

# Changes in a fish assemblage after a coral bleaching event

David J. Booth<sup>1,\*</sup>, Giglia A. Beretta<sup>2</sup>

<sup>1</sup>Department of Environmental Sciences, University of Technology, Westbourne Street, Gore Hill, New South Wales 2065, Australia

<sup>2</sup>School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia

**ABSTRACT:** Large-scale bleaching events are major disturbances to coral health and community structure, but may also affect other coral reef taxa, such as fishes. In 1997–1998, wide-spread coral bleaching and mortality occurred across the Great Barrier Reef, caused by increases in sea surface temperatures resulting from El Niño Southern Oscillation. As part of this event, in February–March 1998, there was extensive bleaching within One Tree Island lagoon (southern Great Barrier Reef), such that almost 12 mo later there was a significant reduction of live coral cover at some sites. We monitored the distribution of adults and recruitment of damselfishes (Pomacentridae) to sites within One Tree Island in 1993–1995 and in 1999. Fish species that normally associate with live corals showed relatively lower recruitment at bleached sites compared to the same sites pre-bleaching or to recovered sites and, as a result, species diversity and assemblage structure of recruits changed. Compared to 1993/1995 densities, adult *Pomacentrus wardi*, *P. moluccensis* and *Chrysiptera rollandi* densities dropped at bleached sites, but not at unbleached sites. While *P. moluccensis* directly associate with live corals, the other 2 species do not. This study has demonstrated that indirect effects of bleaching can include changes in assemblage structure of reef fish adults and recruits.

**KEY WORDS:** Coral bleaching · Damselfishes · Fish diversity · Live coral cover · Recruitment

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

The distribution and abundance of coral reef fishes are in part determined by the availability of suitable habitat (e.g. Bouchon-Navaro 1986, Hixon & Beets 1993, Booth & Beretta 1994, Caley & St. John 1996, Munday et al. 1997) and habitat preferences of incoming larvae (reviewed by Booth & Wellington 1998). Such preferences can be for live coral cover, rubble, and conspecifics (e.g. Sweatman 1983, Booth & Beretta 1994, Tolimieri 1995, Booth 1995). Also, distributions of reef fish can be drastically altered at local scales by differential patterns of post-settlement mortality through juvenile interactions with predators and habitat complexity. Despite these habitat/fish interactions, most

coral reef fishes are flexible within broad groupings, regarding habitat occupied.

While very few fish taxa are obligate corallivores (Hixon 1997), many preferentially settle on live corals (e.g. Booth & Beretta 1994, Munday et al. 1997). Therefore, loss of live corals may alter fish assemblage composition (Wellington & Victor 1985). In turn, fishes may enhance coral diversity (e.g. Glynn & Colgan 1988). Degradation of coral reef habitat may therefore affect densities of coral reef fishes, either by enhancing densities of herbivores (e.g. Wellington & Victor 1985, Glynn & Colgan 1988), or reducing densities of obligate corallivores (Ohman et al. 1998). However, evidence for these phenomena is scarce.

Bleaching of corals refers to the paling of coral tissue caused by the expulsion of symbiotic dinoflagellates and associated pigments, in many cases resulting in temporary shutdown of coral host metabolism (up to

\*Email: david.booth@uts.edu.au

90 % of carbon available to corals is from zooxanthellae photosynthesis; Muscatine 1991) or death (see reviews by Brown 1997 and Hoegh-Guldberg 1999). While direct effects of bleaching on coral physiology and demography have been increasingly studied (Hoegh-Guldberg 1999), to date little attention has been paid to possible indirect consequences of coral bleaching on other members of coral reef communities, such as fishes (but see Lindahl et al. 2001, Victor et al. in press).

The 1997-1998 El Niño Southern Oscillation (ENSO) event led to extensive levels of coral bleaching and mortality worldwide (Wilkinson et al 1999). Bleaching along the entire Great Barrier Reef (GBR) in early 1998 afforded a unique opportunity to study the indirect consequences of coral bleaching on damselfish assemblages at One Tree Island, southern GBR, in the course of long-term fish and coral monitoring. Here we provide quantitative estimates of post-bleaching impacts on mortality in reef corals and a guild of reef fishes in One Tree Island Lagoon by documenting long-term differences in live coral cover at 8 sites after the 1997-1998 bleaching event. Simultaneously at each site, we examine changes in density and diversity of benthic damselfishes, and link change in coral cover due to bleaching to changes in damselfish populations.

