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Community responses to UV radiation. I. Enhanced UVB effects on biomass and community structure of filamentous algal assemblages growing in a coral reef mesocosm

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Abstract Four treatments (PAR; PAR+UVA; PAR + UVA+UVB enhanced by 20% from ambient levels; ambient levels of UVB) were performed using a combination of metal halide lights, UV lamps and cutoff filters over developing assemblages of filamentous algae in a coral reef mesocosm. Exposure to enhanced UVB initially reduced the standing crop by 67% as compared to the productivity of the assemblages grown under PAR and PAR+UVA. Treatment reversal from PAR to enhanced UVB restricted temporarily the growth of the brown alga *Ectocarpus rhodochondroides*. While the spores of this species are inhibited by UVB, the sporophytes seem to be capable of adapting to UVB exposure. The effects of ambient UVB levels on biomass production and community composition were less pronounced, while exposure to UVA did not affect productivity or community composition. All effects due to UVB exposure gradually diminished as succession progressed. Community composition and biomass production were fully restored 1 to 2 weeks after the cessation of exposure to enhanced UVB.

Introduction

The increase in solar ultraviolet-B radiation (UVB; 280 to 320 nm) due to stratospheric ozone depletion (Cutchis 1974; Molina and Molina 1992) has raised much scientific and public concern during the last years. Mathematical models (Madronich et al. 1995) show that adverse effects are expected in the years to come. Atmospheric ozone (O_3) is the principal absorber of energy in the UVB region of the solar spectrum (Stolarski 1988). The quantity of ozone in the atmosphere is only 3 mm in thickness if condensed to standard temperature and pressure. Yet it is sufficient to truncate the solar spectrum abruptly at approximately 290 nm (Caldwell 1979). Peak global losses of ozone are expected around the year 1998, coinciding with peak stratospheric chlorine and bromine abundances (World Meteorological Organization 1995). Based on extrapolation of current trends, the maximum ozone loss relative to the late 1960s will likely be about 12 to 13% at northern midlatitudes in winter/spring. Such a change will be accompanied by a 15% increase in surface erythemal radiation, the part of ultraviolet light responsible for the tanning response of the human skin. The term "erythemal radiation" describes the wavelength band starting approximately at 300 nm and extending through 360 nm, thus overlapping part of the UVB and part of the UVA bands. While the solar incidence of biologically damaging wavelengths is still increasing, that of wavelengths greater than 320 nm, i.e. UVA radiation and photosynthetically active radiation (PAR), will remain virtually unaffected.

UV radiation affects the biology of living organisms and the balance of natural ecosystems. The inhibition of marine primary productivity by increased levels of solar UV radiation may have a significant global-scale climatic impact (Kelly 1986). Aquatic ecosystems alone fix approximately half of our planet's yearly amount of carbon available for the production of new living tissue (Houghton and Woodwell 1989; Behrenfeld and Falkowski 1997). In doing so, they remove carbon dioxide, a gas responsible for the greenhouse effect. Macroalgae are major primary producers in intertidal habitats and provide food (directly or through detritus) to a wide variety of invertebrates and fish (Mann 1972; Duggins et al. 1989). Therefore, changes in macroalgal productivity or diversity due to elevated UVB are likely to bring about disorders at all trophic levels of coastal marine food webs. UV inhibits the growth of many marine primary producers including benthic and planktonic microalgae (Worrest 1983; Jokiel and York 1984), green algae (Halldal 1964), kelps (Wood 1987)

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Erratum
The revised name for *Ectocarpus rhodochondroides* is *Asteronema rhodochortonoides* (Mueller and Parodi 1994, Phycologia 33: 471-474).

and several shallow and deep-water species of red algae (Halldal 1964; Maegawa et al. 1993).

Ultraviolet radiation has been shown to damage the photosynthetic systems of macroalgae (Agrawal 1992) and to inhibit photosynthesis of individual thalli of macroalgae (Häder et al. 1996a, b, 1997). Differences in macroalgal sensitivity to UV have been reported. Benthic algae from deep water habitats were found to be at least twice as sensitive to irradiation below 370 nm as high-intertidal dwellers (Polne and Gibor 1982). Unfiltered, natural, UV-containing sunlight resulted in photopigment destruction and elevated concentration of UV-absorbing substances in the tropical red alga *Eucheuma striatum* (Wood 1989). These effects were not observed when the UV component of sunlight was selectively removed by UV filters. Species of deep-water benthic algae were more sensitive to UVB radiation compared to intertidal benthic algae and seagrasses as measured by inhibition of variable fluorescence (F_v) of the fluorescence rise curve (Larkum and Wood 1993). The authors speculated that this was due to the adaptative capability of intertidal algae to accumulate UV-screening compounds such as mycosporine-like amino acids (MAAs). Two of the organisms studied, *Ecklonia radiata* (a brown alga) and *Posidonia australis* (a seagrass), showed poor F_v recovery 32 h after a 5-min exposure to UVB, suggesting the presence of long-term photosynthetic inhibition. Enhanced UVB radiation reduced the chlorophyll content and photosynthetic rates of *Prasiola crispa*, an Antarctic terrestrial green alga (Post and Larkum 1993). The authors predict that further depletion of stratospheric ozone may reduce algal productivity, even of those species containing high levels of UV-absorbing pigments. Solar UVB also inhibited the growth of thallus segments of the green alga *Ulva expansa* in outdoor cultures, while supplemental UVB inhibited the growth of this alga to a greater extent (Grobe and Murphy 1994).

