Massive corals are regularly spaced: pattern in a complex assemblage of corals

R. Endean*, Ann M. Cameron, Helen E. Fox**, Robert Tilbury***,
Leanne Gunthorpe****

Department of Zoology, The University of Queensland, Brisbane 4072, Australia

ABSTRACT: In November 1994, 955 colonies of scleractinian coral occupied approximately 17% of a 15 × 7 m study area which formed part of an intertidal platform near the reef crest at Heron Island Reef off the NE Australian coast. Of these colonies 468 (49%) were massive corals and 487 (51%) were non-massives. When 50 colonies belonging to unidentified species of *Porites* were excluded there remained 418 massive corals belonging to 28 species and 12 genera. Twenty of these species were represented by fewer than the mean number of 13 colonies and 44% of all colonies of the massive corals present belonged to the species *Favites abdita*, *Montastrea curta* and *Montastrea annuligera*. Although the colonies of massive corals rarely exceeded 50 cm in diameter, they fell into a wide range of sizes. However, the majority of colonies of most species had diameters >10 cm. Mean annual growth rates varied among species and among colonies of the same species but for most colonies was ≤0.5 cm in diameter yr^{-1} The total number of colonies of massive corals (excluding colonies of the genus *Porites*) increased from 382 to 418 from November 1991 to November 1994, with settlement slightly in excess of mortality each year. However, the total area occupied by massive corals remained essentially constant during this period. Most species of massive corals showed no mortality and the low mortality exhibited by each of the remaining species was compensated for by settlement of new colonies. The massive coral colonies were regularly spaced, with a mean centre to centre spacing distance of 27.5 ± 15 cm (SD), a mode of 17 cm and a median of 24 cm. Nearest neighbours were rarely of the same species. We propose that the establishment and maintenance of a structural matrix of massive coral colonies exhibiting the regularly spaced pattern described are based on the release of allelochemicals from these colonies.

KEY WORDS: Community structure · Massive corals · Regular spacing pattern

INTRODUCTION

The occupancy of space on coral reefs by corals has been studied by several workers including Goreau (1959), Lewis (1970), Loya (1972), Connell (1973, 1976), Maragos (1974), Stimson (1974), Dana (1976), Bak & Engel (1979), Sheppard (1979), Bradbury & Young (1982, 1983), Done (1982), Wallace & Bull (1982), Wellington (1982) and Abel et al. (1983). Some attempted to determine the patterns of dispersion exhibited by colonies of particular coral species. Colonies of most species showed an aggregated (clumped) dispersion whilst those of other species were usually dispersed randomly. However, Stimson (1974) found that colonies of *Pocillopora meandrina* at Hawaii were uniformly dispersed and Abel et al. (1983) found that the Caribbean corals *Siderastrea siderea* and *Agaricia agaricites* had abnormally uniform or regular dispersions. Others attempted to categorise coral assemblages by the extent of the contribution to the total coral cover made by particular species. Their attention was focused frequently on relatively short-lived opportunistic species which are often abundantly

*E-mail: acameron@zoology.uq.edu.au
Present addresses:
  **Department of Integrative Biology, University of Califor-
     nia, Berkeley, California 94720, USA
 ***WBM Oceanics Australia, PO Box 604, Market Street,
     Melbourne 8007, Australia
****Victorian Fisheries Research Institute, Department of
     Conservation and Environment, PO Box 114, Queenscliff
     3225, Australia

represented. These species often form what are virtually single species stands (zones) in particular habitats and their abundance facilitates the collection of statistical data. However, it has been pointed out (Endean & Cameron 1990) that opportunists comprise a minority of the species in complex coral assemblages. Such species-rich assemblages usually occur on platforms or gently sloping regions of consolidated reef substratum that are not subjected to frequent and severe physical disturbances such as heavy wave action or pronounced accumulation or movement of sediments. Numerous long-lived massive coral species, termed persisters, many of which occur at low population density and are considered to be rare, occur in complex assemblages. Indeed, it is axiomatic that the high species richness exhibited by complex assemblages results from a high incidence of rare species. These rare species warrant consideration in any attempt to determine patterns of space occupancy in such assemblages. Their importance stems from virtual constancy in their population sizes and population structures arising, in part, from their marked ability to retain their living space despite disturbances that cause high turnover rates of the opportunistic species with which they co-exist (Cameron & Endean 1985, Endean & Cameron 1985).

Competition for space involving aggressive interactions has been suggested to be a major factor responsible for the spatial patterns exhibited by the various species constituting coral assemblages (see review by Lang & Chornesky 1990). However, Bradbury & Young (1982) asserted that the spatial patterns of reef-flat corals at Heron Island Reef, Great Barrier Reef (GBR), were random with respect to species and that aggressive interactions among scleractinians are not a major structuring force in coral communities. This generalisation was criticised by Sheppard (1985) on the basis that Bradbury & Young (1982) did not use a scale of measurement appropriate to the interactive reach of corals. More importantly in our view, it would appear inevitable that only very small portions of complex coral assemblages were actually sampled by the methodology employed. Because of this, the generalisations made by Bradbury & Young (1982) may not be applicable to complex coral assemblages. It has been postulated that colonies of persistent species in complex assemblages are regularly spaced (overdispersed) and that toxicity may be a factor fundamental to the production of such ordered patterns of distribution (Endean & Cameron 1990). Although these hypotheses have not been tested in the field, this line of reasoning has been followed by Licuanan & Bakus (1993), who suspected a current-modulated pattern in the distribution of corals, and by Maida et al. (1995a, b), who found that a soft coral's presence limited the survival of settled spat of hard corals in a current-related manner.

A complex coral assemblage was observed in a moat-like structure about 5000 m^2 in area, seawards of the reef crest on the northern side of Heron Island Reef. The coral assemblage contained many massive coral species (approximately 30) as well as several branching and encrusting non-massive species. The massive coral colonies appeared to be regularly spaced. The colonies of non-massive species were scattered and did not form a dense assemblage as they did seawards of the structure. It was decided to examine the distribution of corals, initially massive corals, in this complex coral assemblage over a period of several years . It was anticipated that the study would enable determination of the patterns of dispersion exhibited by massive corals in a complex assemblage, and would provide information on the genesis of such patterns and insight into possible mechanisms underlying such patterns.