We predicted losses of recruits and adult damselfishes that associate strongly with live coral cover at sites that experienced bleaching, but not of other species of damselfishes. Consequently, we predicted changes in damselfish assemblage structure due to bleaching.

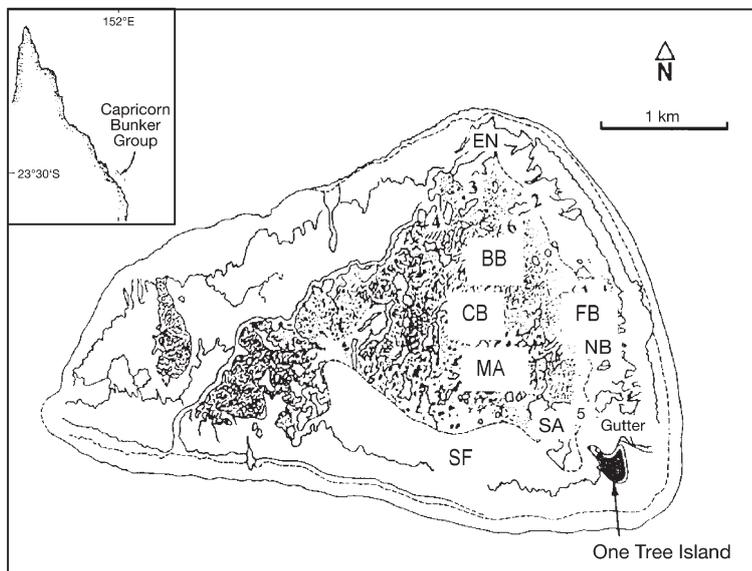


Fig. 1. One Tree Island lagoon, indicating location of One Tree Island, and the 8 study sites: First Bank (FB), Sand Flats (SF), Shark Alley (SA), Entrance (EN), Big Bommies (BB), Maze (MA), Centre Bommie (CB) and No Bommies (NB)

## MATERIALS AND METHODS

**Coral cover.** In February 1995 and January 1999, repeat benthic video transects and surveys of adult and recruit damselfish were conducted in One Tree Island Reef lagoon (23° 30' S, 152° 06' E). One Tree Island Reef lagoon is ponded, with irregular tidal cycles and incomplete tidal flushing (Ludington 1979) The sites surveyed represented 4 inner-lagoonal and 4 edge sites within the main lagoon (1st lagoon) of One Tree Island Reef (Fig. 1). These sites have been surveyed for live coral cover and fish densities on an irregular basis since 1993 as part of a long-term study of fish recruitment (e.g. Booth et al. 2000).

At each of 8 sites, video transects were taken along the middle of 5 permanent 15 m transects that had been established since 1993 to quantify the percent coral cover at fish-recruitment monitoring sites (Fig. 1). In 1995, a Sony Hi-8 Handicam in an Amphibico housing was used, and in 1999, a Sony Digital (VX-700) video camera in a Stingray housing was used. In both cases, the camera was moved along the transects at approximately 70 cm distance above the substrate, generating a field-of-view of approximately 0.4 m<sup>2</sup>. Footage obtained in this way was sampled on a 55 cm colour television, by pausing the tape at 50 regular frames for each transect. For instance, if the duration of the footage for a transect was 10 min, the tape was paused every 12 s. In each paused view, the substrate cover under each of 5 fixed points on the screen was recorded. Cover categories were necessarily broad, given the poor resolution

of the Hi-8 video, although we identified corals to family, genus or species level, as well as life-forms (see English et al. 1994). However, in this paper we only present 2 categories (live coral cover, and pocilloporids) to evaluate an overall effect of loss of live cover on fishes. Branching species, such as *Pocillopora damicornis* often support newly recruited damselfishes (Booth et al. 2000) and were easily identified from video images.

### Damselfish recruit and adult densities.

Censuses of damselfish recruits were conducted over the summer period (December to February) in 1993-1994, 1994-1995, and in January to February 1999, and also at 1 site (Shark Alley) in 1996. The transects varied in width from 1.5 to 4 m, depending on the depth of water adjacent to each site, resulting in variation in transect area from 25 m<sup>2</sup> (Shark Alley) to 63 m<sup>2</sup> (Entrance). Transects were not of fixed width, since many species recruited along natural boundaries (e.g. the reef or sand interface at

the foot of the reef), and these would have been missed if transect width were fixed (see Booth et al. 2000). During censuses we swam slowly along the transect, counting and identifying all recruit-sized (15 to 18 mm total length, TL) damselfish. During April 1995 and April 1999 (and in July 1996 at 1 site), adults of 3 common species of damselfish (*Pomacentrus moluccensis*, *P. wardi* and *Chrysiptera rollandi*) were also censused within transects, and densities expressed as number per 100 m<sup>2</sup>.