Despite the ecological and economic importance of attached macroalgal communities, literature on the effects of UV radiation on this community type is rather scarce (Santas 1989; Schreiber and Pennock 1995). The present study is a laboratory approach for assessing the effects of enhanced solar UVB on tropical algal turf, a community dominated by filamentous algae responsible for a major part of the primary productivity associated with coral reefs (Adey and Goertmiller 1987). As with all light experiments carried out indoors, an unavoidable shortcoming of this attempt was the imperfect simulation of the solar spectrum both in its composition and intensity variation. However, the information provided can be useful if interpreted in combination with data collected in field studies under natural conditions (Santas et al. 1998).

Materials and methods

All experiments were conducted simultaneously at the "Living Coral Reef" mesocosm of the National Museum of Natural History, Smithsonian Institution, Washington, DC. The mesocosm includes more than 300 taxa of marine animal and plant organisms and simulates the physical and chemical parameters encountered in the Caribbean Sea (Adey 1983). During its 5-year operation period prior to this investigation, the "Living Coral Reef" was repeatedly inoculated with living specimens from a natural coral reef habitat nearby the field station of the Smithsonian's Marine Systems Laboratory located on the Turks and Caicos Islands. The mesocosm's water purification system, a series of algal turf scrubbers (ATS; Adey 1983), was used for the culture and exposure of algal assemblages to UVB. An ATS (Fig. 1) consists of a tray, a wave generator, and an artificial substrate (polypropylene screening) for attachment and growth of algal spores. Water pumped from the mesocosm into the wave generator at the upstream end of the tray flows over the growing algal turf, and returns to the mesocosm via a sedimentation tank. No conventional filtration is used, since the microorganisms (bacteria, algae, protozoa, filter feeders, etc.) living in the mesocosm maintain a water quality comparable to that of the natural habitat (Adey and Loveland 1991).

Care was taken to standardize other parameters influencing community development. Flow rate and wave frequency were set at 34.02 liters min^{-1} and one wave per 20 s, respectively, in all ATSs. The depth of the water column overlying the algal attachment substrate was 3 cm. Polypropylene screen (mesh size 1 mm) was stretched around a Plexiglas sheet fitting tightly into the recessed bottom of the trays. The flat substrate design minimized turbulence and illumination variations.

In order to minimize container effects, each of the three ATSs employed was divided longitudinally into two equal parts using an opaque partition positioned parallel to the flow (Fig. 1), for a total of six parts. One part of each ATS was used as a UV treatment, while the other was used as a control (PAR only). For the PAR treatment, one replicate sample was obtained from each ATS ($n = 3$), whereas for each UV treatment, replicates were harvested from 10 × 10 cm quadrats ($n = 3$) within the same ATS part. This scheme provided partial true replication (that of the PAR treatment), useful in assessing container effects on the developing assemblages. Ideally, a minimum of 12 parts (six ATSs) should have been used to provide equal replication (three replicates per treatment and four treatments). However, the above experimental design was implemented because only three ATSs are available for experimental uses at the Smithsonian Coral Reef Mesocosm Exhibit.

Light treatments

In Phase 1 (weeks 1 to 6), four treatments were performed (Table 1) aiming to separate the effects of PAR, UVA and UVB at two levels (high and low): (a) PAR + UVA + high UVB (enhanced by 20% over ambient incidence levels, designated hereafter as HUV), (b) PAR + UVA + low UVB (ambient incidence levels; designated hereafter as LUV), (c) PAR + UVA (designated hereafter as UVA), and (d) PAR (designated hereafter as the control; C1, C2, C3).

In Phase 2 (weeks 7 to 11), the two treatments in the two halves of each ATS were reversed to investigate (a) the recovery of assemblages after the elimination of UV and (b) the response of already established assemblages to UV exposure.

A 400 W metal halide lamp suspended directly above each ATS provided photosynthetically active radiation (PAR) and UVA. A *Westinghouse FS-40 sunlamp suspended on the side of each ATS* (Fig. 1) provided an additional 15% of the total UVA and all of the UVB radiation for the HUV and LUV treatments. Cellulose acetate was used to exclude UVC produced by the FS-lamps (unfiltered peak output at 254 nm). The desirable UVB irradiance was achieved by using cellulose acetate foil of different thicknesses and by adjusting the distance of the FS-40 lamps from the attachment substrate. This combination of light sources resulted in non-homogenous irradiation of the substrates. However, the desirable light conditions were achieved over a narrow elliptical area, which was used for sampling (Fig. 1).

Spectral measurements were performed before ATS commissioning at the Smithsonian's Photobiology Laboratory in Rockville, Maryland. PAR photon flux in all treatments was set at 703 ± 1% μE m^{-2} s^{-1} (Table 1), approximately two-thirds of the

