A comparison of the population ecology of reef flat corals of the family Faviidae (Goniastrea, Platygyra).

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

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R. C. Babcock
26 May 1986

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TABLE OF CONTENTS

Abstract				1
Chapter 1	Introduction			2
Chapter 2	Distribution			5
2.1	Introduction			5
2.2	Methods			7
		2.2.1	spatial distribution	7
		2.2.2	sedimentation	9
2.3	Results			9
		2.3.1	spatial distribution	9
		2.3.2	sedimentation	17
2.4	Discussion			19
Chapter 3	Growth Rates			22
3.1	Introduction			22
3.2	Methods			23
		3.2.1	alizarin staining	23
		3.2.2	X-ray analysis of annual growth bands	23
		3.3.3	juvenile growth rates	24
3.3	Results			25
		3.3.1	alizarin staining	25
		3.3.2	X-ray analysis of annual growth bands	27
		3.3.3	juvenile growth rates	28
3.4	Discussion			32
Chapter 4	Reproduction			39
4.1	Introduction			39
4.2	Methods			40
		4.2.1	gametogenic cycles	40
		4.2.2	size specific fecundity	40
		4.2.3	spawning observations	41
		4.2.4	larval development and settlement	43

	4.3	Results		44
			4.3.1 gametogenic cycles	44
			4.3.2 size specific fecundity	48
			4.3.3 spawning observations	58
			4.3.4 larval development	63
			4.3.5 larval settlement	66
	4.4	Discussion		66
			4.4.1 gametogenic cycles	66
			4.4.2 size specific fecundity	69
			4.4.3 spawning observations	71
			4.4.4 larval development and behaviour	79
Chapter 5		Population dynamics		83
	5.1	Introduction		83
	5.2	Methods		84
			5.2.1 annual population surveys	84
			5.2.2 juvenile mortality	86
	5.3	Results	5.3.1 size-frequency distributions	87
			5.3.2 population dynamics	95
			5.3.3 age frequency distribution	107
			5.3.4 juvenile mortality	112
	5.4	Discussion		114
Chapter 6		Life Tables		124
	6.1	Introduction		124
	6.2	Age determination and age distribution		125
	6.3	Age- specific fecundity schedules		125
	6.4	Rate of increase		127
	6.5	Mortality and survivorship		127
	6.6	Life tables		128
	6.4	Discussion		140
References				146
Appendix 1				157

Figures

2.1 Map of study sites 8
2.2 Cross reef distribution, Geoffrey Bay 10
2.3 Cross reef distribution, Pioneer Bay 11
2.4 Sedimentation at Geoffrey and Pioneer Bays 18
3.1 Juvenile growth rates 31
3.2 Size - age relationships; G. aspera, G. favulus and P. sinensis. 38
4.1 Gametogenic cycles; G. aspera, G. favulus and P. sinensis. 46
4.2 Annual temperature cycles 47
4.3 Size - fecundity relationships, Geoffrey Bay 49
4.4 Size - fecundity relationships, Pioneer Bay 50
4.5 Spawning records, 1981 - 1985 60
4.6 Hour of spawning, 1982 - 1984 62
4.7 Early embryonic stages 65
4.8 Embryonic and larval stages 67
4.9 Spawning and tidal cycles 77
5.1 Size-frequency distributions and total cover of populations, Geoffrey Bay 88
5.2 Size-frequency distributions and total cover of populations, Pioneer Bay 89
5.3 Size-frequency distributions and total cover of populations, pooled bays 90
5.4 Age-frequency distributions and total cover of populations, Geoffrey Bay 91
5.5 Age-frequency distributions and total cover of popualtions, Pioneer Bay 92
5.6 Age-frequency distributions and total cover of populations, pooled bays 93
5.7 Size-frequency distributions as a function of their size in the previous year, G. aspera 97
5.8 Size-frequency distributions as a function of their size in the previous year, G. favulus 98
5.9 Size-frequency distributions as a function of their size in the previous year, P. sinensis 99
5.10 Age and size of G. aspera, G. favulus, and P. sinensis at Geoffrey Bay 109
5.11 Age and size of G. aspera, G. favulus and P. sinensis at Pioneer Bay 110

5.12 Age specific mortality of G. aspera, G. favulus and P. sinensis 111
5.13 Juvenile mortality, G. aspera, G. favulus and P. sinensis 113
5.14 Juvenile mortality, composite graph for G. favulus and P. sinensis 113
5.15 Typical colonies of G. aspera and P. sinensis 116
5.16 Reef flats of Geoffrey Bay and Pioneer Bay 117
6.1 Survivorship of G. aspera, G. favulus and P. sinensis from horizontal life tables 136
6.2 Survivorship of G. aspera, G. favulus and P. sinensis from vertical life tables 137
6.3 Age specific fecundity rates 139

ABSTRACT

The spatial distribution, abundance and growth rates of Goniastrea aspera, G. favulus and Platygyra sinensis were studied at two fringing reefs in the central Great Barrier Reef region. All three species exhibited similar degrees of spatial aggregation, despite the reproductive behaviour of G. favulus which was the only one of the species to spawn eggs with benthic development. Growth rates and recruitment rates in G. aspera and G. favulus were positively related to abundances at the two sites. Growth rates of both adults and juveniles were also used to estimate colony ages.

Gametogenic cycles and size specific fecundities were determined for each species at both sites. Goniastrea aspera, G. favulus and P. sinensis were among a large number of species studied which were observed to participate in annual mass spawning events. These mass spawnings are predictable and take place on only a few nights a year, after full moons in October and November. Studies of development subsequent to spawning showed that larvae did not become mobile for at least 36 hours, and the first larvae were capable of settling only after 4 to 5 days. Frequency distributions and rates of mortality based on both size and age were studied in marked quadrats at the two sites.

Frequency distributions based on size differed in some respects from those based on age, particularly with respect to the older age classes which decreased in mean size in many populations. Mortality patterns showed greater similarities between the two methods, however differences were again apparent in the older/larger classes since partial mortality to individuals is not accounted for in age based measurements. Finally, life tables were generated for each species. The life history patterns of G. aspera, G. favulus and P. sinensis appear to demonstrate a number of trade-offs that can be made between traits such as egg size, egg number, larval mortality, age at first reproduction, and mean colony age and generation times.

CHAPTER 1 INTRODUCTION

In the last decade the population biology of scleractinian corals has received an increasing amount of attention, and a number of studies have been published which have sought to illuminate various aspects of what has been a field in which curiously little has been known (Connell 1973). Much has, however, been published about spatial and temporal patterns of coral communities (see Done 1983 for a review). A more complete understanding of coral communities can be gained by increasing our knowledge of the populations of which they are composed. Studies of the spatial distribution, reproduction, rates of growth, recruitment and mortality of individual species all have obvious relevance to organization at the population, as well as the community level.

Existing studies of coral populations have usually concentrated on a few aspects of their biology, such as spatial distribution (Stimson 1974; Lewis 1974a,b; Dana 1976), reproduction (Lewis 1974a; Kojis and Quinn 1981,1982a; Rinkevich and Loya 1979; Harriott 1983), recruitment (Rylaarsdam 1983; Sakai and Yamazato 1984), age structure (Dodge and Vaisnys 1977; Loya 1976a), and dynamic aspects of coral populations (Connell 1973, Loya 1976, Harriott 1983, Hughes and Jackson 1985, Van Moorsel 1985). There have been many studies of coral growth (see Buddemeier and Kinzie, 1976 for a review), but the majority of these have been concerned purely with coral growth and growth rates, rather than growth as it might relate to aspects of coral populations.

To date there have been only two studies published which have attempted to construct life tables for anthozoan populations. These are the studies of Grigg (1977), who constructed life tables for two species of gorgonian, and Fadlallah (1983a) who produced a life table for the solitary ahermatypic scleractinian Balanophyllia elegans. There are a number of attributes of populations of colonial or clonal organisms which hinder the construction of

classical life tables, to the extent that this may even be impossible. Life tables must be based on the ages of individuals in populations, however in many species of coral, age (as well as individual status) may be difficult to determine with any degree of confidence, due to factors such as colony fission and fusion, and both positive and negative growth (Hughes and Jackson 1980). For this reason, size may be more relevant than age in understanding the demographic behaviour of some coral populations, particularly those in which there is a high rate of fragmentation or asexual propagation (Hughes 1984). The disadvantage of this approach is that it does not allow population size and population genetics to be considered at the same time (Hickman 1979). There has also been a lack of knowledge concerning the reproductive behaviour and fecundity of many corals, as well as difficulties in detecting new recruits at an early stage, making it difficult to obtain data on reproductive output and early age classes. If fecundities are known, it may be necessary to assume that populations are self-seeding in order to compile full life table data, an assumption which is likely to be invalid in many species. If these problems can be satisfactorily overcome there are a number of benefits to be gained by describing the properties of populations in the form of life tables since they facilitate comparison among corals, as well as between corals and other organisms. In addition life tables incorporate time scales, and therefore possess a component which is absent from other analyses such as the use of probability matrices.

This study, which was carried out on two sites on the central Great Barrier Reef, attempts to draw on all of the aspects mentioned above in its examination of the population biology of Goniastrea aspera, G. favulus and Platygyra sinensis. The spatial distribution and abundance of the three species at each site was examined in relation to growth rates and aspects of reproductive biology. Information on growth rates, in addition to its relevance to patterns of abundance, can also be used to age corals.

Studies of the reproductive biology of G. aspera, G. favulus and P. sinensis revealed that they were among a large number of scleractinian species now known to participate in a predictable mass spawning phenomenon. The predictability of this event made it

possible to obtain information on the development of the larvae of the species which were the targets of this study. Investigations of other aspects of the reproduction of G. aspera, G. favulus and P. sinensis were carried out to obtain information on differences in the gametogenic cycles and fecundity of populations at each site. The dynamics of the populations were also examined using both size and age based methods, making it possible to draw comparisons among the populations at both levels. Finally, age based population data were combined with data on fecundity to produce horizontal life history tables for G. aspera, G. favulus and P. sinensis.

CHAPTER 2. DISTRIBUTION

2.1 INTRODUCTION

The populations of Goniastrea aspera, G. favulus and P. sinensis on which this study is based are situated on the reef flats of the fringing reefs of two inshore high islands in the Central Great Barrier Reef. These were Geoffrey Bay at Magnetic Island, and Pioneer Bay at Orpheus Island (Fig. 2.1). These reefs are subject to a higher degree of fine sedimentation than reefs further offshore for several reasons. These are principally the input of silt from coastal rivers, the resuspension of bottom sediment in the relatively shallow waters surrounding the islands, and the resuspension of sediment from the shores of the islands themselves. While the reefs of both Islands are quite similar in many respects all the above factors result in a higher rate of sedimentation at Magnetic Island since it is situated closer to the mainland. The two sites also differ in that the reef at Geoffrey Bay faces the prevailing south easterly wind and swell, while Pioneer Bay faces the north west and is exposed to direct wave action much less frequently.

Coral communities on the reef flats of both bays are dominated by the branching Montipora digitata, along with massive corals, especially the favids Goniastrea aspera, G. favulus and Platygyra sinensis. Goniastrea aspera is characteristic of nearshore fringing reefs and rocky shores, especially those subject to high sedimentation (Babcock 1980). Goniastrea favulus is more widespread in its distribution and while it is present on many inshore reef flats its distribution extends to inner and middle shelf reefs (Kojis and Quinn 1981; Done 1982). Platygyra sinensis also has a more widespread cross-shelf distribution, however it is most common on inshore reef flats (Bull 1982). All three species have a widespread geographic distribution throughout the Indo-Pacific and have been described as being abundant at a number of other localities (Abe 1937a, Ditlev 1978, Brown et al. in press).

The within-reef distribution of these three species is almost completely restricted to the reef flat. Occasional colonies of G. aspera and G. favulus are found at depths of up to 1m below datum, and P. sinensis to depths of 2m, but their greatest densities occur on reef flats. The abundance of these species at each site was examined so that it could be related to differences in sedimentation rates at the two bays.

While the distribution of corals on geographic, between reef, and within reef scales has been fairly extensively studied, the small scale patterns of dispersion of corals have received less attention. Studies of spatial patterns have been used extensively in the botanical literature in investigating the ecology of plant populations (Kershaw 1974) but have only been applied to coral populations relatively recently. Lewis (1974a) attributed the contagious distribution of the Caribbean species Favia fragum to aggregated settlement by the large, well developed planulae released by this species. The clumped distribution of the hydrocoral Allopora californica on the California coast was also attributed to rapid larval settlement (Little-Ostarello 1976). Competition between larvae and adults was proposed as being responsible for the uniform distribution of Pocillopora meandrina at Hawaii (Stimson 1974). Juveniles of P. meandrina have subsequently been shown to have a higher mortality in the vicinity of large colonies (Polachek 1978). The influence of micro-habitat selection by larvae, and fragmentation of adult colonies have also been suggested as being responsible for the contagious distributions of Agaricia agaricites (Lewis 1974b) and Porites astreoides (Lewis 1974a; Dana 1976).

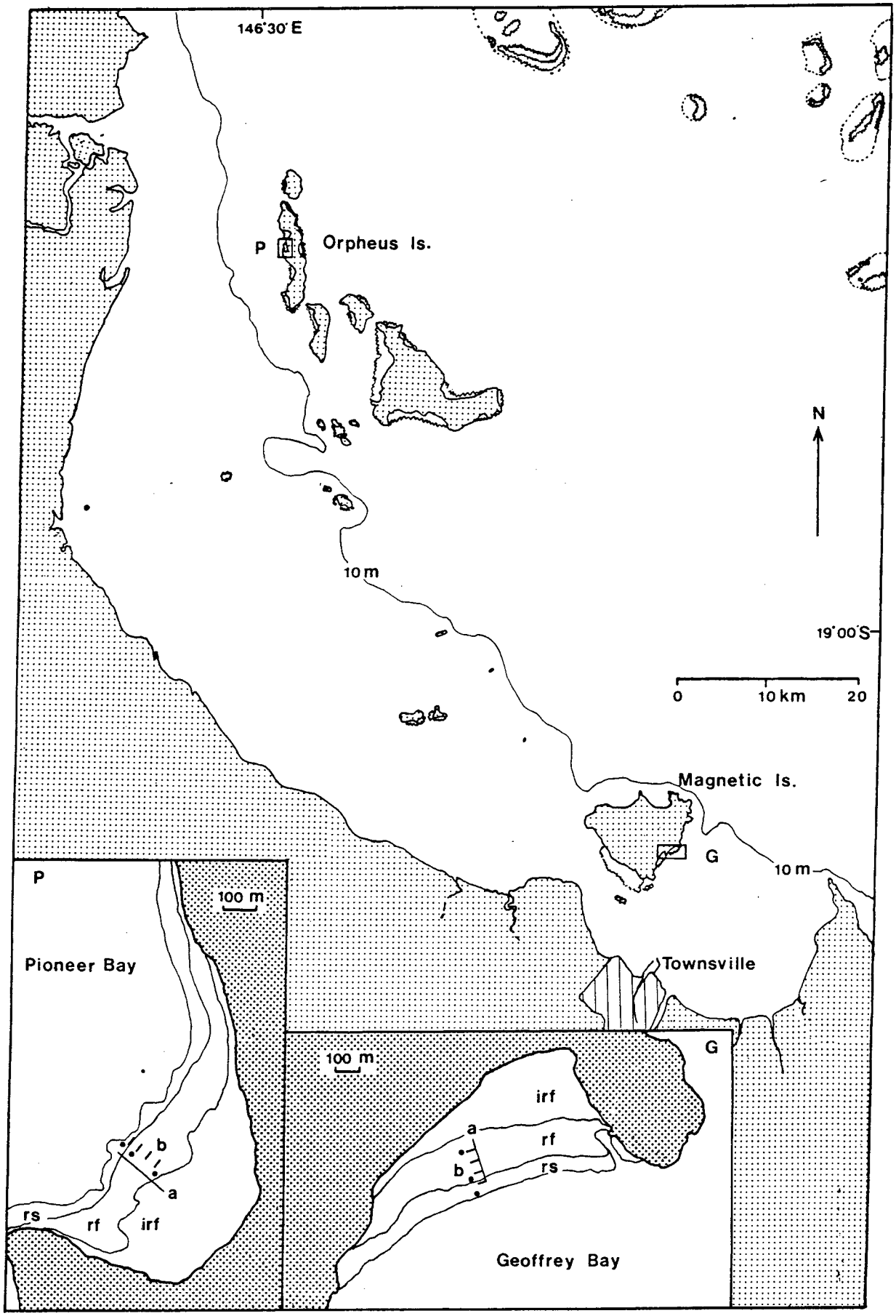
Almost all of these species release well developed planulae, many of which may have restricted dispersal or are capable of rapid settlement. Except in the case of Allopora californica (Little-Ostarello 1976), for which aggregations were found only around female colonies, there is little conclusive evidence to support explanations of the aggregated distributions of coral species. It is clear that larval behaviour is widely assumed to play a significant role in determining the spatial patterns observed in adult coral populations, and that for a number of species fragmentation or mortality of juveniles may also play a role.

The spatial patterns of the species Goniastrea aspera, G. favulus and Platygyra sinensis were investigated in an attempt to determine whether differences in the reproductive behaviour of these species influenced their distributions. Goniastrea favulus has a spawning behaviour which differs from that of the other two species. It has sinking eggs which stick to the substrate around the parent colony. Kojis and Quinn (1981) have suggested that this may result in the retention of larvae in the adult habitat. Goniastrea aspera and P. sinensis spawn buoyant eggs which are likely to result in the widespread dispersal of larvae.

2.2 METHODS

2.2.1 Spatial distribution.

The cross-reef distribution of Goniastrea aspera, G. favulus and Platygyra sinensis was investigated using two different quadrat methods. In the first method a transect was laid perpendicular to the reef-front at both sites (Fig. 2.1) and pairs of $1m^2$ quadrats placed on either side of the transect at 5m intervals. The number and size of colonies in each quadrat was recorded. In addition four transects of continuous $1m^2$ quadrats were laid across the reef parallel to the reef front, at intervals of 30m (Fig 2.1). These transects were 30m long at Geoffrey Bay, and 16m long at Pioneer Bay. The higher overall density of corals at Pioneer Bay provided sufficient numbers of colonies for demographic and spatial analysis in the shorter-length transects. In addition to recording the number and size of colonies in these quadrats, distance to the nearest-neighbour of the same species was measured at the inner three transects. The sizes of hemispherical colonies were estimated by measuring the height of the colony, the greatest diameter, and the diameter perpendicular to that. For microatolls two sets of measurements were made. The area of living coral was measured by obtaining a circumference or length of the strip of living tissue around the perimeter of the microatoll, and multiplying that by the mean height of the living portion of the colony. In addition the two diameters (maximum and perpendicular) of the microatoll were measured. Nearest-neighbour measurements were made from the centre of each colony to the centre


146°30'E
P
Orpheus Is.
N
10 m
19°00'S
0
10 km
20
Magnetic Is.
G
10 m
P
100 m
Pioneer Bay
Townsville
100 m
G
irf
a
rf
b
rs
b
a
rs
rf
irf
Geoffrey Bay

of the nearest colony of the same species.

Data from the parallel transects were also used to describe the small-scale spatial distribution of the species, using both a quadrat method, Morisita's I_δ (Elliott 1977) and a point to point method based on nearest-neighbour distances (Clark and Evans 1954).

2.2.2 Sedimentation

Sedimentation rates at both sites were obtained by means of sediment traps placed at three positions across the reef. These were the inner reef flat, outer reef flat and the bottom of the reef slope (5m depth). Three traps were placed at each position. The traps were constructed from plastic tubes 25mm in diameter and 250mm long, which were attached vertically to steel stakes driven into the reef. The tops of the traps were positioned 250mm above the surface of the substratum. Traps were changed at approximately monthly intervals between April and October 1983. Sediment was removed from the traps, rinsed twice with fresh water on tared filter paper (Whatmans No.1), and dried prior to weighing.

2.3 RESULTS

2.3.1 Spatial distribution

The mean density of colonies of all three species combined was approximately twice as high at Pioneer Bay ($2.4m^{-2}$) as it was at Geoffrey Bay ($1.1m^{-2}$), based on data from the parallel transects. Most of this difference was due to the increased density of Goniastrea favulus at Pioneer Bay. Differences in density between bays were significant for all species (Chi-squared contingency tables, G. aspera, Chi-squared = 120, $p<.01$; G. favulus, Chi-squared = 22, $p<.01$; P. sinensis, Chi-squared = 17, $p<.01$) Densities of populations of Platygyra sinensis and G. aspera were slightly higher at Geoffrey Bay than at Pioneer Bay, however the density of G. favulus was 20 times higher at Pioneer Bay than at Geoffrey Bay (Table 2.1). Population densities obtained from cross-reef transects (Fig. 2.2, 2.3) agreed with those obtained from the

Figure 2.2 Distribution of *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis* at Geoffrey Bay.

Open bars on histograms indicate cross-reef transects, solid bars parallel transects.

A: *G. aspera*

B: *G. favulus*

C: *P. sinensis*

D: elevation of reef flat at cross-reef transect (metres above datum). Elevations surveyed by J. Collins.

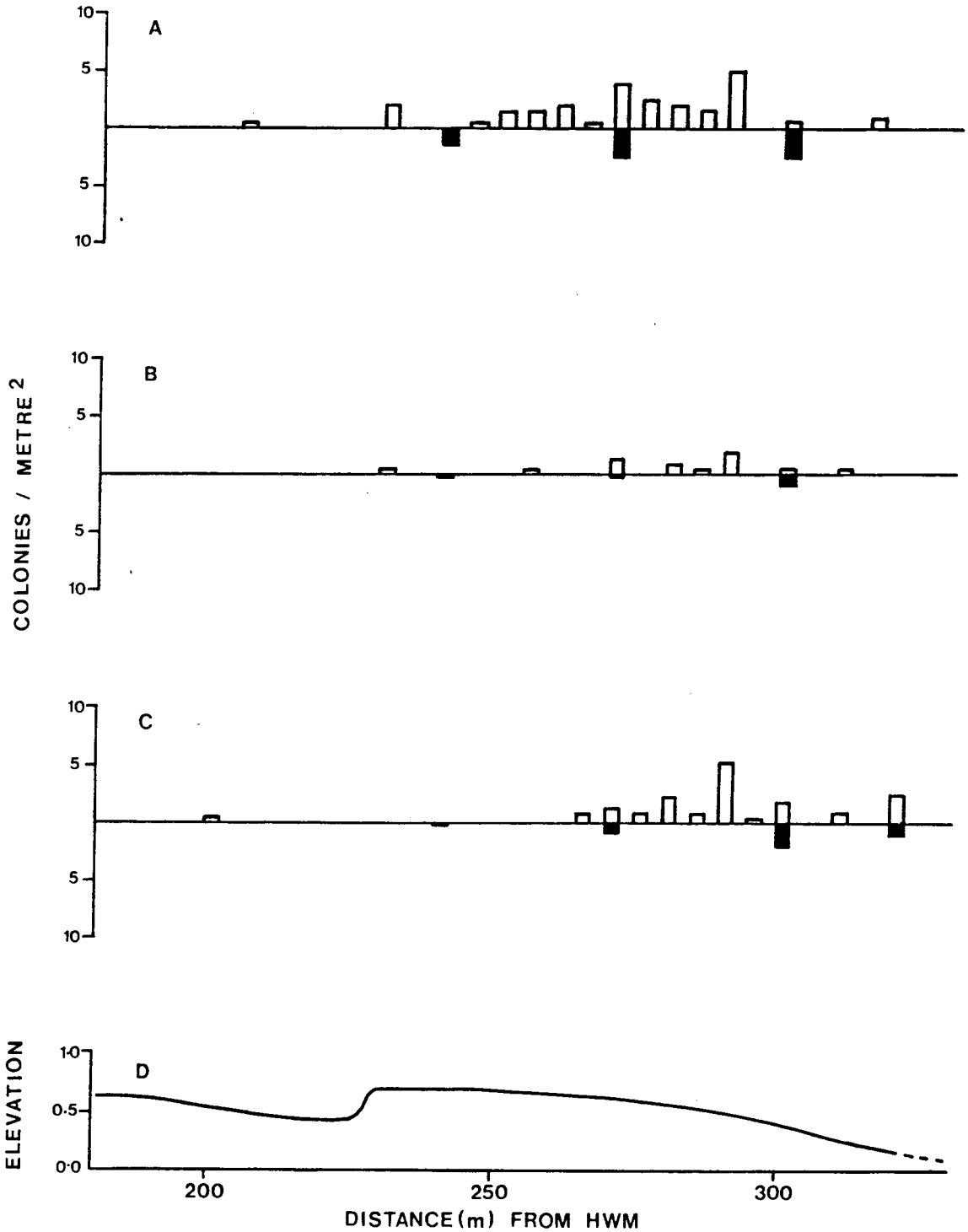

A
B
C
D
10
5
5
10
COLONIES / METRE 2
1·0
0·5
0·0
ELEVATION
200
250
300
DISTANCE (m) FROM HWM

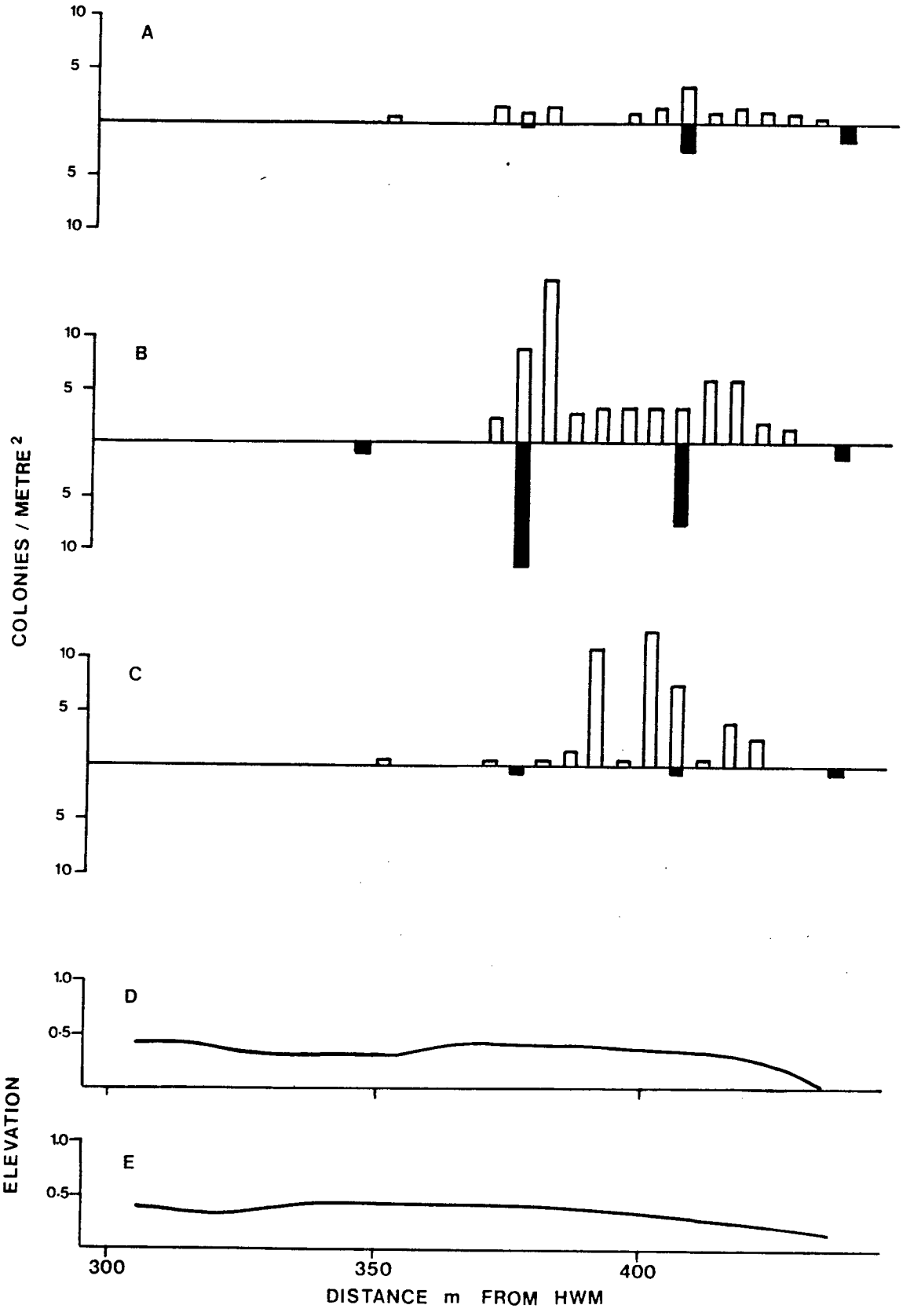
Figure 2.3 Distribution of *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis* at Pioneer Bay.

Open bars on histograms indicate cross-reef transect, solid bars parallel transects.

A: *G. aspera*
B: *G. favulus*
C: *P. sinensis*

D: elevation of reef flat at cross-reef transect
E: elevation of reef flat at site of parallel transects.

Elevations surveyed by J. Collins.
Elevations in metres above datum.


A
B
C
D
E
10
5
5
10
1.0
0·5
COLONIES / METRE²
ELEVATION
300
350
400
DISTANCE m FROM HWM

parallel transects except in the case of P. sinensis which occurred more frequently on the cross-reef transect at Pioneer Bay than at Geoffrey Bay. It may therefore be prudent to conclude that there is little difference in relative density between the two sites for this species.

Table 2.1 Goniastrea aspera, G. favulus and Platygyra sinensis. Density (no. of colonies m^{-2}) from 4 pooled parallel transects. Cover from inner 3 transects.

	G. aspera	G. favulus	P. sinensis
Geoffrey Bay			
density	1.7	0.4	1.1
% cover	0.06	0.013	0.94
Pioneer Bay			
density	1.3	5.4	0.6
% cover	0.005	0.017	0.009

The pattern of distribution of each species across the reef flats at Geoffrey and Pioneer Bays is shown in Figures 2.2 and 2.3. None of the species is abundant in the inner areas of the reef flat which are dominated by accumulations of fine sandy sediment. Abundances peak on the outer reef flat, and gradually decrease as the level of the reef flat drops (Figs. 2.2, 2.3). There do not appear to be any consistent trends in distribution within the outer reef flat for any of the species, apart from a tendency towards highest densities in the central areas of the outer reef flat. This is not to say that there is no variability in the distribution across the reef flat observed at either bay, for example the distribution of Goniastrea favulus appears to be skewed towards the outer end of the reef flat at Geoffrey Bay, while at Pioneer Bay it is skewed towards the inner end.

The small-scale spatial distribution pattern or patchiness of populations of each species was studied for all four parallel transects at both bays using Morisita's index I_δ (Table

2.2). For this measure a value of $I_\delta < 1$ indicates a regular distribution, $I_\delta = 1$ indicates a random distribution, and $I_\delta > 1$ a clumped distribution. For the inner three transects nearest-neighbour distances were also analysed (Table 2.3). In this method the index is R, where R>1 indicates a regular distribution, R=1 indicates a random distribution, and R<1 indicates a clumped distribution. Clumped distributions were observed at both bays for all three species, however the degree and consistency of clumping found varied slightly between transects, species and bays. Platygyra sinensis was clumped at the majority of transects at both bays. Goniastrea aspera was clumped more frequently at Geoffrey Bay than at Pioneer Bay while G. favulus showed the opposite tendency and was more frequently clumped at Pioneer Bay than at Geoffrey Bay. A general tendency towards clumping is shown by the results for pooled transects in all species.

While some disagreement might be expected due to differences in the power of the two tests, the results of the two different methods agreed in the majority of cases. Where discrepancies do occur, in all but one instance they involve cases where the distance method failed to show a departure from randomness, while the quadrat method showed significant clumping. This may reflect a clumped pattern with random dispersion within clumps (Goodall and West 1979).

Table 2.2 *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis*. Analysis of small-scale pattern at four transects from Geoffrey and Pioneer Bays using Morisita's index of dispersion (I_δ). Bold type indicates a significant departure from randomness.

	G. aspera	*G. favulus*	*P. sinensis*
Geoffrey Bay			
inner			
I_δ	0.6	5.0	3.3
Chi-squared	13.7	53.0	47.4
p	>.05	**<.01**	**<.01**
middle			
I_δ	1.1	1.1	0.8
Chi-squared	36.0	30.4	23.0
p	>.05	>.05	>.05
outer			
I_δ	1.7	2.4	1.3
Chi-squared	82.2	68.4	45.5
p	**<.01**	**<.01**	**<.05**
far outer			
I_δ	6.4	-	1.8
Chi-squared	66.0	-	47.2
p	**<.01**	-	**<.05**
pooled			
I_δ	2.0	3.6	1.8
Chi-squared	324.0	244.0	228.0
p	**<.01**	**<.01**	**<.01**

Table 2.2 (cont.)

	G. aspera	G. favulus	P. sinensis
Pioneer Bay			
inner			
I_δ	-	3.8	-
Chi-squared	-	54.2	-
p	-	<.01	-
middle			
I_δ	1.8	1.2	2.5
Chi-squared	19.6	42.5	33.9
p	>.05	<.01	<.01
outer			
I_δ	1.2	1.1	3.8
Chi-squared	23.6	29.8	45.3
p	>.05	<.05	<.01
far outer			
I_δ	0.9	1.4	1.8
Chi-squared	13.1	22.9	25.1
p	>.05	>.05	<.05
pooled			
I_δ	1.5	1.9	2.5
Chi-squared	82.1	382.9	103.6
p	<.01	<.01	<.01

Table 2.3 Goniastrea aspera, G. favulus and Platygyra sinensis. Nearest-neighbour analysis of small scale spatial patterns from three transects at Geoffrey Bay and Pioneer Bay. Bold type indicates significant departure from random distribution. - indicates no colonies present.

	G. aspera	G. favulus	P. sinensis
Geoffrey Bay			
inner			
R	0.7	1.2	0.3
p	**<.01**	>.05	**<.01**
middle			
R	0.8	1.0	0.8
p	**<.01**	>.05	>.05
outer			
R	0.9	1.1	1.0
p	**<.05**	>.05	>.05
pooled			
R	0.8	1.0	0.8
p	**<.01**	>.1	**<.01**
Pioneer Bay			
inner			
R	-	0.2	-
p	-	**<.01**	-
middle			
R	0.6	0.9	0.6
p	**<.01**	**<.01**	**<.01**
outer			
R	1.1	0.8	0.8
p	>.05	**<.01**	>.05
pooled			
R	0.8	0.7	0.7
p	**<.01**	**<.01**	**<.01**

It was possible to compare the degree of aggregation in populations of the three species at both bays using nearest-neighbour distances (Clark and Evans 1954). Comparison of pooled transects for Goniastrea aspera, G. favulus and Platygyra sinensis showed no significant differences between species at either bay, using a one-way ANOVA (Table 2.4). When both transects and bays were pooled there was again no difference between species in the degree of aggregation, using the same analysis (Table 2.4). Nearest-neighbour distances for each individual species were also compared between bays, and no differences could be detected (G. aspera, $F=1.1$, $p>.05$; G. favulus, $F=1.6$, $p>.05$; P. sinensis, $F=1.9$, $p>.05$; one way ANOVA, completely randomized design).

Table 2.4 Goniastrea aspera, G. favulus and Platygyra sinensis. Analysis of variance for nearest-neighbour distances with transects pooled, and with transects and bays pooled. (One-way ANOVA, completely randomized design).

	transects pooled (Geoffrey Bay)	transects pooled (Pioneer Bay)	transects and Bays pooled
F	1.4	1.1	0.2
p	>.05	>.05	>.05

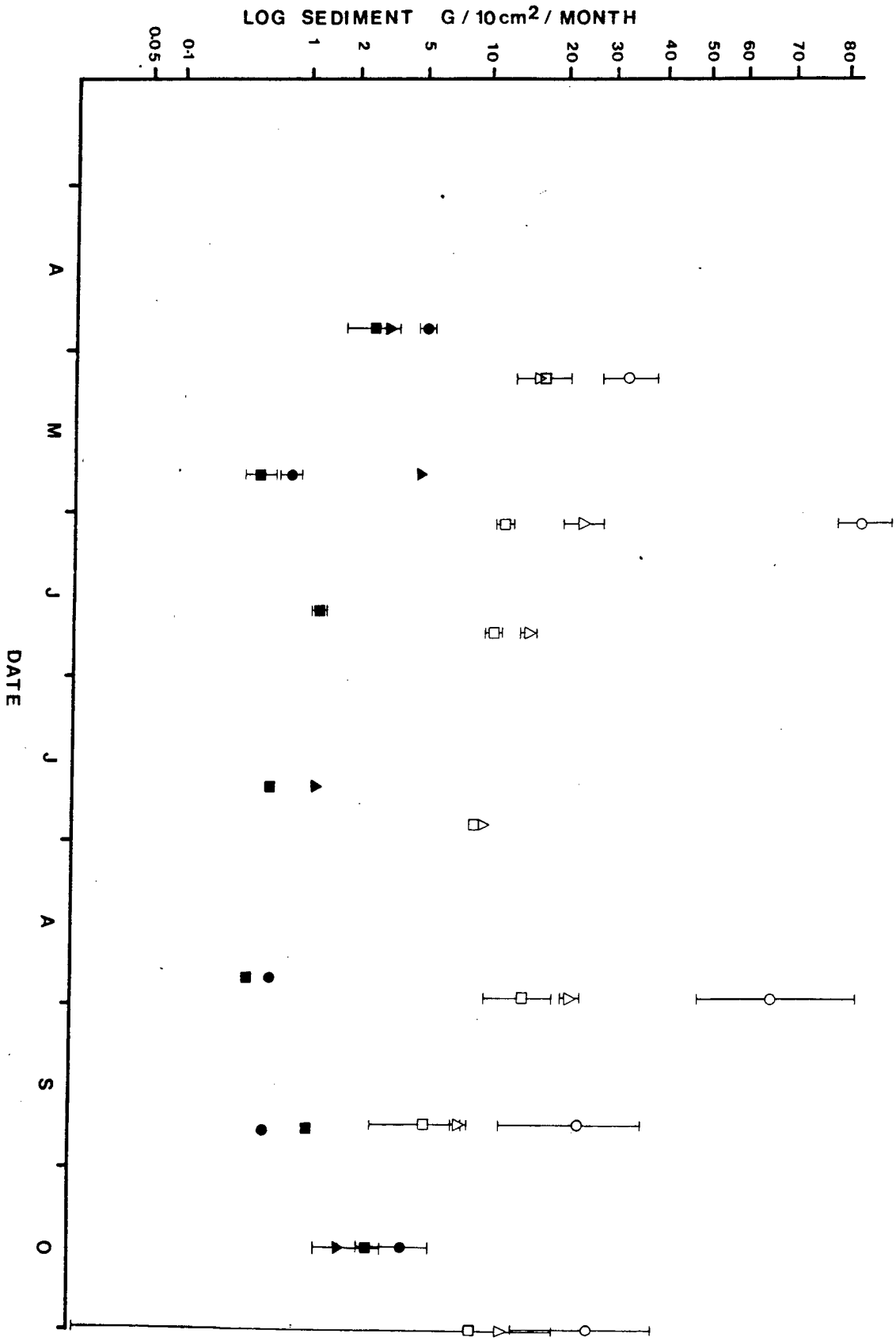
2.3.2 Sedimentation

Clear differences were demonstrated in the degree of sedimentation found at Geoffrey and Pioneer Bays. Sediment traps at Geoffrey Bay collected an average of 24g/month/10cm^2 over the seven months of monitoring, while those at Pioneer Bay consistently received less sediment and averaged only 1.6g/month/10cm^2 (Figure 2.2). There was significant variation between sites in rates of sediment accumulation at Geoffrey Bay, ($F=25.1$, $p<.01$, one-way ANOVA, completely randomized design) with traps on the outer reef flat (45g/month/10cm^2) having higher rates than those on the inner reef flat (14.8g/month/10cm^2) or reef slope

Figure 2.4 Sedimentation at Geoffrey and Pioneer Bays.

