Reproductive ecology and population dynamics in a scleractinian coral community.

Thesis submitted by

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Abstract

Patterns of scleractinian distribution and abundance, reproductive ecology, recruitment and mortality were studied over a 2 year period on a patch reef site at Lizard Island, Great Barrier Reef. The purpose of the study was to examine aspects of the population ecology of a range of coral species, and to determine the relationships between community structure and the ecology of the component species in that community. In particular, an attempt was made to examine dynamic aspects of community structure.

In a series of five 10m x 1m transects, 117 scleractinian species were recorded. Coral cover was significantly higher on the shallow reef top (2m deep) than at the reef base (< 9m deep), but there were no significant differences in number of colonies, number of species, Shannon's diversity index, Pielou's evenness, or mean size class of colonies between the two sites. Coral species showed distribution patterns that could be related to a depth gradient.

Reproductive ecology of five scleractinian species present in this community, *Lobophyllia corymbosa* (Forskal), *Favia favus* (Forskal), *Porites lutea* (Edwards and Haime), *Porites australiensis* (Vaughan) and *Pocillopora damicornis* (Linnaeus) was studied for two years. All but *P. damicornis* released gametes that were probably fertilized externally. Two major reproductive patterns were found amongst the 4 non-viviparous species: *L. corymbosa* and *F. favus* were simultaneous hermaphrodites and

released gametes over several days in summer; *P. lutea* and *P. australiensis* were dioecious and released gametes over several weeks to several months respectively, also in summer. The predominance of non-viviparous species amongst those sampled supports the generalization that a brief annual spawning period with larvae developing externally may prove to be the dominant form of sexual reproduction in hermatypic corals.

The fifth species, *Pocillopora damicornis* showed indications of seasonality in gametogenesis and planula release at Lizard Island, in contrast with several previous reports on the species at other locations. Gametogenesis occurred predominantly in winter, and planulae were released with lunar periodicity that was dependent on the season. *P. damicornis* planulae settled preferentially on biologically conditioned, algal-covered substrata, rather than unconditioned, bare coral substrata, but showed subsequent mortality inversely related to this settlement preference.

Coral mortality rate varied amongst these five species. *P. damicornis* had the highest mortality, followed by *L. corymbosa*, the massive *Porites* species, and *F. favus* in order of decreasing mortality rate. Mortality was very high during a summer period when extensive bleaching (=loss of zooxanthellae) was noted. For most species, mortality rate declined with increasing colony size.

There were no significant differences in recruitment (at >1cm diameter) or mortality rates between colonies in shallow and deep transects over an 18 month period. Between 32% and 48% of all colonies recorded in transects died during the 18 month study period. Despite the potential for large changes in generic abundances as a result of the high rate of turnover in coral colonies, there was usually less difference in the same transect over time than there was between neighbouring transects, i.e. the composition of the coral fauna tended to be maintained over time. Recruitment and mortality rates varied greatly among genera, but were similar in genera from the same families.

Coral spat recruited exclusively onto the lower and vertical surfaces of coral blocks used as settlement plates. Fish grazing on plates in shallow water and sediment deposition in deeper water were concluded to be primary causes of spat death. Spat of three families were abundant. Acroporids were most abundant and recruited mainly in summer, but at low densities at other times. Pocilloporids were second most abundant and recruited evenly throughout the year. Poritids were least abundant of these families and recruited almost exclusively in summer. These temporal patterns could be related to known spawning times of some coral species. Spat were most abundant in shallow sites, but the familial composition of spat was similar at deep and shallow sites. The deep/ shallow variation in abundances of spat on settlement plates, and the fact that these differences were not reflected in recruitment at 1cm diameter in transects, raises questions as to whether either settlement space or availability

of planulae limit recruitment.

Overall, both coral species diversity and colony mortality rate (which may be assumed to reflect the degree of disturbance at a site) did not vary significantly between the deep and shallow sites. This is consistant with the intermediate disturbance model of diversity maintenance. However, the fact that coral composition at the site did not change over 18 months is consistent with equilibrium models of diversity maintenance. A mechanism for succession in the absence of major interspecific competition is proposed, and a number of processes, both equilibrium and non-equilibrium, are concluded to play a role in the maintenance of high diversity in this community.

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DECLARATION

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 is given.

IN SUPPORT OF THE THESIS

The following publications have derived from work connected with the production of this thesis, and a copy of the publication or manuscript is included in the back of the thesis:

Harriott, V.J. (1983) Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. Coral Reefs 2:9-18.

Harriott, V.J. (in press) Reproductive seasonality, settlement, and post-settlement mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. Coral Reefs.

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To anyone I may have forgotten, my apologies and thanks.

CHAPTER 1

General Introduction

The population ecology of scleractinian corals was comprehensively reviewed by Connell (1973). This review drew attention to many shortcomings in the knowledge of the life histories and population dynamics of the majority of coral species. These shortcomings were again highlighted by Pearson (1981).

Aspects of coral population ecology include reproduction, larval ecology, recruitment, growth, competition, mortality and abundance patterns. There has been considerable work in these fields since 1973.

Coral distribution, abundance and diversity patterns have received most attention. Studies, frequently incorporating the use of line transects (Loya, 1978), have been carried out for many purposes: for identification of zonation patterns (Bak, 1975; Pichon and Morrissey, 1981); for analysis of changes in diversity with depth (Loya, 1972; Porter, 1972a); to monitor changes in coral communities following damage (Loya, 1976 a; Dollar, 1982; Rogers *et al.*, 1983); and to examine successional patterns (Grigg and Maragos, 1974).

Few studies, apart from those specifically following recovery of reefs after damage have incorporated an assessment of the dynamic aspects of coral communities. Exceptions include studies by Connell (1978, 1979) and Bak and Luckhurst (1980).

The importance of reproductive ecology and early settlement and survival in determination of community structure has increasingly been recognized (Lang, 1970; Dana, 1976; Bak and Engel, 1979; Goreau *et al.*, 1981; Wallace and Bull, 1981; Birkeland *et al.*, 1981; and many others). Our understanding of coral reproductive ecology has been greatly advanced by the recent contributions of Rinkevich and Loya (1979 a, b) and Kojis and Quinn (1981 a, b, 1982). In particular, Kojis and Quinn (1982) have suggested that the spawning of externally fertilized gametes may be the dominant mode of sexual reproduction in hermatypic corals. In addition, a series of papers on settlement patterns of coral spat has created interest in coral recruitment, an area in which very little information was previously available (Birkeland, 1977; Birkeland *et al.*, 1981; Wallace and Bull, 1981; Sammarco and Carleton, 1981).

Coral mortality has received little attention in the years since Connell's review. Loya (1976b) studied recruitment and mortality of *Stylophora pistillata* in a reef flat habitat, and Bak and Luckhurst (1980) estimated mortality in a mixed species assemblage over 5 years.

Studies of coral growth are numerous (Buddemeier and Kinzie, 1976), but most studies have been concerned with the physiological aspects of the calcification process, and few with the ecological consequences of the coral growth rates. Techniques used in the measurement of coral growth rates have become increasingly sophisticated, and for this reason a study of coral growth rates was considered to be beyond the scope of this thesis.

Competition amongst coral species has received considerable attention, with the result that its existence is generally unquestioned, but its significance as a factor controlling coral distribution and abundance, and hence community structure, has been the subject of some controversy (Sheppard, 1979, 1981, 1982; Bradbury and Young, 1981b; Cope, 1981; Bak *et al.*, 1982).

Despite these studies of many aspects of coral ecology, only a few authors have attempted to integrate data on the population ecology of coral species with a study of the contribution of these attributes to community structure, such as that attempted by Connell in 1973. Loya (1976 b), Bak and Engel (1979) and Bak and Luckhurst (1980) have used this broad approach, and their results have contributed greatly to an understanding of the dynamics of the communities concerned.

Perhaps the area of greatest interest to coral ecologists over the last 5 years has been the process of maintenance of high diversity, in particular the roles of disturbance and succession in this process. This body of theory has evolved from studies on

rocky intertidal areas where the roles of competition, predation and physical disturbance in community patterns have received attention over many years (e.g. Menge and Sutherland, 1976; Sousa, 1979). Fishelson (1973), Loya (1976a), and Grassle (1973) have all proposed that mortality of coral colonies through disturbance prevents monopolization of space by a few coral species, and hence acts to increase coral diversity. Grigg and Maragos (1974) postulated that diversity first increases then decreases during succession, and that succession would be interrupted at different stages in regions with different disturbance regimes.

Theories on diversity maintenance applicable to rainforests and coral reefs were reviewed by Connell in 1978. Models of diversity maintenance via disturbance include the "intermediate disturbance" hypothesis. This hypothesis states that, in the absence of disturbance, diversity increases then decreases during succession owing to competitive exclusion of competitively inferior species by a few dominant species. Disturbances of intermediate magnitude and frequency maintain the community at high levels of diversity, at a stage before competitive exclusion reduces diversity.

The disturbance theories of diversity maintenance have been discussed, extended and tested by many authors, for example Huston (1979) and Denslow (1980) for forest situations; Dollar (1982), Karlson (1980) and Grigg (1983) for coral reefs; and Osman and Whitlach (1978) in general terms. A problem in

comparative work is the determination of how "high" diversity is, and how "intermediate" disturbance is.

In this study, the distribution, abundance and diversity patterns of a scleractinian community in a patch reef environment at Lizard Island, northern Great Barrier Reef, were investigated. Aspects of the population ecology of some component species in the community (reproductive ecology, settlement, recruitment and mortality) were studied, and the interactions between coral ecology and community structure were assessed. Some questions that are addressed by this study are:

1. Did coral species' abundances vary with depth?
2. At what taxonomic level were distribution patterns clearest?
3. What were the major reproductive patterns in the community?
4. Did corals exhibit settlement preferences that were related to their distribution patterns as established colonies?
5. Did coral mortality rates vary amongst the coral species and was mortality related to recruitment rate?
6. Was any theory of diversity maintenance generally applicable to this scleractinian community?
7. Do field studies of coral recruitment shed light on the mechanism of succession in coral communities?

CHAPTER 2

Scleractinian community structure.

2.1 Introduction

Many factors have been proposed which could determine the distribution and abundance of scleractinian corals. These include settlement strategies (Goreau *et al.*, 1981; Lewis, 1970,1974 a,b; Stimson, 1974), predation (Porter, 1972 b; Glynn, 1976; Neudecker, 1979; Wellington, 1982), competition (Connell, 1973; Sheppard 1979), and physical factors such as wave stress and sedimentation (Rosen, 1971; Pichon, 1978 a; Hubbard, 1974; Bradbury and Young, 1981 a). Information available on many of these factors was recently reviewed by Sheppard (1982). These controls on coral populations will vary in their effect in different geographical regions, and will operate at different spatial and temporal scales (e.g. compare Goreau *et al.* (1981) on spatial patterns of spat settlement in an aquarium with Bradbury and Young (1981 a) on spatial patterns of corals across an entire reef top).

Before the factors that control coral distribution and abundances can be understood, the underlying distribution patterns must be known. Descriptions of coral communities are amongst the most common of coral reef studies. Early work was reviewed by Stoddart (1969a, b) and a list of subsequent studies is given in Sheppard (1982).

At the time of Stoddart's (1969 a) review, comparative work suffered from a lack of uniformity of methodology, frequently owing to practical limitations as well as to the differing objectives of the authors. More recently, methods incorporating a series of line transects parallel with the depth gradient appear to have been adopted as a relatively standard technique. Studies that have utilized this technique include Loya (1972), Porter (1972 a), Grigg and Maragos (1974), Pichon and Morrissey (1981), Bull (1982), Dollar (1982), Rogers *et al.* (1983) and many others. Assessments of the suitability and problems encountered in this and other methods have been published by Loya (1978), Pichon (1978 b), Goodwin *et al.* (1976), Done (1981) and Dodge *et al.* (1982).

While results of early distribution studies were frequently presented graphically, cluster analysis has recently been used extensively in analysis of patterns of coral distribution. It has been used both to identify distribution patterns along environmental gradients (e.g. Loya (1972), Pichon and Morrissey (1981), Bull (1982)) and also to identify coral species associations from field data (Ott and Auclair, 1977; Dinesen, 1982; Done, 1982).

In this study, the choice of survey methodology was constrained by the multiple purposes of the study, which were to identify patterns of community structure and to monitor the population dynamics of the community over time. For the second purpose, the number of colonies included needed to be as large as

possible. Thus a series of five 10m x 1m transects were chosen as the sampling unit, in which patterns of coral distribution and abundance, as well as recruitment and mortality of colonies, could be assessed. The results of the analysis of community structure (species distributions, abundance, and colony sizes) are given in this section, and an assessment of the dynamic nature of the community is presented in Chapter 6.

2.2 Study site and methods

Lizard Island (14° 41' S, 145° 28' E), and its associated islands, reefs and oceanographic conditions have been described in detail by Pichon and Morrissey (1981).

The patch reef used as the site for all work described in this thesis is illustrated in figure 1, and the location of the transects and other studies is shown in figure 2. The water depth at mean low tide was approximately 1m to 2m above the tops of coral colonies on the reef top, and 9m to the base of the patch reef at the lower limit of distribution of most corals.

Corals were studied in five 10m X 1m transects distributed along a depth gradient. Transects were spaced approximately 10m apart, with transects 1 and 2 on the reef top, transect 3 on the reef slope in approximately 5m water depth, and transects 4 and 5 at the base of the patch reef in 8m and 9m water depth respectively. Transects were permanently marked by 1cm diameter steel stakes hammered into the reef. A fibreglass tape-measure taut between the two stakes marked the midline of the transect,

FIGURE 1: Aerial photograph of the study site showing the location of the patch reef relative to Palfry Island. (▲)

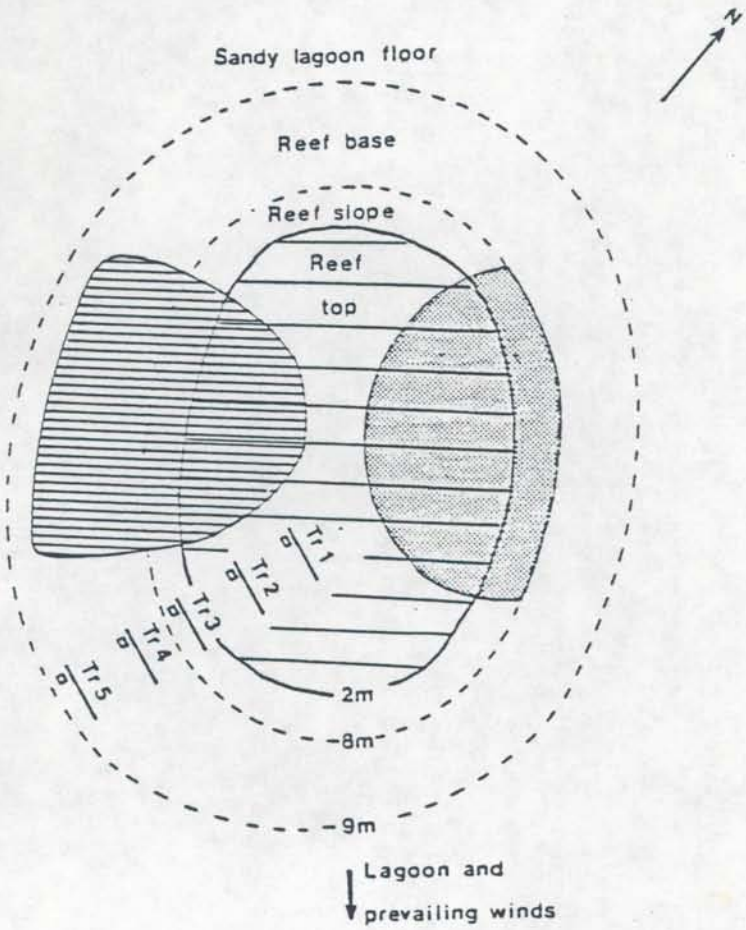


FIGURE 2: A diagramatic representation of the study reef showing the location of transects 1 to 5 and collecting sites. The 2m, 8m and 9m isobaths are marked, and the length of the transect lines is 10m. Colonies of *Pocillopora damicornis* were collected from the stippled area for planulae release experiments, and tagged colonies were monitored for mortality and reproductive condition in the stripped area. The small squares near the transects shows the location of settlement plates.

and a metre stick was used to ascertain the width. In April 1982, each transect was mapped as a series of 10 contiguous $1m^2$ quadrats and each colony was identified to generic level in the field. Transects had been mapped on 10 occasions over a 20 month period prior to the final assessment of species abundances in April 1982. Maps were drawn on a 1:10 scale on underwater paper, and included all colonies either entirely or partially within the 10m x 1m bounds of each transect.

In April 1982, a sample of the skeleton of each colony was collected to allow identification of colonies to species level. Colonies were bleached in a concentrated chlorine solution, washed, dried, and were identified by myself, Dr. M. Pichon or Dr. C. Wallace. Identifications were based on the taxonomic monographs of Veron and Pichon (1976, 1982), Veron *et al.* (1977) and Wallace (1978). Where colonies could not be collected, or were lost or destroyed during the collection and transportation process, field identifications to genus were used.

Coral cover in each transect for each species was calculated from the scale maps. Each colony outline was cut out from maps, grouped with others of the same species, and weighed to the nearest 0.001g. Weight for each species was expressed as a percentage of the total weight for the maps of each transect. There were some difficulties inherent in mapping a three dimensional coral reef surface on a two dimensional map (Pichon, 1978 b). For this reason, no attempt was made to analyse the spatial arrangement of colonies (e.g. nearest neighbour

analysis) from the maps, and estimates of coral cover and colony diameter were only approximate.

Colony diameter was measured from the maps. Largest diameter was assigned to one of 7 size classes, where the maximum size of each size class was approximately double that of the previous class, e.g. class 1= 1 to 3cm; class 2= 4 to 6cm; class 3= 7 to 12cm; class 4= 13 to 25cm; class 5= 26 to 50cm; class 6= 51 to 100cm; class 7= >100cm.

Cluster analyses were performed on both abundance and cover estimates for each transect. The Clustan I C (Wishart, 1975) series of programmes was used, using squared euclidian distance as a measure of dissimilarity, and Ward's fusion strategy on log (n + 1) transformed data. Use of these techniques is discussed in Wishart (1975).

Many diversity indices have been used in coral studies, and the majority of studies have found the various diversity indices to be highly correlated with each other (Loya, 1972; Pichon and Morrissey, 1981), but not always (Sheppard, 1980). Here, number of species, Shannon's diversity, and Pielou's evenness were calculated for both abundance and cover data. Formulae for these indices are given in Loya (1972). This combination of indices allowed the relative influence of the species number and evenness components of diversity to be assessed.

2.3 Results

2.3.1 Species distribution and abundance

To determine whether transect size was sufficient to sample the species present, cumulative species numbers with addition of quadrats was plotted (figure 3). (Loya, 1972; Glynn, 1976). The number of species present begins to level for most transects at about quadrat 6, and the curves are similar to those presented by Loya (1972). A plot of cumulative Shannon's diversity would level even more quickly because of the relatively small effect on the diversity index of the addition of a number of rare species (Loya, 1972; Glynn, 1976). Quadrat-type sampling is more likely than transect methods to sample relatively rare species (Goodwin *et al.*, 1976; Dodge *et al.*, 1982), so the number of species per transect is likely to continue to rise slowly for longer transects.

Figure 4 demonstrates that the majority of species are relatively rare. Approximately 50% of species in each transect are represented by only 1 or 2 individuals, and few species were represented by more than 25 colonies.

Results for abundance (= number of colonies) and cover for each species in each transect, with full species names, are given in Appendix 1. In total 117 species were recorded in the $50m^2$ of transects. A summary of the results for each transect is given in table 1.

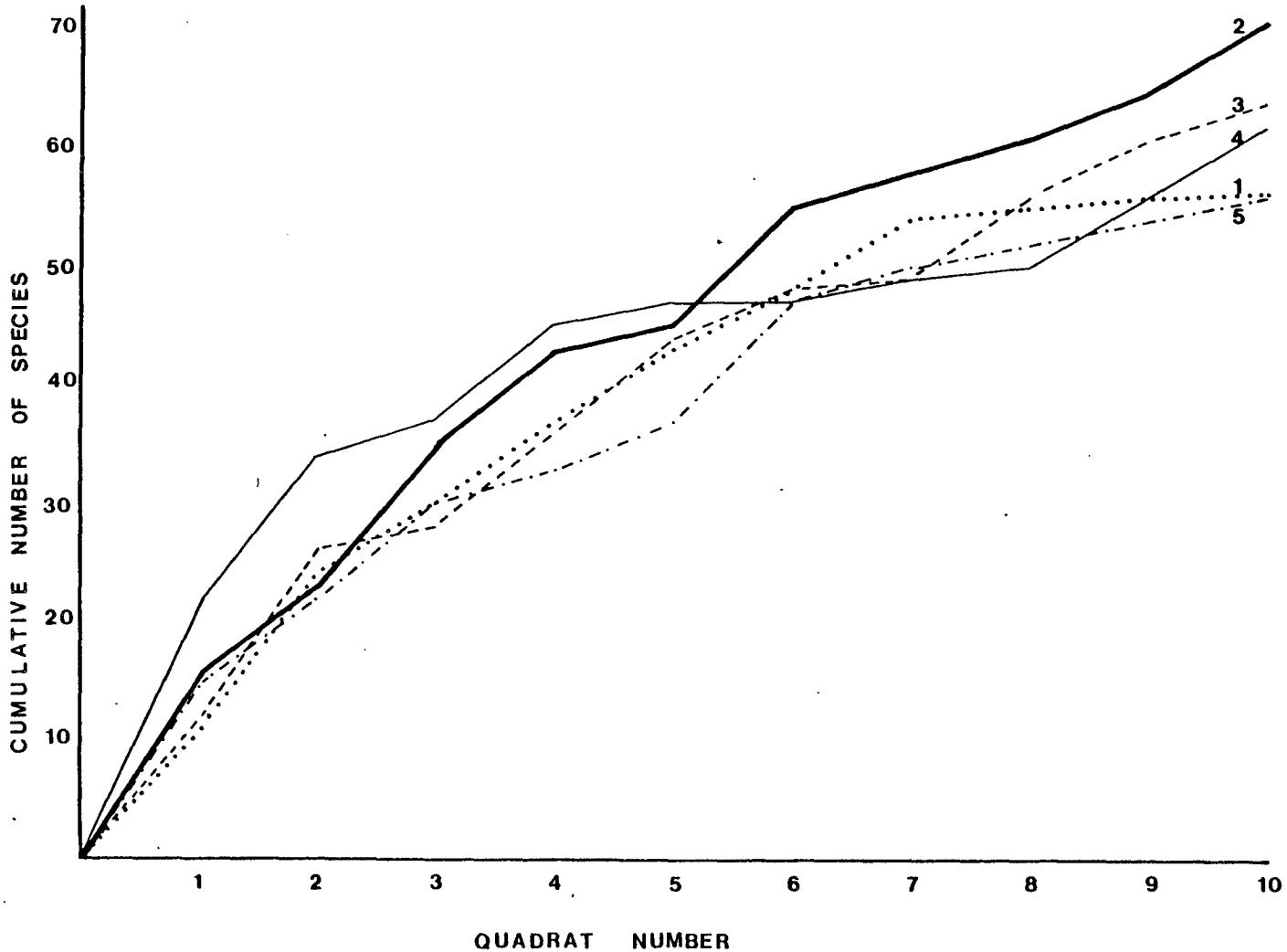


FIGURE 3: Cumulative species numbers for the addition of each $1m^2$ of area, up to $10m^2$, for transects 1 to 5.

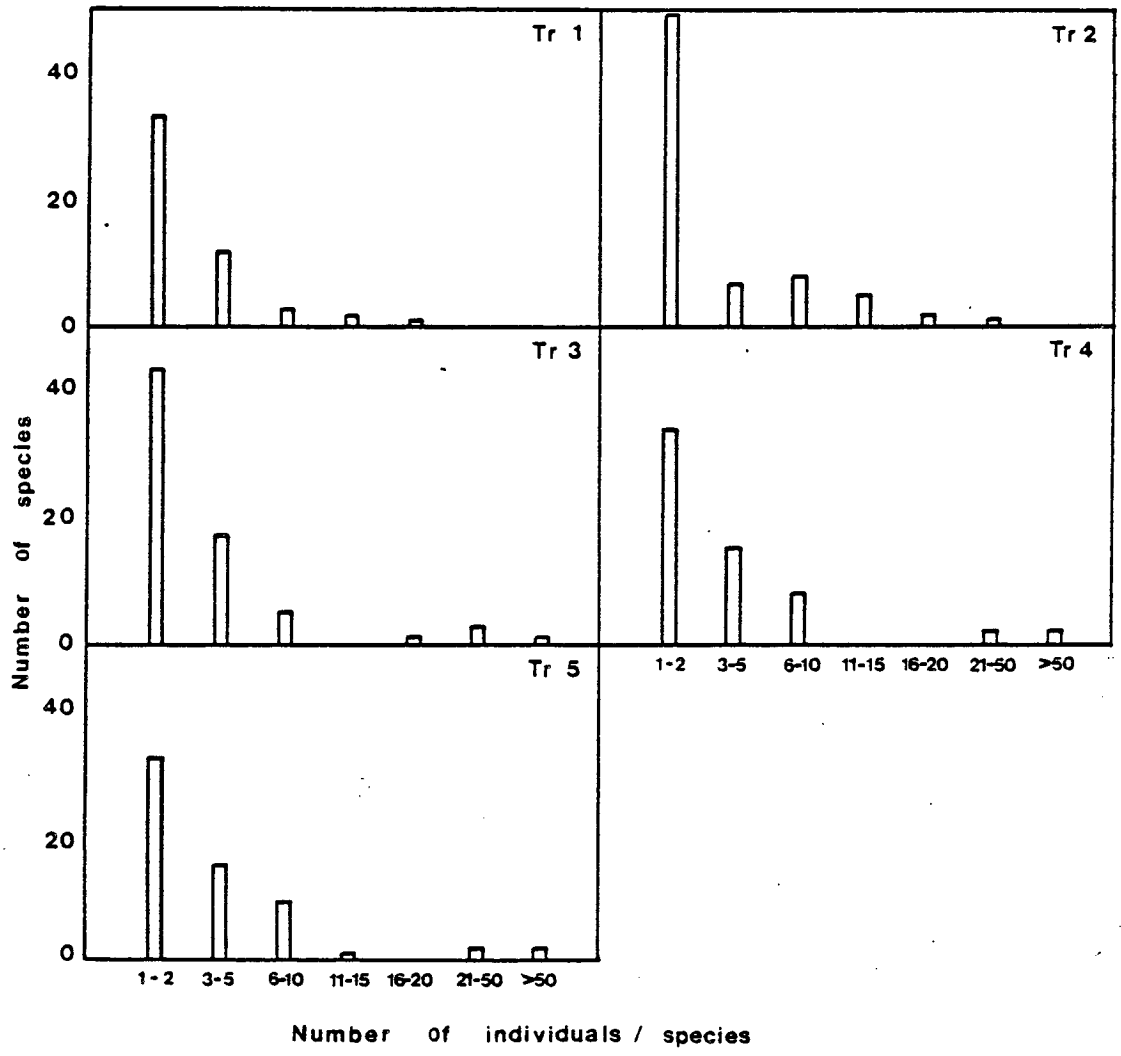


FIGURE 4: The frequency distribution for number of individuals per species for transects 1 to 5.

TABLE 1: Patterns of species abundance and diversity in transects 1 to 5.

	1	2	3	4	5	All transects
Number of colonies	271	327	401	369	405	1173
Number of species	57	71	63	62	59	117
Coral cover (%)	40	48	51	16	29	37
Species/quadrat	13.7	16.9	15.3	14.7	15.3	15.2
Mean size class	2.96	2.67	2.61	2.21	2.59	
Shannon's diversity						
Abundance	3.47	3.66	2.99	3.19	2.97	
Cover	2.62	2.44	2.19	2.42	2.06	
Pielou's evenness						
Abundance	0.86	0.86	0.72	0.78	0.74	
Cover	0.65	0.57	0.53	0.59	0.51	

To test whether there were differences in community structure between shallow (transects 1 and 2) and deep (transects 4 and 5) sites, a number of two sample *t*-tests were performed. There were no significant differences in number of colonies, number of species, Shannon's diversity, Pielou's evenness and number of species per quadrat between the two shallow and two deep sites ($P(T) > 0.05$), but coral cover was significantly higher in the shallow than the deep transects ($P(T) = 0.05$).

Species were not evenly distributed across transects; some species were more abundant in shallow transects and others in deeper transects (table 2). Few species were abundant in both deep (4 and 5) and shallow (1 and 2) transects, and there was a clear indication of a zonation pattern in species distribution across the approximately 7m depth gradient.

2.3.2 Cluster analysis

Analyses were performed on both abundance and cover estimates at the taxonomic levels of species, genus and family (figure 5).

At all taxonomic levels, transects 4 and 5 were similar to each other, as were transects 1 and 2. This would be the expected result, considering the locations of the two sets of transects on the reef base and top respectively. Transects 4 and 5 were more similar to each other than transects 1 and 2 were in all cases.

TABLE 2: Patterns of species abundance and distribution in transects 1 to 5 for abundant coral species. - = <5 colonies; * = 5 to 9 colonies; ** = 10 to 19 colonies; *** = 20 to 50 colonies; ✱ = >50 colonies.

	1	2	3	4	5
E. horrida	*	-	-	-	
A. palifera	*	-		-	
M. verrucosa	-	*	-	-	-
M. monasteriata		**		-	
G. fascicularis	**		*	-	-
G. astreata	**	**	*	-	-
M. tuberculosa	**	**	*		
F. halicora	*	*	-	-	-
P. damicornis	*	*	*	-	-
S. hystrix	*	*	*	-	-
A. brueggemanni	*	**	*	-	-
G. edwardsi	*	**	*	*	*
G. pectinata	*	*	-	*	-
P. australiensis	**	**	***	*	*
P. annae/lichen	***	***	✱	✱	***
P. lutea	**	**	***	***	***
S. pistillata	-	-	*	*	-
A. myriophthalma	-	*		*	*
P. lobata	-	**	**	***	✱
P. vaughani	-	**	***	✱	✱
L. purpurea	-	*	-	*	**
F. favus	-	-	*	**	**
E. lamellosa	-		-	*	
C. serailia	-		-	*	-
P. cylindrica			-	*	*
C. microphthalma	-	-	-	-	**

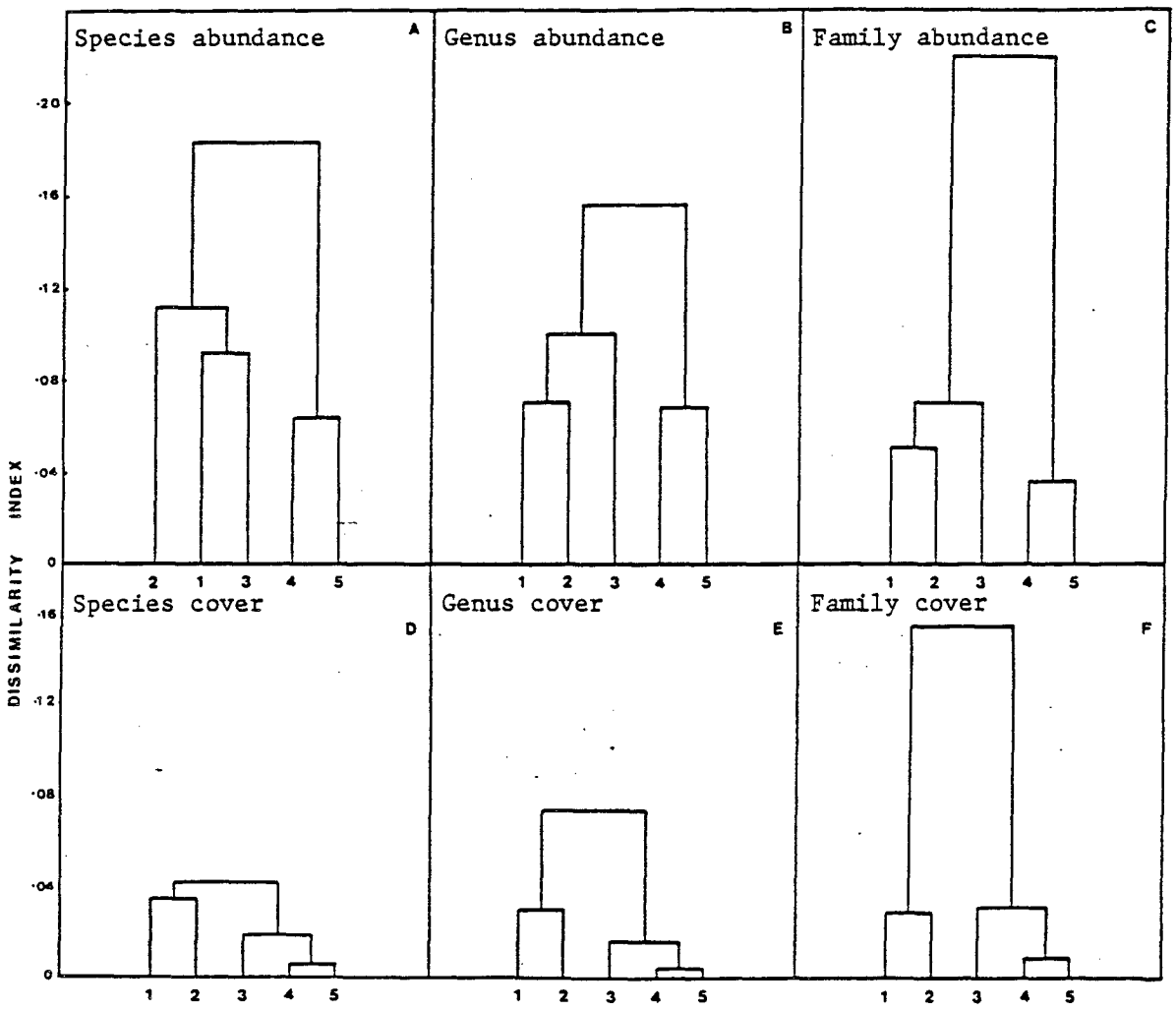


FIGURE 5: Dendrograms for cluster analysis of coral abundance and cover for data at species, genus and family level. The analysis incorporates the squared euclidian distance dissimilarity index and Ward's fusion strategy.

Transect 3 was similar to transects 4 and 5 with respect to coral cover, while in the abundance analysis transect 3 was more similar to transects 1 and 2.

In all cases, there was a distinct deep/shallow split between transect 1 and 2 and transects 4 and 5. The major difference in the results of analyses at different taxonomic levels was in the distinctness of this split. Transects showed a greater similarity within, and greater differences between clusters at higher taxonomic levels.

2.3.3 Size frequency distributions

Size frequency distributions of colonies in transects 1 to 5 are shown in figure 6. Despite the higher cover in shallow transects, there was no significant difference in mean size class of colonies between the two shallow and the two deep sites (table 1; $T = 1.42$, $P(T) > 0.05$). However, transects 4 and 5 each had only 3 colonies in size classes 6 and 7 (>50cm diameter), compared with 7,8 and 8 in size classes 6 and 7 for transects 1,2 and 3 respectively. Thus the difference in coral cover between shallow and deeper sites is largely the result of the presence of a relatively small number of large colonies in the shallower transects.

K-W test is appropriate here

The majority of colonies in all transects were small, i.e. in size classes 1 and 2, or less than 6cm diameter. Only 7% of colonies were over 25cm in diameter and only 2% were greater than 50cm in diameter. In an analysis of the population dynamics of

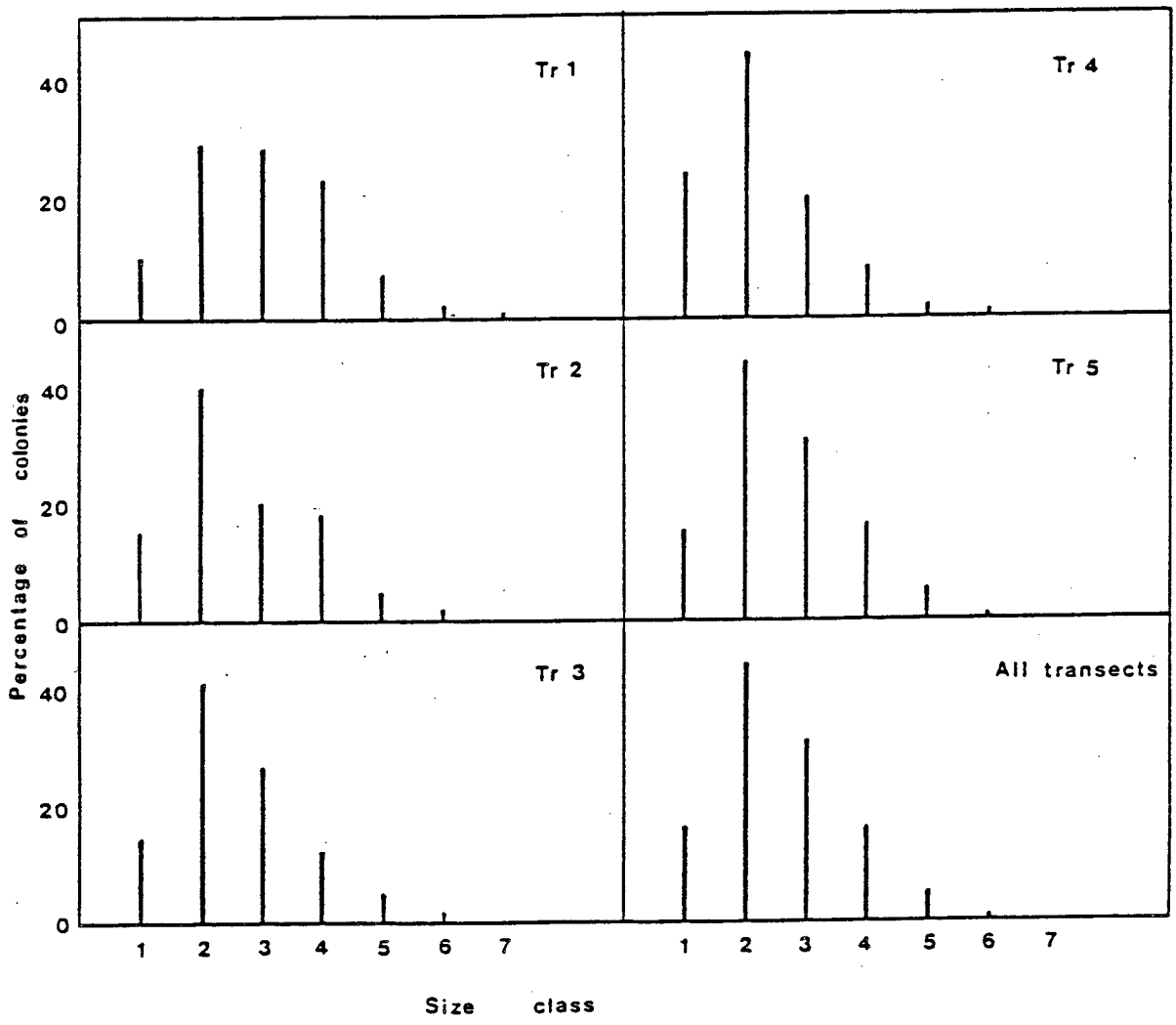


FIGURE 6: Size frequency distributions for colonies in transects 1 to 5, and for all transects pooled. For ease of comparison between sites, frequencies are expressed here as the percentage of the total number of colonies in the transect.

such a community, small colonies are a major component of the community and should be taken into consideration.