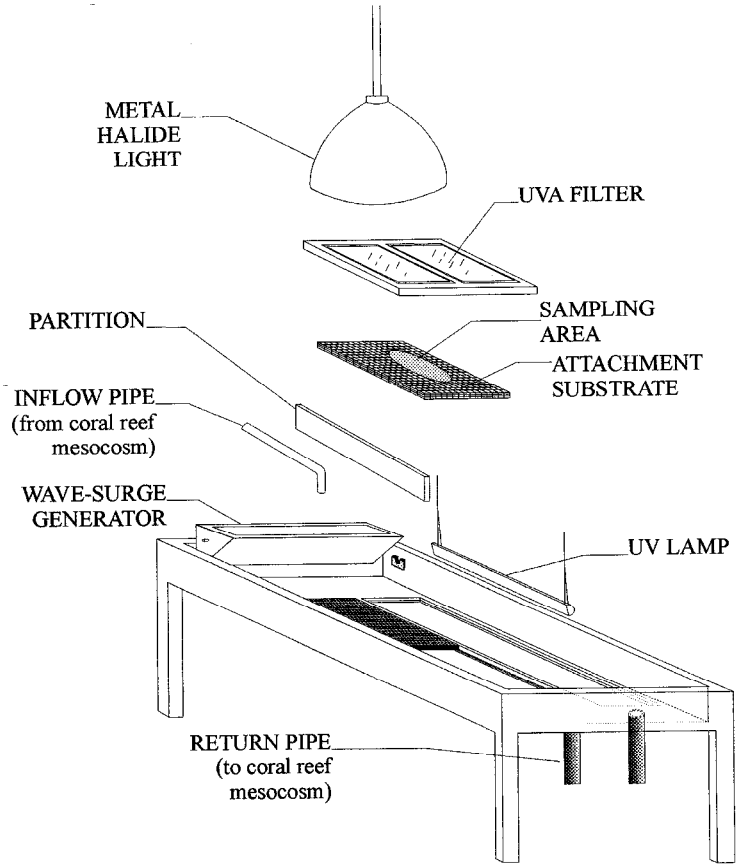


Fig. 1 Algal turf scrubber (ATS) used for mesocosm experiments. One half of each ATS was used for exposure to UV radiation, while the other half as a control (exposure to PAR only)

solar flux of a typical clear summer noon in the Caribbean Sea (latitude 21°N) at a depth of 60 cm below water surface. The spectrum of the metal halide lights is given in Fig. 2a; that of the Westinghouse FS-40 sunlamps, as modified by cellulose acetate filters, is given in Fig. 2b and c. A Plexiglas filter was placed in front of the metal halide lamp to block out UVA radiation in the controls (Fig. 1). UVA photon flux ranged between 40.44 and 48.01 $\mu E\ m^{-2}\ s^{-1}$ (Table 1). UVA irradiance was ca. 15% lower in the UVA treatment since the FS-40 lamp was omitted and metal halide light was used as the only UVA source. UVB photon flux was 4.2 $\mu E\ m^{-2}\ s^{-1}$ in the HUV treatment and 3.5 $\mu E\ m^{-2}\ s^{-1}$ in the LUV treatment. UVC transmitted by the cellulose acetate filters amounted to 0.04% of the total irradiance (Table 1).

The photoperiod was 14 h light:10 h dark throughout the experiment. Before starting the experiment the ATSs were thoroughly cleaned and water flow was initialized in all ATSs at the same time. All treatments and experiments described herein were performed simultaneously.

Biomass

Biomass was measured by scrape-harvesting the elliptical area with the appropriate irradiance conditions (Fig. 1) every 7 d for a total of ten times (Phase 1: weeks 2 to 6; Phase 2: weeks 7 to 11). Following sample biomass collection, the entire rectangular area of each ATS part was harvested to maintain homogeneity of growth conditions. After biomass harvesting, the recessed bottom of the trays was thoroughly cleaned to prevent establishment of grazers in the ATSs. The collected algal biomass was strained free of salt water, allowed to dry for 6 h at 60 °C, and then to constant weight at 80 °C.

To assess the variation of biomass and community indices between treatments within weeks, one-way analysis of variance was performed separately on each week's data, followed by multiple comparisons tests (Tukey's studentized range test). Differences are reported at the 0.05 level of statistical significance.

Table 1 Irradiances (in $\mu E\ m^{-2}\ s^{-1}$) used in the mesocosm experiment

Treatment	Light source/Filter	PAR	UVA	UVB	UVC
PAR + UVA + high UVB	Unfiltered metal halide, FS-40/thin cellulose acetate foil	703.10	47.56	4.20	0.32
PAR + UVA + low UVB	Unfiltered metal halide/no Plexiglas, FS-40/thick cellulose acetate foil	705.05	48.01	3.50	0.38
PAR + UVA	Unfiltered metal halide/no Plexiglas	709.56	40.44		
PAR	Metal halide/ UV-opaque Plexiglas	697.82			

(*UVC*: 240–280 nm; *UVB*: 280–320 nm; *UVA*: 320–390 nm; *PAR*: 700–390 nm)

