Predation on massive corals: are devastating population outbreaks of *Acanthaster planci* novel events?

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ABSTRACT: Coral communities on many reefs of the central third of Australia's Great Barrier Reef have been subject to major damage by population outbreaks of the crown-of-thorns starfish *Acanthaster planci* twice since the 1960's. The interval between outbreaks on individual reefs was approximately 15 yr. This study compares size and damage frequency distributions of major taxa of scleractinian reef corals of massive morphology on 2 sets of 6 reefs of this region. One set of reefs had experienced major population outbreaks of *A. planci*, one set had not. All major reef types found in the area were represented in the sets which spanned 3 degrees of latitude. On both reef sets, representatives of the families Faviidae, Poritidae and Mussidae comprised ca 90 % of the massive corals present. However, the relative proportions of these taxa differed markedly between the 2 reef sets, with members of the Faviidae predominant on non-outbreak reefs and members of the Poritidae predominant on outbreak-affected reefs. Massive coral assemblages on outbreak reefs possessed only ⅓ the colonies on unaffected reefs and approximately half the surviving corals on the outbreak reefs exhibited damage of > ⅓ their colony surface areas. Few large (old) colonies occurred on the outbreak reefs, whereas such large corals were common on unaffected reefs. As most massive corals are slow-growing, long-lived and have lower rates of recruitment than corals of other morphology, continuing starfish reinfestation coincident with reestablishment of a coral cover by the faster-growing, more opportunistic corals will not allow sufficient time for recovery of the massive coral assemblages. They will be replaced by algae and non-massive coral assemblages in the intervals between outbreaks. The recent devastating outbreaks appear to be abnormal perturbations coincident with large-scale human activities on the Great Barrier Reef, rather than integral features of reef ecology.

INTRODUCTION

Predation on corals by the crown-of-thorns starfish *Acanthaster planci* (Linné, 1758) has caused major damage to coral communities of the Great Barrier Reef (GBR) and elsewhere in the Indo-West Pacific region since the 1950's (Endean & Cameron 1985, Moran 1986, Moran et al. 1988, Endean & Cameron 1990). Large populations of the starfish kill entire colonies of most coral species despite individual preferences for different coral types in some circumstances (Moran 1986). The first recorded outbreaks of *A. planci* on the GBR occurred in the 1960's and embraced reefs in the

central third of the ecosystem (Endean 1973). Following predation of the majority of a reef's corals, most of the starfish disappeared. Within 10 to 15 yr rapidly-growing branching and plate-like corals had reestablished an extensive coral cover on parts of many reefs (Endean & Cameron 1985). Formation of such a coral cover has been studied at several reefs of the GBR (Endean 1976) and particularly at Green Island Reef and John Brewer Reef (Pearson 1981, Done 1985, Fisk et al. 1989).

Many reefs of the central GBR experienced a second outbreak during the 1980's (Endean & Cameron 1985, Moran 1986). Whether such population outbreaks of *Acanthaster planci* are a contemporary phenomenon or are part of an ecological pattern that has persisted for thousands of years on the GBR is a contentious issue

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(Moran et al. 1986, Moran & Bradbury 1989, Walbran et al. 1989, Keesing et al. in press). Of particular significance for resolution of the controversy concerning the novelty or otherwise of the starfish outbreaks is predation on corals of massive growth form (Cameron & Endean 1985, Endean & Cameron 1985, Done 1987, 1988, Endean et al. 1989, Cameron et al. in press). In contrast with rapidly-growing encrusting, branching and plate-like corals which are susceptible to many forms of perturbation affecting coral reefs and which have high turnover rates, the slow-growing massive corals are resilient to normal perturbations that occur on coral reefs, and they are typically long-lived. Many have longevities of the order of centuries (Nozaki et al. 1978, Druffel 1982, Isdale 1984, Potts et al. 1985). At least 100 of the ca 330 scleractinian species recorded from the GBR exhibit massive morphology. They represent 30 genera of the 9 families Poritidae, Faviidae, Mussidae, Oculinidae, Agariciidae, Caryophylliidae, Merulinidae, Acroporidae and Siderastreidae (Veron 1986).