2.4 Discussion

2.4.1 Species diversity

The patch reef study site at Lizard Island contains a diverse coral assemblage. Of the approximately 320 scleractinian coral species on the Great Barrier Reef (M. Pichon, personal communication), 117 species or over one third of the total were recorded in the $50m^2$ of transects examined.

which were species observed outside of Transects

In other studies on the Great Barrier Reef, Pichon and Morrissey (1981) reported a similarly diverse coral fauna for a reef flat and reef slope study area on the seaward side of Lizard Island, only a few kilometres from my study site. In a series of thirty one 30m line transects, they recorded 119 scleractinian species. Bull (1982) reported 78 species of 33 genera at two sites on an inshore fringing reef at Magnetic Island near Townsville.

In these studies, coral diversity was high relative to many other geographical regions. In the Red Sea, Loya and Slobodkin (1971) reported 97 scleractinian species from Eilat, and Loya (1972) recorded from 5 to 34 species per 10m line transect. In the Caribbean, most regions contain only 42 to 50 species (reviewed by Bak (1975), and most studies include fewer than 35 species (e.g. Ott and Auclair (1977), Bak (1975), Rogers *et al.* (1983)). In Bermuda, Dodge *et al.* (1982) reported 15 species,

with a maximum of 10 species per 10m x 0.5m transect. Grigg (1983) reports that 42 scleractinian species occur in Hawaii, but Dollar (1982) recorded only 22 species during the course of his extensive study, with 3 species contributing 97% of the coral cover. Similarly, the eastern Pacific region is very low in species numbers (Porter, 1972 b; Glynn, 1976; Wellington, 1982). Any theories on the regulation of coral abundance and distribution which are tested in such low diversity systems may not be generally applicable to more diverse systems, where for example, the effects of predation (Wellington, 1982) may be diffused over many species.

In the community studied here, the number of individuals per species was generally low (figure 4), and the majority of species were represented by only a few colonies. A similar relationship was found by Loya and Slobodkin (1971) and Sheppard (1980) for Red Sea and Indian Ocean localities.

Coral species diversity was consistently high in each transect (table 1) and did not differ significantly between the two shallower and two deeper transects. This result contrasts with many other reports of changes in species diversity with depth. Over a similar depth gradient (2m to 9m)in reef front habitats, species diversity increased in studies by Loya (1972), Porter (1972 a), Glynn (1976), Bak (1975) and Sheppard (1981). These and other results are discussed in Sheppard (1982). Pichon and Morrissey (1981) found no change in the number of species (38, 36, 37) in line transects at 3, 5 and 10m respectively on

the fore-reef slope at Lizard Island.

Any single hypothesis to account for the high diversity of corals at the patch reef site at Lizard Island must be applicable to both the reef top habitat, which has the greatest potential for physical disturbance, and the deeper reef base habitat. The intermediate disturbance hypothesis (Connell, 1973) would be consistent with a conclusion that disturbance was equal in rate and/or intensity at all sites. This will be discussed further in Chapters 6 and 8.

2.4.2 Determinants of species distribution

Species were not evenly distributed across the depth gradient from reef top to reef base; some were more abundant in shallow water and others in deeper water (table 2).

Cluster analyses demonstrated that the two shallow reef top sites were similar to each other, and the two reef base sites were similar to each other in coral species abundance and cover. The reef slope transect resembled the shallower transects with respect to coral species abundance, and the deeper transects with respect to coral species cover. The fluctuating nature of these associations may reflect the intermediate location of transect 3 on the reef slope.

The clearest differences in coral composition between shallow and deep sites were apparent at taxonomic levels higher than species. This is consistent with the finding of Bradbury

and Loya (1978) that spatial patterns for corals were clearer at higher taxonomic levels. Here, it seems that families and genera respond to environmental changes along a depth gradient, but at the spatial scale sampled, the species within the genera show variability in their distributions.

The distribution patterns described here may have resulted from many factors or combinations of factors. These include:
1. Species might settle (or recruit asexually) preferentially in a particular set of environmental conditions, and these recruitment patterns might determine adult distribution patterns.
2. Species might recruit randomly or evenly, followed by differential post-settlement survival because of inherent differences in physiological tolerances. These tolerances might be characteristic of genera or families, and could account for the distinct distribution patterns observed at these levels.
3. Species might settle randomly or evenly, and biological processes such as predation and competition might modify distributions as colonies grow.

Published results provide evidence for all of these possibilities. Harrigan (1972), Lewis (1970, 1974 a,b) and Stimson (1974) give evidence for settlement preferences, or the effects of settlement patterns on distribution of adult corals. Bak and Engel (1979), however, have found no correlation between abundance of juvenile and adult corals of the same species.

Variable tolerances to wave movement, light and sediment form the basis for the coral distribution models of Hubbard (1974), Rosen (1971) and Pichon (1978a). Whether corals show distribution patterns relative to their nutritional requirements for particulate food and light has been the subject of much speculation (see discussion in Sheppard (1982)).

Porter (1972 b), Glynn (1976), Glynn *et al.* (1972), Neudecker (1979) and Wellington (1982) amongst others, have discussed the effects of predation, particularly by *Acanthaster planci* and coral reef fishes, on coral distribution. These studies however, have been concerned with only a few species, or low diversity coral communities.

Recently, the role of interspecific competition via shading and overtopping (Connell, 1973; Porter, 1976) and interspecific aggressive feeding (Lang, 1970, 1973; Sheppard, 1979 and many others) in the determination of coral distribution and community structure has been questioned (Sheppard, 1981, 1982; Bradbury and Young, 1981; Cope, 1981; Bak *et al.*., 1982). Emphasis now appears to be on the localized, rather than community wide, nature of the results of competition.

A more complex hypothesis to account for patterns of species distribution is that the combination of species present will depend on the size and frequency of disturbance, since different disturbance regimes will favour species assemblages adapted to different successional stages (Denslow, 1980; Miller, 1982). Such differences will be reflected in the relative recruitment

and competitive ability of the species (1 and 2 above). For example, in an area with frequent, large disturbances, "r-selected", "opportunistic" or "ruderal" (Grime, 1979) type species might predominate. The species composition of such assemblages will depend on the life history characteristics of the available species, and on the frequency and magnitude of the disturbances.

In the following chapters, data on the reproductive ecology, settlement and early survival, and mortality of scleractinian corals in the community described here, are presented. The influence of these life history traits on the corals' population ecology is assessed, and the results provide evidence to support or refute some of the above hypotheses on determinants of community structure.

CHAPTER 3

Reproductive ecology of 4 non-viviparous coral species.

3.1 Introduction

Until recently, data on scleractinian reproduction has been scarce (Rinkevich and Loya, 1979 a; Connell, 1973) and this has lead to generalizations based on few observations (Stimson, 1978; Rosen, 1981). In particular, many of the early studies were of viviparous species and this resulted in the implication in the literature that this is the general rule for corals (Hyman, 1940; Stimson, 1976).

Recent long term studies of coral reef scleractinian reproduction (Rinkevich and Loya, 1979 a,b; Kojis and Quinn, 1981 a, b, 1982; Oliver, 1979; Babcock, 1980; Bothwell, 1981; Harrison *et al.*, in press) have indicated that a high proportion of corals are not viviparous.

Several major variations in reproductive patterns are now known for scleractinians:

a. Hermaphroditic species that brood planulae (Rinkevich and Loya, 1979 a,b; Harrigan, 1972).

b. Dioecious species that brood planulae (Kojis and Quinn, 1981 b).

c. Hermaphroditic species that release ova and sperm with external fertilization (Kojis and Quinn, 1981 a, b,1982; Oliver, 1979; Babcock, 1980)

d. Dioecious species that release ova and sperm with external fertilization (Willis, in prep.; Fisk, 1981; Kojis and Quinn, 1981 b).

Within these categories, there are many variations in factors such as number of gonads, period of spawning, number of eggs, reproductive seasonality, positions of male and female gonads and lunar periodicity which result in enormous variation in overall reproductive strategies.

Several authors have proposed hypotheses relating mode of reproduction in scleractinian corals with ecology or morphology of the species. Stimson (1978) proposed that shallow water species might reproduce in a manner likely to retain reproductive products in the parental habitat. Loya (1976 a) related reproductive characteristics of a species to its position on an r/K spectrum of life history strategies. Rinkevich and Loya (1979 a) suggested that small polyped, branching species might produce gonads in the coelenteron and be more likely to brood planulae, while large polyped or massive species might spawn large numbers of eggs. Kojis and Quinn (1982) suggested that hermaphroditism with simultaneous release of gametes might promote fertilization in relatively uncommon species.

Reproductive ecology of five scleractinian species, representing a range of taxa, polyp size and growth form, was investigated at the Lizard Island study site. In this chapter, data are presented for four of the species, and results for the fifth species, *Pocillopora damicornis*, are given in Chapter 4.

Observations were made on gonad structure, mode of reproduction and ovum size and number for each species. Results are compared with those available for other scleractinian species and are used to test the applicability of several of the above hypotheses on reproductive ecology. In addition, scleractinian species on the Great Barrier Reef show great variability in reproductive seasonality. Temperature and lunar periodicity have been cited as major regulating factors for marine invertebrate reproductive cycles (Giese and Pearse, 1974), and their role in determining seasonality and spawning period is investigated.

3.2 Methods

Methodology followed that of Kojis and Quinn (1981 a) in that tagged colonies were sampled repeatedly for periods of up to two years. This enabled reproduction to be followed in individuals as well as the population as a whole. Between June 1980 and May 1982, colonies were sampled at six to eight week intervals. They were sampled on S.C.U.B.A. from depths of 2 m to 9 m (figure 2) using a hammer and chisel. Samples were collected from 10 colonies each of *Favia favus* (Forskal) (figure 7) and *Lobophyllia corymbosa* (Forskal) (figure 8) in each sample period, with a colony being replaced once it was reduced to approximately half its original size, or when it died. Overall, 17 *F. favus* and 14 *L. corymbosa* colonies were sampled over the 23 month period.

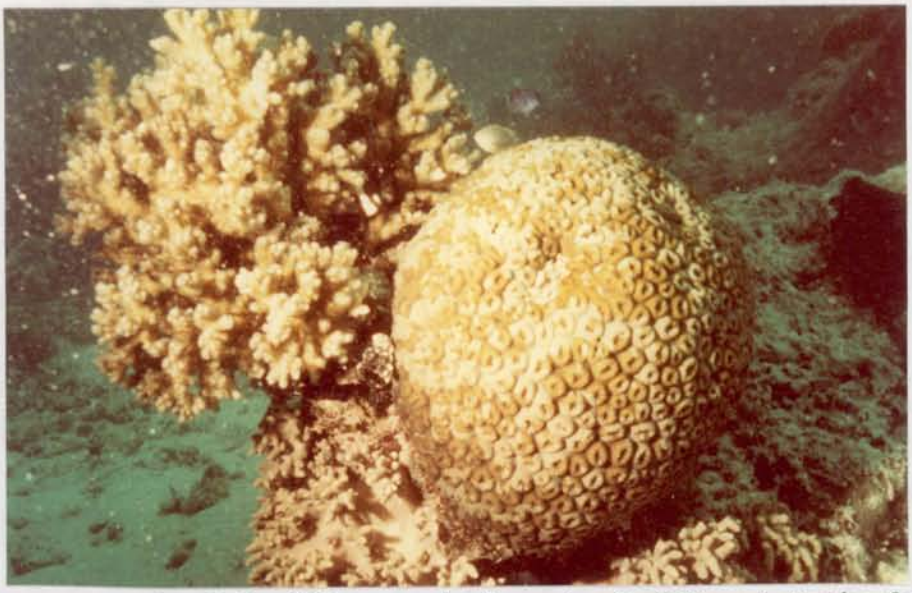


FIGURE 7: Photograph of *Pocillopora damicornis* (left) and *Favia favus*.

FIGURE 8: Photograph of *Lobophyllia corymbosa* colony.

FIGURE 9: Photograph of a massive *Porites* colony.

Porites lutea (Edwards and Haime) and *Porites australiensis* (Vaughan) (figure 9) are very similar taxonomically and cannot be separated in the field (Veron and Pichon, 1982). The initial sample of nine *Porites* colonies consisted of five colonies of *P. lutea* and four colonies of *P. australiensis*. Close to the spawning period in 1981, sample size was increased to 10 *P. lutea* colonies and 9 *P. australiensis* colonies.

From late November to late December 1981, *Porites* colonies were sampled at intervals of two to three weeks. Similarly, samples from additional untagged colonies of *F. favus* and *L. corymbosa* were collected every two to three days and examined fresh under a dissecting microscope for signs of gonad activity or recent spawning. Colonies of each species were held in aquaria with a flow-through sea water system. Outlets were filtered with plankton netting, and aquaria were kept under 50% or 75% shadecloth. Aquaria were monitored for signs of reproductive products.

Regular samples were fixed in 10% sea water formalin, and were either decalcified after two to three days, or were transferred to 70% alcohol and decalcified after several weeks. *Porites* species were decalcified over two to three days in a solution of approximately 10% formic acid and 5% formalin. *Favia* and *Lobophyllia* samples were decalcified in the above solution during the first 14 months of collection, after which a solution of approximately 5% hydrochloric acid and 3% formalin was used. The second solution gave more rapid decalcification than the

former, and the results were comparable for the purposes of dissecting microscope examination. For histological purposes, decalcification in hydrochloric acid provided adequate results, but long decalcification in HCl prevented nuclear staining with haematoxylin. Treatment during the staining process can overcome this problem (Luna, 1968). All decalcified tissue was stored in 70% alcohol.

All *Porites* samples were examined histologically. Samples were dehydrated, cleared, embedded in paraffin and sectioned at approximately 8μm. Sections were taken from two to four regions of the tissue, 300μm to 500μm apart to ensure that some slides contained tissue from the reproductive region of the polyps. Sections were stained in Mayer's haematoxylin and eosin. Maximum egg diameters were measured from sections using stage and ocular micrometers.

Because of their large polyp size, reproductive condition of *L. corymbosa* and *F. favus* could easily be assessed using a dissecting microscope. Egg diameters were measured from preserved specimens using stage and ocular micrometers, and number of ova per gonad and number of gonads per polyp were counted. Representative samples of stages in gonad development were prepared histologically as for *Porites* species. For each of the four species, mean egg or testes diameter for a colony was calculated from measurements of at least 10 eggs or testes per colony.

To obtain an estimate of colony size at first reproduction, and to ascertain the effect of colony size on sex, colonies over a range of sizes were sampled for each species during summer 1981. Samples of *L. corymbosa* and *F. favus* collected on 20 and 29 November 1981 were examined fresh using a dissecting microscope. *Porites* samples collected on 8 December 1981 were examined histologically and a piece of skeleton was retained for taxonomic identification.

3.3 Results

3.3.1 Gonad structure and development

Lobophyllia corymbosa is a simultaneous hermaphrodite in which ovaries and testes develop separately and adjacent on the same mesentery. Ovaries commenced development between January and April , and testes between October and November. However, one of the 14 colonies sampled contained only testes. As spawning period approached, two to three gonads per mesentery were common, although ovaries appeared to merge as eggs enlarged. Each ovary was generally associated with a testis that developed orally, relative to the ovary. Mature ova were orange and testes were cream to light brown. Representative gonad structures are shown in figure 10.

Favia favus is a simultaneous hermaphrodite with ovaries and testes intermingled within a single gonad. Ovaries commenced development in June to August and testes in August to December. Two gonads per mesentery were common, with gonads at the aboral

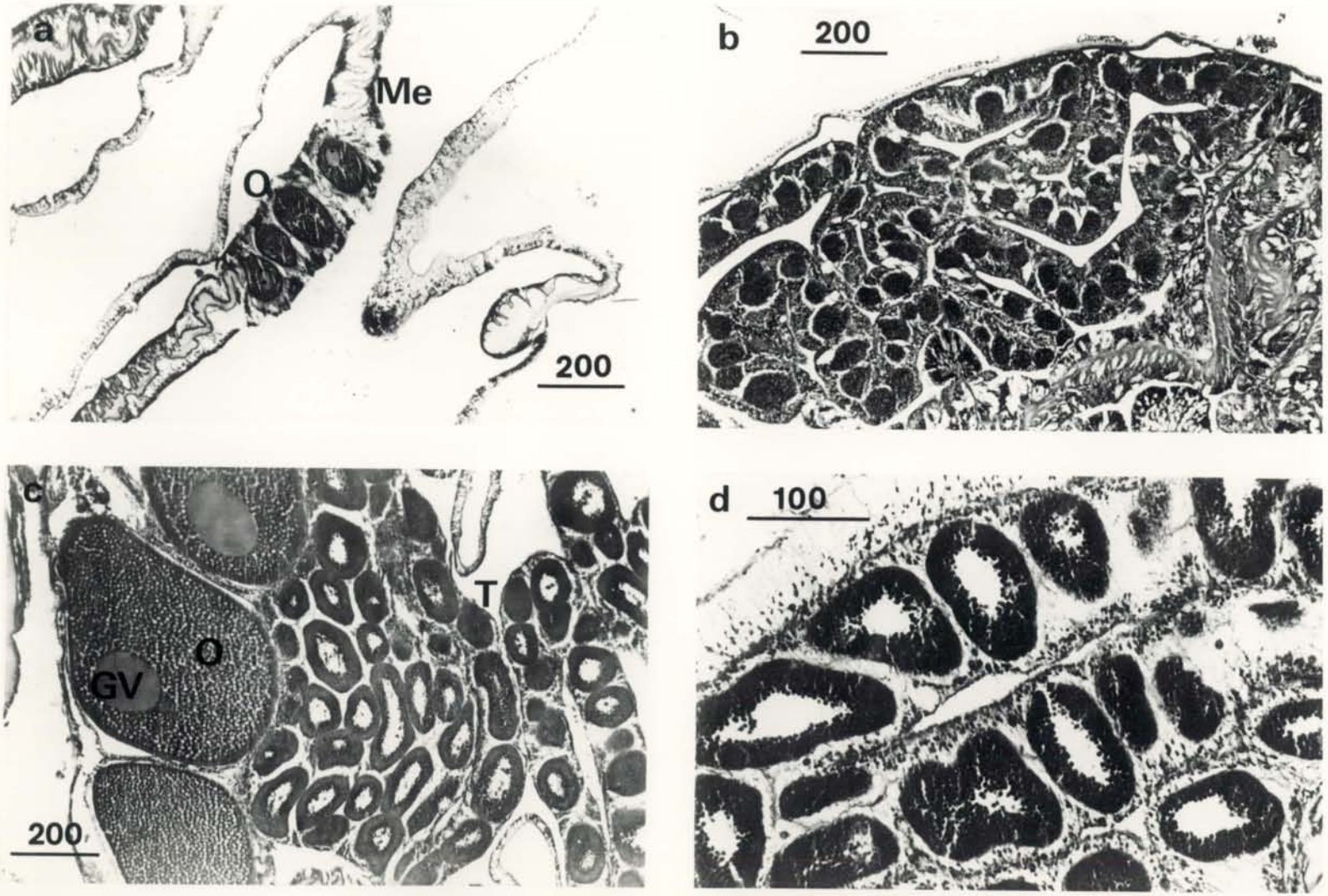

a
Me
O
200
b
200
c
T
GV
O
200
d
100

FIGURE 10: Photomicrographs of *Lobophyllia corymbosa* showing representative gonad structure.

(a) Immature oocytes in mesenteries of a polyp sampled in June 1980.

(b) Immature testes in a polyp sampled in October 1981. Testes lack a lumen.

(c) Adjacent eggs and testes in a polyp sampled November 1981.

(d) Testes in a polyp sampled November 1981 showing testes lumen.

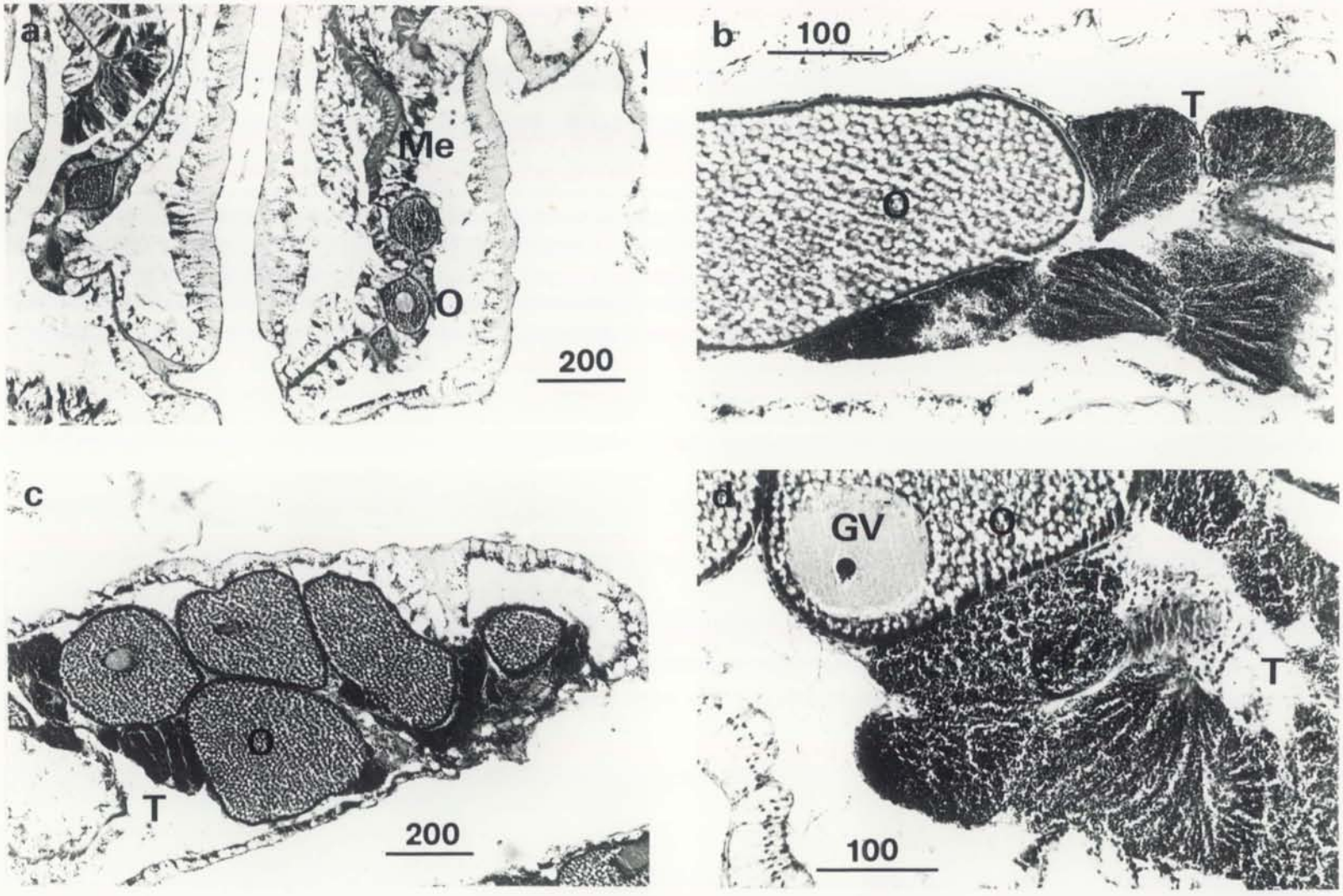
In figures 10 to 13 scale bars are in μm units.

O= oocyte; T= testes; ME= mesenteries; GV= germinal vesicle; M= mouth of polyp.

end of the polyp developing first. Mature eggs were blue or grey and testes were whitish. Representative gonad structures are shown in figure 11.

For both *L. corymbosa* and *F. favus*, initial gonad development was not synchronized, either within or between colonies, but synchrony became apparent as spawning approached. Very small polyps of both species contained either no gonads or smaller gonads than those of large polyps. In *L. corymbosa*, several small polyps contained testes only, and the proportion of gonadal material that was ovary increased with increasing polyp size.

Gonad structure was virtually identical for *P. lutea* and *P. australensis* (figures 12 and 13). Both species were dioecious, with colony size unrelated to sex. Gonads were located in the mesenteries with one gonad per mesentery i.e. 12 gonads per polyp. *Porites* gonads under the dissecting microscope resembled strings of beads, with 4 to 8 ova per female gonad. Eggs developed over a four to six month period for *P. lutea* and over a two to seven month period for *P. australensis*. Testes developed in one to two months for each species and matured at about the same time as the ovaries. Ova of various sizes were present in the same ovaries at the same time, even very close to the spawning period. Some ova were retained following spawning and eventually degenerated. No hermaphroditism was recorded for either species. Sex ratio for colonies sampled was 13 males:7 females for *P. lutea* and 5 males:8 females for *P.*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100

FIGURE 11 : Photomicrographs of *Favia favus* showing representative gonad structure.

(a) A gonad containing immature oocytes in the mesenteries of a polyp sampled in August 1980.

(b) A more mature gonad in August 1980 with oocytes and immature testes.

(c) Mature gonads sampled in December 1980.

(d) Testes and oocytes sampled 1 to 2 days before spawning occurred. Testes lack a lumen and the germinal vesicle is still present in the oocytes.

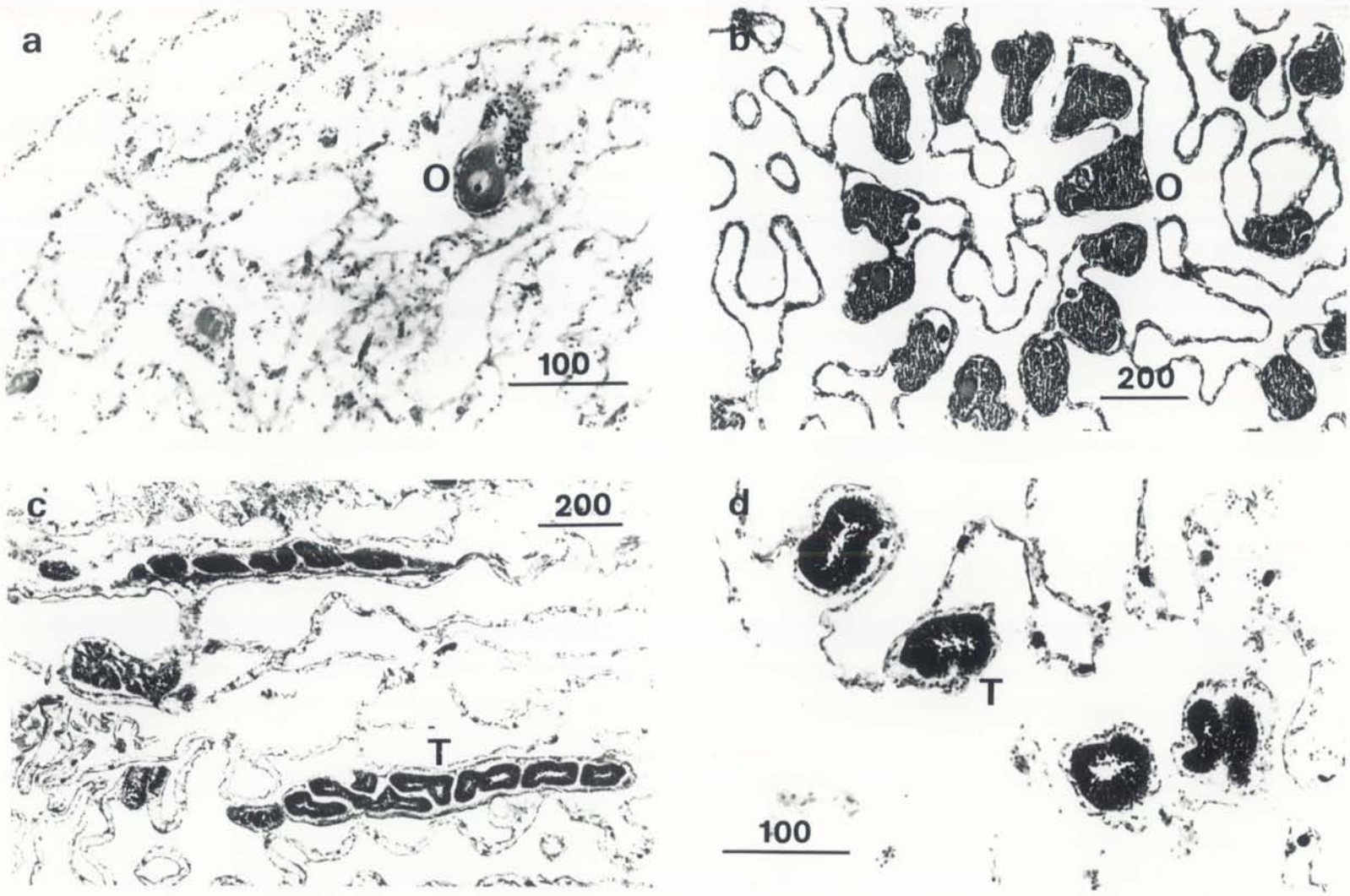

a
O
100
b
O
200
c
200
T
d
T
100

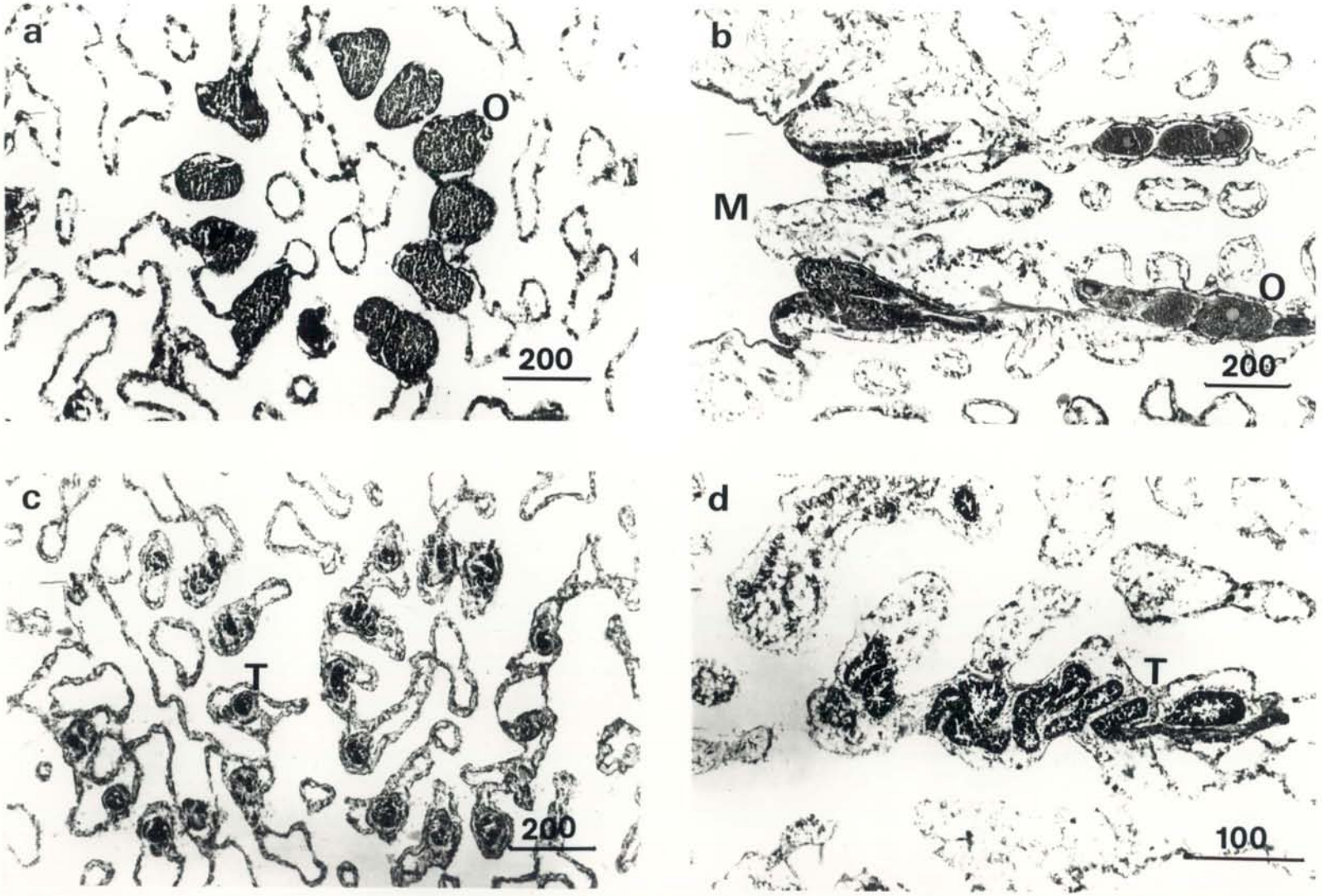
FIGURE 12 : Photomicrographs of *Porites lutea* showing representative gonad structure.

(a) A very small oocyte in a colony sampled in October 1980.

(b) Transverse section of a mature female polyp sampled in December 1981.

(c) Longitudinal section of male polyps sampled in November 1981, showing testicular loculi.

(d) Transverse section of testes sampled December 1981.


a
O
200
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M
O
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c
T
200
d
T
100

FIGURE 13 : Photomicrographs of *Porites australiensis* showing representative gonad structure.

(a) Transverse section of mature female polyp sampled December 1981.

(b) Longitudinal section of a polyp sampled in November 1981 showing the location of the gonad relative to the polyp mouth.

(c) Transverse section of a male polyp sampled in November 1981.

(d) Longitudinal section of a male polyp sampled in December 1981, showing testicular loculi.

australiensis. Representative sections of gonad structures for *P. lutea* and *P. australiensis* are shown in figures 12 and 13.

Gonad development was synchronized within colonies of each *Porites* species, but there was considerable variation in degree of gonad development between colonies, particularly early in the annual cycle. Even very close to the spawning period there was a wide range in gonad size within each species. This can be partly attributed to the very rapid increase in gonad size shortly before spawning, hence a small lag in attaining maturation will result in a wide variation in gonad sizes in the population.

3.3.2 Breeding seasonality

Although gamete release was not observed for any of the four species, several factors provide evidence that each species released gametes that were fertilized externally, and not internally brooded planulae. These factors are:

a. Planulae were never observed either under the dissecting microscope or in sections despite regular sampling over two years

b. Testes did not mature and spawn before ovaries as might be expected if fertilization was internal

c. Spawning occurred over a very short period in each species, while planulating species tend to spawn over a relatively extended period (Kojis and Quinn, 1981 b; Marshall and Stephenson, 1933)

d. For *L. corymbosa* and *F. favus*, the period between presence and absence of eggs and testes was less than two days, so if

internal fertilization had occurred in this time, then the period of larval retention must be very brief.

It is most probable that gametes are shed and fertilized externally as occurs in *Goniastrea favulus* (called *G. australensis* in Kojis and Quinn (1981 a)). In the following results, spawning of gametes is assumed to have occurred when eggs or testes are present in one sample and absent in the next.

Figure 14 shows changes in mean egg diameter and testes diameter for each species. For *L. corymbosa* and *F. favus*, egg diameter increased steadily until the November/ December sample, then declined to 0 by January each year. In December 1981, samples collected at intervals of two to three days indicated that mature ovaries and testes were present on 15 December and absent on 17 December for both species. Spawning was complete with no traces of ovaries or testes in samples collected on 17 December.

Colonies of both species kept in aquaria from 7 December did not spawn at the same time as field colonies. Examination of these colonies on 22 December showed the continued presence of mature ovaries and testes. Delayed spawning of aquarium-held colonies has also been demonstrated for *Porites andrewsi* by Kojis and Quinn (1981 b).

One *Favia* colony in 1980 and a different colony in 1981 contained no gonads in the November/December sample, indicating spawning by at least a portion of the population in November.

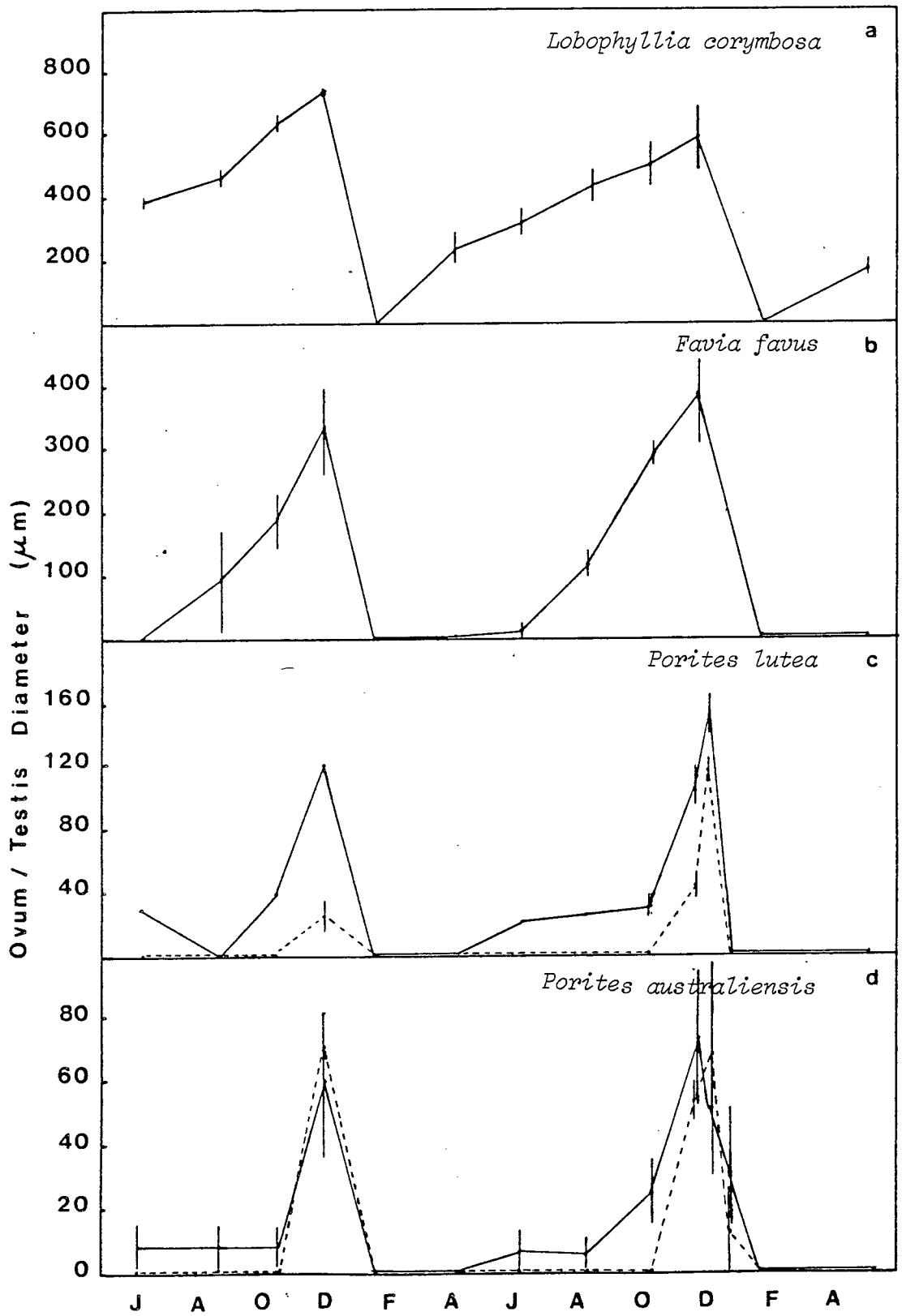


FIGURE 14: Seasonal changes in mean egg diameters and/or testes diameter for 4 coral species, a. *Lobophyllia corymbosa;* b. *Favia favus;* c.*Porites lutea*; d. *P. australiensis*. Solid lines represent eggs, broken lines represent testes, vertical bars show standard errors. For *P. lutea*, results for egg diameters from June 1980 to August 1981 are based on 1 colony only.

