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UVB radiation and depth interaction during primary succession of marine diatom assemblages of Greece

Abstract—Exposure to UVB radiation caused shifts in the species composition of diatom assemblages developing on ceramic tiles in a natural marine habitat near Korinthos, Greece. These differences in community structure were more pronounced during the first month of community development. The diatom species *Mastogloia crucicula* and *Nitzschia constricta* were sensitive to both UVA and UVB radiation, while *Amphora delicatissima, Amphora veneta, Opephora olsenii, Synedra baccilaris,* and *Synedra robusta* were excluded by exposure to UVB but not to UVA. *Amphora robusta, Cocconeis fluminensis, Mastogloia erythraea,* and *Mastogloia ovalis* were absent from 0.5 m while *Nitzschia bilobata* was present only in 1.0 m. *Mastogloia badjikiana, Mastogloia labuensis, Nitzschia lanceolata,* and *Synedra laevigata* were present during different stages of succession. The fact that differences in community structure do 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 increase in solar UVB irradiation caused by the rapid decline in stratospheric ozone concentrations has been confirmed by satellite measurements (Molina and Molina 1992). The deterioration of this phenomenon, as predicted by mathematical models (Madronich et al. 1995), has brought about scientific and public concern about the expected global-scale adverse effects in the future.

The impact of solar UV radiation on aquatic ecosystems and their primary productivity has been the subject of intensive investigations in recent years (Donkor et al. 1993; Häder 1993; Hessen et al. 1995; Häder et al. 1995; Williamson 1995). Because marine habitats exceed in size the terrestrial habitats almost by a factor of two, severe UV effects in the marine environment are expected to have a significant global-scale climatic impact (Caldwell et al. 1995; Liu et al. 1995). Several studies focus on UV effects on phytoplankton productivity (Häder and Schäfer 1994; Kim and Watanabe 1994; Gerber and Häder 1995a), while others focus on changes in motility, photoorientation, and velocity caused by UV (Gerber and Häder 1992; Gerber and Häder 1995b; Schäfer et al. 1993; Tirlapur et al. 1993; Nielsen et al. 1995).

In contrast to the plethora of phytoplankton studies, literature on the effects of UV radiation on periphyton, i.e. algae found attached to many types of substrate, is rather scarce (Santas 1989; Schreiber and Pennock 1995; Santas et al. 1996). Periphytic communities are ecologically and economically important due to their high productivity and their diversified flora and fauna. The present study investigates the combined role of solar UV radiation and depth during the process of ecological succession and establishment of Mediterranean diatom assemblages.

The experiment was conducted at a distance of 50 m from an east-facing rocky shore of Saronikos Gulf, near Korinthos, Greece (37°58′N, 23°0′E). Nine treatment combinations (3 UV regimes × 3 depths) were performed as shown in Table 1. The filters used were UV-transmitting plexiglass (Plexiglas GS 2458) with plastic foil cutoff filters (295 Ultraphan; PR Montagefolie 320 nm Art. Nr. 10155 099; and 395 Ultraphan UV Opak; thickness, 0.3 mm). Each experimental unit consisted of eight 10 × 10-cm ceramic tiles placed on a polypropylene screen fixed onto a 0.75-inch, 45 × 90-cm PVC frame.

Two replicates for each of the nine treatment combinations were suspended from PVC rafts anchored at one end only to allow free swinging of the apparatus with the current. Attenuation of the photosynthetically active radiation (PAR: 400–700 nm), UVA (320–395 nm), and UVB (290–320 nm) bands in the water column was measured with an Optronic 752 double monochromator spectroradiometer. Average daily doses were obtained using three sharp band sensors (Gröbel, Ettlingen) for PAR, UVA, and UVB calibrated against the Optronic spectroradiometer. The signals from the sensors were amplified, digitized, and stored in a dedicated computer (Visual Basic program Windose written by Michael Lebert, Univ. of Erlangen, Germany).

Table 1. Mesocosm experimental design ($n = 2$).

Depth	Cutoff filter		
	290 nm	320 nm	390 nm
0.5 m	PAR + UVA + UVB at 0.5 m	PAR + UVA at 0.5 m	PAR at 0.5 m
1.0 m	PAR + UVA + UVB at 1.0 m	PAR + UVA at 1.0 m	PAR at 1.0 m
1.5 m	PAR + UVA + UVB at 1.5 m	PAR + UVA at 1.5 m	PAR at 1.5 m

To prevent alteration of the transmittance properties due to overgrowth, the filters were cleaned regularly every 2–3 d. The filters were preburnt by a 15-d exposure to full sunlight before the experiments. Spectral transmission of the filters remained stable throughout the 2-month duration of the study.

