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Patterns and consequences of coral bleaching in Micronesia (Majuro and Guam) in 1992-1994

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Abstract—Loss of zooxanthellar symbionts from coral hosts, or "bleaching" has been increasingly noted since the 1980's, and often attributed to elevated sea water temperatures. Here we document the first bleaching events recorded in Micronesia, one on Majuro Atoll in 1992 and another on Guam in 1994. The first caused up to 99% mortality of *Acropora*, altering the community structure of affected lagoonal fringing reefs from *Acropora*-and-*Porites*-dominated to *Porites*-dominated. Mortality of other scleractinians was low, but the common soft coral *Lobophytum pauciflorum* underwent large-scale dieback. Mortality in Majuro lagoon increased from west to east, peaking in the metropolitan area at the east end. The bleaching event on Guam was island-wide, in the warm season but not associated with unusually high temperatures, and associated with little mortality. Fifty-one of 75 surveyed taxa of corals bleached on Guam and 15 of 25 taxa on Majuro. Both scleractinians and alcyonaceans exhibited consistent species-specific sensitivity to bleaching among these and other locations in the tropical Pacific basin. The cause of these bleaching events is unclear, but the pattern on Majuro is suggestive of anthropogenic influence. Lack of bleaching at rural Mili Atoll 25 km from Majuro and lack of above average temperatures on Guam and Majuro suggest that regional ocean warming was not involved in either event.

Introduction

Coral bleaching events have become common since the 1980's in most major oceanic regions where coral reefs are present (Williams & Bunkley-Williams

1990, Glynn 1993, Brown 1997). Bleaching is manifested as a whitening of coral tissues, resulting from a loss of zooxanthellae. Bleaching is generally stress-related and can be elicited by a variety of stressors (Glynn 1993). Increases in sea surface temperature >1ºC above the seasonal maximum are a common cause of bleaching, and the increasing prevalance of bleaching in recent years has been viewed as a harbinger of global warming (Brown 1997).

To date no bleaching events have been described from Micronesia however, between Palau and the Marshall Islands. There is relatively little species-level information from the Indo-West Pacific on the susceptibility of different corals to bleaching. Our study describes bleaching events on Majuro Atoll (Marshall Islands) in 1992 and Guam (Mariana Islands) in 1994. We list species of scleractinian and alcyonacean corals affected, explore potential causes, and describe the consequences of the bleaching events.

Materials and Methods

Majuro: Coral bleaching was first noticed at Majuro on Telap Islet (Site 6B; Fig. 1), on the lagoonal fringing reef and its slope, on 13 December 1992 during a brief stop by GP. The abundance and condition of all scleractinians and alcyonaceans encountered was recorded. Abundance was recorded on a qualitative 5-point scale from rare (unique colony), through uncommon, average, common, to abundant (dominant species). Bleaching was also recorded on a 5-point scale: no bleaching; minor bleaching = ca. <30% of colonies affected; moderate bleaching = ca. 30-60% of coralla affected; strong bleaching = ca. >60% of colonies affected; and dead = recently dead colonies, presumed due to bleaching. Additional information on bleaching was obtained from Phil Kelly, who dove and videotaped lagoonal reefs on Majuro (Site 7B; Fig. 1) and neighboring Mili Atoll between 5-12 December, 1992. Majuro was revisited on 27 May 1993, and 5 lagoonal (‘B’) and 3 outer reef (‘A’) sites along the southern length of the atoll were checked for evidence of bleaching and recent mortality (Fig. 1).

Guam: We recorded bleaching incidence at seven sites between 3-14 October and three more until 29 December, 1994. Seven sites were on the leeward (western) fore reef, one on the windward fore reef, and two in Apra Harbor, a large, artificially semi-enclosed lagoon with patch reefs (Fig. 2). At each site we noted which species bleached among common milleporans, scleractinians, alcyonaceans and anemones. The incidence of bleaching was quantified for some common species by checking every colony encountered.

Voucher specimens of soft corals were deposited in the Zoological Museum, Tel Aviv University (Israel, see Benayahu, 1998). Voucher specimens of *Acropora* species were deposited at the Museum of Tropical Queensland (Townsville, Australia). Other scleractinians are well known, their identification follows the local field guide (Randall & Myers 1983), and were not vouchered.

