

# The role of water temperature and UV radiation in the recovery of the experimentally bleached coral *Pocillopora damicornis* from the eastern Pacific Ocean (Panamá)

L. D'Croz<sup>1,2</sup> and J.L. Maté<sup>1,3</sup>

## ABSTRACT

Field observations and experiments clearly demonstrate the role of elevated water temperature plays in inducing bleaching in the coral *Pocillopora damicornis*. However, the effect of UVR on the corals is not clear. To study the coral-zooxanthella symbiosis during simulated post-ENSO scenarios, colonies of *P. damicornis* were exposed to elevated water temperature and ambient UVR until they bleached. The significant decline of zooxanthellae and photosynthetic pigments resulting in bleaching occurred after 41 days of exposure. Bleached corals were then exposed for 48 days to four experimental conditions to test the effects of water temperature (slightly elevated and ambient) and UVR (ambient and reduced) on six symbiosis attributes. Corals kept under ambient water temperature regained zooxanthellae and the concentration of chlorophylls regardless of the exposure to UVR. Corals under slightly elevated water temperature and reduced UVR remained pale. The condition of corals exposed to slightly elevated water temperature and UVR continued to decline in time. Results indicated that exposure to slightly elevated water temperature, UVR, and their synergy hampered the recovery of experimentally bleached corals.

**Keywords** Coral bleaching, Recovery, *Pocillopora damicornis*, Temperature, UVR

## Introduction

Coral bleaching is related to environmental conditions such as those associated with El Niño Southern Oscillation (ENSO) events (Glynn 1996, Brown 1997, Hoegh-Guldberg 1999). Field and experimental observations have concluded that elevated water temperature is the most important trigger to coral bleaching, particularly for coral species in the Pacific Ocean (Hoegh-Guldberg and Smith 1989, Brown and Suharsono 1990, Glynn and D'Croz 1990, Hoegh-Guldberg and Salvat 1995, Brown et al. 1996). However, clear skies, low wind velocity, calm seas, and high water transparency may cause higher penetration of sunlight in the water column, particularly the ultraviolet radiation (UVR), and this may also play a role in the bleaching of the corals (Lesser et al. 1990, Gleason and Wellington 1993, Kinzie 1993).

*Pocillopora damicornis*, a branching coral which is the major reef-building species on the Pacific coast of Panamá (Glynn and Maté 1997), experienced widespread bleaching and die-off during ENSO related sea warmings (Glynn 1990, Glynn et al. in press). The experimental simulation of ENSO warmings replicated the changes in the coral-zooxanthella symbiosis usually observed during field studies (Glynn and D'Croz 1990) and suggested that increases of 2° to 4° C above the mean sea surface temperature for several weeks can induce bleaching and eventually mortality in *P. damicornis*. However, while there is little doubt as to the effect of elevated water temperature on the bleaching of corals, the role of UVR is not that clear. The experiment by Glynn et al. (1992) suggested that there is no relation between the exposure to

UVR, alone or in synergy with elevated water temperature, and the bleaching of *P. damicornis*.

However, high solar radiation has been implicated in coral bleaching (Lang et al. 1988, Goenaga et al. 1989, Gleason and Wellington 1993). Brown et al. (2000) points out that this is not necessarily due to UVR but to an increase in the photosynthetically active radiation (PAR). This is also consistent with the light dependent mechanism for thermal stress proposed by Jones et al. (1998).

Because water temperature remains slightly higher for several weeks after a major sea warming event, in this experiment we have studied the coral-zooxanthella symbiosis in experimentally bleached colonies of the coral *P. damicornis* exposed to simulated post-ENSO scenarios. We have tested the effects of exposure of corals to slightly elevated water temperature and ambient UVR.