The developing communities were sampled three times by removing one tile from each experimental unit during the period of 1 September–13 October 1994. The samples were processed for community analysis of the diatom assemblage using mild acid digestion of the cell contents (Hasle and Fryxel 1970). After enumeration of the diatom valves, results were expressed as percentages and analyzed by clustering and MDS ordination (Primer software; Plymouth Ma-

rine Laboratory). This ordination technique has been widely applied in ecology during the last 15 yr (Field et al. 1982). Using the sample similarity matrix resulting from clustering (based for example on the Bray–Curtis similarity index), the method determines the dimensional map of points best representing these similarities as follows. The final number of dimensions is predefined by the user to be usually two or three. A dimensional map is initially drawn at random. Regression is then performed among the ranked distances of points given by the similarity matrix. The regression's goodness-of-fit is measured by the stress value, calculated by the formula

$$\text{Stress} = \Sigma_j \Sigma_k (d_{jk} - \bar{d}_{jk})^2 / \Sigma_j \Sigma_k d_{jk}^2,$$

Table 2. Common and dominant diatom species and species responsible for temporal differences (succession column), differences between light (radiation band column), and depth (depth column) treatments.

Common	Dominant	Succession	Radiation band	Depth
Achnanthes brevipes	*Cocconeis placentula*	*Mastogloia badjikiana**	*Amphora delicatissima*‡	*Amphora robusta*¶
Amphora coffeaeformis	*Mastogloia badjikiana*	*M. labuensis**	*A. veneta*‡	*Cocconeis fluminensis*¶
A. inariensis	*M. decussata*	*Nitzschia lanceolata*†	*Cocconeis diminuta*§	*Mastogloia erythraea*¶
A. ostrearia	*M. labuensis*	*Synedra lanceolata*†	*Mastogloia cruciculal*‖	*M. ovalis*¶
A. ovalis	*M. lanceolata*		*Nitzschia constricta*‖	*Nitzschia bilobata*#
A. robusta	*M. smithi*		*Opephora olsenii*‡	
A. ventricosa	*Nitzschia constricta*		*Synedra baccilaris*‡	
Bacillaria paxilifer	*Rhopalodia constricta*		*S. robusta*‡	
Cocconeis scutellum	*Synedra bacillaris*			
Mastogloia corsicana				
M. decipiens				
M. elliptica				
M. erythraea				
M. paradoxa				
M. pisciculus				
M. pussila				
M. punctifera				
Navicula carinifera				
Nitzschia dissipata				
N. panduriformis				
N. peridistincta				
O. olsenii				
Rhaphoneis amphiceros				
R. surirella				
Rhopalodia acuminata				
R. gibberula				
S. ovata				

* Present in weeks 1–6 of development.
† Present only after 6 weeks of growth.
‡ Present only under PAR + UVA.
§ Present only under PAR + UVA + UVB.
‖ Present only under PAR.
¶ Absent 0.5 m.
# Present only in 1.0 m.

Fig. 1. Clustering of diatom assemblages. Primary succession stages are very clearly reflected in the formation of three distinct assemblage clusters corresponding to the three sampling dates: 15 September 1994 (1); 29 September 1994 (2); 13 October 1994 (3). There is a great similarity between replicate assemblages on the first two sampling dates. Key: A, PAR + UVA; B, PAR + UVA + UVB; R, PAR; S, 0.5 m; M, 1.0 m; D, 1.5 m; AM, AM'; replicates.

where $\bar{d}_{jk}$ is the distance between sample points j and k that 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. The position of the points on the map is altered by the program and the value of stress is calculated again. This procedure is repeated for as many times as necessary until stress reaches its minimum value.

Daily surface irradiance averages were 10,500 kJ m^{-2} (PAR), 750 kJ m^{-2} (UVA), and 14 kJ m^{-2} (UVB). Irradiance levels for the three bands at 1.5 m were 33.5% lower than immediately below surface for PAR, 13.8% for UVA, and 6.7% for UVB. A major part of the visible light attenuation was accounted for by the reduced penetration of the long wavelengths (irradiance at 1.5 m was 42% lower than immediately below surface between 600 and 700 nm).

A few days after the placement of the experimental apparatus in the water, a thin layer of debris and bacteria started to develop over the ceramic tiles. One week later, the appearance of a golden-brown color in that layer marked the establishment of pennate diatom species, the early photosynthetic colonizers of newly available substrate in aquatic environments. The occurrence of nonpennate forms was scarce and most likely due to adventitious sedimentation of phytoplankton on the tiles. Pennate diatoms (Table 2) constituted the main taxonomic component of the developing periphytic communities throughout the end of this study. A total of 159 diatom taxa were recorded

during the course of the experiment under the nine treatment combinations.

