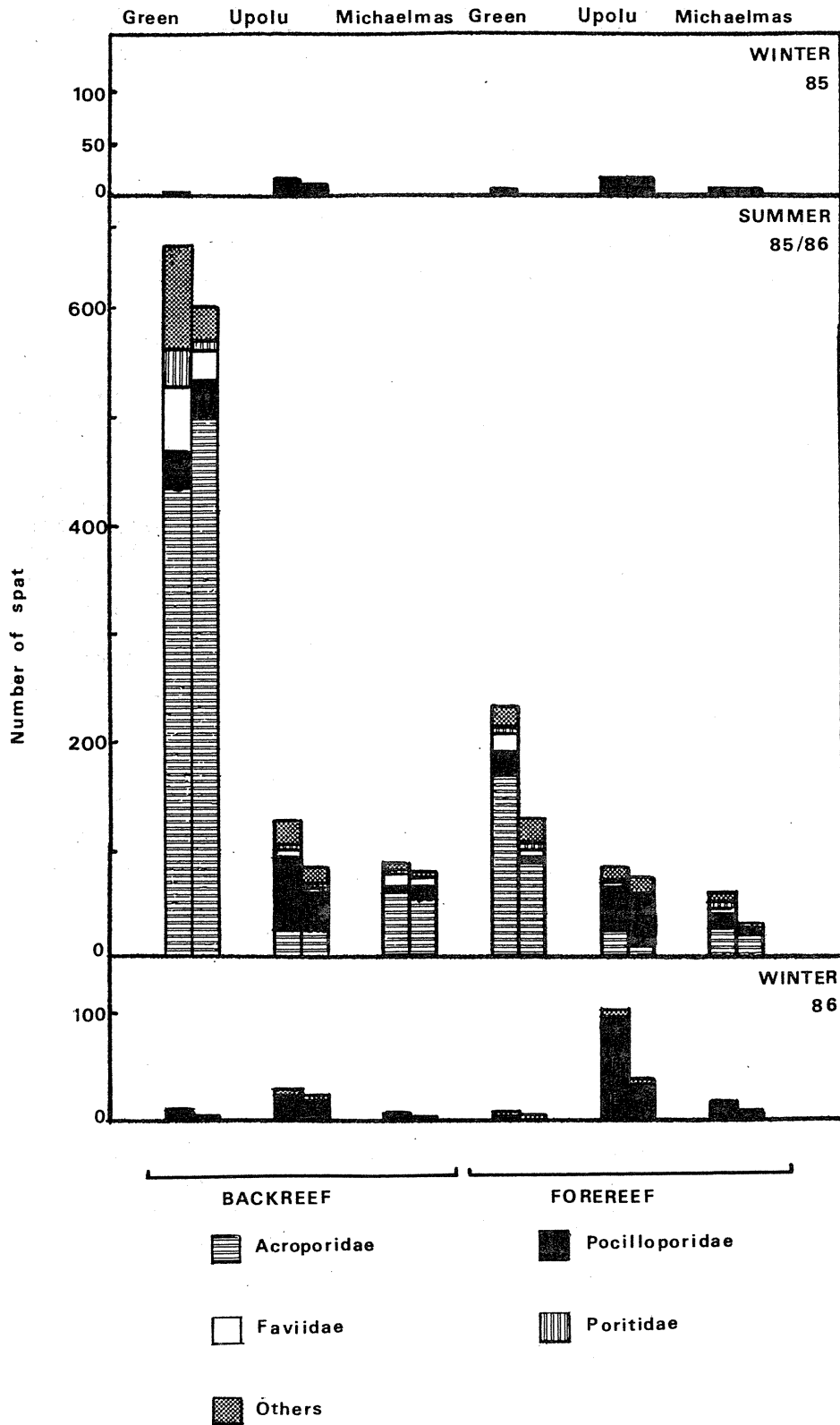
Spat numbers settling on plates over the summer period were analysed by an analysis of variance of log-transformed abundance data which indicated that there was significant variation in spat numbers both amongst the three reefs, and between forereef and backreef sites at each reef (table 1). For all reefs, there was higher recruitment at backreef than forereef sites, and a similar pattern was found at nearby Middle Cay Reef during the same period (Harriott and Fisk 1987b). Green Island had the greatest number of recruits, followed by Upolu Reef then Michaelmas Reef.

Table 2. Results of ANOVA for differences in log-transformed spat abundance with reef (Green, Upolu, Michaelmas) and reef zone (forereef, backreef).

