

REPORT

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## El Niño related coral bleaching in Palau, Western Caroline Islands

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**Abstract** Mass coral bleaching is currently viewed as a major threat to the long-term health of coral reef communities. Here we quantify coral bleaching in Palau coincident with the 1997/1998 El Niño Southern Oscillation event and with local sea surface temperatures of 31 °C, which were 1.0–1.25 °C higher than long-term, satellite-derived climatological maximum monthly means for the region. We sampled nine sites, including protected lagoon and fringing reefs, vertical reef walls, and exposed barrier reefs. The percentage of living scleractinian coral tissue that was bleached was  $53.4 \pm 6.2$  (range: 32.3–79.3,  $n=8$  sites) at 3–5 m depth and  $68.9 \pm 6.2$  (45.7–91.7,  $n=6$  sites) at 10–12 m and did not differ significantly between depths. The overall mean percent cover of bleached scleractinians was  $18.9 \pm 1.5$  (mean  $\pm$  1 SE,  $n=9$  sites), while the cover of healthy corals was only  $15.6 \pm 2.0$ . Nearly half (48%) of 946 surveyed colonies belonging to 20 scleractinian taxa were totally bleached, while 15% were partially bleached. Overall, the results indicate that the 1998 coral bleaching episode in Palau was relatively severe and widespread across depths, sites, habitats, and coral taxa.

**Keywords** Coral bleaching · Disturbance · El Niño · Palau · Sea surface temperature

### Introduction

Coral reefs throughout the world are currently experiencing accelerated degradation (Wilkinson 1992, 1999; Sebens 1994). The changes generally comprise reduced coral cover, fish abundance, and overall species diversity (Wilkinson 1992; Hughes 1994; Edmunds and Bruno 1996; Jackson 1997). Although there are certainly many causal factors (e.g., overfishing, outbreaks of coral diseases and predators, sedimentation and nutrient inputs; Sebens 1994; Jackson 1997; Wilkinson 1999), coral bleaching is currently viewed as a major agent of change in coral reef communities (Brown 1997; Hoegh-Guldberg 1999). Bleaching refers to the loss of symbiotic dinoflagellates (zooxanthellae) from the host tissue of scleractinians and other cnidarians, a reduction in zooxanthellae pigmentation, or both (Hoegh-Guldberg 1999). Bleaching is considered to be a response to environmental stresses including elevated seawater temperature (Hoegh-Guldberg and Smith 1989; Jokiel and Coles 1990; Gates et al. 1992), high irradiance (Lesser et al. 1990; Gleason and Wellington 1993), calm weather (Jaap 1979), and decreased salinity (Goreau 1964). Effects on coral populations range from total recovery in 1 or 2 months to mortality rates of nearly 100% (Glynn 1984, 1990; Harriott 1985; Fitt et al. 1993). On a scale of months to years such high mortality rates may not affect many other reef inhabitants since the dead coral skeletons remain in place and should continue to provide spatial refuge. However, prolonged recovery and subsequent bioerosion can result in habitat loss with cascading effects on numerous fish and invertebrate species (Glynn 1993; Sebens 1994).

Although biologists have been aware of localized bleaching for over a century (Glynn 1993), mass bleaching episodes that result in large-scale coral mortality were first recorded in the early 1980s (Glynn 1983).

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Since then there have been several similar bleaching events on reefs around the world (e.g., Roberts 1987; Lang et al. 1992; Hoegh-Guldberg and Salvat 1995; Brown 1997), and there is strong evidence that the frequency and severity of bleaching have increased (Glynn 1991, 1993; Goreau 1992; Hoegh-Guldberg and Salvat 1995; Brown 1997; Winter et al. 1998; Hoegh-Guldberg 1999). A leading explanation for such mass bleaching events is the interactive effect of increased tropical sea surface temperatures with El Niño Southern Oscillation events (ENSO) (Hoegh-Guldberg 1999), which also may be increasing in intensity (Stone et al. 1999; Fedorov and Philander 2000). The most recent widespread bleaching event occurred in association with the 1997/1998 ENSO, which resulted in sea surface temperatures 1–4 °C above normal summer highs over a broad geographic range, and by some measures was the strongest ENSO on record (McPhaden 1999). Coincident mild to catastrophic bleaching was reported from many locations worldwide including the Caribbean, Indian Ocean, East Africa, Southeast and East Asia, and the Eastern and Western Pacific (Baird and Marshall 1998; Berkelmans and Oliver 1999; Hoegh-Guldberg 1999; Wilkinson 1999; Aronson et al. 2000).

The purpose of this study was to document widespread coral bleaching in the Republic of Palau, Western Caroline Islands, that was associated with the 1997/1998 ENSO. We assessed the 1998 bleaching event in Palau using several methods, including line transects at numerous sites, and qualitative in situ and aerial surveys over a larger area. We quantified the percentage of living coral cover that was bleached at one or two depths (3–5 and 10–12 m) at nine sites to determine the spatial extent of the bleaching across sites, depths, and habitats. A variety of habitat types were sampled, including highly protected lagoon and fringing reefs, vertical reef walls, exposed barrier reefs, as well as reefs with both high and low tidal current velocities. We also surveyed 964 colonies from five sites and 20 coral taxa to determine how general the bleaching was within the Scleractinia.

### Initial qualitative observations

The first indications of coral bleaching in Palau were seen in late June 1998, as small portions of healthy coral colonies became light in color. By mid-July it was evident that numerous species were starting to bleach, and through August the extent of bleaching increased markedly. In September 1998 aerial surveys undertaken to assess the geographic extent of bleaching indicated that bleaching was evident throughout the Palau archipelago. Bleaching of large colonies, particularly *Porites lutea* and *P. lobata*, could be seen from 2,500 m altitude. Qualitative observations suggested that bleaching intensity peaked during September and October, with large numbers of colonies of numerous species totally bleached or already dead. In situ surveys using SCUBA in lagoon areas indicated bleaching was common to

depths of at least 35–40 m. On outer reef drop offs, bleaching was observed to depths of 55–60 m, the lower limits of most colonial scleractinians in Palau (P. Colin, unpublished data). Many other coral reef organisms were bleached including a majority of colonies of common Alcyoniid soft corals such as *Sarcophyton* spp. and *Lobophyton* spp., and a large number of giant clams (*Tridacna gigas*).

