Soft coral abundance on the central Great Barrier Reef: effects of *Acanthaster planci*, space availability, and aspects of the physical environment

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Abstract. The distribution and abundance of soft coral genera on reefs of the central Great Barrier Reef was investigated in relation to reef position, recent history of disturbance, wave exposure, substratum slope and depth. Eighty-five 25 m long transects were surveyed at 10 m depth on windward sides of 14 mid- and outer-shelf reefs. A further 75 transects in different zones on one mid-shelf reef (Davies Reef) between 5 and 30 m depth were investigated. The crown-of-thorns starfish *Acanthaster planci* had caused large-scale mortality of scleractinians on eight of these reefs five to ten years prior to the study, and as a result, scleractinian cover was only 35–55% of that on the six unimpacted reefs. On the impacted reefs, stony corals with massive and encrusting growths form had smaller average colony diameters but similar or slightly lower numerical abundance. In contrast, mean colony size, cover and abundance of branching stony corals showed no difference between impacted and unimpacted reefs. Twenty-four genera of soft corals (in eight families) were recorded, and none showed different abundance or cover in areas of former *A. planci* impact, compared to unaffected sites. Similarly, no difference was detected among locations in the numbers or area cover of sponges, tunicates, zoanthids, *Halimeda* or other macro-algae. Mean soft coral cover was 2 to 5% at 10 m on sheltered mid-shelf reefs, and 12 to 17% on more current-exposed reefs. Highest cover and abundances generally occurred on platforms of outer-shelf reefs exposed to relatively strong currents but low wave energy. On Davies Reef, cover and colony numbers of the families Nephtheidae and Xeniidae were low within the zone of wave impact, in flow-protected bays and lagoons, on shaded steep slopes, and at depths above 10 and below 25 m. In contrast, distributions of genera of the family Alcyoniidae were not related to these physical parameters. The physical conditions of a large proportion of habitats appear "sub-optimal" for the fastest growing taxa, possibly preventing an invasion of the cleared space. Thus, in the absence of additional stress these shallow-water fore-reef zones appear sufficiently resilient to return to their pre-outbreak state of scleractinian dominance.

Introduction

Soft corals (Cnidaria: Octocorallia) achieve high abundance on many coral reefs (Benayahu and Loya 1981; Tursch and Tursch 1982; Dinesen 1983; Dai 1990) and can have a negative effect on stony coral growth and survivorship (Maida et al. 1995). The Xeniidae and the Nephtheidae, two of the three most common octocoral families on the Australian Great Barrier Reef, have been commonly described as "fugitive" organisms, with high rates of growth and of asexual reproduction (e.g., Benayahu and Loya 1985, 1987; Fabricius et al. 1995b; Karlson et al. 1996). These traits should permit rapid population responses when environmental conditions change. In contrast, many members of a third common family, the Alcyoniidae, are characterized by slow growth, low rates of reproduction and mortality, and considerable persistence (Fabricius 1995).

Population outbreaks of the coral-eating starfish *Acanthaster planci* provide a large-scale setting for an investigation of the influence of rapid increases in available space on the abundances of soft corals, and of other sessile macro-benthos groups. On the Great Barrier Reef, the creation of open patches by outbreaks of the starfish is more extensive than that caused by any other natural or anthropogenic disturbance (Pearson 1981; Moran 1986). After the corals have been eaten, their skeletons initially (within days to weeks) become covered with filamentous and coralline algae. Later they may be colonized by surviving reef benthos and by larval recruits (e.g. Done et al. 1991). Soft corals are rarely eaten by *A. planci*, even in later stages of an outbreak when the preferred scleractinian food is reduced by up to 95% (Keesing 1990). This observation, together with the rapid colonizing ability of some soft corals, suggest that they have the capacity to increase in abundance after the selective removal of stony corals.

Several anecdotal reports and untested predictions of soft coral assemblages replacing scleractinian communities after *A. planci* outbreaks or other perturbations have been made (Fishelson 1973; Nishihira and Yamazato 1974; Endean 1976; 1987; Benayahu and Loya 1981;

Table 1. Characteristics of the 14 study reefs: history of recent *Acanthaster planci* outbreaks (Moran 1986; outbreak records before 1980 based on an unpublished database of the Australian Institute of Marine Science), "low" = *Acanthaster* densities below outbreak levels; location on the continental shelf (O, outer-shelf; M, mid-shelf reef), ranked according to their exposure to oceanic swells (1, least exposed; 5, most exposed); percent cover of common groups of macro-benthos (mean of 5–8 25 m line transects ± standard error per reef)