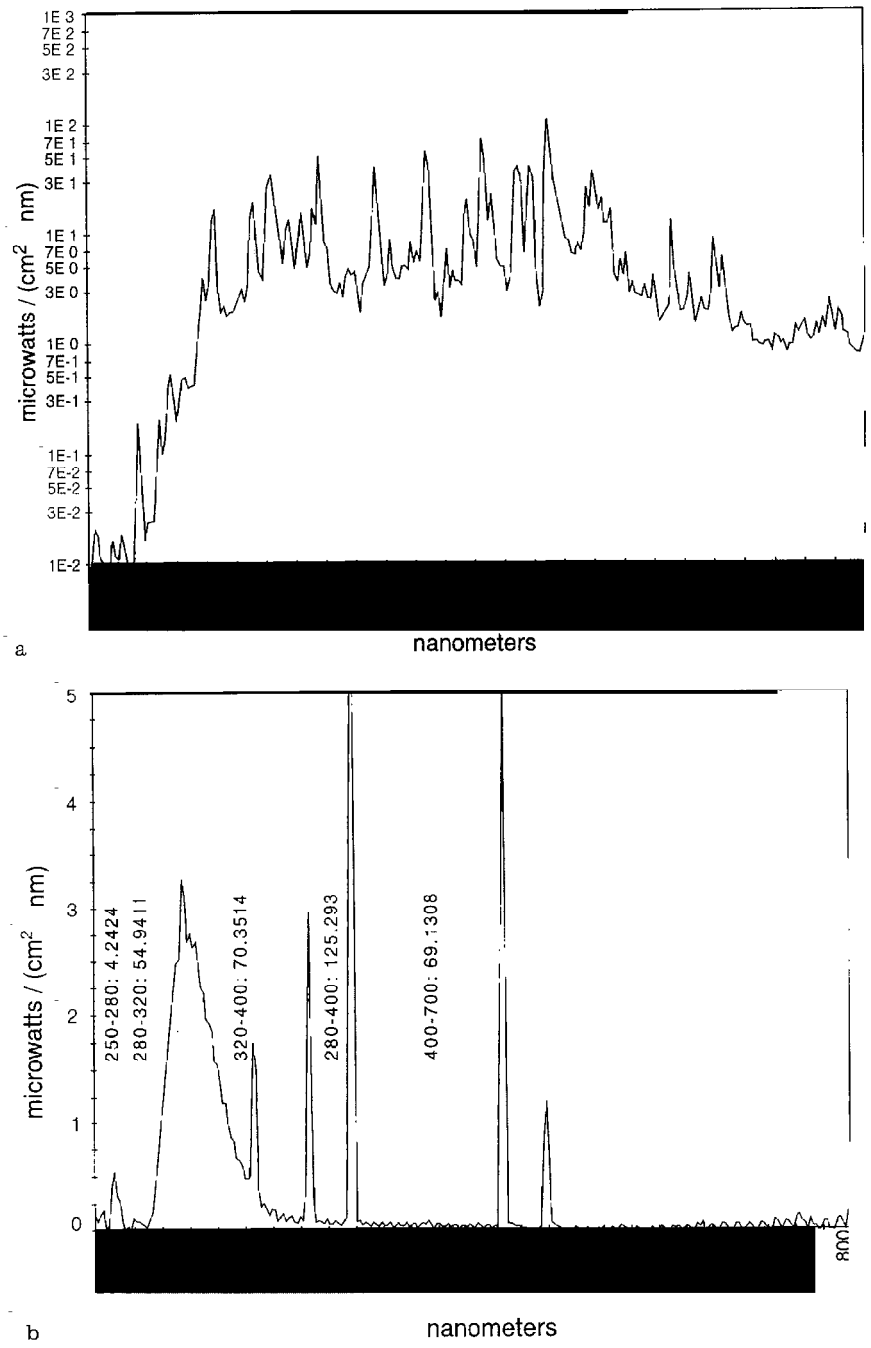


Fig. 2 a Spectrum of metal halide light. Spectrum of FS-40 sunlamp filtered by **b** thin cellulose acetate (high UVB treatment) and **c** thick cellulose acetate (low UVB treatment). Numbers on graphs (b and c) represent total irradiance for corresponding wavelength bands at a distance of 20 cm from the light bulb

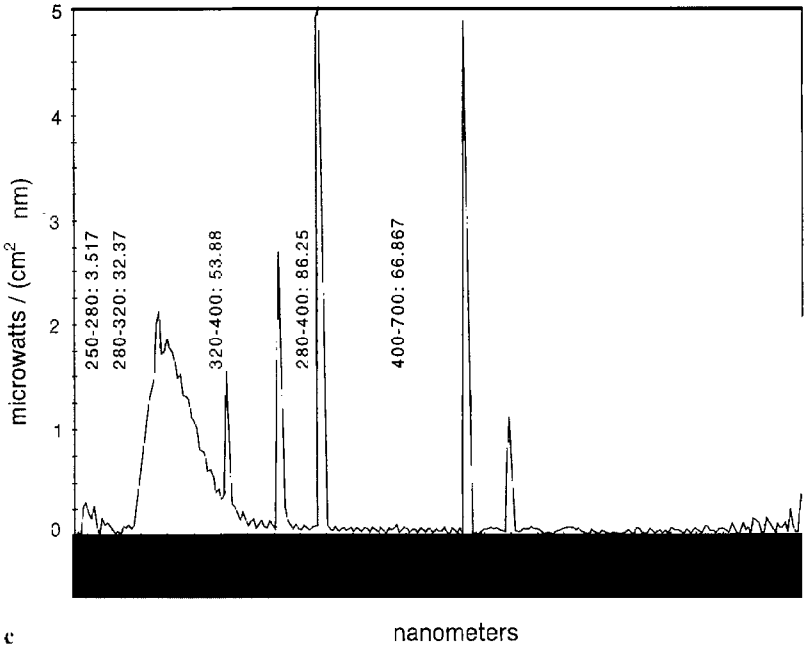
Community analysis

The biomass harvested from each ATS was homogenized by gentle mixing. Every week, three random replicate alga samples per treatment were obtained and mounted in glycerol for counting. In each replicate slide, 15 optical fields were counted using a Zeiss microscope equipped with a 11 × 11 counting grid inserted in one of the eyepieces. In a given optical field, a species received a count of "1" for each occurrence underneath each of the 121 grid cross points. Species abundance was expressed as percentage cover by dividing the total number of individuals of each species by the total number of individuals of all species enumerated in all optical fields of all slides and multiplied by 100. Community structure was analyzed by clustering ("Primer" Software; Plymouth Marine Laboratory).

