

Effects of ultraviolet radiation on corals and other coral reef organisms

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Abstract

The discovery of the importance of solar ultraviolet radiation (UVR) as a factor affecting the biology of coral reefs dates only to about 1980. Interest has heightened during the past five years owing to the demonstration of loss of stratospheric ozone through human activities. We have only begun to document gross, qualitative effects of UVR on coral reef organisms, usually in experiments comparing the biological response to the presence or absence of UVR through the use of UV-cutoff filters, or to varying levels of UVR in transplantation studies. Most such studies have not distinguished between the effects of UVA (320–400 nm) and those of UVB (290–320 nm), although in the context of global change involving stratospheric ozone loss, it is the latter wavelengths that are relevant. To date we have been addressing physiological and ecological questions, not yet attempting to evaluate quantitatively the impact of forecast increases in solar UVB penetration. Interacting and synergistic effects of UVR with increased temperature, pollutants, sedimentation, visible light, etc. have scarcely been studied but will be essential to understanding and predicting the fate of coral reefs under conditions of global change.

Here we comprehensively review the effects of UVR on corals and other reef macroorganisms, mindful that although much is known of proximal effects, little of this knowledge is directly useful in making long-term predictions regarding the health of coral reefs. We conclude that even small anthropogenic increases in UVB levels will have sublethal physiological manifestations in corals and other reef organisms, but that this will have relatively small impact on the distribution of reef corals and coral reefs, perhaps affecting their minimum depths of occurrence.

Keywords: corals, ozone depletion, ultraviolet (UV) radiation, UVB

Introduction: the ultraviolet environment

The decrease of stratospheric ozone from anthropogenic inputs of chlorinated fluorocarbons has resulted in an increase in harmful ultraviolet-B radiation (UVB, 290–320 nm) reaching the earth's surface (Madronich 1992; Madronich *et al.* 1994). The majority of the solar UVB reaching the sea surface is within the 300–320 nm waveband (Frederick *et al.* 1989; Kirk 1994). Although earlier concerns were centred on the Antarctic with the advent of the seasonal 'ozone hole' there, the natural concentration of stratospheric ozone generally is less near the equator than at higher latitudes (Cutchis 1982), which together with the lower solar zenith angle there, means that the tropics receive more ultraviolet radiation (UVR).

Thus, tropical ecosystems have an evolutionary history of exposure to high fluxes of UVR (Green *et al.* 1974; Frederick *et al.* 1989). Wavelengths above 330 nm are unaffected by ozone depletion, whereas a 5% decrease in stratospheric ozone could cause a 10% increase in DNA-weighted UVB dose (Cutchis 1974). In absolute terms, even small percentage decreases in ozone that may occur above the tropics would be important because the UVB irradiance there is already high; therefore, the absolute increase in weighted doses for the same percentage reduction in ozone would be greater, although the relative enhancement of biological effects increases with latitude (Madronich 1992).

Satellite and ground data for 1979–94 show no significant change in stratospheric ozone over the tropics (20°N–20°S), where a downward trend of 2% per decade is

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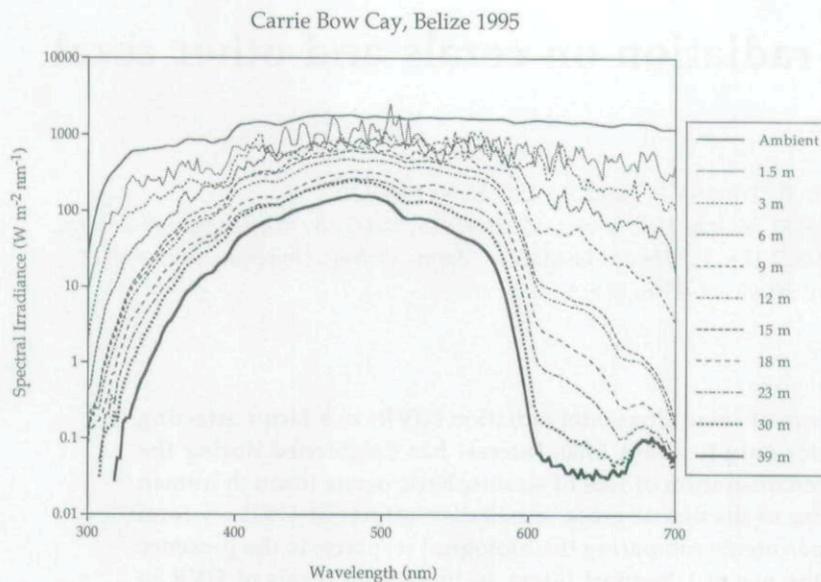


Fig. 1 Depth profile of spectral data (300–700 nm) recorded on the fore reef at Carrie Bow Cay, Belize (17°N), July 1995, 12.00–12.30 hours, using a LiCor LI-1800UW scanning spectroradiometer (LiCor, Lincoln, Nebraska) placed at the various depths using SCUBA. The time between scans was \approx 3–4 min. The cosine-corrected collector and sensors have a nominal bandwidth of 8 nm and were programmed to scan from 300 to 700 nm in 2 nm intervals. Curves represent the means of three scans for each depth. Source of data: MP Lesser (unpublished).

equalled by the 95% confidence limits (World Meteorological Organization 1995). However, in areas of slightly higher latitude (20–30°N), the trend of ozone depletion (–2 to –4% per decade) is higher and less variable (Stolarski *et al.* 1992; Madronich 1992; World Meteorological Organization 1995). During the same time calculated DNA-weighted doses at 5°S and 5°N latitude increased by $5.1 \pm 2.3\%$ (SD) and $4.1 \pm 2.7\%$, respectively, and DNA-weighted doses at 15°S and 15°N latitude increased by $2.8 \pm 2.1\%$ and $6.3 \pm 2.4\%$, respectively (Madronich *et al.* 1994). Many subtropical coral reefs (Caribbean, Hawaii, northern Red Sea) lie within these latitudes, and the data predict that UVB irradiances could increase in the future in these regions before beginning to recover in the next half-century (Madronich *et al.* 1994).

Recent analyses also show that during the month of July many geographical areas, including Hawaii, the Red Sea, and the Caribbean, will likely be subjected to significant increases in the weighted doses of UVB irrespective of the interannual variability in cloud cover in as little as 30 years (Lubin & Jensen 1995). The decrease in the variability of cloud cover affecting UVR reaching tropical ecosystems is important because any decreases in stratospheric ozone, and subsequent increases in UVB, over these areas would not be ameliorated by cloud cover. In general, the high transparency of tropical ocean waters allows UVR to penetrate to depths of 20 m or more (Jerlov 1950; Smith & Baker 1979; Fleischman 1989; Gleason & Wellington 1993; Fig. 1; Table 1). Taken together, these data suggest that coral reef ecosystems will eventually be exposed to slightly higher irradiances of UVR, particularly the UVB portion of the spectrum, than they have been during their recent history.

Although tropical waters generally are more transparent to UVR than temperate waters, the water column

overlying coral reefs in coastal areas is susceptible to terrigenous inputs, upwelling, and variations in dissolved organic matter that can affect its optical properties (absorption and scattering) (Kirk 1994). Kaneohe Bay in Hawaii is actually a tropical estuary and has a vertical attenuation coefficient (K_d , m^{-1}) of \approx 1 at 320 nm, whereas Moku Manu (an offshore reef) has an attenuation coefficient of 0.2 at 320 nm (Lesser unpublished). Because of such variability, accurate underwater measurements of UVR, preferably spectral irradiance, are important. There are few instruments to accomplish this, and none are perfect for the task; accordingly, few published data exist for waters overlying coral reefs. Recent comparison-testing for the commercially available instruments has shown their generally good agreement with each other and radiative transfer models (Kirk *et al.* 1994). Their use through the bathymetric range (0–40 m) of most corals should provide reasonable data when the instruments are consistently calibrated with NIST-traceable standards and by intercomparison. As an example, unweighted UVB has been measured down to 30 m and UVA down to 39 m on the barrier reefs of Belize (Fig. 1; Table 1), but the biological effects, if any, of such radiation at these depths has not been studied.

Effects of UVR on corals and reef organisms

Scleractinian corals containing endosymbiotic dinoflagellates (zooxanthellae, genus *Symbiodinium*) are important contributors to reef photosynthetic production in nutrient-poor tropical waters receiving high solar irradiance. Whereas heterotrophy is important in many species of coral, the principal input of carbon for most species comes from autotrophy (Muscatine 1990). Therefore, zooxanthellate corals must expose themselves to sunlight,

Table 1 Integrated values of unweighted UVR, UVB and photosynthetically active radiation (PAR) for the depth profile at Carrie Bow Cay, Belize (17°N), in June 1995, at 12.00–12.30 hours. ND, not detected. $1 \text{ W} = 1 \text{ J s}^{-1}$. For details of instrumentation and data collection, see caption to Fig. 1

Depth (m)	UVR (W m^{-2}) 300–400 nm	UVB (W m^{-2}) 300–320 nm	PAR (W m^{-2}) 400–700 nm	PAR ($\mu\text{mol quanta m}^{-2}\text{s}^{-1}$) 400–700 nm
Ambient	62.80	3.842	524.7	2105
1.5	36.31	1.047	254.1	1005
3	15.34	0.4622	188.8	759
6	9.584	0.0922	150.4	601
9	5.104	0.0195	102.4	411
12	4.658	0.0184	86.6	336
15	3.973	0.0129	67.9	264
18	2.351	0.0069	42.4	165
23	1.830	0.0027	32.6	126
30	1.411	0.0018	28.1	108
39	0.684	ND	17.1	66

including its UV component, and the photic environment is a crucial determinant of their productivity, physiology, and ecology (Chalker *et al.* 1988; Falkowski *et al.* 1990). The differential sensitivities to UVR in the life processes of various coral species and morphs, and of species of *Symbiodinium*, suggest that increasing fluxes of UVR will affect the community structure of coral reefs, although the extent to which this will occur is difficult to predict, especially because the biological effects on corals of environmentally relevant UVR have only just begun to be evaluated. Thus, we will comprehensively review the effects of UVR on corals and other reef organisms, discerning effects of UVA and UVB where possible, with a view toward identifying the information required to evaluate the impact of projected increases in solar UVB reaching coral reefs.

