

## Indicators of UV Exposure in Corals and Their Relevance to Global Climate Change and Coral Bleaching

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### ABSTRACT

A compelling aspect of the deterioration of coral reefs is the phenomenon of coral bleaching. Through interactions with other factors such as sedimentation, pollution, and bacterial infection, bleaching can impact large areas of a reef with limited recovery, and it might be induced by a variety of stressors including temperature and salinity extremes, and ultraviolet light. Under conditions of ocean warming, often associated with calm and stratified waters, photobleaching of UV-absorbing chromophoric dissolved organic matter (CDOM) is increased, and penetration of both UV-B and UV-A is greatly enhanced. Indices of UV-specific effects in coral tissue are needed to test whether UV increases, associated with global climate change, are harmful to corals. To address this challenge, we have evaluated UV-specific effects in corals and have characterized factors that alter penetration of UV radiation over coral reefs.

An immunoblotting assay was developed to examine UV-specific lesions (thymine dimers) in coral and zooxanthellae DNA. We observed dose-dependent increases of thymine dimers in coral (*Porites porites* var *porites*) exposed to artificial solar irradiance in a solar simulator, although effects were not strictly proportional.

UV measurements were made in July 1999 at Eastern Sambo reef and nearby sites, including profiling along transects from reef to shore. Results of these analyses indicate that the coral at Eastern Sambo reef (at 3-4 meters) were receiving UV-B radiation that was equivalent to 25 to 30% of surface UV irradiance. However, the water just inside the reef in Hawk Channel (located closer to land) was considerably more opaque to UV. This water photobleached with loss of UV absorbance and fluorescence when it was exposed to simulated solar radiation. These results indi-

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cate that photobleaching of the DOM and transport of near-shore water out over the reefs might play a key role in controlling UV penetration to the reef surface.

**Key Words:** corals, coral bleaching, photobleaching, dissolved organic matter, thymine dimers, biomarkers.

## INTRODUCTION

The overall degradation of coral reefs, measured by declining coral abundance and species diversity as well as increases in macroalgae and reef skeletal erosion, has been documented in the Florida Keys (Dustan 1977; Ginsberg 1993; Porter and Meier 1992; Sebens 1994). Declines in reef health have been attributed to anthropogenic impacts including nutrient inputs, increased sediment loading, and global climate change (Williams and Bunkley-Williams 1990; Hallock *et al.* 1993; Leichter *et al.* 1996; Hoegh-Guldberg 1999; Barber *et al.* 2001). These changes are contributing to the elevated occurrence of coral bleaching, coral diseases, and overall ecological deterioration of the Florida Keys reef tract.

Coral bleaching might be the sign of coral reef degradation that is most closely linked to climate change. Bleaching, through interactions with other factors such as sedimentation, pollution, and bacterial infection, can contribute to the destruction of large areas of reef with limited recovery (Williams and Bunkley-Williams 1990; Glynn and Weerdt 1991; Brown 1997). Records of coral bleaching from 1870 to the present indicate that the severity, and frequency have reached unprecedented levels (D'Elia *et al.* 1991; Glynn 1993). Only three bleaching events were reported between 1876 and 1979, compared to over 60 bleaching episodes from 1980 to 1993 (Glynn 1993). Most recently, the El Nino Southern Oscillation (ENSO) conditions during 1997 to 1998 induced worldwide bleaching from the Western Atlantic to the Great Barrier Reef. Although numerous studies have been conducted to evaluate the adaptive capacity of reef corals to physical environmental stress (Brown 1997 for review), recent reports speculate that the frequency and severity of coral bleaching will continue to rise, with annual bleaching events occurring in the Caribbean as early as the year 2020 (Hoegh-Guldberg 1999). If these predictions prove accurate, then the prognosis for recovery from large bleaching events might be poor.

