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Community responses to UV radiation. II. Effects of solar UVB on field-grown diatom assemblages of the Carribean

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Abstract The effects of ambient solar UV on community productivity and structure were assessed during primary succession of benthic diatoms on artificial substrate in a coral reef of the Caribbean. Artificial substrates, partially enclosed by UV cutoff filters, were placed at a depth of 60 cm below surface. During the initial colonization stages, the assemblages exposed to the full solar spectrum had a mean productivity 43.4% lower than the assemblages exposed to PAR + UVA only. Some differences in species diversity of assemblages under the different UV treatments were also observed. Sensitive species to UVB exposure were *Mastogloia angulata*, *M. ovata*, *M. paradoxa*, *Nitzschia longissima*, *Plagiogramma staurophorum*, *Rhopalodia musculus*, and *Surirella ovata*. These UVB effects gradually diminished as succession proceeded; 5 to 6 weeks after the placement of the substrates in the water, no significant differences in productivity were observed between the different treatments, while after 6 weeks of growth, species diversity and evenness were higher, although not statistically significant, in the UVB-exposed assemblages. During the first 2 weeks of growth, the productivity under PAR + UVA was significantly lower than that under PAR only.

Introduction

During the last decade, the amount of stratospheric ozone has been reduced by 3% (World Meteorological Organization 1995). Anthropogenic diminution of the stratospheric ozone layer results in increased incidence of UVB (280 to 320 nm) at the Earth's surface (Kerr and McElroy 1993). Such an increase might have a significant effect on primary producers and other aquatic organisms in the upper ocean layers (Kelly 1986; Häder and Worrest 1991; Smith and Cullen 1995). In Antarctic waters, UVB inhibition of phytoplankton photosynthesis increases linearly with time of exposure (Smith et al. 1992).

Biologically detrimental UVB radiation can penetrate to ecologically significant depths in marine and freshwater systems (Jerlov 1964; Smith and Baker 1981). Photosynthesis can be reduced by as much as 25% in the top 10 to 20 m due to increased UVB radiation (Holm-Hansen 1990). Possible consequences to aquatic systems include reduced biomass production and changes in species composition, biodiversity and foodwebs (Kelly 1986; Häder et al. 1995). Damage by enhanced solar UV radiation at the molecular, cellular, population and community levels has been demonstrated in phytoplankton (Häder 1993). UVA has also been shown to inhibit the growth and photosynthesis of freshwater phytoplankton (Kim and Watanabe 1994). In species of red and brown macroalgae, photosynthesis and growth are impaired by UV radiation (Wood 1987, 1989). In these algal categories, photoinhibition by other bands of the solar spectrum has also been reported (Nultsch et al. 1990; Hanelt et al. 1994).

Worrest et al. (1978) studied the effects of enhanced simulated solar ultraviolet radiation (UVA and UVB) upon a marine community, recruited in a flow-through apparatus under laboratory conditions. The authors concluded that increased exposure to UV depressed chlorophyll *a* concentrations, reduced biomass, increased autotrophic indices and decreased community diversity. Some of these initial results (reduction in biomass, depression of chlorophyll *a* concentration, lower radiocarbon uptake rates) were confirmed in a subsequent study (Worrest et al. 1981b) that utilized a similar experimental apparatus but more extensive replication. Shifts in species composition of an artificial plankton assemblage were detected in another study by Worrest et al. (1981a), suggesting a significant impact

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upon successional patterns and primary producer–consumer trophodynamics of natural communities.

Short-term experiments with UV-radiation screening confirm that UV radiation can reduce the growth rates of benthic diatom communities in shallow freshwater during the summer, at mid-northern latitudes (Bothwell et al. 1993). In situ prolongation of UV exposure increased diatom biomass and community diversity, an effect attributed to grazing; grazing populations of shallow, freshwater habitats may be more susceptible to UVB damage than primary producers. The altered trophic-level interactions, in turn, produced greater effects on diatom communities than the direct effects of UVB (Bothwell et al. 1994).

Direct UVB effects on diatom assemblages grown on ceramic tiles in a natural marine habitat in Saronicos Gulf, Greece included shifts in species composition (Santas et al. 1997) and temporary inhibition of biomass production (Santas et al. 1996). These differences in community structure were more pronounced during the first month of community development. The fact that such differences did not persist at later successional stages suggests that periphytic communities of the upper euphotic zone possess adjustment mechanisms to the stress posed by increased solar ultraviolet radiation. The present study examines the effects of solar UV radiation on the productivity and structure of diatom assemblages of a typical Carribean coral reef.

Materials and methods

The experiment was conducted in the waters off Grand Turk, Turks and Caicos Islands (21°2′N; 71°3′W). The experimental apparatus was placed in a lagoon, 0.5 km from the east shore of Grand Turk, in the vicinity of some reef patches (Fig. 1). Each experimental unit was a partial enclosure comprising (a) an artificial substrate (5 mm mesh polypropylene screen) for algal spore attachment and growth supported by a 2-cm-PVC frame filled with iron reinforcing bar as weight, and (b) a dome of different combinations of cutoff filters open at both ends. All the units were suspended from 8-cm-PVC rafts at a depth of 60 cm (Fig. 2). The entire experimental apparatus was anchored so as to allow free current flow through the partial enclosures.

