ABSTRACT

THE EFFECTS OF ULTRAVIOLET RADIATION ON SKELETAL GROWTH AND BLEACHING IN FOUR SPECIES OF HAWAIIAN CORALS

By

Gwen Davies Goodman

May 1991

Coral bleaching has been attributed to many factors, including increased exposure to ultraviolet radiation (UV). The effects of partial and full spectrum UV on coral skeletal growth and bleaching were investigated. Responses were species-specific and depth-dependent. *Montipora verrucosa, Pocillopora damicornis,* and *P. danai* collected from 1 m maintained or increased their calcification rates when exposed to partial UV or shielded from UV. *M. verrucosa* collected from 1.5 m exhibited bleaching via zooxanthella loss regardless of the UV treatment, probably because of reduced salinity and water temperature. *M. verrucosa* collected from 8.5 m bleached only when exposed to increased intensities of PAR, while *Porites compressa* collected from 8.5 m bleached only when exposed to increases in both PAR and UV. All bleaching resulted from loss of zooxanthellae rather than loss of pigment from zooxanthellae. Lower surface augmentation of color via zooxanthella increases often occurred with a corresponding decrease in upper surface zooxanthella density.
THE EFFECTS OF ULTRAVIOLET RADIATION ON SKELETAL GROWTH AND BLEACHING IN FOUR SPECIES OF HAWAIIAN CORALS

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By Gwen Davies Goodman
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WE, THE UNDERSIGNED MEMBERS OF THE COMMITTEE,
HAVE APPROVED THIS THESIS

THE EFFECTS OF ULTRAVIOLET RADIATION ON SKELETAL
GROWTH AND BLEACHING IN FOUR SPECIES
OF HAWAIIAN CORALS

By
Gwen Davies Goodman

COMMITTEE MEMBERS

Alan C. Miller, Ph.D. (Chair)  Biology

Charles P. Galt, Ph.D.  Biology

Jy-Shéy Ho, Ph.D.  Biology

ACCEPTED AND APPROVED ON BEHALF OF THE UNIVERSITY

Fredrick H. Shair, Ph.D.
Dean, School of Natural Sciences

California State University, Long Beach
May 1991
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INTRODUCTION

In the early 1970s, Molina and Rowland (1974) found that substances commonly known as chlorofluorocarbons (CFC's) could rise into the stratosphere and destroy the Earth's protective ozone shield, subsequently allowing greater levels of ultraviolet radiation to reach the Earth's surface. CFC's not only reduce the ozone layer, but they also absorb outgoing infrared radiation, contributing to the "greenhouse effect" and global warming. In light of the recent discovery of the ozone hole over Antarctica (Gribbin, 1985), a renewed interest has developed concerning the importance of CFC's on ozone depletion and the potential effects of increased ultraviolet radiation on a variety of organisms.

Solar ultraviolet radiation, or full spectrum UV, is usually defined as the portion of the electromagnetic spectrum between x-radiation (200 nm) and visible light (400 nm) (Caldwell, 1981). Because separation of the electromagnetic spectrum into units is arbitrary, the upper boundary of UV light is sometimes defined differently. However, since photosynthetically active radiation (PAR), the portion of the spectrum utilized for photosynthesis, is generally defined as the quantum flux within the 400 to 700 nm range (McCree, 1981), it is advantageous to accept the 400 nm wavelength as the boundary separating UV and PAR (Jokiel and York, 1982). The ultraviolet portion of the spectrum can then be subdivided further: UV-A, or near-UV, occurs between 320 and 400 nm, UV-B, or middle-UV, occurs
between 280 and 320 nm, and UV-C, or far-UV, is found between 200 and 280 nm (Caldwell, 1981).

Although wavelengths shorter than 280 nm (UV-C) do not reach the Earth's surface (Baker et al., 1980), the other wavelengths do and can affect organisms in various ways. UV-A wavelengths alone elicit a number of responses, from interfering with oxidation-reduction reactions in cells of several marine organisms (Zigman and Hare, 1976) to increasing the formation of oxygen radicals, which can damage DNA (Peak and Peak, 1983). UV-B, which is the band of ultraviolet wavelengths absorbed principally by stratospheric ozone (Horvath et al., 1985), damages nucleic acids (Smith, 1969; Setlow, 1974) and inhibits chloroplast function (Jones and Kok, 1966), and hence, is biocidal. Current theory holds that life on land could not have evolved without some sort of shielding from these middle-UV wavelengths (Elliot and Rowland, 1986).

Harmful effects from exposure to ultraviolet solar radiation can be mitigated by organisms in three ways (Calkins and Blakefield, 1986): through behavioral avoidance, by shielding through increased cellular pigmentation, and via multiple DNA repair systems (e.g., photoreactivation). In spite of these mechanisms of adaptation, it is well documented that certain wavelengths of UV light are nevertheless harmful to many organisms since they damage biomolecules such as cell membranes (Murphy, 1983), nucleic acids, and both structural and enzyme proteins, thus creating genetic aberrations (Harm, 1980; Hader and Tevini, 1987). In humans, detrimental effects from excessive UV exposure include accelerated aging (Harm, 1980), carcinogenesis of
the skin (Moan and Peak, 1989), keratitis of the cornea, and cataracts (Hader and Tevini, 1987). In various photosynthetic organisms, exposure to UV has been shown to increase oxygen toxicity (Lesser and Shick, 1989), mutation rates (Harm, 1980), and respiration rates (Carpenter, 1985), and to also inhibit photosynthesis (Bell and Merinova, 1961; Smith et al., 1980) and primary production (Worrest, 1983; Caldwell et al., 1983). In addition, a 5% decrease of primary productivity in aquatic ecosystems for a 16% decrease in stratospheric ozone has been predicted (Worrest, 1983).

Since the ozone layer is naturally thinnest near the equator (Baker et al., 1980), tropical waters are inherently exposed to higher levels of ultraviolet radiation than temperate waters. In addition, these waters are more transparent to UV light than temperate zone waters (Jerlov, 1950; Smith and Baker, 1979) because they are low in particulate matter, which is responsible for the rapid attenuation of UV through scattering and absorption. Consequently, UV radiation often penetrates several meters into these clear waters. Tropical waters contain large numbers of hermatypic corals, each containing in their tissues endosymbiotic, photosynthetic dinoflagellates called zooxanthellae [Symbiodinium (= Gymnodinium) microadriaticum]. These corals, along with free-living algae, help form the basis of the coral reef's food web, but, more importantly, form the structural foundation for all organisms living in this ecosystem. A significant decrease in ozone and a concomitant increase in UV radiation could result in severe damage to tropical marine systems and, therefore, potentially cause socioeconomic
problems for many people that rely on coral reef ecosystems for food and economic benefits.

One possible consequence of an increase in UV radiation reaching the corals is bleaching, which is defined as paleness of the coral tissue due to either the expulsion of the zooxanthellae (Trench and Blank, 1987) or the decrease in zooxanthella pigment (Hoegh-Guldberg and Smith, 1988); i.e., either the zooxanthella cells are expelled from the coral tissue or the cells remain in the tissue but lose their pigments. Global bleaching events in corals have occurred since 1979 (Bunkley-Williams and Williams, 1990), with severe episodes occurring most recently from 1986 to 1988 in the Caribbean (Goenaga et al., 1989). Such bleaching has been attributed to lowered salinities resulting from high levels of precipitation (Goreau, 1964), elevated water temperatures (Jokiel and Coles, 1977; Hoegh-Guldberg and Smith, 1988), lowered air temperatures (Walker et al., 1982), increased water turbidity (Acevedo and Goenaga, 1986), and exposure to intensified levels of solar radiation (Jokiel and York, 1982; Hoegh-Guldberg and Smith, 1989).

In many aquatic organisms, tolerance to solar UV radiation seems to be limited to normal, ambient exposure (Calkins and Thordardottir, 1980). When tolerance and exposure are equal, a sudden or severe increase in UV radiation adversely affects these organisms, unless they can acclimate (Calkins and Blakefield, 1986). In the marine environment, a variety of sessile reef organisms, which have no mechanisms of acclimation and, therefore, live only in shaded areas,
died or were severely damaged when exposed to full sunlight including UV (Jokiel, 1980).