**Data analysis.** Changes in coral cover at each site were tested using paired *t*-tests (1-tailed,  $n = 5$  transects per site). Based on these results, sites were categorised as 'affected' if live cover dropped significantly and 'not affected' if cover did not change. One-tailed tests were used, since we had a firm prior prediction that cover would drop at affected sites (see Sokal & Rohlf 1995). Changes in density of adult and recruit damselfishes, and recruit diversity (Shannon-Wiener Index,  $H'$ ) at each location were tested using nested 2-factor ANOVA, with factors bleaching (affected or unaffected) and location ( $n = 8$ , nested within bleach factor). All dependent variables were logarithmically transformed to produce normally distributed data prior to analysis, except recruit densities, which were normalised as a percentage of total recruitment in that year, so an arc-sine transformation of data was used.

## RESULTS

### Changes in live coral cover

Cover of live hard corals ranged from 2 to 50% among all 40 transects (over the 8 sites) in 1994. When each site was resurveyed in 1999, live coral cover had dropped significantly at 4 of 8 sites (paired 1-tailed *t*-tests,  $0.001 < p < 0.04$ , Fig. 2a), and had not significantly changed at the other 4 sites for 'affected' sites ( $0.13 < p < 0.30$ , Fig. 2a). The 4 former sites showing significant loss of live coral cover were categorised as 'affected' by bleaching, and the unchanged or recovered 4 sites are hereafter termed 'unaffected'. At a higher level of taxonomic resolution, a similar pattern was seen for pocilloporid corals separately (Fig. 2b). The most common pocilloporid species in One Tree Island lagoon were *Pocillopora damicornis*, *Seriopora hystrix*, and *Stylophora pistillata*. Of the sites previously classified as 'affected', 2 sites had only negligible pocilloporid cover over the course of the study, and the 2 other sites exhibited no change in coral cover (paired *t*-tests,  $0.07 < p < 0.1$ , Fig. 2b). 2 of the 4 sites previously classified as 'affected' showed significant drops in pocilloporid cover (paired *t*-tests,  $0.03 < p < 0.04$ , Fig. 2b), while 1 site had only negligible pocilloporid coral cover.

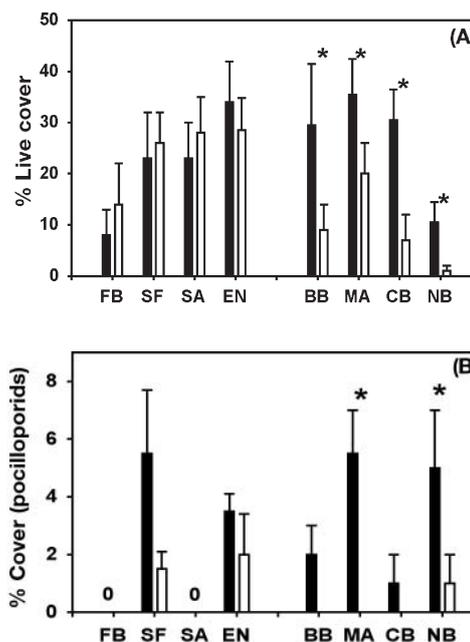


Fig. 2. (A) Percent live coral cover, and (B) percent live pocilloporid cover, at each of 8 study sites in One Tree Island lagoon in February 1995 (■) and February 1999 (□) (mean  $\pm$  SE,  $n = 5$  transects at each site, paired *t*-tests, data arcsine transformed \*: Significant difference, *t*-test,  $p < 0.05$ )

At all sites, coral colony structure and therefore habitat complexity (rugosity) had been preserved in bleached corals, although at some sites (e.g. No Bommies), considerable algal growth had covered bleached corals.

### Fish recruitment and recruit diversity vs live coral cover

Since overall recruitment of pomacentrids varied among the 3 years (e.g. *Pomacentrus moluccensis* total recruitment to transects: 297 in 1993/94, 43 in 1994/95 and 456 in 1999; *P. wardi* 123, 73, 64; *Chrysiptera rollandi* 298, 86, 82: Booth et al. 2000), recruitment of these species at each site was expressed as a proportion of total recruitment for each year. Nested ANOVA (Table 1) showed no significant difference between affected and unaffected sites overall, although recruitment was extremely variable among sites (Fig. 3).