Although bleaching has been correlated with increased temperatures, many studies have concluded that solar irradiance might also be implicated as a stressor producing additive or synergistic effects (Shick *et al.* 1996; Brown 1997 for reviews; Brown *et al.* 2000). Some investigations have focused on UV-induced bleaching (Gleason and Wellington 1993; Kinzie 1993). Other studies have concluded that photosynthetically active radiation (PAR) is responsible for the bleaching; these studies indicated that elevated temperatures render zooxanthellae more susceptible to PAR-induced photoinhibition and oxidative stress (Warner *et al.* 1996; Jones *et al.* 1998; Hoegh-Guldberg and Jones 1999; Hoegh-Guldberg 1999). Field data documenting increased frequency of bleaching on more exposed surfaces of coral support the potential significance of interactions between temperature and solar radiation (Williams and Bunkley-Williams 1990; Brown *et al.* 2000). Further research is needed to resolve the potential mechanisms of interaction between temperature

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and solar irradiance as well as to determine which wavelengths are most effective in inducing coral bleaching.

An important gap in the coral literature is the absence of research on DNA damage and repair. DNA is generally considered the principle target of UV damage in many types of animal tissue (Mitchell and Karentz 1993). Techniques to evaluate UV-induced DNA damage and repair in aquatic organisms have been limited by the lack of availability of antibodies raised against the cyclobutane dimers and other photoproducts. Currently, only a few antibodies available worldwide have been used in investigations related to aquatic organisms (Gieskes and Buma 1997; Vetter *et al.* 1999; Malloy *et al.* 1997). In this study, we report a technique based on use of a commercially-available anti-thymine dimer antibody (Kamiya, Inc.). This technique enables us to characterize DNA damage and repair associated with UV irradiance and to evaluate DNA damage in combination with studies of photoprotection mechanisms, such as pigment induction. Once UV-induced responses are characterized, then synergistic effects of temperature and UV in combination can be better understood. In particular, direct DNA damage associated with UV radiation, in combination with electrophilic attack on DNA associated with oxidative stress, may be a mechanism of temperature and UV synergy.

On a global basis, solar UV-B radiation is most intense in the tropics and subtropics (Madronich *et al.* 1995; Herman *et al.* 1996), and because the UV tolerances of marine organisms are so poorly understood, it is possible that even small increases in UV exposure may be biologically significant. Most people associate increased UV-B irradiance with ozone depletion; however, in the tropical oceans it might also be associated with global warming.

There is concern that UV-B exposure in the upper ocean is enhanced during periods of ocean warming and stratification, that result in calm water conditions of exceptionally high clarity (Gleason and Wellington 1993; Fitt and Warner 1995; Glynn 1996; Shick *et al.* 1996). Several recent studies have shown that warm conditions and stratification favor increased UV-B penetration into lakes (Schindler *et al.* 1996; Leavitt *et al.* 1997; Morris and Hargreaves 1997) and oceans (Vodacek *et al.* 1997; Siegel and Michaels 1996). This effect has been attributed to reduced inputs of UV-absorbing dissolved organic matter (DOM) into the water from land during periods of drought, reduction in inputs of DOM from deeper water by stratification, and loss of DOM from photobleaching and other pathways.

Analyses over a 43-year period (1950-1992) show that the North Atlantic area of NE trades west of 40°W along 10°N to 20°N has experienced higher sea-surface temperatures and low wind speeds associated with ENSO conditions (Enfield and Mayer 1997). Moreover, tropical storms have decreased over the North Atlantic during the 1940's to the mid 1990's (Landsea and Nicholls 1996). These results suggest that waters over coral assemblages in South Florida have been experiencing lower wind stress and warmer temperatures in recent years, conditions that favor more intense stratification, greater photobleaching of CDOM, and deeper UV-B penetration.

The possibility exists that a variety of large-scale changes in sea surface temperatures and UV penetration might interact to cause, or perhaps enhance, the frequency of coral bleaching. Research is needed to assess temporal and spatial patterns of UV-B and UV-A irradiance on coral reefs as well as to detect UV-induced

damage. If UV contributes to coral bleaching, then monitoring efforts must include not only assessment of sea surface temperatures and indices of bleaching, but also UV measurements over reefs and indicators of UV-specific damage. We have developed a program to assess UV in the reef environment and UV-specific DNA damage in zooxanthellae and coral. Preliminary findings and potential implications are discussed below.

