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The Role of Recruitment in Coral Community Regeneration

Thesis submitted by

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for the degree of Doctor of Philosophy in
the Department of Marine Biology at
James Cook University of North Queensland

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Abstract

Green Island reef has been subjected to at least two severe outbreaks of crown of thorns starfish (*Acanthaster planci*) in the last thirty years. The most recent outbreak occurred in the early 1980's. This study commenced in 1985 with the aim of investigating coral recovery following this outbreak, with an emphasis on the recruitment process. The study of Green Island coral communities produced conclusions on coral regeneration based on approximately nine years data on recruitment and of other influential events. These events included two cyclone impacts, minor outbreaks of *Drupella* spp, and the effects of small increases in *A.planci* numbers.

The main characteristic of the recovery process was one of rapid and significant increase in coral (ranging from 15% to 50% cover) between the fourth to the ninth year post-*A.planci*. The observed rapid increase was due to the dominance of fast growing *Acropora* spp. Diversity at Green Island in 1990 was moderate with approximately 25-30% (or 80-100 species) of the total species recorded from the Great Barrier Reef.

Recruitment was investigated during two phases: an early recruitment phase where microscopic (<2 mm diameter) recruits were studied on artificial settlement substratum; and a visible recruitment phase, where annual recruits (>2 mm diameter) were followed on natural substrata on the reef slope. Spatial and temporal variability in both annual early and visible recruitment was evident from this study. However, longer term patterns were detected as follows: (1) three reefs separated by several kilometers showed consistently different early recruit abundance and composition of major families; (2) specific zones on these different reefs showed consistent relative abundance of early recruits; (3) at a smaller spatial scale, specific positions within an individual reef had comparatively different early recruit densities and composition to other positions on the same reef; (4) relatively different densities of early recruits occurred along a depth gradient, which on Green Island ranged from 3 m to 6 m depth. Visible recruit abundance and composition generally reflected early recruitment variations at several spatial and temporal scales, with the exception of massive species. Massive species were very abundant in the visible recruitment community but not in the early recruitment pool. Either the settlement plate technique was under sampling this component, or the relative abundance estimates of the early recruit taxa reflect substantially higher survival rates for the massive corals.

This study covered a period where a change in successional phases took place. An inhibition model via overtopping of arborescent and plate *Acropora* spp could explain the observed pattern. A significant decrease in visible recruitment occurred during a relatively brief time when there was a rapid expansion in overtopping colony morphologies, despite the continuing high abundance in early recruits at the same sites. Relatively minor disturbance events also occurred during the study (especially in the latter period) which created a more complex and less predictable mosaic of reef patches with different conditions and therefore at different successional stages.

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Statement of Sources

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references given.

D A Fisk

29 April 1997

Chapter 1. Introduction

An understanding of the characteristics of natural recovery and replenishment of coral reef biota is essential to the long term management and viability of the Great Barrier Reef (GBR). In particular, this knowledge can be used to predict the response of reefs to natural perturbations. Consequently, our understanding of the possible impact of anthropogenic perturbations is improved. Disturbances to coral reefs may result in the mortality of sessile reef organisms which in turn may or may not result in changes to reef structure and topography. The degree of disturbance and subsequent ability of a reef to recover is usually associated with physical (damage and/or dislodgment, Woodley *et al* 1981, Dollar 1982, Coles 1984) or non physical disturbances (Pearson 1981, Porter *et al* 1981), respectively. Disturbances not resulting in structural changes in the short to moderate term (5-10 years) can include disease and predation on coral tissue such as is caused by crown of thorns starfish (*Acanthaster planci*). Recovery of reefs from disturbances can be via larval colonisation and growth of remnant fragments.

Spatial and temporal data on the contribution of recruitment in the natural regeneration and maintenance of reef communities are required to understand the role of disturbance. Spatial studies of recruitment require intensive measurement of a number of sites over a discrete period of time (eg, Sammarco & Andrews 1988), whereas temporal aspects of recruitment require repeat measurements of representative habitats over a five to ten year time period (Doherty and Williams 1988). This information can be attained from three sources: observations of static and dynamic patterns of recruitment, manipulative experiments, and natural experiments.

Reef fish and scleractinian corals have been the major foci of studies on the recruitment process within the GBR (see reviews by Doherty and Williams 1988 (fish), and Harrison and Wallace 1990 (corals)). This substantial collective body of work has revealed a number of paradigms relating to the supply of larval recruits to a reef and the influence of this process in community structure and in the local demography of species (Coe 1985). In particular fish recruitment has been associated with variations at all the spatial and temporal scales studied to date (Doherty and Williams 1988). The predictability of fish recruitment in a reef system improves in studies with larger spatial scales. Conversely, predictability decreases with increasing in the temporal scales (Doherty and Williams 1988). Furthermore, consistent variation in fish recruitment at small scales has apparently been due to habitat selection by larvae and at larger scales to environmental gradients (Doherty and Williams 1988). Significant spatial and temporal variation in recruitment has been documented for corals where variation among sites has been documented. Temporal variations, however, confound many of these spatial patterns (Baggett & Bright 1985, Wallace 1985a).

It is accepted that replenishment via larval recruitment is pivotal to the recovery process, though processes affecting the post recruitment period will also determine the rate of recovery from a perturbation, both within and among reefs, as well as between habitats and at smaller scales (Keough & Downes 1982). The spatial and temporal scales over which similarities and differences in recruitment are expressed (and the scales of research studies) need to be defined and kept in mind whenever generalisations are made on this process (Hatcher et al 1987). There are many studies on marine benthic organisms where there is strong evidence of spatial and temporal variability in the arrival of new propagules (eg, Dayton 1984, Keough 1984, Underwood and Denley 1984, Connell 1985, Gaines & Roughgarden 1985, Gaines Brown and Roughgarden 1985).

The role of hydrodynamics in the dispersal and transport of larvae is one of the more influential parameters to consider when addressing recruitment processes (Butman 1987, Johnson & Preece 1988). In general, movement of water within the GBR is under the influence of the slow southerly moving Eastern Australian Current and east-west tidal movements, both of which are heavily altered when wind generated currents are present (Wolanski & Pickard 1985, Black et al 1995). Hydrodynamic features which are closely associated with larval transport and distribution patterns include water mass fronts, gyres and eddies, and areas with differential water motion speeds (or larval retention zones) (Sammarco & Andrews 1988, Willis and Oliver 1990; Kingsford Wolanski & Choat 1991). These processes are predicted to operate on recruitment patterns for multi species pools of larvae. However, using hydrodynamics to predict recruitment patterns is not always possible for reef fish (Doherty and Williams 1988); corals (Wallace 1985b); or some other marine invertebrates (Hurlbut 1991), but is probably related to behavioral differences between species, density dependent mortality, and to post settlement differences in species specific responses to localised factors such as substrate type and predation (Keough & Downes 1982).

Recovery of coral communities after severe crown-of-thorns starfish infestations has been studied in a number of Pacific Ocean locations (Great Barrier Reef: Endean and Stablum 1973; Endean 1976; Pearson 1981; Done 1985; Endean and Cameron 1985; Done *et al*

1988; Guam: Colgan 1982; and, Japan: Nishihiri and Yamazato 1974). After *A.planci* outbreaks have reduced hard coral cover severely, benthic organisms other than corals (e.g., macroalgae, soft corals) can sometimes dominate areas previously occupied by corals, but it is more common for the hard coral community to gradually return. In almost all studies of recovery following severe *A.planci* outbreaks, the early successional stages of the coral community were dominated by faster growing species of hard coral, and in particular, species of *Acropora* (Pearson 1981). The contribution to the recovering community of coral remnants which survive *A.planci* predation is dependent on the degree of damage to the colonies and the types of species surviving the outbreak (Done *et al* 1988). With the exception of areas where colonies show high partial mortalities (Endean *et al* 1989) and where intact colonies of species less preferred as prey by *A.planci* remain, the remnants generally are insignificant contributors to the post-outbreak communities. Species less preferred by *A.planci* typically remaining after severe outbreaks include many massive growth form species and species which are protected by episymbionts (Glynn 1983), or colonies within patches of some territorial fish (Glynn and Colgan 1988). The rate and type of recovery from *A.planci* outbreaks is therefore largely dependent on the dynamics of larval recruitment to the impoverished portions of affected reefs.

The nature of recovery of coral communities that occurs following *A.planci* infestation has been the subject of several investigations in recent years. In particular, the dynamics of the massive species have been stressed with reference to long term reef structure, and the demography of massive corals has been used to estimate the frequency of past starfish outbreaks at reefs with unknown outbreak histories (Endean and Cameron 1985, Done 1985 1987 1988; Done *et al* 1988; Endean *et al* 1989; Cameron *et al* 1991). Concern has been raised by the above authors as to the consequences of high mortality of these important reef building components of the coral community. Done (1987 1988) modeled the expected recovery times for *Porites* spp. under various community parameters and concluded that for most populations of *Porites* spp. the minimum recovery times were in excess of fifty years. Cameron and Endean (1985) estimated that several centuries may be required on some reefs to restore massive coral populations to their pre-*A. planci* structure. They stated that the scope of such major impacts support the possibility of such starfish outbreaks being outside the range of perturbations naturally occurring on reefs.

The emphasis of the above authors on the massive corals is pivotal to the understanding of the a reef's history of crown-of-thorns outbreaks as the population structure of massives is a good indicator of the "naturalness" or otherwise, of severe outbreaks. The apparent rapid recovery of *A.planci*-affected reefs using percent cover as the main index of recovery, without consideration to the structure of the recovering community (eg, Colgan 1981; Pearson 1981), does not give a true indication of the initial impact of the starfish nor of the recovery potential.

The extent of live coral cover at Green Island reef (lat.16^{0}46'S, long.145^{0}19'E) has been severely affected twice since early 1960 (Fisk *et al* 1988). There are few data available on the structure of coral communities on Green Island reef prior to 1960 and during the interval between the two starfish outbreaks. This study has taken advantage of a natural experimental situation where coral cover was severely reduced to less than five percent over a major proportion of a whole reef (pers.obs.) and the medium term recovery process was then investigated with an emphasis on recruitment patterns. During both previously recorded outbreaks, the starfish moved in two distinct waves from the eastern end of the reef around to the north-western end via both northern and southern slope edges (Fisk *et al* 1988). Estimates of the number of starfish occupying the reef during this period ran into the millions (Endean and Stablum 1975). Data on recovery of the hard coral community has been collected by the author on an annual basis from 1985 to 1990 (inclusive), that is, a period five to ten years after the starfish outbreak had eaten the majority of corals on this reef. The aim of this long-term study was to monitor the recovery of coral communities and to generate specific questions and hypotheses regarding the regeneration of severely devastated reefs.

After a few years of this monitoring program, it became obvious that characteristics of coral recruitment were pivotal to the understanding of the recovery process. Therefore, additional experiments were introduced and sampling designs modified to build on the existing database so as to answer specific questions relating to recruitment. One aspect of recruitment that became a major focus was the contrast between rates and patterns of recruitment of massive and faster growing species. Details on the nature and importance of recruitment patterns to the recovery process at Green Island will be described in terms of these two major structural groups using the following representatives occurring at Green Island: the faster growing groups (*Acropora* spp., Pocilloporidae, and encrusting forms) and the massive species (from the families Mussidae, Poritidae, and Faviidae).

In this study, recruitment refers to the appearance of organisms following a period of time after settlement when attachment and metamorphosis has occurred and growth has begun (Keough and Downes 1982). The meaning and use of larval settlement and recruitment terms has been the subject of debate in the literature. Keough and Downes (1982) thought that the distinction was important following their evaluation of most of the relevant literature at the time which was dominated by studies of rocky shore intertidal communities or invertebrate fouling communities. Connell (1985) suggested that from a theoretical perspective, recruitment could be used as an estimator of settlement rates as long as mortality of settlers is density independent. Holm (1990) contended that this requirement was too strict and was not important when settlement density was low. In fact, if mortality is density-independent over the maximum range of settlement densities recorded in any particular study, then within the aims of that study, methods which identify early recruitment can be used as an index of settlement. This argument is adopted here where the beginning of coral settlement is defined as that point where the laying down of a coral skeleton has commenced. Even if death occurs at this point, and providing erosion and overgrowth from other organisms is not severe, the remaining coral skeleton can be detected as a newly settled coral or early recruit.

For this project I studied two coral recruitment phases and refer to them as: (i) "early recruitment", where recruits are usually not visible to the unaided eye, being approximately >0.2 mm to <2 mm diameter in size; and (ii), "visible recruitment" where corals can be seen on natural substrata underwater and are usually >2 mm diameter in size. Some studies have suggested that there are differences between the initial recruitment assemblage on artificial substrata and the local established population (Wallace and Bull 1981, Harriott 1985, Sammarco 1991). The distinction between early recruitment and visible recruitment was made in this study as most other studies on coral recruitment have only ever investigated one of these phases, usually inferring characteristics about the phase not studied. This is the first project that looked at both phases simultaneously and attempted to establish the relationship between them.

The objective of a simultaneous study of early and visible recruitment was to identify the relative influence of either phase on the recovering adult community. In particular, this study seeks to establish at what temporal and spatial scales do the most influential determinants of community structure occur.

The questions addressed in this study were:

Early Recruitment

(1) Does the abundance and composition of early recruits vary between reefs over different spatial and temporal scales?

(2) Does early recruitment vary within a reef over different spatial and temporal scales?

(3) Are there areas within a reef where significant differences in early recruitment are predictable?

Visible Recruitment

(4) Is the pattern of early recruitment reflected in the visible juvenile recruit communities?

(5) Are there significant temporal and spatial differences in visible juvenile recruitment at Green Island Reef?

(6) What is the effect of community structure (with respect to the formation of an overtopping canopy) on the visible recruitment rate?

Regeneration Processes

(7) What is the importance and relative contribution of massive coral species in the coral regeneration process?

(8) What is the contribution of non-larval visible recruitment (or asexually produced results) to the regeneration processes at Green Island?

(9) Can succession be described in terms of ecological models?

Chapter 2. GENERAL METHODOLOGY AND STATISTICS

2.1. Description of Study Sites

The location of all reefs and sites used in the early and visible recruitment studies are shown in Figure 2.1 (a-d). Upolu and Michaelmas reefs were included in the early recruitment studies along with Green Island reef because all 3 reefs are suitable for tests of inter reef comparisons of early recruitment patterns. The reefs are suitable for the above tests because: (1) all are situated on the inner mid shelf edge of the GBR and are approximately equidistant apart; (2) all have cays in the NW sectors and would be expected to have similar hydrodynamic conditions in the fore reef and back reef locations; (3) all have experienced similar *A. planci* outbreaks in the past (in terms of timing and degree of disturbance, pers.obs.) and therefore would be expected to be undergoing similar recovery phases. Figures 2.1 (a-d) show the location of the reefs on the continental shelf and the location of study sites within each reef. Numbers on the aerial photos (Figure 2.1 (b-d) indicate sites at approximately 3 m depth where early recruitment data and/or visible recruitment data were collected. At Green Island (Figure 2.1 (b)), sites #1, #3, #5, and #7 included additional deeper positions at approximately 6m depth (with B suffix, compared to 3 m depth sites with an A suffix) to investigate the influence of depth on both early recruitment and visible recruitment of corals.

At Green Island reef, fore reef sites were approximately 150 m apart on an upper slope terrace which had a more gentle slope than adjacent deeper and shallower slope areas. This portion of the reef was exposed to the predominant SE Trade Winds which impinge at a small angle to the reef perimeter and not directly onto the sites. Back reef sites were approximately 250 m apart. The back reef consisted of a shallow reef perimeter slope (approximately 2 m depth) and an extensive sand apron interspersed with patch reefs where the sites were located.

All sites were relocated at each monitoring period using compass bearings and particular physical characteristics of each site.

2.2. Statistical Analyses

There are general statistical details which are common to all sections of this study. To avoid repetition, the common features of all analyses from each chapter are outlined below. More specific information is included in the relevant chapters and in sections where analytical methods differ from the general approach.

2.2.1. Repeated Measures Analysis of Variance (ANOVAR)

Both early recruitment and visible recruitment studies utilised permanent sample positions or quadrats, respectively. Therefore, samples over time were not independent, which is an assumption of univariate ANOVA techniques (Winer 1962). To overcome this statistical limitation and to retain the most powerful analyses possible, the repeated measures analysis of variance (ANOVAR) procedure was adopted. Most tests included a number of fixed main factors and a nested term. All of these analyses were run on the SYSTAT statistical package (SYSTAT Inc., Illinois; Wilkinson 1990). As there were no random factors in the ANOVAR models, the use of the two residual mean squares (MS for between and within subjects terms) would result in over powerful tests and pseudoreplication errors (Green 1993). Consequently, the denominator mean squares from the next level above the residual term in the ANOVAR results table were used. In all cases, this term was non-significant (using the residual error term in this case) which did not invalidate this approach (Underwood 1993).

Groups of dependent variables representing sample times were tested for homogeneity of variances separately,ie, each year's sample was tested for homogeneity of variances. When one or more groups were non-homogeneous, the data were transformed. Recruit abundances were log (x+l) transformed and proportions of recruits were arcsine transformed to improve homogeneity of variances (Snedecor and Cochran 1980). Variances were tested for homogeneity using Bartlett's test prior to formal testing of hypotheses. Levene's test of homogeneity of variances was carried out on transformed and untransformed data which were showing significant results from Bartlett's test. Levene's test can overcome shortcomings of the Bartlett test which is very sensitive to non-normality of data, by conducting ANOVA tests of absolute differences from the cell means (Snedecor and Cochran 1980). When Levene's test showed heterogeneous variances, equivalent non-parametric analyses were carried out.

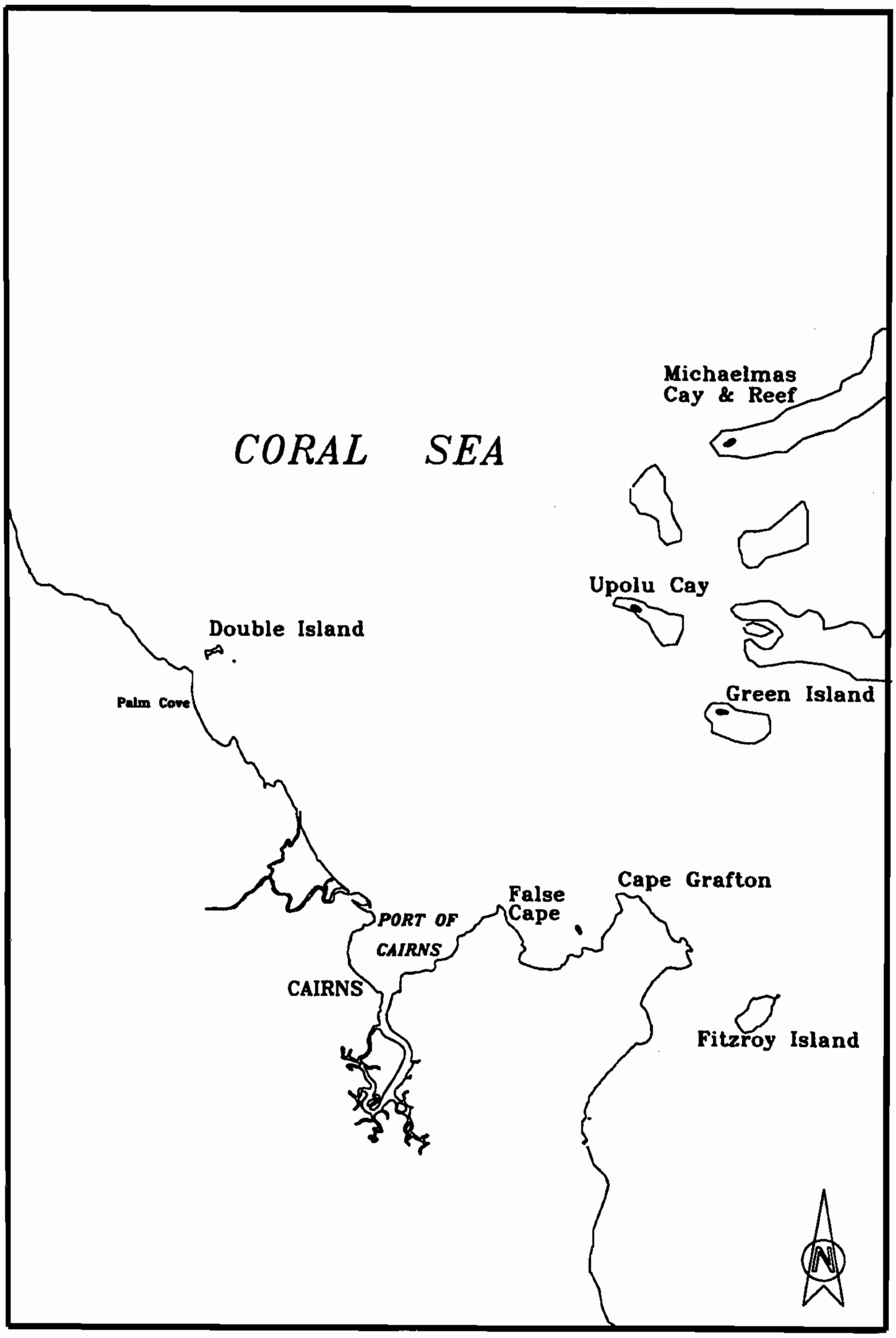


Figure 2.1(a). Map of reefs used in the early recruitment study (Chapter 3). Green, Upolu, and Michaelmas cays and reefs are shown with their relative position to each other on the continental shelf. Green Island is approximately sixteen nautical miles from the port of Cairns.

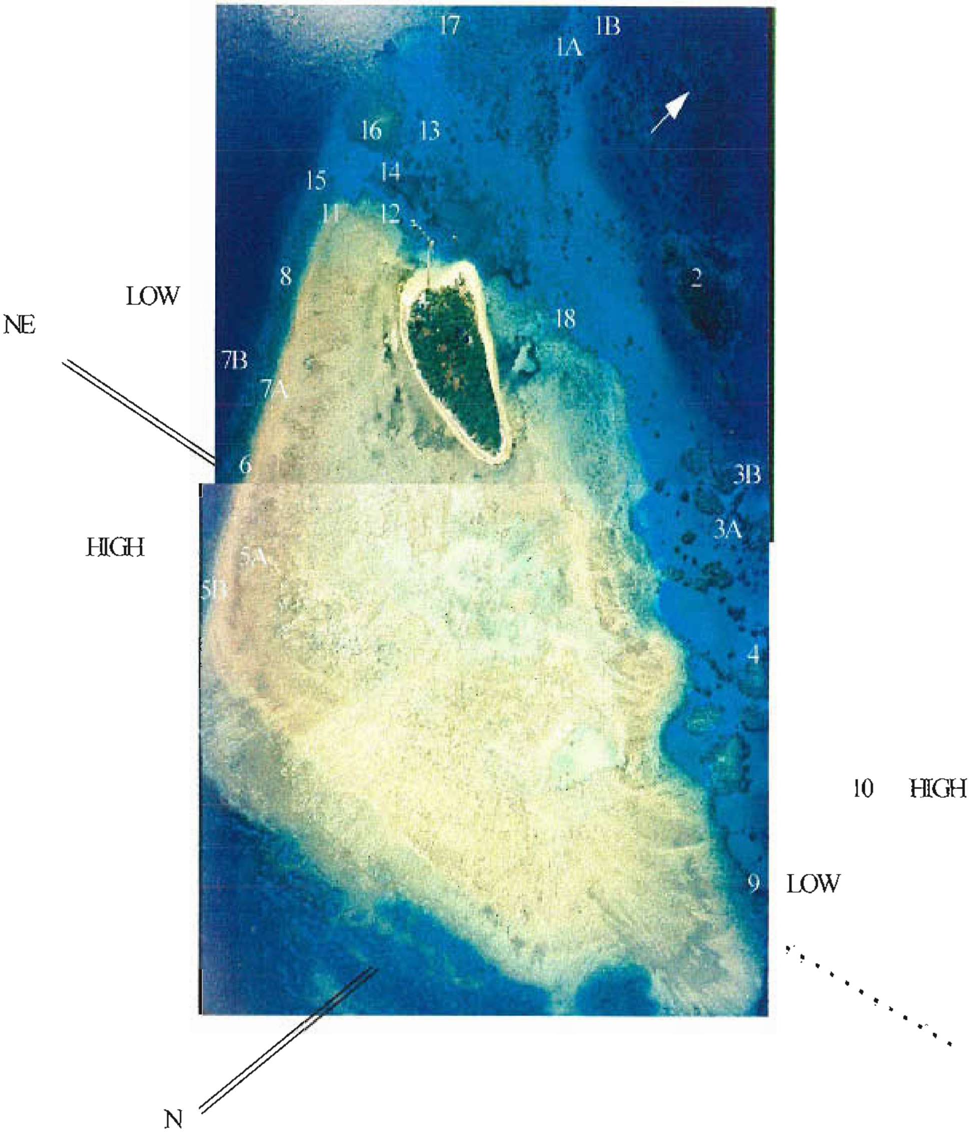


Figure 2.1 (b). Aerial photo of Green Island reef and cay (approx. 500 m long) showing the position of all sites. Double lines indicate the position of coral spawn slicks in December 1990. The slick on the western reef edge formed with light NE winds, whilst the slick at the southern edge formed with light N winds. The dotted line (eastern edge) is where tidal convergence often appears (see Discussion Chapter 3). "HIGH" and "LOW" are potential high and low larval retention areas predicted from models (see Chapter 3). The arrow indicates magnetic north.

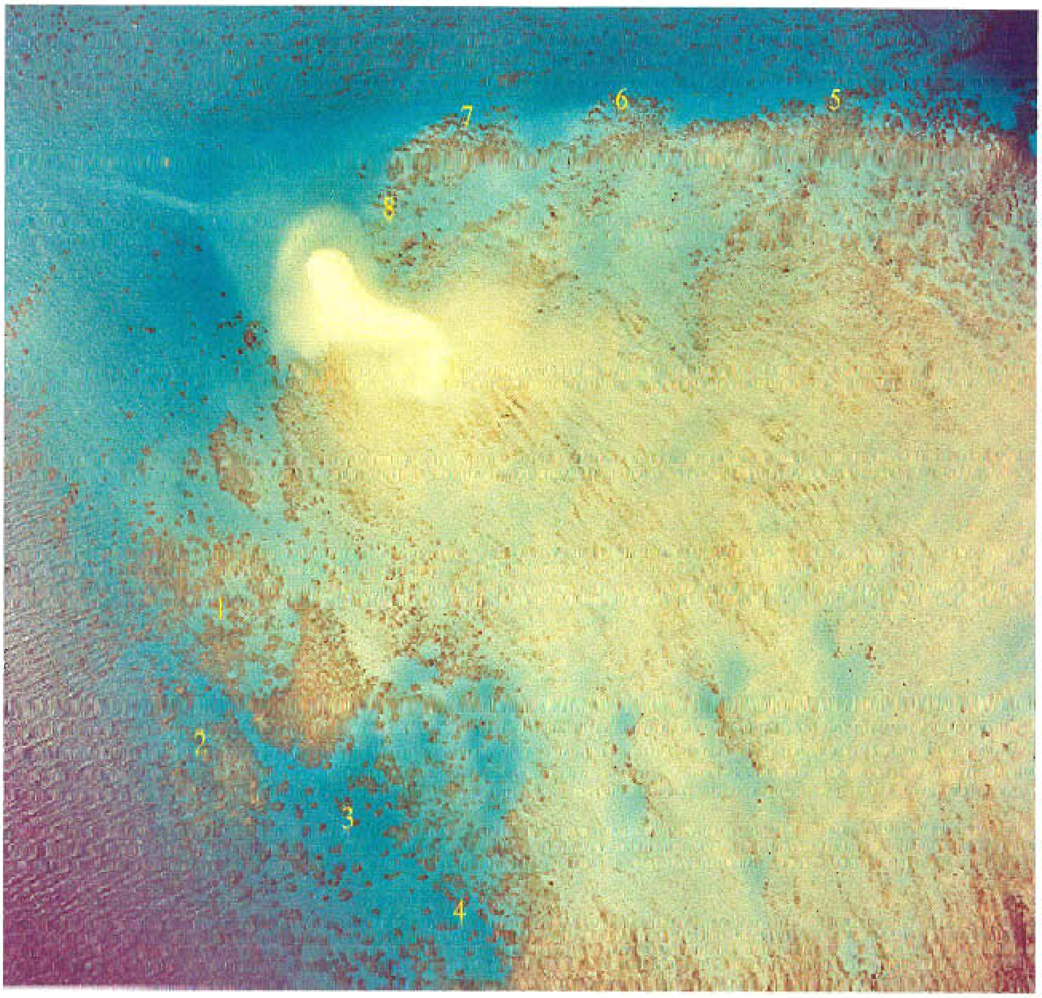


Figure 2.1.(c) Aerial photo of Upolu cay (approx. 50 m long) and part of the reef showing the position of sites used in the early recruitment study (Chapter 3). Magnetic north is towards the top of the page.

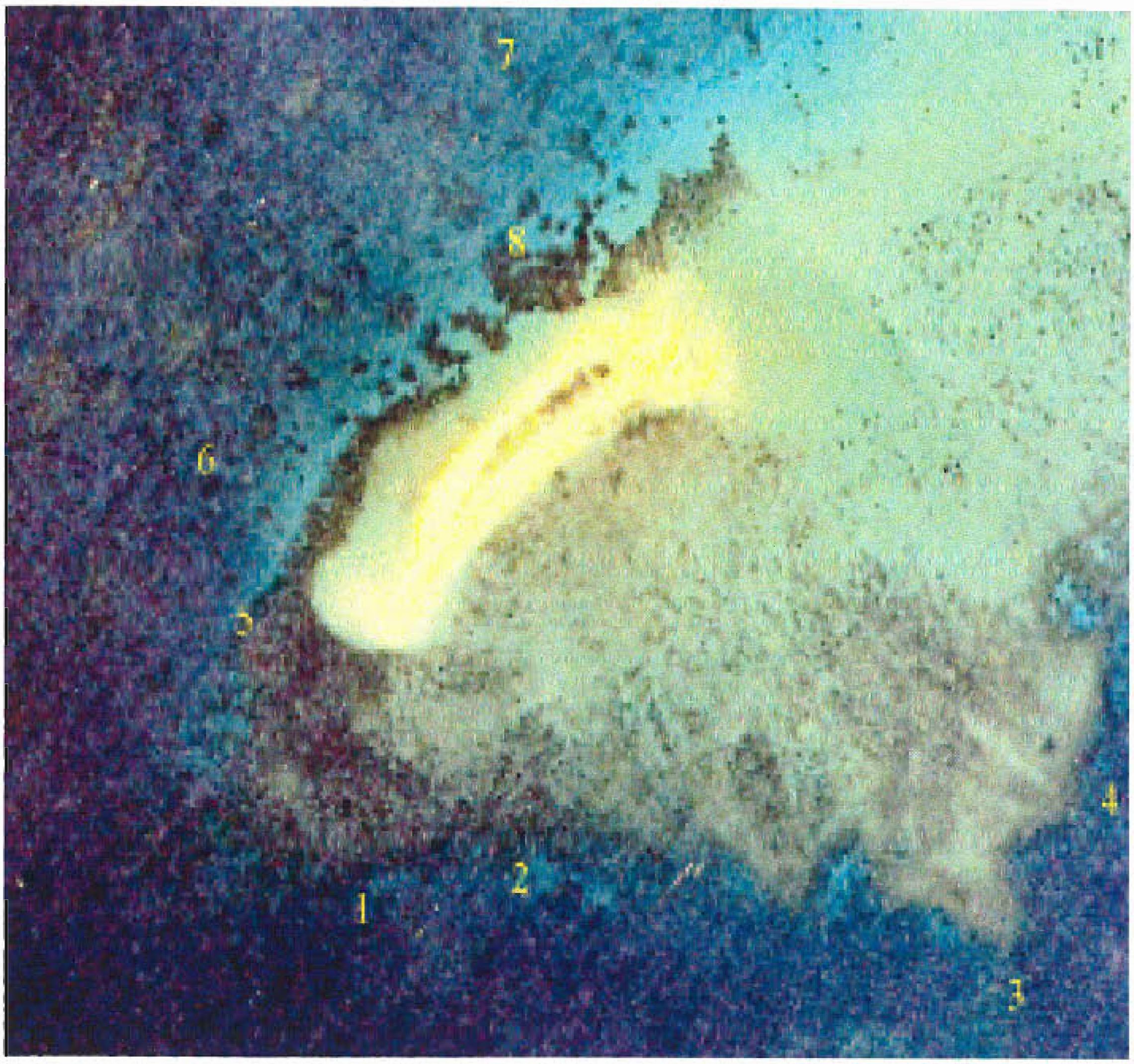


Figure 2.1.(d) Aerial photo of Michaelmas cay (approx. 250 m long) and part of the reef showing the position of sites used in the early recruitment study (Chapter 3). Magnetic north is towards the top of the page.

ANOVAR also require homogeneous covariances or compound symmetry of variances of all possible pairs of repeated measures (Winer 1962, Arnold 1981, Moser *et al* 1990). When this assumption is not met, multivariate analyses of repeated measures are recommended as this assumption does not apply in these tests (Winer 1962). Two statistics (Greenhouse-Geiser (G-G) and Huynh-Feldt (H-F) epsilon) can be used with the repeated measures analyses to estimate the degree of violation of the compound symmetry. These statistics allow univariate tests with adjusted probability levels to have similar power to the standard univariate tests when compound symmetry fails (Moser *et al* 1990; Tabachnick and Fidell 1989). Huynh-Feldt corrections adjust for some shortcomings of the G-G corrections (Wilkinson 1990) so use of the H-F values were followed here. H-F values close to or equal to 1 show that compound symmetry has not been violated or only marginally so. As a further check on this assumption, SYSTAT gives the P-value for both standard and adjusted (via both G-G and H-F epsilon) univariate tests, and where close agreement in the P-values is shown between the standard and adjusted results then violation of compound symmetry is assumed to be negligible or non-existent (Potvin *et al* 1990; Wilkinson 1990).

Tukey's *a posteriori* tests were carried out on significant main (between subject) effects in the ANOVAR. In these cases, main effect differences were tested for each separate sample time.

2.2.2. Power of Non-Significant Results

Power is the probability of detecting a true difference. That is, it is the complement of Type II error, which is the error level of accepting the null hypothesis when in fact it should be rejected. Power calculations were performed on untransformed data for all non-significant results of ANOVAR and other non-parametric tests, using methods outlined in Cohen (1977). The power of non-significant results was calculated using the actual differences in means of the analysed data. The purpose is to help interpretation of non-significant results by indicating the probability of type II error for that particular result. The 4 variables used to estimate power from tables supplied by Cohen (1977) were the following:

$\alpha = 0.1$;

n' = adjusted no.of cases (= denominator df / (numerator df+1))+1;

μ = numerator df;

f = effect size (= e_m/e = std.dev.pop.means / residual std.dev., where $e_m = \sqrt{(\Sigma(m_l - m)^2/k)}$, and m_l = indiv. Mean in each case, m = overall mean, k = no.cases).

In the above power calculations, appropriate degrees of freedom and numerator terms were used according to the particular between or within-subject terms under consideration (Cohen 1977). In almost all cases, the numerator degrees of freedom were so small that the potential of a high power estimate greater than 20 was not possible (see Tables in Cohen 1977).

2.2.3. Multivariate Ordination and Classification

A full description of the techniques briefly described here can be found in Clarke (1993). Non-metric multi-dimensional scaling (MDS) ordination was used to search for patterns in the early and visible recruitment data sets using the PRIMER suite of programs (Plymouth Routines in Multivariate Ecological Research, Plymouth Marine Laboratory). The multivariate MDS is species- or taxa-dependent and is more sensitive to differences between sites and times than are equivalent univariate tests (Warwick and Clarke 1991). That is, these methods compare communities using the identity of species or taxa as well as their relative importance with respect to abundance. MDS uses a measure of similarity between all pairs of sites as a means of constructing a 2-dimensional (or multidimensional) plot where sites with similar species or taxa compositions group together, while more dissimilar sites are further apart. An index called stress is also calculated, which is a measure of how well the differences in species composition between each pair of sites are preserved in a MDS plot. The lower the stress value, the more accurately the MDS plot represents the true relationship between points. Stress values greater than 0.2 are likely to produce plots which will be interpreted inaccurately (Clarke 1993).

In certain cases, *a posteriori* significance testing for differences among groups of sites was performed using the ANOSIM simulation test (Clarke and Green 1988) which is a multivariate equivalent of ANOVA. The taxa most responsible for the Bray-Curtis dissimilarity between groups of sites were determined using the SIMPER program which calculates the percentage contribution of individual taxa to the average dissimilarity between pairs of groups (Warwick 1993).

Before all tests, data were double square root transformed and the sites compared using the Bray-Curtis similarity measure (Bray and Curtis 1957). The choice of transformation and similarity indices follows the recommendations of Field *et al* (1982). This degree of transformation results in a reduction in the effects of dominant taxa over less dominant taxa, and will aid in the differentiation between sites with many and few species (Clarke and

Green 1988). The Bray-Curtis similarity is not affected by joint absences but still gives more weight to abundant species than rare species when comparing samples (Field *et al* 1982). Hierarchical cluster analysis of samples was included as a check on the adequacy of MDS ordinations. The clustering methods use group-average linking of the same similarity matrix produced for the MDS analyses (Clarke 1993).