Overt effects: death, inhibition of growth, and bleaching

MacMunn (1903), in discussing the pigments in azooxanthellate (non-symbiotic) dendrophylliid corals, was apparently the first to state that UVR is potentially damaging to corals. Catala-Stucki (1959) subsequently noted that most corals suffer when exposed to high doses of artificial UVR (from 'Wood tubes,' hydrogen lamps emitting at 254 and 360 nm), which, if prolonged, may be fatal. In their studies of UV-absorbing and fluorescing compounds (see below), Shibata (1969) and Kawaguti (1973) speculated that the compounds served as filters that protected corals and their zooxanthellae from UVR.

Experimental manipulations of coral reef organisms in the field beginning c. 1980 confirmed that UVR could be an environmentally relevant stressor. Jokiel (1980) demonstrated that cryptic reef epifauna were killed by acute exposure to solar UVR in shallow water and

suggested that the structure of coral reefs was affected by the relative UV tolerances of their constituent species. Specimens of *Plerogyra sinuosa* transplanted from 25 m to 5 m depth and shielded from solar UVR remained healthy for six months, whereas unshielded specimens died within one month, implicating UVR as the cause of death (Vareschi & Fricke 1986). Scelfo (1986) confirmed a depth-dependent sensitivity to UVR in *Montipora verrucosa*, colonies of which died within two days of transplantation from 10 m depth into shallow aquaria in full sunlight, but which survived if protected from UV wavelengths < 380 nm. Siebeck (1981, 1988) likewise documented depth-related differences in tolerance to (artificial) UVR (275–400 nm) in several coral genera: on average, UV tolerance in colonies of four species collected at 1.5 m depth was about double that of conspecifics collected at 18–20 m, as indicated by LD₅₀ values. UV effects were ameliorated by treating the corals with visible light following UV exposure (see 'Photoreactivation,' below). Exposing corals collected at 2–4 m depths to UV levels ≈30% of direct solar irradiance and temperatures 1.3–1.8 °C above ambient in aquaria resulted in higher mortalities in *Acropora valida* colonies than in conspecifics shielded from UVR, although there was no effect of UVR on survival of *Pocillopora damicornis* colonies exposed to these experimental conditions (Glynn *et al.* 1993).

Gleason & Wellington (1995) collected planula larvae of *Agaricia agaricoides* from colonies living at 3 m and 24 m and incubated them *in situ* at 3 m in differentially filtered chambers receiving photosynthetically active radiation (PAR) only, PAR + UVA, or full solar irradiation (PAR + UVA + UVB). Survival of all planulae was uniformly high under PAR and PAR + UVA conditions, but decreased to ≈64% in 3 m larvae exposed to PAR + UVA + UVB at 3 m, and to ≈25% in 24 m larvae exposed to the same conditions. This appears to be the first study

demonstrating a UV wavelength-specific effect on mortality in any life history stage of corals.

Sublethal effects of the UV component of sunlight include depressed calcification and skeletal growth. Roth *et al.* (1982) showed that uptake of ^{45}Ca by *Pocillopora damicornis* was negatively correlated with natural levels of UVA (380 nm). Likewise, natural levels of solar UVR depressed skeletal growth in colonies of *Pocillopora damicornis* compared with those grown under a 400 nm cutoff filter (Jokiel & York 1982). Inhibition of growth was not seen in a similar experiment by Glynn *et al.* (1993) on this species and *Acropora valida*, which were grown under 350 nm cutoff filters. The different results in these two studies suggest an effect of UVA wavelengths between 350 and 400 nm. The generally greater sensitivity to UVR of brown than green morphs of *Porites astreoides* included a depression of skeletal growth by natural UVR in the former (Gleason 1993). Stimson (1996) speculated that the wave-like outward growth form of table- or plate-like corals resulted from the annual cycle of UVB irradiance inhibiting growth on the upper surface of the colony.

Bleaching, principally via the loss or expulsion of endosymbiotic algae from the hosts' tissues, is one of a suite of responses to various environmental stressors (Brown & Howard 1985). Although localized bleaching often can be attributed to particular events such as heavy rainfall, aerial exposure during exceptionally low tides, thermal intrusions, etc. (Coffroth *et al.* 1990; Glynn 1993, 1996 this volume), elevated seawater temperature, sometimes associated with El Niño warming events, is generally regarded as the most likely primary factor in geographically widespread bleaching (Atwood *et al.* 1992; Glynn 1993, 1996; Goreau & Hayes 1994). However, the correlation is not exact, and elevated water temperatures and conditions promoting them (low cloud cover, reduced circulation, doldrums) may interact with other factors, such as increased penetration of solar radiation, including UVR and PAR, into clear seawater (Glynn 1993).

Thus, Harriott (1985) suggested that the mass bleaching of corals on the Great Barrier Reef during the warmest part of the year was caused in part by increased penetration of UVR, because bleaching occurred only on the upper and unshaded surfaces of colonies and extended to deep colonies only in very clear water. Similar reasoning was offered by Fisk & Done (1985) to explain bleaching elsewhere on the GBR, and by Goenaga *et al.* (1989) for bleaching in the Caribbean, although analysis of meteorological data could not confirm these contentions (Coffroth *et al.* 1990), and in none of these cases was UVR measured.

Lesser *et al.* (1990) experimentally demonstrated significant independent effects of solar UVR and elevated temperature in reducing the number of zooxanthellae per

polyp in portions of a clonal colony of the zoanthid *Palythoa caribaeorum*. Jokiel (1980) had earlier induced bleaching of a coral reef sponge by acutely exposing it to solar UVR, and Wood (1989) noted the photodestruction of chlorophyll and carotenoids by UVR in a red alga transplanted from shallow Hawaiian reefs to uncovered aquaria in full sunlight. Conversely, Jokiel & York (1982) could not experimentally induce bleaching in colonies of *Pocillopora damicornis* collected from 1 m depth and exposed to unattenuated sunlight in shallow aquaria. Glynn *et al.* (1993) found that UVR ($\approx 30\%$ of direct irradiance) resulted in greater loss of zooxanthellae in *A. valida* and *P. damicornis* from 2 to 4 m than in shielded conspecifics, but only at elevated temperatures.

Noting that much of the bleaching during the 1987 and 1990 events in the Caribbean occurred at depths > 20 m, Goenaga *et al.* (1989) and Gleason & Wellington (1993) hypothesized that the exceptional clarity of seawater during prolonged calm periods (doldrums) allowed UVR to penetrate more deeply and cause bleaching. To simulate the increase in UVR exposure that would occur under such conditions, Gleason & Wellington (1993) transplanted colonies of *Montastrea annularis* (morphotype not given) from 24 m to 18 m and 12 m, exposing them either to ambient irradiance or screening them from UVR < 390 nm. After 21 days, colonies transplanted to 12 m and exposed to UVR were paler and had significantly fewer zooxanthellae per cm^2 than transplanted colonies shielded from UVR at this depth. Although this study did not test wavelength-specific effects of UVR on bleaching, the authors calculated that, in clear seawater, UVA at 24 m can reach 141% of the mean levels that caused experimental bleaching, while UVB (measured at 300–320 nm) can reach 74% of the irradiance that caused bleaching at 12 m. Whether UVA wavelengths in particular are implicated for bleaching the deeper colonies during clear water conditions remains uncertain. As emphasized by Dunne (1994), the UV shields used by Gleason & Wellington (1993) also attenuated PAR by 8%, but the independent effect of PAR was not tested; thus it is also unknown whether this small decrease in visible light contributed significantly to the effect attributed to the exclusion of UVR.

Bleaching and tissue damage in intertidally exposed colonies of *Goniastrea aspera* could not be attributed to ambient UVB radiation (Brown *et al.* 1994a), and although an effect of PAR was apparent, the proximal cause of bleaching (heating, desiccation, photochemical processes) was unknown, nor was an effect of UVA ruled out. Fitt & Warner (1995) implicated UVA and blue light by measuring the decline in quantum yield (F_v/F_m , the ratio of variable to maximal chlorophyll fluorescence), a harbinger of bleaching, in zooxanthellae isolated from colonies of *Montastrea annularis* maintained at elevated

temperature (32 °C) under variably filtered sunlight for up to three days. These experiments demonstrated no effect of UVB exposure on F_v/F_m in zooxanthellae; UVA (320–395 nm) had the greatest effect, and blue light (395–495 nm) also depressed F_v/F_m .