The experiments were conducted during the periods 25 April to 6 June 1987 (first run) and 30 August to 3 October 1987 (second run). Using a combination of cutoff filters two treatments were performed in the first run: (a) PAR + UVA and (b) PAR + UVA + UVB; $n = 3$ (UVB: 295 to 320 nm; UVA: 320 to 375 nm; PAR: 375 to 700 nm; wavelength ranges as delimited by the cutoff filters); three were performed in the second run: (a) PAR, (b) PAR + UVA and (c) PAR + UVA + UVB; $n = 3$. In order to prevent alteration of the transmittance properties due to fouling, the filters were cleaned regularly every 2 d. Weather conditions were mostly sunny with 2 or 3 cloudy days per month. Average irradiances of the three bands were measured with an International Light IL1350 spectroradiometer using SED038/PAR/W UVA and SED240/UVB/W UVB filters. Irradiance values at noon for PAR, UVA and UVB were 1588.3, 163.7 and 3.0 μE m^{-2} s^{-1} (first run); and 1525.7, 158.9 and 2.9 μE m^{-2} s^{-1}(second run).

Algal samples were obtained by random sampling, and species abundance was determined as percentage cover by microscope counts. Standing crop was measured every 7 d for a total of six times for each experiment. Standing crop was estimated by harvesting the same area of substrate at each sampling time. The collected algal biomass was strained free of salt water, and dried to constant weight at 80 °C. A part of the harvested biomass was processed for diatom identification using the H_2O_2 digestion method (Patrick and Reimer 1966). Means determined statistically different by one-way analysis of variance, performed separately on the weekly data, were further analyzed by multiple comparisons tests (Tukey's studentized range test). Results are reported at the 0.05 level of statistical significance.

The Shannon diversity (H'), Pielou evenness (J) and Margalef species richness indices were calculated for diatom assemblages based on the formulae:

$$H' = -\sum p_i \cdot \log_2 p_i \quad \text{(Shannon 1948)},$$

$$J = H'/H_{\max} \quad \text{(Pielou 1966), and}$$

$$\text{Species richness} = (S-1)/\ln N \quad \text{(Margalef 1951)},$$

where p_i is the relative abundance of the ith species in the sample, S is the number of species in the sample, and N is the total number of individuals in the sample.

The Shannon index takes into account both the total number of species and the degree of even distribution of individuals among species. When all species in a sample are equally abundant, maximum diversity, $H_{\max}$, is obtained and it is calculated as $H_{\max} = \log_2 S$. Evenness (J) ranges between 0 and 1 and provides an indication of how homogeneously individuals in a sample are distributed among species. A sample in which all species are represented by equal numbers of individuals has an evenness value of 1. The Margalef species richness index provides reasonable independence from sample size by normalizing over the natural logarithm of the total number of individuals counted.

Due to technical reasons and physical constraints, community analysis was carried out only during the first run. Therefore, the separation of PAR and UVA effects on community composition treatment was not possible. After the enumeration of diatom valves

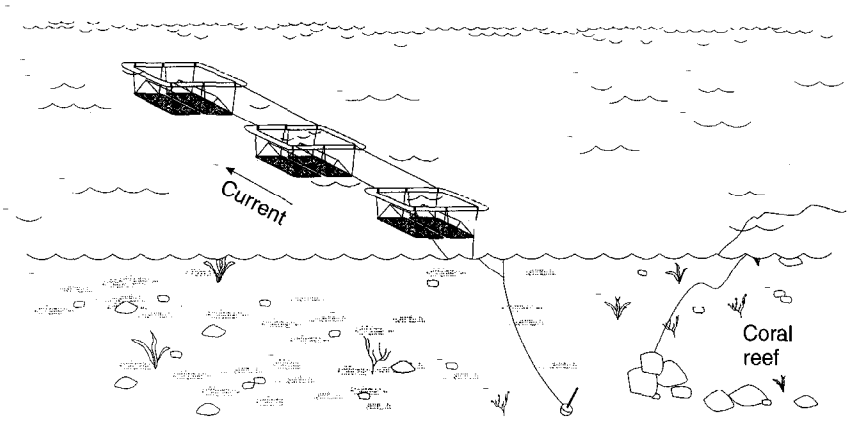

Fig. 1 General view of field experimental apparatus. Growth substrates suspended at a depth of 60 cm below surface. The tier of rafts was anchored only on one end to allow free swinging of the experimental apparatus and current flow over the growing algal mats