The idea that massive corals are primarily responsible for determining the basic structure of complex coral communities was proposed by Cameron & Endean (1985) and Endean & Cameron (1990). The long-term nature of the process of recovery of coral communities from catastrophic destruction was emphasized by these authors, who noted that for complete recovery of a complex coral community from extensive damage caused by an *Acanthaster planci* outbreak the massive corals must attain population size structures comparable with those existing before the *A. planci* outbreak. Decades to centuries are required for this to occur because of the low levels of recruitment (Endean et al. 1989, Fisk & Harriott 1990, Cameron et al. in press) and low growth rates (Buddemeir & Kinzie 1976, Babcock 1989, pers. obs.) of the majority of massive corals. Thus massive coral communities provide a convenient window through which to view the effect on coral reefs of successive *A. planci* outbreaks separated by intervals of the order of 10 to 15 yr, the observed intervals between the only documented *A. planci* outbreaks on reefs of the GBR.

Provided that an adequate pool of propagules is available and environmental conditions remain favourable for coral settlement and growth, it is probable that restoration of a cover of fast-growing opportunistic corals will continue to occur in the face of repeated *Acanthaster planci* outbreaks. Indeed, the presence of an extensive coral cover is obviously a prerequisite for an *A. planci* outbreak. In contrast, it is doubtful whether populations of the slow-growing and persistent massive corals can replace their losses in the face of repeated destruction by the crown-of-thorns starfish (Cameron & Endean 1985, Endean & Cameron 1985). It is a prime purpose of this study to determine whether

marked changes occur in the structure of massive coral communities after *A. planci* outbreaks.

Because of difficulties experienced when attempts are made to attribute damage to coral colonies on a particular reef unequivocally to *Acanthaster planci* predation, the study was designed to reveal whether numbers of massive coral colonies on reefs affected by *A. planci* outbreaks in recent years were markedly depleted when compared with numbers of massive coral colonies on nearby reefs that were not affected by *A. planci* outbreaks. If impoverishment of the massive coral assemblages occurs during outbreaks, differences in the levels of damage, in size (age) structures and possibly the relative abundances of different taxa of massive corals represented in the two reef sets should become apparent. This study sought to detect such differences.

Done (1987) modelled recovery of a mixed species assemblage of massive corals of the genus *Porites* at John Brewer Reef. By using different scenarios based on life history parameters (including recruitment rates, extent of destruction of different size classes, numbers of remnants, survivorship and growth rates) he made prognoses about the recovery of *Porites* spp. communities in the face of repeated *Acanthaster planci* outbreaks. These prognoses ranged from the communities holding their ground to local extinction. However, Endean et al. (1989) noted that *Porites* spp. appeared to be exceptional among massive coral taxa as far as resistance to *A. planci* predation, and hence recovery after *A. planci* outbreaks was concerned. Although colonies of *Porites* can be killed by *A. planci* (Done 1988, Done et al. 1989), they are frequently protected from total predation by the presence of inquiline worms and scallops (DeVantier et al. 1986, DeVantier & Endean 1988). The data we obtained for massive corals other than *Porites* spp. on several reefs led to the conclusion that massive coral assemblages could not recover if *A. planci* outbreaks continued to recur at ca 15 yr intervals (Endean et al. 1989). In view of the importance of establishing the generality of this conclusion for the management of coral reefs, it was decided to extend our earlier studies to embrace additional reefs so that coral communities on reefs of all major types and subjected to a variety of environmental factors in the area affected by *A. planci* outbreaks were examined. Also, in view of the resistance exhibited by *Porites* spp. it was decided to take into account possible differences in resistance to *A. planci* predation exhibited by different taxa by examining all the principal taxa of massive corals encountered during surveys of these reefs. A comprehensive database on which to make prognoses about recovery of massive coral assemblages in the central region of the GBR after *A. planci* outbreaks should then be available.

METHODS

Reefs of all major types ranging from inner shelf fringing reefs to outer shelf platform reefs in the central region of the GBR have been affected by *Acanthaster planci* outbreaks so a variety of reef types was included in the present study (Table 1). Different environmental conditions – including synthetic chemicals in run-off from the Queensland mainland (Endean 1976) – to which different reefs are subjected were thereby taken into account.