▲ = inner reef flat site;
● = outer reef flat site;
■ = reef slope site.

Hollow symbols represent data for Pioneer Bay, solid symbols represent data from Geoffrey Bay. Error bars represent one standard deviation (n = 3). Symbols without error bars indicate that less than three samples were obtained.


LOG SEDIMENT G / 10cm2 / MONTH
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(11.1g/month/10cm^2). There were no significant differences in sediment accumulation between sites at Pioneer Bay. This was probably due to the greater exposure of Geoffrey Bay, where breaking waves result in a greatly increased resuspension of sediments, especially coarser grades, at the outer edge of the reef. Sediment characteristics varied qualitatively between bays, with sediment from Pioneer Bay being composed almost entirely of silt or fine grades, while sediment contained in traps at Geoffrey Bay, especially those from the outer reef flat, contained a much higher proportion of sand and coarser grades of sediment. Wave action is also likely to play a major role in this difference.

2.4 DISCUSSION

Studies of the small scale spatial pattern of Goniastrea aspera, G. favulus and Platygyra sinensis at both Geoffrey Bay and Pioneer Bay indicate that a clumped distribution is present for all species at both sites. The degree and consistency of clumping vary both spatially (between bays and between transects) and between species, however these differences did not prove to be significant when the degree of clumping was compared using nearest-neighbour distances. It has been postulated that the sticky sinking eggs of G. favulus might be an advantage to this species since they would help retain larvae in the adult habitat (Kojis and Quinn, 1981). The significance of this possibility is brought into question by the comparison of the spatial distribution of G. favulus with that of G. aspera and P. sinensis. It might be expected that if the reproductive behaviour of G. favulus helped to retain larvae in the vicinity of the parent, populations of this species would display a more aggregated distribution than those of G. aspera or P. sinensis which have reproductive behaviours that tend to disperse larvae away from the parent (Babcock 1984; Babcock et al. 1986). Since this is not the case it appears that other factors such as larval settlement behaviour, variability in microhabitats, and differential mortality of juveniles are likely to be more important than reproductive behaviour in determining adult distribution patterns.

Differences in the density of populations between bays were most

pronounced for G. favulus, which was much more abundant at Pioneer Bay than at Geoffrey Bay. Differences were smaller between populations of the other two species; G. aspera, which was more common at Geoffrey Bay, and P. sinensis for which there was little difference in density at the two sites. These relative differences are borne out by observations made on other reefs on Magnetic Island and in the Palm Islands group. Done (1982) found that Goniastrea favulus is generally more abundant on reefs further offshore than it is on inshore reefs, while G. aspera is restricted to inshore habitats. It was the most abundant species of scleractinian found in Townsville Harbour (Babcock 1980), and is the dominant species on the reef flats of Pandora Reef (Done 1982), an inshore reef situated between Townsville and the Palm Islands group. Platygyra sinensis is found on reefs across the entire shelf, though it is more conspicuous on reefs furthest inshore.

Differences in growth rates of G. aspera and G. favulus (Chapter 3.3) agree well with their observed distribution patterns. Within each species, populations at the sites at which a significantly greater growth rate was recorded also occurred in significantly higher densities. For P. sinensis, where there was no significant difference in growth rate between sites, there was no clear difference in relative abundance. It may be possible to explain the positive relationship between growth rate and density by comparing sedimentation rates at both sites and relating this to the general distribution pattern of each species.

Sedimentation is the most obvious difference in physical parameters between Geoffrey and Pioneer Bays. Recorded differences in sedimentation rate are due both to the generally more turbid nature of the waters surrounding Magnetic Island, and the aspect of Geoffrey Bay which is exposed to the prevailing south-easterly wind and swell. Differences in temperature at the two sites are small (Ch. 4.3) as are differences in salinity, except in periods of unusually heavy rainfall. Increases in sedimentation rates have been correlated with slower growth rates in Montastrea annularis (Dodge et al. 1974; Aller and Dodge 1974; Dallmeyer et al. 1982; Dodge and Lang 1983) and with general distribution and community patterns of corals (Stoddart 1969; Hubbard and Pocock 1972; Loya

1976b; Bull 1982; Brown et al. in press). Increased sedimentation may adversely affect corals in a variety of ways, either by the energetic cost of sediment removal, or by reducing light penetration.

CHAPTER 3 GROWTH RATES

3.1 INTRODUCTION

Although coral growth has been studied for at least the last 100 years (see Buddemeier and Kinzie 1976 for review), it was not until relatively recently that it began to be studied as a question relevant to the population biology of these animals (Connell 1973). Since then there have been a growing number of studies which address the growth of corals as part of an effort to understand coral demography, as well as the population and community dynamics of corals (Loya 1976a, Rylaarsdam 1983, Van Moorsel 1985, Hughes and Jackson 1985). It is necessary, for example, to know how fast a coral grows in order to predict how a population will react to varying environmental conditions (Hughes 1984) or make inferences about factors which may have influenced it in the past (Done in prep). In order to do this accurately any variation in growth with age must be known. The growth of corals, expressed as linear skeletal extension, remains constant during adult life (Van Moorsel 1985), with a few specialized exceptions that appear to display determinate growth (Buddemeier and Kinzie 1976). Growth during the juvenile phase of life has been assumed by some authors (Connell 1973, Buddemeier and Kinzie 1976) to be more rapid than that of mature colonies. Evidence now exists, although it is still patchy, that the reverse may in fact be the case. Stylophora pistillata grows less in the first year than in older year classes (Loya 1976a), and the growth rates of Pocillopora damicornis in the first 6 months (Sato 1985) are much less than those reported for adult colonies elsewhere in the literature (Buddemeier and Kinzie 1976).

The growth rates of Goniastrea aspera, G. favulus and Platygyra sinensis were examined using a variety of methods at two sites in order to assess whether there were any differences between species or sites which might be related to variation in size or abundance. Data were obtained from colonies from a wide range of sizes so that

any effect of size on growth rate could be determined.

3.2 METHODS

3.2.1 Alizarin Staining

Colonies of Goniastrea aspera, Goniastrea favulus and Platygyra sinensis were stained in situ using the dye Alizarin Red S (Barnes 1972, Lamberts 1978). Colonies were enclosed in plastic bags which were tied at the base of the colonies by a drawstring. The dye was then released from plastic vials previously placed inside the bags to produce concentrations of 10 to 15 mg/l for 3hrs. The colonies stained were selected to cover as wide a size range as possible (1.5 to 17 cm mean radius). Goniastrea aspera was stained in April 1983; G. favulus and Platygyra sinensis were stained in June 1983. Several colonies of Platygyra sinensis from Geoffrey Bay at Magnetic Island were also stained in July 1983. All colonies were collected in August 1984 and bleached to remove the tissue, after which they were measured to determine their mean radius (height, maximum diameter, and diameter at right angles to that). The bleached skeletons were then sectioned along the axis of their greatest diameter to produce a central slab of approximately 1cm thickness. The growth subsequent to staining was then measured using vernier calipers at 5 points and the slab retained for x-ray examination.

3.2.2 X-ray analysis of annual growth bands

All corals which were stained at Pioneer Bay were collected and sectioned through the estimated origin of the colony, along the greatest diameter to produce a 1cm thick slab. Stained corals from Geoffrey Bay were also collected, along with a number of other corals of all three species which were located adjacent to the study site there. These were then sectioned as described above. The stained corals from both bays provided a basis for verification of an annual banding pattern and identification of the seasons during which bands were deposited.

The slabs were analysed using a Shimadzu x-ray instrument (model MD

100P) at 52Kv, 100MAs using Kodak Min R x-ray film. Growth bands were measured from the negatives, starting from the most recent bands on the outside of the colony and continuing towards the centre of the colony until the bands became obscured by changes in the growth orientation of the colony or bioerosion. Measurements were made with calipers from the center of each band along the axis which provided the longest continuous record of growth. Where clear banding existed along more than one axis up to 3 transects were measured, and these were averaged for each year (Dodge and Vaisnys 1977). Measurements were accurate to approximately ± 0.3mm.

3.2.3 Juvenile growth rates

Larvae of Goniastrea aspera, G. favulus and Platygyra sinensis were obtained during the annual spawning period of these species at Geoffrey Bay and Pioneer Bay, and cultured using the methods described in Ch. 4. Larvae of G. favulus were successfully raised to settlement at Pioneer Bay in 1982. The juveniles were settled onto 8cm square plates of Porites skeleton in aquaria. The plates were threaded onto stainless steel rods by means of holes drilled in their centres, and held about 1cm apart using sections of plastic tubing. The rods were then fixed to the reef flat at approximately the level of spring low tide so that the plates were oriented vertically. In 1983 larvae of all three species were raised at both Pioneer and Geoffrey Bays. Settlement plates cut from faviid species (Platygyra and Favia) were used in addition to Porites plates. In addition, some Platygyra sinensis were deployed at Geoffrey Bay on pieces of a plastic culture jar in which they had settled. All species suffered virtually total mortality at Pioneer Bay in 1983 due to bacterial infections in the aquaria which destroyed the newly settled planulae. (G. favulus also suffered very high mortality at Geoffrey Bay). The plates containing the remaining spat (G. aspera and P. sinensis) were deployed in the same fashion as the plates from the previous year. Juveniles settled in 1982 were measured at intervals of several months, while plates deployed in 1983 were initially examined at between one and two weeks after deployment, and thereafter at measured intervals of several months.

Coral plates were recovered and held in aquaria for periods of two

days to a week while they were being measured and censused, since juveniles were too small to be counted or measured in the field. The plates were placed in shallow plastic trays and examined using a dissecting microscope. The largest diameter of the coral and that at right angles to it were measured using a micrometer eyepiece in order to obtain a mean diameter. Care was taken to record the dimensions of the skeleton, rather than the polyp.

3.3 RESULTS

3.3.1 Alizarin staining

Of the 128 colonies stained at Pioneer Bay, 93 were used for growth rate measurements (Table 3.1). The remaining 35 (27%) did not take up the stain or were so poorly stained that measurement was not possible. Poor staining may have been the result of low stain concentrations due to leakage from the bags, however some individual variation in stain uptake between colonies was also apparent. Based on growth increments standardized to 12 months, (Table 3.1) Platygyra sinensis grew more rapidly than either Goniastrea aspera ($t=7.4$, $p<.001$) or G. favulus ($t=5.4$, $p<.001$). Platygyra sinensis also grew faster at Pioneer Bay than at Geoffrey Bay ($t=2.56$, $p<.02$), but the sample size at Geoffrey Bay was comparatively low ($n=8$). Goniastrea favulus at Pioneer Bay grew slightly faster than G. aspera ($t=2.78$, $p<.01$).

Table 3.1 Growth of Goniastrea aspera, G. favulus and Platygyra sinensis based on growth increment after alizarin staining at Pioneer Bay and Geoffrey Bay (P. sinensis only).

species	n	mean colony size (cm mean radius)	mean annual growth increment (mm)	range of growth increment (mm)
Goniastrea aspera	39	5.6	3.3	1.4 - 7.7
G. favulus	33	4.2	4.0	2.6 - 6.5
Platygyra sinensis (Pioneer Bay)	23	6.7	5.7	3.6 - 8.6
Platygyra sinensis (Geoffrey Bay)	8	6.7	4.4	2.8 - 6.2

Table 3.2 Relationship between colony size (mean radius) and growth rate.

species	n	size range	correlation coefficient
Goniastrea aspera	39	1.5 - 12.6	-0.15
G. favulus	33	1.6 - 8.0	-0.18
Platygyra sinensis	31	2.6 - 16.8	-0.14

For each species the growth increment was related to the size of the colony (arithmetic mean radius) by linear regression, but there were no significant correlations (Table 3.2, $p > 0.05$).

3.3.2 X-ray analysis of annual growth bands

Comparison of alizarin staining bands and banding patterns revealed by x-rays confirmed that the usual pair of one dense and one less dense band was laid down every year. The dense bands were laid down during the summer period, and the less dense bands in winter.

Of the 178 corals x-rayed, 126 produced readable growth bands (Table 3.3). When populations of the three species from Geoffrey and Pioneer Bays were compared, it was found that at both sites the growth rate of Platygyra sinensis was more rapid than that of either Goniastrea aspera (Geoffrey Bay $t=16.5$, $p<.001$; Pioneer Bay $t=17.9$, $p<.001$) or G. favulus (Geoffrey Bay $t=13.4$, $p<.001$; Pioneer Bay $t=20.3$, $p<.001$). Pooling the data for both bays produced the same result (Table 3.3) with P. sinensis growing faster than either G. aspera ($t=23.9$, $p<.001$) or G. favulus ($t=23.2$, p,.001). Comparison of P. sinensis populations at the two different sites showed no significant difference in growth rate ($t=1.8$, $p>.05$).

Growth rate data pooled for both bays for Goniastrea aspera and G. favulus showed no difference in growth rate between the species, ($t=.5757$, $p>.5$). However differences were apparent when the site was considered in the analysis. Goniastrea aspera grew faster than G. favulus at Geoffrey Bay, ($t=2.7$, $p<.01$), but the opposite was the case at Pioneer Bay where G. favulus grew more rapidly than G. aspera ($t=4.0$, $p<.001$). Sample populations of G. favulus grew more rapidly at Pioneer Bay than at Geoffrey Bay ($t=4.7$, $p<.001$), while those of G. aspera grew more rapidly at Geoffrey Bay than at Pioneer Bay ($t=1.93$, $p=.053$). There was no significant difference in the growth rate of P. sinensis between bays ($t = 1.81$, $p = 0.07$).

Table 3.3 *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis*. Annual growth rates as measured from x-ray analysis of density banding.

species	n colonies	n bands measured	mean (mm/yr)	range (mm)	SD
GEOFFREY BAY					
G. aspera	26	302	4.1	2-9.5	1.1
G. favulus	17	214	3.8	2-7.8	0.8
P. sinensis	19	209	6.4	3.1-10.9	1.6
PIONEER BAY					
G. aspera	20	220	3.9	1.7-8.1	0.9
G. favulus	25	153	4.3	2.2-8.6	1.1
P. sinensis	19	190	6.8	2.1-12.7	2.2
BAYS POOLED					
G. aspera	46	522	4.0	1.7-9.5	1.1
G. favulus	42	367	4.0	2.0-8.6	0.9
P. sinensis	38	399	6.6	2.1-12.7	1.9

Density band measurements were also used to examine how much of the variability in growth rate within a given species could be attributed to site, colony, and year to year differences using a two-way ANOVA, randomised block design. The last 7 years of growth were analysed from 20 colonies of each species. These were chosen haphazardly, ten from each bay. This was done to produce a balanced data set more amenable to statistical manipulation. With respect to between site differences the results produced by these tests (Table 3.4) are similar to those described above for the entire data set (Table 3.3). Between site differences however account for a relatively small proportion of the total variability, the bulk of which must be assigned to between colony variation and year to year differences in growth (Table 3.4). For this reason data from x - ray analysis of growth rates, rather than alizarin staining data, will be used to estimate colony ages, since estimates based on x - ray data incorporate annual variability over several years.

Table 3.4 Goniastrea aspera, G. favulus and Platygyra sinensis. Annual growth rates derived from x-ray analysis of growth bands. Two-way ANOVA, randomized block design.

	G. aspera			G. favulus			P. sinensis		
	SS	F	p	SS	F	p	SS	F	p
Bay:	0.6	2.5	>.05	16.6	57.1	<.01	1.0	0.9	>.05
Colony:	26.7	8.9	<.01	22.5	6.1	<.01	184.8	10.9	<.01
Year:	39.3	12.6	</01	20.4	5.5	<.01	113.2	7.8	<.01

3.3.3 Juvenile growth rates

The planulae and newly settled juveniles of all three species lack symbiotic zooxanthellae. Spat of *Goniastrea aspera* and *Platygyra sinensis* examined 5 days after deployment on the reef at Geoffrey Bay in 1983 also lacked zooxanthellae, as determined by both ultraviolet fluorescence microscopy and ordinary light microscopy of squashed live juveniles. Juveniles of these species examined after 10 days on the reef at Pioneer Bay (also in 1983) contained numerous zooxanthellae.

Table 3.5 *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis*. Mean diameter of juvenile corals (mm). n = no. of juveniles measured.

Pioneer Bay 1983

G. favulus	4 mo	5.8 mo	8.5 mo	15 mo
n	16	7	4	1
mean	1.1	1.5	1.7	0.2
SD	0.8	0.8	0.5	- (n=1)

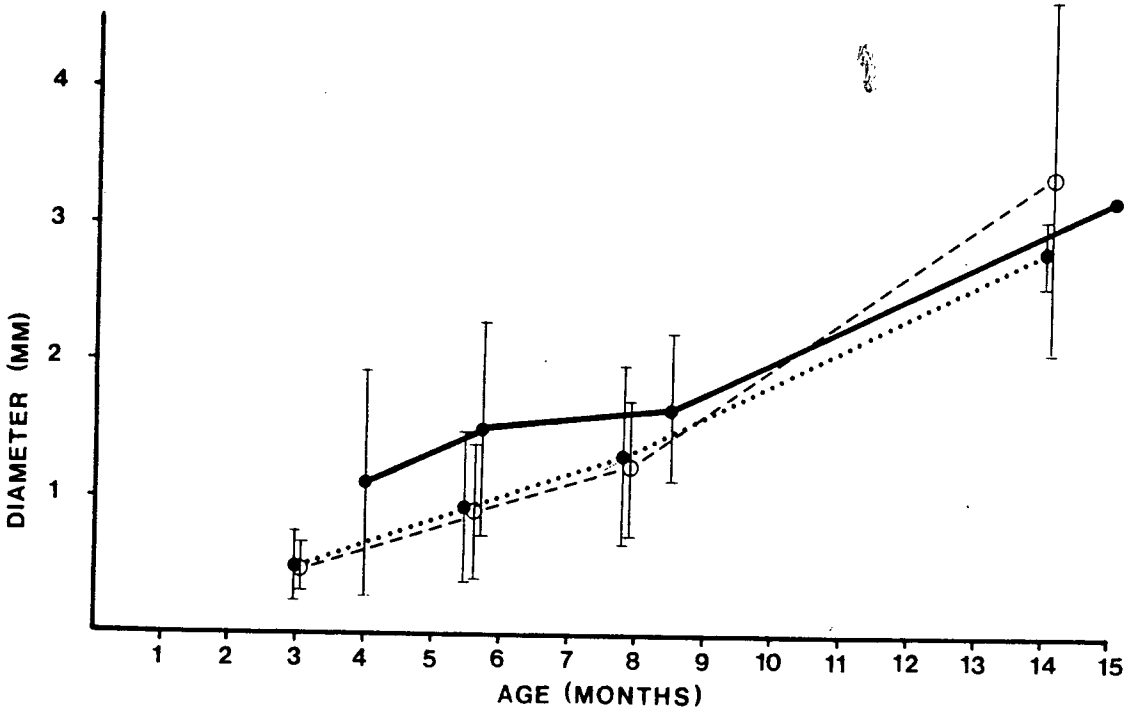
Geoffrey Bay 1984

G. aspera	3 mo	5.5 mo	7.8 mo	14 mo
n	69	98	56	3
mean	0.5	0.9	1.3	2.8
SD	0.2	0.6	0.7	0.3
P. sinensis				
n	79	111	72	3
mean	0.5	0.9	1.2	3.4
SD	0.2	0.5	0.5	1.3

Fig. 3.1 Juvenile growth rates of *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis*.

G. aspera: dotted line
G. favulus: solid line
P. sinensis: dashed line

Error bars indicate standard deviation.


DIAMETER (MM)
4
3
2
1
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2
3
4
5
6
7
8
9
10
11
12
13
14
15
AGE (MONTHS)

In the first year following settlement juvenile corals grew at quite similar rates (Table 3.5). Growth was slower in the first 6 to 8 months than it was in the subsequent period. There were no obvious differences between species in rate of growth during either period (Fig. 3.1). The growth of juveniles was much slower than that of adult corals. For example, based on adult growth rates (Table 3.3) juveniles of G. aspera, G. favulus and P. sinensis might be expected to average 8.2mm, 8.6mm and 12.8mm in diameter respectively after 12 months, however the actual size of juveniles at that age was much less (Table 3.5, Fig. 3.1).

3.4 DISCUSSION

The comparison of Alizarin staining and x-ray density bands provided the necessary confirmation of the annual nature of the deposition of band pairs as well as making it possible to ascertain the season during which the various bands were deposited. In each species the low density band was laid down during the winter months. This is in general agreement with the findings of most other studies of banding patterns in corals (summary in Highsmith 1979). Some differences were apparent in the annual growth of corals as determined by these methods. Growth as determined by Alizarin staining was slower than that measured from x-ray growth bands. In the case of Goniastrea favulus this was not significant, however for both G. aspera and Platygyra sinensis there was a significant bias in the results (Table 3.6). It is considered most likely that these differences are derived from the stained colonies, either through reduced growth as a result of staining, or by underestimation of the growth increment when measurement, since measurements were made from the outer edge of the stain band. The overestimation of the width of x-ray bands is less likely since measurements were made in a serial fashion, with each measurement beginning at the point at which the preceding measurement ended.

Table 3.6 Goniastrea aspera, G. favulus and Platygyra sinensis. Comparison of mean annual growth rates (mm/yr)at Pioneer Bay as determined by Alizarin and x-ray methods.

	growth (Alizarin)	growth (x-ray)	t	p	df
G. aspera	3.3	3.9	-3.0	.002	102
G. favulus	3.9	4.3	-1.8	.07	118
P. sinensis	5.7	6.8	-3.6	.0003	180

The growth rates of G. aspera, G. favulus and P. sinensis are slower than those of other species of these genera, or other massive corals (esp. Porites spp.) reported in the literature (Buddemeier et al. 1974). It is interesting to note that the only coral from a reef flat site sampled by Buddemeier et al. a colony of Goniastrea parvistella, had a growth rate of 1.3-1.5 mm/yr. The growth rate of P. sinensis does fall within the range of those reported for Platygyra spp. (4.9 - 12mm), some of which were P. sinensis, by Weber and White (1974).

Platygyra sinensis grew more rapidly than either Goniastrea species. While there was no difference in the growth rates of G. aspera and G. favulus when sites were pooled, significant differences were apparent both within and between species when sites were considered separately (3.3.2). Goniastrea favulus grew more quickly at Pioneer Bay than at Geoffrey Bay, while the opposite was true of G. aspera. In addition G. favulus grew more rapidly than G. aspera at Pioneer Bay, while the opposite was true at Geoffrey Bay. It is possible that these differential growth rates reflect differences in habitat suitability, and correspond or contribute to the observed variation in abundance of these two species at Pioneer and Geoffrey Bays (2.2.1).

Goniastrea favulus, a species not common in close proximity to the mainland coast, displayed a slower growth rate at Geoffrey Bay,

which is subject to a relatively high degree of sedimentation, than it did at Pioneer Bay, which is comparatively free of the effects of sediment. Differences in the growth rate of G. aspera, which is most abundant in the turbid inshore areas, are more difficult to explain, since increased sedimentation or sediment related factors are usually associated with reduced growth rates in corals. Factors such as higher light levels or decreased nutrient concentrations may be responsible for the growth rate of this species at Orpheus Is. The more widespread species P. sinensis displayed no difference in growth rate between the two sites. For each of these species the site with the greater growth rate corresponded to the site with the greater abundance as well as with general patterns of abundance.

A number of studies have demonstrated that mortality in colonial corals is size dependent (Connell 1973; Loya 1976a; Rylaarsdam 1983; Hughes and Jackson 1985). It may therefore be possible to explain relative abundances of populations at each site in terms of growth rates. Populations of faster growing corals will become larger more quickly and thus may suffer a lower rate of mortality. For example the G. favulus population at Pioneer Bay grows more quickly than at Geoffrey Bay, and might therefore suffer a lower relative mortality rate, since colonies will become larger more quickly. This lower mortality rate would eventually result in a population with a higher density at Pioneer Bay, which was in fact what was found (Ch. 2).

Juveniles of all three species showed slow rates of linear skeletal extension in comparison with adults of the same species (Tables 3.3, 3.5). The rate of growth increased as juveniles grew, but this was still less than half the adult rate after 15 months. This contrasts with general speculation that corals calcify more rapidly in the early stages of growth just after settlement (Buddemeier and Kinzie 1976). In addition the growth rates of juveniles of G. aspera, G. favulus and P. sinensis were found to be considerably slower than those reported on the literature for the post-settlement stages of other species of scleractinians (Table 3.7). Significantly slower growth rates have also been shown by Wallace (1983) for natural recruits, although most of these could not be specifically identified. It is possible that the ability of juvenile corals to survive without significant growth for substantial periods of time,

especially in cryptic habitats (Wallace unpublished data), is the functional equivalent of seed dormancy in plants (Harper 1977).

Failure to recognise the slow growth of new recruits may result in significant underestimation of age (Connell 1973) which could have pronounced effects on demographic studies. It should be noted that these three species, as well as Acropora millepora (Babcock 1985) and those reported by Wallace (1983 and pers. comm.) are broadcast spawners. All of the other species in Table 3.7 are planulating species. Of the planulating species, Pocillopora damicornis and Stylophora pistillata have been characterized as opportunistic species (Connell 1973, Loya 1976a). The relatively rapid growth rates of these two species are consistent with such suggestions.

Table 3.7 Growth of juvenile corals.

species	mode of reproduction	mean diameter (mm)	age	source of diameter estimates
Goniastrea aspera	spawns gametes	1.3	7.8mo	direct measurement n=54
G. favulus	spawns gametes	1.7	8.5mo	direct measurement n=4
Platygyra sinensis	spawns gametes	1.2	7.8mo	direct measurement n=72
Acropora millepora (Babcock 1985)	spawns gametes	5.1	9.3mo	direct measurement n=5
Pocillopora damicornis (Sato 1985)	planulates	5-10	6mo	direct measurement n=54
Porites astreoides (Vaughan 1919)	planulates	12	12mo	direct measurement n=15
Favia fragum (Vaughan 1919)	planulates	12	12mo	direct measurement n=30
Cyphastrea ocellina (Edmondson 1928)	planulates	3	3.5mo	direct measurement n=1
Stylophora pistillata (Loya 1976a)	planulates	13	12mo	mean radius of 1st yr size class n=20

It is possible to derive a reasonably accurate estimate of colony age using growth rate data obtained from x-rays of adult corals as well as measurements of juvenile corals (Fig. 3.2). The initial part of the relationship is derived from actual measurements of spat. The intermediate phase is more speculative, and is based on the assumption that primary polyps will continue to grow at the observed rate until they reach the diameter of adult polyps (~7mm) at the end of the third year. Alternatively, if the growth rate of the juvenile polyps continued to increase in the second year after settlement as it did in the initial year (Fig. 3.1), adult polyp size might be obtained after only two years. Growth during this stage is assumed to be largely two dimensional. Once adult polyp dimensions are obtained growth is assumed to be three dimensional and adult growth rates are applied linearly since there was no evidence of size dependent change in growth rate (3.3.1).

Taking into account the possible increase in juvenile growth rate in the second and third year, as well as the confidence limits on adult growth into account, colony size can be used to place an age on colonies with a conservative accuracy of $\pm$2yr. This can be done by using the following formula:

$$age = [(r - 3j)/a] + 3$$

where - r = arithmetic mean radius of colony
j = mean annual radial growth rate of juveniles (first three years)
a = mean annual adult growth rate

While there are inherent difficulties in the use of the size of corals in estimating their age (Hughes and Jackson 1980) it is important to attempt to gain an understanding of the age structure of populations. This will make it possible to understand the population dynamics of corals in conventional terms, and have a number of implications for current theories regarding topics such as speciation in corals (Potts 1983,1984a).

Fig. 3.2 Size - age relationships.

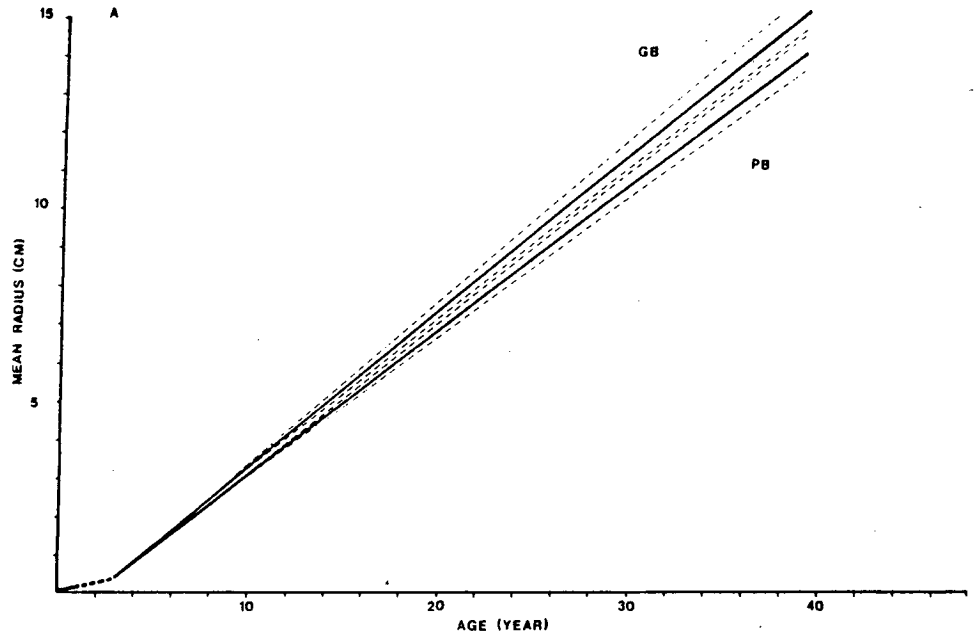
A. Goniastrea aspera.

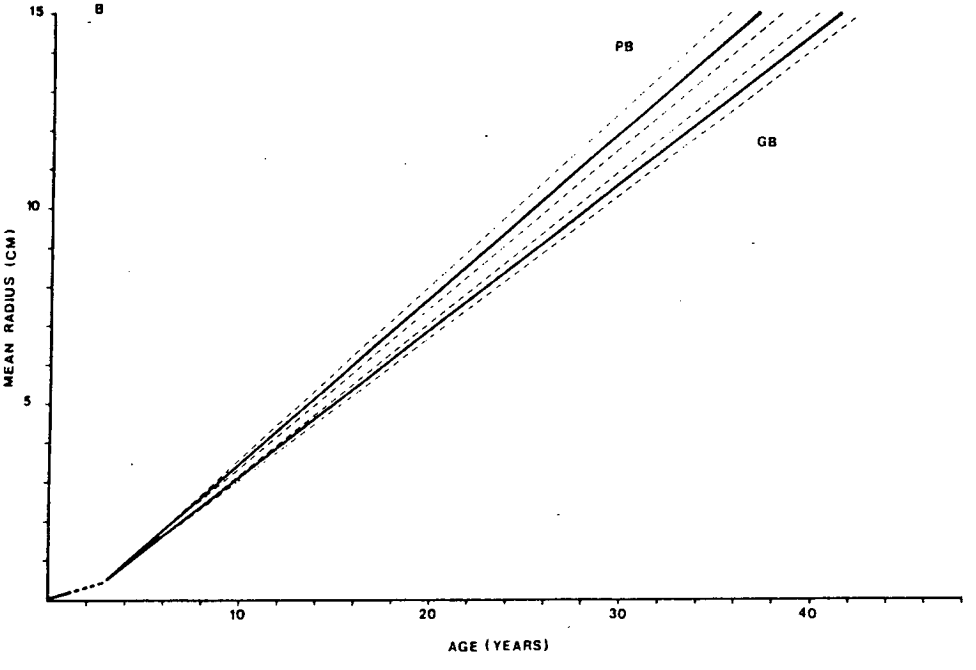
B. G. favulus.

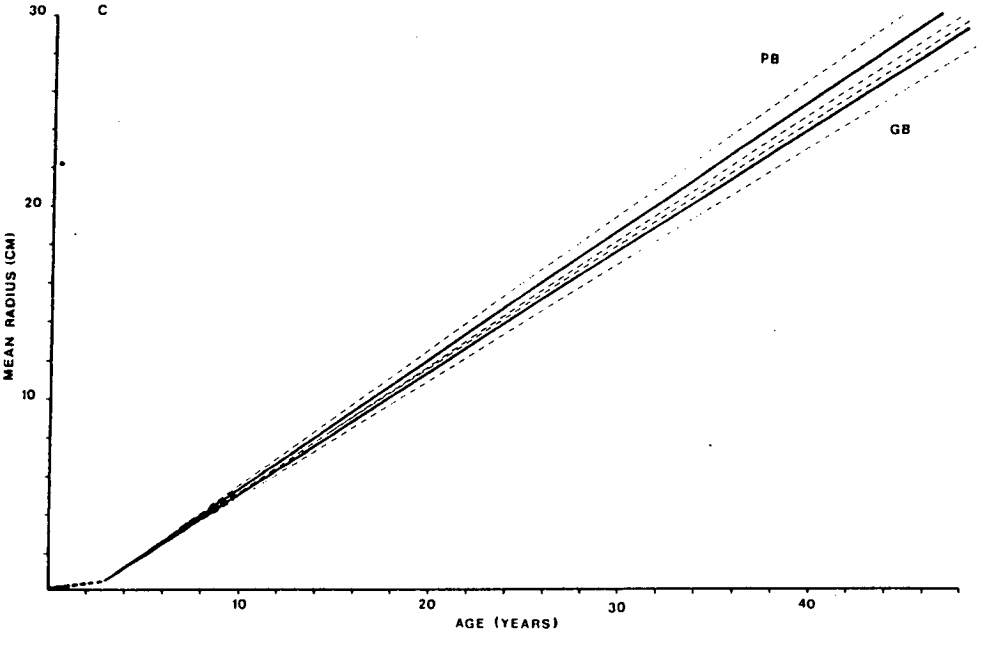
C. Platygyra sinensis.

PB: Pioneer Bay; GB: Geoffrey Bay.

Means and 95% confidence limits based on adult growth rates as determined at each site. See text for full explanation of methods used in estimating both adult and juvenile size - age relationships.


A
GB
PB
MEAN RADIUS (CM)
15
10
5
10
20
30
40
AGE (YEAR)


B
PB
GB
MEAN RADIUS (CM)
15
10
5
10
20
30
40
AGE (YEARS)


C
PB
GB
MEAN RADIUS (CM)
30
20
10
10
20
30
40
AGE (YEARS)

CHAPTER 4 REPRODUCTION

4.1 INTRODUCTION

Reproduction plays a central role in the study of the population biology of all organisms. The lack of information on the sexual reproduction of scleractinians (as well as most other aspects of their population biology) was highlighted by Connell (1973). Since that time knowledge of reproduction in this group has grown rapidly, focusing mainly on modes of reproduction and gametogenic cycles, (Szmant-Froelich *et al.* 1980; Kojis and Quinn 1981, 1982a,b; Harriott 1983a, Babcock 1984; Harrison *et al.* 1984; Willis *et al.* 1985; Babcock *et al.* 1986; and a review by Fadlallah 1983b), but also including investigations of size at first reproduction, fecundity and larval behaviour (Rinkevich and Loya 1979; Kojis and Quinn 1981; Harriott 1983a; Babcock 1984; Szmant-Froelich 1985). These studies have led to a better understanding of coral population biology as well as to important results relevant to the general reproductive biology of invertebrates, for example the mass spawning of corals (Harrison *et al.* 1984). A number of questions have been raised by these discoveries, particularly in relation to details of the physiology and ecology of coral reproduction which influence reproductive patterns in both immediate and evolutionary terms. This increased knowledge of the reproductive biology of corals has also provided the opportunity to make comparisons between corals and terrestrial plants when considering such aspects of life history patterns as relative energetic investments in reproduction and mating patterns.

In this chapter a number of aspects of the reproductive biology of *Goniastrea aspera*, *G. favulus* and *P. sinensis* will be considered, including gametogenic cycles, size at first reproduction, colony fecundity, spawning behaviour, and larval development and behaviour. The mass spawning behaviour of scleractinian corals on the GBR, in which *G. aspera*, *G. favulus*, and *P. sinensis* participate, is also discussed.

4.2 METHODS

4.2.1 Gametogenic cycles

Gametogenesis in Goniastrea aspera, G. favulus and P. sinensis was monitored at both Geoffrey and Pioneer Bays between 1982 and 1984. Samples were collected at approximately monthly intervals by chipping off several polyps from three adult (> 10cm diameter) colonies of each species. Since different colonies were sampled each time, the total number of colonies sampled for each species at each bay was between 20 and 30 colonies. Samples from March to November 1983 were fixed in 10% sea water formalin, decalcified in 4% formic acid, and paraffin embedded prior to sectioning. (previous studies had shown that this was the period of time during which gametogenesis occurred - Kojis and Quinn 1981; Babcock 1984). Serial sections were cut at 6µm, and representative sections mounted for microscopic examination. Maximum diameters of each oocyte revealed in serial sections were measured using a micrometer eyepiece. Five oocytes were measured from each of three colonies.

In addition to these histological samples, corals sampled in 1982 and 1984 were examined visually at the time of collection for the presence of mature gonads in order to monitor the possibility of asynchronous gametogenesis in part of the population. Mature gonads in these species are visible to the naked eye (Babcock 1984) and would be detected in such examinations.

Temperatures at each site were recorded at Geoffrey and Pioneer Bays in 1983 using max-min thermometers deployed at 5m. These were situated at the same sites as the 5m sediment traps (Fig. 2.1).