A total of 13 species of pomacentrids recruited into transects during the study (Table 2). Of 9 species recruiting to affected sites in 1994-1995, only 5 species recruited in 1999. Four species decreased significantly in density over the 5 yr period, while 5 species did not differ significantly in recruitment (Table 2). Of 11 species recruiting to unaffected sites, 9 recruited in 1999

Table 1. *Pomacentrus moluccensis*, *Chrysiptera rollandi* and *P. wardi*. Nested ANOVA for (a) % change in recruitment and recruit diversity ( $H'$ ), and (b) % change in adult pomacentrids as functions of factors 'Bleach' (whether sites were categorised as affected or unaffected by bleaching) and Site ( $n = 4$  sites nested within each Bleach treatment). Significant p-values are in **bold**, and all data conformed with assumptions of normality and equality of variance after transformation

(a)		% Recruitment			Recruit diversity					
Source	df	MS	F	p	MS	F	p			
Bleach	1	0.024	1.50	0.24	95.3	6.50	<b>0.02</b>			
Site (Bleach)	6	0.016	1.04	0.44	18.4	1.26	0.33			
Error	16	0.016			14.6					
(b)		<i>P. moluccensis</i>			<i>C. rollandi</i>			<i>P. wardi</i>		
Source	df	MS	F	p	MS	F	p	MS	F	p
Bleach	1	0.018	5.5	<b>0.03</b>	0.025	8.05	<b>0.01</b>	0.100	30.0	<b>0.001</b>
Site (Bleach)	6	0.006	1.7	0.19	0.003	1.01	0.45	0.061	18.44	<b>0.001</b>
Error	16	0.003			0.160			0.003		

and 1 new species recruited in 1999. Three species dropped in recruit abundance over the 5 years, while 3 increased and 5 did not change significantly (Table 2). Recruit diversity (Shannon-Wiener Index,  $H'$ ) dropped significantly at 5 sites, including the 4 affected sites (Fig. 4), and nested ANOVA (Table 1) indicated that the drop in diversity was significantly greater at affected sites.

#### Changes in adult pomacentrid densities: 1994 to 1999

There was no significant change in the density of adults of 3 common pomacentrid species in any of the

4 unaffected sites between 1994 and 1999, with the exception of a loss of *Pomacentrus wardi* at the Entrance site. In addition, a survey of adults at the Shark Alley site showed that densities in July 1996 were also not significantly different to densities in 1994 and 1999, suggesting little fluctuation in densities over a scale of 5 yr (paired  $t$ -tests, 1-tailed 5% significance level, Fig. 5). In contrast, densities of adults of all 3 species at all 4 affected sites dropped significantly from 1994 to 1999. Nested analyses of variance (Table 1) indicated that adult densities of all 3 species dropped significantly more at affected than unaffected sites overall.

There was a linear positive relationship between mean adult density and live coral cover among sites in 1999 ( $r^2 = 0.49$ ,  $n = 8$  sites,  $p < 0.05$ , Fig. 6b) but not in 1994 ( $r^2 = 0.03$ ,  $p > 0.05$ , Fig. 6a).

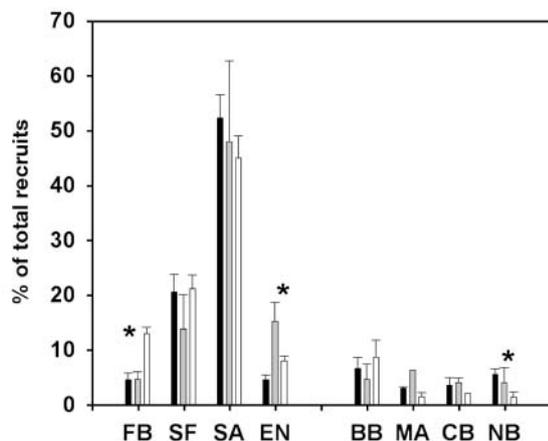


Fig. 3. *Pomacentrus moluccensis*, *P. wardi*, *Chrysiptera rollandi*. Recruitment (% of total recruitment) of common pomacentrids before and after the 1998 bleaching event in One Tree Island lagoon, at 8 study sites. The 4 leftmost sites were classified as 'unaffected' and the others as 'affected' by bleaching. Mean  $\pm$  SE,  $n = 5$  transects at each site, paired  $t$ -tests, data arcsine transformed \*: Significant difference,  $t$ -test,  $p < 0.05$ . 1993/94: black bars; 1994/95: grey bars; 1999: white bars

## DISCUSSION

The bleaching event of 1998 affected most shallow sites within One Tree Island lagoon, but while some sites appeared to have recovered by January 1999, some sites remain devastated with respect to live coral cover. In parallel, densities of damselfish adults, and diversity of recruits dropped at sites where coral cover had dropped significantly, which is likely to be a result of the bleaching event 10 mo beforehand. This suggests deleterious effects of above-normal water temperature on damselfish assemblages through changes in live coral cover.