Hermatypic corals, however, have evolved photo-protective pigments in the form of mycosporine-like amino acids (Dunlap and Chalker, 1986) that shield the zooxanthellae from the harmful effects of UV radiation in the UV-B region (Shibata, 1969; Kawaguti, 1969). These amino acids are located in the coral ectoderm (Kawaguti, 1944) and are collectively called S-320, since their peak absorption occurs at 320 nm (Shibata, 1969). However, the production of these specialized compounds requires energy expenditure that might otherwise be used for increased growth or for reproduction (Jokiel and York, 1982). Since zooxanthellae are imperative in the nutrition and calcification of corals (Muscatine, 1980; Cook, 1983), corals with reduced densities of zooxanthellae or zooxanthellae with reduced photosynthetic pigment concentrations may be more susceptible to disease and to competition for light and space from other corals and macroalgae. Therefore, a greater degree of tolerance to UV radiation, along with the ability to increase the production of S-320, should offer a competitive advantage of survival to some species of corals.

In the past fifteen years, much research has been performed on various aspects of the effects of light on coral growth and calcification (Dustan, 1975; Coles and Jokiel, 1978; Roth et al., 1982; Rinkevich and Loya, 1984), as well as on the effects of solar radiation on the symbiotic zooxanthellae (Houck et al., 1977; Kevin and Hudson, 1979; Dustan, 1982; Dubinsky et al., 1984; Muscatine et al.,
1984; Kinzie et al., 1984; Siebeck, 1981 and 1988; Vareschi and Fricke, 1986). These studies indicate that exposure to solar radiation, including UV, is an important physical factor affecting the reef environment.

Jokiel and York (1982) found that the Hawaiian coral, *Pocillopora damicornis*, which was collected from 1 m and naturally exposed to high incident levels of full spectrum UV, demonstrated no changes in either zooxanthella density or pigment concentration when shielded from UV radiation. Those colonies that were shielded from UV radiation did, however, exhibit a greater skeletal growth than those exposed to UV radiation. In this study, Jokiel and York were concerned with the effects of the combined wavelengths of UV radiation on shallow-water corals only. In addition, Roth et al. (1982) found that *P. damicornis* exposed to radiation at wavelengths of 380 nm displayed a decreased calcification rate, but only when this radiation was separated from visible light. They suggested that this near-UV inhibition may result from a balance between the negative effects of near-UV radiation and the positive effects of the combination of near-UV and visible light. However, Roth et al. (1982) did not examine the effects of the entire band of wavelengths that comprise near-UV radiation.

Using long-term monoculture experiments on zooxanthellae, Jokiel and York (1984) discovered that, whereas short-term growth photo-inhibition was caused by exposure to PAR, long-term growth photo-inhibition was due almost entirely to UV radiation. These experiments were, however, conducted on isolated zooxanthellae, which
might be expected to respond differently to those found in situ since they are not protected by the photoprotective pigments located in the host coral. For the corals *Stylophora pistillata* and *Seriatopora hystrix*, Hoegh-Guldberg and Smith (1989) concluded that, while elevated temperatures seem to be responsible for zooxanthella expulsion, exposure to sudden increases in solar radiation may cause bleaching through zooxanthella pigment loss.

Although most hermatypic corals do produce photo-protective pigments, it is apparent from these studies that exposure to UV radiation can affect corals to various degrees; and, in addition, species-specific responses still need to be examined. In particular, no studies have addressed the effects of UV-A alone on skeletal growth and bleaching in either shallow- or deeper-growing corals, nor have the specific mechanisms responsible for bleaching in deeper-water corals exposed to full spectrum UV been examined.

The purpose of this study was to answer the following questions: 1) How does UV-A affect the skeletal growth of three shallow-water Hawaiian corals? 2) Does UV-A cause bleaching in either the shallow- or deeper-water form of one species of these corals? 3) If bleaching results from exposure to full sunlight (UV + PAR), what role does UV play; i.e., are the effects of UV plus PAR compensatory, additive, or synergistic? 4) If bleaching does occur from exposure to either UV-A or full spectrum UV, is this mechanism a result of reduced zooxanthella density or a decrease in zooxanthella pigment concentration? 5) If bleaching is a direct result of a reduction in density of zooxanthellae in a specific region of the
coral, could some of these microalgae actually be undergoing an avoidance response by moving to shaded/protected areas of the coral?
MATERIALS AND METHODS

I performed this study between 5 June and 28 August 1989 at the Hawaii Institute of Marine Biology (HIMB), located on Coconut Island in Kaneohe Bay, Oahu, Hawaii (Fig. 1). This bay is situated on the windward side of Oahu and is protected by Oahu's barrier reef. I collected all corals from Checker Reef (21° 25'N, 157°46'W), which is a patch reef located approximately 1000 m north of Coconut Island (Fig. 1). I measured the amount of PAR and UV radiation striking Coconut Island hourly from 1 June to 24 August 1989 with a Weathertronics 1150 Series Data Acquisition system.

Skeletal Growth

The Effects PAR only and Partial UV on Shallow-water Corals

To measure the effects of PAR only and partial wavelengths of UV radiation on skeletal growth, I collected corals from the reef flat of Checker Reef at a depth of approximately 0.5-1.5 m and subjected them to various light treatments. I collected these corals from a shallow depth rather than a deep one to control for factors that may influence growth, such as temperature, pressure, and salinity.

I collected 70 colonies measuring 7-10 cm in diameter of *Porites compressa*, *Montipora verrucosa*, and a combination of *Pocillopora damicornis* and *P. danai* from the reef and carefully transported them in temporary aquaria to Coconut Island in a manner that minimized stress from crowding and stagnant water. I selected
Figure 1. Map of Oahu, Hawaii, showing the location of Coconut Island, where the Hawaii Institute of Marine Biology (HIMB) is located, and Checker Reef, the coral collection site.
these corals because they represent the four most common species comprising the reefs of Kaneohe Bay. *Pocillopora damicornis* and *Porites compressa* are relatively fast growing branched corals and are generally found on the windward side of a reef. *P. danai* and *M. verrucosa* are slower growing corals; *P. danai* is found on the leeward edge of the reef, while *M. verrucosa* is found just off the reef edge on the windward side.

At HIMB, I placed the corals on vinyl-covered mesh screens and deposited them on the forereef of Coconut Island at a depth of 0.2-1.5 m for six days to reduce any stress that may have occurred during transport. To measure linear skeletal growth, I stained the corals by placing them in temporarily closed-system aquaria that contained 20 ppm of Alizarin Red-S (Lamberts, 1974). The stain was incorporated into the skeleton for 12 hrs in sunlight.

After the staining procedure was completed, I transported the corals to the lee side of Coconut Island where they would remain submerged under 25 cm of water and exposed to various light treatments for 50 days. I then randomly distributed 10 colonies each of *P. compressa*, *M. verrucosa*, and a combination of *P. damicornis* and *P. danai* according to positions I had marked previously on a 1 m² vinyl-covered mesh platform. Using monofilament line, I attached them to the platform approximately 5 cm apart in order to minimize stress due to competition from neighboring colonies.

Each platform was suspended from a single PVC float under one of three treatments: "No UV," "Partial UV," and "Full UV." The "No UV" treatments were covered with a UV-stabilized polycarbonate filter
(Rohm and Tuffok brand), which was opaque to UV radiation but approximately 95% transparent to wavelengths in the PAR region (Fig. 2). The "Partial UV" treatments were covered by a polyester film (Dupont Mylar brand), which in many studies has been shown to block out ultraviolet radiation below 320 nm (Jokiel and York, 1982; Jokiel, pers. comm.), thus transmitting approximately 90% of the energy in the UV-A and PAR regions. However, upon analysis using different Beckman spectrophotometers both at the HIMB and at California State University, Long Beach, I found that the particular batch of Mylar employed transmitted wavelengths > 295 nm. Therefore, I actually measured the effects of partial wavelengths of UV radiation, not just UV-A, on growth and bleaching. The "Full UV" treatment was covered with a fluorohaloocarbon film (Allied Chemical Corp. Aclar brand), which is approximately 93% transparent to all wavelengths of the solar spectrum (Fig. 2). I used this filter to control for the slight reduction in the transmittance of PAR that occurs with the two preceding filters. I replicated each treatment twice (Fig. 3).