Primary succession stages are reflected in the formation of three distinct assemblage clusters corresponding to the three sampling dates (Figs. 1, 2). The separation of the UV (PAR + UVA + UVB) treatment (Fig. 3a, b) suggests that solar UVB has a discernible effect on community structure during the early stages of primary succession (Fig. 3a, b). A close relationship of the replicate assemblage pairs of all treatment combinations was observed. The separation of the different communities became less clear as succession progressed (Fig. 3c).

The separation of the assemblages into three depth groups was quite clear on the first sampling date (Fig. 4a) but does not persist at later stages of community development (Fig. 4b, c).

Similarity percentage analysis indicated that structural differences were primarily due to differences in the abundance of dominant and common diatoms (Table 2, first two columns). The remaining taxa groups include diatom species (Table 2, last 3 columns) accounting for the structural differences observed (1) during different succession stages, (2) between light treatments, and (3) with depth treatments.

There are many studies on the solar UV radiation effects on isolated marine photosynthetic organisms (Archer 1995; Hansson 1995; Schreiber and Pennock 1995, Stewart 1995; Tamigneaux et al. 1995). Focusing on individual organisms, however, is a rather simplistic approach for explaining phenomena at the ecosystem level. The under-
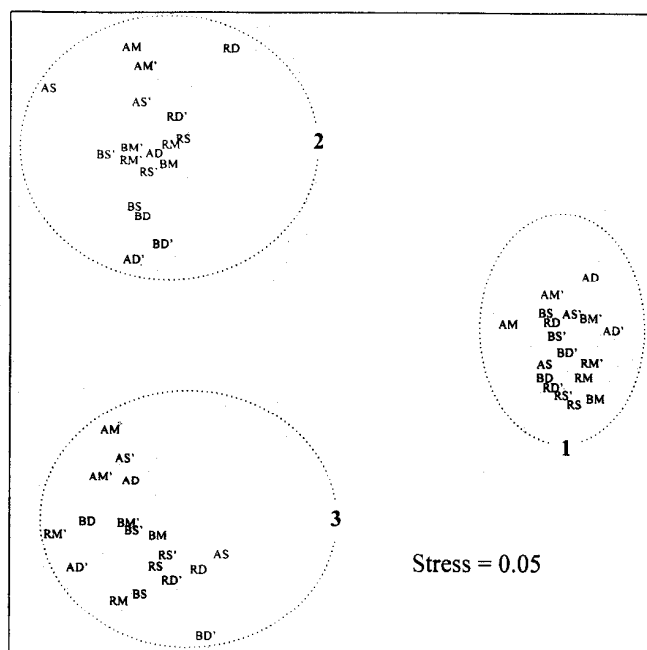
Fig. 2. MDS ordination of diatom assemblages. The separation of the three succession stages is particularly clear (groups 1, 2, 3). For key, see legend to Fig. 1.

standing of large-scale UV effects involves long-term field investigations examining the interaction of more than one environmental factor on biological systems. Recently, due to the greenhouse effect emergency, a few attempts have been made to study the interaction of UV radiation with CO_2 (Bowes 1993; Melillo et al. 1993; Yakimchuk and Hoddinot 1994).

The waters at the test site were quite clear. The attenuation of UVB (6% between 0 and 1.5 m) was lower than UVA and PAR (13.8 and 33.5%, respectively). In the east Mediterranean, Jerlov (1970) found a reduction of 14% per meter depth for UVB penetration, measured as radiation at 310 nm, while for UVA (at 375 nm) the corresponding value is 5%. The same author classified these waters among the ones of the earth's clearest, rivaling the clarity of the Sargasso Sea (type I). The difference in measurements is attributed to two reasons: (1) in the present study irradiance was measured for the full range of the three light bands, whereas Jerlov measured attenuation at a single wavelength for each band; and (2) local differences in the optical properties of waters within the eastern Mediterranean area.