CHAPTER 3. Early Recruitment of Corals Using Ceramic Tiles

3.1. Introduction

Coral recruitment studies have shown significant temporal and spatial variation over a wide range of scales (Harrison and Wallace 1990), making it difficult to describe patterns in early recruitment. Dispersal and local availability of coral planulae can influence the rate of early recruitment to a reef or to a location within a reef. The relative abundance of early recruit taxa can also indicate: (1) competitive advantages of different life history strategies used by major taxa; (2) the influence of these strategies on community succession; and (3) the nature and speed of recovery (Connell and Slayter 1977).

Coral life history strategies result in larval production by two modes (broadcast spawning with external development, and internal brooding), which have different potential consequences for the supply of recruits. The majority of species produce coral larvae from a mass spawning event in early summer on the Great Barrier Reef (GBR) (Babcock *et al* 1986). Development from external spawning and fertilisation to settlement-competence stage requires between two and six days (Babcock and Heyward 1986; Harrison and Wallace 1990), during which time the developing planulae move with the prevailing currents. The average swimming speeds of fully developed planulae are slow, they are effectively passive meroplanktonic larvae (Harrison and Wallace 1990). In contrast, brooded larvae usually settle within a few hours or days after they are released (Harrison and Wallace 1990). At the same time, some brooded planulae (e.g., *Pocillopora damicornis*) apparently can delay settlement and potentially drift for up to one hundred days (Richmond 1987). The time spent in the plankton and the behaviour of water masses clearly determines the degree of dispersal of planulae both within a reef and between groups of reefs. Coral recruitment shows distinct seasonality in many areas, which is probably due to the short larval life of most corals and the fact that the majority of GBR species are broadcast spawners (Harrison and Wallace 1990). However, not all coral recruitment is seasonal. Brooded larvae from the families Pocilloporidae, some Poritidae, and possibly Isoporan Acroporidae, release larvae throughout the year (Harriott 1985; Wallace 1985a,b).

Two opposing viewpoints in the literature center on the relative significance of the contribution to recruitment of planulae to seed natal or distant reefs (Willis and Oliver 1989). Spawn slicks formed after mass spawning events have shown rapid inter-reef movement (Willis and Oliver 1989), demonstrating the ability of inter-reef dispersal and the potential supply of propagules from outside the parent reef. Self-seeding of reefs is generally expected to be prominent amongst brooding coral species because of the advanced developmental stage of the released propagules (Stoddart 1983; Harriott 1992). In contrast, gamete producing species have a longer development time before they are competent to settle, and as a consequence they are expected to be transported longer distances.

Because of the developmental time required by the majority of broadcast spawning species, the movement and behaviour of water masses are expected to be very influential in the dispersal and potential recruitment patterns of corals. Hydrodynamics are therefore implicated in the following: (1) the retention of planulae within a reef (Sammarco and Andrews 1988); (2) the movement of planulae to distant reefs (Harrison *et al* 1984; Babcock and Heyward 1986; Oliver and Willis 1987; Willis and Oliver 1989); and (3) the concentration of planulae within particular reef locations (Harriott and Fisk 1987, 1988). Time-averaged hydrodynamic models have been used to predict resident periods of water masses within individual reefs, and to predict distances and directions that larvae can be transported (Dight *et al* 1990; Black and Gay 1987; Black and Moran 1991; Black *et al* 1990 1991). While very useful models have come out of these studies, the accuracy of the models in predicting local larval availability and the degree of connectivity of reef systems still needs to be tested empirically. The limitation of time averaged models is that at any particular time, the degree of similarity of wind and current conditions (and hence particular characteristics of local water movements) to the average long-term condition may be low. Oliver *et al* (1992) issued such a caution from a multi-disciplinary study of coral dispersal and localised water current measurements regarding the use of coral recruitment as a way of validating larval dispersal models. The ability of time- and spatially-averaged models to predict dispersal patterns and concentrations of larvae have to be applied as generalised models of long term within-reef distribution patterns (Oliver *et al* 1992).

Dight *et al* (1990) modeled the long-shore water flow patterns in the Cairns section of the GBR and showed that Green Island would frequently be in the direct path of longshore water flow in both north and south directions. Therefore, because of its position on the continental shelf, Green Island reef would potentially receive frequent supplies of water borne coral larvae under most common wind conditions. In addition, models of water movements within Green Island reef have been run for neutrally buoyant larvae during average early summer conditions (Black and Gay 1987). These models predicted a number of areas of potentially high and low larval retention within Green Island reef and the immediate surrounding waters. These specific locations were predominantly on or near shallow reef areas and hence lent themselves to a test of the hydrodynamic model for this reef, assuming that wind conditions during the critical dispersal stages of the study periods were similar to the time-averaged conditions. That is, interpretation of results have to take into account the actual wind conditions during the critical dispersal phase for each separate experimental period.

Temporal recruitment patterns have been found to extend to inter-annual variations within the same sites (Baggett and Bright 1985; Fitzhardinge 1985; Wallace 1985a,b). However, these studies were restricted to small areas within single reefs so it is not known if this pattern is present at larger individual- or multi-reef scales.

Spatial patterns in coral recruitment have also been demonstrated from studies of early recruitment between sites at spatial scales less than whole reefs (Babcock 1988; Baggett and Bright 1985; Wallace 1985b). Geographic differences in abundance and composition of early recruitment were noted in two studies at spatial scales of hundreds of kilometers (Fisk and Harriott 1990; Sammarco 1991). Harriott and Fisk (1987 1988) have reported significant taxonomic and numerical differences between single back reef and fore reef sitess located at three different reefs at scales at one to three km (Green, Michaelmas and Upolu Reefs, northern GBR). It is not known if the above back reef and fore reef location differences are consistent at a number of sites within each location, or between a number of seasons. This study investigated the back reef/fore reef location pattern in the above three reefs by incorporating within-site variability over approximately 10 m spatial scales. At a smaller spatial scale, Wallace (1985a) found taxonomic differences in relative abundance between exposed and cryptic shaded habitats. Also, Fisk and Harriott (1993) demonstrated a significant reduction in recruit abundance under plate and arborescent *Acropora* spp. colonies in comparison to nearby unshaded positions. Taxonomic differences between the shaded and exposed positions were also suggested by these data but because of the small sample size it was not feasible to make an unequivocal conclusion on this point.

Studies of coral recruitment using artificial substrata such as ceramic tiles can reflect characteristics of the very early recruitment phase and possibly the rate of successful settlement of corals (Harrison and Wallace 1990). Successful settlement in this instance is the phase following larval searching behaviour and begins with attachment and metamorphosis, resulting in the formation of a recognisable skeleton. Wallace (1985a) thought that counts of recruit skeletons on settlement plates were a good estimate of successful settlement when predators could be excluded and where immersion times of the plates did not allow overgrowth by other benthic organisms. Estimates of recruitment are generally regarded as a good representation of settlement when mortality of settlers is density independent (Connell 1985, Davis 1988; M^{c}Guiness and Davis 1989, Hughes 1990, Sutherland 1990). Early recruitment estimates as defined here will not account for the loss of individuals from the available pool of planulae during the period of searching behaviour and prior to attachment and metamorphosis. The size of newly settled coral larvae is generally related to the size of mature planulae, which are commonly approximately 2 mm diameter (Stephenson 1931, Yonge 1932; Jell 1980; Fisk 1981; Van Moorsal 1983; Babcock 1985). The smallest sizes of early recruits on the tiles in this study were approximately 2 mm diameter, indicating that the recruitment estimates reported in this study are recording most newly settled and metamorphosed corals.

Choices of substrate orientation by settling planulae appear to vary according to particular light and sedimentation regimes (Carleton and Sammarco 1987; Fisk and Harriott 1990; Harrison and Wallace 1990; Babcock and Davies 1991). With increasing depth, corals show a trend towards settlement in more exposed positions compared to more sheltered preferences in shallower depths (Rogers *et al* 1984; Baggett and Bright 1985; Harriott 1985; Wallace 1985a,b). There are indications that some taxa (e.g., some Faviidae and ahermatypic species) prefer more cryptic shaded habitats than others in similar depth regimes (Wallace 1985a).

The techniques used in this study give a good estimate of successful settlement and early recruitment densities because after attachment of the larvae, a skeleton is laid down with recognisable septa within one to five days (Vandermeulen and Watabe 1973; Jell 1980; Babcock 1985). It is from this successful settlement stage that early recruits can be detected using a dissecting microscope even if the attached newly settled coral dies. The advantages and efficacy of using ceramic tiles for experimental substratum in comparison to natural substrata for early recruitment studies are outlined in Harriott and Fisk (1987). The most important advantages of ceramic tiles are that surface type, available area, and surface orientation are standardised. Retrieval and replacement of settlement substrata also allows for the standardisation of the degree of conditioning of the surfaces within each sample period. Conditioning results in the appearance of a micro-biotic film which is shown to be important to the settling larvae's choice of substrate (see review in Harrison and Wallace 1990). Regular replacement of recruitment substrata also minimises the possible effects of interaction and competition from other organisms (Osman *et al* 1989).

Aspects of early coral recruitment which addressed the aims of this study outlined in Chapter 1 were:

- seasonal and inter-annual differences in composition and abundance of early recruits at Green Island reef and 2 nearby reefs, leading to conclusions on characteristics of whole reef early recruitment;
- depth differences in early recruitment at Green Island reef;
- spatial patterns at Green Island with respect to hydrodynamic model predictions and to longer term trends.

3.2. Methods

Commercially available ceramic tiles were used as sampling surfaces to measure early recruitment of corals. For the summer period (October/November to April), tiles were immersed prior to the annual mass spawning period (usually November) and left in the field for up to 6 months. Over this period the juvenile corals grew to 2-20 mm in diameter. All tiles were replaced for the winter sample commencing in approximately April, resulting in clean surfaces being available for consecutive summer and winter periods.

The ceramic tiles (15 cm x 15 cm) were attached to galvanised weldmesh racks raised approximately 20 cm above the substrate. Each rack contained 3 pairs of tiles placed horizontally above and below the mesh. Some tiles were occasionally lost from these racks so the third tile pair was added as a reserve pair in case of such losses. When all three pairs were retrieved, the two most spatially separated pairs (approximately 15 cm apart) on a rack were chosen for analysis (Figure 3.2.1).

Tiles were drilled in the center and a nut and bolt used to hold the pairs rigidly together on both sides of the rack mesh. This method produced an approximately 1 cm gap between the upper and lower tiles which proved to be a favorable cryptic settlement habitat for corals. At all times the glazed surfaces of tiles faced upwards and the unglazed surface faced the substrate. This arrangement presented coral planulae with the best surface (the unglazed surface) for attachment in the most favorable orientation determined by trial and error from previous studies (Harriott and Fisk 1987,1988; Fisk and Harriott 1990). Racks were pinned to the substrate using one meter long steel rods and replaced by removing rods from one side only, leaving the new rack and tiles in exactly the same position as the previous rack.

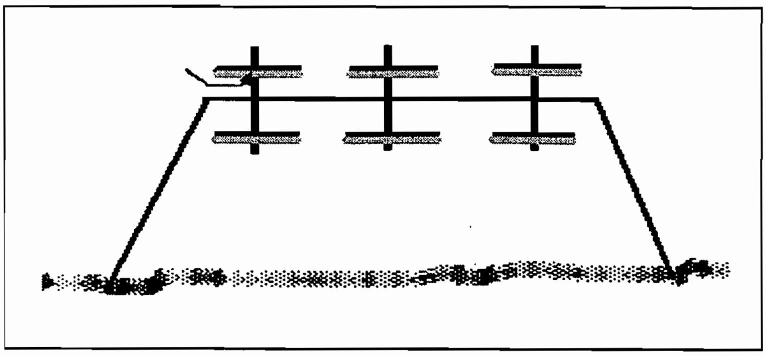


Figure 3.2.1. Illustration of the arrangement of ceramic tiles used in the study of early recruitment of corals. Three pairs of tiles were arranged on the horizontal section of mesh and held in place by bolts placed in the center drilled holes. The glazed sides of the tiles are facing upwards (the darker lines on the horizontal tiles). The cryptic habitat or 'gap' position is shown in one pair by the arrow.

The provision of a cryptic habitat in the form of a gap between the settlement tiles as part of a complex sampling unit (see below), also acts as an exclusion mechanism of macro-grazers and may provide a critical habitat for settlement of certain taxa. Almost all early recruits counted on the tiles were located on the surface of the tile itself and not on other organisms which had settled on the tiles during the immersion period. A low proportion of recruits were overgrown by other organisms and those that had been overgrown were usually detected when the soft tissue organisms were removed. Furthermore, the skeletal remains of encrusting organisms such as bryozoans and bivalves, were sufficiently thin that overgrown coral recruits could be detected underneath the skeletons of these organisms.

Tiles were individually tagged, cleaned of algae and organic matter for several days with concentrated chlorine bleach, then rinsed in water and dried. The unglazed surfaces of both the upper and lower tiles of each pair were examined with a dissecting microscope and coral recruits located by circling each corallium with a pencil. The tile surfaces were then photocopied and re-examined to identify each coral using the photocopy as a map and compilation sheet.

Coral recruits were identified to family level where possible using photos of settled juveniles of known coral species (Harriott 1983; Babcock unpublished; Jell 1975). Severely damaged and heavily fouled corals were grouped with unidentified corals into an "unknown" category. Corals which were damaged or fouled were not common (estimated < 5% of all recruits). This "unknown" group also included uncommon cases of very recent settlers (within 36-48 hours of settlement) where a basal plate and rudiments of septa were present (see Jell 1975 for photographic examples). A small number of taxa (less than 10 per sample period) could be identified to genus with a good degree of certainty. These included early recruits of the genus *Millepora* and the hydrocoral *Heliopora coerula* which were readily recogised because of their distinctive morphology and colours. The Isoporan Acropora group (either *A.palifera*, *A.cuneata.* or *A.brueggemanni*) were also recognisable due to their unusually large size (and by other features, see Babcock (unpubl.)) from the very early recruitment phase.

3.2.1. Annual and Inter-Reef Patterns in Early Recruitment for Green, Upolu and Michaelmas Reefs

Sampling racks were located at eight sites per reef at Green Island Reef, Upolu Reef, and Michaelmas Reef (Figure 2.1 (b-d)), for two summers (1988-89, 1989-90) and one winter (1988). Upolu reef is approximately ten kilometers north of Green Island reef, and Michaelmas reef is a further nine kilometers north of Upolu reef. Four sites were established in back reef and fore reef locations within each reef, with distances between sites within a location kept at approximately 200-300 m. The sites within a location were chosen to give clear back and fore reef positions with respect to the cay on each reef. Within each site, two racks were placed approximately 10-15 m apart at approximately 3 m depth. All of the sites were used repeatedly for the whole study period except at Upolu Reef where two of the sites initially established in the fore reef were not relocated at the post 1989-90 summer sample and so new sites were established close by.

Repeated measures ANOVA (ANOVAR) was used to test for summer differences in early recruitment abundance between Green, Upolu, and Michaelmas Reefs, in addition to tests of differences between back reef and fore reef locations (Figure 3.2.1.1). All factors within the model were fixed. Nested terms in the model included sites within location, and replicate racks within sites. Differences in recruitment between the two summer periods were also determined along with the time x reef and location interaction terms. The null hypotheses were: Ho_1 : there was no difference between the three reefs; Ho_2 : there was no difference between back reef and fore reef locations at the three reefs, Ho_3 : there was no difference between the two summers; Ho_4 : there was no difference in time trends among reefs; and

Ho_5 : there was no difference in time trends among back reef and fore reef locations. The data were analysed using a number of variables : (i) total recruits per rack (pooled total from two pairs of tiles); (ii.) number of recruits per rack not including the Pocilloporidae family which is predominantly a planulating family; (iii) total recruits per rack found in the cryptic habitat, that is, on the unglazed underside of the two top tiles from each rack; and (iv), the number of recruits found in the cryptic habitat excluding the Pocilloporidae. Indices (iii) and (iv) above were included to gauge the impact of large grazing animals such as fish and echinoids which were presumably excluded from this area because of the small gap (<1 cm) between the top and bottom tile of each pair.

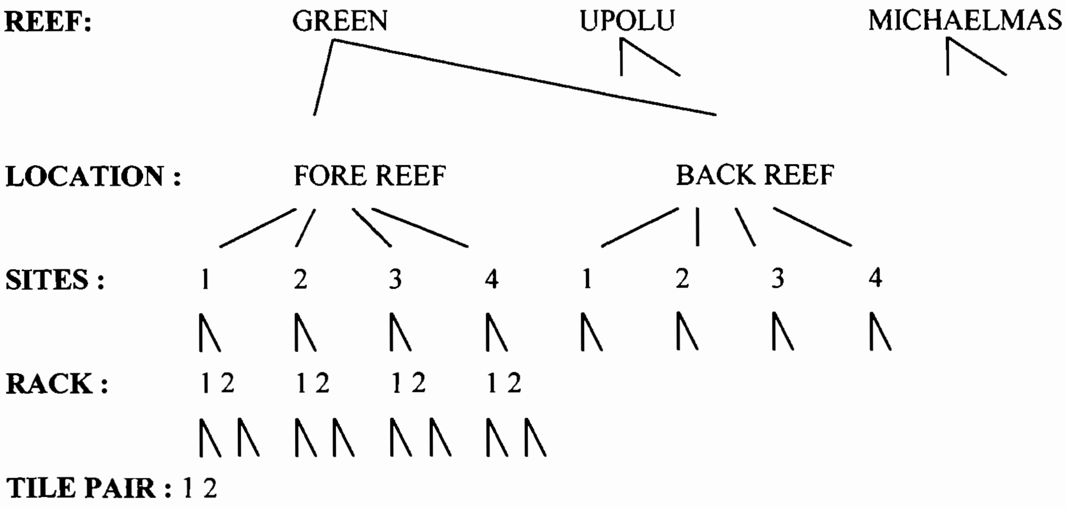


Figure 3.2.1.1. Schematic representation of the experimental design used for summer early recruitment studies of three reefs.

A 2-way ANOVA investigating differences between reefs and locations was run on the winter 1988 data using a similar sampling design to the ANOVAR above except that data from a single tile pair from each site was treated as a replicate sample for back reef and fore reef locations. The smaller sample size was used for the winter data to confirm previous recruitment studies showing relatively lower abundance, and dominance by planulating coral taxa. Variables which were tested included total recruits per rack, and total recruits found in the cryptic habitat (same as above). The null hypotheses were that there was no difference in recruit abundance between reefs or between locations during the winter period.

3.2.2. Taxonomic Composition

Multidimensional Scaling (MDS) ordination and clustering analyses were used to compare taxonomic composition of spatial and temporal early recruitment data from Green, Upolu, and Michaelmas reefs for the winters of 1987 and 1988, and the summers 1988-89 and 1989-90. The data matrix was comprised of seven taxa groups (Acroporidae, Pocilloporidae, Poritidae, Faviidae, *Heliopora* spp., *Millepora* spp., and an unknown/unidentified group) and twenty-four sites (eight from each reef).

The mean number of taxa per tile pair (from a single rack) was used as a representative sample for each site. The total number of tile pairs used to calculate each site mean (for the three seasons) ranged from ten to thirteen pairs because of some tile losses within each sample period. One tile pair per site was included from the winter 1987 sample and up to four tile pairs per site were used from samples of each of the other three seasons. It was thought worthwhile to include all data including the winter samples as equal sampling within seasons was maintained at all 3 reefs. In the latter three season samples, data were used from up to two tile pairs from each of two replicate racks set approximately 10 m apart within each site.

3.2.3. Depth Differences in Early Recruitment at Green Island

An additional two racks were deployed in deeper positions (average 6m depth) at two sites in the back reef and two in the fore reef at Green Island (Figure 2.1(b), sites 1B, 3B, 5B, 7B). This study was run from winter 1988 to the end of winter 1990 and racks were replaced after approximately each six month period, resulting in data for two winter and two summer periods. The racks were used at the same sites where permanent quadrats were located on natural substratum. These quadrats were mapped annually for visible recruits (below) so that comparisons between early and visible recruitment characteristics could be made.

Abundances of early recruitment were compared with ANOVAR using the summer recruitment rates in the shallower (3 m) and deeper (6 m) sites. The null hypothesis was that there is no difference in early recruit abundance between the shallow and deeper positions. To check for possible changes in settlement orientation preferences in the deeper sites (Rogers *et al* 1984; Fisk and Harriott 1989; Babcock and Davies 1991), an additional tile was added to the uppermost top position of each tile pair with the unglazed surface facing upwards. This arrangement gave early recruits an opportunity to settle on the same surface type available in other tile orientations. The additional uppermost tile was added to each tile pair combination in the deeper racks for the 1988-89 summer only (earlier experiments showed little to no recruitment to top upper surfaces in shallow water (Harriott and Fisk 1987)). If there was a shift in preferences of settlement orientation, this surface orientation and the appropriate settlement surface would have been included in subsequent experimental designs.

3.2.4. Spatial Consistency of Early Recruit Abundance at Green Island

At Green Island, eight shallow locations (approximately 3 m depth, site numbers #1 to #8 including sites with A suffix, Figure 2.1(b)) within each site were re-sampled for four summers from 1986-87 to the 1989-90 summer, using the same techniques as described above. Tests for spatial consistencies were made of the total numbers of early recruits, and the number of early recruits of Acroporidae and Pocilloporidae. One tile pair from a single rack at each site was processed for these analyses as losses of some tile pairs occurred in earlier years. Differences between the eight sites (using ranked recruitment abundance) were analysed using the non parametric Friedman 2-way ANOVA. The null hypothesis was that the sites do not display a predictable ranking in their abundance.

3.2.5. High-Low Larval Retention Areas at Green Island

From the hydrodynamic models of Black and Gay (1987), a number of predicted areas of relatively high and low larval concentrations were identified at Green Island. The predictions for Green Island indicated that two distinct pairs of high-low areas existed with similar conditions in each. These areas were easily identified on the model map but were not sufficiently accurate to confidently locate locations to less than approximately 100 m. If the predictions were true, early recruitment rates would be expected to be relatively different in the low and high areas. At each of the two high and two low larval retention areas, four replicate racks were positioned within 10 m of each other (sites #9, 10; and sites #5a, 7a; Figure 2.1(b)). Two tile pairs per rack were used as replicates within each position. The high-low pairs used for this test were within approximately 500 m of each other, with one high-low pair in the fore reef and another pair in the back reef. The distances between high and low areas within each of the pairs was approximately 200 m in both cases. Reef areas with suitable hard substrata were available in all areas at approximately 3 m depth. Early recruitment rates were assessed for the summer periods of 1988-89 and 1989-90 using the same sites and approximately the same rack positions for the two time periods.

A nested ANOVA was used to determine the significance of differences in abundance of early recruits between predicted low and high larval retention areas for each summer sample period separately. I justify this approach by noting that the predicted high-low areas are defined by using (long term) time-averaged wind speed and direction data for the early summer period. Therefore there is a reasonably high chance of differences in wind conditions between individual years which will result in differences in the intensity and duration of cells of high and low water movement. It is likely that this was the case for the two summers (see Results below, Fitzroy Island wind data, Bureau of Meteorology, National Climate Centre). The null hypothesis was that there was no difference in abundance between the low and high predicted larval retention areas.

Tests were done using pooled early recruit abundance, Pocilloporidae only, pooled non-Pocilloporidae; and pooled recruits and pooled non-Pocilloporidae recruits from the gap habitat.

3.3. Results

3.3.1. Taxonomic Composition

The composition of early recruits pooled from summers 1988/89 and 1989/90 for the three study reefs, showed a clear dominance of Acroporidae in both summers and at all reefs (Table 3.3.1.1). Upolu Reef was an exception in summer 1989/90 where Pocilloporidae were relatively more abundant than the Acroporidae. The general trends in relative abundance of taxa are in contrast to the winter pattern (Table 3.3.1.1) where Pocilloporidae were markedly dominant at all reefs.

REEF	YR.	ACR.	POC.	POR.	FAV.	UNK.	TOT.
GREEN	88/89	79.7%	7.2%	1.3%	0.4%	11.5%	8843
	89/90	71.3%	23%	0.8%	0.2%	4.7%	5308
UPOLU	88/89	62%	32.3%	0.4%	0%	5.3%	3457
	89/90	24.5%	66.8%	0.2%	0.4%	8.1%	1423
MICH.	88/89	71.8%	14%	2.4%	1.1%	10.7%	1881
	89/90	71.9%	21.3%	3.9%	0%	2.9%	1161
POOLED		70.3%	20.1%	1.2%	0.3%	8.1%	22073
WINTER 1987 :							
GREEN		0%	88%	6%	0%	6%	33
UPOLU		1%	96%	0%	1%	2%	123
MICH.		2%	82%	13%	1%	2%	102
POOLED		1.2%	89.5%	5.8%	0.8%	2.7%	258

Table 3.3.1.1. Pooled composition of taxa of early recruits for 2 consecutive summers. Data are from 32 (Upolu, Michaelmas) to 56 tile pairs (Green). Yr = summer period; Acr. = Acroporidae; Poc. = Pocilloporidae; Por. = Poritidae; Fav. = Faviidae and Mussidae; Unk. = unknown or unidentified/damaged, or other uncommon taxa (*Heliopora* spp. and *Millepora* spp.); Tot. = total number of recruits.

3.3.2. Inter- and Intra-Reef Patterns

Individual reefs showed significant differences in mean abundance of recruits between the two summers. There were also inter-annual differences in relative abundance between reefs (Table 3.3.2.1; Figure 3.3.2.1(A)). Inter-reef differences in recruitment were a result of relatively lower recruit abundance in summer 1988/89 at Michaelmas in contrast to higher similar abundance at Green and Upolu Reefs. Nonetheless, the rank order of Green, Upolu and Michaelmas reefs in terms of mean abundance was consistent for the two consecutive summer periods. Using means and 95% confidence limits (Table 3.3.2.1) some consistent patterns in pairwise comparisons of the reefs were evident. These included similar abundance between Green and Upolu reefs, and a consistent higher abundance at Green Island reef compared to Michaelmas reef. Michaelmas and Upolu reefs showed more variable patterns, with higher abundance at Upolu in the summer 1988/89 and similar abundance at the two reefs in the following summer.

REEF	SUMMER 1988/89	SUMMER 1989/90
GREEN	136.6 (36)	78.5 (20)
UPOLU	115.6 (24)	47.2 (16)
MICHAELMAS	58.6 (12)	35.3 (12)

Table 3.3.2.1. Mean number of early recruits per tile pair and 95% confidence limits (in brackets) from the three study reefs and for two consecutive summer periods.

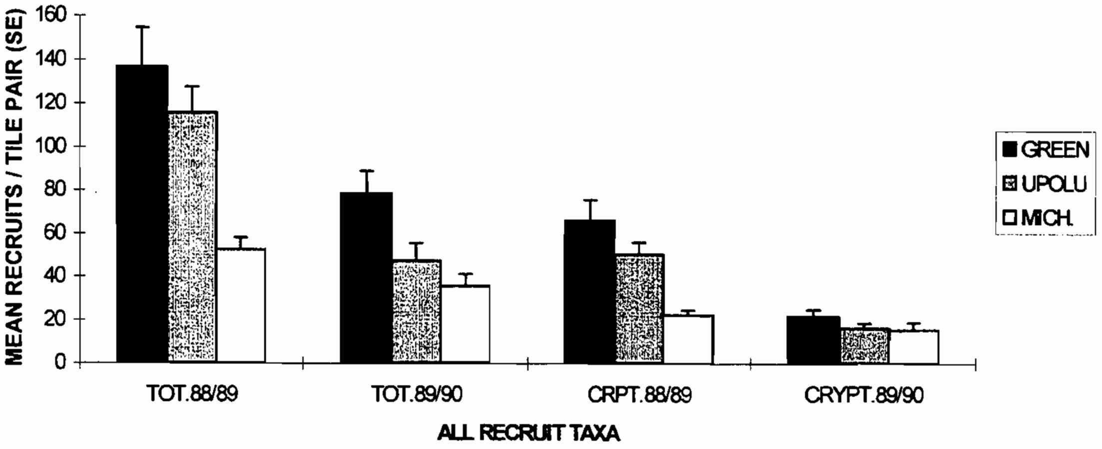
Repeated measures ANOVA (ANOVAR) support the above conclusions where a significant difference was detected in total early recruitment between Green, Upolu, and Michaelmas reefs, as well as between back reef and fore reef locations but there were also significant reef x location interactions (see summary results in Table 3.3.2.2(A); Figure 3.3.2.2.(A), and details in Appendix 3.3.1.1). There was a significantly higher recruitment in the 1988/89 summer compared to the following summer, but the tests also indicated significant interactions between the two time periods and the three reefs. Figure 3.3.2. l(A) shows the interactions of these above factors, where Green and Upolu recorded higher means in 1988/89 summer compared to the following summer, but Michaelmas recorded approximately similar mean results in both summers.

Total early recruitment differences between back reef and fore reef locations showed a stronger pattern to the above pooled reef differences. Significantly higher mean recruit abundances in back reef locations compared to fore reef locations were primarily the result of large differences at Upolu and Michaelmas reef in 1989/90 summer (Figure 3.3.2.2(A)). A similar pattern of higher back reef abundance compared to abundances in the fore reef was shown for two consecutive summers at Upolu reef. Michaelmas reef showed a more variable pattern between the two summers, with similar abundances in the back and fore reef locations in the first summer, but higher back reef abundances compared to fore reef in the second summer. In contrast, there was no difference between locations for both summers at Green Island reef.

Early recruits from non-Pocilloporidae taxa showed almost identical patterns to total early recruitment (ANOVAR results, Table 3.3.2.2). The only difference was an additional significant interaction term (Year x Reef x Location). As with the total recruitment data above, summer 1988/89 was a better recruitment year for non-Pocilloporidae recruits compared to summer 1989/90 (Figure 3.3.2.1(B)). This means that the potential influence of brooding planulating species (principally Pocilloporidae) on recruitment patterns between reefs and locations was not significant enough to affect conclusions on the total recruitment pattern.

There were significant differences in total early recruitment in the cryptic habitat between the three reefs, as well as between the two locations and the two summers (Table 3.3.2.2; Figure 3.3.2.1(A), Figure 3.3.2.2.(B)). Only the year x reef interaction term was significant, which is a result of differences in recruit patterns between the two summers. There was a higher recruitment rate and a difference in abundance between reefs in summer 1988/89 but not in the following summer. In summer 1989/90, there were lower recruitment rates overall and no clear difference in abundance among the three reefs.

(A) Total Early Recruitment :All Surfaces (Tot) and Cryptic Habitat



(B) Non Pocilloporidae : All Surfaces (Tot) and Cryptic Habitat

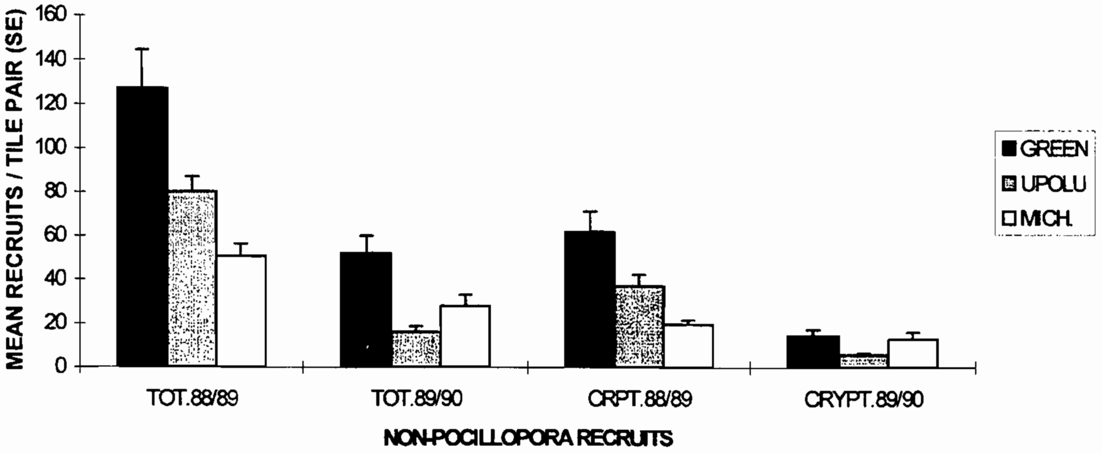
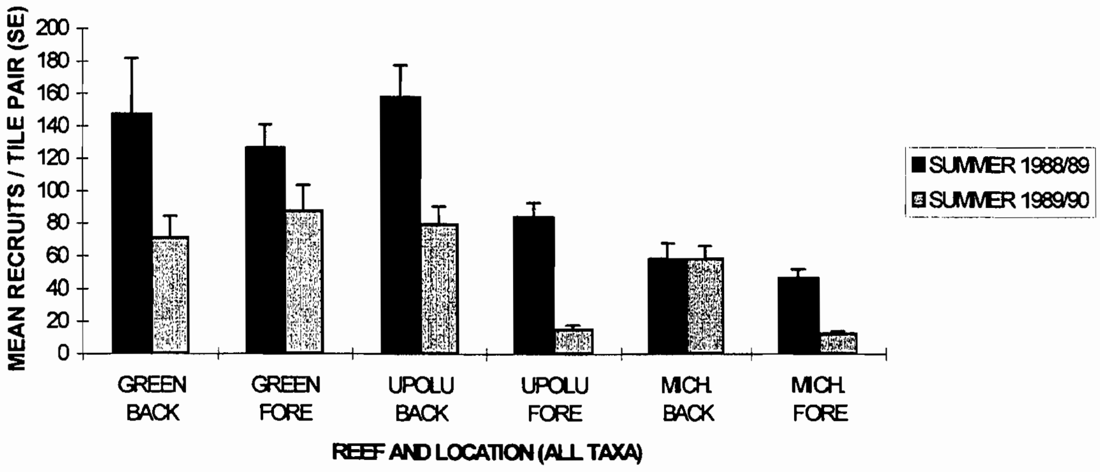


Figure 3.3.2.1. Mean early recruitment for two consecutive summers at Green, Upolu, and Michaelmas reefs. Mean values are calculated from sixteen racks per reef from each summer using data from (A) two tile pairs per rack pairs (all surfaces) for total early recruitment; and (B) early recruitment in the cryptic habitat (the top inner tile surface from two tile pairs).

(A) Total Early Recruitment Back and Fore Reefs : All Surfaces



(B) Cryptic Habitat Early Recruitment Back and Fore Reef

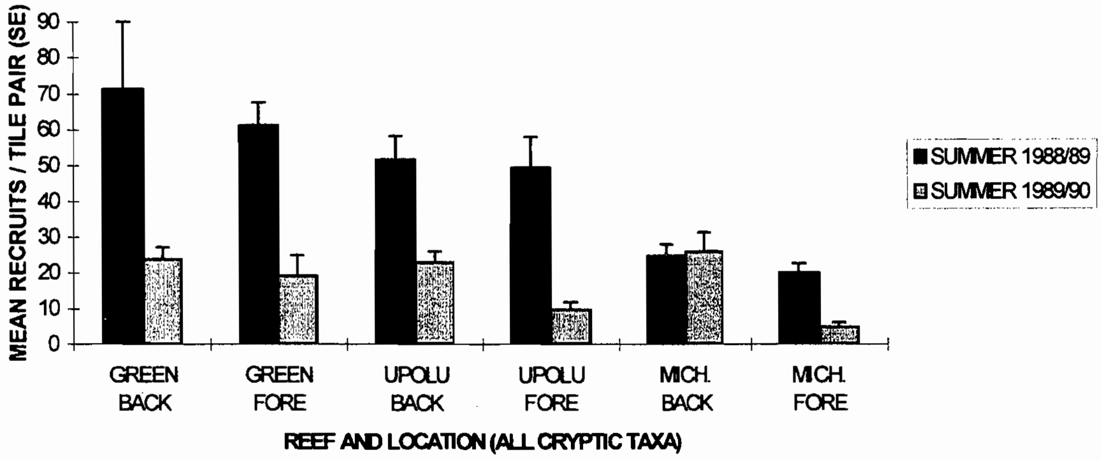


Figure 3.3.2.2. Early recruitment in the fore reef and back reef locations from two consecutive summers at three study reefs (A-C). (A) total recruits (all surfaces); (B) cryptic early recruitment; (C) cryptic non Pocilloporidae; (D) total and cryptic habitat early recruitment from winter 1988. Mean values are calculated from sixteen racks per reef from each summer using data from two tile pairs per rack pairs (all surfaces) for total early recruitment; and early recruitment in the cryptic habitat (the top inner tile surface from two tile pairs).