Reef	*A. planci* Outbreaks	Exposure – Rank order	Stony corals	Turf algae	Coralline algae	Soft corals	Sponges	Zoanthidae
Chicken	No	O-5	34.8 ± 3.2	33.7 ± 3.2	14.8 ± 4.0	9.3 ± 2.5	2.6 ± 1.3	1.0 ± 0.3
Bowl	No	O-4	31.5 ± 2.9	37.7 ± 3.4	14.9 ± 1.4	10.7 ± 1.6	1.1 ± 0.5	0.8 ± 0.2
Coil	No	O-4	33.5 ± 3.0	28.8 ± 7.5	24.2 ± 5.6	8.6 ± 0.9	0.5 ± 0.2	0.4 ± 0.3
Faraday	No (low 1984)	M-3	20.4 ± 2.8	38.9 ± 2.0	16.7 ± 4.1	17.1 ± 2.5	1.6 ± 0.5	0.3 ± 0.2
Centipede	No (low 1987)	M-2	32.4 ± 2.5	31.5 ± 6.7	11.2 ± 4.2	5.6 ± 1.4	4.3 ± 1.6	3.2 ± 1.6
Davies	No (low 1971, 1989)	M-2	32.4 ± 0.9	31.9 ± 2.3	13.8 ± 1.8	4.3 ± 0.6	1.0 ± 0.2	2.0 ± 0.2
Needle	1984–1985	O-4	22.6 ± 2.9	45.4 ± 4.1	24.6 ± 3.5	2.7 ± 0.5	2.1 ± 1.1	0.1 ± 0.1
Fork	1971, and before 1986	O-4	27.3 ± 2.0	33.0 ± 4.6	20.5 ± 3.0	6.3 ± 1.6	2.1 ± 0.5	6.7 ± 0.7
Dip	1983–1985	O-4	13.6 ± 2.0	35.5 ± 4.9	24.6 ± 4.3	14.1 ± 2.0	1.4 ± 0.7	0.1 ± 0.1
18-025	Before 1988	O-3	18.4 ± 2.9	43.2 ± 7.1	19.4 ± 5.5	12.3 ± 0.6	2.9 ± 0.5	1.7 ± 2.2
Yankee	1984–1987	M-3	15.3 ± 2.2	53.6 ± 5.5	13.0 ± 3.5	12.2 ± 4.2	2.9 ± 0.5	1.6 ± 0.6
Grub	1970–1971, 1985–1986	M-2	18.7 ± 4.8	47.7 ± 6.5	15.9 ± 2.8	7.5 ± 1.1	5.1 ± 1.3	2.1 ± 0.8
Rib	1966–1969, 1983–1984	M-1	22.8 ± 3.3	59.9 ± 3.5	8.0 ± 0.7	5.0 ± 0.9	1.5 ± 0.8	0.9 ± 0.3
Brewer	1969–1971, 1983–1985	M-1	11.5 ± 2.0	57.9 ± 4.2	11.4 ± 2.5	4.8 ± 2.3	3.0 ± 0.9	7.4 ± 2.2
Mean	All	O	25.9 ± 2.8	36.8 ± 2.1	20.4 ± 1.5	9.2 ± 1.3	1.8 ± 0.3	1.5 ± 0.8
Mean	All	M	21.6 ± 2.6	45.6 ± 4.3	12.9 ± 1.0	7.8 ± 1.8	2.8 ± 0.5	2.5 ± 0.8
Mean	No	All	30.5 ± 1.9	33.3 ± 1.6	15.9 ± 1.6	9.0 ± 1.9	1.9 ± 0.5	1.3 ± 0.4
Mean	Yes	All	18.7 ± 1.4	47.0 ± 3.2	17.2 ± 2.0	8.1 ± 1.4	2.6 ± 0.4	2.6 ± 0.9

Endean et al. 1988; Chou and Yamazato 1990; Devantier 1995). However, Pearson (1981) found no responses by soft corals to *A. planci* infestations on five 1 m² plots on John Brewer Reef (Great Barrier Reef) between 1974–78, after an outbreak had decimated stony coral cover in 1970–71. Similarly, Birkeland and Lucas (1990) emphasized the lack of evidence for an increase in alcyonaceans after the removal of scleractinians. A theoretical ecological model of shifts in community composition after *A. planci* outbreaks produced a pattern of slow increase in soft coral abundance to levels of up to 50% above initial abundances (Bradbury and Mundy 1989).

Disturbance and competition can act synergistically in shaping reefal communities (Hughes 1989). If, after disturbance, soft corals or other benthic groups invade reef substratum, recovery of stony coral populations could be severely delayed. Accordingly, the objective of this investigation was to determine if there were differences in area cover and abundance of specific soft coral taxa between reefs that were and were not recently affected by *A. planci*. Differences in cover, abundance and colony sizes of the relatively fast-growing branching stony corals and the slower-growing massive and encrusting stony coral taxa, and in cover and abundance of several other common macro-benthos groups (sponges, zoanthidae, tunicates, macroalgae, and *Halimeda*) were also assessed. The study thus addresses the consequences of increased space availability on reef community structure. A further objective of the study was to assess the potential effect of some abiotic parameters (current and wave exposure, substratum angle, and water depth) on cover and abundance of common soft coral taxa, as very little information exists about the habitat requirements of soft corals.

Methods

Study sites

Fourteen adjacent mid- and outer-shelf reefs on the central Great Barrier Reef were selected, aiming at covering an equal number of reefs with, and without, recent *Acanthaster planci* infestations (Moran 1986; Bass et al. 1988, 1989), and an equal number each on mid- and outer-shelf positions on the continental shelf (Fig. 1, Table 1). Due to the small number of reefs without recent crown-of-thorns outbreaks, the sampling design could not be fully balanced, and the surveys were carried out on eight *A. planci* impacted reefs (IR) and six non-impacted reefs (NIR). The reefs were ranked according to estimates of exposure (distance to the edge of the continental shelf, and shelter from upstream reefs). Assessments were carried out at 10 m depth on the windward side of each of the 14 reefs between April and November 1992.

Benthic assemblages were also investigated along depth gradients and between geomorphological zones on Davies Reef (Fig. 1) in order to assess the relationships of physical parameters to the distribution and abundance of octocorals. Five sites were established at the windward and the leeward side, and in the lagoon, and one at each of the north and south reef flanks. Transects were censused along depth contours at 5 m depth increments as follows: windward side 5 to 30 m; leeward 5 to 25 m; flanks 5 to 20 m; lagoon 5 to 15 m. The deepest transect depth for the sites reflect differences in the base of the reef.

