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ORIGINAL ARTICLE

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The effects of ultraviolet radiation on the planktonic community of a shallow, eutrophic estuary: results of mesocosm experiments

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Abstract This paper describes the results of pelagic mesocosm experiments designed to test the effects of enhanced and reduced ultraviolet radiation (UV) on the planktonic community of a Baltic Sea estuary. The Darss-Zingst estuary consists of a series of brackish lagoons with high concentrations of chlorophyll and dissolved organic matter. The shallow depth of the estuary ensures that organisms in the water are regularly exposed to high levels of photosynthetically active radiation (PAR) and UV. During the summer of 1995 and 1996, four 1-m^3 mesocosms were filled with water from the mid-point of the estuary. Each compartment was equipped with a pump to simulate natural rates of wind-induced vertical mixing. The mesocosms were hung in the estuary from a floating raft and were shielded from above by filters to give the spectral treatments PAR only, PAR+UV-A, and PAR+UV-A+UV-B. Enhanced levels of UV-B, i.e. twice that of midday sunlight, were provided in a further treatment by artificial sunlamps. Experiments were conducted for periods of 3–14 days. No significant effects of enhanced or reduced UV-B were observed on chlorophyll a concentrations or photosynthetic performance, although the PAR-only treatment did show higher final chlorophyll concentrations in two of the trials. Phytoplankton pigment composition was measured by in vivo absorption and fluorescence excitation spectra, and was similar in all mesocosm treatments indicating that there were no major differences in functional group composition. Bacterial secondary production rates as measured by thymidine incorporation increased with time in all mesocosms, probably due to enhanced production of phytoplankton exudate. There was evidence for a small depression of secondary production by enhanced UV-B, but only on certain days. Microzooplankton generally increased in all mesocosms to population densities higher than those observed in the estuary, and tended to reach higher final values in the mesocosms exposed to UV. It is concluded that vertical mixing which reduces the residence time of planktonic organisms in the surface layers, and high concentrations of chromophoric, dissolved organic matter, which greatly reduce the penetration of UV-B, combined to protect the planktonic community from UV-B damage.

Keywords Ultraviolet radiation · Phytoplankton · Zooplankton · Bacteria · Mesocosm

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Introduction

The concentration of ozone in the stratosphere is expected to decrease throughout the first part of the new millennium, allowing greater quantities of ultraviolet-B radiation (UV-B; 280–320 nm) to reach the surface of the earth. A wealth of scientific evidence now shows that aquatic processes can be impacted by both UV-B and UV-A radiation (320–400 nm) in many different ways, with examples ranging from photolysis of refractory dissolved organic material, to DNA damage of zooplankton and fish eggs at the higher trophic levels [see Vincent and Roy (1993), Williamson (1995), Franklin and Forster (1997) for overviews of the subject]. Despite the rapid increase in research into the effects of UV-B, it is still difficult to predict the types and extent of ecosystem changes to be expected as aquatic ecosystems become exposed to more short-wavelength solar radiation in the future. Many UV-B experiments to date have been performed under laboratory conditions, using artificial irradiances, and using cultured organisms with no prior history of UV-B exposure. Tolerances of natural populations acclimated to solar exposure may be considerably

higher. The co-occurrence of other stressors such as nutrient limitation, extremes of temperature, supersaturating oxygen concentrations or high pH values will modify the response of natural phytoplankton assemblages to increased UV-B. Also, the complexity of potential interactions and feedbacks between phytoplankton and zooplankton as well as with bacteria and other components of the microbial food web make even more difficult the assessment of ecosystem responses to increased UV-B.