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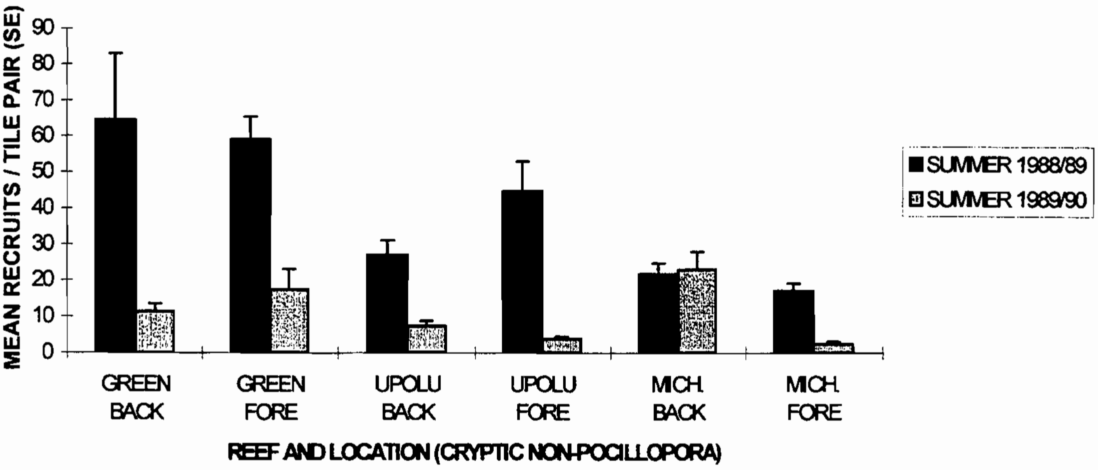
(C) Cryptic Habitat - Non Pocilloporidae



(D) Total Recruitment for Winter 1988

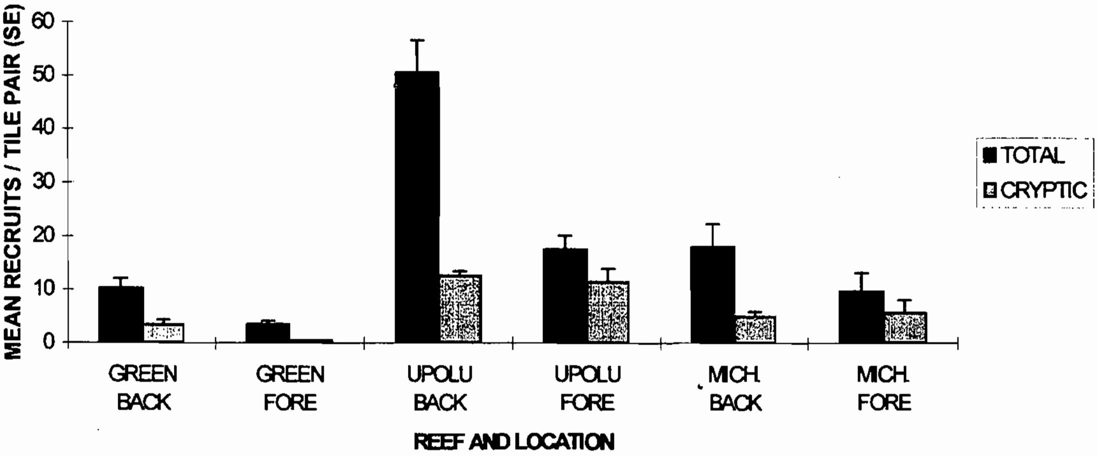


Figure 3.3.2.2. Early recruitment in the fore reef and back reef locations from two consecutive summers at three study reefs (A-C). (A) total recruits (all surfaces); (B) cryptic early recruitment; (C) cryptic non Pocilloporidae; (D) total and cryptic habitat early recruitment from winter 1988. Mean values are calculated from sixteen racks per reef from each summer using data from two tile pairs per rack pairs (all surfaces) for total early recruitment; and early recruitment in the cryptic habitat (the top inner tile surface from two tile pairs).

Recruitment patterns in the cryptic habitat indicate that in the absence of possible grazing influences on the bottom surface tile, the significant differences between the three reefs and between the two locations were clearer because fewer significant interactions were detected. There would therefore appear to have been some effect on the data of a grazing type of impact at certain reefs and locations, but the effect was not consistent across all sites.

FACTOR	TOT	NOPC	CRY.	NOPC CRY.	(B)W88 TOT
(A)POOLED RECRUITMENT					
REEF (R)	S	S	S	S	S
LOC. (L)	S	S	S	NS	S
R x L	S	S	NS	S	S
YEAR (Y)	S	S	S	S	
Y x R	S	S	S	S	
Y x L	NS	NS	NS	S	
Y x R x L	NS	S	NS	S	
(C) ANOVAR - DEPTH					
DEPTH (D)	S	S	NS		
YEAR (Y)	S	S	S		
D x Y	S	S	S		

Table 3.3.2.2. ANOVAR results of early recruitment between Green, Upolu, and Michaelmas Reefs (REEF), and between back reef and fore reef locations (LOC). Differences between two consecutive summers (YEAR) are also tested. TOT.= total recruits from two pooled tile pairs per rack (all surfaces); NOPC.= pooled non-Pocilloporidae; CRY= recruits from two top inner side tiles (= cryptic habitat) per rack; NOPC.CRY= non-Pocilloporidae from two top inner tiles per rack; W88 TOT= total recruits from pooled tile pairs (2) per rack, from winter 1988, - = not tested; S and NS = significant or not significant (respectively) at P=0.05; (B) Winter 1988 (Green Is.) results; (C) Depth effects (Green Is.) using data from two depths and two summers.

Non-Pocilloporidae early recruits found in the cryptic habitat were significantly different between the three reefs, and between years (Table 3.3.2.2). All interaction terms were significant and were the result of a complex pattern in relative abundance. Lower mean abundance values were recorded in the second (1989/90) summer at Green and Upolu reefs but Michaelmas reef was very similar in both summers (Figure 3.3.2.1(B)). The relative mean abundance was similar at the three fore reef locations during both summers, but the reef rank order more or less reversed in the back reef from one summer to the next (Figures 3.3.2.2(C)).

REEF	ACR.	POC.	POR.	UND.	TOT.
GREEN	1.8%	95.4%	0%	2.7%	219
UPOLU	0.9%	97%	0.6%	1.5%	993
MICH.	1.4%	85%	12.7%	0.9%	434
POOLED	1.2%	93.6%	3.7%	1.5%	1646

Table 3.3.2.3. Percentage composition of recruit taxa for three reefs (separately and pooled) from winter 1988. Poc. = Pocilloporidae; Acr. = Acroporidae; Por. = Poritidae; Mich. = Michaelmas Reef; Und. = Unidentified, Tot. = Total recruits.

Early recruitment data in winter 1988 showed significant differences between the three reefs and between the back and fore reef locations but the reef x location interaction term also showed a significant result (Table 3.3.2.2). There were generally lower recruit abundances at Green Island compared to Upolu and Michaelmas in both back and fore reef locations (Figure 3.3.2.2(D)). Upolu had significantly higher recruit abundance to the other two reefs, particularly in the back reef. Pocilloporidae recruits were the dominant taxa at all three reefs during winter in contrast to the dominance of Acroporidae in the summer period. Michaelmas recorded a relatively higher proportion of Poritidae recruits in comparison to the other two reefs (Table 3.3.2.3).

3.3.3. Combined Seasonal and Inter-Reef Patterns

The two-dimensional plot from the MDS ordination (Figure 3.3.3.1) shows three broad homogeneous reef site groupings with the exception of a few sites which are more closely associated with other reefs than with their own reef group.

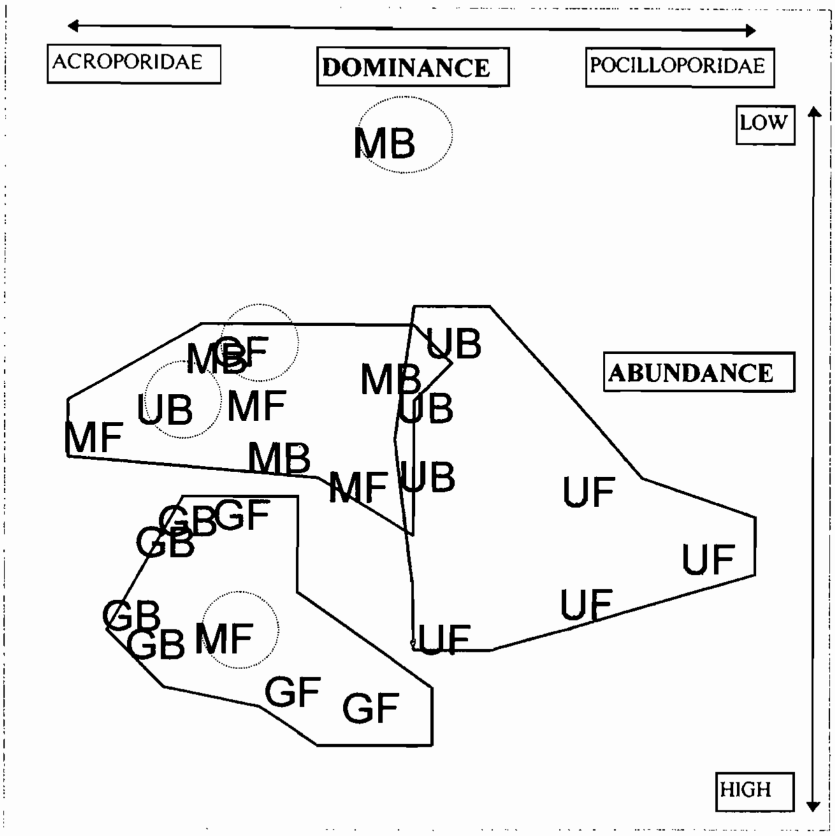


Figure 3.3.3.1. Multidimensional scaling ordination plot (2-dimensional) of early recruitment patterns from Green (G), Upolu (U), and Michaelmas reefs (M). Sites located in the back reef (B) and the fore reef (F) are also indicated. Lines are encircling groups of eight sites from each of the three reefs. Data are drawn from mean recruits/tile pair from winter 1987 and 1988, and from the summers 1988/89 and 1989/90. Seven taxa are included in the matrix. Stress = 0.18.

Upolu Reef sites show the greatest degree of dissimilarity compared to sites from the other two reefs. Green Island and Upolu Reef sites were also generally clumped separately from each other with the exception of single sites from each reef. The pattern of site association is the result of major gradients of change in taxonomic composition and numerical abundance. An axis from the right hand side to the left hand side of the plot represents a gradation of sites with a dominance of Pocilloporidae to sites with a dominance of Acroporidae. A second axis from bottom to top of the plot represents sites with high to low mean total number of recruits, respectively. Clear similarities are also evident within most sites from the fore reef and back reef at Green and Upolu reefs but not at Michaelmas reef.

Figure 3.3.3.1 MDS conclusions are supported by the results of ANOSIM and SIMPER analyses on the same similarity matrix used for the MDS plot. A l-way analysis of similarities (ANOSIM) indicated that the three reefs were significantly different from each other (P=0.001) with respect to composition of taxa and recruit abundance. Pairwise comparisons of each pair of reefs showed significant differences between all site pairs (P=0.01). Acroporidae and Pocilloporidae recruits ranked first and second (respectively) as to their relative contribution to the similarity of sites within each reef (results from SIMPER analyses). The combined percentage contribution to the degree of dissimilarity between reefs (for two summers and two winters) of these two taxa was 57%, 64%, and 58%, for Green, Upolu, and Michaelmas reefs, respectively. In conclusion, the relative proportions of the Acroporidae and Pocilloporidae were most important to the discrimination of early recruitment patterns at the inter-reef scale. This result may also explain the pattern of fore and back reef sites in the MDS plot.

3.3.4. Depth Differences in Early Recruitment at Green Island

In the first summer of this part of the study, very few recruits(<5 /tile) were found on the top outer surface indicating that no distinctive change in preferred surface orientation was occurring in the deeper positions used in this study. As a consequence, this additional surface was not included in the following analyses.

Total recruit abundances were significantly higher in the 6 m sites compared to the 3 m sites (Table 3.3.2.2). However, this pattern was not consistent for consecutive summers (significant depth x year interaction, Table 3.3.2.2). Figure 3.3.4.1 shows that significant differences were due to a combination of pronounced lower depth abundance at shallow sites in summer 1989/90, and similar abundances at both depths in the first (1988/89) summer. Non-Pocilloporidae recruits showed an identical pattern to the total recruitment pattern (Table 3.3.2.2; Figure 3.3.4.1). A different pattern was exhibited by recruits in the cryptic habitat where the significant interaction term is indicating that recruit abundances were higher at shallower sites in summer 1988/89. Consequently, the ANOVAR is indicating that there is no significant differences between the 2 depths overall.

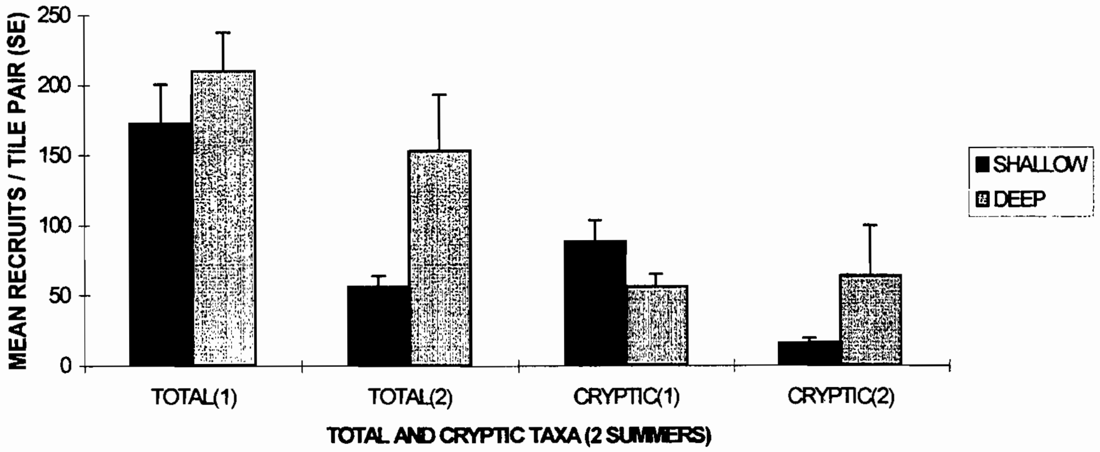
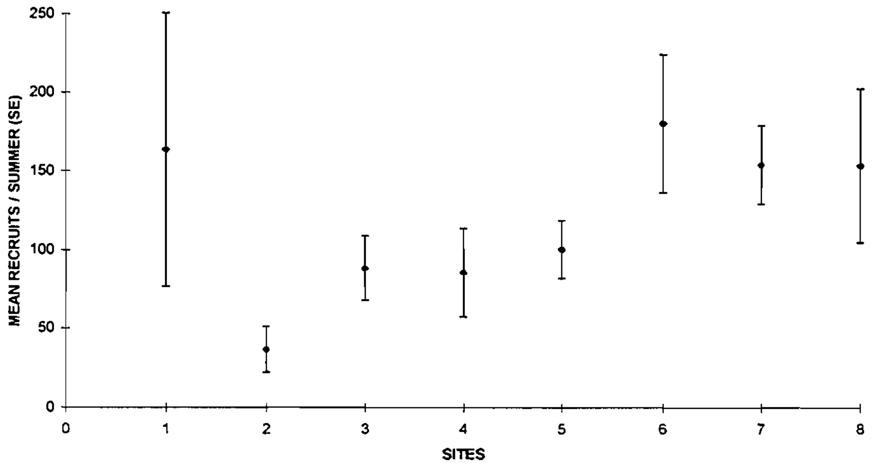


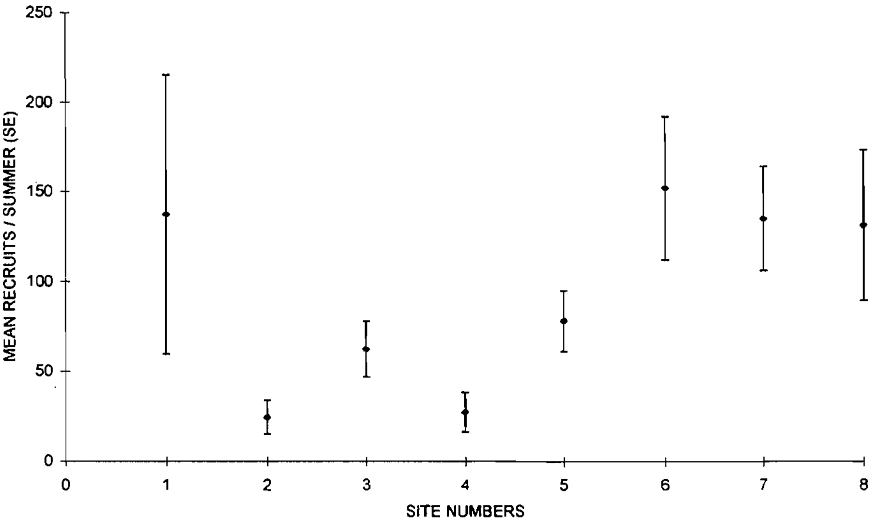
Figure 3.3.4.1. Depth comparisons of Green Island total early recruitment data (from two consecutive summers, (1) 1988/89 and (2) 1989/90). Data are presented from all surfaces and from the cryptic habitat. Shallow = approximately 3m depth; Deep = approximately 6m depth.

3.3.5. Spatial Consistency of Early Recruitment

No consistent spatial pattern of pooled (total) or Pocilloporidae early recruits was detected among eight sites on Green Island (data from four consecutive summers from 1986-87 to 1989-90, Figures 3.3.5.1 (A-C), Table 3.3.5.1). The null hypothesis was that the sites do not agree predictably in their ranking. In contrast, a consistent pattern of site ranking was demonstrated by recruits of Acroporidae.



(A) Total Early Recruitment



(B) Acroporidae Early Recruitment

Figure 3.3.5.1. Spatial consistency of early recruitment at eight sites around Green Island for four consecutive summer periods from 1986/87 to 1989/90. Data are presented as (A) total recruits, (B) Acroporidae, and (C) Pocilloporidae.

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(C) Pocilloporidae Early Recruitment

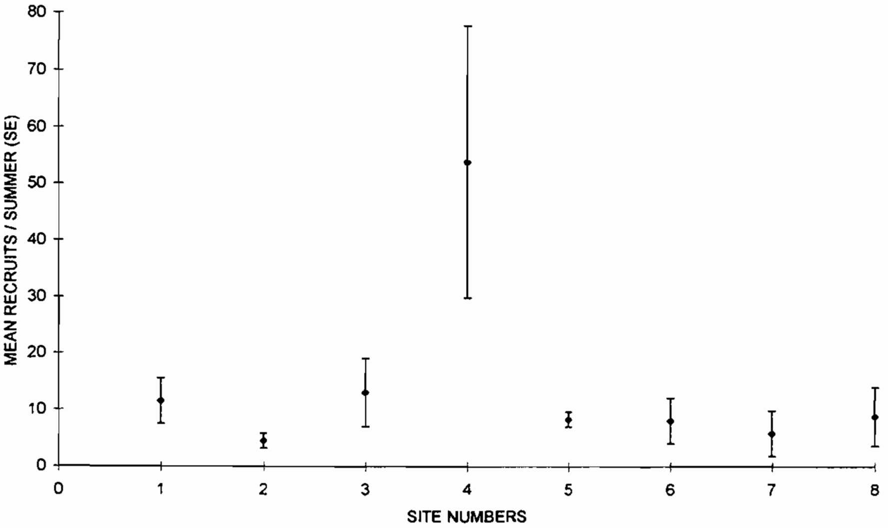


Figure 3.3.5.1. Spatial consistency of early recruitment at eight sites around Green Island for four consecutive summer periods from 1986/87 to 1989/90. Data are presented as (A) total recruits, (B) Acroporidae, and (C) Pocilloporidae.

VARIABLE	FRIEDMAN STATISTIC	P
TOTAL RECRUITS	13.83	0.054 (NS)
ACROPORIDAE	19.52	0.007 (S)
POCILLOPORIDAE	12.77	0.078 (NS)

Table 3.3.5.1. Results of non-parametric Friedman's test for spatial consistency of abundance of early recruit at eight sites at Green Island for four consecutive summer periods. Significant level (P) is set at 0.05, and degrees of freedom = 7.

Figure 3.3.5.1 shows the spatial consistency of early recruitment for each Green Island site using the mean number of recruits per summer for 4 consecutive summers. Total and Acroporid recruits have relatively similar patterns as the latter is a major component of the total recruit numbers. The total recruit test (Table 3.3.5.1) was only marginally non-significant and the main reason for this was the substantial variability in abundance of taxa (particularly Acroporidae) at site #1 (Figures 3.3.5.1(A,B). Site #4 clearly had a larger component of Pocilloporidae in its pool of early recruits compared to all other sites (Figure 3.3.5.1(C)).

3.3.6. High and Low Larval Retention Areas at Green Island

Green Island reef has areas identified by hydrodynamic modeling (located on the map in Figure 2.1(b)) as having high and low probabilities for larval retention and consequently high or low potential for early recruitment. These high-low areas showed different recruitment results over two consecutive summers (ANOVA, Table 3.3.6.1 and Appendix 3.3.6.1).

Total recruitment was significantly different between the pre-defined high and low larval retention areas in both years. However, the relative abundance of recruits reversed between the two years with the first year supporting the model predictions (ratio mean recruits/tile pair = 118:99, high:low), while the second year showed mean ratios of 60:98 (high:low). Pocilloporidae were significantly different between the high-low areas in the first year but not the second year.

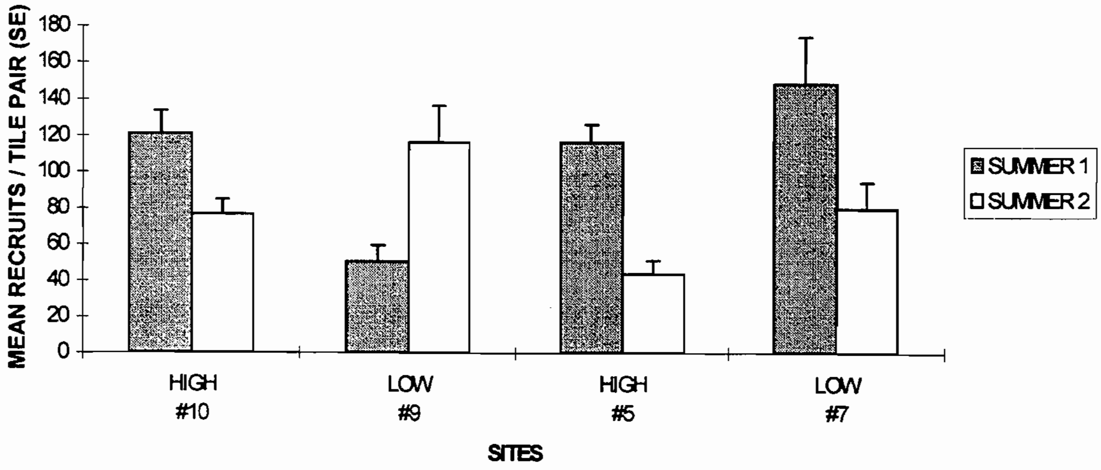
Figure 3.3.6.1(A-C) illustrates the variable patterns of total early recruitment recorded in each of the two summers. In the first summer, the high-low pair of sites #10 and #9 agreed with the predicted pattern, but the reverse of the predicted pattern was shown in sites #5 and #7. In contrast, the predicted pattern was reversed in both high-low pairs in the second summer.

Non-Pocilloporidae had a similar inverse relationship as the total recruits between the two years. Non-Pocilloporidae in the cryptic top inner tile position showed a significant result supporting the modeling predictions in the second year (ratio mean recruits/tile pair = 13:8, high:low). Pocilloporidae results supported the modeling predictions in the first year but not in the second year.

VARIABLE	YEAR	P
TOTAL RECRUITS	1988/89	0.036 (S)
	1989/90	0.001 (S)
NON-POCILLOPORIDAE	1988/89	0.174 (NS)
	1989/90	0.273 (NS)
TOTAL CRYPTIC	1988/89	0.210 (NS)
	1989/90	0.801 (NS)
NON-POCILL.CRYPTIC	1988/89	0.115 (NS)
	1989/90	0.025 (S)
POCILLOPORIDAE	1988/89	0.014 (S)
	1989/90	0.572 (NS)

Table 3.3.6.1. Summary results of ANOVA tests of untransformed early recruitment abundance between pre-defined high and low larval retention areas. The experiment was repeated for two consecutive summer periods but because of inter-annual variation in wind related water movements, the two years were tested separately. Total Cryptic = total recruits in the cryptic top inner tile cryptic habitat; Non-Pocill.Cryptic = non-Pocilloporidae recruits in the top inner tile cryptic habitat. Significance level (P) is set at P=0.05, and NS = not significant, S = significant.

(A) Total Early Recruitment



(B) Non Pocilloporidae Early Recruitment

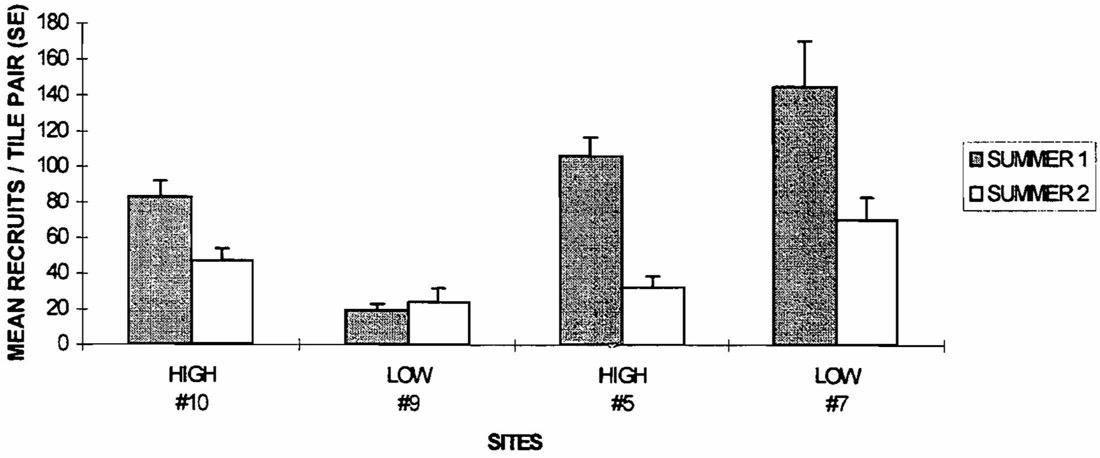


Figure 3.3.6.1(A,B). Early recruitment patterns of (A) total recruits, and (B) non-Pocilloporidae, for two consecutive summers at two pairs of relatively close sitess representing areas of hypothesised high and low larval retention areas. Recruit data are from all surfaces of each tile pair. Sitess refer to the following: H#10 = "high" recruitment site #10, L#9 = "low" recruitment site #9 close to #10 site; H#5 = "high" recruitment-site; L#7 = "low" recruitment site close to #5 site.

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(C) Pocilloporidae Early Recruitment

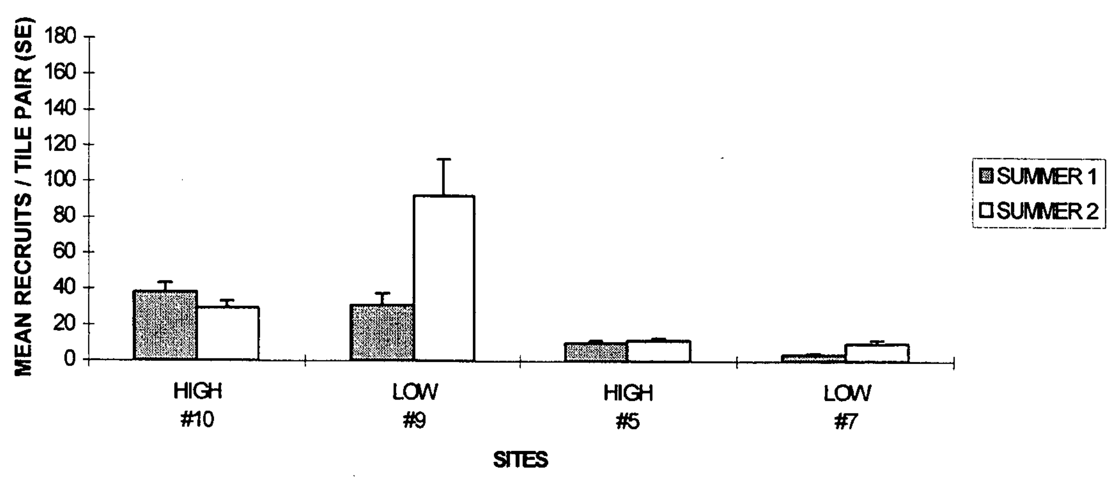


Figure 3.3.6.1(C). Early recruitment patterns of Pocilloporidae for two consecutive summers at two pairs of relatively close sitess representing areas of hypothesised high and low larval retention areas. Recruit data are from all surfaces of each tile pair. Sitess refer to the following: H#10 = "high" recruitment site #10, L#9 = "low" recruitment site #9 close to #10 site; H#5 = "high" recruitment-site; L#7 = "low" recruitment site close to #5 site.

YEAR	SITE 5 (HIGH)	SITE 7 (LOW)	SITE 9 (HIGH)	SITE 10 (LOW)
1	9.0	3.3	56.0	31.3
2	30.2	11.6	86.8	41.4

Table 3.3.6.2. Percentage of Pocilloporidae early recruits (of the total recruits) at each of the larval retention experimental sites for the years 1988/89 (year 1) and 1989/90 (year 2).

The contribution of the Pocilloporidae towards the total abundance pattern was particularly significant at the northern sites (#9, #10) in both years, and at site #5 in year 2 (Table 3.3.6.2). In contrast to the total and non-Pocilloporidae recruit patterns, the percentage contribution of Pocilloporidae in both summers matched the predicted pattern for high and low retention areas (Table 3.3.6.2), though the ANOVA analyses using numbers of

Pocilloporid recruits were significant in year 1 but not in year 2 (Table 3.3.6.1; Figure 3.3.6. l(C)). This discrepancy is because the predicted pattern was reversed over the 2 separate years by agreeing with the prediction in the first year in the high-low sites (#10, #9), but agreed with the predicted pattern (or approximately so) in the other two site pairs (#5, #7) in both years.

3.4. Discussion

3.4.1. Inter-Reef, Within Reef, and Seasonal Patterns of Early Recruitment

This study has demonstrated that similar reefs within the mid shelf zone (defined by their position on the continental shelf of the Great Barrier Reef) have different taxonomic and relative abundance characteristics of early recruitment. That is, there are differences in the rank abundance of major families such as the Acroporidae, Pocilloporidae, and Poritidae, between reefs. Variability in spatial pattern was evident over scales of 10 m to several km. In addition, significant variability was shown over temporal scales of six months to five years within a reef. Habitat variability was demonstrated in two of the three study reefs (Upolu and Michaelmas) where there were generally higher abundances in the back reef compared to the fore reef. Also, there are differences in the overall mean recruitment between reefs. These results are consistent with findings of similar variability among habitats and between years in fish recruitment over similar spatial and temporal scales on the GBR (Doherty and Williams 1988).

The relative abundance of recruits of Acroporidae and Pocilloporidae was found to contribute most to the differences between the three study reefs. Fisk and Harriott (1990) and Sammarco (1991) noted major differences in taxonomic composition of early recruitment between near shore reefs and mid and outer shelf reefs of the Great Barrier Reef, respectively. This study confirms the mid shelf pattern noted by both the above studies where the majority of recruits are from the Acroporidae family. Sammarco (1991) also recorded differences in patterns of recruitment between mid shelf and outer shelf reefs but his study was inconclusive because the data did not separate the effects of transplantation of settlement plates which were moved between reef zones and the effects of differences in seasonal recruitment patterns.

This study indicated that at similar depths and at spatial scales over several kilometers, total summer recruitment varied significantly between years. Temporal variations in early recruitment between summer periods have been noted by Baggett and Bright (1985), Wallace (1985a,b), and Fisk and Harriott (1990). In Wallace's (1985) four year study, major temporal variation in early recruitment occurred in the shallow reef flat and crest sites while the deeper sites had relatively consistent recruitment.

The taxonomic composition of early recruits over the summer period confirms similar conclusions from previous studies on the Great Barrier Reef (Harriott 1985, Wallace 1985(a,b), Wallace *et al* 1986, Fisk and Harriott 1990, Sammarco 1991). That is, summer recruits are mainly composed of the families Acroporidae, Pocilloporidae and Poritidae (in decreasing rank abundance), and in most studies, these three families comprise more than 90% of all early recruits. Furthermore, Acroporidae generally represent between 50% and 90% of all summer early recruitment. In contrast, the winter period recruitment was dominated by Pocilloporidae and the abundance of total recruits were relatively low compared to the summer period. A similar conclusion was noted by Harriott (1985) from her eighteen month study of a single patch reef at Lizard Island.

The potential influence of recruits from planulating (eg, brooding) species as opposed to broadcast species did not significantly affect the overall conclusions in this study. This was an important finding despite the relatively low number of known brooding species on the GBR (14 from 147 species studied, Willis *et al* 1985). For example, other studies have indicated that there are reefs where there is a significant proportion of recruits from planulating species in summer (Babcock 1985). For the two year period of this study, the contribution of brooding species to the total early recruitment pool was significant in terms of abundance, particularly during the winter months. The Pocilloporidae were the major brooding group at these reefs with very few brooders such as the Isoporan *Acropora* spp recruits (Willis *et al* 1985), *Heliopora* spp recruits (external brooders, Babcock 1990), and likely planulating *Porites* species. Brooding *Porites* spp (Kojis and Quinn 1981) may be significant contributors in winter to the higher total abundance of recruits of this family at Michaelmas reef.

On a broader scale to the present study, differences in composition and abundance of early recruitment between Pacific and Caribbean Oceans have been noted by Sammarco (1985). The major difference was in taxonomic composition where the Caribbean reefs appear to be dominated by *Agaricia* and *Porites* spp. (Bak and Engel 1979, Tomascik 1991, Smith 1992), compared to the Pacific where Acroporidae are dominant. An additional difference not noted by Sammarco (1985) is the apparent dominant advantage of the brooding mechanism in the Caribbean. For example, Smith (1992) noted that *Porites astreoides* (98% of all recruits in his study) was a brooding species and its pattern of recruitment contrasted with other poorly recruiting broadcaster species also present in his Bermuda study. In contrast, *Agaricia* spp. was the most abundant recruit from studies at East Florida Gardens (Baggett and Bright 1985) and St. Croix (Rogers *et al* 1984). It has been demonstrated from the Pacific and Indian Oceans, that early recruitment at some temperate coral reef locations are also dominated by brooding coral species (e.g., Lord Howe Island, Harriott 1992; and, by inference from genetic studies, at Rottnest Island Western Australia, Stoddart 1988).

3.4.2. Depth Comparisons

The present study at Green Island reef has been the only study to date to present an investigation of both spatial and temporal aspects of depth effects on recruitment. Here, recruitment at two different depths at Green Island reef was not consistent over 2 summer periods. In the first year there was little difference in recruitment with depth, and in the second year there was a distinct preference by recruits for the deeper (6 m) sites. Depth variation in abundance has been described in a number of studies, but these data were usually unreplicated either spatially or temporally, resulting from annual or inter annual studies down a single site slope (Birkeland 1977; Birkeland *et al* 1982; Bak and Engel 1979; Wallace and Bull 1982; Wallace 1985a); or from a small number of sites (Harriott 1985; Sammarco 1991; Rogers *et al* 1984). Sammarco (1991) also compared a small number of sites from three reefs situated at different cross-shelf positions on the GBR. From these studies certain depths showed relatively higher or lower recruitment but the patterns differed between areas. As a result, studies have concluded that shallow sites (<2 m depth) can have the highest recruitment in certain studies (Harriott 1985); high inter annual variations in other studies (Wallace 1985a; Wallace and Bull 1982); or conversely, sites at 12-18 m depth showed relatively higher recruitment (Birkeland 1977; Birkeland *et al* 1982; Rogers *et al* 1984; Sammarco 1991). In contrast, Bak and Engel (1979) recorded little variation in abundance over a depth range of 3-37 m in a study from the Caribbean.

Depth differences in recruitment rates among the above studies need to be assessed in the context of regional differences in light and sedimentation regimes as these factors can influence recruitment (Birkeland 1977; Birkeland *et al* 1982, Sammarco and Carleton 1982; Rogers *et al* 1984; Wallace and Bull 1982). Environmental conditions were not mentioned in any of the studies investigating depth differences so comparisons of for example light and sedimentation regimes between these studies is not possible to explain the variation in results. In general terms, light increases and sedimentation decreases on the GBR from inshore to offshore reefs (pers.obs.). The difference in recruitment patterns at Green Island reef could have been a result of very different environmental conditions that favored recruitment at both depths in the first year, but favored only the deeper sites in the second year. Willis and Oliver (1988) noted that the distribution of coral planulae in the water column soon after mass spawning varied according to wind strength which probably affected the degree of mixing, but by the fifth day after spawning, similar densities were observed down to 20 m depth. If this is generally true for patches of planulae, temporal environmental variability within sites (which affect settlement selection by the planulae) is implicated by the available data as being the reason for the seasonal relative differences in recruit abundances between depths.

3.4.3. Spatial Consistency Between Sites

This study has demonstrated that there is a consistent pattern of relative abundance of Acroporidae early recruits at the eight Green Island sites. Wallace (1985a) also noted a consistent pattern over a five year period, with occasional deviations, at her reef slope series of sites extending to 20 m depth within a single area. Wallace's study showed that each depth site had a characteristic rate of recruitment relative to the others. The present study indicated that differential early recruitment on a broader spatial scale (kilometers) and at the same depth (3-6 m) can also occur consistently, particularly for broadcast spawning species.