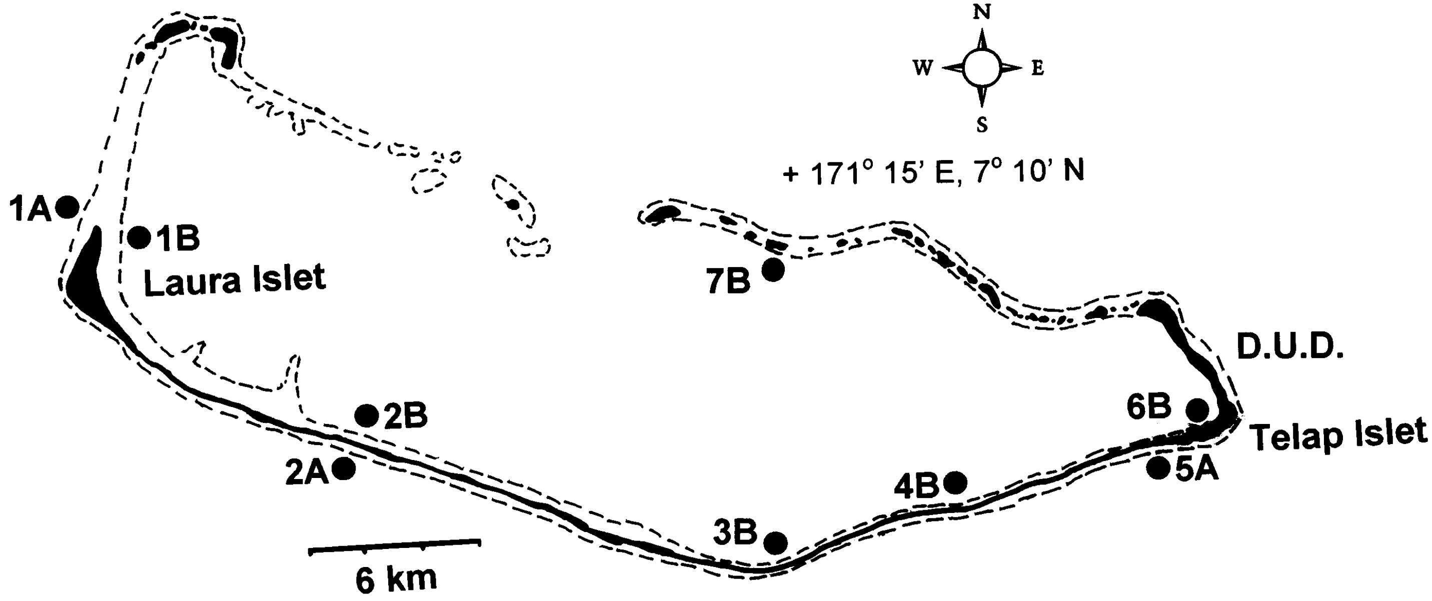

Figure 1: Map of Majuro Atoll, with sites of bleaching survey marked. Dashed line: fringing reef margin; solid areas: islets. D.U.D. = local name for Darrit-Uliga-Dalap islets, the metropolitan center of the Marshall Islands.