Factor	d.f.	F-ratio	P(F)
Reef	2	39.83	3.4×10^{-4}
Reef Zone	1	20.97	3.8×10^{-3}
Interaction	2	3.33	0.11
Error	6		

Spat that settled in winter were almost exclusively of the family Pocilloporidae (figure 8). On the summer plates, Pocilloporidae were the most abundant taxa only on the plates from Upolu Reef. On Green and Michaelmas Reefs, spat from the family Acroporidae dominated on summer plates.

Figure 8. Summary of spat settlement on plates at Green, Upolu, and Michaelmas Reefs, for an 18-month period.



2.4 DISCUSSION

2.4.1 Recruitment patterns

Spat preference for the lower and 'gap' habitat for all reefs and sites is consistent with the results reported by Harriott and Fisk (1987b). Uppermost surfaces were least favoured, probably because of their propensity for collection of sediment and their susceptibility to grazing, especially by fish (Harriott 1985).

The concentration of spat recruitment in summer at most reefs has been reported previously (Harriott 1985; Wallace and Bull 1982; Wallace 1983, 1985a, 1985b, 1985c) and can be attributed to the phenomenon of the majority of coral species on the Great Barrier Reef spawning in a short period in late spring and early summer (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). This results in the availability of large numbers and a variety of planulae in the water during summer, while only some Pocilloporidae and a few planulating *Acropora* species are known to spawn consistently in winter (Harriott 1983b; Kojis 1986).

There is evidence that planulae of pocilloporid corals are able to settle rapidly and may in fact settle close to their reef of origin. Many pocilloporids brood larvae, which are sometimes asexually produced (Stoddart 1984), and in other cases are not (Ayre and Resing 1986). The larvae of *Pocillopora damicornis*, the best studied of the Pocilloporidae, are capable of settlement 12 to 24 hours after release (Harrigan 1972; Harriott 1983b; Richmond 1982), in contrast to the larvae of non-brooding species which require a minimum of about 4 days before settlement can occur (Babcock 1985).

The cover of pocilloporid corals at the forereef of Upolu Reef was approximately twice that found on Green or Michaelmas forereefs (unpublished line transect data), and pocilloporid spat were approximately twice as abundant at Upolu, compared with the other two reefs. This suggests that local recruitment may be a major factor in the reported high density of pocilloporid recruits at Upolu Reef.

The data on summer recruitment can be used to test the hypothesis that if reefs are predominantly self-seeding, then the depauperate nature of the adult coral population at Green Island would result in lower recruitment rates than for less-damaged reefs. The results contradict this prediction, and the fact that recruitment rates at all sites at Green Island were higher than at any of the sites on the other two reefs (which are less damaged, unpublished data) is strong evidence that the recruits came largely from outside Green Island. This result is consistent with the predictions from oceanographic data and known larval life periods given in Williams et al. (1984) that, over a larval period of approximately one week, larvae are likely to be moved long distances from the parent reef.

2.4.2 Dispersal pathways

A larval dispersal path that would yield the specific recruitment patterns on the three reefs reported here can be predicted from the oceanographic conditions during the period following the peak spawning period for corals on this part of the Great Barrier Reef. During early summer, the currents are predominantly wind-driven apart from the influence of the East Australian Current moving to the south-east (longshore) in periods of calm wind (Wolanski and Pickard 1985; Wolanski and Bennett 1983; Church 1983).

The mass spawning of corals in 1985 occurred on the evenings of 2 and 3 December (R. Babcock, pers. comm.). The most recent data available indicate that many corals are competent to settle as little as four days after spawning (Babcock 1985). Oliver and Willis (1987) report that mass spawning of corals can result in the formation of slicks containing very large densities of living coral larvae compared to the water around them.

Table 3. Wind speed and direction at Fitzroy Island for the 2 weeks following the time of the mass spawning of corals in 1985 (Bureau of Meteorology data). Speed is in knots.