I constructed this apparatus so that the treatment filters were on top of the PVC float and remained out of water, while the mesh screens were suspended below the float and remained submerged at all times (Fig. 3). This ensured that no aquatic organisms would colonize the filters and diminish transmittance of the appropriate wavelengths of radiation. I cleared the filters daily of rainwater and salt encrustation. To avoid damage to the filters and float by high wind or waves, I placed the apparatus at a lagoon entrance on the lee side of Coconut Island. However, the flow rate of this water is
Figure 2. Transmission characteristics of the three UV filters used in this study where UV is the portion of the electromagnetic spectrum between 200 and 400 nm and PAR is the portion between 400 and 700 nm. The Full UV filter is transparent to all wavelengths of the solar spectrum down to 200 nm, including full spectrum UV radiation and PAR. The Partial UV filter transmits wavelengths down to 295 nm, including some UV-B, all of UV-A, and PAR. The No UV filter transmits wavelengths down to 400 nm, including PAR, but blocks out all wavelengths of UV. Transmittance of the wavelengths of solar radiation reaching the Earth's surface is included as a reference (Baker et al., 1980).
Figure 3. Experimental float and filter apparatus used for the skeletal growth study. Each 1 m² UV filter treatment was replicated twice and placed in a random order on top of the PVC float. Corals were suspended from the float and surrounded with opaque plastic to prevent the transmittance of refracted rays from other filters or the surrounding water. The entire apparatus was situated in the lee of Coconut Island.
TOP VIEW

FILTERS

- Full UV
- Partial UV
- No UV

SIDE VIEW

FILTER

- 1m² Mesh Platform with Coral Colonies
- Opaque Plastic on Four Sides
- Submerged 0.25m
much slower than that found across the reefs of Kaneohe Bay, so I replaced one control set of 30 corals onto the reef and left it uncovered to simulate natural growing conditions.

After 50 days, I determined skeletal growth by measuring the new skeleton formed since the corals were stained. To expose the skeleton, I placed the corals in fresh water and removed the tissue using a high pressure water hose. New carbonate material deposited since staining with alizarin red was clearly visible and was measured to the nearest 0.1 mm with vernier calipers on 10 randomly selected branches. The light treatment of the individual corals was revealed after I measured growth to prevent subconscious biasing of the data. I analyzed the data using a two-way ANOVA and Tukey-Kramer a-posteriori tests.

Microalgal Density and Pigment Concentration

The Effects of PAR only, Partial UV, and Full Spectrum UV on Shallow- and Deeper-water Corals

I examined the effects of PAR only, partial UV plus PAR, and full spectrum UV plus PAR on zooxanthella density and pigment concentration in the "shade-loving" species, Montipora verrucosa, collected from the reef edge at two depths: 1 m and 8.5 m. At the reef edge, M. verrucosa forms thickened, upright branches, while at depth its morphology is plate-like. Because many coral colonies are a result of asexual reproduction through cloning, I collected one large colony from each depth for the experiments to avoid error due to genetic differences. I transported the two colonies to Coconut Island, allowed them to acclimate to aquarium conditions for two days, and
broke them into fragments roughly equal in size to provide numerous clones.

I placed the fragments on wire racks in an outdoor aquarium at HIMB. This aquarium (152 cm long x 75 cm wide x 15 cm deep) was located in full sunlight, oriented with its long axis in an east-west direction, and separated into three light treatments. The sides and bottom of the aquarium were opaque to sunlight. I fitted each treatment filter placed across the top of the aquarium with black plastic on either side, such that any refracted or reflected light penetrating a specific filter was prevented from entering an adjacent treatment (Fig. 3). The aquarium was supplied with seawater from Kaneoke Bay at a rate of 20 l min⁻¹ and was vigorously aerated within each treatment; this ensured near saturation levels of dissolved oxygen, optimal water motion (Jokiel, 1980), thorough mixing, and temperatures of 25±2°C under the treatment filters.

*M. verrucosa* growing at 1 m is naturally exposed to high incident levels of UV radiation. Therefore, I subjected the fragments to three treatments: "No UV", "Partial UV", and "Full UV" (control). These three treatments were covered by the polycarbonate, Mylar, and Aclar filters described previously in the skeletal growth experiment.

*M. verrucosa* growing at 8.5 m is naturally exposed to about 4% of the UV levels found at the surface (pers. observ.). Therefore, I subjected the fragments to four treatments: "No UV + Shade" (control), "No UV," "Partial UV," and "Full UV." The "No UV + Shade" treatment was covered by the polycarbonate filter and fitted with a
black mesh shade cloth such that the amount of PAR transmitted through it was decreased by 25%, approximating the decrease in visible light for those corals growing at a depth of 8.5 m. The "No UV," "Partial UV," and "Full UV" treatments were covered by the polycarbonate, Mylar, and Aclar filters, respectively.

I determined the zooxanthella density and pigment concentration for six randomly selected samples (three for zooxanthella counts and three for pigment analysis) by extracting a core starting from the irradiated surface tissue and continuing through the carbonated skeleton and the non-irradiated tissue on the underside, using a sharpened cork borer (1 cm in diameter). Since I analyzed both irradiated (upper) and non-irradiated (lower) surfaces separately, I parted the core surfaces using a razor blade. In addition, I normalized zooxanthella density and pigment concentration to the surface area of the core.

The cores that I analyzed for zooxanthella density were fixed in formalin and stained with Lugol's solution for 24 hrs. I then placed these cores in 10 ml of 20% acetic acid for 48 hrs, which decalcified the skeleton and left a pellet of tissue. To break up the individual microalgal cells, I ground the resulting pellet with a Radnoti tissue grinder. I determined zooxanthella density by sampling the cells eight times using a two chamber hemacytometer and a phase contrast microscope.

The cores that I analyzed for pigment concentration were ground in 100% acetone in a darkened room using a mortar and pestle. I then exposed the cores to a known volume of 100% acetone at 0 °C for 48 hrs
to extract the chlorophyll pigments. I cleared the samples of suspended material via centrifugation and analyzed them with a Beckman DU-70 spectrophotometer using a 1 cm quartz cell; the extinction coefficient for chlorophyll a was determined at 663 nm and for chlorophyll c at 630 nm. I calculated pigment concentration (mg/ml) using the equations determined by Jeffrey and Humphrey (1975):

\[
\text{Chlorophyll a} = 11.43 \, E_{663} - 0.64 \, E_{630}
\]

\[
\text{Chlorophyll c} = 27.09 \, E_{630} - 3.63 \, E_{663}
\]

where \( E_x \) is the extinction coefficient at wavelengths indicated by the subscripts. I normalized the resulting values to zooxanthellae density to obtain pigment per cell (mg).

In preliminary tests, I terminated the experiments when fragments under at least one filter bleached completely, since linear trends could not be compared among all the treatments after that point. Although the corals in this experiment had not yet fully bleached because of inclement weather, it was terminated after six days since there was no coral left to sample. Corals were sampled on days 1, 3, 4, 5, and 6 to determine zooxanthella density and pigment concentration. I terminated the experiment conducted on fragments collected from 8.5 m after 10 days when at least one treatment contained bleached corals; I sampled the corals on days 1, 3, 4, 5, 6, and 10.

Since each fragment I sampled did not contain the same density of zooxanthellae or concentration of pigments at the start of an experiment, it was more accurate to compare filter treatments by analyzing for differences in the linear trends, which reflect changes
in zooxanthella density and pigment over time, rather than the mean loss or gain of zooxanthellae over time. For this analysis, I used the two-way ANOVA test for significance (SAS, 1987). A regression analysis and randomization test with 1000 iterations were used to compare the slopes of the lines to a slope of zero within each treatment. In addition, in an effort to determine the relative contribution of zooxanthella loss or cellular pigment loss to bleaching, I compared the slopes of the linear regression lines within each treatment to a slope of zero using Student’s t and randomization tests (Sokal and Rohlf, 1981).

The Effects of PAR only, Full Spectrum UV only, and Full UV plus PAR on Deeper-water Corals

In the following experiment, I examined the effects of increases in PAR only, full spectrum UV only, and full UV plus PAR on bleaching in two deeper-water corals. For this study, I selected two perforate corals (defined as corals with tissue extending into the skeleton). I collected two "shade-loving" species, Montipora verrucosa and Porites compressa, from the fore-reef at a depth of 8.5 m, transported them to Coconut Island, and acclimated the colonies in an outdoor aquarium for three days. Since P. compressa assumes a finger-like morphology even at depth, I placed the finger fragments on their sides in the aquarium. In this situation, the upper surface sampled was the surface in direct contact with solar radiation, while the lower surface was shielded.

I placed fragments of each of the two colonies on wire racks in the aquarium described in the previous microalgal density and pigment
concentration experiment. I subjected the fragments to four treatments: "No UV + Shade" (control), "No UV," "Full UV + Shade," and "Full UV." The "No UV + Shade," "No UV," and "Full UV + Shade" treatments were covered with the polycarbonate and shade cloth, polycarbonate only, and Aclar filters, respectively. The "Full UV + Shade" treatment was covered by an Aclar filter fitted with the black mesh shade cloth described previously, which reduced the transmittance of PAR and UV by 25%.