Similarly, for *L. corymbosa*, one colony spawned in November 1981.

Porites lutea and *P. australiensis* show overlapping but not identical spawning seasonality. Egg diameter increased slowly at first and then rapidly as spawning season approached. Testes development was late and very rapid.

For *Porites lutea*, all colonies spawned between 27 November 1980 and 20 January 1981; and between 5 December and 21 December 1981. For *P. australiensis*, all colonies spawned between 27 November 1980 and 20 January 1981. The next summer, one colony spawned between 12 October and 26 November; three between 26 November and 5 December; two between 5 December and 21 December; and two between 21 December and 23 January.

3.3.3 Ovum size and fecundity

Results are shown in table 3. An estimate of the average number of eggs per mature gonad and average number of mature gonads per polyp is listed. Number of mature polyps in a colony 10 cm in diameter was estimated from counts of polyps in a colony or sub-sample of a colony (for *Porites*) of each species.

For *L. corymbosa* and *F. favus*, ovum diameters were measured from both dissected specimens and from histological sections. There was a shrinkage factor of 20% to 30% attributable to histological processing. This factor accounts for the discrepancy in egg diameter of *P. lutea* between that

TABLE 3: Comparative egg size and fecundity for four coral species. Egg counts are approximate.

Species	Mature egg diameter (μm)	Egg/polyp	Polyp Diameter (cm)	Polyps/colony 10 cm diameter	Eggs/colony 10 cm diameter
L. corymbosa	600*/750**	2,800	2.5	10	28,000
F. favus	360*/500**	1,200	1.0	100	120,000
P. lutea	180*	72	0.1	3,000	216,000
P. australensis	150*	72	0.1	3,000	216,000

* measured from sections

** measured from dissected gonads

reported here measured from histological sections, and the result of 297 μm found by Kojis and Quinn (1981 b) measured from dissected eggs.

3.3.4 Colony size at first reproduction

Colony size at first reproduction is difficult to determine for *L. corymbosa* because of taxonomic difficulties in distinguishing single polyps of *Lobophyllia* species from each other and from solitary mussids. In five colonies of *L. corymbosa* (6 to 10 cm diameter) each containing two to ten polyps, all large polyps contained ovaries and testes. Small polyps, as mentioned earlier, frequently contained no gonads or testes only. This result implies that the factor limiting gonad production for this species is likely to be polyp size, rather than colony size and it is likely that large single polyps of this species would also contain gonads.

For *F. favus*, the relationship between colony size and gonads is shown in figure 15. All but one colony greater than 4 cm in diameter contained gonads and all colonies less than 4 cm diameter contained no gonads. One small colony contained male gonads only. This phenomenon of adolescent protandric hermaphroditism at the colony level has previously been reported for *Goniastrea favulus* (Kojis and Quinn, 1981 a).

For *P. lutea* and *P. australiensis*, the relationship between colony size and reproduction is less clear (figure 15), possibly complicated by asexual reproduction by fragmentation

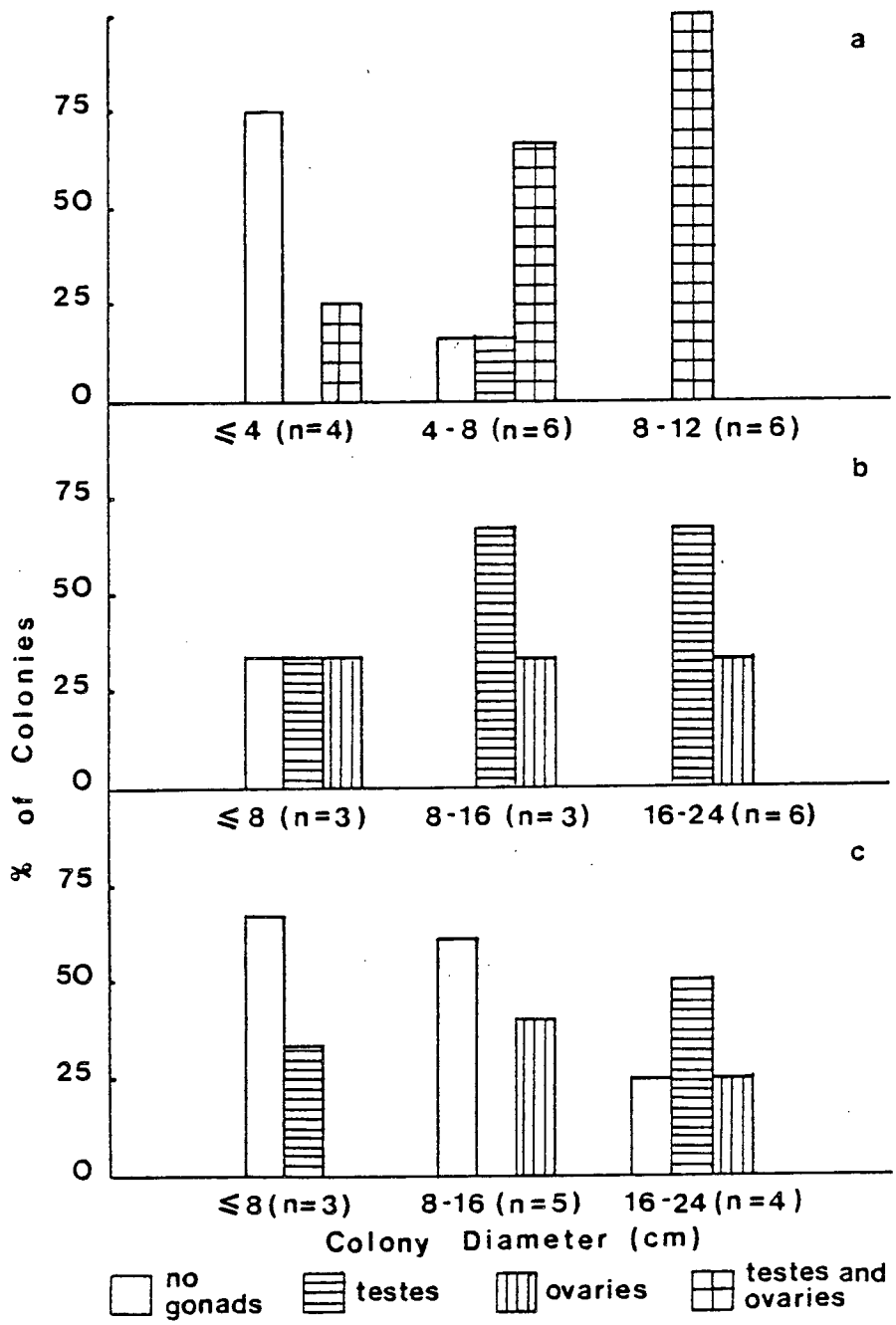


FIGURE 15: Relationship between colony diameter and presence and sex of gonads for small colonies of a. *Favia favus*; b. *Porites lutea* and c. *Porites australiensis*.

(Highsmith, 1980; Kojis and Quinn, 1982). In species that reproduce asexually, colony size is unrelated to age of the colony and any relationship between gonad production and size would be distorted.

For *P. lutea*, all colonies over 8 cm diameter contained gonads, but of three colonies less than 8 cm diameter, one had no gonads, one had testes and one ovaries. For *P. australiensis*, four of the six colonies that did not contain gonads were over 8 cm diameter. This may be partly attributable to the extended spawning period of *P. australiensis* since several colonies may already have spawned by 8 December when the samples were collected. There is no relationship between colony size and sex for either species, and no colony changed sex during the course of the study so it is probable that colonies stay the same sex throughout their lifetime.

3.4 Discussion

3.4.1 Gonad structure

In the four species studied, two of the four major patterns described for scleractinian corals occur; a. hermaphroditic with release of gametes (*L. corymbosa* and *F. favus*); and b. dioecious with release of gametes (*P. lutea* and *P. australiensis*).

Kojis and Quinn (1981 b) described two patterns of reproduction found within the family Poritidae, dioecious with release of gametes and dioecious with release of planulae. At

Lizard Island, *Porites lutea* and *P. australiensis* are both dioecious and release gametes that are fertilized externally, similar to *P. lutea*, *P. lobata* and *P. cylindrica* (= *andrewsi*) from Heron Reef (Kojis and Quinn, 1981 b).

Gonad structure for *F. favus* is similar to that described for other faviids from the Great Barrier Reef region, eg. *F. pallida* (=*doreyensis*, Marshall and Stephenson, 1933); *Goniastrea favulus* (Kojis and Quinn, 1981 a); *G. aspera* (Babcock, 1980); and *Favites abdita* and *Leptoria phrygia* (Kojis and Quinn, 1982). In all these cases, ovaries and testes are intermingled on the same mesentery, with ova developing early in the gametogenic cycle and testes developing shortly before spawning. At other locations, *Favia favus* in the Red Sea releases large numbers of pinkish-red eggs in aquaria (Rinkevich and Loya, 1979 a), which supports the evidence presented here for external fertilization; while in contrast the Atlantic species, *Favia fragum* releases planulae over three to four months (Lewis, 1974).

Not authors of species

Marshall and Stephenson (1933) described reproductive structures in several unnamed *Lobophyllia* species. Their descriptions were similar to that given here, i.e. separate ovaries and testes with testes generally found orally relative to ovaries and on the same mesenteries. Testes and ovaries each developed over a longer period in *L. corymbosa* than they did in *F. favus*.

The tendency for testes to begin development later than ovaries in many species may account for the large number of corals listed by Connell (1973) in which only eggs have been reported. In *Favia favus*, testes were present for only one to four months per year and would easily have been missed by infrequent sampling.

Rinkevich and Loya (1979 a) proposed that when gonads develop in the body cavity (usually in branching or small-polyped species) the number of ova is reduced during oogenesis and the species brood planulae. In contrast, species developing gonads in their mesenteries (usually large-polyped or massive species) have numerous large ova and expel gametes. The present and other recent studies do not in general support this proposal (Szmant-Froelich *et al.*, 1980; Kojis and Quinn, 1981 b). *Favia favus* and *L. corymbosa* fit the pattern of large-polyped species that release large numbers of gametes, but *Porites* species fit into the classification less easily. They are small-polyped species (branching in the case of *P. cylindrica*) in which gonads develop in the mesenteries. Some species produce relatively small numbers of ova per polyp and spawn gametes, and other species are known to brood planulae (Marshall and Stephenson, 1933; Kojis and Quinn, 1981 b). *Montipora ramosa* and *Acropora formosa* are small-polyped branching species which are hermaphroditic and spawn gametes (A. Heyward, personal communication; Oliver, 1979). In fact, external fertilization appears to be the rule rather than the exception for *Acropora* species (Bothwell, 1981).

3.4.2 Ovum size and number

Few comparative data are available on numbers of mature eggs per polyp or per colony for scleractinian species, although Rinkevich and Loya (1979 a) discuss some patterns from earlier observations. The results in table 3 exhibit two trends, the interpretation of which depends on whether the polyp or the colony is considered to be the reproductive individual. Justification of the view adopted here that the colony can be considered as an individual is given in Connell (1973).

For the four species at the polyp level, the number of eggs per polyp and egg diameter both increased with increasing polyp size. However the contribution to relative fecundity of the number of eggs per polyp is overbalanced by the relative numbers of polyps per colony. Thus at the colony level, the frequently cited inverse relationship between egg size and numbers (Emlen, 1972; Stearns, 1976) holds for colonies of similar sizes for the four species studied. *Porites* species allocate their reproductive resources to a large number of small eggs, and *F. favus* and *L. corymbosa* to a decreasingly small number of larger eggs. However, the potentially high fecundity of *Porites* species is reduced because the species is dioecious and some proportion of the population releases sperm only.

In other studies providing comparable data, Fisk (1981) found approximately 3600 and 7000 eggs per polyp for the deep water solitary corals *Heteropsammia cochlea* and *Heterocyathus aequicostatus* respectively. Number of eggs per polyp is greater

for these corals than for the other species listed here, and egg size is intermediate (each approximately 200 μm diameter).R. Babcock (personal communication) found approximately 180,000 eggs in a colony of *Goniastrea aspera* 10 cm in diameter. Egg diameter was 280 μm for preserved eggs and 350 μm for fresh eggs so this coral is intermediate in both egg size and colony fecundity between the *Porites* species and *Favia favus* at Lizard Island.

3.4.3 Reproductive seasonality and lunar periodicity

All four species studied at Lizard Island spawned in early summer (figure 14). Other studies on the Great Barrier Reef have reported a variety of spawning times for corals, with the majority of species spawning in October to January. Data on spawning season and lunar periodicity from this and other studies on the Great Barrier Reef are summarized in table 4.

In general, most species spawned in late spring and summer, and brooding species generally spawned over a longer period than those with external fertilization. The wide range of spawning periods for different species in the same geographical locality indicates that if exogenous factors trigger spawning (Giese and Pearse, 1974), then they must be species specific.

Temperature is frequently cited as a potential controlling factor in the reproductive cycles of marine invertebrates (Orton, 1920; Giese and Pearse, 1974). Figure 16, which shows annual water temperature changes near Heron Island (23°27' S), Magnetic Island (19°11' S) and Lizard Island (14°40' S), indicates that

TABLE 4: Spawning times for corals from the Great Barrier Reef

Species	Location and Author	Spawning Period	Lunar Phase	Spawned Product
Lobophyllia corymbosa	L.I. (1)	mid-December	*	gametes
Porites australensis	L.I. (1)	November to January	none	gametes
P. lutea	L.I. (1)	December	*	gametes
P. lutea	H.I. (2)	January to February	*	gametes
P. lobata	H.I. (2)	early to mid-December	*	gametes
P. andrewsii	H.I. (2)	early to mid-December	*	gametes
P. murrayensis	H.I. (2)	mid November to April	none	planulae
P. haddoni (=stephensoni)	Low (3)	summer and autumn	none	planulae
Favia favus	L.I. (1)	mid-December	*	gametes
F. pallida	Low (3)	November or December	-	-
Favites abdita	H.I. (4)	mid-November	*	gametes
Leptoria phrygia	H.I. (4)	mid-December	*	gametes
Goniastrea favulus	H.I. (5)	late October to November	*	gametes
G. favulus	M.I. (6)	mid to late October	*	gametes
G. aspera	M.I. (7)	mid to late October	*	gametes
Acropora formosa	M.I. (8)	October and November	*	gametes
Heteropsammia cochlea	W.R. (9)	January to June	none	gametes
Heterocyathus aequicostatus	W.R. (9)	April to June	none	gametes
Turbinaria mesenterina	M.I. (10)	May or June	none	gametes
Pocillopora damicornis	Low (3)	all year	full moon or new moon	planulae

* between full and last quarter moon. 1. This paper. 2. Kojis and Quinn (in press). 3. Marshall and Stephenson (1933). 4. Kojis and Quinn (1982). 5. Kojis and Quinn (1981). 6. Babcock (1980). 7. Babcock(in prep) 8. Oliver (in prep) 9. Fisk (1981). 10. Willis (in prep) L.I. = Lizard Island; H.I. Heron Island; Low = Low Isles; M.I. = Magnetic Island; W.R. = Wistari Reef.

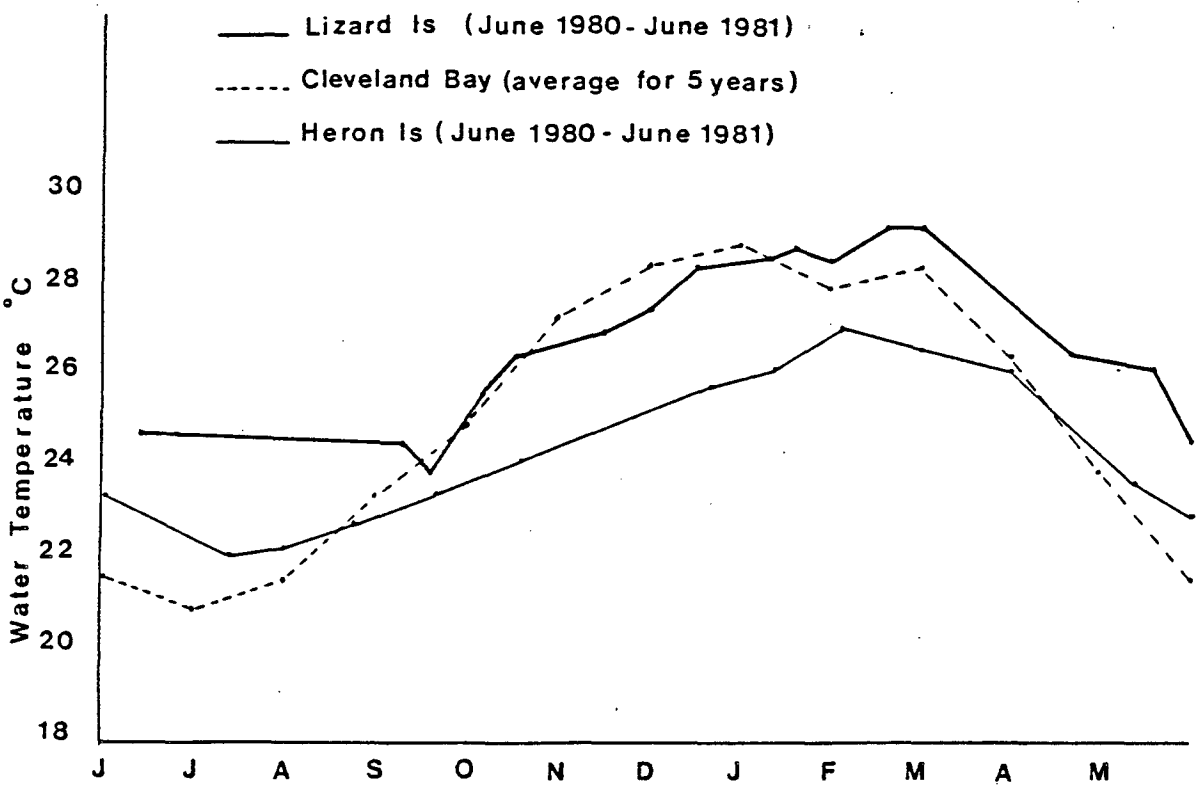


FIGURE 16: Seasonal changes in surface water temperature at three locations in the Great Barrier Reef Province. Data are from Walker (1981) for Cleveland Bay, and from C.S.I.R.O. Cronulla for Lizard Island and Heron Island.

there is a distinct summer/ winter variation in water temperatures, even at Lizard Island, the most northern of the locations. Variations would be even greater in the shallow water sites at each location, than in the open water where the given temperatures were measured.

There are distinct differences in the temperature regimes at the three locations. Temperature at Cleveland Bay, in which Magnetic Island is situated, is more variable than the other two sites. This correlates with a shallower (10 m), more inshore location relative to Heron Reef and Lizard Island.

At Lizard Island, relative to Magnetic Island, temperature is higher in winter and begins to rise later, but is similar from September to March, i.e. over the main breeding period. All four species at Lizard Island spawned in December, while most species at Magnetic Island spawned in October or November. This may reflect the earlier rise in temperature at Magnetic Island, or may simply reflect inherent differences between taxa as the same species have not yet been followed at both sites.

At Heron Reef, temperatures rise more slowly and are lower overall in summer, relative to the northern sites. This is not reflected in distinctly different reproductive seasonalities at southern and northern locations. All but one species studied at Heron Reef (i.e. *P. lutea*) spawned at the same time as or earlier than species studied at Lizard Island.

Unfortunately in only two cases have the same species been studied at different geographical locations on the Great Barrier Reef. *Porites lutea* at Lizard Island spawned in early December and at Heron Island spawned in late January/ February (Kojis and Quinn, 1981 b). This may reflect differences in the temperature regime at the two locations, i.e. spawning occurred at about 27°C in each case. *Goniastrea favulus* studied at Magnetic Island spawned in mid to late October (Babcock, in press) and at Heron Island in late October to November (Kojis and Quinn, 1981 a). In 1981, the Heron Island population spawned predominantly one month later than the Magnetic Island population (B. Kojis, personal communication). Temperatures were lower during the spawning period at Heron Island than at Magnetic Island, and the role of temperature in regulation of the reproductive cycle remains unclear.

The influence of lunar phase on spawning has been examined for a number of marine invertebrates (Giese and Pearse, 1974). It has a major influence on planulae release in *Pocillopora damicornis* on the Great Barrier Reef and in Hawaii (Marshall and Stephenson, 1933; Harrigan, 1972; Chapter 4), and in *Stylophora pistillata* at Palau (Atoda, 1947a), but not in the Red Sea (Rinkevich and Loya, 1979 b).

For species that release gametes annually, there is a correlation between lunar phase and period of gamete release. On the Great Barrier Reef, most species for which data are available spawn in the period between the full and last quarter moon,

irrespective of the month (table 4).

Synchronization of spawning in a particular period has the advantage to the coral of increasing the probability of fertilization. The cue for this synchronization with lunar phase is not obvious from observations to date, but the lack of spawning in aquarium held colonies supports a proposal that tides, rather than light associated with lunar periods, may provide the answers.

The length of the spawning period is one of the few apparent differences in reproductive ecology between the two *Porites* species studied. Their similarity in gonad and egg structure, and the overlap in the spawning period is of interest in terms of the close taxonomic relationship between the two species. Reproductive isolation via non-overlap of spawning period has been cited as a factor preventing cross-fertilization and possibly promoting speciation in closely related species (Rae, 1978; Harriott, 1980). It would be interesting to test whether cross-fertilization between the two species is possible in aquaria.

The relationship between reproductive seasonality and temporal aspects of spat recruitment onto coral block substrata are discussed in Chapter 7.

3.4.4 Sex ratio of *Porites* species

At Heron Reef, *Porites* colonies sampled by Kojis and Quinn (1981 b) on the reef flat were predominantly female (*P. lutea*, 3 males: 41 females; *P. lobata*, three males: 40 females). At Lizard Island, sex ratio for *P. lutea* was 13 males: 7 females and for *P. australiensis* was 5 males: 8 females. Kojis and Quinn (1981 b) proposed that the local abundance of one sex (and colour) at Heron Reef might reflect a high degree of asexual reproduction in the population, resulting in proliferation of one genotype, hence sex. The lack of dominance of one sex in *Porites* populations at Lizard Island indicates that disproportionate representation of the sexes is not an inherent feature of *Porites* populations, and supports the view that frequent asexual reproduction has occurred on Heron reef flat. The absence of this feature from the Lizard Island population might reflect a lesser significance of asexual reproduction in the relatively less physically disturbed back reef area, compared to a reef flat. To test this hypothesis, it would be valuable to compare sex ratios in colonies from lagoonal or back reef habitats at Heron Reef with those found on the reef flat.

3.4.5 Hypotheses concerning reproductive strategies

Results of this paper and from other recent studies add significantly to the body of data with which to test several theories on reproduction in corals that have been proposed in recent years.

Stimson (1978) proposed that shallow water corals would reproduce in a manner likely to retain propagules in the parental habitat. More recent studies suggest that mode of reproduction is related to more complex factors than habitat alone. Of the seven species studied on Heron reef flat by Kojis and Quinn (1981 a, b, 1982), six species reproduce by release of externally fertilized gametes. Only one of these six species has a mechanism specifically designed to promote retention of gametes on the reef flat. All four species studied at Lizard Island were non-reef flat species, and did not planulate, as would be predicted by Stimson's theory. However pocilloporid corals are also widely distributed in the same habitats to at least 9 m in depth and three pocilliporid species were observed to planulate in aquaria (Chapter 4 and personal observations).

Kojis and Quinn (1982) have suggested that a brief annual spawning period with larval development external to the parent colony will be the dominant form of sexual reproduction amongst hermatypic corals. This is supported in full by results in this paper and other recent work.

They also suggested that a strategy of hermaphroditism with simultaneous release of ova and sperm, and possible self-fertilization, will maximize reproductive success in relatively sparsely distributed species. While such a strategy may enhance reproductive success, it is not restricted to rare species. *Acropora formosa* and *Favia favus* are amongst the most common species in the northern Great Barrier Reef (M. Pichon,

unpublished data), yet both are hermaphroditic with epidemic spawning of gametes.

On the other hand, the species that were not hermaphroditic with epidemic spawning of gametes (*P. damicornis* and other pocilloporids, *Porites* species) were relatively abundant (Chapter 2), as the hypothesis would predict. In these cases, epidemic spawning may not be necessary to ensure fertilization. In addition, *Porites* species are known to reproduce asexually by fragmentation and success in sexual reproduction may be less important in maintenance of their populations than it is for other species. The relationship between reproductive strategy, abundance and asexual reproduction warrants further investigation.

CHAPTER 4

Reproduction and settlement in *Pocillopora damicornis*

4.1 Introduction

Early work on scleractinian reproduction centered almost exclusively on species releasing planulae, particularly pocilloporids, and resulted in the dogma that most corals reproduced viviparously. Recent studies have shown this assumption to be invalid (Szmant-Froelich et al., 1980; Kojis and Quinn, 1982; Chapter 3), with the majority of species releasing externally fertilized gametes.

Pocillopora damicornis (figure 7) is the best studied scleractinian species with respect to patterns of planula release and settlement preferences. Major studies of seasonality and lunar periodicity of planulae release in this species have been carried out in Palau (Atoda, 1947 a), Hawaii (Harrigan, 1972; Richmond and Jokiel, in press), Enewetak (Stimson, 1978; Richmond and Jokiel, in press) and Low Isles, Great Barrier Reef (Marshall and Stephenson, 1933). All these studies found planula release throughout the year, but with variable lunar periodicity and intensity.

None of these studies has investigated the gametogenic cycle underlying the pattern of planula release (as was done for *Stylophora pistillata* by Rinkevich and Loya, 1979 a), nor have they sampled repeatedly from the same colony to find if a colony

breeds throughout the year. To obtain more detailed information on the reproductive biology of *P. damicornis*, a histological study was combined with data on planula release in aquaria, for a population of this species at Lizard Island, on the Great Barrier Reef.

In addition, several experiments were performed on settlement preferences and early survival of juvenile *P. damicornis*. Previous studies have examined settlement preferences (Harrigan, 1972) and the effects of biological disturbance and competition on spat survival (Vine, 1974; Sammarco, 1982, Sammarco and Carleton, 1981; Sato, 1982). This study investigated how settlement preferences affect subsequent juvenile survival in a one species system in no-disturbance and low-disturbance environments.

4.2 Methods

4.2.1 Histological studies

Tagged colonies of *P. damicornis*, 15 to 40 cm in diameter, were sampled at 6 to 8 week intervals between June 1980 and May 1982. Colonies were sampled from depths ranging from 3m to 8m. Samples from other untagged colonies were collected at approximately weekly intervals in October/ November 1981, December 1981/ January 1982, and April/ May 1982. These additional collections allowed assessment of small scale changes in gonad development, and of whether repeated sampling influenced the reproductive state of tagged colonies.

Branches 3 to 6 cm long were fixed in seawater formalin, decalcified in approximately 10% formic acid with 5% formalin, and stored in 70% alcohol. Samples were embedded in paraffin, sectioned at approximately 8 μm through 3 regions of the tissue separated by approximately 1mm, and stained with Mayer's haemotoxylin and eosin. Slides were examined for male and female gonads and planulae. In most cases, sections through ~50 to 150 polyps per sample were examined.

4.2.2 Planula release

Planulae release in aquaria was monitored regularly for periods of 1 to 4 weeks from June 1981 to May 1982. In each period, five to 15 *P. damicornis* colonies, each 10 to 25 cm diameter were collected from the study site and transferred to a flow-through seawater aquarium system. The aquarium system at Lizard Island Research Station draws its water from an adjacent reef flat, and some coral colonies have been known to live at least 2 years in the system. Corals were treated in one of two ways, depending on availability of aquaria:

a. Corals were left in flow-through aquaria with plankton netting covering the outlet.

b. Corals were in flow-through aquaria daily, and were in non-flowing aquaria or buckets from approximately 8 p.m. to 8 a.m..

Planulae were released only at night and in both treatments planulae were counted at about 8 a.m.. There were no observed differences in frequency of planula release or colony condition between the two treatments. Daily records of planula release were kept for individual colonies. In June 1980 and August 1980, colonies were kept for the extent of the observation period. In October 1981 to May 1982, few planulae were released and corals were replaced each 7 to 10 days to ensure that the low planula yields recorded were not the result of aquarium stress. The numbers of planulae released by colonies was unrelated to the length of time in aquaria, so there was no indication of any effect of collection (Marshall and Stephenson, 1933) or stress (Loya and Rinkevich, 1979) that could result in premature or retarded release of planulae.

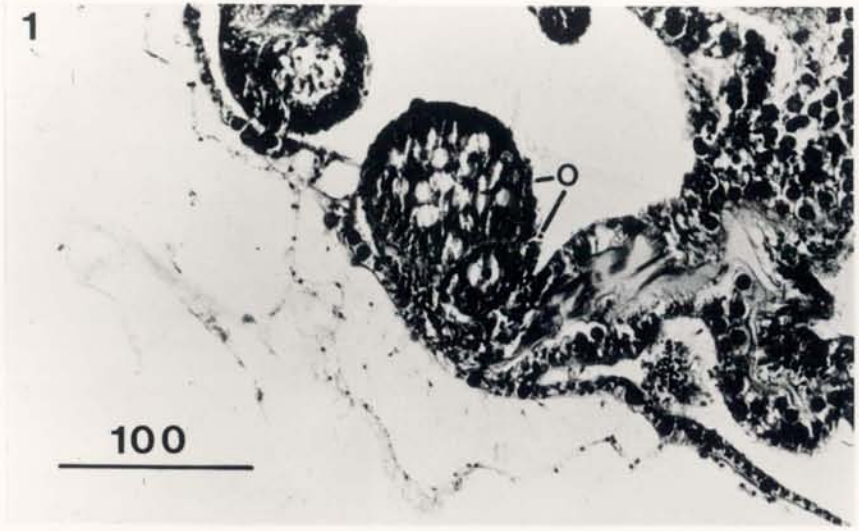
4.2.3 Settlement and survival

Planulae collected on 16 to 18 June 1981 were put into a large aquarium with 8 settlement blocks (each 5cm x 5cm x 1.5cm) that had been cut with a band-saw from a large *Porites* colony. Four of the blocks had been submerged at the study site for the previous 4 months and were covered with a layer of filamentous green algae and other organisms, but no coral spat were recorded (these are called the algal blocks). The other 4 blocks had not been in the sea, but had been soaked in seawater for 1 hour prior to commencement of the experiment (called bare blocks). Blocks were leaned against the aquarium wall such that all surfaces were available for settlement.

Planulae settled on the blocks and the aquarium walls 1 to 4 days after release. After 1 week, blocks were placed in a smaller aquarium for 2 months. Filamentous algae grew extensively on both sets of blocks during this period, and were approximately 1 to 2 mm high on the bare blocks and 5 to 10 mm high on the algal blocks.

In August 1981, 9 weeks after settlement of the planulae, blocks were removed briefly from aquaria, examined for living and dead corals with a dissecting microscope, and replaced in aquaria. Such examinations of newly settled corals had been carried out on a related project, without apparent increased coral mortality, at least in observations over the next few days. Counts of living and dead corals would underestimate the number of dead corals as the skeletons may be very small when the coral died, or may be covered by algae or other encrusting organisms.

In August, the 8 blocks were subjected to two different treatments, with approximately equal numbers of living corals in each treatment. One set (bare blocks no. 1 and 2 and algal blocks no. 5 and 6) was kept in the aquarium and the other set (bare blocks no. 3 and 4 and algal blocks no. 7 and 8) was taken to the study site and placed in a semi-protected location amongst the branches of a dead *Acropora* colony and well above the sediment. The blocks were not accessible to large fish, but were exposed to small fish and invertebrates. In October 1981, all blocks were again counted for living corals.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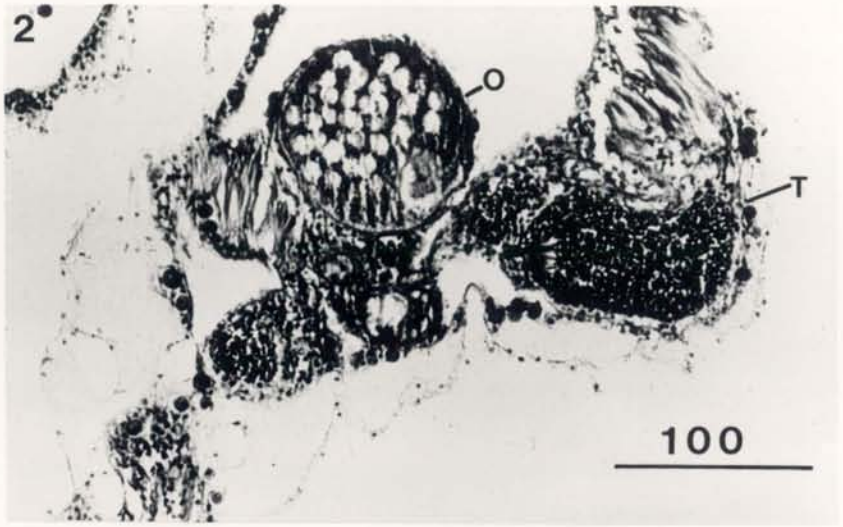
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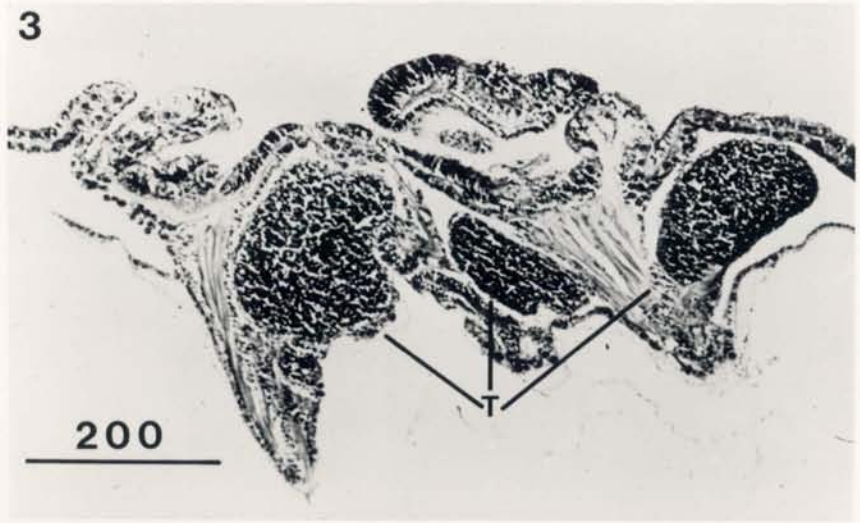
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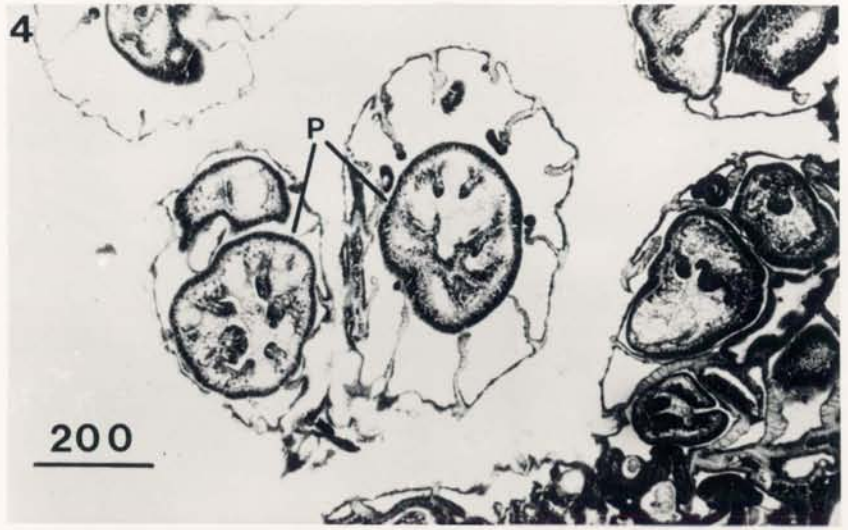
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FIGURE 17: Representative stages in gonad maturation for *Pocillopora damicornis*. Scale bars are in μm.

17.1 Stalked ovary showing two oocytes, one large and one small.

17.2 Ovary and testis in the same polyp. Ovary contains only one large oocyte.

17.3 Mature testes occupy most of the coelenteron.

17.4 Planulae in the coelenteron show development of mesenteries.

O=oocyte; T= testes; P= planulae.

TABLE 5: Results for histology of colonies sampled repeatedly P = planulae; ♂, male; ♀, female; ⚥, both male and female gonads; X, colony dead or too small to be sampled; dash, no gonads or planulae; blank, no sample taken.

	1980				1981						1982		Initial colony diameter (cm)
	June	Aug	Oct	Dec	Jan	Apr	June	Aug	Oct	Nov	Jan	Apr	
1	⚥	-	-	-	-	-	P ♂	-	-	-	X		15
2	-	-	P	-	-	-	P ♀	-	-	-	♂	X	25
3	⚥	♂	-	-	-	-	♂	-	-	⚥	X		40
4	-	-	-	-	-	♂	P ♂	-	-	-	⚥	♀	40
5	♂	-	-	-	-	-	♂	P ♂	-	X			40
6	♂	-	-	-	-	-	P	-	♂		♂	⚥	30
7	-	-	-	-	-	-	-	-	-	-	-	♂	30
8	-	-	-	-	X								25
9	-	-	-	X									30
10	-	⚥	-	-	-	⚥	P	-	P ♂	-	-	⚥	25
11				-	-	-	P	-	-	-	-	♂	35
12					-	-	P	-	-	-	-	⚥	30
13								⚥		-		⚥	25

Of 172 colonies sampled histologically, 61 contained some reproductive material; 53 had male gonads, 29 had female gonads and 10 contained planulae (32 had various combinations of these). A high percentage of specimens had male gonads, and many had only male gonads. When testes and ovaries occurred in the same colony, the testes were often mature even when oocytes were still very small. Small (<200μm) or apparently immature planulae were not found in sections, suggesting that the period of post-fertilization development may be very brief.

There were no obvious changes in gonad development in samples collected repeatedly over a one month period from 2 April 1982 to 5 May 1982 (table 6). This result suggests that the sampling interval used (approximately 2 monthly) was adequate to sample major changes in gonad structure. Samples collected from both tagged and untagged colonies on 29 April 1982 (table 6) were similar in their degree of gonad development, indicating that repeated sampling did not adversely effect gametogenesis in *P. damicornis*. In fact, fewer tagged colonies than untagged colonies lacked gonads.