Date	0600		0900		1500	
	Dirn.	Speed	Dirn.	Speed	Dirn.	Speed
2/12	NE	2	NNW	2	NNE	4
3/12	NNW	4	NW	4	NNW	6
4/12	ENE	8	ENE	5	NW	3
5/12	SE	12	SE	15	NNW	4
6/12	E	8	E	8	E	12
7/12	ESE	12	E	12	E	12
8/12	SE	11	SE	9	SE	10
9/12	SE	6	SSE	4	NE	13
10/12	WNW	1	SE	2	ESE	3
11/12	NW	5	NW	5	NW	8
12/12	NNW	3	NW	4	NW	8
13/12	NW	10	NW	6	E	3
14/12	W	3	NW	5	NE	5
15/12	NE	6	NNW	8	NNW	12

Wind records for Fitzroy Island, near Green Island, during the early part of December 1985 (table 3) show a period of northerly winds from 2 to 4 December, southerly or easterly winds from 5 to 7 December, and a period from 7 to 9 December when winds were from the south-east. These data suggest that larvae from corals which spawned on the evenings of 2 and 3 December would have drifted south-eastward for 2 or 3 days then moved to the north-west from 7 to 9 December. Under these circumstances, it is likely that larvae of corals that spawned on Michaelmas, Arlington or Upolu Reefs could have settled on Green Island Reef. There is a break in the reefs to the north of Michaelmas Reef that could account for the failure of a net southerly drift of larvae to recruit at Michaelmas Reef. The formation of

relatively small but dense patches of larvae within slicks (Oliver and Willis 1987) and the relatively large area of water compared to reef adds an element of chance to the probability of large numbers of larvae 'hitting' a reef.

Williams et al. (1984), Wolanski and Jupp (1984), and Wolanski et al. (1986) describe the pattern of eddies in the lee of reef systems, and discuss their possible role in retaining particles, particularly reproductive products close to the reef. Williams et al. (1984) conclude that the systems are unlikely to retain particles for more than a few days and would therefore have a limited role in determining recruitment patterns. It is possible, however, that eddies play a major role in retaining reproductive products briefly as they move past a reef, once they have been in the water mass for several days and are competent to settle. In the circumstances described here, an eddy formed by the current from the south 4 to 7 days post-spawning might have trapped larvae in the leeward reefs long enough to account for the higher numbers of recruits in the backreefs of all the reefs studied.

If the factors discussed here have had a major role in determining recruitment patterns, we should be able to predict recruitment patterns in this reef set from oceanographic conditions during the summer spawnings. For example, the relative abundance of spat between reefs should be different if the strength and direction of winds in the week following spawning varies greatly from that reported for 1985. An increased number of widely spaced settlement plate sets have been deployed to test this hypothesis, and we plan to study this reef set for several years to document long term trends in recruitment patterns.

There are several management implications for a finding of wide dispersal of larval products. Firstly, there have been predictions that recovery times following crown of thorns starfish predation on reefs as badly damaged as Green Island will be slow because of a lack of larval recruits when the adult corals on the same reef are mostly dead (Endean 1976; Pearson 1981). This would clearly not be the case, and the predictions of plentiful larval recruits presented here are born out by the observation of very large numbers of small corals in the field at Green Island 5 years after the starfish damage (sections 1 and 3).

Secondly, if the pattern of heavier than average larval recruitment at Green Island holds true for many years, perhaps because of the conditions prevalent during summer, then we could question whether a high density recruitment of A. planci larvae might not also occur and be a factor in the propensity for Green Island to suffer outbreaks of the starfish.

Finally, evidence of this type adds to the body of literature on the interconnectedness of reef systems indicating that individual reefs must be managed as part of a larger system. Damage to reefs 'upstream' may impact on 'downstream' reefs, particularly if one of the reefs is the usual source of recruits for the other.

3 POPULATION DYNAMICS OF JUVENILE CORALS AT GREEN ISLAND

3.1 INTRODUCTION

When the majority of the hard corals on the reef at Green Island were killed by Acanthaster planci, the coral community was freed from any competition for space with other corals, and patches of dead coral substrate were created which were potential recruitment sites for new corals.

The early phase of the recovery process for corals is little studied because the colonies are not clearly visible for several years (Wallace 1983). The relationship between initial settlement onto the bare surface, subsequent recruitment, and the abundance of larger colonies is significant in our understanding of the dynamics of the recovering reef community. Here, we investigate the juvenile coral populations on two types of dead coral surface approximately five years post-A. planci, and subsequent recruitment to those same sites.

Preliminary results for the first three samples that cover a 10-month period are presented here. The study is on-going, and the results of the longer term study will be presented separately.

3.2 METHODS

Two easily recognised and readily available substrates were chosen for our permanent quadrats. These were dead standing plate Acropora (A. hyacinthus plates), and smoother clean limestone substrates (e.g. dead Porites colonies). We sampled five of each substrate at each of two depths (3m and 6m) in both a forereef and a backreef site. The settlement plates referred to in section 2 were located in these same areas.