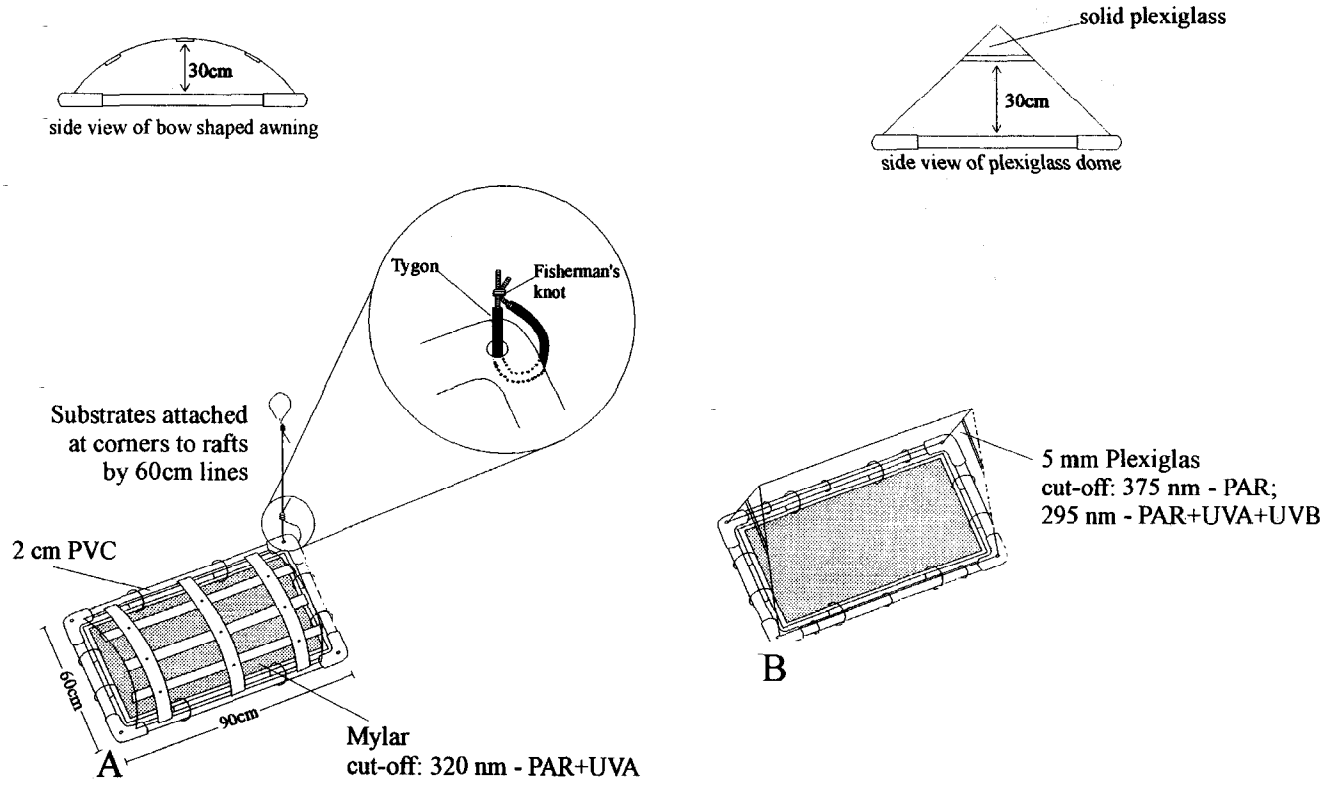

Fig. 2 Field enclosure design. UV transparent Plexiglas was used for the PAR + UVA + UVB treatment (*bottom right*, cutoff at 295 nm); Mylar (*bottom left*, cutoff at 320 nm) for the PAR + UVA treatment; and regular Plexiglas (cutoff at 375 nm) for the PAR treatment

using a light microscope equipped with an eyepiece grid, the results were expressed as percentage cover and analyzed by clustering and multi-dimensional scaling (MDS) ordination ("Primer" software; Plymouth Marine Laboratory). This ordination technique determines the dimensional map of points best representing the similarities of different assemblages. The similarity values result from a clustering procedure based on selected indices such as the Bray–Curtis similarity index. Regression is then performed among the ranked physical distances of points given by the similarity matrix. The goodness-of-fit of the regression is measured by the *stress* value, calculated by the formula (Field et al. 1982):

$$\text{Stress} = \sum_j \sum_k \left(d_{jk} - \bar{d}_{jk}^2\right) \Big/ \sum_j \sum_k d_{jk}^2$$

where $\bar{d}_{jk}$ is the distance between sample points j and k which corresponds to the given dissimilarity d_{jk}. Stress values between 0 and 1 indicate excellent configurations, values between 1 and 2 are considered satisfactory, while values > 2 show virtually random configurations (Clarke and Warwick 1989).

Results

A total of 160 diatom taxa were found under all treatments (Table 1). In addition to diatoms, other taxa present on the artificial substrate included representatives of the genera: *Bryopsis*, *Cladophora*, *Enteromorpha*, *Ceramium*, *Polysiphonia*, *Heterosiphonia*, *Herposiphonia*, *Ectocarpus*, *Schizothrix*, *Calothrix*, *Oscillatoria*, etc. The weekly harvesting procedure prevented the establishment of a diversified microfauna. The most common microinvertebrates encountered were species of nematodes, amphipods and unidentified decapod larvae. None of these organisms, however, reached substantial abundances during the course of the experiments.

Species present in the PAR + UVA + UVB treatment only were *Ardissonea fulgens*, *Cocconeis nummularia*, *Diploneis crabro*, *Fragilaria brevistriata* and *Mastogloia ovalis*. The most abundant taxa in the same treatment were *Mastogloia shmidtii*, *Nitzschia behrei*, *N. constricta* var. *parva* and *Synedra undulata*. Species present in the PAR + UVA treatment only were *Mastogloia angulata*, *M. ovata*, *M. paradoxa*, *Nitzschia longissima*, *Plagiogramma staurophorum*, *Rhopalodia musculus*, and *Surirella ovata*. The most abundant species in the same treatment were *Diatoma vulgare*, *Licmophora remulus*, *Striatella unipunctata*, *Synedra distinguenda*, and *Synedra ulna*.

The 3-week averages (weeks 2, 3, 4) of the mean diatom productivity values ($n = 3$) of the PAR + UVA + UVB treatment were 43.4% (first run) and 36.2% (second run) lower than the corresponding values for the PAR + UVA treatment (Fig. 3a, b). The means of the two treatments were statistically different in weeks 2 through 4 in the first run (Fig. 3a), and in weeks 2 and 3 in the second run (Fig. 3b). The productivity curves of the different treatments converged in the last 2 weeks of both runs.