## METHODS

UV profiles of the water column were obtained at a series of sites along the Florida Keys on a cruise aboard the *OSV Peter W. Anderson* (Patterson 2000). These profiles were obtained using a Biospherical PUV 550/500 instrument at sites ranging from the Dry Tortugas in the western Keys to Elkhorn Reef in the eastern Keys. A Biospherical PUV 550/500 instrument also was used to make direct measurements of UV reaching the coral surface at the Eastern Sambo site where underwater diurnal coral experiments were conducted. Additional UV measurements were made using a Satlantic OCP-100 free-falling instrument during July 1999 at sites in the Lower Keys that were located close to coral reefs at Looe Key and at the Eastern Sambo site. These measurements included those at a series of stations that were located along a south-north transect from the Atlantic Ocean outside the Eastern Sambo reef across Hawk Channel, the 7 to 10 km zone that is located between the Lower Keys fringing reefs and the land. Water samples were concurrently obtained at these sites, and absorption and fluorescence spectra of the filtered (0.2 m) water samples were measured. UV-visible absorption spectra were obtained using an Agilent 8453E UV-Visible Spectroscopy System. Fluorescence spectra were measured using a ISA SPEX Fluorolog 3 Spectrofluorometer and a Shimadzu Model RF-10AxL Fluorometer. Sigma Stat (SPSS Inc.) was used to perform exponential regressions on the UV-depth profiles and non-linear exponential regressions on the UV spectral data. Irradiation of coral and water samples was conducted in an Atlas Suntest CPS solar simulator equipped with a water bath to control the temperature. Doses to water were equivalent to estimated sea surface mid-day values for August and approximately twice the levels reported for coral exposures (see Figure 5).

Thymine dimers were measured using an immunoblotting technique that we have recently developed using a commercially available antibody. Briefly, frozen coral samples were homogenized with a mortar and pestle in Tris EDTA (TE) buffer, and DNA was extracted using a Qiagen Dneasy Kit. Next, DNA was blotted onto a nitrocellulose membrane, vacuum baked, blocked for 30 min using 5% milk in phosphate-buffered saline with 0.2% Tween 20 (PBST) and incubated with primary antibody (Kamiya, Inc.) overnight. Subsequently, blots were washed four times for 10 min in PBST, then secondary antibody was applied at 1:5000 concentration (Fab complex goat anti-mouse antibody conjugated to horseradish peroxidase) for 1 h and washed four times for 20 min in PBST. Chemiluminescent substrate (Pierce) is applied and visualized on X-ray film. Films are analyzed for densitometric differences using a flatbed scanner. Relative pixel intensity is determined using image analysis software (Scion Image, NIH). Data presented here are expressed as pixel intensities; however, laboratory standards are being developed that will enable us to quantify the number

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of thymine dimers per kilobase of DNA. Finger coral (*P. porites*) were irradiated in a SunTest solar simulator for 1, 2, and 4 h to determine whether a dose response to UV light occurred.

### RESULTS

The UV irradiance in water over and near the coral reefs at depth  $z$ ,  $E(\lambda, z)$ , could be related to the irradiance immediately below the water surface,  $E(\lambda, 0)$ , by the exponential relationship:

$$E(\lambda, z) = E(\lambda, 0) e^{-K_d(\lambda) z} \quad (1)$$

where  $K_d(\lambda)$  is the diffuse attenuation coefficient of the water at wavelength  $\lambda$ . Values of  $K_d(\lambda)$  were determined by exponential regressions using data for depths where the irradiance was  $>1\%$  of  $E(\lambda, 0)$  ( $r^2 > 0.98$  in the UV region). Analyses of the UV and visible spectral data for the dissolved substances in filtered water samples ( $0.2 \mu\text{m}$ ) from the sites near Eastern Sambo reef (Figure 1) indicated that they could be closely described by a non-linear exponential function, as observed with other seawater samples (*e.g.*, Blough *et al.* 1993):