At the time of the initial mapping in November 1985, coral cover was very low in the sample quadrats, although some juvenile corals were present in all quadrats. We used a 1m x 1m quadrat subdivided by string into 25 equal smaller squares to aid accurate relocation of individual colonies. The quadrat location was defined by two steel stakes which were usually marked in two corners of a quadrat. Compass bearings and hand drawn maps aided relocation of each set of quadrats.

The dead Acropora plates varied in size (mean=0.57m², range=0.23 to 1.0m²) and outlines of the plate shape were recorded on the map of the quadrat. The area of the plate was measured from the maps using a planimeter. The solid substrates were a constant 1m². Recruitment and abundance figures were then calculated per m² for the plates.

Juveniles were defined in this study as those with a mean diameter less than or equal to 20cm. Colonies were identified to generic level. At the first census, most colonies had an encrusting morphology with height less than 1cm, so colonies were measured along the longest horizontal axis and along the horizontal axis

perpendicular to this. At the time of the second census, many colonies had changed in morphology to the adult type colony shape and a height measurement was also taken.

Colonies were mapped and measured in November 1985, the quadrats were censused for presence/absence of colonies in May 1986, and the colonies were re-mapped and measured in September 1986.

Two of the marked dead Acropora plates on the forereef disappeared between the first two census periods, almost certainly due to the effects of Cyclone Winifred (Harriott and Fisk 1987a). There were therefore reduced samples for the study of recruitment during the year and a subsample of four of the five quadrats per site was used in the analyses. Mortality and recruitment rates were calculated in two ways: by including the plates lost during the cyclone and by excluding them from an analysis. Where a reduced sample set was used, the four quadrats were chosen randomly for the recruitment analyses, and the quadrats with the four highest initial colony numbers used for the mortality analyses. Each colony was given a unique number for tracing through time and all data were included in a database management program.

3.3 RESULTS

3.3.1 Fission and fusion rates

Over the study period 13 colonies were added to the total number of colonies under examination via the splitting or fission of colonies present at the commencement of the study. In addition, 8 colonies merged or fused to other colonies, thereby reducing the number of colonies under examination. Colonies which underwent fission or fusion were not included in estimates of recruitment or mortality, respectively.

3.3.2 Abundance of juveniles

Corals from the families Acroporidae and Faviidae were the most abundant juveniles for all substrates, depths, and sites pooled (table 4).

A 3-way ANOVA of juvenile abundance per m^2 showed a significant effect ($p < 0.01$) of site (forereef versus backreef) on juvenile density, and a significant interaction between the factors depth and substrate type (table 5).

Juvenile density was higher in the backreef than the forereef. The interaction between the factors depth and substrate is illustrated in figure 9. At the shallow sites, densities were similar on plates and solid substrates, while at 6m, juveniles were far more abundant on the solid substrates than on the dead plates.

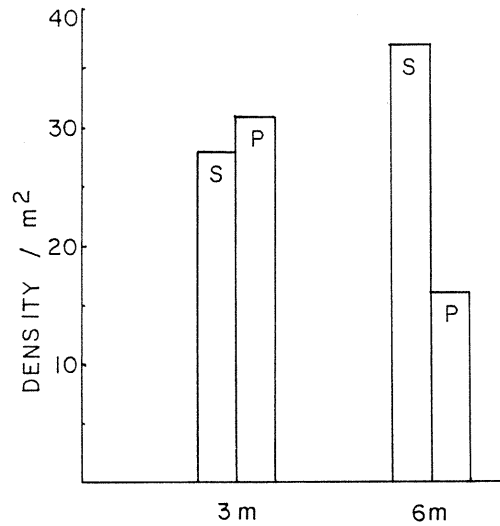
Table 4. The relative abundance of the major families and genera of juveniles pooled for all substrates, depths, and sites. Only those genera with 20 or more records are listed here (=86% of all records).

Families	No.	% of Records	Genera	No.	% of Records
Acroporidae	552	43	<u>Acropora</u>	438	35
Faviidae	366	28	<u>Porites</u>	195	15
Poritidae	200	16	<u>Favia</u>	142	11
Pocilloporidae	56	4	<u>Montipora</u>	109	9
Mussidae	52	4	<u>Leptastrea</u>	74	6
			<u>Favites</u>	59	5
Total	1226	95	<u>Stylophora</u>	38	3
			<u>Cyphastrea</u>	25	2
			<u>Lobophyllia</u>	22	2
			Total	1102	86

Table 5. Results of a 3-way ANOVA of initial density of juveniles per m² in November 1985, with respect to the factors: substrate type (dead plates and solid substrates), depth (3m and 6m), and site (forereef and backreef). *=significant.