4.3.2 Reproductive seasonality

In histological samples, gonad and planulae development were highest in the May/ June (winter) period each year, and lowest in the December to February (summer) period (figure 18).

TABLE 6: Frequencies of colonies with planulae and male and female gonads in samples collected between 2 April 1982 and 7 May 1982. Colonies with combinations of these have been counted twice.
P = planulae; * = sample from tagged colonies.

	2 April	25 April	29 April	29* April	5 May
P	0	0	0	0	0
♂	2	2	3	6	4
♀	2	2	3	5	2
No Gonads	3	3	2	0	2
Number of Colonies	6	5	5	7	6

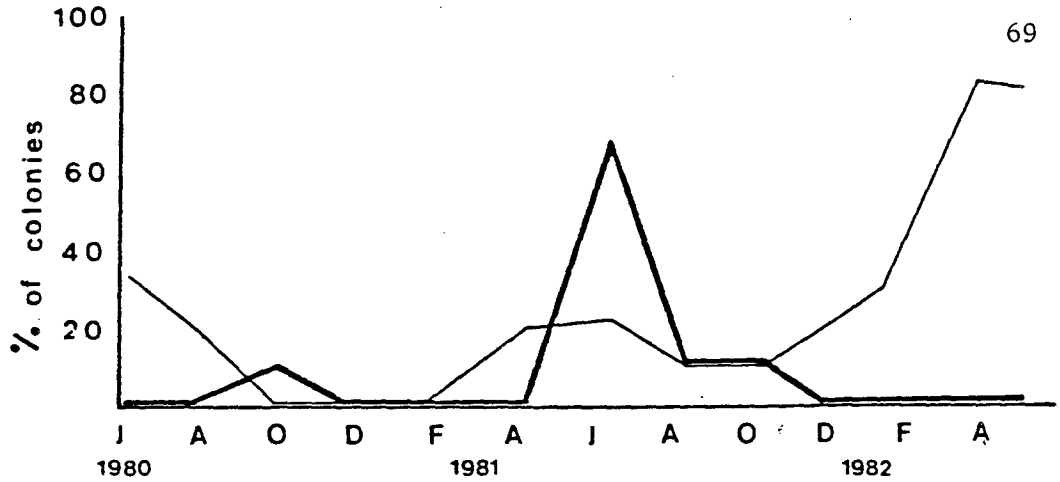

FIGURE 18: Changes in the percentage of colonies sampled histologically that contained planulae (heavy line), or gonads and no planulae (light line). Samples were taken between June 1980 and May 1981.

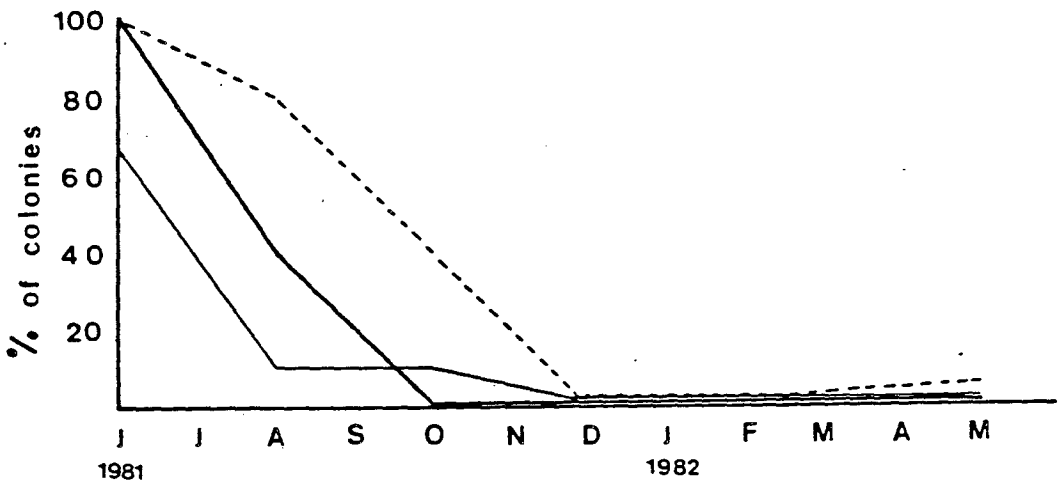

FIGURE 20: Percentage of colonies from histological samples that contained planulae, shown with the percentage of colonies in aquaria that released more than 5 planulae per week (dashed line); and more than 100 planulae per week (heavy line). Samples were taken between June 1981 and May 1982, and the lines show a similar pattern over time.

In aquaria, planula release over a one year period declined from a peak in June 1981 to very small numbers released in October 1981, none from December 1981 to March 1982, and a few in April 1982 (figure 19). From 26 November 1981 to 2 February 1982, planulae released were counted on 50 of the 69 days. This included 6 collections each of 10 colonies. In total, 3 planulae were released during this sample period, on three separate days. The sample period covered 4 new moons and 2 full moons (planula release by *P. damicornis* on the Great Barrier Reef has been reported to occur predominantly on the new moon in summer (Marshall and Stephenson, 1933)). These results indicate that there was little or no planula release in most colonies during summer 1981/82.

Histological results reflect the results of aquarium release experiments (figure 20), i.e. when planulae were not found in histological sections, then very few planulae were released in aquaria. There is a seasonal change in the number of planulae released and in the number of colonies containing planulae or gonads, with the greatest reproductive activity during the study period occurring in winter (figures 18 and 19). There are indications of some variation in gametogenic activity from year to year, i.e. gonads were present more frequently in summer 1981/82 than they were in 1980/81.

Number of planulae released in aquarium experiments varied greatly between colonies. In June 1981, planula release per day for the colonies sampled was >500, 140, 60, 18, 8, over a five

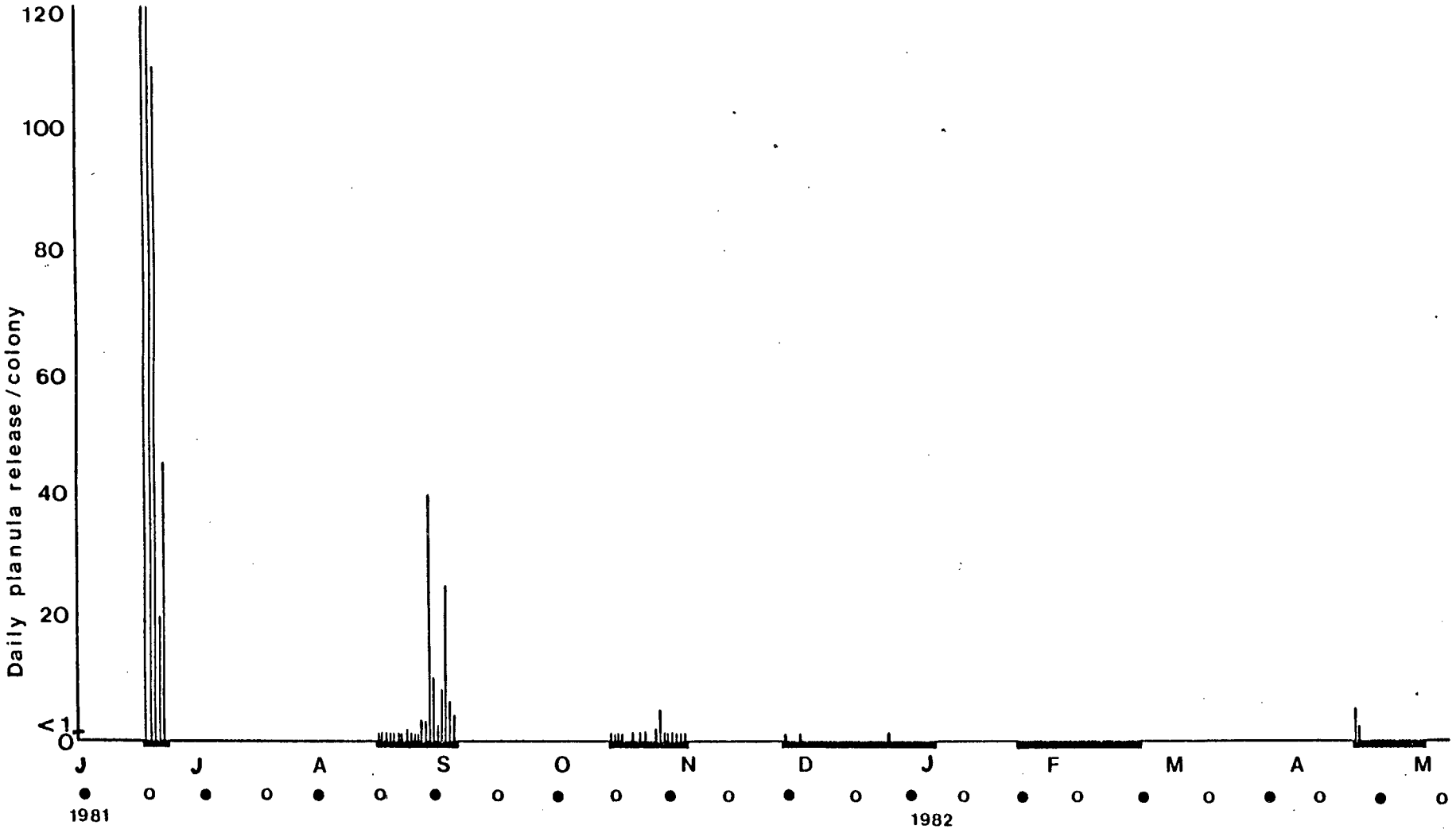

FIGURE 19: Number of planulae released per colony for samples of 5 to 15 colonies of *Pocillopora damicornis* between June 1981 to May 1982. Solid line under x-axis represents the sample periods, open circles show the time of the full moon and full circles show the time of the new moon.

day period, and in August 1981 the figures were 47, 36, 0, 0, 0 , during the 5 days of maximum planula release. Over the one year sampled, 4,400 planulae were released by 19 out of the total of 120 colonies sampled, but 60% of the total planulae yield came from one colony.

4.3.3 Lunar Periodicity

Planula release in June 1981 and April 1982 occurred about the time of the full moon,and in August and November 1981 it occurred predominantly about the time of new moon (figure 19). Planula release at other times was too infrequent to allow detection of any pattern.

4.3.4 Settlement patterns

In August 1981, 281 corals were counted on the eight settlement blocks; 85% on algal blocks and 15% on bare blocks (table 7). 19% of colonies on algal blocks were living and 63% of colonies on bare blocks were living (table 8). There was a significant difference in the frequency of living and dead corals between the 2 block types (χ^2=36.2, P(χ^2)< 0.01).

Between August and October 1981, 73% of corals on bare blocks and 17% of corals on algal blocks survived. Relative survival rates in the field and aquaria are listed in table 8. There was no significant difference in frequency of living and dead corals between blocks in the field or aquarium situation (χ^2 =0.30, P(χ^2)= 0.42). Over the four month period, survival was

TABLE 7: Frequency of living and dead corals on settlement blocks in August and October 1981.

Treatment	BARE BLOCKS			ALGAL BLOCKS		
	August 81		October 81	August 81		October 81
	Dead	Living	Living	Dead	Living	Living
Aquarium from	1	6	3	48	13	1
June to October	10	6	6	26	10	2
Aquarium June to August, Field August to October	4	10	6	39	6	2
	0	4	4	82	17	3
TOTAL	15	26	19	195	46	8

TABLE 8: Percentage survival rates of Pocillopora damicornis colonies on settlement blocks. In each case, frequency of living and dead corals was significantly dependent on substrate type at the $p = 0.01$ level, using X^2 contingency table analysis.

Treatment	Bare Blocks	Algal Blocks	Combined
Aquarium (June to August)	63%	19%	26%
Aquarium (August to October)	75%	13%	34%
Field (August to October)	71%	22%	40%

10% for all corals; 46% on bare blocks and 3% on algal blocks.

4.4 Discussion

4.4.1 Gonad structure and development

Gonad structure of *P. damicornis* is similar to that described for the other pocilloporid *Stylophora pistillata* (Rinkevich and Loya, 1979 a). The arrangement of gonads attached to the mesentery by stalks may be typical of pocilloporids, rather than of brooding corals in general (c.f. Rinkevich and Loya 1979 a).

Maximum egg diameter was 100μm, compared to measurements of 20μm for *P. damicornis* from Hawaii, 100μm for *P. meandrina* from Hawaii, and 200μm for *S. pistillata* from the Red Sea (from Rinkevich and Loya, 1979a). Egg diameters for non-brooding species at Lizard Island ranged from 150μm for *Porites australiensis* to 600μm for *Lobophyllia corymbosa* (Chapter 3), i.e. the eggs were considerably larger in the non-brooding species.

For *P. damicornis* , testes appear to develop and mature before ovaries, and this may be a mechanism that reduces self-fertilization in this species. Two factors suggest that the growth of planulae must be very rapid; first the large difference in the size of the largest eggs found (approx. 100μm) and the size of typical planulae (approx. 200μm), and second the appearance of planulae in colonies followed over time (table 1) when samples taken 2 months earlier had either small or no

gonads. An alternative, that planulae of *P. damicornis* are produced asexually, has been proposed by J. Stoddard (cited in Richmond and Jokiel, in press). Clarification of the developmental process of planulae of this species will require extensive further investigations.

4.4.2 Reproductive seasonality

This study is the first report of seasonality in planula development and release in *Pocillopora damicornis*. Previous reports have indicated planula release throughout the year, with lunar periodicity (Atoda, 1947 a; Harrigan, 1972; Stimson, 1978; Richmond and Jokiel, in press), although Marshall and Stephenson (1933) at Low Isles noted that numbers of planulae released were highly variable throughout the year. In other pocilloporids, *Stylophora pistillata* and *Seriatopora hystrix* have been reported to breed continuously at Palau (Atoda, 1947b,1951), while *Stylophora pistillata* has been found to have seasonal breeding in the Red Sea (Rinkevich and Loya, 1979 b), and at Lizard Island (Y. Loya, personal communication).

There is no obvious explanation for the unexpected finding of seasonality in planulae release in this species at Lizard Island, in contrast with other locations where observations have been made. There are no apparent environmental differences between the Lizard Island site and the Low Isles site where observations of Marshall and Stephenson (1933) were made, nor does it seem likely that the two populations would be genetically

isolated, considering the potential for wide dispersal of *P. damicornis* planulae (Richmond, 1981; Richmond and Jokiel, in press).

This study, however, is the first to follow individual colonies of *P. damicornis* over time, and such techniques may reveal more seasonal variability in reproductive activity than the more frequently used technique of pooling results from a number of different colonies in each sample period.

Both Harrigan (1972) and Marshall and Stephenson (1933) have reported that only a fraction of the colonies in their samples released planulae in any one period. Some of the variability in planulae release in Harrigans's results may be attributed to the fact that she did not differentiate two morphs of *P. damicornis* that have since been found to release planulae on different lunar phases (Richmond and Jokiel, in press). Harrigan found that 39% of colonies released planulae in aquaria (compared with 16% in this study) and numbers of planulae released ranged from 19,803 to 723 per month. Similarly, in her study, only a few colonies released large numbers of planulae and the major contribution of a colony to its total fecundity may occur within a short period, despite the release of small numbers of planulae at other times.

The results of Marshall and Stephenson (1933) are difficult to interpret because of the small size and irregular spacing of their samples. Large numbers of planulae were counted in April, May, June, December and February, and few planulae were counted in September, January and March. Thus, while there was variation

in planula production from month to month, release of planulae was not confined to the winter months as was recorded in the present study. The peak period of larval release in *P. damicornis* may be variable in space or time and does not necessarily correspond to the common summer spawning peak that has been found for many other scleractinians (Chapter 3).

Overall, the results suggest that *P. damicornis* colonies at Lizard Island show both seasonal and inter-colony variation in numbers of planulae released. Further studies, following gametogenic cycles at approximately weekly intervals are needed to fill present gaps in the knowledge of the interactions between reproductive ecology of populations and their component individuals.

4.4.3 Lunar periodicity

Lunar periodicity of *P. damicornis* planula release is consistent with that described for Low Isles (Marshall and Stephenson, 1933), i.e. planulae were released on the full moon in winter, and on the new moon in summer.

The range of patterns of lunar periodicity for *P. damicornis* is wide. Atoda (1947 a) at Palau, Stimson (1978) and Richmond and Jokiel (in press) at Enewetak, found planula release on the new moon. Harrigan (1972) at Hawaii found planula release to be variable, but to occur predominantly from full moon to new moon, while Richmond and Jokiel (in press) found that two morphological variants of the species at Hawaii released planulae

from the first quarter to full moon, and third quarter respectively.

Lunar periodicity of *P. damicornis* planula release is a geographically variable phenomenon, and shows variation even within one locality (eg Hawaii). This variability implies a flexibility in the reproductive ecology of the species that could well include the reported variation in reproductive seasonality/synchrony. Such variability is significant when considering the genetic isolation or otherwise of populations and the dispersal potential of planulae (Richmond and Jokiel, in press).

4.4.4 Settlement and survival of juveniles

Authors have suggested that several factors influence coral spat settlement and survival, including settlement preferences, predation, grazing pressure, competition with algae and other organisms, and sedimentation (Dart, 1972; Harrigan, 1972; Vine, 1974; Schuhmacher, 1974; Sato, 1982; Sammarco, 1982; Sammarco and Carleton, 1981).

Dart (1972) and Vine (1974) inferred that filamentous algae inhibit coral settlement, while grazing to bare rock encourages settlement but disturbs older colonies. However, Sammarco and Carleton (1981) found that spat settlement was higher within damselfish territories (high algal cover) than in areas exposed to fish grazing. They attributed this to some combination of the factors (a) variable levels of biological disturbance (b)

settlement preferences of spat (c) spat-specific predation outside territories.

In this study, preferential settlement of *P. damicornis* larvae on conditioned algal coated substrate over unconditioned, bare coral substrate has been demonstrated. This supports the observations of Harrigan (1972) on settlement preferences on a wide variety of surfaces. Subsequent survival of spat, however, appears to be inversely related to the density of the algal cover. Once settled, spat may require either slow growth or cropping of the algal layer to prevent competitive dominance by algae. However, intensive grazing to bare rock would kill spat directly. Spat survival requires a balance between algal dominance and death by biological disturbance.

The poor ability of spat to settle on bare rock, where survivorship was high in the absence of predation, may reflect the rarity of this substrate type in the field, or there may be selective pressure caused by higher predation/disturbance effects on bare rock.

In the field situation, spat survival was slightly lower on bare blocks and slightly higher on algal blocks relative to the aquarium situation, but not significantly so. This indicates that factors that correlate with the field situation (i.e. lower light, increased grazing pressure, increased sediment and water movement) had a smaller effect on coral survival than did the substrate on which the corals were found. The slightly greater survival of corals on algal blocks in the field relative to the

aquarium (22% versus 13% in aquaria) may be owing to the slightly increased grazing pressure and its repression of algal dominance.

The factors that affect spat survival are complex, and act at different stages of colony growth. These results for *P. damicornis* cannot be applied directly to other species, since it is likely that differences in settlement preferences and spat survival play a role in determining the distribution patterns of adult corals (Stimson, 1974; Lewis, 1974a, b). Settlement patterns of pocilloporids and other coral families in a field situation are compared in Chapter 7.

CHAPTER 5

Coral mortality before and during a mass bleaching event.

5.1 Introduction

Mortality rates are an integral part of the life history strategies and population dynamics of scleractinian corals (Bak and Luckhurst, 1980), and have relevance to theories on community structure and diversity (Connell, 1973, 1978). There are few published quantitative assessments of coral mortality under natural conditions. The studies of Loya (1976 b) for *Stylophora pistillata* in the Red Sea, and of Connell (1973) for a mixed species assemblage on Heron Reef were carried out predominantly in reef flat and reef crest habitats respectively. These areas are potentially highly physically disturbed , and the high mortality rates reported in these studies might be considered to be unrepresentative of coral communities in general.

Bak and Luckhurst (1980) assessed mortality for colonies of several species over 30 cm in diameter, at depths of 10 to 40 m at Curacao. The mortality rates of 2% to 19% annually that they reported were comparable with the results of Connell (1973). Bak and Engel (1979) have reported on mortality in juvenile corals (<4cm) and found mortality rates of approximately 50% annually.

Loya (1976 a) has suggested that the pocilloporid *S. pistillata* is an r-strategist because of the high mortality and recruitment rates exhibited by the species. In contrast, Rosen

(1981) says that corals can generally be considered as relatively K-selected, or competitors/ stress-tolerators (Grimes, 1979), because of their longevity and low turnover.

In this study, mortality of three coral species and one species group was assessed. The species covered a range of polyp sizes, growth form and taxa, and their reproductive ecology was studied simultaneously (Chapter 3). This study was carried out on a back reef area at depths of 2m to 9m, where physical conditions were probably intermediate between those in the studies of Connell (1973) and Bak and Luckhurst (1980).

The study period overlapped with a period in summer 1981-82 in which widespread bleaching (=loss of zooxanthellae) was reported in shallow water corals from many areas of the Great Barrier Reef. Such bleaching has previously been reported in corals and is associated with stresses such as lowered salinity, darkness and high temperatures (Yonge and Nicholls, 1931; Goreau, 1964; Jokiel and Coles, 1974, 1977). The mortality of the study species during the bleaching event was quantified and compared to that for the one year period prior to the bleaching. Some causes for the bleaching are proposed.

This study has value in adding to the few published estimates of coral mortality under "natural" conditions, which provide a baseline against which mortality following unusual or catastrophic conditions (such as cyclones or severe pollution) could be measured.

5.2 Methods

Mortality was assessed for the same species whose reproductive ecology was studied, i.e. *Pocillopora damicornis*, *Favia favus*, *Lobophyllia corymbosa* and the *Porites lutea/ australiensis* group. The latter two species could not be separated in the field, and because their distributions, abundance and reproductive ecology (Chapters 2 and 3) were very similar, it was considered valid to pool them for mortality analysis.

On 8 January 1981, tags were placed close to 20 colonies of each species. The colonies were mapped, and measured to the nearest 1 cm diameter. Depth of colonies ranged from 2m to 8m at low tide (figure 2).

On 7 April 1981, 21 August 1981, 2 December 1981 and 7 May 1982, the tagged colonies were relocated and recorded as living or dead. When a tag could not be found, one of two options was followed. If a colony of the same species and size was found in the mapped position, the tag was assumed to have been destroyed and the colony was retagged. The most obvious source of tag loss was fish grazing. If no tag or colony could be found, the colony was counted as "lost", and was not included in the analyses. In this manner, the mortality estimate derived was probably an underestimate, as it is likely that many of the lost colonies were in fact dead.

For the purposes of this study, death was defined as tissue death, or removal or destruction of the skeleton. It is probable that in some cases, breakage of skeletons results in living fragments (Highsmith, 1980, 1982) but these were considered as recruits from asexual reproduction rather than as a continuation of the original colony.

When colonies died or were lost, an equivalent number of new colonies of a similar size were tagged to keep the sample size for each time interval close to 20. Thus, the total number of observations for each species was approximately 80.

For *P. damicornis*, the age of each colony was estimated on the following basis. It was known from settlement experiments (Chapters 4 and 7) that the diameter of a 1 year old *P. damicornis* colony was approximately 1cm. Linear extension rates for colonies with a diameter of 5cm and above are approximately 2.5 cm/year (Buddemeier and Kinzie, 1976, Stephenson and Stephenson, 1933), and are likely to be less for smaller colonies (personal observations). Using this information, a relationship between diameter and age was obtained (table 9). From these approximate ages, a survivorship curve could be calculated.

5.3 Results

Of the colonies tagged in January 1981, 1/18 (6%) of *F. favus*, 2/13 (15%) of the *Porites* species, 4/20 (20%) of *L. corymbosa* and 8/18 (44%) of *P. damicornis* colonies died in the 16 months to May 1982.

TABLE 9: Estimated age from colony diameter, annual mortality for each size class, and survival per 100,000 spat for Pocillopora damicornis

Year	Range of diameter (cm)	Annual mortality	No. of survivors /100,000 spat
1	0.2 to <1	99.6%	400
2	1 to <4	49%	204
3	4 to <7	25%	153
4	7 to <12	25%	115
5	12 to <17	25%	86
6	17 to <22	27%	63
7	22 to <27	27%	46
8	27 to <32	27%	33
9	32 to <37	0%	33
10	37 to <42	0%	33
11	42 to <47	0%	33
12	47 to <52	0%	33

When the number of living colonies at the beginning and end of a defined period is known, mortality for any other time period can be calculated using the following formulae.

The instantaneous mortality rate (m) can be calculated from survival data for a known period of time (t_1).

$$m = \frac{\ln Nt_1 - \ln N_0}{t_1}$$

The number of individuals surviving for a second period (t_2) can be calculated from m.

$$Nt_2 = N_0 e^{t_2 m}$$

Hence mortality rate can be calculated.

$$\text{Mortality} = \frac{N_0 - Nt_2}{N_0} \times 100\%$$

where N_0= number of individuals at time 0

Nt_1= number of individuals living at time t_1

Nt_2= number of individuals living at time t_2

In this study, the length of the period between successive observations ranged from 3.5 to 5 months. For each observation period and each species, 4-monthly mortality rate was calculated, and the results are shown in figure 21. All species showed some temporal variation in mortality rate over the first three periods, but in each case, mortality was greatest in the final observation period from December 1981 to May 1982.

The annual mortality rate was calculated for the period from January 1981 to December 1981, and for the period from December 1981 to May 1982 (table 10). In all cases, mortality was higher

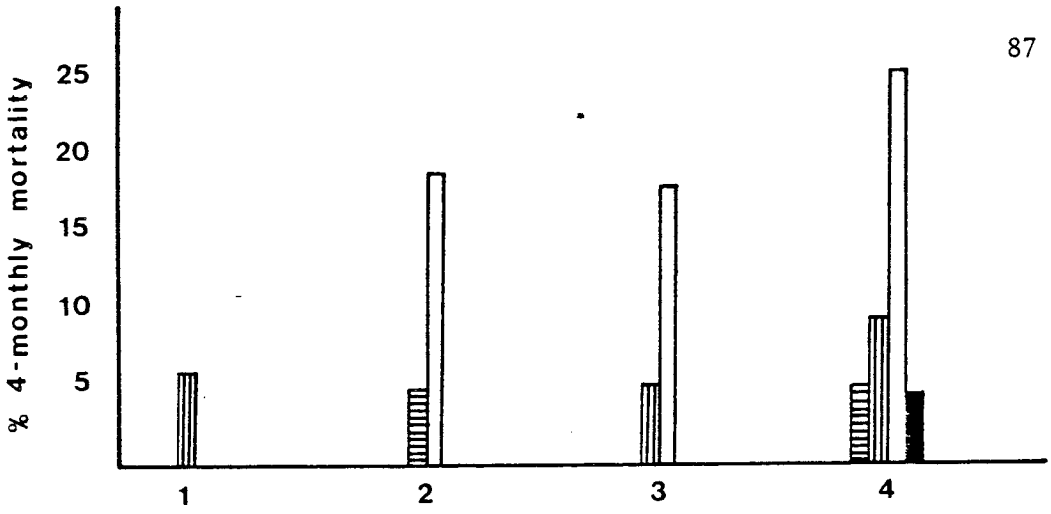

FIGURE 21: Percentage 4-monthly mortality in the sample periods 1 (January 1981 to April 1981), 2 (April 1981 to August 1981), 3 (August 1981 to December 1981), and 4 (December 1981 to May 1982) for *Pocillopora damicornis* (open bars), *Lobophyllia corymbosa* (vertical lines), massive *Porites* species (horizontal lines) and *Favia favus* (solid bars).

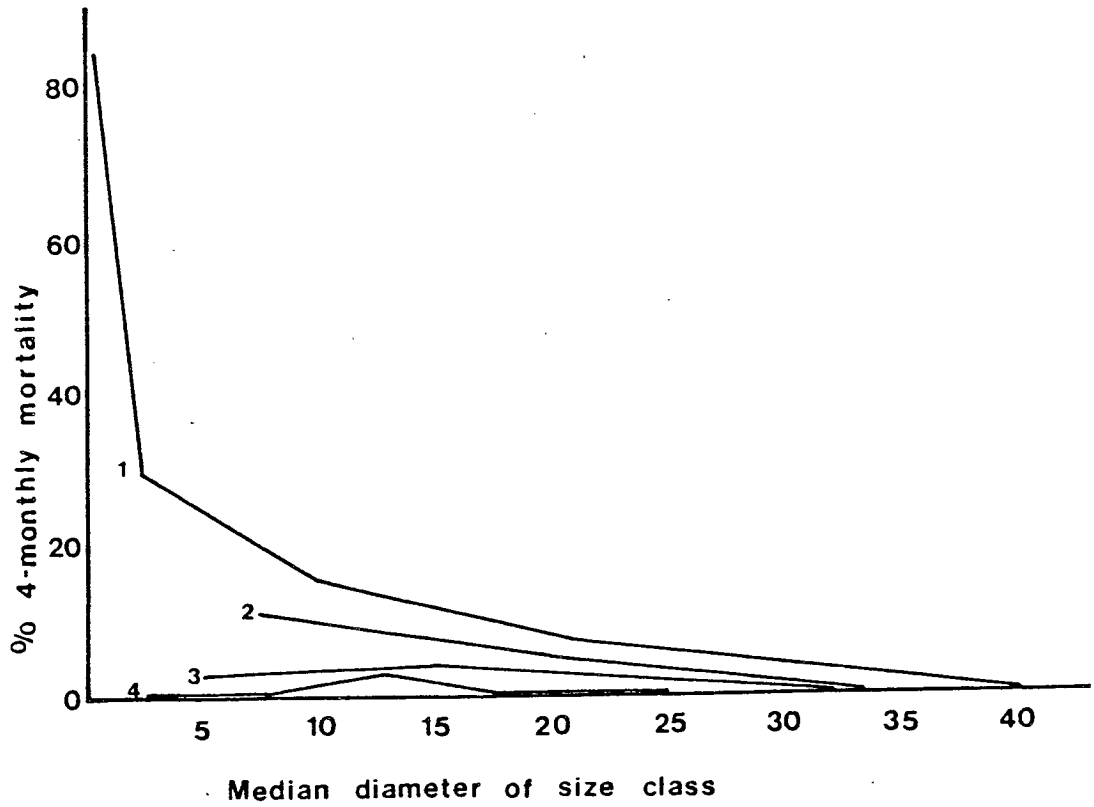

FIGURE 22: Percentage 4-monthly mortality for *Pocillopora damicornis (1)*, *Lobophyllia corymbosa (2)*, massive *Porites (3)*, and *Favia favus (4)* at several size classes.

TABLE 10: Annual mortality rate, calculated from mean 4-monthly mortality rate for January 1981 to December 1981, and for December 1981 to May 1982.

Species	Jan 81 → Dec 81	Dec 81 → May 82
Pocillopora damicornis	31%	58%
Lobophyllia corymbosa	12%	23%
Porites species	5%	15%
Favia favus	0%	12%

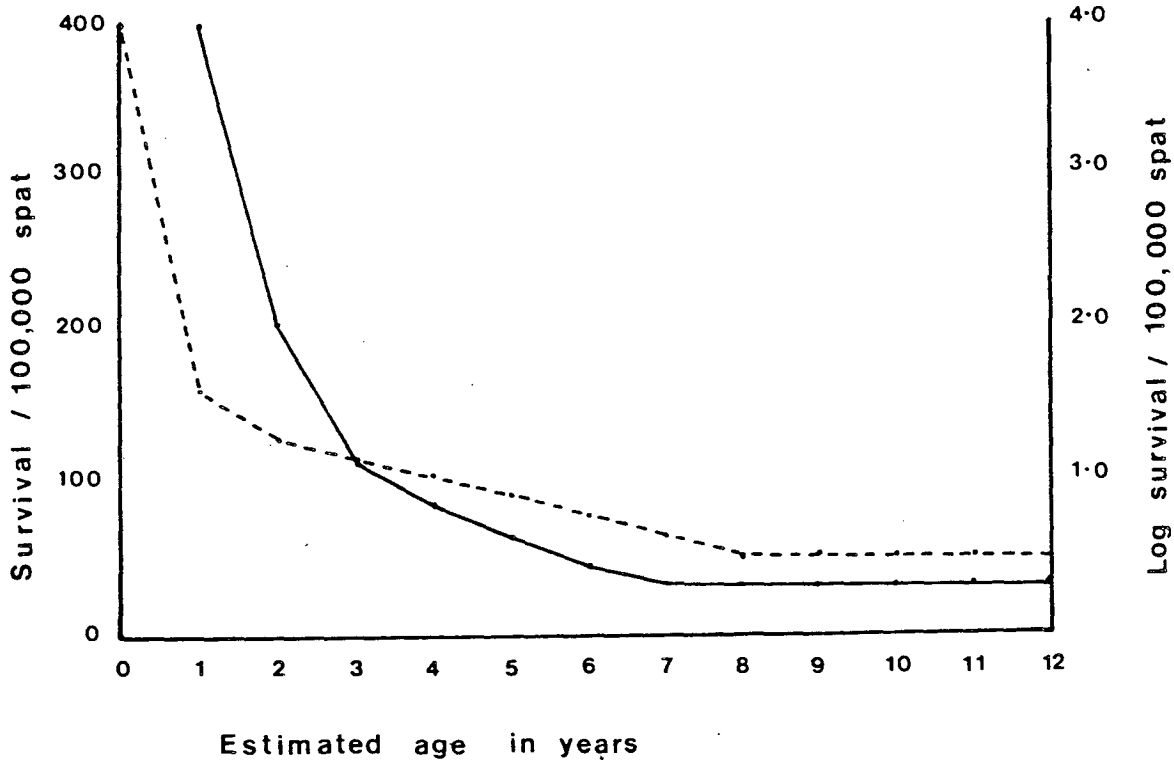

FIGURE 23: Survivorship curve for *Pocillopora damicornis*, from raw data (solid line), and on a log scale (dashed line).

in the latter than the former period. For all species pooled and for *P. damicornis*, frequencies of living and dead corals were significantly dependent on the time period (χ^2 contingency table analysis, $P(\chi^2)<.01$). The number of dead corals was too low for the other species to permit testing.

Fisher exact test not possible

To ascertain the relationship between mortality and size, individuals were allotted to a size class, the range of which depended on the species. The mean 4 monthly mortality rate was calculated for each size class, and the relationship is shown in figure 22. In general, mortality decreased with increasing size class, indicating that smaller individuals are more susceptible to mortality than larger ones. For *P. damicornis*, the plot was extended by including data on the mortality rate of 2 month old spat in the field (Chapter 4). The mortality rate of 60% for 2 months gives a 4 monthly rate of 84% for young spat. Similar data were not available for the other species.

Using the procedure for age determination outlined previously, ages were assigned to *P. damicornis* colonies. Mortality rate estimates for each size class were applied and a survivorship curve from 0 to 12 years for 100,000 newly settled spat was calculated (figure 23). The mortality rates used excluded the 4 monthly period from December 1981 to May 1982, because it was considered that bleaching resulted in unusually high mortality.

delete

Despite the inherent simplifications in age determination and size related mortality (Connell, 1973; Hughes and Jackson, 1980), the method produced a good representation of a type 3 survivorship curve (Deevey, 1947), when results were plotted both untransformed and as a semi-log transformation (figure 23).

5.4 Discussion

5.4.1 Causes of mortality

Mortality rates of the 4 scleractinian coral species showed (a) variation in magnitude amongst different species, (b) temporal variation and (c) a decrease with increasing size class.

Frequently, causes of mortality could not be determined but the most common observed causes were the following:

1. Physical damage as a result of wave action, bioerosion or both produced colonies that had been overturned or broken into fragments. Some percentage of fragments survived and this has been considered to be a common means of reproduction and redistribution for some species (Highsmith, 1980, 1982).

2. Predators, in particular grazing fish and *Acanthaster planci*, were frequently seen to damage living coral. Generally, predation caused damage to only part of a colony, but death of the entire colony sometimes resulted, particularly for small colonies. Scarid grazing most commonly affected *Porites* species, leaving series of parallel teeth marks on the surface of the colonies (personal observations; Glynn *et al.*, 1972). *Acanthaster planci* was present in low to moderate numbers (0 to 2

per $100m^2$) throughout the study and preyed upon many species, but affected *Acropora* species most seriously.

3. Tissue death by infection or unknown causes was occasionally observed particularly in small *P. damicornis* colonies.

4. A mass bleaching event occurred sometime between December 1981 and April 1982. Zooxanthellae were expelled from large areas of tissue in coral colonies at the study site, at nearby reefs, and at reefs near Townsville (personal observations; figure 24). Many small colonies were completely bleached and subsequently died, although many larger colonies were reinfected with zooxanthellae over subsequent months and recovered completely. In the Lizard Island area, bleaching occurred exclusively on the upper surface of corals, generally at depths of less than 10 m , but occasionally in deeper waters where water was clear. On branching colonies, the upper surfaces of branches were frequently bleached white, while the lower and any shaded surfaces of the same branches retained normal colouration.

Expulsion of zooxanthellae by corals has previously been reported as a response to stresses such as high temperature (Shinn, 1966; Jokiel and Coles, 1974, 1977; Coles, Jokiel and Lewis, 1976), fresh water influx (Goreau, 1964; Egana and DiSalvo, 1982), and extended darkness (Yonge and Nicholls, 1931; Franzisket, 1970).

There is some evidence that the stress in the case of bleaching reported here is caused by radiation, since the bleaching occurred only on the upper and unshaded surfaces of

FIGURE 24: Photograph showing bleaching of coral tissue of a faviid coral in the summer of 1981/82. In many colonies, there was a subsequent re-invasion of zooxanthellae and complete recovery.

or re-population (from residual resident cells)

colonies, and because of the restriction of bleaching to colonies in shallow or very clear waters. The bleaching occurred during a summer period of unususlly low rainfall and cloud-free days. Siebeck (1981) and Jokiel and York (1982) have discussed the potentially damaging effects of the presence of UV radiation on corals, and the significance of UV blocking agent in coral tissue (Shibata, 1969). Unusually high levels of UV radiation are a possible cause of the stress that caused bleaching in this case, although no measurements of UV irradiance levels are available for the period and location. Detrimental synergistic effects of environmental variables have been reported by Coles and Jokiel (1978). They noted that interactions between physical factors are most important near the limits of tolerance of a given factor. The bleaching in this case occurred during the period of high water temperature (figure 16), which may in itself stress corals (Jokiel and Coles, 1974, 1977).

5.4.2 Life history strategies

The mortality rates found in this study are comparable with those reported by Loya (1976 b) of about 30% annual mortality for the pocilloporid *S. pistillata*, and with those of Connell (1973) of 0% to 30% annually in a mixed species population. Bak and Luckhurst (1980) reported a somewhat lower mortality rate (2% to 19%) but this may be associated with the larger size of colonies in their samples (> 30 cm diameter).