Field data

Percentage cover, colony size and numbers of soft corals, hard corals and other macro-benthos (sponges, zoanthids, tunicates, macroalgae, and *Halimeda*), and 'space' were estimated using line intercept and belt transects, where 'space' (or unoccupied substratum) was defined as the proportion of consolidated hard substrata covered by filamentous or coralline algae but not occupied by macro-invertebrates or macro-algae. Between 5 and 8 25 m long transects were

were recorded. Three pairs of genera (*Nephthea/Stereonephthya*, *Xenia/Heteroxenia*, and *Isis/Rumphella*), were each treated as one category, as not all colonies could be distinguished with certainty.

Tunicates	Macroalgae	Halimeda	Others
0.1 ± 0.1	1.4 ± 0.3	0.0 ± 0.0	2.1 ± 0.7
0.2 ± 0.1	0.5 ± 0.2	0.9 ± 0.4	2.1 ± 0.5
0.0 ± 0.0	0.1 ± 0.1	3.6 ± 1.6	0.0 ± 0.0
0.1 ± 0.1	0.6 ± 0.4	2.0 ± 1.1	1.9 ± 0.1
0.8 ± 0.4	0.6 ± 0.3	9.3 ± 4.4	1.7 ± 0.2
0.2 ± 0.1	0.6 ± 0.2	14.4 ± 1.9	0.4 ± 0.1
0.1 ± 0.0	1.0 ± 0.6	1.1 ± 0.8	0.5 ± 0.1
0.9 ± 0.2	0.4 ± 0.1	0.9 ± 0.0	2.8 ± 0.2
0.1 ± 0.1	0.7 ± 0.3	8.8 ± 1.5	0.8 ± 0.4
0.2 ± 0.2	0.3 ± 0.2	0.2 ± 0.4	3.3 ± 0.6
0.3 ± 0.1	0.2 ± 0.1	0.0 ± 0.1	1.4 ± 0.4
0.6 ± 0.4	1.1 ± 0.6	0.1 ± 0.1	6.0 ± 0.4
0.1 ± 0.0	0.2 ± 0.1	0.4 ± 0.2	2.1 ± 0.3
0.2 ± 0.1	1.1 ± 0.8	1.0 ± 0.8	1.6 ± 0.4
0.2 ± 0.1	0.6 ± 0.2	2.2 ± 1.1	1.0 ± 0.1
0.3 ± 0.1	0.6 ± 0.1	3.8 ± 1.9	0.8 ± 0.1
0.2 ± 0.1	0.6 ± 0.2	4.9 ± 2.0	1.1 ± 0.4
0.3 ± 0.1	0.6 ± 0.1	1.5 ± 1.0	1.2 ± 0.5

investigated on each reef along the 10 m depth contour (85 transects in total). The angle of the slope was measured along the transects every 2 m, and the readings later averaged to one value for each transect. Tape intercepts were recorded to the nearest centimetre. Sixteen benthic categories based on growth forms and higher taxonomic groups were distinguished (see Reichelt et al. 1986). In addition, soft coral abundance and colony sizes were assessed within a 50 cm wide strip along the same transect. Soft corals were identified to genus, and the longest and shortest diameters of each colony

Data analysis

The line transect data were analyzed for cover, abundance (number of observations), and chord length of each of the 16 benthic categories after substracting the length of sand and loose rubble from the total transect length. The belt transect data, also standardized to hard substrate only, were analyzed for cover and abundance of each soft coral genus. Chord lengths (intercepts) were used as a relative measure of diameters of colonies or patches (Marsh et al. 1984; Mundy 1991). A two-way analysis of variance was used to assess the effects of crown-of-thorns impact and shelf position on the variables. The data were averaged over transects for each reef, and the analysis was weighted by the number of transects within each reef. For the ANCOVAs of the 11 most common soft coral genera (belt transects), slope was used as a covariate. Differences in the soft coral assemblage (represented by the six soft coral genera with greatest mean cover) were assessed using a two-way MANCOVA, with slope angle as the covariate. ANCOVAs, again with slope as the covariate, were also used to test for the effect of depth and location on soft coral cover and abundance at Davies Reef. Log-transformations for abundance data and arc-sin square-root transformations on the proportion of cover were carried out where appropriate to reduce heteroscedasticy. Variance is represented by standard errors of means throughout.