Factors	d.f.	Mean Squares	F-test Ratio	P(F)
Site	1	1974.02	11.04	0.002 *
Depth	1	207.03	1.16	0.29
Substrate	1	198.01	1.11	0.30
Site x Depth	1	148.24	0.83	0.37
Site x Substrate	1	70.24	0.39	0.54
Depth x Substrate	1	1600.23	8.95	0.005 *
Site x Depth x Substrate	1	87.01	0.49	0.49
Error	32	5722.00		

Figure 9. The initial abundances of juvenile corals at Green Island Reef, expressed as an interaction of the factors depth and substrate type. S=solid substrates, P=dead Acropora plates.



3.3.3 Recruitment 1985-86

Table 6 shows the results of a 3-way ANOVA with 4 replicates for each of the two substrate types, two depths and two sites. Only the factor 'site' had a significant effect on recruitment, with higher recruitment on the backreef than the forereef site.

Table 6. Results of a 3-way ANOVA of recruitment rates of corals with respect to the factors: substrate type (dead standing plates, solid substrates), depth (3m and 6m) and site (forereef, backreef).
*=significant.

Factors	d.f.	Mean Square	F-test Ratio	P(F)
Site	1	318.8	34.1	5×10^{-6} *
Depth	1	5.3	0.6	0.46
Substrate	1	16.5	1.8	0.20
Site x Depth	1	9.0	1.0	0.34
Site x Substrate	1	22.0	2.4	0.13
Depth x Substrate	1	0.8	0.1	0.78
Site x Depth x Substrate	1	19.5	2.1	0.16
Error	24	9.3		

Recruitment rates of the families are given in table 7. The recruitment rates of the different families closely reflect their previous abundance in the juvenile coral community, with acroporids being the fastest recruiters, as well as the most abundant juvenile corals.

Table 7. Abundance of juvenile coral recruits by family.

Family	% of initial abundance	% of subsequent recruits	% on smooth limestone	% on dead plates
Acroporidae	43	42	41	45
Faviidae	28	30	26	40
Poritidae	16	12	14	7
Mussidae	4	7	9	3
Pocilloporidae	4	2	-	-

3.3.4 Mortality

Table 8 gives the results of 3-way ANOVAs on the effects of depth, site and substrate type on mortality rates. When mortality due to loss of the whole substrate (i.e. dead plate) was excluded, there was no significant effect for any factor (table 8A). However, when mortality due to plate loss was included (using all five quadrats in each data set), there was a significant difference in mortality due to substrate type (table 8B).

Table 8. Results of a 3-way ANOVA of mortality rates of juvenile corals with respect to the factors: substrate type (dead plates and solid substrates), depth (3m and 6m) and site (forereef and backreef). Percentage data was arcsin transformed. * = significant.

A. Mortality due to plate loss not included.

Factors	d.f.	Mean Sq.	F-test Ratio	P(F)
Site	1	96.6	0.35	0.56
Depth	1	3.3	0.01	0.91
Substrate	1	780.2	2.83	0.11
Site x Depth	1	67.2	0.24	0.63
Site x Substrate	1	41.8	0.15	0.70
Site x Depth x Substrate	1	888.3	3.26	0.08
Error	24	275.4		

B. Mortality due to plate loss included.

Site	1	12.4	0.03	0.86
Depth	1	2.6	0.007	0.93
Substrate	1	2284.7	5.85	0.02*
Site x Depth	1	97.0	0.25	0.62
Site x Substrate	1	523.4	1.34	0.26
Site x Depth x Substrate	1	867.7	2.22	0.15
Error	32	390.8		

The difference between the data sets indicates that there is not higher mortality of juveniles of dead plates, but that plates are more susceptible to catastrophic damage such as that caused by Cyclone Winifred.

There were no clear differences in the mortality rates of the major families i.e. Acroporidae (26%), Faviidae (25%) and Poritidae (26%).

3.3.5 Net changes

Net changes in the number of colonies for each of the factors (sites, depths, substrates) for the 10-month period: November 1985 to September 1986, are summarised in table 9.

Solid substrates showed a net increase in all sites and depths, while dead Acropora plates showed a net decline in numbers in shallow sites and a net increase in deeper sites, for both forereef and backreef sites.