Manipulating the natural solar radiation incident on a system containing all relevant trophic levels, over several generation times, can solve some of these problems. Experimental enclosures, or mesocosms, containing several trophic levels can be used for this purpose. Mesocosm experiments must be run long enough for interactions between the different ecosystem components to develop (Oviatt 1993). In order to draw meaningful conclusions, it is essential to simulate natural conditions as closely as possible within the mesocosm. Replication of natural radiation field is therefore of great importance when examining the effects of UV and high levels of photosynthetically active radiation (PAR; 400–700 nm). Relatively small mesocosms can be suitable for examining photobiological processes in eutrophic and hypertrophic shallow lakes or lagoons. In such water bodies the attenuation of both UV and PAR is strong due to high concentrations of both dissolved and suspended particulate matter, and the whole photic zone may be compressed into a depth of <1 m. In such cases the natural light gradient can be simulated quite well in an enclosure (Rijkboer et al. 1993).

The usefulness of mesocosms or other forms of manipulated natural systems for testing the complex effects of UV on marine and freshwater communities has been recognised in recent years (Demers et al. 1998), and the use of such methods is becoming more common. Bothwell et al. (1994) used cut-off filters to screen areas of river bed from solar UV – the result was a dramatic change in the composition of the benthic flora and fauna. A reduction in primary production was observed when benthic diatom mats were exposed to natural UV-B plus additional UV-B from artificial fluorescent lamps (Sundbäck et al. 1997). Decreased algal production was also observed in UV-B-exposed pelagic mesocosms, but effects were not detected on higher trophic levels (Keller et al. 1997).

This work describes the use of mesocosms in two sets of experiments in 1995 and 1996 to investigate the effects of reducing or enhancing the UV incident on the water column of a shallow, tideless estuary. The Darss-Zingst estuary is typical of the many hypertrophic coastal lagoons or “boddens” which occur along the southern shoreline of the Baltic Sea. It receives large inputs of inorganic nutrients from its catchment area. In winter, when biological activity is low the concentrations of nitrate frequently exceed 200 µg l^{-1}. This excess of nutrients fuels a large spring phytoplankton bloom and by summer, when the experiments described here took place, a large phytoplankton biomass is established and the external concentrations of nutrients are greatly reduced. Algal growth during this phase is largely dependent on recycled rather than external sources of macronutrients.

The shallow average depth of 2 m, and presence of turbulent mixing, ensures that planktonic organisms are regularly exposed to surface sunlight, and are therefore at risk from enhanced UV-B. Small mesocosms (~1 m^3) have already been used successfully to investigate pool sizes and flow of carbon through the estuarine food web, and to test the effects of nutrient additions on the pelagic communities (Schiewer et al. 1997).

The aim of the first set of experiments was to artificially increase the UV-B stress on the pelagic system by a factor of two. This was a common goal of all partners participating in the UV-MAOR (UV radiation effects on MArine ORganisms) project. The second set of experiments compared the responses of UV-screened mesocosms to ones exposed to the full solar spectrum.

Materials and methods

Design and construction of mesocosms

The mesocosms used in these experiments were designed to simulate the physical conditions in the water column of a shallow, turbid, hypertrophic estuary such as the Darss-Zingst bodden chain, and their construction is described in detail in Schiewer (1997). Large fibre-reinforced polyethylene bags with a volume of 1 m^3 and a depth of 1 m were hung from a supporting metal framework (Fig. 1). The whole apparatus was positioned directly in the estuary, next to a small jetty belonging to the field station of the Uni-

Fig. 1 Situation of 1,000-l experimental mesocosms in the Darss-Zingst estuary at the harbour of Zingst during June 1996. The Plexiglas lid of one compartment has been lifted to allow the investigator to measure the dissolved oxygen concentration in the water column

versity of Rostock at Zingst. Plastic drums (50 l) attached to the corners of the framework were used for flotation. The bags were filled with water collected directly from the estuary. As the aims of the mesocosm experiments were primarily to examine phytoplankton responses to UV, the water was filtered during filling through 100-µm gauze to remove the larger grazers. Approximately 4 h was required to fill all four compartments. The open waters of the Darss-Zingst estuary are subject to almost continuous wind-induced vertical mixing (Schubert et al. 2001 this issue), therefore mixing was simulated in the mesocosms by submerging small centrifugal water pumps at the bottom of the compartments. The pumps drew in water from the bottom, and directed it upward to the surface, thus ensuring a continuous circulation with a turnover time of approximately 2 h.