The degree of influence of dispersal mechanisms will have an effect on the arrival of propagules from other reefs and from other parts of the same reef. Brooding species tend to settle near to the adults (Stoddart 1988) in the absence of strong water movement, therefore, brooding species' recruitment can also affects the interpretation of spatial patterns of overall coral recruitment. In the present study, a single site on Green Island clearly had a relatively large Pocilloporidae component to its recruitment pool. Consistent local supply of larvae of brooding species should increase the probability of abundance consistencies between sites but the remaining sites showed a similar relatively low abundance of recruits of brooding taxa over four summers. High abundance of recruits of planulating species were recorded by Babcock (1988) where there was a significant difference among sites for a single summer. Here, recruitment patterns of brooding taxa also did not correlate with the recruit pattern of spawning species, strengthening the prediction that brooding taxa recruitment will be different to broadcast taxa recruitment patterns. The difference is probably due to the tendency of the former to remain in the plankton for shorter time periods than do the latter.

3.4.4. High and Low Larval Retention Areas

Results from most taxonomic groups in the larval retention experiment did not generally support the predicted pattern from the Green Island hydrodynamic model over a two year period, though a significant difference between the high-low areas was detected in both summers for pooled coral recruits (despite the fact that the predicted high-low areas recorded the reverse rank order). The exception was the recruitment pattern of recruits of Pocilloporidae which showed a significant difference (in the rank order of the prediction) between a high-low pair in the first summer. Pocilloporidae should be expected to be strongly sourced from local populations and to recruit locally on a frequent basis (Stoddart 1988, Harrison and Wallace 1990). Therefore, the concept of larval retention within a reef may be more applicable to self-seeding processes involving locally produced planula than to intra- and inter-reef supplies of broadcast recruits. In contrast, Sammarco and Andrews (1988) and Andrews *et al* (1988) reported on a study which tested recruitment to a single pair of high-low larval retention areas on Helix Reef (GBR). The model was verified with wind and tide data from a single summer datum, and the majority of early recruits recorded were not brooding taxa (eg, Pocilloporidae). Despite the single sample period (one summer) in this experiment, it has been the best test of the hypothesis to date. Also, the results are in contrast to the above conclusions from Green Island on the applicability of the hypothesis to brooding taxa.

Since the early recruitment data from all tested groups provide a relatively accurate confirmation of high and low areas in the first year of the present study for one of the site pairs (#10, #9), the discrepancy in the second high-low site pair may indicate fine spatial scale inaccuracies of the model. The inaccuracies were possibly due to the relatively short distances between predicted high and low retention areas (sites #5, #7, respectively) and an insufficiently small grid size used in the model. Alternatively, the placement of recruitment panels may not have replicated the predicted position of high and low retention areas. Such inaccuracies were illustrated by the reversal in relative abundance of total recruits between high and low areas along the southern slope pair (#5, #7) between the two summers, and similar total abundance in the first year between the northern high-low areas (#10, #9).

Alternatively, the northern and southern high-low differences may not occur simultaneously each summer period. That is, conditions favorable for a high-low recruitment pattern to be established at one location are probably not present at the other location during that same time period.

Surface coral slicks correlate well with higher concentrations of live planulae in the plankton (Oliver and Willis 1987), consequently the presence and behaviour of coral slicks can be used as an indication of the presence and behaviour of high larval density areas. The model predictions for Green Island are also partially backed up by my observations of the behaviour of mass spawning slicks around Green Island during the 1990/91 summer (following the second sample year). A large coral spawn slick was located along the S-SE slope region during the four days following the mass spawning night in early December, and the slick was orientated roughly parallel to the crest (see Figure 2.1(b) for an illustration of this description). The surface slick feature was indicative of a relatively high abundance of live planulae below water to a depth of at least 1 to 2m (pers.obs.). In calm conditions and in northeasterly winds, the slick was generally located in the southern end of the reef edge (within the region of the "high retention" area and site #5), but moved to a more westerly position along this edge when easterly winds increased (that is, in the vicinity of the "low retention" area and site #7). The slick tends to be located in the south east section of the reef in northerly winds. During this time there was not a similar well defined planulae concentration on the north eastern reef edge as predicted by the model. However, under other wind conditions I have frequently observed a tidal convergence region in this area where other plankton are concentrated. The concentrations are obviously a result of tidal water masses converging from different directions in this corner of the reef.

3.4.5. Hydrodynamic Processes

Hydrodynamic processes are implicated in the spatial and temporal variations in early recruitment outlined in this study. The supply of larvae to reefs is from adults within the parent reef (self-seeding) or from distant reefs upstream (inter-reef dispersal). Oliver and Willis (1987) and Willis and Oliver (1988) concluded from their multi-disciplinary studies that boundary layers between water masses (Hamner and Wolanski 1988), and wake and eddy systems behind reefs can cause concentrations of larvae. These larval patches vary in space and time and persist after surface slicks originating from mass spawning events have broken up (Willis and Oliver 1988). These authors also concluded that inter-reef dispersal is possible for broadcast spawners during all wind conditions and that the self-seeding of reefs, particularly in lagoons, can occur in calm wind conditions.

Sammarco and Andrews (1988) thought that self-seeding mainly occurred at their study reef though the data they presented did not support this conclusion. The concept of self-seeding reefs has been postulated by hydrodynamic numerical models (Black *et al* 1991; Black 1988) particularly where there are areas within reefs which have relatively lower water speeds and presumably relatively higher larval retention times. The question of the existence or not of predicted areas with different residence times of water masses may be connected to the existence of features associated with topographically-controlled fronts and current shear (Oliver *et al* 1992).

Ideally, real time wind and tidal current data should be included in any test of models using long term wind and current data, as annual differences in these factors can vary significantly. Currents are predominantly wind-driven in the region of the three study reefs except under calm conditions where the weak East Australian Current influences the motion of water masses (Wolanski and Pickard 1985). Both mechanisms result in mainly southerly water flow during the period when most coral larvae are present in the water column. Models of hydrodynamics in the Cairns section of the Great Barrier Reef (Dight *et al* 1988,1990) indicate that Green Island reef is in the direct path of most wind generated longshore currents, whereas Upolu and Michaelmas reefs are more marginally located with respect to these currents. This could in itself offer an explanation for the higher abundance of total recruits at Green Island compared to the two reefs to the north, assuming inter-reef larval transport is occurring, and that the influence of within reef brooding species is not significant.

Eddy formation in the lee side of a reef would be expected to enhance larval availability (both natal and external) in these locations (Willis and Oliver 1988). The results of this study suggest that mechanisms such as broad eddy formations in the lee of each reef could be influencing the differences in relative abundance between the fore and back reef locations. Spatial patchiness within back or fore reef locations can be further explained by the concept of predicted areas of higher and lower larval retention. However, hydrodynamic models using long term current and wind averaged conditions were not confirmed empirically in this study. The exception to this was for Pocilloporidae recruits which fitted the predicted pattern in one of the two summers. Wind directions and speeds for the period four to six days after the mass spawning times in the second (1989) summer generally were not typical of long term wind patterns, which show a predominantly northerly wind direction (Table 3.4.1).

From my observations on local slick behaviour, the more easterly wind direction in November 1989 would mean a movement towards the west of water masses with relatively high planula concentrations, especially associated with a slick (ie, towards low retention site #7). This pattern was reflected in Pocilloporidae recruitment, but not non-Pocilloporidae recruitment, for that summer. The conclusion on the influence of larval retention mechanisms is therefore equivocal as the local presence of adult Pocilloporidae populations may also explain the observed pattern, given that large populations do exist near predicted high retention areas in the vicinity of sites #5 and #10 (pers.obs.).

The pattern of visible juvenile recruitment in areas where detailed early recruitment data are available is the subject of the next chapter. The large variations shown in the composition and abundance of early recruits among sites where visible recruitment was studied, should be useful in demonstrating the degree of control recruit supply has on the visible recruitment dynamics of corals at Green Island.

YEAR	DATE	DAYS AFTER	WIND SPEED	WIND DIR.	NOTES
1988	28 NOV.	0	6	SSE	
	29 NOV.	1	3	NE	
	30 NOV.	2	6	NNE	
	1 DEC.	3	0	CALM	
	2 DEC.	4	14	S	RAIN
	3 DEC.	5	0	CALM	
	4 DEC.	6	10	SE	
1989	17 NOV.	0	8	E	
	18 NOV.	1	6	N	SLICK
	19 NOV.	2	6	NNE	SLICK
	20 NOV.	3	10	ENE	SLICK
	21 NOV.	4	10	S	RAIN
	22 NOV.	5	6	E	RAIN
	23 NOV.	6	12	ESE	

Table 3.4.1. Meteorological observations (at 3 pm) of wind speed and direction from nearby Fitzroy Island during the annual mass spawning periods at Green Island during 1988 and 1989. Rain records may indicate that winds were variable and short lived. 'Slick' refers to slick formation on Green Island reef. Wind speed is in knots, and 'wind dir' refers to the compass direction of the wind. 'Days after' refer to the number of days following mass spawning nights.

Chapter 4. Visible Coral Recruitment in Quadrats

4.1. Introduction

Recruitment studies on coral reefs have generally been instantaneous (ie, from a single sample time) and broad scale, with interpretation of recruitment inferred retrospectively (Endean 1976). Alternatively, the data have been recorded remotely (eg, by still photography) with recruitment not interpreted *in situ* (Connell 1973; Done 1985); or recorded *in situ* but over a relatively short time (1-3 yrs) and/or at frequent intervals (1-2 mo) (Harriott 1983; Cameron *et al* 1988, Done *et al* 1988, Gittings *et al* 1988). Methods used to repeatedly map defined areas vary among studies with either approximate or exact areas mapped at each sampling time. The former method risks recording the same individual in successive times if growth is slow and recruitment is defined as the sum of all colonies of some small dimension. The former approach also has the potential to interpret the appearance of a new colony as a recruit when it is the result of a fission event or fragmentation event.

The characteristics and dynamics of small visible recruits on natural substrata are important aspects in the study of coral reef recovery as predictions can be made on the regeneration periods and successional processes which lead to the diversity of coral communities observed on the GBR.

Spatial and temporal variation in the densities of juvenile recruits was an important aspect to address in this study since there were significant differences around Green Island in the annual supply of early recruits (Chapter 3 results). The study was designed to complement the early recruitment studies in Chapter 3 which were addressing the supply of new recruits. The aim of this study was to identify quantitative and qualitative differences in visible recruitment (both temporally and spatially) in order to assess the relative influence of post settlement processes.

4.2. Methods

Visible recruitment was followed by repeated mapping and measuring of juvenile corals within permanently marked quadrats on dead standing *Acropora* plates and consolidated substrata. The exact re-positioning of quadrats was done with the aid of previously mapped and identified juvenile corals on the substratum surfaces, along with the relocation of at least one steel stake on or near the dead plate, or in at least two of the four corners of the consolidated substratum quadrats.

The spatial scales I chose to study at Green Island included location differences over 1 to 2 km between back reef and fore reef; sites within locations separated by distances of 100 m to 200 m; differences between 3 m and 6 m depths within each of the sites chosen for the location comparisons; and differences between the two main types of natural substrata which were separated by distances of 1 to 5 m. Using this design it was hoped that both substrate variability and spatial differences in recruitment would be adequately addressed. The 1 m^2 quadrats were located at four sites on Green Island reef, each with groups of three or five quadrats (depending on the study, see following methods section) at two depths (3 m and 6 m) ranging over a portion of slope approximately 20 m x 10 m in area. Deeper sites were established directly down the slope from the shallower sites. Figure 4.2.1.1 gives a diagram of the statistical design of the visible recruitment studies.

Site selection was partially guided by notable features of the slope topography which would aid in relocation under most climatic conditions (Figure 2.1(b); sites 1A, 1B, 3A, 3B, 5A, 5B, 7A, 7B). Sites with the A suffix are all at or about 3 m depth, while sites with the B suffix are at or about 6 m depth. The positions of the permanent quadrats were selected in a haphazard manner with choice partially determined by all or some of the following factors : there was an obvious number of small and already established juvenile corals present within the quadrat; most of the area of a consolidated m^2 quadrat did not include rubble, soft coral colonies, or other large macro-benthos; and quadrat positions were chosen so that all quadrats were able to be relocated under low visibility conditions which meant that all quadrats were not more than approximately 5 m apart. This means that the recruitment data represent the maximum rate expected for the most readily available substrata. This is important when relationships are drawn between early recruitment on artificial tile surfaces (which represent maximum settlement conditions for larvae) and visible recruitment to natural substrata.

Each census was conducted annually during the late spring to early summer period (late October to early December). The time interval between successive visits was important. Too long an interval would result in underestimates of the actual recruitment rate, where a recruit appears and dies between censuses. An annual census on the other hand may miss such shorter term events. As a result, estimates were not made of the number of visible recruits that settled and died in the first approximately 6 months. A preliminary survey of the first four six month periods of study at Green Island indicated that more than 98% of recruits recorded at the end of the first six month period were also present at the end of that year. Thus, the shorter interval mapping (ie, every 6 months) was not continued.

Within each of the two sites established in 1985, monitoring of five consolidated substrata quadrats (1 m^2) and five dead standing *Acropora* plates was established. In November 1988, three replicate quadrats at 3 m and 6 m depth and for each of the two substratum types, were established in two additional sites at back reef and fore reef positions. This meant that from 1988 to 1990, a total of 64 quadrats were monitored (32 consolidated and 32 dead plates) for annual recruitment. Additional data are also available for longer term trends from a subset of 40 quadrats which were followed from 1985 to 1990 (Figure 4.2.1.1).

Recording *in situ* recruitment on the same dead coral plate over a number of years will not yield absolute densities of recruits for comparison with inter annual densities, but it can estimate annual relative recruitment rates between years (which would be the natural pattern on a reef). That is, this approach carries an assumption that conditions with respect to fouling communities and competition from other coral recruits are similar on all mapped dead plates within each year. The same assumption is made for the annual mapping of quadrats which are consolidated substrata. Rates of recruitment were standardised for the dead plate substrata data by converting recruitment rates per area of dead plate to recruitment per 1 m^2. Three dead plates disappeared (presumably they were broken off in storms and displaced elsewhere or broken up) during the five year study period. All were replaced in the following census period by the closest adjacent plate in similar condition. The most current dead plate outlines were drawn underwater on a 1:10 scale utilising a 1 m^2 quadrat subdivided into 25 smaller grids.

Visible recruits as small as 2 mm diameter (and sometimes smaller) were recorded at each census period. Corals at this size are almost certainly recruits which have settled and survived through the first year, following the previous census (Harrison and Wallace 1990; observations from early recruitment plates, Chapter 3). Corals were identified to species level wherever possible, though many small colonies could only be identified to genus. Maximum diameter was used for all indices of size as the majority of colonies were slightly oval to circular in shape. A 1 m^2 metal quadrat, subdivided with thin nylon rope into twenty-five equal smaller sections (each 20 cm x 20 cm), was used to map colonies and to re-position the quadrat each year in relation to the previous years map. Colonies which had recruited or had undergone fission during the previous year were also noted. Daughter colonies from fission events were not included in estimates of recruitment but were treated separately in the results. This demarcation was chosen so that a distinction could be made between larval recruitment and other forms of recruitment.

After each census, the maps were photocopied and kept for cross-referencing with previous maps, and individual colonies from the previous year's census identified. All new recruit colonies were then given unique identification numbers. The data were entered into a DBASE IV database. The data book aided in interpretation of links between closely associated colonies, particularly those which fused or had undergone fission. Records were also made in the field on the likely origin of colonies if they were interpreted as not being the result of larval recruitment.

The analyses of trends in visible recruitment concentrated on recruitment rates of *Acropora* species (combined) compared to the massive corals (defined here as the combined rates from Poritidae, Mussidae, and Faviidae species). Recruitment trends in other major taxa found in abundance on the early recruitment tiles were also investigated.

4.2.1. Temporal Trends

Data from the forty quadrats which were mapped for visible recruits for five years were pooled for descriptive statistics. As well, investigations of changes in the proportion of recruits of *Acropora* spp and massive species over the five years and between the two locations, depths and substrate types, were carried out using Chi-square tests. The null hypothesis was that there were no differences in the proportion of recruits of *Acropora* spp and massive species recruits either between years, locations, depths or substrata over the five years.

The accuracy of the technique adopted here for the time made available for field studies meant that replication was relatively low and the more powerful univariate analytical techniques were not always best suited to the interpretation of the data. Pattern seeking, multivariate techniques and recent advances in statistical treatment of such data has fortunately advanced to the point where this study design is information rich whilst retaining maximum accuracy and precision.

Diversity indices based on numbers of colonies of visible recruits were calculated using the PRIMER software package. The indices were: species richness (as Margalef's D), Shannon-Wiener diversity (H') using $\log_e$ in calculations, evenness (as Pielou's J), and Simpson's dominance index. K-dominance plots were calculated using the same visible recruitment data input files used in the above analysis to assess the degree of dominance of recruits from Green Island sites followed for five years. Plots are presented for comparisons among years, locations and 3 m and 6 m depths. The plots contrast with the above diversity indices, as they emphasise dominance over richness. That is, they reduce the weighting of abundant taxa (Field *et al* 1982) and therefore do not provide a measure of species richness but rather an inverse relationship with diversity (Lambshead *et al* 1983; Magurran 1988). ANOVAR was used to test for differences in these diversity indices among the five years, two locations, and two depths. Genera were pooled from all quadrats within each site to give realistic estimates of visible recruitment diversities at each site. The two depths within each site were used as replicates, and therefore the test of depth effects was not available.

In the univariate ANOVAR analyses, the main effect of location in the ANOVAR was not taken into consideration due to the lack of replication (only one back reef and fore reef site was followed for the five year period). The other factors of depth and substratum were treated as fixed effects. The within-subjects main effect of year is the major theme in these data, along with the interaction terms of year with substratum and depth. The interaction term between substratum and depth is not relevant to temporal change. A diagram of the statistical design for both temporal and spatial analyses is presented in Figure 4.2.1.1.

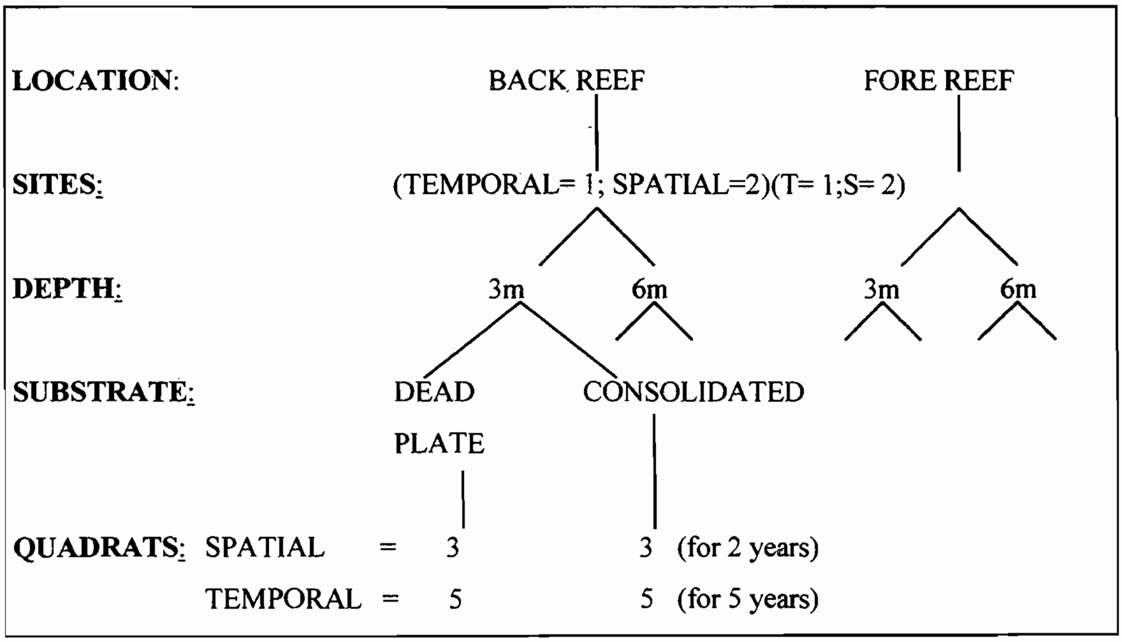


Figure 4.2.1.1. Statistical design used for the analysis of visible recruitment data. One site each (with two depths) in the back reef and the fore reef was used for the temporal analysis (covering five years from 1986 to 1990). Two sites each in the back and fore reef locations were used for the spatial analyses, covering two years of data from 1989 and 1990.

In only one variable (pooled hard coral recruitment rate) did the transformed variances remained heterogeneous according to Bartlett's and Levene's test for homogeneity, so a non-parametric test (Kruskal-Wallis test) was employed using time as the grouping factor.

Statistical treatment of the five year temporal data used the between-subject sources of variation which were the same as for the two year spatial study, though the main focus of investigation was the within-subject factor of year (see Appendices 4.3.1-2 for details of ANOVAR (repeated measures) designs for both the temporal and spatial studies). The within-subject factor of year in the spatial study was secondary to the aims of this section though results were incorporated when significant differences were detected as this period is concerned with the shorter temporal trends between 1988 and 1990.

A posteriori general linear contrasts (Wilkinson 1990) were conducted on the within-subject main effect (time) whether a significant result was produced or not. Tests (probability value at $\alpha = 0.05$) were made of a range of combinations of years from tests of adjacent year means, to differences between varying combinations of means from one or more years. Most interest was on the time period up to 1988 and the two following census years. This appeared to be a period in the successional process where a distinct change in the processes affecting the community occurred (see discussion).

The SYSTAT output included equivalent multivariate analyses for the within subject (temporal) terms. Results for Pillai trace analyses were noted, and where significant multivariate results differed with the equivalent (non-significant) ANOVAR test factor, the multivariate outcome was adopted as it is considered to be a conservative test (Tabachnick and Fidell 1989).

4.2.2. Spatial-Habitat Trends

The spatial study was primarily concerned with the main (between-subjects) effects of location (back reef/fore reef), substrate (consolidated/dead plate), and depth (shallow/deep). Similar ANOVAR to the temporal trend analyses were used to investigate spatial patterns of visible recruitment for the two year period from 1988 to 1990 (see Figure 4.2.1.1 for a diagram of the statistical design). Three quadrats from the two sites used in the temporal analysis were used here along with the three quadrats from each of two additional sites established in 1988.

Quadrats were mapped in the same sequence as the initial census, and the first three quadrats from sites established in 1985 were chosen for the spatial pattern investigations. The data used here contained many zeros (particularly for 1990) when individual quadrats were used as sample replicates. Therefore, recruitment rates were pooled for three quadrats from each site and depth, which further reduced the power of statistical tests. The two sites in each location were nested terms and all of the factors were considered to be fixed. The time factor was used to investigate a shorter period from 1988 to 1990 which I considered important because it was the period where a definite transition in recruitment patterns occurred in the coral community. This transition correlated with a rapid increase in the formation of an overtopping canopy in most of the quadrats and in the surrounding community. The following categories of coral were tested : combined hard coral, *Acropora* spp., Faviidae, Poritidae, and combined massives (Faviidae, Poritidae, and Mussidae).

4.2.3. Multivariate Analysis of Visible Recruit Data

Non-parametric multidimensional scaling ordinations were run on the genera of recruits, testing for patterns in the spatial-habitat parameters and the two sample years. The PRIMER software package (Plymouth Marine Labs) was used for all multivariate analyses. After the MDS plots were produced, differences between these parameters were evaluated using the non-parametric randomisation procedure ANOSIM (Clarke and Green 1988; Clarke 1993). Where ANOSIM tests showed significant differences between stations or locations, the genera contributing the most to the differences between sites or location pairs were determined using a technique called SIMPER (similarity percentages) (Clarke 1993). SIMPER provides a list of taxa ranked in order of their contribution to the average dissimilarity among station pairs.

4.2.4. Effect of Overtopping on Visible Recruitment

Recruitment to substrata underneath overtopping colonies was estimated by noting the position of recruits in the field with respect to the edge of overtopping colonies. Recruits were not included in the estimates of recruits under colonies if they were clearly in an area of substratum overtopped by a colony during the previous year (ie, they were within 2 cm of the colony margin). This distinction should have allowed for those recruits which initially settled in unshaded positions but were subsequently overtopped by rapidly growing margins of the larger colonies between census times. The identification of recruits and of the overtopping species in each case were recorded. This investigation only used colonies from within the quadrats. The presence of overtopping colonies in the quadrats increased over time as the number of overtopping colonies within the quadrats increased.

The proportion of each quadrat shaded by an overtopping colony was estimated from the field maps by calculating the percentage of each 1/25th of every quadrat with greater than 50% of the area having an overtopping colony present. The mean % area of all quadrats with an overtopping colony present was then calculated for each annual census.

4.2.5. Non-Larval Visible Recruitment

Incidences of recruitment into quadrats from sources other than larval settlement were determined in the field using criteria on colonies having more than one of the following attributes : unusually large sizes when first recorded; unusual shapes (especially asymmetrical shapes); presence of limited or no attachment base; and colonies of the same species and colour in relatively close positions to colonies recorded from the previous census. The types of recruitment which relate to the above processes include fragmentation of colonies through colony breakage; immigration of loose colonies from outside the quadrat; ingrowth of colonies from outside the quadrat perimeter; and fission colonies from asexual division of colonies already present within quadrats. The latter probably often occurred as a result of fish grazing activities.

Chi squared tests were run on the frequencies of immigrants, ingrowing colonies, and fission colonies, using both changes over the five year period and differences between major taxa. The null hypotheses were : H_1: there is no difference over time in frequencies of the main sources of non larval recruitment; and H_2: there is no difference in the frequencies of recruit sources among the major taxa. The taxa categories included *Acropora* spp, *Montipora* spp, Faviidae, Poritidae, Pocilloporidae, and all other (pooled) minor taxa.

4.2.6. Plate Disintegration Rates

Areas of dead plates were estimated from the maps using a planimeter and the scaled drawings of dead plate outlines from each census. Their initial sizes varied from 0.3 m^2 to 1 m^2 in area (mean=0.58 m^2, SE=0.05). The areas of most plates continually reduced in size so each year's estimate of recruitment had to be adjusted to the area of dead plate remaining at the time of that census. All dead plates used in this study were probably killed during the 1980-81 crown of thorns outbreak on this reef. That is, all plates were assumed to have been dead for at least four years at the start of the study. The thickness of the dead plates and the current prevalence of the two plate species (*Acropora hyacinthus* and *A.cytherea)* suggest that the dead plates were most likely from these same two species. The more or less similar composition of the epiphytic communities and similar size range of juvenile corals on the plates appeared to support this assumption of the approximate time of death of the plates.

4.3. Results

4.3.1. Temporal Trends

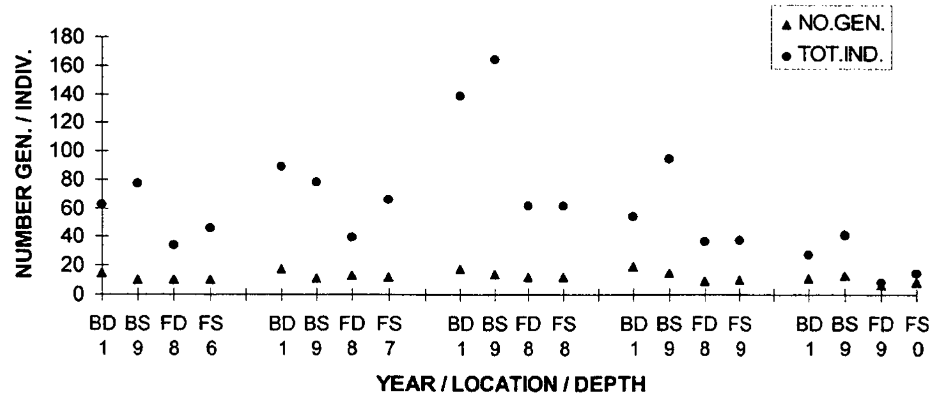
A total of 1841 visible recruits were recorded from the five year study period. The recruits were composed of 46.2% *Acropora* spp, 32% massives species, and 21.8% other recruits. There were 689 massive recruits, with 29% from the family Poritidae and 63% from the family Faviidae.

TAXON		1986	1987	1988	1989	1990
All Taxa	mean	4	5.5	7.3	5.6	2.4
	se	0.5	0.8	1.2	1.0	0.7
Massives	mean	1.8	2.0	3.0	1.6	1.0
	se	0.2	0.3	0.5	0.3	0.3
Acropora spp.	mean	1.9	2.7	3.9	3.0	0.9
	se	0.3	0.4	0.7	0.5	0.2

Table 4.3.1.1. Summary statistics of visible recruitment (mean per m^2, and standard error (se)) from five years of juvenile dynamics at two sites (one each in the fore reef and back reef). Data were pooled from quadrats with two substrate types (dead plates and consolidated) and two depth ranges (approximately 3 m and 6 m) within each site.

The annual recruitment pattern of these major taxa groups is presented in Table 4.3.1.1. The proportion of *Acropora* spp to massive species visible recruits varied over the five year period (χ^2 value = 9.94, df = 4, P = 0.0415). There were also variations between the two locations in the ratio of pooled recruits over a five year period as well as in *Acropora* spp recruits, but not in the ratio of massive recruits (Table 4.3.1.2). Variations in the proportion of *Acropora* spp and massive recruits on the two substratum types also occurred over the five years, but not for pooled recruits. Proportions of any of the recruit classes did not vary between the two depths during the five years (Table 4.3.1.2).

(A) Number of Genera and Total Individuals



(B) Margalef's Richness, Shannon-Wiener, Pielou's Evenness, and Simpsons Dominance

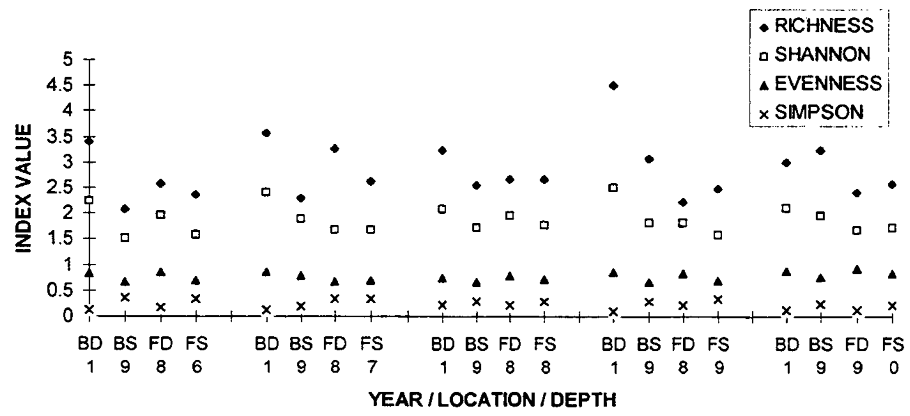


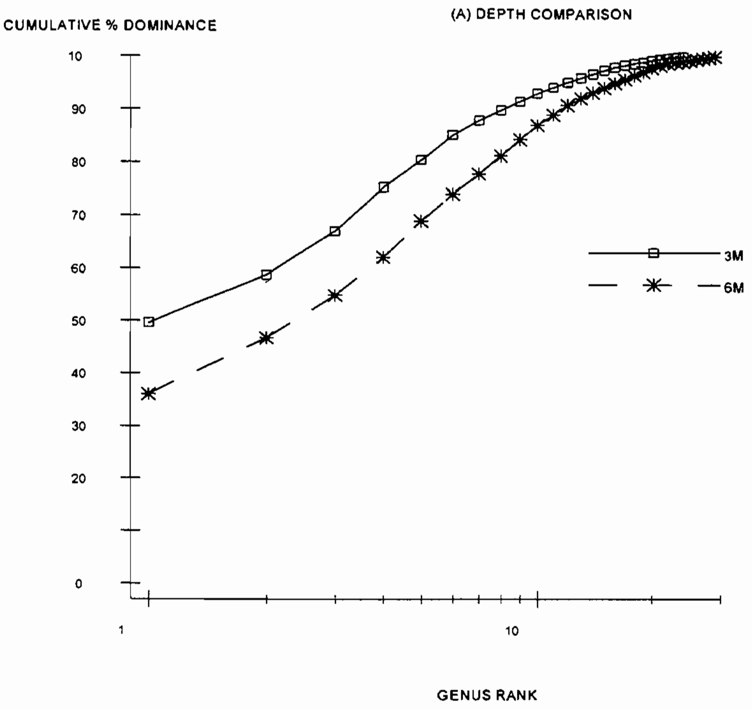
Figure 4.3.1.1. Generic diversity of pooled visible recruits from four sites: (A) numbers of genera and individuals; (B) four diversity indices that include both genera and numbers of individuals in their calculations. Data are from the five year temporal data set and are expressed in relation to the spatial parameters of location and depth, and time. The x axis represents sites from left to right following each census year (1986 to 1990), then each location (back reef (B), fore reef (F)), and two depths of deep (6 m, D) and, shallower (3 m, S) sites. The top graph shows the number of genera and the individual number of visible recruits. The bottom graph shows the four diversity indices of richness (Margalef's), Shannon-Wiener, evenness (Pielou's J), and Simpsons dominance index.

The relationship between generic diversity and spatial and temporal parameters is shown in figure 4.3.1.1. The top graph (A) shows the variability in numbers of individuals in comparison with the relatively constant number of genera. The bottom graph (B) compares four different indices which emphasise richness (Margalef's), evenness (Pielou's J), or dominance (Simpsons). None of these indices were significantly different among years or locations except for the total number of individuals which were different among years (as was as the year x location interaction term; ANOVAR, Appendix 4.3.1.1).

	POOLED		ACROPORA		MASSIVES	
	χ^2 value	P	χ^2 value	P	χ^2 value	P
LOCATION	10.42	0.034	11.43	0.022	4.59	0.33
DEPTH	8.49	0.075	7.4	0.12	4.46	0.35
SUBSTRATE	8.5	0.08	9.9	0.042	9.91	0.042

Table 4.3.1.2. Chi-square tests using three types of visible recruits and comparing differences in ratios of each type between two locations, two depths and two substrates from 1986 to 1990. Significant results at P level of 0.05 are highlighted.

K-dominance plots (Figure 4.3.1.2) calculated for comparisons among years, locations, and depth, show (A) that 3 m depth sites have a lower diversity but higher dominance than the 6 m sites; (B) that there is very little difference in diversity and relative dominance between the back reef and the fore reef; and (C) that in 1986 and 1988, visible recruitment was less diverse than in 1990; recruitment dominance plots from 1987 and 1989 were different in shape to the other three years and crossed most other plots, indicating relatively different visible recruitment characteristics for these years; also, it is apparent that in the moderately abundant genera, the most changes occurred in dominance between years (as shown in the mid sections of the curves).



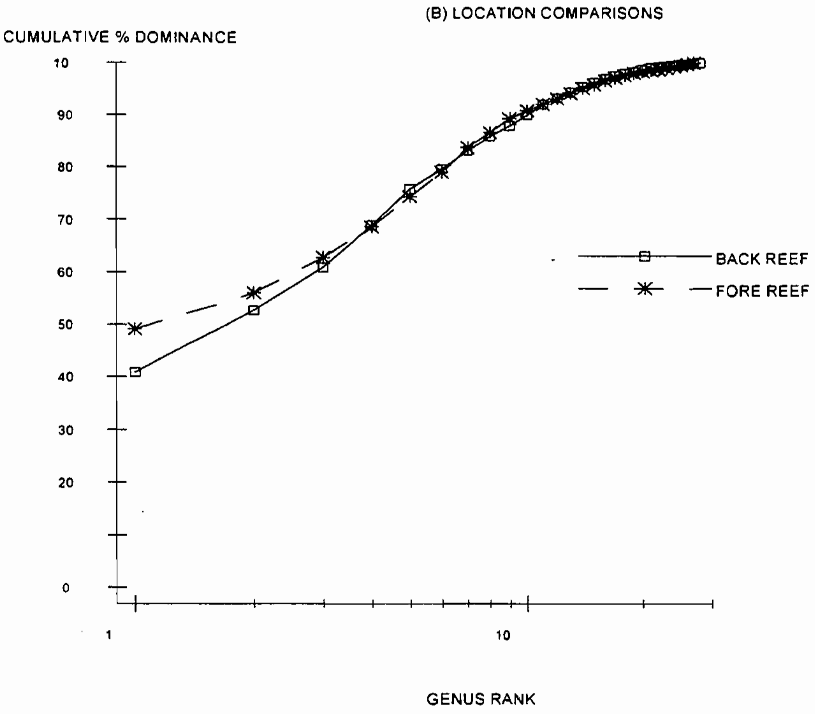


Figure 4.3.1.2. Dominance plots of generic visible recruitment comparing (a) depth (3 m and 6 m); (b) location (back reef, fore reef); and (c) years (1986-90).