Results

Effects of Acanthaster history

Turf and coralline algae

Five to 10 years after the outbreaks of *A. planci*, the proportion of consolidated substratum covered with turf
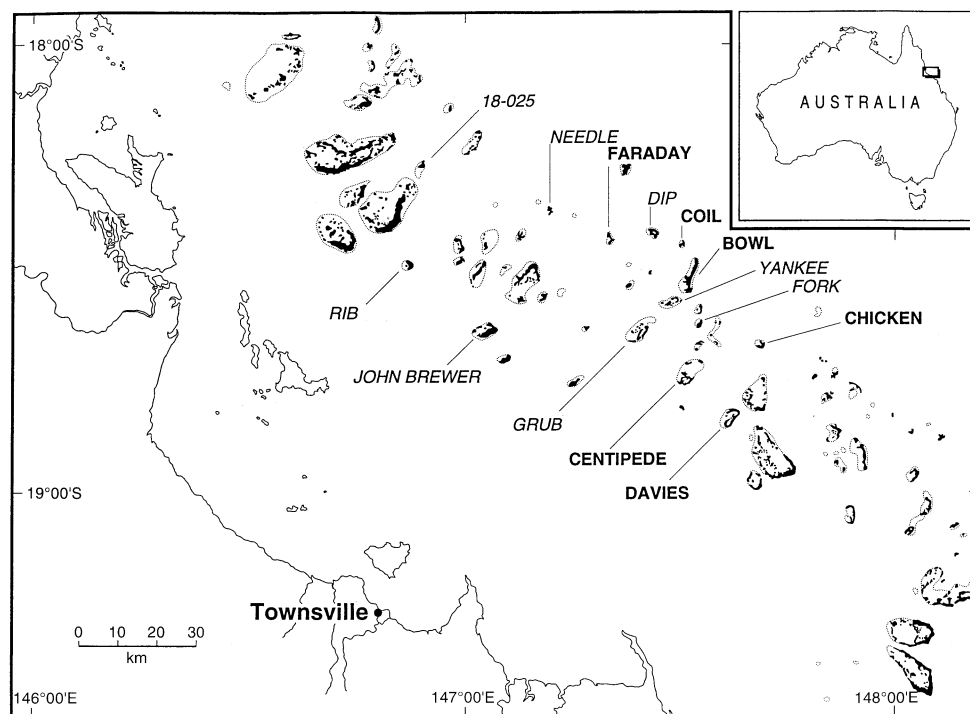

Fig. 1. Locations of study reefs. Eight reefs (*italics*) had high densities of *Acanthaster* 5 to 10 years prior to the benthos assessment (Table 1), the other 6 reefs (bold letters) were unaffected by *Acanthaster*

Table 2. *P*-values for effects of crown-of-thorns history (COT), position on the continental shelf (Shelf), and COT by Shelf of two-way ANOVAs of mean abundance (colony number), percent cover, and chord length (indicating colony or patch diameter) of turf algae (TA), coralline algae (CA), massive corals (CM), encrusting corals (CE), branching corals (CB), and soft corals (SC). Data based on means of 14 reefs (85 line transects)

Response	Source	TA	CA	CM	CE	CB	SC
Abundance	COT	**0.031***	**0.027***	**0.014***	0.120	0.454	0.826
	Shelf	0.177	**0.017***	0.643	0.565	0.077	0.504
	COT by Shelf	0.428	0.061	0.373	0.920	0.314	0.650
Cover	COT	**0.002***	0.654	**< 0.001***	**0.004***	0.171	0.294
	Shelf	0.054	**0.004***	0.375	0.699	**0.047***	0.192
	COT by Shelf	0.070	0.366	0.086	0.394	0.926	0.179
Chord length	COT	0.058	0.213	**< 0.001***	**< 0.001***	0.311	0.427
	Shelf	0.217	**0.031***	0.270	0.091	0.093	0.367
	COT by Shelf	0.082	0.855	0.060	0.370	0.987	0.280

$*P < 0.05$

algae (Table 1) was significantly higher on impacted reefs (IR: 47.0% ± 3.2 SEM) compared to non-impacted reefs (NIR: 33.3% ± 1.6; Table 2). Fifty percent of the space covered with turf algae occurred in patches > 50 cm chord length. Patches ⩽ 10 cm chord length were highly abundant on both reef types, but held only 3.3% of the space covered by turf algae. The high turf cover on IR was due to the greater number of patches covered with turf ($P < 0.001$), and not due to greater mean patch sizes. For coralline algae, the patterns were less pronounced (Table 2). The number of patches with coralline algae was slightly higher on IR, however neither mean chord length nor cover varied significantly between IR and NIR (cover: 17.2% ± 2.0, versus 15.9% ± 1.6; $P > 0.05$).

Stony corals

Mean stony coral cover was 40% lower on IR than NIR (Table 1). The differences were mostly due to smaller colony sizes of massive and encrusting taxa (Table 2). Cover of massive and encrusting stony corals on IR were 30 to 50% of that on NIR, whereas colony numbers were significantly lower only in the massive forms. The mean chord lengths (a measure of colony diameters) in both groups were significantly shorter on IR (7.4 ± 0.4, $n = 8$, versus 10.4 cm ± 0.6, $n = 6$ for encrusting corals; and 8.6 ± 0.5 versus 12.0 cm ± 0.7 for massive corals). In branching corals, there was no effect of crown-of-thorns impact on cover, abundance and colony sizes (IR: 8.4% ± 1.4, NIR: 9.4% ± 0.9, $P = 0.017$; Table 2). Contrary to the relatively slow-growing massive and encrusting corals, branching corals seemed to have regrown to initial colony sizes, as the mean chord length for branching corals was similar on IR and NIR sites (11.2 cm ± 0.7, versus 11.8 ± 0.8, $P > 0.05$). Cover of branching stony corals was significantly lower at mid-shelf positions (7.2% ± 0.9 SEM, $n = 7$) compared with outer shelf sites (10.6% ± 1.2, $n = 7$, $P = 0.002$).