MATERIALS AND METHODS

The corners of a rectangular area, 15 × 7 m, aligned so that its long axis was approximately parallel with the reef edge, were marked with steel pegs driven into the substratum in December 1983. This study area forms part of an extensive (approximately 500 m long by approximately 10 m wide) but shallow, moat-like structure between the reef crest and the reef edge. Initial surveys of the habitat indicated that an area of approximately 105 m^2 contained most of the massive coral species present. The structure itself runs parallel with the reef edge and is situated on the northern side of Heron Island Reef (23° 26' S, 151° 57' E) to the east of the feature known locally as the 'Blue Pool'. Several such structures occur along the perimeter of the northern side of the reef. The floor of the study area is of dense consolidated reef fabric, for the most part devoid of coral sand and sloping slightly seawards. Areas sparsely covered by low algal turf fill the spaces among coral colonies and among other sessile animals present.

On low water of neap tides, the moat-like structure remains full of water and averages about 0.6 m in depth but it drains considerably at low water of spring tides, only a few cm of water then remaining on its seaward side. Tidal range in the area is approximately 3 m. Although protected from the direct effects of waves and swell generated by the prevailing south-easterly winds, the study area is exposed to waves and swell generated by winds with a northerly component.

Initially the 15 × 7 m area was divided into areas of 1.0 m^2 by use of a 1.0 m^2 quadrat placed on parallel chains that were 1 m apart with markers at 1 m intervals. Every macroscopic sessile animal located in each

1.0 m² of the grid system thereby established was recorded. Corals were identified to species except for colonies of the genera *Porites, Acropora, Stylophora* and *Montipora*. Also, some small colonies of massive corals were initially identified to genus only. Identifications were based on the works of Veron & Pichon (1976, 1980), Veron et al. (1977) and Veron (1986). From November 1984 to November 1990 the position of each massive coral present was determined each year in late November or early December by reference to fixed points in the grid system At the same time, the appearance of new colonies and the demise of colonies that were present the previous year were noted. Also recorded were any changes in the sizes and shapes of colonies since the previous visit. In order to determine the size of each massive colony, 2 measurements (error = ±5 mm) were made each year using a metre rule and large dividers. The first measurement was of the greatest horizontal extent of the colony and the second was made normal to the first through the midpoint of the colony, again in the horizontal plane. The average of these yielded the size (average diameter) of the colony.

Relocation of coral colonies by reference to the grid system was time-consuming and problems were encountered in relocating small colonies, particularly when visits coincided with periods of neap tides and/or heavy wave action. It was therefore decided in November 1991 to facilitate the location and measurement of each colony by plotting annually the position and size of each colony to scale on a map of the whole study area. The position of each colony relative to adjacent colonies was determined by measurement (centre to centre and edge to edge) and confirmed by photography. Measurements of the major and minor horizontal axes of each colony (as described above) were used when plotting the respective sizes of colonies on the map. In November 1994 the position and size (to scale) of each non-massive coral colony present were added to the map. This paper deals with data collected from November 1991 to November 1994 inclusive. The number of colonies of each massive species was determined each November (see Table 1). In 1994 a species-area curve was plotted and frequency distributions of colonies among species were determined (see Fig. 1). Size frequency groupings based on colony area were established for species of massive coral represented by 6 or more colonies in 1994 (see Fig. 2) and size frequency distributions for species represented by fewer than 6 colonies were also obtained (see Table 2). Areas equivalent to diameters of 5 cm and multiples thereof were used for the size categories. The maximum size attained by each species of massive coral was also determined (see Table 3). Changes in sizes of colonies between successive annual visits were recorded (see

Tables 4 & 5). Also, we obtained information on demise of colonies, net settlement between visits and alterations in areas occupied by colonies over this period.

Measurement (accuracy ±5 mm) of the minimum distances between neighbouring coral colonies was made in November 1994 for nearest neighbour analysis. For each of the 418 massive coral colonies (excluding those of *Porites* spp. all of which were too small to be identified in the field and are not included in the results), the distance to its nearest neighbour was measured from colony edge to colony edge, at the nearest points in each case. Coral colonies that settled in 1992, 1993 and 1994 were also mapped to scale, and each settler's nearest neighbour (edge to edge) was determined. The mean intraspecific spacing distance was calculated for each massive coral species represented by 6 or more colonies in 1994 (see Table 6). This was done by measuring the distance to the nearest neighbour of the same species from colony centre to colony centre for each colony. In 1994 the number of instances when a colony had a member of the same species as its nearest neighbour was determined for species with 6 or more colonies and the number of instances when a colony had a member of the same genus as its nearest neighbour was determined for *Favia, Favites, Goniastrea, Montastrea* and *Platygyra*. The binomial distribution test was used to determine whether the number of colonies that had the same species (or genus) as nearest neighbour was more or less than expected by chance. Interactions between neighbouring colonies observed between November 1991 and November 1994 were recorded.

In order to determine the distribution pattern of the colonies of massive corals, the actual distribution was compared with simulated random distributions. For this process, the centre of each massive colony was used to establish x-y co-ordinates for the colony with reference to the major (15 m) and minor (7 m) axes of a m² grid system superimposed to scale on a map of the colonies present in 1994. Each colony's nearest neighbour within the study area (using centre-to-centre measurements) was determined and the distance separating the members of each nearest neighbour pair recorded (see Fig. 3). The actual mean spacing distance (the mean distance separating the members of each pair of nearest neighbours in the study plot) was then calculated.