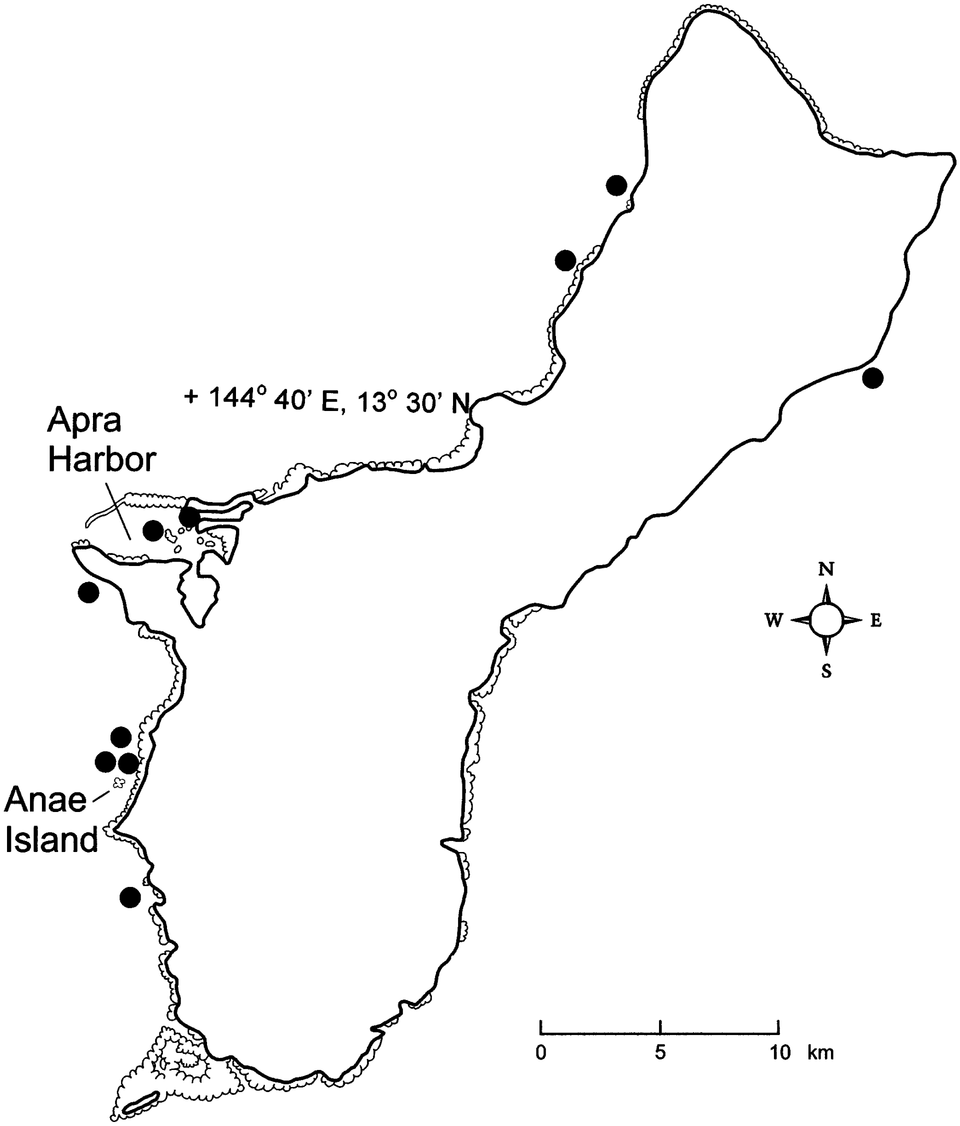

Figure 2: Map of Guam, with sites of bleaching survey marked.

Results

MAJURO

Extensive bleaching was noted on a lagoonward fringing reef on Telap Islet (Site 6B, Fig. 1) on 13 December 1992. The landward end of this reef had a slight, ponded moat with localized stands of *Montipora digitata*, and continued seaward as a relatively flat, shallow rubble platform. Coral cover increased from none to moderate on this platform, with alternating beds of *Montipora digitata* and *Acropora-Porites rus* lagoonward. The reef slope past the platform had coral communities dominated by *Porites rus,* with *Porites cylindrica,* massive *Porites* spp., and *Acropora* spp. abundant, and gave away to a sandy slope at a depth of ~5m.

Acropora spp. were highly bleached or recently dead, with only 3-4 unbleached colonies among several hundred seen. The *Acropora* community included at least *Acropora digitifera, A. cerealis, A. latistella, A. valida,* and *A. nasuta;* all species were strongly affected. Colonies ranged from partly to completely bleached, to dead. Dead colonies ranged from those killed perhaps a couple of weeks earlier, covered by algal turf but with skeletal structure intact, to apparently recently killed colonies with little algal growth. Several fully-bleached *Acropora* retained pale blue branch tips. Part of the variation in bleaching response was depth/zonation related: while the *Acropora* spp. on the reef platform were all dead, many colonies on the lagoon slope were alive. Bleaching dominated at all depths checked however, with bleached and dead *Acropora* were also the rule at the foot of the fringing reef slope at 5m.

Lobophytum pauciflorum was the only common soft coral, and was second to *Acropora* in severity of bleaching response. All surviving colonies were pale (pale yellowish to light brown), had numerous lesions, sagging instead of erect lobes, and retracted polyps. Most colonies had large areas missing or disintegrating. *Lobophytum pauciflorum* appears to lay down a solid base of spiculite, as has been described for the related genus *Sinularia* (Konishi 1981, Schumacher 1997). These solid bases form a characteristic, relatively smooth, regular, convex “attachment scar”, exposed under disintegrating colonies. Such attachment scars were common, ranging from fresh to heavily fouled, and attest to considerable and protracted mortality of *Lobophytum* in the area (see below).

Bleaching in other corals varied, with 60% (N=25) of the taxa showing some bleaching, but no other coral species had mortality (Table 1). Common or abundant corals other than *Acropora* were little affected. Several *Porites* species were common to dominant; all were little or un-affected. *Montipora digitata* and *Pocillopora damicornis,* the two other common species were also little affected, even though the former was the only coral in the moat, a ponded habitat where water overheated during the day. Among corals of average abundance, two species, *Pavona cactus* and *Fungia fungites,* were affected moderately, and one, *Lobophyllia hemprichii,* strongly (Table 1). The only other soft coral seen, a single *Sarcophyton,* appeared unaffected.

Similar bleaching occurred in the mid-northern Majuro lagoon (Site 7B on Fig. 1), but not in the lagoon of neighboring Mili Atoll. Lagoonal fringing reefs at 1-3 m depths at Site 7B had a similar reef assemblage to that of Site 6B (above): dominated by *Porites (P. cylindrica* and *P. rus* especially) and *Acropora* (a multispecies assemblage of mostly corymbose forms). While all *Acropora* colonies were bleached or dead, no bleaching was evident among *Porites* in the video footage. Mortality is estimated to have been between 25-50% among *Acropora.*

Table 1. Bleaching on lagoonal fringing reef of Telap Islet, Majuro, 13 December 1992.