Widespread bleaching occurred across One Tree Island lagoon in early 1998 (R. Sweatapple and M. Waugh pers. comm.), and was extensive at adjacent Heron Island reef where up to 80% of corals were affected on the reef flat and 70% on the reef slope (K. Townsend pers. comm.). Sea surface temperature

Table 2. Recruitment of pomacentrid species (mean  $\pm$  SE) onto transects (n = 5) at affected and unaffected/recovered sites within One Tree Island lagoon, 1994–1995 (pre-bleaching) and 1999 (post-bleaching). \*: Significant difference, paired *t*-tests, 1-tailed,  $p < 0.05$

Species	Affected sites (n = 4)		Unaffected sites (n = 4)	
	1994-1995	1999	1994-1995	1999
<i>Amblyglyphidodon curacao</i>	0.38 $\pm$ 0.13	0*	0.36 $\pm$ 0.15	0.04 $\pm$ 0.04*
<i>Chromis viridis</i>	0.35 $\pm$ 0.24	0*	0	0
<i>Chrysiptera rollandi</i>	0.91 $\pm$ 0.24	0.75 $\pm$ 0.75	4.28 $\pm$ 0.97	2.25 $\pm$ 1.75
<i>Chrysiptera talboti</i>	0	0	0.11 $\pm$ 0.06	0*
<i>Dascyllus aruanus</i>	0.49 $\pm$ 0.18	0.43 $\pm$ 0.43	0.08 $\pm$ 0.08	0.08 $\pm$ 0.08
<i>Dischistodus melanopus</i>	0.44 $\pm$ 0.22	0.33 $\pm$ 0.33	1.39 $\pm$ 0.86	1.41 $\pm$ 0.44
<i>Dischistodus</i> sp.	0.13 $\pm$ 0.13	0*	0	0.43 $\pm$ 0.25*
<i>Neoglyphidodon melas</i>	0.08 $\pm$ 0.04	0*	0.04 $\pm$ 0.04	0.18 $\pm$ 0.18
<i>Pomacentrus amboinensis</i>	0	0	0.53 $\pm$ 0.24	0.41 $\pm$ 0.31
<i>Pomacentrus bankanensis</i>	0	0	0.12 $\pm$ 0.07	0.12 $\pm$ 0.07
<i>Pomacentrus flavicauda</i>	0	0	0.04 $\pm$ 0.04	0*
<i>Pomacentrus moluccensis</i>	1.40 $\pm$ 1.25	2.98 $\pm$ 1.68	4.38 $\pm$ 2.01	13.25 $\pm$ 1.31*
<i>Pomacentrus wardi</i>	0.29 $\pm$ 0.13	0.24 $\pm$ 0.16	1.17 $\pm$ 0.26	2.23 $\pm$ 0.64*

(SST) data indicated that water temperatures from Heron reef exceeded the 'bleaching threshold' for ca. 2 mo in 1997-1998, but not significantly in 1998-1999. At nearby Heron Island, recovery of overall coral cover was high 6 mo after the event. However, Heron reef is not ponded at low tide, and it is likely that elevated temperatures persisted longer in One Tree lagoon.

The marked drop in live coral cover attributed to bleaching at One Tree occurred in the central region of the lagoon. At these sites, flushing is minimal during tidal cycles (Ludington 1979), and water temperatures may remain high for longer periods than sites on the edge of the lagoon (data not shown). Lower fish recruitment at affected (inner) sites may be partly a result of oceanographic processes (see Booth et al. 2000), but drops in abundance of adults and recruit diversity at affected sites, and not at unaffected sites are unlikely to have an alternative oceanographic explanation. Pocilloporids corals, favoured by recruits of many fish species, were heavily impacted by the bleaching event, although only rare at some sites prior to bleaching. Other studies (Glynn 1984, Gleason 1993, Salvat 1993, Hoegh-Guldberg & Salvat 1995, Marshall & Baird 2000, Mumby et al. 2001) have found the fast growing pocilloporids highly susceptible to bleaching events, exhibiting high mortality.