In one of the early laboratory studies exposure to enhanced simulated solar UV radiation resulted in decreasing the diversity of a marine community (Worrest et al. 1981b).
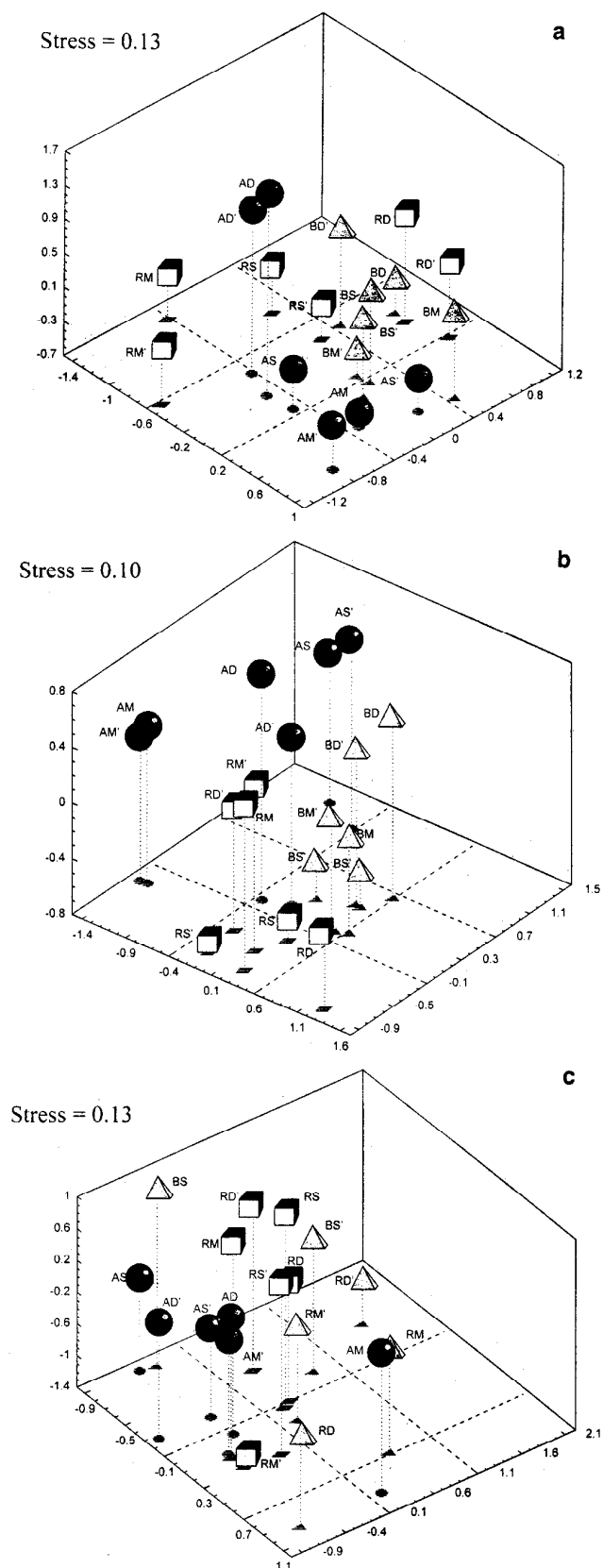
Fig. 3. Clustering by UV treatment. Cubes, PAR; spheres, PAR + UVA; pyramids, PAR + UVA + UVB. The effect of UVA and UVB (c) on community structure is more pronounced during the early stages of primary succession (a, b). For key, see legend to Fig. 1.