This experiment also continued until one treatment contained bleached corals (10 days); I sampled both species on days 1, 2, 3, 4, 5, 7, and 10. The sampling method and subsequent analysis of zooxanthella densities and pigment concentrations were the same as those described in the previous section.
RESULTS

Responses by corals to ultraviolet solar radiation were species-specific and depth-dependent. Shallow water corals maintained or increased their rate of calcification and maintained both zooxanthella populations and pigments when exposed to only partial wavelengths of UV radiation. In addition, when separated from the effects of increased intensities of PAR, full spectrum UV did not cause bleaching in deeper-water corals. When bleaching did occur in any coral exposed to partial or full spectrum UV plus PAR, this phenomenon appeared to stem mainly from the loss or movement of zooxanthellae rather than from the loss of zooxanthella pigment.

Skeletal Growth

The Effects PAR only and Partial UV on Shallow-water Corals

Although the skeletal growth experiment originally included four species of shallow water corals, colonies of *Porites compressa* could not be analyzed because they died before the 50-day experimental period was completed, due to predation by the nudibranch, *Phistella sibogae*. In general, the trends for the remaining species, *Montipora verrucosa*, *Pocillopora damicornis*, and *Pocillopora danai*, show that the slowest growth rates occurred under full spectrum UV with higher growth rates found with either partial wavelengths or no wavelengths of UV (Table 1), although not all of the differences were significantly different (Table 2). In addition, each of the three
Table 1. Skeletal growth rates (mm 50 days$^{-1}$) for Montipora verrucosa, Pocillopora damicornis, and Pocillopora danai under three treatments. The apparatus for these three treatments was situated in the lee of Coconut Island and, hence, was subject to conditions different from those found on the reef. The reef set, placed on the forereef of Coconut Island, was not covered by a filter and was exposed to full spectrum UV plus PAR; it controlled for the unnatural growing conditions.

<table>
<thead>
<tr>
<th></th>
<th>No UV</th>
<th>Partial UV</th>
<th>Full UV</th>
<th>Reef Set</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$n$</td>
<td>Mean</td>
<td>SD</td>
<td>$n$</td>
</tr>
<tr>
<td>Montipora verrucosa</td>
<td>18</td>
<td>3.88</td>
<td>1.42</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>2.69</td>
<td>1.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>3.81</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td>Pocillopora damicornis</td>
<td>6</td>
<td>5.37</td>
<td>0.63</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>4.11</td>
<td>1.50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>6.05</td>
<td>0.97</td>
<td></td>
</tr>
<tr>
<td>Pocillopora danai</td>
<td>13</td>
<td>2.65</td>
<td>0.87</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>1.96</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2.89</td>
<td>0.27</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Results of significance testing by ANOVA (F statistic and probability value) of the skeletal growth rates of *Montipora verrucosa*, *Pocillopora damicornis*, and *Pocillopora danai* under various combinations of treatments. All treatments transmitted approximately ambient levels of PAR. (*) indicates significance at the $p = 0.10$ level, (**) indicates significance at the $p = 0.05$ level.

<table>
<thead>
<tr>
<th>Treatment Comparison</th>
<th>Montipora verrucosa</th>
<th>Pocillopora damicornis</th>
<th>Pocillopora danai</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F$</td>
<td>$p$</td>
<td>$F$</td>
</tr>
<tr>
<td>No UV, Partial UV, Full UV</td>
<td>10.83</td>
<td>0.0001**</td>
<td>2.07</td>
</tr>
<tr>
<td>No UV, Partial UV</td>
<td>1.99</td>
<td>0.17</td>
<td>3.24</td>
</tr>
<tr>
<td>No UV, Full UV</td>
<td>7.75</td>
<td>0.01**</td>
<td>4.43</td>
</tr>
<tr>
<td>Partial UV, Full UV</td>
<td>33.70</td>
<td>0.0001**</td>
<td>17.11</td>
</tr>
<tr>
<td>Reef Set, No UV,</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Partial UV, Full UV</td>
<td>7.71</td>
<td>0.0001**</td>
<td>4.15</td>
</tr>
<tr>
<td>Reef Set, No UV</td>
<td>0.01</td>
<td>0.91</td>
<td>2.10</td>
</tr>
<tr>
<td>Reef Set, Partial UV</td>
<td>3.52</td>
<td>0.08*</td>
<td>8.53</td>
</tr>
<tr>
<td>Reef Set, Full UV</td>
<td>5.49</td>
<td>0.03**</td>
<td>7.08</td>
</tr>
</tbody>
</table>
reef-set species, which were grown under more natural conditions and without a filter to block full spectrum UV, exhibited a significantly faster growth rate than those corals exposed to full UV plus PAR ("Full UV" filter) but grown in the lee of Coconut Island ($p < 0.07$, Table 2).

Skeletal growth in *M. verrucosa* was significantly different among the three UV treatments, "No UV," "Partial UV," and "Full UV" ($p = 0.0001$, Table 2). Mean growth was greatest under the "Partial UV" treatment (Table 1). While the reef-set colonies of *M. verrucosa* exposed to full spectrum UV plus PAR grew significantly faster than the lee-side colonies grown under the "Full UV" treatment ($p = 0.03$, Table 2), the reef-set colonies exhibited no significant difference in growth from those colonies that were shielded from all wavelengths of UV radiation ("No UV," $p = 0.91$, Table 2). In addition, although those colonies of *M. verrucosa* grown under the "Partial UV" filter did not grow significantly faster than the reef-set colonies ($p = 0.08$, Table 2), the data may indicate a trend of faster growth.

In the coral *P. damicornis*, the greatest skeletal growth appeared to occur in those colonies not exposed to UV radiation ("No UV," Table 1); however, growth did not differ significantly among the three UV treatments ($p = 0.16$, Table 2). *P. damicornis* maintained the greatest skeletal growth when grown at high water velocities on the reef (Table 1).

*P. danai* exhibited growth trends similar to those of *M. verrucosa*: skeletal growth significantly differed among the three treatments ($p = 0.002$, Table 2), with the greatest mean growth
occurring in those colonies exposed to only partial wavelengths of UV radiation (Table 1). In addition, the reef set colonies did not grow significantly faster than those colonies shielded from UV radiation ("No UV," \( p = 0.66, \) Table 2), and exposed to partial wavelengths of UV ("Partial UV," \( p = 0.40, \) Table 2). Although growth among the reef-set colonies was not significantly faster than those grown under the "Full UV" filter (\( p = 0.07, \) Table 2), the reef colonies may also be indicating a trend of faster growth.

**Microalgal Density and Pigment Concentration**

**The Effects of PAR only, Partial UV, and Full Spectrum UV on Shallow- and Deeper-water Corals**

For the following experiments, the repeated measures ANOVA test for significance (SAS, 1987) was used to examine the differences in slopes of the lines among treatments, rather than the mean gain or loss of zooxanthella populations or pigment concentrations (Tables 3 and 4). A regression analysis and Student's \( t \)-test with a randomization test (Sokal and Rohlf, 1981) were used to compare the slopes of the lines to a slope of zero within each treatment (Figs. 4-12). In the pigment per cell graphs, the points are a result of the mean chlorophyll concentration \(( n = 3)\) divided by the mean zooxanthella density \(( n = 3)\) for each day. Hence, it is not possible to plot variances for these data (i.e., \( n = 1 \)).

The shallow-water colony of *Montipora verrucosa*, which is normally to exposed high levels of full spectrum UV, exhibited slight visible bleaching on the upper surfaces of fragments placed in all three treatments: "No UV," "Partial UV," and "Full UV."
bleaching stemmed from a significant decrease in zooxanthella densities \((p < 0.05, \text{Fig. 4})\), but may have been tempered by an increase in chlorophyll a per cell \((p = 0.02, \text{Fig. 5})\) and chlorophyll c per cell \((p = 0.10, \text{Fig. 6})\) for those fragments grown under the "No UV" filter only. The slopes of the fragments placed under the three UV treatments, however, did not differ significantly from each other at the \(p = 0.05\) level in zooxanthella density, chlorophyll a per cell, or chlorophyll c per cell on the upper surfaces (Table 3). Slopes for chlorophyll a per cell did differ significantly at the \(p = 0.10\) level among the three treatments; however, this is probably a result of variations in the shape of the lines (Fig. 5) rather than an actual dissimilarity in bleaching via pigment loss (Bradley, pers. comm.).

Among the lower surfaces of the coral fragments, zooxanthella densities, as well as chlorophyll per cell concentrations, did not change significantly over time \((p > 0.30, \text{Figs. 4, 5, and 6})\), with one exception: chlorophyll c per cell from the "No UV" treatment increased significantly \((p = 0.04, \text{Fig. 6})\). In addition, a comparison of slopes among treatments revealed no significant difference for zooxanthella density nor pigment per cell \((p > 0.50, \text{Table 3})\).