Photosynthesis and respiration

Artificial UVB radiation inhibited photosynthesis in *Fungia* spp. collected at 30 m depth, but not in those collected at 1 m (Masuda *et al.* 1993). Paired colonies of *Acropora microphthalmalma* translocated from 2, 10, 20 and 30 m depth to 1 m maintained similar rates of photosynthesis when shielded from solar UVR at 1 m, but colonies originating at 20 and 30 m showed $\geq 30\%$ inhibition of photosynthesis when exposed to UVR (Shick *et al.* 1995). In both *Fungia* spp. and *A. microphthalmalma*, photosynthesis in zooxanthellae isolated from both UV-resistant (shallow-dwelling) and UV-sensitive (deep-dwelling) corals was inhibited by UVR. Collectively, these results indicate a greater resistance of coral photosynthesis to UVR in those living in shallow water than in deep-water conspecifics, and a protective effect of the hosts' tissues on the zooxanthellae *in hospite*. The likely basis for this protection – UV-absorbing compounds – will be discussed below. Acclimatization to solar UVR improved the subsequent photosynthetic performance in colonies of *Montipora verrucosa* exposed to UVR (Kinzie 1993).

Simulated solar UVR depressed photosynthesis in zooxanthellae (probably *Symbiodinium bermudense*: see Banaszak *et al.* 1993) freshly isolated from the tropical sea anemone *Aiptasia pallida* (Lesser & Shick 1989), but less so when photosynthesis was measured in the intact anemone (Shick 1993), again indicating a protective role of the host. Lesser and Shick (1990), using electron microscopy and quantitative stereology, showed that simulated solar UVR significantly decreased the volume fraction of chloroplasts in cultured zooxanthellae from *Aiptasia pallida*. The chloroplast volume fractions for cells *in hospite* were not significantly different for treatments with and without UVR, although the surface density of thylakoid membranes in cultured zooxanthellae was significantly lower than for cells *in hospite*. For cells *in hospite* the surface density of thylakoid membranes was significantly decreased after exposure to UVR. These results again suggest that the host has a role in modifying the microenvironmental irradiance to which zooxanthellae are exposed, and that UVR affects the photomorphogenesis of chloroplasts and their components.

When *S. bermudense* was cultured under conditions designed to simulate those *in hospite*, DNA-weighted UVR (290–400 nm) dosage rates of 0.57 mW m^{-2} depressed maximum photosynthetic capacity, cell-specific content

of chlorophyll *a*, chlorophyll-specific fluorescence, and Rubisco activity (Lesser 1996). These effects were exacerbated at high temperatures. Improvement of photosynthetic performance and fluorescence by the addition of exogenous antioxidants suggested that the effects of UVR were both direct and indirect, in the latter case, mediated by reactive oxygen species (ROS; see 'Photooxidative Stress,' below). The results are consistent with the known effects of both UVR and ROS on the D1 protein in photosystem II of photosynthesis (Renger *et al.* 1989; Tschiersch & Ohmann 1993) and on Rubisco (Asada & Takahashi 1987; Neale *et al.* 1992).

The sensitivity of any biological process to changes in stratospheric ozone and hence UVB irradiance depends largely on its action spectrum, which expresses the relative effect of radiation of the same photon flux density at different wavelengths (Kohen *et al.* 1995). Action spectra and accurate radiometry are essential for making predictions through modelling (Smith *et al.* 1980; Caldwell *et al.* 1986; Coohill 1989) in the event of continued changes in the rate and geographical extent of ozone depletion. Halldal (1968) presented an action spectrum for photosynthesis in zooxanthellae isolated from *Favia pallida* that indicated both photooxidation of chlorophyll at UVB wavelengths $< 300 \text{ nm}$, as well as considerable UVA-stimulated photosynthesis. However, it is unclear whether UVA itself was used photochemically by algal chlorophyll or accessory pigments, or whether UVA-induced fluorescence at longer wavelengths in the host tissue (which tissue probably was present, based on the method used to isolate the zooxanthellae) was responsible for the photosynthesis in the UVA range (see 'Fluorescent Pigments,' below).

The action spectrum for inhibition of photosynthesis by UVR in *Pocillopora damicornis* from Hawaii (Lesser & Lewis 1996) shows a significant increase in the effects of UVB (up to 310 nm), and a decrease in the remainder of the UV spectrum, when compared with action spectra for isolated zooxanthellae and phytoplankton. The shape and the magnitude of the action spectrum for *P. damicornis* reflects both the accumulation of high concentrations of UV-absorbing compounds in *P. damicornis* and that most of these absorb principally in the UVA portion of the spectrum (Lesser & Lewis 1996; Jokiel *et al.* in press). These results seem to contradict the notion that symbiotic microalgae at 1.0 m depth would be fully protected from the effects of UVR on photosynthesis by virtue of living in the host's tissues, although it appears that they are better protected than are cultured phytoplankton or zooxanthellae. One reason for this result is the extremely high biologically effective dose of UVB received in shallow tropical waters (Banaszak *et al.* submitted). The result predicts that subsequent increases in UVB will have

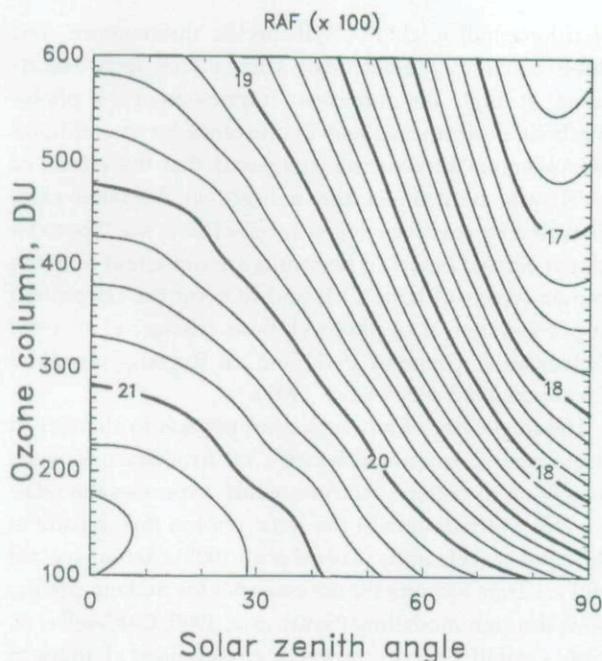


Fig. 2 Radiation amplification factor (RAF) for *Pocillopora damicornis* from Kaneohe Bay, Hawaii, during July 1994. The RAF was calculated using the action spectrum (in 1.0 nm increments) for inhibition of photosynthesis by UVR from 280 to 420 nm (Lesser & Lewis 1996), the atmospheric profiles from the US Standard Atmosphere continental aerosols and a radiation model for 25 km visible range. RAF calculation courtesy of S Madronich, National Centre for Atmospheric Research, Boulder, Colorado.

demonstrable effects on the productivity of this, and possibly other, shallow water coral species.

One way to compare the sensitivities of different biological functions or to compare the same function among diverse taxa is to calculate a radiation amplification factor (RAF) using a radiative transfer calculation for the dose change that results from a small decrease in ozone (1%). The RAF can then be used to determine the increase in *biologically effective* UVB radiation for a given decrease in ozone concentration (Madronich 1992). The RAF from 280 to 420 nm for *P. damicornis* at 1 m depth in Hawaii is 0.20 ± 0.02 , with little variation associated with solar zenith angle or even stratospheric ozone (Fig. 2). Thus, if a 10% reduction in ozone occurred over time above Hawaii, the percentage or power rules (Madronich 1992) would predict that corals at 1 m would receive a 2% increase in biologically effective radiation relative to photosynthesis, with unknown consequences. By comparison, the RAF for photosynthesis in a free-living dinoflagellate, *Prorocentrum micans*, is 0.50 (Madronich 1992); the larger impact in *P. micans* relative to that in the coral may be related to a different suite of UV sunscreens, higher sunscreen concentrations in the coral, longer optical pathlengths in the coral (see 'Myco-

sporine-like amino acids,' below), and the effects of vertical mixing on the amelioration of damage in free-living phytoplankton.

There is no consistent effect of UVR on respiration among corals, isolated zooxanthellae, or free-living algae, and its variable effects can be both acute and long-term. Simulated solar UVR both inhibited photosynthesis and increased respiration above the level of dark respiration in zooxanthellae isolated from *Aiptasia pallida* (Lesser & Shick 1989). Acclimation to UVR in culture and *in hospite* did not affect mitochondrial volume density in these zooxanthellae (Lesser & Shick 1990). Steady-state respiration in zooxanthellae isolated from specimens of the reef anemone *Phyllo-discus semoni* acclimated to solar UVR for ≈ 5 months was about double that of algae isolated from hosts shielded from long-term exposure to UVR (Shick *et al.* 1991). Like Kinzie's (1993) results for solar UVR effects on *Montipora verrucosa* colonies, Masuda *et al.* (1993) found no effect of artificial UVB on coral respiration in *Favia* spp., but saw an acute UVB-induced decrease in respiration in isolated zooxanthellae. It may be that the much larger biomass of the host masks any effects of UVR on respiration of zooxanthellae *in hospite*. Finally, Carpenter (1985) found that solar UVR increased respiration in algal turfs on coral reefs.