Results

The algae of the "Living Coral Reef" mesocosm are representative of Caribbean coral reef habitats similar to the one in the field site of this investigation (Santas et al. 1998). Early substrate colonization occurred through algal spore settlement and spore vegetation. Although this process continued throughout the experiment, vegetative regeneration of the basal cells was responsible for most of the growth between harvests.

Fig. 2c



c

Biomass

The biomass data of the ATS units are plotted in Fig. 3a, b. Two weeks after the beginning of the experiments the standing crop under HUV was 67% lower than that under UVA (Fig. 3a). Although mean biomass production under the HUV treatment tended to be lower than all other treatments throughout Phase 1, this difference was statistically significant only in weeks 2 and 6. The most dramatic difference occurred in the second week of growth, when the biomass production of this assemblage was 3.66 g m^{-2} d^{-1}, a value lower than one-third of the mean biomass production of the controls (12.12 m^{-2} d^{-1}).

During Phase 2, exposure to enhanced UVB of assemblages previously exposed to PAR only did not result in statistically significant biomass differences (Fig. 3b). The increased error bars at the beginning of Phase 2 (weeks 7 and 8) represent higher variation between replicates. This is largely due to the different provenance of the assemblages assigned to the control treatment in this phase (the three Phase 2 controls were exposed to PAR + UVA + enhanced UVB; PAR + UVA + UVB; and PAR + UVA during Phase 1). However, this variation subsides with time and reaches its minimum value in week 10.

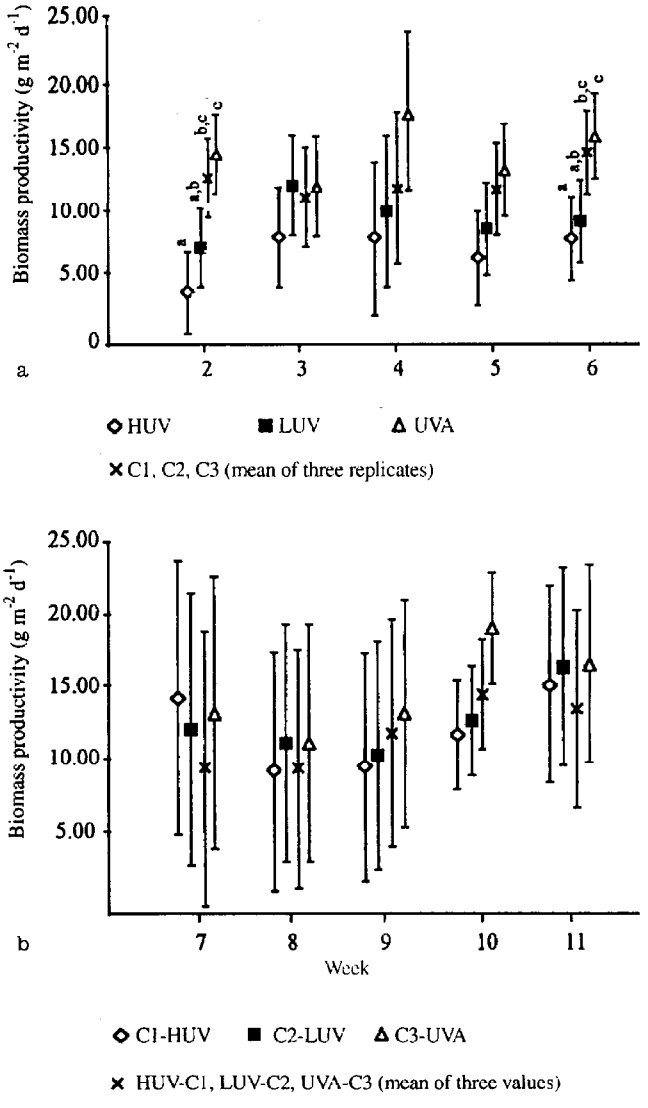


Fig. 3 Biomass production of coral reef mesocosm assemblages. **a** Weeks 1 to 6: primary productivity was lowest under enhanced UVB during the first 6 weeks of growth. Means with the same letter are not significantly different at the 0.05 probability level. **b** Biomass productivity after treatment reversal (weeks 7 to 11). There were no significant productivity differences between any two treatments or dates

A similar trend was observed in the LUV treatment. In Phase 1, this treatment had a lower biomass production than that of the controls except week 3. Mean weekly biomass production of the LUV treatment was intermediate between HUV and the controls, although not significantly different than either of the two (Fig. 3a). During Phase 2, exposure of assemblages previously exposed to PAR only to PAR + UVA + low UVB did not result in statistically significant differences (Fig. 3b).

The standing crop in the UVA treatment tended to be higher than that of all other treatments in both phases (Fig. 3a, b). In weeks 2 and 6 the UVA treatment had a significantly higher biomass productivity than each of the LUV and HUV treatments (Fig. 3a).

Community composition

The green algae *Enteromorpha prolifera* and *Cladophora fuliginosa* (Fig. 4a to f) dominated the initial stages of community development under all treatments. In the HUV treatment (Fig. 4a, left), the cyanobacterium *Schizothrix calcicola* became increasingly abundant and eventually dominated the assemblage in the last 2 weeks of Phase 1. In Phase 2, the abundance of the brown alga *Ectocarpus rhodochondroides* increased dramatically immediately after cessation of exposure to UVB (Fig. 4a, right). The diatom *Licmophora* sp. was the only other species present in substantial numbers after the reversal of treatments.