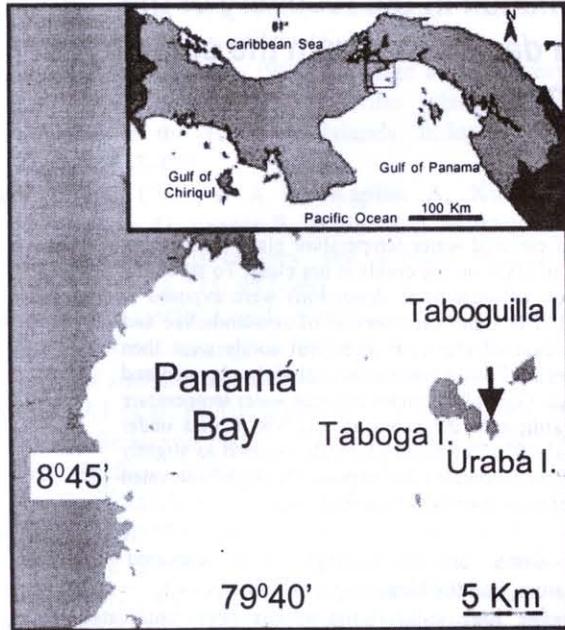
## Methods

Two hundred colonies of *Pocillopora damicornis* (8-10 cm in diameter) were collected at Urabá Island (Gulf of Panamá) at a depth of 4-6 m below mean low water, on May 20<sup>th</sup> 1992 (Fig. 1). Corals were placed in four holding tanks under running seawater filtered through a Strainrite polyester felt bags (pore size of 1 µm), ambient water temperature, and ambient light. After eight days corals had a healthy appearance showing normal coloration and expanded polyps. The initial condition of the endo-symbiosis was assessed by randomly sampling ten corals per tank. Branchlets measuring 2-3 cm in length were clipped from the corals.

<sup>1</sup> Maté: Smithsonian Tropical Research Institute, Box 2072, Balboa, Panamá. dcrozl@naos.si.edu

<sup>2</sup> Universidad de Panamá, Departamento de Biología Marina y Limnología, Estafeta Universitaria

<sup>3</sup> University of Miami, Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, 4600 Rickenbacker Causeway, Miami, FL 33149



**Fig. 1** Collection of *Pocillopora damicornis* at Urabá Island, Bay of Panamá (black arrow).

Coral fragments that were sampled were wrapped in aluminum foil and frozen ( $-20^{\circ}\text{C}$ ) and processed within the next 24 h. Coral tissues were removed with a jet of distilled water from an airbrush. Two aliquots of the resulting suspension were counted with a compound microscope using a hemacytometer to determine the number of zooxanthella cells (3 replicated counts). The suspension was then centrifuged at 2500 G for 10 minutes, the supernatant used for soluble protein analysis, and a solution of 90% acetone in distilled water added to the settled zooxanthella pellets and refrigerated in the dark for 24 h. The extract was analyzed for the concentration of chlorophyll *a* and *c*<sub>2</sub> according to Jeffrey and Haxo (1968). Coral soluble proteins were analyzed according to the method of Lowry (Peterson 1977) using the SIGMA protein assay kit (No. P5656). Coral surface area was estimated using the paraffin method of Glynn and D’Croze (1990). Results were log transformed to normalize the distribution.

#### Experimental bleaching

Healthy corals were selected for the bleaching experiment. One hundred and sixty colonies were distributed in 4 water tanks and gradually exposed to elevated water temperature supplied from a heated reservoir, under indirect sunlight, during 41 days (May 28<sup>th</sup> to July 10<sup>th</sup> 1992) by which time most corals were bleached. The mean ( $\pm$ SE) water temperature in the heated tank was  $30.76 \pm 0.1^{\circ}\text{C}$  (Table 1). Ten bleached corals were randomly sampled per tank and their symbiosis attributes analyzed as previously indicated.

#### Experimental recovery

Bleached corals showing expanded and active polyps were exposed to four experimentally simulated post-ENSO scenarios: slightly elevated water temperature and reduced exposure to ambient UVR (HT-UV), slightly elevated water temperature and exposure to ambient UVR (HT+UV), ambient water temperature and reduced exposure to ambient UVR (AT-UV), and ambient water temperature and exposure to ambient UVR (AT+UV). The experimental set-up consisted of six tanks (77.5 cm in length x 77.5 cm in width x 30.0 cm deep), and their position oriented to directly receive the morning sunlight (07:00-12:00). Raw seawater flowed into two 60 L glass aquaria used as reservoirs for the supply of seawater to the experimental tanks at a rate of approximately 2 liters  $\text{min}^{-1}$ . In both reservoirs seawater was stone aerated and filtered as previously described, before its distribution to the experiment tanks. Aquarium heaters were placed in one of the glass aquarium reservoirs in order to achieve an increase of  $1\text{-}2^{\circ}\text{C}$  above ambient temperature in the experiment tanks. Three tanks were supplied with heated seawater, and the other three with ambient temperature seawater. The water temperature was monitored daily at approximately 12:00 using a mercury thermometer with a resolution of  $0.02^{\circ}\text{C}$ .