Cell division in zooxanthellae

UVR inhibits the growth of zooxanthellae in culture. Jokiel & York (1982, 1984) demonstrated separate, dose-dependent depressions by solar UVA and UVB of growth of *Symbiodinium microadriaticum* (or *S. bermudense*?) isolated from the 'shade-loving' anemone *Aiptasia tagetes* (= *A. pallida*). Lesser & Shick (1989) and Lesser (1996) likewise saw inhibitory effects of simulated solar UVR and artificial UVR at environmentally relevant irradiances on *Symbiodinium bermudense* (isolated from *Aiptasia pallida*) in culture. UVA and UVB had little effect on *S. microadriaticum* isolated from the 'sun-loving' scyphozoan, *Cassiopeia xamachana* (Jokiel & York 1982). Read (1986) also found differences in the UV-sensitivity of growth among cultures of zooxanthellae from taxonomically diverse invertebrate hosts in Hawaii and Enewetak, and only those from the nudibranch *Melibe pilosa* grew at all in full sunlight. Banaszak & Trench (1995a) confirmed a low sensitivity of *S. microadriaticum* from *C. xamachana* to artificial UVR, but found significant growth inhibition by UVR in *S. californium* from *Anthopleura elegantissima* (not a coral reef species). UVR stimulated the development of multiple-layer cell walls in the latter zooxanthellae. These authors found no UV-related differences in cell size in either species of zooxanthella, but Lesser & Shick (1989) found slight increases in cell size (detectable by flow cytometry with sample sizes of 5000) in zooxanthellae

exposed to UVR in culture and *in hospite*. Conversely, Read (1986) noted large but unspecified increases in the sizes of cultured zooxanthellae exposed to solar UVR, perhaps associated with decreased rates of cell division.

Effects of UVR on growth of zooxanthellae *in hospite* has scarcely been studied. In *Pocillopora damicornis*, full solar UVR did not affect the number of zooxanthellae per cm² of coral surface (Jokiel & York 1982), whereas pieces of a clonal colony of *Palythoa caribbaeorum* exposed to solar UVR had fewer zooxanthellae per polyp than did those shielded from UVR (Lesser *et al.* 1990). Morphs of *Porites astreoides* differing in their bathymetric distributions had differing sensitivities to solar UVR, manifested in greater mitotic indices in zooxanthellae isolated from the resistant morph when exposed to UVR (Gleason 1993). Whether species-specific sensitivity to UVR of zooxanthellae in culture or *in hospite* is related to their inherent capacities for repair of UV-related damage, or to the concentrations of UV-absorbing compounds in the zooxanthellae or their hosts, has not been studied systematically. However, the relatively low concentrations or absence of UV-absorbing mycosporine-like amino acids in zooxanthellae from *Anthopleura elegantissima* and *Aiptasia pallida* are correlated with the relatively great sensitivity to UVR in these zooxanthellae (see 'Mycosporine-like amino acids,' below).

Reproduction

Almost nothing is known of the effects of UVR on reproduction in reef corals. The majority of coral species broadcast-spawn their gametes as opposed to brooding planula larvae (Harrison & Wallace 1990), yet the only available information concerns corals that brood planulae and the response of these planulae. The damaging effect of UVR on DNA is well established (e.g. Setlow & Setlow 1962), so the nearly universal phenomenon among corals and many reef invertebrates of broadcast spawning at night might be related to avoiding such damage as well as to avoiding predation. Nocturnal UV avoidance seems especially relevant to sperm, which unlike eggs, are too small to make effective use of UV sunscreens (see Garcia-Pichel 1994; Adams & Shick 1996) and do not accumulate, e.g. mycosporine-like amino acids (Carroll & Shick 1996; see below). Further, sperm must remain viable only for long enough to fertilize the eggs (a matter of minutes to hours during a mass spawning), whereas eggs and larvae developing from them remain in the plankton for much longer, when they are exposed to solar UVR and thus require protection from it.

Exposure to natural UVR resulted in greater release of planulae and decreased skeletal growth in *Pocillopora damicornis* when compared with shielded specimens (Jokiel & York 1982). This relationship might allow corals

to increase reproductive output at the expense of skeletal growth in unstable (shallow) environments, while maintaining higher growth rates in deeper, stable environments. In long-term experiments, exposure to natural levels of UVR did not alter reproductive periodicity compared with shielded specimens but increased planula release throughout the monthly cycle (Jokiel 1985). Planulae of the reef coral *Agaricia agaricites* derived from colonies growing at 3 m were more resistant to UVR than were those from 24 m depth (Gleason & Wellington 1995). The differential mortality in these planulae was related to UVB rather than to UVA or visible light.

Photooxidative stress

In addition to its direct effects, UVR may indirectly damage reef organisms via photochemical reactions that produce reactive oxygen species (ROS). Such reactions transform electronic excitation from the absorption of UVR into chemical energy by activating molecular oxygen (O₂), yielding ROS such as hydrogen peroxide (H₂O₂), superoxide and hydroxyl radicals (O₂^{-•} and •OH, respectively) and singlet oxygen (¹O₂). Most production of ROS does not involve the direct activation of O₂ by UVR. Rather, various photosensitizing molecules in cells (flavins, aromatic amino acids, the reduced pyridine nucleotides NADH and NADPH, porphyrins) absorb, especially, UVA (Tyrrell 1991) and enter an excited state wherein the excitation energy can be transferred to O₂ to form ¹O₂, H₂O₂ or O₂^{-•}, which in turn can lead to the production of extremely reactive •OH in an iron-catalysed Fenton reaction. UVA-generated ROS have multiple toxic effects on organisms, damaging DNA, enzymes, membrane proteins and lipids (especially those containing polyunsaturated fatty acids), photosystem components, etc., collectively resulting in photooxidative stress. Additionally, the photochemical production of ROS in seawater (reviewed by Palenik *et al.* 1991) potentially can damage cell membranes of marine organisms, but there has been virtually no study of this. The intracellular production of ROS increases with O₂ concentration, so that photoautotrophic symbioses producing an excess of O₂ in sunlight would seem particularly vulnerable to the separate and interacting effects of UVR and ROS.

Because of the specialized laboratory techniques necessary to measure most ROS, this chemistry has not figured prominently in studies of the UV photobiology of coral reefs. Most evidence for UV-induced photooxidative stress is indirect—an elevation of the antioxidant defenses against ROS (see 'Antioxidants,' below) under conditions of UV exposure, although differential effects of UVR on oxygen fluxes in zooxanthellate symbioses complicates the interpretation.

Antioxidant defenses (see Halliwell & Gutteridge 1989)

include the enzymes superoxide dismutase (SOD), catalase, and ascorbate (in autotrophs) and glutathione (in animal hosts) peroxidases, the first of which detoxifies $O_2^{\cdot-}$ and the others H_2O_2 . Various water-soluble (ascorbic acid, uric acid) and lipid-soluble (carotenoids, tocopherols) antioxidant molecules scavenge oxygen radicals or quench 1O_2 .

Thus, the higher activity of host SOD in solar UV-exposed specimens of the temperate sea anemone *Anthopleura elegantissima* than in UV-shielded clonemates was taken as a reaction to UV-induced oxidative stress (Dykens & Shick 1984). The elevation of SOD activity in host and zooxanthellae, and of catalase and ascorbate peroxidase in the zooxanthellae from a UV-exposed reef anemone (*Phyllodiscus semoni*), was interpreted similarly, although the opposite response of host SOD in the reef octocoral *Clavularia* sp. may have resulted from higher O_2 fluxes during long-term protection from UVR (Shick *et al.* 1991). Lesser *et al.* (1990) found a significant UV-related elevation of SOD and catalase in the zooxanthellae but only a suggestive trend in these activities in the host tissue of the reef zoanthid *Palythoa caribaeorum*. Lesser & Shick (1989) demonstrated that exposure to UVR at moderate irradiance ($PAR = 375 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) under a solar simulator significantly elevated SOD and catalase activity in cultured zooxanthellae (*Symbiodinium bermudense*) from the tropical anemone *Aiptasia pallida*, but not in zooxanthellae exposed *in hospite* (within the host). This indicates a protective effect of the host on its symbionts under these conditions. However, in full sunlight ($PAR \approx 1700 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), zooxanthellae exposed to UVR *in hospite* had higher activities of SOD, catalase and ascorbate peroxidase than those in which the anemones (*A. pallida*) were shielded from UVR (Lesser 1989).

Spin-trapping experiments on *A. elegantissima* (Dykens *et al.* 1992), which is not a coral reef species, confirmed an enhancement by UVR of $O_2^{\cdot-}$ and $^{\cdot}OH$ in tissues of host and zooxanthellae. Lesser (1996a) used flow cytometry and fluorescent metabolic probes to confirm the elevation by artificial UVR of H_2O_2 and $O_2^{\cdot-}$ in *S. bermudense* cultured at saturating PAR. No such studies have been published for corals, but by extension of the results of UV exposure on the activities of antioxidant enzymes, it is likely that fluxes of ROS are engendered by solar UVR in these symbioses.