Monte Carlo simulations (Sokal & Rohlf 1995) were used to determine whether the colonies present were randomly distributed, regularly spaced or clumped. For the Monte Carlo program, the computer representation of the map of the 15 × 7 m study area was divided into 10 cm × 10 cm sections. Each coral, regardless of actual size, was treated as a 10 × 10 cm square (the median diameter of the actual corals being

9.5 cm) For the simulations, the same number of massive coral colonies (418 excluding colonies of the genus *Porites*) as were present in the study area were distributed randomly in the same plot size 1000 times, generating a normal distribution. The mean spacing distance for each simulation was calculated and these were compared with the actual mean spacing distance. If fewer than 5% of the simulated means were greater than the actual mean, then the coral colonies in the study area were considered to be regularly spaced.

For a second set of simulations, each square metre of the study area was divided into quadrants, yielding a total of 420 quadrants of 0.25 m². Thirty-three of these carried no massive corals from 1991 to 1994 and no non-massive corals in 1994 and were therefore treated as 'forbidden' for the placement of corals in the random simulations.

RESULTS

In 1994 a total of 955 scleractinian coral colonies occupied approximately 17% of the 15 × 7 m study area. Of these, 468 (49%) were massive and 487 (51%) were non-massive corals. Other macroscopic sessile animals present were 2 colonies of alcyonarians, 2 colonies of hydrocorals and 10 clams. The 418 colonies of massive corals present in 1994 and listed in Table 1 represent 28 species belonging to 12 genera. Note that colonies identified to genus only are not included in the species totals in Table 1. The species-area curve revealed that the 105 m² study area contained nearly all the massive coral species in the habitat. Indeed, only an additional 3 species were found in the moat-like structure outside the study area.
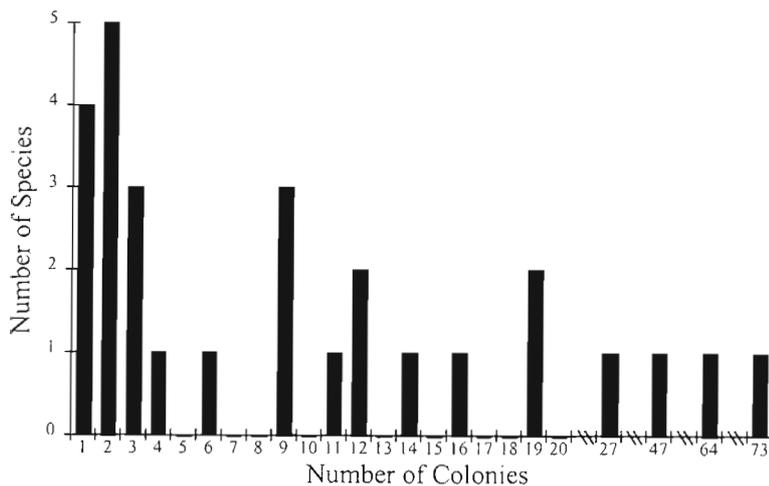

Fig. 1. Frequency distribution of colonies among species of massive coral in the study area in 1994. The mean number of colonies per species was 13 and the modal number was 2. (Note breaks in x-axis)

Many of the massive corals recorded must be regarded as rare. In 1994, 5 species (*Cyphastrea serailia, Favia matthai, Favia stelligera, Favites pentagona* and *Lobophyllia pachysepta*) were represented by the modal number of 2 colonies, 4 species (*Favia rotumana, Platygyra pini, Platygyra sinensis* and *Symphyllia recta*) were represented by 1 colony and 20 of the 28 species by fewer than the mean number of 13 colonies (Fig. 1). Only 3 species were represented by more than 30 colonies. (Note that colonies identified to genus only are not included in Fig. 1.)

Histograms of sizes of the colonies of each species with 6 or more colonies are given in Fig. 2. Sizes of the colonies of species with fewer than 6 colonies are listed in Table 2. It is apparent that colonies of most species were well represented in the 6 to 10 cm and/or the 11 to 15 cm diameter categories. Colonies less than 5 cm in diameter and belonging to *Montastrea curta, Montastrea annuligera, Favites abdita* and *Leptoria phrygia* were relatively common, reflecting the extent of recent settlement of colonies of these species. *Favia pallida, Platygyra daedalea, F. abdita* and *M. curta* were well represented in the 16 to 20 cm in diameter category. Colonies of *Goniastrea australensis, Goniastrea aspera, Goniastrea retiformis, P. daedalea, M. curta, M. annuligera, F. pallida, F abdita, Cyphastrea micropthalma* and *Cyphastrea serailia* embraced the greatest range of size categories. The maximum size attained by each species (Table 3) may have been constrained by the shallowness of the water at low tide.

Annual changes in the mean size of colonies of each species of massive coral are listed in Table 4. Colonies of many species showed little change in size during the 3 yr period. Indeed, the mean annual change in diameter for colonies belonging to 15 of the 28 species was ≤0.5 cm yr^{-1} Some colonies regressed in size. Mean annual growth rates for colonies of the remaining 13 species ranged from 0.5 to 1.0 cm in diameter. That growth rate varied annually among colonies of a particular species is exemplified by the data for *Platygyra daedalea*, shown in Table 5. Over the 3 yr period the average growth rate per colony was ≤0.5 cm in diameter yr^{-1} for 9 of the 25 colonies and between 0.5 and 2.0 cm in diameter yr^{-1} for the remainder.