$$a(\lambda) = c + a(412) * \exp -S(\lambda - 412) \quad (2)$$

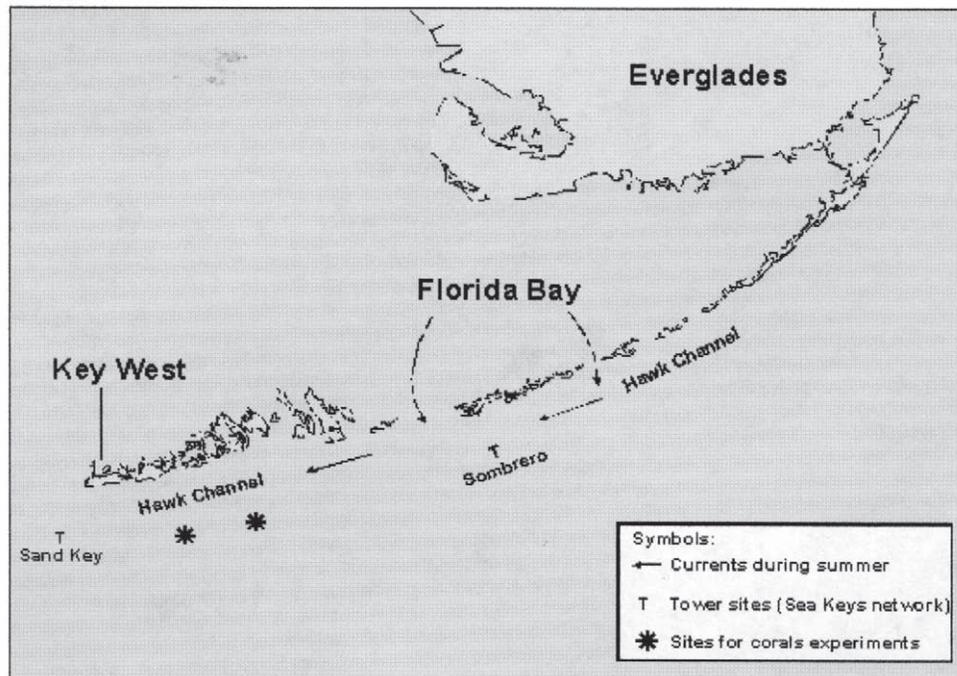
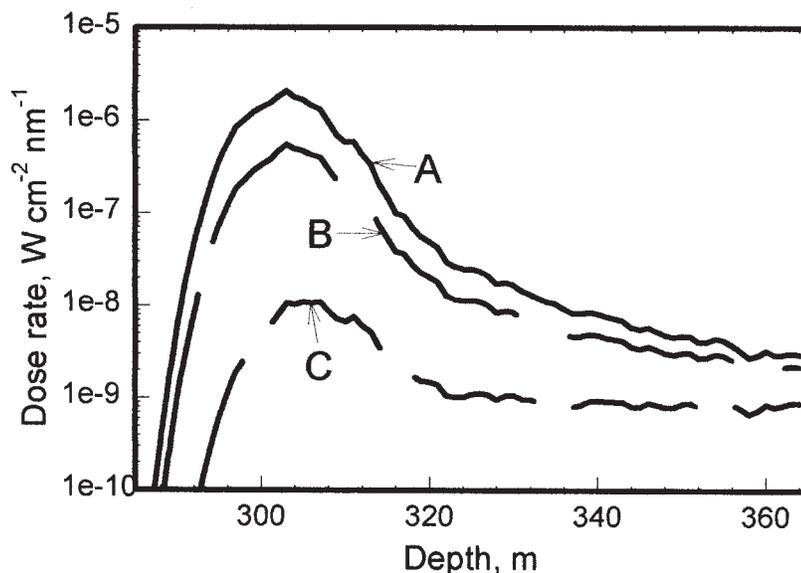


Figure 1. Map of the Florida Keys, USA, and the location of sites used in this study.

where  $\lambda$  is the wavelength in nm,  $a(\lambda)$  is the absorption coefficient of the water ( $\text{m}^{-1}$ ),  $S$  is a spectral slope coefficient that characterizes how rapidly the absorption decreases with wavelength, and the other terms are fitting parameters. Values of  $S$  ranged from 0.018 up to 0.026 for the 300 to 500 nm range and  $r^2$  values for the exponential fits were  $>0.98$  in all cases. The absorption coefficients generally were higher and the slope coefficients lower in Hawk Channel, closer to land. Also, we observed that the slope coefficients were somewhat wavelength dependent, decreasing with increasing wavelength, especially for the clear ocean water outside the reefs. Values of  $K_d(\lambda)$  in the short wavelength UV region ( $<340$  nm) were close to the  $a(\lambda)$  for water samples collected at the same sites [typically  $K_d(\lambda)$  was  $<1.2$  times greater than  $a(\lambda)$ ], indicating that UV attenuation was dominated by dissolved substances in the water, likely the colored dissolved organic matter (CDOM).