Data on colony size and degree of damage (partial mortality) were collected according to the protocol described earlier (Endean et al. 1989) for every massive coral present in transects on the reefs selected for study (Table 1). Thus manta tow surveys on 12 reefs of the central GBR were conducted to locate living and/or remnant assemblages of massive corals (Table 1). Six of the reefs had been affected by major population outbreaks of *Acanthaster planci* and 6 were unaffected. On each reef, at least 3 belt transects each of 300 m² (30 m along-slope by 10 m down-slope) were situated in each region using plastic tapes, at randomly selected distances from the anchoring position. Additional transects, in groups of 3, were examined on some reefs. Logistic restraints precluded a completely balanced sampling design. Transects were positioned on the reef slope from ca 3 to 10 m below crest. Each transect was searched systematically by SCUBA. Each massive coral colony present (representing most massive species known from the GBR) was recorded if at least half of the colony lay within the transect. The maximum diameter (maximum horizontal dimension) of each colony was measured to the nearest 0.5 cm, and it was assigned to one of 3 size classes (1 to 10 cm diameter; 11 to 50 cm diameter; > 50 cm diameter). Counts of very small colonies are probably conservative although every effort was made to census all colonies present. The surface of each colony was inspected so that it could be assigned to one of 3 damage classes: intact or < ⅓ dead surface; ⅓ to ⅔ dead; > ⅔ dead. Counts of totally killed colonies are probably conservative because of the difficulty in detecting those that were overgrown by algae, soft and hard corals, zoanthids and encrusting sponges.

The data set was analysed at both generic and family levels. All comparisons between the 2 reef sets were made using the Wilcoxon Rank Sum test based on the mean abundance of colonies per reef (Lehmann 1975). The test compares differences between the 2 reef sets relative to inter-reef variability within the sets. Significance levels were determined from precise 2-tailed probabilities. The presence of ties makes the test conservative.

RESULTS

On both reef sets the families Faviidae, Mussidae and Poritidae comprised ca 90 % of the colonies present. On reefs unaffected by starfish outbreaks, poritid corals comprised 34 % of the total assemblage (30 % for

Table 1. Details of each reef surveyed including name, location, reef type, year of last major *Acanthaster planci* outbreak (if any), date of survey, number of 300 m² transects and total area surveyed. Reef types are Inner Shelf Platform (ISP), Mid-shelf Platform (MSP), Outer Shelf Platform (OSP), Inner Shelf Fringing (ISF). Transects were located randomly within regions with living or remnant assemblages of massive corals

Reef	Lat. S.	Long. E	Reef Type	Year of *A. planci* outbreak	Date of survey	No. of transects	Total area (m²)
Unaffected reefs							
Low Is.	16° 23'	145° 34'	ISP	–	3 Mar 87	3	900
Hastings	16° 31'	146° 01'	OSP	–	25 Jun 87	6	1800
Fitzroy Is.	16° 56'	146° 00'	ISF	–	2 Mar 87	9	2700
N. Brook Is.	18° 09'	146° 18'	ISF	–	22 Oct 87	9	2700
Normanby Is.	17° 13'	146° 05'	ISF	–	28 Feb 87	9	2700
Davies*	18° 50'	147° 39'	MSP	–	22 Jun 88	3	900
Affected reefs							
Green Is.	16° 46'	145° 58'	ISP	1979–81	19 Feb 87	15	4500
Potter	17° 42'	146° 53'	OSP	1983	26 Feb 87	9	2700
Beaver	17° 51'	146° 29'	MSP	1982–83	20 Jun 87	3	900
Rib	18° 29'	147° 53'	MSP	1983–84	19 Jan 87	3	900
John Brewer	18° 38'	147° 04'	MSP	1983–85	22 Sep 86	9	2700
Holbourne Is.	19° 44'	148° 22'	ISF	1985–87	1 Feb 87	9	2700

* Transects in areas unaffected by *Acanthaster planci* in 1988

Table 2. Composition of massive coral assemblage on reefs unaffected and affected by major *Acanthaster planci* population outbreaks, indicated by the percentages of colonies in different taxa

Coral taxa	% Colonies	
	Unaffected reefs	Affected reefs
Poritidae	34	56
Faviidae	40	31
Mussidae	15	4
Other families	11	9
Porites	30	52
Favia	11	9
Favites	5	5
Goniastrea	10	8
Lobophyllia	11	1
Symphyllia	3	3

Porites), faviids comprised 40 % and mussids comprised 15 %. On affected reefs, poritids comprised 56 % (52 % for *Porites*), faviids 31 % and mussids only 4 % (Table 2).

