Spatial variability of coral bleaching in Palau during a regional thermal stress event in 2010

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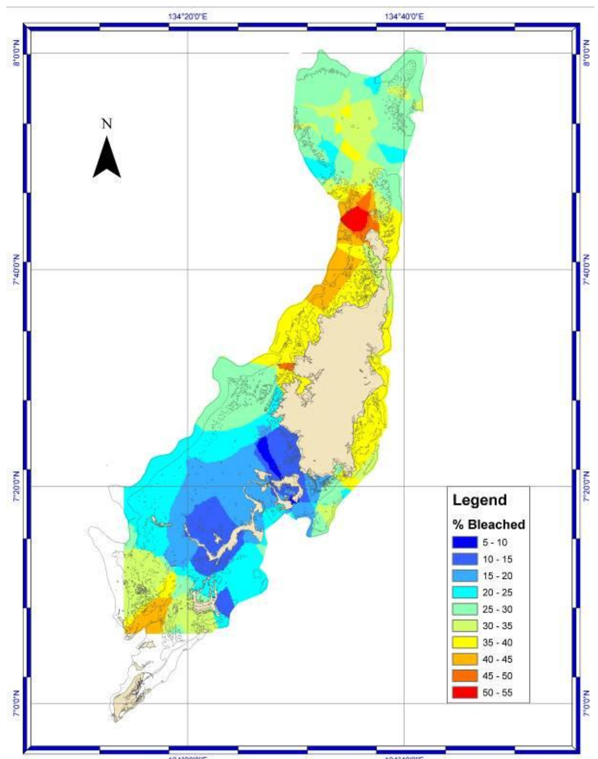

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Executive summary

Thermal stress continues to emerge as a global concern for coral reefs. Yet, most studies are site specific. There are few studies that examine the spatial variability of bleaching response during thermal stress events. This study examined the spatial extent and severity of bleaching in Palau during a regional thermal stress event in 2010. We surveyed coral bleaching at 80 sites using a stratified-random sampling design in July-August 2010. Our objective was to determine whether there were any spatial differences in thermal stress that were habitat or taxa dependent. Coral bleaching was significantly higher on outer and patch reefs than in the bays, and was particularly severe in the northwestern lagoon. While the reefs in the bays may provide a safe haven for some coral species through climate change, these reefs, alone, are not resilient because they are more vulnerable to land-use change than patch and outer reefs. Therefore, protecting nearshore reefs from local disturbances may help buffer the coral reefs of Palau against climate-change induced disturbances.

Introduction

Reef corals are particularly sensitive to increases in water temperature. Corals pale when temperatures are elevated a few degrees above the average seasonal maximum (Glynn 1991). If high temperatures are sustained for several weeks the most temperature-sensitive corals will bleach, losing their endosymbionts and their autotrophic capacity (Hoegh-Guldberg 1999). These corals may subsequently die of starvation (Glynn 1993, Brown 1997; Fitt *et al.* 2001). Coral bleaching events are becoming more frequent as the oceans continue to warm (Hoegh-Guldberg 1999; Hughes *et al.* 2003), and these events are expected to increase in intensity over the coming decades (Hoegh-Guldberg *et al.* 2007; Baker *et al.* 2008).

In 2010, western Micronesia experienced a thermal stress event - with recorded sea surface temperatures as high as 1.5^{o}C above average (Figures 1-3). The earliest signs of bleaching were reported in late June 2010. The outer south-western barrier reefs of Palau showed paling of some coral species. By mid-July, more extensive bleaching was observed. This study was designed to examine the intensity of thermal stress with the extent of bleaching severity and mortality in Palau (Figure 4). There are few records on the spatial variability of bleaching during a regional thermal stress event (but see McClanahan *et al.* 2007; Wagner *et al.* 2010), as most studies are site specific assessments of stress (Loya *et al.* 2001; van Woesik *et al.* 2011).