The deeper-water colony of \(M. \text{ verrucosa}\), which is normally exposed to approximately 96\% less UV and 25\% less PAR than surface corals (pers. observ.), exhibited bleached upper surfaces in those fragments that were exposed to increased levels of PAR found in all treatments without shade, regardless of the type of UV filter. This bleaching was caused by a decrease in zooxanthella populations \((p < 0.001, \text{Fig. 7})\). Within the "Full UV" treatment, this bleaching
may have been tempered by significant increases in both the chlorophyll a per cell \( (p = 0.08, \text{Fig. 8}) \) and chlorophyll c per cell \( (p = 0.06, \text{Fig. 9}) \). Furthermore, the slopes of the zooxanthella populations were significantly different between fragments that were exposed to natural levels of PAR ("No UV + Shade") and those that were exposed to ambient, surface levels of PAR ("No UV, Partial UV, Full UV", \( p = 0.003, \text{Table 4} \)). Significance of differences at the \( p = 0.10 \) level (Table 4) for slopes of both chlorophyll a and c per cell among the four treatments probably reflects an artifact due to the line shape sensitivity of the ANOVA test, rather than actual differences in increases or decreases of these two pigments (Bradley, pers. comm.).

An additional ANOVA was performed to compare those fragments receiving equivalent levels of PAR but different wavelengths of UV radiation. From this comparison, while it visually appeared that bleaching in the upper surfaces was most dramatic in the "Full UV" treatment, neither the slopes of the zooxanthella densities nor the slopes of the pigment per cell concentrations differed significantly when compared among the three UV treatments \( (p > 0.12, \text{Table 4}) \).

Within the lower surfaces of those fragments exposed to all wavelengths of UV ("Full UV"), an visible increase in color intensity was apparent. This phenomenon resulted from an increase in zooxanthella density only \( (p = 0.003, \text{Fig. 7}) \), which differed significantly among the three UV treatments \( (p = 0.003, \text{Table 4}) \). Pigments per cells did not significantly increase \( (p > 0.15, \text{Figs. 8 and 9}) \), or differ among the UV treatments \( (p > 0.22, \text{Table 4}) \).
Table 3. Effects of partial wavelengths of UV radiation on *Montipora verrucosa* collected from 1.5 m. Density of zooxanthellae is abbreviated as zoox, chlorophyll a as chl a, and chlorophyll c as chl c. The slopes of the responses were compared among the different treatments using ANOVA for repeated measures (F statistic and probability value). (*) indicates a significance at the $p = 0.10$ level, (**) indicates significance at the $p = 0.05$ level.

<table>
<thead>
<tr>
<th>Treatment Comparison</th>
<th>Upper Surface</th>
<th>Lower Surface</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>zoox</td>
<td>chl a·zoox^{-1}</td>
</tr>
<tr>
<td>No UV, Partial UV, Full UV</td>
<td>1.21  0.36</td>
<td>4.93  0.06*</td>
</tr>
</tbody>
</table>
Figure 4. The effects of partial wavelengths of UV radiation on the zooxanthella density of *Montipora verrucosa* taken from 1.5 m over six days. The uppermost graph represents the mean amount of UV radiation reaching Coconut Island from 0600 to 1800 hours per day. "U" represents the mean of samples (n = 3) taken from the upper surface of the coral; "L" represents the mean of samples (n = 3) taken from the lower, or underneath, surface. $r^2$ is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the $p = 0.10$ level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the $p = 0.05$ level.
Figure 5. The effects of partial wavelengths of UV radiation on the concentration of chlorophyll a per cell of *Montipora verrucosa* taken from 1.5 m over six days. "U" represents the ratio of the mean \((n = 3)\) chlorophyll a samples to the mean \((n = 3)\) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean \((n = 3)\) chlorophyll a samples to the mean \((n = 3)\) zooxanthella samples taken from the lower, or underneath surface. \(r^2\) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.10\) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.05\) level.
The graph shows the change in chlorophyll a (X10^-6) over 7 days for three different UV exposure conditions: NO UV, PARTIAL UV, and FULL UV. The graph includes linear regression lines with correlation coefficients (r^2) for each condition.

- **NO UV**
  - U: r^2 = 0.906**
  - L: r^2 = 0.012

- **PARTIAL UV**
  - U: r^2 = 0.075
  - L: r^2 = 0.025

- **FULL UV**
  - U: r^2 = 0.272
  - L: r^2 = 0.204
Figure 6. The effects of partial wavelengths of UV radiation on the concentration of chlorophyll c per cell of Montipora verrucosa taken from 1.5 m over six days. "U" represents the ratio of the mean \(n = 3\) chlorophyll c samples to the mean \(n = 3\) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean \(n = 3\) chlorophyll c samples to the mean \(n = 3\) zooxanthella samples taken from the lower, or underneath surface. \(r^2\) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.10\) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.05\) level.
Comparison of chlorophyll content in various UV exposures:

**NO UV**
- U: $r^2=0.712^*$
- L: $r^2=0.765^{**}$

**PARTIAL UV**
- U: $r^2=0.055$
- L: $r^2=0.002$

**FULL UV**
- U: $r^2=0.115$
- L: $r^2=0.368$
Table 4. Effects of partial wavelengths of UV radiation on *Montipora verrucosa* collected from 8.5 m. Density of zooxanthellae is abbreviated as zoox, chlorophyll a as chl a, and chlorophyll c as chl c. The slopes of the responses were compared among the different treatments using ANOVA for repeated measures ($F$ statistic and probability value). (*) indicates significance at the $p = 0.10$ level, (**) indicates significance at the $p = 0.05$ level.

<table>
<thead>
<tr>
<th>Treatment Comparison</th>
<th>Upper Surface</th>
<th>Lower Surface</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>zoox</td>
<td>chl a·zoox$^{-1}$</td>
</tr>
<tr>
<td>No UV + Shade, No UV, Partial UV, Full UV</td>
<td>11.91 0.003**</td>
<td>3.61 0.08*</td>
</tr>
<tr>
<td>No UV, Partial UV, Full UV</td>
<td>2.01 0.21</td>
<td>2.36 0.11</td>
</tr>
</tbody>
</table>
Figure 7. The effects of partial wavelengths of UV radiation on the zooxanthella density of *Montipora verrucosa* taken from 8.5 m over 10 days. The uppermost graph represents the mean amount of UV radiation reaching Coconut Island from 0600 to 1800 hours per day. "U" represents the mean of samples \((n = 3)\) taken from the upper surface of the coral; "L" represents the mean of samples \((n = 3)\) taken from the lower, or underneath, surface. \(r^2\) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.10\) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.05\) level.
Figure 8. The effects of partial wavelengths of UV radiation on the concentration of chlorophyll a per cell of *Montipora verrucosa* taken from 8.5 m over 10 days. "U" represents the ratio of the mean (n = 3) chlorophyll a samples to the mean (n = 3) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean (n = 3) chlorophyll a samples to the mean (n = 3) zooxanthella samples taken from the lower, or underneath surface. \( r^2 \) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.10 \) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.05 \) level.
Figure 9. The effects of partial wavelengths of UV radiation on the concentration of chlorophyll c per cell of Montipora verrucosa taken from 8.5 m over 10 days. "U" represents the ratio of the mean (n = 3) chlorophyll c samples to the mean (n = 3) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean (n = 3) chlorophyll c samples to the mean (n = 3) zooxanthella samples taken from the lower, or underneath surface. $r^2$ is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the $p = 0.10$ level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the $p = 0.05$ level.
The Effects of PAR only, Full Spectrum UV only, and Full UV plus PAR on Deeper-water Corals

In the previous experiment concerning the effects of PAR only, partial UV, and full spectrum UV on coral bleaching, visual bleaching did occur in those deeper-water coral fragments exposed to full spectrum UV plus PAR; however, since those fragments were exposed to increases in intensities of both UV radiation and PAR, bleaching could not be attributed to increases in UV alone. Therefore, the following experiment was designed to determine if bleaching in deeper water corals is a direct response to increased levels of UV radiation, increased intensities of PAR, or both.

Responses to the four treatment filters ("No UV + Shade," "No UV," "Full UV + Shade," and "Full UV") between Montipora verrucosa and Porites compressa collected from 8.5 m were significantly different concerning the slopes of the zooxanthella densities on the upper surfaces ($p = 0.01$, Table 5), but not the lower surfaces ($p = 0.88$, Table 5). In addition, there were no significant differences in slopes for the pigment per zooxanthellae concentrations within either the top ($p > 0.61$, Table 5), or bottom surface ($p > 0.34$, Table 5), although upper-surface chlorophyll c per cell was borderline ($p = 0.06$, Table 5).