The mesocosms were subject to four different spectral treatments, without replication, in 1995. A hinged lid for each mesocosm was formed by a 1.2-m^2 sheet of 3-mm UV-transparent GS 2458 Plexiglas (Röhm, Darmstadt, Germany), which ensured that differences due to reflective loss of solar irradiation were similar for all treatments. The four different spectral treatments then consisted of: PAR (no wavelengths <390 nm; Ultraphan 390 foil), PAR+UV-A (>320 nm; Mylar foil), unfiltered solar, e.g. PAR+UV-A+UV-B, and solar plus enhanced UV-B. The Ultraphan and Mylar filters were taped on to the Plexiglas lids. The UV-B enhancement was provided by two preburned (1500 h) Q-Panel 313 fluorescent lamps suspended under the Plexiglas lid, 0.3 m above the water surface. The tubes were filtered with cellulose acetate to remove wavelengths <290 nm. All filter materials were replaced at intervals of 2–3 days. Replication of the experiments in 1995 was achieved by running the set of four treatments 3 times within the time period 12 June–4 July. The individual experiments ran for 8 days [experiment (Expt) I], 3 days (Expt II) and 6 days (Expt III). The weather was mainly cloudy during Expts I and II, but clear sky conditions were present throughout Expt III. Expt II was prematurely ended due to damage by a storm.

The results of the 1995 experiments, namely that greatly enhanced UV-B had no obvious effect on phytoplankton biomass, but that mixing was perhaps important, determined the design of the experiments in the following year. Only two spectral treatments were used (PAR and PAR+UV-A+UV-B), and each treatment was mixed either constantly with a submerged pump, or intermittently by means of a paddle. The 1996 experiments were run for a longer time period of 14 days (starting 14 June 1996). An additional experiment in 1996 was also performed with 200-l land-based mesocosms which were shaded to 20% of the incident PAR, in order to test the effect of reduced irradiance supply on pigmentation and photosynthetic performance.

Measurement of irradiance

Spectral irradiance measurements were made with a SR-9910 double-monochromator spectroradiometer (Macam Photometrics, Livingston, Scotland). A flat, cosine-corrected light collector connected by a quartz fibre-optic cable to the spectroradiometer was used to take measurements of irradiance at the surface of the mesocosms. These scans were done under the different spectral filters, to allow for reflective losses from the different materials and to account for shading by lamps and the sides of the mesocosm. Underwater measurements of scalar irradiance at different depths within the mesocosms were made with a small, spherical light collector also connected to a quartz cable. The spectral and spatial distribution, and calculated biologically effective irradiances at the surface of the four mesocosms are described in detail by Forster and Schubert (in press). Underwater measurements, from which spectral attenuation coefficients [$K_{(\lambda)}$] were calculated, were performed every day, in each mesocosm, close to solar noon.

Non-spectral continuous recordings of surface irradiance during the period of the experiments were done by means of a global radiation meter located on the roof of the field station, approximately 75 m from the experimental site. Global radiation (300–3000 nm) was converted to PAR (400–700 nm) after direct comparison with a PAR meter (Li-192; Li-Cor, USA).