Table 9. Net changes in number of colonies for the 10-month period: November 1985 - September 1986. Mortality due to plate loss included. P=plates, S=solid.

Sites: Depths: Substrates:	Forereef				Backreef				Total Fore- and Backreef
	3m	6m	3m	6m	3m	6m	3m	6m	
	P	S	P	S	P	S	P	S	
Initial Nos:	131	106	26	142	75	185	67	230	962
+ Recruits:	15	25	11	26	23	68	21	65	254
- No. Dead:	42	18	8	21	41	30	14	63	237
=	104	113	29	147	57	223	74	232	979
Net change =	-27	+7	+3	+5	-18	+38	+7	+2	+17

3.3.6 Growth rates

The preliminary results for growth rates of juvenile corals showed no apparent pattern with respect to depth or substrate type. However, there appears to be a clear difference between genera in growth rate, and corals of the same genus almost invariably grew faster in the forereef than the backreef (table 10). Further analysis of growth patterns will await the continuation of this section of the project over a longer time period. A significant number of corals of all types exhibited no growth or negative growth over the 10-month period.

Table 10. The mean increase in diameter (cm) over 10 months, of the major juvenile coral genera at the forereef and backreef sites.

Genus	Forereef	Backreef	All corals
<u>Acropora</u>	2.8	1.4	2.11
n=	122	110	232
<u>Montipora</u>	2.3	1.1	1.68
n=	30	33	63
<u>Porites</u>	0.8	0.3	0.41
n=	30	77	107
<u>Favia</u>	0.8	0.5	0.62
n=	23	46	69
<u>Favites</u>	0.8	0.1	0.34
n=	14	20	34
<u>Leptastrea</u>	0.7	0.3	0.53
n=	16	14	30
<u>Cyphastrea</u>	-0.4	0.4	0.01
n=	7	7	14
<u>Goniastrea</u>	1.1	0.4	0.63
n=	4	8	12
<u>Platygyra</u>	1.8	0.7	1.50
n=	7	3	10
<u>Stylophora</u>	1.2	1.2	1.2
n=	3	18	21

3.4 DISCUSSION

From this study, we have shown that juvenile corals were more abundant and recruited more rapidly on a backreef site compared to a forereef site. This result is consistent with results from our study of coral spat recruitment, where higher recruitment rates were found in the backreef than the forereef (Harriott and Fisk 1987b, sec. 2.3).

Juvenile corals of the families Acroporidae, Faviidae, and Poritidae recruited to Green Island Reef during the study period in the same relative abundance as the established juveniles, indicating that a consistent recruitment pattern over the last few years would alone have given rise to the current taxonomic status of the coral population, without the need to invoke differential post-recruitment mortality. In fact, the combination of recruitment and mortality as expressed in the net turnover measurements acted to maintain the observed structure of the juvenile community. Wallace (1985c) also concluded that larval recruitment largely determined species composition at her study reef where recovery was in progress after heavy A. planci predation.

In addition, juvenile corals were recorded in approximately the same relative taxonomic composition, at the family level, as the coral spat on settlement plates (section 2). This supports the hypothesis that a pool of recruits of similar taxonomic composition has been added to Green Island Reef for several spawning seasons at least.

Juvenile pocilloporid corals have been relatively scarce at the study sites, both as established juveniles and juvenile recruits. The family Pocilloporidae is the only abundant winter spat at Green Island, so perhaps post-settlement mortality may therefore be occurring which is more or less specific to the pocilloporids.

Initial results indicate that juvenile coral mortality rates did not differ significantly between depths or sites examined here, nor did they differ greatly between the dominant families. Destruction of the dead plates was the only factor that had a large impact on the juvenile mortality.

Growth rate, measured as change in mean diameter, was consistently greater in the forereef site than the backreef site. Acropora and Montipora increased in diameter at three to eight times the rate of the faviid and poritid corals measured. Stylophora grew at approximately half the rate of Acropora and Montipora.

The net increase in colony numbers in three of the four study sites and depth combinations indicates that Green Island Reef is in an early successional stage where the number of colonies increases over a number of years before space becomes limited and competition eventually reduces the number of colonies (Pearson 1981). Other studies on communities at later successional stages (Harriott 1983a; Hughes and Jackson 1985) have shown relatively constant colony numbers and constant diversity despite high turnover rates. High turnover of colonies was observed in our study (mortality rates: 13%-52% per year), but net increases in colony numbers also occurred.