## Methods

### Study location and sites

The Palau archipelago in the Western Pacific (07°N, 134°E) is a group of hundreds of small and large islands and lagoons surrounded by an extensive barrier reef. Palau has the highest shallow water marine species diversity found in Micronesia, with nearly 400 species of scleractinian corals reported (Veron 1986, 1995; Maragos and Cook 1995), plus at least 200 species of other anthozoans.

Six of the nine sites that were sampled quantitatively (Fig. 1, Table 1; Risong Lagoon, Ot Lagoon, No Name, Ngerikuul Pass, Wonder Pass, and Big Drop Off) were located in the southern rock island region of Palau which consists of hundreds of small limestone islands that are often surrounded by a narrow (5–30 m), shallow (1–5 m depth) shelf/fringing reef that ends at a near-vertical drop-off that usually extends to 20–30 m in depth. The rock island sites are all protected from open ocean swells but experience a range of local tidal flow conditions (J. Witman, unpublished data). The other three sites (West Pass, Siaes Reef, and Short Drop Off) were located on the 120-km-long, exposed outer barrier reef.

### Quantitative survey techniques

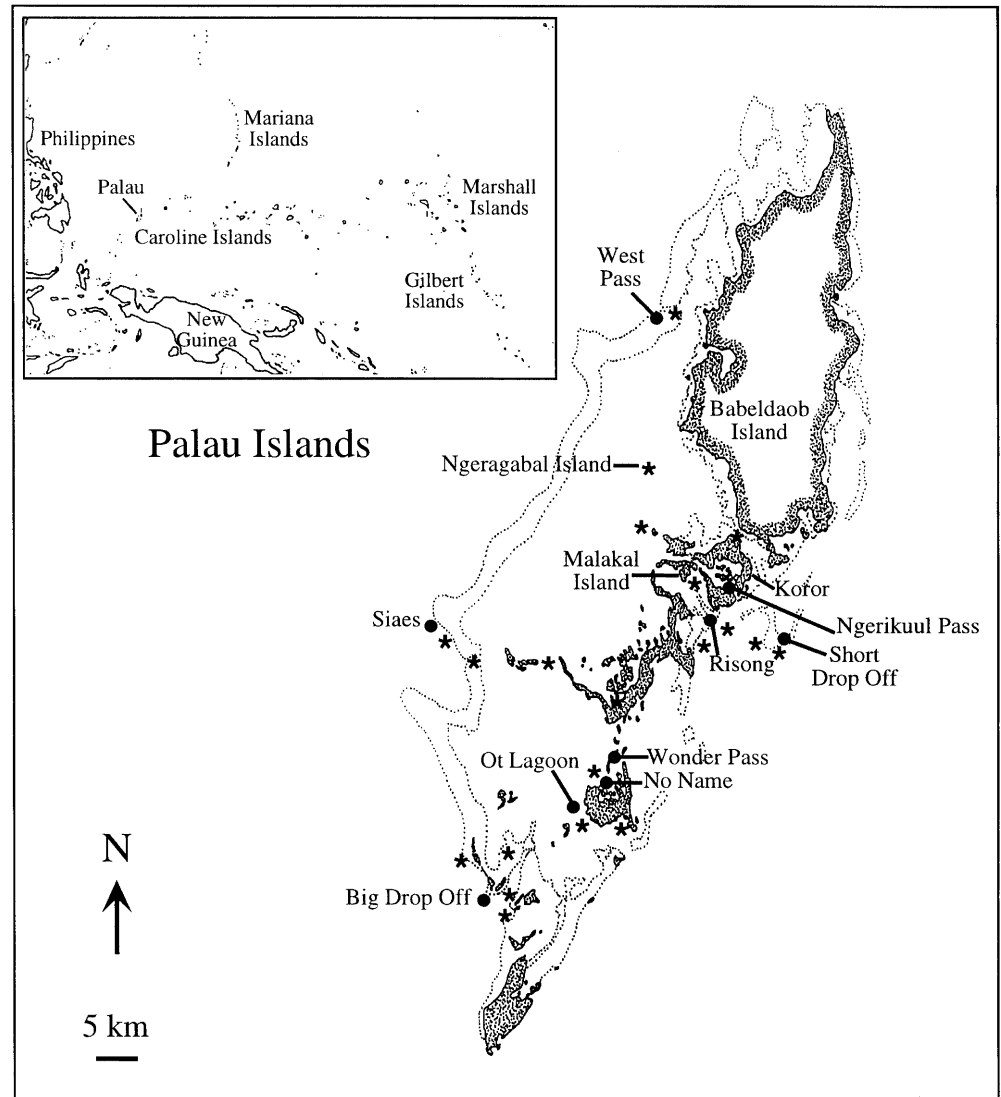
The spatial extent of scleractinian bleaching was quantified in November 1998 using the point-intercept technique (Lang et al. 1992) in two depths: at 3–5 m on the horizontal fringing reefs or reef crests at eight sites, and at 10–12 m on vertical rock and reef walls at six sites. Three non-overlapping, horizontal 20-m transect lines were haphazardly placed at each sampled depth/site combination. The sessile organisms and substrate directly beneath the point of each 10-cm increment were characterized as one of four categories: healthy coral (coral tissue with apparently “normal” coloration), bleached coral (coral tissue that was obviously pale or white in appearance), recently dead coral (corals that had apparently died in the last few weeks – this category includes both the “just dead” and “recently dead” categories of Lang et al. 1992), and other (which included bare substrate, dead coral skeletons, and space occupied by other organisms). Means and standard errors were calculated from the three replicate transects at each depth/site combination.

We examined variation in bleaching at the colony level within and among coral taxa in five 1×30-m video transects placed along the 10- to 12-m depth contour (one per site at five sites: West Pass, Ot lagoon, No Name, Siaes, and Ngerikuul Pass). Video transects were analyzed in the laboratory by scoring each coral colony (or individual coral polyp in the case of solitary corals) that fell within the transects as healthy, partially bleached, or totally bleached (>90% of the coral tissue was pale or white). These data were pooled across sites for analysis.