While overall decreases in adult damselfish density and recruit diversity occurred at affected sites, there were no clear effects on rates of recruitment. Given the strong preference for live branching corals by some species, such as *Pomacentrus moluccensis* (Booth et al. 2000), this is hard to explain. However, during 1999 surveys, *P. moluccensis* recruits were observed mainly on live branching corals at all sites (pers. obs.) and it may be that suitable habitat is not limiting for recruits, even at bleached sites. In addition, adult damselfish

are very aggressive towards confamilial recruits (Doherty 1982, Jones 1987, Forrester 1990), so the losses of adults reported here at affected sites may have been advantageous for new recruits, counteracting any negative effects of loss of live cover at these sites.

Some damselfish species were highly patchily distributed on live corals in One Tree Island lagoon, so assessment of density changes of those species using the methods presented here was unsuitable. *Chromis viridis* recruits, for instance, aggregate in large numbers on isolated branching tabulate acroporid corals (pers. obs.). One such group, at the Big Bommie site (Fig. 1) was monitored from 1993 to 1995, in 1996 and in 1999. During all censuses, except in 1999, from 100

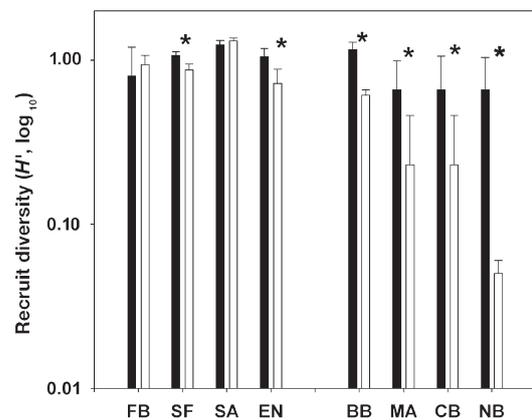


Fig. 4. Overall diversity ( $H'$ ) of pomacentrid recruits before and after the 1998 bleaching event, One Tree Island lagoon, at 8 study sites. The 4 leftmost sites were classified as 'Unaffected' and the others as 'affected' by bleaching (see text). (mean  $\pm$  SE, n = 5 transects at each site, paired *t*-tests, data  $\log_{10}$  transformed \*: Significant difference, *t*-test,  $p < 0.05$ ) 1995: black bars; 1999: white bars

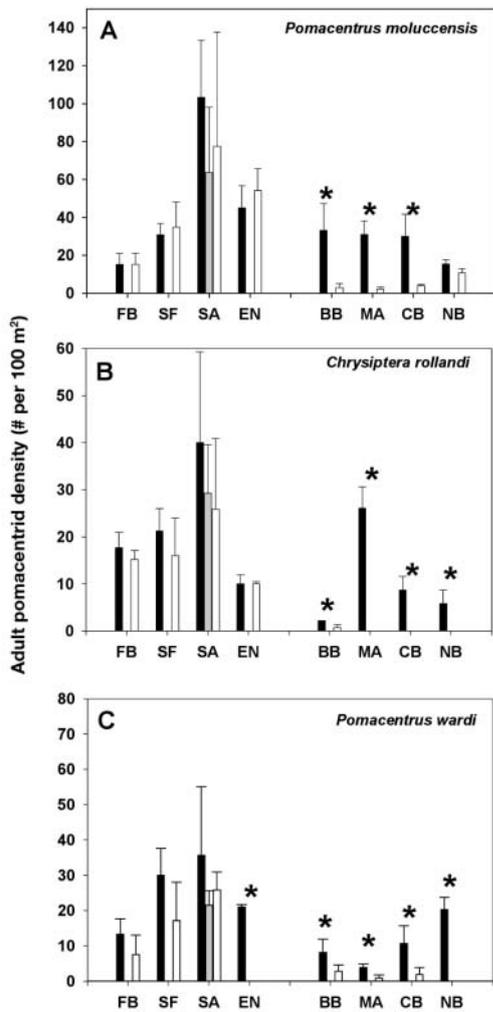


Fig. 5. *Pomacentrus moluccensis*, *P. wardi*, *Chrysiptera rollandi*. Density of adult pomacentrids, before (1995 black bars) and after (1999 white bars) the 1998 coral bleaching event, One Tree Island lagoon, at 8 study sites. The 4 leftmost sites were classified as ‘affected’ and the others as ‘unaffected’ by bleaching (see text). Data for one site, Shark Alley, are also included for 1996 grey bars. (mean  $\pm$  SE, n = 5 transects at each site, paired t-tests, \*: Significant difference, t-test, p < 0.05)

to 200 recruits of a range of size classes were observed on the coral head, which appeared healthy. In 1999, the coral head was dead and covered by algae, and no *Chromis viridis* recruits were seen. Therefore, it is likely that recruitment of some fish species was seriously reduced as a result of coral bleaching and subsequent colony mortality, but different sampling methods will need to be employed to detect such effects.