One of the main aims of the mesocosm experiments in 1995 was to expose the planktonic community to doubled levels of unweighted surface UV-B. This was a difficult challenge, as the radiative flux at the surface is constantly changing due to changes in solar elevation and to weather systems moving across the region. A maximum integrated (280–320 nm) solar UV-B value of 2.3 W m^{-2} was measured under clear sky conditions at Zingst, in June 1994. By adjustment of the height of the fluorescent UV lamps suspended above the surface of the mesocosm, it was possible to irradiate with an additional mean UV-B of 2.4 W m^{-2}, which meets the requirement for a doubling of the natural midday fluence rate. However, the instantaneous enhancement of UV-B would have been much greater than planned under cloudy conditions, therefore the irradiance time on cloudy days was reduced accordingly by shortening the length of time that the lamps were on. The maximum length of time that the lamps were on was for 6 h, during a completely cloudless day in Expt III of 1995. This gave an extra daily unweighted UV-B dose of 48 kJ m^{-2}, compared to the natural daily UV-B dose of 60 kJ m^{-2} under clear-sky summer conditions. The lowest daily enhancement given was 17 kJ m^{-2} (lamps on for 2 h) during an overcast day in Expt I. However, fluence rates weighted by a biological weighting function such as that for DNA damage (Setlow 1974) were increased by a factor much greater than two at the water surface, due to the presence of shorter UV-B wavelengths in the artificial lamp spectrum (Forster and Schubert in press).

Physical and chemical parameters in the water column

Temperature and dissolved oxygen concentration of the water in the mesocosms were measured 3 times day^{-1} (0900, 1300, 1700 hours) throughout the course of the experiments. On chosen days, the measurement frequency was increased to every 2 h in order to improve the resolution of the diurnal changes. The oxygen concentration near the surface of the mesocosms was measured with a Clarke-type electrode connected to a portable oxygen meter (WTW, Germany), after first thoroughly mixing the water column. Water samples were also collected and brought immediately (<10 min) to the laboratory for measurement with a pH meter (WTW). Samples for nutrient analyses were filtered through Whatman GFF filters and either measured immediately or frozen at –20°C. Concentrations of dissolved nitrate, nitrite, ammonium and phosphate were determined spectrophotometrically using an autoanalyser.

Biological parameters

Samples were collected 3 times day^{-1} from all four mesocosms, and from the estuarine water next to the mesocosms, with a 1-l plastic container. The sample was stored in dim light in the field station, and sub-samples were immediately taken for the following analysis. Optical methods, rather than traditional methods of counting cells, were used to enable us to follow broader changes in the community structure at a high temporal resolution.

In vivo absorption (300–800 nm) was measured in a 1-cm quartz cuvette placed at the entrance to the integrating sphere attachment of a dual-beam spectrophotometer (Lambda II; Perkin-Elmers, USA). With this method, and with optically-thin suspensions, much of the forward-scattered light is captured by the detector and losses due to scattering are minimal. The measurements approximate the true absorption of the suspension, and gives information on the abundance of pigments within the sample. The ratios of absorption peaks in areas of strongest pigment absorption were compared, e.g. 620 nm for the cyanobacterial pigment phycocyanin and 675 nm for chlorophyll a. The sample was then filtered through a GF-92 filter (Schleicher and Schüll), and the filter extracted overnight at 4°C in the solvent *n,n*-dimethylformamide. The optical density of the extract was measured in a spectrophotometer, and the equations of Porra et al. (1989) were used to estimate the concentrations of chlorophyll a and b. Chlorophyll c-containing species are present at low concentrations is the Darss-

Zingst estuary in summer, and the contribution of this pigment was ignored.

The GF-92 filtrate was collected and its absorption was also measured in a 1-cm quartz cuvette, relative to a distilled water blank. Absorption of the filtrate in the UV region gives a good estimate of the concentration of chromophoric, dissolved organic materials (cDOM) in the water (Morris et al. 1995). These compounds are a major contributor to UV attenuation in coastal and estuarine areas.

Further information on photosynthetically active pigments, and hence the abundance of different algal groups, was derived from measurements of the fluorescence excitation spectra for photosystem (PS) II. This measurement was made on unconcentrated natural samples, at room temperature, in the presence of the PS II inhibitor 3-(3,4-dichlorophenyl)-1,1-dimethylurea to ensure that the fluorescence yield was maximal and constant throughout the scan. Samples were scanned from 350 to 650 nm in 1-cm cuvettes in a Hitachi F-3000 spectrofluorimeter. The emission wavelength was set to the in vivo PS II maximum of 685 nm. The advantage of fluorescence excitation spectra measurements over absorption measurements is that only the pigments active in transfer of energy to PS II are visualised (Neori et al. 1988). Scans of a GF-92 filtrate showed that interference by non-photosynthetic components such as cDOM was minimal at this emission wavelength.