Using the diffuse attenuation and absorption coefficients to estimate UV penetration into the seawater, the TUV model of Madronich (1993) to estimate surface solar spectral irradiance at these sites, and the Setlow action spectrum for DNA damage (Setlow 1974), we computed dose rates of DNA-damaging UV at Eastern Sambo and a nearby site in Hawk Channel (Figure 2). The coral reefs at Eastern Sambo were receiving considerable exposure to DNA-damaging radiation during July, approximately 25 to 35% of surface UV irradiance at a depth of 3 to 4 meters (Figure 2). The water just inside the reef in Hawk Channel and closer to land was



**Figure 2.** DNA-damaging weighted irradiance estimated for the near surface and at a depth of 4.0 meters for Eastern Sambo coral reef and for a mid-Hawk Channel site located in the Florida Keys. The Hawk Channel site was located 4 km north of the Eastern Sambo coral reef. The dose rates noted as follows are integrated over the UVR region (280 to 400 nm): A, near surface, dose rate =  $2.2 \times 10^{-5}$   $\text{W cm}^{-2}$ ; B, depth = 4.0 m at Eastern Sambo reef, dose rate =  $6.6 \times 10^{-6}$   $\text{W cm}^{-2}$ ; C, depth = 4.0 m at mid-Hawk Channel site, dose rate =  $1.8 \times 10^{-7}$   $\text{W cm}^{-2}$ .

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nearly two orders of magnitude more opaque to UV (Figure 2). Underwater measurements of the diurnal variation of solar UV irradiance (305, 320, 340, and 380 nm) and PAR reaching the reef surface at the Eastern Sambo site also were made (Figure 3). The substances in the water samples from Hawk Channel photobleached with loss of UV absorbance and fluorescence and an increase in the spectral slope coefficient  $S$  when the water was exposed to simulated solar radiation (Figure 4). These data indicate that interactions between photobleaching of the CDOM and climate-sensitive transport of near-shore water out over the reefs might play a key role in controlling UV penetration to the reef surface.

Coral exposed to simulated solar radiation showed increased thymine dimers with increased exposure time, representing doses of 0.468, 0.935, and 1.870 joules  $\text{cm}^{-2}$  of DNA damaging UV, based on the Setlow action spectrum (Figure 5). Effects were not strictly proportional to dose. This could be a result of a variety of methodologic issues that are now under investigation and/or DNA repair in the coral at low doses. Additional research in our laboratory has demonstrated that thymine dimers are also detected under realistic field exposure conditions (unpublished data).

## DISCUSSION

The initial results reported here suggest that UV intensities reaching Florida Keys reefs may be linked to climate-sensitive transport of CDOM over the reefs and its interaction with photobleaching of the CDOM. Because CDOM absorbs UV-B much more strongly than it absorbs visible radiation, it tends to reduce exposure of the corals to harmful UV-B radiation, while allowing most of the essential photosynthetically active radiation to reach the reef surface. Likely sources of the CDOM include sea grasses that are abundant near the reefs and in Hawk Channel, on-shore mangroves, and transport of CDOM from Florida Bay, a region that lies south and west of the Everglades in south Florida. Tidal channels between the Florida Keys