**Table 1** General information on the experimental conditions during the bleaching and recovery of *P. damicornis*. \*\*\*:  $P < 0.001$ , \*\*:  $P < 0.01$ , and ns: non significant.

Condition	Mean $\pm$ SE (n)	P
1. Acclimation (20 May – 27 May 1992)		
a. Ambient water temp.	28.20 $\pm$ 0.40 (7)	
2. Experimental bleaching (28 May – 09 Jul 1992)		
a. Elevated water temp. ( $^{\circ}\text{C}$ )	30.76 $\pm$ 0.10 (31)	***
b. Ambient water temp. ( $^{\circ}\text{C}$ )	29.03 $\pm$ 0.16 (31)	
3. Experimental recovery (10 July – 28 August 1992)		
a. Elevated water temp. ( $^{\circ}\text{C}$ )	30.30 $\pm$ 0.10 (43)	***
b. Ambient water temp. ( $^{\circ}\text{C}$ )	28.68 $\pm$ 0.14 (43)	
c. UVR in (-UV) tanks ( $\text{W}\cdot\text{m}^{-2}$ )	0.03 $\pm$ 0.002 (45)	***
d. UVR in (+UV) tanks ( $\text{W}\cdot\text{m}^{-2}$ )	2.15 $\pm$ 0.07 (45)	
e. PAR in (-UV) tanks ( $\text{W}\cdot\text{m}^{-2}$ )	330.86 $\pm$ 20.1 (45)	ns
f. PAR in (+UV) tanks ( $\text{W}\cdot\text{m}^{-2}$ )	332.69 $\pm$ 27.1 (45)	
Elevated water temp.: bleaching vs. recovery		**
Ambient water temp.: bleaching vs. recovery		ns

Mean temperature ( $\pm$ SE) for the heated tanks was  $30.30^{\circ}\text{C} \pm 0.10$  and  $28.68^{\circ}\text{C} \pm 0.09$  for the ambient temperature tanks (Table 1). Half of each tank’s upper surface was covered by an acrylic panel (1 cm thick) tested to block out 99% of the UVR (Glynn et al. 1992); the other half was exposed to ambient light.

Discrete measurements of the solar irradiation were carried using the radiometer IL 1400A (International Light Inc.) equipped with PAR and UVR (356-367 nm) detectors. Mean PAR at 2-3 m depth on the collecting site was 200.1 watts m<sup>-2</sup> (± 21.0, n = 15 readings) and UVR was 1.52 watts m<sup>-2</sup> (± 0.16, n = 15). ANOVA tests showed that the difference in water temperature between the heated and ambient treatments (p<0.01), and between full and reduced exposure to ambient UVR was significant (p<0.01), but that the difference in PAR in tanks with and without the acrylic panels was not (Table 1).

Twenty corals were placed in each tank: 10 colonies were in the half side of the tank covered by the acrylic panel (reduced UVR), and the other 10 were directly exposed to sunlight. Corals were visually monitored for any change in color or and mortality during the 48 days of recovery (10 July to 28 August 1992). At the end of this period, branchlets were clipped from 5 randomly selected corals per treatment replicates and processed for the symbiosis attributes, as previously described. Results were tested for temperature and UVR effects using an ANOVA with tanks nested within temperature (Systat 1998).