In the second run, the PAR treatment had the highest productivity in week 2, while in weeks 3 and 4, the treatment with the highest productivity was PAR + UVA (Fig. 3b). Mean PAR + UVA + UVB productivity was

Table 1 Pennate diatom species list

1. *Achnanthes brevipes*	41. *D. smithi*	81. *M. ignorata*	121. *N. frustulum*
2. *A. hungarica*	42. *D. subadvena*	82. *M. labuensis*	122. *N. laevis*
3. *A. inflata*	43. *D. suborbicularis*	83. *M. laminaris*	123. *N. longissima*
4. *A. lanceolata*	44. *D. weissflogi*	84. *M. lanceolata*	124. *N. panduriformis*
5. *Amphora biggiba*	45. *Donkinia recta*	85. *M. ovalis*	125. *N. peridistincta*
6. *A. coffeaeformis*	46. *Fragilaria brevistriata*	86. *M. ovata*	126. *N. sigma*
7. *A. decussata*	47. *F. constricta*	87. *M. ovulum*	127. *N. vidovichii*
8. *A. graeffi*	48. *F. construens*	88. *M. paradoxa*	128. *Opephora gemmata*
9. *A. inariensis*	49. *F. pinnata*	89. *M. peragalli*	129. *O. martyi*
10 *A. ostrearia*	50. *Grammatophora hamulifera*	90. *M. pisciculus*	130. *O. olsenii*
11. *A. robusta*	51. *G. oceanica*	91. *M. punctifera*	131. *Ostrupia powelli*
12. *A. veneta*	52. *G. undulata*	92. *M. pussila*	132. *Plagiogramma pulchellum*
13. *A. ventricosa*	53. *Gyrosigma acuminatum*	93. *M. schmidtii*	133. *P. staurophorum*
14. *Anorthoneis excentrica*	54. *G. attenuatum*	94. *M. smithi* (sp.2)	134. *Pleurosigma angulatum*
15. *Ardissonea crystallina*	55. *Licmophora gracilis*	95. *M. splendida*	135. *Podocystis adriatica*
16. *A. fulgens*	56. *L. grandis*	96. *M. staurophora*	136. *P. spathulata*
17. *Auricula complexa*	57. *L. ehrenbergii*	97. *M. subaffinis*	137. *Rabdonema adriaticum*
18. *A. minuta*	58. *L. juergensii*	98. *M. subaffirmata*	138. *R. minutum*
19. *Bacillaria paxillifer*	59. *L. oedipus* (sp.1)	99. *M. sublatericia*	139. *Rhaphoneis ampiceros*
20. *Caloneis linearis*	60. *L. reichardtii*	100. *M. tenera*	140. *R. nitida*
21. *Campylodiscus fastuosus*	61. *L. remulus*	101. *M. undulata*	141. *Rhopalodia constricta*
22. *Climacosphenia elongata*	62. *Mastogloia angulata*	102. *M. varians*	142. *R. gibberula*
23. *C. moniligera*	63. *M. asperula*	103. *M.* sp.1	143. *R. musculus*
24. *Cocconeis disculus*	64. *M. asperuloides*	104. *Navicula carinifera*	144. *Stauroneis (Gregori)*
25. *C. dirupta*	65. *M. barbadensis*	105. *N. cincta*	145. *S. spicula*
26. *C. diruptoides*	66. *M. binotata*	106. *N. crucigera*	146. *Striatella unipunctata*
27. *C. fluminensis*	67. *M. citrus*	107. *N. flanatica*	147 *Surirella fastuosa*
28. *C. nummularia*	68. *M. cocconeiformis*	108. *N. florinae*	148. *S. ovata*
29. *C. ornata*	69. *M. corsicana*	109. *N. ramosissima*	149. *Synedra distinguenda*
30. *C. placentula*	70. *M. cribrosa*	110. *N. subrinkocephala*	150. *S. hennedyanna*
31. *C. scuttelum*	71. *M. crucicula*	111. *Nitzschia acuminata*	151. *S. laevigata*
32. *C. sublittoralis*	72. *M. decussata*	112. *N. acuta*	152. *S. provincialis*
33. *Ctenophora pulchella*	73. *M. elegans*	113. *N. apiculata*	153. *S. pulchella* fm. *constricta*
34. *Cymatosira lorenziana*	74. *M. elliptica*	114. *N. behrei*	154. *S. ulna*
35. *Denticula tenuis*	75. *M. erythraea*	115. *N. bilobata*	155. *S. undulata*
36. *Diatoma vulgare*	76. *M. fimbriata*	116. *N. commutata*	156. *S. toxonoides*
37. *Dimmerogramma minor*	77. *M. gibbosa*	117. *N. constricta*	157. *Tabularia fasciculata*
38. *Diploneis bombus*	78. *M. gigantea*	118. *N. constricta* var. *parva*	158. *Toxarium undulatum*
39. *D. crabro*	79. *M. horvathiana*	119. *N. dissipata*	159. *Trachyneis aspera*
40. *D. puella*	80. *M. ineaqualis*	120. *N. elegantula*	160. *Tropidoneis lepidoptera*

significantly lower than PAR in week 2 only. In week 5, PAR + UVA + UVB productivity was higher than both PAR and PAR + UVA, but the difference was not statistically significant.

Community analysis was based on the presence and percentage cover of diatom species. The mean total numbers of species and species richness under PAR + UVA + UVB were lower than under PAR + UVA throughout the experiment. However, the only significant difference was that the total number of species was lower ($F = 7.89$; $df = 1, 4$; $p < 0.05$) in the PAR + UVA + UVB treatment in week 3. The means of the two treatments converged at the end of the experiment (Fig. 4a, b). The mean total number of species ranged between 47.67–72 and 61.67–90.67 in the PAR + UVA + UVB and PAR + UVA treatments, respectively. The highest mean number of species (90.67) occurred in week 5 in the PAR + UVA treatment, the lowest number (47.67) in week 2 in the PAR + UVA + UVB treatment.