In M. verrucosa, upper-surface bleaching via zooxanthellae loss occurred in only those treatments where the fragments were subjected to increased intensities of PAR ("No UV," "Full UV," $p < 0.001$, Fig. 10), regardless of the UV treatment. In addition, while significant
Table 5. Effects of full spectrum UV radiation on *Montipora verrucosa* and *Porites compressa* collected from 8.5 m. Density of zooxanthellae is abbreviated as zoox, chlorophyll a as chl a, and chlorophyll c as chl c. The slopes of the responses were compared among the different treatments using ANOVA for repeated measures (F statistic and probability value). (*) indicates significance at the \( p = 0.10 \) level, (**) indicates significance at the \( p = 0.05 \) level.

<table>
<thead>
<tr>
<th>Treatment Comparison</th>
<th>Zoox</th>
<th>Chl a-zoox(^{-1})</th>
<th>Chl c-zoox(^{-1})</th>
<th>Zoox</th>
<th>Chl a-zoox(^{-1})</th>
<th>Chl c-zoox(^{-1})</th>
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</thead>
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<tr>
<td></td>
<td>( F )</td>
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<td>( F )</td>
<td>( p )</td>
<td>( F )</td>
<td>( p )</td>
</tr>
<tr>
<td><em>M. verrucosa</em> vs. <em>P. compressa</em>:</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>No UV+Shade, No UV, Full UV+Shade, Full UV....</td>
<td>5.05</td>
<td>0.01**</td>
<td>0.27</td>
<td>0.61</td>
<td>4.17</td>
<td>0.06*</td>
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<td><em>M. verrucosa</em>:</td>
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<td></td>
<td></td>
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<tr>
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<td>30.57</td>
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<td>0.96</td>
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<td>8.01</td>
<td>0.07*</td>
<td>0.94</td>
<td>0.37</td>
<td>0.01</td>
<td>0.92</td>
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<tr>
<td>No UV, Full UV...</td>
<td>0.59</td>
<td>0.49</td>
<td>0.12</td>
<td>0.74</td>
<td>22.20</td>
<td>0.003**</td>
</tr>
<tr>
<td><em>P. compressa</em>:</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No UV+Shade, No UV, Full UV+Shade, Full UV....</td>
<td>9.87</td>
<td>0.005**</td>
<td>0.58</td>
<td>0.46</td>
<td>1.10</td>
<td>0.31</td>
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<tr>
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<td>0.91</td>
<td>0.47</td>
<td>0.52</td>
<td>0.24</td>
<td>0.64</td>
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<td>No UV, Full UV...</td>
<td>27.40</td>
<td>0.006**</td>
<td>0.18</td>
<td>0.69</td>
<td>8.10</td>
<td>0.06*</td>
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</tbody>
</table>
Figure 10. The effects of full spectrum UV radiation on the zooxanthella density of Montipora verrucosa taken from 8.5 m over 10 days. The uppermost graph represents the mean amount of UV radiation reaching Coconut Island from 0600 to 1800 hours per day. "U" represents the mean of samples (n = 3) taken from the upper surface of the coral; "L" represents the mean of samples (n = 3) taken from the lower, or underneath, surface. \( r^2 \) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.10 \) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.05 \) level.
Figure 11. The effects of full spectrum UV radiation on the concentration of chlorophyll a per cell of *Montipora verrucosa* taken from 8.5 m over 10 days. "U" represents the ratio of the mean \( (n = 3) \) chlorophyll a samples to the mean \( (n = 3) \) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean \( (n = 3) \) chlorophyll a samples to the mean \( (n = 3) \) zooxanthella samples taken from the lower, or underneath surface. \( r^2 \) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.10 \) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.05 \) level.
Figure 12. The effects of full spectrum UV radiation on the concentration of chlorophyll c per cell of *Montipora verrucosa* taken from 8.5 m over 10 days. "U" represents the ratio of the mean \( (n = 3) \) chlorophyll c samples to the mean \( (n = 3) \) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean \( (n = 3) \) chlorophyll c samples to the mean \( (n = 3) \) zooxanthella samples taken from the lower, or underneath surface. \( r^2 \) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.10 \) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.05 \) level.
differences in zooxanthella densities occurred among the slopes of all four treatments \( (p = 0.0001, \text{Table 5}) \), no significant difference occurred among the "No UV + Shade" and "Full UV + Shade" treatments \( (p = 0.07, \text{Table 5}) \), nor among the "No UV" and "Full UV" treatments \( (p = 0.49, \text{Table 5}) \). Although the "No UV + Shade" / "Full UV + Shade" treatment comparison for zooxanthellae is significant at the \( p = 0.10 \) level, this may, again, be due to the line shape sensitivity of the ANOVA test since the magnitude of the measurements was similar in each of the two treatments compared (Bradley, pers. comm.). No significant differences occurred for either pigment per cell among the "No UV + Shade" / "Full UV + Shade" treatment comparison.

While upper-surface bleaching in both the "No UV" and "Full UV" treatments resulted mainly from losses in zooxanthellae, within the "No UV" treatment significant decreases occurred in both chlorophyll a \( (p = 0.01, \text{Fig. 11}) \) and chlorophyll c \( (p = 0.02, \text{Fig. 12}) \) per cell, while within the "Full UV" treatment, a significant increase in chlorophyll a per cell \( (p = 0.001, \text{Fig. 11}) \) occurred. Moreover, a comparison of slopes for these two treatments yielded no significant difference for chlorophyll a per cell \( (p = 0.74, \text{Table 5}) \), but did result in a significant difference for chlorophyll c per cell \( (p = 0.003, \text{Table 5}) \).

Increases in lower-surface zooxanthella densities occurred in those coral fragments grown under both the "No UV" and "Full UV" treatments \( (p < 0.001, \text{Fig. 10}) \). No significant changes in the slopes of lower-surface zooxanthellae occurred in either the "No UV + Shade" or the "Full UV + Shade" treatments \( (p > 0.11, \text{Fig. 10}) \). In
addition, while treatment comparisons for the lower-surface zooxanthella populations resulted in significant differences among all four treatments \( (p = 0.01, \text{Table 5}) \), no differences were seen within the "No UV + Shade" / "Full UV + Shade" comparison \( (p = 0.69, \text{Table 5}) \), or the "No UV" / "Full UV" comparison \( (p = 0.37, \text{Table 5}) \). There were no lower-surface increases in chlorophyll a or chlorophyll c per cell among any of the four treatments (Figs. 11 and 12, respectively). Furthermore, treatment comparisons for both pigments per cell resulted in no significant differences \( (p > 0.36, \text{Table 5}) \) except with chlorophyll c per cell compared between the "No UV" and "Full UV" treatments \( (p = 0.03, \text{Table 5}) \). In this case, differences may again be due to the line shape sensitivity of the ANOVA test (Bradley, pers. comm.).

In contrast to \textit{M. verrucosa}, \textit{P. compressa} upper-surface bleaching via zooxanthella loss occurred only in those fragments exposed to the combination of PAR and UV radiation ("Full UV," \( p = 0.001, \text{Fig. 13})\). No bleaching via zooxanthellae or chlorophyll per cell loss occurred in those fragments shielded from increased intensities of PAR ("No UV + Shade," "Full UV + Shade," \( p > 0.28, \text{Figs. 13, 14, and 15})\), nor in those fragments shielded from UV but exposed to increased PAR ("No UV," \( p > 0.09)\). These results are reflected by the treatment comparisons for the upper surfaces zooxanthella slopes of \textit{P. compressa} (Table 5): significant differences at the \( p = 0.05 \) level found in the four treatment comparison are actually due to differences among the "No UV" / "Full UV" treatments.
Similar to *M. Verrucosa*, an increase in zooxanthella density within the lower surfaces of *P. compressa* was apparent only in those fragments grown under the "Full UV" treatment (*p* = 0.02, Fig. 13). No significant increases among the lower surfaces were observed for either type of chlorophyll per cell (*p* > 0.62, Figs. 14 and 15). In addition, significant differences for lower-surface slopes compared among the various treatment combinations occurred only for zooxanthellae compared among the four treatments (*p* = 0.01 Table 5).
Figure 13. The effects of full spectrum UV radiation on the zooxanthella density of *Porites compressa* taken from 8.5 m over 10 days. The uppermost graph represents the mean amount of UV radiation reaching Coconut Island from 0600 to 1800 hours per day. "U" represents the mean of samples \((n = 3)\) taken from the upper surface of the coral; "L" represents the mean of samples \((n = 3)\) taken from the lower, or underneath, surface. \(r^2\) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.10\) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.05\) level.
Figure 14. The effects of full spectrum UV radiation on the concentration of chlorophyll a per cell of *Porites compressa* taken from 8.5 m over 10 days. "U" represents the ratio of the mean \((n = 3)\) chlorophyll a samples to the mean \((n = 3)\) zooxanthella samples taken from the upper surface of the coral. "L" represents the ratio of the mean \((n = 3)\) chlorophyll a samples to the mean \((n = 3)\) zooxanthella samples taken from the lower, or underneath surface. \(r^2\) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.10\) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \(p = 0.05\) level.
Figure 15. The effects of full spectrum UV radiation on the concentration of chlorophyll c per cell of *Porites compressa* taken from 8.5 m over 10 days. "U" represents the ratio of the mean (n = 3) chlorophyll c samples to the mean (n = 3) zooxanthellae samples taken from the upper surface of the coral. "L" represents the ratio of the mean (n = 3) chlorophyll c samples to the mean (n = 3) zooxanthellae samples taken from the lower, or underneath surface. \( r^2 \) is the coefficient of determination, (*) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.10 \) level, (**) indicates that the slopes of the regression lines are significantly different from a slope of zero at the \( p = 0.05 \) level.
DISCUSSION