(Figure 4.3.1.2. continued over page)

(Figure 4.3.1.2. continued from the previous page)

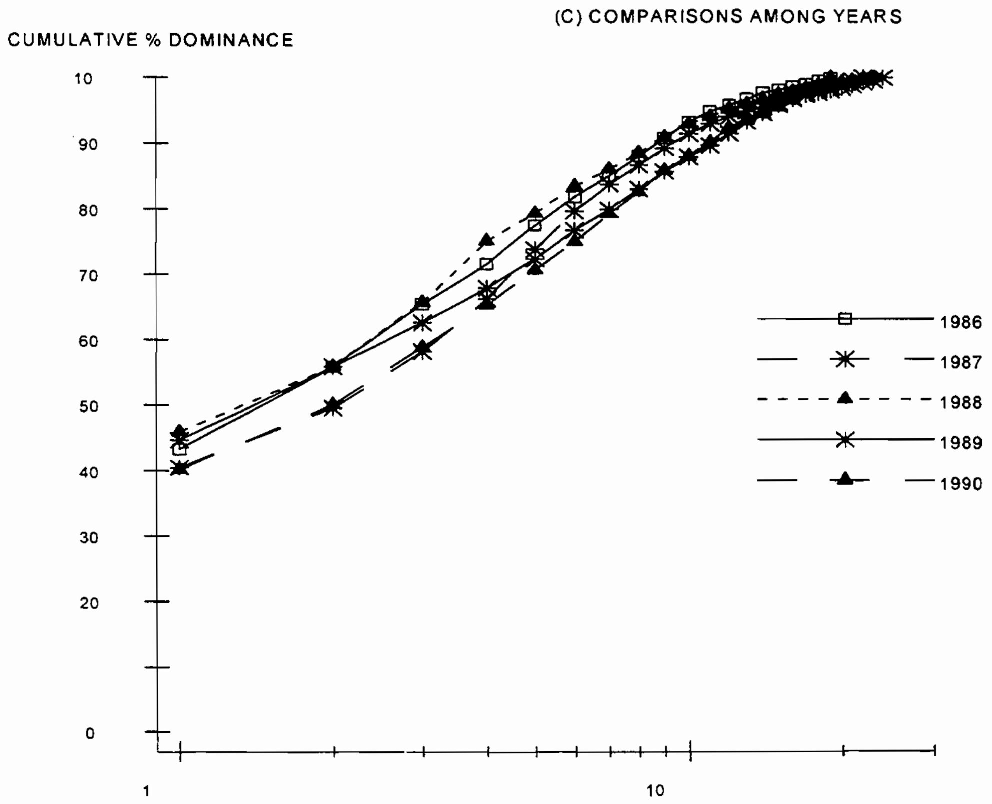
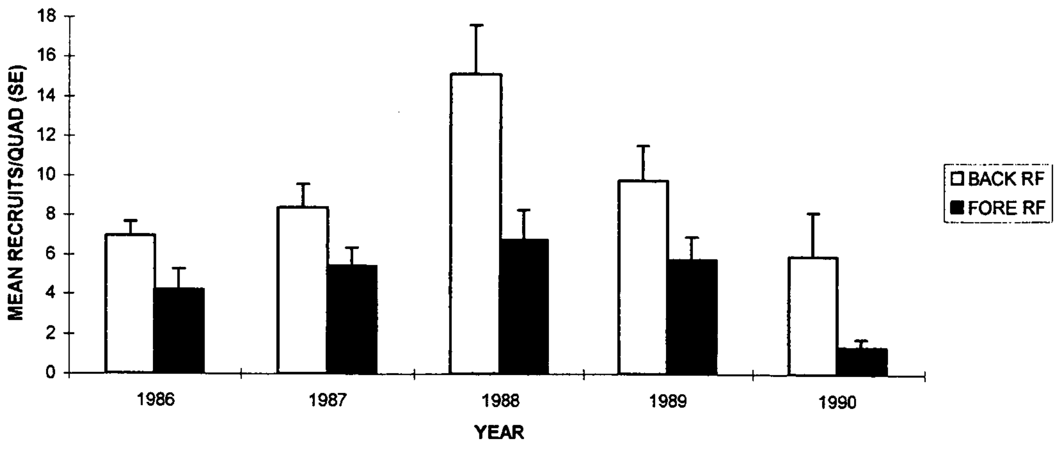


Figure 4.3.1.2. (Continued) Dominance plots of generic visible recruitment comparing (a) depth (3 m and 6 m); (b) location (back reef, fore reef); and (c) years (1986-90).

POOLED RECRUITMENT



MASSIVES RECRUITMENT

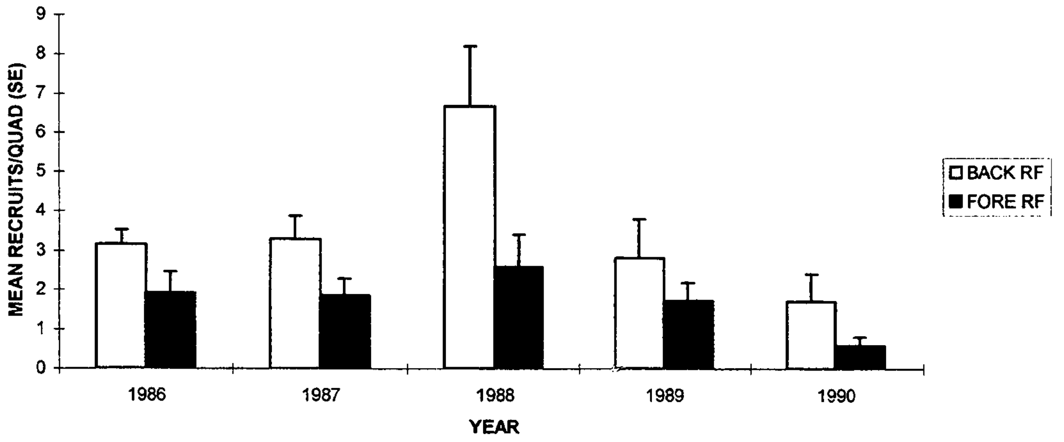


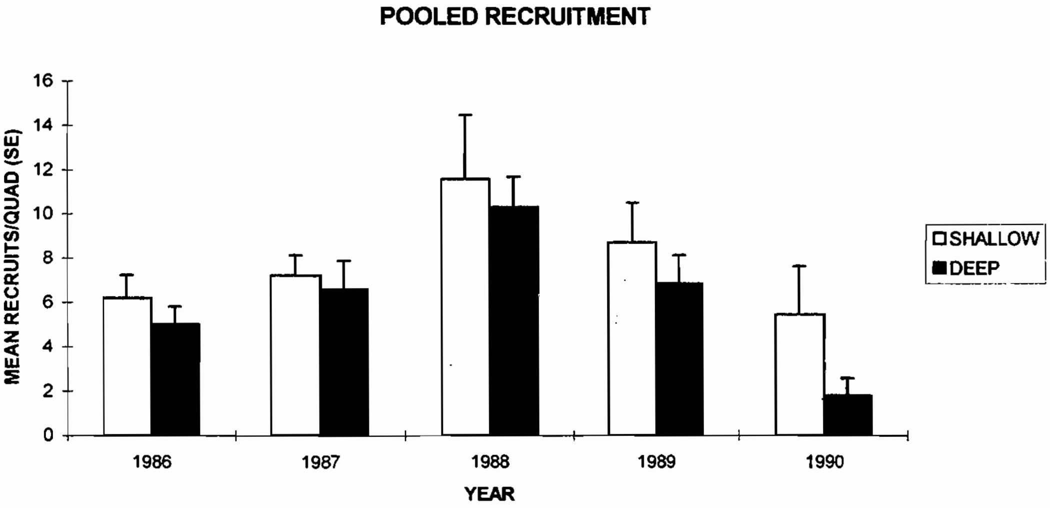
Figure 4.3.1.3. Annual visible recruitment over a five year period from 1986 to 1990. Data are presented as recruits per standardised 1 m^2 quadrat comparing back reef and fore reef patterns for pooled recruits and massive coral recruits.

Pooled taxa recruitment rates showed heterogeneous variances after transformation so a Kruskal-Wallis test was done using time as the grouping variable. The analysis indicated a significant difference in recruitment between years with a range of 3.9 to 5.5 cols/m^2 (K-W statistic=47.2, $P<0.001$; df=4). Figure 4.3.1.3 shows annual recruitment rates between fore reef and back reef locations rising to a peak in 1988 and then falling in the subsequent years. Mean annual recruitment was consistently higher in the back reef compared to the fore reef for both pooled recruits and massive recruits (Figure 4.3.1.3). There were very similar pooled recruitment rates between the two depth regimes (Figure 4.3.1.4) and the two substrate types (Figure 4.3.1.5).

The same conclusion to the non parametric tests was reached when a univariate repeated measures analysis of pooled recruitment was run (see Appendix 4.3.1.2) to investigate *a posteriori* contrasts of combinations of years. Results suggests a clear difference in the combined recruitment rates before and after approximately 1989. *A posteriori* contrasts of adjacent pairs of year means were not significant except for the contrast between 1989 and 1990 which was significant ($P<0.001$; 1989 = 7.7 recruits/m^2, SE=1.1; 1990 = 3.9 recruits/m^2, SE=1.2). Multivariate repeated measures analysis also indicated that there was a significant difference between years (Pillai trace = 0.48, P = 0.001, df = 4,29).

Recruitment rates of *Acropora* spp were not significantly different between years, nor were any of the habitat (spatial) parameters significant in the 5 year data (Appendix 4.3.1.2). However, the multivariate measure, Pillai trace, indicated a significant difference in *Acropora* spp. recruitment between years (Pillai trace = 0.33, P = 0.02, df = 4,29). Tukeys tests showed the significant differences were between 1985 and 1988 mean recruitment (P = 0.012), as well as between 1988 and 1990 mean recruitment (P = 0.001).

Recruitment rates of combined massive species was significantly different between years, but a number of interaction terms involving the year term (Figures 4.3.1.3 & 4; Appendix 4.3.1.2) were also significant. *A posteriori* tests showed no significant differences between adjacent pairs of year means. The recruitment rates of massive species at different depths (Figure 4.3.1.4) and on different substrata (Figure 4.3.1.5) showed a peak in 1988 and then a decline in subsequent years. The multivariate Pillai trace test indicated that recruitment between years was significantly different (Pillai trace = 0.49, P = 0.001, df = 4,29).



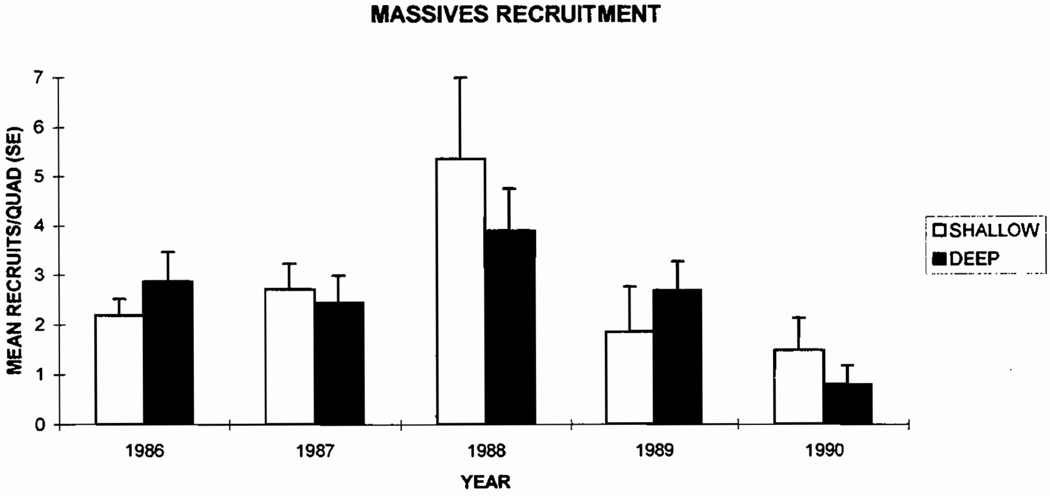
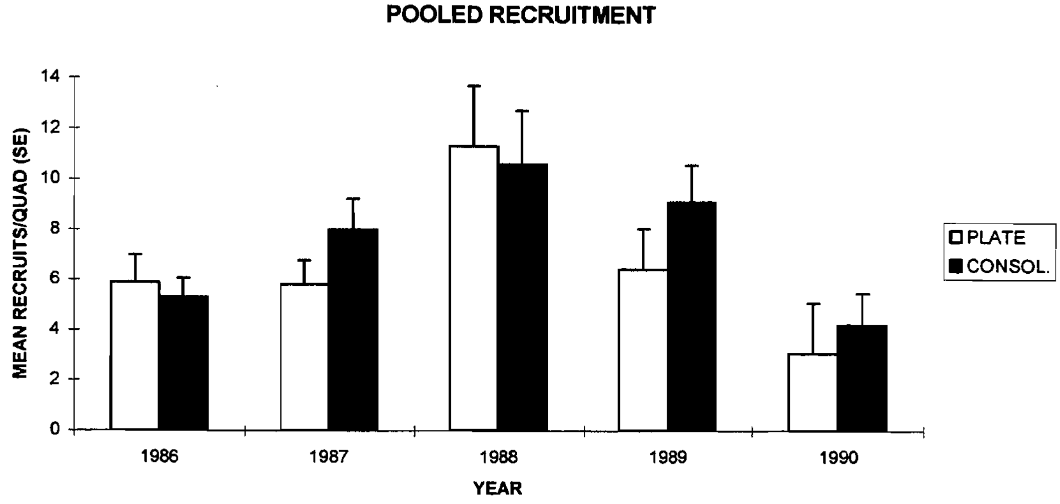


Figure 4.3.1.4. Annual visible recruitment from 1986 to 1990. Data are presented as recruits per standardised 1 m^2 quadrat comparing 3 m and 6 m depth patterns for pooled recruits and massive coral recruits.



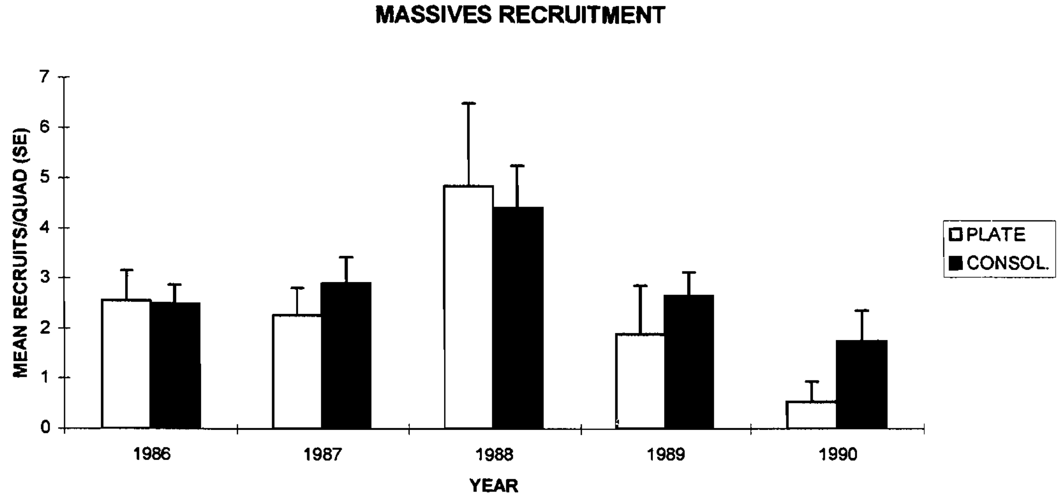


Figure 4.3.1.5. Annual visible recruitment over a five year period from 1986 to 1990. Data are presented as recruits per standardised 1 m^2 quadrat comparing dead plate and consolidated substratum patterns for pooled recruits and massive coral recruits.

4.3.2. Spatial-Habitat Trends

Recruitment rates of pooled taxa were not significantly different between back reef and fore reef locations, between shallow (3 m) and deeper areas (6 m), nor between dead plates and consolidated substrata (ANOVAR results, Appendix 4.3.1.3). The power of all non-significant results were low, ranging from 0.05 to 0.16. Mean values for the spatial and habitat parameters from each census year are presented in Table 4.3.2.1.

		HC	ACR	FAV	POR	MAS
YEAR	1988-89	8.8(1.2)	4.9(0.9)	1.4(0.4)	1.0(0.2)	2.5(0.5)
	1989-90	3.8(1.0)	2.2(0.9)	0.6(0.2)	0.3(0.1)	1.0(0.3)
LOC	BACK	6.4(1.2)	3.1(0.9)	1.1(0.3)	0.8(0.2)	1.9(0.5)
	FORE	6.2(1.1)	4.0(0.8)	0.9(0.3)	0.5(0.2)	1.7(0.4)
DEPTH	SHALL.	7.8(1.4)	5.0(1.1)	1.2(0.4)	0.7(0.2)	1.9(0.6)
	DEEP.	4.8(0.7)	2.1(0.5)	0.8(0.2)	0.6(0.2)	1.7(0.3)
SUBSTRATE	PLATE	5.5(1.3)	4.1(1.1)	0.6(0.3)	0.5(0.2)	1.1(0.4)
	CONS.	7.1(1.0)	3.0(0.5)	1.4(0.3)	0.9(0.2)	2.5(0.4)

Table 4.3.2.1. Juvenile coral recruitment means and standard errors (brackets) per quadrat for a range of spatial-habitat parameters. Data are from the years 1988-89 and 1989-90, where mapping of three permanent quadrats per site/habitat parameter was carried out in early summer (October-November) each year.

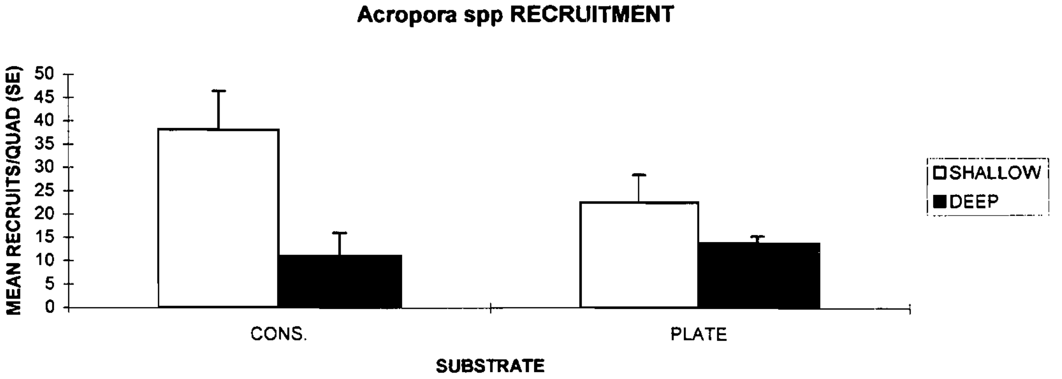


Figure 4.3.2.1. Spatial patterns of *Acropora* spp visible recruits comparing substratum types (consolidated and dead plates) with two depths (shallow 3 m, deep 6 m) for the 1989 and 1990 years.

Acropora spp. recruitment rates were not significantly different between back reef and fore reef locations, the two substratum types, or between the two census years (Appendix 4.3.1.3, Table 4.3.2.1). Recruitment of *Acropora* differed between the two depth regimes with higher recruitment in shallow quadrats compared to the deeper quadrats. However, there was a significant interaction between depth and substratum with similar mean recruits per quadrat recorded on shallow and deep dead plates, but higher means recorded on shallow consolidated substrata (Figure 4.3.2.1).

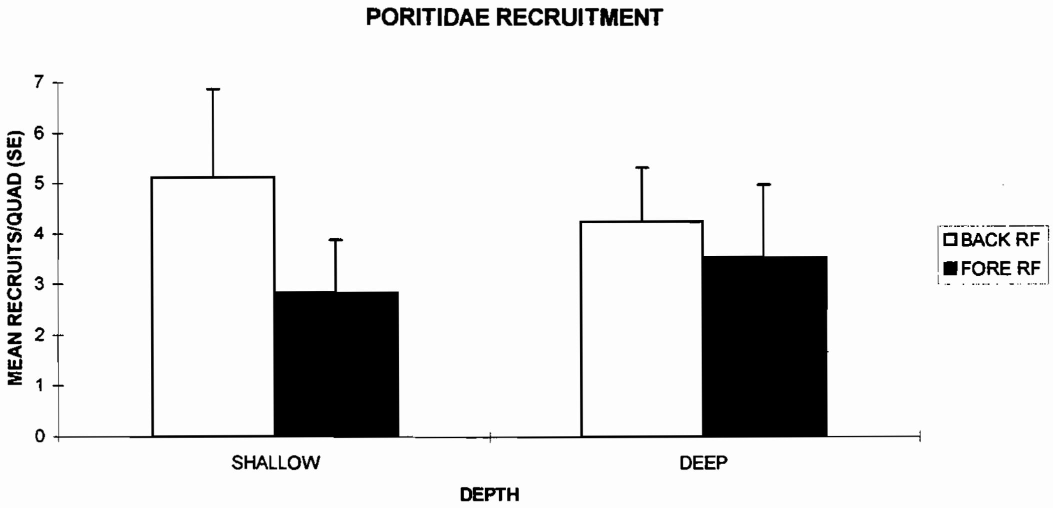


Figure 4.3.2.2. Spatial patterns of Poritidae visible recruits comparing two depths (shallow 3 m and deep 6 m) with back reef and fore reef locations.

Recruitment rates of Poritidae were significantly different between back reef and fore reef locations, and between the two substratum types (Appendix 4.3.1.2, Table 4.3.2.1). Mean recruitment onto dead plates was lower (0.5 cols./m^2) than onto consolidated substrata (0.9 cols./m^2). The power of non-significant results were low, ranging from 0.1 to 0.19. However, the location by depth interaction term was significant indicating that mean recruitment per quadrat was higher in the back reef shallow depths (mean = 0.85, se = 0.4) compared to the fore reef shallow recruitment rate (mean = 0.5, se = 0.2). In contrast, the recruitment rates were similar at both locations in the deeper areas (mean back reef = 0.7, se = 0.2; mean fore reef = 0.6, se = 0.2).

Faviidae and combined massive coral recruitment rates were not significantly different for any of the tested parameters and the power of non-significant tests were low, ranging between 11 and 17 (Appendix 4.3.1.2, Table 4.3.2.1).

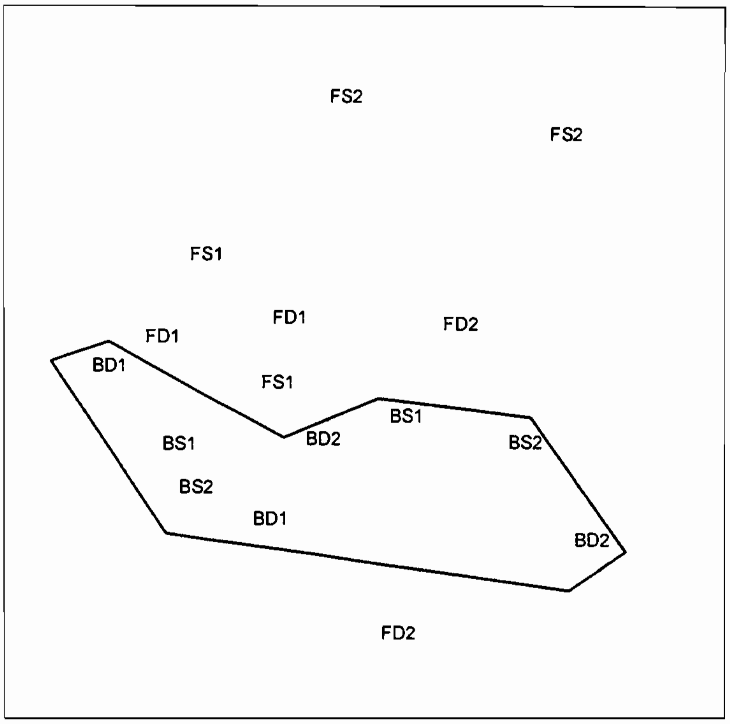


Figure 4.3.3.1. Multidimensional scaling plot (MDS) of visible recruits from the 1989 and 1990 spatial study. The relative abundance of genera were used to calculate Bray-Curtis similarities between back reef and fore reef locations (B, F), shallow 3 m and deep 6 m depths (S, D), and years (1989 = 1, 1990 = 2). For example, FD2 refers to one of two fore reef deep sites from 1990. The back reef data are circled to clarify the plot. Stress = 0.14.

4.3.3. Multivariate Spatial and Temporal Analysis

The two dimensional MDS plot of visible recruitment data (Figure 4.3.3.1) from 1988-89 and 1989-90 shows some similarities within the back reef and fore reef sites, but the ANOSIM analysis did not indicate a significant difference between these locations (P = 0.3). There was no clear difference in shallow or deeper sites over time, which was supported by the non-significant ANOSIM result (P = 0.7). There was some indication of a difference between the two census years with samples from 1988-89 positioned to the left hand side of the plot and 1989-90 samples positioned more to the right hand side. However, the ANOSIM analysis did not indicate a significant difference between years (P = 0.2). The multivariate analyses therefore indicated that there were no significant differences in recruitment of genera between any of the spatial/habitat parameters or between the two year's samples.

(I) 1988-89 VS 1989-90			(II) SHALLOW VS DEEP		
GENUS	%CON	CUM%	GENUS	%CON	CUM%
Montipora	8.11	8.11	Favid	7.1	7.1
Fungia	6.91	15.03	*Fungia*	6.59	13.68
Pocillopora	6.61	21.63	*Porites*	6.32	20.0
Favid	6.3	27.94	*Galaxea*	6.2	26.2
Lobophyllia	5.73	33.66	*Montipora*	5.95	32.15
Favites	5.47	39.13	*Lobophyllia*	5.93	38.08
Favia	5.38	44.51	*Goniastrea*	5.74	43.82
Porites	5.35	49.86	*Stylophora*	5.45	49.27
Goniastrea	5.29	55.15	*Favia*	5.38	54.65
Stylophora	5.22	60.37	*Pocillopora*	5.31	59.96
Acropora	5.05	65.42	*Acropora*	5.17	65.14
Galaxea	4.84	70.25	*Favites*	4.96	70.1
Cyphastrea	3.88	74.14	*Pavona*	3.97	74.07

Table 4.3.3.1. Results of similarity analyses (SIMPER) showing the percentage contribution (% CON.; and Cumulative % (CUM%)) of visible recruit genera to the average dissimilarity between the two sample years (I) and between the two depth regimes (II).

SIMPER analyses of the percentage contributions to the dissimilarity between years and between shallow and deep sites were used to describe trends in recruitment which may be present but which were not strong enough to cause statistically significant results. These results (Table 4.3.3.1) indicated that 12 of the same taxa (of a total of 28 taxa) contributed approximately 75% of the total dissimilarity between years and depths. In addition, each taxon contributed very similar percentages, which probably accounted for the non significant ANOSIM results. The two lowest ranked genera in this table are the only taxa not appearing in both analyses of year and depth comparisons.

4.3.4. Effect of Overtopping Colonies on Visible Recruitment

Table 4.3.4.1 outlines the differences between open and understorey recruitment patterns and the extent to which the quadrats were shaded by overtopping colonies. Only one colony was identified as having recruited under an overtopping colony in the first four years from 1986 to

1989 (Table 4.3.4.1). In contrast, there were nine colonies from the 1990 census (or 6% of all recruits for this year) which were recorded as having recruited under other colonies. At the same time, there was a fifty percent increase in the mapped area of quadrats with overtopping colonies present between 1987 and 1990. The recruitment rate to unshaded areas of quadrats averaged approximately $8/m^2$ and variations in this rate were more or less directly proportional to the total number of recruits recorded in the quadrats each year. There was a low positive linear relationship between the mean density of all recruits and the mean area of unshaded space in the quadrats (linear regression analysis for five census years, $r^2 = 0.33$).

Recruits found on substrata underneath colonies in 1990 included five *Acropora* and five massive genera (one colony each of *Platygyra*, *Favia*, *Lobophyllia*, *Galaxea*, and *Porites*). Six of the ten recruits were found under overtopping colonies from open arborescent species namely, *Acropora formosa*, *A.nobilis*, and *A.valenciennesi*. Three recruits were found under thick corymbose plate *Acropora* (*A.nasuta*, *A.millepora*), and one recruit was found under a table *Acropora* (*A.hyacinthus*).

4.3.5. Non Larval Visible Recruitment

Table 4.3.5.1 summarises the frequency and types of non larval recruitment recorded in the quadrats for the five year period from 1986 to 1990. Daughter colonies from fission events accounted for 75.4% of all non larval recruits. An additional 20.3% of recruits were from immigration of fragments into the quadrats, while 4.3% of recruits were due to growth of colonies into the quadrat area from outside the quadrat perimeter.

There were significant differences over the five years of the study in the frequency of three types of non larval recruitment (P = 0.034, Chi-sq. = 16.63, df = 8). The main difference between years was due to immigrating fragments which were generally higher in 1988 and 1990, and in the frequency of fission colonies which was relatively higher in 1987 compared to the other years.

There were also significant differences in the taxonomic composition of the 3 major sources of non-larval recruitment (P = <0.001, Chi-sq. = 115.7, df = 10). In particular, *Acropora* spp dominated the immigrating fragments, while *Montipora* spp and Faviidae were dominant in the fragmentation recruits.

	1986		1987		1988		1989		1990	
	TOT	UND	TOT	UND	TOT	UND	TOT	UND	TOT	UND
AC	62	0	86	1	127	0	180	0	67	4
MO	13	0	18	0	29	0	17	0	5	0
FA	51	0	50	0	7	0	63	0	29	2
MU	7	0	11	0	7	0	19	0	7	1
PO	19	0	24	0	31	0	41	0	16	1
PC	6	0	9	0	5	0	26	0	10	0
OC	1	0	3	0	3	0	14	0	7	1
TOT	166	0	218	1	293	0	221	0	98	9
MEAN /m^2	4		6		9		11		6	
% SHADE	0.7		6		16		24		35	

Table 4.3.4.1.. The number of recruits found under overtopping colonies contrasted with total recruitment to the quadrat area (and the percentage area of quadrats with overtopping colonies). Data are from one back reef and one fore reef site where visible recruitment was followed for five years (from a total of forty quadrats). TOT=total number of recruits; UND=recruits recorded under overtopping colonies. Taxa shown here include : AC (*Acropora* spp), MO (*Montipora* spp), FA (Family Faviidae), MU (Family Mussidae), PO (Family Poritidae), OC (Family Oculinidae), and TOT (pooled recruits); MEAN/m^2 is the mean recruitment rate to the total unshaded quadrat area; % SHADE refers to the mean percentage area per quadrat which has been overtopped.

4.3.6. Plate Disintegration Rates

The dead plate areas in 1985 ranged in size from 0.3 m^2 to 1 m^2 with a mean of 0.58 m^2 (SE=0.05). There was a steady decline in mean plate size to a mean of 0.31 m^2 in 1990 (Figure 4.3.6.1). The annual loss rate of plate area for the five year period was very consistent (mean loss in area = 0.05m^2 / yr, se = 0.01, no.of measurements = 108). The combined area of the mapped quadrats decreased from 30.8 m^2 in 1986 to 25.9 m^2 in 1990 due to the erosion of dead plate margins.

SOURCE	AC	MO	FA	PO	PC	OT	TOT
IMMIGRATION	31	2	0	2	7	0	42
INGROWTH	2	1	0	1	1	4	9
FRAGMENTATION	18	34	68	20	2	14	156
TOTAL :	51	37	68	23	10	18	207
	1986	1987	1988	1989	1990		
IMMIGRATION	3	5	14	7	13		
INGROWTH	0	4	2	1	2		
FRAGMENTATION	24	56	27	21	28		
TOTAL	27	65	43	29	43		

Table 4.3.5.1. Summary of the non larval recruit taxa and their origin from Green Island quadrats over the period of 1986-90. Data are from the initial forty quadrats established in 1985; Immigr. = immigrant fragments, Ingrow. = ingrowing colonies from the quadrat perimeter, Fission = number of daughter colonies from fission events; AC = *Acropora* spp; MO = *Montipora* spp; FA = Faviidae; PO = Poritidae; PC = Pocilloporidae; OT = other taxa.

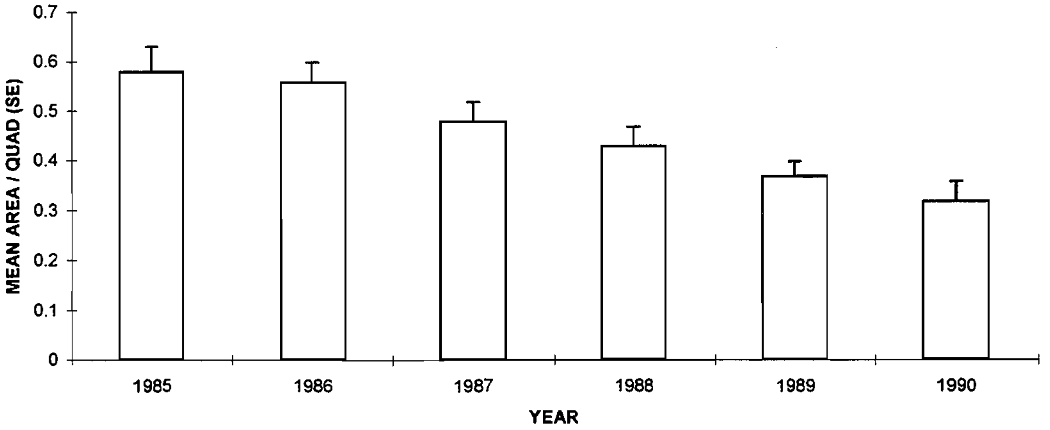


Figure 4.3.6.1. The annual mean area of mapped dead plates (m^2) between 1985 and 1990. Data are from one back reef and one fore reef location (ten plates from each location). The plates are equally distributed between a 3 m site and a 6 m site within each location.

4.4. DISCUSSION

4.4.1. Temporal Patterns

One of the strengths of this study is its relative longevity (5yr) with respect to annual trends in visible coral recruitment on a reef. Significant inter-annual variation in the relative abundance of visible recruits was concluded from this study and could be due to differences in supply of larvae, or differences in post settlement mortality. Comparable temporal studies on the GBR have also indicated that there are inter-annual variations in fish recruitment which also involves a plankton phase (Doherty and Williams 1988; Fowler *et al* 1992). The studies on fish and this study on corals suggest that large scale physical processes (ie, oceanographic and meteorological phenomena) are driving these patterns. In Chapter 3, temporal variation in the supply of early recruitment onto artificial substrata was confirmed but it remains to be shown if the degree of variation in supply is sufficient to influence the variations in abundance of visible recruits. This will be examined in Chapter 5.

The annual recruitment of visible recruits was multispecific, but with a strong dominance of *Acropora* spp. This result is similar to studies from other reefs and from other studies on recovery following *A. planci* outbreaks on the GBR (Pearson 1981; Wallace and Bull 1986; Done *et al* 1988). Although insufficient numbers of individual genera were recorded in the quadrats to allow formal statistical testing for the majority of genera, it was shown that pooled taxa, such as the massives, do show inter-annual variability in visible recruitment patterns which differ from those of *Acropora* spp. These differences were due to the significant interactions between habitat and years, which suggests that variation in post settlement mortality rates due to habitat characteristics may also play a part in the inter-annual variation of visible recruits. Conflicting results have been reported with fish recruitment studies, where both multispecific (Doherty and Williams 1998) and single species recruitment patterns (Fowler *et al* 1992) have been shown to have different yet significant inter-annual variation. Visible recruitment of corals displayed distinct differences in relative abundance of genera. Species differences may be stochastic, due to the time by space interactions shown in the spatial study results. Alternatively, post settlement mortality may be creating these differences among coral taxa either separately or in conjunction with stochastic recruitment. Watson (1995) concluded from his one year study of juvenile corals at Lizard Island that mortality of recruits was a function of size rather than taxon. Processes affecting post settlement mortality would therefore favor the faster growing forms over the slower growing forms.

Recruitment of massive corals showed very similar inter-annual fluctuations and the proportion of *Acropora* spp recruits to massive coral recruits varied over the five year period. This suggests that factors other than large scale processes (eg, habitat selection or post settlement mortality) are significantly influencing massive coral survival.

From the spatial analysis study, visible recruitment of *Acropora* spp. varied significantly between the periods before and after 1989. The combined massives and 3 families of massive corals (Faviidae, Poritidae, and Mussidae) also displayed this pattern. Eight years after the last starfish outbreak on Green Island, it appears that shading may be influencing visible recruitment. One such influence could be a rapid increase in a canopy of live coral during this time. This suggests that the same factors influencing reduction in early recruitment may be operating on visible recruits in the quadrats. Fisk and Harriott (1993) demonstrated that an overtopping coral canopy can reduce the numbers of available larvae settling in an area. The correlation between a reduction in visible recruitment and the establishment of large colonies of *Acropora* spp. adjacent to the quadrats has been documented elsewhere in this chapter. Fisk and Harriott (1993) noted that the canopy effect on early recruitment rates also extends to the more open arborescent *Acropora* spp. which are common in the Green Island reef communities. This study has shown that visible recruitment density appears to be related to the supply of early recruits (allowing for the halving of available unshaded substrata within the quadrats). The relative paucity of annual visible recruits recorded under the coral canopy within quadrats indicates that early recruitment is suppressed and/or survival is reduced due to the shading effect of overtopping colonies. Since visible recruitment densities in 1990 were not lower than most previous years, a relatively lower supply of recruits from the previous summer,ie, relatively lower early recruitment densities in the 1989/90 summer, cannot be an alternative explanation for the observed

4.4.2. Spatial Patterns

There were significant differences in visible recruitment of *Acropora* spp and Poritidae between locations. The factor location influenced recruitment patterns more than substratum type or depth. All recruits pooled and *Acropora* spp had significantly higher abundances in the back than the fore reef locations over the five year period. This is not surprising given the dominance of the latter taxon in total recruitment. Studies of fish recruitment have also demonstrated considerable within-reef, inter-reef, and regional variations in recruitment

(Doherty and Williams 1988; Fowler *et al* 1992). Therefore, it appears that factors influencing recruitment patterns in animals with larval phases are operating at scales which probably affect both corals and fish in a similar way. However, the characteristic patterns of recruitment in one group will not necessarily help in predicting patterns in the another group because of differences in behaviour and settlement selection prerequisites. Also, species-specific fish recruit patterns at one reef were not useful in predicting patterns at other reefs (Doherty and Williams 1988). A similar relationship in corals could not be investigated in this study due to the difficulty of identifying juveniles beyond genus level.