Mortality rate varied among species in the present study. Mortality of *P. damicornis* was greater than that of any other species at all size classes (figure 22). Mortality for *F. favus* and *Porites* species was low and that of *L. corymbosa* was intermediate in magnitude. Franzisket (1970) noted that a *Pocillopora* species had high mortality in the absence of light, relative to three other coral species. He correlated its high mortality with its high metabolic rate, and concluded that the species' stringent ecological requirements made it poorly adapted to withstand environmental change. Jokiel and Coles (1974) also found that *Pocillopora meandrina* showed low tolerance for artificially raised temperatures, relative to other species, and Glynn (1976) found higher mortality rates for *P. damicornis* than for other species in both field and experimental situations. *Pocillopora* species probably expend large amounts of energy on the production of large, well-developed planulae, and in the present study, *P. damicornis* was highly successful at recruitment, relative to its abundance (Chapter 6 and 7). In this manner, its population can be maintained despite high mortality rates, and narrow physiological tolerances, i.e. there is a trade-off between reproductive effort, maintenance and mortality (Law, 1979).

Rosen (1981) stated that zooxanthellate corals in general are remarkable for their longevity and low turnover; that is, on an r/K life history spectrum they are relatively K selected (Stearns, 1976), and are competitors or stress tolerators rather than ruderals (Grime, 1979). The coral species

studied exhibited a range of mortality rates that varied from very high (approx. 40% per year) to very low (less than 5% per year). The corals also exhibited a range of recruitment success in a concurrent experiment (Chapters 6 and 7). Thus Rosen's assumption of uniformly low recruitment and mortality in corals may be an over-simplification.

Good

Certainly, *P. damicornis*, and the other pocilloporid *S. pistillata*, have life history features which place them on the r-selected/ ruderal extreme of a life history spectrum (Loya 1976a), at least in terms of mortality rate and recruitment success. On the other hand, coral species abundant in turbid or low light habitats are probably stress tolerant, while those with high digestive dominance or overshading abilities (Connell, 1973; Lang, 1970, 1973) may be good competitors (*sensu* Grime (1979)).

5.4.3 Fragmentation

Highsmith (1982) proposed that species that are adapted to fragment would put little energy into sexual reproduction and skeleton maintenance. These species would have high mortality rates (as defined here) and would produce many fragments. However, while 4 of the 5 species studied here (*P. damicornis*, *L. corymbosa* and massive *Porites*) are known to survive following fragmentation (personal observations, Highsmith, 1980, 1982) they have a range of mortality rates, and modes of sexual reproduction (Chapters 3 and 4) that do not show the relationship with the species' propensity to fragment that was proposed by Highsmith

(1982).

Highsmith also argues that fragmentation that results in pieces with surface area greater than 100 cm^2 will not result in high mortality of fragments. In this case, fragmentation would have enormous advantages in reproduction with little cost in increased mortality. However, the results presented here indicate that for some coral species, mortality continues to decline until colonies are quite large (figure 22), and this factor would decrease the selective advantage of fragmentation to produce small colonies. In addition, unattached fragments will have a higher mortality rate than an attached colony the same size, because the fragment will be more prone to physical disturbances (e.g. abrasion), and because a fragment may be deposited in an unsuitable habitat. Thus, while it is apparent that in some cases fragmentation is a successful means of dispersal, its value relative to the associated increased mortality may be somewhat less than that attributed by Highsmith.

5.4.4 Survivorship curve

Mortality rates generally decreased with increasing size for all species. A similar relationship was found by both Connell (1973) and Loya (1976 b). Bak and Engel (1979) found an annual mortality of over 50% for small corals (<4cm diameter), far higher than comparable mortality of an adult population (Bak and Luckhurst, 1980). Small colonies are more susceptible to most factors causing tissue death than larger ones, possibly because

the area of tissue remaining following damage is too small to regenerate.

The survivorship curve for *P. damicornis* is the typical type 3 curve of Deevey (1947) repeated in Odum (1971), that would be expected for a marine organism producing many small offspring, i.e. very high mortality in juveniles and decreasing mortality rates with increasing age. Survivorship curves for the other scleractinian species studied here would be expected to follow a similar pattern if data were available for the early stages. This contrasts with the survivorship curve for the temperate coral *Balanophyllia elegans* from California (Fadlallah, 1983). *B. elegans* releases rapidly settling non-pelagic larvae with low mortality, and has a type 2 survivorship curve, i.e. mortality rate is similar throughout the life cycle. The reproductive ecology of *B. elegans* contrasts with any reported for tropical coral species (Chapter 3, Harrison *et al.* in press; Kojis and Quinn, 1981a, b, 1982).

5.4.5 Ecological consequences

The relatively high mortality for several coral species in this study supports a concept of generally high turnover in scleractinian communities. The results of Loya (1976b) and Connell (1973), from shallow water reef flat habitats are shown here to be consistent with results from deeper and more sheltered waters. A similar pattern of relatively high mortality and changes in the spatial relationships of living corals was

demonstrated by Bak and Luckhurst (1980) in an even less physically disturbed habitat than the one described here.

These results contribute to the small amount of baseline data on "natural" mortality in corals, that can be compared with estimates of coral mortality following some unusual occurrence, such as the mass bleaching or a pollution event.

Occasional mass mortality must influence the abundance and distribution of organisms as much as, or more than, the normally encountered day to day mortality in the populations (Yamaguchi, 1975; Loya 1976 a; Fishelson, 1973). Such events might prevent long term survival of some species in areas where their normal physiological tolerances are exceeded only occasionally, particularly if they recruit infrequently.

CHAPTER 6

Population dynamics in mapped transects

6.1 Introduction

There are few studies of the dynamics of coral populations over time compared with the many studies of coral distribution and community structure based on samples taken at one time only (see review by Stoddard, 1969a; and references listed in Chapter 2). Exceptions include Connell (1974, 1978, 1979), Loya (1976 b,c), Bak and Luckhurst (1980), and Dollar (1982). Studies concerning damage to, and recovery of coral communities following severe perturbations were reviewed by Pearson (1981) and in Rogers *et al.* (1983). The studies of Connell (1973, 1978, 1979) and Bak and Luckhurst (1980) involved analysis of changes in patterns of space occupancy by corals in marked quadrats, while Loya (1976c), Dollar (1982) and Rogers *et al.* (1983) have studied changes in community structure using line transects. Loya (1976b) studied the population of *Stylophora pistillata* that settled on artificial substrata.

The studies listed above have indicated the dynamic state of many coral populations, in contrast to expectations from the formerly frequently- assumed association between high diversity and stability (see review by Goodman, 1975). The prevalence of frequent physical disturbance and high mortality rates in these studies has resulted in the formation of, and support for,

non-equilibrium hypotheses of diversity maintenance, predominantly the intermediate disturbance hypothesis of Connell (1978).

Knowledge of the extent to which instability of reef components varies between reef sites is limited by the small number of sites around the world in which such studies have been carried out. There have also been few attempts to quantify how different coral taxa are affected by disturbance and how they contribute to the high turnover in coral communities (e.g. Bak and Luckhurst, 1980).

This study integrates measurement of short term temporal patterns of coral recruitment and mortality (on a scale of 2 months), with an assessment of the net effect of these changes over a longer period (20 months). Coral mortality is defined as in Chapter 5, and colony abundance is defined as the number of colonies greater than approximately 1cm in diameter.

Keough and Downes (1982) have distinguished between settlement, and recruitment which is measured by an observer some time after settlement. In the following chapters, spat recruitment refers to the presence of small corals, less than 1cm in diameter, observed some time following settlement. There may or may not have been mortality of spat subsequent to settlement. Coral recruitment will be discussed in this chapter and refers to the establishment of corals 1cm or more in diameter, i.e. at a size visible to the naked eye and probably more than one year old. There is undoubtedly mortality prior to this stage.

Population dynamics for 5 sites and for 24 generic groups are compared, and an assessment is made of how these patterns of recruitment and mortality affect community structure at the 5 sites. The applicability of equilibrium and non-equilibrium models of diversity maintenance to the community is discussed.

6.2 Methods

The five 1m X 10m transects described in Chapter 2 were mapped on 10 occasions at approximately 2-monthly intervals between June 1980 and February 1982. Colonies were mapped on a 1:10 scale, freehand on underwater paper. At each census from August 1980, a copy of the map produced on the previous census was used a guide, and missing or new colonies were marked on the map. In this way, the majority of non-cryptic coral colonies over 1 cm diameter were mapped. Disturbance to corals in the transect was kept to a minimum during the mapping process. The maps produced were compared to photographs of the transects taken in August 1980, June 1981 and February 1982, to check the accuracy of mapping of colony shapes and positions.

Colonies were identified to generic level when possible. For many of the species present (Chapter 2), underwater identification to specific level would have been impossible. Faviids in particular were difficult to separate even at generic level, and some genera were grouped to decrease the error associated with identifications. Generic groups, listed in table 11, are hereafter refered to by the name of the dominant genus.

TABLE 11: Abundance in February 1982 and estimated errors in identification to generic level for all genera or generic groups recognized. Genera included in each group are given below.

Category	Abundance	Identification errors (%)	Category	Abundance	Identification errors (%)
Porites	585	0.3	*Turbinaria*	21	0
Favia[1]	138	4.3	*Stylophora*	19	0
Acropora	131	3.0	*Lobophyllia*[4]	17	5.9
Goniastrea[2]	113	10.8	*Goniopora*	15	0
Montipora	97	1.0	*Mycedium*[5]	13	15.0
Galaxea	53	0	*Merulina*	8	12.5
Seriatopora	30	0	*Pavona*	5	20
Cyphastrea	29	6.9	*Euphyllia*	5	0
Astreopora	29	3.4	*Pectinia*	3	0
Pocillopora	28	0	*Symphyllia*	3	0
Fungia[3]	28	3.6	*Hydnophora*	3	0
Echinopora	21	0	*Diploastrea*	0	-

[1] *Favia, Favites, Montastrea*

[2] *Goniastrea, Platygyra, Leptoria, Leptastrea*

[3] *Fungia, Heliofungia, Lithophyton, Herpetoglossa*

[4] *Lobophyllia, Scolymia*

[5] *Mycedium, Echinophyllia*

Accuracy of identifications was checked in April 1982, when all colonies from transects were collected and identified to species level (Chapter 2). Their confirmed identification was compared to the field designation (table 11). Most errors occurred in identification of very small colonies. Overall, 96.4% of the colonies were correctly identified to generic level, and a further 1% could not be identified, generally because of their small size or inaccessibility.

Possible mapping errors were checked by comparing three consecutive census maps for each sample period and transect. If a colony was recorded as lost in the middle census, but reappeared in the same location in the third census, then it was assumed to have been overlooked in the second period and was added to the map. To be counted as dead, a colony had to be missing from at least 2 consecutive census maps.

Partial mortality (Hughes and Jackson, 1980) was not estimated in this study, i.e. if only a small proportion of the coral tissue remained alive, the colony was not marked as lost. Colony fission (=death of coral tissue separating two living sections of the same original colony) caused some difficulty in the censusing process. Generally, the two living sections of the original colony were considered to be separate colonies (c.f. Loya, 1978) hence one of the two pieces was considered to be a recruit, and the process to be a form of asexual reproduction. This approach can be justified on the grounds that once separated, the colonies are independent with respect to

mortality, reproduction etc.

6.3 Results

6.3.1 Colony turnover

Data on number of recruits and number of dead colonies for all transects, times and genera are presented in Appendix 2. Between the first two census periods, June 1980 and August 1980, high numbers of recruits were recorded (figure 25). This is probably attributable to an improvement in my ability to recognize and map small colonies, and is unlikely to reflect exceptionally high recruitment. For this reason, results for the period prior to August 1980 are not included in subsequent calculations.

Total numbers of recruits, dead colonies, colony abundances and net turnover are shown in table 12. Because both recruitment and mortality were numerically very high during the study period, relative to the number of colonies present at any one time, there was a potential for large changes in the taxonomic composition of transects. To determine whether the generic composition of each transect was more similar in one transect over time than it was in neighbouring transects, a cluster analysis was performed on 10 sites; generic abundance in transects 1 to 5 in both August 1980 and February 1982. Methodology for the cluster analysis followed that described in Chapter 2, and results are shown in figure 26.

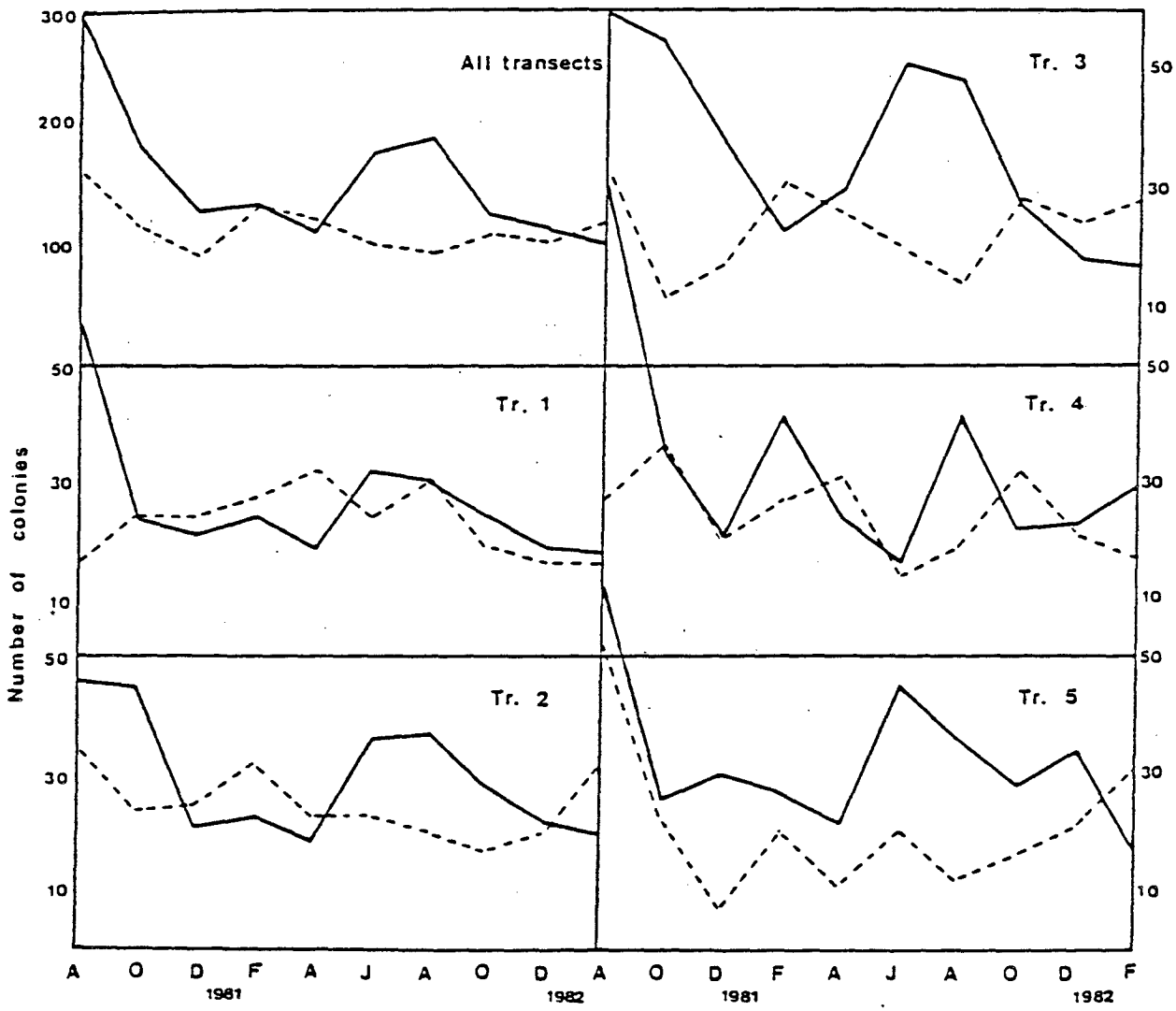

FIGURE 25: Changes in the number of recruits (solid line) and dead colonies (dashed line) between August 1980 and February 1982. Results for August 1982 were not included in subsequent analyses.

TABLE 12: Population parameters for transects 1 to 5 between August 1980 and February 1982.

	1	2	3	4	5	TOTAL
Number of colonies in August 1980	239	245	226	227	232	1169
Number of recruits	211	251	308	252	265	1287
Number of dead colonies	212	215	199	217	161	1004
Net turnover after 18 months	-1	+36	+109	+35	+104	+283

TABLE 13 : Number of recruits in each sample period between April 1981 and February 1982, and number that died before February 1982, for all transects pooled. The number that recruited but died between consecutive sample periods could not be calculated.

Sample Time	Total number of recruits	Dead by Feb. '82	% mortality
April 1981	104	54	52
June 1981	151	68	45
August 1981	171	62	36
October 1981	114	44	38
December 1981	119	26	22
February 1982	100	0	0
TOTAL	759	254	33

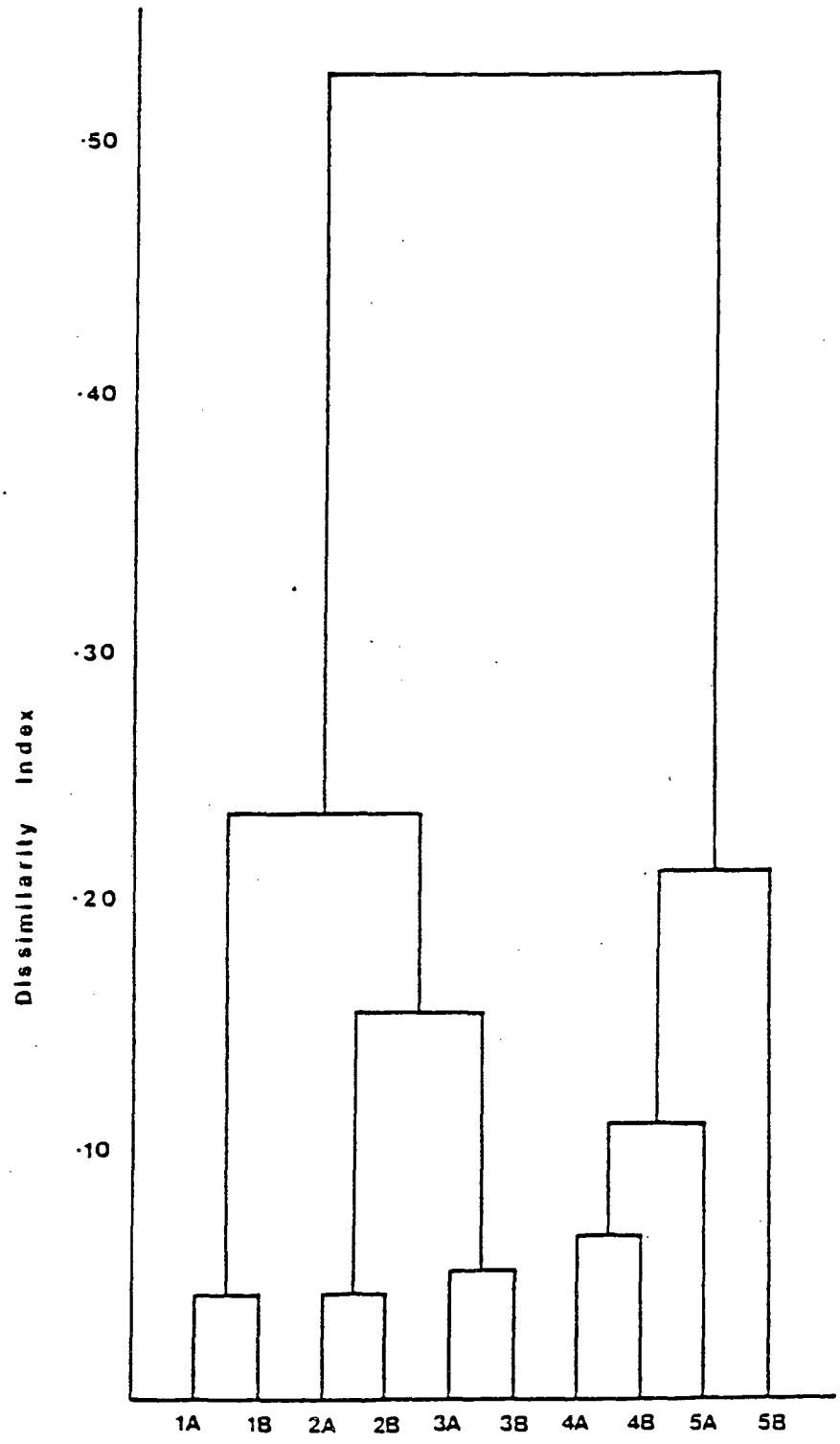

FIGURE 26: Dendrogram showing the dissimilarity between generic composition of transects 1 to 5 at time A (February 1982) and time B (August 1980).

For transects 1 to 4, generic abundance was more similar in one transect at different times than it was in adjacent transects. In transect 5, generic abundance in February 1982 was more similar to that of transect 4 than it was to transect 5 in August 1980. In this case, the potential for a large change in generic abundance has been realized.

In this study, transects were censused at 2-monthly intervals, more frequently than most coral studies. To compare these results with those that would have resulted from an annual census, fate of new recruits over a one year period was followed. The number of new recruits in each two month period from April 1981 (i.e. recruited after February 1981) to February 1982 was counted. Each recruit was traced through consecutive maps, and the number that died before February 1982 was counted. These colonies would not have been included in an annual census in February 1981 and 1982. Results are shown in table 13.

Approximately 50 % of recruits in April 1981 were dead by February 1982. Of all recruits over a one year period, 33% were dead by the end of the period. Thus an annual census would have underestimated recruitment and mortality by a factor of about 1/3. Most of these colonies are very small, and would not greatly effect the appearance of the community, although their potential to influence community structure is great.

6.3.2 Recruitment

Recruitment rates for each genus at each time and transect were analysed using a three way analysis of variance (table 14). Only the 10 most abundant genera were used in the analysis because most other genera were rare in several transects. The results demonstrate that genus is a significant factor in determination of recruitment rate, but time and transect number are not.

The relationship between colony abundance and number of recruits for genera, with transects and times pooled, is shown in figure 27. There is a significant positive correlation between abundance and recruitment ($r= 0.92$; $d.f.=24$), i.e. the most abundant genera have the most recruits.

Thus, for all transects pooled, recruitment reflects generic abundance. For each genus separately, the distribution of recruits amongst the 5 transects might reflect the distribution of all colonies in that genus, or recruits might be distributed differently from the total population.

To test these alternatives for each genus, a series of χ^2 contingency table analyses were performed. These tested whether, for each genus, both recruits over the 18 months (from appendix 2), and all colonies in August 1980 were distributed similarly amongst the 5 transects. Results are given in table 15. Of the 11 genera that were abundant enough to be tested, 5 genera had recruits that were distributed in the same pattern as all

TABLE 14: Three way analysis of variance of recruitment rate by genus, transect number and time for arcsine transformed proportions.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	Signif.
Main effects					
Genus	7430.5	9	825.6	4.47	0.001
Transect	927.7	4	231.9	1.25	0.29
Time	1845.9	8	230.7	1.25	0.27
2-way interactions					
Genus x transect	7758.5	36	215.5	1.17	0.25
Genus x time	13676.1	72	189.9	1.03	0.43
Transect x time	4625.5	30	144.5	0.78	0.80
Explained	36264.2	161	225.2	1.22	0.07
Residual	53252.9	288	184.9		
Total	89517.1	449	199.4		

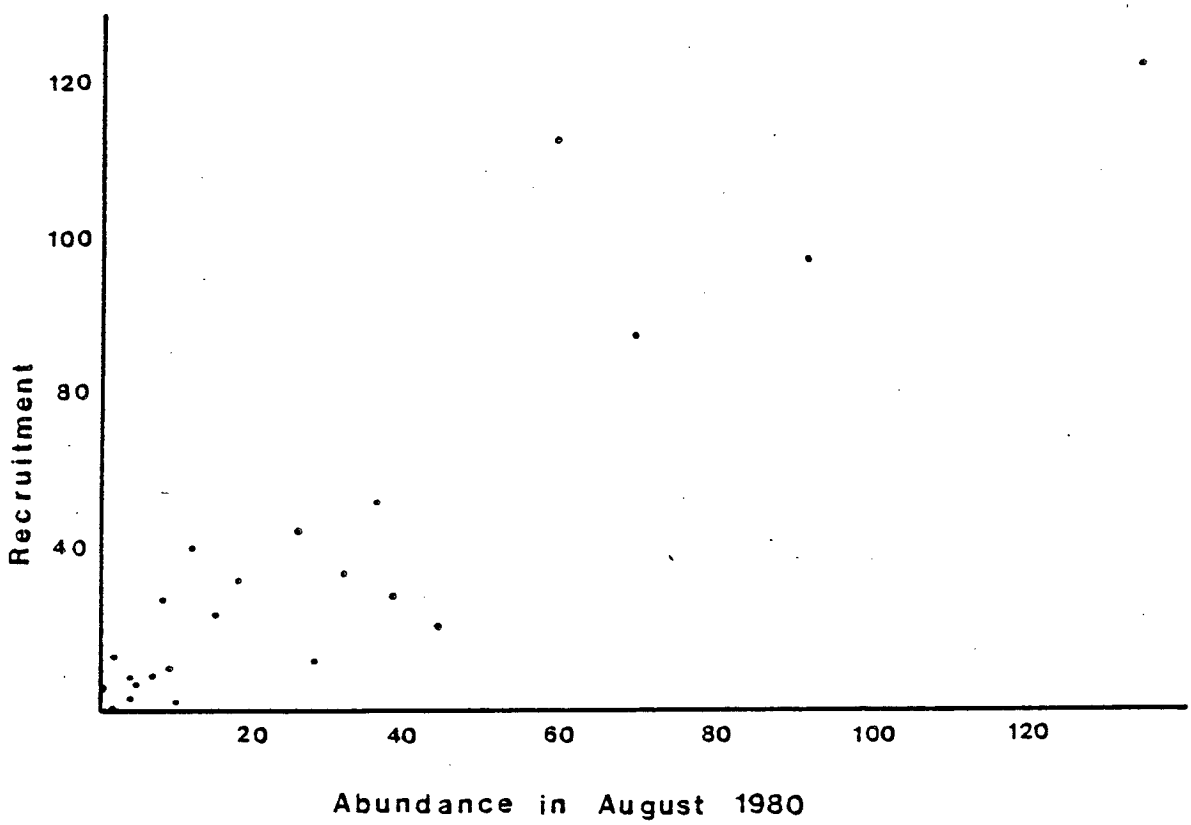

FIGURE 27: The relationship between abundance in August 1980, and subsequent recruitment over the next 29 months, for 23 genera. *Porites* was not included because of the scale of the figure, and had an abundance of 499, and 319 recruits.

why not plot log-log

TABLE 15: Results of χ^2 contingency table analyses to determine whether new recruits are distributed amongst transects 1 to 5 in the same way that all colonies are, for genera where frequency of colonies per transect generally exceeded 5. Further explanation is given in the text.

Genus	χ^2	P (χ^2)	Dependence
Pocillopora	16.73	<.01	**
Stylophora	3.69	.45	
Seriatopora	5.76	.22	
Acropora	17.37	<.01	**
Montipora	13.18	<.01	**
Astreopora	5.79	.21	
Porites	13.61	<.01	**
Fungia	2.68	.61	
Galaxea	4.69	.32	
Favia	10.47	.03	*
Goniastrea	10.35	.03	*

* significant at 0.05 level

** significant at 0.01 level

TABLE 16: Results of analysis of variance for differences in mean recruitment rate between selected coral families.

Family	Mean	S.D.
Pocilloporidae	0.17	0.04
Acroporidae	0.13	0.01
Faviidae	0.14	0.05
Poritidae	0.07	0.00

Source	S.S.	D.F.	M.S.	F	P(F)
Between	0.217	3	0.072	38.65	0.01
Within	0.015	8	0.002		
Total	0.232				

colonies, and 6 genera had recruits with significantly different distribution patterns amongst the 5 transect from all colonies of that genus. Recruits of *Pocillopora, Acropora, Montipora, Favia* and *Goniastrea* were more abundant than expected in deep transects, while *Porites* recruits were more abundant than expected in shallow water.

A one way analysis of variance was performed to test for differences in mean recruitment rate between genera of different families, for the four families that had more than one genus per family in the transects (table 16). There were significant differences in mean recruitment rate between families.

6.4.3 Mortality

Changes in mortality rate for each genus at each site and time were analysed by three way analysis of variance (table 17). There was a significant effect of time on mortality rate. The significant interaction effect between genus and transect made interpretation of the results for these factors difficult. The relationship between mortality rate and transect number for different genera are illustrated in figure 28. The effect of transect number on mortality rate varies for the different genera considered. There was no clear pattern of change in mortality rates across transects, and this was supported by the S.N.K. range tests for differences in mortality rates between transects (table 17), which showed high overlap in mortality rate between all transects except transects 4 and 5 which both occur in deep

TABLE 17: Three way analysis of variance of mortality rate by genus, transect number and time, for arcsine transformed proportions.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	Signif.
Main effects					
Genus	10370.7	9	1152.3	7.61	0.001
Transect	2039.2	4	509.8	3.37	0.01
Time	3773.7	8	471.7	3.11	0.002
2-way interactions					
Genus x transect	9150.3	36	254.2	1.68	0.011
Genus x time	8795.0	72	122.2	0.81	0.862
Transect x time	7106.5	32	222.1	1.47	0.055
Explained	41235.5	161	256.1	1.69	0.001
Residual	43604.7	288	151.4		
Total	84840.2	449	189.0		

S.N.K. range tests (underlining = means not sign. different, p=0.05)

(i) Mean mortality for each genus, transects and times pooled

Gal.	Por.	Astr.	Gonias.	Ser.	Mont.	Fav.	Fung.	Pocil.	Acrop.
3.04	11.17	14.42	14.46	15.69	16.14	17.50	18.46	19.98	20.25

(ii) Mean mortality for each transect, genera and times pooled.

Transect	5	3	1	2	4
	11.79	14.41	14.74	16.49	18.12

(iii) Mean mortality for each time, genera and transects pooled. The time is numbered chronologically from October 1980 which equals time 1.

Time period	2	6	5	9	4	7	8	3	1

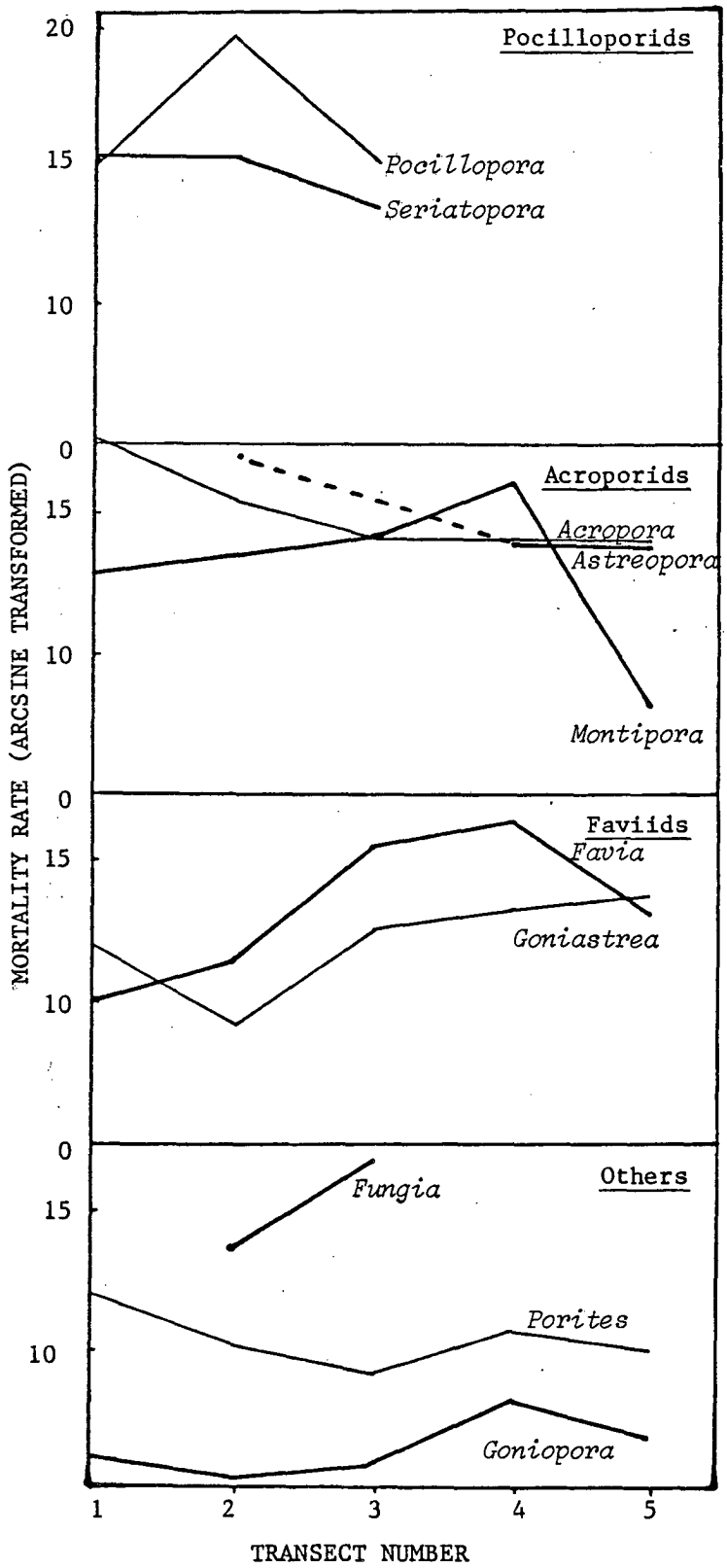

FIGURE 28: Changes in mortality rates in transects 1 to 5 for the 10 genera tested, with mortality pooled over time. Only transects where the mean number of colonies for a genus was over 3 are included.

water.

To examine the relationship between recruitment and mortality, it was necessary to increase the sample size by pooling results over time and transects. This was considered to be justified in the case of mortality because variation in genera explained the largest proportion (35%) of variation in mortality rate, and because of the large overlap between transects and times shown by the S.N.K. tests. There was a positive correlation between recruitment and mortality (figure 29; r=0.74, d.f.=16), and there was a tendency for genera from the same families to group together.

6.4 Discussion

6.4.1 Colony turnover

This study shows that an analysis of transect data taken at annual intervals would have underestimated recruitment and mortality by about 1/3, compared with data collected at 2-monthly intervals. The underestimate involves mainly small colonies that have high mortality rates (Chapter 5). It seems likely that much of community structure is determined by the action of physical and biological pressures on small colonies (settlement preferences, differential mortality, limitation of distribution according to physiological tolerances) (Dana, 1976; Goreau *et al.*, 1981; Birkeland *et al.* 1981). Lack of information on the population dynamics of these early stages should be recognized in studies where sampling is infrequent, or when sampling

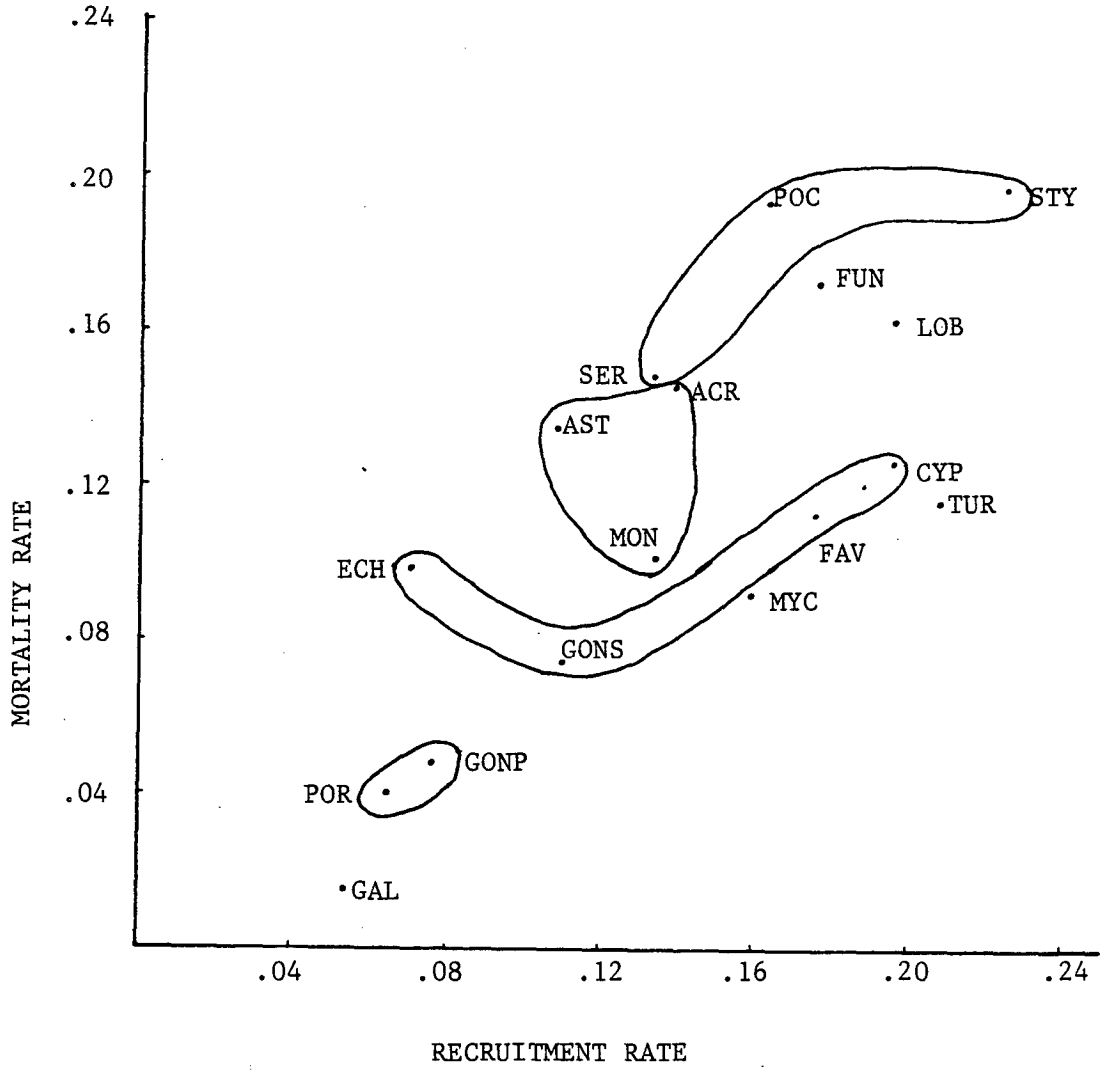

FIGURE 29: The relationship between recruitment and mortality rates for the most abundant genera (mean number of colonies $\geqslant$ 10). Genera in the same families are enclosed within the solid lines.

methodology precludes data on colonies of this size (eg. Done, 1981; Bak and Luckhurst, 1980).

Connell (1973) found that 50% of the colonies that settled in one sample period had died by the following year. Although the data are not directly comparable, this result is similar to that obtained here. In addition, Connell found that large, older colonies were the most stable component of the population, and that was also true in this study.