The foregoing studies provide evidence for the UV-induced production of ROS in symbiotic coral reef and temperate anthozoans, but there has been scant study of any resultant oxidative damage. Lesser & Shick (1990) found a significant UV-related increase in the volume fraction of accumulation bodies (associated with cell ageing and autophagy) in cultured *Symbiodinium bermudense*, and decreases in the volume fraction of

chloroplasts and the surface density of thylakoid lamellae of zooxanthellae exposed to UVR *in hospite*. The correlation of indicators of ROS production with UV exposure and observed bleaching in *P. caribaeorum* (Lesser *et al.* 1990) implicates UV-induced oxidative stress as one mechanism eliciting bleaching.

Defences against UVR

Behaviour. Most corals are permanently fixed to the reef framework and cannot relocate to alter their photic environment, but the expansion and contraction of the living tissue can vary its exposure to sunlight. In the case of *Coeloseris mayeri*, fully retracting the tissue exposes the skeleton and increases reflection of UVA about threefold compared with the partially retracted state, although UVB reflectance is unaffected (Brown *et al.* 1994b). Such behaviour might be especially protective against UVA if the tissue is covered by a thick layer of mucus containing a sunscreen absorbing UVR in this range (Drollet *et al.* 1993; see 'Mycosporine-like amino acids' below).

Melanin. The velvet-black colour of certain azooxanthellate dendrophyllid corals appears to be due to melanin, which, as is well known in vertebrates, probably acts as a sunscreen (MacMunn 1903; also see Kawaguti 1973). A similar pigmentation is seen in the holothuroid echinoderm *Stichopus chloronotus* (Shick unpublished), which is abundant on shallow reef flats in full sunlight. Although melanin may be an effective sunscreen in these non-photosynthetic organisms, it blocks PAR in addition to UVR, so it is less suited to protecting photoautotrophic symbioses. Moreover, some melanins are photo-oxidizable and in turn may generate ROS and initiate lipid peroxidation (Kohen *et al.* 1995), so they seem doubly ill-suited as photoprotectants where O_2 concentrations are high.

Fluorescent pigments. Kawaguti (1944, 1969, 1973) demonstrated the dissipation of high-energy UVR via its absorption and subsequent fluorescence at longer (visible) wavelengths by green pigments concentrated in granules in certain ectodermal cells of various zooxanthellate corals. UV-induced fluorescence was likewise noted in diverse Pacific, Caribbean and Red Sea species by Catala-Stucki (1959), Logan *et al.* (1990) and Schlichter *et al.* (1994). Kawaguti (1969, 1973) reported an absorption maximum of 320–330 nm for the green fluorescent pigment in *Lobophyllia robusta* and *Oulastrea crispata*, although the absorption spectra apparently were determined for aqueous extracts of coral tissues, not purified pigments, and thus might have included other hydrophilic UV-absorbing compounds (see below). It is clear that when activated at 380 nm, the pigment solution fluoresced at

450–510 nm, leading Kawaguti to suggest that the pigment both protected the coral from UVR and transformed damaging wavelengths into photosynthetically useful ones. Whereas the relative importance of the latter function is questionable under bright sunlight in shallow water, the photosynthetic role of UVA-induced blue-green fluorescence by host pigments is presumably enhanced in *Leptoseris fragilis* living at ≈ 100 m depth at low PAR (Schlichter & Fricke 1990), especially because the fluorescence in this species more closely matches the absorption maximum of chlorophyll. UV-induced fluorescence may help certain corals to inhabit cryptic and other light-limited environments (Schlichter *et al.* 1994). The chemical identity of these fluorescent pigments remains unknown. They apparently are distinct from the minimally UV-absorbing, non-fluorescent, dimeric protein-based pink and blue pigments (chromophore unknown) in host tissues of acroporiids and pocilloporids (Dove *et al.* 1995).

Mycosporine-like amino acids. Shibata (1969) originally detected 'S-320' materials having an absorption maximum at that wavelength in aqueous extracts of *Acropora* spp., *Pocillopora* sp. and an unidentified cyanobacterium from the Great Barrier Reef. Absorption peaks in the range ≈ 320 – 340 nm are common in many coral reef organisms (e.g. Figure 3), and S-320 substances are now known to be the mycosporine-like amino acids (MAAs), a family of water-soluble compounds (not 'pigments,' for they are colourless) having an aminocyclohexenone or aminocyclohexenimine chromophore. Substitution of the chromophore by nitrogen or various imino acids and imino alcohols at the C1 position determines the particular absorption maximum of each MAA, which ranges from 309 to 360 nm (Fig. 4). Glycine is the common substituent at the C3 position in all structurally identified MAAs except mycosporine-aurine in *A. elegantissima* (Stochaj *et al.* 1994) and mycosporine-methylamine:threonine in *P. damicornis* (Wu Won *et al.* 1995), which incorporate the sulfonic amino acid, taurine, and a methylamine group, respectively.

The concentration of S-320 or MAAs in reef benthos collected from shallow water is generally higher than that in conspecifics from deeper sites or shaded habitats (Dunlap *et al.* 1986; Olson 1986; Scelfo 1986; Drollet *et al.* 1993; Gleason & Wellington 1993; Shick *et al.* 1995; Fig. 3) where exposure to UVR is less. Similarly, MAA concentrations are higher in exposed epidermal tissues than in internal organs of reef holothuroids (Shick *et al.* 1992), high in the ocular lenses of fishes (Dunlap *et al.* 1989), and even vary between exposed and shaded portions of the same colony in *Porites compressa* (Hunter 1985). Moreover, transplanting corals and other reef anthozoans, and macroalgae, from greater to lesser depths, or maintaining them in aquaria exposed to solar

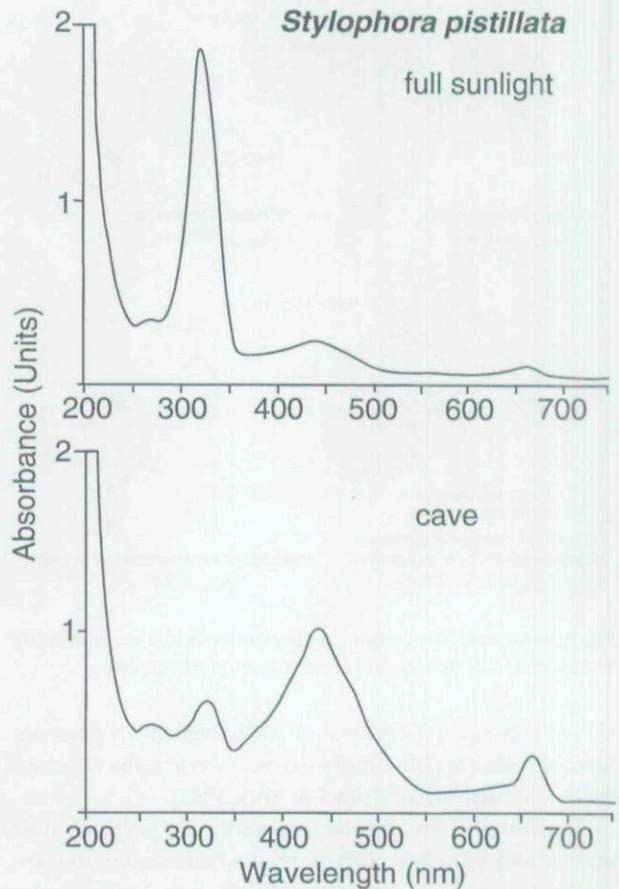


Fig. 3 Absorption spectra for methanolic extracts of same-size pieces of colonies of *Stylophora pistillata* collected from a fully sunlit site, and from inside a cave ≈ 3 m away, at 5 m depth on Grub Reef, Great Barrier Reef. The spectra evince acclimatization to UVR and PAR: the peak at 327 nm associated with MAAs is larger in the specimen from full sunlight, whereas the peaks at 441 and 665 nm associated with chlorophyll and accessory pigments are larger in the specimen from the dimly lit cave, presenting a classic example of photoacclimatization. Source: JM Shick (unpublished data).