Pulse-amplitude-modulated chlorophyll fluorescence was used to estimate the photosynthetic activity of samples from the mesocosms. In 1995, 25 ml of sample was taken out of the mesocosm and dark incubated for 10 min before being filtered onto a GF-92 filter for measurement. Concentration on a filter was necessary to increase the signal:noise ratio to acceptable levels. The ratio of variable-to-maximum fluorescence (F_v/F_m), was then measured with a PAM-101 modulated chlorophyll fluorometer (Walz, Effeltrich, Germany). A weak, pulsed red LED was used as measuring light, and a Schott KL-1500 to provide a pulse of saturating light in order to measure the dark-adapted F_v/F_m. This parameter gives an estimate of the maximum photochemical efficiency of PS II reaction centres, and is sensitive to a variety of environmental stressors. Reductions in F_v/F_m are caused, for example, by nutrient limitation (Berges et al. 1996) or by exposure to short-wavelength UV (Forster et al. 1997). Samples for fluorescence measurements during the 1996 campaign were concentrated by centrifugation at 3,000 rpm for 10 min, which was sufficient to pellet approximately 90% of the total chlorophyll in the sample. The algal pellet was resuspended in approximately 10% of its original volume, and placed in a 3-ml cuvette, located directly at the end of the PAM fibre-optic. Measurement of F_v/F_m was made after a total of 15 min dark acclimation.

Bacterial production rates were measured during Expt I and II in 1995 with the method of Fuhrmann and Azam (1982). Samples were removed from the mesocosms at 0900 hours, inoculated with ^{3}H-thymidine and incubated at constant temperature in the laboratory for 1 h. Then, glutaraldehyde was added to stop biological activity, and the samples were later counted in a liquid scintillation counter. Bacterial abundances and biomasses were estimated from epifluorescence microscopy of DAPI-stained samples.

The abundance and biomass of zooplankton was estimated by counting formaldehyde-fixed samples after preconcentration of 1 l of sample on a 55-µm mesh. The conversion factors of Heerkloss et al. (1991) were used to obtain biomasses from microscopic counts.

Results

Environmental conditions during the period preceding the experiments

Experiments took place in June 1995 and June 1996, during a period when relatively stable physical and chemical parameters characterised the water column.