The H' and J values ranged between 2.08–2.44 and 0.483–0.578 for the PAR + UVA treatment, while in the PAR + UVA + UVB treatment H' and J ranges were 2.00–2.23 and 0.482–0.555 (Fig. 4c, d). No significant differences were observed. The highest diversity values (H') occurred in week 5 in the PAR + UVA assemblage. Individuals were most evenly distributed among species (highest J) in week 2 under the PAR + UVA treatment.

The lowest values for both H' and J occurred in week 4 in the PAR + UVA + UVB treatment. The H' and J values of the PAR + UVA + UVB treatment remained lower than those of the PAR + UVA treatment throughout most of the experiment (Fig. 4c, d). In week 6, however, this relation was reversed: species diversity and evenness of the PAR + UVA + UVB treatment exceeded that of the PAR + UVA treatment.

Figures 5 and 6 summarize the results of nearest-neighbour clustering; Fig. 7 is the outcome of hierarchical ordination. In week 2, the six assemblages form a group that is clearly separated from the other dates (encircled in Figs. 5, 7), probably indicating a time effect. The six assemblages cluster again in week 3. However, the separation of this group is not as clear as in week 2, as shown by the nested pattern of clustering

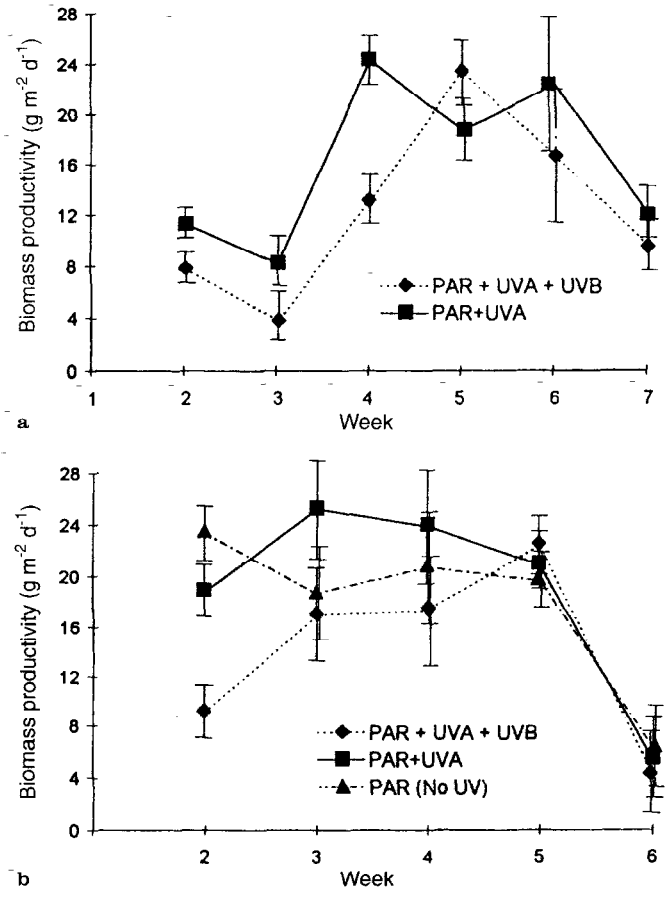

Fig. 3 Biomass productivity of benthic diatom assemblages: **a** first run, **b** second run. Statistical significance determined by separate one-way analysis of variance within weeks

(Fig. 5). Similarity between replicates was highest in week 4, when the three replicates of each treatment form two distinct groups (Fig. 6). In week 6, treatment separation is suboptimal, while in weeks 2, 3 and 5 no distinct clustering pattern between treatments is observed.

Discussion and conclusions

The reduced productivity of the PAR + UVA + UVB treatment during the first 4 weeks suggests that benthic algal assemblages are most sensitive to UVB during the spore establishment and vegetation stages. The exclusion of UVB had a similar transient effect on the productivity of diatom assemblages of the Mediterranean Sea (Santas et al. 1996); exposure of Mediterranean diatoms to ambient solar UVB-inhibited productivity during the first 2 weeks of growth – although to a lesser extent than reported here – and also affected community structure. The difference between the findings of the two studies can be explained by the fact that, in the Mediterranean study, standing crop measurements were obtained by harvesting different substrate areas, while in the present study, the same substrate area was harvested week after week. The harvesting of the same area was a periodic disturbance, which probably delayed succession and caused the prolonged manifestation of UV effects.

By contrast, exposure to enhanced UVB reduced the productivity of filamentous algal assemblages grown in laboratory mesocosms for a period of 6 weeks (Santas et al. 1998). Productivity was restored to normal levels only after removing UVB. Exposure of mature filamentous algal assemblages to enhanced UVB did not affect productivity or community structure, while exposure to UVA seemed to have a rather beneficial effect on the growth of filamentous algae.

The productivity fluctuation patterns were very similar among the different treatments. This phenomenon has been related to the fluctuation of parameters such as PAR, current and wave action, turbidity, grazing, etc. (Adey and Steneck 1985; Adey and Goertmiller 1987). At present, it remains unknown whether such factors enhance or mask the effects of solar UV. Negative UVB effects, for example, may be balanced by positive UVB influences on algal community composition, such as control of UV-sensitive grazers (Bothwell et al. 1994), thereby relieving some of this growth-inhibiting pressure. In the present study, the influence of grazers was minimal due to their exclusion by the frequent harvesting procedure.

During weeks 3 and 4 UVA appeared to enhance the growth of the diatom assemblages. Beneficial UVA effects have been reported for *Ulva lactuca* L. and *Trailliella intricata* (Halldal 1964). These algae were shown to utilize UVA and a part of the UVB spectrum in photosynthesis. In addition, ^{15}N-ammonium uptake was enhanced by UVA for the marine tropical diatom *Bellerochea yucatanensis* v. Stosch (Döhler 1995). However, uptake rates of ^{15}N-ammonium decreased upon exposure to UVA of high intensity and UVB radiation in the marine haptophycean *Pavlova lutheri* (Droops) Green strain Plymouth CC 75 and *Pavlova* sp. (Döhler and Buchmann 1995). Strong damage by low-intensity UVA on ^{15}N incorporation into amino acids was observed. Since most UVA studies have focused on physiological effects on single species, further research is required to elucidate the role of UVA on community productivity and structure.