Soft corals

Soft corals were the second-most common group of sessile macro-invertebrates after the stony corals. Total soft coral cover varied between 1 and 27% on the transects at 10 m depth (range for hard corals: 8 to 48%). The family Alcyoniidae represented 44% of the total soft coral cover, the Xeniidae 25%, Nephtheidae 17%, with 5 less common families accounting for most of the remaining 14%

(Table 3). *Sinularia* was the genus with highest cover, whereas *Efflatounaria* and *Xenia* were the most abundant taxa in terms of numbers of colonies. Ten genera accounted for 88% of the soft coral cover in this region, while 14 additional genera and several rare gorgonian genera (unidentified) were found in low abundance and cover. Taxa which occurred in very low frequencies included the azooxanthellate, cave-inhabiting *Minabea*, *Scleronephthya*, *Siphonogorgia* and other Nidaliidae, and members of the family Melithaeidae.

Total number of soft corals, mean colony size, and mean soft coral cover were all unrelated to previous crown-of-thorns impact (Table 2). Relative soft coral cover was 8.1% ± 1.4 on IR, and 9.0% ± 1.9 on NIR. Colony numbers were 0.95 ± 0.34 per meter transect tape on IR, and very similar (0.97 ± 0.23 m^{-1}) on NIR. AN-COVAs on cover and colony numbers of the three most common families showed no crown-of-thorns or shelf effects (Table 4a, and Fig. 2). The proportion of the supposedly fast-growing Nephtheidae and Xeniidae relative to the more persistent, slow-growing, slow-recruiting Alcyoniidae was not enhanced in areas of increased space availability (2-way ANCOVA on the ratio [log (nephtheid) + log(xeniid cover))/(log(alcyoniid cover)], $P > 0.05$). The residuals from the ANCOVAs on the 3 families were uncorrelated ($\chi^2_{(3)} = 1.33$, $P = 0.722$), and thus no information, additional to that derived from the univariate analyses, would be expected from a MANOVA.

The ANCOVAs for individual taxa indicated no significant effects of *A. planci* history on cover and colony numbers for any of the 11 most common genera (Table 4a, and Fig. 3). Both *Efflatounaria* and *Xenia* had significantly *lower* cover on IR, however the differences became insignificant in analyses where slope was included as covariate. A MANCOVA on percent cover of the 6 most common soft coral genera showed a statistically significant effect of shelf position and slope angle (Table 4b). Furthermore, it indicated a marginal effect ($P = 0.058$) of crown-of-thorns impact, due to the reduced cover of the two xeniid genera.

Other macro-benthos

None of the other macro-benthos forms (sponges, tunicates, zoanthids, macro-algae and *Halimeda*) showed significant differences in percent cover between IR and NIR (Table 1, $P > 0.05$). Zoanthidae were common on

Table 3. Soft coral community composition, and percent cover (proportion of total consolidated substrate) on 14 mid- and outer-shelf reefs of the central Great Barrier Reef at 10 m depth. Data based on observations of 7,956 individuals in 85 belt transects of 25×0.5 m (total area surveyed: 1063 m^2)

Taxon	Colony number (% of total)	Relative cover (%)	Total cover (%)
Alcyoniidae	**14.82**	**46.32**	**2.40**
Sinularia	8.68	29.32	1.53
Sarcophyton	2.79	7.01	0.36
Lobophytum	1.49	7.02	0.36
Alcyonium	0.83	1.14	0.06
Parerythropodium	0.54	0.97	0.05
Cladiella	0.49	0.70	0.04
Xeniidae	**47.07**	**24.28**	**1.27**
Efflatounaria	22.94	16.66	0.86
Xenia and *Heteroxenia*	22.00	5.70	0.30
Sympodium	1.21	1.09	0.06
Anthelia	0.69	0.31	0.02
Cespitularia	0.23	0.52	0.03
Nephtheidae	**21.81**	**15.33**	**0.86**
Nephthea and *Stereonephthya*	7.58	8.19	0.49
Lemnalia	6.76	3.68	0.19
Paralemnalia	4.95	2.05	0.11
Capnella	1.80	0.94	0.05
Dendronephthya	0.72	0.47	0.02
Asterospiculariidae			
Asterospicularia	**9.18**	**3.34**	**0.17**
Briareidae			
Briareum	**0.99**	**5.11**	**0.26**
Isididae			
Isis and *Rumphella*	**1.47**	**1.50**	**0.07**
Clavulariidae			
Clavularia	**0.43**	**1.11**	**0.06**
Plexauridae			
Plexaura flava	**1.12**	**0.61**	**0.03**
Other genera	**3.11**	**2.56**	**0.06**
Sum	**100.00**	**100.00**	**5.18**

several sites, but cover was highly variable (0.1 to 7.4%) and not related to any of the environmental parameters measured. The same was found for the locally abundant and highly aggregated alga *Halimeda*.

Soft coral distribution

Position on continental shelf

Soft coral cover at 10 m depth was highest on reefs such as Faraday, Dip, Yankee, and Reef 18025, which were near the edge of the continental shelf (Table 1). Cover on these reefs ranged from 12.2% to 17.1% of the consolidated substratum. These values correspond to 20.1 to 35.7% of total macro-benthos cover (commonly referred to as 'live cover'). In comparison, soft coral cover was low on the 5 mid-shelf reefs closest to the shore (7.9% $\pm$ 2.1), and on the five outer-most reefs (8.6% $\pm$ 1.57). Overall, the highest cover of soft corals in the region was encountered on platforms of outer-shelf reefs at 15 to 25 m depth (visual estimate: 25 to >50% of consolidated substratum, not censused). Species asssemblages were generally very

similar on outer-and mid-shelf habitats. For most taxa, no significant differences in cover between both reef types were observed, except in *Asterospicularia* (Table 4a) which had high numbers on outer-shelf reefs but very low abundances on the mid-shelf. Otherwise, taxa were relatively evenly distributed among the mid- and outer-shelf reefs.