4.2.2 Size specific fecundity

In order to establish how colony fecundity changes with age or size, colonies of a range of sizes, including both the largest and smallest colonies available, were sampled from each species at both Geoffrey and Pioneer Bays in 1983. Collection of samples took place three weeks before spawning at Geoffrey Bay, and one week before spawning at Pioneer Bay. Approximately 50 colonies were sampled

from each species at Geoffrey Bay, and 30 colonies from each species at Pioneer Bay. Sampling was deliberately biased towards small to medium sized colonies in order to increase accuracy in determining size at first reproduction. The colonies chosen were all hemispherical in growth form to reduce the likelihood of possible age effects on fecundity (Kojis and Quinn 1985, Szmant-Froelich 1985) in colonies which were remnants of older colonies. Colony sizes were measured (using the methods described in Chapter 2), prior to chipping off samples which were fixed in 10% formalin and decalcified in 4% HCL. Oocytes were counted in 5 mesenteries from each of 3 chosen polyps from every sample. Counts were made using a stereo dissecting microscope. The diameter of 20 freshly spawned eggs of each species were measured to obtain average egg diameters.

Since colony fecundity also varies as a simple consequence of the surface area of a colony in these species, the average number of septa per corallite as well as the mean number of corallites per cm^2 was measured for each species. Ten corallites from each of five colonies of G. aspera, G. favulus and P. sinensis were haphazardly selected and the number of primary septa (those connected to the columella) were counted. On each of these colonies the number of polyps in a $4cm^2$ quadrat was also counted to provide the mean number of polyps per unit area. This information could then be used in conjunction with data from the polyp dissections to provide estimates of the total egg production from a colony.

4.2.3 Spawning observations

The presence of ripe coral gonads can be determined in the field on the basis of egg colour and sperm maturity (Harrison et al. 1984). The eggs of G. aspera are visibly pigmented 1 to 2 months before spawning, and testes are visible only in the month prior to spawning (Babcock 1980). Fully mobile sperm are visible in live testes squashes only in the final week before spawning (Acropora formosa, Oliver 1979, Babcock 1980). Using these criteria, in addition to previous information regarding the timing of spawning in Goniastrea aspera (Babcock 1980) and G. favulus at Heron Is. (Kojis pers. com.)

and Magnetic Is. (personal observations), spawning times were estimated and colonies were observed to determine actual spawning times. Experience gained in predicting the timing of spawning during the early stages of this study greatly facilitated data collection in subsequent years.

A variety of methods were used to obtain data on the spawning times of corals. Direct observations of spawning were made on corals *in situ*, corals moved to underwater observation posts, and corals in aquaria. At night corals were shielded as much as possible from artificial illumination and frequent brief observations were made using flashlights. Spawning activity was also inferred by indirect means, including the disappearance of gonads between sequential samples from tagged colonies in the field or in aquaria, or the presence of sperm or eggs in aquaria. Details of these observations varied from year to year and are outlined below.

1981 At Magnetic Island daily sequential samples were taken from *Goniastrea aspera* and *G. favulus* from the 16th to 20th of October. These species as well as *Platygyra sinensis* were also observed in aquaria.

1982 Aquarium observations were made on both *G. aspera* and *G. favulus* from Magnetic Island on the 5th and 6th of November. Field observations were also made on the 6th of November at Magnetic Island. At Orpheus Island, field and aquarium observations were made on *G. aspera*, *G. favulus* and *P. sinensis* from the 3rd to 6th of December. Observations were also made on a number of additional species which were found to have ripe gonads (see Appendix 1).

1983 Field observations and sequential field samples were used to determine spawning times of the study species at Magnetic Island between the 25th and 26th of October. The same methods, in addition to aquarium observations, were used at Orpheus Island between the 22nd and 26th of November. At both sites a large number of other species were observed at the same time (Appendix 1).

1984 Field and aquarium observations as well as sequential field samples were carried out at Magnetic Island between October 13th and

17th on G. aspera, G. favulus and P. sinensis. Samples of G. favulus and P. sinensis from Magnetic Is. were collected on October 18th and December 6th. At Orpheus Island aquarium observations were made on all three species between the 13th and 16th of November. Other species observed are listed in Appendix 1.

1985 Aquarium observations were conducted using corals from Magnetic Is. from the 29th of October to the 1st of November, and at Orpheus Island from the 30th of November to the 2nd of December. Other species observed are listed in Appendix 1.

Details of numbers of colonies sampled or observed are included in Table 4.4.

4.2.4 Larval development and settlement

Fertilized eggs were obtained principally during the predictable coral spawning seasons at Magnetic Island in October and Orpheus Island in November, 1983. Less extensive additional observations were made on material collected in 1984 and 1985 including examination of freshly spawned live eggs for the presence of polar bodies. Colonies of G. aspera, G. favulus and P. sinensis were collected and placed in aquaria prior to spawning. After spawning eggs and sperm were collected by suction into plastic wash bottles and the gametes of all species were then transferred into 4 litre plastic jars full of seawater. The jars were sealed by placing 60µm plankton mesh across the mouths. The mesh was held in place using lids which had had their centres cut out to allow sea water to pass through. The jars were then transferred to the sea and attached by a line to an anchored buoy where they floated semi-submerged at the sea surface. The gametes were therefore held at ambient surface seawater temperature and provided with continuous multidirectional agitation by wave action.

Development was monitored by retrieving the cultures periodically and pipetting out subsamples. Live embryos were examined using a stereo-dissector microscope prior to fixing in either 10% formalin - 1% $CaCl_2$ - 5% acetic acid, 2% glutaraldehyde buffered

by .1M sodium cacodylate, or 100% acetic ethanol for egg-sperm bundles (1 part glacial acetic acid to 3 parts absolute ethanol by volume).

Preserved specimens were mounted and oriented for sectioning in 2% agar. The agar blocks were trimmed to 3mm thickness, embedded in paraffin and sectioned at 5µm. A Gomori trichrome was used to stain early developmental stages, however for later developmental stages a progressive ferrous sulphate - haematoxylin sequence (Lillie and Fulmer 1976) gave superior results and was used for most of the material.

The settlement preferences of the larvae of Goniastrea aspera were examined for a variety of substrata. In 1983, 5 day old larvae were placed in an aquarium with freshly cut coral plates and small Tridacna shells (mean diameter of 7cm) taken directly from the outer reef flat. The coral plates were cut from either Porites or Platygyra colonies, and were approximately 1cm in thickness and 8cm square. Ten plates of each type were used. The clam shells from the reef flat were covered by crustose and turf algae, as well as a variety of other organisms, in stark contrast to the newly cut clean surfaces of the coral plates. In 1984 larvae were offered a choice of two types of cut coral plate, either Platygyra or Porites. Ten plates of both types were conditioned in the sea for 3 weeks prior to settlement. In both experiments substrata were removed from aquaria and and the number of planulae which had settled on them was scored after 2 days using a dissecting microscope. Only the two main surfaces of the coral plates were scored, and the edges left uncounted since edges could not be examined while keeping the plates underwater.

4.3 RESULTS

4.3.1 Gametogenic cycles

Goniastrea aspera, G. favulus and Platygyra sinensis were all simultaneous hermaphrodites with eggs and testes intermingled in the same mesenteries. Gametogenesis was synchronous within populations.

Oocytes developed for approximately 6 months in G. aspera and P. sinensis, beginning in late April or May and culminating in synchronous spawning events in mid October and mid November. Oogenesis in Goniastrea favulus took place over a more extended period, lasting at least 7 to 8 months (Fig. 4.1). Oocytes of G. favulus sampled in March had mean diameters of 50 to 75μm, indicating that oogenesis was probably initiated 1 to 2 months earlier, in January or February, and the total period of gametogenesis is likely to be 8 or 9 months in length. The mean diameter of spawned eggs was 360μm for G. aspera, 430μm for G. favulus and 405μm for P. sinensis.

Despite the difference in the month of spawning between Geoffrey Bay and Pioneer Bay (4.3.3), the initiation of oogenesis probably occurred at almost the same time in G. favulus and P. sinensis at both bays (Fig. 4.1). In all three species development proceeded so that by June oocytes were of similar sizes at both bays. Differences in the rate of oocyte development became apparent in G. aspera and P. sinensis only 2 to 3 months before spawning, in late August and September when oocytes from colonies at Geoffrey Bay began to grow more rapidly. Goniastrea favulus did not display this trend, perhaps due to the longer period of gametogenesis. Even though oocyte diameters in colonies at Pioneer Bay were very similar to those in Geoffrey Bay colonies in mid October, they did not contain any testes. In G. aspera and P. sinensis testis formation was also initiated one month later in Pioneer Bay populations than in Geoffrey Bay populations.

Differences in the rate of oocyte development in G. aspera and P. sinensis coincided with changes in sea water temperatures at the two sites (Fig. 4.2). Temperatures in the shallow (<10m) waters surrounding Magnetic Island began to rise more rapidly than those at Pioneer Bay which is further offshore. Maximum temperatures at Geoffrey Bay during this period were generally higher than maxima at Pioneer Bay, and minumum temperatures at Pioneer Bay were slightly lower than those at Geoffrey Bay. Temperatures during the spawning period were approximately 27 degrees at both Geoffrey Bay and Pioneer Bay.

Figures

Fig. 4.1 Gametogenic cycles of G. aspera (GA), G. favulus (GF) and P. sinensis (PS), 1983.
Solid line: Geoffrey Bay populations
Dashed line: Pioneer Bay populations
t: testes present in samples
Error bars represent one standard deviation (n = 15).

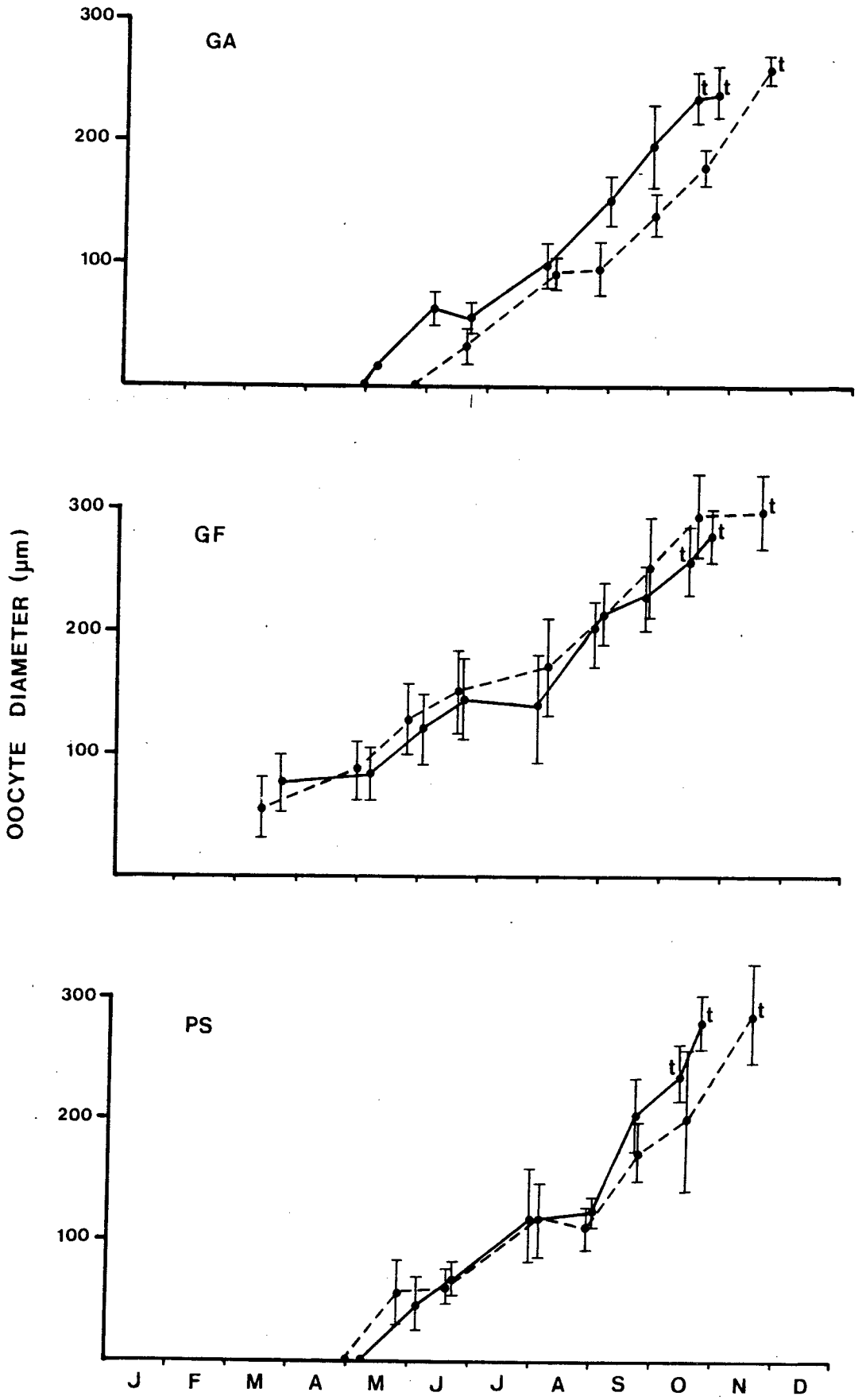
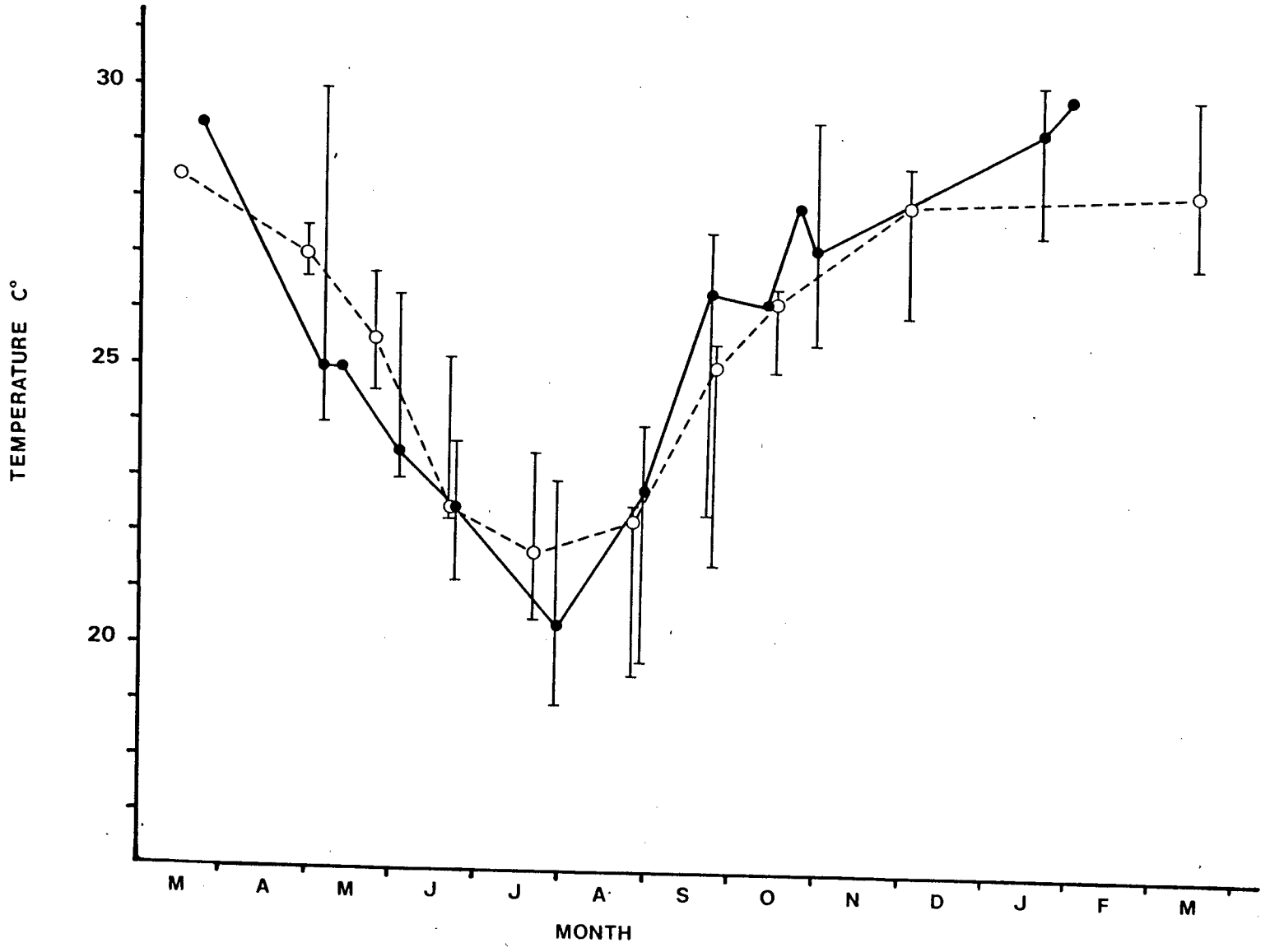

GA
GF
PS
300
200
100
OOCYTE DIAMETER (µm)
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 4.2 Annual temperature cycles 1983 - 1984. Solid line: Geoffrey Bay; dashed line: Pioneer Bay. Error bars represent temperature maxima and minima.


30
25
20
TEMPERATURE C°
M
A
M
J
J
A
S
O
N
D
J
F
M
MONTH

4.3.2 Size specific fecundity

Colony fecundity expressed as numbers of eggs per mesentery increased with size in Goniastrea aspera, G. favulus and Platygyra sinensis (Figs. 4.3, 4.4) until fully mature levels of fecundity were reached. Of the three species, G. aspera became reproductive at the smallest size, with eggs beginning to appear in mesenteries of colonies over 5cm² in area (4 - 5 years old Ch. 4). Goniastrea favulus was found to first become reproductive at slightly larger sizes, between 10 and 15cm² (5 - 6 years), while P. sinensis colonies were not reproductive until they reached sizes greater than 25 to 35cm² (5 - 8 years; Figs. 4.3, 4.4). Although the size at first reproduction was similar at both bays, the rate at which fecundity increased appeared to differ between bays. In each species full fecundity was reached at smaller colony sizes and younger ages at Pioneer Bay than at Geoffrey Bay, However maximum fecundities were similar at both bays (Figs. 4.3, 4.4). Maximum average egg numbers per mesentery were approximately twice as high in Goniastrea aspera (10 - 13) as in G. favulus (4 - 6) or Platygyra sinensis (4 - 7).

The number of egg bearing mesenteries varied between species. Each polyp is divided by the skeletal septa into lobes which contain the mesenteries and there are usually two mesenteries in each of these lobes. In G. aspera both of these mesenteries were egg bearing, however in G. favulus and P. sinensis there was usually only one egg bearing mesentery in each lobe in the populations studied. These differences are accounted for in estimates of mean numbers of eggs per mesentery. Within any given species the number of eggs in the mesenteries of a polyp was often variable, and this was especially true in smaller colonies. Colonies with mean egg numbers per mesentery of less than two, for example, often had mesenteries which contained no eggs but often possessed testes. In all three species, colonies which had very few mesenteries containing eggs might contain a much higher number of mesenteries with testes. This trend reached its fullest development in Goniastrea favulus in which some small colonies were found to contain only testes. Of the G. favulus colonies in which no eggs were found, 33% contained testes at Geoffrey Bay and 8% at Pioneer Bay.

Fig. 4.3 Fecundity (mean number of eggs per mesentery) in relation to colony size (surface area) and age at Geoffrey Bay. Plot of five point running-means.

GA: *G. aspera*

GF: *G. favulus*

PS: *P. sinensis*

Surface area scale square-root transformed.

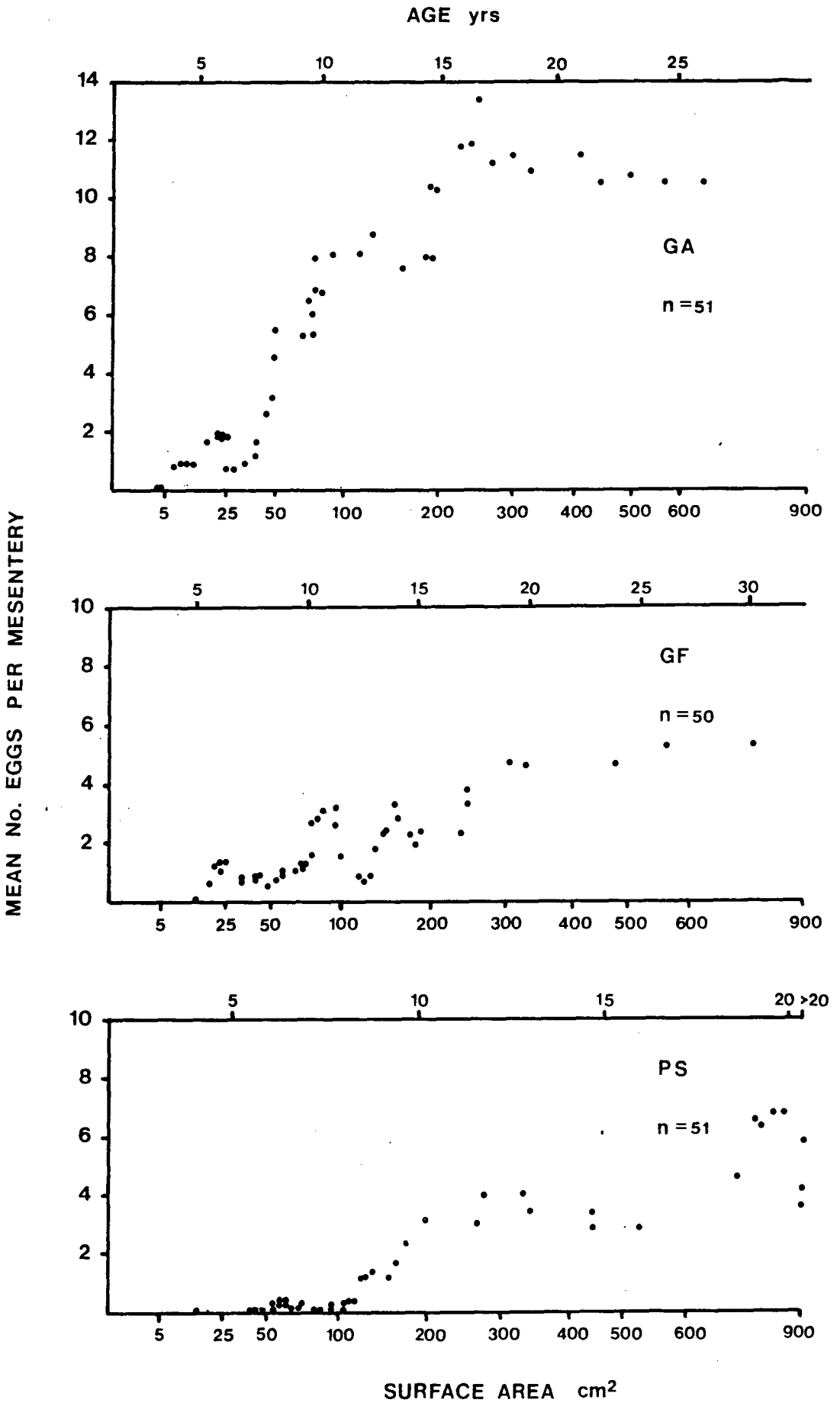

AGE yrs
5
10
15
20
25
14
12
10
8
6
4
2
GA
n = 51
5
25
50
100
200
300
400
500
600
900
MEAN No. EGGS PER MESENTERY
5
10
15
20
25
30
10
8
6
4
2
GF
n = 50
5
25
50
100
200
300
400
500
600
900
5
10
15
20 >20
10
8
6
4
2
PS
n = 51
5
25
50
100
200
300
400
500
600
900
SURFACE AREA cm²

Fig. 4.4 Fecundity (mean number of eggs per mesentery) in relation to colony size (surface area) and age at Pioneer Bay. Plot of five point running-means.

GA: *G. aspera*
GF: *G. favulus*
PS: *P. sinensis*.

Surfacre area scale square-root transformed.

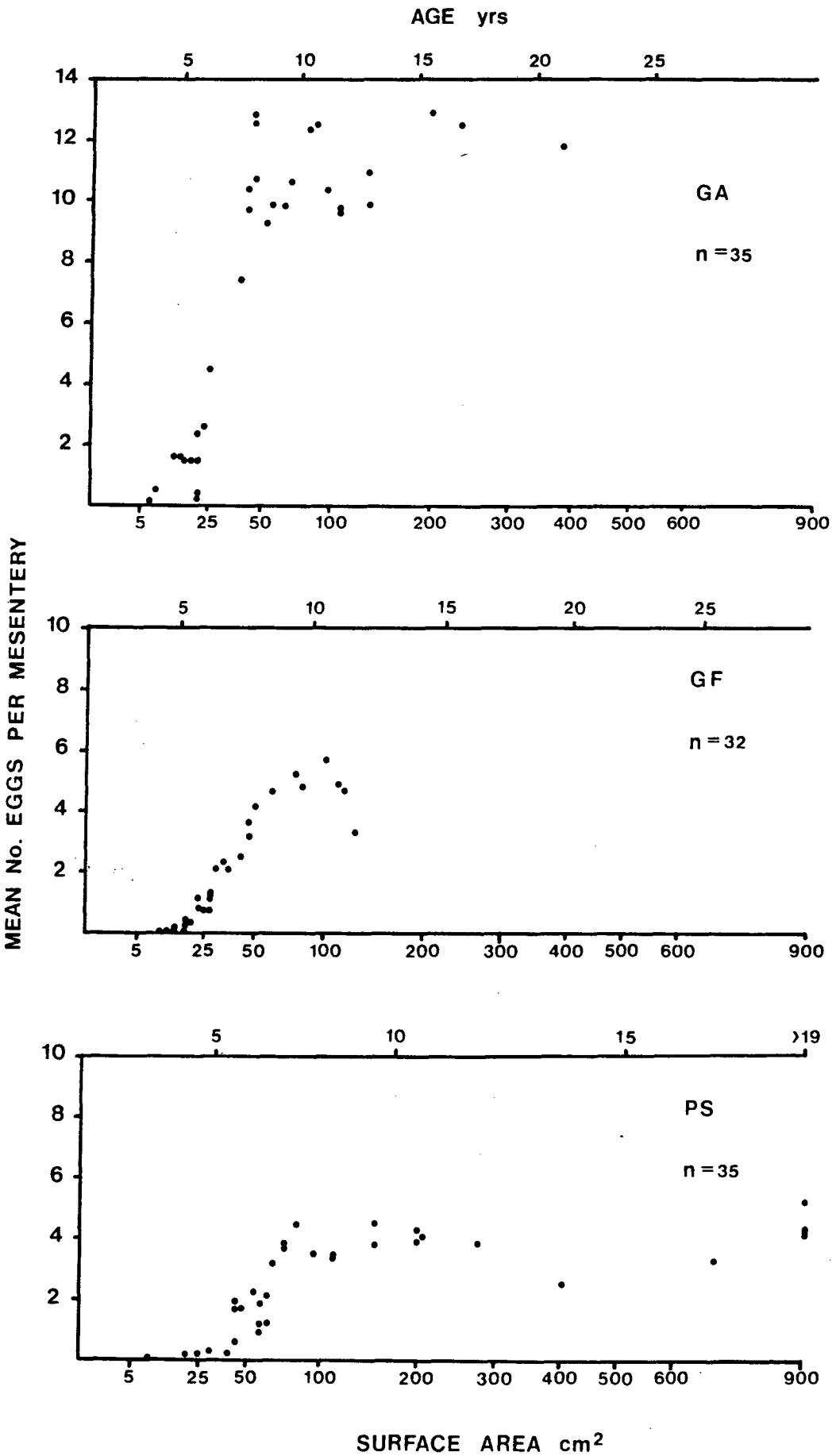

AGE yrs
5
10
15
20
25
14
12
10
8
6
4
2
GA
n = 35
5
25
50
100
200
300
400
500
600
900
MEAN No. EGGS PER MESENTERY
GF
n = 32
PS
n = 35
>19
SURFACE AREA cm²

Table 4.1 Colony size and polyp fecundity. Figures enclosed in brackets represent colonies in which only testes were found. N; number of colonies sampled.

Size class	% repro-ductive	mean number of eggs per mesentery	N
Geoffrey Bay			
G. aspera			
0 - <40	42	0.9	20
40 - <80	100	5.4	10
80 - <120	100	8.0	3
120 - <160	100	8.2	2
160 - <200	100	7.7	4
200 - <240	100	20.9	1
240 - <280	100	10.5	3
280 - 320	100	14.8	1
>320	100	10.6	7
G. favulus			
0 - <40	46(7.6)	0.8	13
40 - <80	91(16.7)	0.8	12
80 - <120	100(14)	2.8	6
120 - <160	100	1.9	7
160 - <200	100	3.7	1
200 - <240	100	1.3	3
240 - <280	100	3.8	2
280 - 320	100	5.5	1
>320	100	5.3	5
P. sinensis			
0 - <40	0	0	5
40 - <80	15	0.3	15
80 - <120	11	0.3	9
120 - <160	40	1.4	5
160 - 200	50	1.2	2
>200	100	4.7	17

Table 4.1 (cont.)

Pioneer Bay

G. aspera			
0 - <40	38	1.7	13
40 - <80	100	11.0	9
80 - <120	100	10.6	6
120 - <160	100	12.3	2
160 - <200	100	14.5	1
200 - 240	100	14.0	1
>240	100	10.3	3
G. favulus			
0 - <40	47(5)	0.8	20
40 - 80	100	3.7	6
>80	100	4.4	6
P. sinensis			
0 - <40	33	0.1	6
40 - <80	76	2.2	13
80 - <120	100	2.8	4
120 - 160	100	3.9	2
>160	100	4.1	10

Table 4.1 (cont.)

Pooled

G. aspera			
0 - <40	57	1.3	33
40 - <80	100	8.1	19
80 - <120	100	9.8	9
120 - <160	100	10.3	4
160 - <200	100	9.1	5
200 - <240	100	17.5	2
240 - <280	100	11.4	4
280 - 320	100	14.8	1
>320	100	10.5	10
G. favulus			
0 - <40	57(6)	0.7	33
40 - <80	88(11)	1.8	18
80 - <120	100(14)	2.8	7
120 - <160	100	2.1	8
160 - <200	100	3.1	2
200 - <240	100	1.3	3
240 - <280	100	3.8	2
280 - 320	100	5.5	1
>320	100	5.3	5
P. sinensis			
0 - <40	18	0.1	11
40 - <80	46	1.3	26
80 - <120	38	1.1	13
120 - <160	71	2.0	7
160 - 200	75	3.6	4
>200	100	4.2	25

Table 4.2 Colony age and polyp fecundity. Percent of colonies in reproductive condition and mean number of eggs per mesentery. Figures in brackets represent colonies in which only testes were found. N; number of colonies sampled.

age class	% repro-ductive	mean number of eggs per mesentery	N
Geoffrey Bay			
G. aspera			
0 - <5	25	0.6	8
5 - <10	63	3.1	22
10 - <15	100	7.9	9
15 - <20	100	12.8	6
20 - 25	100	10.7	4
>25	100	11.0	2
G. favulus			
0 - <5	0	0	3
5 - <10	80(10)	1.1	20
10 - <15	100(12.5)	1.0	16
15 - <20	100	3.1	7
20 - 25	100	5.3	1
>25	100	5.3	3
P. sinensis			
0 - <5	0	0	4
5 - <10	21	0.5	29
10 - <15	100	3.6	7
15 - <20	100	5.6	6
20 - 25	100	4.1	2
>25	100	4.0	3

Table 4.2 (cont.)

Pioneer Bay

G. aspera			
0 - <5	66	0.5	3
5 - <10	84	6.3	19
10 - <15	100	11.0	8
15 - <20	100	14.3	2
20 - 25	100	10.6	2
<25	100	9.6	1
G. favulus			
0 - <5	0	0	6
5 - <10	76(5)	2.0	20
10 - 15	100	4.7	5
P. sinensis			
0 - <5	40	0.1	5
5 - <10	81	2.7	22
10 - <15	100	2.6	3
15 - <20	100	2.4	2
20 - 25	100	5.1	1
>25	100	5.5	3

Table 4.2 (cont.)

Pooled

G. aspera			
0 - <5	36	0.6	11
5 - <10	70	4.6	41
10 - <15	100	9.4	17
15 - <20	100	13.1	8
20 - 25	100	10.6	6
>25	100	10.5	3
G. favulus			
0 - <5	0	0	9
5 - <10	75(8.8)	1.0	34
10 - <15	100(9.5)	2.7	21
15 - <20	100	3.1	7
20 - 25	100	5.3	1
>25	100	5.3	3
P. sinensis			
0 - <5	22	0.1	9
5 - <10	47	1.4	51
10 - <15	100	3.3	10
15 - <20	100	4.9	8
20 - 25	100	4.4	3
>25	100	4.7	6

The mean number of interseptal lobes per polyp, and the mean number of septa cm^{-2} was determined for each species, as follows:

G. aspera 23.7, (S.D. = 5.9); 3.4 polyps cm^{-2}
G. favulus 3.2, (S.D. = 6.8); 3.7 polyps cm^{-2}
P. sinensis 20, (S.D. = 5.2); 4.1 polyps cm^{-2}

The fecundity of colonies of a given size was then calculated by multiplying the number of eggs per mesentery by the number of interseptal lobes per polyp and by the mean number of polyps cm^{-2} (Table 4.3). Colony fecundities in Tables 4.1 and 4.2 do not always increase uniformly, due to irregularities in the estimates in numbers of eggs per mesentery caused by low numbers of colonies sampled in some size classes.

Table 4.3 Mean fecundity of fully mature colonies of *G. aspera*, *G. favulus* and *P. sinensis* from Geoffrey and Pioneer Bays. Fully mature colonies were taken to be those greater than $200cm^2$ in size, based on Figs. 4.3 and 4.4, with the exception of *G. favulus* at Pioneer Bay, for which colonies of over $100cm^2$ were used (Fig. 4.4).

	mean no. of eggs per mesentery	S.E. of means	eggs cm^{-2}
Geoffrey Bay			
G. aspera	11.7	0.3	949
G. favulus	3.9	0.2	340
P. sinensis	4.0	0.2	325
Pioneer Bay			
G. aspera	11.2	0.5	902
G. favulus	4.9	0.3	422
P. sinensis	3.6	0.3	290
Pooled Bays			
G. aspera	11.6	0.2	935
G. favulus	4.3	0.1	368
P. sinensis	4.4	0.1	350

4.3.3 Spawning observations

Spawning of Goniastrea aspera, G. favulus and Platygyra sinensis was found to occur on only a few nights after the full moon, usually in October at Magnetic Island, and in November at Orpheus Island. Individual colonies and populations of each species spawned over a period of one or two nights, although colonies held in aquaria often spawned over a period of up to four nights, presumably due to disturbance by lights and handling. The actual night of spawning varied between the 3rd and 6th night after full moon over a period of 5 years, but usually occurred on the 4th and 5th nights after full moon (Table 4.4).

Since lunar months are not the same length as calendar months the full moon in any given month will fall 11 to 12 days earlier in successive years. This meant that corals spawned earlier and earlier in the month in each successive year, until a critical point was reached where the corals switched to the following full moon. The result of this was that spawning at each site tended to fall within a "window" of appropriate spawning dates (Fig 4.5).

All three species tended to spawn during the same month at each site although there were instances of spawnings being split over two months both within and between species. In 1984 at Magnetic Island the population of Goniastrea aspera spawned after the October full moon, while populations of G. favulus and Platygyra sinensis spawned after both the October and November full moons, with the majority of the populations spawning after the November full moon. In 1985 G. favulus at Pioneer Bay spawned after the October full moon while both G. aspera and P. sinensis spawned after the November full moon (Table 4.4).

Table 4.4 Spawning records records of Goniastrea aspera, G. favulus and P. sinensis from 1981 to 1985. Night of spawning and the number of colonies observed is given, as well as the method of observation. a: spawning observed in aquaria; f: spawning observed in field; n: colonies observed but did not spawn; ( ): spawning inferred from sequential field samples or from the presence of eggs in aquaria. *: colonies resampled on December 8 and were not found to contain any eggs, assumed to have spawned after the November full moon; +: colonies contained no gonads and are assumed to have spawned after the full moon in October.

	Night after Full Moon								
	Magnetic Island October				Orpheus Island November				
	3	4	5	6	2	3	4	5	6
1981									
G. aspera	-	5(f), 3(a)	3a						
G. favulus	-	5(f), 3(a)	2a						
P. sinensis									
1982									
G. aspera		2a	-				2a	2f,3a	
G. favulus		3a	-				1f,4a	3a	
P. sinensis			14f	1a			2a	4a,9f	
1983									
G. aspera	18f	17f, 6(f)	-		-	1f,4a	10(f)		
G. favulus	13f	19f, 2(f)	-		-	2a	2f, 10(f)	4a	
P. sinensis	12f	18f,	-		-	4f,2a	10(f)	4a	
1984									
G. aspera	-	2f,8a	8f		-	6a	5a	3a	
G. favulus	-	1a	16n*			1a	4a	3a	
P. sinensis	-	2a	2a,2f 28n*			-	3a	15a	
1985									
G. aspera	-	4a	2a		-	2a	8a		
G. favulus	-	5a	-		>30n+				
P. sinensis	-	1a	3a		-	4f	3a		

Fig. 4.5 Spawning records for G. aspera, G. favulus and P. sinensis 1980 - 1985.