In the LUV treatment, *Ectocarpus rhodochondroides* appeared in week 3, became dominant 2 weeks before treatment reversal and remained dominant (Fig. 4c, left). *Licmophora* sp. was present in Phase 2 (Fig. 4c, right), while *Cladophora fuliginosa* persisted in significant quantities throughout the duration of the experiment.

In the UVA treatment (Fig. 4e) and the controls (Fig. 4b, d, f), *Ectocarpus rhodochondroides* was the dominant species throughout the experiment. Treatment reversal caused some changes in the abundance of subdominant species, but not in that of the dominant species (Fig. 4b, d, f, right).

The weekly harvesting disturbance and thorough cleaning of the ATS trays prevented the establishment of grazers in the ATS trays. Occasionally, some amphipods and tubeworms were observed underneath the Plexiglas sheet supporting the attachment substrate (plastic screen). These occurrences were rare and were not likely to have any measurable impact on community development.

During Phase 1, algal assemblages developing under the high and low UVB treatments formed a distinct cluster, separated from the rest of the treatments in weeks 3 to 5 (Fig. 5). In week 6, the LUV and HUV treatments dissociate from each other but are still individually distinguished from the rest of the treatments. The UVA treatment was most similar to the control replicate within the same ATS (C3) in weeks 3, 4 and 6, possibly suggesting a container effect. However, all three controls along with the UVA assemblage tend to form a single higher-order group in weeks 3 to 6, indicating that: (1) treatment effects are stronger than container effects, and (2) the effects of the UVA treatment are not clearly distinguishable from those of PAR.

During Phase 2, the similarity among all treatments is generally much higher than in Phase 1. In week 7 (Phase 2), the assemblage previously exposed to high UVB is still separated from the other assemblages despite treatment reversal, probably indicating a lag effect. In weeks 10 and 11, the effects of UVB reappear as evidenced by the grouping of the HUV and LUV treatments. However, the separation of this group from the other treatments is weaker than in Phase 1.