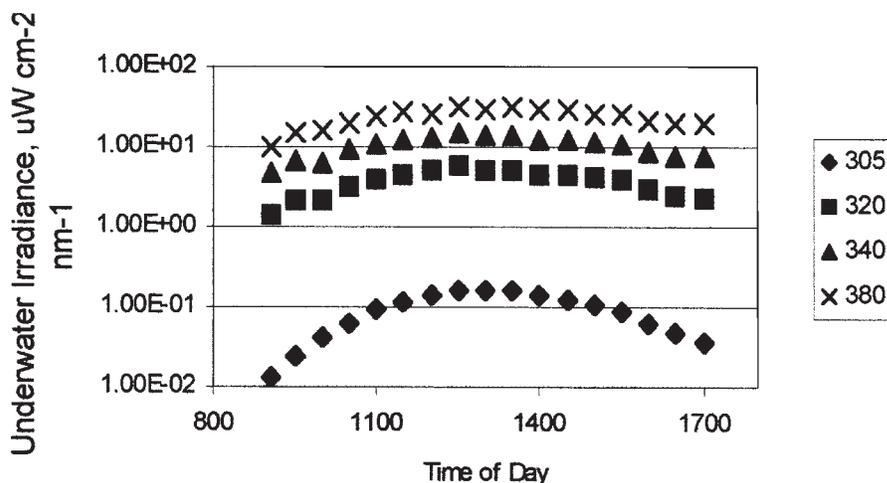
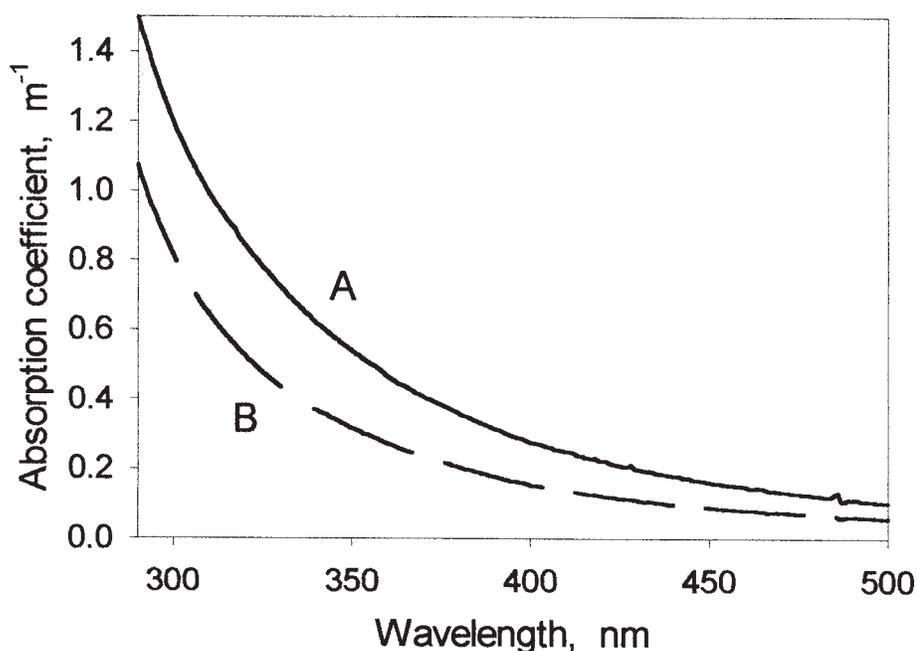


Figure 3. Diurnal variation in UV irradiance reaching the coral reef surface (depth 4.0 m) at Eastern Sambo reef, Florida Keys on July 21, 1999.



**Figure 4.** Decrease in UV absorption coefficients (photobleaching) of the CDOM in a mid-Hawk Channel Florida Keys water sample on exposure to simulated solar radiation. [Irradiance measured using calibrated Optronics Model 754 Spectroradiometer was  $1.24 \times 10^{-4} \text{ W cm}^{-2}$  in the UV-B region (280 to 315 nm) and  $3.71 \times 10^{-3} \text{ W cm}^{-2}$  in the UV-A (315 to 400 nm), approximately equivalent to mid-afternoon solar radiation during July in the Florida Keys on a clear day]. A, prior to irradiation; B, after 18 h of irradiation in solar simulator.

connect Florida Bay to the Atlantic coastal zone of the Keys and this CDOM generally moves in a westerly direction along Hawk Channel in the Middle and Lower Keys (Lee *et al.* personal communication; Lee and Williams 1999). Climatic factors, such as regional shifts in precipitation frequency and intensity over the Everglades, can strongly affect the amounts of CDOM that enter Hawk Channel from Florida Bay. Human activities, such as the large scale changes in Everglades hydrology that have occurred since the early 1900s, likely interact with climatic changes to alter CDOM concentrations in waters around the Keys. Photobleaching of the CDOM in the surface waters of Hawk Channel and in stratified water outside the reefs might also play an important role in this overall picture.