Survivorship of visible settlers for all massive corals was 84% (27/32) for the first year (November 1992 to November 1993) and 72% (23/32) for the 2 yr (November 1992 to November 1994). For *Favites abdita* the comparable figures are 50% and 50% respectively; for *Montastrea annuligera* they are 100% and 50% respectively; for

Table 1. Genera and species (excluding species of *Porites*) of massive coral colonies in the 105 m² plot on Heron Island Reef crest from 1991 to 1994. Number of colonies (N), mortality (M) and settlement (S) in each year for each species are shown. (Where a colony was too small for identification to the species level, the genus only is listed)

| Species	1991 N	1991–1992 M	S	1992 N	1992–1993 M	S	1993 N	1993–1994 M	S	1994 N
Acanthastrea										
A. echinata	12	0	0	12	0	0	12	0	0	12
Cyphastrea										
C. micropthalma	4	0	0	4	0	0	4	0	0	4
C. serailia	2	0	0	2	0	0	2	0	0	2
Cyphastrea sp.	2	1	0	1	0	0	1	0	0	1
Favia										
F. favus	3	0	0	3	0	0	3	0	0	3
F. matthai	2	0	0	2	0	0	2	0	0	2
F. pallida	16	0	0	16	0	0	16	2	0	14
F. rotumana	1	0	0	1	0	0	1	0	0	1
F. stelligera	2	0	0	2	0	0	2	0	0	2
Favia sp.	0	0	0	0	0	0	0	0	4	4
Favites										
F. abdita	65	4	2	63	2	0	61	2	5	64
F. chinensis	11	0	0	11	0	0	11	0	0	11
F. complanata	18	0	2	20	0	0	20	1	0	19
F. halicora	15	0	2	17	0	2	19	0	0	19
F. pentagona	1	0	1	2	0	0	2	0	0	2
Favites sp.	17	2	6	21	0	3	24	4	12	32
Galaxea										
G. fascicularis	0	0	1	1	0	0	1	1	0	0
Goniastrea										
G. aspera	10	1	0	9	0	0	9	0	0	9
G. australensis	11	1	1	11	2	0	9	0	0	9
G. favulus	16	5	1	12	0	3	15	3	0	12
G. retiformis	15	0	0	15	0	0	15	0	1	16
Goniastrea sp.	0	0	2	2	0	1	3	1	1	3
Hydnophora										
H. exesa	1	0	0	1	0	0	1	1	0	0
H. microconos	5	0	0	5	0	0	5	0	1	6
Leptastrea										
L. purpurea	1	1	0	0	0	0	0	0	0	0
Leptoria										
L. phrygia	6	0	2	8	0	0	8	0	1	9
Leptoria sp.	0	0	0	0	0	0	0	0	2	2
Lobophyllia										
L. pachysepta	5	1	0	4	0	0	4	2	0	2
Montastrea										
M. annuligera	40	1	2	41	0	1	42	3	8	47
M. curta	64	4	8	68	5	2	65	1	9	73
M. magnistellata	1	1	0	0	0	0	0	0	0	0
M. valenciennesi	2	0	0	2	0	0	2	0	1	3
Montastrea sp.	1	1	1	1	1	0	0	0	1	1
Platygyra										
P. daedalea	26	1	1	26	0	0	26	0	1	27
P. pini	1	0	0	1	0	0	1	0	0	1
P. sinensis	2	1	0	1	0	0	1	0	0	1
Platygyra sp.	0	0	0	0	0	1	1	0	0	1
Psammocora										
P. contigua	3	0	0	3	0	0	3	0	0	3
Symphyllia										
S. recta	1	0	0	1	0	0	1	0	0	1
Total	382	25	32	389	10	13	392	21	47	418
Total no. of genera	13			13			13			12
Total no. of species	31			30			30			28
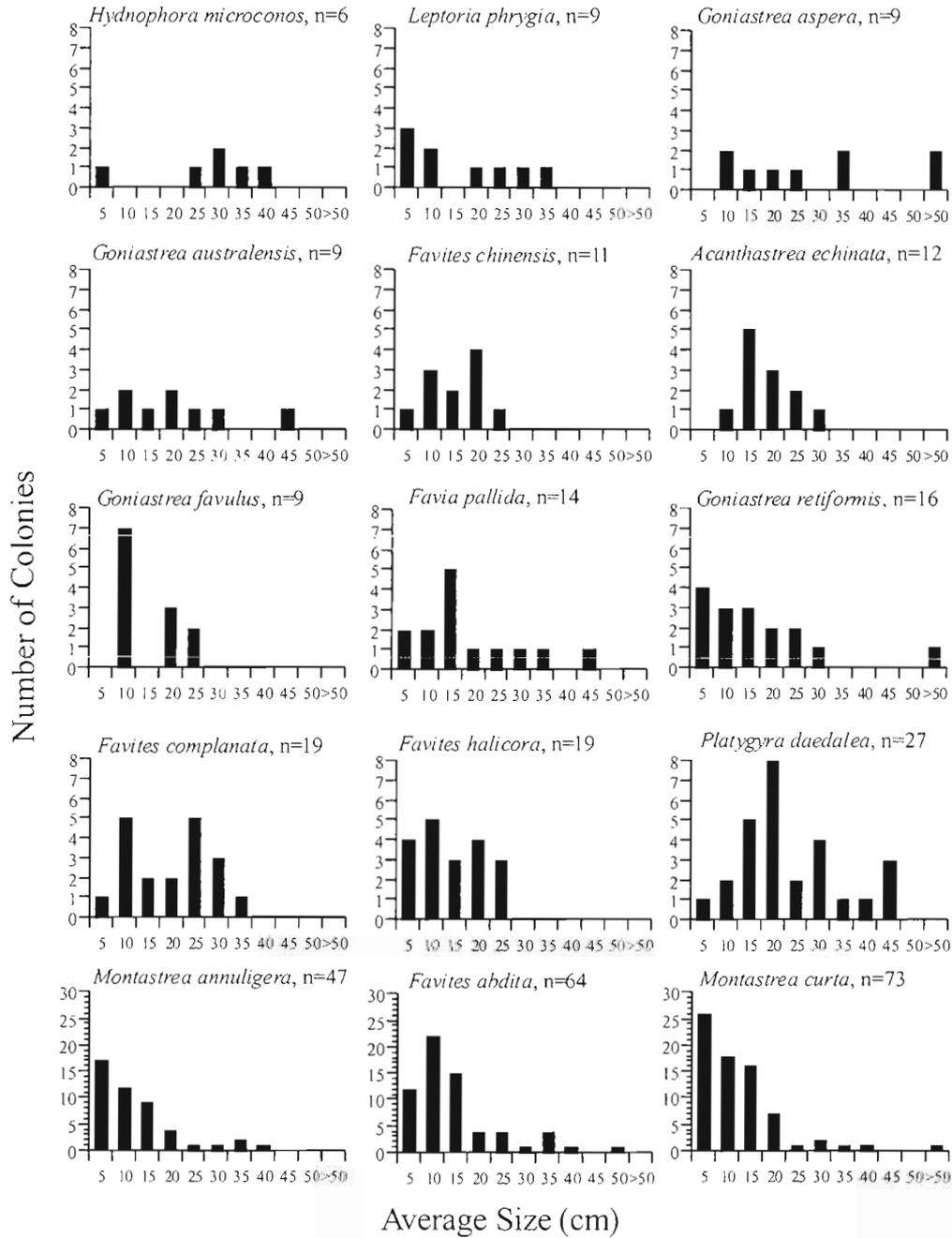
Fig. 2. Histograms showing size distributions of colonies of massive coral species with 6 or more colonies in 1994. Corals are grouped into 5 cm size classes equivalent to an average diameter of < 5 cm, 6–10 cm, 11–15 cm, etc., although the colonies were treated as ellipses in calculation of area