## Results

### Experimental bleaching

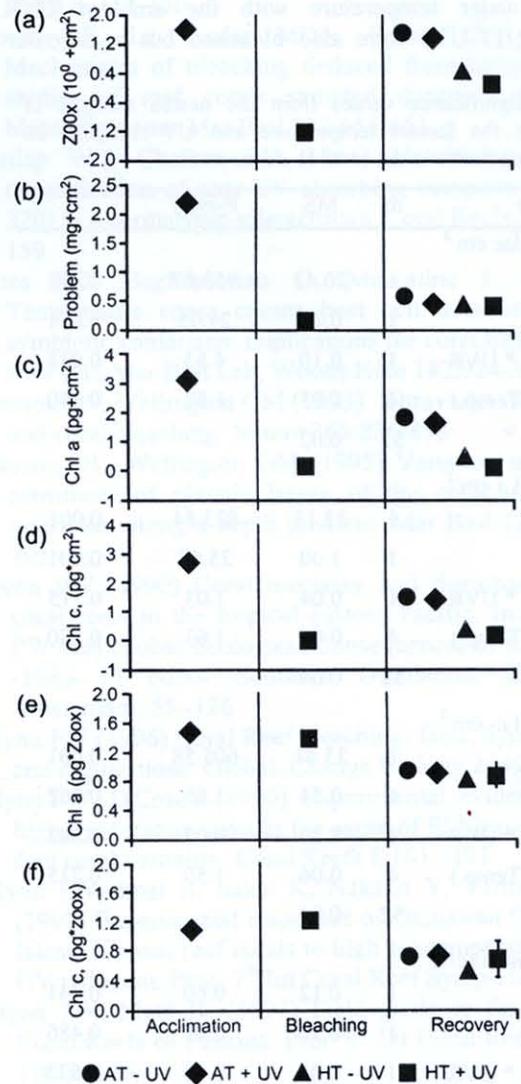
Only three *P. damicornis* colonies died during the bleaching phase of this experiment when 160 coral colonies were exposed to 30.76° C of water temperature for 41 days. Corals had their colorless polyps with a healthy appearance as noted by the expanded and highly active polyps. No mortality was recorded in the control group of corals.

Bleached coral colonies suffered significant decline in the density of zooxanthellae, chlorophyll *a* and *c*<sub>2</sub> per area (Figs. 2a-d). No significant changes were noted in the content of chlorophylls in the zooxanthellae (Figs. 2e-f) and in the concentration of soluble proteins (Fig. 2b). Analyses of variance indicated that differences in all symbiosis attributes were highly significant except in the chlorophylls per zooxanthella between the acclimated and bleached corals (see Fig. 2).

### Experimental recovery

Bleached corals exposed under slightly elevated water temperature (treatments HT+UV and HT-UV) had survivorship close to 60% (n=35), whereas, all corals returned to ambient water temperature (treatments AT+UV and AT-UV) survived (n=60). The appearance of surviving corals was remarkably different in corals at ambient water temperature (28.5° C) than at elevated water temperature (30.30° C). *P. damicornis* maintained at ambient water temperatures gradually regained the natural golden-brown coloration. Polyps were mostly expanded and activity was high. Corals under heated treatments remained bleached during these 48 days of additional exposure to elevated water temperature, and polyp condition steadily deteriorated during this time. Polyps in

most of the cases were retracted into the coral skeleton and showed little activity. This was especially evident in corals exposed to HT+UV which were the most affected (Fig. 2).



**Fig. 2 a-f** Natural logarithm means (± SE) in zooxanthella densities, chlorophyll (*a*, *c*<sub>2</sub>) concentrations, and soluble proteins in *Pocillopora damicornis* after 8 days of acclimation, 41 days of experimental warming when corals were bleached, and 48 days of exposure to simulated post-ENSO conditions. HT-UV: slightly elevated water temperature and reduced exposure to ambient UVR, HT+UV: slightly elevated water temperature and exposure to ambient UVR, AT-UV: ambient water temperature and reduced exposure to ambient UVR, and AT+UV: ambient water temperature and exposure to ambient UVR.

Corals returned to ambient water temperature levels rapidly regained their zooxanthellae regardless of the presence of UVR (Fig. 2a). In contrast, corals maintained

under slightly elevated water temperature did not regain their zooxanthellae complement and remained severely paled or bleached during the recovery experiment. The most negative impact was observed in the HT+UV treatment and zooxanthella levels in those bleached corals were in the order of  $10^4 \text{ cm}^{-2}$  (Fig. 2a). Corals exposed to elevated water temperature with the ambient UVR removed (HT-UV) were also bleached but to a lower

**Table 2** Significance values from the nested analysis of variance of the factors temperature and UV radiation on symbiosis attributes in the coral *P. damicornis*.