G. aspera

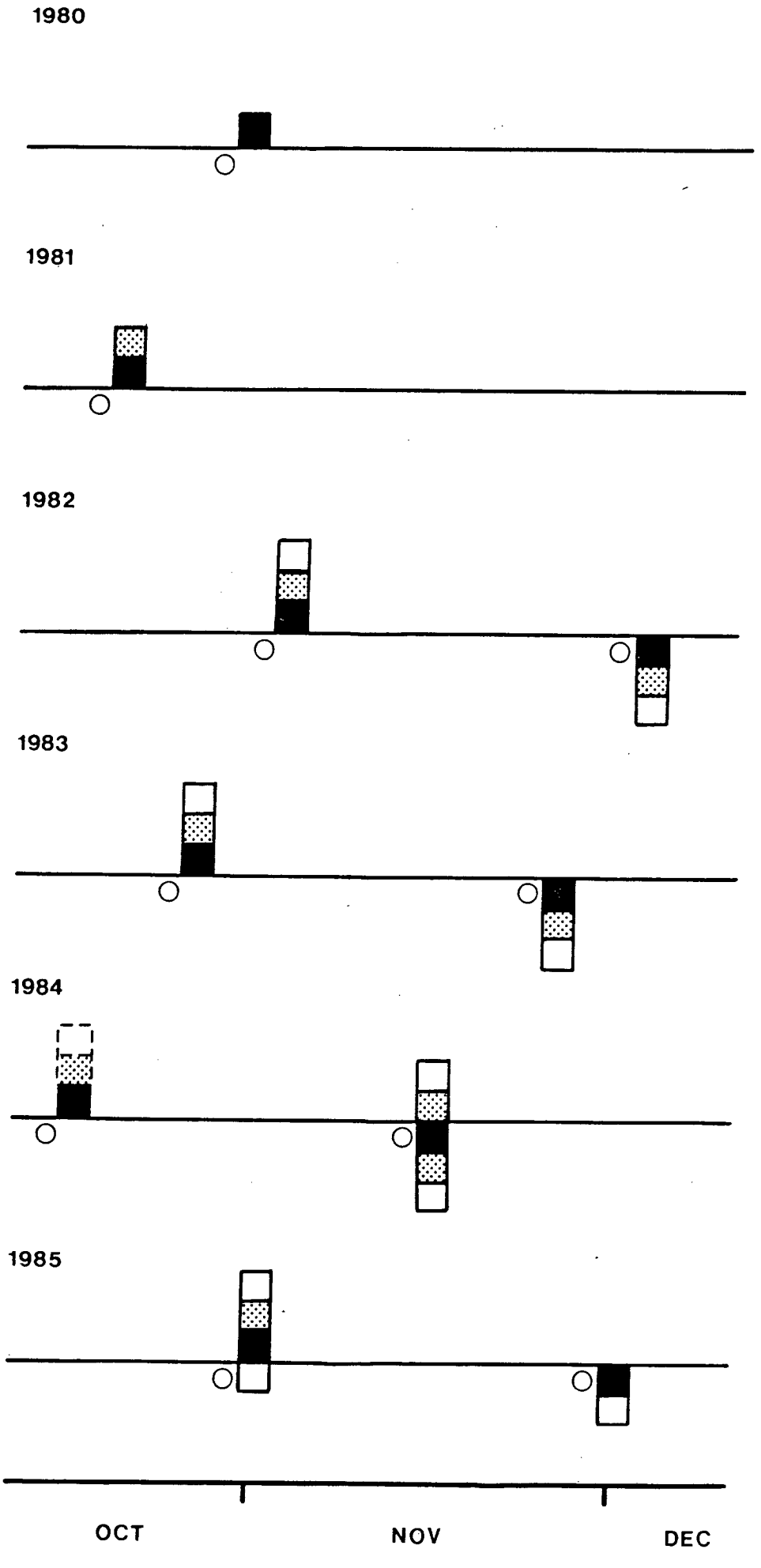
G. favulus

P. sinensis.

Partial spawning of populations.

time of full moon.

Records for Geoffrey Bay above axis, Pioneer Bay below axis. 1980 data from Babcock 1980.


1980
1981
1982
1983
1984
1985
OCT
NOV
DEC

Spawning in each species occurred after dark, and different species spawned at slightly different times (Fig 4.6). Goniastrea favulus spawned earliest, and was recorded as releasing gametes between 25min and 2hrs 10min after sunset. Goniastrea aspera and Platygyra sinensis spawned between 3 and 4 hrs after sunset (Fig. 4.6). These results include both field and aquarium observations. Spurious aquarium observations resulting from disturbance by lights have been omitted. The hour of spawning remained relatively constant in relation to the time of sunset for each species over the period 1982 - 1984. Although the hour of spawning roughly coincided with the of low tide, tides varied considerably in relation to spawning time, with low tide falling both before and after observed spawnings (Fig. 4.6).

A variety of spawning behaviours were observed in the three species. Platygyra sinensis released round egg-sperm bundles (Fig. 4.7) which were slowly squeezed out through the mouths of the polyps, while Goniastrea aspera rapidly ejected numerous irregularly shaped egg-sperm bundles from each polyp. The bundles of G. aspera appeared to correspond to the contents of individual mesenteries. In both of these species spawning tended to occurr throughout the colony at the same time, although on several occasions only part of a colony of G. aspera was observed to spawn, with the rest of the colony spawning several minutes later. The egg-sperm bundles were buoyant and floated rapidly toward the surface after being released. The spawning behaviour of G. favulus was quite different to that of the other species with eggs and sperm being released separately. Eggs were negatively buoyant and enclosed in a gelatinous mucous envelope which caused them to adhere to the parent colony or nearby substratum. Eggs and sperm could be released at the same time but were often released separately, with eggs being released first followed 1/2 to 1 hour later by jets of sperm.

Mass spawning was observed in a number of additional species of scleractinian (Appendix 1) which showed patterns of timing and behaviour very similar to those described for G. aspera, G. favulus and P. sinensis. There was some variation in the night and hour of spawning, with some species releasing gametes before, and some after the period in which G. aspera, G. favulus and P. sinensis were

Fig. 4.6 Time of spawning of G. aspera (GA), G. favulus (GF) and P. sinensis (PS) in relation to sunset and time of low tide, 1982 - 1984.

▼ : times of low tides on spawning nights.

Horizontal lines indicate time and duration of spawning in relation to sunset.

Dates of spawning observations. Only field observations are included.

a: 5/11/82

b: 5/12/82

c: 6/12/82

d: 25/10/83

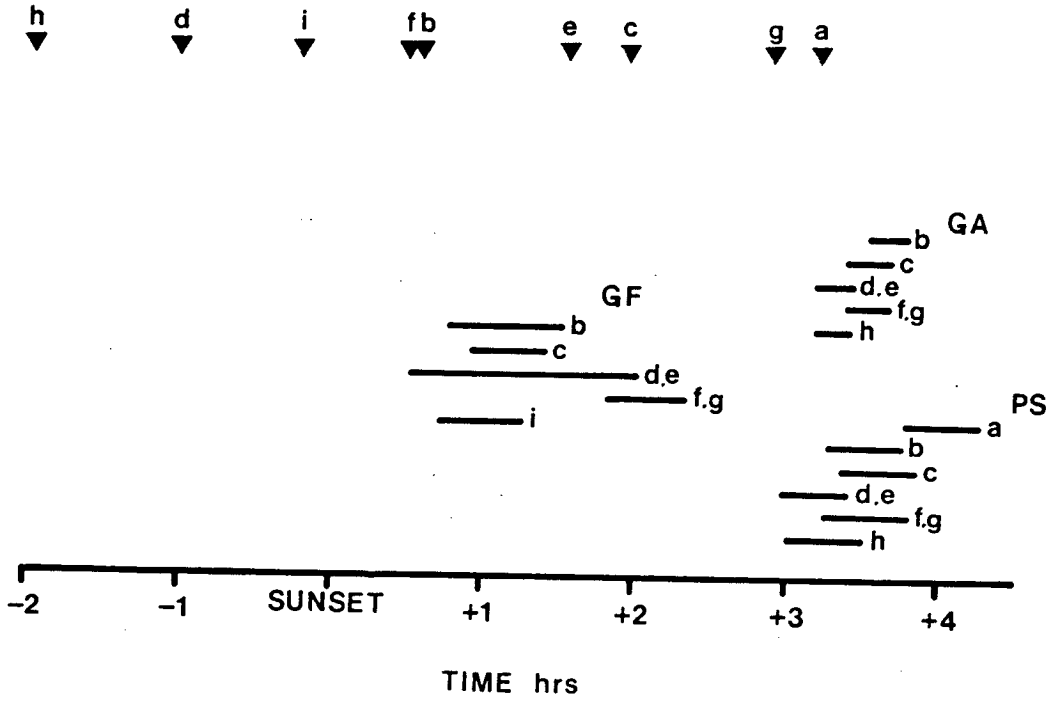
e: 26/10/83

f: 24/11/83

g: 25/11/83

h: 14/10/84

i: 12/11/84


h
d
i
f b
e
c
g
a
GA
b
c
d.e
f.g
h
GF
b
c
d.e
f.g
i
PS
a
b
c
d.e
f.g
h
-2
-1
SUNSET
+1
+2
+3
+4
TIME hrs

observed to spawn. The details of observations made on other species are published in Harrison et al. (1984), Willis et al. (1985), and Babcock et al. (1986).

4.3.4 Larval development

The use of plastic jars floating in the sea proved to be an extremely successful way of culturing embryos. Continuous agitation in many directions, ventilation and ambient seawater temperature are factors likely to have contributed to this success, since the same containers placed on mechanical to-and-fro agitators produced inferior results. Up to 10,000 larvae could be raised in each 4 litre jar, and most appeared healthy after 48 hrs. Larvae held at higher concentrations often showed signs of deteriorating condition after only 12 hours.

Polar bodies were observed in freshly spawned eggs of Goniastrea aspera and G. favulus. None were found on the eggs of Platygyra sinensis; However only a limited number of eggs from this species were examined and their polar bodies may have been overlooked. Additional observations of polar bodies were made on two other scleractinian species, Favia pallida and Pectinia lactuca. The first polar body was already visible in freshly spawned eggs of G. favulus, and the second was released 30 to 45min after spawning. In all other species in which polar bodies were observed, the first polar body was released at between 30 to 60min after spawning, followed by the second polar body approximately 15 to 30min later.

In Goniastrea aspera and P. sinensis sperm clots (sensu Miller 1981) were observed. Some of these may have been formed in response to breakage of the egg membrane however in many cases they were observed to form at the site of polar body release, and polar bodies could be seen associated with the sperm clot. Individual clots could not be followed for long enough to determine whether cleavage originated at the site of aggregation, however in G. favulus cleavage was observed to originate from the point of polar body release and sperm were visible in the initial cleavage furrow in sections of P. sinensis (Fig. 4.7).

In all three species the first signs of cleavage were observed between 1.5 to 2 hours after spawning with subsequent cleavages occurring approximately every hour. Cleavages were equal and radial in G. aspera and P. sinensis (Fig. 4.7), shifting to a pseudospiral pattern of cleavage as development progressed to the 8-cell stage and beyond. Goniastrea favulus exhibited very similar development, with a variable tendency towards slightly unequal divisions in the early stages (Fig. 4.7).

Embryos of all species had developed into hollow blastulae (Fig. 4.8) after 7 hours and by 10 hours both live and histological examination revealed that embryos were beginning to flatten and invaginate (Fig. 4.8). Live embryos at this stage had the appearance of concave/convex discs and could be distinguished from unfertilized eggs without the aid of a microscope. Embryos collected from slicks of coral larvae at the surface of the sea on the morning after spawning were almost all at this stage of development.

Formation of a pharynx by invagination of the ectoderm was noted in all three species within 24 hrs and a gut cavity with well differentiated endoderm was formed between 24 and 36 hrs. The endoderm was highly vacuolated, largely occluding the cavity at this stage, and there was a distinct mesogleal layer (Fig. 4.7). At this stage the larvae were spherical or slightly ovoid and still quite buoyant, concentrating near the surface. By 48 hrs after spawning larvae were fully mobile and capable of maintaining their position at or near the bottom of culture vessels or aquaria, although only a small proportion did so. The majority of larvae concentrated themselves near the surface until about 4 to 5 days old when the majority of larvae were found at the bottom of containers. Development during this period involved further cellular differentiation and the formation of mesenteries prior to settlement (Fig 4.8).

Larvae of Goniastrea aspera and Platygyra sinensis began to settle and metamorphose inside the culture vessels during subsampling between 4 and 5 days after spawning, and when transferred to aquaria containing conditioned settlement substrata, most had settled by 6 to 7 days after spawning. Larvae of G. favulus were transferred to

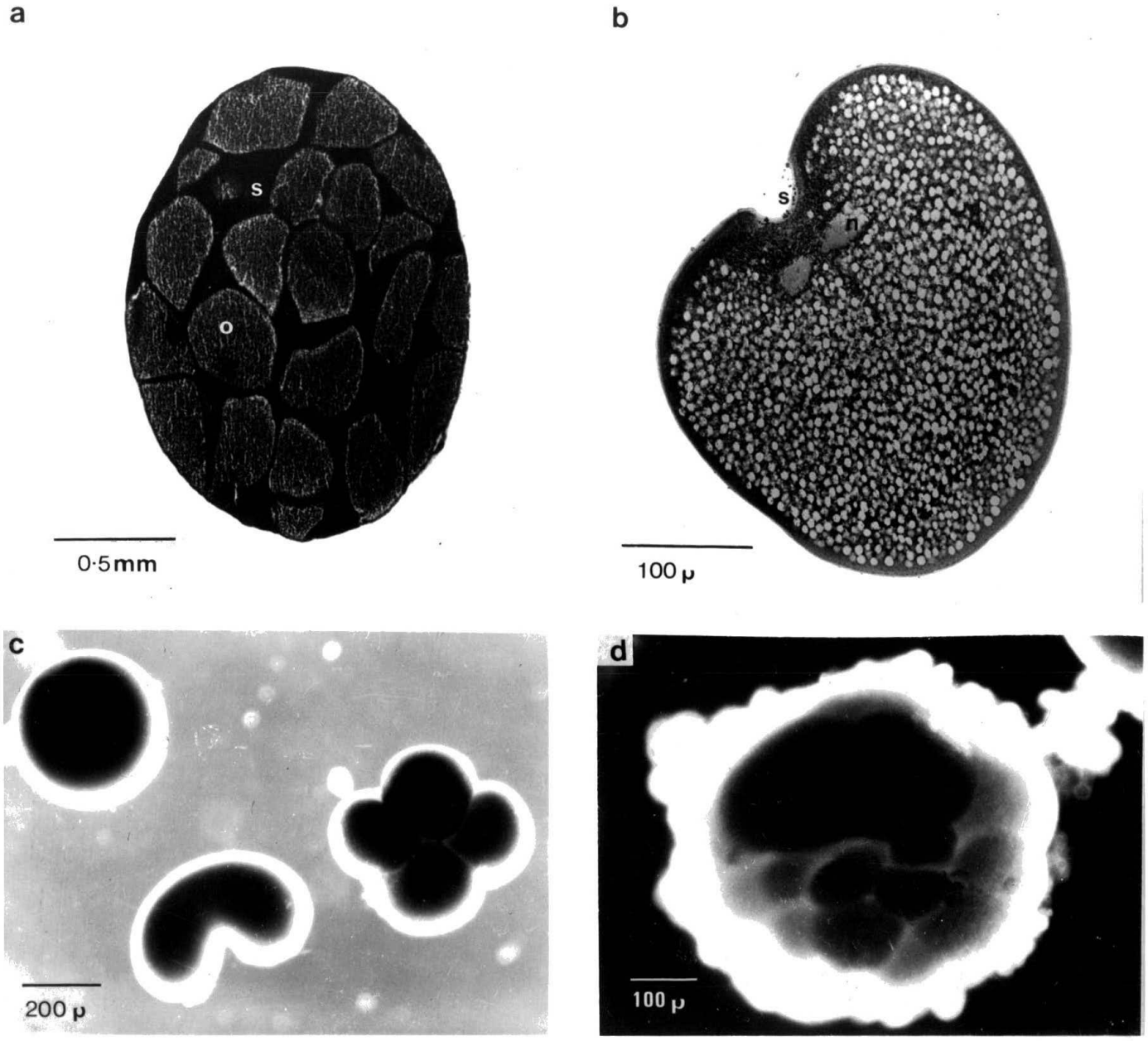
Fig 4.7 Pre-fertilization and early embryonic stages.

a. Egg-sperm bundle of *P. sinensis* shortly after spawning. o: oocyte; s: sperm.

b. First division cleavage in an egg of *P. sinensis* sperm are still present at the site of cleavage (and presumably fertilization). n : nucleus; s: sperm.

c. Egg, two cell and four cell stages of division in *P. sinensis*.

d. *G. favulus* embryo demonstrating unequal cleavage.


a
s
o
0·5mm
b
s
n
100 μ
c
200 μ
d
100 μ

aquaria after 4 days, but only a relatively small number had settled by five days. By the eighth day after spawning however most of the larvae of this species had also settled. By 9 to 10 days after spawning small percentages of larvae continued to swim in the aquaria even though by that time the great majority had metamorphosed.

4.3.5 Larval settlement

The larvae of Goniastrea aspera exhibited marked preferences for certain types of experimental substrata. Conditioned clam shells had approximately 10 times as many corals settled on them (1258) as did freshly cut coral plates (167) ($t = 2.39$, $p < .05$). Larvae were about 50% more likely to settle on plates cut from favid corals than those cut from Porites ($t = 4.64$, $p < .001$).

4.4 DISCUSSION

4.4.1 Gametogenic cycles

The gametogenic cycles displayed by Goniastrea aspera, G. favulus and Platygyra sinensis were typical of those found in other colonial scleractinians, especially those of the family Faviidae, a number of which have been studied previously in detail (Marshall and Stephenson 1933; Kojis and Quinn 1982; Harriott 1983a; Szmant-Froelich in press). The pattern found in most favid corals is that of hermaphroditic colonies with a 5 to 9 month gametogenic period, synchronous throughout the colony, with testes developing only in the last month before spawning. Exceptions to this pattern are Favia fragum, which planulates and has an extended breeding period and overlapping gametogenic cycles within colonies (Szmant-Froelich et al. in press), and Montastrea cavernosa (Szmant-Froelich in press), and Diploastrea heliopora (pers. obs.) which are gonochoric.

The timing of the initiation of gametogenesis has recently been

Fig. 4.8 Embryonic and larval stages.

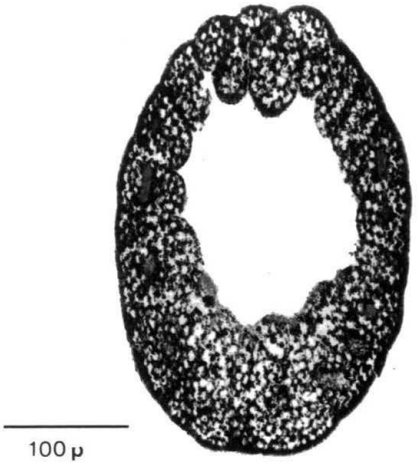
a. Blastula of P. sinensis, L.S. 7hrs old.

b,c. Invaginating blastulae of P. sinensis, L.S. 10hrs.

d. Planula of P. sinensis. The gut is fully formed and endoderm (en), mesoglea (m), and ectoderm (ec) are well differentiated. L.S. 26hrs.

e. P. sinensis planula showing further differentiation of the ectoderm, a well formed pharynx (p), and mesenteries (me). L.S. 6.5 days.

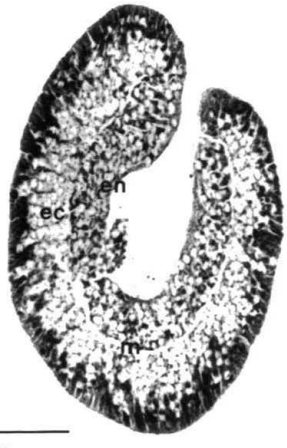
f. An 8 day old larva of P. sinensis. This larva had metamorphosed just prior to settlement. Six mesenteries are present, of which the two directives are better developed and possess well differentiated mesenterial filaments. T.S.



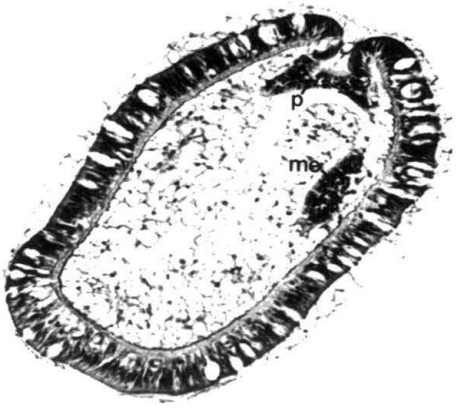
100 µ

50 µ

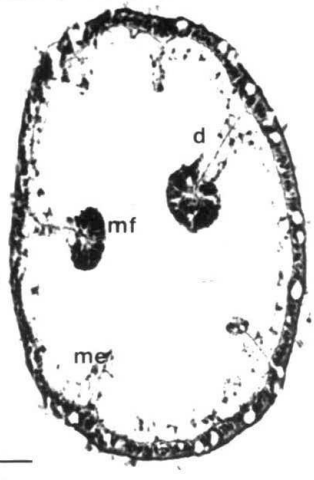
50 µ



100 µ



100 µ



100 µ

suggested as a factor in determining the date of spawning in Pocillopora verrucosa in the Red Sea (Fadlallah 1985). In that species gametogenesis began at the same time as low winter sea temperatures began to rise. The results of the present study suggest that reproductive seasonality is probably under more complex control, since even though oocyte development started at different times in the three different species in this study, they all spawned at the same time (Fig. 4.1). In addition populations of G. favulus and P. sinensis which spawned one month apart began to develop oocytes at the same time, and in all three species oocyte diameters were the virtually the same at both bays during the intermediate stages of oogenesis. The recent discovery of a mass spawning of scleractinians on the west coast of Australia (Simpson 1985) in March, during a period of falling temperatures, indicates the possibility of a large degree of genetic determination of spawning seasonality, rather than a totally physiological relationship between temperature and gametogenesis.

While physiological controls such as temperature may not absolutely determine spawning season or the timing of spawning on wide geographic scales, they may be influential at local scales where there is likely to be a high degree of larval exchange between reefs (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986), such as those dealt with in this study. The more rapid warming of waters around Magnetic Island in Cleveland Bay may result in earlier maturation and spawning of corals at Geoffrey Bay. Oocyte development in G. aspera and P. sinensis at Geoffrey Bay is accelerated relative to that observed in these species at Pioneer Bay. The formation of testes prior to spawning may also be under the influence of temperature. Populations of G. favulus had very similar rates of of oogenesis at both bays, even up to the time of spawning, however testes were formed one month later in the population at Pioneer Bay. This apparent influence of temperature on testis development may also affect G. aspera and P. sinensis, which also form testes one month later at Pioneer Bay than at Geoffrey Bay. It is possible that temperature influences the timing of spawning more by its effect on the timing of testis formation than by its effect on oogenesis in G. aspera, P. sinensis as well as G. favulus. Without direct evidence from controlled experiments a

cautious interpretation of the relationship between temperature and gametogenesis is necessary, but temperature and changes in temperature have been shown to play important roles in the reproductive cycles of other invertebrates (Orton 1920; Korringa 1947; Campbell 1974; Schroeder and Hermans 1975). Clinal variations in temperature with depth have also been shown to have corresponding variations in the timing of reproductive season in populations of the octocorals Muricea californica and M. fruticosa on the California coast (Grigg 1979).

4.4.2 Size specific fecundity

Fecundity in colonial scleractinians has two components. Firstly, fecundity increases as the colony grows and more polyps are formed, and secondly, the fecundity of individual polyps can increase with age or size (Marshall and Stephenson 1933; Rinkevich and Loya 1979; Kojis and Quinn 1981; Babcock 1984). Changes in polyp fecundity, usually expressed as number of eggs per mesentery, is primarily a function of colony size, although there appear to be age or historical effects as well (Kojis and Quinn 1985; Szmant-Froelich 1985). All three species in this study exhibited a roughly sigmoidal increase in fecundity as measured by number of eggs per mesentery. There was the result of a pre-reproductive phase of 4 to 8 years, followed by an 'adolescent' period during which fecundity increased to adult levels.

A number of differences were observed between species in their potential fecundity and the rate at which colonies matured. Platygyra sinensis became reproductive at larger sizes (~50 cm^2, or 2.8cm mean radius) than did either Goniastrea species (15 - 25 cm^2, or 1.5 - 2cm mean radius), but since P. sinensis grows more rapidly the age at which reproductive activity begins is similar in all three species at around 5 years old (Fig. 4.3). This lends some support to the experimental findings of Kojis and Quinn (1985, for G. favulus), and Szmant-Froelich (1985) that there is a historical component (age) involved in changes of polyp fecundity. If the three species were to be ranked in terms of the onset of reproductive activity, G. aspera is the most precocious, with some colonies possessing gonads after only four years. This species also

reached adult levels of fecundity more quickly than did G. favulus (5 - 6yrs) or P. sinensis (5 -8yrs) at Geoffrey Bay. In general, adult levels of polyp fecundity were reached by each species at sizes of between 100 and 200 cm^2 (4 - 5.5cm mean radius). Kojis and Quinn (1981) estimated the age of first reproduction of G. favulus at Heron Island to be 4 - 7 years, which agrees well with the results of this study.

Estimates of age at first reproduction in other colonial scleractinians range from 1.5-2yrs for Stylophora pistillata (Rinkevich and Loya 1979) and 2yrs for Favia fragum (Szmant-Froelich et al. in press), to 4yrs for Porites lutea (Harriott 1983), 4-5yrs for Acropora granulosa, A. hyacinthus, A. loripes and A. valida (Wallace 1985), and 5-6yrs for Montastrea annularis (Szmant-Froelich in press). Apart from Favia fragum and Stylophora pistillata these values are all surprisingly similar to each other and to the results obtained in this study, especially given the wide morphological range of species cited. Both F. fragum and Stylophora pistillata are planulating species. There appears to be a trend among scleractinians for species with an early age of first reproduction and short life span to brood larvae (Ch. 6).

Within each species there were differences between bays in the rate at which mean number of eggs per mesentery increased, as well as in the upper limit of polyp fecundity achieved. Adult levels of fecundity were achieved at between 10 to 15 years in populations of all three species. Differences in rate of change were relatively greater than those in maximum fecundity. All the species matured more rapidly at Pioneer Bay than at Geoffrey Bay, however this trend did not correspond well with differences in growth rates observed at the two bays (Ch. 3). For example G. favulus grew faster and matured sooner at Pioneer Bay than at Geoffrey Bay, while in contrast G. aspera grew more quickly at Geoffrey Bay, but still matured sooner at Pioneer Bay. Differences in fecundity between sites which may be related to physical factors have been demonstrated in other scleractinians (Acropora palifera, Kojis and Quinn 1984), however it is not clear what factors might cause the earlier development to full maturity of populations at Pioneer Bay. Populations at Pioneer Bay were found to have a longer period of

gametogenesis than those at Geoffrey Bay. Maximum fecundity was lower in the populations of G. favulus at Geoffrey and Pioneer Bays (5 to 6 eggs per mesentery, Figs. 4.3, 4.4) than in the population studied by Kojis and Quinn at Heron Island (over 7). This may be due in part to the larger average size of this species at Heron Island (Ch. 4; Kojis and Quinn 1981). This is especially true of the population at Pioneer Bay where large colonies of this species are relatively rare.

The numbers of eggs per mesentery reached by G. aspera were approximately twice those found in G. favulus and P. sinensis (Table 4.3). Since the eggs of G. aspera were about half the volume of the eggs of the other two species it is possible that egg number varies as a result of the architectural constraints of the polyp. Producing larger eggs may mean that fewer can be fit into the available space. In terms of reproductive success, small eggs may be individually less likely to survive than larger ones, but this disadvantage can be overcome by producing eggs in large numbers (Stearns 1976).

4.4.3 Spawning observations

Populations of Goniastrea aspera, G. favulus and Platygyra sinensis spawn gametes for external fertilization during an annual spawning event which occurs over a period of two nights following full moons in October or November on the Great Barrier Reef. The synchrony of spawning observed in these and other species (e.g. Acropora formosa Oliver 1979) encouraged research into the spawning behaviour of a large number of other species which led directly to the discovery of the mass spawning of corals on the central Great Barrier Reef (Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). The mass spawning of corals has now been shown to involve species from most scleractinian families, as well as a number of alcyonaceans (Babcock et al. 1986). The number of species which have been observed to participate in this phenomenon is now in excess of 133 (Willis et al. 1985; personal observations) and

includes almost 40% of scleractinian species on the GBR. For the sake of brevity the mass spawning will be discussed here mainly in terms of the results of this study for G. aspera, G. favulus and P. sinensis. The phenomenon has been discussed in wider terms in the papers cited above and these should be referred to for further details concerning other species.

The mass spawning phenomenon is unique in the literature on reproductive biology in its predictability, synchrony and the number of species involved. Other examples of highly predictable, highly synchronized annual reproductive cycles occur in marine organisms. Spawning may occur on only one or two nights a year (e.g. in Eunice viridis and Comanthus japonica Korringa 1957; Kubota 1981) or it may occur with a definite periodicity within a more extended breeding season (Centrechinus (Diadema) setosa), Leuresthes tenuis, Neofibularia nolitangere, Clunio marinus, Fox 1924; Korringa 1957; Reiswig 1970; Neumann 1981). Although a number of species of hydromedusae have been reported to spawn together at Friday Harbour, USA (Miller 1979), the spawning occurs over an extended period. There are some parallels between the mass spawning of corals and two groups of periodic cicadas in North America which emerge synchronously to reproduce every 13 and 17 years, with three different species involved in each emergence (Lloyd and Dybas 1966). The synchronous flowering of tropical tree communities in Central America (Janzen 1967) is probably the closest parallel at the community level, with approximately 100 species flowering at the same time, during the dry season. This flowering season lasts for about two months, a much more extended period than that observed in coral communities on the central GBR. Although the mass spawning season of corals may last for just over a month (e.g. in split spawning years, Fig. 4.5), it is episodic, and occurs only for brief periods during that time. Marine organisms may have a factor constraining optimal times for spawning, in the form of tides, which does not exist in terrestrial communities.

Proximate factors

Several factors have been implicated as proximate cues in synchronizing the mass spawning of scleractinian corals. These cues

appear to "operate on increasingly fine time scales: annual sea temperature patterns, monthly lunar or tidal cycles, and diel light cycles" (Babcock et al. 1986). Sea temperature patterns have been discussed above (4.4.1) as they relate to gametogenic cycles. Temperature appears to influence the final maturation of gametes only on a local basis, and on wider geographic scales there may be other, as yet unidentified ultimate factors which determine the season of spawning (Simpson 1985). This idea has been stated by Janzen (1967) in relation to tropical tree communities when he stated that the seasonal peak in flowering was "the result of selection for sexual reproduction at the most opportune time in the year, rather than the result of immutable physiological processes which can only occur at that time of the year".

A strong relationship between lunar phase and spawning time was evident in the spawning of G. aspera, G. favulus and P. sinensis, as well as other corals involved in mass spawning. Observations show that spawning occurs after nightfall following the first full moon subsequent to the maturation of gonads. Goniastrea aspera, G. favulus and P. sinensis usually spawned on the 4th and 5th nights after the full moon, however spawning night ranged between the 3rd to the 6th night after full moon. Lunar periodicity has been well documented in brooding corals (Abe 1937b; Atoda 1953; Lewis 1974a; Rinkevich and Loya 1979, Richmond and Jokiel 1984) and in gamete releasing species (Kojis and Quinn 1981, 1982a,b; Harriott 1983a; Babcock 1984; Harrison et al. 1984; Willis et al. 1985; Babcock et al. 1986). A wide range of other marine organisms also display distinct lunar periodicity in their reproductive behaviour (Korringa 1957; Johannes 1978; Kubota 1981). In particular the spawnings of Comanthus japonica (Kubota 1981) and Eunice viridis (Caspers 1984) are similar to many corals in that they occur on only a few days once a year. It is also interesting to note that in the planulating species Favia fragum, the only brooding scleractinian species in which both gametogenesis and embryogenensis have been documented, gamete release also occurs 4 to 5 days after full moon (Szmant-Froelich et al. in press).

Observations of the mass spawning of corals in the Dampier Archipelago in Western Australia have shown that spawning there

occurs mainly on the eighth and ninth nights after the full moon which fall during or just before periods of neap tides (Simpson 1985). Simpson argues that this evidence indicates some role for tides, specifically neap tidal periods, as proximate factors entraining and influencing the night of spawning. While this is possible, it should be remembered that there is likely to be very limited genetic exchange between coral populations in eastern and western Australia. Populations in the two regions may therefore be exhibiting an adaptive, rather than a physiological response to different tidal cycles - using moonlight to achieve the same net result of spawning just on or before neap tides.

It has been shown that the timing of the release of planulae in races of Pocillopora damicornis at Hawaii can be manipulated experimentally by means of artificial moonlight (Jokiel et al. 1985). This indicates that moonlight can be detected by corals and that it can act as a factor entraining reproductive rhythms. Other factors such as pressure (Naylor and Atkinson 1972) and water motion (Neumann 1978) may act as zeitgeibers for a tidal rhythm, but they have not yet been demonstrated for coelenterates. The time of spawning of G. aspera, G. favulus and P. sinensis (Fig. 4.6) was much more closely correlated with time of sunset than with the time of the low tide which occurred on the nights of spawning. In addition, colonies of all three species kept in tideless conditions in aquaria spawned at the correct time in relation to light regimes (Babcock 1984). It therefore seems likely that moonlight itself is acting as the cue which synchronizes the mass spawning of corals, rather than the effects of tides.

Spawning tends to occur after a specific period of darkness, ranging from 30 minutes in G. favulus, to 3 to 4 hours after sunset for G. aspera and P. sinensis (Fig. 4.6). It is probable that the final sequence of events leading to the release of gametes is set in motion by the onset of darkness, once the gametes are fully differentiated. Babcock (1984) showed that for G. aspera in aquaria, the hour of spawning could be controlled by manipulating the light-dark cycle. Similar biological mechanisms using diel changes in light appear to be widespread in coelenterates (Campbell 1974; Honneger et al. 1980; Yoshida et al. 1980).

Ultimate causes

Successful synchronization of gamete release within populations, however it is achieved, maximizes the probability of achieving fertilization. While temperature, moonlight and sunlight may be used to synchronize spawning, they are not necessarily the factors which ultimately determine the optimal time for spawning to take place. For example, moonlight can be used to predict the tidal regime. This use of one signal to gain information about another, perhaps less easily detectable factor, has been shown to exist in a number of arthropod species (Tevis and Newell 1962; Hoffman 1978). The significance of the precise time during the lunar/tidal cycle at which coral spawning occurs, (at night, around the time of low tide), may be related to the need to avoid predation while still producing high concentrations of gametes in order to maximize fertilization. Spawning at night minimizes predation by visual feeders such as planktivorous fish species.

It is also possible that the timing of spawning is related to the advantage of reduced dispersal of gametes prior to fertilization. On the nights following the full moon, particularly the 4th and 5th nights, low tide falls between late afternoon and midnight on the central GBR. The amplitude difference between this low tide and the following low tide is small (<0.5m), resulting in an extended period of slack water (Fig. 4.9) during which the majority of coral species spawn. Thus it is possible that the timing of spawning is ultimately due to the advantage of increased fertilization during periods of low water motion.

Evidence which supports the importance of tides as an ultimate factor in determining the timing of spawning can be obtained from Goniastrea favulus. This species spawns during the daylight at Heron Island (30mins to 1hr,30min before sunset, Kojis and Quinn 1981), but after dark on reefs off Townsville (25min to 2hrs,10min after sunset). In both cases however spawning occurs around low tide. Tides in the Townsville region always occur one half hour or more later than those at Heron Island (Maxwell 1968). Spawning

during low tide has been postulated as a mechanism for increasing the concentration of gametes in other animals (McDowall 1969). This may be especially important for G. favulus since it is a species restricted to reef flats, and its eggs are negatively buoyant and not released in egg-sperm bundles as occurs in other species such as G. aspera and P. sinensis. Corals in Western Australia spawn at the same phase of the tidal cycle as corals on the GBR, around periods of low tidal range during neap tides (Simpson 1985). This gives further weight to the argument that tidal conditions are an important ultimate factor in determining the time of spawning. This is true whether or not tides may also act as proximate cues for spawning synchrony as suggested by Simpson.

The interspecific synchrony of coral spawning on the GBR is the most significant and unusual aspect of the mass spawning phenomenon. This synchrony may be the result of species responding independently to physical factors in order to maximize reproductive success. The buoyant properties of eggs and egg-sperm bundles (in all mass spawning species except G. favulus), modes of reproduction, and larval development (Babcock and Heyward in press) of species involved in the mass spawning are very similar; therefore the physical constraints which determine optimal spawning times for each species are also likely to be similar.

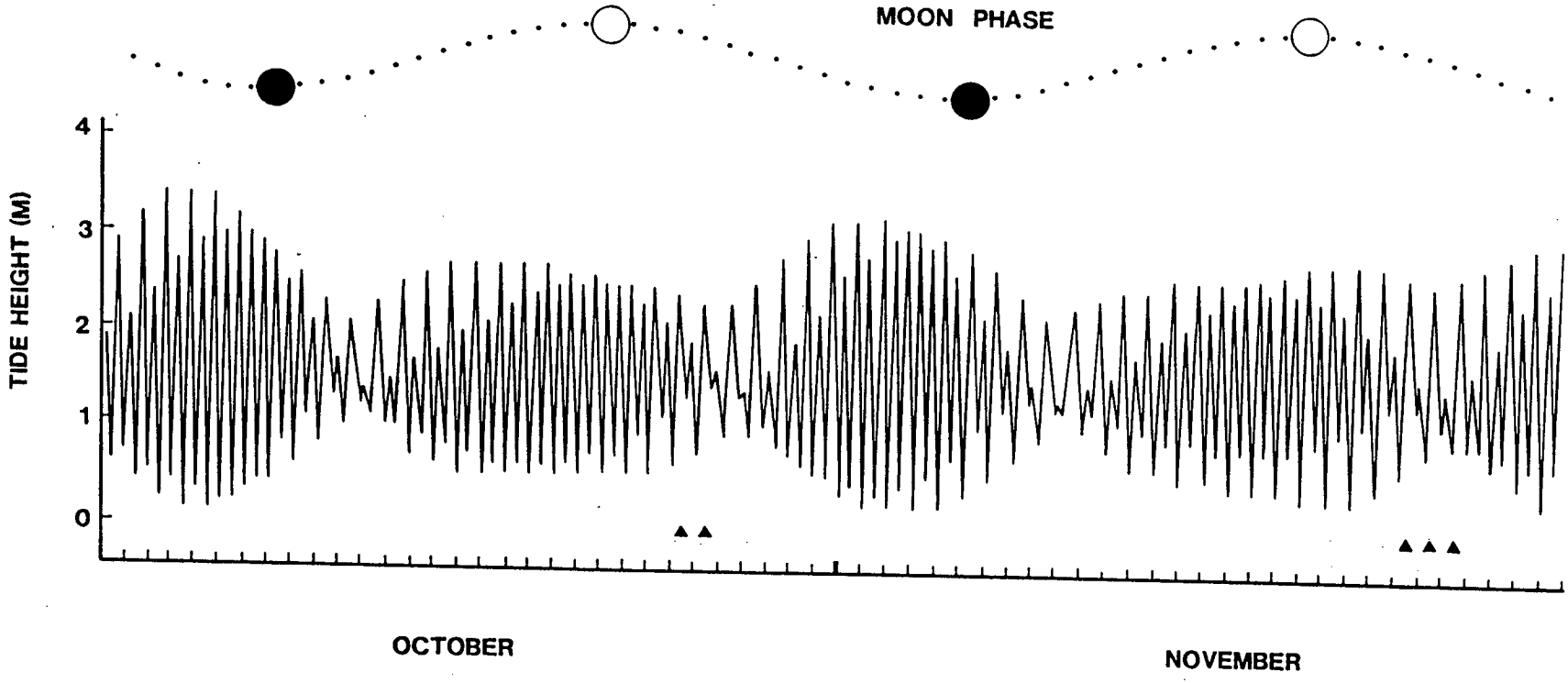
It has also been suggested (Harrison et al. 1984) that the chances of survival of planktonic eggs and larvae would be increased during synchronous multispecific spawning, by satiating predators. A number of planktivorous fish species have been observed eating coral eggs, including species of Abudefduf, Neopomacentrus, and Pomacentrus, which picked off egg-sperm bundles as they were released. This activity was observed only during the crepuscular period, when there was still sufficient light for visual feeding. These observations are significant in that mass spawning occurs during the period of darkness between sunset and moonrise, after the third night following full moon, thus limiting the impact of visual predators. These observations demonstrate that predation does occur, and that there may be a relationship between the timing of spawning and the need to reduce predation. However, they do not constitute evidence to support the predator satiation hypothesis, they merely

Fig. 4.9 Spawning of *G. aspera*, *G. favulus*, and *P. sinensis* in relation to tidal amplitude, October and November 1983.