Montastrea curta they are 70% and 50% respectively. From November 1991 to November 1994 (Table 1) the total number of colonies of massive species in the study increased from 382 to 418, with settlement somewhat in excess of mortality each year. However, colonies of most species showed no mortality during this period whilst mortality was compensated for by settlement in others. Indeed, the total area occupied by massive corals during

this period remained essentially constant being 10.13, 10.23, 10.85 and 10.25 m^2 between 1991 and 1994. Although more colonies of non-massive species than massive colonies (487:468, respectively) were present in 1994, the area occupied by non-massive colonies was substantially less than that occupied by massive colonies.

The mean centre to centre spacing distance of the 418 massive corals present in 1994 was 27.5 ± 15 cm

Table 2. Size distributions of massive coral species with fewer than 6 colonies in 1994. Increments represent the area equivalent to an average diameter of <5 cm, 6–10 cm, 11–15 cm, etc., although the colonies were treated as ellipses in calculation of area

Species	No. of colonies	Equivalent average diameter (cm)										
		<5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	>50
Cyphastrea												
C. micropthalma	4		1				1					2
C. serailia	2				1							1
Favia												
F. favus	3		2	1								
F. matthai	2									2		
F. rotumana	1				1							
F. stelligera	2		1	1								
Favites												
F. pentagona	2			1						1		
Lobophyllia												
L. pachysepta	2	1	1									
Montastrea												
M. valenciennesi	3	1	1	1								
Platygyra												
P. pini	1	1										
P. sinensis	1		1									
Psammocora												
P. contigua	3	2		1								
Symphyllia												
S. recta	1									1		
Total	27	5	7	5	2	0	1	0	2	2	0	3

(SD), with a mode of 17 cm and a median value of 24 cm (Fig. 3). The mean spacing distance generated from the 1000 simulations in the Monte Carlo program was 26.5 cm, and 4.2% of the simulations had mean spacing distances greater than the actual mean, indicating that the corals were regularly spaced. When we excised the 33×0.25 m^2 portions of the study area that were devoid of massive species from 1991 to 1994 and in 1994 were also devoid of non-massive corals (an

area of 8.25 m^2, or 7.86% of the total area), the mean spacing distance of the 1000 simulations was 26 cm. After the excisions, only 0.7% of the simulations had mean spacing distances greater than the actual mean, indicating that the massive coral colonies were regularly spaced at the 1% significance level.

Colonies of different species had mean spacing distances (centre to centre) that varied (Table 6). The mean centre-to-centre spacing distances separating

Table 3. Maximum sizes attained by colonies belonging to species of massive corals represented in the plot in 1994. Sizes were calculated from measurements of major and minor axes of colonies, which were treated as ellipses. A significant portion of the calculated area of a colony noted as 'patchy' was dead

Species	Maximum area (cm^2)	Notes	Species	Maximum area (cm^2)	Notes
Acanthastrea echinata	615		*Goniastrea australensis*	1257	
Cyphastrea micropthalma	3487	Patchy	*Goniastrea favulus*	325	
Cyphastrea serailia	2199	Patchy	*Goniastrea retiformis*	2104	Centre dead
Favia favus	106		*Hydnophora microconos*	990	
Favia matthai	1500		*Leptoria phyrgia*	990	
Favia pallida	1308		*Lobophyllia pachysepta*	43	
Favia rotumana	228		*Montastrea annuligera*	1103	
Favia stelligera	99		*Montastrea curta*	3102	Patchy
Favites abdita	1693		*Montastrea valenciennesi*	85	Patchy
Favites chinensis	456		*Platygyra daedalea*	1221	
Favites complanata	767		*Platygyra pini*	1	
Favites halicora	491	Patchy	*Platygyra sinensis*	47	
Favites pentagona	1014	Patchy	*Psammocora contigua*	118	
Goniastrea aspera	10249	Patchy	*Symphyllia recta*	1148	

Table 4. Number of colonies (No.), size (average diameter in cm), and average yearly change in diameter (Δ) of colonies of massive coral species that persisted from November 1991 to 1994 inclusive, ordered by average annual growth (Avg.) over the 3 years. The minimum and maximum changes in diameter from 1991 to 1994 are indicated by Min. and Max., respectively