UVR, often causes increases in S-320 or MAA concentrations (Jokiel & York 1982; Scelfo 1986; Wood 1989; Shick *et al.* 1991; Gleason 1993; Glynn *et al.* 1993; Kinzie 1993), although species and morphs differ in their responsiveness of accumulating UV-absorbing materials. Despite exceptions to the foregoing relationships (Scelfo 1985; Gattuso 1987; Lesser *et al.* 1990; Shick *et al.* 1991; Stochaj *et al.* 1994), the general positive correlation between UVR exposure and MAA concentration, together with the high molar extinction coefficients ($\epsilon \approx 28$ – 50 000) of MAAs in the range of environmentally relevant UVR, has been taken as good circumstantial evidence for a photoprotective role of MAAs. By incorporating multiple MAAs having different absorption maxima, corals have a broadband filter that in theory protects them from most ambient

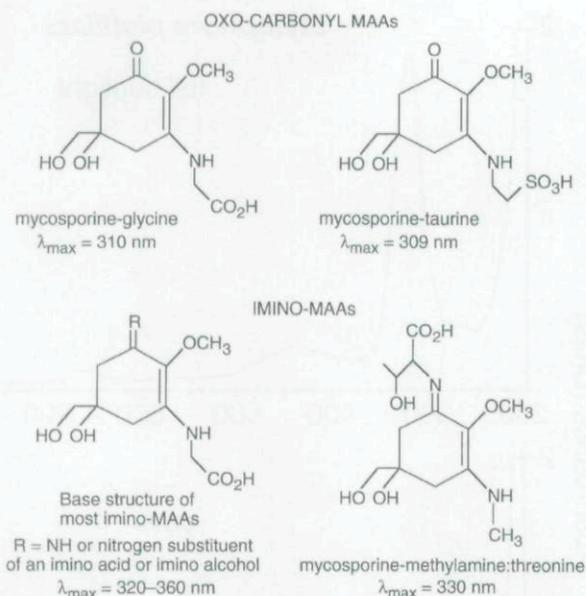


Fig. 4 Structures of mycosporine-like amino acids, taxonomically widespread UV sunscreens among marine organisms.

UV wavelengths (Dunlap *et al.* 1986) but which does not filter out photosynthetically active wavelengths required by the zooxanthellae (Jokiel & York 1982).

Accordingly, the greater resistance to UVR of host tissues and planulae, and of photosynthesis by zooxanthellae *in hospite*, in shallow-water than in deeper-water corals (Siebeck 1981, 1988; Masuda *et al.* 1993; Gleason & Wellington 1995; Shick *et al.* 1995) is intuitively satisfying. Likewise, the greater abundance in shallow water of MAA-rich green morphs than MAA-poor brown morphs of *Porites astreoides*, and the higher mitotic indices of zooxanthelle *in hospite* in the green morphs exposed to UVR, support the hypothesis that MAAs are UV photoprotectants. Experimentally elevating S-320 concentration by prior exposure to UVR predictably decreased the sensitivity of photosynthesis to UVR in colonies of *Montipora verrucosa* (Kinzie 1993), although additional protective mechanisms (e.g. antioxidant enzymes: Lesser *et al.* 1990; Shick *et al.* 1991) might also have been induced.

Factors other than UVR that vary inversely with depth (e.g. PAR and water movement) may also affect the concentration of MAAs in corals (Lesser *et al.* 1990; Jokiel *et al.* in press), but this does not negate a role of MAAs as UV photoprotectants. Such covarying factors may even offer an experimental means to alter MAA concentrations independently of UV exposure and thus avoid induction of other UV-protective mechanisms (see Garcia-Pichel *et al.* 1993). Exposure to elevated temperature, even in the presence of UVR, may depress MAA concentrations (Lesser *et al.* 1990; Glynn *et al.* 1993; Lesser 1996), so that thermal depression of these UV defenses might be involved in coral bleaching.

Because MAAs probably are synthesized in the shikimic acid pathway that is absent from metazoans, MAAs in corals are presumed to originate in their zooxanthellae (Dunlap & Chalker 1986). Despite their algal origin, > 95% of the total amount of MAAs in *Acropora microphthalma* occur in the host animal's tissues (Shick *et al.* 1995), perhaps being translocated from the zooxanthellae, which have the same qualitative complement of MAAs. Thus, photosynthesis in colonies of this coral from 2 m and 10 m depth was not inhibited by full solar UVR when measured at 1 m, but UVR did inhibit photosynthesis in zooxanthellae isolated from these colonies. Similarly, Masuda *et al.* (1993) found no reduction of photosynthesis following artificial UVB exposure of shallow-water specimens of *Fungia* spp., whereas photosynthesis was reduced after exposing their isolated zooxanthellae to UVB. Such studies suggest that the host's tissues, probably because of their high concentrations of MAAs, form the first line of defence for the symbiosis and protect the algal endosymbionts (see also Jokiel & York 1982).

Zooxanthellae in the reef anemone *Phyllodiscus semoni* contain 40% of the mycosporine-glycine present in the symbiosis during prolonged shielding from UVR, but 95% of this MAA when the symbiosis is exposed to sunlight for ≈ 5 months (Shick *et al.* 1991). Tropical zooxanthellae (*S. microadriaticum*) synthesize MAAs (stimulated by UVR) in culture and translocate them to the symbiotic scyphozoan, *Cassiopeia xamachana*, when *in hospite* (Banaszak & Trench 1995b). In culture, *S. bermudense* increases its MAA content when UVR is present (Lesser 1996), but the MAA concentration in the anemone *Aiptasia pallida* symbiotic with this zooxanthella is very low and unaffected by acclimation to UVR in the laboratory (see Shick 1993). In contrast to the foregoing examples, the temperate zooxanthellae (*S. californium*) in *A. elegantissima* contain little or no MAAs *in hospite* (Stochaj *et al.* 1994; Banaszak & Trench 1995b), nor do these zooxanthellae synthesize MAAs when cultured in the presence of UVR (Banaszak & Trench 1995b). Therefore, species of zooxanthellae differ in their capacity to synthesize, accumulate and translocate MAAs. If such variability occurs among algal and cyanobacterial endosymbionts inhabiting diverse host species and morphs, it may be involved in differential UV-induced bleaching among coral reef symbioses.

A dietary origin of the MAAs present in both zooxanthellate and naturally apozooxanthellate specimens of *A. elegantissima* has been suggested (Stochaj *et al.* 1994; Banaszak & Trench 1995b). Trophic accumulation of MAAs may be the rule for non-symbiotic reef consumers such as holothuroid echinoderms (see Shick *et al.* 1992), as has been demonstrated experimentally in a boreal sea urchin (Carroll & Shick 1996). The origin (dietary,

endosymbiotic or both) of MAAs in most symbiotic reef invertebrates remains an open question.

The variable effects of UVR on ultrastructure, growth and photosynthesis in zooxanthellae *in vitro* seem related to their individual MAA concentrations (cf. Jokiel & York 1982; Shick *et al.* 1991, 1995; Shick 1993; Banaszak & Trench 1995a; Lesser 1996), although the small individual size of zooxanthellae optically constrains the effectiveness of intracellular sunscreens (Raven 1991; Garcia-Pichel 1994). This is because the total UV absorption by an intracellular sunscreen is determined by its concentration and the optical pathlength (cell radius). Because metabolically active microalgae are limited in the concentration of osmotically active sunscreens such as MAAs that they can accumulate without disrupting cellular water balance, this fact, together with their small size (c. 4–5 μm radius in *Symbiodinium* spp.), limits the effectiveness of intracellular MAAs.

Thus, although *Symbiodinium bermudense* doubles its total intracellular concentration of MAAs when cultured in the presence of UVR, and action spectra show a decrease in the wavelength-dependent effects of UVR, at the organismal level photosynthetic performance is still reduced (Lesser 1996). Specifically, culture growth decreases by 45% and the maximum rate of photosynthesis in these zooxanthellae is depressed by about 24% when measured in the presence of UVR as compared with measurements in the absence of UVR. Similarly, simulated solar UVR depresses photosynthesis in *S. bermudense* freshly isolated from its host *A. pallida* (Lesser & Shick 1989), which, however, affords some UV protection to algal photosynthesis *in hospite* despite the rather low concentration of MAAs in the symbiosis (Shick 1993). The slight protection of the zooxanthellae *in hospite* may be related to the longer optical pathlength over which UVR can be absorbed during its passage through the host.

The data in Gleason & Wellington (1995) for planula larvae of *Agaricia agaricoides* allow calculation of the relevance of these optical considerations in nature. In planulae (radius $\approx 500 \mu\text{m}$) collected from colonies living at 3 m depth, mycosporine-glycine accounts for $\approx 99\%$ of the total larval MAA concentration and constitutes $\approx 1.63\%$ of their dry mass (assuming that biomass is $\approx 50\%$ protein). Planulae collected at 24 m, where the daily dose of biologically effective (DNA-weighted) UVB (300–320 nm) irradiance is 33 times less, and the daily dose at 310 nm is 70 times less than at 3 m, have 0.54% of their dry mass as mycosporine-glycine. From these data and the relationships in Garcia-Pichel (1994), we calculated that the sunscreen factor, S , in 3-m planulae at 310 nm (λ_{max} of mycosporine-glycine, which has a broad absorption peak between 300 and 320 nm) is 0.98 and that S in 24-m planulae is 0.94—i.e. mycosporine-glycine is 94–98% efficient in absorbing UVB at 310 nm before it reaches

other cellular targets in these larvae. Thus, acclimatization to the 33–70-fold greater ambient UVB/310 nm dose at 3 m involves an increase in S of 0.04 via a threefold increase in MAA concentration compared with that in planulae produced in 24-m colonies. Therefore, a 24-m planula moved to 3 m would receive an effective weighted UVB/310 nm dose (not absorbed by mycosporine-glycine) 1.3–2.8 times greater ($33\text{--}70 \times 0.04$) than that in a native 3-m planula having a higher MAA concentration. This is in good agreement with the 2.6-fold greater mortality in 24-m planulae (64% mortality) compared with native 3-m planulae (25%) during exposure of both to full sunlight at 3 m (Gleason & Wellington 1995).