Species	Abundance	Status
Scleractinia		
Pocilloporidae		
Pocillopora damicornis (Linné)	common	minor bleaching
Acroporidae		
Acropora spp.*	common	strong bleaching & dead
Montipora digitata (Dana)	common	minor bleaching
Astreopora sp.	rare	no bleaching
Siderastreidae		
Psammocora contigua (Esper)	uncommon	no bleaching
Agariciidae		
Pavona varians Verrill	uncommon	minor bleaching
Pavona divaricata (Lamarck)	average	minor bleaching
Pavona decussata (Dana)	rare	no bleaching
Pavona venosa (Ehrenberg)	uncommon	minor bleaching
Pavona cactus (Forsskål)	average	moderate bleaching
Fungiidae		
Ctenactis sp(p).	uncommon	no bleaching
Fungia fungites (Linné)	average	moderate bleaching
Poritidae		
Porites rus (Forsskål)	abundant	no bleaching
Porites massive sp(p).	common	no bleaching
Porites cylindrica Dana	common	minor bleaching
Mussidae		
Symphyllia ?recta (Dana)	rare	no bleaching
Lobophyllia hemprichii (Ehrenberg)	average	strong bleaching
Faviidae		
Favia sp.	rare	no bleaching
Octocorallia		
Helioporidae		
Heliopora coerulea (Pallas)	rare	no bleaching
Alcyoniidae		
Lobophytum pauciflorum (Ehrenberg)	common	dead to strong bleaching
Sarcophyton sp.	rare	no bleaching

See Methods for description of abundance and status categories.

* *Acropora* species were not identified in the field; the following species were kindly identified by Carden Wallace (Museum of Tropical Queensland) from samples taken: *Acropora digitifera* (Dana), *Acropora cerealis* (Dana), *Acropora latistella* (Brook), *Acropora valida* (Dana), *Acropora nasuta* (Dana).

A few *Lobophytum* colonies visible on the videotape looked pale and yellowish, and appear to have been bleaching. In contrast Mili lagoon had numerous normal *Acropora* colonies, both small corymbose and large tabular forms, with only an occasional bleaching colony.

When Site 6B was resurveyed on 27 May, 1993, almost all the *Acropora* were dead, but other scleractinians showed little/no mortality. The only living *Acropora* encountered were a few surviving colonies of *Acropora latistella* at 3-5m depth.

Over 50% of the coral cover was lost locally in areas where *Acropora* dominated parts of the reef tract. The extent of colony mortality of *Lobophytum* was more difficult to judge, but is estimated, on the basis of barren attachment scars, at ca. 50% of colonies. Almost all surviving colonies had partial mortality, with colony centers frequently dead, but colony edges surviving as fragments around a central, smooth, dome-shaped attachment scar. Thus the total loss may have been ca. 80% of *Lobophytum* cover. Surviving colonies were still yellowish and had their polyps withdrawn, but appeared more pigmented and intact than in December.

Other than the paleness of *Lobophytum*, the only bleaching encountered in May 1993 was on the outer reef flat of Laura (Site 1A, Fig. 1). This reef flat had localized bleaching, limited to, but widespread among, species of *Acropora*. *Acropora nasuta*, *A. aspera* and *A.* sp. showed bleaching (ca. 20-30% of colonies affected), while *A. ?humilis* and several locally rare *Acropora* species showed no bleaching. Other corals showed no bleaching, and included: common/abundant: *Pocillopora damicornis*, *Montipora digitata*, *Porites cylindrica*, *Porites* spp., *Pavona varians*, *Pavona divaricata;* uncommon & rare: *Montipora* spp., *Astreopora myriophthalma*, *Porites lichen*, *Porites rus*, *Gardineroseris planulata*, *Fungia fungites*, *Favia mathaii*, *Favia* sp., *Platygyra daedalea*, *Cyphastrea serailia*, *Favia ?favus*, *Favites ?complanata*, *Goniastrea pectinata*, *Leptastrea purpurea*, and *Heliopora coerulea*. The fore reef off the reef flat had ca. 75% coral cover, dominated (ca. 2/3 of cover) by *Acropora (Isopora)* sp., with other *Acropora* species also common, and showed no bleaching.