### Sea surface temperature measurements

Sea surface temperature (SST) was measured bi-weekly at an offshore reef area (Short Drop Off) using a hand-held mercury thermometer, beginning > 1 year prior to the bleaching event. We also

**Fig. 1** Map of study sites in Palau. *Circles* Quantitatively sampled sites; *stars* qualitatively surveyed sites



**Table 1** Coordinates and descriptions of sites used in quantitative bleaching surveys in Palau. Flow data (Witman, unpublished) were obtained using the dissolution block technique (Thompson and Glen 1994)

Site	Coordinates	Characteristics
Big Drop Off	07°06.32'N, 134°15.25'E	Rock island, med. flow
Ngerikuul Pass	07°19.26'N, 134°29.78'E	Rock island, high flow
No Name	07°14.80'N, 134°23.02'E	Rock island, low flow
Ot Lagoon	07°09.48'N, 134°20.53'E	Rock island, low flow
Risong	07°18.45'N, 134°28.85'E	Rock island, low flow
Wonder Pass	07°10.88'N, 134°21.65'E	Rock island, high flow
Short Drop Off	07°16.47'N, 134°31.50'E	Barrier reef, med. flow
Siaes	07°18.79'N, 134°13.43'E	Barrier reef, high flow
West Pass	07°32.52'N, 134°28.25'E	Barrier reef, high flow

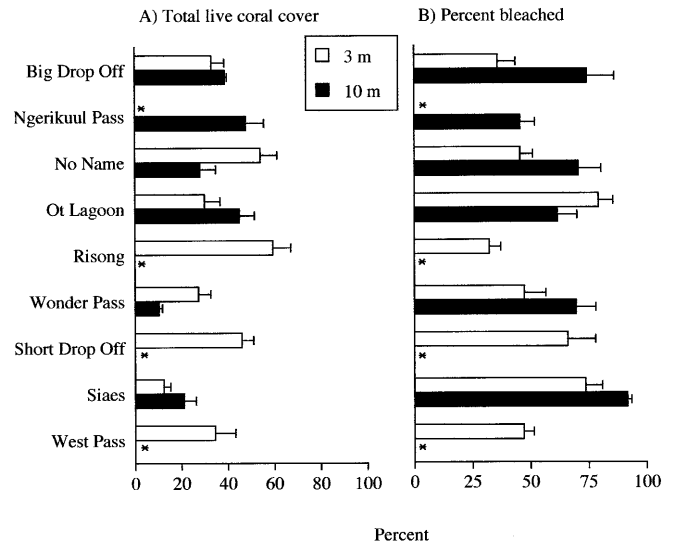
consulted the large-scale (50-km) SST Coral Bleaching “HotSpot” anomaly images, provided by the United States National Oceanic and Atmospheric Administration, National Environmental Satellite Data and Information Service (NOAA/NESDIS, <http://psbgi1.nesdis.noaa.gov:8080/PSB/EPS/SST/climohot.html>), as a forecasting tool for potential bleaching conditions. These images are based on multi-channel, night-time-only satellite AVHRR [advanced very high resolution radiometer on NOAA polar orbiting environmental satellites (POES)] SST data (Walton et al. 1998), and highlight SST anomalies that are greater than 1° above the

maximum monthly mean (MMM) climatological SST at each pixel. The MMM climatology was developed from satellite SST spanning the years 1984–1993, exclusive of 1991/1992 (due to aerosol contamination from the Mt. Pinatubo eruption). Degree-heating week (DHW) accumulations of these SST HotSpot anomalies ([http://psbgi1.nesdis.noaa.gov:8080/PSB/EPS/icg/dhw/dhw\\_new.html](http://psbgi1.nesdis.noaa.gov:8080/PSB/EPS/icg/dhw/dhw_new.html)) commence at the 1 °C threshold and provide an estimate of the residence time of anomalously warm water in the region and are included in this analysis. In addition, we incorporated 15-year SST time series data for several sites around Palau using NASA/JPL

Oceans Pathfinder Best SST (AVHRR) data at 9-km resolution (<http://podaac.jpl.nasa.gov/sst/>; see also Kearns et al. 2000; Kilpatrick et al. 2001). High (9-km) resolution HotSpot maps were also prepared from the Pathfinder Best SST data and a 9-km Pathfinder-based MMM climatology [1985–1993 inclusive (aerosols corrected); Liu et al. 2000; Toscano et al. 2000, unpublished data). These are presented to illustrate the detailed water heating around the Palau islands.

**Results and discussion**

The results of our surveys indicate that the 1998 coral bleaching in Palau was relatively severe and widespread across depths, sites, habitats, and coral taxa. The mean percent cover of bleached scleractinian corals was  $18.9 \pm 1.5$  (mean  $\pm 1$  SE,  $n=9$  sites), and the cover of healthy corals was only  $15.6 \pm 2.0$  (when pooled across sites and depths). The overall percentage of living scleractinian coral tissue that was bleached (i.e. bleaching severity) was  $53.4 \pm 6.2$  (range of site means = 32.3–79.3,  $n=8$  sites) at 3–5 m and  $68.9 \pm 6.2$  (45.7–91.7,  $n=6$  sites) at 10–12 m and did not differ significantly between depths (Fig. 2;  $t=1.741$ ;  $df=1,12$ ;  $P>0.05$ ). Although bleaching severity varied significantly among sites within depth strata (3–5 m,  $F_{7, 15}=6.28$ ,  $P<0.01$ ; 10–12 m,  $F_{5, 12}=3.25$ ,  $P<0.05$ ), the lowest recorded percentage at any site/depth combination was  $32.3 \pm 4.8$  ( $n=3$  transects, Fig. 2). Among-site variation in the degree of bleaching could have been due to variability in the susceptibility of locally dominant species to thermal stress and might explain why bleaching intensity did not correspond to any obvious site characteristics. For example, bleaching severity did not vary significantly between barrier reef and rock island sites (Kruskal–Wallis test of 3- to 5-m transect data:  $\chi^2=1.088$ ,  $df=1$ ,  $P=0.296$ ).