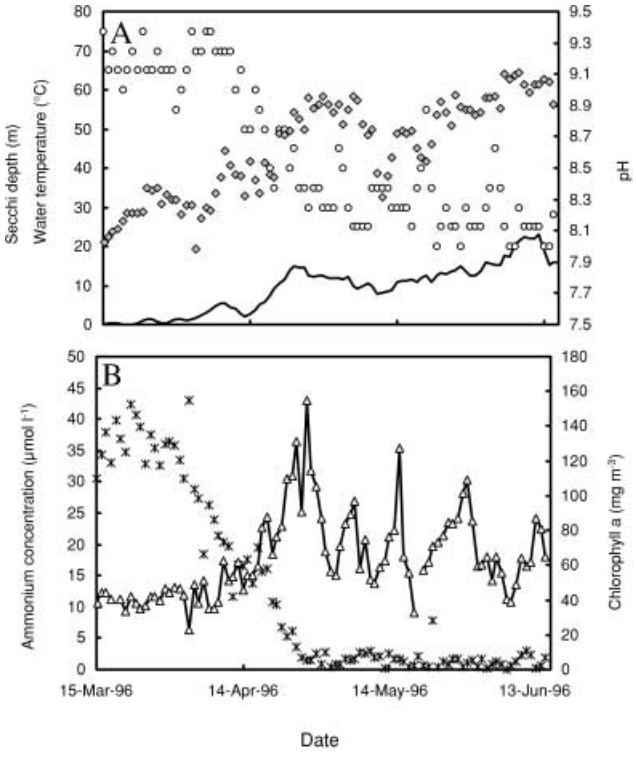

Fig. 2A, B Data describing the physical, chemical and biological state of the Darss Zingst estuary in the 3-month period before the 1996 mesocosm experiments (Expts). **A** shows daily measurements of water temperature (*solid line*), pH (*filled diamonds*) and Secchi depth (*open circles*) taken at the University of Rostock field station at Zingst. **B** shows daily measurements of ammonium concentration in µmol l^{-1} (*stars*) and chlorophyll a concentration (*open triangles*). The onset of higher daily irradiances and warmer temperatures in March triggered the development of a dense phytoplankton bloom which peaked in early May. High phytoplankton densities throughout the late spring and summer period are accompanied by high pH, low nutrient availability and low transparency of the water column

Earlier in both years, increasing water temperatures and daily irradiances in April had triggered the development of dense phytoplankton blooms (Fig. 2a). During April and early May, bloom formation quickly reduced the supply of inorganic nutrients and decreased the transparency of the water column – as shown for ammonium concentrations and Secchi depth, respectively (Fig. 2b). As phytoplankton biomass increased, photosynthetic drawdown of carbon dioxide and bicarbonate causes the pH in the estuary to increase, occasionally to values >9, and supersaturation of the water column with oxygen was regularly observed.

Physical and chemical parameters in the water column

During the mesocosm experiments, concentrations of phosphate ranged between 0 and 2.2 µmol l^{-1} and concentrations of combined nitrate+nitrite+ammonium ranged between 0.32 and 4.1 µmol l^{-1} with the bulk of the values being <2 µmol l^{-1}. Nitrate concentrations were

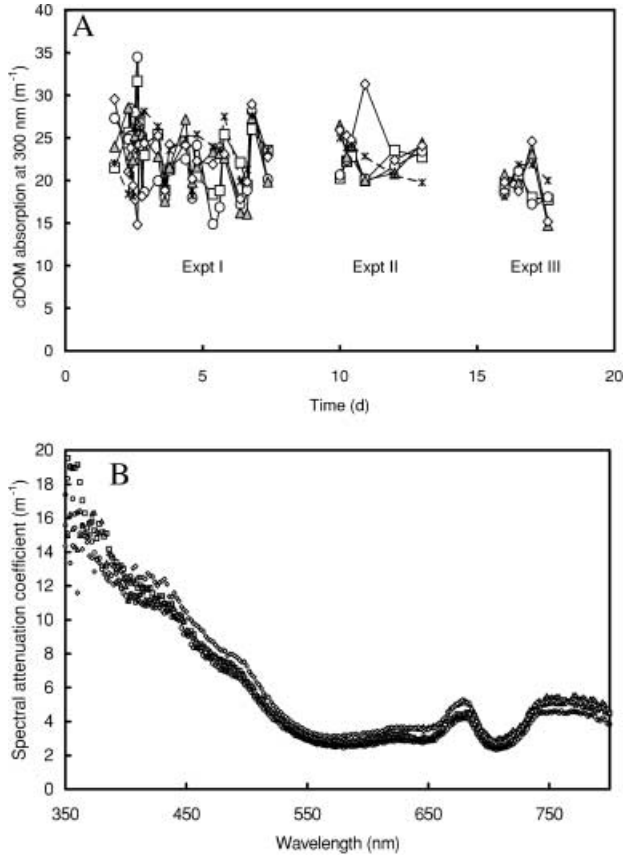

Fig. 3 Optical conditions in the mesocosm compartments during the experiments of 1995. **A** shows the ultraviolet (UV) absorption of a 0.8 µm filtrate at 300 nm. Absorption in this region is due to coloured, dissolved organic materials (*cDOM*). **B** shows the close similarity of spectral attenuation coefficients for scalar irradiance measured directly in the water column of the four mesocosms on 17 June 1995 (day 4 of Expt I). Calculation of attenuation coefficients <350 nm was not possible, as insufficient irradiance at these wavelengths penetrated the water column. Treatments and symbols are photosynthetically active radiation (PAR; *open diamonds*), PAR+UV-A (*open squares*), PAR+UV-A+UV-B (*open circles*), PAR+UV-A+enhanced UV-B (*filled triangles*), estuarine water (*stars*)