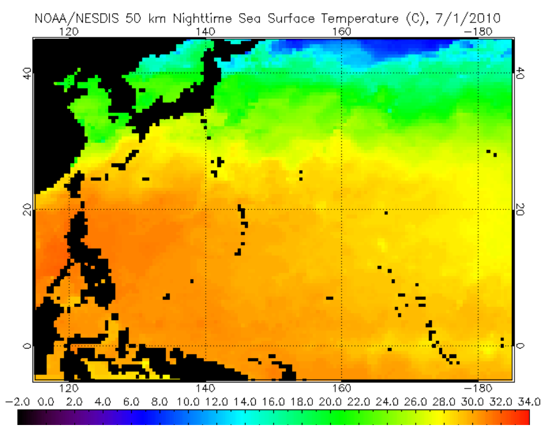

Figure 1. Sea surfaces temperatures in Micronesia, 1 July, 2010.

Coral bleaching and mortality is dependent on the intensity and duration of the temperature stress. For example in 1998 reefs in southern Japan that were exposed to temperatures 3^{o}C above the summer mean lost nearly 85% of .the corals (Loya *et al.* 2001), showing major long-term transitions in species composition (van Woesik *et al.* 2011). Whereas in the same year, nearby reefs exposed to temperatures 1.8^{o}C above the summer mean showed only subtle, mortality induced, shifts in size-frequency distributions (Roth *et al.* 2010). Although coral bleaching and mortality is dependent on the intensity and duration of the temperature stress, bleaching is also dependent on a number of other

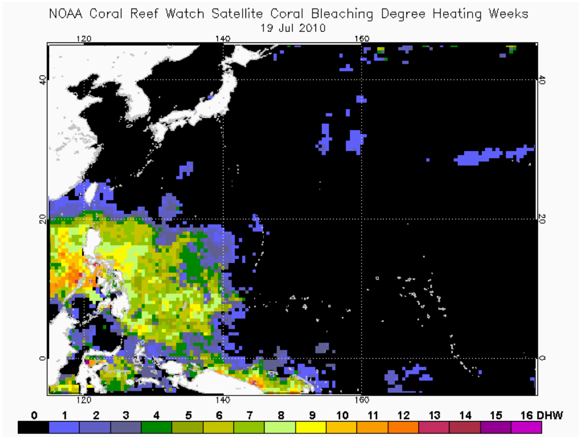

Figure 2. Degree heating weeks 19 July 2010.

variables including: (i) the composition of the coral community that is subjected to the thermal stress (Loya *et al.* 2001; McClanahan 2004), (ii) the daily and seasonal variation in temperature to which the reef corals are exposed (McClanahan and Maina 2003), (iii) the recent history in exposure to irradiance (Dunne and Brown 2001; Mumby *et al.* 2001; Brown *et al.* 2002), and (iv) the exposure to high concentrations of dissolved inorganic nitrogen concentrations (Wooldridge and Done 2009; Wagner *et al.* 2010).

Reefs under the same temperature stress, supporting different coral species, show different responses (McClanahan 2004). For example, reefs supporting mainly pocilloporids and acroporids are more likely to bleach than reefs supporting faviids and massive *Porites* (van Woesik 2001). Given the same species composition, the extent of thermal tolerance is also dependent on geographic locality and habitat type. Biogeographic regions experience temperature 'zones', upon which natural selection has acted (Craig *et al.* 2001; Smith-Keune & van Oppen 2006; Barshis *et al.* 2010). Such adaptations determine the temperature tolerances of the coral populations. For example, the corals in the northern Great Barrier Reef experience average temperatures of ~28.5°C in the warmest months, whereas corals in the southern Great Barrier Reef rarely experience temperatures above 27°C (Smith-Keune & van Oppen 2006; Wooldridge and Done 2009). Therefore, it is no surprise that under a regional temperature stress event in 1998, the northern nearshore reefs, which were adjusted to warmer temperatures, showed less bleaching than the southern nearshore reefs (Berkelmans and Oliver 1999).

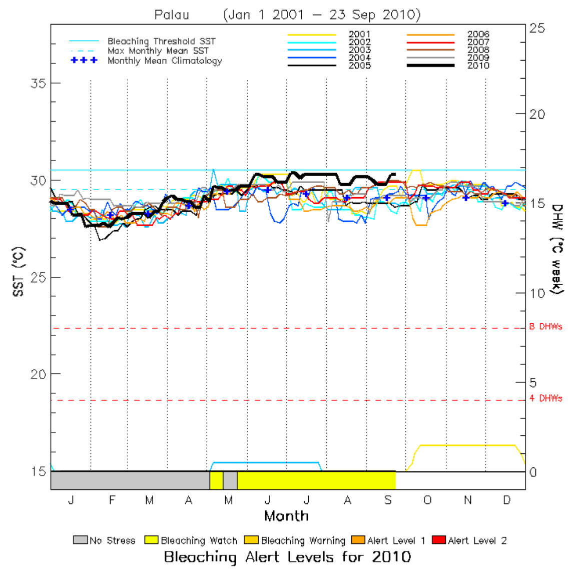

Figure 3. Annual sea surface temperatures for Palau from 2001 to 2010.