Species	No.	Average diameter (cm)							Avg.	Min.	Max.
		1991	1992	Δ91–92	1993	Δ92–93	1994	Δ93–94			
Platygyra pini	1	9.5	3.0	−6.5	1.0	−2.0	1.5	0.5	−2.5	−8.0	−8.0
Psammocora contigua	3	15.5	15.0	−0.5	15.0	0.0	10.0	−5.0	−2.0	−9.5	0.5
Cyphastrea micropthalma	4	45.5	39.0	−6.5	44.0	5.0	40.5	−3.5	−1.5	−13.5	−1.0
Favia favus	3	10.5	10.5	0.0	10.0	−0.5	8.5	−1.5	−0.5	−4.0	0.5
Favites halicora	16	13.0	13.5	0.5	13.5	0.0	13.0	−0.5	0.0	−14.5	5.5
Montastrea valenciennesi	3	10.0	10.0	0.0	9.0	−1.0	10.0	1.0	0.0	−1.0	1.0
Montastrea annuligera	37	12.0	12.5	0.5	12.0	−0.5	12.0	0.0	0.0	−14.5	7.5
Favites chinensis	11	13.0	13.5	0.5	13.0	−0.5	13.0	0.0	0.0	−7.0	4.0
Favites abdita	58	13.0	13.5	0.5	14.0	0.5	13.5	−0.5	0.0	−8.5	7.5
Montastrea curta	58	11.5	11.5	0.0	12.5	1.0	12.0	−0.5	0.0	−12.0	10.5
Cyphastrea seralia	2	35.0	36.0	1.0	38.5	2.5	35.5	−3.0	0.0	−0.5	1.5
Goniastrea australensis	8	19.0	20.0	−1.0	21.0	1.0	19.5	−1.5	0.0	−7.0	3.5
Goniastrea favulus	9	12.5	12.5	0.0	13.0	0.5	14.0	1.0	0.5	−1.5	3.0
Leptoria phrygia	6	20.0	20.5	0.5	21.5	1.0	21.0	−0.5	0.5	−4.0	5.0
Favites complanata	17	16.5	18.0	1.5	18.5	0.5	17.5	−1.0	0.5	−11.5	6.5
Favia stelligera	2	7.5	6.5	−1.0	8.0	1.5	9.0	1.0	0.5	1.0	3.0
Favia matthai	2	41.5	43.0	1.5	43.0	0.0	43.5	0.5	0.5	1.0	3.0
Platygyra daedalea	25	16.0	17.0	1.0	17.0	0.0	18.0	1.0	0.5	−4.0	5.5
Acanthastrea echinata	12	13.5	14.5	1.0	15.5	1.0	15.5	0.0	0.5	−2.0	5.5
Favia pallida	14	14.0	15.0	1.0	15.5	0.5	16.0	0.5	0.5	−0.5	6.5
Goniastrea aspera	9	34.0	36.0	2.0	36.5	0.5	37.0	0.5	1.0	−5.0	7.0
Favia rotumana	1	15.0	17.0	2.0	15.5	−1.5	17.5	2.0	1.0	2.5	2.5
Platygyra sinensis	1	5.5	6.0	0.5	7.5	1.5	8.0	0.5	1.0	2.5	2.5
Symphyllia recta	1	36.0	39.0	3.0	38.0	−1.0	38.5	0.5	1.0	2.5	2.5
Favites pentagona	1	41.0	55.5	14.5	51.0	−4.5	43.5	−7.5	1.0	2.5	2.5
Lobophyllia pachysepta	2	3.0	6.0	3.0	5.0	−1.0	5.5	0.5	1.0	0.5	5.0
Goniastrea retiformis	15	13.0	14.5	1.5	14.0	−0.5	15.5	1.5	1.0	−1.0	8.0
Hydnophora microconos	5	26.0	27.5	1.5	29.0	1.5	29.5	0.5	1.0	1.5	9.0

nearest-neighbour (same species) colonies of *Montastrea curta*, *Favites abdita* and *Montastrea annuligera*, the 3 commonest species, were 61 ± 38 cm (SD), 67 ±
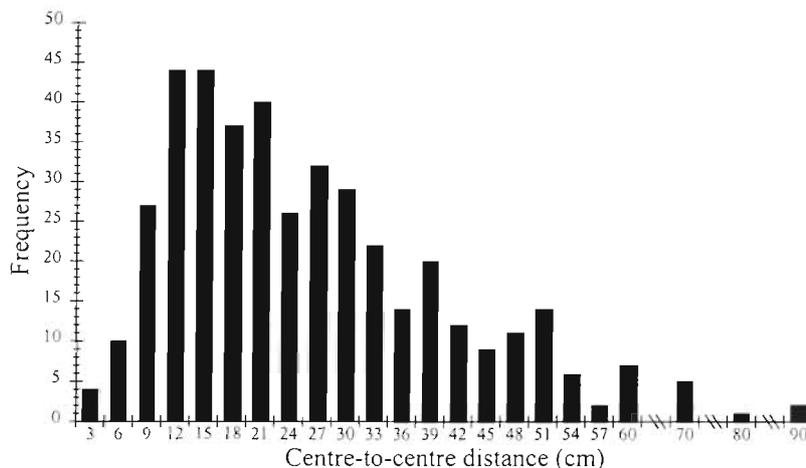

Fig. 3. Frequency distribution of the centre-to-centre spacing distances for the massive coral colonies (excluding *Porites* spp.) in the study area in 1994, based on the centre coordinates of the nearest neighbour of each coral. Distances are grouped into intervals of ≤ 3 cm, 4–6 cm, 7–9 cm, etc.