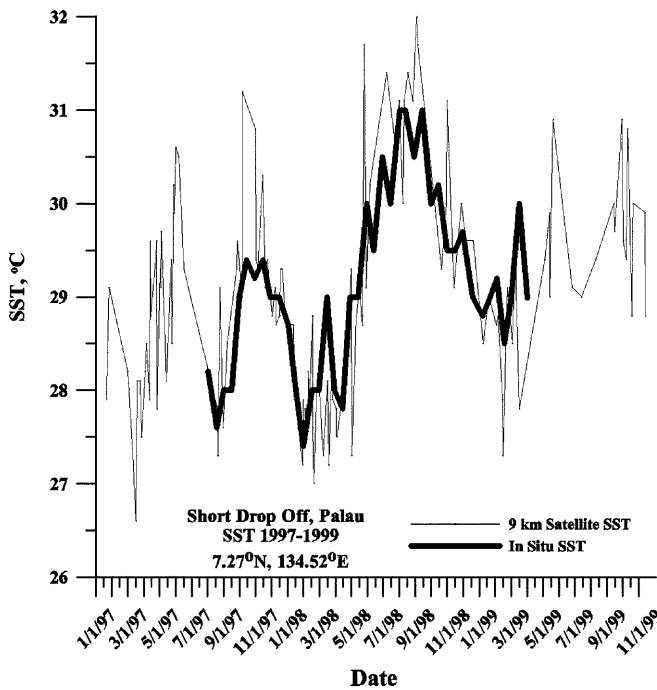


**Fig. 2** Percentage of the substratum that was covered by **A** live scleractinian corals (including bleached and non-bleached tissue), and **B** the percentage of that live coral tissue that was “bleached.” Data are from quantitative point-intercept sampling at nine sites in Palau. Bars represent untransformed means  $\pm 1$  SE,  $n=3$  transects/site; asterisks site/depth combination was not sampled

The percent cover of recently dead scleractinians ranged from 0–6.6 among sites. Our point-intercept sampling took place 12–16 weeks after the beginning of severe bleaching and it is possible that many coral colonies died and were overgrown weeks before we quantified the occurrence of recently dead corals. For example, dead skeletons of tabular Acroporids (e.g. *A. tenuis* and *A. hyacinthus*), still in growth position, were very common at depths of 1–10 m at many of the sites we surveyed. However, Palau was affected by a poorly documented *Acanthaster planci* outbreak during

**Table 2** Percentage of colonies (or individual polyps in the case of solitary species) of each scleractinian taxa that displayed “normal” or “healthy” coloration, and those that were partially or totally bleached (i.e. > 90% of surface area). Data were pooled from 1x30-m-band video transects at five sites

Taxa	Percent healthy	Percent bleached	Percent partially bleached	Total no.
<i>Acropora</i> sp.	62	32	6	47
<i>Astreopora</i> sp.	41	50	9	22
<i>Favia</i> sp.	16	71	13	80
<i>Favites</i> sp.	23	61	17	168
<i>Fungia</i> sp.	28	51	21	121
<i>Galaxea</i> sp.	60	20	20	5
<i>Goniopora</i> sp.	95	0	5	20
<i>Heliofungia actiniformis</i>	100	0	0	11
<i>Lobophyllia</i> sp.	8	83	9	88
<i>Montipora</i> sp.	92	5	4	83
<i>Pachyseris speciosa</i>	17	58	25	12
<i>Pavona</i> sp.	65	10	25	20
<i>Pectinia paeonia</i>	18	53	29	17
<i>Physogyra lichtensteini</i>	14	86	0	7
<i>Platygyra</i> sp.	41	55	5	22
<i>Pocillopora</i> sp.	60	20	20	25
<i>Porites</i> sp.	35	42	23	168
<i>Psammocora contigua</i>	0	100	0	25
<i>Scolymia</i> sp.	88	13	0	8
<i>Turbinaria</i> sp.	47	13	40	15
Totals	37	48	15	964

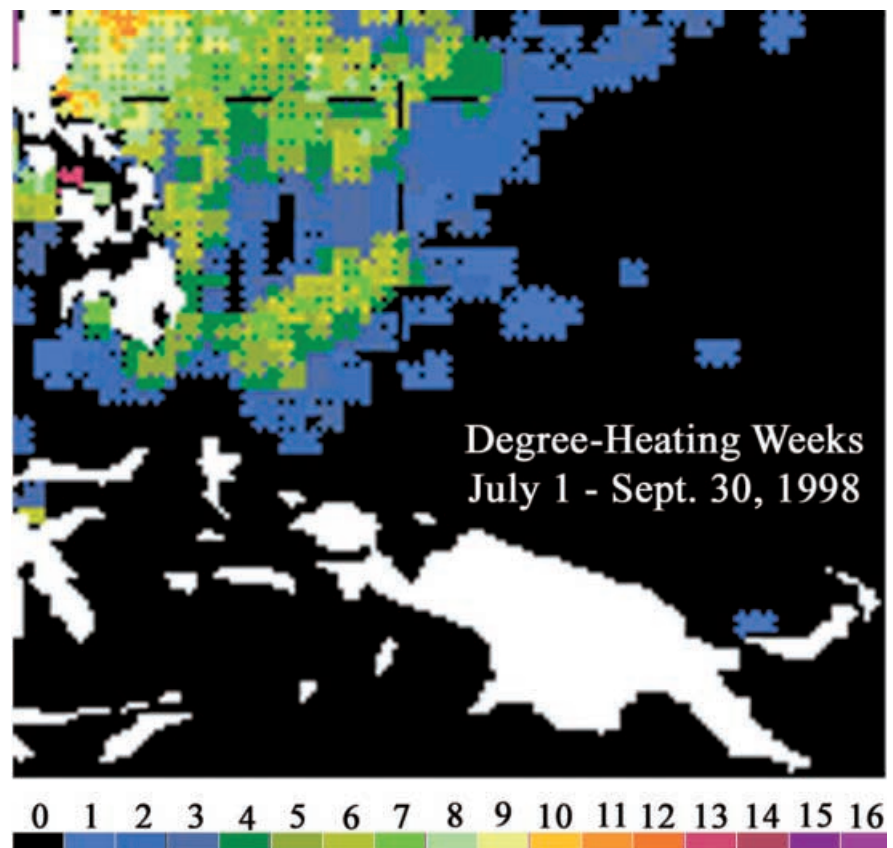


**Fig. 3** SST data at the Short Drop Off site in Palau for 1997–1999. In situ measurements were made by hand and 9-km night-time satellite SST data are from the NASA/JPL AVHRR Oceans Pathfinder program

the mid to late 1990s which caused near total coral mortality at some sites (P. Colin, personal observations). Because plating species of *Acropora* are a preferred prey of *A. plani* (Birkeland 1982; Colgan 1987), it is unclear whether predation or bleaching (or some other factor) caused the mortality of these normally common species.