○ : full moon

● : new moon

▲ : spawning observed


MOON PHASE
TIDE HEIGHT (M)
4
3
2
1
0
OCTOBER
NOVEMBER

show that the timing of spawning may be advantageous for individuals, regardless of the number of other colonies or species which are spawning at the same time. In order to prove that predator satiation might be a factor contributing to the multispecific nature of the mass spawning phenomenon it must be shown that the proportion of eggs and larvae which escape predation is proportional to the number of species spawning at any one time.

It is now known that the mass spawning of scleractinian corals occurs not only on the GBR but in Western Australia as well. The phenomenon does not appear to occur in the Red Sea, where coral species spawn over a period of several months, and during a variety of different lunar phases (Shlesinger and Loya 1985). In the Caribbean Sea, some corals spawn together (Acropora cervicornis and Diploria strigosa), but a greater number spawn or planulate at various times throughout the year (Szmant-Froelich, in press). Slicks of scleractinian larvae have been reported from Bermuda (Butler 1980, S. Wyers pers. comm.) which are similar to slicks observed as a result of coral spawning on the GBR. Variation in physical factors, such as tidal amplitude and annual sea temperature range, which may determine the most favorable spawning period, appear to be more pronounced on the GBR (Maxwell 1968) and the coast of Western Australia (Simpson 1985) than in the Red Sea (Shlesinger and Loya 1985) or Caribbean (Olhorst 1980). This may more sharply define the period of time during which conditions are optimal for reproductive success on the GBR and Western Australia, thereby concentrating the reproductive season of many corals into a relatively brief period of time.

Although there are a number of similarities in the timing of mass spawning between corals on the GBR and in west Australia in relation to the time of day and phase of the tidal cycle during which spawning occurs, there are also several significant differences. These are principally the relationship of lunar phase and annual temperature cycles with spawning. Differences in these factors have already been discussed in terms of their possible role as proximate cues, and because of the differences between the two regions it seems reasonable to assume that they are not the ultimate factors which determine the day or season of spawning (indeed this

has never been suggested). It may be possible to explain the difference in the season of spawning in terms of seasonal wind and current patterns (Simpson 1985), since spawning in both regions takes place at times when prevailing wind patterns are changing, resulting in an increased likelihood of prolonged periods of calm weather (Walker and Collins 1985; Simpson 1985). This cannot however be a full explanation since these wind and current patterns must change twice every year. One common aspect of seasonal current patterns in relation to mass spawning at the two sites is that spawning takes place when prevailing surface circulation shifts from generally northerly to southerly movement. The adaptive significance, if any, of this similarity is not clear.

4.4.4 Larval development and behaviour

Observations on the developmental rates of *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis* are consistent with those reported for other gamete spawning species of scleractinian (Szmant-Froelich *et al.* 1980; Kojis and Quinn 1982a; Krupp 1983; Babcock and Heyward in press). Larvae of all three species studied developed into mobile ciliated larvae between 1 and 2 days. These rates are comparable to those observed in planulae collected in the field (Bull 1986).

Despite the fact that *Goniastrea aspera* and *G. favulus* are capable of varying degrees of self-fertilization (Heyward and Babcock 1986), the observation that polar body release is not completed until some time after spawning indicates that self-fertilization will not occur prior to the release of gametes and the break-up of egg-sperm bundles (Fig. 4.7). By the time eggs are capable of being fertilized, the presence of gametes from a large number of different colonies makes cross-fertilization more likely than self fertilization.

Early cleavage patterns observed in *G. aspera* and *P. sinensis* were very similar to each other and to those observed in other corals with external fertilization (Szmant-Froelich *et al.* 1980; Babcock and Heyward in press), with the first cleavages being equal. The

slightly larger eggs of G. favulus which are benthic, develop in a slightly different manner with a relatively greater tendency towards unequal cleavages. In P. sinensis the cleavage furrow was initiated at the probable site of sperm entry, near the nucleus (Fig 4.7). Similarly, cleavage in the temperate scleractinian Astrangia danae was found to be initiated adjacent to the nucleus (Szmant-Froelich et al. 1980). Studies on the eggs of Hydrozoans (e.g. Orthopyxis, Miller 1981) have shown that fertilization can only occur at a point on the egg adjacent to the nucleus. The cleavage pattern in all three species was similar to that observed in Astrangia danae in that cleavage began in a radial plane and subsequently rotated into a pseudospiral formation (Szmant-Froelich et al. 1980).

Endoderm formation in G. aspera, G. favulus and P. sinensis examined both histologically and as whole mounts indicated that endoderm formation was by invagination, as was found in the embryos of all other gamete spawning species of scleractinian so far examined. In most anthozoans endoderm formation is by invagination (Mergener 1971), however in Favia fragum (Szmant-Froelich et al. in press) and Meandrina areolata (Boschma 1929), (which are both brooding species), endoderm formation is by a process of delamination.

Since the eggs of G. aspera and P. sinensis are buoyant and larvae do not become mobile until 1 to 2 days after spawning, dispersal away from the parent reef is likely unless local current patterns such as topographic eddies (Williams et al. 1985) result in the retention of a particular water mass near the parent reef. This conclusion applies to the larvae of the majority of corals which spawn gametes for external fertilization, e.g. mass spawning species, since all of them except G. favulus also have buoyant larvae and have similar developmental rates (Babcock and Heyward in press). The smaller eggs of Porites cylindrica (mean diameter 231μm) developed more rapidly and were mobile after only one day (Kojis and Quinn 1982a). While the eggs and larvae of G. favulus may have a lower chance of dispersal immediately after spawning, larvae raised in aquaria are found swimming in the water column once they become mobile, and there is still a chance of significant dispersal in this species. This is reflected in small scale dispersion patterns in populations of this species which do not show a greater

degree of aggregation than those of closely related species with more dispersive eggs (Ch. 2).

Larvae of G. aspera, G. favulus and P. sinensis were found to be capable of settlement after 4 to 5 days, with the majority of larvae having settled by seven to eight days after spawning. Again, similar results were obtained for the larvae of other gamete spawning species with the majority of larvae settling between 5 and 10 days (Babcock and Heyward in press). Larvae of Porites cylindrica raised in aquaria by Kojis and Quinn (1982a) settled after 7 days. These settlement times are shorter than those previously reported for Acropora formosa and A. hyacinthus of 16 to 36 days (Harrison et al. 1984), G. favulus 17 to 20 days (Kojis and Quinn 1981), and G. aspera which could not previously be induced to settle in aquaria (Babcock 1984). These reports were based solely on larvae raised in aquaria. The technique of rearing larvae using in situ culture vessels employed here as well as the use of conditioned settlement substrata, appear to have influenced the earlier settlement times obtained in this study.

Clearly these results, as well as the previous findings of Harrison et al. (1984) and Babcock and Heyward (in press) necessitate a re-assessment of the assumptions made by various authors that scleractinian communities (Done 1982) and populations (Potts et al. 1985) are self-seeding. There may well be a certain degree of self-seeding taking place, however there is little or no evidence to support this assumption except in cases where species are known to release rapidly settling larvae. For corals which are broadcast spawners, the most parsimonious conclusion, in the light of available evidence on the development and behaviour of coral larvae, is that most larvae are swept clear of the parent reef and only a small proportion may return there. These proportions should be determined by combined oceanographic and plankton studies. The relative contribution these larvae make to recruitment on the parent reef, as opposed to larvae from other reefs, must also be assessed.

Although scleractinian larvae are transported passively in the plankton for the first one to two days, after this time they are mobile, and may be able to determine their position in the water

column. Furthermore, once larvae encounter a reef or other suitable substrata for settlement, they can make active choices concerning settlement preferences. Goniastrea aspera larvae showed marked preferences for conditioned surfaces and surfaces with particular textural characteristics (e.g. plates ut from favid corals). The larvae of Pocillopora damicornis (Harrigan 1972; Harriott 1983b) showed a preference for settlement on conditioned substrata, and the larvae of Alcyonium sidereum have been shown to have increased rates of settlement in the presence of various red algae (Sebens 1983). Larvae of Xenia macrospiculata and Parerythropodium f. fulvum were found to prefer to settle on substrata with a rough texture (Benayahu and Loya 1984). That such preferences are likely to influence the choice of microhabitat in which scleractinian larvae choose to settle has long been assumed, but has only recently begun to be rigorously examined. Benayahu and Loya (1984) have shown that the effect of substrate type and orientation on settlement behaviour in two species of tropical alcyonaceans corresponds well with the distribution of newly settled polyps in the field. Most studies however, which have sought to demonstrate such effects have relied on investigating settlement after the fact by studying recruitment. While this approach is certainly valid up to a point, it cannot differentiate between the roles of settlement, and post-settlement mortality, in producing the observed recruitment patterns. This is another area which deserves further study in the future, with particular reference to hermatypic scleractinians.

CHAPTER 5 POPULATION DYNAMICS

5.1 INTRODUCTION

Demographic studies of modular organisms should ideally take into account two levels of population, the genetic individual or genet, as well as its sub-units, ramets (Harper 1977; Hughes and Jackson 1985). Populations of ramets may have quite different characteristics to those of their corresponding genets (Harper and Bell 1979), especially where there is the potential for a high level of vegetative propagation (Hughes 1984). Because individuals may be subject to a wide range of circumstances, the number of sub-units of which they are composed may also vary widely. It may be very difficult to determine which of the ramets originate from the same genet, and unless this can be done it is pointless to approach the population dynamics of modular organisms using traditional age-based life tables. Modular organisms may also display both positive and negative growth, therefore the relationship between age and size of an individual can be very poor (Hughes and Jackson 1980). In such cases methods based on size alone may be more useful for understanding and predicting population dynamics (Werner and Caswell 1977; Hughes 1984). This is the approach taken recently by Hughes and Jackson (1985) for several populations of foliose corals in Jamaica. In these corals there was a poor correlation between size and age due to factors such as variability in individual growth rates, partial mortality, and fission and fusion of colonies.

Despite the usefulness of the size-based approach, it does not include the influences which age may have on factors such as fecundity or survivorship (Hughes 1984). Perhaps more importantly population dynamics based on size alone cannot be used to examine the time scale of population dynamics as they affect genetic processes in the species. In this study species were used which build a 'massive' skeleton that remains to provide evidence of the history of individuals. For this reason genets could be defined and

ages could be estimated providing a means of obtaining both age-based, and sized-based population parameters. No other study of colonial coral populations has attempted to examine both of these aspects of demography. The probability of failing to recognize ramets was minimal because of the massive nature of the skeleton, its slow growth, and the relatively small sizes attained by Goniastrea aspera, G. favulus and Platygyra sinensis. Past studies have been based solely on colony size with only cautious inferences (if any) made regarding the age of colonies (Connell 1973; Loya 1976a; Harriott 1985; Hughes and Jackson 1985; Potts et al. 1985). In most of these studies it was impossible to incorporate any estimate of post-settlement mortality rates in the overall picture of population dynamics.

This study, attempts to consider all these aspects of the populations of Goniastrea aspera, G. favulus and Platygyra sinensis, relatively common, small to intermediate sized massive corals of Indo-Pacific reef flats. Since most of the corals subjected to this kind of study in the past have been sub-tidal, and either branching or foliose species, this study also provides an opportunity to compare aspects of scleractinian coral life history patterns and assess current generalizations with respect to other growth forms.

5.2 METHODS

5.2.1 Annual Population Surveys

Population counts and measurements were carried out between June and August of 1982, 1983 and 1984, during afternoon spring low tides which exposed the reef flats for periods of over 3 hours at a time. Sample populations were those present in the three inner transects at both Geoffrey and Pioneer Bays (Ch. 2, Fig. 2.1). The transects were permanently marked by steel stakes which were driven into the reef flat at 5m intervals. A tape measure was stretched along them and a $1m^2$ quadrat positioned astride the tape at one metre intervals to form a continuous belt of quadrats which could be re-established each year (Ch. 2).

Colonies were recorded only if their centres fell within the quadrats. A number was assigned to every colony and its species and quadrat were recorded. Measurements of colony dimensions and nearest-neighbour distances were taken as described in section 2.2.1. In addition to this information, data on the growth form of the colony was recorded, such as whether the colony was an intact hemispherical form, a microatoll or other damaged form, or a tissue fragment of a microatoll (the skeleton usually remained unfragmented). Where colonies were the product of fission, this also was recorded so that it was possible to establish both the number of colonies (ramets) and the number of individuals (genets). Because of the massive growth form of these species daughter colonies were usually identifiable as such since they were obvious fragments of an original colony. The diameter of the original colony as well as any subsequent growth of the daughter colony could therefore be measured. Where separate individuals were fused with each other (sensu Babcock 1984) this was also recorded. In these cases of fusion between non-daughter colonies the skeletons are cemented onto each other, but tissues remain separate (Collins 1978). The fusion of daughter colonies, in which tissues re-connect, reforming a single colony, were also recorded. A combination of all this data and the relatively low densities in most quadrats made it possible to re-identify individual colonies without individual marking.

All measurements were carried out in situ using calipers to measure diameters and heights. In cases where this was not possible due to the position of the colony, a tape measure was used instead. A tape was always used to measure the tissue dimensions of microatolls or fragments of microatolls which presented relatively two dimensional surfaces. The arithmetic mean radius of hemispherical colonies and microatolls was calculated from diameter and height measurements. Surface areas (size) were approximated as the surface area of either a hemisphere (for hemispherical colonies) - using the mean radius, or a cylinder (for colonies with relatively two dimensional surfaces such as microatolls) - by multiplying the mean dimensions of the living tissue.

It was felt that the method used was the most accurate that could

be employed to obtain demographic data and to measure size changes, with perhaps the exception of photographing colonies colonies individually. Since a significant proportion of colonies were microatolls, or were relatively small and cryptic (especially at Pioneer Bay), photographic censuses and measurements proved to be unsuitable. Living portions of most microatolls were barely visible in $0.5m^2$ photographs since they were oriented perpendicular to the plane of the photograph, and small colonies in cryptic positions were usually obscured. Although there are disadvantages to *in situ* measurements, in that actual photographs over a number of years cannot be compared and measured, there are even greater drawbacks to photographic methods when applied to these species, in terms of accuracy of both counts and measurements. Due to the slow growth rate of these species (Ch. 3), margins of error on *in situ* size measurements were relatively large, and were not considered to be accurate enough for growth rate measurements. The often complex growth form further complicated any attempts to measure individual growth rates. However, net changes in colony size, expressed as surface area, could be adequately estimated.

5.2.2 Juvenile Mortality

Mortality rates were determined for juvenile *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis* on *in situ* settlement plates (Ch. 3.2.3), at Pioneer Bay (1982-83), and Geoffrey Bay (1983-84). An additional measure of juvenile mortality was obtained for *G. favulus* at Pioneer Bay in 1984-85 using the same methods as in previous years. Measurements of mortality in 1982 and 1983 commenced when settlement plates were retrieved for growth measurements after several months. Newly settled juveniles of *G. favulus* at Pioneer Bay in 1984 were counted prior to placement on the reef. Conditioned coral plates were used in that year (Ch. 3) which provided greater contrast with the pale translucent appearance of the juvenile corals. This provided an accurate estimate of juvenile mortality in the first months after settlement. Reliable counts were not possible in 1982 and 1983 since unconditioned plates were used in those years. A further estimate of mortality in the first few months was obtained for *P. sinensis* at Geoffrey Bay from

juveniles which had settled on the inside of their plastic larval culture jar. The jar was cut up and pieces deployed at Geoffrey Bay, at the same site as the coral plates. When the plastic fragments were retrieved, both live polyps and the skeletons of dead juveniles could be counted, providing accurate information on mortality during this period. Unfortunately these plastic fragments were washed away after the first census. Observations of the settlement plates were terminated after 14 to 15 months, either when all of the original population was dead, or when the remaining few individuals were used for skeletal specimens.

5.3 RESULTS

5.3.1 Size-frequency distributions

The size-frequency distributions, number of colonies, and the mean colony size of each species are displayed in Figs. 5.1-5.3 In addition these figures show the proportion of the total surface area of each population represented in the various size classes. The overall size distributions of Goniastrea aspera and G. favulus at Geoffrey Bay resemble each other quite closely with the majority of colonies falling in the first two size classes. In contrast the population of Platygyra sinensis contained a much higher proportion of large colonies (Fig. 5.1). These large colonies contributed by far the greatest proportion of surface area to the population of P. sinensis, while the proportion of total surface area contributed by the various size classes for G. aspera and G. favulus was relatively evenly distributed between the size classes. The mean size of P. sinensis was approximately three times that of either Goniastrea species (Table 5.1). The contribution of 'microatolls' (i.e. microatolls, colonies resulting from fission or having suffered substantial injury in the past) was highest in the largest size classes. These types of colonies were also represented in most other size classes but at much lower frequencies. Platygyra sinensis colonies had a larger mean size and subsequently the frequency of microatolls was highest in this species.

Fig. 5.1 Geoffrey Bay. Size frequency distributions and total cover of *G. aspera* (GA), *G. favulus* (GF) and *P. sinensis* (PS). Solid portions of the histograms represent frequencies of hemispherical undamaged colonies, open bars represent frequencies of microatolls, damaged colonies or colonies resulting from fission. Arrows indicate mean colony size. N = number of colonies.

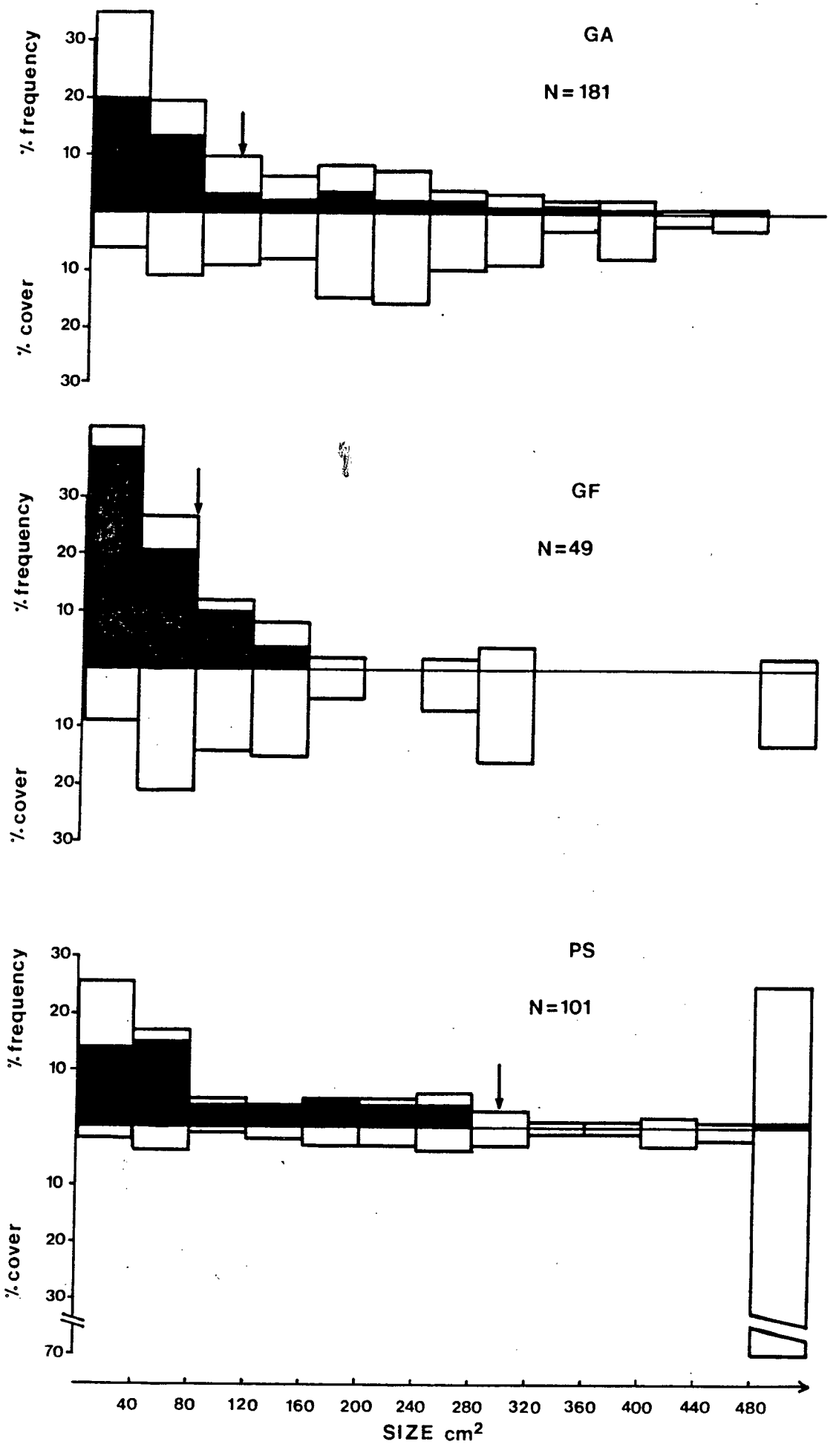

GA
N=181
% frequency
% cover
30
20
10
10
20
30
GF
N=49
% frequency
% cover
30
20
10
10
20
30
PS
N=101
% frequency
% cover
30
20
10
10
20
30
70
40
80
120
160
200
240
280
320
360
400
440
480
SIZE cm²

Fig. 5.2 Pioneer Bay. Size frequency distributions and total cover of G. aspera (GA), G. favulus (GF) and P. sinensis (PS). Solid portions of the histograms represent frequencies of hemispherical undamaged colonies, open bars represent frequencies of microatolls, damaged colonies or colonies resulting from fission. Arrows indicate mean colony size. N = number of colonies.

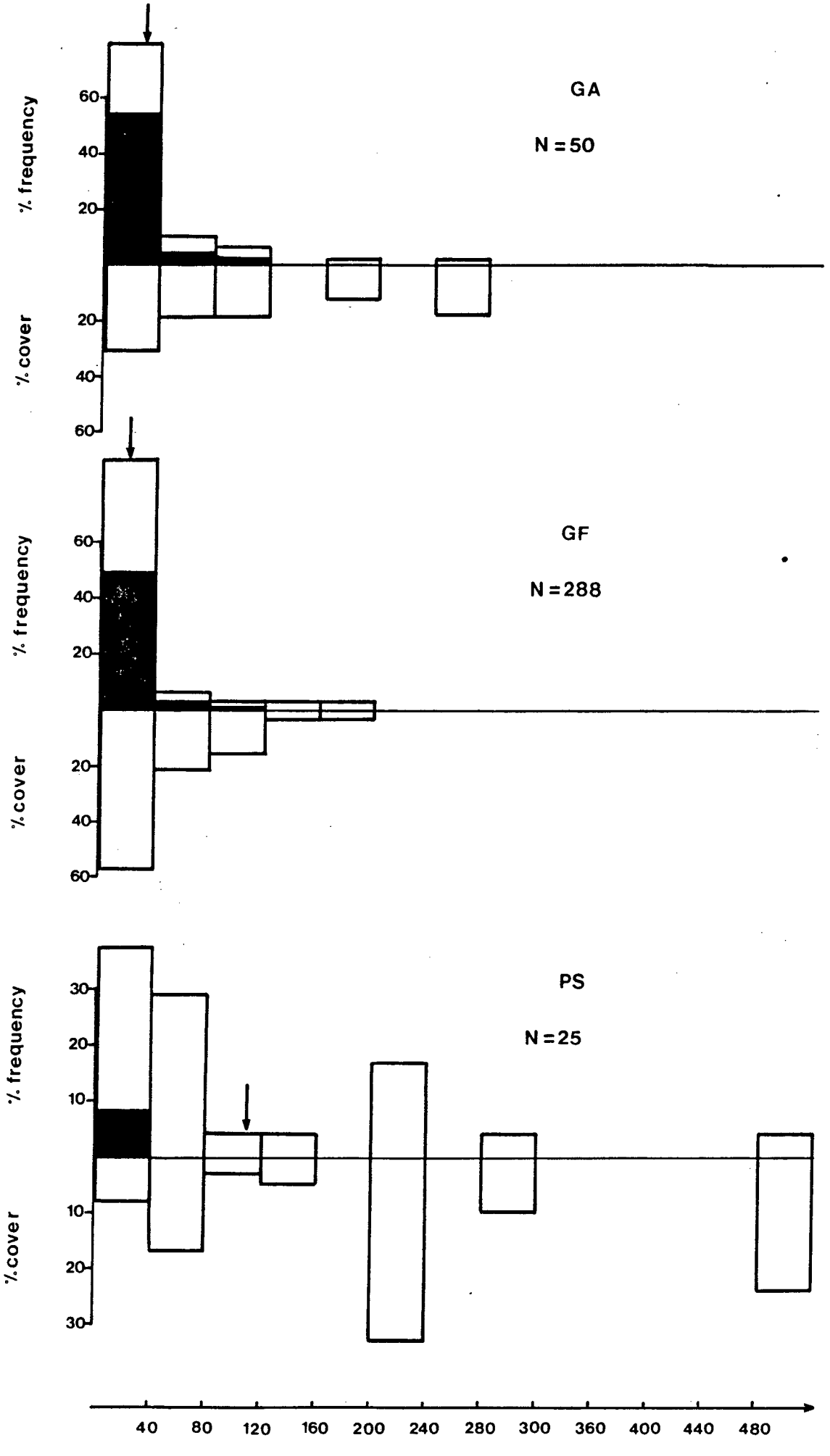

GA
N = 50
% frequency
% cover
60
40
20
20
40
60
GF
N = 288
% frequency
% cover
60
40
20
20
40
60
PS
N = 25
% frequency
% cover
30
20
10
10
20
30
40
80
120
160
200
240
280
300
360
400
440
480

Fig. 5.3 Pooled Bays. Size frequency distributions and total cover of G. aspera (GA), G. favulus (GF) and P. sinensis (PS). Solid portions of the histograms represent frequencies of hemispherical undamaged colonies, open bars represent frequencies of microatolls, damaged colonies or colonies resulting from fission. Arrows indicate mean colony size. N = number of colonies.

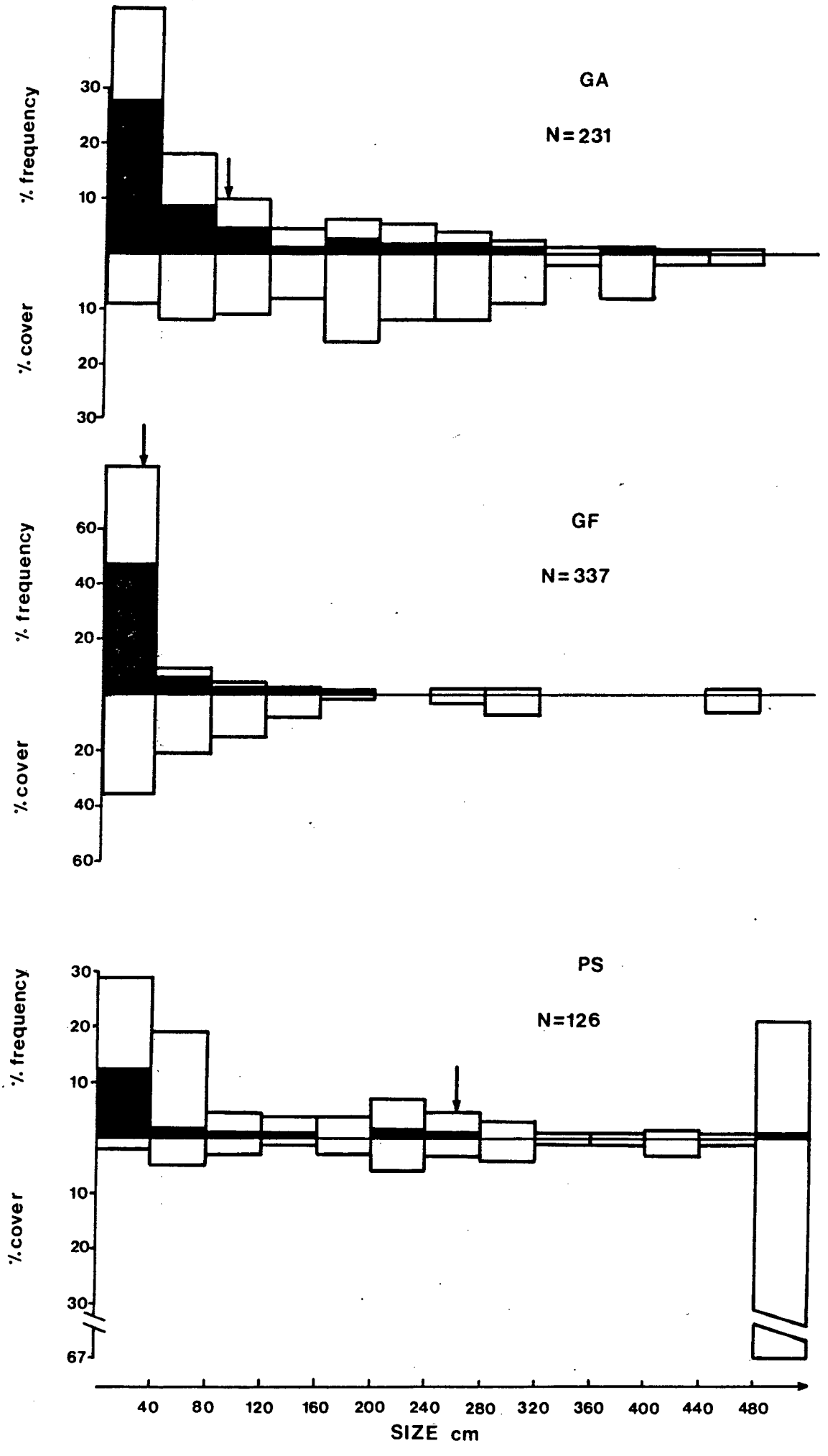

GA
N=231
% frequency
% cover
30
20
10
10
20
30
GF
N=337
% frequency
% cover
60
40
20
20
40
60
PS
N=126
% frequency
% cover
30
20
10
10
20
30
67
40
80
120
160
200
240
280
320
360
400
440
480
SIZE cm

Fig. 5.4 Geoffrey Bay. Age frequency distributions and total cover of *G. aspera* (GA), *G. favulus* (GF) and *P. sinensis* (PS). N = number of individuals. Arrows indicate mean age.

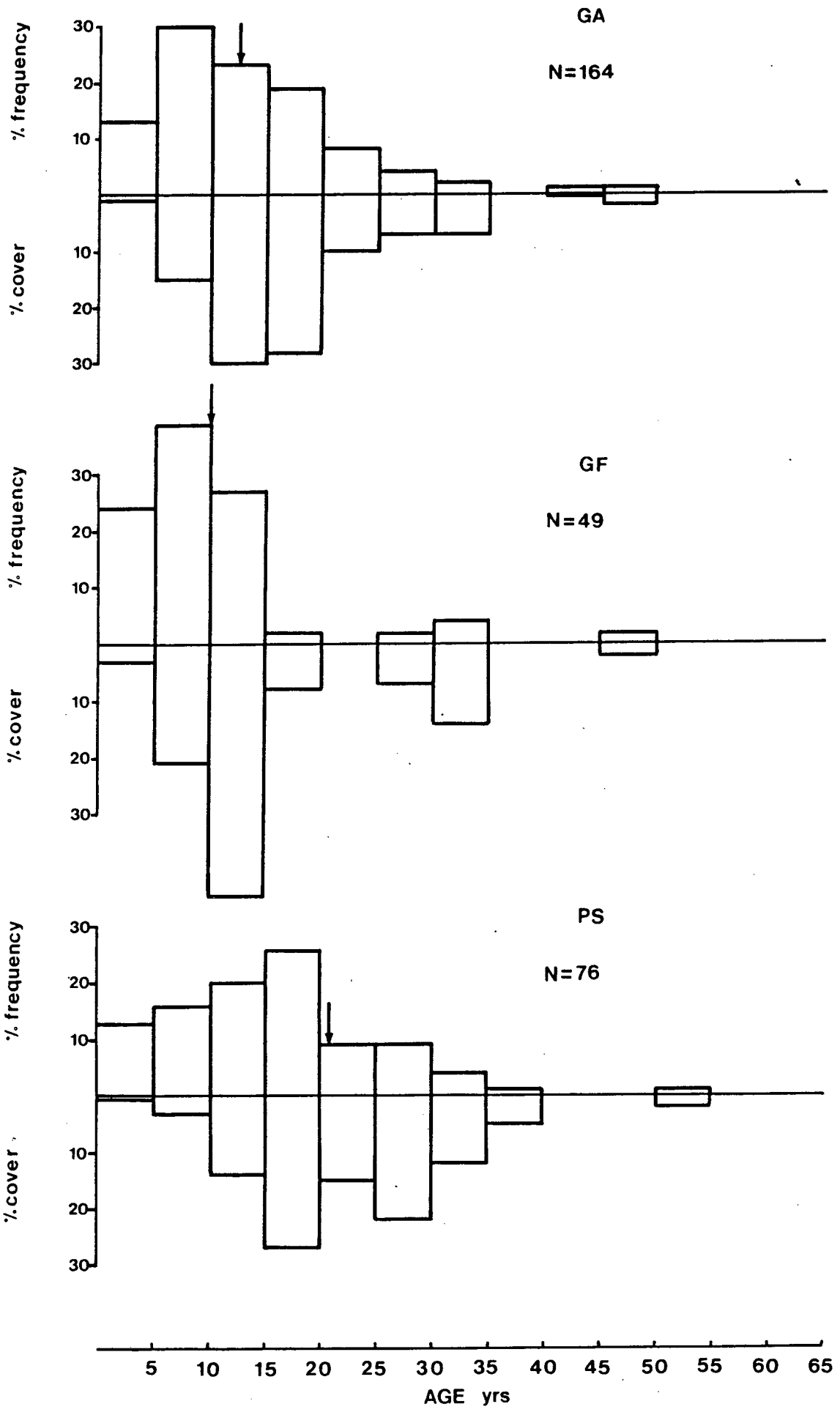

GA
N=164
% frequency
% cover
30
20
10
10
20
30
GF
N=49
% frequency
% cover
30
20
10
10
20
30
PS
N=76
% frequency
% cover
30
20
10
10
20
30
5
10
15
20
25
30
35
40
45
50
55
60
65
AGE yrs

Fig. 5.5 Pioneer Bay. Age frequency distributions and total cover of *G. aspera* (GA), *G. favulus* (GF) and *P. sinensis* (PS). N = number of individuals. Arrows indicate mean age.

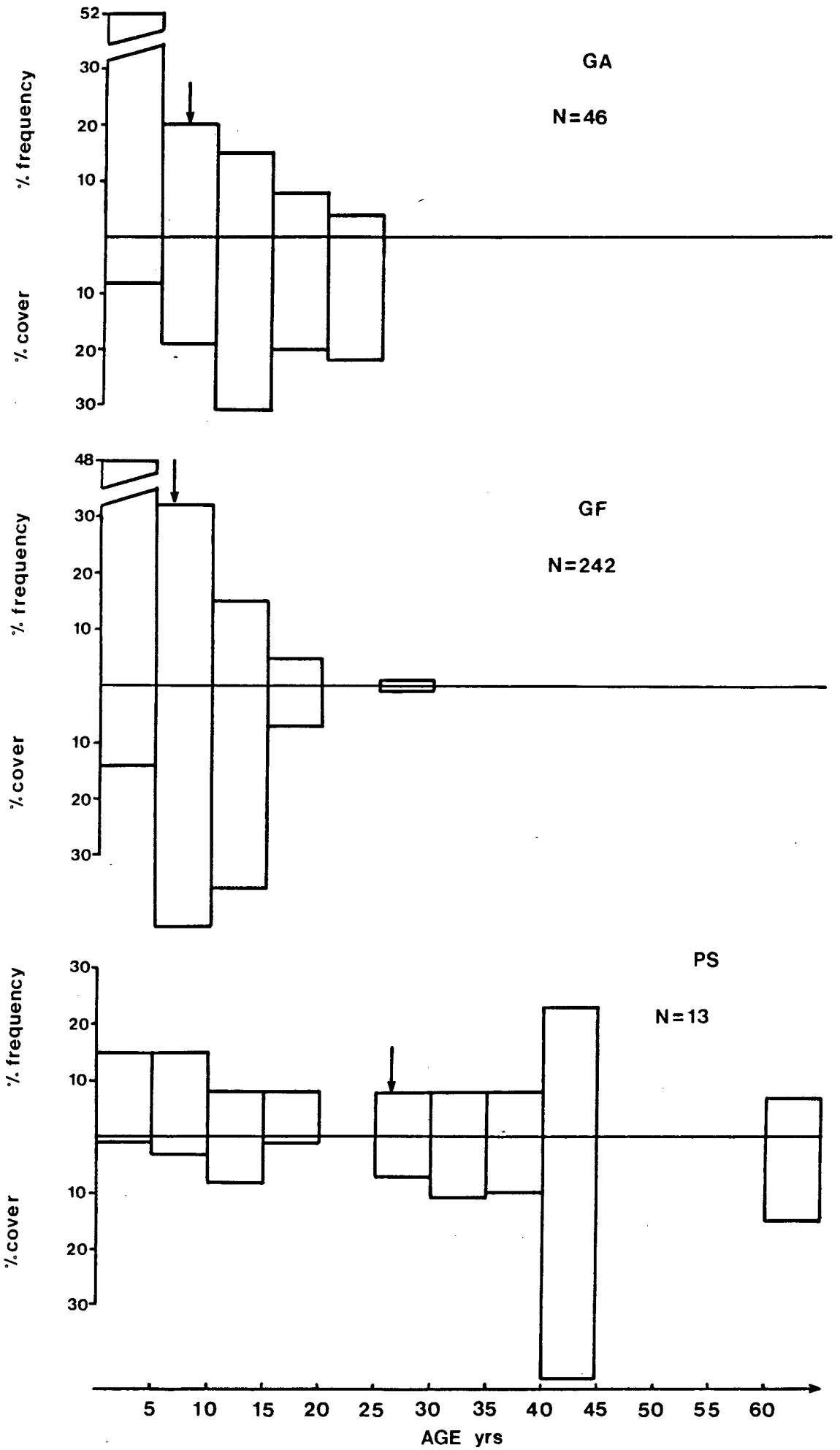

GA
N=46
% frequency
% cover
52
30
20
10
10
20
30
GF
N=242
% frequency
% cover
48
30
20
10
10
20
30
PS
N=13
% frequency
% cover
30
20
10
10
20
30
5
10
15
20
25
30
35
40
45
50
55
60
AGE yrs

Fig. 5.6 Pooled Bays. Age frequency distributions and total cover of *G. aspera* (GA), *G. favulus* (GF) and *P. sinensis* (PS). N = number of individuals. Arrows indicate mean age.