41 cm and 78 ± 43 cm respectively. The nearest-neighbour records for each of the massive species were also examined for the 15 species with 6 or more colonies in 1994. If *F. abdita*, *M. curta* and *M. annuligera* are excluded, there were only 3 instances in a total of 163 of a nearest neighbour being of the same species. These were 1 recently settled colony of *Favites complanata*, 2 specimens of *Goniastrea retiformis* (which may well be 'splinter' colonies from a larger colony) and 2 colonies of *Platygyra daedalea* which were touching. For *F abdita* (n = 64) there were 8 colonies of which the nearest neighbours were also *F. abdita* and, of these, none was closer than 4 cm, edge to edge. For *M. curta* (n = 73) there were 6 colonies the nearest neighbours of which were also *M. curta* and of these, only 1 was closer than 4 cm, edge to edge. For *M. annuligera* (n = 47) there were 7 colonies with the same species as nearest

Table 5. Size (diameter in cm) and yearly change in diameter (Δ) of the 25 individual colonies of *Platygyra daedalea* that persisted from 1991 to 1994, ordered by average annual growth over the 3 years (Avg.). Sizes were calculated from measurements of major and minor axes of the colonies

Colony	1991	1992	Δ91–92	1993	Δ92–93	1994	Δ93–94	Avg.
1	27	28.5	1.5	22	−6.5	23.25	1.25	−1.3
2	35.5	34.75	−0.75	36	1.25	33.5	−2.5	−0.7
3	37.5	36.5	−1	40.5	4	36.5	−4	−0.3
4	22	22	0	21	−1	22	1	0.0
5	12	12.5	0.5	8.5	−4	12.75	4.25	0.3
6	36.5	37	0.5	37	0	37.5	0.5	0.3
7	21	21	0	25.5	4.5	22	−3.5	0.3
8	8.75	10.5	1.75	9.5	−1	10.25	0.75	0.5
9	12.5	13	0.5	12.5	−0.5	14	1.5	0.5
10	12.25	13.5	1.25	13.5	0	14.25	0.75	0.7
11	6	5.5	−0.5	5.5	0	8	2.5	0.7
12	10	11.5	1.5	12	0.5	12.25	0.25	0.8
13	15.5	18	2.5	17.5	−0.5	17.75	0.25	0.8
14	4.5	6	1.5	6	0	7	1	0.8
15	37	37	0	38	1	39.5	1.5	0.8
16	2	3	1	3.5	0.5	4.75	1.25	0.9
17	8	9	1	10.5	1.5	10.75	0.25	0.9
18	12	13.5	1.5	12	−1.5	14.75	2.75	0.9
19	6.5	8	1.5	8	0	9.75	1.75	1.1
20	14.5	16	1.5	16	0	18	2	1.2
21	7	9.5	2.5	9.5	0	10.5	1	1.2
22	5.5	7	1.5	7.5	0.5	9.25	1.75	1.3
23	25	28	3	27	−1	29	2	1.3
24	4	5.75	1.75	6.5	0.75	8.25	1.75	1.4
25	19.5	22	2.5	24.5	2.5	24.75	0.25	1.8
Avg	16.1	17.2	1.1	17.2	0.0	18.0	0.8	0.6

Table 6. Number of colonies (No.), mean intraspecific spacing distance (centre to centre) and standard deviation (SD) and median spacing distance for each species with 6 or more individuals occurring in the 105 m² plot in 1994. All measurements are in cm

Species	No.	Centre to centre		
		Mean	SD	Median
Montastrea curta	73	61	38	50
Favites abdita	64	67	41	55
Montastrea annuligera	47	78	43	73
Platygyra daedalea	27	114	47	115
Favites halicora	19	116	32	127
Goniastrea retiformis	16	123	62	126
Favites complanata	19	125	74	116
Goniastrea aspera	9	131	79	167
Goniastrea favulus	12	134	91	78
Favia pallida	14	137	71	131
Goniastrea australensis	9	157	82	144
Leptoria phrygia	9	164	37	159
Acanthastrea echinata	12	207	7	173
Favites chinensis	11	233	110	244
Hydnophora microconos	6	245	71	234

chance (p < 0.05, binomial test). However, this test yielded random results when applied to nearest-neighbour records for *M. annuligera* and *F. abdita*. Two of the 5 well-represented genera yielded non-random results according to the binomial test. More colonies of species of *Favia* were nearest neighbours to other colonies of *Favia* than expected by chance (p > 0.95). Fewer colonies of species of *Montastrea* (p < 0.05) were nearest neighbours to other colonies of *Montastrea* than expected by chance.

In 1994 the mean nearest neighbour edge-to-edge distance for all 418 colonies of massive corals was 15.5 ± 14 cm (SD), the mode being 5.0 cm and the median being 10.0 cm. There were 92 instances of edge-to-edge nearest neighbour distances as close as 4 cm (the maximum interactive reach for any of the species of corals studied). Despite their proximity, there were very few interactions among these adjacent colonies. In only 10 instances over the 3 yr period did deaths of some polyps appear to have stemmed from aggressive interactions. None of these interactions resulted in deaths of entire colonies and stand-offs involving the previously interacting colonies were occurring by December 1994. It is possible that stand-offs have already occurred in the cases of the other closely adjacent colonies that showed no indication of aggressive interactions.

DISCUSSION

The species richness of the massive corals in the study area was high. Although fewer colonies of massive species (468) than those of non-massive species (487) were present in 1994, many of the non-massive colonies were small and the massive corals provided more of the coral cover in the area than did non-massives. Even so, total scleractinian coral cover comprised only approximately 17% of the study area. Other sessile animals scarcely accounted for another 0.5% The bulk of the cover was provided by epibenthic felt (see Thomassin 1976) on a substratum of consolidated reef rock.

Corals often occupy less than half the area apparently available (Endean 1974, Sheppard 1985). In our study area the total coral cover was less than 20% of the total area available and the area occupied by mas-

neighbours, and none of these was closer than 4 cm, edge to edge. *M. curta* was less likely to have another *M. curta* as its nearest neighbour than expected by

sive corals was approximately 10% of the area. It has never been determined whether the space surrounding colonies of persistent corals is indeed available throughout the year for settlement of the larvae of either persistent or opportunistic corals, or, in the longer term, for recruitment of corals.

The total area occupied by massive corals from November 1991 to November 1994 remained essentially constant but there was an increase in the total number of colonies of massive corals, settlement being slightly in excess of mortality each year. It remains to be seen how many of the recent settlers are recruited to the breeding population of each species since mortality among them was substantial. Established colonies of most species showed either no mortality or mortality of <10% yr^{-1} (Table 1). Some colonies had attained relatively large sizes (Table 3, Fig. 2) indicating their long-term persistence.