The ecological interpretation of the different ecological indices is as follows (Legendre and Legendre 1983). Diversity can be viewed as a function of environmental stability (higher H' values indicate more stable environments), and has two components: the number of species and the evenness of their frequency distribution. For instance, a community with a given total number of species of which only a few are dominant will have a lower H' than a community with the same total number of species but a more even frequency distribution. The number of species is proportional to the number of realized niches, i.e. sets of environmental conditions not shared by sympatric species (Hutchinson 1957, 1965). Species richness has a very similar ecological interpretation to the total number of species, but bears the advantage of being relatively independent of sample size.

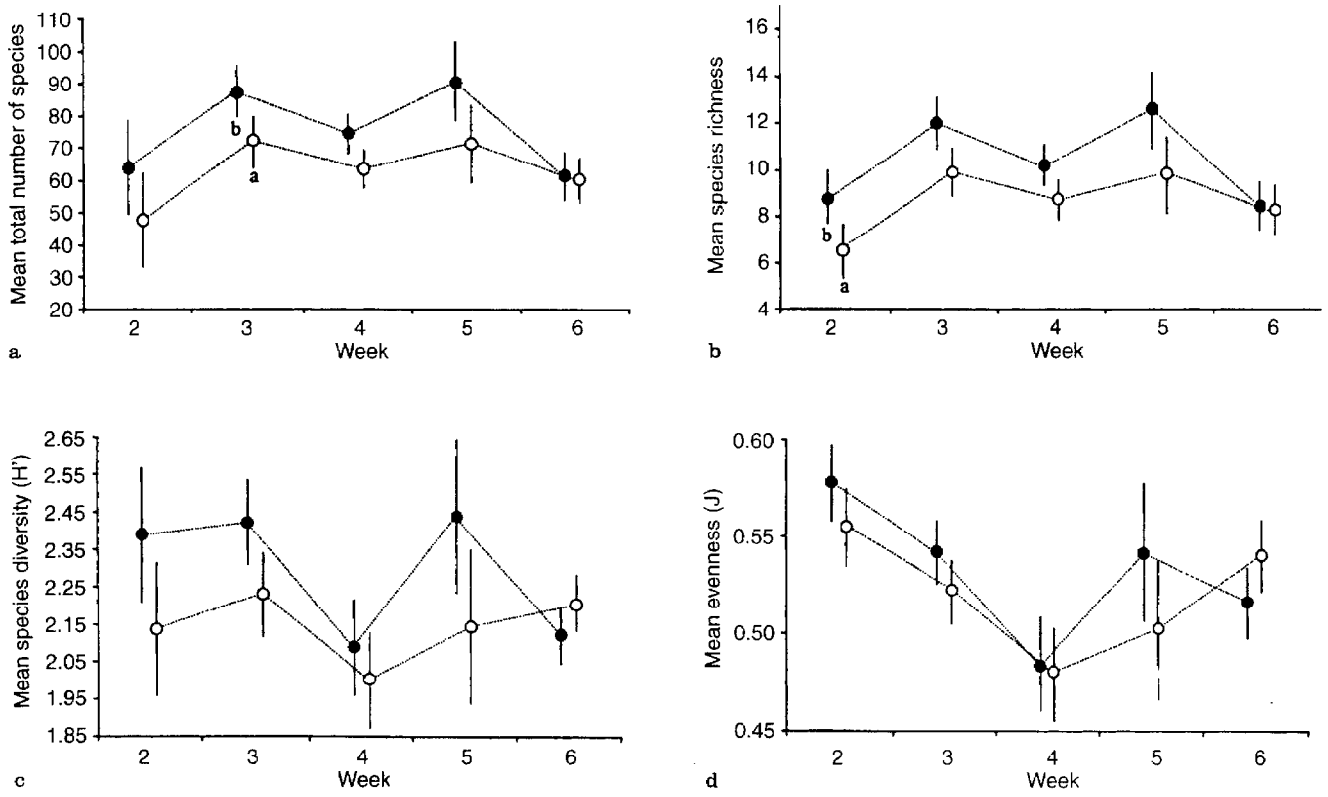

Fig. 4 **a** Total number of species; **b** Margalef index of species richness; **c** Shannon index of species diversity (H'); **d** Pielou index of evenness (J). Significant difference between treatments found only in week 3 for mean total number of species (○ PAR + UVA + UVB; ● PAR − UVA)

The evenness is inversely proportional to the degree of biological activity (production, life cycles, energy flow between trophic levels, etc.) in a given environment. Lower evenness values are indicative of stress. Based on the above, the maximum H' value in week 5 (Fig. 4c) is probably due to the high values of both total number of species and evenness (Fig. 4a, d). In week 4 a local minimum of species diversity and evenness occurred (Fig. 4c, d). This decrease in the H' and J indices is not accompanied by a decrease in productivity (Fig. 3), and is the combined result of a reduction in the total species number with an increase in the dominance of certain species. These were *Licmophora* sp., *Synedra* sp., *Navicula* sp., *Nitzschia* sp., *Stauroneis* sp., and *Mastogloia* sp. A common feature of these species is that they are larger and more elongated than the majority of the other diatom species present. Their presence, however, is related to season and/or succession rather than tolerance to UVB, as these species were present in both treatments.