Of all colonies recorded in the transects, 53% recruited during the 18 month study period, and a similar percentage died. The high turnover of colonies did not generally result in large changes in generic abundance in the transects. This contrasts with observations on population changes in coral reef fishes (Sale, 1983; Doherty, 1983). Their studies of fish communities on patch reefs over a time period comparable with my study indicated large changes in relative abundances of fish species, attributed to high mortality and recruitment rates, and the variable abundance and species composition of the fish recruits.

The relative stability of generic abundances in this study also contrasts with the predictions of the non-equilibrium hypotheses of diversity maintenance (e.g. the intermediate disturbance hypothesis) that "High species diversity is maintained only when the species composition is continually changing" (Connell, 1978, p. 1303). At the spatial scale of this study, generic composition was stable over an 18 month period, despite high coral mortality and recruitment.

Good!

At progressively smaller spatial scales, the probability of finding changes in species composition over time increases, down to the case where a colony is replaced by a colony of the same or a different species once it dies. Similarly, the probability of finding changes in the community increase with the increasing time period over which observations are made. Bohnsack (1983) has discussed the effects of sampling interval and spatial scale on interpretations of the stability or otherwise of reef fish communities. As Bohnsack points out, the interpretation of dynamic nature of communities is scale dependent, and this makes interpretation of processes of diversity maintenance, presently quite rigidly separated into equilibrium and non-equilibrium models (Connell, 1978), difficult to apply to field studies. Concepts of diversity maintenance will be discussed further in Chapter 8.

6.4.2 Spatial patterns

There were no clear differences between recruitment and mortality rates in deep and shallow transects. The similarity of mortality rates at shallow and deep sites is unexpected, since shallow areas are often considered to be subject to greater physical stress, hence with a higher colony turnover than deeper sites (Connell, 1979; Fishelson, 1973; Loya, 1972; Grassle, 1973; Glynn, 1976; Bak and Luckhurst, 1980). In this case, the shallowest site was at a depth of approximately 3m, and did not resemble a reef flat typical of shallow water habitats with strong physical forces. The small depth gradient (3m to 9m) in

this study may have been insufficient to result in the major changes in physical parameters with depth found in other studies.

Causes of mortality (Chapter 5) varied with depth. The effects of predation by *Acanthaster planci* were most severe in shallow water where *Acropora* colonies were abundant. Predation by *A. planci* was most severe during the first 6 months of the study and probably accounts for the fact that there was a net decrease in the number of colonies in transects 1 and 2 during this period (figure 25). Spatial rearrangement of colonies with subsequent damage or death appeared to occur more frequently in shallow transects following strong winds and storms, despite the absence of overall higher mortality in shallow areas. In deeper transects, occasional periods of heavy sediment deposition appeared to contribute to colony death, particularly for small colonies.

6.4.3 Generic patterns

There was a complex set of relationships between abundance, recruitment and mortality such that relative abundances of genera remained nearly constant over 18 months. Recruitment tended to maintain abundance, since the most abundant genera had the highest number of recruits. Connell (1973) also found that recruitment was in proportion to abundance. In addition, there was a positive correlation between recruitment rate and mortality rate, and this would also play a role in maintaining the relative abundances of the different genera.

Recruitment rate varied among genera in different families, and a similar relationship would be expected for mortality (figure 29). Of the 4 major families, pocilloporids had the greatest relative number of recruits, followed by faviids, acroporids and poritids.

The relationship between abundance of adults and number of recruits has received much attention from both coral and fish workers (Done, 1981; Bak and Engel, 1979; Doherty, 1983 and many others). If abundance of recruits reflects adult abundance, then recruitment alone may be a major determinant of distribution patterns. If abundance of recruits is different from that of adults, then either the population is in a state of flux and the composition of the adult population is dependent on variable recruitment, or post-recruitment events such as differential survival or biological interactions (competition, predation) determine distribution and abundance.

Bak and Engel (1979) found no direct relationship between abundance of coral recruits at different depths, and abundance of adult colonies at the same depths. They considered this to be evidence for the influence of post-recruitment factors on coral distribution.

For 6 of the most abundant genera in this study (*Pocillopora, Porites, Acropora, Montipora, Favia* and *Goniastrea*), distribution of recruits over 18 months amongst the 5 transects did not reflect distribution of established colonies in the transects. Since distribution patterns of coral genera

did not change greatly over the study period (i.e. the population is not in a state of flux as a result of temporally variable recruitment), there is evidence that post-recruitment events have a major effect on distribution of these genera.

For the other 5 genera (*Stylophora*, *Seriatopora*, *Astreopora*, *Fungia* and *Galaxea*), in which distribution of recruits reflected that of established colonies, recruitment patterns alone would be sufficient to explain the distribution patterns observed.

Bak and Luckhurst (1980) found that, although cover of various community components remained constant over extended periods, the specific composition of the coral community showed large variations. Whether species show the same degree of consistency over time, such as that exhibited here by genera warrants further investigation.

CHAPTER 7

Temporal and spatial patterns of spat recruitment.

7.1 Introduction

Because most coral species are non-motile, factors influencing patterns of juvenile recruitment have significant effects on distribution and abundance of adult corals. The degree to which populations on coral reefs are limited by resource availability (particularly space) versus availability of recruits has recently been discussed by Doherty (1981) and Williams (1980) for reef fishes, and by Birkeland *et al.* (1981) for corals. The two alternatives have important implications in determining variability in natural populations. In addition, for corals the relative effects of substratum selection by planulae, and differential post-settlement mortality of spat, in determining coral distribution and community structure are largely unknown (Chapter 6, Sheppard, 1982, Done, 1982).

Thus the major questions concerning the effect of coral recruitment on community structure are:

1. Are planulae evenly dispersed between reefs, within reefs, and within reef zones; or is recruitment predominantly local (e.g. Neudecker, 1981)?
2. How many planulae are available, i.e. does the availability of planulae limit recruitment, or is there competition for settlement space among a large pool of planulae (e.g. Birkeland

et al., 1981)?

3. Do corals exhibit settlement preferences that correspond to their distribution patterns (Bak and Engel, 1979)?

4. Is there differential post-settlement mortality that contributes to coral abundance and distribution (Done, 1982)?

Several studies have contributed towards answering some of these questions. Although little information is available on large scale dispersal abilities of coral planulae, Harrigan (1972) and Richmond (1981) have determined that *Pocillopora damicornis* planulae can survive for long periods without settling. Birkeland *et al.* (1981) have raised the question of space limitation in spat settlement, and many authors have discussed settlement preferences, particularly in relation to causes of mortality of spat (Harrigan, 1972; Lewis, 1974; Schuhmacher, 1974; Birkeland, 1977; Bak and Engel, 1979; Sammarco, 1982; Sammarco and Carleton, 1981; Wallace and Bull, 1981, Neudecker, 1981).

In this study, spat recruitment (at <1cm diameter) at 5 sites on a patch reef at Lizard Island is described for a 16 month period. Recruitment patterns are related to the distribution patterns of adult colonies in adjacent areas (transects 1 to 5), and to available information on reproductive seasonality of the corals. Some of the major questions of coral recruitment are discussed.

7.2 Methods

The location of transects 1 to 5 was described in Chapter 2. A set of settlement plates was placed at 5 sites, within one metre of transects 1 to 5 (figure 2), e.g. site 1 is adjacent to transect 1. Grids constructed from "weldmesh" 22cm square reinforcing iron were attached to stakes, and settlement plates were attached to the grids (figure 30).

Settlement plates for each period were 4 coral blocks, each 5cm x 5cm x 2cm, cut with a band saw from a *Porites* colony, and 4 plastic Petri dishes, 9 cm diameter. Two holes were drilled in diagonally opposed corners of the coral blocks and the blocks were suspended horizontally from the grid. Preliminary experiments showed that spat settled preferentially on the lower surface of blocks, and a horizontal orientation of the blocks gave maximum preferred settlement surface. Petri dishes were suspended vertically from one point (figure 30).

In each sample period, settlement plates were collected and replaced by fresh plates. All samples had been submerged approximately 4 months at the time of collection. Plates were collected in April 1981, and every 2 months thereafter until April 1982, a total of 7 samples covering 16 months immersion.

When settlement plates were collected, they were examined with a light microscope and spat were photographed live. Plates were labelled and bleached in a concentrated chlorine solution. Bleached plates were reexamined and the position of colonies was

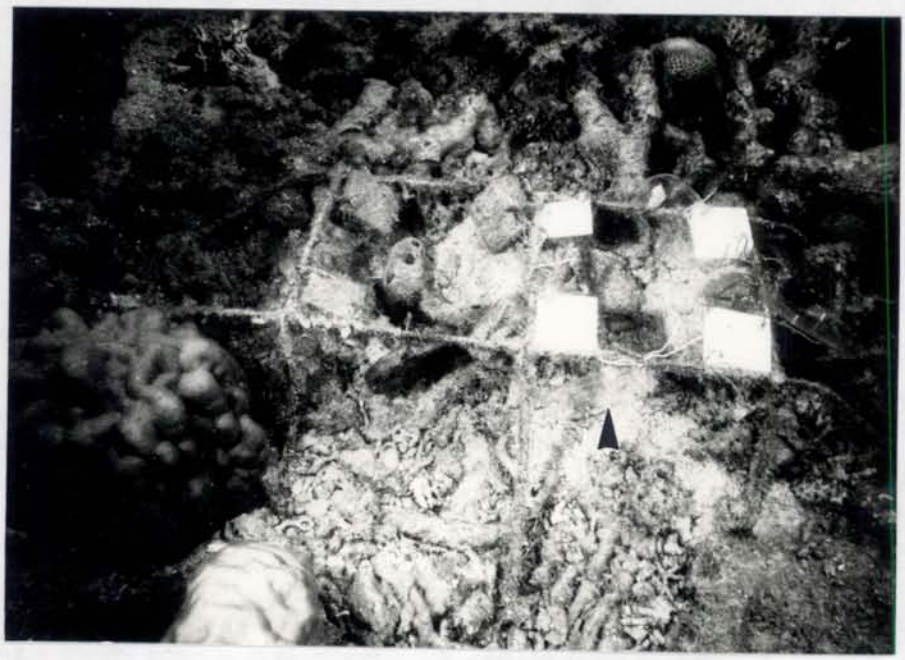

FIGURE 30: Photograph showing the grids used for attachment of settlement plates, and the orientation of the coral blocks used as a settlement surface. The location of one Petrie dish is shown by the dark arrow.

marked. Colonies were counted and identified where possible, and scanning electron micrographs were taken of a variety of spat types.

In addition to the regularly collected plates, two additional sets of plates, each of 20 coral blocks and 10 Petri dishes, were set near transects 2 and 5 in summer 1981/82. These plates gave additional data on recruitment on shallow versus deep sites at the time of maximum settlement. To ascertain growth rates of spat, colonies that settled on coral blocks deposited randomly on the reef top at the study area were collected, labelled, photographed live, and returned to the study site. The colonies were rephotographed on successive sample periods for as long as the corals lived.

7.3 Results

7.3.1 Taxonomy

Over 90% of spat could be identified to family level, and belonged to one of three families, Pocilloporidae, Acroporidae, and Poritidae. Types of spat within families could be recognized but could not be consistently identified to generic or specific level.

Planulae from the pocilloporids, *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* were raised to several months old spat in aquaria (figure 31, 32). Although some distinctive differences are noticeable in large spat, I could not confidently separate the species when small. *Acropora*

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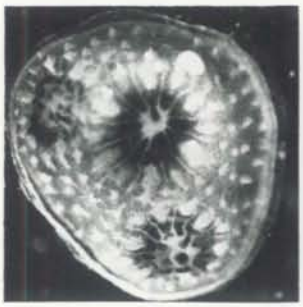

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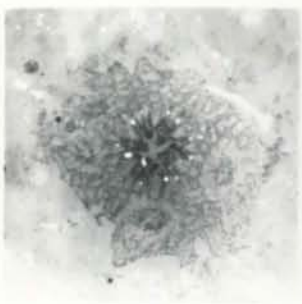

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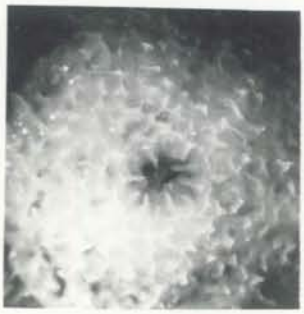


viii.

FIGURE 31: Spat of pocilloporid carals, and *Acropora brueggemanni* that were raised from planulae released in aquaria.

(i) Scanning electron micrograph of *Pocillopora damicornis* spat (X27)

(ii) Scanning electron micrograph of *Stylophora pistillata* spat (X54)

(iii) Scanning electron micrograph of *Seriatopora hystrix* spat (X27)

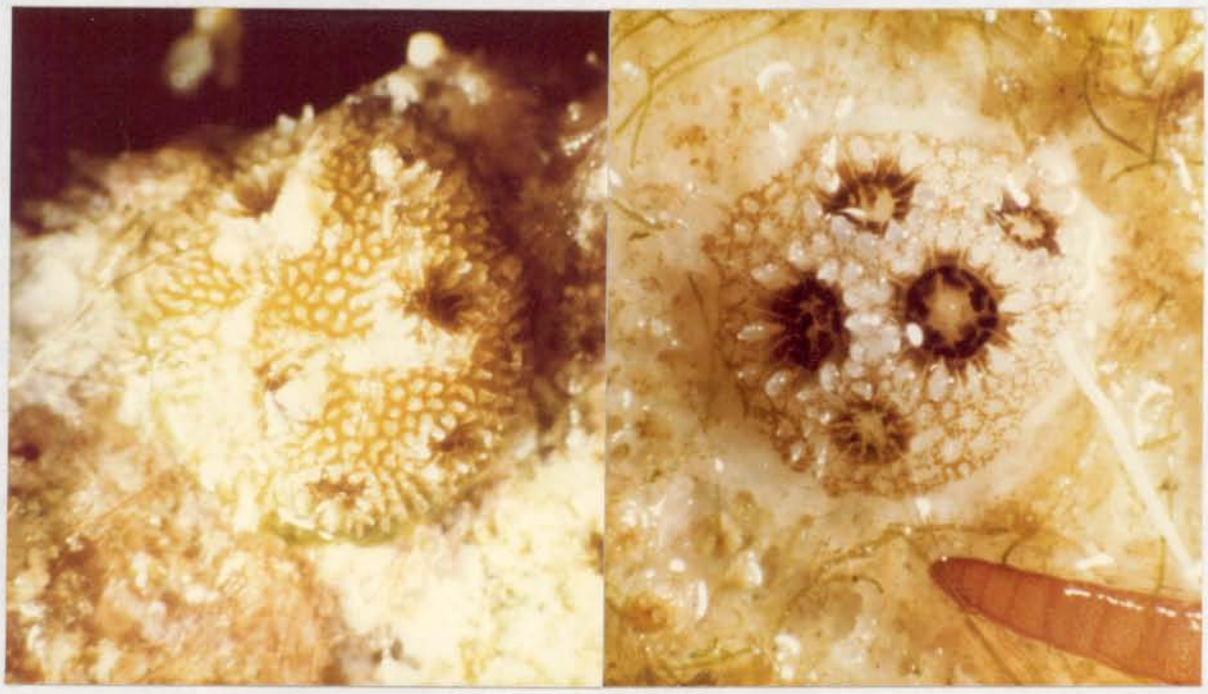
(iv) Live *P. damicornis* spat, 8 weeks old (X 52)

(v) Colony of *P. damicornis* from aggregated settlement of planulae in aquaria (X 10)

(vi) Live *S. hystrix* spat, 1 week old (X 16)

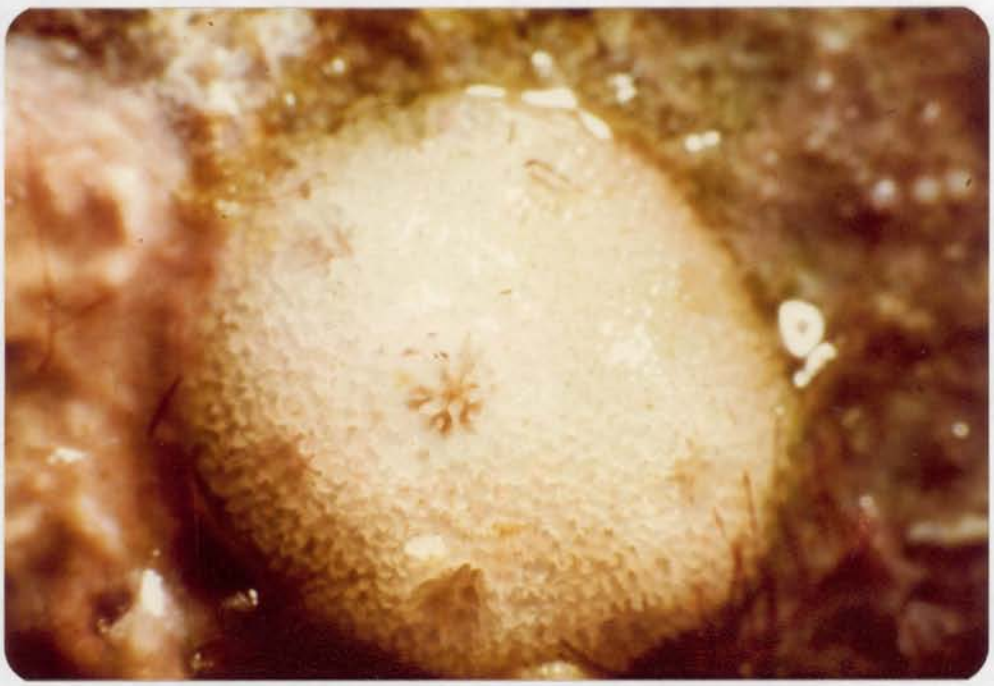
(vii) *S. hystrix*, settled in aquarium (X 16)

(viii) *Acropora brueggemanni* spat, settled in aquarium at 2 weeks old (X 16)



a.

b.



c.

FIGURE 32: Colour plates of coral spat. (a) pocilloporid coral; (b) *Seriatopora hystrix* spat raised from planulae released in aquaria; (c) *Acropora brueggemani* spat approximately 1 week old from planulae raised in aquaria.

brueggemanni was also reared from planulae (figure 31, 32). Poritid spat were distinguishable by their small size and distinctive septae. Jell (1980) gives electron micrographs of recently settled *Porites* spat. In figures 32 to 35, a range of spat types are shown with their taxonomic designation.

7.3.2 Growth of spat

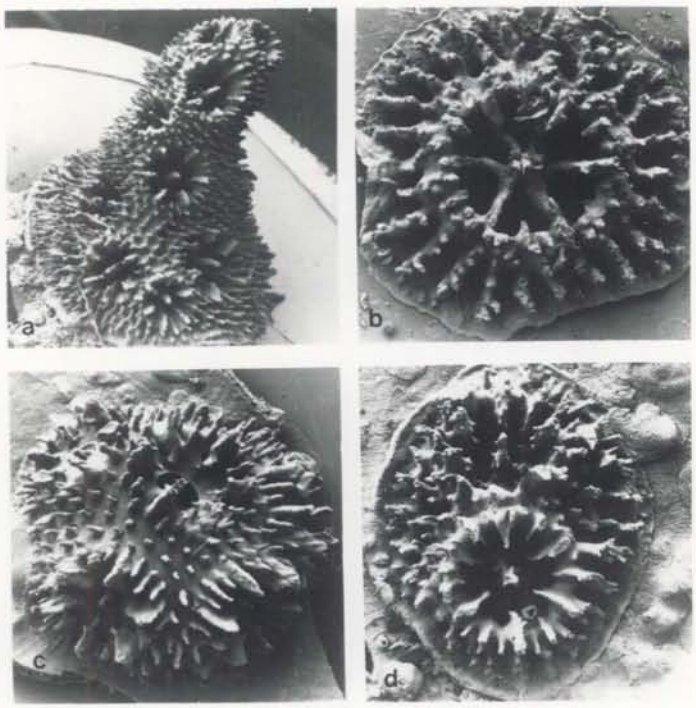
The largest spat recorded on plates that had been submerged for 4 months was approximately 2.5 mm diameter. No spat larger than 4 mm diameter and 5 mm high was found on plates submerged up to 9 months. Consequently, corals 1cm in diameter, under conditions at the study site, are probably at least 1 year old (c.f. Connell, 1973).

The growth of newly settled corals was slow (figure 36) despite the apparent health of most colonies. Mortality rate of spat in the field was high, but was probably somewhat elevated by repeated collection.

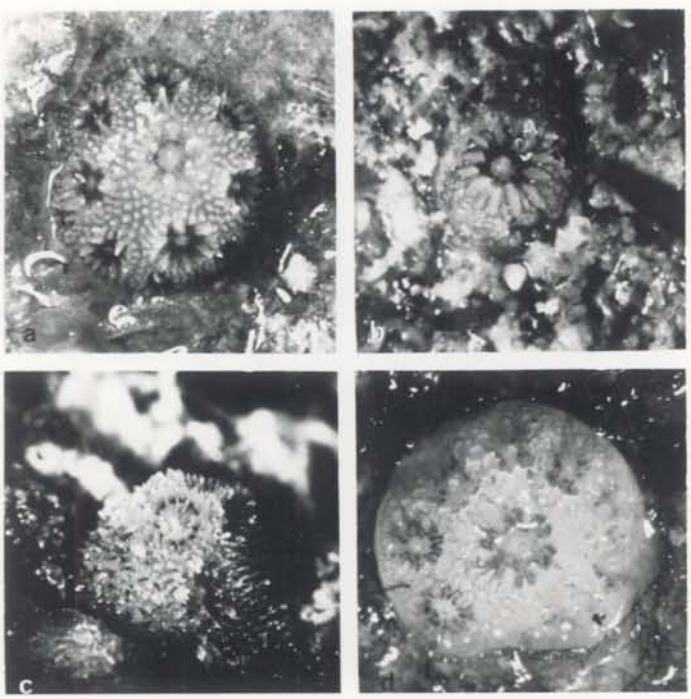
7.3.3 Orientation effect

Spat were found exclusively on the lower and vertical surfaces of coral blocks. On Petri dishes, spat were most frequently found under the upper rim of the dishes.

The factors limiting recruitment of spat on upper surfaces appear to be predominantly fish grazing and sedimentation. In shallow water, growth of filamentous algae is rapid and grazing



i.

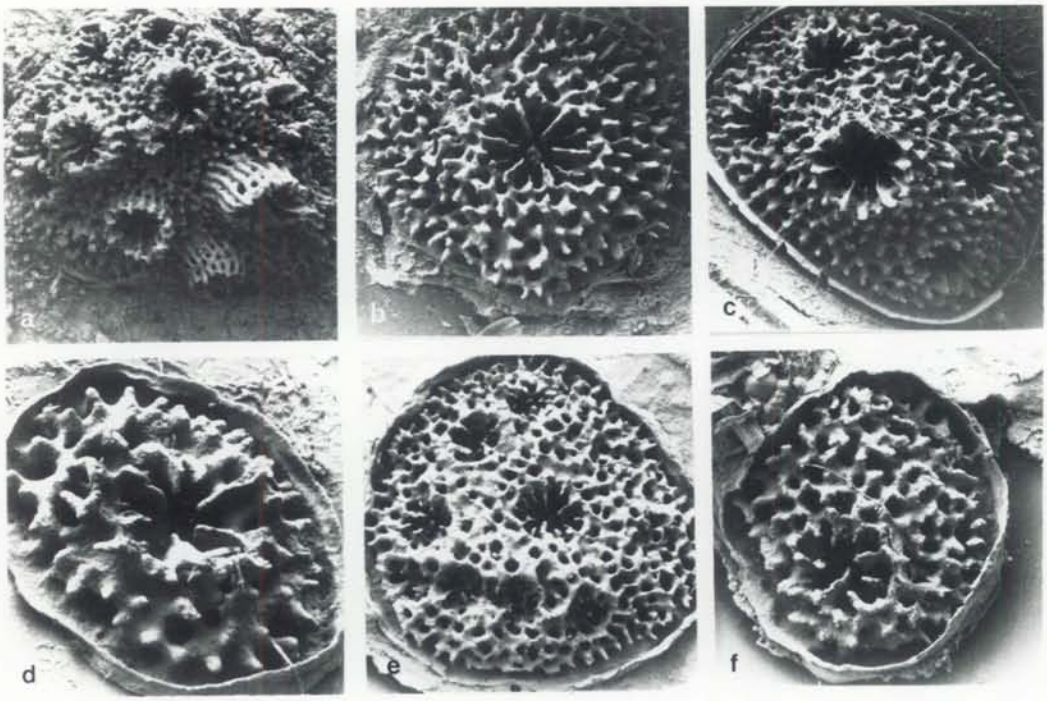


ii.

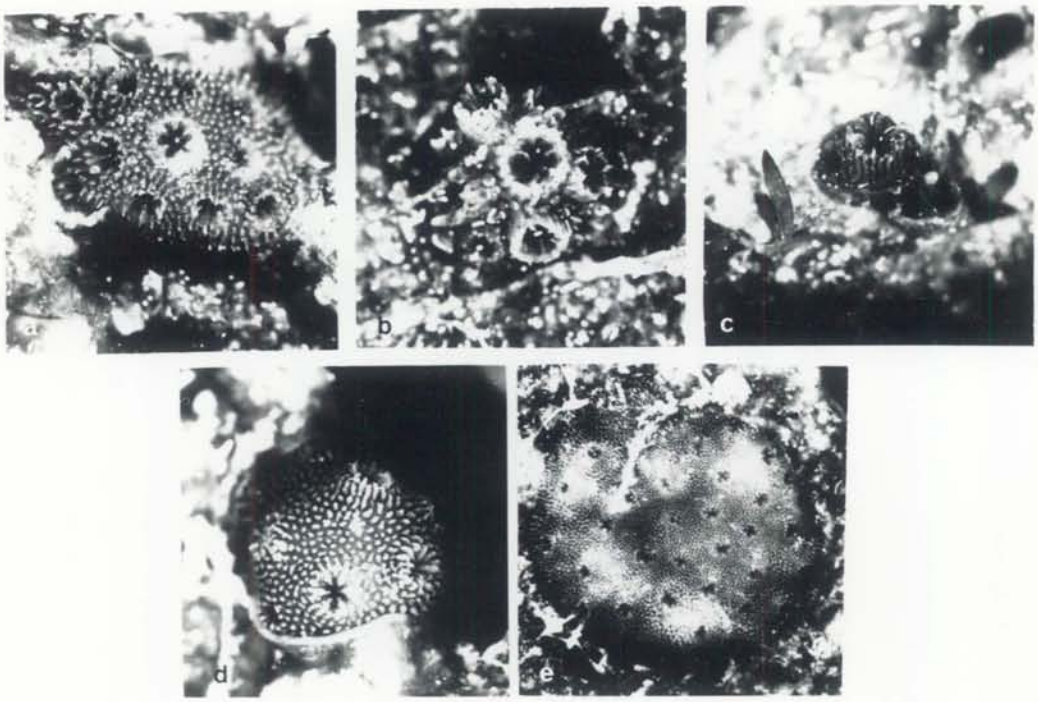
FIGURE 33: Representatives of spat from the family Pocilloporidae that settled on plates in the field.

(i) Scanning electron micrographs of pocilloporid spat
   a. November 1981, X 10
   b. February 1982, X 40
   c. April 1981, X 27
   d. February 1982, X 40

(ii) Photomicrographs of living pocilloporid spat
   a. August 1981, X 16
   b. December 1980, X 16
   c. February 1982, X 16
   d. December 1980, X 16



i.



ii.

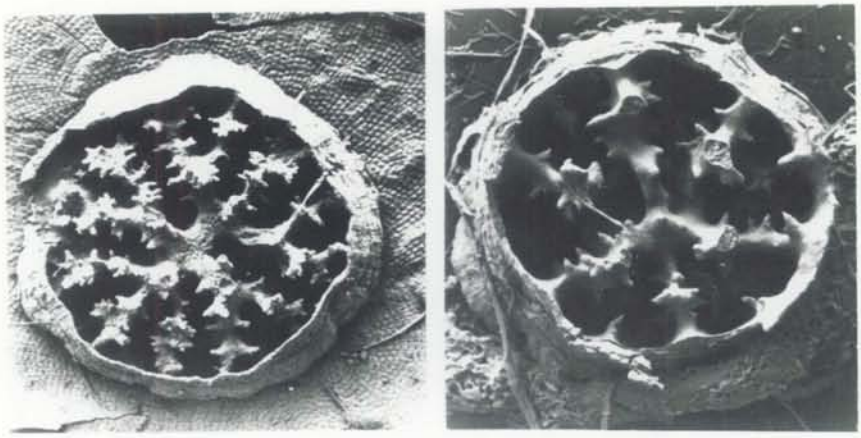
FIGURE 34: Representatives of spat from the family Acroporidae that settled on plates in the field.

(i) Scanning electron micrographs of acroporid spat

a. February 1982, X 13
b. February 1982, X 27
c. October 1981, X 20
d. December 1981, X 54
e. April 1982, X 20
f. April 1981, X 20

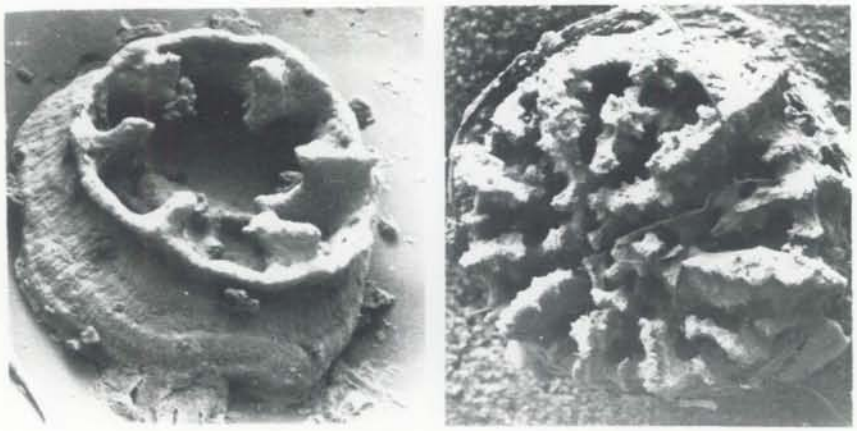
(ii) Photomicrographs of living acroporid spat

a. April 1981, X 16
b. April 1981, X 16
c. April 1981, X 16
d. April 1981, X 16
e. December 1981, X 16



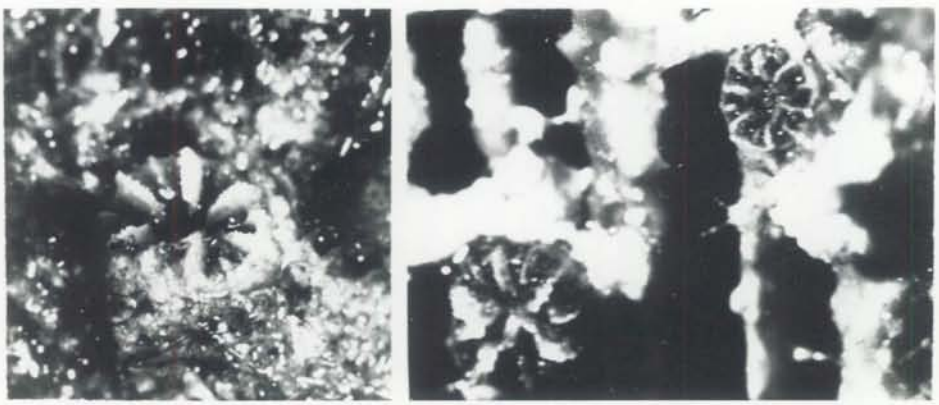
a b

i.



a b

ii.



a b

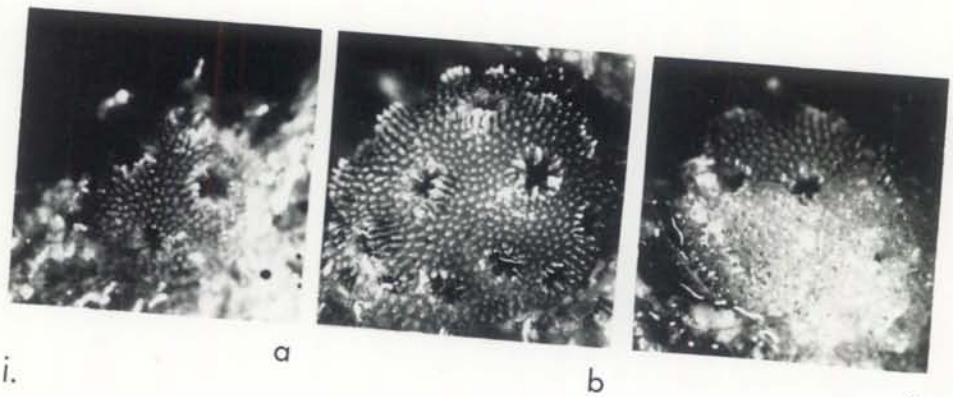
iii.

FIGURE 35: Representatives of spat from the family Poritidae, and from other less common families, that settled on plates in the field.

(i) Scanning electron micrographs of poritid spat
  a. October 1981, X 54
  b. February 1982, X 80

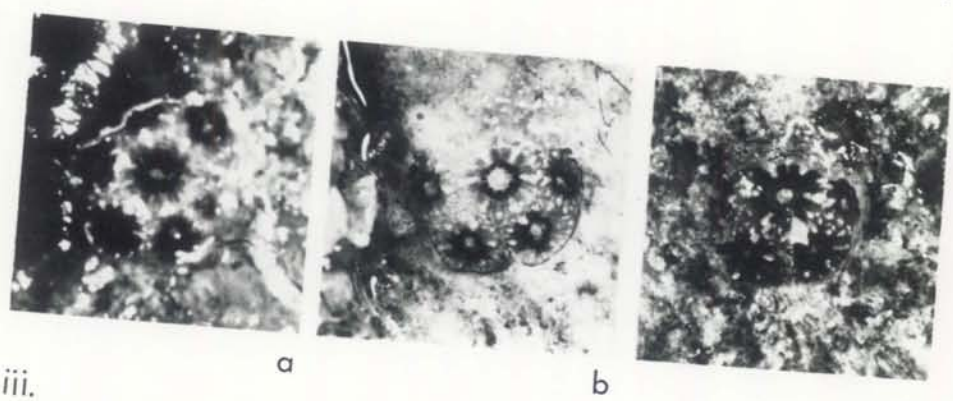
(ii) Scanning electron micrographs of spat of unknown taxa
  a. April 1982, X 100
  b. February 1982, X 35 (possible ahermatype)

(iii) Photomicrographs of living corals
  a. April 1981, X 16; ? *Galaxea*
  b. February 1982, X 52; as ii b above.

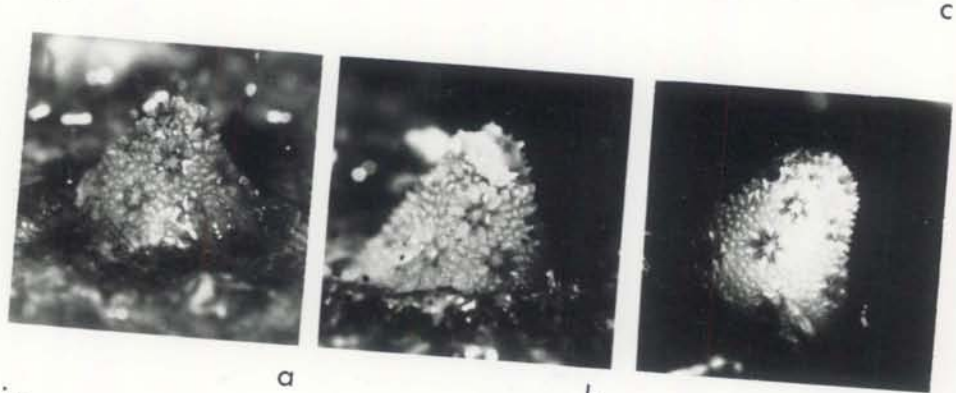


i. a b c

ii. a b c



iii. a b c



iv. a b c

FIGURE 36: Photomicrographs of living coral colonies, photographed live over a period spanning 4 to 6 months. Corals were returned to the field between photographs.

(i) Acroporidae a. June 1981
b. August 1981
c. October 1981

(ii) Pocilloporidae a. June 1981
b. October 1981
c. December 1981

(iii) Pocilloporidae a. June 1981
b. August 1981
c. December 1981

(iv) Pocilloporidae a. August 1981
b. October 1981
c. December 1981

pressure was high. The upper surfaces of coral blocks were almost invariably scored with teeth marks interspersed with areas of high algal crop, while algal cover was uniformly dense on the lower surface of the blocks (figure 37). In deeper waters, algal growth and fish grazing was low, but there was heavy deposition of sediment, as a result of movement of sediment-ladened water out of the lagoon with tidal changes. Coral blocks in the deeper sites were usually covered in a 1mm to 2mm thick layer of fine sediment at the time of collection. Such a sediment layer would prevent attachment of planulae to the block surface and could smother any planulae that did settle. The relative effects of settlement preferences and early mortality could not be separated in this study.

7.3.4 Nature of the settlement surface

Petri dishes were frequently lost from grids before collection, particularly in the shallow sites (see sample sizes in Appendix 3). Strong water movement broke the plates from the grid. Loss of some dishes made comparison of temporal and spatial settlement patterns on the two surfaces difficult, so results for Petri dishes were restricted to differences in abundance and taxonomic composition between the two surfaces.

A comparison of spat abundances was complicated by the vertical orientation of the Petri dishes, which would tend to reduce settlement, and the larger surface area of the Petri dishes (approx. $155cm^2$ c.f. $90cm^2$ for coral blocks), which

(a)

(b)

FIGURE 37: A coral block settlement plate from transect 1, showing upper and lower surfaces. The upper surface shows the teeth marks of grazing fishes (a), and on the lower surface, algae is ungrazed (b).

might increase settlement. At each site, there was no significant difference between the mean number of spat on coral blocks and Petri dishes (Appendix 3; 5 sets of t-tests, $p(T) > 0.05$).

The relative frequency of different families of spat was found to be significantly dependent on type of settlement surface when all transects and times were pooled ($\chi^2=9.78$, $P(\chi^2) < 0.05$). When shallow (1 and 2) and deep (3,4,5) sites were analysed separately, it was found that the relative abundance of spat families was not dependent on type of settlement surface at the deep sites ($\chi^2=11.95$, $P(\chi^2= 0.80)$, but was dependent at the shallow sites ($\chi^2= 11.95$, $P(\chi^2) < 0.01$). At the shallow site, there were more pocilloporids and fewer poritids on Petri dishes than coral blocks. Wallace and Bull (1981) also reported a higher frequency of pocilloporids on Petri dishes relative to a coral surface.

7.3.5 Seasonality of settlement

Data for numbers and types of spat that settled at each site in each period are given in Appendix 3. Changes in spat abundance and type on coral blocks over time for all sites pooled are shown in figure 38.

Spat recruitment was greatest on plates collected from December to April (120 spat) and least on plates collected from June to October (41 spat).