Overall, there were markedly fewer massive corals, irrespective of colony size or degree of damage, on the affected reefs than on the unaffected reefs, with the difference being significant for the total assemblage and for the families Faviidae and Mussidae but not for the Poritidae (Table 3). For corals with $< \frac{1}{3}$ colony damage there were significant differences between the 2 reef sets in numbers of colonies of all these major taxa (Table 3). The depauperate state of the entire assemblage, of the families Faviidae, Mussidae and Poritidae

Table 3. Mean numbers ha^{-1} (with standard errors) of massive corals on both reef sets and the percentages by which the means for affected reefs differ from those for unaffected reefs. Corals of families other than those named represented ca 10 % only of the assemblage on both reef sets. (A) All corals, irrespective of colony size or damage; (B) corals with $< \frac{1}{3}$ damage

|	Mean numbers ha^{-1}		p	% Differ- ence
	Unaffected reefs	Affected reefs		
A				
All massive corals	4015 (727)	1471 (103)	··	63
Poritidae	1369 (475)	824 (238)		40
Faviidae	1621 (584)	449 (134)	·	72
Mussidae	606 (280)	63 (43)	··	90
B				
All massive corals	3454 (791)	727 (209)	··	79
Poritidae	1060 (379)	382 (117)	·	64
Faviidae	1462 (505)	195 (69)	··	87
Mussidae	594 (244)	44 (30)	··	92
Significance of differences between reef sets (Wilcoxon rank sum test): · p≤0.05; ·· p≤0.01				

and of a representative genus, *Favia*, on the affected reefs is shown in Figs. 1 to 5. Two general trends are apparent from these figures: (1) there were substantially fewer corals in all 3 size classes on the affected reefs than on the unaffected reefs, the exception being poritid recruits < 10 cm in diameter, which were similar in numbers on both reef sets; (2) many of the surviving corals on affected reefs exhibited substantial colony damage. For corals with $< \frac{1}{3}$ colony damage, there were significantly fewer large colonies (> 10 cm diameter) in most taxa on the affected reefs than on reefs unaffected by outbreaks (Table 4).

Approximately half the corals present on affected reefs had suffered partial mortality exceeding $\frac{1}{3}$ their colony surfaces (Figs. 1 to 5). Since badly damaged corals do not regrow over their own coralla (Hughes & Jackson 1980, Done 1987), these colonies have been reduced to much smaller sizes. By contrast, most corals on unaffected reefs were intact or exhibited only low levels of colony damage, generally restricted to $< \frac{1}{3}$ colony surface area. The family Poritidae, composed predominantly of the genus *Porites*, exhibited comparitively greater levels of such background mortality than other taxa on unaffected reefs (Fig. 4).

DISCUSSION

Colonies of massive corals on reefs unaffected by *Acanthaster planci* outbreaks exhibited negligible background mortality, apart from that shown by representatives of the family Poritidae (Endean et al. 1989). Some of the partial mortality exhibited by *Porites* spp. had resulted from self-shading during colony growth (DeVantier & Endean 1989). Interspecific interactions and sedimentation were probably responsible for much of the remaining partial mortality (L.M.D. own obs.). By contrast, many of the surviving corals on reefs affected by *A. planci* outbreaks exhibited substantial colony damage, generally in excess of $\frac{1}{3}$ colony surface area and often exceeding $\frac{2}{3}$ of the original colony surface. Although most corals on the affected reefs had obviously suffered predation by *A. planci* during the recent outbreaks, as evidenced by typical starfish feeding scars, some of the damage could have been caused by other agencies. It was for this reason, and in the absence of detailed before, during and post-outbreak studies that massive coral communities on reefs that had been affected by *A. planci* outbreaks were compared with those on unaffected reefs. Allowance was thereby made for destruction of massive corals by agencies other than *A. planci*.