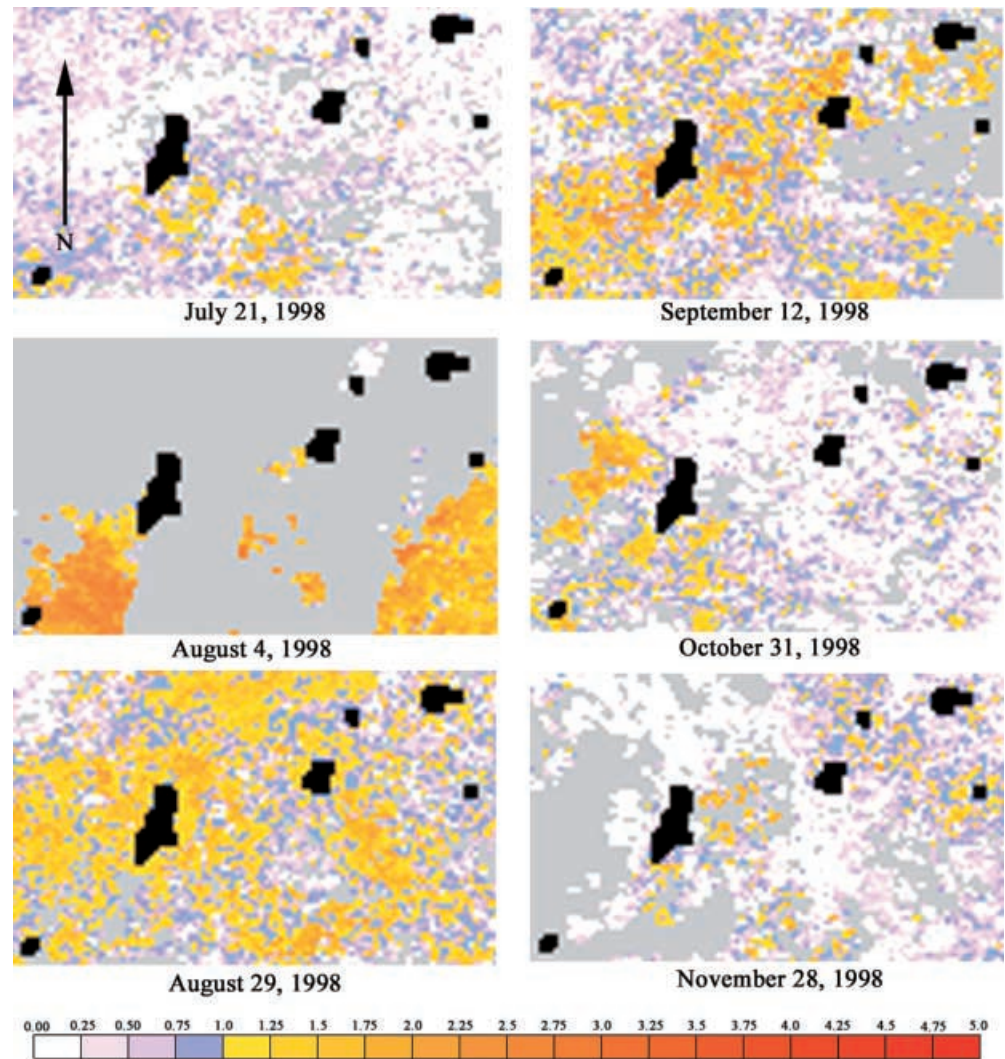
Nearly half (48%) of the 946 colonies surveyed in the video transects (pooled across 20 taxa) were totally bleached, and 15% were partially bleached (Table 2). However, there was considerable variation among taxa and a few (e.g. *Goniopora* spp. and *Montipora* spp.) displayed much lower bleaching frequencies. Such taxa-specific bleaching susceptibility could result in a major shift in species composition on reefs that have been severely or repeatedly bleached (Glynn 1993). Interestingly, at the generic level, the relative bleaching frequencies we recorded in the quantitative surveys do not correspond to the order of susceptibility reported from previous Pacific bleaching episodes in which *Acropora* spp. was the most susceptible and *Porites* spp. was the least susceptible taxa (Gleason 1993; Hoegh-Guldberg and Salvat 1995). Variation within genera may account for the discrepancies between our results and previous reports. For example, qualitative surveys (Table 3) indicated considerable variation in bleaching susceptibility among Acroporid species as some had apparently experienced nearly 100% mortality (e.g. *A. echinata* and

**Fig. 4** Portion of NOAA/NESDIS Degree Heating Weeks (DHW) chart for the eastern hemisphere, covering the period 1 Jul–30 Sept 1998. DHW accumulations begin when the HotSpot anomaly (at each pixel) reaches the 1 °C level. One DHW is equivalent to 1 week of SST 1 °C above the MMM climatological value. Two DHW are equivalent to 2 weeks of SST 1 °C above the MMM, or 1 week of SST 2 °C above the MMM. Four to seven DHW had accumulated around the Palau region during this period, mainly during August and early September (see HotSpot anomaly maps in Fig. 5)





**Fig. 5** Time series of 9-km HotSpot anomalies for the waters surrounding Palau during 1998. Landmasses and shallow water areas are masked in *black*. *Gray areas* indicate no satellite retrievals due to cloud cover. The scale indicates the level of SST anomaly above the satellite-derived maximum monthly mean (MMM) SST. The 1 °C threshold level, above which coral bleaching is likely to occur, is indicated in *yellow*