Although colonies rarely exceeded 50 cm in diameter, a wide range of sizes was found in most massive species. Because of the very low growth rates (≤ 0.5 cm in diameter yr^{-1}) of most colonies and because the majority of colonies of most species had diameters greater than 10 cm, their ages appear to span decades. Thus physical disturbance capable of killing established colonies has not been responsible for the low cover of massive corals observed in the study area since 1983. Certainly no marked physical disturbances such as severe cyclones that might cause large scale mortality of massive corals have been recorded at Heron Island Reef since 1983.

The difficulties of relating size of coral to age are well known (see Hughes & Jackson 1980, Hughes & Connell 1987) and the actual ages of the colonies in the study area could not be determined. Although some colonies showed mean annual increments consistent with published radial growth rates of approximately 5 mm yr^{-1} (1 cm in diameter yr^{-1}) for species of *Platygyra* and *Goniastrea* (Babcock 1985), many colonies did not show detectable changes in size within the limits of experimental error and some colonies had definitely regressed in size. Also, colonies of some species (e.g. *Goniastrea favulus*) had apparently reached maximum size, as larger specimens were not observed elsewhere on the Heron Island Reef flat. Intrinsic factors may have been responsible for the slowing of growth as maximum size was approached (see Soong 1993). Then too, the growth rates of massive corals present may have been affected adversely by the physical as well as biological conditions prevailing in the study area. The tops of several of the colonies, particularly those on the shallower lagoon side of the study area, were dead, indicating that the potential for growth of these colonies in the vertical plane was restricted. In this regard, the shallowness of the water at low tide

would prevent branching corals from competing with massive corals by overtopping. However, some colonies of massive corals in the deeper reef edge side of the study area remained covered by water during most low tides yet showed very low growth rates. The possibility that biotic factors were involved in slowing growth and limiting the sizes attained by some colonies in the study area should be considered. During the study period instances of partial or complete mortality of established colonies of most species of massive corals were few.

Sheppard (1985) accounted for some of the vacant space in the vicinity of corals in terms of their interactive reach. For approximately 50 species this ranged from 0.4 to 4.0 cm. Clearly interactive reach is effective in maintaining apparently unoccupiable space in the immediate vicinity (within 4 cm) of established colonies. It must thus be important in determining the fate of some settling propagules but its importance to established colonies is not so clear (see e.g. Bak et al. 1982). In the complex assemblage at Heron Island Reef, the incidence of obvious interactions among coral colonies was extremely low. Moreover, the radius of the apparent zone of vacant space surrounding each colony was usually much greater than could be accounted for by interactive reach. The mean edge-to-edge spacing distance between adjacent coral colonies was 15.5 ± 14 cm (SD), with a median of 10 cm and a mode of 5 cm. If coral colonies grew closer than approximately 4 cm (edge to edge), destructive interference (overgrowth, partial destruction of polyps) was rarely apparent, and stand-offs appeared to have occurred when colonies were so close. In the few instances when colonies of the same species were nearest neighbours, only colonies of *Platygyra daedalea* appeared capable of abutting on one another without fusion. Perhaps different morphs of this species are involved (see Miller 1994).

Because instances of direct interference between coral colonies were few it is possible that competitive interactions were expressed in a more subtle fashion. For example, growth suppression in some coral colonies may have been caused by allelochemicals exuded from adjacent colonies. That one scleractinian species found at Heron Island Reef has the potential to release toxic exudates adversely affecting other scleractinians was demonstrated by Gunthorpe & Cameron (1990).

The low population densities of most species of massive coral should be emphasised. Approximately one-third of the species in the 15 × 7 m study area were represented by only 1 or 2 colonies and approximately two-thirds of the species were represented by fewer than the mean of 13 colonies. Only 3 species were represented by more than 30 colonies. No meaningful

description of this complex coral community could be made on the basis of the numerical dominance of colonies of a particular species or on the basis of extent of cover by colonies of a particular species. No small group of species characterises this assemblage. It is a diverse assemblage comprised of a large number of persistent massive species, most of which are rare, and a number of branching species, some of which have a high turnover and are considered to be opportunists. Overall, the massive coral colonies are not randomly distributed. Nor are they clumped. On the contrary, massive coral colonies in the complex assemblage studied were regularly spaced.

The mean intraspecific spacing distances of nearest neighbours (centre to centre) for the 15 species with 6 or more colonies varied. For the 4 commonest species the intraspecific spacing distance is inversely related to relative abundance, but this relationship is not so clear for the other 11 species. Although the mean intraspecific spacing distance calculations made involved 83 % of the total number of colonies of massive species present, they pertain to only 15 of the 28 species present in 1994, and we are faced with the problem that almost half the species of this rich assemblage are too rare to be included in the analyses.

We have shown that in a complex coral community massive coral colonies are regularly spaced. Also, we have noted that there appears to be a zone (greater than that of interactive reach) around each massive coral colony where recruitment of new coral colonies is inhibited. If the apparent zones of inhibition surrounding existing coral colonies overlap, no opportunities may be presented for effective settlement of coral larvae. Such settlement could occur only when one or more existing colonies in the complex assemblage are killed, a rare occurrence in the case of persistent massive corals. However, space in complex assemblages made available by the deaths of massive corals or space unsuited because of unfavourable physical features for long-term occupancy by corals may be occupied temporarily by opportunists such as *Pocillopora damicornis*, further adding to the complexity of the system.

In the complex community studied, the persistence of individuals of massive corals, their low mortality, low rates of recruitment and low rates of growth result in a constancy of colony numbers and a constancy of population size frequencies not previously documented in coral reef biology. We are currently examining the possibility that established massive corals constitute a structural matrix from which chemical compounds are released. We propose that the compounds are essentially toxins that effectively produce a zone of chemical inhibition around each established coral colony that restricts the settlement of new colonies within the zone and slows the growth of the polyps of neighbouring colonies, thereby limiting the extent of their intrusion into the zone. All this would result in the colonies of massive corals present in the complex assemblage studied being regularly spaced.

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