During the second recorded outbreak series in the 1980's, outbreaks were observed on reefs in the region (e.g. Green Island Reef) almost as soon as a coral cover
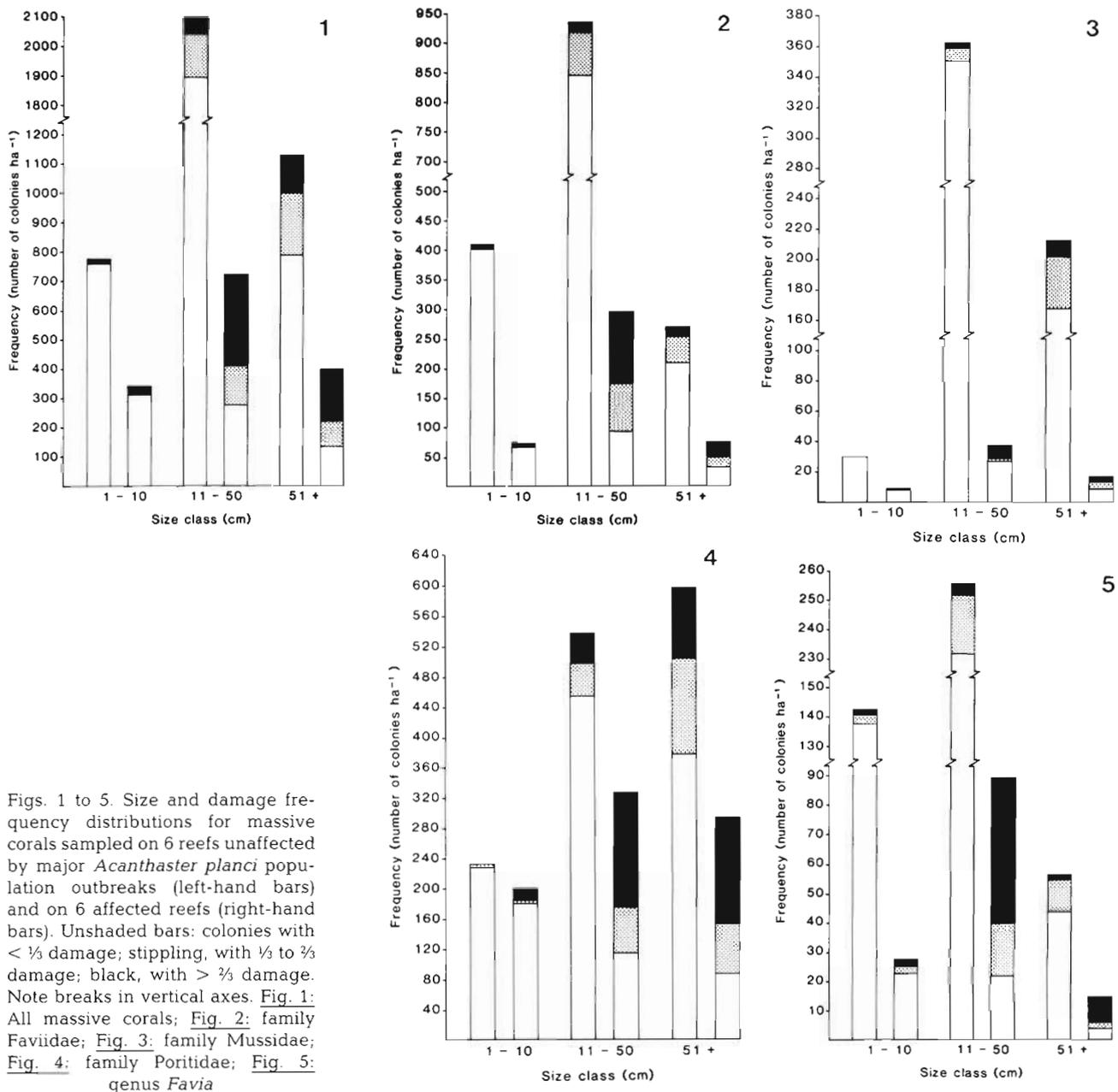
Figs. 1 to 5. Size and damage frequency distributions for massive corals sampled on 6 reefs unaffected by major *Acanthaster planci* population outbreaks (left-hand bars) and on 6 affected reefs (right-hand bars). Unshaded bars: colonies with < ⅓ damage; stippling, with ⅓ to ⅔ damage; black, with > ⅔ damage. Note breaks in vertical axes. Fig. 1: All massive corals; Fig. 2: family Faviidae; Fig. 3: family Mussidae; Fig. 4: family Poritidae; Fig. 5: genus *Favia*

was reestablished. If reinfestation by *Acanthaster planci* continues to be coincident with recovery of a coral cover by fast-growing branching and plate-like corals, the massive coral assemblage cannot recover and will continue to be degraded, the complexity of the coral communities will be reduced and a state of impoverishment will ultimately result.