In the present study, the diatom species excluded by exposure to UVB, were *Mastogloia angulata*, *M. ovata*, *M. paradoxa*, *Nitzschia longissima*, *Plagiogramma*

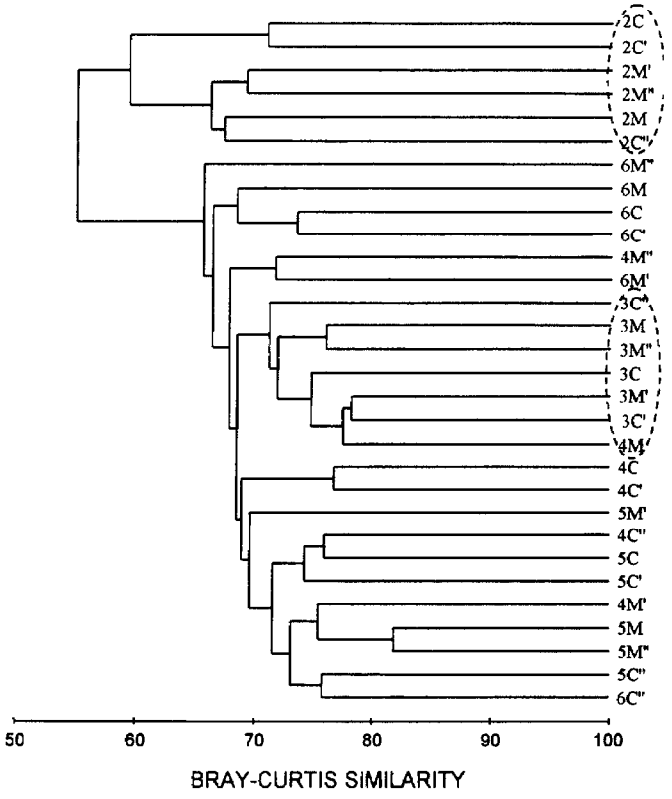

Fig. 5 Community similarity between the coral reef diatom assemblages (all samples) (*C*: PAR − UVA + UVB; *M*: PAR + UVA; *number of primes* indicate replicates; *numbers preceding letters* correspond to growth weeks; *encircled assemblages* show strong similarity)

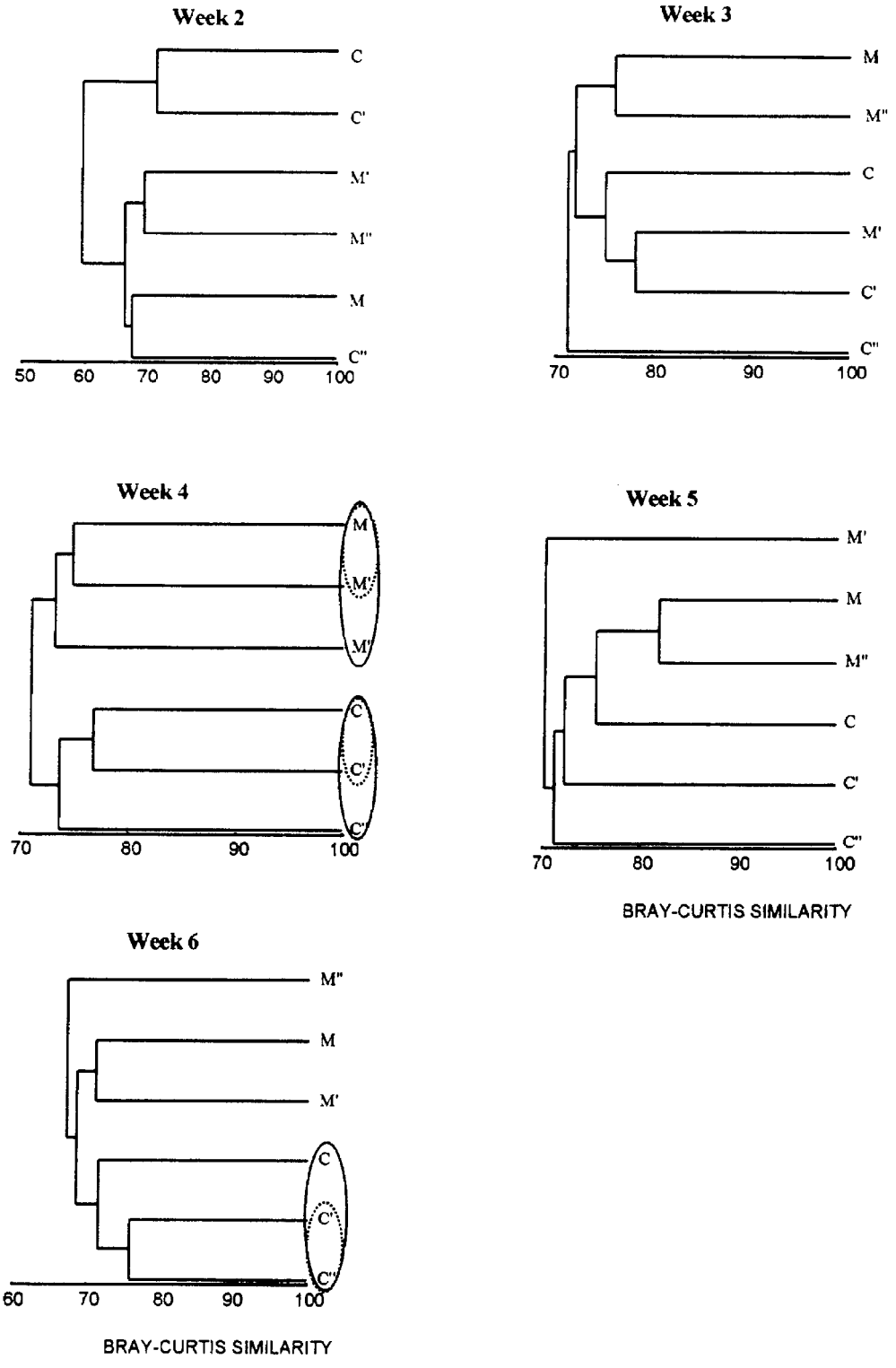

Fig. 6 Weekly clustering of diatom assemblages (*abbreviations*, see Fig. 5)