While recent coral mortality was not evident among any of the western sites (1A, 1B, 2A, and 2B), recently killed corals were common at all central and eastern locations (3B, 4B, 5A, and 6B; Fig. 1). In the lagoon, sites 1B and 2B had abundant live *Acropora*, peaking at 80% *Acropora* cover on the fringing reef crest at Site 2B. In contrast, Site 3B had an abundance of dead *Acropora*, peaking on the fringing reef crest, where all the *Acropora* were recently dead, but mortality decreased rapidly with depth. At Site 4B, 62% (N=87) of *Acropora* colonies at 0-2 m were dead; low levels of mortality were evident at 5 m as well. At both sites, dead *Acropora* were in comparable condition (skeleton intact, calices discernible, endolithic algal penetration shallow) to those known to have died from bleaching at Site 6B. Evidence for *Lobophytum* mortality was noted at Sites 2B and 3B in addition to 6B. The only fore reef site (5A) surveyed along the eastern part of the atoll, showed recent mortality of *Pocillopora* spp. (*P. eydouxi* and *P. verrucosa*) and *Acropora cytherea*. Most of the *Pocillopora* colonies were dead, as were 67% (N=18) of the large *Acropora cytherea* tables that once dominated the slope at 6-8m. Dead colonies were intact, and appeared fresh; live portions had not grown appreciably compared with neighboring dead branches, indicating that the mortality was recent. It is not clear whether the fore reef mortality was bleaching related, however it was roughly contemporaneous with the lagoonal bleaching event. No recent mortality was evident at the westernmost two outer reef slope sites (1A, 2A).

Table 2. Bleaching on Guam, Oct.-Dec. 1994.

Species	Incidence	Comments
Milleporina		
Milleporidae		
Millepora platyphylla Hemprich & Ehrenberg	3/3	strong bleaching
Scleractinia		
Astrocoeniidae		
Stylocoeniella armata (Ehrenberg)	1/2	minor bleaching
Pocilloporidae		
Pocillopora damicornis (Linné)	3/4*	
Pocillopora eydouxi Milne Edwards & Haime	0/1	
Pocillopora meandrina/verrucosa complex	7/7	moderate bleaching
Seriatopora aculeata Quelch	2/2	strong bleaching
Stylophora mordax (Dana)	5/6	none to strong bleaching
Acroporidae		
Acropora cf. *palmerae* Wells	0/1	common, no bleaching
Acropora danai (Milne Edwards & Haime)	0/4	common, no bleaching
Acropora humilis (Dana)	0/2	common, no bleaching
Acropora surculosa (Dana)	0/3	common, no bleaching
Acropora tenuis (Dana)	2/2	2 colonies total, both bleaching
Acropora palifera (Lamarck)	3/3	moderate bleaching
Acropora monticulosa (Brüggemann)	1/1	moderate bleaching
Acropora valida (Dana)	4/4	minor-moderate bleaching
Acropora wardi Verrill	1/1	minor bleaching
Acropora verweyi Veron & Wallace	3/3	strong bleaching (80%; N=25 at 1 site)
Astreopora myriophthalma (Lamarck)	0/2	
Montipora foveolata (Dana)	2/2	strong bleaching (96%; N=25 at 1 site)
Montipora verrucosa (Lamarck)	1/1	minor bleaching
Montipora spp.	8/8	strong bleaching
Siderastreidae		
Coscinaraea columna (Dana)	1/1	
Psammocora superficialis Gardiner	0/1	
Psammocora profundacella Gardiner	0/1	
Agariciidae		
Gardineroseris planulata (Dana)	2/2	
Pachyseris speciosa (Dana)	1/1	strong bleaching
Pavona varians Verrill	1/2	
Pavona decussata (Dana)	0/1*	N=1*
Pavona frondifera (Lamarck)	1/1*	moderate bleaching at *: 28% (N=40)
Fungiidae		
Fungia scutaria Lamarck	0/1	
Poritidae		
Alveopora sp.	3/4	moderate-strong bleaching
Goniopora spp.	0/1	

Porites (Porites) massive spp.	3/4 *	minor bleaching overall, but 10% (N=20) at *
Porites (Porites) cylindrica Dana	1/1*	moderate bleaching at *: 20% (N=10)
Porites (Synaraea) rus (Forsskål)	1/3*	bleaching only at *: 14% (N=43)
Porites (Synaraea) sp. 1	3/3	strong bleaching
Oculinidae		
Galaxea fascicularis (Linné)	1/3	
Mussidae		
Acanthastrea echinata (Dana)	1/3	moderate bleaching
Lobophyllia hemprichii (Ehrenberg)	1/2*	minor bleaching, no bleaching at *
Lobophyllia corymbosa (Forsskål)	0/1*	N=1*
Merulinidae		
Hydnophora microconos (Lamarck)	1/1	
Merulina ampliata (Ellis & Solander)	0/1	
Faviidae		
Cyphastrea serailia (Forsskål)	0/2	
Diploastrea heliopora (Lamarck)	1/2	
Echinopora lamellosa (Esper)	0/1	
Favia mathaii Vaughan / *pallida* (Dana)	2/4	minor-moderate bleaching
Favia stelligera (Dana)	3/3	minor-strong bleaching
Favites abdita (Ellis & Solander)	1/1	minor bleaching
Favites flexuosa (Dana)	1/1	
Favites russelli (Wells)	3/3	
Goniastrea edwardsi Chevalier	3/3	strong bleaching, some mortality
Goniastrea pectinata (Ehrenberg)	2/3	
Goniastrea retiformis (Lamarck)	1/2	minor bleaching
Leptastrea ?transversa Klunzinger	0/2	
Leptastrea purpurea (Dana)	0/1*	N=3*
Leptoria phrygia (Ellis & Solander)	2/4	minor-moderate bleaching
Montastraea curta (Dana)	2/2	strong bleaching (92%; N=25 at 1 site)
Oulophyllia crispa (Lamarck)	0/2	
Platygyra daedalea (Ellis & Solander)	1/2	
Platygyra pini Chevalier	2/3	
Coralliomorpharia		
?Rhodactis sp.	1/1	
Actiniaria		
Entacmaea quadricolor (Rüppel & Leuckart)	1/1	
Octocorallia		
Helioporidae		
Heliopora coerulea (Pallas)	0/1	
Alcyoniidae		
Asterospicularia randalli Gawel	0/2	common, not bleaching
Lobophytum pauciflorum (Ehrenberg)	1/1	strong bleaching, some mortality
Lobophytum batarum Moser	1/1	
Sarcophyton glaucum (Quoy & Gaimard)	0/2	common, not bleaching