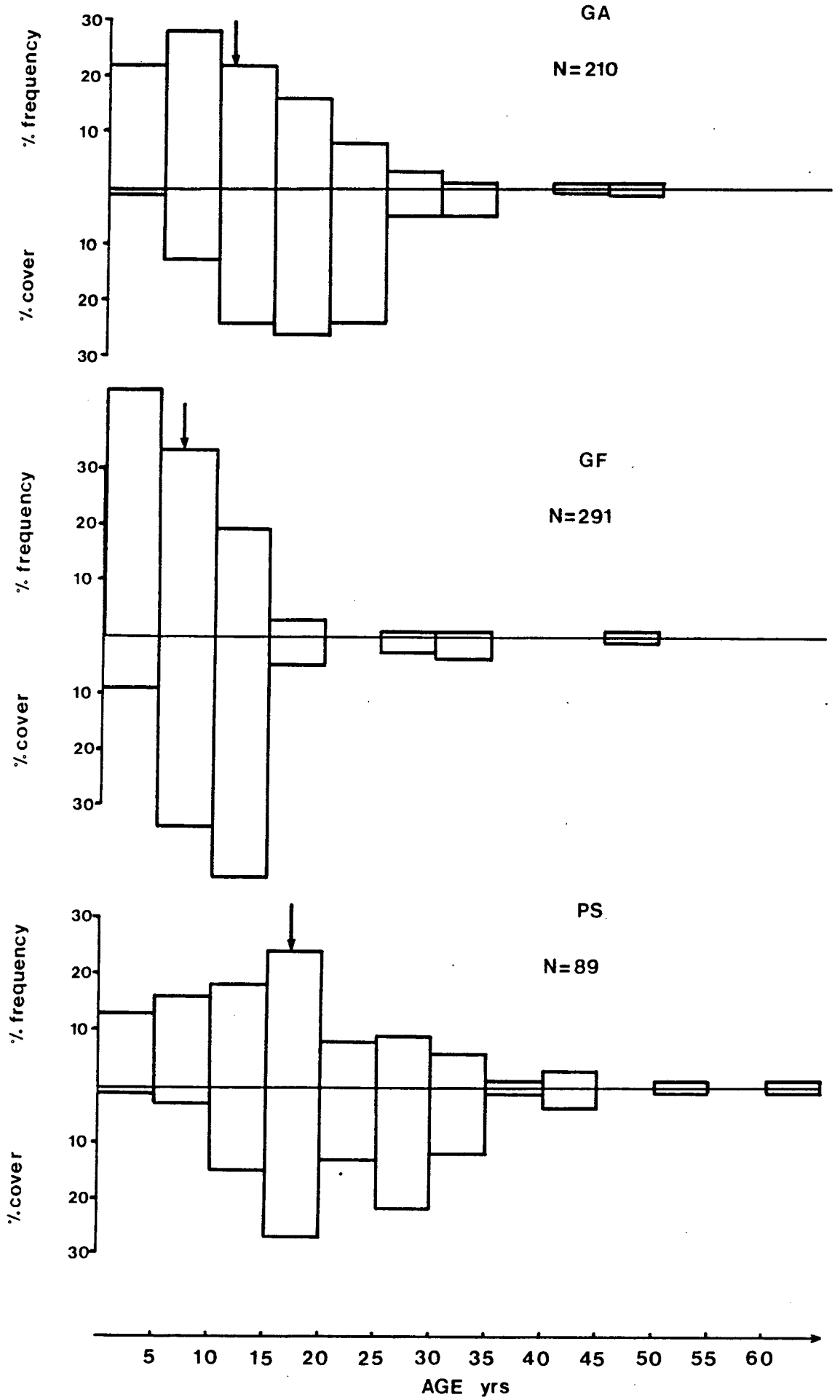

GA
N=210
% frequency
% cover
30
20
10
10
20
30
GF
N=291
% frequency
% cover
30
20
10
10
20
30
PS
N=89
% frequency
% cover
30
20
10
10
20
30
5
10
15
20
25
30
35
40
45
50
55
60
AGE yrs

Table 5.1. *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis*. Sample size, total cover, and mean cover m^{-2} 1984.

	Study Sites		
	Geoffrey Bay	Pioneer Bay	Pooled Bays
Sample size			
G. aspera	181	50	231
G. favulus	49	288	337
P. sinensis	101	25	126
Total cover (cm^2)			
G. aspera	19077	1493	20570
G. favulus	3902	5040	8942
P. sinensis	29957	2764	32721
Cover m^{-2}			
G. aspera	212	33	152
G. favulus	43	112	66
P. sinensis	333	61	242

Populations of *Goniastrea aspera* and *G. favulus* at Pioneer Bay again displayed trends which were similar (Fig. 5.2), but which were different to those displayed by these species at Geoffrey Bay. The smallest size class of the Pioneer Bay populations was by far the most abundant, and the largest colonies were only about half the size of the largest colonies from Geoffrey Bay. Mean colony sizes were much smaller than those for the Geoffrey Bay populations, falling within the smallest size class for both species (Table 5.1). The mean colony size of *Platygyra sinensis* was again larger than that of the other two species, but this species also showed a size frequency distribution skewed towards the smaller classes relative to the Geoffrey Bay population, with fewer large colonies at Pioneer Bay. Total cover contributed by each size class showed patterns similar to those at Geoffrey Bay for *G. aspera* and *P. sinensis*. The

preponderance of small colonies of G. favulus at Pioneer Bay however resulted in this size class dominating in terms of total cover. Data was pooled for both bays (Fig. 5.3) to provide a general picture of the size structure of populations of all three species and for use in the compilation of life tables (Ch. 6). These data reflect the trends for individual bays discussed previously, since they are influenced by the relative numeric dominance of species at different bays. For example, mean size of G. favulus for pooled bays and the proportion of total cover contributed by the smallest size classes were heavily influenced by the larger number of colonies at Pioneer Bay. Overall, colonies of P. sinensis were larger than those of either Goniastrea species, and large colonies were much more significant, both numerically and in terms of total cover. The two Goniastrea species were similar in most respects, however colonies of G. favulus were slightly smaller than those of G. aspera (Table 5.1).

5.3.2 Population dynamics

Mortality Populations were divided into 40cm² size classes for examination of size frequency distributions. The largest size classes were pooled for the purposes of examining transitional probabilities (change of size class). Whole colony mortality rates were similar in all species at both bays during the period of the study. Overall mortality ranged between 12% and 24% per year (Table 5.2), and no consistent trends were apparent between species or bays. Total numbers in the sample populations decreased for the Goniastrea species at both Pioneer and Geoffrey Bays in 1982-83, but remained virtually constant over the period 1983-84. In contrast, total numbers of P. sinensis increased at both bays during 1982-83, remaining constant at Geoffrey Bay in the following year, while dropping back to the 1982 level at Pioneer Bay. Net changes in population numbers varied from -10% for G. aspera and -9% for G. favulus, to +13% for P. sinensis at Geoffrey Bay. Net changes at Pioneer Bay were smaller, with +2% for G. aspera, +1% for G. favulus, and no change at all for P. sinensis. Most of the decrease at Geoffrey Bay came from high mortality of the first size class in 1982-83, while the increase in numbers of P. sinensis

during that period was caused principally by larval recruitment into the smallest size class (Table 5.5) rather than by fission.

Total cover for populations did not always correspond to changes in total colony number (Table 5.3). For example, although numbers of P. sinensis colonies increased at both bays in 1982-83, the total amount of cover decreased. Turnover in all populations was relatively high, with annual tissue loss due to partial mortality of colonies as well as whole colony mortality ranging from 10% to 41%. The two greatest losses of total cover both occurred in 1982-83, in the population of P. sinensis at Pioneer Bay (41%), and G. aspera at Geoffrey Bay (40%). The majority of losses in that year were caused by partial mortality in the largest size classes, with partial mortality to the largest colonies contributing almost all of the loss to the G. aspera population, and just one colony contributing almost half the total loss to P. sinensis. The majority of populations showed a net tissue loss over the two year period, however there were also cases of net increase in cover, due to a combination of growth, recruitment, and in a small number of cases, the immigration of unattached colonies.

Rates of whole and partial colony mortality were strongly dependent on colony size. The probability of a colony moving into another size class or staying in the same size class are shown for each of the study populations in Figs. 5.7 - 5.9. The most likely fate of colonies in all size classes was to remain in the same size class, while the next most likely outcome was to move into either of the adjacent size classes. The highest probability of whole colony mortality was always found in the smallest size class, ranging from 54% for P. sinensis at Pioneer Bay, to 18% for G. favulus at Pioneer Bay. The largest size class of P. sinensis tended to either remain in the same size class, or shrink down to one of the two smallest size classes. This was as a result of fission of the large colonies, which produced either a number of small colonies, or one or more small colonies, with part of the original colony remaining in the largest size class.

Fig. 5.7 Goniastrea aspera. Size frequency distributions of colonies as a function of their size in the previous year. Frequencies are from data combined for 1982-83 and 1983-84.

GB = Geoffrey Bay

PB = Pioneer Bay

Pooled = data for both bays pooled

Size classes (cm^2):		
	1	0-40
	2	41-80
	3	81-120
	4	>120

Colonies below abscissa represent colonies which died completely.

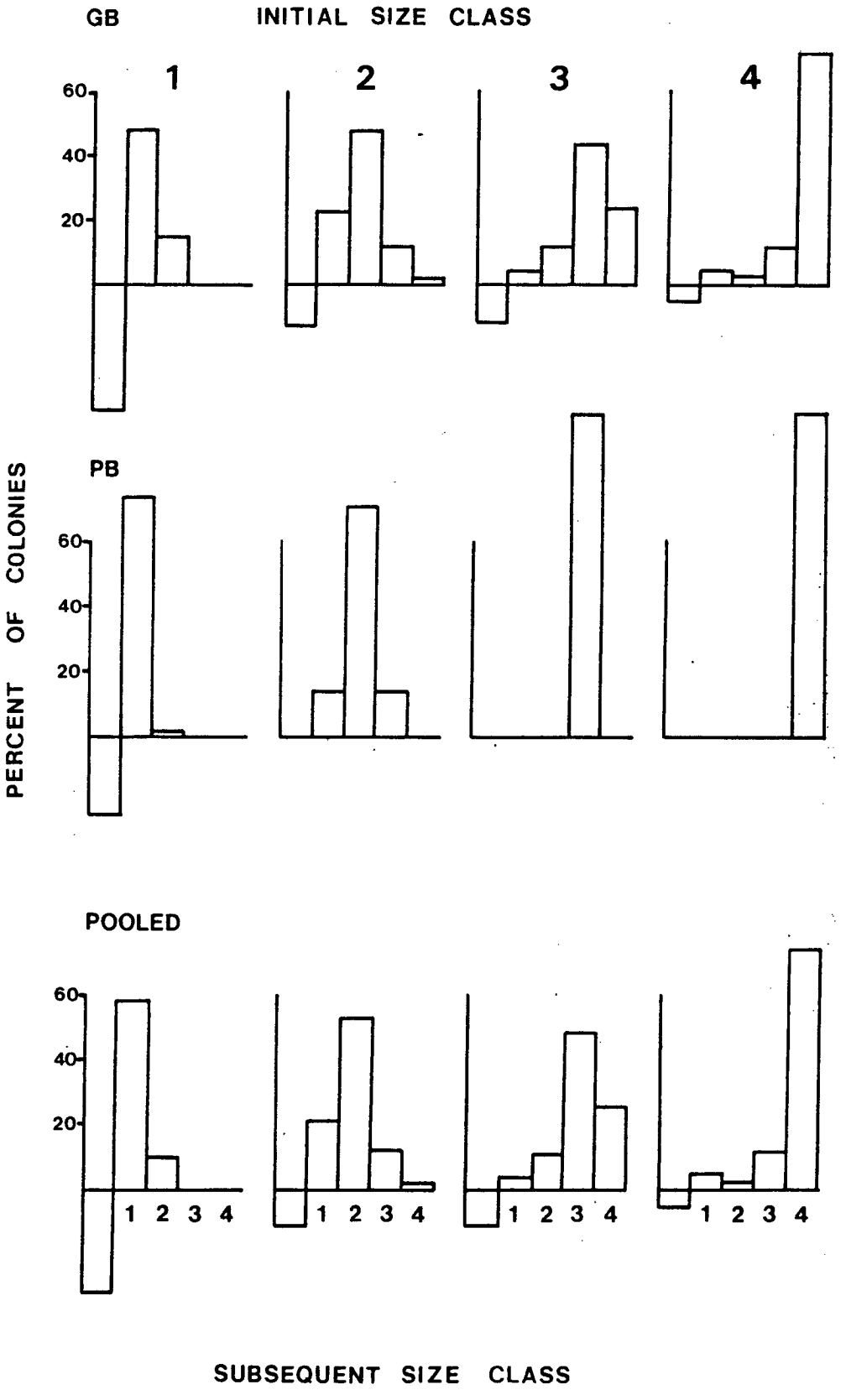

GB
INITIAL SIZE CLASS
1
2
3
4
60
40
20
PB
PERCENT OF COLONIES
POOLED
1 2 3 4
SUBSEQUENT SIZE CLASS

Fig. 5.8 *Goniastrea favulus* Size frequency distributions of colonies as a function of their size in the previous year. Frequencies are from data combined for 1982-83 and 1983-84.

GB = Geoffrey Bay

PB = Pioneer Bay

Pooled = data for both bays pooled.

Size classes (cm^2):		
	1	0-40
	2	41-80
	3	81-120
	4	>120

Colonies below abscissa represent colonies which died completely.

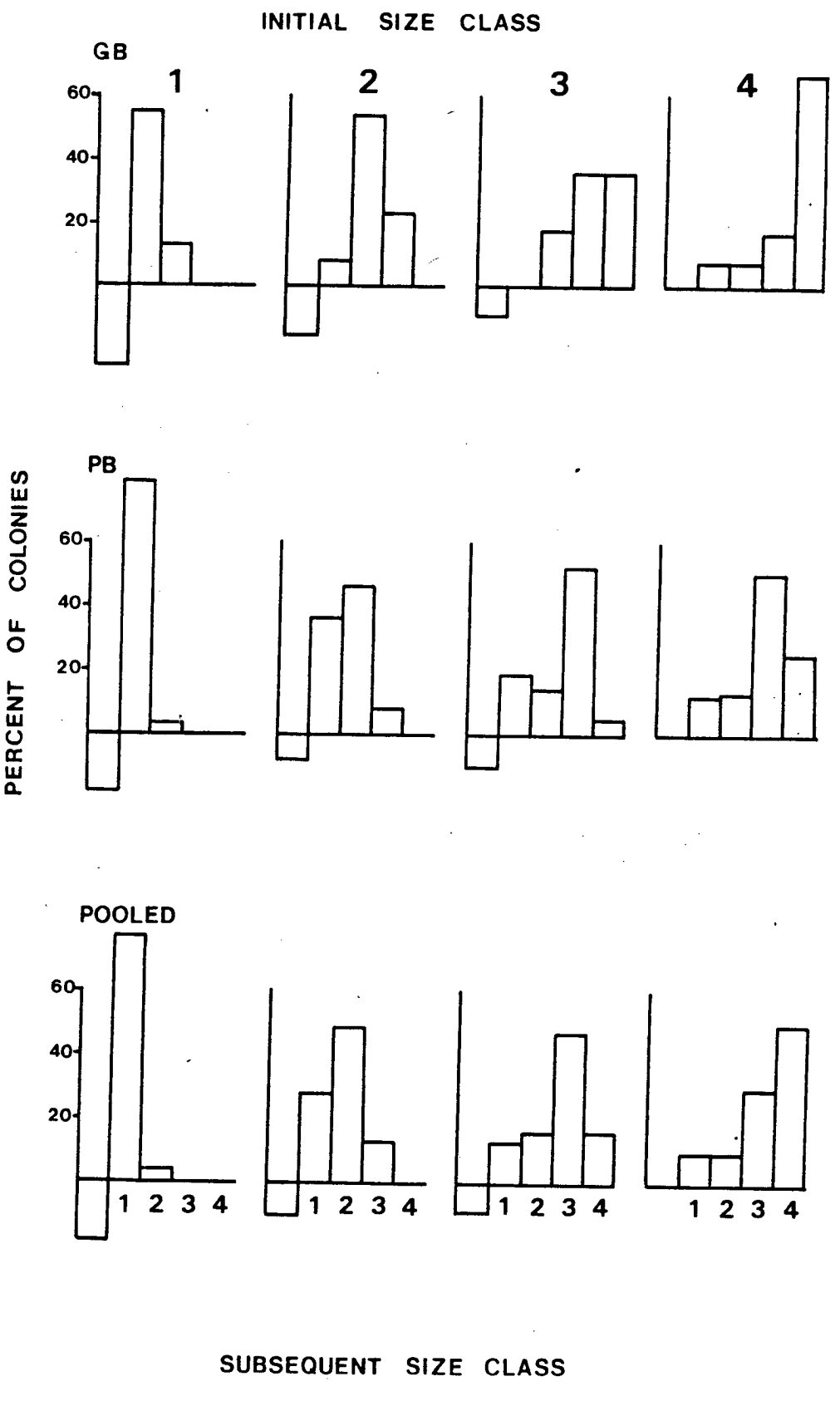

INITIAL SIZE CLASS
GB
1
2
3
4
60
40
20
PB
PERCENT OF COLONIES
POOLED
1 2 3 4
SUBSEQUENT SIZE CLASS

Fig. 5.9 *Platygyra sinensis*. Size frequency distributions of colonies as a function of their size in the previous year. Frequencies are from data combined for 1982-83 and 1983-84.

GB = Geoffrey Bay

PB = Pioneer Bay

Pooled = data for both pooled

Size classes (cm^2):		
	1	0-40
	2	41-80
	3	81-120
	4	>120

Colonies below abscissa represent colonies which died completely.

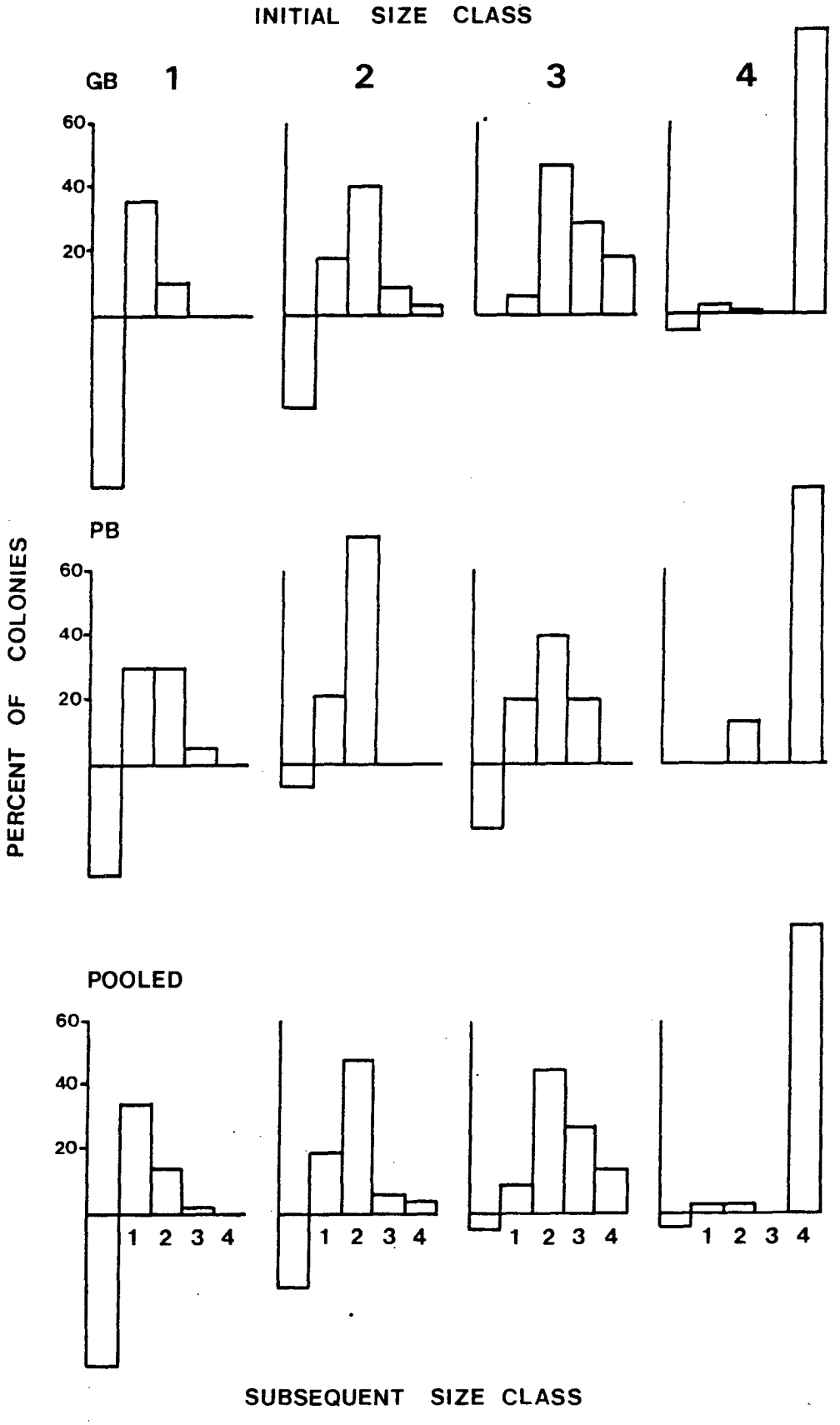

INITIAL SIZE CLASS
GB
1
2
3
4
60
40
20
PB
POOLED
PERCENT OF COLONIES
1 2 3 4
SUBSEQUENT SIZE CLASS

Table 5.2 *Goniastrea aspera*, *G. favulus* and *P. sinensis*. Whole colony mortality, Geoffrey and Pioneer Bays.

	1982			1983			1984
	n	mortal-ity	%	n	mortal-ity	%	n
Geoffrey Bay							
G. aspera	202	49	24	180	25	14	181
G. favulus	54	12	22	51	8	16	49
P. sinensis	90	16	18	102	20	20	101
Pioneer Bay							
G. aspera	53	10	19	50	10	20	50
G. favulus	292	45	15	288	47	16	288
P. sinensis	25	3	12	29	6	21	25

Previous damage to colonies also had a significant influence on the probability of further damage. The fate of colonies of each species was scored according to change in surface areas as either positive (growth) or negative (partial or whole colony mortality) and pooled for both years of the study. The frequency of positive and negative scores was then compared between previously undamaged colonies (hemispherical) and colonies which were noted to have sustained significant damage at some time in the past (microatolls, parts of microatolls, or other previously damaged colonies). The results were analysed by 2 x 2 contingency tables with data pooled for both bays (Table 5.4). For both *G. aspera* and *G. favulus*, previously damaged colonies were more likely to sustain a loss in colony size than were undamaged hemispherical colonies. Previous history of colonies of *P. sinensis* did not have a significant influence on their subsequent fate, perhaps partially as a consequence of relatively low sample numbers, especially of uninjured colonies.

Total colony mortality (Table 5.4) showed no significant relationship between previous partial mortality and the probability of subsequent whole colony mortality.

Table 5.3 *Goniastrea aspera*, *G. favulus* and *P. sinensis*. Total cover and tissue turnover at Geoffrey and Pioneer Bays, 1982 -1984. Area values are cover totals for all transects (cm^2).

	1982				1983				1984
	total area	area loss (%)	area gain (%)	net change (%)					total area
Geoffrey									
G. aspera	25.6	40	17	-23	19.5	17	14	-2	19.1
G. favulus	3.5	25	25	+1	3.5	11	24	+13	3.9
P. sinensis	35.2	26	13	-12	30.9	17	14	-3	29.9
Pioneer									
G. aspera	1.4	10	22	+12	1.6	19	13	-6	1.5
G. favulus	6.6	28	17	-12	5.9	30	16	-14	5.0
P. sinensis	4.3	41	9	-33	2.9	18	21	-4	2.8

Table 5.4 *Goniastrea aspera*, *G. favulus* and *Platygyra sinensis*. Influence of previous partial colony mortality on the probability of subsequent damage. Chi-squared analysis, 2 x 2 contingency tables. Bays pooled for 1982-83 and 1983-84.

	Chi-squared	p
Partial mortality		
G. aspera	32.25	<.001
G. favulus	19.3	<.001
P. sinensis	1.75	>.05
Total mortality		
G. aspera	0.36	>.05
G. favulus	2.99	>.05
P. sinensis	1.73	>.05

Recruitment Two components of recruitment were considered, larval recruitment and the formation of new colonies by fission. Recruits originating from larval settlement were considered to be those small colonies, not obviously originating from fission, which appeared in the quadrats in 1983 and 1984. The smallest colonies counted were approximately 1cm in diameter, and were thus likely to be over 2 years old (Ch. 3) before they became visible and 'recruited' into the population.

Levels of recruitment for *G. aspera*, *G. favulus* and *P. sinensis* were similar at both Bays, with a total rate of 0.52 recruits m^{-2} at Geoffrey Bay, only slightly lower than the 0.6 recruits m^{-2} at Pioneer Bay. This was despite a roughly two-fold difference in total density between the bays (Table 5.5). Variation in recruitment rates for each species showed a significant positive

correlation with species density at both bays (Table 5.5; $r = 0.894$, $.05>p>.01$).

The contribution of colony fission to recruitment was relatively minor in both Goniastrea species, but played a greater role in Platygyra sinensis, especially at Pioneer Bay (Table 5.5). The mean size of dividing colonies was usually much larger than the mean colony size, thus large colonies appear to be more likely to divide than smaller ones. The larger mean colony size of P. sinensis may therefore have contributed to the higher probability of fission in this species. The mean annual probability of fission showed a direct correspondence with mean colony size for each population except G. favulus at Pioneer Bay, which had a relatively high probability of colony fusion considering the very small mean colony size. The overall proportion of colonies in each population which were produced by fission (i.e. colonies which may have split at any time in the past, not necessarily during the time of the study) closely reflected the rates of fission observed during the study. (Table 5.6). The mean annual probability of fission (Hughes and Jackson 1985) was calculated by dividing the number of parent colonies observed by the total number of colonies in the population.

Table 5.5 Larval recruitment over two years at Geoffrey and Pioneer Bays.

	G. aspera			*G. favulus*			*P. sinensis*		
	83	84	mean	83	84	mean	83	84	mean
Geoffrey Bay									
no. of recruits	21	24	22.5	8	5	6.5	24	12	18
recruits m^{-2}	.23	.26	.25	.09	.06	.07	.26	.13	.2
adult density m^{-2}	2	2	2	.6	.5	.6	1.1	1.1	1.1
Pioneer Bay									
no. of recruits	6	10	8	35	36	35.5	4	1	2.5
recruits m^{-2}	.13	.22	.17	.8	.4	.4	.09	.02	.03
adult density m^{-2}	1.1	1.1	1.1	6.4	6.4	6.4	0.6	0.6	0.6

Table 5.6 Formation of new colonies by fission, 1982-83 and 1983-84. Population sizes are for 1982 and 1983 'parent' populations. Mean colony sizes are for 1984, as are proportions of colonies in population formed by fission.

Geoffrey Bay

	G. aspera		*G. favulus*		*P. sinensis*	
	82-83	83-84	82-83	83-84	82-83	83-84
no. colonies produced by fission	8	3	1	0	4	7
no. of parent colonies	5	2	1	0	3	6
no. colonies in population	202	180	54	51	90	101
mean size of parent colonies (cm^2)	329	217	605	-	346	352
mean size of all colonies (cm^2)	106		79		299	
mean annual probability of fission	0.028		0.009		0.047	
proportion of population formed by fission (including prior to study)	0.09		0.04		0.23	

Table 5.6 (cont.)

Pioneer Bay

	G. aspera		G. favulus		P. sinensis	
	82-83	83-84	82-83	83-84	82-83	83-84
no. of colonies produced by fission	1	0	6	11	3	1
no. of parent colonies	1	0	4	11	2	1
no. of colonies in population	53	50	292	288	25	29
mean size of parent colonies (cm^2)	10	-	75	37	594	530
mean size of all colonies (cm^2)	30		18		545	
mean annual probability of fission	0.009		0.029		0.055	
proportion of population formed by fission (including prior to study)	0.08		0.15		0.48	

Fusion of daughter colonies was a rare occurrence, and only three instances were recorded during the period of the study, one in each species. All of these fusions were between parts of microatolls which had reconnected. Skeletal fusion (as opposed to tissue fusion) of unrelated individuals of the same species was common although no new instances of this were observed during this study. Based on 1984 values Goniastrea aspera at Geoffrey Bay had the highest incidence of this phenomenon, involving 14% of all colonies, followed by P. sinensis at Geoffrey Bay (6%) and G. aspera and G. favulus at Pioneer Bay (4% and 1%). Since the tissues of these individuals do not fuse, they were always scored as separate colonies.

5.3.3 Age frequency distribution

Age structure It was possible to estimate the age of colonies using measurements of their mean radius or diameter and applying the formulae for estimation of age developed in Ch. 3.4 Where two or more daughter colonies were involved, they were counted as a single individual whose age was based on the diameter of the original colony. Age-frequency distributions produced from this data (Figs 5.4 - 5.6) often differed from size-frequency distributions for the same populations (Figs. 5.1 - 5.3), as did the distribution of the proportion of total cover contributed by each size class. Populations of Goniastrea aspera and G. favulus at Geoffrey Bay showed a lesser contribution from the youngest age class than would be indicated from the size-frequency distribution, and colonies which fell into the mid-range of age classes were most abundant. A similar trend was apparent in Platygyra sinensis at Geoffrey Bay, with the difference that the older age-classes continued to decrease in abundance. This was despite the fact that the size-frequency distribution of this species was bi-modal, due to the large number of large sized colonies. The population of P. sinensis at Pioneer Bay showed the same pattern, although less clearly, perhaps due to the small sample size. Due to the strong dominance of the smallest size classes at Pioneer Bay, the youngest age-class dominated there, in contrast to the Geoffrey Bay populations. The majority of total cover for all populations was contributed by the middle age classes, again with the exception of

the Goniastrea populations at Pioneer Bay which were dominated by large numbers of small colonies. The overall picture provided by pooling the data for both bays consolidated the trends described above, with middle age-classes dominating numerically and in terms of their contribution to total cover. Once again the numerical dominance of small colonies of G. favulus resulted in the youngest age class being the most numerous, however the total area contributed by this class was quite small and the middle age classes were dominant in terms of cover.

In very general terms, colony size was positively correlated with age, however there was a very interesting trend among colonies in the older age classes. Mean colony size in the oldest age classes of many of the populations decreased in relation to mean colony size in the middle age classes (Figs. 5.10, 5.11). This was probably due to the higher probability of fission of larger, (usually older) colonies.

The mean ages of the populations studied ranged from 7.3 years for Goniastrea favulus to 26.2 years for P. sinensis, both at Pioneer Bay. Mean ages of both Goniastrea species were less than those of P. sinensis (Figs. 5.4 - 5.7).

Age specific mortality rates The recorded frequencies of mortality of colonies in each of the age classes above were pooled for the period of the study to provide age specific mortality rates for each population. Mortality here did not include the death of single daughter colonies, but was only recorded when an entire genet disappeared. Mortality was highest in the first age class, with mortalities ranging from 21% to 69%, but dropped rapidly after the age of ten years to values below 10% (Fig. 5.12).

Net change in numbers of individuals (genets) was relatively minor over the two year period of the study, with both increases and decreases being recorded (Table 5.7). The only species to show any consistent trend in population size at both bays was G. favulus, which decreased slightly in numbers at both Geoffrey Bay and Pioneer Bay. The greatest change in numbers occurred in G. aspera at Geoffrey Bay between 1982 and 1983, where there was a 20% decrease

Fig. 5.10 Age and size of *G. aspera* (GA), *G. favulus* (GF) and *P. sinensis* (PS) at Geoffrey Bay. Error bars represent one standard deviation.

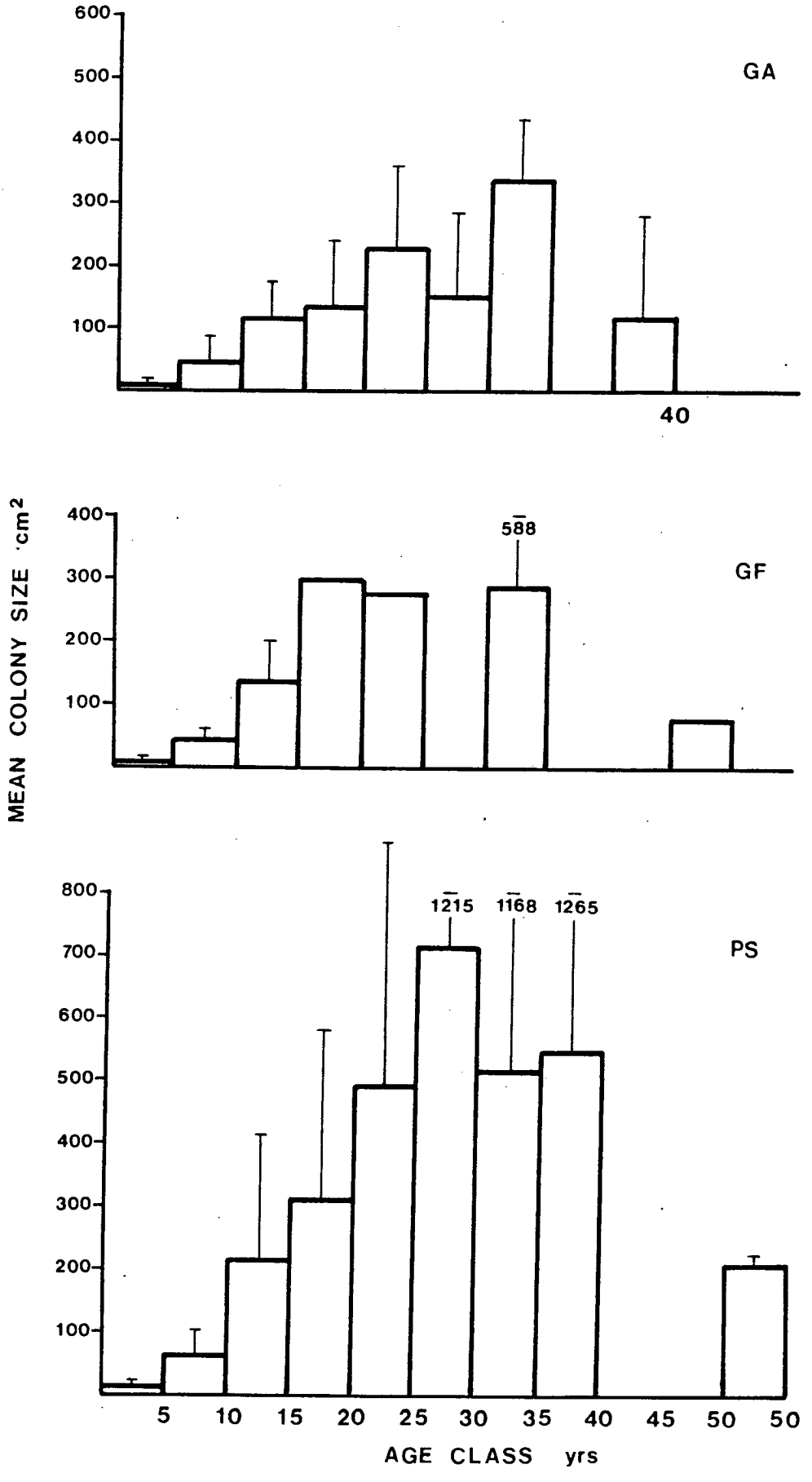

GA
600
500
400
300
200
100
40
GF
400
300
200
100
588
MEAN COLONY SIZE ·cm²
PS
800
700
600
500
400
300
200
100
1215
1168
1265
5
10
15
20
25
30
35
40
45
50
50
AGE CLASS yrs

Fig. 5.11 Age and size of *G. aspera* (GA), *G. favulus* (GF) and *P. sinensis* (PS) at Pioneer Bay. Error bars represent one standard deviation.