In this regard, the results of the present study are unequivocal. Reefs of the GBR that have been affected by major *Acanthaster planci* outbreaks since the 1960's carried assemblages of massive corals possessing only ca ⅓ the colonies on nearby unaffected reefs. Moreover, the massive coral assemblages on affected

reefs have lost most large (old) colonies, a situation that differs markedly from that on unaffected reefs. This trend was most marked for the Faviidae and Mussidae. Such effects were lessened for the Poritidae by the relatively faster growth rates of *Porites* spp. and their defence by inquilines from total predation by *A. planci*. Furthermore, approximately half the surviving massive corals on affected reefs have been reduced substantially in size (exhibiting damage of > ⅓ their surface areas).

As well as the difference in the size (and age) structures of massive coral populations on affected reefs, the relative abundances of the taxa represented are differ-

Table 4. Mean number ha⁻¹ (with standard errors) of massive corals either intact or with only slight damage (< ⅓ surface area) in 3 size classes (1 to 10 cm diameter, 11 to 50 cm, 51+ cm) on the 2 reef sets, and percentages by which the means for affected reefs (A) differ from those for unaffected reefs (U)

Coral taxa	Diameter 1 to 10 cm				Diameter 11 to 50 cm				Diameter 51+ cm			
	U	A	p	%	U	A	p	%	U	A	p	%
All massive corals	764 (343)	312 (93)		59	1987 (226)	279 (82)	··	85	793 (221)	136 (29)	··	83
Poritidae	228 (129)	181 (64)		28	455 (161)	115 (32)	·	75	378 (89)	87 (21)	··	77
Faviidae	403 (235)	67 (25)		83	848 (215)	94 (33)	··	89	211 (55)	34 (12)	··	84
Mussidae	30 (11)	8 (5)	·	73	351 (128)	27 (19)	··	92	168 (105)	9 (7)	·	95
Porites	215 (129)	176 (66)		18	337 (143)	87 (25)	·	74	342 (84)	79 (22)	·	77
Favia	138 (88)	23 (8)		83	232 (72)	22 (4)	··	91	44 (19)	4 (3)	·	91
Favites	47 (25)	8 (3)		83	123 (40)	14 (8)	··	89	16 (7)	2 (2)		88
Goniastrea	151 (81)	27 (11)		82	193 (47)	24 (7)	··	88	18 (4)	2 (1)	··	89
Lobophyllia	15 (6)	4 (3)		73	247 (122)	8 (5)	··	97	128 (95)	1 (1)	·	99
Smphyllia	6 (2)	1 (1)		83	60 (15)	18 (13)	·	70	34 (12)	8 (6)	·	76

Significance of differences between reef sets (Wilcoxon rank sum test) is represented thus: · p ≤ 0.05; ·· p ≤ 0.01

ent. Faviidae and Mussidae were poorly represented on affected reefs whereas collectively they dominated the taxa on unaffected reefs (Table 2). By contrast, colonies of *Porites* spp. constitute more than half the assemblage on affected reefs but less than ⅓ of the total colonies on unaffected reefs. Thus, as well as an overall depletion in numbers of massive coral colonies, marked changes in the proportion of colonies carrying extensive areas of damage, in the size (age) structure of massive coral communities and in the relative abundances of massive corals of different taxa following *A. planci* outbreaks are already in evidence.

At least some massive coral species have long pre-reproductive periods, of the order of 5 to 8 yr (Kojis & Quinn 1985, Babcock 1989). On attaining reproductive age, such small colonies produce relatively few gametes in comparison with large colonies. Thus the reduction in numbers and sizes of corals on outbreak-affected reefs is likely to be compounded in the longer term by a marked reduction in reproductive output, further slowing recovery. Because of the geographical extent of the devastated region (in excess of 3 degrees of latitude, Johnson et al. 1989) and the probable larval connectedness of reefs of the region (Oliver & Willis 1987), it is possible that sexually-produced recruits for initiation of recovery are becoming scarce. If recruitment and survivorship of remnants between outbreaks remain low (Babcock 1989, Endean et al. 1989, Fisk & Harriott 1990), many taxa of the assemblage might be expected to become extinct locally. For example, corals of the family Mussidae on affected reefs were represented by only 10 % of the numbers found on reefs unaffected by the outbreaks (Table 3). Even despite the relatively greater resistance of *Porites* spp. to *Acanthaster planci* predation compared with the susceptibility of other massive corals (Endean et al. 1989), some