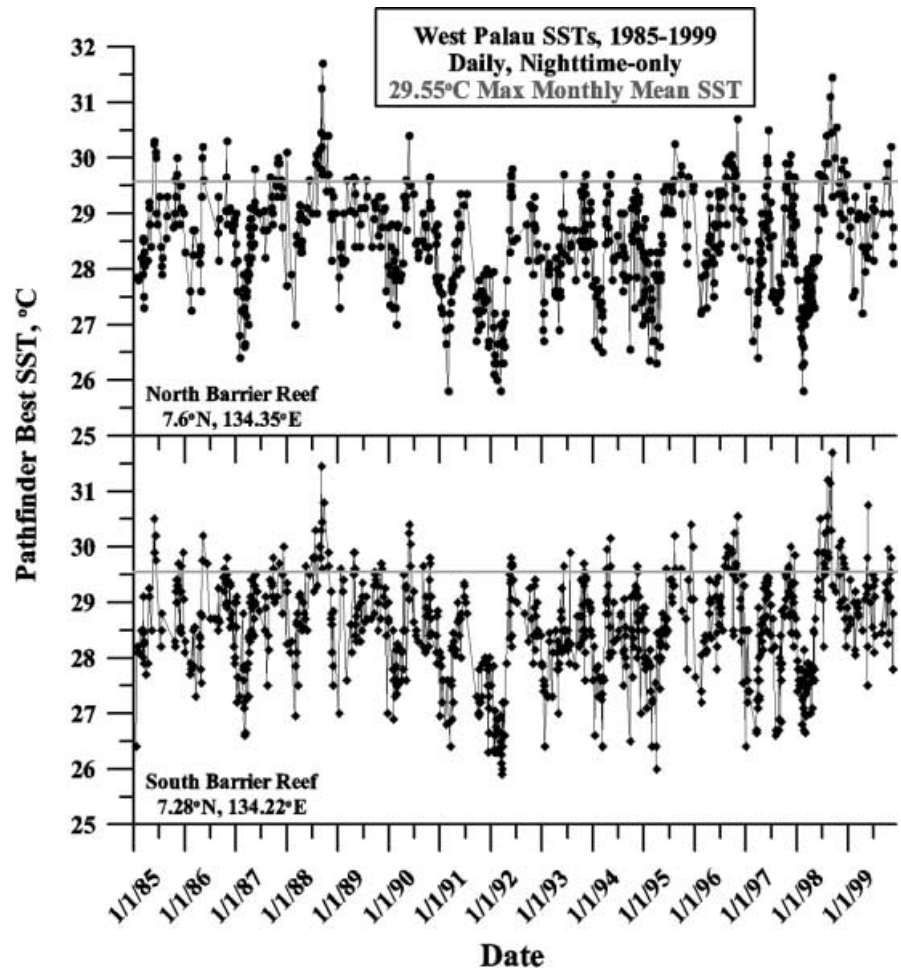


*A. hyacinthus*), while other species appeared unaffected (e.g. corymbose Acroporids). Despite strong variation among taxa, gross colony morphology was not obviously related to bleaching as some species with massive (e.g. *Porites lutea*), branching (e.g. *Acropora formosa*), tabular (e.g. *Acropora hyacinthus*), plating (e.g. *Pachyseris speciosa*), and free-living (e.g. *Fungia fungites*) morphologies all exhibited high frequencies of bleaching (Tables 2 and 3). Hoegh-Guldberg (1999) has suggested that variation among taxa in bleaching susceptibility may be caused by differences in tissue thickness. However, the absence of a repeatable susceptibility hierarchy indicated by this and previous studies (e.g. Williams and Bunkley-Williams 1988) seems to preclude a universal explanation.

The exact causes and mechanisms of coral bleaching have proved difficult to elucidate (Brown 1987; Edmunds 1994) and remain controversial (Warner et al. 1999). Nonetheless, a number of experimental laboratory studies have demonstrated the importance of increased water temperature (Hoegh-Guldberg and Smith 1989; Glynn and D’Croze 1990; Gates et al. 1992; review in Brown 1997), and many past mass bleaching episodes

were correlated with sea surface temperatures 1–4 °C above normal summer highs (Glynn 1984; Gates 1990; Hoegh-Guldberg and Salvat 1995; Brown et al. 1996; Winter et al. 1998). For example, the 1983/1984 ENSO caused 2–3 °C SST increases and was related to especially severe bleaching and high rates of coral mortality in the Eastern Pacific (Glynn 1983, 1984, 1990). Glynn (1993) suggests that SST increases of 3–4 °C for 1–2 days or 1–2 °C for several weeks are required to cause severe thermal bleaching. Local temperature records indicate that surface water temperatures at the Short Drop Off site in Palau were 31 °C for a period of at least 30 days, during the late summer of 1998 (Fig. 3), when ENSO-related increases in SST peaked in the Western Pacific (McPhaden 1999). NOAA/NESDIS 50-km DHW maps indicated that the equivalent of 4–7 weeks of thermal stress had accumulated over the 12-week period spanning 1 July through 30 September 1998 (Fig. 4). High-resolution (9-km; Toscano et al. 2000; Liu et al. 2000) HotSpot maps focused on Palau (Fig. 5) show temperature anomalies above the MMM SST of 29.55 °C beginning in late July 1998, with warmth

**Fig. 6** Fifteen-year nighttime satellite SST records for northern and southern areas of the outer barrier reef on the western side of Palau. Satellite data are from the NASA/JPL AVHRR Oceans Pathfinder program. Night-time SST were above the HotSpot temperature threshold at both sites for almost all of the latter half of 1998, and exceeded the 1 °C level during August and September 1998



peaking in August and remaining around the Palau islands into September and October. Long-term satellite SST for sites around Palau (Fig. 6) indicate that SST between July and November 1998 were above the 29.55 °C, 9-km MMM, and exceeded that threshold by at least the 1 °C anomaly level for periods considered sufficient to induce coral bleaching.

Although correlative, the results of this study suggest that ENSO-related SST increases are likely to be the cause of the 1998 bleaching in Palau. However, it is not possible to rule out other factors in either the bleaching or recent coral mortality documented in this study. For instance, ENSO events can also be associated with unusually calm periods that can enhance shallow subtidal irradiance levels (Lesser et al. 1990; Gleason and Wellington 1993). Although, somewhat controversial (Warner et al. 1999), it is thought that increased visible and UV light can induce bleaching or increase its severity (Lesser et al. 1990; Gleason and Wellington 1993; Hoegh-Guldberg 1999). Thus, increases in irradiance may have contributed to this mass bleaching event.

The effects of the 1998 bleaching in Palau are difficult to assess in more detail because of the lack of quantitative baseline data. A qualitative rapid ecological

assessment of Palau's reefs in 1992 reported that "coral reefs in Palau are in excellent condition supporting diverse and abundant coral reef, seagrass, mangrove, and lagoon ecosystems," and "only a few coral reef areas have been subjected to anthropogenic impacts" (Maragos and Cook 1995). Ultimately, the effects of the 1998 bleaching will be determined by rates of coral recovery and mortality and subsequent regrowth and recruitment. Moderate to severe mortality of corals that were bleached in 1998 could reduce coral cover to <10–20% at a number of rock island and barrier reef sites.

As of September 2000, there appears to have been very little recovery of bleached corals following the return of SST to normal levels (P. Colin, personal observations). Preliminary estimates of mortality based on reefs that were originally sampled with low-altitude (300 m or less) aerial photographs and resampled using SCUBA indicate that bleaching-related mortality was relatively high for some massive reef-building species. For example, at one patch reef in the central lagoon near the small island of Ngeragabal (Fig. 1), colonies of *Porites* spp. that were bleached in September were dead by December 1998 in nearly all cases ( $n = 100$  colonies). However, not all *Porites* spp. colonies on this reef bleached. Non-bleached colonies were not evident in the

aerial photographs, and of 491 *Porites* spp. colonies surveyed at this site, 40% were found to be alive, 30% were heavily damaged by bleaching but a portion was still alive, and 30% were completely dead. These results are concordant with qualitative observations at numerous other sites during early 1999, which suggested that bleaching-related mortality, although variable, was high for some species.