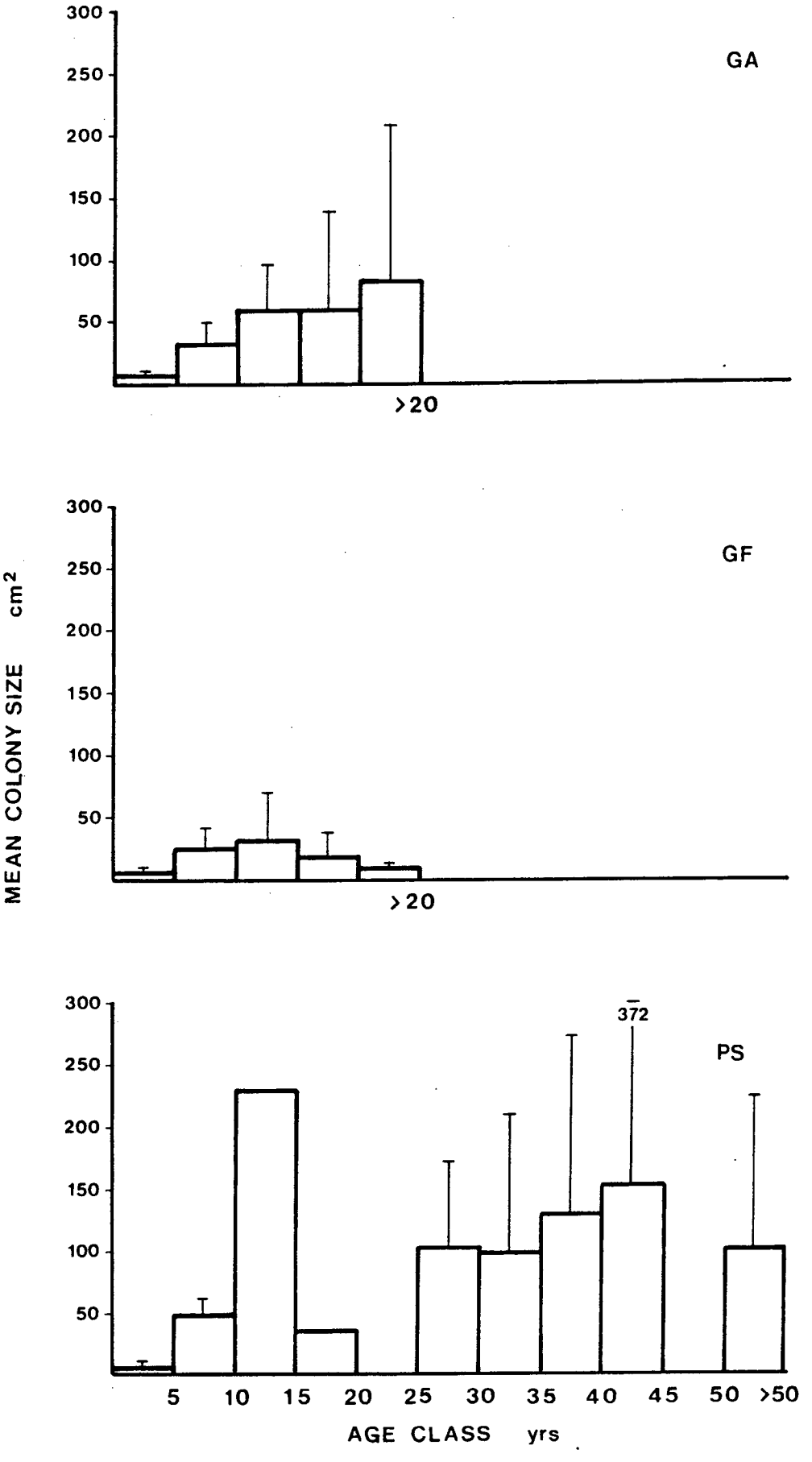
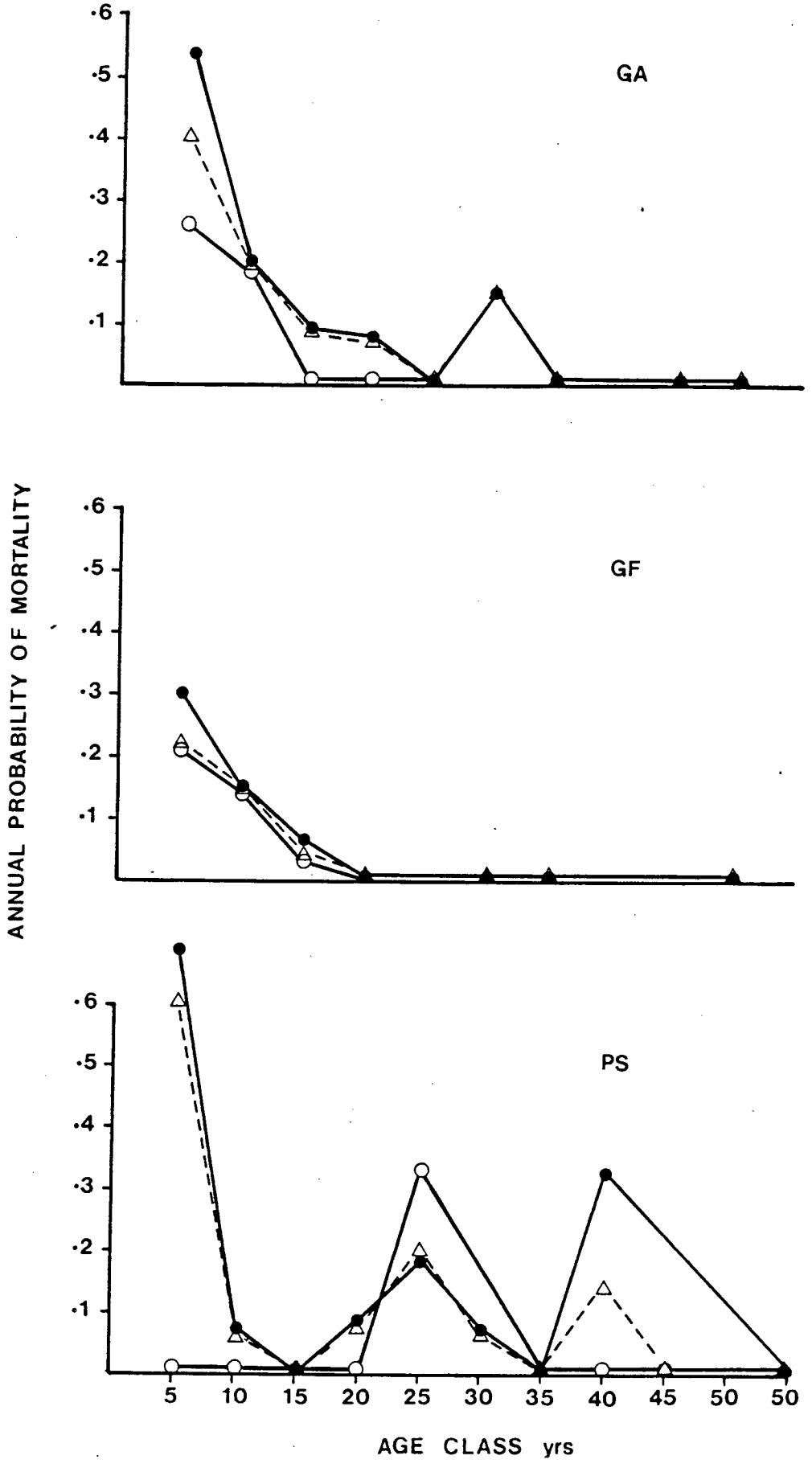

GA
GF
PS
MEAN COLONY SIZE cm²
300
250
200
150
100
50
>20
372
5
10
15
20
25
30
35
40
45
50
>50
AGE CLASS yrs

Fig. 5.12 Age specific mortality, G. aspera (GA), G. favulus (GF) and P. sinensis (PS). Data was combined for the periods 1982-83 and 1983-84 to provide mean annual probability of mortality.

Geoffrey Bay

Pioneer Bay

Bays pooled


GA
GF
PS
·6
·5
·4
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·2
·1
5
10
15
20
25
30
35
40
45
50
50
ANNUAL PROBABILITY OF MORTALITY
AGE CLASS yrs

in number of individuals, followed by a 12% increase in the following year. These fluctuations were caused mainly by mortality in the youngest age class in 1983 - 83 (Fig. 5.12), followed by average recruitment (Table 5.5) and good survival of colonies in the 5 - 15 year age groups.

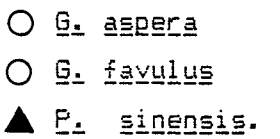
Table 5.7 Population sizes, 1982-1984 based on genetically distinct individuals.

	1982	1983	1984
Geoffrey Bay			
G. aspera	183	147	164
G. favulus	51	51	49
P. sinensis	62	74	76
Pioneer Bay			
G. aspera	44	42	46
G. favulus	251	247	242
P. sinensis	15	14	13

5.3.4. Juvenile mortality.

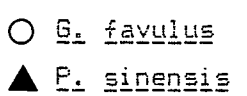
The post-settlement stages (between settlement and 'visual' recruitment) of all three species suffered high mortality (>95%) during the first 14 - 15 months after settlement (Fig. 5.13). Rates of mortality in juveniles, based on counts begun 3 months after settlement, were very similar in all species. The highest mortality occurred in the younger stages, from 3 to 6 months after settlement (36% - 44%), and dropped gradually over the subsequent months. Two additional records of mortality, which included the first months after settlement which were missing in the other records, gave even higher rates of mortality. Platygyra sinensis on plastic fragments at Geoffrey Bay had a mortality of 79% in the first three months, and G. favulus (on coral plates) at Pioneer Bay suffered 98% mortality in the first 7 months after settlement. These initial (0 - 3 and 0 -7 months) mortality data were combined with the mortality data for P. sinensis and G. favulus during the subsequent period (3 - 14 and 3 -15 months) to produce a composite graph of mortality for

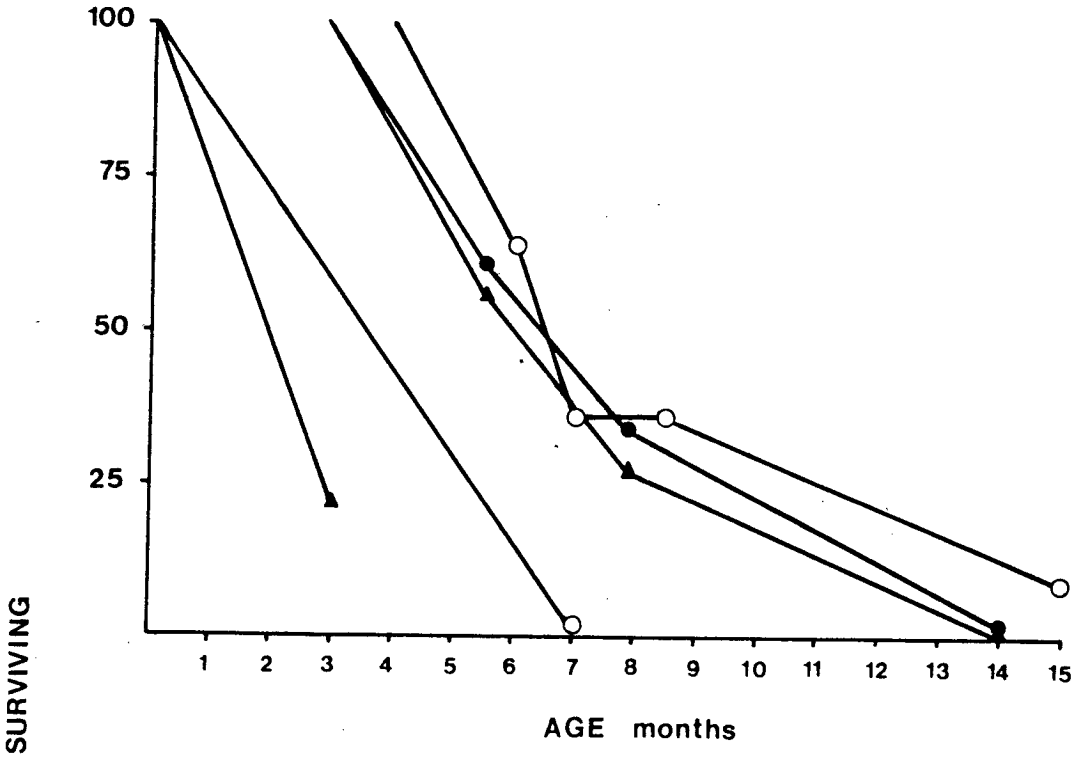
Fig. 5.13 Juvenile mortality. Age in months after settlement.

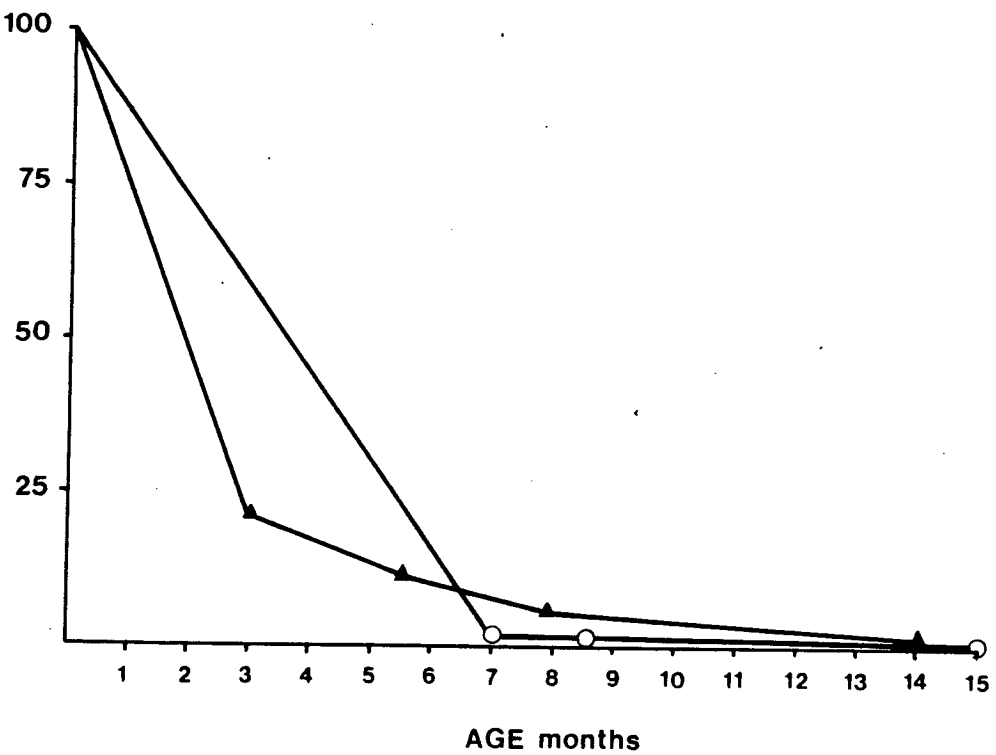


For further details of the origins of data see text.

Fig. 5.14 Juvenile mortality. Composite graph of juvenile mortality derived by combining data for immediate post settlement mortality with separate mortality data obtained for later juvenile stages. Graphs were compiled assuming that juvenile P. sinensis counted at 3 and 7 months after settlement have suffered the same mortality as those on other substrata in the immediate post settlement period.




100
75
50
25
PERCENT SURVIVING
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE months


100
75
50
25
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE months

these two species, from settlement to 14 and 15 months (Fig. 5.14). While the two types of initial mortality data are not directly comparable, since they involve different experimental cohorts under slightly different conditions, the composite graphs are very similar.

5.4 DISCUSSION

Population structure Clear differences in population size-structure and mean colony size were observed between Platygyra sinensis and the two Goniastrea species at both bays (Figs. 5.1-5.3). Goniastrea aspera and G. favulus populations were dominated numerically by small colonies, which made significant but variable contributions to overall cover, while P. sinensis populations were generally dominated by larger colonies, especially in terms of total cover. Mean colony size of P. sinensis was about 3 times that of either Goniastrea species, a result which cannot be entirely explained by differences in growth rate since P. sinensis grows only about 1.7 times faster (Ch. 3).

The proportion of colonies which were microatolls, or had suffered major damage at some time in the past was almost twice as high in P. sinensis (82%) as in G. aspera or G. favulus (50% and 49%; Fig. 5.4). In addition, the proportion of colonies in the population which were products of fission was also much greater in P. sinensis (46% - 76%) than in either Goniastrea species (Table 5.6). Thus it appears that to a certain extent, these populations are following the pattern found in other coral populations, where species in which fission plays a major role in colony formation are less dominated by small size classes than are those in which recruitment is the major source of recruits (Hughes and Jackson 1985). Platygyra sinensis also attains a larger size than the other species, which further increases its chances of fission (Table 5.6; Hughes and Jackson 1985). The overall rate of sexual recruitment was also higher in both Goniastrea species than it was in P. sinensis (Table 5.5).

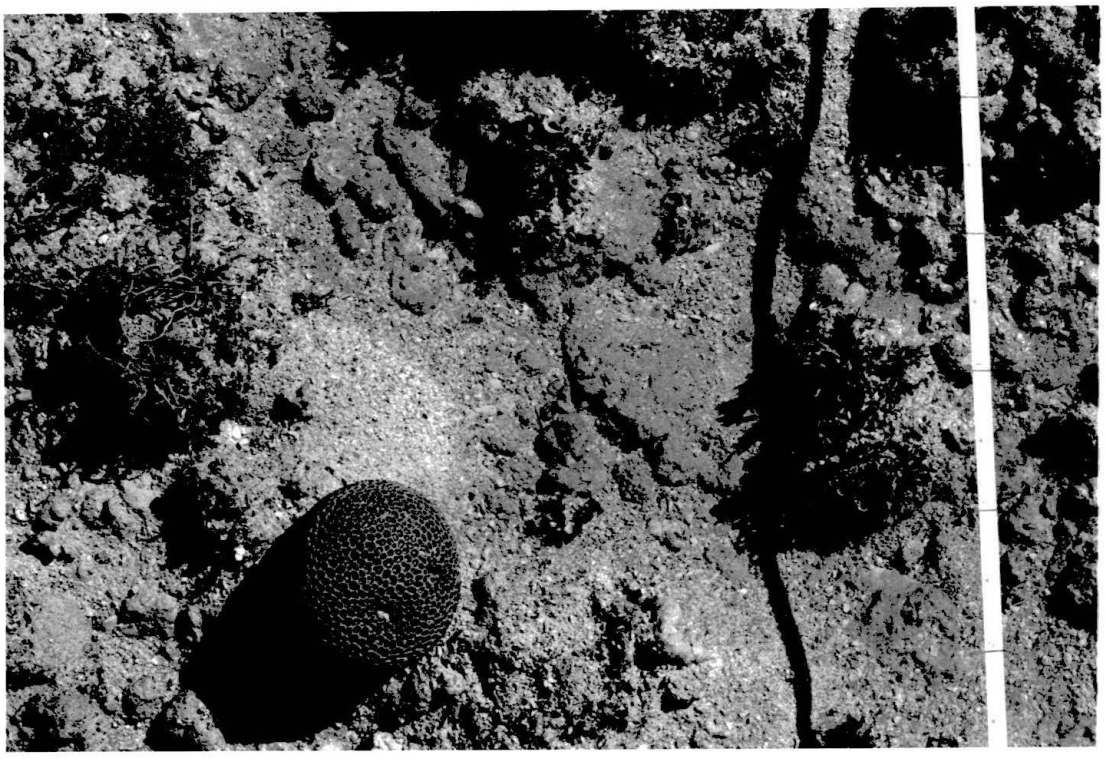
Size frequency distributions of all species were skewed towards the

smaller size classes at Pioneer Bay in comparison to Geoffrey Bay and all species also had smaller mean sizes (Figs. 5.1-5.2). Overall there was a higher proportion of 'microatolls' or otherwise damaged colonies at Pioneer Bay than at Geoffrey Bay, especially in the smallest size classes,, where the proportion of these colonies was 41% in G. favulus, and 29% in P. sinensis (Fig. 5.2). Most true microatolls are formed by exposure during spring low tide, when desiccation and exposure to direct sunlight kill off the top of the colony. This often results in microatolls with their tops inclined at right angles to the sun's direction during low tides (Fig. 5.15). Not all colonies showed this type of damage; however other causes of mortality can only be speculated upon. For example, the level of the reef flat at Pioneer Bay is lower than that of Geoffrey Bay (Ch. 2), and subsequently exposed for shorter periods during low tides. As a consequence partial mortality might be expected to be lower at Pioneer Bay than at Geoffrey Bay. The explanation for this may lie in the nature of the reef flat at Pioneer Bay, which has a more three-dimensional structure than the reef flat at Geoffrey Bay (Fig. 5.16). Due to the cryptic nature of much of the settlement of these species, a large number of colonies are situated on the edges of small depressions or cracks in the reef surface. Since the surface of the reef flat is essentially quite level, this may result in an increased probability of rubble, macroalgae, sponges, and other corals falling on top of colonies and damaging them, resulting in increased partial mortality. In contrast, the majority of colonies at Geoffrey Bay grow above the general level of the reef flat and are less likely to be covered or damaged by wave entrained objects.

Data describing the population structure of Goniastrea favulus in other parts of the Pacific region are available from Heron Island in the southern Great Barrier Reef (Kojis and.Quinn 1981), and from Phuket, on the western coast of Thailand (Brown et al. in press). Size-frequency distributions of populations around Phuket were very similar to those found in this study when converted to equivalent size classes, and had a mean size corresponding to between 25cm^2 and 49cm^2 (based on maximum diameters only), compared with mean sizes of 18cm^2 to 80cm^2 for Pioneer and Geoffrey Bays respectively. The general pattern was also similar at Heron Island, however large colonies were more abundant, and subsequently

Fig. 5.15 Top. A typical hemispherical colony of Goniastrea aspera at Geoffrey Bay.

Bottom. An inclined microatoll of Platygyra sinensis at Geoffrey Bay.



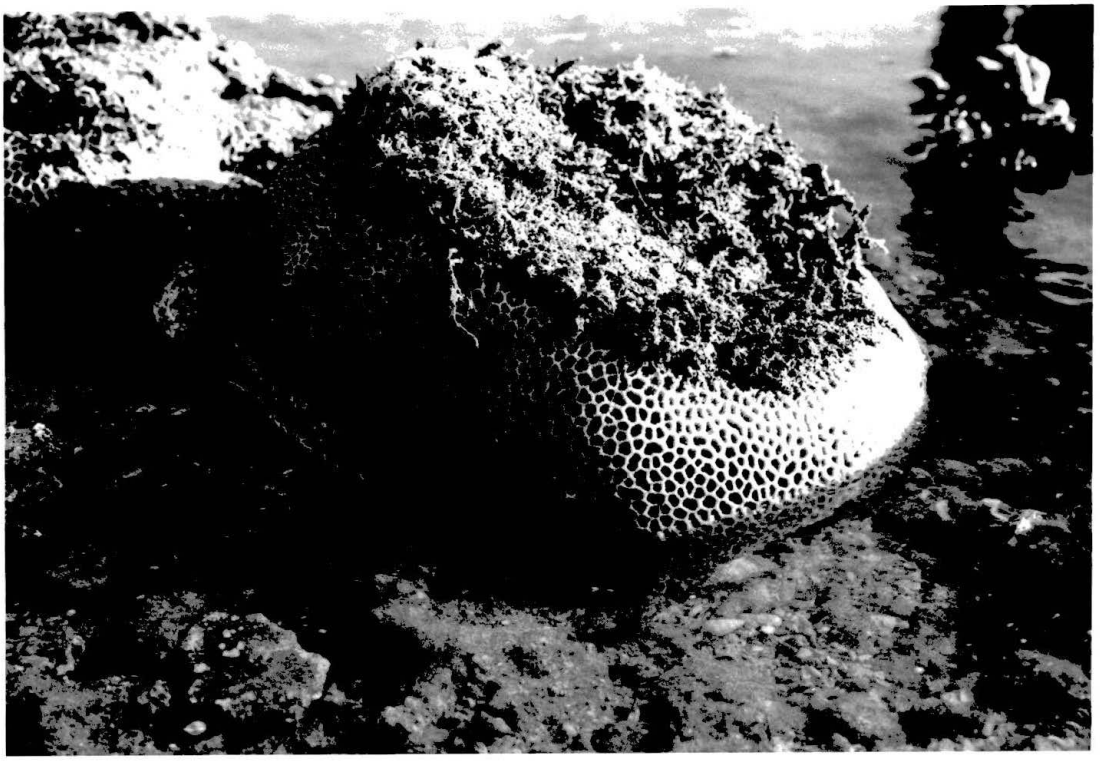
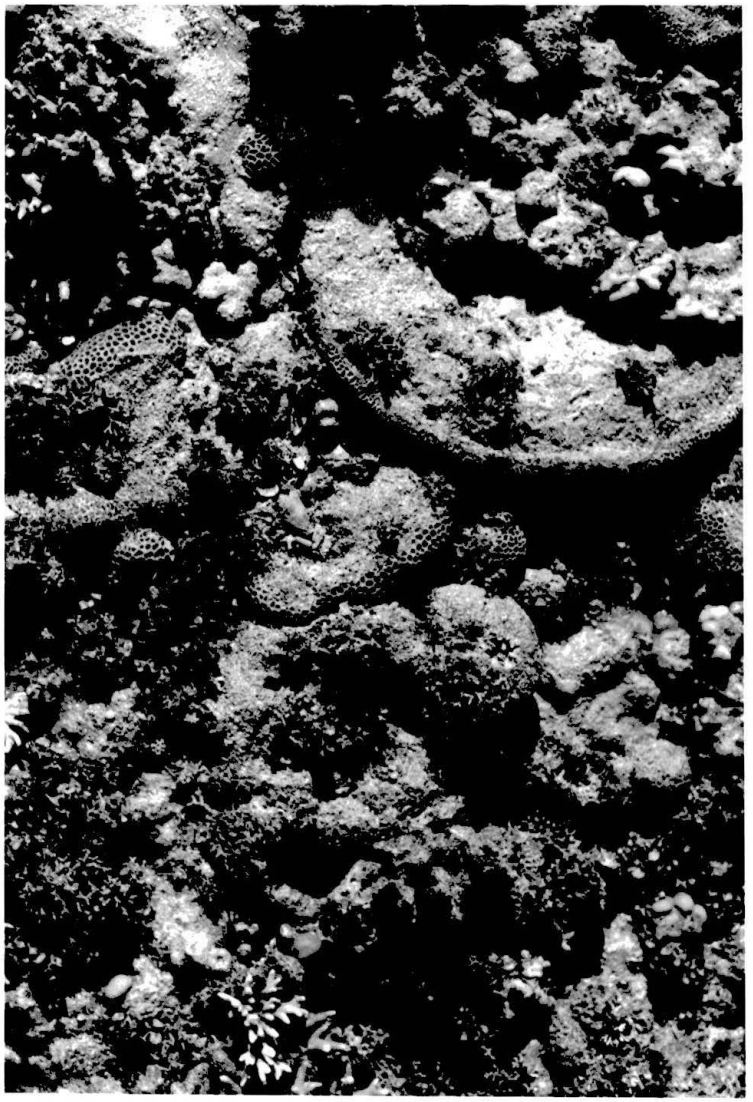


Fig. 5.16 Top. The reef flat at Geoffrey Bay, with both microatolls and hemispherical colonies of G. aspera. Note that the surface of the reef flat is composed of a large proportion of rubble, and that the colonies project above its relatively level surface.

Bottom. The reef flat at Pioneer Bay, with a typical large microatoll of P. sinensis and numerous small colonies of G. favulus. The reef flat of this bay was more complex in its structure, and colonies were less likely to project above the general level of the reef flat.



the mean colony size was larger there (127cm^2).

Short of either following populations for very long periods of time, or studying newly recruited cohorts of short-lived species, the solution to some of the problems of ageing corals may be reached by choosing species or populations in which the problems mentioned above are reduced to manageable levels. Certain massive species are probably better suited to attempts at ageing than foliose or branching forms. Corals such as massive Porites can be individually cored and accurately aged, or their ages can be estimated from growth rates and diameters (Potts et al. 1985). Estimations can only be carried out where the original colony remains intact, or if the divided parts remain firmly connected. Since daughter colonies of Goniastrea aspera, G. favulus and Platygyra sinensis usually remained firmly connected after fission it was possible to define genetic individuals. Estimation of the ages of individuals was then possible, using knowledge of both juvenile and adult growth rates. The formulae used to estimate age are believed to be the most accurate possible. They incorporate both adult and juvenile growth, and the adult growth rates used are based on x-radiographic measurements which incorporate both individual, year to year, and between site variability. Relatively large numbers, especially of the Goniastrea species, and the lumping of age classes increased the generality of any conclusions drawn from these estimates. Thus it was possible to examine populations at the level of colonies or modules, as well as at the level of genetic individuals.

Comparisons of size- and age-based population structures reveal a number of differences. There were overall differences of between 9% and 29% between the number of morphologically and genetically distinct colonies (ramets vs. genets) (Table 5.8). These levels of clonal input to the population are not insignificant, but are lower than those found in corals with other growth forms. The open branching Acropora cervicornis was estimated by Neigel and Avise (1983) to have about a 40% difference, however this was only based on a simulated population. A suite of foliose species studied by Hughes and Jackson (1984) had an overall difference (based on very conservative estimates) of at least 24% between the number of ramets and genets.

Table 5.8 Numbers of colonies (ramets), and genetic individuals (genets) in the study populations, 1984.

	ramets	genets	% difference
Geoffrey Bay			
G. aspera	181	164	9
G. favulus	49	49	0
P. sinensis	101	76	25
Pioneer Bay			
G. aspera	50	46	8
G. favulus	288	242	16
P. sinensis	25	13	48
Pooled Bays			
G. aspera	231	210	9
G. favulus	337	291	14
P. sinensis	126	89	29

The youngest age class (visible recruitment to 5 years) was the most abundant only in the populations of *G. aspera* and *G. favulus* at Pioneer Bay. In all other populations one or more of the older age classes were more numerous than the youngest. This may have a number of causes: either the populations are declining, or recruitment may be episodic. Juvenile survival may be sufficiently variable to cause significant differences in abundance, even when averaged over a number of years. Since populations which showed both declines and increases in overall population size displayed this trend (Table 5.7), the latter explanation seems more likely.

The most interesting aspect of the age-based population structure is the relative contribution to total cover made by the various age classes. In all cases the most significant contribution was made by intermediate aged colonies, in contrast to the size-based population structure where the largest colonies, perhaps not surprisingly, contributed the bulk of total cover in most cases. The oldest colonies however were not the largest in size and contributed a relatively small proportion of the total cover (Table 5.6, Figs.

5.4-5.6). The reason for this lies in the probability of injury (partial mortality) being greater for larger colonies (Figs 5.7-5.9), and that once injured, the likelyhood of further injury is greater than for colonies which have not been injured in the past (Table 5.3). As colonies grow older and larger, the probability of some kind of damage occurring to them increases for a number of reasons. Larger colonies project further above the reef flat and are exposed for longer periods of time and more frequently. They are thus more likely to become microatolls. Random deleterious events are also more likely to affect colonies as they grow and cover more space. Bioerosion of the substratum or the skeleton of the coral at the attatchment point may also increase over time resulting in the dislodgement of colonies.

Given the increased probability of further damage to already damaged colonies, the older portions of some populations in habitats on reef flats at Geoffrey and Pioneer Bay appear to suffer a mean downward trend in colony size (Figs. 5.10, 5.11). This may be equivalent in its demographic consequences to a period of senescence in these species. On theoretical grounds, senescence is not expected to occur in colonial organisms such as corals (Harper 1980). In the corals studied here (Ch. 3) and most other colonial corals (Van Moorsel 1985) growth is indeed indeterminate and there appears to be no sign of physiological senescence. A number of coral species have been shown to be very long-lived (Porites spp., Potts et al. 1985) or to have a high probability of great age (Acropora cervicornis, Neigel and Avise 1983; foliose species, Hughes and Jackson 1985). All of these are sub-tidal species or populations, so it is possible that the occurrence of such a period of senescence is restricted to particular species and habitats, such as those studied here. It should be emphasized that that this trend must be considered a characteristic of populations (and perhaps only some populations) rather than of individuals. Some colonies may continue to grow optimally until they are destroyed completely, however the mean size of the oldest age classes in this study did not continue to increase.

Population dynamics Mortality in all three species was inversely proportional to both colony age (Fig.5.12), and colony

size (Figs. 5.7 - 5.9). Similar trends have been found in all previous studies of coral mortality (Connell 1973; Loya 1976a; Rylaarsdam 1983; Harriott 1985; Hughes and Jackson 1985; Wallace 1986). The simplest explanation for this, put forward by Jackson (1979), suggested that the likelihood of any event completely killing a small colony is greater than that for larger colonies, where there is a higher probability of part of the colony may remaining unaffected. As a corollary, it should be expected that although large colonies have a lower rate of total mortality they will have a higher incidence of partial mortality. This was indeed demonstrated by Hughes and Jackson (1985) for foliose species at Discovery Bay in Jamaica, and for the three species in this study (Figs. 5.7 - 5.9). For reef flat species such as G. aspera, G. favulus and P. sinensis, the chance of partial mortality is further increased by emersion and other factors described previously. The rigours of the intertidal habitat may also be responsible for the high turnover rate found in these corals (Tables 5.2, 5.3) which are comparable to those of foliose species (Hughes and Jackson 1985). Foliose corals might have been expected to have a much higher turnover due to their morphology which is more prone to fragmentation. In addition rubble or sediment of large particle size may be less easily removed from flat surfaces than from the convex surfaces of massive species.

Despite their massive growth form and relatively small potential size, which should tend to reduce the probability of colony fission, high rates of colony fission were found in a number of populations in this study. However, when the mean annual probabilities of fission were averaged for the six populations of massive corals in this study, a value of 0.029 was obtained, compared with a value for eight populations of foliose Caribbean species of 0.05 (Hughes and Jackson 1985, Table 4). It is likely that the rates for open branching species are even greater.

Colony fission has been described as being advantageous in many species of corals (review in Highsmith 1982; Hughes and Jackson 1985) since it provides a means for the rapid occupation of space, and spreads the risk of mortality of the whole genotype (Highsmith 1982). Highsmith concluded that a number of corals appear to have

incorporated fragmentation into their life histories, but the massive faviids on the reef flats of Geoffrey and Pioneer Bays are not among them. Fission in G. aspera, G. favulus and P. sinensis is probably best considered a form of partial mortality in these slow growing species, and a cost rather than a benefit . Although there may be a significant number of clonally related colonies in some populations (especially P. sinensis), previously damaged colonies are more likely to suffer further damage, and age frequency distributions indicate that many older colonies are reduced significantly in size (Figs. 5.3 - 5.6), in some cases below the reproductive threshold (Ch. 4). While fragmented colonies may survive for some time, perhaps eventually exceeding their original size, they probably make a relatively minor contribution to total recruitment and dispersal considering the substantial larval recruitment in these species.

Juvenile mortality The rate of mortality of corals in the first year of life (Fig. 5.13) was much higher than that in any of the older age classes. This is consistent with the trend of size dependent mortality found among the older members of the population. The trend is in fact evident even within the first year, with mortality in the first few months being higher than in the latter part of the year. There are very few records in the literature with which to compare these mortality rates. Most field studies have been based on visible recruits usually more than 10mm in diameter, and never less than 5mm in diameter (Bak and Engel 1979; Rylaarsdam 1983; Van Moorsel 1985). These corals are likely to be at least 6 months to 1 year old (Babcock 1985). Mortality in Acropora millepora (86%) in the period 3.4 to 9.3 months after settlement (Babcock 1985) was similar to that found in favid species in this study. The mortality rates of these species, which are all gamete spawning species, appear to be rather higher, at least 95%, than rates for other corals raised in situ. Porites astreoides had a mortality of 74% in the first year (Vaughan 1912), while Pocillopora damicornis in the first three months on uconditioned blocks (equivalent to the substratum used here) suffered only 29% mortality. This should be compared with the 79% mortality suffered by Platygyra sinensis in the first three months. Mortality of

Pocillopora damicornis at Okinawa in the first six months was between 83% and 96% on caged, vertically oriented dishes (Sato 1985). This was the treatment most similar to the experimental conditions used here. Other treatments used by Sato, such as uncaged, and upward and downward facing dishes produced very different results, with mortalities on unprotected upward-facing dishes reaching 100% after only two weeks. Porites astreoides and Pocillopora damicornis are both planulating species, and as further studies in post settlement mortality are carried out it will be interesting to see whether the trend of lower juvenile mortality in planulating species than in gamete-spawning species is borne out. Clearly the role of microhabitat in early survival, especially in relation to larval settlement behaviour, needs to be further investigated before completely realistic estimates can be made of juvenile coral mortality and the role it plays in the maintainance and distribution of coral populations. The results of Sakai and Yamazato (1984) appear to be particularly interesting in this regard since their mortality rates of newly settled corals on denuded natural substrata are much lower than those recorded on experimental substrata.

CHAPTER 6 LIFE TABLES

6.1 INTRODUCTION

Despite recent increases in the number of studies on the topic of coral population biology there remain few studies which have attempted to construct classical life tables for corals, and none of the life tables which have been constructed have been for hermatypic scleractinians. Life tables have been published for two temperate species of gorgonian (Muricea californica and M. fruticosa) by Grigg (1977), and for the ahermatypic scleractinian Balanophyllia elegans by Fadlallah (1983a). Studies of the population biology of hermatypic scleractinians have concentrated on various facets of their ecology such as reproduction (Goniastrea favulus, Kojis and Quinn 1981), age structure (Diploria strigosa, Dodge and Vaisnys 1977), and dynamic aspects of coral populations (Connell 1973; Loya 1976; Harriott 1983b; Hughes and Jackson 1985). None have combined all of these aspects in the form of life tables and there are a number of reasons for this. The principal difficulty lies in establishing the age and individual status of colonial organisms, in which colony size may be poorly linked to age, and in which clonal propagation may even separate individuals into several colonies. Lack of knowledge of the reproductive and larval biology of corals has also presented problems in the compilation of full life table data (Ch. 1).

In Goniastrea aspera, G. favulus and P. sinensis, limitations which restrict the use of life tables for many corals can be largely overcome. Each species produces a massive skeleton which serves as a record of the growth and history of individuals, preventing the decoupling of size and age. The skeletons of these corals possess annual density bands which, although they were not used to age individual corals, do allow accurate determination of mean growth rates which incorporate variations in annual growth rates. Age estimates also included the period of slow juvenile growth found in these species. In addition, the reproductive biology of these species is now well known, making it possible to calculate age-

specific fecundities for the populations. In this chapter I attempt to construct life tables for these species based on data presented in the previous chapters, and compare them with data available for other scleractinians. Information on fertility schedules, generation times and larval development will also be discussed in relation to theories relating to the evolution and biogeography of Indo-Pacific Scleractinia.

6.2 AGE DETERMINATION and AGE DISTRIBUTION

Ages of colonies were estimated from skeletal size by the formula described in Chapter 2, using the appropriate values for juvenile and adult growth rates for each species and population. These estimates assume that all colonies which were the product of fission could be recognized as such and the appropriate measurements made. Although it is possible that this assumption was violated in some cases these instances are likely to have been rare, due to the skeletal characteristics of the species, as discussed above. Age structures are all based on 1984 populations and are in the form of 5 year age classes, apart from the initial age class of 0 - 2 yrs in the horizontal life tables (Tables 6.1 - 6.3), which represents the period of time between spawning and visible recruitment. Five year age-classes, while they may sacrifice precision, probably represent a conservative degree of accuracy when confidence limits on age determinations (Ch. 4) are taken into account. In addition, pooling of year classes into 5 year intervals facilitated the construction of age frequency distributions, especially for the older age-classes where numbers were low. Although it is probably impossible to achieve total accuracy of age determination in any coral population, without very long term studies, the information gained by an age-based approach to coral populations makes such attempts worthwhile. This is especially true in light of our present lack of knowledge in this area.

6.3 AGE-SPECIFIC FECUNDITY SCHEDULES

The fecundity of colonies of each species was estimated on the basis

of colony size and the size-specific fecundity relationship for each population (Ch. 4). The surface area of colonies and the mean number of egg bearing mesenteries per cm^2 was multiplied by the size-specific fecundity (mean number of eggs per mesentery) (Ch. 4) of individuals in each age-class. Where individuals consisted of a number of daughter colonies, the fecundity of each colony was calculated separately and then summed to provide the total fecundity for the individual. Age-specific fecundity schedules (m_x) were calculated using the observed age distributions, pooled for both bays. In the case of empty age classes m_x values were estimated by taking an average of the values of the four adjacent age classes, or the two adjacent age classes where only one was present on one side of the missing value. Populations from both bays were pooled for the construction of life tables for two reasons: Firstly, some populations were too small to provide adequate numbers for the construction of separate life tables, and secondly so that estimates of the size of the zero age-class could be obtained from population fecundities. If the size of the zero age class was estimated from the fecundities of populations at each bay it would be necessary to assume self-seeding of populations. This assumption is not likely to be valid due to the dispersive nature of the eggs and larvae of these species. Consideration of pooled populations takes into account a well mixed resevoir of larvae, and since the populations at Geoffrey and Pioneer Bays are broadly representative of populations on fringing reef flats of the central Great Barrier Reef region, pooled populations are assumed to represent 'regional' populations.