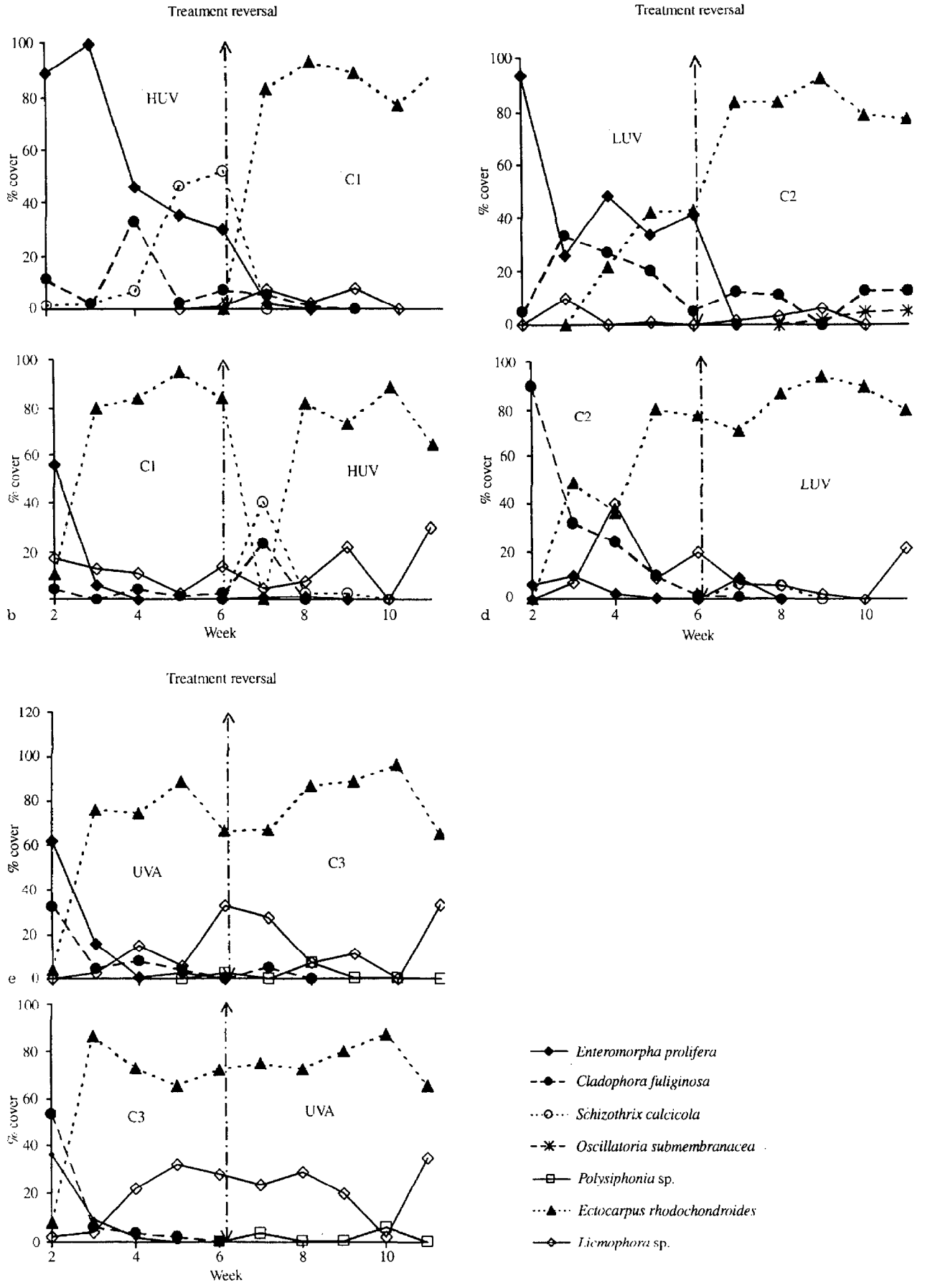
Discussion

During Phase 1, UVB affected the species composition and relative abundance of algal assemblages (Fig. 5, weeks 2 to 6). Such structural differences were not discernible during weeks 7 to 9, but reappeared towards the end of Phase 2, when the LUV and HUV assemblages group together again (Fig. 5). This cluster is more similar to the C1–C2 C3–UVA group than in Phase 1, indicating smaller differences in species composition, which are primarily due to the increased relative abundance of the subdominant diatom *Licmophora* sp. in these assemblages (Fig. 4b, d). These findings suggest that periphytic algal assemblages are more sensitive to UVB during the stages of early substrate colonization. Sensitivity to UV during the settlement stages has also been reported by Lüning (1980) for survival, growth and reproduction of gametophytes of the brown alga *Laminaria* sp.

During Phase 1, UVB reduced biomass productivity (Fig. 3a), while no significant differences in biomass production were found in Phase 2 (Fig. 3b). Bothwell et al. (1994) found an increase in the primary productivity of communities exposed to UVB radiation compared to communities protected from UVB radiation. This "paradox" was attributed to a suppression of grazer population growth by UVB, which, in turn, resulted in enhanced primary productivity. In the absence of UVB, increased grazing restricted algal growth, suggesting that grazing effects on primary productivity may be more pronounced than UVB inhibition. In the present study, however, such effects were not observed, since grazers were excluded by the frequent, thorough scraping of the attachment substrates and cleaning of the ATSs. The absence of significant biomass differences

►

Fig. 4a–f Abundance of dominant algal species in mesocosm experiment. Each graph represents the development of a single algal assemblage. After week 6 (*broken vertical line*) the light regime was reversed over the growing assemblages


Treatment reversal
HUV
C1
% cover
Week
Treatment reversal
LUV
C2
% cover
Week
b
C1
HUV
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Week
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LUV
% cover
Week
Treatment reversal
UVA
C3
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Week
e
C3
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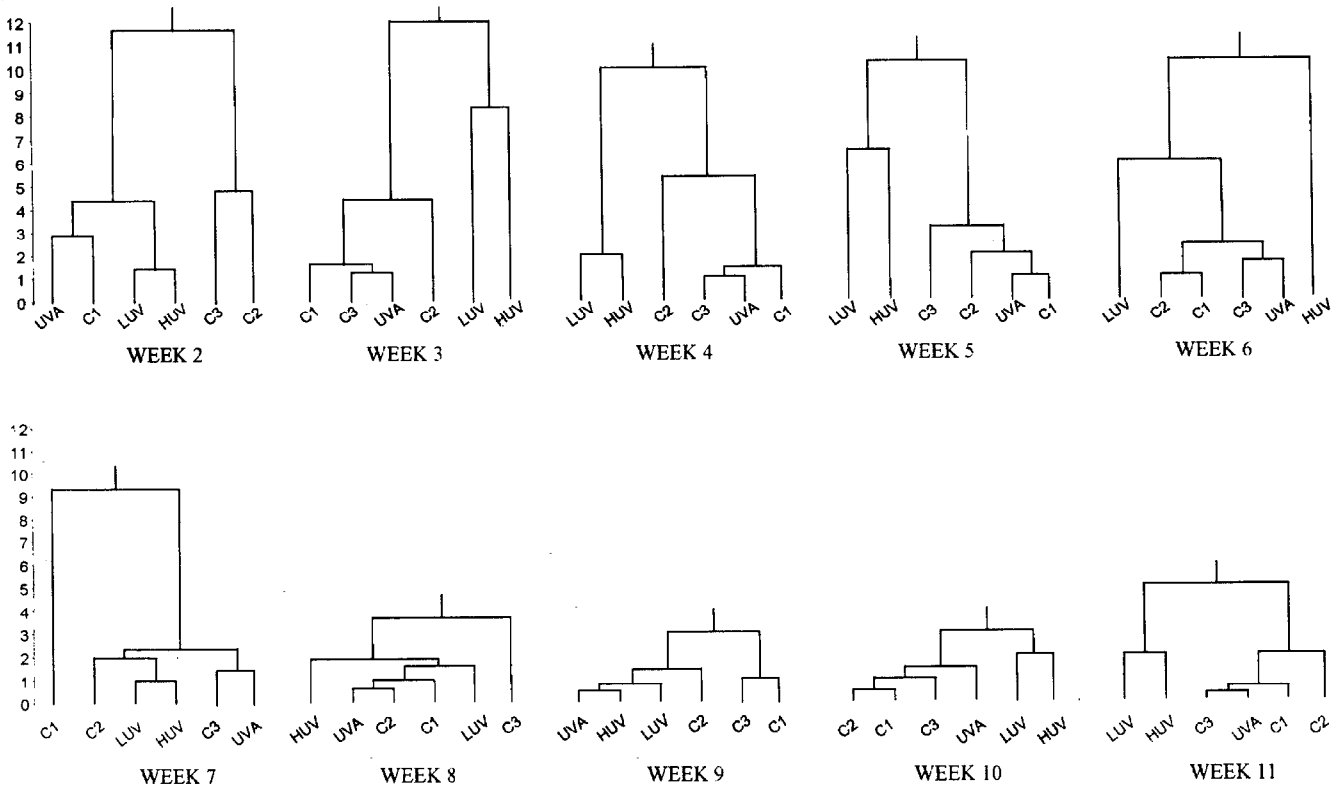
Enteromorpha prolifera
Cladophora fuliginosa
Schizothrix calcicola
Oscillatoria submembranacea
Polysiphonia sp.
Ectocarpus rhodochondroides
Licmophora sp.



suggests that the primary production of established marine periphytic communities and, therefore, the productivity may be unaffected by increasing irradiances of solar UVB. This may be possible if increased productivity by UV-tolerant species offsets the reduction in productivity of UV-intolerant species.