Densities of adults of species that do not usually directly associate with live corals, such as *Chrysiptera rollandi* and *Pomacentrus wardi*, dropped markedly at bleached sites relative to unaffected sites. Rea-

sons may include general degradation of habitat at bleached sites, or highly unfavourable conditions at bleached sites during the high-temperature event of early 1998, such as buildup of macroalgae (pers. obs.). In 1999, the structural integrity of bleached corals had not changed noticeably, suggesting that changes were not simply a product of change in habitat complexity (sensu Roberts & Ormond 1987). Predictions of which species would be most affected by bleaching and other disturbances, based species requirements, must be made with caution.

There was no significant relationship between live coral cover and adult pomacentrid densities in 1994, but post-bleaching, a significant among-site relationship was evident (Fig. 6). Effects of reduced live cover may only be apparent at low coral cover, since in 1999, 3 sites had less than 10% cover and low adult densities.

Table 2 suggests that several changes in damselfish recruit abundance were independent of the bleaching event. *Amblyglyphidodon curacao* recruitment dropped significantly at all sites from 1993 to 1999, while *Pomacentrus moluccensis* increased over the same period. Also, the dramatic drop in density of *P. wardi* adults at the Entrance site, while unexplained, did not appear to be bleaching-related. These examples highlight the stochastic nature of recruitment, and caution against

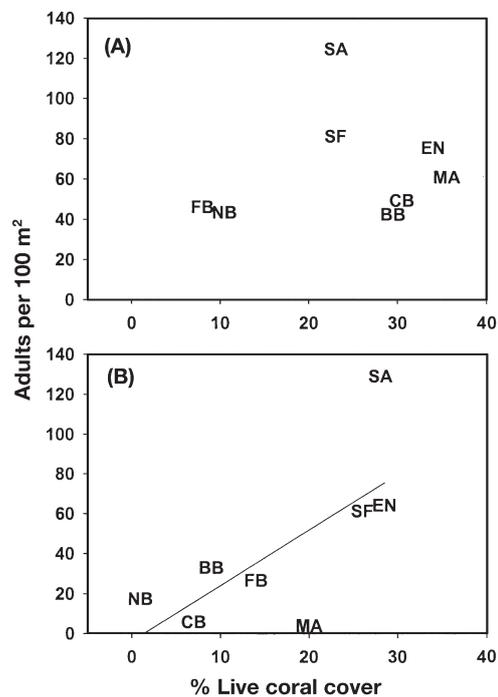


Fig. 6. Relationship between mean live coral cover at each of 8 sites within One Tree Island lagoon, and mean density of adult damselfish (*Pomacentrus moluccensis*, *P. wardi* and *Chrysiptera rollandi*). (A) 1994:  $r^2 = 0.03$ , p > 0.05; (B) 1999:  $r^2 = 0.49$ , p < 0.05). Site codes as in Fig. 1

the hasty attribution of cause and effect in explaining changes in recruitment through time.

More detailed links between fish distribution and changes in habitat that resulted from the bleaching event were not possible due to lack of resolution of video records. High-resolution digital technology was unavailable for earlier habitat censuses, and taxonomic resolution of substrate type at this time was necessarily broad. The use of high-resolution video and direct observations of substrate will considerably enhance our ability to link changes in fish assemblages to concomitant changes in habitat through disturbances such as bleaching. Given that the incidence of bleaching is likely to rise over the next decades (Hoegh-Guldberg 1999), it is critical that links between bleaching and aspects of the coral reef community be explored.

Bleaching effects on corals are now well documented (see reviews by Brown 1997, Hoegh-Guldberg 1999). This study is one of the few to consider indirect effects of bleaching on reef fish, which are important components of coral reef communities. Indirect effects of bleaching of corals on fish assemblages could therefore have far-reaching effects on coral reef ecosystems, since many fish species facilitate or retard coral settlement or growth/health (e.g. Hixon 1997). Reefs such as at One Tree Island, with limited tidal flushing, may be especially susceptible to persistent bleaching, and so at these locations, bleaching effects on fish communities may be more significant.