Davies Reef

Location and depth: at outer slope sites, total soft coral cover and species numbers were highest at depths of 15 to 25 m (Fig. 4). Assemblages at this depth were dominated by *Nephthea*, *Efflatounaria*, *Sarcophyton*, *Sinularia*, *Plexaura* and *Isis*. In shallow water, Nephtheidae were rare on the windward compared to the leeward side. By contrast, xeniid cover was generally higher on the windward compared to the leeward side down to 20 m depth. The distribution of the Alcyoniidae was relatively even (around 1%), excepting some shallow back reef sites which had mean alcyoniid cover of up to 10%. Lagoonal areas had generally very low soft coral cover (Fig. 4), and only a few taxa were present in a fraction of the transects

Table 4a. Two-way ANCOVAs of percent cover of the most common soft coral groups on 14 mid- and outer-shelf reefs of the Great Barrier Reef. Probabilities of no difference in cover between crown-of-thorns impacted and unaffected (COT), and outer- and mid-shelf reefs (Shelf). Slope angle was used as the covariate in the design

Taxon	COT	Shelf	Slope	COT by Shelf
Xeniidae	0.531	0.633	0.807	0.807
Nephtheidae	0.300	0.131	**0.029***	0.969
Alcyoniidae	0.080	0.532	0.601	0.610
Efflatounaria	0.082	0.387	**0.028***	0.399
Xenia	0.126	0.584	0.117	0.106
Asterospicularia	0.721	**0.002***	**< 0.001***	0.114
Nephthea	0.128	0.856	**0.048***	0.983
Lemnalia	0.898	0.594	0.062	0.671
Paralemnalia	0.683	0.287	0.235	0.756
Capnella	0.322	0.433	0.535	0.931
Lobophytum	0.197	0.152	0.057	0.267
Sarcophyton	0.444	0.425	0.298	0.638
Sinularia	0.679	0.102	0.951	0.951
Briareum	0.710	0.546	0.748	0.412

*$P < 0.05$.

Table 4b. MANCOVA testing the effect of COT and Shelf on the cover of the six most widely distributed and common soft coral taxa (*Efflatounaria*, *Xenia*, *Nephthea*, *Sarcophyton*, *Sinularia*, and *Briareum*). Slope was included as the covariate

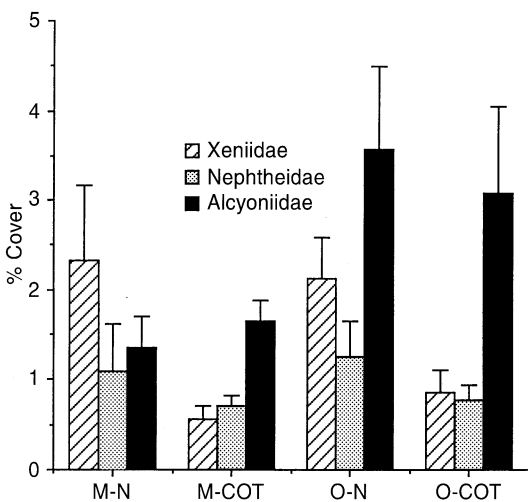| Source	Wilk's Lambda	F	df	P
COT	0.106	5.610	(6, 4)	0.058
Shelf	0.061	10.241	(6, 4)	0.020
Slope	0.067	9.234	(6, 4)	0.025
Shelf by COT	0.158	3.541	(6, 4)	0.121

Fig. 2. Percent cover of the three most common soft coral families Xeniidae (*hatched*), Nephtheidae (*grey*), and Alcyoniidae (*black*) at mid-shelf (*M*) and outer-shelf reefs (*O*), with (*COT*) and without (*N*) previous crown-of-thorns outbreaks. Error bars indicate 1 SEM

(mostly *Sinularia*, *Briareum*, *Efflatounaria*, and some Isidae, *Lobophytum* and *Sarcophyton*). Lagoonal sites at 5 m depth were mostly free of soft corals, except on a few platforms where some *Efflatounaria*, *Sarcophyton*, *Xenia*,
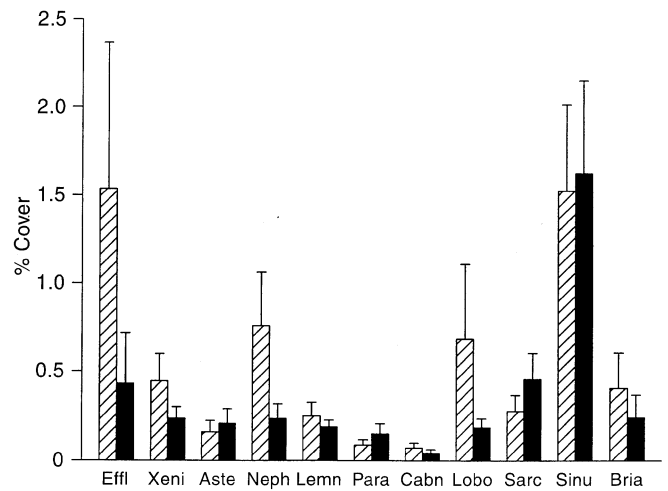

Fig. 3. Mean percent cover of the 11 most common soft coral genera on crown of thorns unimpacted (*hatched bars*) and impacted reefs (*filled bars*). Error bars indicate 1 SEM

Nephthea and *Sinularia* covered up to 3% of the substratum.