The actual increase in mortality (2.6-fold) is greater than that predicted (1.3-fold) by the increase in the integrated UVB (300–320 nm) dose, which may indicate the enhancement of additional UV defenses (e.g. DNA repair) in the 3-m planulae compared with their 24-m conspecifics. It is also noteworthy that despite the absorption of 98% of incident UVB at 310 nm by mycosporine-glycine in the 3-m planulae, they nevertheless suffer 25% mortality under the experimental conditions. These coral larvae may thus be living at the edge of their tolerance for UVB, at least under the additional stress of handling. Assuming that MAA concentrations in 3-m planulae are near the physiological maximum, compensation for subsequent increases in solar UVB would necessarily involve defensive mechanisms other than MAAs, such as DNA repair. The predominance of UVA-absorbing MAAs in *P. damicornis* seemingly leaves this coral particularly susceptible to the effects of UVB (Jokiel *et al.* in press).

UVA had no effect on the survival of the planulae of *A. agaricoides*. This is intriguing because these planulae contain no MAAs absorbing in that range. Interestingly, Dunlap & Yamamoto (1995) have shown that mycosporine-glycine but not imino-MAAs (see Fig. 4 for structures) has antioxidant activity, so that the greater concentration of mycosporine-glycine in 3-m planulae might also enhance their defenses against the indirect, ROS-mediated effects of UVA as well as having its role in blocking UVB. Gleason & Wellington (1995) did not study enzymic defenses against oxidative effects of UVA, but such defenses might also be relevant to the resistance of the larvae to UVA exposure in the absence of UVA-absorbing MAAs (see Shick *et al.* 1995; Lesser 1996).

Mycosporine-glycine ($\lambda_{\text{max}} = 310 \text{ nm}$) and palythine ($\lambda_{\text{max}} = 320 \text{ nm}$) are the predominant MAAs in zooxanthellate anthozoans on the Great Barrier Reef (Dunlap & Chalker 1986; Dunlap *et al.* 1986; Shick *et al.* 1991, 1995) and on Caribbean reefs (Gleason & Wellington 1995; but see Gleason 1993). As noted by Dunlap & Yamamoto (1995), the presence of high concentrations of mycosporine-glycine in these oxygenic photoautotrophic symbioses is consistent with its antioxidant function. The

imino-MAA palythine provides an additional defense against direct UVB effects but does not have antioxidant activity. The predominance of these particular MAAs, which have the shortest-wavelength absorption maxima of all MAAs identified in coral reef organisms, may be related to the relatively high UVB-transparency transparency of tropical seawater compared with eutrophic seawater. The occurrence of UVA-absorbing imino-MAAs (e.g. shinorine, porphyra-334, asterina-330) shows considerable taxonomic variation among zooxanthellate and azooxanthellate reef organisms (e.g. Dunlap *et al.* 1989; Shick *et al.* 1991, 1992 1995; Gleason 1993; Dunlap & Yamamoto 1995; Jokiel *et al.* in press). Although generally consistent with a sunscreen function, their distribution and relative abundance may be complicated by the dietary habits of the consumers (see Carroll & Shick 1996).

Finally, various other natural products present in coral reef organisms absorb UVR to varying extents, but there has been little consideration of these as potential sunscreens. Because the hydrophilic MAAs presumably occur primarily in the cytosol and protect intracellular components, the question arises whether lipophilic UV sunscreens may be sequestered in the cell's plasma membrane as a first line of defense.

Antioxidants. Enzymic antioxidants such as superoxide dismutase, catalase, and ascorbate and glutathione peroxidases that may protect against ROS-mediated effects of UVR already have been discussed in the section on 'Photooxidative Stress'. Beyond the aforementioned properties of mycosporine-glycine, little is known of non-enzymic, 'small molecule antioxidants' in coral reef organisms. Uric acid, an antioxidant more potent than mycosporine-glycine (see Dunlap & Yamamoto 1995), is much more concentrated in zooxanthellate than in experimentally apozooxanthellate specimens of *Aiptasia pallida*, but its concentration in zooxanthellate specimens in the field appears unrelated to irradiance of the habitat (Tapley *et al.* 1988; Shick *et al.* in preparation).

Considering their striking colours and demonstrated role in photoprotection in higher plants, algae and cyanobacteria, there has been surprisingly little study of carotenoids in colourful corals. MacMunn (1903) noted the absence of 'lipochromes' (= carotenoids) from dried specimens of azooxanthellate dendrophyllid corals. Later studies by, especially, D. L. Fox and coworkers (see review by Goodwin 1984), confirmed the presence in hydrocorals and octocorals of predominantly astaxanthin, with smaller amounts of β -carotene and zeaxanthin. Native carotenoids scarcely absorb UVR and thus do not function as sunscreens, and although certain carotenoproteins do absorb UVR (Cheesman *et al.* 1967), no sunscreen role has been proposed for them. Nevertheless, an association of higher carotenoid concentrations with more brightly

lit habitats has been discerned in azooxanthellate sea anemones (see Shick 1991).

The protective effects of carotenoids are manifested in their quenching of activated photosensitizers and singlet oxygen ($^1\text{O}_2$) and as chain-breaking antioxidants (Krinsky 1993; Kohen *et al.* 1995). Thus, the anticarcinogenic (Krinsky 1993) and antiphotooxidative (Paerl 1984) effects of carotenoids following exposure to UVR are a consequence of their antioxidant, not UV-absorbing, properties. The antioxidant effects of carotenoids have been studied largely *in vitro* by measuring their ability to inhibit lipid peroxidation.

The predominance of astaxanthin (as opposed to β -carotene) in the admittedly few corals that have been studied might be related both to the greater antioxidant potency of the former (Krinsky 1993), and to the tendency of the latter to have prooxidant effects at high P_{O_2} (Burton & Ingold 1984), of some relevance in an oxygen-producing symbiosis. The latter authors suggested accordingly that, in humans, β -carotene might be expected to accumulate in membranes where the P_{O_2} is low, and α -tocopherol (vitamin E) to accumulate in lipid domains under high P_{O_2} , because the latter is a better antioxidant under such conditions. By analogy, β -carotene might not be expected to predominate in the hosts' membrane systems of zooxanthellate corals, but if present, it would vary positively with α -tocopherol, with which it has synergistic effects, perhaps because α -tocopherol inhibits the prooxidant effects of the β -carotene peroxy radical (Krinsky 1993). β -carotene and α -tocopherol might also be expected to vary positively with ascorbic acid (vitamin C), which regenerates α -tocopherol from its radical form. Although the chemistry is daunting to most marine biologists, the role of carotenoids in UV photoprotection in coral reef organisms warrants study.

Photoreactivation. The effects of UVB radiation in particular include its absorption and subsequent damage to the chromophore DNA (in both host and zooxanthellae, and in their mitochondria and chloroplasts). Formation of UVB-induced cyclobutane-type pyrimidine dimers has not, to our knowledge, been measured in the DNA of any coral reef macroorganisms. However, certain reef species apparently can repair such damage in the process of photoreactivation. This involves the splitting of such dimers by the enzyme photolyase when activated by UVA or blue light, as in the following examples.

Siebeck (1981, 1988) demonstrated that the LD_{50} of UVR in colonies of *Turbinaria mesenterina* and several genera of faviid corals could be increased by their subsequent exposure to white light and its spectral components. Blue-violet wavelengths ≈ 450 nm had the greatest photoreactivating effect, a result consistent with the known action spectrum for enzymic photorepair (Harm

1980; Mitchell & Karentz 1993). Carlini & Regan (1995) measured DNA photolyase activities in three genera of subtropical opisthobranch molluscs, but could find no correlation between enzyme activity in the snails and the potential for UVB exposure in their respective natural habitats. It is unknown whether the degree of photoreactivation or photolyase activities are subject to acclimation by varying exposure to UVB, but the question has relevance to projected increases in UVB reaching reef ecosystems.

Monitoring

Monitoring UVR over large areas is prohibitive owing to the cost of instruments having a suitably high degree of accuracy and resolution. Data collected using different types of instruments and measurement units faces the problem of intercalibration and comparison. One approach would be to invest in a few high-resolution spectroradiometers, similar to the NSF-UV monitoring program initiated in response to the Antarctic ozone hole, and coupling these measurements to radiative transfer models of both the atmosphere and the water column for coastal and open tropical waters. These stations could then be used for intercomparison of commercially available, and other, radiometers or spectroradiometers being used today. Additionally, in areas where using any instrument may not be feasible, there are chemical actinometers (e.g. *o*-nitrobenzaldehyde) that have high absorption in the UVB (but generally cover the spectrum from 300 to 400 nm) that can be deployed inexpensively in a manner analogous to the Caribbean Coastal Marine Productivity (CARICOMP) monitoring program. The available chemical actinometers have various absorption spectra and quantum yields; some have been used previously (Fleischmann 1989) but all should be used with caution (Morales *et al.* 1993) and would probably be limited to assessing relative changes in total UVR.