Although the corals *Montipora verrucosa*, *Pocillopora damicornis*, and *Pocillopora danai* normally thrive under incident doses of ultraviolet radiation that might damage or kill other coral reef epifauna (Jokiel, 1980), colonies grown under full spectrum UV filters exhibited less growth than those colonies placed under partial UV and no UV filters or grown without any filter but exposed to all wavelengths. In addition, although symbiotic dinoflagellates are UV sensitive when separated from their animal host (Calkins and Thordardottir, 1980; Jokiel and York, 1982), when exposed to natural, reduced intensities of PAR, neither full spectrum UV nor partial wavelengths of UV radiation caused bleaching in the *M. verrucosa* or *Porites compressa* colonies examined. These two responses to ultraviolet radiation probably resulted from the presence and production of the photo-protective pigments, S-320, in the coral tissue.

**Skeletal Growth**

S-320 is responsible for blocking the biocidal portion of the UV spectrum (UV-B) but is largely transparent to the UV-A wavelengths (Kawaguti, 1944). Since the production of the S-320 pigments needed for protection from UV-B entails a high metabolic cost (Kawaguti, 1944), it would not be surprising for corals shielded from UV-B to exhibit enhanced skeletal growth (Jokiel and York, 1982). In fact, significantly faster skeletal growth did occur in both *M. verrucosa* and *P. danai* when grown under the "No UV" treatment than when grown
under the "Full UV" treatment (Table 2). Jokiel and York (1982) obtained similar results for *P. damicornis*; and, while the same trend was shown for *P. damicornis* in this study, no significant difference between the two treatments was found (Table 2), possibly due to the low sample size (Table 1).

Near UV radiation has been shown to participate in photosynthesis (Steeman Nielsen, 1975). In symbiotic organisms, UV-A wavelengths stimulate fluorescence in the green animal pigments and are then re-emitted at longer wavelengths, absorbed by the pigments of the algae, and used for photosynthesis (Kawaguti, 1969). Since zooxanthellae may increase calcification rates through the translocation of organic carbon produced in photosynthesis (Pearse and Muscatine, 1971; Muscatine et al., 1984), it follows that increases in the efficiency of photosynthesis by harnessing added wavelengths of light might translate into greater skeletal growth rates. In addition, Roth et al. (1982) found that while wavelengths solely in the UV-A region decreased calcification rates, UV-A + PAR together created a net positive effect. Subsequently, those corals protected from UV-B but grown in the presence of UV-A + PAR might be expected to show an even greater skeletal growth since they do not have to devote energy to the production of S-320; and they have additional wavelengths of light available for photosynthesis. Because the Mylar filter used in this study transmitted some of the shorter wavelengths in the UV-B region, this response to UV-A + PAR could not be demonstrated. However, both *M. verrucosa* and *P. danai* grew significantly faster under the "Partial UV" treatment than under the "Full UV"
treatment (Table 2); and, since the production of S-320 was still required, enhanced calcification by UV-A wavelengths may have occurred. Again, a lack of significant difference in growth rates of *P. damicornis* colonies may have been due to the low sample size.

Therefore, it appears that corals shielded from partial wavelengths of UV-B and from full spectrum UV radiation may be able to increase skeletal growth either by channeling more energy towards growth rather than towards the production of photoprotective pigments, or by harnessing additional wavelengths of energy for photosynthesis.

Jokiel (1978) found enhanced photosynthesis and calcification in corals growing in high wave energy habitats; and Dennison and Barnes (1988) observed a 25% reduction in photosynthesis, respiration, and calcification in *Acropora formosa* subjected to reduced water motion. In addition, Houck et al. (1977) found that in *P. damicornis* linear skeletal growth reached a sharp optimum between 26 and 27 °C, then dropped off drastically with increasing temperature, while growth in *M. verrucosa* reached a maximum at approximately 25 °C then decreased slowly with increasing temperature.

In the present study, *M. verrucosa* and *P. damicornis* were collected from the windward edge of Checker Reef and were subsequently subjected to reduced flow rates and higher water temperatures (between 27 and 28.5 °C) when placed in the lee of Coconut Island. Colonies of both of these species exhibited slower skeletal growth rates when grown under the full UV plus PAR filter ("Full UV" treatment) than those colonies subjected to full spectrum UV plus PAR but
grown without a filter on the forereef (Table 2). P. danai, which was collected from the leeward edge of Checker Reef where it is naturally exposed to lower flow rates than those corals growing on the forereef, did not grow significantly slower in the lee of Coconut Island under the "Full UV" treatment compared to the more natural reef-set samples; however, this $p$ value is close to the 0.05 level of significance and may have reached this significance level if a larger sample size had been used (Tables 1 and 2).

Therefore, the combined effects of UV radiation, lowered flow rates, and higher water temperatures may be more pronounced in those species normally found in high energy environments on the forereef. In addition, since there was no significant difference in skeletal growth among colonies of any the species grown on the reef and shielded from UV ("Reef set" / "Full UV", $p > 0.178$, Table 2), the damaging effects of exposure to full spectrum UV on corals growing under optimal reef conditions may be similar to the detrimental effects of higher water temperatures and lowered flow rates on corals shielded from UV radiation.

**Microalgal Density and Pigment Concentration**

**Upper Surfaces of the Coral Fragments**

As mentioned previously, the photoprotective pigments, S-320, are largely transparent to UV-A wavelengths (Kawaguti, 1944); and UV-A has been shown to participate in photosynthesis (Steeman Nielsen, 1975). Therefore, one might expect zooxanthella populations within corals normally exposed to surface levels of full spectrum UV
radiation, but now shielded from UV-B and exposed to UV-A + PAR, to be maintained at the original density. In this study, although slight bleaching did occur in *M. verrucosa* collected from the reef edge and exposed to partial wavelengths of UV with PAR, the same effect occurred in both the "No UV" and "Full UV" treatments. Bleaching in all three treatments appeared to result from a loss of zooxanthellae only (Fig. 4). In some cases *in situ* bleaching has been attributed to lowered salinities as a result of intense precipitation (Goreau, 1964), although manipulative studies conducted by Hoegh-Guldberg and Smith (1989) showed that reduced salinities without a corresponding high increase in water temperature had no effect on two corals collected from the Great Barrier Reef, Australia. Heavy rainfall, as shown by the much reduced UV levels (Fig. 4), occurred during the initial 5 days of this experiment, resulting in decreased temperatures and lowered salinities. While there was no significant difference in the slopes compared among the three treatments (Table 3), all other variables within the treatments were the same except for the band of UV wavelengths transmitted through the filters. Therefore, the slight bleaching that occurred in all three treatments may be attributed to lowered salinities and lower water temperatures.