Table 2, cont.

Sinularia discrepans Tixier-Durivault	1/1	strong bleaching
Sinularia gaweli Verseveldt	1/1	
Sinularia gyrosa (Klunzinger)	1/1	
Sinularia maxima Verseveldt	1/1	strong bleaching, some mortality
Sinularia peculiaris Tixier-Durivault	1/1	strong bleaching
Sinularia polydactyla (Ehrenberg)	0/2	common, not bleaching
Sinularia paulae Benayahu	0/1	
Sinularia sp. unidentified	1/1	strong bleaching

Incidence: number of sites where bleaching was observed over number of sites where species was observed.

Comments: notes on incidence of bleaching for species studied in more detail.

Identifications above follow Randall & Myers (1983) except for the following corrections: *Acropora* cf. *palmerae* for their *A. monticulosa, A. danai* for their *A. irregularis, A. monticulosa* for their *A. smithi, A. valida* for their *A. variabilis, A. verweyi* for their *A. squarrosa.* Alcyonacean taxonomy follows Benayahu (1998).

*: data includes one site from patch reef in Apra Harbor at mouth of Piti Channel (4 Nov. 1994); this site receives heated effluents from a nearby powerplant, thus bleaching here is likely above background levels.

N = number of colonies studied.

GUAM

During an island-wide bleaching event on Guam in 1994 fall, considerable variability was evident among species in bleaching incidence. Bleaching was recorded in 68% (N=75) of taxa encountered (Table 2). The most heavily bleached species among common hard corals were *Millepora platyphylla*, most species of *Montipora*, *Acropora verweyi*, *Seriatopora aculeata*, *Pachyseris speciosa*, *Porites (Synaraea)* sp. 1 *(sensu* Randall & Myers 1983), *Goniastrea edwardsi,* and *Montastraea curta.*

Species of certain genera or families appeared more prone to bleaching than others. Thus pocilloporids generally bleached extensively: *Pocillopora* and *Stylophora* species showed moderate bleaching at most sites, and *Seriatopora aculeata* bleached heavily. Acroporids also tended to bleach, with most *Montipora* (all encrusting to submassive) species moderately to heavily bleached, and about half of the *Acropora* species moderately to heavily bleached. Among *Acropora, A.* cf. *palmerae, A. danai, A. humilis, A. surculosa* did not bleach at any location; while *A. wardi, A. tenuis, A. palifera, A. monticulosa, A. valida,* and *A. verweyi* bleached at every surveyed site. In contrast, most poritids bleached little, except for the morphologically unusual *Porites (Synaraea)* sp. 1, and the few colonies of *Alveopora* encountered. Faviids showed a range of response, with *Goniastrea edwardsi* and *Montastrea curta* being most severely affected (Table 2).

Among soft corals, *Asterospicularia randalli,* and species of *Sarcophyton* were not observed to bleach. Two of the common species of *Lobophytum* bleached, with *L. pauciflorum* bleaching so heavily that several colonies were dying. Among *Sinularia* species there was considerable variation in bleaching response (Table 2).

Discussion

BLEACHING RESPONSE

Although there are considerable data on bleaching susceptibility of corals and other organisms in the Western Atlantic and East Pacific (e.g., Williams & Bunkley-Williams 1988, 1990, Glynn 1990), there is as yet little species-level information on bleaching susceptibility for Indo-West Pacific taxa (but see Fisk & Done 1985, Hoeksema 1991). This is in part attributable to the taxonomic challenge posed by this vast, diverse and taxonomically inadequately explored area. It is clear that while most if not all photosymbiotic organisms can bleach, there is considerable variation among taxa in propensity to bleaching. Susceptibility to bleaching is in part genetically/phylogenetically controlled, and some clones (e.g., Jokiel & Coles 1990, Edmunds 1994), species (e.g., Williams & Bunkley-Williams 1988, 1990, Hoeksema 1991) and even higher taxa (e.g., Gleason 1993) are more prone to bleaching than others. Additional variability in bleaching response arises from the differential susceptibility of different zooxanthellar taxa to bleaching (Rowan et al. 1997).