Reef-building corals have inhabited shallow tropical waters for > 200 million years (Stanley 1981). However, they only generated coral reef habitats intermittently during periods when water temperature and ocean chemistry were favorable to high calcification rates (Veron 1995). During numerous periods of non-optimal environmental conditions, scleractinians experienced high extinction rates, were largely restricted to habitat refuges, and generally did not create large structures (Veron 1995). If tropical sea temperatures continue to increase or if ENSO events become more frequent or severe, reef-building corals may not be able to maintain their current role as habitat providers to numerous reef-dependent taxa (Sebens 1994; Brown 1997). Because of the critical importance of coral reefs to tropical marine species diversity and human economic interests, their fate should be regarded as a pressing scientific, conservation, and social issue.

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## Appendix

The additional Table 3 shows bleaching of various cnidarian species from qualitative observations at 24 sites in Palau (1998).

**Table 3** Bleaching of various cnidarian species from qualitative observations at 24 sites in Palau (1998)

Species	Bleaching level and estimated mortality
<b>OCTOCORALLIA</b>	
<i>Lobophytum</i> several spp.	Extremely high (90% +), high mortality of large colonies
<i>Sinularia</i> spp.	High, in most species mortality 90% +, species specific
<b>HEXACORALLIA</b>	
Milleporidae	Some mortality seen
<b>SCLERACTINIA</b>	
Astrocoeniidae	
<i>Stylocoeniella</i>	High, high mortality
Pocilloporidae	
<i>Palauastrea ramosa</i>	Low, low mortality
<i>Pocillopora damicornis</i>	Bleaching variable (0–50% bleached), low mortality
<i>Pocillopora eydouxi</i>	High with high mortality
<i>Pocillopora</i> spp.	High with high mortality
<i>Seriatorpora</i> spp.	High with high mortality

**Table 3** Continued

Species	Bleaching level and estimated mortality
<i>Stylophora</i> spp.	High with high mortality
Acroporidae	
<i>Acropora echinata</i>	Very high, mortality approaching 100%
<i>Acropora formosa</i>	High, high mortality
<i>Acropora</i> spp. arborescent	Variable by species
<i>Acropora hyacinthus</i>	Very high, mortality approaching 100%
<i>Acropora</i> other tabulate	High, but one unidentified species moderate, mortality high
<i>Anacropora</i> spp.	Total mortality in limited areas while others were unaffected
<i>Astreopora</i> spp.	
<i>Montipora</i> spp.	Moderate, moderate mortality
Poritidae	
<i>Alveopora</i> spp.	Relatively little bleaching and mortality seen
<i>Goniopora stokesii</i>	
<i>Goniopora</i> spp.	Variable by habitat, low mortality? Locally high, moderate mortality, some species not affected
<i>Porites lobata/lutea</i>	Moderate, moderate mortality (10–40%)
<i>Porites rus</i>	Low to moderate, low to moderate mortality
<i>Porites cylindricus</i>	High to moderate, high to moderate mortality
<i>Porites nigrescens</i>	
Siderastereidae	
<i>Psammocora contigua</i>	Moderate to high, moderate mortality
<i>Psammocora digitata</i>	High, high mortality, tips bleached first
Agariciidae	
<i>Leptoseris gardineri</i>	High, high mortality
<i>Leptoseris papyracea</i>	High, high mortality
<i>Pachyseris rugosa</i>	Variable but generally high, high mortality
<i>Pavona cactus</i>	
<i>Pavona clavus</i>	High, high to moderate mortality
<i>Pavona minuta</i>	High, high mortality
Fungiidae	
<i>Cycloseris</i> spp.	No bleaching seen
<i>Diaseris</i> spp.	No bleaching seen
<i>Fungia</i> spp.	Variable, often high mortality, habitat and species specific?
<i>Podabacia crustacea</i>	Moderate, mortality unknown
Other fungiids	
Oculinidae	
<i>Acrhelia horrecens</i>	Moderate to high, moderate mortality
<i>Galaxea astreata</i>	High, high mortality in all areas, one of the most affected species
Pectinidae	
<i>Mycedium elephantotus</i>	Moderate, moderate mortality
<i>Pectinia lactuca</i>	High, high mortality
<i>Pectinia peonia</i>	High, high mortality
Mussidae	
<i>Cynaria lacrymalis</i>	High, mortality appears low
<i>Lobophyllia corymbosa</i>	High, high mortality
<i>Lobophyllia nataii</i>	High, high mortality
<i>Lobophyllia hemprichii</i>	High, high mortality
<i>Lobophyllia pachysepta</i>	High, high mortality
<i>Symphyllia</i> spp.	High, high mortality
Merulinidae	
<i>Hydnophora</i> spp.	Low, but variable, low mortality



Table 3 Continued

Species	Bleaching level and estimated mortality
<i>Merulina</i> spp.	Moderate to high, moderate mortality
Favidae	
<i>Barabattoia amicornum</i>	Low to moderate, mortality unknown
<i>Caulastrea furcata</i>	No bleaching seen
<i>Diploastrea heliophora</i>	Variable, often distinct color (bleaching) variation
<i>Favia/Favites</i> spp.	Variable, high in some, moderate mortality
<i>Goniastrea</i> spp.	Variable bleaching among species, high mortality in some
<i>Leptoria</i> spp.	Variable, but generally moderate
<i>Oulophyllia</i> spp.	High in some areas, mortality high
<i>Platygyra</i> spp.	High in some areas, mortality unknown
Caryophylliidae	
<i>Catalaphyllia jardinei</i>	Low to none
<i>Euphyllia divisa</i>	High, mortality unknown
<i>Euphyllia glabrescens</i>	High, mortality unknown
<i>Euphyllia parancora</i>	High, mortality unknown
<i>Physogyra lichtensteini</i>	Very high, high to near total mortality of polyps
<i>Pleurogyra sinuosa</i>	Generally high bleaching and mortality, some colonies unaffected
Dendrophyllidae	
<i>Dendrophyllia</i> spp.	Azooxanthellate, no bleaching
<i>Tubastraea</i> spp.	Azooxanthellate, no bleaching
<i>Turbinaria bifrons</i>	Locally high bleaching, mortality high
<i>Turbinaria peltata</i>	Locally high bleaching, mortality high