communities of *Porites* spp. could withstand as few as 2 or 3 further *A. planci* outbreaks comparable with those of the 1980's under modelling conditions of failed recruitment and high background mortality (Done 1988, Done et al. 1989). The capacity of the massive coral assemblage as a whole to recover from further *A. planci* outbreaks is considerably less than that of *Porites*. For many taxa of massive corals, growth rates are only half those of *Porites* spp. Mortality of massive coral colonies generally has been much greater than that suffered by *Porites* spp. (Endean et al. 1989), and the mortality of surviving remnants of massive corals can be high. For example, colony remnants < 10 cm in diameter on one reef had suffered 50 % mortality 1 yr after an *A. planci* outbreak through overgrowth by other sessile organisms (Endean et al. 1989). In view of these factors it can be predicted that massive coral communities are unlikely to withstand even the 2 or 3 further *A. planci* outbreaks required for local extinction of *Porites* spp. in the worst case scenario presented by Done (1988).

The observed interval between outbreak episodes on reefs devastated twice by the starfish is ca 15 yr. It is unlikely that further outbreaks could occur on these reefs prior to their acquisition of a cover of fast-growing corals and there would appear to be no a priori reason why outbreaks should occur at intervals much longer than the time taken for reefs to acquire such a coral cover. Although some authors link restoration of coral cover per se with recovery following *Acanthaster planci* outbreaks (Walbran et al. 1989), complete recovery requires reestablishment of the abundances and size distributions of the constituent species (Endean et al. 1989). It will be determined by the persistence of unaffected colonies, by the survivorship and growth of colony remnants and by the level of recruitment of new colonies. Comparison of colony

numbers, of the levels of damage exhibited, and of the size structures of massive coral assemblages found on both affected and unaffected reefs, taken in conjunction with the slow growth rates of many massive coral species of ca 0.5 to 1.0 cm radially per year (Buddemeir & Kinzie 1976, Babcock 1985, pers. obs.) indicates that 10 to 15 yr are clearly insufficient for recovery of the massive coral assemblage. Indeed, massive corals growing at 0.5 cm radially per year which colonized reefs immediately following the 1960's outbreaks would have attained diameters < 15 cm in the period prior to the second outbreak series. Colonies of such sizes are highly susceptible to being killed outright in a single *A. planci* predation episode. The time scale on which the continuing degradation of the GBR must be viewed is the ecological one based on the longevities of massive corals. Many colonies of massive coral species in the assemblage persist for decades to centuries. Some of the colonies measured were several metres in diameter and are hundreds of years old.

The data presented support the view advanced by Endean & Cameron (1985) that the longterm impoverishment of reefs whose hard coral cover has been devastated by *Acanthaster planci* twice in the past 20 yr is now probable. The basic structure of the communities will be lost as a result of the destruction of massive corals. Further loss of massive corals during *A. planci* outbreaks occurring at 15 yr intervals may lead to the local extinction of such corals with the possible exception of *Diploastrea heliopora* (Cameron et al. in press) and some *Porites* spp. Our prognosis for reefs in the central region of the GBR, in the absence of effective control measures, is that there will be continued outbreaks of *A. planci* following restoration of coral cover by fast-growing, opportunistic species, resulting in a gradual breakdown in the structure of the complex coral communities on these reefs. The communities of massive corals will lose adult colonies and will become dominated progressively by prereproductive recruits, provided sufficient sexual reproduction occurs to supply the affected reefs with propagules. In the intervals of approximately 15 yr between successive *A. planci* outbreaks the reefs will probably carry covers consisting predominantly of algae for 8 to 10 yr followed by branching and plate corals for 5 to 7 yr.

Repeated outbreaks of the intensity of those of the past 20 yr could not have occurred in the century prior to the 1960's on reefs of the central third of the GBR, otherwise, the reefs would not carry the numbers and size structures of massive corals observed during this study. Indeed, were outbreaks of the intensity of those of the past 20 yr regular or cyclical features of coral reef ecosystems prior to the 1950's, the complex assemblage of long-lived massive corals we have described could not exist.

The information presented is consistent with the view that the outbreaks on the GBR are novel events, peculiar to the latter half of the 20th century and coincident with large-scale human activities on the GBR, rather than integral features of reef ecology in the region. One hypothesis that has been proposed to account for these outbreaks is that of removal of predators of the starfish, principally piscine and molluscan predators of juvenile and sub-adult starfish (Endean 1973, 1977, McCallum 1987, McCallum et al. 1989, Ormond et al. 1990). This hypothesis still requires testing, even though it has been proposed in various forms for almost 20 yr.

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