The process which appears to have the major influence on the early successional stages in the development of the coral community appears to be recruitment of the broadcast spawning species. Acropora spp. are the most dominant and successful group of recruits, with greatest abundances, recruitment rates and growth rates. The recovering coral community at Green Island is Acropora dominated, as has been described for other post-A. planci reefs (Pearson 1981, sec.1).

For corals such as Pocillopora damicornis, successful recruitment as juveniles was limited. However as it was also one of the corals most resistant to predation by A. planci, and relatively large remnant patches have survived at Green Island (section 1) it is unlikely to suffer local extinction at Green Island. On the other hand, if a preferred coral prey species was dependent for dispersal on a brooding reproductive cycle (where propagules tend to settle close to parents), or vegetative reproduction by fragmentation (Wallace 1985c), it is conceivable that the species could be entirely removed from a reef system for long periods by repeated intensive A. planci outbreaks.

Incomplete predation by A. planci of colonies of important reef-building corals can result in substantial remnant populations (Done, 1985). These remnants may provide resistance against species composition change on a whole reef scale, and result in the persistence of many genotypes. The contribution of remnants to juvenile coral community composition was not assessed at Green Island because so many years had passed since the last A. planci outbreak.

The recruitment and juvenile studies from this project suggest that the contribution of remnants is not significant in comparison to the contribution of larval recruitment in the recovery and re-establishment of the coral community.

The juvenile coral population mapped in this study will be recensused in future years. These data should allow analysis of small scale changes in the community structure as the colonies become larger, and factors such as interspecific competition and overgrowth will have an increasing role to play. The long term stability or otherwise of the juvenile recruitment patterns reported here can then be tested.

4 **ACKNOWLEDGMENTS**

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5 **APPENDIX Transect data for Green Island (1985)**

Site	Repli- cate	Depth (m)	Hard Coral %	Soft Coral %	No. Cols	Mean Inter- val	Rubble	Sand	<u>Helio- pora</u>
<hr/>									
1	a	0.5	1.6	25.0	5	9.4	3.7	45.8	0.0
	b	0.5	7.0	9.5	23	9.2	5.7	25.8	0.0
	c	0.5	7.9	21.1	21	11.3	12.0	27.8	0.0
	d	0.5	5.8	15.7	11	16.0	17.3	25.1	0.0
2	a	3.0	9.0	10.2	7	38.6	1.1	0.0	0.0
	b	2.0	14.0	3.3	9	46.5	18.9	1.2	0.0
	c	2.0	0.8	0.3	3	8.7	28.9	0.0	0.0
	d	2.0	5.6	4.2	5	33.4	35.0	0.0	0.0
3	a	3.0	11.8	8.1	35	10.1	23.3	5.0	0.0
	b	3.0	4.7	6.3	16	8.9	30.7	3.7	0.0
	c	3.0	3.0	1.8	21	4.3	29.9	3.5	0.0
	d	3.0	2.5	3.3	20	3.7	36.1	3.6	0.0
4	a	6.0	4.6	1.9	37	3.7	3.0	0.0	0.0
	b	6.0	4.1	0.0	20	6.1	14.1	11.3	0.0
	c	6.0	2.1	0.7	19	3.3	11.4	4.9	0.0
	d	6.0	5.2	0.5	31	5.0	10.7	2.7	0.0
5	a	2.0	2.6	0.2	19	4.1	64.0	12.0	0.0
	b	2.0	2.7	0.9	16	5.1	83.2	1.8	0.0
	c	2.0	2.7	3.6	11	7.5	47.3	14.8	0.0
	d	2.0	1.7	9.7	13	3.8	53.9	5.3	0.0
6	a	5.0	5.5	10.0	23	7.2	15.5	36.5	0.0
	b	5.0	5.5	6.1	24	6.8	13.3	31.5	0.0
	c	5.0	3.6	5.9	22	5.0	20.1	35.2	0.0
	d	5.0	7.7	5.4	26	8.9	9.6	39.1	0.0
7	a	2.0	14.0	18.9	22	19.0	7.4	12.7	0.0
	b	2.0	14.0	18.9	23	14.7	6.1	13.9	0.0
	c	2.0	16.5	23.7	16	31.0	11.6	35.7	0.0
	d	2.0	3.5	7.2	17	6.2	44.8	20.5	0.0