The differential responses imposed by habitat characteristics may also play a role in the response of corals to thermal stress. For example, corals on reef flats that experience daily temperature fluctuations that can exceed 6°C are less likely to bleach during regional temperature increases than corals in habitats with lower temperatures fluctuations (Maina and McClanahan 2003). Clearly, acclimation to dynamic, eurythermal conditions makes corals more tolerant to regional thermal stress. The extent to which corals bleach under temperature stress is also highly dependent on the intensity of irradiance (Iglesias-Prieto *et al.* 1992; Brown *et al.* 2002; Takahashi *et al.* 2004). Suspended particles in nearshore environments are known to reduce irradiance (Golbuu *et al.* 2007), which in turn can reduce bleaching susceptibility. For example, Wagner *et al.* (2010) showed that nearshore corals growing in turbid conditions with low irradiance were less prone to bleaching, despite homogeneously elevated temperatures. Notably, localities with high nutrient concentrations were exceptions to these trends and showed extensive bleaching. A similar response was observed on the Great Barrier Reef, where Wooldridge and Done (2009) suggested that corals in localities with low- water quality, measured as high satellite-derived-chlorophyll-a concentrations, were more likely to bleach in 1998 and in 2002 than corals in localities with high-water quality.

In 1998, the reefs of Palau were subjected to extensive thermal stress and widespread coral mortality (Bruno *et al.* 2001). Bruno *et al.* (2001) sampled nine sites, six of which were in the sheltered lagoon around the Rock Islands, and three of which were on outer reefs. While comprehensive datasets were collected at each site, the study was conducted in November, 1998, two months after the temperatures peaked, and the most vulnerable species may have already died. Moreover, the study was not spatially extensive enough to identify localities that may have tolerated thermal stress. Here we study the spatial variation in the extent of coral bleaching during a moderate regional thermal stress event in 2010, when the sea surface temperatures were 1.5^{o}C above average. The main objectives of this study were to determine whether (i) there were any spatial differences in thermal stress in Palau in 2010, (ii) which corals were most thermally tolerant, and (iii) whether colony size influenced the probability of bleaching. The study addresses whether, in the face of climate change, a coral-reef system, such as Palau, could prioritize conservation resources toward specific localities, some of which may tolerate regional thermal stress events better than other localities.

Methods

Study location and environmental variables

Palau is located in western Micronesia (07° 30 N, 134° 30 E) (Fig. 4). The archipelago is about 700 km long. We focused our efforts on the reefs in the vicinity of the main island of Babeldaob, which supports outer barrier, patch, and fringing reefs in bays (Golbuu *et al*. 2007) (Fig. 4).

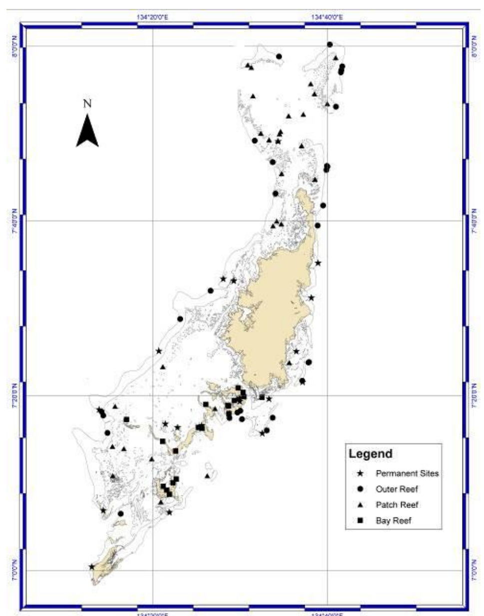

Figure 4. Eighty study sites, stratified by bays (n=20), patch reefs (n=30), and outer reefs (n=30) that were examined for coral bleaching in July 2010.