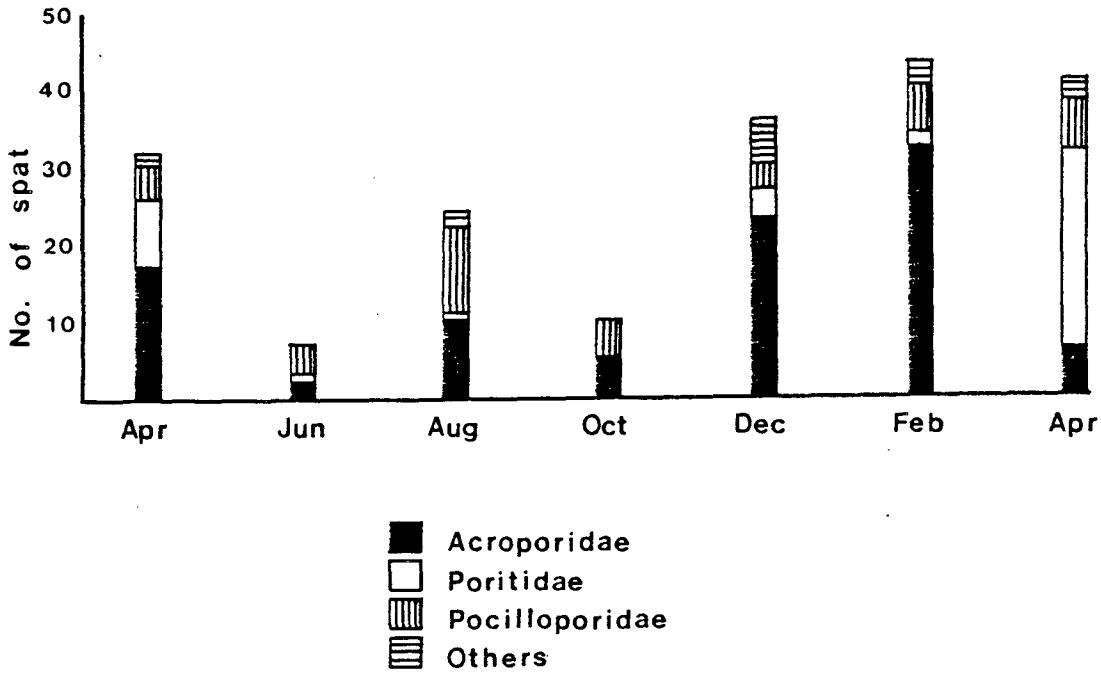


FIGURE 38: Changes in the number of coral spat on coral blocks for all transects pooled for sample periods from April 1981 to April 1982.

Recruitment of pocilloporids occurred uniformly throughout the year, relative to other families. They were most abundant in August, on plates collected 2 months after the release of large numbers of planulae by *Pocillopora damicornis* in aquarium experiments (Chapter 4). At Lizard Island, *P. damicornis* released planulae predominantly in winter, while colonies of *Stylophora pistillata* and *Seriatopora hystrix* were observed to spawn in summer (personal observations; Y. Loya, personal communication). Thus pocilloporids were releasing planulae at all times of the year, and this would account for the relatively even spatfall.

Poritids had low recruitment at all times apart from April each year. *Porites lutea* and *P. australiensis* spawned in mid-December in two successive years (Chapter 3). Several other *Porites* species are also known to have a brief summer spawning period, although at least one *Porites* species releases planulae over a longer period (Kojis and Quinn, 1981 b). Synchronized December spawning in poritids would account for the pre-April recruitment peak.

Acroporid recruitment peaked between October and February, but there was a low level of settlement at all other times. Many *Acropora* species spawn in a brief spring/summer period each year (Harrison *et al.*, in press). Settlement of propagules released in October or November would account for the summer recruitment peak a few months before that of the poritids. Isoporan *Acropora* species release well developed planulae for extended periods each

year relative to the non-isoporan *Acropora* species (B. Kojis, personal communication). The isoporans *A. brueggemanni* and *A. palifera* are the most abundant acroporids at the study site (Appendix 1), and settlement of their propagules could acount for the small amount of recruitment throughout the year. *Acropora* spat that settled in winter resembled the *A. brueggemanni* spat that settled in aquaria (e.g. figure 34 (i)c).

7.3.6 Spatial settlement patterns

Table 18 lists the numbers and types of spat that recruited at sites 1 to 5 during the study period. Fewer spat recruited at deeper sites (3,4,5) than at shallower sites (1,2). A one-way anova showed significant differences between the mean number of spat/ coral block amongst the 5 sites (table 19). T-tests for differences between pairs of transects showed that there was no significant difference in the mean number of spat between transects 1 and 2, and between transects 3,4 and 5 ($P(T) > 0.05$); but that the number of spat on blocks from these two groups (i.e. shallow versus deep) were significantly different from each other ($P(T) < 0.001$).

Figure 39 shows the distribution of spat of the three major coral families at each of the 5 sites, and abundances of established colonies of each family in the adjacent transects (Chapter 2). To determine whether spat were distributed amongst the 5 transects in the same relative frequency that established colonies were, χ^2 contingency table analyses were performed for

TABLE 18: Abundance of spat on coral blocks in transects 1 to 5 for all samples pooled.

	Tr 1	Tr 2	Tr 3	Tr 4	Tr 5	Total
Pocilloporidae	16	10	8	3	2	39
Poritidae	30	8	0	4	1	43
Acroporidae	29	53	0	3	10	95
Others	6	5	2	2	1	16
TOTAL	81	76	10	12	14	193

TABLE 19: Results of analysis of variance for effects of Transect number on mean number of spat per coral block

Transect No.	Mean	S.D.
1	2.96	2.78
2	2.67	2.75
3	0.36	0.62
4	0.39	0.79
5	0.50	1.37

Source	S.S.	D.F.	M.S.	F	P(F)
Between	195.76	4	48.94	13.45	.000
Within	491.18	135	3.64		
Total	686.94	139			

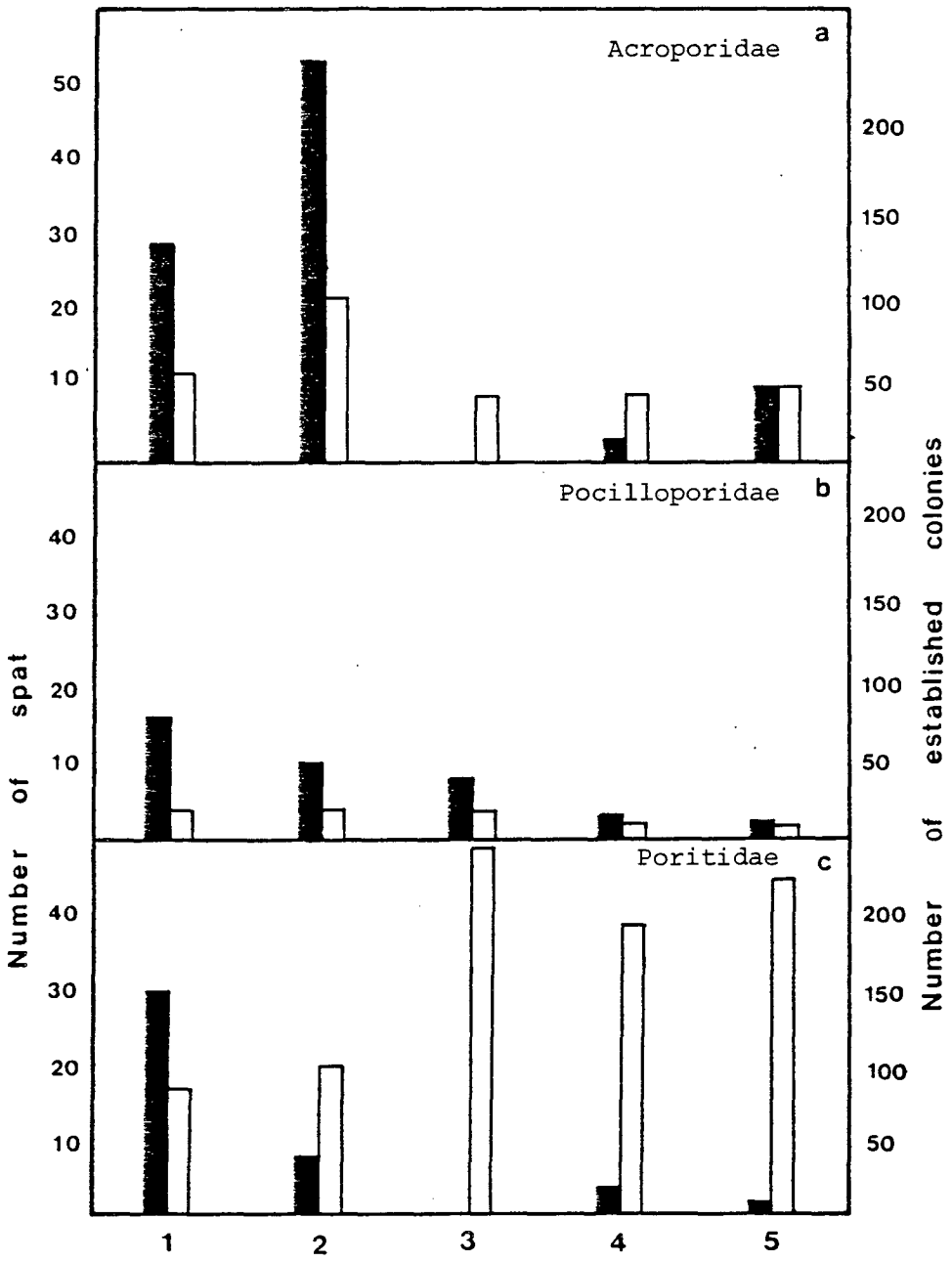


FIGURE 39: Number of coral spat (dark bars and left scale) and number of established colonies (open bars and right scale) in transects for acroporids, pocilloporids and poritids.

abundance data for spat and established colonies (Chapter 2), for each family. For acroporids and poritids, there were significant differences in the distributions of spat and established colonies (χ^2= 36.0, P(χ^2) < 0.001; χ^2 = 140.0, P(χ^2) < 0.001 respectively). Pocilloporid spat were not distributed differently from established colonies (χ^2 = 4.8, P(χ^2) = 0.31).

For all sites pooled, different families showed markedly different abundances of spat, relative to the abundance of established colonies. Pocilloporids had the most abundant spat/colony (0.54), i.e. they were the most successful recruiters, followed by acroporids (0.30) and poritids (0.05).

To test whether the relative abundance of the three major spat families varied with depth, two χ^2 contingency table tests were performed. There was a significant dependence of spat type on site of the settlement plates in the first test, where each site was considered separately (χ^2=57.16, P(χ^2)< 0.01). However when the results from transects 1 and 2, and transects 4 and 5 were pooled and tested, to reduce the effect of small scale variation of recruitment success, the taxonomic composition of the spat was found to be independent of whether the site was shallow or deep (χ^2=0.95, P(χ^2)=0.81). At both deep and shallow sites, approximately 50% of the spat were acroporids, and 20 % each were poritids and pocilloporids. Similarly, analysis of the spat that settled on deep and shallow sites in the separate experiment of summer 2081/82 (table 19) showed no significant dependence of spat type on depth (χ^2=2.19, P(χ^2= 0.53).

TABLE 20: The number and type of spat that settled on the additional set of coral blocks placed at the deep and shallow sites in summer 1981/82.

Taxa	Shallow	Deep
Acroporidae	13	9
Pocilloporidae	15	4
Poritidae	14	9
Others	3	2
	45	24

7.4 Discussion

7.4.1 Distribution of spat on plates

Spat settled exclusively on the bottom and sides of coral settlement blocks. The factors that prevented settlement or killed spat on upper surfaces appeared to be fish grazing pressure in shallow water and sediment in deeper water. Physical factors regulating spat survival that have been postulated in the literature are numerous. Birkeland (1977) noted that grazing fish avoided corals as small as 3mm. Corals in this study were generally smaller than 2mm, and there was no evidence that fish avoided the corals. Nor were grazing fishes found to avoid corals in the studies of Bak and Engel (1979), Neudecker (1979) and Wellington (1982). Birkeland (1977) also found that algae frequently trapped sediment which smothered corals unless the algae were grazed by fish. In his study, algal growth was slowed at deeper sites and this accounted for the greater abundance of corals on the upper surface of settlement plates at depth.

In a comparable study at Guam, Birkeland *et al.* (1981) again found a change in orientation of spat with depth. Once more, they attributed changes in orientation and abundance of spat to a combination of light requirements and algal growth, where rapid algal growth traps sediment and kills spat.

Wallace and Bull (1981) also found a change in preferred orientation of settling from lower to upper surface with increasing depth. Bak and Engel (1979) interpret a change in the

orientation from vertical to horizontal with increasing depth for *Agaricia agaricites* as indicating selection by planulae of optimum light conditions. In most of these studies, sediment was a factor causing death of juveniles only in shallow water, compared to the present study where sediment deposition was highest in deeper waters. The effect of sediment probably accounts for the absence of a change in orientation of spat recruitment with depth that has been reported by these other authors.

Schuhmacher (1974) found 80% of coral settlement in ridges and small crevices and attributed this to effects of sedimentation and sea urchin grazing on upper horizontal surfaces. Lewis (1974) found that planulae of *Favia fragum* in aquaria were attracted to dark corners and the undersides of objects on the bottom. Again, he assumed that avoidance of predators was the selective pressure accounting for evolution of this behaviour in an organism normally dependent on light (c.f. Goreau *et al.*, 1981).

In this study, corals that were monitored for growth (figure 36) survived for up to 6 months on the underside of pieces of coral lying on the bottom, although growth rate was slow. In order to survive, planulae may have to settle cryptically on the underside of ledges, on dead coral (Birkeland and Randall, 1981), or in cracks and crevices (Schuhmacher, 1974), then grow in a cryptic location until they have attained a size refuge from competition with algae and from accidental grazing (Brock, 1979).

Subsequently, they must either grow into the light (Birkeland, *et al.*, 1981) from their cryptic location, or they are dependent on chance movement of the substrate to which they are attached into a suitable light regime (eg by turning over of coral rubble or bioerosion causing collapse of dead coral substrate under which spat have settled). Mortality of spat would be very high at these stages.

Thus the factors affecting substratum selection and survival of spat vary greatly depending on the physical and biological conditions at the site. Corals may preferentially settle away from predators (Lewis, 1974; Schuhmacher, 1974), amongst filamentous algae (Chapter 4, Sammarco and Carleton, 1981), or at variable substratum angles depending on light (Bak and Engel, 1979). Spat on upper horizontal surfaces may be killed by filamentous algae, by sediment, or by grazing (this study, Schuhmacher, 1974, Birkeland, 1977; Bak and Engel, 1979; Brock, 1979; Wellington, 1982).

7.4.2 Temporal patterns

Discussion of temporal patterns is limited by the fact that plates were submerged at the study site for a total of only 16 months. Thus, the contribution of annual variability in spat settlement cannot be assessed from this study.

During the study period, there was large temporal variation in spat settlement, with most settlement in summer. Peak settlement follows the period when mass spawning of gametes by

scleractinian corals has been reported by Harrison *et al.* (in press), and many other coral species have also been found to breed (Chapter 3, Kojis and Quinn, 1981 a, b, 1982).

The summer/ winter variation in spat abundance in this study is less than that found by Wallace and Bull (1981) at Broadhurst Reef, where 13 spat were recorded on plates collected in October 1980, and 1847 spat were recorded on plates collected in February 1981. Wallace and Bull's study area is predominated by non-isoporan *Acroporas* (C. Wallace, personal communication), the majority of which appear to spawn in summer (Harrison *et al.*, in press). Broadhurst Reef may lack input of planulae at other times from pocilloporids and isoporan *Acropora* species which were more abundant at the Lizard Island study site than at Broadhurst Reef (Appendix 1). The difference between the sites gives some evidence that there may be an effect of local abundance of breeding colonies on the abundance of spat, i.e. there could be some differentiation of the planula pool between sites or reefs that may account for the relative abundances of different species at those sites (Done, 1982).

7.4.3 Spatial variation in settlement

Spat recruitment was greater at shallow sites than deeper ones for both coral blocks and Petri dishes. Wallace and Bull (1981) also found the highest abundance of spat at shallow sites, but Birkeland (1977) and Birkeland *et al.* (1981) found the highest recruitment at intermediate depths. Bak and Engel (1979)

found little difference in the number of coral recruits at depths between 3m and 37m, although the composition of the spat changed.

Despite the far greater abundance of spat on settlement plates in shallow water than in deep water in this study, there was no corresponding difference between deep and shallow transects in the recruitment rate of coral colonies at visible size (Chapter 6). This discrepancy has several possible explanations:

1. Spat abundance may be temporally variable between years such that spat have settled more heavily in deeper transects in other years.

2. There may be higher post-settlement mortality of spat in shallow than in deep areas, resulting in similar recruitment at visible size. Possibly higher algal growth, hence higher grazing pressure in shallow water results in higher spat mortality.

3. A paucity of suitable settlement substrata in shallow waters may naturally limit settlement in shallow water to a level comparable to that in deeper waters, despite the higher density of planulae in the shallow water. Provision of artificial substrata in this study may have increased numbers of planulae settling to well above the natural levels. This factor may operate in conjunction with explanation 2 above, in that scarcity of good settlement sites may force planulae to settle in unsuitable sites where chances of death are increased.

4. If corals of some species (eg some poritids) recruit successfully in shallow water but are not abundant there as adults (Chapter 6), then there may have been a redistribution of

colonies from shallow to deep water as a result of fragmentation (Highsmith, 1982). Thus asexual reproduction by fragmentation may be an important source of recruitment into deeper waters.

Birkeland *et al.* (1981) found that spat recruitment was unrelated to the size of settlement plates and postulated that (a) recruitment may be more a function of the number of newly created patches suitable for coral settlement than of patch size, and (b) planulae may not recruit to all available space, i.e. space is not limiting for spat settlement, but number of planulae may be. The latter hypothesis is in accord with recent proposals on factors limiting coral reef fish recruitment (Williams, 1980; Doherty, 1981).

It is possible, however, that settlement space that has been experimentally provided eg. by Birkeland *et al.* (1981), may be much greater than that which is available naturally, so that extrapolations about limiting numbers of planulae under natural conditions are difficult to make. The degree to which recruitment is controlled by either limitation of settlement space or number of recruits cannot be determined from this study, but spat recruitment rates on coral blocks indicate that planulae are not abundant at deeper sites, and alternatively that suitable settlement space away from the effects of grazing and algal growth may be limited at shallow sites.

Despite the differences in spat abundance between deep and shallow sites, there was little variation in the familial composition of spat. This implies that the spat available for

settlement at each site were a homogenous mixture of available planulae. There was no apparent preference for different depths and conditions by different families, even though the adults of those families were distributed very differently (Chapter 2).

There was no direct relationship between abundance of spat and established colonies in transect 1 to 5 for acroporids and poritids. In Chapter 6, abundances of recruits at 1cm or more were also shown to be unrelated to abundances of all colonies over the depth gradient for *Acropora*, *Montipora* and *Porites*. Thus there is strong evidence that post-settlement mortality plays a role in determining the distribution patterns of established colonies of these taxa.

Pocilloporid spat were distributed in a way that did not differ significantly from the distribution of established colonies. From Chapter 6, recruits of *Seriatopora* and *Stylophora* were distributed similarly to all colonies, but recruits of *Pocillopora* had a different distribution from all colonies. In this family, at least for the non-*Pocillopora* genera, settlement patterns may be a significant determinant of colony distribution.

Bak and Engel (1979) found little relationship between abundances of juvenile and adult corals in a study to species level in the Caribbean. Their study and this one indicate that differential survival following relatively uniform settlement may be a significant phenomenon in determining coral community structure.

Post-settlement mortality, determined largely by physiological tolerances may account for distribution patterns of corals at family level, on a between reef zone scale. At within habitat scales, there was variability of recruitment frequency at family level that may be attributable to substratum selection or to chance.

Done (1982) discussed the relative effects of pre-settlement dispersal of planulae, and post-settlement differential mortality in determining coral distribution patterns on a "between reef" scale, and concluded that "self-seeding" of reefs may play a role in the determination of species distribution patterns. From the present study, it seems likely that "within-reef zone" scale differences in distribution of coral families can be accounted for by differential mortality according to physiological tolerances from a relatively homogenous planulae pool. Whether a particular planulae pool is characteristic of a reef zone, an individual reef, or an oceanographic region cannot be determined from presently available data. The degree of dispersal of reproductive products within and between reefs, and hence the discreteness of reefs and reef zones has important theoretical and reef management implications, and remains a priority area for reef research.

In summary, it appears that, in this study, coral spat were fairly uniform in taxonomic composition, and were abundant in shallow waters. Coral spat were found predominantly on the underside of substrata, to avoid (or as a result of) grazing

pressure in shallow water and heavy sediment in deeper water. There was some differential settlement dependent on the nature of the settlement surface. Settlement space that affords high survival, free from the effects of grazing organisms and death from sediment smothering may be limiting in natural conditions, particularly in shallow waters. Peak settlement occurred in late summer, following the period of most intensive spawning activity, but some corals settled throughout the year. Families showed different recruitment success relative to their abundance in the established community, with pocilloporids the most successful, followed by acroporids with poritids least successful of the three major spat families. Abundance of adult colonies showed no direct relationship with abundance of spat for acroporids and poritids, but appeared to be related for pocilloporids.

CHAPTER 8

Conclusions

8.1 Summary

This study is the first to examine in detail, many aspects of the population ecology of a range of coral species on the Great Barrier Reef. The results obtained provide answers, or at least clues, to many problems concerning the structure and dynamics of coral communities, and the ecology of their component species. As a result, there is a clearer picture of the complexity of the relationships that occur in such a highly diverse community. The major findings of the study are as follows:

Coral species showed distribution patterns that could be related to a depth gradient in a patch reef habitat. Coral cover was higher in shallow than in deep transects, but there were no differences in number of colonies, coral diversity, and mean colony size between the shallow and deep sites.

Of the five coral species whose reproductive ecology was studied, four released externally fertilized gametes during a brief period in summer, and one species released well developed planulae for an extended period in winter.

Coral mortality rate varied temporally, as well as amongst the five species studied. Mortality rate was generally highest in small individuals and decreased with increasing size class. During an unusual mass bleaching event, coral mortality increased greatly, and such events might be a major determinant of coral distribution patterns in the long term.

In five transects censused over 18 months, the number of coral recruits (at 1cm or more diameter) and colony mortality were not significantly different for shallow and deep sites. The most abundant genera had the highest number of recruits. For genera with high recruitment rates relative to the number of colonies present, mortality rates were also high. Recruitment and mortality rates varied between genera from different families. For the most abundant genera, distribution of recruits was significantly different from distribution of all colonies of those genera. This indicates that differential post-recruitment mortality may determine distribution patterns of these genera.

Coral spat recruited more abundantly on shallow than deep settlement plates, but the taxonomic composition of spat did not vary with site. Highest spat recruitment occurred in summer, following the period when most coral species are known to spawn on the Great Barrier Reef. Acroporids were the most numerous spat, but pocilloporids were most successful relative to the number of colonies at the site. Again, distribution patterns of coral spat of 2 out of 3 major families were not related to distribution patterns of established colonies amongst the 5

transects.

Overall, differential post-settlement mortality, possibly as a result of differing physiological tolerances, seems more likely than selection of suitable settlement substrata to play a major role in determining distribution patterns of major coral taxa.

8.2 Diversity and disturbance

The concept that interruption of succession at different stages will result in systems of different diversity was described by Connell (1978, 1979) as the intermediate disturbance hypothesis. The theory has been modified by several authors. e.g. Dustan (1979), who incorporated concepts of rate of population growth to explain some anomalies in earlier theories; and Miller (1980), who expanded the model to include changes in both magnitude and rate of disturbance.

Here, species diversity, measured by both number of species and Shannon's diversity index, did not vary significantly between shallow and deep sites. The intermediate disturbance hypothesis would predict that levels of disturbance should not differ greatly between these sites. Assuming that disturbance must, by definition, cause death of coral colonies, which in turn begins the successional process, then coral mortality rates can be used as a measure of the amount of disturbance.

As predicted by the model, there were no significant differences in coral mortality rates between sites, despite the observed greater effect of water movement, predominantly wave action, at the shallow site. Other causes of coral mortality in deeper sites resulted in similar levels of mortality overall.

However, non-equilibrium models of diversity maintenance, including the intermediate disturbance model, by definition apply to systems where community composition is changing (Connell, 1978). In this study, despite high colony turnover, the community composition was very similar at the beginning and end of an 18 month period. During this time, the number of recruits was sufficiently high to more than replace all colonies in the transects at the beginning of the period (table 13). There was a high potential for change in the community, through recruitment and mortality, that was not realized.

Connell (1978) predicted that in communities where species composition is in equilibrium, diversity will be low. That was not the case in the community described here. Equilibrium hypotheses of diversity maintenance include the role of niche diversification, circular networks, and compensatory mortality. There was evidence for the action of some of these factors in this study, for example, there was clear separation of some species along a depth gradient (Chapter 2).

In this community, diversity was maintained at a high level in the presence of high mortality (=disturbance), but without a resultant dramatic change in community composition. The factors

that operate to influence diversity are clearly complex.

8.3 Succession

The literature concerning the theories of and evidence for succession is extensive and has been reviewed by Connell and Slatyer (1977) and by McIntosh (1980). The majority of succession models are based on studies of terrestrial plant communities, and few involve marine communities.

Pearson (1981) has noted that the mechanism by which one suite of species replaces another during succession is not clear. Many authors have suggested that monopolization of space by a competitively dominant species is a mechanism that reduces diversity during the latter stages of succession. Recent work, however, has indicated that competitive mechanisms, in general, may be relatively unimportant as determinants of coral community structure (Sheppard, 1981; Bradbury and Young, 1981). Where coral cover is not high, and where coral growth is not restricted to two dimensions (as in a reef flat community), competitive interactions may not greatly restrict coral survival.

A simple model for succession in a coral community in the absence of strong competitive interactions is described here. It is consistent with the "inhibition" model proposed by Connell and Slatyer (1977), i.e. that early colonizers resist the invasion of subsequent colonizers, which can grow only when the dominant residents are damaged or killed, thus releasing resources. The limiting resource in this case is proposed to be suitable

settlement space.

In many coral reef communities, coral cover is well below 100%, for instance in this study it ranged from 16% to 51%. Assumptions of space limitation for adult coral colonies in such communities may be invalid, particularly in communities where growth in three dimensions is possible, e.g. non-reef flat communities. However areas of suitable settlement space, free from the effects of competition with algae, grazing and sediment deposition may be scarce at some sites (Chapter 7), even when coral cover is relatively low. In this study, corals settled preferentially in cryptic locations (Chapter 7) and were never observed to recruit onto either smooth, algal platform or sand, which comprised the majority of substrata at the study site.

Secondary succession begins with the creation of settlement space as the result of a disturbance that results in the death of one or more established coral colonies, i.e. a disturbed patch is created in the mosaic of patches that comprise the community (Osman and Whitlach, 1978). Since a coral colony had previously lived in this position, and since the skeletal remains of the colony provide shelter for newly settled spat (Birkeland and Randall, 1981), the location is likely to be a suitable settlement space.

The high recruitment success of a few opportunistic coral species has frequently been noted (Stephenson and Stephenson, 1933; Grassle, 1973; Loya, 1967 c). Recruitment success appears to be related to the production of well developed

planulae for extended periods each year (Loya, 1976 c;Chapter 7).

Dana (1976) has noted "If a few species have both a large and frequent reproductive output, their larvae may nearly always be available to colonize patches of reef substrate made suitable for settlement by recent disturbances. Subsequent invasion by other species, perhaps competitive dominants through growth form or aggressiveness, may be quite difficult as favourable settling space has been usurped by the opportunistic species."

The majority of coral species spawn for only a brief period each year (Chapter 3), and their propagules are likely to be available for settlement for only one or two months after the summer spawning period.

Because of the greater availability of their propagules, opportunistic species are likely to predominate during early successional stages after a moderate disturbance. However, as Connell and Slatyer (1978, p.1123) note "Since the early succession species are shorter lived, they will be replaced more often than would the longer-lived late succession species. If propagules of these later species are available for invasion, then after several years of transitions the latter species will tend to accumulate, with the result that the early species will gradually decrease in relative abundance."

There is evidence from this study (Chapters 5 and 6) for variations in mortality rates as well as recruitment success amongst coral species, with the opportunistic pocilloporid

species having high mortality. Pearson (1981) has noted that mortality rates of coral colonies during succession decreases over time. This would be a result of both the increasing size of the colonies and of the succession of species from short-lived to long-lived species.

The relative abundances of the non-opportunistic species that eventually dominate the community would be determined by chance settlement and differential survival with respect to the species' physiological tolerances. These factors probably act relatively early in the life of a colony. In the absence of any major disturbance, coral colonies could grow large, and coral cover get high, so that death of a colony might result in growth of an established colony into the space formerly held by the dead colony, before any new recruits can become established. In this way, competition between large colonies and new recruits may be significant. At very high coral cover, competition between established colonies may limit colony growth in the direction of the competitive interaction. Occasional mass mortalities would return the community to a very early successional stage, when the successional process would begin again.

A community is a mosaic of patches of different sizes and ages since disturbance (Osman and Whitlach, 1978). If small disturbances, on the scale of death of single colonies occur frequently, then parts of the community will be in different successional stages, and the community as a whole will be diverse. Thus, high diversity in coral communities can occur -

even in the absence of a large scale physical disturbance and strong competitive exclusion. High diversity is maintained by many factors including partitioning of habitat along a depth gradient (Chapter 2), higher mortality of the most abundant recruiters during the successional process, and because of chance recruitment events in a potentially limited settlement space. The roles of these and other processes in diversity maintenance will depend largely on the spatial and temporal scale of any study undertaken to detect and measure the processes.

APPENDIX 1: Colony abundance and cover (in parenthesis) for coral species in transects 1 to 5 in April 1982.

	1	2	3	4	5
Pocillopora damicornis	9(3.00)	6(0.39)	5(0.03)	4(0.04)	3(0.47)
Stylophora pistillata	1(0.21)	3(0.34)	9(0.64)	6(0.03)	2(0.21)
Seriatopora hystrix	7(0.18)	9(0.21)	5(0.16)	1(0.04)	2(0.04)
Stylocoeniella guentheri	0	0	0	1(0.01)	2(0.02)
Acropora acuminata	0	1(0.02)	0	0	0
A. breuggemanni	7(0.31)	10(1.20)	6(1.76)	3(0.06)	1(0.01)
A. cerealis	0	1(0.02)	0	0	0
A. cuneata	0	1(0.02)	0	0	0
A. cytherea	1(6.44)	1(0.02)	0	0	0
A. delicatula	1(0.05)	0	0	0	2(0.11)
A. divaricata	1(0.30)	5(2.29)	0	0	0
A. florida	0	4(1.95)	0	0	0
A. formosa	0	1(0.02)	0	0	0
A. humilis	0	2(0.68)	0	0	0
A. hyacinthus	0	0	1(0.02)	0	0
A. intermedia	0	0	1(0.02)	0	0
A. longicyathus	0	0	0	1(0.02)	0
A. nasuta	0	1(0.30)	1(0.04)	0	1(0.03)
A. palifera	5(2.90)	4(0.43)	0	1(0.02)	0
A. sarmentosa	1(0.42)	0	2(0.05)	0	1(0.03)
A. tenuis	0	1(0.25)	2(0.90)	0	1(0.02)
A. microphthalma	0	0	1(0.01)	0	0
Montipora verrucosa	2(0.02)	7(0.26)	4(0.09)	2(0.03)	3(0.10)
M. hispida	0	2(12.30)	0	0	0
M. danae	1(0.29)	0	1(0.09)	2(0.10)	3(0.09)
M. tuberculosa	16(0.77)	15(0.72)	6(0.14)	0	0
M. monasteriata	0	15(0.06)	0	1(0.02)	0
M. hoffmeisteri	0	0	1(0.04)	0	0
M. c.f. floweri	0	1(0.02)	0	0	0
M. aequituberculata	1(0.06)	3(0.04)	2(0.06)	2(0.02)	0
M. venosa	0	1(0.06)	0	5(0.15)	3(0.09)
M. granulata	0	0	0	2(0.03)	1(0.01)
M. millipora	1(0.02)	2(0.04)	1(0.02)	3(0.04)	5(0.04)
M. incrassata	2(0.06)	2(0.92)	0	0	1(0.02)
M. subtilis	0	2(0.24)	0	0	0
Astreopora myriophthalma	3(0.07)	5(0.02)	0	6(0.17)	5(0.10)
A. listeri	0	1(0.02)	1(0.02)	2(0.07)	1(0.01)
A. randalli	0	0	0	0	3(0.04)
Psammocora haimeama	0	0	1(0.01)	0	0
P. profundicella	1(0.07)	0	1(0.03)	0	0
Porites annae/lichen	35(1.16)	32(0.85)	104(1.88)	58(0.75)	35(0.94)
P. australiensis	11(2.99)	16(10.38)	24(10.21)	9(2.08)	8(0.81)
P. cylindrica	0	0	1(0.02)	5(0.19)	7(3.69)
P. lobata	3(0.03)	11(1.30)	17(12.13)	29(4.42)	54(12.14)
P. lutea	18(9.58)	18(8.49)	29(13.33)	29(4.31)	29(5.71)
P. mayeri	4(0.23)	1(0.05)	2(0.04)	1(0.27)	0
P. murrayensis	0	0	0	1(0.02)	0
P. nigrescens	2(0.07)	0	0	0	0
P. rus	3(0.66)	1(0.05)	5(0.54)	0	0
P. solida	2(0.23)	1(0.07)	3(3.47)	0	4(0.20)
P. stephensoni	0	0	2(1.09)	0	0
P. vaughani	2(0.02)	14(0.28)	49(0.70)	52(0.88)	86(1.89)

Goniopora lobata	0	0	0	1(0.02)	1(0.01)
G. minor	0	2(0.04)	4(0.13)	0	0
G. norfolkensis	0	0	1(0.03)	0	0
G. tenuidens	0	1(0.04)	0	3(0.07)	0
Pavona varians	4(0.07)	2(0.02)	2(0.01)	1(0.02)	1(0.01)
Leptoseris sp.	0	0	0	1(0.02)	1(0.03)
Coscinarea columna	0	1(0.02)	0	1(0.02)	1(0.02)
Heliofungia actiniformis	0	0	0	0	1(0.02)
Fungia fungites	1(0.04)	1(0.02)	1(0.01)	0	0
F. horrida	0	0	2(0.01)	0	0
F. concinna	0	1(0.02)	1(0.01)	1(0.02)	0
F. granulosa	0	0	1(0.03)	0	0
Herpetoglossa simplex	0	0	1(0.17)	0	0
Litophyton edwardsi	0	2(0.02)	0	0	1(0.01)
Galaxea astreata	12(0.51)	10(0.57)	7(0.24)	4(0.17)	4(0.18)
Galaxea fascicularis	12(1.04)	0	6(0.43)	1(0.06)	1(0.10)
Echinophyllia orpheensis	0	0	0	1(0.04)	2(0.05)
E. echinata	0	0	0	3(0.01)	0
Mycedium elephantotus	0	0	4(0.12)	3(0.02)	2(0.04)
Pectinia paeonia	0	1(0.02)	0	0	0
Scolymia vitiensis	0	0	1(0.01)	1(0.02)	0
Acanthastrea echinata	0	1(0.03)	0	0	0
Lobophyllia hemprichii	0	0	1(0.10)	1(0.02)	0
L. corymbosa	0	1(0.13)	0	1(0.06)	2(0.04)
L. pachysepta	0	2(0.03)	1(0.01)	2(0.07)	0
Symphyllia recta	3(0.23)	1(0.02)	0	0	0
Favia stelligera	1(0.04)	0	0	0	0
F. favus	2(0.18)	2(0.09)	5(0.09)	10(0.18)	17(0.25)
F. pallida	2(0.14)	2(0.10)	0	1(0.02)	1(0.09)
F. matthai	1(0.03)	2(0.05)	1(0.02)	2(0.01)	0
F. maxima	0	1(0.04)	0	1(0.02)	1(0.02)
F. lizardensis	5(0.40)	1(0.03)	2(0.07)	0	1(0.02)
Barabattoia amicorum	0	0	1(0.04)	0	1(0.02)
Favites abdita	2(0.04)	2(0.12)	0	1(0.02)	0
F. halicora	5(0.08)	6(0.07)	4(0.05)	3(0.02)	4(0.04)
F. flexuosa	0	0	0	1(0.04)	2(0.05)
F. pentagona	0	0	0	1(0.02)	0
Goniastrea retiformis	2(0.03)	2(0.21)	0	0	0
G. edwardsi	5(0.16)	13(0.16)	7(0.07)	7(0.09)	9(0.18)
G. pectinata	6(0.27)	8(0.44)	2(0.04)	7(0.09)	4(0.04)
Platygyra daedalea	3(0.23)	1(0.13)	0	0	1(0.02)
P. lamellina	0	1(0.02)	0	0	0
P. sinensis	1(0.02)	0	0	0	0
P. pini	1(0.18)	3(0.07)	1(0.04)	3(0.48)	1(0.02)
Leptoria phrygia	0	2(0.17)	1(0.05)	0	0
Hydnophora excesa	0	1(0.02)	0	0	0
H. rigida	0	0	1(0.02)	0	0
Montastrea curta	0	2(0.02)	0	0	0
M. magnistellata	1(0.05)	0	0	1(0.01)	0
M. valenciennesi	1(0.02)	1(0.05)	2(0.02)	2(0.02)	1(0.04)
Diploastrea heliopora	0	0	0	0	0
Leptastrea purpurea	3(0.12)	6(0.05)	2(0.04)	6(0.15)	10(0.15)
Leptastrea pruinosa	1(0.07)	1(0.04)	1(0.02)	0	1(0.01)
Cyphastrea serailia/	2(0.06)	0	3(0.30)	6(0.07)	3(0.07)
C. microphthalma	1(0.02)	2(0.02)	2(0.02)	4(0.03)	12(0.18)

C. japonica	1(0.02)	0	0	1(0.02)	0
Echinopora lamellosa	2(0.02)	0	3(0.05)	5(0.16)	0
E. horrida	6(4.57)	1(0.02)	2(0.03)	3(0.15)	0
E. mammiformis	0	0	1(0.02)	0	0
Merulina ampliata	2(0.02)	0	2(0.10)	3(0.03)	4(0.03)
Euphyllia glabrescens	0	0	0	0	1(0.01)
E. ancora	0	1(0.02)	1(0.38)	0	0
Turbinaria frondens	0	0	0	0	3(0.19)
T. stellulata	0	0	0	0	1(0.06)
T. reniformis	1(0.05)	1(0.02)	1(0.07)	2(0.02)	4(0.12)
Coeloseris mayeri	2(0.04)	1(0.02)	0	1(0.02)	0

APPENDIX 2: Number of recruits (+) and dead colonies (-) in transects censused from August 1980 to February 1982.