Source	df	MS	F-ratio	P
<b>Zooxanthellae <math>\text{cm}^{-2}</math></b>				
Temp.	1	20.43	953.07	0.001
UVR	1	0.62	29.05	0.001
Temp. * UVR	1	0.10	4.53	0.038
Tank (Temp.)	4	0.03	1.82	0.140
Error	52	0.02	-	-
<b>Chlorophyll <math>a \text{ cm}^{-2}</math></b>				
Temp.	1	32.13	823.84	0.001
UVR	1	1.00	25.67	0.001
Temp. * UVR	1	0.04	1.03	0.315
Tank (Temp.)	4	0.06	1.63	0.180
Error	52	0.04	-	-
<b>Chlorophyll <math>c_2 \text{ cm}^{-2}</math></b>				
Temp.	1	23.41	605.58	0.001
UVR	1	0.14	3.65	0.062
Temp. * UVR	1	0.00	0.02	0.882
Tank (Temp.)	4	0.06	1.50	0.215
Error	52	0.04	-	-
<b>Soluble proteins <math>\text{cm}^{-2}</math></b>				
Temp.	1	0.12	0.60	0.441
UVR	1	0.10	0.49	0.486
Temp. * UVR	1	0.05	0.23	0.633
Tank (Temp.)	4	0.48	2.33	0.068
Error	52	0.21	-	-
<b>Chlorophyll <math>a \text{ zooxanthella}^{-1}</math></b>				
Temp.	1	0.11	0.83	0.366
UVR	1	0.01	0.06	0.813
Temp. * UVR	1	0.07	0.52	0.473
Tank(Temp.)	4	0.11	0.86	0.495
Error	52	0.13	-	-
<b>Chlorophyll <math>c_2 \text{ zooxanthella}^{-1}</math></b>				
Temp.	1	0.25	0.92	0.343
UVR	1	0.19	0.68	0.414
Temp. * UVR	1	0.11	0.39	0.534
Tank (Temp.)	4	0.40	1.44	0.234
Error	52	0.28	-	-

extent than those of the HT+UV treatment. Zooxanthella density in this treatment was an order of magnitude higher than in the HT+UV treatment (Fig. 2a). The response of chlorophyll  $a \text{ cm}^{-2}$  to the experimental conditions mirrored those observed for the density of zooxanthellae. Water temperature and UVR both independently and synergistically had significant effects on zooxanthellae  $\text{cm}^{-2}$  (Table 2). Corals returned to ambient water temperature levels rapidly increased the levels of chlorophyll regardless of their exposure to UVR.

Coral colonies maintained at elevated water temperature continue to lose chlorophyll with the most bleached colonies being those in the HT+UV treatment (Fig. 2c). The concentration of chlorophyll  $c_2 \text{ cm}^{-2}$  was significantly affected only by water temperature (Table 2). Corals returned to ambient water temperatures rapidly regained the concentration of chlorophyll per area regardless of UVR (Figs. 2c-d), while corals maintained under elevated water temperature remained pale-bleach and with lower concentration of chlorophylls. No significant differences were observed in the concentration of chlorophylls per zooxanthella and in the concentration of soluble proteins per area (Table 2). Also, there is no tank effects on any of the symbiosis attributes considered.

## Discussion

This experiment demonstrated that the recovery of thermally stressed *P. damicornis* can be hampered by exposure to high sub-lethal water temperatures, exposure to UVR, or by the synergy between these factors. The coral-zooxanthella symbiosis may be individually or synergistically affected by elevated water temperature and UVR, as shown in attributes such as the density of zooxanthellae, and the concentration of chlorophyll  $a$  (Table 2). However, elevated water temperature is the most important factor determining the fate of bleached corals due to thermal stress. Corals rapidly recovered their zooxanthellae complement and photosynthetic pigments when temperature returned to normal conditions, regardless of the level of UVR (Fig. 2). In this regard, coral species may show different strategies to cope with high irradiance: (a) the presence of mycosporine-like amino acids (MAAs) which provides protection against exposure to short-wavelength radiations (Dunlap et al. 1986, Shick et al. 1996); (b) a photobiological system where fluorescent pigments regulate the light exposure which reaches the zooxanthellae (Salih et al. 2000); and (c) polyps retracting deep into the coral skeleton, as in *Porites* spp. (Hoegh-Guldberg 1999).