We undertook a rapid assessment of the extent of coral bleaching from 28 July to 12 August, 2010. We used a stratified-random sampling approach to differentiate the reefs as either: (i) bays, (ii) patch reefs, and (iii) outer reefs. Stratification of Palau's reef habitats was based on the 2005, National Oceanic and Atmospheric Administration (NOAA) benthic habitat maps of Palau (Battista *et al.* 2007). The habitat shapefiles were accessed using Arc9.3® from which random points were selected using the Hawths-extension toolbox (Hawths® 2009). We pre-selected random points for each habitat, surveying 30 sites on the outer reefs, 30 sites on the patch reefs, and 20 sites in the bays (Fig. 1). The survey targeted the shallow coral-reef assemblages between 2-5 m, primarily because we wished to adequately survey the most species-rich strata. Within each site, we haphazardly laid down 3 x 30 m fiberglass transect tapes, and took 30, 1 m^2 photographs along each transect. Within each photo frame, each coral colony, with its center inside the 1 m^2 fame, was identified and measured to the nearest centimeter, and assessed for the extent of bleaching, as either (i) no bleaching, (ii) pale, or (iii) bleached. Some coral colonies simultaneously showed all three responses, which were reported as percentages. We focused our spatial analyses on colonies that were > 50% bleached. In total 34,397 coral colonies were assessed for bleaching in Palau during the 2010 thermal stress event.

Data analysis

To examine whether the thermal stress caused differential mortality, we calculated the first difference in coral cover across sequential sampling periods. These data were analyzed using General Linear Models. We examined the raw data for violations of normality using normal probability plots, and violations of homogeneity of variances using the Levene's test. Bleaching prevalence was also spatially interpolated for the entire sampling domain using kriging, by applying Gaussian functions for best-fit modeling (Wagner *et al.* 2008).

Results and Discussion

Bleaching prevalence

The study focused on bleaching prevalence, in order to determine the proportion of the population which was bleached, and thereby accounting for differences in coral colony densities across habitats. Coral bleaching was significantly higher on outer reefs (5.2 ± 0.1, mean ± standard error) and patch reefs (5.4 ± 0.2) than in the bays (3.9 ± 0.20) (one-way ANOVA, p<0.001); Fig. 4). Similarly, there was significantly higher bleaching of *Pocillopora* on the outer reefs than in the bays (ANOVA, p<0.001; Fig. 5a). There were no significant differences however in bleaching of *Acropora* and *Porites* colonies among habitats (Figs. 5b & 5c). Faviids showed a similar bleaching trend as *Pocillopora*, with significantly less bleaching in the bays than on patch and outer reefs (Fig. 5d). There was no relationship between bleaching prevalence and coral colony size across all habitats.

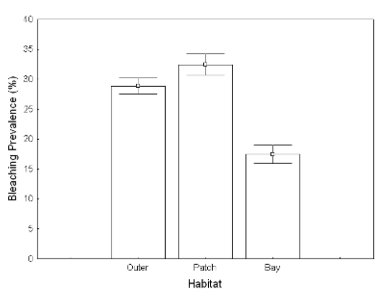

Figure 4. Bleaching prevalence, which is the proportion of colonies that bleached within each population, stratified by habitat type, for the thermal stress event in Palau in 2010.