Site	Repli- cate	Depth (m)	Hard Coral %	Soft Coral %	No. Cols	Mean Inter- val	Rubble	Sand	<u>Helio- pora</u>
8	a	2.0	23.4	6.0	39	18.0	2.1	0.0	0.0
	b	2.0	12.5	3.4	29	13.0	35.2	0.0	0.4
	c	2.0	20.2	0.0	46	13.2	7.7	0.0	0.0
	d	2.0	8.3	2.3	23	10.9	14.7	0.0	0.0
9	a	6.0	14.1	8.7	28	15.1	15.9	7.4	0.0
	b	6.0	5.3	16.4	15	10.7	38.5	0.0	0.3
	c	6.0	4.9	9.5	16	9.1	8.9	22.3	0.0
	d	6.0	19.2	20.2	22	26.2	10.5	16.6	0.0
10	a	5.0	6.7	26.0	21	9.5	6.8	0.0	0.0
	b	5.0	9.4	23.4	28	10.1	0.5	0.0	0.0
	c	5.0	4.4	22.7	14	9.4	24.0	0.0	0.0
	d	5.0	6.6	10.4	17	11.6	34.6	0.0	0.0
11	a	3.0	8.8	18.2	11	23.9	52.3	0.3	0.0
	b	3.0	3.9	20.2	8	19.3	19.1	0.0	0.0
	c	3.0	2.0	30.3	5	11.8	7.7	0.0	0.0
	d	3.0	6.8	32.1	18	11.4	26.4	0.0	0.0
12	a	1.0	6.7	12.0	12	16.8	48.8	0.0	4.2
	b	1.0	6.4	26.5	16	11.9	43.5	1.5	2.0
	c	1.0	9.5	20.5	27	10.5	41.5	0.0	0.9
	d	1.0	14.2	15.1	40	10.7	33.4	0.0	1.8
13	a	5.0	1.9	20.3	7	8.3	6.8	9.5	0.0
	b	5.0	2.3	9.5	8	8.8	10.7	38.7	0.0
	c	5.0	3.4	13.6	12	8.4	12.8	29.2	0.0
	d	5.0	2.7	18.0	13	6.2	18.3	10.0	0.0
14	a	0.0	1.3	0.0	9	4.4	31.4	0.0	0.0
	b	0.0	2.0	0.0	10	6.1	2.1	0.0	0.0
	c	0.0	2.0	0.0	7	8.6	0.0	0.0	0.0
	d	0.0	1.8	0.0	6	9.2	0.0	0.0	0.0
15	a	0.0	4.1	0.0	19	6.5	62.5	22.1	0.0
	b	0.0	20.5	0.0	35	17.6	24.0	20.3	0.0
	c	0.0	52.3	0.0	44	35.6	3.5	12.6	0.0
	d	0.0	37.0	0.0	32	34.7	40.6	8.5	0.0
16	a	0.0	28.2	0.0	48	17.6	0.0	51.9	0.0
	b	0.0	27.7	0.0	39	21.3	0.0	63.4	0.0
	c	0.0	11.6	0.0	18	19.3	1.4	64.5	0.0
	d	0.0	13.7	0.0	22	18.7	6.1	61.8	0.0
17	a	2.0	5.3	21.9	9	17.6	20.2	7.3	0.0
	b	2.0	17.6	30.1	26	20.3	7.4	0.3	0.0
	c	2.0	6.5	10.8	15	12.9	19.1	9.3	0.0
	d	2.0	4.8	15.0	10	14.4	23.7	9.0	0.0
18	a	0.0	3.0	49.5	16	5.7	2.3	2.7	0.0
	b	0.0	2.9	24.3	19	4.5	8.0	16.0	0.0
	c	0.0	2.3	17.8	14	4.9	44.2	3.3	0.0
	d	0.0	2.8	8.0	6	13.8	55.3	11.0	0.0
19	a	2.0	5.4	25.9	13	12.5	29.0	0.0	13.8
	b	2.0	2.5	36.9	7	10.6	32.4	0.0	6.0
	c	2.0	2.7	23.5	10	8.1	41.0	0.0	5.5
	d	2.0	3.9	54.5	7	16.7	9.5	0.0	13.7
20	a	6.0	0.8	29.6	2	12.0	30.3	19.2	0.0
	b	6.0	1.9	56.4	6	9.3	8.6	0.3	6.2
	c	6.0	0.6	36.4	3	6.0	18.0	9.6	0.0
	d	6.0	0.7	64.3	2	11.0	4.7	1.5	13.5

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