Notes
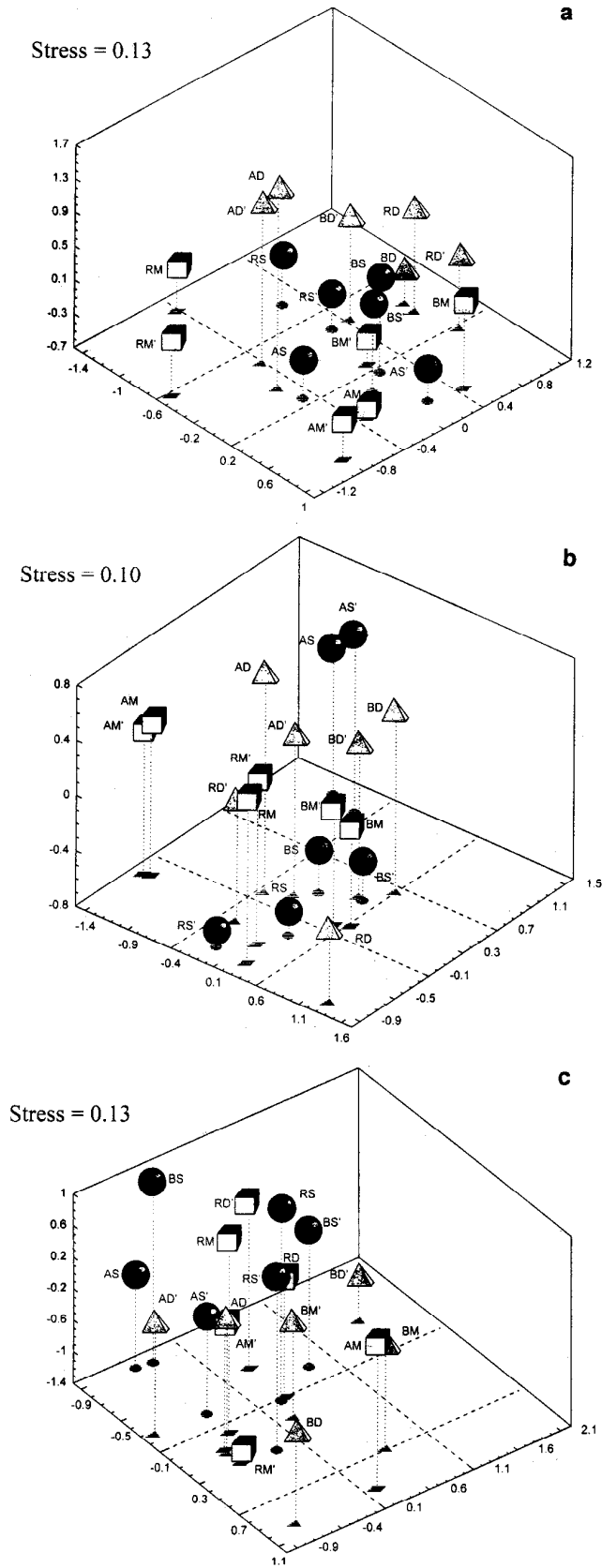
Shifts in the species composition of laboratory-grown assemblages suggest a significant impact of UV radiation on the succession and trophodynamics of natural communities (Worrest et al. 1981*a*).

Similarity percentage analysis indicated that the temporal differences in community structure are mainly due to the changing abundance of *Mastogloia badjikiana*, *Mastogloia labuensis*, *Nitzschia lanceolata*, and *Synedra laevigata*. The former two of these species appear during the early stages of community development, while the latter two appear only after 6 weeks of community development. These species are cosmopolitan, most frequently encountered in temperate and tropical marine and brackish waters. The fact that the differences observed were primarily due to differences in the abundance of dominant and common diatoms suggests that in assessing solar UV effects, community structure is a safer criterion to use than isolated indicator species.

Species contributing to the dissimilarity among the different UV radiation treatments are *Amphora delicatissima*, *Amphora veneta*, *Cocconeis diminuta*, *Mastogloia crucicula*, *Nitzschia constricta*, *Nitzschia longissima*, *Nitzschia marginulata*, *Nitzschia punctata*, *Opephora olsenii*, *Rhopalodia brebissonii*, *Surirella striatulla*, *Synedra baccilaris*, and *Synedra robusta*. One of these species, *C. diminuta*, is present only under PAR + UVA + UVB radiation, while *M. crucicula* and *N. constricta* appear only under the PAR treatment. *A. delicatissima*, *A. veneta*, *O. olsenii*, *S. baccilaris*, and *S. robusta* were present only under PAR + UVA. Most of these species are widely distributed in warmer oceans (polyhalobiotic), while some are found in brackish and marine waters.

A third distinct group of species contributed to the dissimilarity of the different depth assemblages. This group consisted of the species *Amphora robusta*, *Cocconeis fluminensis*, *Mastogloia erythraea*, *M. ovalis*, *Nitzschia bilobata*. More specifically *A. robusta*, *C. fluminensis*, *M. erythraea*, and *M. ovalis* are present at 1.0 and 1.5 m but not at 0.5 m. The dissimilarity between 1.0 and 1.5 m is mainly attributed to the absence of *N. bilobata* from 1.5 m.

The weakening of structural differences at later successional stages is explained partly by the inherent capacity of periphytic communities to adapt to increased solar UVB irradiance and partly by the masking interaction effects of depth and primary succession. Bothwell et al. (1994) have pointed out the interaction of grazing with solar UV on diatom productivity. Other factors such as nutrient availability, wave action, and temperature may have similar effects on community structure and productivity. In conclusion, we think that predictions of community responses to elevated UVB cannot be made with-

Fig. 4. Clustering by depth. Spheres, 0.5 m; cubes, 1.0 m; pyramids, 1.5 m. The separation of the assemblages into three depth groups is quite clear on the first sampling date (a) but does not persist persist at later stages of community development (b, c). For key, see legend to Fig. 1.

out taking into account its long-term interaction with other environmental factors.

Regas Santas
Charalambia Lianou

OikoTechnics Institute
Kefallenias 50
GR-16342, A. Helioupolis, Greece

Daniel Danielidis

Department of Biology
University of Athens
Greece

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