Slope inclination: on Davies Reef, slope angle had a strong effect on the cover and abundance of a range of genera. *Nephthea*, *Asterospicularia*, *Plexaura* and *Isis*, the family Nephtheidae, and the total soft coral cover, were significantly related to the substratum slope when analyses were carried out on transects as sampling units ($P < 0.05$ in all cases). The numbers were highest on horizontal terraces and in gradually sloping areas, and lowest on steep slopes, vertical walls and overhangs. *Nephthea*, *Lemnalia*, *Asterospicularia*, *Plexaura flava* and most Xeniidae rarely occurred on slopes steeper than 60°, and *Isis* was only found on platforms with less than a 35° angle. In contrast, the common taxa *Sinularia*, *Sarcophyton*, *Briareum* and *Lobophytum* were not affected by the substratum slope, and the first three of these genera were the major community component on steeply sloping reef surfaces.

Substrate inclination also appeared to contribute to differences in assemblages on windward and leeward sides of Davies Reef, where reef morphology differed, particularly below 20 m depth. On the leeward side, the sampling area at 20 and 25 m was between 50 and 150 m away from the base of the reef slope on an almost horizontal bottom surface. In contrast, the reef formed an extended terrace at 17 to 20 m on the windward side, but dropped with a slope angle of 30 to 45° below 20 m. Horizontal areas had consistently higher soft coral cover (ranging from 6 to 11%) than the steeper slopes (0.8 to 5%) at the same depth. At 25 m, cover was significantly lower on the windward slope (1.3% ± 0.4, $n = 3$) than the leeward terrace (5.6% ± 1.3, $n = 3$). In the lagoon, patch reefs had very low soft coral cover (range: 0 to 0.1%) on vertical walls, but had higher cover (range: 1.4 to 3.9%) on gradually sloping reef patches and flat platforms.
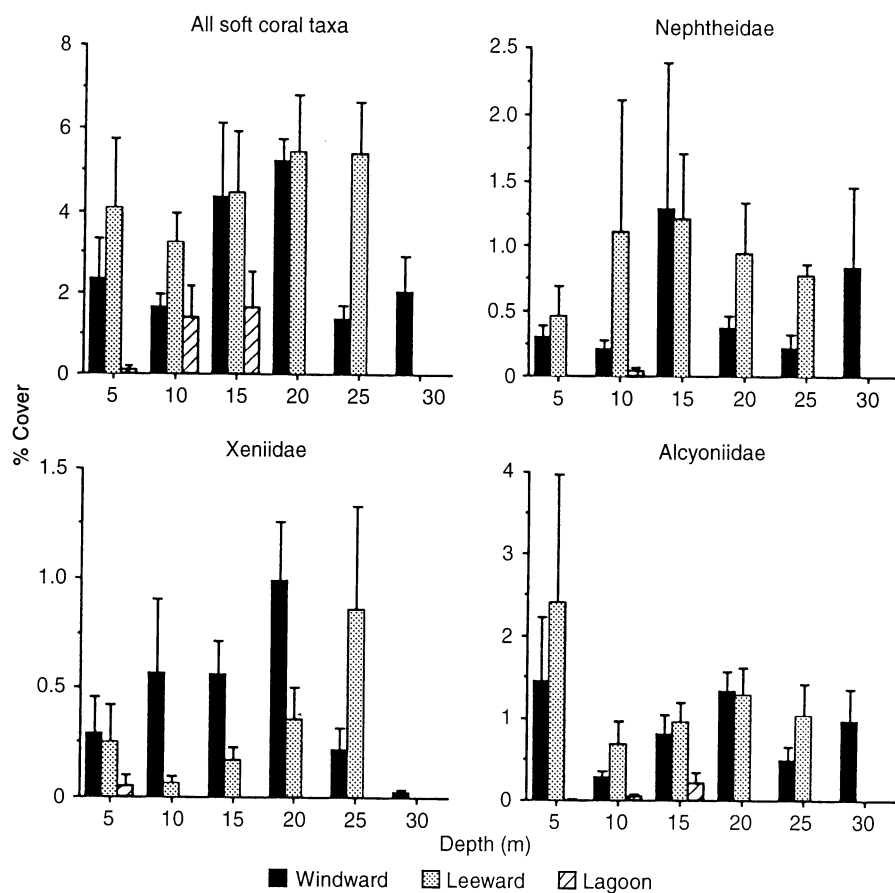
Fig. 4. Soft coral cover at Davies Reef on the windward (*black bars*), leeward (*grey bars*) and lagoon (*hatched bars*) sites. Note the different scales on the y-axis. Data based on 75 belt transects (25 × 0.5 m). Error bars indicate 1 SEM

Discussion

Space limitation versus demographic restraints

Soft coral communities showed little tendency to take advantage of increased available space due to *A. planci* outbreaks. No differences in percent cover and colony numbers were evident 5 to 10 years after such outbreaks had removed a large proportion of stony coral. On at least four of the reefs, scleractinian cover may have been low for longer than 20 years as previous crown-of-thorns outbreaks had already occurred there in the late 1960s (Table 1). The reason for the common perception of an increase in soft corals may be that they are much more conspicuous where hard corals are sparse than in areas of high coral cover. Their coloration and shape stand out against algae, but blend in with scleractinians.