There were clear differences in area available for settlement between dead plates (<1 m^2) and consolidated substrata (a constant 1m^2). Furthermore, there was a gradual reduction in area of the dead plate surfaces over time. Coral skeletons left *in situ* after tissue death are generally regarded to provide space for other reef organisms (Connell and Keough 1985; Reichelt and Bradbury 1984; Wallace *et al* 1986; Reichelt 1988). The mean areas of the dead plates in 1989 and 1990 were smaller than in previous years, though the rate of reduction was quite regular (average of 0.5m^2/yr) over the course of the study. The condition of the dead plate substrata compared to the consolidated substrata is pivotal to the understanding of the spatial trends outlined in this study, such as location differences. Dead plates disintegrated from the outer edges towards the centre. The centre was usually more steeply sloped and was where sediment and detritus collected (pers.obs.). This affected the area of suitable substratum for settlement of coral recruits. In addition, the reduction in substratum area of dead coral plates over time could explain the relatively lower recruitment rates of all major taxa onto the dead plates.

The higher number of recruits recorded under colonies in 1990 correlates with a greater area of the quadrats being under live coral canopy compared to previous times, and is probably related to dramatic growth in some canopy species between 1989/90 and 1990 (see Chapter 5). In particular, some arborescent *Acropora* spp. colonies substantially increased in size between census periods in the latter part of the study. Fisk and Harriott (1993) also noted relatively more recruits settled under arborescent colonies than under tabulate colonies. A rapid increase in canopy area, along with the relatively minor shading effect of this growth form, probably allowed some recruitment to occur and/or allowed the survival of recruits settling within the previous year.

The contribution of non-larval recruitment to the composition of the regenerating coral communities was relatively minor. Most of this was colony fragmentation, which was most likely due to grazing impacts of fish. The mean size of fission colonies was small (generally less than 5 mm diameter) and turn over was high (pers.obs). In contrast, Done *et al* (1988) noted a substantial non larval contribution to the recovery of a coral community at John Brewer Reef four years after an *A. planci* outbreak.

4.4.3. Composition of Visible Recruits

The annual number of genera of visible recruits remained relatively constant from 1986 to 1990 and all diversity indices of annual visible recruits did not change significantly during this period. However, differences were detected in dominance curves from sites at different depths (using relative abundance of genera), indicating differences between depth habitats in visible recruit composition. Genus richness and Shannon's index also frequently showed higher values for deeper sites within locations. In contrast, variations among annual dominance curves suggested temporal differences in larval composition. If there were similarities between years in environmental conditions affecting survival of early recruits, the variations in dominance could explain the differences in composition of visible recruits at the 2 depths. Specific temporal variations in composition have also been found for reef fish (Doherty and Williams 1988; Fowler *et al* 1992) suggesting that similar mechanisms are influencing larval supply to reefs. In contrast, multivariate analyses (at the generic level) generally supported the univariate results for the tested major taxa,ie, there are significant differences in abundances of visible recruits between years. Differences in the presence of moderately abundant taxa are probably causing the inter annual variations (this can be seen in the crossing over of dominance curves in the moderately abundant section of the k-dominance curve in Figure 4.3.1.2 (c)).

4.4.4. Massive Coral Characteristics

A number of studies of coral regeneration suggested that structural components of the community are important to the long term recovery (Endean and Cameron 1985, Done 1985,1987,1988; Done *et al* 1988; Endean *et al* 1989; Cameron *et al* 1991). In particular, the role and dynamics of the massive corals in the regeneration process has been stressed. The massive corals can be viewed as the solid building-block components of a reef, whilst encrusting and branching forms contribute infill. In this context, massive colonies would be expected to provide reef stability in the structural sense; contribute substantially to whole reef growth; provide the majority of preferred settlement substrata for new corals; and be an integral part of the diversity or complexity of the reef community. Massive corals are generally slow growing so the relative abundance of massive corals can be used to gauge the ecological consequences of *A. planci* outbreaks, ie, provide a retrospective assessment of the intensity and frequency of past starfish outbreaks (Endean *et al* 1989; Cameron *et al* 1991). Therefore the population dynamics of massive corals, particularly their recruitment, growth, and survival rates, are important to reef recovery following major perturbations.

The apparent paucity of remnants of massive corals (pers.obs.) at the beginning of this study (1985) contrasts with observations of Woodhead (1970) following a starfish outbreak on Green Island in 1966. Thus, the earlier outbreak generally resulted in partially killed massive colonies (Woodhead 1970). Cameron and Endean (1982) suggested that on certain reefs, such as Green Island, the second *A. planci* outbreak in 1979-81 occurred before hard corals had recovered from the previous outbreak. The apparent reduction in abundance of massive coral colonies on a reef supports the suggestion that starfish outbreaks of such intensity and frequency are unusual events over the relatively long time periods of a reef's development (Cameron and Endean 1982; Cameron *et al* 1991).

The Faviidae, Poritidae, and Mussidae, comprised almost all (91%) of all the massive families on Green Island. The relative abundance of massive coral families in quadrats on Green Island by late 1990 differed from that recorded on similarly damaged reefs studied by Cameron *et al* (1991). These researchers reported on a suite of starfish affected reefs south of and including Green Island reef. Although the same three families accounted for 90% of massives colonies in Cameron *et al*'s (1991) study, the relative abundance differed to that recorded in this study in the following way: Poritidae (56% compared to Green Island (29%)), Faviidae (31% compared to 63% at Green Island), and non-Poritidae (44% compared to 71% at Green Island). The difference between the present study and the study of Cameron *et al* (1991) can be understood by the following points: (1) the reefs studied by Cameron *et al* (1991) were affected after 1981 (when the outbreaks on Green Island had ceased) and so would have been at earlier recovery phases than Green Island; (2) the emphasis of the study by Cameron *et al* (1991) was on the large massive colonies (>10 cm) and the authors noted that the abundance of colonies <10 cm diameter were probably under estimated which is in contrast to the present Green Island reef study which generally focused on colonies <10 cm diameter. The differences in the scale of investigation of these 2 studies lead to contrasting conclusions. That is, the Green Island reef study demonstrated that massive taxa can recruit very well to COTS damaged reefs. This is in contrast to Cameron *et al* (1991) who concluded that massives poorly recruit after major disturbances.

Done *et al* (1988) reported that 58% of non-Poritidae massives comprised the recovering population at John Brewer Reef and most were Faviidae. John Brewer Reef had a large starfish outbreak until 1983, and Done et al (1988) were reporting on recovery at this reef 5 years after the outbreak. The period of time after a starfish outbreak is an important variable to include in comparisons, as is the sampling effort and the scale of the study. The present study is perhaps the most fine scale spatial study of the three, with Cameron *et al* (1991) at the other extreme. In comparison to the other studies, the present study records very early visible recruitment. Due to the relatively slow growth of massives, different conclusions could be made on the rates of increase in abundances, and the mechanisms controlling the successional process of the massive corals. The choice of study areas could also result in the differences outlined above, for example, Cameron *et al* (1991) purposely chose areas where relatively high abundances of massives were located by manta-tow surveys. Also, the degree of effort per unit area invested in each of the three studies is an important influence on conclusions drawn from estimates of abundance, as is the difference in topographic complexity of the reef surface. The more sampling effort, the more colonies that usually will be found. When comparisons of recruitment rates between studies are required, the finer the spatial scale of the study, the more accurate the estimates should be. Therefore, the estimates from the present study can be taken as the most accurate available for a severely affected reef from the Great Barrier Reef. However, the extrapolation of such fine scale estimates of visible recruitment to broader spatial scales (eg, whole reefs or multi-reef scales) should be made with caution.

Studies of regenerating reefs affected by starfish from outside the GBR are less common. Colgan (1982) reported on the status of communities in Guam 11 years after an *A. planci* outbreak. In this study, up to 31% of colonies in the regenerating communities were reported as massive taxa but the generic composition was not included. This result is very similar to the proportion of massive visible recruits recorded at Green Island (31% of all taxa were massives). The nature of recovery may be different from that seen on the GBR and in the present study, even when comparisons are made during a similar period of time that has elapsed after a starfish outbreak. Also, the contribution of colony remnants following starfish feeding is possibly more important in the Guam study. Colgan (1982) reported that immediately after the passing of the starfish, non-preferred prey species remained, including certain massive species (*Galaxea* spp. and *Porites* spp.).

AUTHOR	PERIOD	REC.	POR.	NON-POR.
Fisk (this study)	5yr	3.0	29%	71%
Connell (1973)	8yr	1.0	100%	0%
Harriott (1983)	1.5yr	9.0	47%	53%
Endean et al (1988)	*	0.3*	50%	50%
Done et al (1988)	5yr	0.22	43%	57%
MEAN (5 Studies)		2.7	54%	46%

Table 4.4.1. Comparisons of visible recruitment rates (recruits/m^2/yr) of pooled massive corals (REC) and relative proportions of Poritidae (POR) and non-Poritidae (NON-POR) from five studies on the GBR * no time period available when recruitment was estimated.

Recruitment of massive corals ranged from 1-5/m^2/yr on Green Island with an annual mean for the five years of 3/m^2/yr. The proportion of non-Poritidae recruits at Green Island reef for the five year period of the present study was 71%. Recruitment rates from other post-*A. planci* studies of all massive corals combined as well as for non-Poritidae massives, are generally not as high as those recorded in this study (Table 4.4.1). Density of massive coral recruits (<5 cm dia) from the studies of Endean *et al* (1988) averaged 0.33/m^2 while massive recruit rates from the Done *et al* (1988) on John Brewer Reef were 0.22/m^2/yr with Poritidae 0.1/m^2/yr and non-Poritidae 0.12/m^2/yr. Only Harriott's (1983) study recorded a higher combined massives recruitment rate than the present study. The relatively high recruitment estimate can be explained by a number of unique factors associated with this study. Harriott's (1983) study concentrated on a single patch reef which was dominated (numerically and with respect to cover) by *Porites* spp. This patch reef was also partially affected by an *A. planci* infestation during the latter stages of the study. *A. planci* predation frequently leaves remnant patches of live corals, particularly in less preferred corals such as *Porites* spp and Harriott made no distinction between remnants and true recruits. Also, Harriott (1983) did not distinguish between larval and fission recruitment in her estimates. Done *et al* (1988) and Endean *et al* (1988) both concluded that recruitment of massives was very low by inferring from the abundances of the smallest size classes in their respective study plots. Making such inferences ignores turnover rates of small colonies and is dependent on net gain in small colonies over the period of study to register positive recruitment rates.

At Green Island reef, Poritid visible recruits were a substantially lower proportion of the total massive coral recruitment pool in comparison to other published studies (Table 4.4.1). Endean *et al* (1988) presented data which indicated that approximately 50% of the smallest size classes (1-5 cm dia) in starfish affected reefs were Poritidae and 50% were non-Poritidae. The time period for recruitment to occur in Endean *et al* (1988)'s study is impossible to estimate. The distinction between remnants and true recruits cannot be estimated and this makes recruit density/per unit time calculations not applicable.

These comparative data are not for the same post-*A. planci* period as the present study, so the recovery phases may be different. The present study recorded the highest proportion of non-Poritidae recruits of all studies, but Green Island reef may be an atypical reef in that it appears to receive greater numbers of recruits compared to at least two other nearby reefs (Fisk and Harriott 1990; this study). However, this does not explain the relatively higher abundance of non-Poritidae recruits at Green Island. Two explanations may account for this result: (1) non-Poritidae massive corals may have a much higher survival rate to visible size compared to Poritidae massive; (2) alternatively, there may be fewer Poritidae recruits present in the larval pool compared to the non-Poritidae massives. However, settlement plate studies measuring early recruitment on Green Island have demonstrated that the Poritidae are much more abundant on plates than non-Poritidae massives (Fisk and Harriott 1990; this study). Therefore, the first explanation suggesting higher relative survival of non-Poritidae compared to Poritidae appears to be the more likely.

Connell (1973) reported that recruitment of massive corals made up 20% of all recruits at his reef flat sites on Heron Island over an eight year period, though it should be noted that these sites were not recovering from *A. planci* predation. However, most of the visible massive recruits in the Heron Island study were Poritidae. At a predominantly non-*A. planci* affected reef at Lizard Island, Harriott (1983) reported that massives comprised 53% of all recruits over an eighteen month period at a back-reef patch reef in depths ranging from 1 m to 9 m. Further breakdown of Harriott's recruitment data shows that of all visible recruits 26% were Poritidae, 25% were Faviidae, and 2% were Mussidae. The latter study was compiled from data collected every two months and so is from a more frequent temporal series than any other data, including the present study, where sampling was conducted annually.

The lower recruitment rates recorded in the literature before this study (not considering Harriott's (1983) data) was proposed as one reason that massive coral recovery will be slow to regain pre-*A. planci* levels of massive coral community composition (Cameron *et al* 1991). This aspect of their demography is also significant for projections of recovery times (Done 1987,1988; Cameron *et al* 1991; Endean *et al* 1988). As a result, differences in recruitment estimates between the studies reported above are quite large and could result in very different modeling outcomes to that proposed by Done (1987,1988) for example.

The availability of larvae of massive corals (see early recruitment results, Chapter 3) at Green Island contrasts with the visible recruitment rates recorded in the permanent quadrats. The quadrats show very high recruitment of Poritidae and non-Poritidae massive corals compared to very low recruitment of these groups onto the settlement plates (Fisk and Harriott 1990; Harriott and Fisk 1988; this study). Two possible explanations for this difference between early and visible recruitment are: (1) the settlement plates are not suitable for most non-Poritidae massives; (2) post-settlement survival is much higher for massives compared to the more abundant early recruits from the Families Acroporidae and Pocilloporidae. Recruits (including other massive taxa) which are very different to the major families mentioned above are also rare in all studies.

In the next chapter, a broader scale investigation of the characteristics of the regenerating coral community on Green Island will be presented.

Chapter 5. Changes in the Coral Community at Green Island

5.1. Introduction

A number of studies have investigated the recovery of coral reefs following *A. planci* infestations (Pearson and Endean 1969; Woodhead 1970; Pearson 1974, 1981; Wallace 1983,1985a; Colgan 1987; Done *et al* 1988; Endean *et al* 1988). Conclusions based on these studies vary due to natural differences in recovery potential between different reefs, and to differences in methodology. The predicted or estimated rate of growth or increase in colony size leads to projections of recovery times, and these factors account for much of the differences between studies. Studies of recovery varied with respect to the interval between initial impact and post impact observations. Some included a series of observations over time at the same reefs (eg, Pearson and Endean 1969; Woodhead 1971) or of the same permanently marked site(s) within reef(s) (eg, Pearson 1974, 1981; Colgan 1987; Done *et al* 1988). Most studies did not compare patterns within marked sites with broader scale patterns at that reef. Yet most studies assumed that conclusions on recovery patterns from limited numbers of study sites applied to larger spatial scales.

Recovery of reefs following *A. planci* outbreaks does not always display the same pattern as recovery from other natural perturbations. The major difference lies in the nature of the physical damage caused by disturbances such as storm damage and by selective mortality agents like disease, as opposed to that caused by *A. planci*. Such impacts are likely to lead to changes in reef surface topography and to the creation of patches of dead standing corals. The latter outcome may approximate the effect of low to medium *A. planci* infestations. The influences of remaining structural features of reefs affected by *A. planci* on key processes such as recruitment are important to recovery rates. For example, the formation of a canopy has been shown to influence recruitment to the shaded substratum in permanent quadrats (Chapter 4).

The aim of this chapter was to investigate links within the major coral groups (namely, *Acropora* spp and massive taxa), and across different spatial scales of coral recruitment and the resultant community composition within one reef (Green Island reef). Two approaches were used. In the first approach, early recruitment (Chapter 3) and visible recruitment (Chapter 4) were investigated for the degree of association between these two recruitment phases.

Secondly, a study was done to determine if recruitment trends and coral composition of the permanent quadrats were reflected in coral community patterns at a broader spatial scale. Patterns in the composition of corals in the adjacent community were investigated to determine if the visible recruitment patterns of relative abundance in the permanent quadrats (Chapter 4) were occurring at a larger spatial scale.

5.2. Methods

Data on coral cover and relative abundance of species estimated from line intercept transects and belt transects, respectively, were used to determine if similar processes affecting recruitment rates were present in communities adjacent to the quadrats. Community composition in areas adjacent to the permanent quadrats, and in a series of sites spread around Green Island reef, was assessed using belt transects.

Figure 2.1 indicates the location of all study sites. Percent cover was estimated along four thirty meter long line intercept transects. Two back reef and four fore reef sites were used. Corals were identified *in situ* to species level where possible. Transects were randomly placed in the same area for the years 1985 to 1988 (inclusive). In 1988, the line transects were permanently marked using steel pickets to indicate the beginning of each line. As well, steel rods and masonry nails were used at ten meter intervals along each line. That is, coral cover data from 1989 to 1990 (inclusive) were from transects which were permanently fixed. By 1993, most markers, with the exception of the starting pickets, had been lost. Transects were re-established by using the pickets as the starting point and placing the tapes in the previous line directions.

Belt transects were used in 1993 to assess the relative composition of regenerating coral communities at a total of seventeen sites from back reef and fore reef locations (Figure 2.1). Data from additional sites not used in this study were collected as part of a separate monitoring program by the author in a comparable manner to the present study. It was thought that this data would be useful to gain a more complete assessment of the whole-reef recovery pattern`. This included sites where permanent quadrats were established. At each site, four belt transects each 10 m by 0.3 m wide, were used to assess community composition. Each belt transect was located at the start of the line intercept discussed above. Three of the back reef sites were in shallow reef flat habitats. Five were located in the back reef area close to the cay. Five sites were located along the fore reef slope with three sites in 3 m depth and two sites at 6 m depth.

Most of the remaining sites in the back reef were at approximately 3 m depth, with only one site at 6 m depth. Most back reef sites were in shallower depths because coral communities usually did not exist at depths deeper than approximately 4 m. Greater than 50% of the colony had to be within the belt for inclusion in the sample. Species were identified, the maximum diameter of each colony measured, and colony fragments recorded.

Changes in mean maximum diameter (MMD, measured in cm) of colonies in the permanent quadrats were followed by plotting the annual MMD as well as the mean annual change in MMD of colonies. Three growth forms of *Acropora* spp were used in this part of the study. They were : arborescent *Acropora* spp (*A. formosa*, *A. nobilis*, *A. grandis*), tabulate *Acropora* spp (*A. hyacinthus*, *A. cytherea*, *A. latistella*), and corymbose *Acropora* spp (all other plate colony forms). Comparisons were made between mean diameters and mean change in diameters of *Acropora* spp and massive colonies from sites in the back reef and fore reef and sites at 3 m and 6 m depths within each of these two locations. These measurements were made as part of the annual census of visible recruitment in the permanent quadrats. The aim was to compare changes in colony size so that trends in visible recruitment could be put into a local context and that possible causes of observed recruitment patterns could be described.

Multidimensional scaling (MDS) techniques (described in Chapter 2), and descriptive statistics of community composition were used on abundances of genera and of species. Data from all sites assessed by belt transects were compared to each other to test for similarities in communities around Green Island reef.

The relationship between visible recruitment and the composition of regenerating coral communities was investigated by running Spearman rank correlations on the number of genera of visible recruits in the permanent quadrats and in the adjacent community. Visible recruits monitored in quadrats (using pooled sites and three of the four sites separately) over five years were used for these analyses. One of the four sites where permanent quadrats were mapped (located on a small back reef patch reef) was excluded from this aspect of the investigation because line transect data were not recorded for this site (due to insufficient area for transects to be deployed).

Diversity indices were calculated for visible recruitment from the five year temporal data set (Chapter 4). Genera abundance in the quadrats were pooled from adjacent shallow and deep sites (site numbers with suffixes A and B, see Figure 2.1). Diversity indices were also calculated from belt transect data collected in 1993 (described above) in the adjacent coral community. Comparisons of diversity indices were made between the pooled visible recruits and the community composition in areas adjacent to the quadrats to assess the possible influence of recruitment on the established coral community. Three of the four sites monitored for visible recruits over a five year period (Chapter 4) were used in this comparison. The site not used here was in a shallow back reef area where insufficient hard substratum was present for establishing belt transects.

The relationship between early recruitment as recorded on the ceramic tiles (Chapter 3) and visible recruitment in quadrats (Chapter 4) was investigated using Spearman rank correlations. Three sites established in 1985 and monitored for a five year period were analysed separately using pooled recruitment data from each of the two programs where early recruitment on tiles were paired with visible recruitment in quadrats from the following year. Each row in the input data represented a separate year of data. It was assumed that over a one year period most new visible recruits in the quadrats settled from the previous year annual mass spawning period in addition to minor spawning and planulating events outside this period. Pooled data from sites established in 1988, in addition to sites established in 1985, were analysed for one period using the 1989 early recruit data and the 1990 visible recruit data. In all analyses, pooled recruits, *Acropora* spp recruits, and pooled massive recruits were tested.

5.3. Results

5.3.1. Coral Cover

Total coral cover and changes in colony dimensions of *Acropora* were closely related (Figures 5.3.1.1, 5.3.1.2). The latter influenced the trends in total coral cover substantially. *Acropora* spp constituted a major component of the total hard coral cover at all sites. Cover of massives remained less than 5% at all sites and times. Mean total coral cover (Figure 5.3.1.1) increased in all fore reef sites up to 1990. However, cover was lower at all fore reef sites in 1993. The two back reef sites exhibited the same increase up to 1990 but not the same reduction in cover as the fore reef sites after 1990.

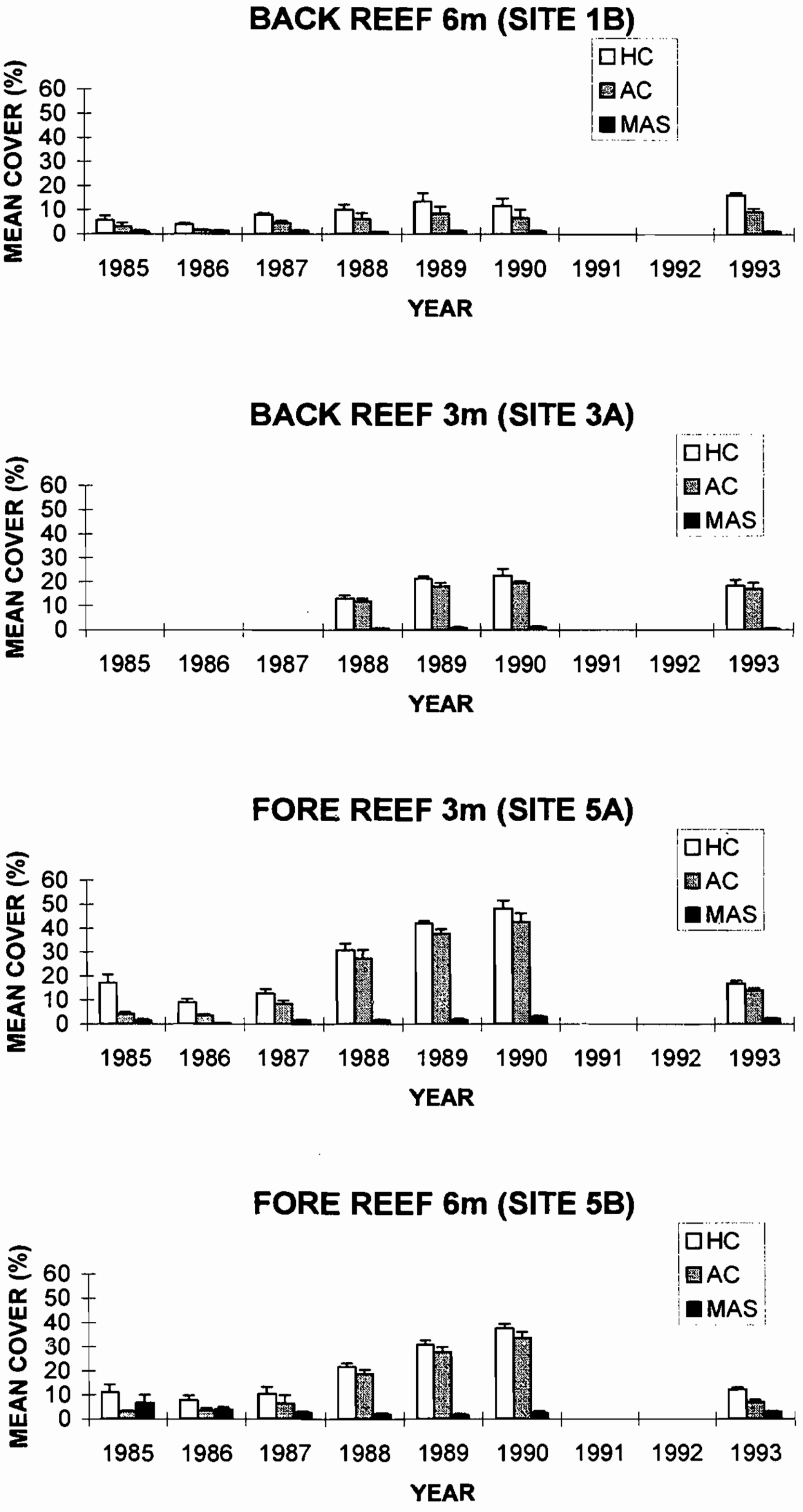


Figure 5.3.1.1. Mean percent cover of hard coral, *Acropora* spp, and massives from sites where permanent quadrats were established to study visible recruitment. No data were recorded for 1991 and 1992. **(Figure 5.3.1.1 continued over page)**

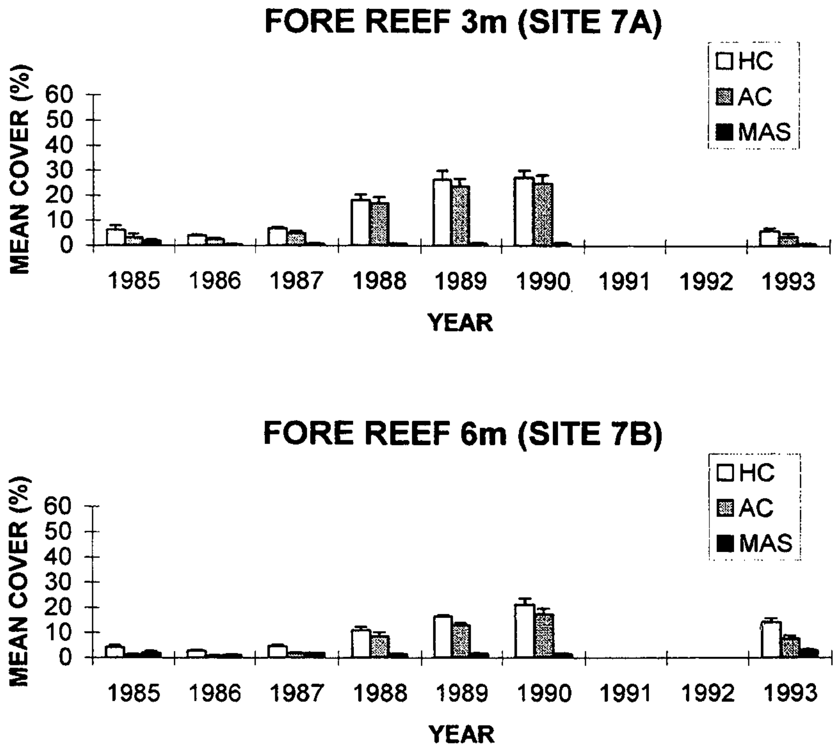


Figure 5.3.1.1. (Continued from previous page) Mean percent cover of hard coral, *Acropora* spp, and massives from sites where permanent quadrats were established to study visible recruitment. No data were recorded for 1991 and 1992.

Changes in mean maximum diameter (MMD) of *Acropora* spp and massive corals in quadrats showed clear differences with respect to location and depth (Figure 5.3.1.2-5). *Acropora* spp showed greater colony sizes and greater increases in MMD in the fore reef compared to the back reef, and greater growth at 6 m depth compared to 3 m depth. Massive corals also generally were larger and grew more quickly in the fore reef compared to the back reef , but were larger and grew more quickly in 3 m depth than at 6 m depth. Pooled mean maximum diameter from all sites over five years for *Acropora* spp and massive colonies, showed a steady increase up to 1990 for *Acropora* spp, with no noticeable increase in the massives (Figure 5.3.1.2). Mean change in MMD of *Acropora* spp increased to 1989 and dropped in 1990. MMD of massives was steady with a slight decline over time.

Three growth forms of *Acropora* spp increased in MMD over time (Figure 5.3.1.3). Arborescent forms displayed the highest increase, followed by tabulate and corymbose forms. Changes in MMD ranked similarly among the three growth forms.

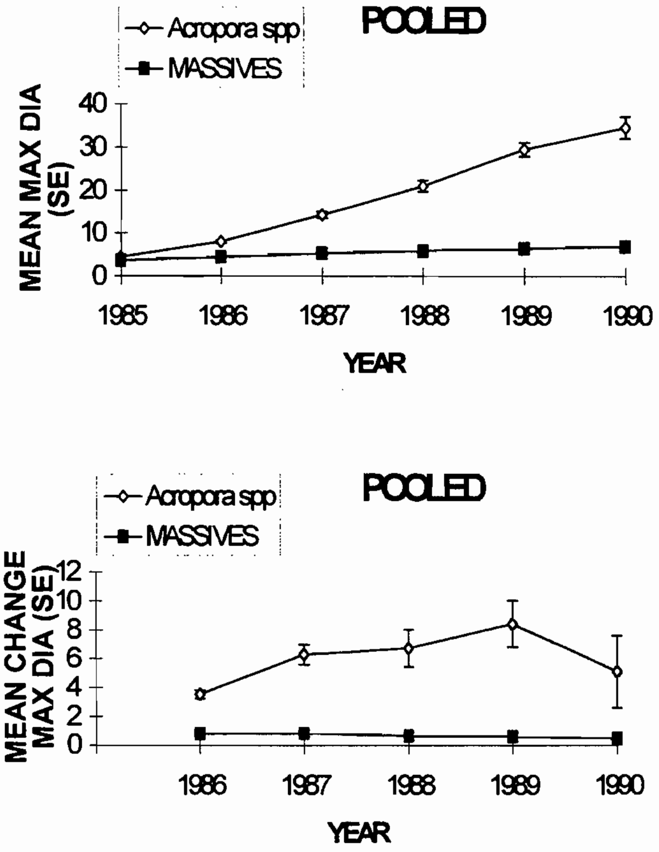
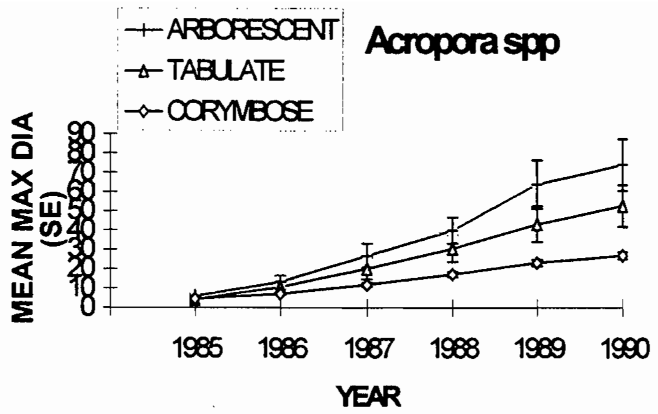


Figure 5.3.1.2. Mean maximum diameter (MMD, cm/yr) of *Acropora* spp and massive colonies (left) pooled from all sites over five years. Open circles represent pooled *Acropora*, closed squares represent pooled massives. Changes in MMD (cm/yr) is shown on the right. Data are from 138 to 145 colonies per year for each of the two taxa groups.



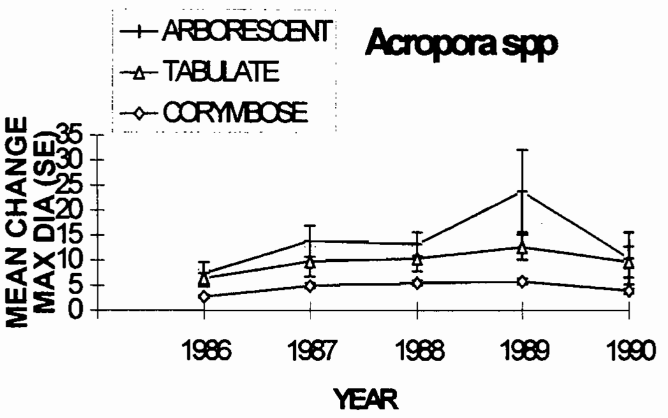


Figure 5.3.1.3. Mean maximum diameter (MMD, cm/yr, top) and mean change in MMD (cm/yr, bottom) for three growth forms of *Acropora* spp. Data are from 82 to 84 colonies per year for corymbose forms, 10 colonies per year for tabulate forms, and 12 colonies per year for arborescent forms.

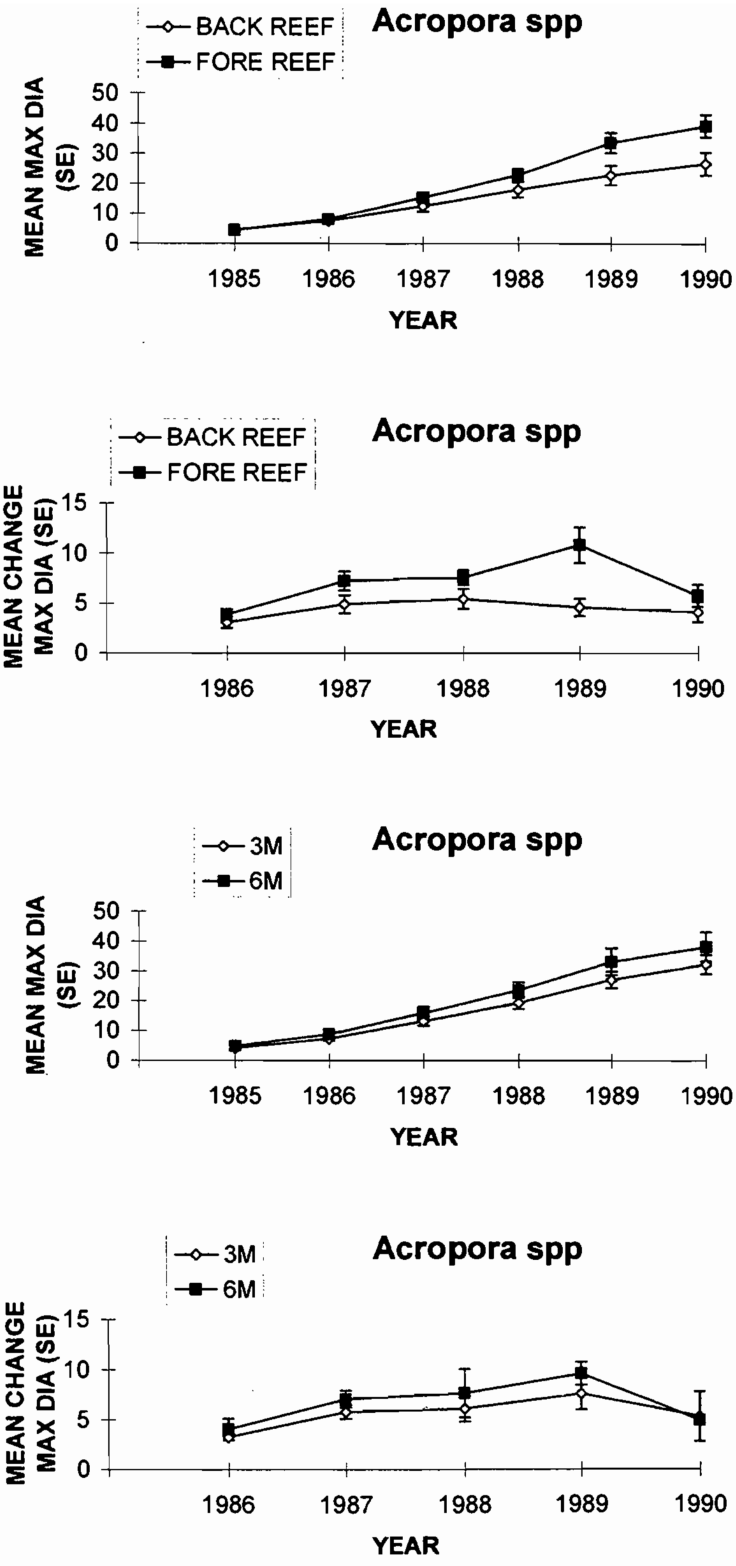


Figure 5.3.1.4. Effects of location (top two graphs) and depth (bottom two graphs) on MMD and annual changes in MMD of *Acropora* spp. Data for MMD are from 48 colonies per year (fore reef) and 94 colonies per year (back reef); and from 86 colonies per year (from 3 m depth) and 58 colonies per year (from 6 m depth).