Generation times, defined as the mean age of the mothers of a set of new-born individuals in a population (Charlesworth 1980), was calculated using the age-specific fecundity schedules for each species.

6.4 RATE OF INCREASE

The observed per capita rate of increase (r) for each species was calculated from the three estimates of population size in 1982, 1983 and 1984 using the following formula:

$$r = \frac{\Sigma Nt - (\Sigma N)(\Sigma t)/n}{\Sigma t^2 - (\Sigma t)^2/n}$$

where N = natural log of population size at each census, t = time units of one year, scaled so that the time of the first census equals one, and n = the number of estimates (Caughley 1977). Alternative estimates of r were obtained from life table data. These were in the form of r_c, the capacity for increase (Southwood 1978), calculated as the natural log of the sum of $l_x m_x$ divided by the generation time of the population.

6.5 MORTALITY and SURVIVORSHIP

Age-specific mortality rates observed between 1982 and 1984 (Ch.5) were used to calculate annual mortality rates for each age-class in the construction of horizontal life tables (Tables 6.1 - 6.3). Horizontal life tables include an age class (0 -2 yrs) not present in the vertical life tables. Individuals in this size class could not be observed, since this period includes the larval and juvenile stages (hence the lack of an f_x value), however it was possible to estimate mortality from the size of the zero age class and the mean annual recruitment rate. Recruits are likely to become visible only after 2 years (Ch. 3), thus this estimate of mortality includes mortality both before and after settlement.

Vertical life tables were also constructed from the age frequency distributions of each pooled population. The primary assumption for the compilation of vertical life tables is that they can only be made for populations with a stable age distribution. this assumption is clearly invalid for the populations in this study, as indicated both by their age distributions (Fig 5.6) and by the observed rates of increase of the populations over the period of the

study. The procedure can however still be carried out if corrections are made (Caughley 1977). It was thus necessary to carry out several procedures prior to calculating values for these life tables. The sampled frequency was corrected by multiplying it by a correction factor (e^{rx}) based on the observed rate of increase of the populations. It was then necessary to smooth the corrected frequencies from f_1 onwards, by fitting a curve to the observed frequencies. A number of formulae were tried, including log-polynomials and probits (Caughley 1977), as well as several other monotonically decreasing functions ($y = a - bx$; $y = ae^{-bx}$; $y = ax^{-b}$; $y = 1/(a + bx)$; $y = a - b \ln x$; Grigg 1975). The goodness - of - fit of the smoothed frequency distributions with the corrected frequency distributions were compared to determine the formula which provided the best fit. For each species the formula: $y = a - b \ln x$ produced the highest value for Chi-squared, and appeared to be the closest fit when frequencies were plotted and compared graphically. Consequently this formula was used for age frequency smoothing in the construction of vertical life tables.

Both horizontal and vertial life tables as described above have certain drawbacks and limitations when used for comparatively small populations such as those studied here. Age specific mortalities observed over a relatively short period of time may be different in detail from those that might be observed over longer periods. A number of assumptions are necessary in the construction of vertical life tables, and operations such as smoothing of data in the life table may introduce numerical attributes of formulae which have no strict biological basis. Since far fewer assumptions were necessary in the construction of horizontal life tables than for vertical life tables, the former must be preferred. However in general it may not always be possible to study populations for long enough to obtain mortality data on which these life tables are based. It is therefore instructive to compare the results of the two methods in this case.

6.6 LIFE TABLES

Age specific survivorship and fecundity schedules for Goniastrea

aspera, G. favulus and Platygyra sinensis are presented in Tables 6.1 - 6.3 (horizontal life tables) and 6.4 - 6.6 (vertical life tables). Survivorship curves for all three species were of the classic type III form (Deevey 1947), with mortality acting most heavily on the youngest individuals (Figs. 6.1 and 6.2). Survivorship in the oldest age classes (Tables 6.1 - 6.3), as determined from mortality of individuals observed in the field, indicated very low rates of mortality of individuals. There were in fact very few instances of individuals dying over the period of the study, however mortality of parts of individuals (i.e. colonies resulting from fission) was often observed (Ch. 5). Life tables are not designed to take partial mortality into account (there are other methods such as size class transition probabilities which can be used to deal with this; Hughes 1984; Ch. 5), however it should be noted that the oldest colonies in the various populations should not be considered immune to the processes of mortality. Vertical life tables for G. aspera and G. favulus did produce higher mortalities in the older age classes, truncating the older portion of the populations relative to the observed distributions. In the vertical life table for P. sinensis the older portion of the population was not truncated and was in fact emphasized by the calculation of the life table. In all three cases this is the result of the correction factor which was negative for G. aspera and G. favulus, and positive for P. sinensis. The correction assumes that the observed increase or decrease in the population is a persistant feature, rather than merely a trend observed during the relatively brief period of the study which might be reversed or cancelled over a longer period.

Overall survivorship was higher for G. favulus than for G. aspera or P. sinensis (Figs. 6.1 and 6.2), with the major difference between the species occurring in the first age class.

The observed per capita rate of increase for each population was: G. aspera: $r = -0.035$; G. favulus: $r = -0.02$; and P. sinensis: $r = +0.035$. Recruitment was fairly constant throughout the study, and most of the deviation from population stability was the result of mortality to the populations in the period 1982 to 1983 (Ch. 5.3.2). There was little agreement between the observed rates of increase

Table 6.1 Horizontal life table for Goniastrea aspera. +: below size of visible recruitment; *: values estimated from adjacent age classes. See text for explanations.

x (pivotal age class)	f_x	l_x	s_x	m_x	$l_x m_x$
0	17200623	1.00	1.77×10^{-6}	0	0
2	+	1.77×10^{-6}	0.59	0	0
5	45	1.05 "	0.80	898	.00094
10	52	0.84 "	0.91	20979	.01762
15	45	0.76 "	0.92	74238	.05642
20	34	0.70 "	1.00	167261	.11708
25	16	0.70 "	0.85	304431	.21310
30	6	0.59 "	1.00	125377	.07397
35	2	0.59 "	1.00	522198	.30809
40	0	0.59 "	1.00	210112*	.12397
45	1	0.59 "	1.00	3015	.00178
50	1	0.59 "	1.00	89858	.11202

$R_o = 1.02499$

Table 6.2 Horizontal life table for *G. favulus*. +: below size of visible recruitment; *: values estimated from adjacent age classes. See text for explanations.

x (pivotal age class)	f_x	l_x	s_x	m_x	$l_x m_x$
0	1914348	1.00	2.20×10^{-5}	0	0
2	+	2.20×10^{-5}	0.78	0	0
5	127	1.71 "	0.86	146	.00249
10	94	1.47 "	0.96	4511	.06631
15	55	1.41 "	1.00	17331	.22436
20	8	1.41 "	1.00	18728	.26406
25	0	1.41 "	1.00	78394	1.10535
30	2	1.41 "	1.00	44851*	.63230
35	1	1.41 "	1.00	232667	3.28060
40	0	1.41 "	1.00	128560*	1.81269
45	0	1.41 "	1.00	128560*	1.81269
50	1	1.41 "	1.00	24453	.34479

$R_o = 9.5656$

Table 6.3 Horizontal life table for *P. sinensis*. +: below size of visible recruitment; *: values estimated from adjacent age classes. See text for explanations.

x (pivotal age class)	f_x	l_x	s_x	m_x	$l_x m_x$
0	10968205	1.00	1.87×10^{-6}	0	0
2	+	1.87×10^{-6}	0.4	0	0
5	12	0.75	0.94	0	0
10	14	0.70	1.00	2956	.00206
15	16	0.70	0.92	97757	.06842
20	21	0.65	0.79	141087	.09171
25	7	0.51	0.93	226089	.11530
30	8	0.47	0.86	338340	.15901
35	5	0.41	1.00	277127	.11362
40	1	0.41	1.00	53863	.02208
45	3	0.41	1.00	140654	.05767
50	0	0.41	1.00	97335*	.03990
55	1	0.41	1.00	99095	.04062
60	0	0.41	1.00	97412*	.03993
65	0	0.41	1.00	97412*	.03993
70	1	0.41	1.00	95730	.03924

$R_o=0.8295$

Table 6.4 Vertical life table for G. aspera. *: values estimated from adjacent age classes. See text for explanation..

x (pivotal age class)	f_x	f_x (corrected)	f_x (smoothed)	l_x	s_x	m_x	$l_x m_x$
0	17200623	17200623	17200623	1.00	2.6×10^{-6}	0	0
5	45	37.8	45.0	2.6×10^{-6}	0.69	898	.0233
10	52	40.8	30.4	1.8 "	0.72	20979	.03776
15	45	26.6	21.9	1.3 "	0.69	74238	.09650
20	34	16.9	15.8	0.9 "	0.66	167261	.15053
25	16	6.6	11.2	0.6 "	0.66	304431	.18265
30	6	1.8	7.4	0.4 "	0.50	125377	.05015
35	2	0.6	4.1	0.2 "	0.40	522198	.10443
40	0	0	1.3	0.1 "	0	210112*	.01680
45	1	0.2	0	0	0	0	0
50	1	0.2	0	0	0	0	0

R_o=0.6421

Table 6.5 Vertical life table for G. favulus. *: values estimated from adjacent age classes. See text for explanation.

x (pivotal age class)	f_x	f_x (corrected)	f_x (smoothed)	l_x	s_x	m_x	$l_x m_x$
0	1914348	1914348	1914348	1.00	5.4×10^{-5}	0	0
5	127	114.8	103.0	5.4×10^{-5}	0.65	146	.00784
10	94	76.9	66.9	3.5 "	0.69	4511	.15788
15	55	40.7	45.7	2.4 "	0.76	17331	.41594
20	8	5.4	30.7	1.6 "	0.61	18728	.29964
25	0	0	19.0	0.99 "	0.50	78394*	.77610
30	2	1.1	9.6	0.50 "	0.22	44851	.22425
35	1	0.5	2.1	0.11 "	0	232667	.25593
40	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0
50	1	0.4	0	0	0	0	0

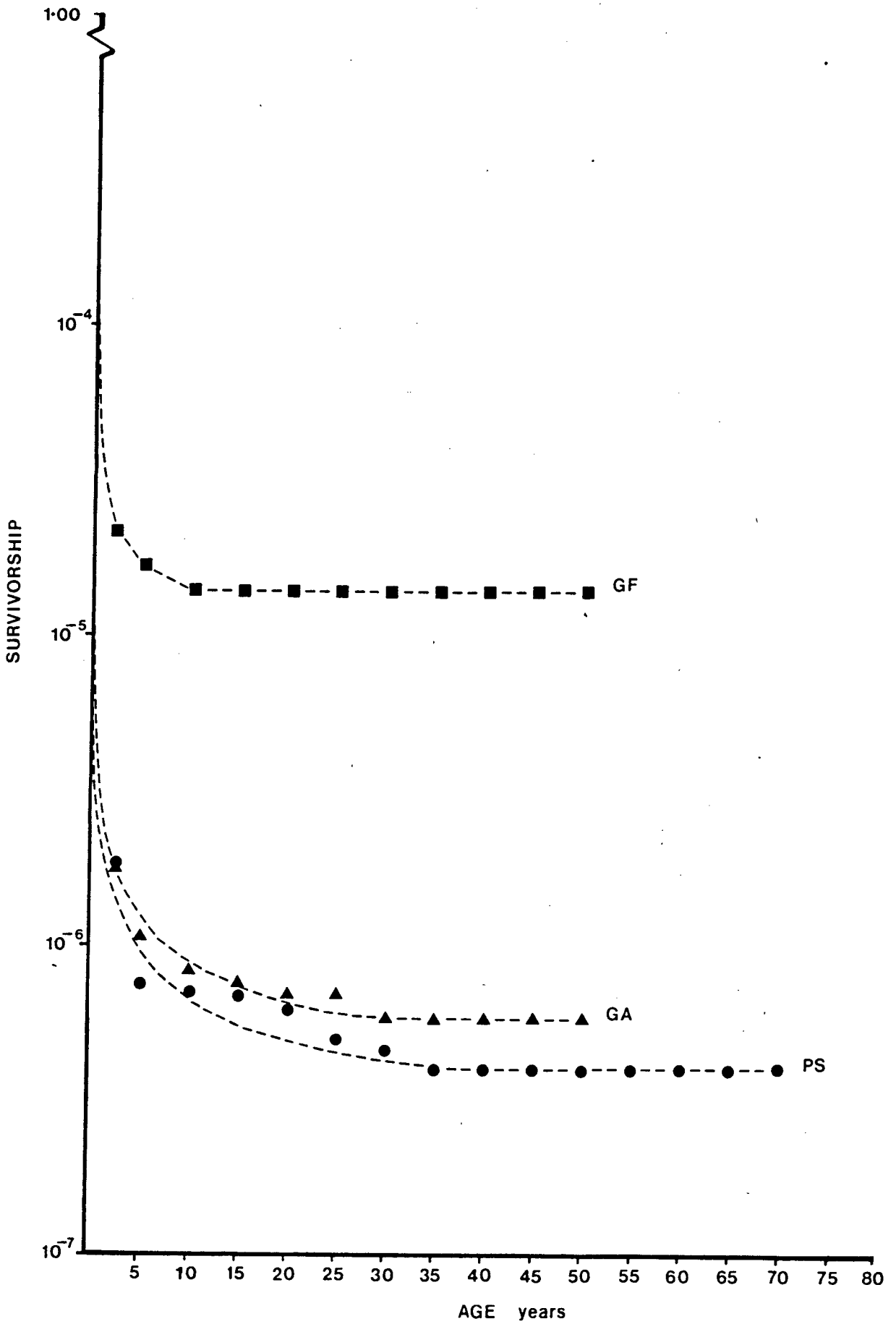
R_o=2.1376

Table 6.6 Vertical life table for P. sinensis. *: values estimated from adjacent age classes. See text for explanation.

x (pivotal age class)	f_x	f_x (corrected)	f_x (smoothed)	l_x	s_x	m_x	$l_x m_x$
0	10968205	10968205	10968205	1.00	2.60×10^{-6}	0	0
5	12	14.3	28.8	2.6×10^{-6}	0.81	0	0
10	14	19.7	23.1	2.1 "	0.86	2456	.00515
15	16	27.0	19.7	1.8 "	0.83	97757	.17596
20	21	42.2	17.4	1.5 "	0.93	141087	.21163
25	7	16.7	15.6	1.4 "	0.93	226089	.31652
30	8	22.8	14.1	1.3 "	0.92	338346	.43984
35	5	17.0	12.8	1.2 "	0.92	277127	.30483
40	1	4.1	11.8	1.1 "	0.89	53863	.05763
45	3	14.5	10.7	0.98 "	0.92	140654	.13784
50	0	0	9.9	0.90 "	0.91	97335*	.08760
55	1	6.8	9.1	0.82 "	0.93	99095	.08125
60	0	0	8.4	0.76 "	0.92	97412*	.07403
65	0	0	7.7	0.70 "	0.93	97412*	.06818
70	1	11.6	7.1	0.65 "	0	95730	.06222

R_o=2.0127

Fig. 6.1 Survivorship of *G. aspera*, *G. favulus* and *P. sinensis* (pooled populations) from horizontal life tables. GA: *G. aspera*; GF: *G. favulus*; PS: *P. sinensis*. Age in years.


1·00
10^{-4}
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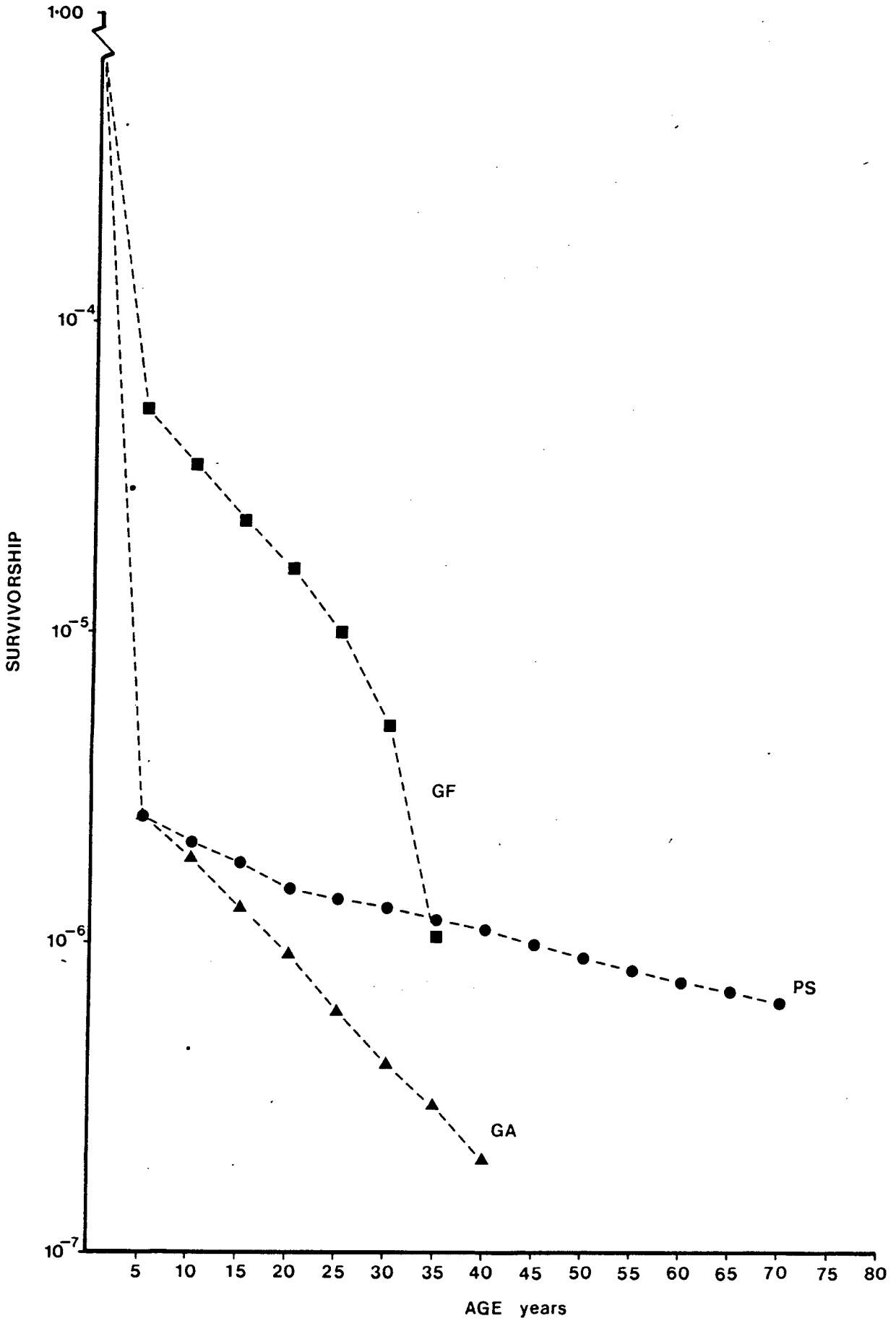
45
50
55
60
65
70
75
80
AGE years

Fig. 6.2 Survivorship of *G. aspera*, *G. favulus* and *P. sinensis* (pooled populations) from vertical life tables. GA: *G. aspera*; GF: *G. favulus*; PS: *P. sinensis*. Age in years.


1·00
10^{-4}
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SURVIVORSHIP
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GA
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70
75
80
AGE years

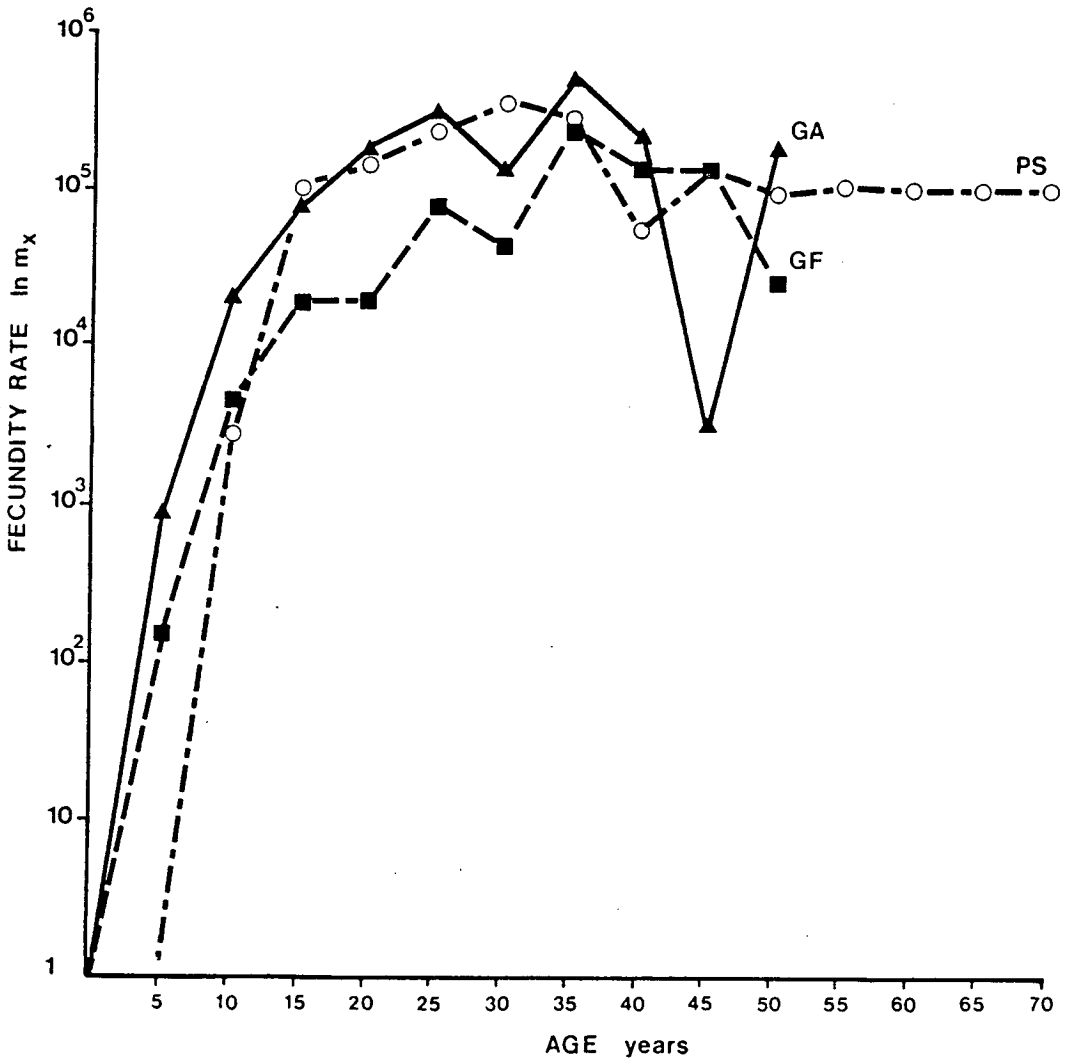
and the r_c values calculated from either of the sets of life tables, or even among the values calculated from the life tables. However most of the values were close to zero (Table 6.7), apart from the r_c value for the G. favulus horizontal life table of .145. High survivorship observed in the older age classes may be responsible for this.

Table 6.7 Observed rate of increase and capacity for increase (r_c) from horizontal and vertical life tables for G. aspera, G. favulus and P. sinensis.

	G. aspera	G. favulus	P. sinensis
r (observed)	-.035	-.02	.035
r_c (horizontal)	.0014	.145	.0069
r_c (vertical)	-.025	.049	.026

The age specific fecundity schedules (Fig. 6.3) for each species show that colony fecundity increases rapidly once reproductive age is reached. The average reproductive output per individual tended to be greatest in the middle age classes, with the oldest individuals often having reduced fecundity. Variability in reproductive potential increased in the older age classes, since total fecundity is a function of colony size and colony size showed the greatest variability among the oldest colonies (Figs. 5.10 and 5.11). The oldest age classes did contain individuals with very high fecundities, however they also contained the highest proportions of colonies which were the product of colony fission and partial fission. This tended to reduce the reproductive potential many of the colonies since size has an important influence on colony fecundity (Ch. 4.3.2). Mean generation times in each population were G. aspera: 18yrs; G. favulus: 16yrs; and P. sinensis: 27yrs.

Fig. 6.3 Age specific fecundity rate of *G. aspera*, *G. favulus* and *P. sinensis* (pooled populations). GA: *G. aspera*; GF: *G. favulus*; PS: *P. sinensis*. Age in years.


FECUNDITY RATE ln m_x
10^6
10^5
10^4
10^3
10^2
10
1
5
10
15
20
25
30
35
40
45
50
55
60
65
70
AGE years
GA
PS
GF

6.4 DISCUSSION

Survivorship to visible recruitment was between 2.6×10^{-6} and 5.3×10^{-5} in the three species, a similar rate to that estimated for Muricea californica (3.5×10^{-7}) and M. fruticosa (4.9×10^{-6}) on the California coast (Grigg 1977). Survivorship curves were of the same general form (Type III) in G. aspera, G. favulus and P. sinensis, with very similar levels of mortality in G. aspera and P. sinensis, and slightly lower levels of mortality in G. favulus. This is largely due to what appears to be lower levels of mortality in G. favulus in the first age class. The difference is most likely to be the result of larval mortality since mortality rates of newly settled juveniles of all three species in the first year of life were very similar (Ch. 5.3.3). The benthic development of the eggs of G. favulus may have the effect of reducing larval mortality in the first one to two days since the dispersal and dilution of eggs prior to their becoming mobile larvae is reduced during this period. A certain degree of self-seeding of G. favulus populations is implicit in this conclusion, however this is not entirely contradictory to the conclusions drawn from the spatial dispersion patterns of adult populations which do not show an unusual degree of aggregation in this species (Ch. 2). Larvae may move around sufficiently during the period between achieving mobility and settlement to obscure any spatial relationship between adult and offspring at small scales, while still tending to remain in the vicinity of their original habitat (i.e. a particular bay or reef).

After high initial mortality in the 0 - 2 and 2 - 5yr age classes, mortality in G. aspera, G. favulus and P. sinensis gradually decreased until by the time the oldest age classes were reached, zero mortalities were recorded in the horizontal life tables (Fig. 6.1). While very few of the older individuals died completely during the period of the study, there was a considerable amount of mortality to parts of individuals, often involving whole daughter colonies. This trend of very little mortality in the oldest age

classes was very similar to that found in Pocillopora damicornis (Harriott 1985) at Lizard Island, It should be noted however that the oldest colonies in that study were estimated to be aged 12 years, therefore P. damicornis suffers a higher overall rate of mortality than any of the corals considered in this study. These results emphasize the fact that for clonal organisms, e.g. plants and corals, colony size rather than individual age is often more important in making predictions about the demographic fate of individuals.

Age specific fecundity schedules for G. aspera, G. favulus and P. sinensis showed rapid increases in fecundity after reproductive age was reached, due to a combination of increased polyp fecundity and increased surface area. Mean colony fecundity decreased in the older age classes as a result of decreases in mean surface area of older individuals and the colonies of which they were composed. The total number of larvae produced by each population was quite large (Tables 6.1 - 6.3), providing a potentially very high r_{max}. However it is clear from the values of r calculated from observed changes in population numbers and from values of r_c that r_{max} was never near being attained. Low survival rates in the first age class which are most likely to be the result of high levels of larval mortality appear to be the main factor limiting the increase of these populations, as has been found in populations of the gorgonians Muricea californica and M. fruticosa (Grigg 1977).

A comparison of the life history patterns of G. aspera, G. favulus and P. sinensis suggest that a number of trade-offs are being made in optimizing reproductive success (Table 6.8). Goniastrea aspera was the most fecund species, and had the smallest eggs, while G. favulus had the largest eggs, but produced them in the lowest numbers. Platygyra sinensis was intermediate in both egg number and egg size, although these fell much closer to the values for G. favulus than G. aspera (Table 6.8). The relativley low number of eggs produced by G. favulus appears to be compensated for by lower rates of larval mortality in this species than in G. aspera and P. sinensis. While rates of larval mortality in both G. aspera and P. sinensis were similar, Platygyra colonies were usually larger and older than those of G. aspera, perhaps compensating to some extent

for relatively low egg production per unit area and high larval mortality. Mean age, generation time and age at first reproduction of P. sinensis were greater than for either of the two Goniastrea species. Goniastrea favulus had the lowest mean age and generation time of the three species, with with G. aspera occupying the intermediate position.

Life history patterns of other scleractinians appear to extend trends found in G. aspera, G. favulus and P. sinensis. Goniastrea aspera, G. favulus and P. sinensis are all long lived organisms, which produce large numbers eggs that are small in relation to the larvae of brooding corals. Goniastrea aspera, G. favulus and P. sinensis all suffer high larval mortality, begin reproduction at around 5 years old, and do not reach adult levels of fecundity until they are 10 to 15 years old. Two long lived species of gorgonian, Muricea californica and M. fruticosa (Grigg 1977) exhibit patterns of reproduction and mortality very similar to those of Goniastrea and Platygyra. The ahermatypic scleractinian Balanophyllia elegans produces large benthic planulae which settle very close (< 1m) to the parent (Gerrodette 1981). Survivorship curves of this species most closely resembles the type II curve (Fadlallah 1983a), in which mortality, including larval mortality, is more or less independent of age. This species reproduces at an early age (1.5 years) and has a life span of under 10 years (Fadlallah 1983a). Although no estimates of larval mortality are available for Favia fragum, this species releases well developed planulae which are capable of rapid settlement (Lewis 1974), and are likely to suffer a low mortality in comparison to larvae of other members of the Faviidae such as Goniastrea and Platygyra which are gamete spawners. Favia fragum reaches reproductive size after two years, and colonies never attain large sizes (Szmant Froelich et al. in press). Stylophora pistillata, which has been described as a fugitive species (Loya 1976), is another short lived species which broods planulae. Massive Porites species are perhaps the longest lived of all scleractinians (Potts et al. 1985), yet their eggs are among the smallest of all scleractinians (Kojis and Quinn 1982a). The common assumption of a positive correlation between high larval dispersal and high larval mortality appear to be supported by these data. Life history patterns with high levels of juvenile mortality are

often asociated with long lived organisms and delayed onset of reproduction (Bell 1976; Stearns 1976). The available data also support this generalization. There appears to be a general trend towards early reproduction and brooding in short lived corals, and for broadcast spawning in longer lived species, as was suggested by Fadlallah (1983). Apparently, short lived species must produce larvae with a high probability of survival in order to ensure their continuity, while longer lived species can afford the gamble of greater dispersal and its advantages (Palmer and Strathman 1981).

Table 6.8 Life history traits of G. aspera, G. favulus and P. sinensis. All values for pooled populations (both bays).

	G. aspera	G. favulus	P. sinensis
egg size(um)	360	420	405
fecundity (eggs cm^{-2})	935	340	350
survivorship to 2yrs ('larval' mortality)	$1.8x10^{-6}$	$2.2x10^{-5}$	$1.9x10^{-6}$
age at first reproduction	4-5 yrs	5-6 yrs	5-8 yrs
mean age of population	11.2 yrs	7.1 yrs	17.3 yrs
mean generation time	18 yrs	15.5 yrs	27 yrs

Data now available on the population biology of scleractinian corals should be taken into account when assessing theories concerning intraspecific variability and speciation observed in this group in the Indo-Pacific. Potts (1983, 1984b) has speculated that a number of the life history attributes of scleractinians, in combination with habitat disruptions caused by sea level fluctuations throughout the quaternary, have inhibited speciation and contributed to the relatively high degree of intraspecific variability observed in corals. The basic mechanism proposed is that corals responded to regular changes in habitat (and to a certain extent geographic isolation) caused by sea level fluctuations with increased intraspecific variation. This variability was fixed in populations, but did not result in speciation for the following reasons: first, generation times of species might be too long for speciation to occur, (e.g. massive Porites species, long lived clones of fragmenting corals such as branching Acropora species). Second, intermediate disturbances (sensu Connell 1979) prevented competitive exclusion of new (or old) genotypes. Third, inbreeding may have maintained variability in populations where larvae settle near their parents, especially in long-lived species. Finally, dispersal of larvae between subpopulations would maximize variation in the population as whole and prevent genetic divergence of sub-populations.

I consider that these mechanisms may have to be re-evaluated, since a number of the processes proposed above to maintain variation appear to have limited validity and are even contradictory. Generation times of Goniastrea aspera, G. favulus and P. sinensis are not exceptionally long, between 15 and 30 years, which would allow between 100 and 200 generations to pass during the average quaternary sea level stand of 3200 years (Potts 1984b). This is almost within the level set by Potts (10^3 to 10^6 generations) for substantial evolutionary change. While corals such as massive Porites and those with a high degree of clonal propagation may well have longer generation times, they are not necessarily typical of most scleractinians. Within the Indo-Pacific Faviidae for example, most species do not achieve extremely large sizes and are likely to have generation times with lengths of the same order as the species in this study. The Faviidae are well known for their intraspecific

variation in growth form, much of which is probably genotypic (Veron et al 1977). Genetically based variability in growth form has been demonstrated in species of Acropora (Potts 1984b). Of the nine species of Acropora studied by Wallace (1985), recruitment by fragmentation was dominant in only three, with the others showing high levels of larval recruitment. (It should be noted however that the Acropora species studied by Potts (1984b) release well developed planulae which may settle near their parents.) Intermediate scale distubances are not unique to coral reefs and are also likely to affect other reef organisms, even if at slightly lower frequencies relative to their average life spans.

While backcrossing may occur in corals there is no reason to believe that this is occurring at unusually high frequencies. The majority of corals on the Great Barrier Reef for example are now known to spawn gametes (Babcock et al. 1986) which do not develop into mobile larvae for approximately 36 hours, and are not capable of settlement for at least four days (Babcock and Heyward in press). The majority of larvae are therefore likely to be dispersed away from their parents (Bull 1986), even if factors such as local eddy systems, which might retain them near the parent reef are invoked (e.g. Potts et al. 1985). It is not clear whether Potts (1983) proposed that both backcrossing due to limited dispersal, as well as maximization of variation due to a high degree of dispersal and gene flow, acted at the same time or on the same organisms. This should be clarified, since though their effect may be the same their mechanisms are quite different. Varying abilities to self-fertilize have been shown to exist in some hermaphroditic mass spawning scleractinians (Heyward and Babcock 1985). While this is a potential source of inbreeding, only one of the four species studied (G. favulus), showed appreciable amounts of self-fertilization. There was however a suggestion that self-fertilization might occur only after the period during which most of the cross-fertilizations took place. It seems most likely then that the fixation of rare alleles by self-fertilization may play only a minor role in certain species.

In view of the available information on the demography and larval development of corals, dispersal and gene flow between populations appear to be the most realistic of the mechanisms proposed by Potts

for maintaining variability without allowing speciation, perhaps augmented by intermediate generation times. A high proportion of scleractinians are now known to have relatively dispersive larval stages (Harrison et al. 1984; Babcock and Heyward in press; Ch. 3), which should provide for substantial gene flow between populations. This may have prevented populations from becoming totally isolated in ocean basins, even during periods of low sea level. Dispersive larvae would also have facilitated the persistance of genotypes adapted to particular sets of conditions in refugia at times of rapid habitat change during sea level transgressions. It may be unnecessary to invoke futher mechanisms to prevent speciation and maintain variation, except for specific cases where evidence indicates that a combination of characteristics such as extremely long generation times and non-dispersive sexually produced larvae exist.

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APPENDIX 1.

Corals other than Goniastrea aspera, G. favulus and Platygyra sinensis which were observed spawning 1982 - 1985. These observations have all been published in detail elsewhere (Harrison et al 1984; Willis et al 1985; Babcock et al 1986). The species listed here are only those for which I carried out the sole or major proportion of the observations. Since they lie outside the strict terms of reference of this thesis, these species will only be listed here, and details can be obtained from the references listed above (enclosed).

1982 (Harrison et al 1984)

ACROPORIDAE

Acropora formosa Orpheus Is.
A. listeri
A. longicyathus
A. millepora Orpheus Is.
A. nasuta

FAVIIDAE

Favia pallida
F. rotumana
Favites chinensis
Goniastrea retiformis

OCULINIDAE

Galaxea astreata

1983 (Babcock et al 1986)

Magnetic Island

FAVIIDAE

Barabattoia amicorum
Cyphastrea chalcidicum
Echinopora lamellosa
Favia lizardensis
F. pallida
Favites abdita
F. halicora
F. pentagona
F. russelli
Favites sp.
Montastrea magnistellata
M. valenciennesi
Platygyra daedalea

OCULINIDAE

Galaxea astreata
G. fascicularis

PORITIDAE

Goniopara minor
G. palauensis

Orpheus Island

ACROPORIDAE

Acropora cerealis
A. formosa
A. millepora
A. nasuta
A. tenuis
Astreopora myriophthalma
Montipora tuberculosa

AGARICIDAE

Pachyseris rugosa

P. speciosa

CARYOPHILLIDAE

Euphyllia divisa

Physogyra lichtenstieni

FAVIIDAE

Caulastrea furcata

Echinopora gemmacea

Favia bennettae

F. pallida

F. veroni

Favites abdita

F. complanata

F. flexuosa

F. halicora

Goniastrea palauensis

G. pecinata

G. retiformis

Montastrea magnistellata

Oulophyllia crispa

Leptoria phrygia

Platygyra daedalea

P. lamellina

P. pini

MERULINIDAE

Clavarina triangularis

MUSSIDAE

Acanthastrea echinata

Lobophyllia corymbosa

L. hemprichii

OCULINIDAE

Galaxea fascicularis

PECTINIDAE

Echinophyllia orpheensis

Mycedium elephantotus

Oxypora lacera

Pectinia alcicornis

P. peonia

PORITIDAE

Goniopora lobata

Goniopora sp. 1

Porites cylindrica

P. lobata

1984 (Willis et al 1985)

Magnetic Island

CARYOPHYLLIDAE

Euphyllia ancora

E. divisa

DENDROPHYLLIIDAE

Turbinaria frondens

FAVIIDAE

Cyphastrea chalcidicum

F pallida

Favites complanata

F. pentagona

Goniastrea palauensis

Montastrea valenciennesi

Platygyra daedalea

MUSSIDAE

Lobophyllia hemprichii

OCULINIDAE

Galaxea fascicularis

PECTINIDAE

Pectinia lactuca

PORITIDAE

Goniopora lobata

G. norfolkensis

Orpheus Island

AGARICIDAE

Pachyseris speciosa

CARYOPHYLLIDAE

Physogyra lichtenstieni

FAVIIDAE

Favia matthai

Favia pallida

F. rotumana

Favites abdita

F. chinensis

F. flexuosa

F. halicora

Goniastrea pectinata

G. retiformis

Leptoria phrygia

Montastrea curta

M. magnistellata

Oulophyllia crispa

MUSSIDAE

Lobophyllia hemprichii

PORITIDAE

Porites cylindrica

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