Adverse UVB effects on algal productivity may be milder than expected, since, unlike the abrupt UVB increase in Phase 2 of this laboratory assay, the increase in solar UVB occurs gradually over many years. Such gradual change in solar UV, combined with the capacity of many algal species to maintain high growth rates under high levels of UV and PAR (Jokiel and York 1984), may allow for adaptations of algae at the individual, species and community levels. However, there is evidence that grazer and bacteria populations may be more susceptible to UVB damage than algae (Bothwell et al. 1994; Herndl et al. 1993).

The differences in the species composition of the algal turf assemblages during the early stages of primary succession were largely due to the inhibition of *Ectocarpus* sp. spore germination by UVB. This brown alga was the dominant species in the absence of UVB. Its relative abundance declined temporarily after sudden exposure to enhanced UVB to increase soon again to pre-exposure levels (Fig. 4b). This suggests that unlike UVB-sensitive spores, *Ectocarpus* thalli are capable of adapting to a certain degree of UVB stress. Therefore, substrate colonization through vegetative regeneration of prostrate thalli left on the substrate after harvesting was possible during the second phase.

Fig. 5 Farthest neighbor clustering of mesocosm algal assemblages

Enteromorpha prolifera dominated young communities exposed to enhanced UVB (Fig. 4a). After the initial colonization stages, however, *Schizothrix calcicola*, replaced *E. prolifera*, while in the absence of UVB the abundance of *E. prolifera* declined rapidly (Fig. 4b; weeks 2 to 6). This increased tolerance of *E. prolifera* spores for UVB exposure partly explains the high abundance of this species during colonization of newly available substrate in the HUV and LUV treatments. Species of the genera *Enteromorpha*, *Cladophora* and *Ectocarpus* are frequently observed in surface layers of coastal waters exposed to high irradiance levels. The abundance of such species near the surface may be partly due to their increased UVB tolerance – a competitive advantage over species characterized by more rapid growth, efficient reproduction and/or chemical defense strategies but with a reduced UVB tolerance. Under the specific shallow water, UVB exposure and periodic harvesting conditions of this study, however, *S. calcicola* seems to have a medium-term competitive advantage over *E. prolifera*. In the absence of UVB, *Ectocarpus rhodochondroides* quickly replaces *Enteromorpha prolifera*, *C. fuliginosa* and *S. calcicola*. UV-screening pigments and shading by the outer cell layers may provide considerable protection for the main bulk of the thallus of macrophytes. This phenomenon is best exemplified by some species of the red alga *Jania*, often abundant at or near the surface. The outer, often bleached or necrosed cell layers of *Jania* spp. provide protection for the inner thallus. *Jania* thalli in turn provide shading

protection to algae of smaller stature growing in close association under the canopy of their larger neighbors.

UVA seems to have a rather beneficial effect on community productivity, since, in most cases, the standing crop of the UVA treatment was higher than that of the PAR treatment.

A weakness of the experimental design has been the exposure of the algal assemblages to a spectrally fixed light field. In nature, during the course of a day, the spectral balance of sunlight may vary several-fold with the solar zenith angle, ozone thickness, atmospheric conditions, etc. (Prézelin et al. 1994). Seasonal differences in irradiance and spectral balance are even more pronounced. For example, the daily PAR and UVB doses of a bright, mid-summer day can be 23 and 34 times higher than those of a cloudy, late-fall day in the Mediterranean (Santas et al. 1997). With regard to spectral balance, the same study reported that the late October UV-B/PAR ratio was 2.42 times lower than the corresponding early August value. Another possible source of error might have been the imperfect filtration of UVC by the cellulose acetate cutoff filters. However, the amount of UVC radiation transmitted through these filters was only a small percentage (0.04%) of the total irradiance (Table 1). Due to these limitations the results of this laboratory assay alone cannot be safely viewed as an accurate prediction of natural community responses to increased UVB. However, the data provide a comparison on the tolerance and behavior of common tropical species of filamentous algae. The assessment of UVB effects would probably be more realistic in carefully planned field studies. In such attempts, however, the possibility of masking or enhancement effects resulting from the lack of control over other confounding factors cannot be excluded. Therefore, a complementary experimental design should include both laboratory and field experiments (see Santas et al. 1998 for field studies).

Future research should take account of the interaction between UVB radiation and other factors complicating the interpretation of photobiological phenomena, such as trophic interactions, shading, grazing, UV screening pigment content, etc. Physiological studies are also needed to clarify the issue of differential sensitivity of algae during different stages of their life cycle. Since biological systems are subject to a wide variety of such interactions, caution should be applied in extrapolating from single-factor laboratory studies to global-scale effects of the expected increase in solar UVB.

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