A generalized characterization of soft corals as 'colonizers' and 'pioneers' is certainly inappropriate. Larval settlement success in soft corals appears low compared to many stony corals (Stephenson and Stephenson 1933; Benayahu and Loya 1987; Fabricius 1995), and asexual reproduction by budding or colony fission may be the predominant mode of propagation for many taxa. The lack of population response after *A. planci* outbreaks in common soft corals may therefore be related to demographic restraints including low rates of growth, low larval recruitment success, or processes such as density-dependent mortality (Karlson et al. 1996). The effect of these factors on space occupation has been modelled theoretically and previous studies suggest that a certain proportion of space will remain vacant if settlement rates are low or mortality is high and/or density dependent (Hughes 1984; Roughgarden et al. 1984, Bence and Nisbet 1989). The evidence presented here also suggests that most soft coral species are not constrained by competition for space with stony corals. The restricted ability of octocorals to colonize space rapidly after disturbance could mean that hard corals will be able to re-establish successfully before an increase in octocoral abundance can be observed.

Control by physical parameters

The finding that soft coral populations are not denser where space availability is enhanced cannot necessarily be extrapolated from shallow-water areas to other depths or to flow-protected near-shore zones. Rather, processes of recolonization and growth may be habitat-specific (Done et al. 1991). The most favourable habitats on the central Great Barrier Reef, where cover, numerical abundance and species numbers were highest, were sites located on outer-shelf reefs on platforms exposed to unobstructed water flow and below the impact zone of storm waves. Less suitable physical conditions (steep slopes, wave exposed shallow water, or shelter from flow) are likely to retard individual and population growth of soft corals after a disturbance.

Frequent damage to colonies by storm waves, in combination with low larval recolonization rates and habitat selection of the larvae, may keep wave-exposed shallow water zones depauperate of wave vulnerable taxa (Massel and Done 1993). At reefs on the shelf break, waves can exert strong drag forces to depths reaching far below 10 m (e.g., Chicken, Coil, Bowl Reef). Highest soft coral abundance shifts to greater depths with increasing distance from the land and increasing wave exposure. Cover is greatest at 2 to 6 m on near-shore reefs, around 15–20 m at Davies Reef on the mid-shelf, and luxuriant soft coral cover of >55% occurs from 18 m depth down to at least 30 m on exposed reefs such as Myrmidon Reef (K. Fabricius, unpublished data; Dinesen 1983; Reichelt et al. 1986).

This study indicates that physical parameters exert a strong control on soft coral distribution. Soft corals are passive suspension feeders, and dependent on water flow for particle transport. Both slow and very fast flow speeds depress feeding efficiency and growth rates (Fabricius et al. 1995b). It is unknown how slope angle affects soft coral cover and colony numbers, but again nutritional aspects appear to take effect. Most taxa depend on light for photosynthesis. A wide azimuth angle provides long exposure to photosynthetically active irradiance, which is of particular relevance at greater depth where periods of photosynthetic saturation are short in a majority of soft coral taxa (Fabricius and Klumpp 1995).

It appears that a large proportion of the reef (i.e., substratum on steep slope, at great depth, in zones of wave exposure, and at flow speeds to fast and too slow for efficient feeding) provide "sub-optimal" conditions for many soft coral taxa.

Coexistence of soft and stony corals

In sessile organisms, competition for space is usually tightly interlinked with competition for other resources (Buss 1979; Sebens and Thorne 1985). Coexistence of soft and stony corals, which together dominate many reef communities of the Indo-Pacific, may be facilitated by differences in the utilization of food resources. Both phototrophy and heterotrophy differ considerably between these two groups (Fabricius and Klumpp 1995; Fabricius et al. 1995a, b). Their dependence on irradiance, particulate food and flow may be sufficiently different to considerably reduce the overlap of ecological niches. Mechanisms of aggression or defence by hard corals (e.g., extracoelenteric digestion by mesenterial filaments, sweeper tentacles, and immunological responses) seem not to be activated, or are ineffective, against neighbouring soft corals (Sheppard 1979), so that aggressive interactions between soft and stony corals are rarely observed in the field. Moreover, soft corals are frequently competitively superior over neighbouring scleractinians under experimental conditions (e.g., Sammarco et al. 1985; Alino et al. 1992). An inverse relationship between soft and hard coral abundances, such as reported by Dinesen (1983), and Reichelt et al. (1986), seem to be more the result of different habitat requirements than of present-day competitive interactions.

Resilience of coral reefs after episodic and long-term disturbance

Availability of space, and active competition for space can act as major limiting factors in sessile marine communities (Dayton 1971; Connell 1976; Sebens 1976; Lang and Chornskey 1990). Nevertheless, none of the soft corals, nor any of the other sessile macro-benthos groups examined here (other than hard corals) showed differences in abundances between *A. planci* impacted and unimpacted reefs. The data indicate that soft corals do not replace scleractinian communities after catastrophic or episodic hard coral mortality. Instead, some fast-growing and fast-recruiting scleractinian taxa may eventually colonize the vacant space before a response in soft coral cover becomes apparent. Processes may be similar after other episodic disturbances to hard corals, such as cyclones. Previous reports of soft coral dominance following *A. planci* infestations were mostly from reefs which were additionally stressed by increased sedimentation, due to land development, erosion and dredging (e.g., Nishihira and Yamazato 1974; Chou and Yamazato 1990). It remains to be investigated whether non-episodic disturbances, in particular chronically increased rates of sedimentation or eutrophication, promote abundances of certain soft coral taxa (particularly Alcyoniidae) and are responsible for occurrences of soft coral "take-over" as observed by Chou and Yamazato (1990) or Devantier (1995).

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