## References

- Aronson RB, Precht WF, Macintyre IG, Murdoch TJT (2000) Coral bleach-out in Belize. *Nature* 405:36
- Baird AH, Marshall PA (1998) Mass bleaching of corals on the Great Barrier Reef. *Coral Reefs* 17:376
- Berkelmans R, Oliver JK (1999) Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs* 18:55–60
- Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Mar Biol* 69:175–185
- Brown BE (1987) Worldwide death of corals – natural cyclical events or man-made pollution? *Mar Pollut Bull* 18:9–13
- Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16:S129–S138
- Brown BE, Dunne RP, Chansang H (1996) Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. *Coral Reefs* 15:151–152
- Colgan MW (1987) Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* 68:1592–1605
- Edmunds PJ (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching susceptible clones. *Mar Biol* 121:137–142
- Edmunds PJ, Bruno JF (1996) The importance of sampling scale in ecology: kilometer-wide variation in coral reef communities. *Mar Ecol Prog Ser* 143:165–171
- Fedorov AV, Philander SG (2000) Is El Niño changing? *Science* 288:1997–2002
- Fitt WK, Spero HJ, Halas J, White MW, Porter JW (1993) Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean “bleaching event.” *Coral Reefs* 12:57–64
- Gates RD (1990) Seawater temperature and sublethal coral bleaching in Jamaica. *Coral Reefs* 8:193–197
- Gates RD, Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. *Biol Bull* 182:324–332
- Gleason DF, Wellington GM (1993) Ultraviolet radiation and coral bleaching. *Nature* 365:836–838
- Gleason MG (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* 12:193–201
- Glynn PW (1983) Extensive ‘bleaching’ and death of reef corals on the Pacific coast of Panama. *Environ Conserv* 10:149–154
- Glynn PW (1984) Widespread coral mortality and the 1982–83 El Niño warming event. *Environ Conserv* 11:133–146
- Glynn PW (1990) Coral mortality and disturbances to coral reefs in the tropical Eastern Pacific. In: Glynn PW (ed) *Global ecological consequences of the 1982–83 El Niño-Southern Oscillation*. Elsevier, Amsterdam, pp 55–126
- Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol Evol* 6:175–179
- Glynn PW (1993) Coral reef bleaching: ecological perspectives. *Coral Reefs* 12:1–17
- Glynn PW, D’Croz L (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8:181–191
- Goreau TF (1964) Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. *Science* 145:383–386
- Goreau TJ (1992) Bleaching and reef community change in Jamaica: 1951–1991. *Am Zool* 32:683–695
- Harriott VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. *Mar Ecol Prog Ser* 21:81–88
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world’s coral reefs. *Mar Freshwater 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
- Hoegh-Guldberg O, Smith GJ (1989) The effects of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J Exp Mar Biol Ecol* 129:279–303
- Hughes TP (1994) Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Jaap W (1979) Observations on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys. *Bull Mar Sci* 29:414–422
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16:S23–S32
- Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–162
- Kearns EJ, Hanafin JA, Evans R, Minnett PJ, Brown OB (2000) An independent assessment of Pathfinder AVHRR sea surface temperature accuracy using the Marine-Atmosphere Emitted Radiance Interferometer. *Bull Am Meteor Soc* 81:1525–1536
- Kilpatrick K, Podesta GP, Evans R (2001) Overview of the NOAA/NASA Pathfinder algorithm for sea surface temperature and associated matchup database. *J Geophys Res* 106(C5):9179–9197
- Lang JC, Lasker HR, Gladfelter EH, Hallock P, Japp WC, Losada FJ, Muller RG (1992) Spatial and temporal variability during periods of “recovery” after mass bleaching on Western Atlantic coral reefs. *Am Zool* 32:696–706
- Lesser MP, Stochaj WR, Tapley DW, Schick JM (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8:225–232
- Liu G, Toscano MA, Strong AE, Guch IC, Casey KS (2000) Examination of satellite-derived SST fields for improved early

- warning of coral reef bleaching events. In: Proc American Geophysical Union Fall Meeting, 15–19 Dec
- Maragos JE, Cook CW Jr (1995) The 1991–1992 rapid ecological assessment of Palau's coral reefs. *Coral Reefs* 14:237–252
- McPhaden MJ (1999) Genesis and evolution of the 1997–98 El Niño. *Science* 283:950–954
- Roberts L (1987) Coral bleaching threatens Atlantic reefs. *Science* 238:1228–1229
- Sebens KP (1994) Biodiversity of coral reefs: what are we losing and why? *Am Zool* 34:115–133
- Stanley GD (1981) Early history of scleractinian corals and its geological consequences. *Geology* 9:507–511
- Stone L, Huppert A, Rajagopalan B, Bhasin H, Loya Y (1999) Mass coral reef bleaching: a recent outcome of increased El Niño activity? *Ecol Lett* 2:325–330
- Thompson TL, Glen EP (1994) Plaster standards to measure water motion. *Limnol Oceanogr* 39:1768–1779
- Toscano MA, Strong AE, Guch IC, Casey KS (2000) Improved prediction of coral bleaching using high-resolution HotSpot mapping and DHWs. In: Proc 9th Int Coral Reef Symp, Abstract
- Veron JEN (1986) *Corals of Australia and the Indo-Pacific*. Angus and Robertson, Sydney
- Veron JEN (1995) *Corals in space and time*. Cornell University Press, Ithaca
- Walton CC, Pichel WG, Sapper JF, May DA (1998) The development and operational application of nonlinear algorithms for the measurement of sea surface temperatures with the NOAA polar-orbiting environmental satellites. *J Geol Res* 103:27,999–28,012
- Warner ME, Fitt WK, Schmidt GW (1999) Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. *Proc Natl Acad Sci USA* 96:8007–8012
- Wilkinson CR (1992) Coral reefs of the world are facing widespread devastation: can we prevent this through sustainable management practices? In: Proc 7th Int Coral Reef Symp Publ 1, pp 11–21
- Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. *Mar Freshwater Res* 50:867–878
- Williams EH Jr, Bunkley-Williams L (1988) Bleaching of Caribbean coral reef symbionts in 1987–1988. In: Proc 6th Int Coral Reef Symp Publ 3, pp 313–318
- Winter A, Appeldoorn RS, Bruckner A, Williams EH Jr, Goenaga C (1998) Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs* 17:377–382