Future studies will include determination of the sources and spatial distributions of CDOM over the reefs, use of fluorometry to determine CDOM seasonal distributions at selected sites on the reefs, examination of the influence of particulate matter on UV exposure at the reefs, and studies of factors that affect the photobleaching and other degradation pathways of the CDOM. To determine the mean distributions and seasonal cycles of CDOM at the coral reefs, we have moored Wetlabs Sea Tech CDOM fluorimeters at one of the Coastal Marine Automated Network (CMAN) tower sites that are located in the Lower and Middle Keys. The

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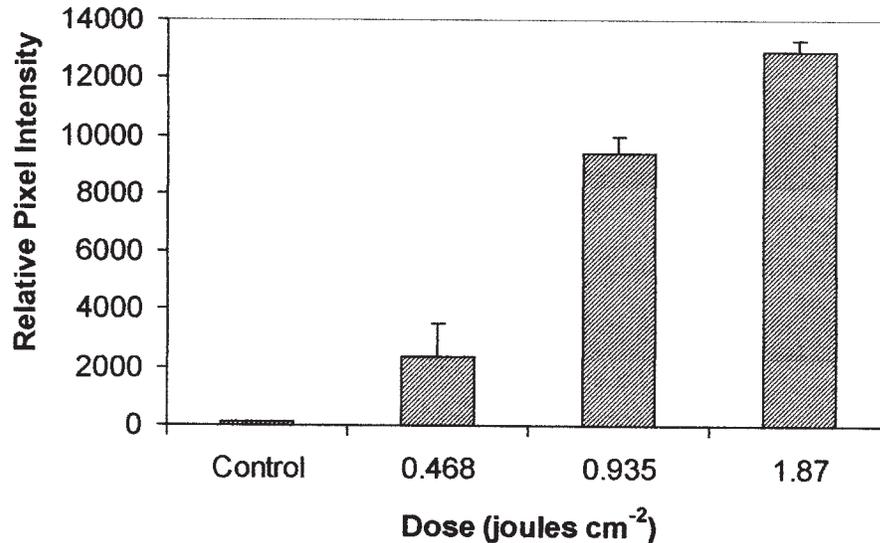


Figure 5. Induction of thymine dimers in *P. porites* using a solar simulator. The average and range of duplicate samples are presented.

CMAN sites also are equipped with instruments that record wind and current observations and other ancillary data such as PAR, transmittance, and chlorophyll fluorescence that might be relevant to evaluations of the sources of the CDOM over the reefs.

The immunoblotting technique we developed will be useful to assess direct DNA damage associated with UV exposure. By making use of a commercially available antibody, our technique can be easily adapted in other laboratories. Development of a standard to convert fluorescence intensity to thymine dimers has involved irradiation of salmon DNA with a calibrated UV source and validation against standards of known dimer quantities. Use of laboratory standard in future studies should facilitate transfer of the technique to other laboratories. Our ongoing research program is also examining natural cycles of DNA damage and repair in both coral and zooxanthellae in combination with pigment induction in several species. These techniques will allow us to study interactive effects of solar irradiance and increased temperature, to determine which wavelengths are responsible for synergistic effects, and characterize the role that DNA damage plays in coral bleaching. We are also developing immunolocalization procedures that will allow us to determine whether thymine dimers are located primarily in coral tissue or zooxanthellae.

Recent authoritative reviews (Brown 1997; Hoegh-Guldberg 1999; Reaser *et al.* 2000; Wilkinson 1998; Wilkinson 2000) concur that increased sea surface temperatures associated with global climate change explain a greater proportion of the occurrences of coral bleaching than any other factor; however, they also confirm that solar radiation has an important secondary or synergistic effect in some instances. To date, there is no consensus regarding the relative effects of increased PAR wavelengths as opposed to UV radiation (Brown 1997). Lesser (1996) observed that elevated temperature and UV radiation cause oxidative stress in zooxanthellae.

More recently, Jones *et al.* (1998) have contended that increased PAR irradiance in combination with increased temperature elicits oxidative stress associated with photoinhibition. By either mechanism, damage to DNA from electrophilic attack may result. We contend that direct DNA damage by UV light should be evaluated as an additional stress on both coral and zooxanthellae. Ultimately, a detailed knowledge of combined stressors is needed to predict the occurrence, and potentially the impact, of coral bleaching worldwide.

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