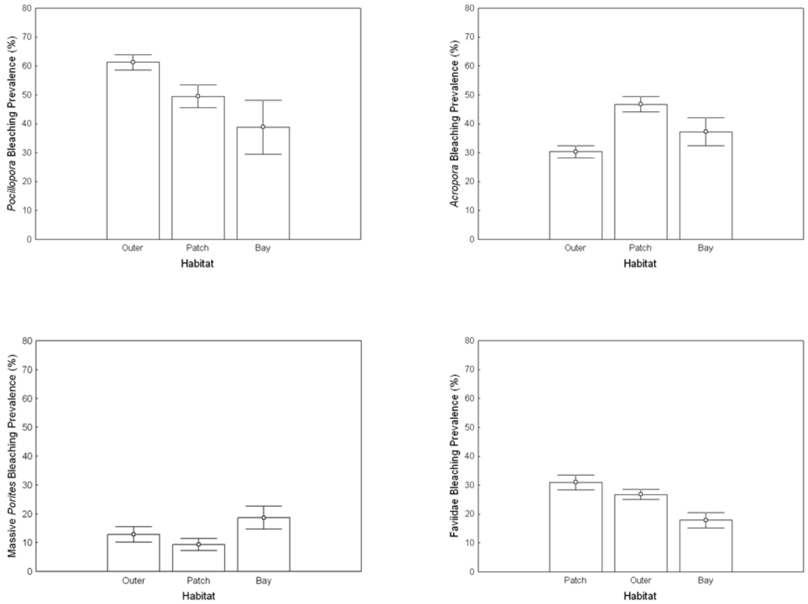

Figure 5. Bleaching prevalence, which is the proportion of colonies that bleached within each population, stratified by habitat type, for *Pocillopora* (top left), *Acropora* (top right), *Porites* (bottom left), and faviids (bottom right).

Islands and persistent corals

The present study shows that habitats respond differently to thermal stress, and that regional persistence is not simply about water temperature. The nearshore reefs of Palau had less bleaching and mortality than the outer barrier and patch reefs, even though the temperatures were as high, if not higher, in the bays. The duration and intensity of irradiance also plays a major role in whether corals bleach or not. Experimental studies show that low irradiance under temperature stress reduces the likelihood of bleaching (Iglesias-Prieto *et al*. 1992; Takahashi *et al*. 2004). Indeed, corals in bays experience less irradiance than corals on outer reefs (see Golbuu et al 2007, their Figure 4). High volcanic islands, in general, have a high variance in the intensity and duration of incoming irradiance (Iwase *et al.* 2008). These different levels of irradiance influence not only coral morphology, but may also cause different intensities of bleaching under the same thermal stress.

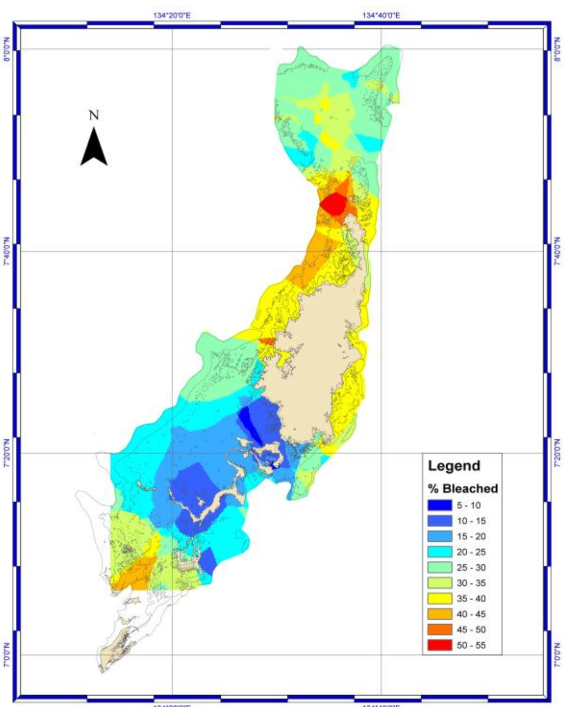

Figure 6. Bleaching prevalence in Palau in July-August, 2010.

Conservation

Still, a higher temperature tolerance nearshore does not suggest that the reefs are resilient. Nearshore reefs are also more affected by land-use change than outer barrier reefs (Golbuu *et al.* 2011). While outer reefs are somewhat removed from direct land-use change, these outer reefs are also more vulnerable to temperature stress events. Therefore, incorporating reefs from a variety of habitat types into conservation plans, and reducing river run-off to the nearshore reefs becomes even more pertinent as we strive to optimize conservation plans under climate-change scenarios.

The study shows that reefs around bays are indeed more tolerant to thermal stress than patch and outer reefs, and the reefs in the bays are therefore valuable refuges to buffer coral-reef ecosystems against climate-change induced disturbances.

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Figure 8. Bleaching in Bay, August 1, 2010.