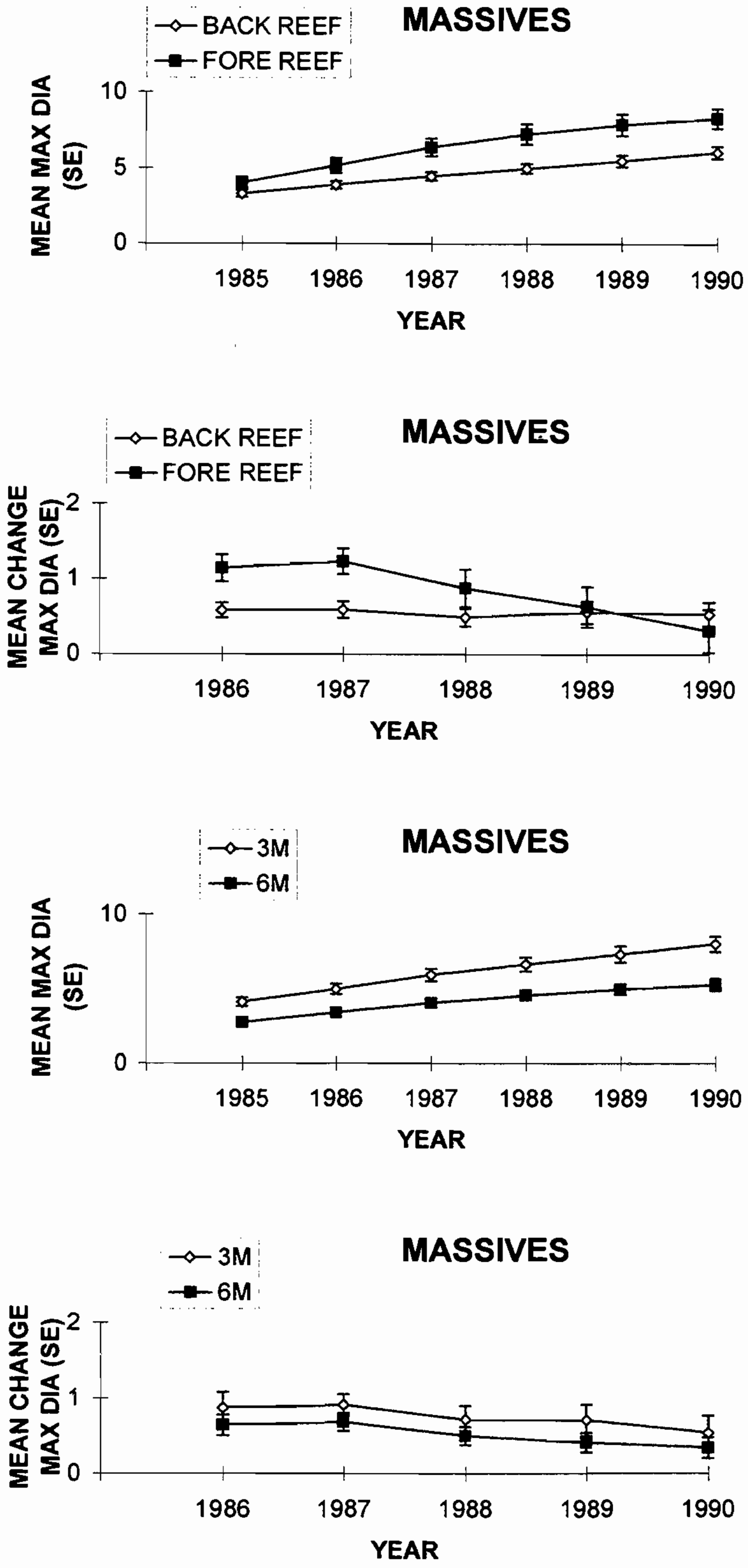


Figure 5.3.1.5. Mean maximum diameter (MMD in cm) and changes in MMD of massive colonies in permanent quadrats at different locations(top two graphs) and depths (bottom two graphs). Data are from 48 to 94 colonies for location effects, and from 58-86 colonies for depth effects.

5.3.2. Adjacent Coral Community Composition and Relative Abundance

Multidimensional scaling (MDS) plots of the relative abundance of both genera and species in 1993 are shown in Figure 5.3.2.1 (a,b). The plot of abundance for genera does not show any clear differentiation between locations (back and fore reef) nor between depths (3 m and 6 m). There is an indication of shallower and deeper site groupings (eg, 3 m sites #9, #5A, #7A, #2, at the top of the plot; and 6 m sites #5B, #7B, #5A at the lower part of the plot). Some habitat differences may also be present. For example, the series of sites situated around the back reef harbour area were an homogeneous group except for #11 on the reef flat.

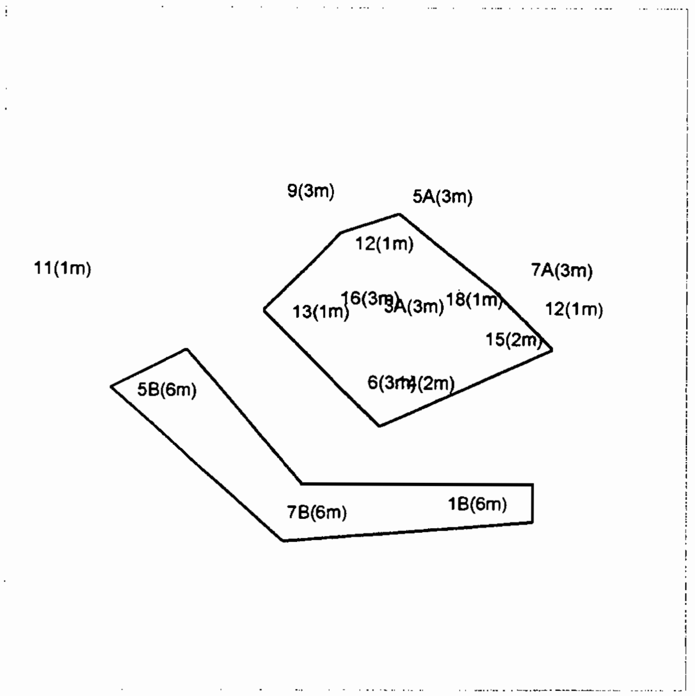
In the species plot (b), sites #11, #12, and #2 were excluded because they were very dissimilar to the other sites and caused excessive overlap in a plot which initially included them. Sites from back and fore reef locations do not show close similarities in the plots, except for the back reef harbour sites (#11-#17). There is also a weak association of some depth related sites in this plot. All data used in the species MDS plot are presented in Appendix 5.3.2.1.

The results of Spearman rank correlations between abundance of visible recruits in permanent quadrats (over a five year period from 1985 to 1990) and abundance of adjacent established coral communities in 1993 are presented in Table 5.3.2.1. There was a high degree of association between the composition of genera of visible recruits and the composition of genera of the adjacent community. Table 5.3.2.2 shows the ranks of pooled visible recruits over five years from pooled back and fore reef sites, with the composition and ranking of genera from belt transects recorded in 1993 in adjacent communities at these same sites.

	SPEARMAN VALUE	P
SITE #7A (FORE 3m)	0.73	<0.001
SITE #7B (FORE 6m)	0.53	<0.001
SITE #1B (BACK 6m)	0.60	<0.001
POOLED ABOVE SITES	0.62	<0.001

Table 5.3.2.1. Spearman rank correlations between visible recruits in permanent quadrats and the composition of adjacent coral communities from 1993 belt transects. The critical value for correlation coefficients for $\nu = (n-2) = 52$, one independent variable, and for $P = 0.05$, is 0.268 (Rohlf and Sokal 1969).

(A) Genus Data



(B) Species Data

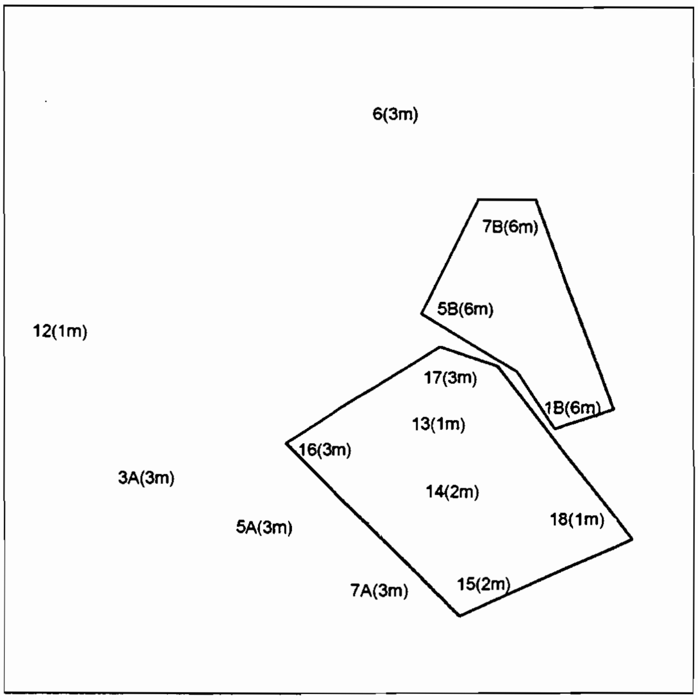


Figure 5.3.2.1(a,b). MDS (2-D) plots of genus and species data from a belt transect survey in 1993. The back reef harbour sites (surrounded by the larger polygon) generally were located in between the two depth extremes. Stress = (a) 0.12; (b) 0.15.

GENUS	VR	R	ADJ	R		GENUS	VR	R	ADJ	R
Acropora	538	1	1198	1		*Montastrea*	1	21	15	23
Porites	121	2	454	2		*Mycedium*	1	21	11	27
Montipora	96	3	206	4		*Oxypora*	1	21	0	36
Faviidae	95	4	14	24		*Podabacia*	1	21	7	29
Favia	80	5	219	3		*Tubastrea*	1	21	0	36
Favites	51	6	142	7		*Goniopora*	0	22	35	15
Lobophyllia	41	7	82	10		*Astreopora*	0	22	25	18
Stylophora	32	8	91	9		*Symphyllia*	0	22	23	19
Goniastrea	29	9	169	5		*Pavona*	0	22	21	20
Platygyra	21	10	69	12		*Heliopora*	0	22	20	21
Fungia	21	11	49	14		*Echinopora*	0	22	8	28
Leptastrea	21	12	130	8		*Hydnophora*	0	22	7	29
Galaxea	15	13	147	6		*Pachyseris*	0	22	7	29
Cyphastrea	12	14	64	13		*Diploastrea*	0	22	5	31
Pocillopora	10	15	71	11		*Merulina*	0	22	4	32
Seriatopora	9	16	29	16		*Euphyllia*	0	22	3	33
Echinophyllia	7	17	17	22		*Polyphyllia*	0	22	3	33
Turbinaria	5	18	12	26		*Sandalolitha*	0	22	3	33
Stylocoeniella	4	19	2	34		*Barabattoia*	0	22	2	34
Mussidae	4	19	0	36		*Coscinaraea*	0	22	2	34
Pavona	4	19	0	36		*Herpolitha*	0	22	2	34
Pectinia	4	19	2	34		*Gardin'seris*	0	22	1	35
Psammocora	3	20	13	25		*Halomitra*	0	22	1	35
Leptoria	3	20	7	29		*Oulophyllia*	0	22	1	35
Acanthastrea	1	21	6	30		Pectiniidae	0	22	1	35
Agariciidae	1	21	0	36		*Plerogyra*	0	22	1	35
Alveopora	1	21	5	31		*Scolymia*	0	22	1	35
Millepora	1	21	26	17						

Table 5.3.2.2. Rank abundance of genera recorded in five years of visible recruitment and the genera in 1993 belt transect surveys of adjacent coral communities. VR = visible recruits; ADJ = 1993 belt transect data from adjacent communities; R = ranks of relative abundance. Very small colonies that could not be identified to genus are listed at the family level of identification,ie, Faviidae, Mussidae, Agariciidae, and Pectiniidae.

5.3.3. Diversity and Dominance

Table 5.3.3.1 summarizes trends in diversity in permanent quadrats for pooled data from four sites (#1A and 1B pooled, 7A and 7B pooled) monitored annually from 1985 to 1990. The similarity indices (Jaccard (C) Index) indicated that in 1985 and 1990 there was similar composition in back reef quadrats, but dissimilar compositions in fore reef. The change in species composition between 1985 and 1990 was relatively similar in the back and fore reef sites. Simpson's dominance index (D) indicated that there was a similar dominance in both back and fore reef sites in 1985. There was a slightly higher dominance in both locations in 1990.

Species richness (Margalef's index) increased over the five year period (Table 5.3.3.1). At the beginning of the study (1985), and at the end of the study (1990) the back reef sites had higher richness than the fore reef sites. In 1990, sixteen *Acropora* species were recorded in the back reef compared to twenty-one species in the fore reef. In comparison, massive species numbered forty-five in the back reef and thirty-seven in the fore reef sites. Massive species in this case included all Faviidae, Mussidae, Poritidae, and Oculinidae.

INDEX	BACK REEF SITE (1A & 1B)		FORE REEF SITE (7A & 7B)	
	1985	1990	1985	1990
NO.COLS	559	649	393	411
RICHNESS (Margalef's)	6.9	8.0	6.5	7.2
DOMINANCE :				
SIMPSONS (D)	0.091	0.069	0.082	0.057
RECIPROCAL (D)	0.910	0.931	0.918	0.943
SIMILARITY :	WITHIN LOCAT'N		WITHIN YEAR:	
	BACK	FORE	1985	1990
JACCARD (C)	0.155	0.734	0.473	0.567

Table 5.3.3.1. Diversity indices of corals in permanent quadrats from pooled shallow and deep sites in two locations in 1985 and 1990. Jaccard's index compares back reef and fore reef locations (by pooling five years of data from both), and the first and last year of data collection.

Diversity indices of visible recruitment and of the adjacent coral community (from belt transects) were similar, indicating a strong influence of the cumulative recruitment pattern on the established communities (Table 5.3.3.2). Similar numbers of genera were recorded in both data sets from two of the sites (1B and 7A), with a higher number of genera recorded in site 7A in the established community than in the visible recruit assemblage. Evenness and Simpson's dominance indices from the three sites ranked in the same order for visible recruits and for the adjacent coral communities. Richness and Shannon-Weiner indices were similar or slightly higher in the adjacent community compared to the recruit assemblage with site 1B ranking highest in both indices and in both data sets. There is an inverse relationship between the number of visible recruit colonies over five years and the number of colonies in the adjacent community in 1993. When the number of colonies is standardised by dividing the number of colonies by the number of genera, this inverse relationship remains the same.

VISIBLE RECRUITS 1985-90 :							
SITE	GE	NO	IN	RI	SH	EV	SI
1B	25	373	15	4.05	2.41	0.75	0.15
7A	22	227	10	3.87	1.88	0.61	0.30
7B	20	180	9	3.66	2.07	0.69	0.22
ADJACENT COMMUNITY 1993							
	GE	NO	IN	RI	SH	EV	SI
1B	24	169	7	4.48	2.58	0.81	0.11
7A	19	191	10	3.43	2.06	0.70	0.21
7B	32	404	13	5.17	2.58	0.74	0.12

Table 5.3.3.2. Comparison of diversity indices of recruitment (pooled visible recruits recorded in permanent quadrats at three sites from 1985-90), and of the adjacent established coral community in 1993 (belt transect data). GE = number of genera; NO = individual number of colonies; IN = standardised index which divides the number of colonies by the number of genera; RI = Margalef's richness; SH = Shannon-Wiener; EV = Pileou's (J) evenness; and SI = Simpson's dominance index.

The established coral community demonstrated differences in diversity in some habitats and some depths (Table 5.3.3.3). The number of genera and individuals, as well as richness and Shannon's index, were higher in the back and fore reef sites than in the reef flat sites. Evenness was higher in the fore and reef flat sites than in the back reef sites. Simpson's dominance was higher in the back and reef flat sites than in the fore reef sites. Mean values of all diversity indices for visible recruitment were similar to means of diversity in the established community (Table 5.3.3.3).

SITE	HABITAT/DEP	GEN	IND	RICH	SHAN	EVEN	SIMP
7A	FORE / 3m	19	191	3.43	2.06	0.698	0.212
7B	FORE / 6m	32	404	5.17	2.58	0.744	0.119
1B	BACK / 6m	24	169	4.48	2.58	0.81	0.113
5A	FORE / 3m	20	173	3.69	2.12	0.709	0.196
5B	FORE / 6m	31	343	5.14	2.72	0.791	0.097
2	BACK / 3m	19	170	3.5	1.72	0.584	0.35
3A	BACK / 3m	22	194	3.99	2.01	0.651	0.269
6	FORE / 3m	20	159	3.75	2.27	0.759	0.143
11	BACK / FLAT	14	69	3.07	2.26	0.857	0.118
12	BACK / FLAT	10	108	1.92	1.4	0.607	0.397
13	BACK / 3m	28	267	4.83	2.45	0.735	0.153
14	BACK / 3m	23	324	3.81	2.21	0.705	0.19
15	BACK / 3m	22	202	3.96	1.99	0.644	0.255
16	BACK / 3m	23	198	4.16	2.21	0.704	0.229
17	BACK / 3m	32	315	5.39	2.55	0.736	0.141
18	FLAT / 1m	20	147	3.81	2.51	0.838	0.109
MEAN BACK RF (N=8)		24.13	230	4.27	2.22	0.70	0.21
MEAN FORE RF (N=5)		24.40	254	4.23	2.35	0.74	0.15
MEAN FLAT (N=3)		14.67	108	2.93	2.06	0.76	0.21
MEAN 3m (N=3)		20.30	186	3.70	2.06	0.69	0.23
MEAN 6m (N=3)		29.00	305	4.90	2.63	0.78	0.11
MEAN VIS.REC.(N=6)		24.7	245	4.3	2.4	0.73	0.17
MEAN NON VIS.(N=10)		21.1	196	3.8	2.2	0.72	0.21

Table 5.3.3.3. Diversity indices of the adjacent established coral community derived from belt transects collected in 1993 from 17 sites spread around Green Island. GEN = number of genera; IND = number of individual colonies ; RICH = Margalef's richness ;SHANN = Shannon-Wiener; EVEN = Pielou's evenness ; and SIMP = Simpson's dominance.

5.3.4. The Relationship between Early Recruitment and Visible Recruitment

Spearman rank correlations between abundance of early recruits and abundance of visible recruits are shown in Table 5.3.4.1. Taxa groups were selected on the basis of relevance to the stated aims of the study and only in cases where sufficient data were available. Visible recruitment of massive colonies at two deeper sites were significantly correlated with early recruitment on artificial substrata in adjacent areas. The majority of early recruits of massive were from the family Poritidae, with only a few from the Faviidae family. No other significant correlations were found.

SITE	VARIABLE	SPEARMAN (CRIT. VALUE)	P
#1B - BACK 6m SITE	TOTAL CORAL	0.05 (0.997)	NS (>0.05)
(ER87/88&VR88),(ER88/89&VR89)	*Acropora* spp	0.05(0.997)	NS (>0.05)
(ER89/90&VR90)	MASSIVES	-1.0 (0.997)	S (<0.05)
#7A - FORE 3m SITE	TOTAL CORAL	-0.4 (0.95)	NS (>0.05)
(ER86/87&VR87),(ER87/88&VR88)	*Acropora* spp	-0.8 (0.95)	NS (>0.05)
(ER88/89&VR89),(ER89/90&VR90)	MASSIVES	-0.2 (0.95)	NS (>0.05)
#7B - FORE 6m SITE	TOTAL CORAL	0.5 (0.997)	NS (>0.05)
(ER87/88&VR88),(ER88/89&VR89)	*Acropora* spp	0.5 (0.997)	NS (>0.05)
(ER89/90&VR90)	MASSIVES	-1.0 (0.997)	S (<0.05)
2xBACK, 4xFORE SITES	TOTAL CORAL	0.46 (0.811)	NS (>0.05)
(ER89/90&VR90)	*Acropora* spp	0.12 (0.811)	NS (>0.05)
	MASSIVES	0.64 (0.811)	NS (>0.05)
	FAVIIDAE	0.00 (0.811)	NS (>0.05)
	PORITIDAE	0.63 (0.811)	NS (>0.05)

Table 5.3.4.1. Spearman rank correlations of abundance of early recruitment (ER, see chapter 3), and abundance of visible recruits in adjacent permanent quadrats (VR, see chapter 4). Comparisons were made at three sites over three and four continuous years, using early recruitment data from one year and comparing these with visible recruitment in the following year. Comparisons were also made between early recruitment in 1989/90 and visible recruitment in 1990 at six sites where both sets of data are available.

5.4. Discussion

Coral cover had increased dramatically at Green Island six to seven years after starfish were reported to have eaten more than eighty percent of the coral on this reef (Pearson 1981). *Acropora* spp were the dominant component of this increase in cover. This result is similar to that of other studies of recovery after *A. planci* outbreaks on the Great Barrier Reef (Pearson 1974, 1981; Done *et al* 1988) where *Acropora* spp dominated the regenerating community.

The present study demonstrated differences in recovery rates between back and fore reef locations and depths. Differential growth rates of corals have been assumed from field observations, for example, Woodhead (1971) assumed that colonies at deeper sites were smaller due to lower growth rates. Differences in recovery between habitats such as location and depth can be at least partly explained by the relatively small differences in *Acropora* spp growth rates, shown in this study. Factors such as differences in the timing of recruitment cannot alone explain observed community differences in regeneration rates among habitats. In the absence or scarcity of *Acropora* spp, communities would be expected to show very different recovery rates in terms of coral cover and composition. This may be the reason for differences reported in natural recovery characteristics from the Caribbean (Hughes 1985) and from Guam (Colgan 1987).

The ability of *Acropora* spp to dominate most regenerating communities on the Great Barrier Reef probably results from their high abundance as larval recruits relative to other taxa, and to their relatively high growth rates. Therefore, *Acropora* spp can be classified as a pioneer genus with respect to succession processes (Connell 1973). All growth forms of *Acropora* spp have high rates of increase in colony diameter, with arborescent colonies ranked highest. Arborescent *Acropora* spp do not form a single colony base like tabulate and corymbose *Acropora* spp do. This feature allows arborescent *Acropora* spp to regenerate from fragments (the other *Acropora* growth forms generally do not) which will be important in regenerating communities where coral remnants are present (Done *et al* 1988) or where asexual recruitment is an important component of a community (eg, Caribbean foliaceous species mainly recruit asexually, Hughes (1985)).

Mean maximum diameter (MMD) of *Acropora* spp increased at a lower rate in 1990. This may have been due to inter colony contact becoming frequent and thus introducing competition for light and space. Tabulate *Acropora* spp, respond to such situations by forming more centrally placed additional whorls within the colony, thereby increasing the colony surface area without further peripheral growth of the colony. The stimulation for this growth response appeared to be the point where inter colony contact or the appearance of very close neighbours occurs. This situation generally appeared in the latter one to two years of the study. The measurement of maximum diameter does not include this growth condition which may have accounted for the decrease in MMD by 1990.

The high abundance of species of massive corals at most sites contrasts with other studies of post *A. planci* recovery (including studies on Green Island reef over the same period (Endean *et al* 1988)). In fact, prior to the 1987 survey, a number of study sites had higher cover of massives than *Acropora* spp. Endean *et al* (1988) made very different conclusions, noting very low recruitment of massive coral eight years after the starfish infestations had passed. This conclusion was based on a broader definition of recruits than the one used here (colonies less than 5 cm dia) and also included individual species with a growth form habit from families other than those included in the more restrictive definition of massives used here. In 1990 (at least two years after Endean *et al*'s surveys of Green Island) the mean maximum diameter of massive corals from the permanent sites was approximately 5 cm. There is also a suggestion of a suppression of growth in massives due to overtopping by *Acropora* spp. Thus, the annual change in mean diameters of massive corals was tending to decrease in the latter part of the study (Figure 5.3.1.2).

The noticeable decrease in coral cover in 1993 (Figure 5.3.1.1) was directly related to impact from cyclone "Joy" which passed close to Green Island soon after the December 1990 survey. Deeper sites were less affected than shallower ones and certain back reef areas were also less damaged (eg, site #3A). It was not only direct storm damage from the cyclone that affected corals but also a subsequent increase in black band disease and an influx of *Drupella* spp recruits, especially affecting species such as *Acropora millepora* (pers.obs.). The combined impact of these events was largely on *Acropora* spp colonies. The storm effects also created more favorable conditions for future settlement by clearing dead standing colonies which were shading underlying substrata. At the same time, the impact of disease and *Drupella* spp created additional dead standing colonies. As a result, patches with large differences in recovery phases were distributed over small spatial scales of possibly one to several metres. Because of these disturbance events, the relationship between recruitment and the adjacent established communities will become less predictable in the future.

Significant correlations between accumulated recruitment over a five year period and established communities was an important finding. There was a difference of three years between the completion of the recruitment part of the study and the collection of data from the established communities. During this interval, many factors could have altered the composition of the visible recruits but it appears that any alterations that may have occurred were minor since the composition in recruitment in quadrats and community composition in adjacent areas was so highly correlated. When the recruitment and established community data were analysed separately, there were some conflicting results. Multivariate analyses of the established communities in 1993 demonstrated relatively homogeneous compositions of genera and species among sites, aside from some depth and habitat effects. Some differences were noted between slope, reef flat, back reef habitats. Similar multivariate analyses of visible recruitment did not detect any clear differences between depths though some minor grouping of sites from back and fore reefs could be seen (Chapter 4). In addition, dominance plots (Chapter 4) of visible recruits showed differences in dominance at different depths but no differences between locations and years. Comparisons of diversity trends among visible recruits in quadrats and adjacent communities in this chapter, however, indicated most measures were similar in value. The exception was the inverse relationship between the number of recruits and the number of colonies in the established community. This may be a further indication of the influence of the dominant canopy forming species on the rate of recruitment. That is, in sites where high numbers of corals are in the established community, the rate of recruitment is relatively lower than in sites with lower numbers of established colonies. From all the data presented, it is apparent that the composition and broad trends in visible recruitment have been demonstrated to be reflected in the adjacent regenerating community. Similar conclusions of a close correlation of visible recruitment with adjacent established communities were reached by Harriott (1985) in her 18 month study of a fringing reef at Lizard Island (GBR).

The more specific comparison of corals in quadrats at two locations over a five year period indicated that changes in composition of the broader coral community at the study sites were higher in the back reef than in the fore reef by 1990. This change in overall community composition occurred despite no significant change in the composition of visible recruits (Chapter 4), suggesting that differential survival among visible recruits between locations was determining broader coral community composition by 1990. That is, up to nine years after the *A. planci* outbreak, Green Island coral community composition is similar in composition to the visible recruitment trends and was beginning to show a new recovery phase where influences due to habitat differences were determining the composition of the established communities. This change in phases of the recovery pattern correlates with the rapid expansion of a live coral canopy, and lead to a differentiation in coral communities with respect to location and depth. In contrast, Pearson (1981) concluded that after 7 years, his study reefs (located along a similar section of the GBR) had recovered to similar pre *A. planci* diversity levels.

A direct relationship between early recruitment and visible recruitment was not demonstrated in this study, except for massive colonies (principally Poritidae) in two 6 m sites. This result may be because the massive species were not accurately represented on the artificial substrata noted and discussed in earlier chapters. Alternatively, the tiles in deeper water may approximate more shaded conditions which Wallace (1983) has suggested may be a requirement for settlement of certain massive and ahermatypic taxa. This may explain the discrepancy between early and visible recruit abundance of this taxon. Harriott (1985) found that the distribution of early recruits and visible recruits at Lizard Island were similar to the established adjacent communities over an eighteen month period. This contrasts with the present study where early recruitment is generally different to visible recruitment and to the adjacent community. Since early recruitment does not generally reflect patterns in the later developmental phases of coral communities (this study), it is at the very early stages of succession (ie, at or immediately after settlement) where differences in the taxonomic composition of later developmental stages has been determined.

Chapter 6. General Discussion and Summary

This study utilised a 'natural' disturbance, the 1980's *Acanthaster planci* infestation, to investigate the role of recruitment in the regeneration process of a coral reef. Recruitment was studied at several spatial and temporal scales, as well as during two different recruitment phases. The broad scope of the study reduced its ability to use powerful question-driven (univariate) analyses and consequently to assess non significant results from such analyses. Despite this, many interesting patterns in early and visible recruitment were found using multivariate techniques. An advantage of using multivariate techniques is that the relative abundance of all or most taxa recorded during the different aspects of the study contributed to the conclusions reached. In comparison, univariate statistics require that the data are reduced to the most abundant taxa or to the investigation of just a few parameters.

6.1. General characteristics and effects of A. planci *on coral communities*

Major *A. planci* outbreaks result in a significant reduction in live coral cover and a corresponding decrease in species diversity (Moran 1986). Not all colonies or all parts of colonies are eaten during a particular infestation, with the degree of damage determined by the density, behaviour and feeding preferences of starfish, and by the colony morphology of different coral species. The contribution of the remnant colonies to regeneration of a community will vary. Done *et al* (1988) concluded that the significance of coral remnants to the regeneration of communities was negligible in the first few years after the passing of a starfish infestation on John Brewer Reef (GBR). It was difficult to gauge the contribution of remnants to the regeneration process at Green Island since the interval between the passing of the outbreak and the commencement of the study was too long (five years from the first observations of an active outbreak). Most likely, the contribution was negligible since very few colonies were encountered where patches of live coral tissue remained on previously large colonies. One exception was the back reef site (#2). Here, high coral cover in 1990 was due to regrowth from the tips of arborescent *Acropora* spp. Such tips often remain since *A. planci* has difficulty in reaching this part of the colony. In 1985 former large colonies at this site were mainly arborescent *Acropora* spp. Therefore, severe predation followed by *in situ* recovery of the same colonies may have already occurred prior to the 1980's outbreak.

An important factor to note is the structural complexity of the reef is generally unaffected immediately after an outbreak (ie, the dead coral skeletons are left intact and in the same position). Other disturbances which result in dead standing coral colonies include tissue death from disease and predation by the gastropod *Drupella* spp. Both these processes were occurring after 1990 though with less impact than that caused by *A. planci* . Despite coral tissue death, the same light regime persists in the underlying substratum. Consequently, since settlement and survival of corals is light dependent, the characteristics of coral recruitment in the underlying substratum also remains the same. However, algal growth and the infill of spaces occurs between branches in dead corymbose and tabulate corals. This occurs relatively rapidly (within a few years, pers. obs.) on *Acropora* spp colonies, resulting in less light penetration under such colonies. Thus, there is a deterioration of ambient light conditions in the understory as the dead colonies decrease light transparency over time. Processes influenced by algal cover and infill of dead skeletons may include other physical characteristics associated with live or recently dead *Acropora* spp colonies, such as different local sedimentation regimes and water flow patterns, which in turn could influence coral recruitment (Harrison and Wallace 1990; Babcock and Davies 1991; Hunte and Wittenberg 1992). At the same time, the perimeter of dead plates gradually break away (or in cases of large physical disturbances, whole dead colonies are removed), thereby increasing favorable conditions for coral recruitment. Conditions for recruitment therefore become more variable as dead standing structures change and as additional disturbances occur.

The behaviour of *A. planci* can also affect the recovery process. Characteristics of recovery are affected by the mechanics of the disturbance, as determined by individual and group feeding behaviour of the starfish. That is, at various starfish densities and under different behaviour responses of *A. planci*, the rate and degree of coral mortality at any location on a reef will vary. At John Brewer Reef (GBR), aggregations of *A. planci* were present on some parts of this reef up to four years after the initial observation of their presence (Moran *et al* 1985) which presumably would lead to significant differences in recovery time within this reef. Also, sections of a reef can be completely denuded of live coral cover in a short period of time, whereas corals in other areas of the same reefs may be only partially eaten. Furthermore, at some sites corals may be left alone or slowly consumed by a small number of remaining *A. planci* following the passing of the majority of starfish in a large aggregation. Therefore, caution must be emphasised when generalisations about a reef's recovery are made without the specific knowledge of the movements and densities of *A. planci* within that reef.

A. planci prefer to eat *Acropora* spp, particularly tabulate and arborescent colonies. In fast moving aggregations, colonies of less preferred species can be left undamaged (unpubl.data). On Green Island, *A. planci* aggregations during the 1960's and 1980's were reported to have moved from south to north along both the western and eastern reef slopes (Fisk *et al* 1988). As the aggregations converged on the north-western reef sector, coral mortality was more severe, with many less preferred species also consumed. During late 1996 and early 1997, Green Island was once again carrying large *A. planci* aggregations (pers.obs.). Observations on starfish behaviour along the southern slope indicated a general south to north movement pattern. This could be a migratory response of the larger *A. planci* cohorts (several cohorts were present in the population) to a dwindling supply of the highly preferred tabulate *Acropora* spp. It was possible that the large *A. planci* had moved from a broad area in the southern reef sector to sections of reef to the north where relatively lower densities of these cohorts existed. Consequently, there have been similar movement patterns of *A. planci* during three separate outbreak periods on Green Island. Repeated patterns of movement of aggragations have been observed on other reefs (eg, John Brewer Reef and Rib Reef (off Townsville), T Done, P. Moran, pers.comm.) This suggests that individual reefs may have characteristic patterns of disturbance by *A. planci* and therefore characteristic patterns of impact and recovery rates within a reef following a starfish infestation will also be repeated over time.

In general, the interval between repeat *A. planci* disturbances, and the relative intensity of the disturbances, will determine which successional phase is reached before the next starfish impact occurs (Karlson and Hurd 1993). Records from Green Island since the 1960's suggest that the frequency and intensity of *A. planci* outbreaks have been sufficient to severely reduce coral cover of all slope communities (Endean *et al* 1988). Due to slow growth rates, the potential recovery of massive corals, in particular, will probably take many decades as postulated by Done (1988) though the density of massives could be greater than previously predicted. However, the current 1997 disturbance at Green Island reef may extend this projected recovery time. Similar warnings have been made for John Brewer Reef (Done 1985) after analysis of the impact on massive corals of repeated outbreaks of *A. planci* on this reef.

6.2. Processes and Factors Affecting Recruitment

The majority of corals on the GBR spawn annually in a brief mass spawning event. Consequently, recruitment of new corals is predominantly limited to a few months in early summer (Harrison and Wallace 1990). Passive or near passive dispersal of coral larvae means that small scale and large scale phenomenon, such as the behaviour of water masses, could be instrumental in the recovery potential of reefs. More specifically, particles can be entrained in periodically formed eddy systems in the wake of objects such as shallow reef structures and islands (Willis and Oliver 1988; Hamner and Wolanski 1988). Water movements in the northern part of the Great Barrier Reef during spawning time are primarily wind driven currents from the north (Wolanski and Pickard 1985). This results in a southerly movement of water masses, which is helped by the southward movement of the long shore East Australian Current. The prevailing conditions probably indicate that most larvae arriving at Green Island come from mid shelf reefs to the north of Green Island. The relative position of Green Island reef on the continental shelf makes this reef more likely to receive propagules drifting in this southerly current than would adjacent, nearby reefs (Dight *et al* 1990). The early recruitment studies indicated that the supply of coral larvae was higher at Green Island than at other nearby reefs, and higher also than at other reefs on the GBR (Harriott and Fisk 1988; Fisk and Harriott 1990; this study). These larvae most likely arrived at Green Island from other reefs, since recruitment was relatively high during a period (around 1986) when there were few corals of reproductive size on Green Island (pers.obs.). This indicates that recovery of a reef is not necessarily limited by a reduction in reproductive corals within a reef, but that recovery might be affected by reduced larval supply from up stream source reefs. Within Green Island reef also, there are at least two potential sets of high and low larval retention areas (one set each in the NE back reef and the S fore reef, see Figure 2.1(b)) which have been predicted from numerical modeling (Black and Gay 1987), and which could be a factor influencing the spatial pattern of recovery. The potential for the concentration of *A. planci* larvae in the high retention areas could help explain the movement patterns of outbreaks from the southern and NE ends towards the N-NW end of the reef.

At or about 1988, many larger colonies on Green Island were of reproductive size and were observed to spawn (pers.obs.) thereby adding to the pool of potential coral recruits, providing self seeding mechanisms (like those predicted in the above numerical models) were present. Certainly, the observations of coral spawning slicks on Green Island (Chapter 3) supports the likelihood of this mechanism being present at least in the latter stages of the study.

Certain brooding species, such as *Pocillopora damicornis*, some *Porites* spp, and *Heliopora coerula*, produce larvae throughout the year or at times of the year outside the peak mass spawning period (Harriott 1993, Stoddart 1988, Babcock 1990). If present in sufficient densities on a reef, such species could dominate larval recruitment on a local (within reef) scale. For example, early recruits at Upolu Reef comprised relatively higher densities of

Pocilloporidae recruits in both summer and winter periods compared to Green and Michaelmas reefs. This appears to correlate with high densities of adult *P.damicornis* colonies on this reef (unpublished data). In contrast, the contribution to total recruitment from these taxa were low at Green Island, despite the presence on this reef of some large mono specific stands of *Pocillopora damicornis* and *Heliopora coerula.*

Coral recruitment at Green Island probably commenced as soon as settlement space became available following *A. planci* predation (Wallace *et al* 1986). Reef recovery likely began while the starfish outbreak was still in progress, since there were large numbers of starfish on the reef for up to 4 years (Endean and Cameron 1985). However, new coral recruits grow very slowly, and generally reach sizes of less than 1 cm diameter in their first one to two years of life (Harriott 1985; Wallace *et al* 1986; Babcock 1989). For this reason, coral recovery is not readily observed during the first three to five years following an infestation. This lag period could explain reports of an absence of regrowth of corals up to five years after *A. planci* infestations.