In manipulative bleaching experiments with the intertidal zoanthid *Palithoa caribaeorum* (Lesser et al. 1990), and with *P. damicornis* (Glynn et al. 1992) the decline in the number of zooxanthellae, and in the concentration of chlorophylls was principally due to elevated water temperatures. While these two studies have shown that UVR was not responsible for the bleaching, a decline in UV absorbing compounds was found when shallow habitat corals were exposed to elevated water temperatures. According to Lesser et al. (1990) photo-protecting molecules are thermally labile and their

concentration decline when corals are exposed to elevated water temperatures.

However, Michalek-Wagner (2000) showed that MAAs in soft corals is not thermally labile, and when exposed to the combination of elevated water temperature and high UVR the concentration of photo-protecting molecules will increase providing additional resistance. These contrasting results might suggest that the MAA mechanism of photo-protection is specific to the symbiotic association, and might also depend on the habitat of the coral. For example, the concentration of UV absorbing compounds is an adaptive photo-protecting mechanism which varies with depth (Dunlap et al. 1986, Gleason and Wellington 1995) and coral species which thrive in shallow water habitats exhibit higher concentration of MAAs, enhancing their resistance to solar irradiance. There is a direct relationship between irradiance of solar UVR and the concentration of MAAs in the coral *P. damicornis* (Jokiel et al. 1997).

The initial 41 day exposure of *P. damicornis* to slightly elevated water temperature, and to a full dose of irradiance likely weakened the chemical photo-protecting mechanism. The steadily decline in the condition of corals subjected to the combination of slightly elevated water temperature and full exposure to UVR (HT+UV) might involve the irreversible disruption of the symbiotic association by a succession of processes including: (a) the loss of photosynthetic capacity due to heat-induced damage to Photosystem II (Iglesias-Prieto 1997, Warner et al. 1996); (b) the reduced photosynthetic-electron transport leading to the production of toxic forms of oxygen (Lesser et al. 1990); (c) histopathological abnormalities in both coral tissue and zooxanthellae (Glynn and D'Croz 1990, Gates et al. 1992, Brown et al. 1995); and (d) the increased metabolism of the host due to high water temperature, and the consequent decline in energy reserves in the form of lipid levels or as somatic tissue (True 2000).

In conclusion, this experiment has shown that elevated water temperature and UVR play an important role during the recovery process of thermally stressed corals.

**Acknowledgements** Authors are grateful to the following people: J. Del Rosario, F. Cedeño, and D. Avila for assistance during the development of the experiments; A. Velarde for logistical arrangements and facilities; P.W. Glynn for advice, and financial support from his NSF grant OCE-9314798, and O. Hoegh-Guldberg, K. Kaufmann, and two anonymous reviewers for comments on the manuscript.