*Acknowledgements.* We acknowledge funding from the Australian Research Council to Drs. P. Doherty, M. Kingsford and D. B., and GBRMPA funding to D. B. Thanks to Ginger Garrison and 3 anonymous referees for constructive comments on an earlier draft of the manuscript, and to Pam and Konrad Beinssen at One Tree Island Research Station for temperature data.

#### LITERATURE CITED

- Booth DJ (1995) Survivorship and growth within social groups of the domino damselfish *Dascyllus albisella*. *Ecology* 76: 91–106
- Booth DJ, Beretta GA (1994) Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* 13:81–89
- Booth DJ, Wellington G (1998) Settlement preferences in coral-reef fishes: Effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Aust J Ecol* 23:274–279
- Booth DJ, Kingsford MJ, Doherty PJ, Beretta GA (2000) Recruitment of damselfishes at One Tree Island lagoon: persistent spatial patterns over two decades. *Mar Ecol Prog Ser* 202:219–230
- Bouchon-Navaro Y (1986) Partitioning of food and space resources by chaetodontid fishes on coral reefs. *J Exp Mar Biol Ecol* 103:21–40
- Brown BE (1997) Adaptations of reef corals to physical environmental stress. *Adv Mar Biol* 31:221–299
- Caley MJ, St John J (1996) Refuge availability structures assemblages of tropical reef fishes. *J Anim Ecol* 65: 414–428
- Doherty PJ (1982) Some effects of density on the juveniles of two species of tropical, territorial damselfishes. *J Exp Mar Biol Ecol* 65:249–261
- English S, Wilkinson C, Baker V (eds) (1994) Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville
- Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish population. *Ecology* 71: 1666–1681
- Gleason MG (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* 12:193–201
- Glynn PW (1984) Widespread coral mortality and the 1982/83 El Niño warming event. *Envir Conserv* 11:133–146
- Glynn PW, Colgan MW (1988) Defense of corals and enhancement of coral diversity by territorial damselfishes. *Proc 6th Int Coral Reef Symp* 2:157–163
- Hixon MA (1997) Effects of reef fishes on corals and algae. In: Birkeland C (ed) Life and death of coral reefs. Chapman & Hall, New York, p 230–248
- Hixon MA, Beets JP (1993) Predation, prey refuges and the structure of coral-reef fish assemblages. *Ecol Monogr* 63: 77–101
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O, Salvat B (1995) Periodic mass-bleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Mar Ecol Prog Ser* 121:181–190
- Jones GP (1987) Some interactions between residents and recruits in two coral reef fishes. *J Exp Mar Biol Ecol* 114: 169–182
- Lindahl U, Ohman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. *Mar Poll Bull* 42:127–131
- Ludington CA (1979) Tidal modifications and associated circulation in a platform reef lagoon. *Aust J Mar Freshw Res* 30:425–430
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155–163
- Mumby PJ, Chisolm JRM, Edwards AJ, Clark CD, Roark EB, Andrefouet S, Jaubert J (2001) Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia. *Mar Biol* 139:183–189
- Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution of coral-dwelling gobies. *Mar Ecol Prog Ser* 152:227–239
- Muscatine L (1991) The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinski Z (ed) *Ecosystems of the World 25: Coral Reefs*. Elsevier, Amsterdam, p 75–87
- Ohman MC, Rajasuriya A, Svensson S (1998) The use of butterflyfishes (Chaetodontidae) as bio-indicators of habitat structure and human disturbance. *Ambio* 27:708–716
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Salvat B (1993) The 1991 Bleaching event in the Society Islands, French Polynesia. *Proc 7th Int Coral Reef Symp* 1:73

- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. WH Freeman, New York
- Sweatman HPA (1983) Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. *Mar Biol* 75:225–230
- Tolimieri N (1995) Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. *Oecologia* 102:52–63
- Victor BC, Wellington GM, Robertson DR, Ruttenberg BI (in press) The effect of the El Niño-Southern Oscillation event on the distribution of reef-associated labrid fishes in the eastern Pacific Ocean. *Bull Mar Sci* 69:279–288
- Wellington GM, Victor BC (1985) El Niño mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68:15–19
- Wilkinson C, Linden O, Cesar H, Hodgson G, Ruebens J, Strong AE (1999) Ecological and socioeconomic impacts of the 1998 coral mortality in the Indian Ocean: an ENSO impact and a warning of future change? *Ambio* 28:188–196

*Editorial responsibility: Charles Birkeland (Contributing Editor), Honolulu, Hawaii, USA*

*Submitted: February 10, 2002; Accepted: July 15, 2002  
Proofs received from author(s): November 18, 2002*