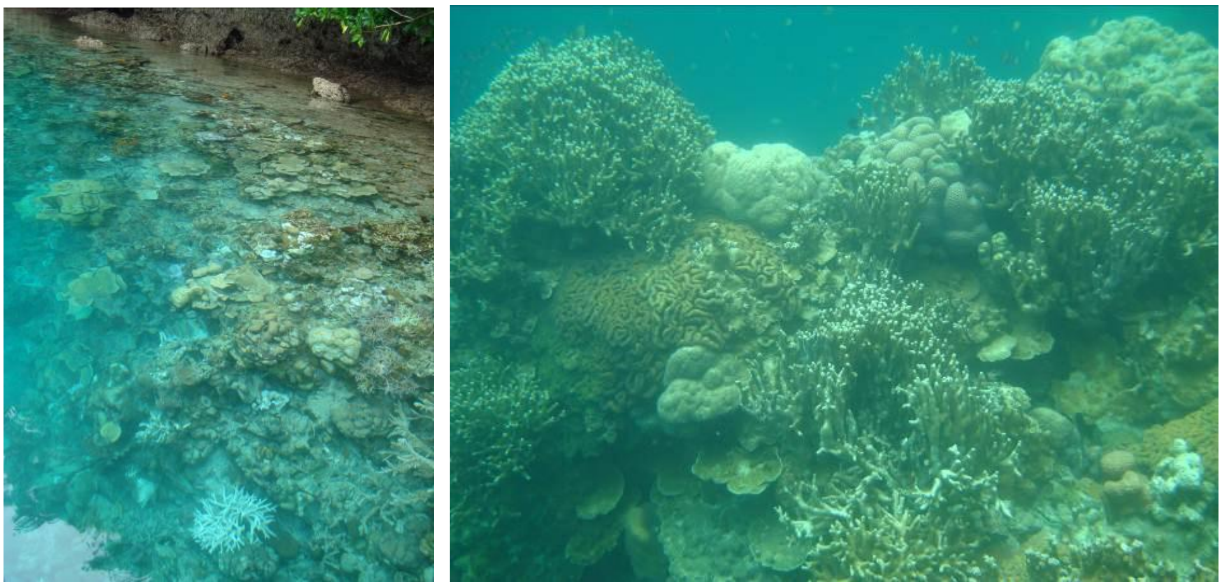

Figure 9. Bleaching on patch reefs, August 3, 2010, 2010; (top) Ebill, and (bottom) Lukes.

Figure 10. Bleaching on outer reefs, August 3, 2010; top (west), and bottom (east).