## References

- Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16(Suppl):129-138
- 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
- Brown BE, Dunne RP, Goodson MS, Douglas AE (2000) Marine Ecology: bleaching patterns in reef corals. *Nature* 404:142-143
- Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8: 163-170
- Brown BE, Le Tissier MDA, Bythell JC (1995) Mechanisms of bleaching deduced from histological studies of reef corals sampled during a natural bleaching event. *Mar Biol* 122:655-663
- Dunlap WC, Chalker BE (1986) Identification and quantification of near-UV absorbing compounds (S - 320) in a hermatypic scleractinian. *Coral Reefs* 5:155 - 159
- Gates RD, Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. *Biol Bull Mar Biol Lab, Woods Hole* 182:324-332
- Gleason DF, Wellington GM (1993). Ultraviolet radiation and coral bleaching. *Nature* 365:836-838
- Gleason DF, Wellington GM (1995) Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Mar Biol* 123:693-703
- 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 -1983 El Niño -Southern Oscillation*. Elsevier, Amsterdam: 55 -126
- Glynn PW (1996) Coral Reef bleaching: facts, hypotheses and implications. *Global Change Biology* 2: 495 - 509
- 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
- Glynn PW, Imai R, Sakai K, Nakano Y, Yamazato K (1992) Experimental responses of Okinawan (Ryukyu Islands, Japan) reef corals to high sea temperature and UV radiation. *Proc. 7<sup>th</sup> Int Coral Reef Symp* 1:27-37
- Glynn PW, Maté JL (1997) Field guide to the Pacific Coral Reefs of Panamá. *Proc 8<sup>th</sup> Int Coral Reef Symp* 1:145 -166
- Glynn PW, Maté JL, Baker AC, Calderón MO (in press) Coral bleaching and mortality in Panamá and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-1983 event. *Bull Mar Sci*
- Goenaga C, Vicente VP, Armstrong RA (1989) Bleaching induced mortalities in reef corals from La Parguera, Puerto Rico: a precursor of change in the community structure of coral reefs? *Carib J Sci* 25:59-65
- Hoegh-Guldberg O (1999) Coral bleaching, Climate Change and the future of the world's Coral Reefs. *Mar Freshwater Res* 50:839-866.
- Hoegh-Guldberg O, Salvat B (1995) Periodic massive 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 CJ (1989) The effect of sudden changes in temperature, light and salinity on the

- population density and export of zooxanthellae from the reef corals *Sylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J Exp Mar Biol Ecol* 129:279-303
- Iglesias-Prieto R (1997) Temperature-dependent inactivation of Photosystem II in symbiotic dinoflagellates. *Proc 8<sup>th</sup> Int Coral Reef Symp* 2:1313-1318
- Jeffrey SW, Haxo FT (1968) Photosynthetic pigments of symbiotic dinoflagellates (zooxanthellae) from corals and clams. *Biol Bull* 135:149-165
- Jokiel PL, Lesser MP, Ondrusek ME (1997) UV-absorbing compounds in the coral *Pocillopora damicornis*: Interactive effects of UV radiation, photosynthetically active radiation, and water flow. *Limnol Oceanogr* 42:1468-1473
- Jones R, Hoegh-Guldberg O, Larkum AWL, Schreiber U (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. *Plant Cell and Environment* 21:1219-1230.
- Kinzie RA III (1993) Effects of ambient levels of solar ultraviolet radiation on zooxanthellae and photosynthesis in the reef coral *Montipora verrucosa*. *Mar Biol* 116:319-327
- Lang JC, Wicklund RI, Dill RF (1988) Depth- and habitat-related bleaching of zooxanthellate reef organisms near Lee Stocking Island, Exuma Cays, Bahamas. *Proc 6<sup>th</sup> Int Coral Reef Symp* 3:269-274
- Lesser MP, Stochaj WR, Tapley DW, Shick 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
- Michalek-Wagner K (2000) The effect of high irradiance and temperature on tissue levels of UV-absorbing MAAs in soft corals. No evidence for thermal lability of MAAs. *9<sup>th</sup> Int Coral Reef Symp* (Abstract page 256)
- Peterson GL (1977) A simplification of the protein assay method of Lowry et al. which is more generally applicable. *Anal Biochem* 83:346-356
- Salih A, Larkum A, Cox G, Kuhl M, Hoegh-Guldberg O (2000) Fluorescent pigments in corals are photo-protective. *Nature* 408:850-853
- Shick JM, Dunlap WC, Jokiel PL (1996) Effects of ultraviolet radiation on corals and other coral reef organisms. *Global Change Biol* 2: 527-545
- Systat (1998). *Statistics*. Version 8.0. SPSS, Inc: 1086 pp
- True J (2000) Changes in the lipid content and tissue thickness variation in the massive coral *Porites* during natural and experimental bleaching events. *9<sup>th</sup> Int Coral Reef Symp* (Abstract page 259)
- Warner ME, Fitt WK, Schmidt GW (1996) The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae *in hospite* from four different species of reef corals: a novel approach. *Plant Cell and Environment* 19:291-299