The taxonomic specificity of bleaching response was similar on Guam and Majuro. *Acropora*, *Pocillopora* (other than *P. damicornis)* and *Lobophytum pauciflorum* were heavily affected on both islands. Among soft corals, *Lobophytum pauciflorum* was the most impacted on both islands. Putative bleaching-associated mortality was encountered only among species of *Acropora*, *Pocillopora* and in *Lobophytum pauciflorum* on Majuro, and in *Lobophytum pauciflorum* on Guam. The high sensitivity of *Acropora* to bleaching and to subsequent mortality is well documented, as is the lesser, but still considerable sensitivity of *Pocillopora* (Fisk & Done 1985, Williams & Bunckley-Williams 1990, Salvat 1992, Glynn et al. 1994, Drollet et al. 1995).

There was little overlap among the *Acropora* species encountered on the two islands, but many species in this large genus appear highly susceptible to bleaching and bleaching-associated mortality. In the severe bleaching episode documented for Majuro, all *Acropora* species were heavily affected. In contrast in the less severe bleaching event on Guam, considerable inter-specific variation in bleaching response was evident. The same hierarchy in bleaching response among *Acropora* species observed in 1994 was evident in a more severe bleaching event in 1996 on Guam (GP, unpublished). Similar variation in susceptibility to bleaching was documented among species of *Acropora* by Fisk & Done (1985), who found *A. hyacinthus* and *A. digitifera* to have been little affected by a bleaching event that decimated other species of *Acropora*. *Acropora digitifera* was not recorded in 1994, but was resistant to bleaching in the 1996 event (GP, unpublished). Susceptibility to bleaching appears to be species specific and geographically widespread. The uniformly high susceptibility of *Acropora* to bleaching at some sites and times (e.g. Majuro Site 6B; Moorea: Hoegh-Guldberg & Salvat 1995) may be the result of the severity of those bleaching episodes, or the low diversity of *Acropora* in the area and consequent absence of less susceptible species. Similar variation in bleaching response is evident among other corals. Most *Montipora* species on Guam bleached heavily, however *M. digitata,* the only common *Montipora* encountered on Majuro showed little bleaching, despite the much more severe nature of the bleaching episode there.

Millepora have generally been found to be particularly susceptible to bleaching, and bleaching-associated mortality (e.g. Glynn 1990, 1993, Williams & Bunkley-Williams 1990, Glynn & de Weerdt 1991) and *Millepora platyphylla* was one of the most severely affected corals on Guam. However in the Society Islands *Millepora* did not bleach heavily (Gleason 1993, Drollet et al. 1995). *Montastrea curta* bleached heavily in the Society Islands (Gleason 1993, Drollet et al. 1995), as in Guam. *Seriatopora hystrix* was especially susceptible to bleaching in Taiwan (Williams & Bunkley-Williams 1990), and also suffered bleaching-associated mortality on the Great Barrier Reef (Done & Fisk 1985). On Guam *Seriatopora aculeata* was one of the most susceptible species. In contrast most *Porites* species (except the unusual *Porites (Synaraea)* sp. 1) appear to be relatively resistant to bleaching at other locations, as on Majuro and Guam (e.g. Gleason 1993, Hoegh-Guldberg & Salvat 1995). These observations support the observation already made in the West Atlantic and East Pacific faunas (Williams & Bunkley-Williams 1988, 1990, Glynn 1990), that there is geographically widespread, taxonomic specificity in bleaching response by anthozoan hosts.

Bleaching response appears to be partly related to the environmental tolerance of species. Corals from habitats exposed to large fluctuations in temperature, such as shallow reef flats, were generally least affected by bleaching. Reef flats have extreme fluctuations in temperature and salinity and are exposed to intense radiation (PAR and UV) because of shallow depths and restricted circulation. Corals that live on reef flats must be physiologically tolerant of such conditions, as must their zooxanthellae. *Montipora digitata, Pavona decussata, Pavona divaricata, Psammocora contigua, Pocillopora damicornis,* several species of *Porites, Leptastrea purpurea,* and *Leptastrea transversa,* are abundant on, and the first three largely restricted to, reef flat biotopes, and these species indeed showed limited or no bleaching. Most notable is the limited response of *Montipora digitata,* a species from a genus that otherwise has high susceptibility to bleaching. In contrast many *Acropora* species require environments with good water exchange, and *Acropora* were heavily impacted by bleaching. Similarly, Warner et al. (1996 cited in Brown 1997) showed that zooxanthellae from the back reef coral *Siderastrea radians* were less temperature sensitive than those of two species of fore reef coral.