A number of early recruitment studies of corals on the GBR have found similar relative abundance of early recruit families to this study (Wallace *et al* 1986; Sammarco 1983; Sammarco and Andrews 1988; Harriott and Fisk 1988; Fisk and Harriott 1990). All report very low densities of recruits of Faviidae and Mussidae, relatively higher abundance of recruits of Poritidae, and consistently high abundance of recruits of Acroporidae and Pocilloporidae. The above generalised relative abundance of early recruit families was not reflected in the correspondingrelative abundance of visible recruits at Green Island.

In summary, this study based on five years continuous data, supports an hypothesis that large (eg, inter reef dispersal patterns) and small spatial scale physical phenomena (eg, substrate type, depth) are influencing coral recruitment patterns and hence the regeneration process at Green Island. However, these patterns do not occur on an annual basis. Rather, they are detectable over longer temporal periods with significant inter annual variability.

6.3. Habitat and Spatial Patterns

It is feasible that specific patterns in recruitment could occur on a broader spatial scale than within a reef,ie, recruitment patterns can be consistent across several reefs within the same time scale. For example, during some years there is potential for consistent variations between back reef and fore reef locations across several reefs similarly placed on the GBR. The settlement plate study indicated a significant difference in early recruitment between back and fore reef locations in cryptic habitats at the three study reefs. One possible explanation could be that there is a grazing effect on recruit mortality rates and hence recruit densities. Grazing by fish and echinoids has been suggested as both a benefit and an inhibitor of coral recruitment (Sammarco 1985; Hughes *et al* 1987). It appears that the intensity of grazing is a determining factor (Hughes *et al* 1987), as is the rugosity of the surfaces being grazed (Carleton and Sammarco 1987).

Following an *A. planci* outbreak, many surfaces will be available on which coral larvae can settle. There is no evidence from this study (pers.obs.) that soft corals or macro algae rapidly dominated large areas of Green Island reef previously occupied by hard coral to the point that subsequent recruitment of hard corals was inhibited for long periods of time, as was predicted by Endean (1976). Soft coral mats covered small areas of low profile substrata in the shallow fore reef but these mats retreated within three or four years (pers. obs.). While there may been some anecdotal evidence of opportunistic use of available free space by non coral organisms, there was not any evidence of a shift in community type following this significant disturbance event (Rogers 1993, Hatcher 1984, Done 1992 a,b, Knowlton 1992). If grazing was responsible for controlling abundance of macro algae, as documented in the Caribbean (Hughes *et al* 1987), then the relative abundance of fish on Green Island was probably sufficient to prevent macro algal dominating.

Over the five years of the study, there were always abundant surfaces of dead tabulate and corymbose *Acropora* spp corals. These have been demonstrated to be suitable for settlement of coral recruits (Wallace *et al* 1986; this study). In addition, there was always ample consolidated hard substratum. The fate of the dead plates remaining after the 1979-81 *A. planci* outbreak was an important factor in the dynamics of coral recovery. Coral recruits using the dead plate surface for settlement were less likely to survive than those which recruited onto solid substratum. This was primarily due to continuous reductions in the surface area of the plates especially towards the periphery of the skeletons where corals settle most frequently. Theoretically, only species capable of survival in the absence of a stable substratum (eg, arborescent *Acropora* spp) should be able to utilise dead plate substrata as a temporary area of establishment. Dead coral plates were also occasionally overturned by storms, and presumably the majority of the new recruits were killed in these cases. Therefore, although dead coral plates provided a suitable surface for recruitment, they were a relatively unstable substratum for long term survival, especially for corals which may need to survive and grow for four to six years before reaching sexual maturity (Harrison and Wallace 1990). Clearly these processes can produce patchiness in the size classes of corals in a regenerating community. This would provide species with low or irregular recruitment rates an opportunity to become established after the early colonizers had initially colonised an area. The shading effect of the dead plates on the understorey substratum would also influence recruitment in the same way as live plates. If similar mechanisms are operating under both live and dead plates, relatively lower recruitment under plate and arborescent skeletons could influence community composition and structure (Fisk and Harriott 1992). At a smaller scale, as the dead plates gradually disintegrate, areas beneath them may become more suitable for coral recruitment.

6.4. Impacts of Disturbance

Natural disturbances on corals either cause physical or tissue damage. An *A. planci* outbreak of the magnitude experienced on Green Island is a severe disturbance from which the reef as a whole takes years to recover. During the five years of this study, Green Island coral communities were subject to a number of relatively less severe impacts as well, which served to make the study of recovery from *A. planci* a more complex task. In addition to a minor recruitment of *A. planci* (whose feeding scars became noticeable in the summer of 1986/87), Green Island was also subjected to two cyclones in 1985 (cyclone 'Winifred') and 1990 (cyclone 'Joy').

Following cyclone 'Joy' there were minor outbreaks of black band disease and a high recruitment pulse of the corallivorous gastropod *Drupella* spp. The latter two disturbances were not wide spread and also acted in a localised or species specific manner, respectively. The majority of disturbances affected *Acropora* spp in particular, and *Drupella* spp appeared to recruit and impact on *Acropora millepora* colonies predominately. The two cyclones caused relatively low impacts which were restricted to shallow water communities, but they differed in their zone of maximum damage. As with all cyclone related disturbances, corals and geomorphological structures varied in their susceptibility to damage (Done 1992c). Cyclone 'Winifred' caused most damage in the north-western sector of the reef whilst damage due to cyclone 'Joy' was predominantly in the southern sectors of the reef (pers.obs.). Damage was restricted to loosely attached colonies or colonies attached to unconsolidated substrata. Both dead standing and live colonies were affected. In contrast, black band disease and *Drupella* spp predation was more dispersed and more specific, with both disturbances leaving new dead standing colonies in both shallow and mid depth ranges. These events had the effect of making substratum available for larval recruitment. In the process, small local patches of two distinct types of available substratum (dead plates and consolidated substratum) were created at only certain parts of the reef. These patches would obviously be at a very different phase of regeneration to the remainder of the reef. That is, recovery trends on this reef were becoming more complex as time progressed. Significant area-specific impacts could therefore influence major habitat related patterns of recruitment and regeneration.

More recently, a relatively larger cyclonic impact on the northern reef sector (March 1997, cyclone 'Justin') caused considerable damage to back reef communities. At the same time a new major *A. planci* outbreak is currently affecting significant portions of Green Island Reef (April 1997) and has reduced coral cover along the southern slope and elsewhere considerably. The combined effect of these events means that Green Island Reef is rapidly returning to a low cover, low diversity coral community similar to that of the early 1980's.

6.5. Successional Phases and Community Composition

The duration of the study of Green Island was too short to be viewed as an extensive study of ecological succession. Successional stages take many decades to develop in coral reef communities. However, some points can be made in a successional context, particularly pertaining to the early stages of community succession. Greene and Shroener (1982) discussed a fixed lottery succession model which is likened to Connell and Slayter's (1977) inhibition model where there is a species by species replacement in a linear fashion as community residents inhibit invasion of subsequent colonists. An inhibitory recruitment phase was reached six to seven years after the last *A. planci* outbreak at Green Island due to the formation of a live coral canopy. Assumptions for this inhibition model require that turnover of species is driven by recruitment and disturbance processes. In this model the community composition gradually shifts towards longer lived species. This is unlikely at Green Island as long as the canopy forming species persist in an area. The model predicts that only disturbance and recruitment rates that can keep pace with the rate of competitive overgrowth will maintain the diversity of such assemblages and prevent them from being dominated by longer lived species. At Green Island, this model would be applicable only if the understorey corals (particularly the massives) can survive long periods as a shaded understorey community, awaiting the removal of the canopy species by a physical disturbance.

An alternative successional end point is predicted when competitive factors dominate and lead to a community composed of species most efficient in utilising space. This alternative model is likened to the tolerance model of Connell and Slayter (1977). Greene and Shroener (1982) suggest that the inhibition and tolerance models could be viewed as two extremes of a more general successional process. However, the fixed lottery model with a linear species by species replacement (or constant probability of species by species replacement) is probably rare in most ecological successions (Usher 1979), and examples in nature of non-linearity are common. Examples of factors causing non-linearity or non-homogeneous species replacements include gregarious settlement of planulae (Lewis 1974; Goreau *et al* 1981; Crisp 1979), and different community structural features which influence recruitment, competition, and disturbance processes (Greene and Shroener 1982).

Small increases in the number of species were observed at Green Island over a five year period when rapid expansion of coral cover occurred. The spatial dominance (of both the substratum and the space directly above the substratum) of plate and arborescent *Acropora* spp, creates a non-linear successional pattern of patchiness in recovery. Competition for unshaded space through rapid growth was probably causing a decrease in suitable areas for recruitment. Under these conditions, the massives could be out-competed due to the superior growth rates of canopy-forming species. The longer term tolerance of massive corals (greater than time periods experienced in this study) to shading from overtopping colonies is not known. However, mean survival rates of massive corals did not significantly vary during the study period, and was not different from survival of *Acropora* spp corals (unpubl.data). In fact, survival rates for all colonies were relatively high, with a mean of approximately 70% for the five years from 1985 to 1990. Therefore, any competitive advantage to massives in having higher survival rates at the very early development stage, is counter balanced by their relatively slower growth rates.

There are a range of indices in this study which point to a period of change around 1988. At this time, the formation of an overtopping canopy of live coral correlates with a change in the dynamics of the coral community, especially with respect to recruitment. The onset of this "competition" phase via shading or overtopping (Sheppard 1981; Stimson 1985; Lang and Chornesky 1990) was predicted as the final phase in recovery following severe *A. planci* predation by Colgan (1982), and as a component of a more general theoretical pathway of community succession by Connell and Slayter (1977). One striking characteristic from the Green Island study was a significant decrease in recruitment rates as this phase emerged. This period of major canopy formation was recorded in the quadrats and in the surrounding community. Evidence for this can be interpreted from the dramatic increase in cover, particularly of *Acropora* spp, in the surrounding community at the same time.

Acropora spp exhibit slow growth in their early years but once a particular size is reached, growth is very rapid, with arborescent corals showing the fastest growth, followed by tabulate and corymbose growth forms. Growth rates of tabulate and corymbose *Acropora* spp are relatively slow in the first few years because they form a broad encrusting colony base. After this stage they are capable of extremely rapid growth and dominance of the space above the substratum. In contrast, arborescent *Acropora* spp establish a base quickly prior to rapid linear extension and branch development. Both growth strategies are effective in rapidly occupying space above the substratum and in contributing to a major proportion of the coral cover estimates. In some of the reef slope sites dominated by *Acropora* spp, total coral approached 50% in 1990, comparable to that seen at sites on undisturbed reefs.

The pattern of *Acropora* spp dominance following *A. planci* outbreaks is similar to that reported from other studies. *Acropora* spp are numerically dominant on recruitment plates, and in many cases comprise over 80% of early recruits at Green Island. They were also numerically dominant as visible recruits in mapped quadrats, although the relative proportion is lower than their abundance as early recruits. For example, over a five year period, 46% of visible recruits were *Acropora* species. Many of the largest *Acropora* spp in the permanent quadrats must have recruited in the first few years following the starfish outbreak, as they all reached the rapid growth phase at approximately 1987-88. At this time, most coral growth rates in the quadrats began to decrease as the *Acropora* spp came into direct contact and shaded each other.

The dynamics of massive corals at Green Island is more complex, and differs from results of past studies. Massive corals were not abundant as early recruits on recruitment plates compared to either *Acropora* spp or Pocilloporidae corals. At Green Island, early recruit abundance was in the range of approximately 1% Poritidae and less than 1% Faviidae or Mussidae. However, these massive coral families were better represented at the visible recruitment stage in the mapped quadrats, where Faviidae comprised 20% and Poritidae 10% of all visible recruits. One possible explanation is that their survival rate between settlement and their appearance in the community at a visible size is higher than the rate for *Acropora* spp recruits. Babcock (1985) has reported slow growth rates for faviid recruits, so it seems likely that most massives were three to five years old when they are first observed in the field. In this study, growth rates of massive corals remained much lower than *Acropora* spp, and the mean rates did not increase during the study period.

Therefore, the often reported apparent failure of massive corals to recover in post-*A. planci* coral communities may be more a function of different developmental time scales rather than low recruitment. Whilst they recruit relatively abundantly to the visible recruitment pool, and survive as well as other taxa, massives make little contribution to live coral cover or to the structure of the coral community within the time frame reported here or for most other published studies, i.e. up to ten years following an infestation. The long term future of the massive corals is dependent primarily on whether or not they are capable of successfully competing with the faster growing canopy forming species. However, as has been suggested by the data presented here, overtopping colonies can reduce recruitment and probably growth and survival of understorey communities, therefore their future viability in these areas is uncertain.

Inter-annual fluctuations in visible recruitment were observed in the juvenile communities and a strong shift in the overall trend was observed around 1988. Correlations have been outlined above, which point towards a change in successional phases from a community with minimal competitive interactions to one with more frequent competition. Early recruitment studies at these same Green Island sites indicated that inter-annual variations in the availability of larvae within a site and between sites can be large, but over a five year period the variance of mean early recruitment rates at each site is generally low. Therefore, it is possible that sites within a reef could have predictable mean early recruitment rates.

In summary, *Acropora* spp would be expected to continue to dominate Green Island communities in the absence of further disturbances such as another *A. planci* outbreak or severe storms or cyclones. The fate of corals, and in particular the massives, in the understorey over a longer time period will be important to the understanding of the recovery processes. The degree of tolerance by massives to the overtopping effects will determine the long term composition of the communities in the absence of disturbances that can eliminate the canopy.

Karlson and Hurd (1993) concluded in their review of disturbances of coral reefs that reefs will 'prove to be mosaics of species assemblages with equilibrial and nonequilibrial dynamics'. This study supports their conclusion through both empirical data on spatio-temporal patterns of recruitment, and through circumstantial evidence of causal factors. Coral reef patches in different successional phases will create the mosaic of species assemblages as will consequent disturbances which will create mosaics with contrasting dynamics in coral communities due to differences in successional phases.

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Appendices

Appendix 3.3.1.1. Summary of ANOVAR analyses of early recruitment comparing (i) three reefs (REEF: Green, Upolu, Michaelmas), two locations (LOC: back reef, fore reef), for two consecutive summers (YEAR). Variables tested include: POOL = pooled recruits; NOPC = non-Pocilloporidae recruits; CRY = cryptic habitat recruits; NOPC-Y = non-Pocilloporidae cryptic recruits; (ii) Winter 1988 early recruitment (W88) for the same parameters as above; (iii) Depth analyses (DEP) from Green Island data. Significant P values set at 0.05 are shown in bold. Df = degrees of freedom; MS = mean square values; P = probability. ALT.ERR = alternate error term used for calculating F statistics.

(i) 3 REEFS		**POOL**		**NOPC**		**CRY**	
SOURCE	**df**	**MS**	**P**	**MS**	**P**	**MS**	**P**
REEF(R)	2	57800	**<0.001**	157	**<0.001**	9558	**<0.001**
LOC(L)	1	48203	**<0.001**	45	**<0.001**	2570	**<0.01**
R x L	2	14311	**<0.001**	83	**<0.001**	288	>0.10
ALT.ERR	8	1125		2		297	
YEAR(Y)	1	111440	**<0.01**	562	**<0.001**	35292	**<0.001**
Y x R	2	9636	**<0.05**	28	**<0.001**	6075	**<0.001**
Y x L	1	502	>0.05	5	>0.05	1040	>0.05
Y x R x L	2	2639	>0.05	24	**<0.05**	305	>0.10
ALT.ERR	8	2895		6		360	
		NOPC.Y		**(ii)W88**			
REEF(R)	2	8354	**<0.001**	5121	**<0.001**		
LOC(L)	1	1	>0.75	5011	**<0.001**		
R x L	2	1986	**<0.005**	1247	**<0.002**		
ALT.ERR	8	181		182			
YEAR(Y)	1	33455	**<0.001**				
Y x R	2	6737	**<0.001**				
Y x L	1	1340	**<0.05**				
Y x R x L	2	953	**<0.05**				
ALT.ERR	8	298					
(iii)DEP		**POOL**		**NOPC**		**CRY**	
DEP(D)	1	4.84	**<0.001**	6	**<0.01**	0.15	>0.5
SIT{DEP}	6	0.8	N/A	0.7	N/A	3.0	N/A
ALT.ERR	8	0.8		0.9		0.7	
YEAR(Y)	1	9.4	**<0.001**	16.7	**<0.001**	22.7	**<0.001**
Y x D	1	1.8	**<0.01**	2.3	**<0.001**	3.6	**<0.001**
ALT.ERR	8	0.2		0.2		0.22	

Appendix 3.3.6.1. Summary of ANOVA testing model predictions of two high and low larval retention pairs of sites (TREATMENTS) within Green Island reef. Four replicate racks per treatment (REP) were deployed with two pairs of tiles per rack (SAM). The experiment was run for two consecutive years but since the wind conditions varied over the two sample times, the experiments were analysed separately. A number of early recruitment parameters were tested including: pooled early recruits (POOLED); Non Pocilloporidae (NON POCIL.); pooled cryptic recruits (CRY); Non Pocilloporidae cryptic recruits (NO POC.CRY); Pocilloporidae only (POCILL.).

	df	**MS**	**P**	**MS**	**P**
(i) POOLED		**(1) 1988/89**		**(2) 1989/90**	
TREATMENT(T)	1	2984	0.04	11552	**0.001**
REP{T}	2	19204	**<0.001**	4773	0.011
SAM{REP{T}}	12	3815	<0.001	2452	0.02
ERROR	16	568		780	
(ii) NON-POCIL.		**(1) 1988/89**		**(2) 1989/90**	
TREATMENT(T)	1	1152	0.2	458	0.3
REP{T}	2	32856	<0.001	4644	<0.001
SAM{REP{T}}	12	3378	0.001	976	0.03
ERROR	16	568		356	
(iii) CRYPTIC		**(1) 1988/89**		**(2) 1989/90**	
TREATMENT(T)	1	458	0.2	4	0.8
REP{T}	2	5494	<0.001	186	0.07
SAM{REP{T}}	12	939	0.01	179	0.02
ERROR	16	268		57	
(iv) NO-POC.CRY		**(1) 1988/89**		**(2) 1989/90**	
TREATMENT(T)	1	713	0.12	205	**0.03**
REP{T}	2	7140	<0.001	399	0.001
SAM{REP{T}}	12	898	0.01	87	0.04
ERROR	16	257		34	
(v) POCILL.		**(1) 1988/89**		**(2) 1989/90**	(transf.)
TREATMENT(T)	1	371	**0.004**	0.3	0.54
REP{T}	2	3068	<0.001	8.34	0.001
SAM{REP{T}}	12	297	<0.001	1.14	0.18
ERROR	16	32		0.7	

Appendix 4.3.1.1. ANOVAR results for a series of diversity indices calculated from visible recruitment data at the level of genus. SHANNON = Shannon-wiener; EVEN. = Pielou's Evenness; NUMBER = number of genera; INDIV = Number of Individuals; SIMPSON = Simpsons Dominance. Significant results at P=0.05 are in bold type.

		(i)SHANNON		**(ii)EVEN.**		**(iii)NUMBER**	
SOURCE	df	MS	P	MS	P	MS	P
BETWEEN							
LOC	1	0.4	NS	0.001	NS	80	NS
DEP	1	0.51	NS	.06	NS	9.8	NS
ERROR	1	0.14		0.001	NS	16.2	
WITHIN							
YR	4	0.01	NS	0.01	NS	12.8	**S**
YR*LOC	4	0.04	NS	0.008	NS	5.5	**S**
YR*DEP	4	0.04	NS	0.004	NS	4.3	NS
ERROR	4	0.01		0.0001		1.2	

		(iv)INDIV.		**(v)SIMPSON**	
SOURCE	df	MS	P	MS	P
BETWEEN					
LOC	1	8832	NS	0.01	NS
DEP	1	848	NS	0.06	NS
ERROR	1	63		0.002	
WITHIN					
YR	4	1026	**S**	0.07	NS
YR*LOC	4	739	**S**	0.007	NS
YR*DEP	4	25.4	NS	0.004	NS
ERROR	4	214.4		0.001	

Appendix 4.3.1.2 Details of ANOVAR (univariate repeated measures) of temporal trends in visible coral recruitment (untransformed) for a five year period from 1985 to 1990. Habitat parameters tested were location (LOC), depth (DEP), and substratum (SUB), using the following taxa groups : (i) Total hard coral (HC); (ii) *Acropora* spp. (AC); (iii) Massives (MA). df=degrees of freedom; MS=mean square; P=probability at 0.05; Significant results at P=0.05 are in bold type. Huynh-Feldt (H-F) epsilon values are indicative of the degree of violation of compound symmetry assumptions. Values of 1 or close to 1 indicate no or minor violations; (*) is the alternative MS term used to calculate the F-statistic here (see Methods).

		(i)HC		**(ii)AC**		**(iii)MA**	
SOURCE	**df**	**MS**	**P**	**MS**	**P**	**MS**	**P**
BETWEEN							
LOC	1	38033	**P<0.05**	21.6	P>0.05	4.1	P>0.05
DEP	1	5508.9	**P<0.05**	18.6	P>0.05	0.04	P>0.05
SUB.	1	2650.5	**P<0.05**	1.7	P>0.05	0.23	P>0.05
LOC*DEP	1	2770.5	**P<0.05**	10.6	P>0.05	0.08	P>0.05
LOC*SUB	1	9518	**P<0.05**	4.6	P>0.05	0.25	P>0.05
DEP*SUB	1	7148	**P<0.05**	2.54	P>0.05	2.41	P>0.05
LOC*DEP*SUB	1	0.027*		9.76*		39.48*	
ERROR	32	64.83		15.34		13.71	
WITHIN							
YR	4	15.99	**P<0.05**	5.33	P>0.05	46.5	**P<0.01**
YR*LOC	4	2.83	P>0.05	1.75	P>0.05	12.25	**P<0.05**
YR*DEP	4	0.74	P>0.05	0.21	P>0.05	6.75	**P<0.05**
YR*SUB	4	1.3	P>0.05	0.48	P>0.05	3.28	P>0.05
YR*LOC*DEP	4	2.44	P>0.05	0.53	P>0.05	6.3	P>0.05
YR*LOC*SUB	4	1.53	P>0.05	1.16	P>0.05	0.58	P>0.05
YR*DEP*SUB	4	2.29	P>0.05	1.52	P>0.05	13.4	**P<0.05**
YR*LOC*DEP*SUB	4	18.48*		19.3*		1.36*	
ERROR	128	38.02		21.54		10.9	
H-F EPSILON::		0.84			0.91		0.8

Appendix 4.3.1.3. Results of ANOVAR (univariate repeated measures) of spatial trends over a two year period of visible coral recruitment for the following taxa : (i) Pooled hard coral (HC); (ii) *Acropora* spp. (AC); (iii) Massives (MA); (iv) Poritidae (PO); (v) Faviidae (FA). LOC=location; SIT{LOC}=site within location; DEP=depth; SUB=substratum; DF=degrees of freedom; MS=mean square; P=probability level. Significant results at P=0.05 are in bold type. (*) is the alternative MS term used to calculate the F-statistic here (see Methods).

		(i)HC		(ii)AC		(iii)MA	
SOURCE	**df**	**MS**	**P**	**MS**	**P**	**MS**	**P**
BETWEEN							
LOC	1	0.04	P>0.75	90.3	P>0.05	0.13	P>0.75
SIT{LOC}	2	19.51	P>0.1	399.3	**P<0.05**	0.95	P>0.5
DEP	1	22.69	P>0.1	902.9	**P<0.03**	0.05	P>0.75
SUB.	1	7.34	P>0.25	116.4	P>0.05	4.8	P>0.25
LOC*DEP	1	1.61	P>0.25	15.5	P>0.1	0.003	P>0.75
LOC*SUB	1	4.98	P>0.25	68.0	P>0.05	0.13	P>0.75
DEP*SUB	1	16.71	P>0.1	235.4	**P<0.05**	1.57	P>0.25
LOC*DEP*SUB	1	27.45*		0.71*		30.92*	
ERROR	6	366.5		148.1		19.06	
WITHIN							
YR	1	48.74	P>0.05	2.4	P>0.25	2.64	P>0.25
YR*LOC	1	13.36	P>0.1	2.2	P>0.25	0.03	P>0.75
YR*SIT{LOC}	2	6.0	P>0.25	0.6	P>0.5	0.13	P>0.75
YR*DEP	1	1.53	P>0.25	0.24	P>0.5	0.004	P>0.75
YR*SUB	1	0.07	P>0.75	0.03	P>0.75	0.04	P>0.75
YR*LOC*DEP	1	7.49	P>0.1	0.8	P>0.5	0.18	P>0.5
YR*LOC*SUB	1	8.09	P>0.1	1.64	P>0.25	0.31	P>0.5
YR*DEP*SUB	1	0.38	P>0.5	0.21	P>0.5	0.42	P>0.5
YR*LOC*DEP*SUB	1	37.31*		229.3*		63.1*	
ERROR	6	165.1		130.0		33.7	

(Appendix 4.3.1.3. Continued over page)

Appendix 4.3.1.3. Continued.

		(iv)POR		(v)FAV	
SOURCE	**df**	**MS**	**P**	**MS**	**P**
BETWEEN					
LOC	1	1494	**P<0.03**	0.8	P>0.5
SIT{LOC}	2	1732	**P<0.03**	2.3	P>0.25
DEP	1	4.33	P>0.25	1.9	P>0.25
SUB.	1	3770	**P<0.25**	6.2	P>0.1
LOC*DEP	1	414.7	**P<0.05**	0.4	P>0.5
LOC*SUB	1	40.7	P>0.05	0.1	P>0.75
DEP*SUB	1	72.7	P>0.05	2.3	P>0.25
LOC*DEP*SUB	1	0.003*		7.2*	
ERROR	6	6.902		6.9	
WITHIN					
YR	1	27.3	P>0.1	2.3	P>0.25
YR*LOC	1	0.9	P>0.5	0.001	P>0.75
YR*SIT{LOC}	2	2.47	P>0.25	0.24	P>0.25
YR*DEP	1	0.2	P>0.5	0.1	P>0.75
YR*SUB	1	3.03	P>0.25	0.01	P>0.75
YR*LOC*DEP	1	0.002	P>0.75	0.08	P>0.75
YR*LOC*SUB	1	1.6	P>0.25	0.01	P>0.75
YR*DEP*SUB	1	0.01	P>0.75	0.3	P>0.25
YR*LOC*DEP*SUB	1	1.24*		22.1*	
ERROR	6	5.8		9.8	

Appendix 5.3.2.1. Numbers of species and taxa recorded from belt transects in 1993 from around Green Island. Taxa are ranked from the most abundant to the least abundant. Sites identified in the first row are shown on the map in Figure 5.2.1.

SITES =	9	2	7A	6	7A	7B	1B	5A	5B	11	18	12	13	14	15	16	17	T
Porites spp	2	4	8	42	28	53	9	28	67	17	16	11	42	39	28	16	45	
Acropora spp	5	24	24	8	55	61	18	8	27	0	18	3	48	57	34	15	35	
Montipora spp	0	4	4	15	5	39	17	4	28	6	10	1	9	6	8	10	15	
Leptastrea purpurea	0	2	0	1	3	40	3	0	22	1	3	2	6	2	1	0	11	
Stylophora pistillata	0	6	6	2	0	3	15	1	7	2	10	0	7	3	3	7	19	
Acropora hyacinthus	0	2	6	2	6	4	1	14	2	0	1	0	3	14	13	7	14	
Galaxea astreata	0	8	16	3	0	2	6	8	12	0	4	0	5	6	1	12	3	
Acropora formosa	0	8	5	7	1	10	1	3	9	0	3	3	4	3	12	8	7	
Goniastrea retiformis	0	0	0	8	7	8	1	11	14	1	1	0	10	10	2	4	6	
Acropora millepora	0	17	5	0	4	0	0	2	2	2	5	4	6	12	8	5	7	
Acropora tenuis	1	15	15	2	1	3	0	3	3	0	2	0	3	11	2	10	5	
Pocillopora damicornis	10	9	2	0	2	5	1	3	1	9	0	0	3	2	7	4	10	
Favia matthai	1	1	1	0	1	2	3	5	6	8	6	2	3	7	9	4	5	
Favites abdita	1	0	3	2	9	4	3	0	4	6	4	1	5	12	3	2	2	
Galaxea fascicularis	0	9	9	2	0	4	2	9	10	0	7	0	4	2	0	0	3	
Lobophyllia hemprichii	0	0	0	0	1	22	3	2	5	0	4	0	12	1	1	3	7	
Acropora nasuta	0	11	2	0	4	4	2	3	2	0	0	0	4	3	7	7	7	
Favia favus	0	0	0	2	6	9	1	2	6	0	3	0	7	5	2	2	7	
Favia spp	0	3	1	3	3	6	2	2	2	0	3	2	3	19	1	0	1	
Acropora elseyi	0	4	4	2	1	0	1	11	5	0	0	0	0	0	4	12	5	
Acropora aspera	0	0	0	0	0	0	0	0	0	1	0	46	0	0	1	0	0	
Favites halicora	0	1	1	3	5	3	2	2	4	0	1	0	8	10	2	1	5	
Fungia spp	0	11	12	0	1	6	0	1	4	0	0	0	2	1	0	5	5	
Heliopora coerulea	28	0	1	0	0	1	0	5	4	0	0	0	0	0	0	0	9	
Acropora nobilis	4	1	3	0	4	4	2	9	1	0	0	0	6	2	0	7	1	
Goniastrea aspera	0	1	1	8	4	5	5	3	2	0	0	0	3	5	0	3	3	
Millepora spp	11	3	0	0	3	0	1	0	1	3	2	0	1	9	2	0	1	
Platygyra sinensis	0	1	1	7	4	4	1	2	3	0	1	2	2	0	2	1	6	
Favia pallida	0	0	2	2	1	4	2	1	2	0	2	0	3	1	4	3	4	
Leptastrea transversa	0	0	5	0	3	0	0	2	0	0	2	1	1	12	2	2	1	
Seriatopora hystrix	2	0	2	0	0	0	13	0	0	0	1	0	3	1	3	6	0	
Acropora sarmentosa	0	0	2	2	0	2	5	0	0	0	1	0	0	3	5	1	8	
Acropora humilis	0	0	2	0	1	4	2	3	2	2	2	1	4	1	1	2	1	
Goniopora spp	0	1	5	2	0	5	0	0	4	0	0	0	0	0	1	2	4	
Cyphastrea serailia	0	1	0	5	1	0	0	0	3	2	4	0	2	3	0	1	1	
Symphyllia recta	0	0	0	0	5	0	1	4	0	0	1	1	2	3	3	2	1	
Acropora latistella	0	2	9	0	0	0	0	1	1	0	0	0	0	1	0	7	1	
Astreopora myriophthalma	0	0	0	0	0	1	4	0	6	1	4	0	2	1	2	0	1	
Cyphastrea microphthalma	2	0	0	1	0	2	0	3	0	0	1	3	4	3	1	1	1	
Acropora florida	0	0	11	2	0	1	0	1	1	0	0	0	2	1	1	1	0	
Cyphastrea chalcidicum	0	0	0	1	0	4	2	0	4	0	2	0	0	2	0	1	5	
Goniastrea edwardsii	0	0	0	0	2	1	4	0	8	0	0	0	4	0	0	0	2	
Platygyra pini	0	0	0	0	0	4	1	0	3	1	3	0	2	4	1	1	0	
Acropora loripes	0	1	0	1	0	3	3	0	0	0	1	0	1	2	0	1	4	
Acropora selago	0	0	0	0	0	2	3	0	1	0	0	0	5	2	0	0	2	
Favia speciosa	0	0	0	0	1	1	0	0	0	1	1	2	0	4	3	1	1	
Montipora digitata	0	0	2	0	0	0	0	0	0	2	1	10	0	0	0	0	0	
Faviid	0	0	3	0	2	1	0	0	0	0	0	0	1	7	0	0	0	
Plesiastrea versipora	0	0	2	1	1	1	2	1	3	0	0	0	1	0	2	0	0	
Acropora gemmifera	0	0	0	2	0	0	0	0	1	0	1	0	0	4	3	0	2	
Echinophyllia aspera	0	0	0	0	0	1	1	1	6	0	1	0	0	0	0	2	0	
Goniastrea favulus	0	0	0	3	0	0	0	0	8	0	0	0	0	1	0	0	0	
Montipora spp (branch)	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Montastrea curta	0	0	1	1	1	3	2	0	1	0	0	0	2	0	0	0	1	
Acropora cytherea	0	0	2	0	0	3	1	2	0	0	0	0	0	1	0	2	0	
Acropora pulchra	0	0	0	0	0	0	0	0	0	0	0	9	0	2	0	0	0	
Mycedium elephantotus	0	0	0	0	0	3	0	0	2	0	0	0	6	0	0	0	0	
Pavona venosa	0	0	1	0	0	3	1	0	1	0	0	0	1	0	0	1	3	
Acropora cerealis	0	2	0	1	0	1	1	0	0	0	0	0	1	2	0	2	0	
Favites spp	0	0	0	0	1	0	2	0	2	0	1	1	1	1	0	0	1	
Psammocora haimeana	0	0	0	1	0	2	1	0	3	0	0	0	1	0	0	0	2	
Turbinaria stellulata	0	0	0	0	1	2	2	0	1	0	2	0	0	0	1	0	1	
Acropora yongei	0	1	6	0	0	0	0	1	0	0	1	0	0	0	0	0	0	
Lobophyllia pachysepta	0	0	0	1	0	7	0	0	1	0	0	0	0	0	0	0	0	
Acropora longicyathus	0	6	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	
Favia lizardensis	0	0	0	0	5	0	0	0	0	0	0	0	0	0	2	0	1	
Goniastrea spp	0	0	0	0	0	0	1	0	0	0	2	0	3	0	2	0	0	
Acropora digitifera	0	0	0	1	2	0	0	3	0	0	0	0	0	0	1	0	0	
Acropora microphthalma	0	1	0	0	0	0	3	0	0	0	0	0	1	2	0	0	0	
Lobophyllia spp	0	0	0	3	2	0	0	0	0	0	0	0	0	2	0	0	0	
Leptoria phrygia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	3	1	
Podabacia crustacea	0	0	0	0	0	3	0	1	2	0	0	0	0	0	0	0	1	
Platygyra spp	0	1	2	0	1	1	0	0	0	0	0	1	0	1	0	0	0	
Acropora grandis	0	1	0	1	0	2	0	0	0	0	0	0	0	0	1	0	1	
Acropora valida	0	2	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	
Echinopora horrida	0	0	0	1	0	1	0	0	4	0	0	0	0	0	0	0	0	

(Cont. over page)

Appendix 5.3.2.1 (cont.)

SITES =	9	2	7A	6	7A	7B	1B	5A	5B	11	18	12	13	14	15	16	17	T
Favia rotundata	0	0	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0	
Montipora verrucosa	0	0	0	0	0	2	2	0	0	0	0	1	1	0	0	0	0	
Acropora carduus	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	
Acanthastrea echinata	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	1	
Alveopora spp	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	1	0	
Diploastrea heliopora	0	0	0	0	0	3	0	0	0	0	0	0	2	0	0	0	0	
Echinophyllia orpheensis	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	2	
Hydnophora rigida	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	
Lobophyllia corymbosa	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	2	
Platygyra daedalea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	3	
Pachyseris speciosa	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	0	0	
Acropora divaricata	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	
Acropora secale	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	
Favites complanata	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	
Favites russelli	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	
Goniastrea australensis	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	
Goniastrea pectinata	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	
Astreopora spp	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	
Favia helianthoides	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	
Goniopora tenuis	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	
Merulina ampliata	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	
Pavona decussata	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	
Sandalolitha robusta	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Polyphyllia talpina	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Acropora samoensis	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	
Barabattoia amicorum	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	
Coscinaraea columna	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Euphyllia ancora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Favia maritima	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Favia stelligera	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
Goniopora fruticosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	
Herpolitha limax	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Hydnophora microconos	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	
Leptastrea pruinosa	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	
Montastrea magnistellata	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	
Montipora spumosa	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
Pavona spp	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
Pectinia spp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	
Psammocora profundacella	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
Pachyseris rugosa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
Stylocoeniella armata	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	
Acropora aculeus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
Acropora austera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
Acropora brueggemanni	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Acropora donei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Acropora granulosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Acanthastrea hillae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Acropora lovelli	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Acropora robusta	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Acropora subulata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Coscinaraea exesa	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Euphyllia glabrescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Echinopora lamellosa	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Echinopora mammiformis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Fungia echinata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Favites flexuosa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Favites pentagona	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Gardineroseris planulata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Goniopora stutchburyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Halomitra pileus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Hydnophora exesa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Montipora foliosa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Montipora foveolata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Merulina scabricula	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
Montastrea valenciennesi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Oulophyllia crispa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Porites cylindrica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Plerogyra sinuosa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pocillopora spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Porites rus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
Psammocora spp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Pavona varians	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Pocillopora woodjonesi	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Scolymia vitiensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
Turbinaria reniformis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
Turbinaria spp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	