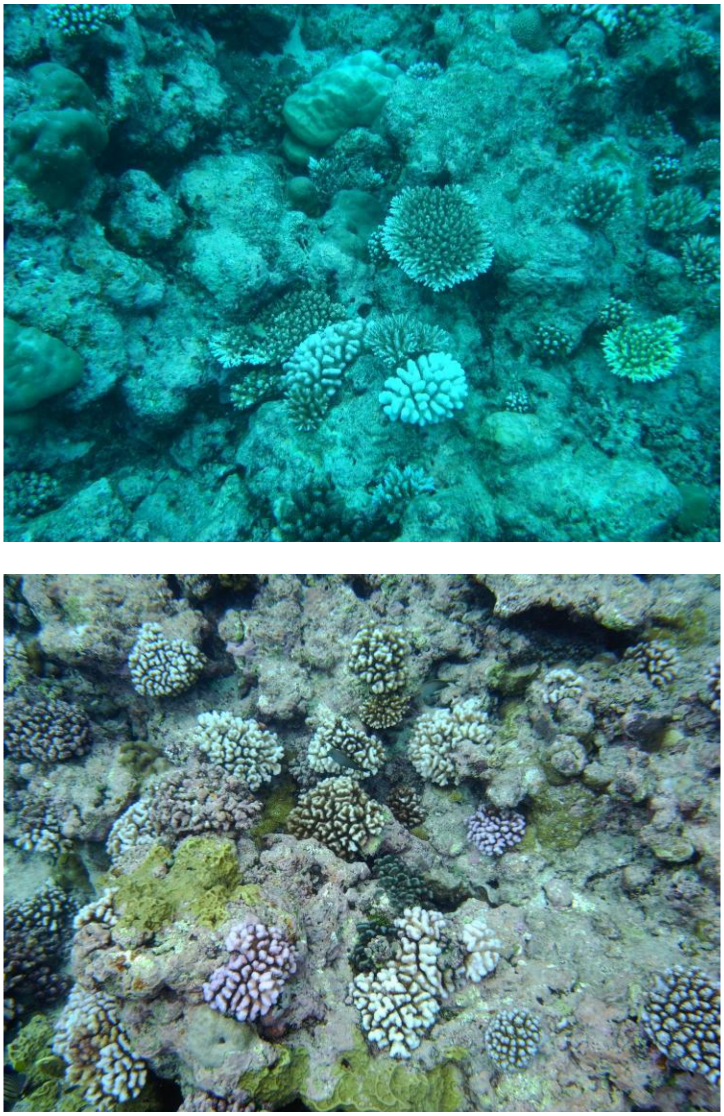

Table 1. Summary of bleaching prevalence in Palau in July-August, 2010.

Family	**Genus**	**Bay reef mean**	**Bay reef Std. dev.**	**Outer reef mean**	**Outer reef Std. dev.**	**Patch reef mean**	**Patch reef Std. dev.**
Acroporidae	*Acropora*	12.05	13.81	59.78	50.41	33.94	30.31
	Astreopora	1.80	0.84	1.83	1.01	6.02	7.53
	Montipora	5.86	8.26	34.82	16.56	14.94	14.36
Agariciidae	*Pachyseris*	1.25	0.42	1.21	0.39	2.75	2.06
	Pavona	6.71	5.69	8.17	11.47	8.69	13.41
Faviidae	*Caulastrea*					1.00	0.00
	Cyphastrea	2.00	1.00	2.29	1.97	2.85	1.86
	Diplostrea	1.00	0.00	1.40	0.66	1.00	0.00
	Echinopora	8.17	11.11	1.96	1.08	3.58	3.40
	Favia	4.74	5.10	5.91	5.31	5.01	6.10
	Favites	9.52	12.38	10.52	8.67	7.47	10.36
	Goniastrea	15.31	24.99	7.45	5.47	5.09	5.92
	Leptastrea			1.00	0.00		
	Leptoria	1.50	0.71	2.93	2.54	1.68	0.77
	Montastrea	4.00	2.83	1.00	0.00	1.00	0.00
	Oulophyllia	1.00	0.00			1.00	0.00
	Platygyra	5.44	4.07	1.44	0.72	1.63	0.87
Fungiidae	*Ctenactis*	3.93	2.42	1.00	0.00	2.59	1.56
	Fungia	8.42	9.44	1.61	0.70	5.63	5.85
	Heliofungia	19.89	14.16				

	Herpolitha	1.00	0.00			1.00	0.00
	Podabacia					1.00	0.00
	Sandalolitha	2.00	0.00			1.50	0.71
Merulinidae	*Hydnophora*	2.50	2.12	3.14	2.38	3.91	4.83
	Merulina	1.75	1.17	1.29	0.49	1.31	0.59
Mussidae	*Acanthastrea*	7.00		2.20	0.84	1.00	0.00
	Lobophyllia	7.00	12.81	1.10	0.22	1.06	0.17
	Symphyllia	5.80	5.67	1.22	0.54	1.19	0.37
Non-Scleractinia	*Heliopora*			4.48	3.47	2.56	1.90
	Millepora			2.26	2.00	1.63	0.96
Oculinidae	*Galaxea*	2.00	1.00	10.07	10.74	2.14	1.63
Pectiniidae	*Echinophyllia*			1.00	0.00	1.00	0.00
	Mycedium	1.00	0.00	1.00	0.00	1.00	0.00
	Oxypora			1.00	0.00	1.00	0.00
	Pectinia	1.50	0.50			1.00	0.00
Pocilloporidae	*Pocillopora*	3.68	5.57	18.91	11.73	8.67	8.65
	Seriatopora	3.60	5.34	7.27	8.20	40.40	47.67
	Stylophora	1.00		3.96	4.55	2.08	1.51
Poritidae	*Goniopora*	10.50	10.94	15.00	0.00		
	Porites	37.74	20.56	9.56	13.00	23.33	30.83
	Porites massive	15.93	14.16	12.92	16.24	10.00	9.88
Siderastreidae	*Coscinaraea*	3.00	0.00			1.00	0.00
	Psammocora	1.42	0.49	1.91	1.22	2.02	1.45