CAUSE OF BLEACHING

The 1994 bleaching event was the first regional bleaching event noted on Guam since the University of Guam Marine Lab was established in 1970 (see

Williams & Bunkley-Williams 1990 for notes on absence of 1987 bleaching event on Guam). A second event that took place on Guam in the 1996 summer (GP pers. obs.) suggests that local bleaching events may be increasing in frequency. Majuro (and other localities in Micronesia) have had little surveillance, so little can be said about the frequency of bleaching events there.

The cause of the 1994 bleaching event on Guam is not clear. Many, but not all recent regional bleaching events can be attributed to protracted exceptionally warm (+1ºC anomaly) water temperatures during the warm season, and/or to intense downwelling of irradiation (UV and/or PAR) (Gleason & Wellington 1993, Glynn 1993, Goreau & Hayes 1994, Brown 1997). Bleaching affected corals around the island, and was evident to a depth of at least 25m. Monthly mean sea surface temperature (SST) peaked at 29.9ºC during 1994 (September), while it ranged between 29.1 - 29.9ºC (29.6ºC mean) between 1989-1996 (NOAA satellite-derived, monthly SST data for vicinity of Guam). Mean monthly SST for August and October 1994 were both 29.7ºC. Although we have no data for irradiance, rainfall was typical for August-November (118 cm vs. 131 cm for 39 year mean; National Weather Center data), suggesting normal cloud cover.

The cause of the 1992 bleaching on Majuro is also unclear. Sea surface temperature around Majuro peaked at 29.9ºC in September-November 1992, slightly higher than the 1989–1996 mean warm season monthly peak of 29.7ºC (range: 29.1–31.1ºC) (NOAA satellite-derived, monthly SST data for vicinity of Majuro). Bleaching was widespread on Majuro, but was limited/absent on Mili Atoll 25 km to the S/SE. This indicates that region-wide ocean warming is unlikely to be the cause of the event. Mortality on Majuro decreased with depth over the limited depth range (ca. 5m) on which most of our study focused. In December 1992, *Acropora* spp. mortality was 100% in the shallowest parts of Site 6B, but some bleached colonies survived in deeper water. By May 1993, mortality was 100% among *Acropora* spp. at <0.5 m depth, but many colonies survived at >1m depth at Site 3B. Such extreme depth stratification in mortality rates is suggestive of UV or PAR downwelling as a potential contributing factor to the mortality. UV is attenuated very rapidly even in clear oceanic waters (Dunne & Brown 1996).

Although bleaching appears to have been widespread in the Majuro lagoon during late 1992, subsequent bleaching-associated mortality exhibited a marked west-to-east gradient across the lagoon. Over 99% of the *Acropora* died on the east end of the lagoon, intermediate numbers died in the east-central and central part of the lagoon, and no mortality was evident on the west end, along the southern shore. The only recent mortality noted on the fore reef was also at the easternmost site surveyed along the southern atoll rim. It is difficult to propose a stressor that would affect corals both in the lagoon and on the outer reef slope and yet exhibit such a west to east gradient. Although the atoll is quite open, the east end is more enclosed than the west end (Fig. 1), and may experience less wave setup, as the predominant wind directions are from the E-NE (Holthus et al. 1992). The southeast fore reef slope would also be potentially calm if wind directions were mainly from the N and NE. Calm waters are especially conducive to

UV and PAR downwelling and to local water heating, and given appropriate environmental conditions, this could have been more severe along the eastern end of the atoll.

Although it is difficult to construe a natural parameter that corresponds to the observed gradient in mortality, the magnitude of human impact does correspond. Human population is concentrated on the eastern end of the atoll, where bleaching-associated coral mortality was greatest. D.U.D. (= local name for Darrit-Uliga-Dalap), the metropolitan center of the Marshall Islands, lies on three islets forming the eastern atoll rim, and has a population density of 7150 people km^{-2} (Holthus et al. 1992). The only area with almost complete *Acropora* mortality was in D.U.D., and mortality decreased with increasing distance from this area both in the lagoon and on the outer reef slope. A similar gradient in mortality of lagoonal corals (again affecting *Acropora* most severely) toward a metropolitan population center was documented in neighboring Tarawa Atoll, Kiribati (Paulay 1997). As hypothesized by Williams & Bunkley-Williams (1990), resilience of hosts to bleaching may decrease with anthropogenic stress, and diffuse anthropogenic influence may have increased the severity of the bleaching response in the eastern lagoon.

CONSEQUENCE OF BLEACHING

The bleaching event on Majuro altered reefs that previously were dominated in large areas by *Acropora* spp. to reefs where *Acropora* are effectively absent. Mortality on these lagoonal reefs appears to have been very selective, with only *Acropora* species and *Lobophytum pauciflorum* affected. Considerable mortality of *Acropora* have been documented at several other Indo-West Pacific reefs (e.g., Fisk & Done 1985, Gleason 1993).

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