(a) All transects pooled

(b) Transect 1

(c) Transect 2

(d) Transect 3

(e) Transect 4

(f) Transect 5

(a) All transects pooled

	Aug.80		Oct.80		Dec.80		Jan.81		Apr.81		Jun.81		Aug.81		Oct.81		Dec.81		Feb.82			
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
Pocillopora	1	6	3	6	6	3	4	10	11	7	6	8	11	7	6	7	5	7	2	9	54	64
Stylophora	4	1	6	4	1	5	5	3	2	7	7	2	5	1	2	2	7	1	1	5	34	30
Seriatopora	11	7	2	4	3	6	7	6	3	5	4	5	4	1	4	4	7	6	2	3	36	40
Acropora	22	12	17	17	12	13	17	28	19	21	28	20	20	27	21	12	13	20	20	18	167	176
Montipora	35	6	10	12	5	4	8	4	12	7	17	11	26	6	12	14	4	10	8	9	102	77
Astreopora	26	0	6	8	5	3	1	9	3	4	3	4	4	3	1	3	5	1	2	3	30	38
Porites	107	66	63	22	46	25	31	23	19	23	50	17	46	18	31	32	20	10	13	23	319	193
Goniopora	4	0	6	0	1	2	3	0	0	1	0	1	0	1	0	0	1	0	0	2	11	7
Pavona	3	1	0	1	0	0	2	0	1	1	2	1	2	1	1	1	1	1	0	2	9	8
Fungia	11	7	8	6	6	3	5	6	5	5	5	7	4	3	5	5	7	7	2	4	47	46
Galaxea	5	1	1	1	5	0	3	1	1	1	1	0	4	0	2	0	2	3	3	1	22	7
Mycedium	0	1	1	1	1	0	0	1	3	0	0	1	4	0	2	1	1	2	2	2	14	8
Pectinia	2	0	1	0	0	2	0	2	1	0	1	0	0	0	0	0	0	0	0	0	3	4
Lobophyllia	5	5	3	2	1	1	3	3	1	4	2	1	7	1	3	6	2	0	3	3	25	21
Symphyllia	1	0	0	0	0	0	0	2	1	1	1	1	0	1	0	0	0	1	0	2	2	8
Favia	17	10	23	11	16	5	20	15	16	10	13	9	20	13	14	11	14	10	12	12	148	96
Goniastrea	20	20	11	12	13	5	10	9	9	12	26	7	18	7	8	7	9	10	13	12	117	81
Hydnophora	0	0	1	0	1	0	1	1	0	1	0	0	2	0	1	0	0	0	0	0	6	2
Diploastrea	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Cyphastrea	6	5	13	4	0	6	6	3	2	1	7	1	3	2	6	2	3	4	2	4	42	27
Echinopora	12	1	1	2	0	2	0	4	2	3	2	2	2	0	0	3	1	2	5	0	13	18
Merulina	5	0	1	1	1	2	0	2	1	1	1	2	1	1	2	0	1	1	1	1	9	11
Euphyllia	0	1	0	0	0	0	2	0	0	1	0	0	2	0	0	0	3	0	0	1	7	2
Turbinaria	3	2	2	2	4	1	2	1	1	3	2	0	4	0	4	1	6	4	4	4	29	16
Unknown	6	11	7	2	4	4	8	4	1	4	3	1	3	2	4	1	5	2	6	2	41	22
Total	308	165	186	118	131	93	138	137	114	123	180	101	192	95	129	112	116	102	101	123	1287	1004

(b) Transect 1

	Aug.80		Oct.80		Dec.80		Jan.81		Apr.81		Jun.81		Aug.81		Oct.81		Dec.81		Feb.82			
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Pocillopora	0	3	1	2	0	1	0	2	2	4	1	2	0	3	0	1	0	0	1	1	5	16
Stylophora	0	0	1	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	3	3
Seriatopora	6	2	0	2	0	2	2	1	0	2	0	3	0	1	1	0	3	1	1	0	7	12
Acropora	5	4	2	9	4	6	9	6	5	11	3	7	6	9	8	3	5	5	5	6	47	62
Montipora	9	0	2	4	2	0	0	1	1	0	4	3	5	4	4	4	0	1	3	1	21	18
Astreopora	3	0	1	1	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	3	4
Porites	18	2	7	2	9	5	7	7	1	3	13	2	9	5	5	8	2	1	3	4	56	37
Goniopora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pavona	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	2	1
Fungia	0	0	1	0	1	0	1	2	0	2	0	0	0	0	0	0	4	0	0	0	7	4
Galaxea	3	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	1	5	2
Mycedium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobophyllia	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	3	2
Symphyllia	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	2	1	6
Favia	2	1	2	2	1	0	1	0	3	1	0	3	2	1	2	0	1	2	1	0	13	9
Goniastrea	3	2	2	1	0	3	0	1	3	2	6	1	5	3	1	0	2	1	1	1	20	13
Hydnophora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diploastrea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyphastrea	0	1	2	1	0	0	2	0	0	0	0	0	0	1	0	1	0	2	0	0	4	5
Echinopora	5	0	1	0	0	1	0	3	1	2	1	2	0	0	0	1	1	1	1	0	5	10
Merulina	1	0	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	4
Euphyllia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Turbinaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	1
Unknown	1	0	1	0	2	2	0	0	0	1	1	0	0	0	0	0	1	0	0	0	5	3
Total	58	16	24	24	21	24	24	27	19	32	32	24	30	30	24	19	19	16	18	16	211	212

(c) Transect 2

	Aug.80		Oct.80		Dec.80		Jan.81		Apr.81		Jun.81		Aug.81		Oct.81		Dec.81		Feb.82			
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Pocillopora	1	1	2	1	2	2	1	4	3	3	2	3	2	0	2	1	1	1	0	3	15	18
Stylophora	0	0	2	2	0	0	3	2	2	3	4	2	1	0	1	1	1	0	0	2	14	12
Seriatopora	2	0	0	1	1	0	3	1	1	3	1	1	2	0	2	2	2	2	1	2	13	12
Acropora	13	1	5	4	4	5	3	14	4	6	8	8	5	10	8	3	5	8	7	4	49	62
Montipora	11	3	6	3	2	3	2	1	2	1	5	5	9	1	5	3	3	4	1	4	35	25
Astreopora	2	0	3	1	1	0	0	1	0	1	0	0	2	1	0	1	0	0	1	2	7	7
Porites	8	18	14	5	4	8	4	2	3	2	4	2	6	3	4	2	2	0	1	2	42	26
Goniopora	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Pavona	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
Fungia	1	1	1	2	0	1	1	0	0	1	1	0	2	0	0	1	1	1	0	2	6	8
Galaxea	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	5	0
Mycedium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lobophyllia	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	2	0	0	2	4	4
Symphyllia	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Favia	2	2	2	1	1	3	3	3	2	0	4	1	2	4	1	1	3	1	2	2	20	16
Goniastrea	1	4	7	3	2	0	2	1	1	1	4	1	1	0	2	1	1	1	3	1	23	9
Hydnophora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Diploastrea	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Cyphastrea	1	1	2	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	3	3
Echinopora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Merulina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphyllia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1
Turbinaria	0	0	0	0	2	0	0	0	0	1	0	0	2	0	1	0	0	0	1	1	6	2
Unknown	1	2	0	1	0	0	1	0	0	1	1	0	0	1	2	0	0	0	1	0	5	3
Total	46	35	45	24	21	25	23	32	19	23	36	23	37	20	28	17	22	20	20	31	251	215

(d) Transect 3

	Aug.80		Oct.80		Dec.80		Jan.81		Apr.81		Jun.81		Aug.81		Oct.81		Dec.81		Feb.82			
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Pocillopora	1	2	0	1	3	0	3	4	2	0	2	0	7	3	3	3	2	5	1	5	23	21
Stylophora	3	1	2	1	1	2	0	1	0	3	1	0	2	0	1	1	2	1	1	1	10	10
Seriatopora	2	4	2	1	0	2	2	2	1	0	2	1	1	0	0	1	2	1	0	1	10	9
Acropora	1	6	5	1	4	2	4	4	6	4	9	5	4	3	1	3	1	5	4	3	38	30
Montipora	9	0	2	1	1	1	0	2	5	2	2	1	5	1	1	4	0	1	2	2	18	15
Astreopora	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0
Porites	22	13	25	0	13	4	5	3	8	7	14	4	14	2	8	6	1	3	4	5	92	34
Goniopora	1	0	2	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	4	2
Pavona	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1
Fungia	7	0	4	1	3	1	1	3	2	1	4	5	1	2	3	2	1	2	0	1	19	18
Galaxea	1	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	5	1
Mycedium	0	0	1	0	0	0	0	0	1	0	0	1	2	0	0	1	0	1	0	0	4	3
Pectinia	1	0	0	0	0	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	2
Lobophyllia	0	1	2	1	0	0	1	1	0	1	1	0	3	1	0	3	0	0	1	0	8	7
Symphyllia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Favia	4	2	6	2	2	1	2	4	1	0	4	0	3	1	2	2	2	2	2	3	24	15
Goniastrea	3	3	1	1	4	1	2	4	1	4	7	0	2	1	0	1	2	0	0	4	19	16
Hydnophora	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	2	1
Diploastrea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyphastrea	1	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	2	3	3
Echinopora	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	4	2
Merulina	0	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	3	2
Euphyllia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Turbinaria	3	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	2	0	0	1	4	4
Unknown	0	0	3	0	2	0	2	1	0	0	1	0	1	0	1	1	1	1	1	0	12	3
Total	61	33	56	11	38	17	23	31	30	26	51	20	48	14	27	28	18	24	17	28	308	199

(e) Transect 4

	Aug.80		Oct.80		Dec.80		Jan.81		Apr.81		Jun.81		Aug.81		Oct.81		Dec.81		Feb.82			
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Pocillopora	0	0	0	1	1	0	0	0	4	0	1	3	2	0	0	2	1	0	0	0	9	6
Stylophora	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	3
Seriatopora	1	0	0	0	1	2	0	2	0	0	0	0	1	0	0	1	0	0	0	0	2	5
Acropora	0	0	2	2	0	0	1	1	2	0	1	0	1	3	1	2	0	1	1	0	9	9
Montipora	6	0	0	4	0	0	6	0	0	4	0	1	2	0	1	1	1	2	2	1	12	13
Astreopora	11	0	1	5	2	1	1	4	0	1	2	0	0	2	1	1	1	1	1	0	9	15
Porites	26	9	9	6	9	6	5	5	4	8	3	0	11	4	5	10	9	2	4	7	59	48
Goniopora	1	0	4	0	0	1	2	0	0	0	0	0	0	1	0	0	1	0	0	1	7	3
Pavona	1	0	0	1	0	0	2	0	0	1	0	0	1	0	0	1	0	0	0	0	3	3
Fungia	2	1	2	2	1	1	1	1	3	1	0	1	0	1	1	2	0	3	1	1	9	13
Galaxea	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	3	2
Mycedium	0	0	0	1	1	0	0	1	2	0	0	0	1	0	0	0	1	0	1	1	6	3
Pectinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobophyllia	4	3	1	0	0	1	1	1	0	2	0	0	1	0	1	1	0	0	2	0	6	5
Symphyllia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Favia	7	1	6	3	4	1	9	6	7	7	1	4	6	4	5	7	2	4	4	1	44	37
Goniastrea	7	4	1	3	2	0	4	1	1	3	3	3	7	2	3	2	2	5	2	1	25	20
Hydnophora	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Diploastrea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyphastrea	3	2	4	2	0	4	1	1	0	0	3	0	2	1	1	1	1	0	1	1	13	10
Echinopora	5	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	3	0	4	4
Merulina	2	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	2	4
Euphyllia	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	2	1
Turbinaria	0	1	1	1	0	0	2	0	1	1	2	0	1	0	1	0	1	2	2	1	11	5
Unknown	3	6	2	1	0	1	3	2	0	1	0	1	2	0	1	0	1	1	4	0	13	7
Total	81	27	35	36	21	20	41	27	24	31	16	14	41	19	22	32	23	21	29	17	252	217

(f) Transect 5

	Aug.80		Oct.80		Dec.80		Jan.81		Apr.81		Jun.81		Aug.81		Oct.81		Dec.81		Feb.82			
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Pocillopora	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	2	3
Stylophora	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	3	0	0	1	5	2
Seriatopora	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	2	0	0	4	2
Acropora	3	1	3	1	0	0	0	3	2	0	7	0	4	2	3	1	2	1	3	5	24	13
Montipora	0	3	0	0	0	0	0	0	4	0	6	1	5	0	1	2	0	2	0	1	16	6
Astreopora	8	0	1	1	2	1	0	2	1	2	1	4	2	0	0	1	2	0	0	1	9	12
Porites	33	24	8	9	11	2	10	6	3	3	16	9	6	4	9	6	6	4	1	5	70	48
Goniopora	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pavona	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	2	2
Fungia	1	5	0	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	1	0	6	3
Galaxea	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	2	0	0	4	2
Mycedium	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	1	1	1	4	2
Pectinia	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Lobophyllia	1	0	0	1	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	1	4	3
Symphyllia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Favia	2	4	7	3	8	0	5	2	3	2	4	1	7	3	4	1	6	1	3	6	47	19
Goniastrea	6	7	0	4	5	1	2	2	3	2	6	2	3	1	2	3	2	3	7	5	30	23
Hydnophora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Diploastrea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyphastrea	1	1	5	1	0	1	3	1	1	1	4	0	1	0	2	0	2	1	1	1	19	6
Echinopora	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Merulina	2	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	3	1
Euphyllia	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
Turbinaria	0	1	1	0	1	0	0	1	0	0	0	0	1	0	0	1	3	1	0	1	6	4
Unknown	1	3	1	0	0	1	2	1	1	1	0	0	0	1	0	0	2	0	0	2	6	6
Total	62	54	26	23	30	7	27	20	22	11	45	20	36	12	28	16	34	21	17	31	265	161

APPENDIX 3: Number of coral spat that have settled on coral blocks (left column) and Petrie dishes (right column) in each sample period. The number of coral blocks in each period is 4, and the number of Petrie dishes is shown at the top of the column.

	April 81		June 81		Aug 81		Oct 81		Dec 81		Feb 82		Apr 82	
Transect 1	n = 1		n = 0		n = 1		n = 2		n = 2		n = 2		n = 0	
Pocilloporidae	1	0	1		8	1	3	0	0	2	1	2	2	
Poritidae	8	0	1		1	0	0	0	3	0	2	1	15	
Acroporidae	12	0	1		3	0	1	0	4	3	7	2	1	
Others	1	0	0		1	0	0	0	4	0	0	0	0	
Transect 2	n = 1		n = 0		n = 4		n = 1		n = 3		n = 4		n = 1	
Pocilloporidae	0	5	0		3	2	2	0	3	0	2	0	0	0
Poritidae	1	0	0		0	0	0	0	0	0	0	0	7	0
Acroporidae	3	3	1		7	0	3	0	17	6	17	3	5	0
Others	0	1	0		1	1	0	0	2	0	0	2	2	0
Transect 3	n = 4		n = 4		n = 4		n = 4		n = 4		n = 4		n = 3	
Pocilloporidae	2	4	3	2	0	0	0	0	0	0	0	1	3	0
Poritidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Acroporidae	0	0	0	0	0	0	0	0	0	5	0	3	0	0
Others	1	0	0	0	0	0	0	0	0	0	1	3	0	0
Transect 4	n = 4		n = 2		n = 4		n = 4		n = 4		n = 4		n = 4	
Pocilloporidae	1	0	0	0	0	0	0	0	0	0	1	8	1	0
Poritidae	0	0	0	0	0	0	0	0	0	0	0	0	4	0
Acroporidae	2	0	0	0	0	0	1	0	0	2	0	0	0	0
Others	0	0	0	2	0	0	0	0	0	0	1	0	1	1
Transect 5	n = 4		n = 4		n = 4		n = 4		n = 4		n = 4		n = 4	
Pocilloporidae	0	0	0	1	0	0	0	0	0	0	2	0	0	0
Poritidae	0	0	0	1	0	0	0	1	1	1	0	3	0	0
Acroporidae	0	1	0	0	0	0	0	1	2	8	8	5	0	1
Others	0	0	0	0	0	0	0	0	0	0	1	1	0	0

REFERENCES

Atoda, K. (1947 a). The larva and postlarval development of some reef building corals II. *Stylophora pistillata* (Esper). Sci. Rep. Tohoku Univ. (4 th Ser) 18: 48-64.

Atoda, K. (1947 b). The larvae and postlarval development of some reef-building corals I. *Pocillopora damicornis caespitosa* (Dana). Sci. Rep. Tohoku Univ. (4th ser.), 18: 24-47.

Atoda, K. (1951). The larvae and postlarval development of some reef-building corals V. *Seriatopora hystrix* (Dana). Sci. Rep. Tohoku Univ. (4th ser.) 19: 33-39.

Babcock, R.C. (1980). The biology of *Goniastrea aspera* in the Townsville region. Honours thesis, James Cook University, 84pp.

Babcock, R.C. (in press). Reproduction and dispersal of two species of reef flat corals, *Goniastrea aspera* Verill and *G. faculus* Dana. Coral Reefs.

Bak, R.P.M. (1975). Ecological aspects of the distribution of reef corals in the Netherlands Antilles. Bijdr. Dierk. 45: 181-190.

Bak, R.P.M. and M.S. Engel (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol. 54(4): 341-352.

Bak, R.P.M. and B.E. Luckhurst (1980). Constancy and change in coral reef habitats along depth gradients at Curacao. Oecologia 47(2): 145-155.

Bak, R.P.M., R.M. Termaat and R. Decker (1982). Complexity of

coral interactions: influence of time, location of interaction and epifauna. Mar. Biol. 69: 215-222.

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc. 3rd Int. Coral Reef Symposium, Miami, V.1: 15-21.

Birkeland, C. and R.H. Randall (1981). Facilitation of coral recruitment by echinoid excavations. Proc. 4th Int. Coral Reef Symp., Manila, Philippines, 1981. V.1: 695-698.

Birkeland, C., D. Rowley and R.H. Randall (1981). Coral recruitment patterns at Guam. Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V.2: 340-344.

Bohnsack, J.A. (1983). Species turnover and the order versus chaos controversy concerning reef fish community structure. Coral Reefs 1: 223-228.

Bothwell, A.M. (1981). Fragmentation, a means of asexual reproduction and dispersal in the coral genus *Acropora*(Scleractinia: Astrocoeniidae: Acroporidae) -a preliminary report. Proc. 4th Int. Coral Reef Symp., Manila, Philippines V. 2: 137-144.

Bradbury, R.H. and Y. Loya (1978). A heuristic analysis of hermatypic corals at Eilat, Red Sea. Am. Nat. 112: 493-507.

Bradbury, R.H. and P.C. Young (1981 a). The effects of a major forcing function, wave energy, on a coral reef ecosystem. Mar. Ecol. Prog. Ser. 5: 229-241.

Bradbury, R.H. and P.C. Young (1981 b). The race and the swift revisited, or is aggression between corals important? Proc.

4th. Int. Coral Reef Symp., Manila, Philippines, V.2: 351-356.

Brock, R.E. (1979). An experimental study of the effects of grazing by parrotfishes and role of refuges in benthic community structure. Mar. Biol. 51: 381-388.

Buddemeier, R.W. and R.A. Kinzie III (1976). Coral growth. Oceanogr. Mar. Biol. Ann. Rev. 14: 183-225.

Bull, G.D. (1982). Scleractinian coral communities of two inshore high island fringing reefs at Magnetic Island, North Queensland. Mar. Ecol. Prog. Ser. 7: 267-272.

Coles, S.L. and P.L. Jokiel (1978). Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa* (Lamarck). Mar. Biol. 49: 187-195.

Coles, S.L., P.L.Jokiel and C.R. Lewis (1976). Thermal tolerance in tropical versus subtropical Pacific reef corals. Pac. Sci. 30: 159-166.

Connell, J.H. (1973). Population ecology of reef-building corals. p. 205-245 In O.A. Jones and R. Endean (Eds.) Biology and Geology of Coral Reefs. V 2, Academic Press, New York. 480 pp.

Connell, J.H. (1978). Diversity in tropcal rain forests and coral reefs. Science 199: 1302-1310.

Connell, J.H. (1979). Tropical rain forests and coral reefs as open, non- equilibrium systems. p. 141-163 In R.M. Anderson, L.R. Taylor and B. Turner. (Eds.) Population dynamics. Proc. Symp.. Brit. Ecol. Soc., Blackwell Scientific Publishers, Oxford.

Connell, J.H. and R.Slatyer (1977). Mechanisms of succession in natural communities and their role in community stability and organization. Am.Nat. 111: 1119-1144.

Cope, M. (1981). Interspecific coral interactions in Hong Kong. Proc. 4th. Int. Coral Reef Symp., Manila, Philippines, V.2: 356-362.

Dana, T.F. (1976). Reef coral dispersion patterns and environmental variables on a Caribbean coral reef. Bull. Mar. Sci. 26: 1-13.

Dart, J.K.G. (1972). Echinoids, algal lawn, and coral colonization. Nature (London) 239: 49-50.

Deevey, E.S. (1947). Life tables for natural populations of animals. Quart. Rev. Biol. 22: 283-314.

Denslow, J.S. (1980). Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46: 18-21.

Dinesen, Z.D. (1982). Regional variation in shade-dwelling coral assemblages of the Great Barrier Reef Province. Mar. Ecol. Prog. Ser. 7: 117-123.

Dodge, R.E., A. Logan and A. Antonius (1982). Quantitative reef assessment studies in Bermuda: a comparison of methods and preliminary results. Bull. Mar. Sci. 32(3): 745-760.

Doherty, P.J. (1981). Coral reef fishes: recruitment limited assemblages? Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V.2: 465-470.

Doherty, P.J. (1983). Recruitment surveys of coral reef fishes as tools for science and management. In: Baker, J.T., R.M.

Carter, P.W. Sammarco and K.P. Stark (Eds.) Proc. Inaugural G.B.R. Conference, Townsville, 1983: 191-196.

Dollar, S.J. (1982). Wave stress and coral community structure in Hawaii. Coral Reefs 1: 71-81.

Done, T.J. (1981). Photogrammetry in coral ecology: a technique for the study of change in coral communities. Proc. 4th. Int. Coral Reef Symp., Manila, Philippines, V. 2: 315-320.

Done, T.J. (1982). Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1: 95-107.

Egana, A.C. and L.H. DiSalvo (1982). Mass expulsion of zooxanthellae by Easter Island corals. Pac. Sci. 36: 61-63.

Emlen, J.M. (1972). Ecology: An Evolutionary Approach. Addison-Wesley Pub., Massachusetts. 493pp.

Fadlallah, Y.H. (1983). Population dynamics and life history of a solitary coral, *Balanophyllia elegans*, from central California. Oecologia 58: 200-207.

Fishelson, L. (1973). Ecological and biological phenomena influencing coral- species composition on the reef tables at Eilat (Gulf of Aqaba, Red Sea). Mar. Biol. 19: 183-196.

Fisk, D.A. (1981). Studies of two free-living corals and their common sipunculan associate at Wistari Reef (Great Barrier Reef). M.Sc. thesis, University of Queensland.

Franzisket, L. (1970). The atrophy of hermatypic reef corals maintained in the darkness and their subsequent regeneration in light. Int. Rev. Gesamten Hydrobiol. 55: 1-12.

Giese, A.C. and J.S. Pearse (1974). Reproduction of marine

invertebrates. V 2. Academic Press, New York. 546 pp.

Glynn, P.W. (1976). Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol. Monogr. 46(4): 431-456.

Glynn, P.W., R.H. Stewart and J.E. McCosker (1972). Pacific coral reefs in Panama: structure, distribution and predators. Geol. Rundsch. 61: 483-519.

Goodman, D. (1975). The theory of diversity-stability relationships in ecology. Quart. Rev. Biol. 50 (3): 237-266.

Goodwin, M.H., M.J.C. Cole, W.E. Stewart and B.L. Zimmerman (1976). Species density and associations in Caribbean reef corals. J.Exp. Mar. Biol. Ecol. 24: 19-31.

Goreau, T.F. (1964). Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science 145: 383-386.

Goreau, N.I., T.J. Goreau and R.L. Hayes (1981). Settling, survivorship and spatial aggregation in planulae and juveniles of the coral *Porites porites* (Pallas). Bull. Mar. Sci. 31(2): 424-435.

Grassle, J.F. (1973). Variety in coral reef communities. In O.A. Jones and R. Endean (eds.) Biology and geology of coral reefs. V.2 : 247-270. Academic Press, New York.

Grigg, R.W. (1983). Community structure, succession and development of coral reefs in Hawaii. Mar. Ecol. Prog. Ser. 11: 1-14.

Grigg, R.W. and J.E. Maragos (1974). Recolonization of

hermatypic corals on submerged lava flows in Hawaii. Ecology 55: 387-395.

Grime, J.P. (1979). Plant strategies and vegetation processes. John Wiley and Sons, Chichester. pp222.

Harrigan, J.F. (1972). The planula larva of *Pocillopora damicornis* : Lunar periodicity of swarming and substratum selection behavior. Ph.D. thesis, University of Hawaii.

Harriott, V.J. (1980). The ecology of holothurian fauna of Heron Reef and Moreton Bay. Master of Science thesis, University of Queensland.

Harrison, P.L., R.C. Babcock, G.D. Bull, J.K. Oliver, C.C. Wallace and B.L. Willis (in press) Mass spawning in tropical reef corals. Science.

Highsmith, R.C. (1980). Passive colonization and asexual colony multiplication in the massive coral *Porites lutea* Milne Edwards and Haime. J. exp. mar. Biol. Ecol. 47: 55-67.

Highsmith, R.C.(1982). Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7: 207-226.

Hubbard, J.A.E.B. (1974). Scleractinian coral behaviour in calibrated current experiment: an index of their distribution patterns. Proc. 2nd. Int. Coral Reef Symp., V. 2: 107-126.

Hughes, T.P. and J.B.C. Jackson (1980). Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. Science 209: 713-715.

Huston, M. (1979). A general hypothesis of species diversity. Am. Nat. 113: 81-101.

Hyman, L.H. (1940). The Invertebrates. I. Protozoa through Ctenophora. McGraw-Hill, New York. 726 pp.

Jell, J.S. (1980). Skeletogenesis of newly settled planulae of the hermatypic coral *Porites lutea*. Acta. Palaeont. Polon. 25: 312-320.

Jokiel, P.L. and S.L. Coles (1974). Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. Pac. Sci. 28: 1-18.

Jokiel, P.L. and S.L. Coles (1977). Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar. Biol. 43: 201-208.

Jokiel, P.L. and R.H. York Jnr. (1982). Solar ultroviolet photobiology of the reef coral *Pocillopora damicornis* and symbiotic zooxanthellae. Bull. Mar. Sci. 32: 301-315.

Karlson, R.H. (1980). Alternative competitive strategies in a periodically disturbed habitat. Bull. Mar. Sci. 30(4): 894-900.

Keough, M.J. and B.J. Downes (1982). Recruitment of marine invertebrates: the role of active lerval choices and early mortality. Oecologia 54: 348-352.

Kojis, B.L. and N.J. Quinn (1981 a). Aspects of sexual reproduction and larval development in the shallow water hermatypic coral, *Goniastrea australensis* (Edwards and Haime, 1857). Bull. Mar. Sci. 31: 558-573.

Kojis, B.L. and Quinn, N.J. (1981 b). Reproductive strategies in four species of *Porites* (Scleractinia). Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V. 2: 145-151.

Kojis, B.L. and N.J. Quinn (1982). Reproductive ecology of two faviid corals (Coelenterata: Scleractinia). Mar. Ecol. Prog. Ser. 8: 251-255.

Lang, J.C. (1970). Interspecific aggression by scleractinian corals. I The rediscovery of *Scolymia cubensis*. Bull. Mar. Sci. 21: 952-959.

Lang, J. (1973). Interspecific aggression by scleractinian corals II. Why the race is not only to the swift. Bull. Mar. Sci. 23: 260-279.

Law, R. (1979). Ecological determinants in the evolution of life histories. p. 81-103 In R.M. Anderson, B.D. Turner and L.R. Taylor (Eds.) Population dynamics. Proc. Symp. Brit. Ecol. Soc., Blackwell Scientific Publ., Oxford.

Lewis, J.B. (1970). Spatial distribution and pattern of some Atlantic reef corals. Nature 227: 1158-1159.

Lewis, J.B. (1974 a). Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. Proc. 2nd. Int. Coral Reef Symp. V. 2: 201-206.

Lewis, J.B. (1974 b). The settlement behaviour of planulae larvae of the hermatypic coral *Favia fragum* (Esper). J. Exp. Mar. Biol. Ecol. 15: 165-172

Loya, Y. (1972). Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. 13: 100-123.

Loya, Y.(1976 a). The Red Sea coral *Stylophora pistillata* is an r strategist. Nature, London. 259: 478-480.

Loya, Y. (1976 b). Settlement, mortality and recruitment of a Red

Sea scleractinian coral population. p 89-100 In G.O. Mackie (Ed.) Coelenterate ecology and behaviour. Plenum Press, N.Y.

Loya, Y. (1976 c). Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. Ecology 57(2): 278-289.

Loya, Y. (1978). Plotless and transect methods. p. In D.R. Stoddard and R.E. Johannes (Eds.) Coral reef: research methods. Monogr. Oceanogr. Methodol. 5, U.N.E.S.C.O., Paris, 581pp.

Loya, Y. and B. Rinkevich (1979). Abortion effects in corals induced by oil pollution. Mar. Ecol. Prog. Ser. 1: 77-80.

Loya, Y. and L.B. Slobodkin (1971). The coral reefs of Eilat (Gulf of Eilat, Red Sea). Proc. Symp. Zool. Soc. Lond. 28: 117-139.

Luna, L.G. (1968). Manual of histological staining methods of the Armed Forces Institute of Pathology. 3rd. edition. McGraw-Hill Book Co., New York. 258 pp.

Marshall, S.M. and T.A. Stephenson (1933). The breeding of reef animals. Part 1. The corals. Scient. Rep. Great Barrier Reef Exped. 3: 219-245.

McIntosh, R.P.(1980). The relationship between succession and the recovery process in ecosystems. p. 11-62 In J. Cairns Jr.(Ed.) The recovery process in damaged ecosystems. Ann Arbor Science Pub. Inc. 167pp.

Menge, B.A. and J.P. Sutherland (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110: 351-369.

Miller, T.E. (1982). Community diversity and interactions between the size and frequency of disturbance. Am. Nat. 120: 533-536.

Neudecker, S. (1979). Effects of grazing and browsing fishes on the zonation of corals in Guam. Ecology 60(4): 666-672.

Neudecker, S. (1981). Effect of substratum orientation, depth, and time on coral recruitment at Guam. Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V.2 : 376 (Abstract).

Odum, E.P. (1971) Fundamentals of ecology. W.B. Saunders and Co., Philadelphia. pp 574.

Oliver, J.K. (1979). Temporal and spatial variations in the growth of *Acropora formosa* (Dana 1846) on a North Queensland fringing reef. Honours thesis, James Cook University.

Oliver, J.K. (in prep.). Sexual reproduction in *Acropora formosa* : seasonality and synchrony of gametogenesis.

Orton, J.H. (1920). Sea-temperature, breeding and distribution in marine animals. J. mar. Biol. Ass. U.K. 12: 339-366.

Osman, R.W. and R.B. Whitlach (1978). Patterns of species diversity: fact or artifact. Paleobiology 4: 41-54.

Ott, B. and A.N. Auclair (1977). Cluster-analytic definition of species ecological groups for a submerged barrier reef in Barbados, West Indies. Int. Revue. Ges. Hydrobiol. 62(1): 41-51.

Pearson, R.G. (1981). Recovery and recolonization of coral reefs. Mar. Ecol. Prog. Ser. 4: 105-122.

Pichon, M. (1978 a). Recherches sur les peuplements a dominance d'anthozoaires dan les recifs coralliens de Tulear

(Madagascar). Atoll Res. Bull. 222: 1-447.

Pichon, M. (1978 b). Problems of measuring and mapping coral reef colonies. In Stoddart, D.R. and R.E. Johannes (Eds.) Coral reefs: research methods. Monogr. Oceanogr. Methodol. 5, U.N.E.S.C.O., Paris, 581pp.

Pichon, M. and J. Morrissey (1981). Benthic zonation and community structure of South Island Reef, Lizard Island (Great Barrier Reef). Bull. Mar. Sci. 31(3): 581-593.

Porter, J.W. (1972 a). Patterns of species diversity in Caribbean reef corals. Ecology 53: 744-748.

Porter, J.W. (1972 b). Predation by *Acanthaster* and its effect on coral species diversity. Am. Nat. 106: 487-492.

Porter, J.W. (1976). Autotrophy, heterotrophy and resource partitioning in Caribbean reef-building corals. Am. Nat. 110: 731-742.

Rae, J.G. (1978). Reproduction in two sympatric species of *Macoma* (Bivalvia). Biol. Bull. 155: 207-219.

Richmond, R.H. (1981). Energetic considerations in dispersal of *Pocillopora damicornis* (Linnaeus) planulae. Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V. 2: 153-156.

Richmond, R.H. and P.L. Jokiel (in press). Lunar periodicity in larval release in the reef coral *Pocillopora damicornis* at Enewetak and Hawaii. Bull. Mar. Sci. 34(1).

Rinkevich, B. and Y. Loya (1979 a). The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. Mar. Ecol. Prog. Ser. 1: 113-144.

Rinkevich, B. and Y. Loya (1979 b). The reproduction of the Red

Sea coral *Stylophora pistillata*. II. Synchronization in breeding and seasonality of planulae release. Mar. Ecol. Prog. Ser. 1: 145-152.

Rogers, C.S., M. Gilnack and H.C. Fitz (1983). Monitoring of coral reefs with linear transects: a study of storm damage. J. Exp. Mar. Biol. Ecol. 66: 283-300.

Rosen, B.R. (1971). Principal features of reef coral ecology in shallow water environments of Mahe, Seychelles. Symp. Zool. Soc. Lond. 28: 163-183.

Rosen, B.R. (1981). The tropical high diversity enigma - the coral's eye view. p. 103-130 in Forey, D.L. (Ed.) The Evolving Biosphere. British Museum (Natural History), Cambridge University Press.

Sale, P.(1983). Temporal variability in the structure of reef fish communities. In: Baker, J.T., R.M. Carter, P.W. Sammarco and K.P. Stark (Eds.) Proc. Inaugural G.B.R. Conference, Townsville, 1983. : 239-244.

Sammarco, P.W. (1982). Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J. Exp. Mar. Biol. Ecol. 61: 31-55.

Sammarco, P.W. and J.H. Carleton (1981). Damselfish territoriality and coral community structure: reduced grazing, coral recruitment, and effects on coral spat. Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V. 2: 525-535.

Sato, M. (1982). Mortality and growth of juvenile coral *Poctllopora damicornis* (Linne). Abstract of M.Sc. thesis, University of Ryukyus, Japan.

Schumacher, H. (1974). On the conditions accompanying the first settlement of corals on artificial reefs with special reference to the influence of grazing sea urchins (Eilat, Red Sea). Proc. 2nd Int. Coral Reef Symposium V. 1: 257-267.

Sheppard, C.R.C. (1979). Interspecific aggression between reef corals with reference to their distribution. Mar. Ecol. Prog. Ser. 1: 237-247.

Sheppard, C.R.C. (1980). Coral cover, zonation and diversity on reef slopes of Chagos Atolls and population structures of the major species. Mar. Ecol. Prog. Ser. 2: 193-204.

Sheppard, C.R.C. (1981). Illumination and the coral community beneath tabular *Acropora* species. Mar. Biol. 64: 53-58.

Sheppard, C.R.C. (1982). Coral populations on reef slope and their major controls. Mar. Ecol. Prog. Ser. 7: 83-115.

Shibata, K. (1969). Pigments and a UV-absorbing substance in corals and a blue-green algae living in the Great Barrier Reef, Australia. Plant Cell Physiol. 10: 325-335.

Shinn, E.A. (1966). Coral growth rate, an environmental indicator. J. Paleont. 40(2): 233-240.

Siebeck, O. (1981). Photoreactivation and depth dependent UV tolerance in a reef coral in the Great Barrier Reef, Australia. Naturwiss. 68: 426-428.

Sousa, W.P. (1979). Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. Ecology 60: 1225-1239.

Stearns, S.C. (1976). Life history tactics: a review of the ideas. Q. Rev. Biol. 51: 3-47.

Stephenson, T.H. and A. Stephenson (1933). Growth and asexual reproduction in corals. Scient. Rep. Gt. Barrier Reef Exped. 3: 167-271.

Stimson, J.S. (1974). An analysis of the pattern of dispersal of the hermatypic coral *Pocillopora meandrina* var. *nobilis* Verill. Ecology 55(2): 445-449.

Stimson, J.S. (1976). Reproduction in some common Hawaiian reef corals. p. 271-279 in G.O. Mackie (Ed.) Coelenterate ecology and behaviour. Plenum Press, N.Y.

Stimson, J.S. (1978). Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. Mar. Biol. 48: 173-184.

Stoddart, D.R. (1969 a). Ecology and morphology of recent coral reefs. Biol. Rev. 44: 433-498.

Stoddart, D.R. (1969 b). Field methods in the study of coral reefs. Proc. Symp. Corals and Coral Reefs, Mar. Biol. Assoc. India: 71-80.

Szmant-Froelich, A., P. Yevich and M.E.Q. Pilson (1980). Gametogenesis and early development of the temperate coral *Astrangia danae* (Anthozoa: Scleractinia). Biol. Bull. 158: 257-269.

Veron, J.E.N. and M. Pichon (1976). Scleractinia of Eastern Australia. Part 1. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. A.I.M.S. Monograph Series V. 1.

Veron, J.E.N. and M. Pichon (1982). Scleractinia of Eastern Australia. Part IV. Family Poritidae. A.I.M.S. Monograph Series V.5.

Veron, J.E.N., M. Pichon, and M. Wijsman-Best (1977). Scleractinia of Eastern Australia. Part II. Families Faviidae, Trachyphyllidae. A.I.M.S. Monograph Series V. 3.

Vine, P.J. (1974). Effects of algal grazing and aggressive behavior of the fishes *Pomaantrus lividus* and *Acanthurus sohal* on coral reef ecology. Mar. Biol. 224: 131-136.

Walker, T.A. (1981). Annual temperature cycles in Cleveland Bay, Great Barrier Reef Province. Aust. J. Mar. Freshwater Res. 32: 987-991.

Wallace, C.C. (1978). The coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) in the central and southern Great Barrier Reef Province. Mem. Qd. Mus. 18(2): 273-319.

Wallace, C.C. and G.D.Bull (1981). Patterns of juvenile coral recruitment on a reef front during a spring summer spawning period. Proc. 4th Int. Coral Reef Symposium, Manila, Philippines, V.2: 345-350.

Wellington, G.M. (1982). Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. Ecol. Monogr. 52(3): 223-241.

Williams, D.McB. (1980). Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). Bull. Mar. Sci. 22: 159-170.

Willis, B.L. (in prep). Reproductive ecology of *Turbinaria mesenterina*- a dioecious autumn/winter spawner.

Wishart, D. (1975). Clustan 1C manual. Computer Centre, University College, University of London.

Yamaguchi, M.(1975). Sea level fluctuations and mass mortality of

reef animals in Guam, Mariana Is. Micronesia 11(2): 227-243.

Yonge, C.M. and A.G. Nicholls (1931). Studies on the physiology of corals V. The effects of starvation in light and in darkness on the relationship between corals and zooxanthellae. Scient. Rep. Gt. Barrier Reef Exped. 1: 177-211.

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