The use of remote sensing platforms for monitoring the gross effects, if any, of UVR, and other stressors, is in its infancy and may include airborne (LIDAR [Light Detection and Ranging], hyperspectral spectroscopy) or underwater platforms (ROV [Remote Operated Vehicle], AUV [Autonomous Underwater Vehicle], UUV [Unmanned Underwater Vehicle]) having sophisticated measurement packages to measure the optical properties of the water column and optical signatures of corals that change in response to their physical environment (Hardy *et al.* 1992; Mazel 1995). Many of these instruments extend into the UV (e.g. Hyperspectral Meter measuring upwelling and downwelling irradiance; 512 channels from 350 to 900 nm), with the promise of full-spectrum UV coverage in the future. There is reason to hope that such instruments will be able to monitor reef areal

coverage and health over large spatial and temporal scales. In particular, the measurement of fluorescent signatures *in situ* with laser line scanning or fast repetition rate fluorometry (Falkowski & Kolber 1993) holds the promise that technologies based on optical signatures can be used to assess the effect of UV and thermal stress on corals non-destructively and before visible signs of deterioration actually occur.

Predicting the effects of increasing UVB on corals and reef communities

Predicting the outcome of any increase in UVB radiation is difficult and needs to be considered with some caution. The highest annual doses of UVB are at the equator, with near uniformity among months in total UVB received (Cutchis 1974). Moving away from the equator, there is a pronounced seasonal change even at tropical latitudes, with UVB showing changes of two- to threefold within six months. This implies that reef corals can acclimatize to changes of this magnitude on an annual basis, so absolute tolerance limits rather than rates of change are our primary focus.

For a first approximation of tolerance, biologists generally use the lethal response of an organism to the environmental factor in question. Unfortunately, there are no LD₅₀ values for reef corals exposed to environmentally relevant UV spectra and dose rates. Maximum LD₅₀ values (with photoreactivating light present) for several reef corals collected at 1–3 m reported by Siebeck (1988) are ≈ 800 – 1100 kJ m^{-2} of broad-band artificial UVR (275–400 nm), *seemingly* about the same as the daily dose of unweighted solar UVR they would receive in nature (≈ 900 – $1000 \text{ kJ m}^{-2} \text{ d}^{-1}$; cf. data in Gleason & Wellington 1995 and Table 1). However, the light sources used by Siebeck were greatly enriched in UVB wavelengths < 300 nm, and the fluences at wavelengths below 295 nm were orders of magnitude greater than those prevailing in nature. Accordingly, these LD₅₀ values cannot be used as absolute measures of coral tolerance to natural UVR, nor do they allow any prediction of the effects of further increases in, specifically, solar UVB radiation, although they can be used to assess relative tolerances among species and colonies from different depths of origin (see 'Overt Effects,' above).

Regarding whether any continued increases in UVR will have any effect on corals and coral reef communities, we present a worst-case scenario based on published historical data for tropical and subtropical systems. At 20°N the maximum ambient dose of UVB at 307.5 nm occurs in June (Cutchis 1974). Assuming at worst a 10.8% total decrease in stratospheric ozone at this latitude since 1969 (i.e. –4% per decade: Madronich 1992), a concomitant 13.6% increase in unweighted UVB radiation at 307.5 nm

at the sea surface (S Madronich, personal communication), and a K_d of 0.25 m^{-1} at that wavelength (Banaszak *et al.* submitted; data from coastal reefs outside Kaneohe Bay, Hawaii), the UVB dose that occurs at 1 m depth now exceeds the maximum June 1969 dose in April through August (with the doses in the other months remaining below the June 1969 maximum).

Applying the RAF for UVR inhibition of photosynthesis in *Pocillopora damicornis* (Fig. 2) to a 10.8% decrease in stratospheric ozone results in a calculated increase of only 2.3% in UVB radiation at 307.5 nm weighted for this process, or a 25.7% increase in DNA-weighted dose. Unfortunately, we do not know how much impact this increase may have had on shallow-water corals that have already been exposed to it, but many species do flourish today at a depth of 1 m, so they presumably have the capacity to have dealt with this increase. At the same rate of ozone loss during the next decade, the cumulative loss from 1969 to 2006 would be 14.8%, which would expose corals at 1 m depth to a 3.2% greater photosynthesis-weighted dose, and a 37.8% higher DNA-weighted dose, than in 1969. Even if this increase were to exceed the LD_{50} of reef corals now living at 1 m, the K_d indicates that they could live at a depth of 2 m without exceeding the 1969 maximum dose at 1 m.

A 'natural experiment' has already occurred that suggests that increases in UVB through projected decreases in stratospheric ozone will not cause mass mortalities or bleaching of coral reefs. The eruption of Mount Pinatubo in June 1991 caused a transient decrease in ozone of about 4% at tropical and subtropical latitudes (Randel *et al.* 1995), but there was no widespread incidence of coral mortality or bleaching during the September–November 1991 ozone decrease (cf. fig. 7 in Randel *et al.* 1995; and fig. 2 in Glynn 1996; this volume). Ozone anomalies persisted for several years after the eruption, and although there were widespread bleaching events across the Southern Hemisphere at latitudes where ozone decreases occurred in 1994, such was not the case in 1992 or 1993. The interpretation is complicated by the unusually cool temperatures worldwide in 1992, also a consequence of the Mount Pinatubo eruption (Hayes & Goreau 1994). On balance, there was no clear effect of short-term ozone depletion on coral well-being.

Our assessment is that the ramifications of the maximum projected increases may include any or all of the following:

1 Based on mortality data alone, the most dramatic effects, if any, will be limited to the upper 1 m of the water column; mass mortalities or dramatic changes in reef coral community composition probably will not result from the small projected increases in UVB, although the minimum depths of occurrence of species may increase.

2 Even small increases in UVB radiation will likely have sublethal effects on photosynthesis, respiration, calcification, growth, and planula release throughout the depth range where the increases occur.

3 Interactive effects, especially with increases in water temperature, will be greater than the sum of the independent effects.

4 Community level processes are likely to be affected with unknown consequences for coral distribution and abundance, but given the variability of the natural environment, we probably will be unable to detect these changes by techniques and monitoring programs currently in use.

In theory, the reef coral component of the community might respond to increased UVB in several ways:

1 Reef corals can acclimatize to changing environmental conditions. The projected increases in UVB could simply fall within the capacity of these organisms to attenuate the damaging radiation with sunscreens, repair UV-induced damage, or otherwise compensate. Most coral species have broad bathymetric and latitudinal distributions and colonies of any given species can generally be found growing under conditions of nearly undetectable UVB to some of the highest levels found on this planet. Using a hypothetical colony of a given species growing at the highest levels of UVR (shallow, equatorial, clear water, arid region) as a benchmark, we can argue that reserve capacity to acclimatize must exist for the remainder of the population (> 95% of which lives at depths > 1 m), if not the entire population. The scant evidence available suggests that planulae of some shallow-water reef corals are near the limits of their tolerance for UVB (Gleason & Wellington 1995). However, the data are too few to generalize and it simply is unknown whether shallow-water adult and larval representatives of a species have reserve capacity to acclimatize to further increases in solar UVB.

2 Selection for UV-resistant species could produce changes in the composition of reef coral communities. Interspecific differences in UV tolerance have been demonstrated experimentally (Siebeck 1981, 1988; Glynn *et al.* 1993). Differential susceptibility to environmental UVB will lead to selection of species that can tolerate higher levels of this stressor.

3 Increases in UVB could lead to selection for UV-resistant variants of the same reef coral species. Intraspecific differences in such resistance have been shown in green and brown morphs of *Porites astreoides* (Gleason 1993). The green morph is more abundant in shallow water and maintains a higher growth rate under conditions of high UVR. Presumably, increased levels of UVB could favour the green morph throughout a broader depth range. The extent to which such variation in UV tolerance reflects genotypic differences or phenotypic (physiological)

plasticity of clonal genotypes has not been studied but seems experimentally tractable (e.g. Potts 1984; Shick & Dowse 1985; Ayre & Willis 1988).

4 Changes could occur in the microalgal component of the coral symbiosis via selection among differentially UV-tolerant species of *Symbiodinium* (Jokiel & York 1982; Banaszak & Trench 1995a) or other photoautotrophs. Different taxa of zooxanthellae show zonation with depth and colonies of single reef coral species can simultaneously host multiple algal endosymbionts in variable proportions (Rowan & Knowlton 1995). A coral host might respond to increasing UVB by switching algal partners, retaining those that maintain or increase its fitness under the new conditions (Karakashian & Siegel 1965; Buddemeier & Fautin 1993). Such switching of algal partners has been demonstrated experimentally in the tropical sea anemone *Aiptasia pulchella* (Kinzie & Chee 1979).

The major needs for predicting future changes related to UVR are:

1 Good estimates of increased spectral irradiance, and
2 Good experiments documenting the effects of the increased spectral irradiance on survival and reproduction. This work will centre on the ability of reef corals and other organisms to acclimatize (field) or acclimate (laboratory) to increased UVB, which will necessitate the simulation of solar spectral irradiance that is elevated particularly at wavelengths < 330 nm. This assessment would include the genetic components of UV resistance (estimated from LD₅₀ values) in coral hosts and endosymbiotic algae, and mechanistic studies of biochemical and other defenses against UVR. There should be emphasis on metabolic processes such as primary production and skeletal growth, and on early life stages, including gametes, fertilization, larval development and settlement, and early development of colonies.

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