staurophorum, *Rhopalodia musculus*, and *Surirella ovata*. In another study carried out in the Mediterranean Sea, the species *Mastogloia crucicula*, *Nitzschia constricta*, *N. marginulata* and *N. punctata* were sensitive to both UVA and UVB, while *Amphora veneta*, *N. longissima*, *Opephora olsenii*, *Synedra baccilaris* and *S. robusta* were excluded by exposure to UVB, but not UVA (Santas et al. 1997). All of the above taxa belong to the Biraphideae, a group with a single raphe on each valve. They are elongated, cosmopolitan, polyhaline forms with the exceptions of *Surirella ovata* (stenohaline) and *Rhopalodia musculus* (meso-euryhaline). The diatom assemblages of the present study differed from those of the Mediterranean both in terms of species and species abundance. However, the assemblages of the two sites included several species in common. Of those, *N. long-*

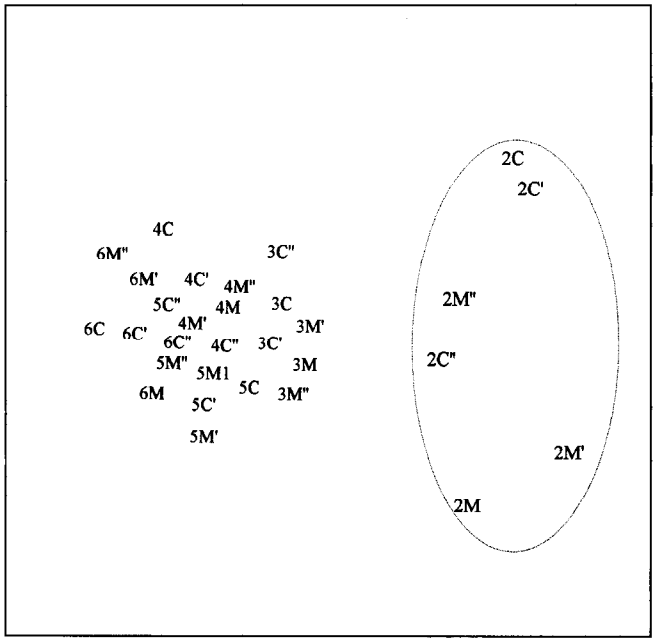

Fig. 7 Multi-dimensional scaling ordination of all the coral reef diatom assemblages. There is a clear time effect in separating the six assemblages of week 2 from the rest of the weeks. However, no separation pattern is clear thereafter (*abbreviations*, see Fig. 5)

issima was the only species excluded by UVB in both studies. This species can be useful in physiological studies for understanding UVB-induced photodamage and photoinhibition. All of the Mediterranean taxa excluded by UVB are also elongated, cosmopolitan forms belonging to the Biraphideae group with the exception of *Synedra* (Araphideae).

The increase of the Shannon index of the assemblages exposed to UVB at the end of the experiment is due to a more homogeneous species distribution rather than an increase in the number of species present. However, whether UVB favors higher species diversity requires further investigation. At later stages, the UVB-exposed diatom assemblages adapted in terms of both productivity and species diversity. It is speculated that such an adaptation may be due to the following three mechanisms: (a) the upper layer of diatom cells may provide some degree of UVB screening to the underlying cell layers; (b) UVB-tolerant species may have a less opportunistic dispersal strategy and colonize the substrate at later stages; and (c) short-term physiological adaptation at the individual and/or population levels may occur. The parallel changes of each of the four community indices in the two treatments (Fig. 4a to d) reflect fluctuations of factors other than light. Such factors include the establishment of grazers, current and wave action, biological cycles, spore availability, etc.

The absence of consistent clustering patterns can be explained by (a) the high numbers of diatom species present in all assemblages and (b) the lack of dramatic differences in the relative species abundances. Differences in community structure are easier to demonstrate in cases of smaller number of species present combined with dramatic differences in relative species abundance (Santas et al. 1998). In the present study, increasing the number of replicate enclosures and samples per assemblage would probably have elucidated differences in community composition. However, such an increase in the sampling effort was not possible due to the physical constraints of the strenuous labor required for (a) the microscopic analysis of community structure and (b) the construction and maintenance of the experimental apparatus in the field.

In conclusion, the findings of this study suggest that:

a. Ambient levels of solar UVB inhibit the productivity of tropical marine diatom assemblages at the early stages of primary succession. However, as succession progresses, productivity is restored to normal levels; ambient UVB levels do not seem to have harmful long-term effects on community productivity and/or structure.
b. On the contrary, exposure of natural communities to ambient levels of UVB may actually sustain the high diversity of tropical marine diatom assemblages by restricting the abundance of dominant species.
c. UVA inhibits the growth of tropical marine diatom assemblages to a lesser extent and for a shorter period during the early stages of primary succession.

Further research is needed on the issues of (a) adaptation mechanisms of natural communities to UVB exposure and (b) the interaction of ambient and enhanced solar UV with other factors affecting primary productivity (different light wavelength bands, grazing, wave action, nutrients, etc.).

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