The *M. verrucosa* colony taken from a depth of 8.5 m in Kaneohe Bay is normally exposed to only about 4% of the UV radiation found at 0.2 m (pers. observ.). However, the fragments of this *M. verrucosa* colony that were exposed to increased, aquarium levels of PAR responded with severe bleaching regardless of the UV treatment (i.e.
"No UV," "Partial UV," or "Full UV," Fig. 7). The control frag­
ments, which were grown under the "No UV + Shade" filter, were ex­
posed to levels of PAR similar to the those found at a depth of 8.5 m
(pers. observ.) at Checker Reef and did not bleach (Fig. 7). While
the concentration of S-320 within the coral decreases with depth
(Dunlap and Chalker, 1986), production of this pigment can increase
in direct response to increases in the intensity of UV radiation
(Jokiel and York, 1982). Furthermore, Jokiel and York (1984) showed
that rapid adaptation to extremely high levels of UV radiation is
possible for many species of microalgae, including zooxanthellae.
Jokiel and York (1984), also observed that short-term photoinhibition
of cultured zooxanthellae was due largely to intensified levels of
PAR, not UV radiation. These results also agree with Houck et al.
(1977) who observed that the "shade-loving" species, M. verrucosa,
shows a direct negative correlation of growth with increased levels
of light, and with Dustan (1982) who found that Montastrea annularis
transplanted from 30 to 15 m, where UV penetration is minimal but PAR
is increased, exhibited reduced growth, severe bleaching, and high
mortality.

Therefore, it appears from experiments performed on M.
verrucosa collected from the reef edge and from 8.5 m that partial
wavelengths of UV radiation (mostly in the UV-A region), when sepa­
rated from PAR, do not affect zooxanthella densities or pigment
concentrations.

In addition, full spectrum UV, when separated from PAR, does
not cause bleaching, either through the loss of zooxanthellae or
through the loss of zooxanthella pigments in *M. verrucosa* collected from 8.5 m. Although concentrations 5-320 were not measured in this study, this phenomenon may stem from the increased production of this pigment in direct response to increases in UV radiation (Jokiel, 1985). Exposure, however, to intensified levels of PAR does cause bleaching via zooxanthellae loss only, as shown by the lack of a significant difference between fragments under the "No UV + Shade" vs. "Full UV + Shade" treatments as well as between fragments under the "No UV" vs. "Full UV" treatments (Fig. 10). In the treatments with shade, bleaching did not occur, regardless of the transmittance of UV. In those treatments without shade, but with subsequent increases in the intensity of PAR, bleaching did occur, again, regardless of the transmittance of UV. Therefore, in the deeper growing colonies of *M. verrucosa* examined, bleaching may have resulted from the inability of the zooxanthellae to photoadapt to increased levels of visible light.

Bleaching in *P. compressa* was similar to bleaching in *M. verrucosa* in that it was due entirely to zooxanthella loss (Fig. 13) rather than loss of zooxanthella pigment (Fig. 14 and 15). *P. compressa* also did not appear to be affected by full spectrum UV when UV was separated from PAR. In contrast to bleaching in *M. verrucosa*, however, exposure to PAR without UV, and exposure to UV with reduced intensities of PAR caused no bleaching. Exposure to UV plus PAR together resulted in severe bleaching, indicating a synergistic effect of UV and PAR in *P. compressa* (Fig. 13).
Chang et al. (1983) studied strains of the zooxanthella, *Gymnodinium microadiaticum*, isolated from three different types of invertebrate hosts and found functional differences in their mechanisms of photo-adaptation. They concluded that the adaptive capabilities of the zooxanthellae was related to the ambient irradiance encountered by the respective host. However, there is much variation in the ability of corals and their zooxanthellae to adapt to high levels of solar irradiance (Siebeck, 1981), possibly due, in part, to genetic differences in the zooxanthellae that the various hosts possess (Jokiel and York, 1982). As mentioned previously, growth in "sun-loving" species is positively correlated with sun exposure (Jokiel and York, 1982), while growth in "shade-loving" species is negatively correlated (Houck et al., 1977; Jokiel and York, 1982).

In addition, "sun" and "shade" zooxanthellae living in different ecotypes of the same coral species may be intolerant to changes in irradiance that occur when the coral is transplanted to new environments (Dustin, 1979). Although *M. verrucosa* and *P. compressa* are both considered "shade-loving" species, they exhibit diverse morphologies: *M. verrucosa* appears as a thickened finger-like form in shallow water and assumes a plate-like form at depth while *P. compressa* is finger-like in both shallow and deep water. Hence, these morphologies may affect the degree of sun tolerance afforded by the different zooxanthellae: deep-water *P. compressa* may be more tolerant to increased levels of PAR, but, when combined with increased levels of UV, is susceptible to severe bleaching.
The actual mechanism responsible for bleaching has been the subject of many recent studies; and it appears that the bleaching process is different with each species of coral, the amount of time that has elapsed between the bleaching event and sampling (Hoegh-Guldberg and Smith, 1989), and the type of environmental stress placed on the corals. In laboratory studies, Hoegh-Guldberg and Smith (1989) found that in *Stylophora pistillata* colonies exposed to reduced salinity and to full sunlight for 10 days, bleaching occurred through the loss of zooxanthella pigment, whereas colonies exposed to highly elevated temperatures bleached via loss of zooxanthellae. In addition, Kleppel et al. (1989) observed that natural *in situ* bleaching of *Montastrea annularis* event was due largely to the loss of chlorophyll c per zooxanthella.

In the present experiments concerning the effects of partial wavelengths of UV on *M. verrucosa*, colonies from both the reef edge and from 8.5 m showed no significant decreases in either chlorophyll a or chlorophyll c per zooxanthella in each treatment, regardless of the type of UV transmitted and the numbers of zooxanthellae lost. Although both of these colonies were also subjected to decreased salinity because of a severe storm that was in the area for the duration of most of the two experiments, bleaching resulted from losses in zooxanthellae only. Those corals that were examined for the effects of full spectrum UV plus PAR were grown under optimal conditions without the effects of a storm. Here, any bleaching that occurred was, again, due solely to a reduction in zooxanthella densities with one exception: the *M. verrucosa* fragments grown under the
"No UV" filter, which also showed a significant decrease in chlorophyll a per cell (Fig. 11). Both chlorophyll a and chlorophyll c per zooxanthella responded similarly for all other treatments in both M. verrucosa and P. compressa in that they did not significantly increase or decrease in concentration. Although more studies are needed to determine the actual mechanism of bleaching, it appears from this study that short-term exposure to PAR, as well as short-term exposure to lowered salinity, causes bleaching in M. verrucosa and P. compressa mainly through a reduction in zooxanthellae. This should, however, be investigated more thoroughly.

Lower Surfaces of the Coral Fragments

No work to date has been published concerning increases in color intensity on underneath surfaces of corals irradiated with light from above, although some researchers have noticed a similar occurrence (Wilkerson, pers. comm.; Hoegh-Guldberg, pers. comm.). In the present study, in those treatments where I saw an increase in color, this event stemmed from a significant increase in zooxanthella density, rather than from an increase in pigment per cell. In addition, when bleaching occurred in corals collected from 8.5 m and exposed to increases in PAR and/or full spectrum UV, an increase in zooxanthellae within the bottom surfaces was measured along with a decrease in zooxanthellae from the upper surfaces. Two possible explanations for this phenomenon are that the doubling time for the zooxanthellae in situ was more rapid than the expulsion rate or that the some of the zooxanthellae from the upper surfaces migrated to the
shaded lower surfaces of the coral, perhaps in direct response to irradiance stresses from above.

Zooxanthella mitotic indexes, which are used to calculate doubling times, were not measured for *M. verrucosa* or *P. compressa* in this study; however, the underside populations of these zooxanthellae doubled in less than 30 days (Figs. 7, 10, and 13). This rate was faster than that observed by Wilkerson et al. (1983) in the coral, *S. pistillata* (42-53 days), and faster than doubling rates published for any coral to date. Therefore it is possible that the zooxanthellae migrated to protected areas of the coral, in addition to being expelled from the host. In this case, bleaching via zooxanthella "loss" may actually be bleaching via zooxanthella movement through expulsion and migration. Hence, although further research detailing this process must be performed, bleaching should be re-examined in many coral species since a new dimension may be added to our understanding of the mechanisms concerned.

In conclusion, one must recognize that UV radiation is not necessarily detrimental to reef-building corals. Degrees of adaptation to increased levels of full spectrum UV alone and with PAR offer a competitive advantage to the various coral species that comprise the reef. Utilization of the UV-A wavelengths may even benefit the corals by adding supplementary energy for photosynthesis, especially for deeper growing corals, since it is this band of UV radiation that penetrates the deepest in clear oceanic waters (Smith and Baker, 1979). Organisms have adapted to the presence of UV radiation throughout their evolutionary history. Although the relationship
between the ozone layer and UV is well known, the discovery of the depletion of this layer has only been recent; and it is unknown whether fluctuations in this layer are part of the global cycle and whether organisms were able to adapt to increases in UV in the past. This study, along with others concerning the ozone layer and the effects of UV radiation on various organisms, will provide baseline data for these types of studies in the future.
LITERATURE CITED