reduced to undetectable levels within the first 3 days of Expts I and II, with the reduction of nitrate being followed by a slight increase in nitrite concentration. Nitrate was undetectable throughout the whole of Expt III. Ammonium concentrations followed no clear trends. Water temperature in the mesocosm experiments ranged from 14.4 to 16.9°C during Expt I, 15.3–20.0°C during Expt II, and 18.3–23.1°C in Expt III.

The estuary also receives a large allochtonous input of dissolved organic materials from its catchment area, including many substances which show strong absorption in the near-UV and UV region. Spectrophotometric measurements of filtered samples at 300 nm showed absorption coefficients of 20 m^{-1} or more in all mesocosm compartments throughout the experiments in 1995 (Fig. 3a) and 1996 (data not shown). There was no evidence for differences in the cDOM concentration within the different mesocosm treatments.

The penetration of PAR and UV into the water is controlled primarily by the concentrations of absorbing particles, e.g. phytoplankton, and of cDOM. Underwater light measurements in the mesocosms always showed similar profiles (Fig. 3b), indicating there were no major differences in the particulate or dissolved loading of the water. Attenuation was lowest in the green region of the spectrum, where phytoplankton and cDOM absorption is weak, and was highest in the UV region. UV-B attenuation coefficients could not be directly measured, as the penetration of this waveband in to the water was so weak (no photons <310 nm were present at the first measuring depth of 10 cm). A conservative attenuation estimate of 30 m^{-1} can be obtained by using a spectral slope (S) value of 0.015 to extrapolate Fig. 3b to 320 nm. This would give a 1% depth for this wavelength of 15 cm.

Chlorophyll a concentration

The concentration of chlorophyll a was used as the main indicator of autotrophic biomass in the mesocosms. Chlorophyll concentrations of the estuarine water at the start of the experiments varied between 40 and 80 mg m^{-3}, as water bodies with different degrees of plankton development passed through the narrowest point of the estuary at Zingst. The daily dose of PAR and UV was extremely low on the first day of Expt I in 1995, with continuous heavy rain falling, but light availability then increased towards the end of the experiment as weather conditions improved (Fig. 4a). Changes in the chlorophyll a concentration of all four mesocosms closely tracked changes occurring naturally in the estuary during the first seven days of Expt I (Fig. 4a). Pigment concentrations increased by >100% during the first 3 days, coupled with a complete removal of nitrate, then slowly declined during the remaining 5 days. The estuarine chlorophyll a concentration only deviated from that of the mesocosms at the end of the experiment ($P<0.05$, Tukey test following model 1 ANOVA), probably due to advection of a more eutrophic water mass into the area. As suggested by the underwater light measurements, the values in each of the mesocosms were similar up until the fifth day, despite the large difference in spectral treatments. Lower chlorophyll values were recorded in the enhanced UV-B treatment during day 5, but this difference disappeared during the final 2 days. The PAR treatment showed significantly higher chlorophyll concentrations at the end of the experiment ($P<0.05$, Tukey test following model 1 ANOVA), coincidental with the onset of higher daily photon doses.

Expt II in 1995 was started immediately after the end of Expt I, and ran for 3 days under similar overcast weather conditions (mean daily PAR dose for Expt I was 33 mol photon m^{-2}, for Expt II 37 mol photon m^{-2}). Again, chlorophyll a concentrations were similar throughout the experiment in all four compartments, with final values ranging from 68 to 73 mg chlorophyll a m^{-3}. Expt II was stopped prematurely to allow filters and lamp holders to be repaired.

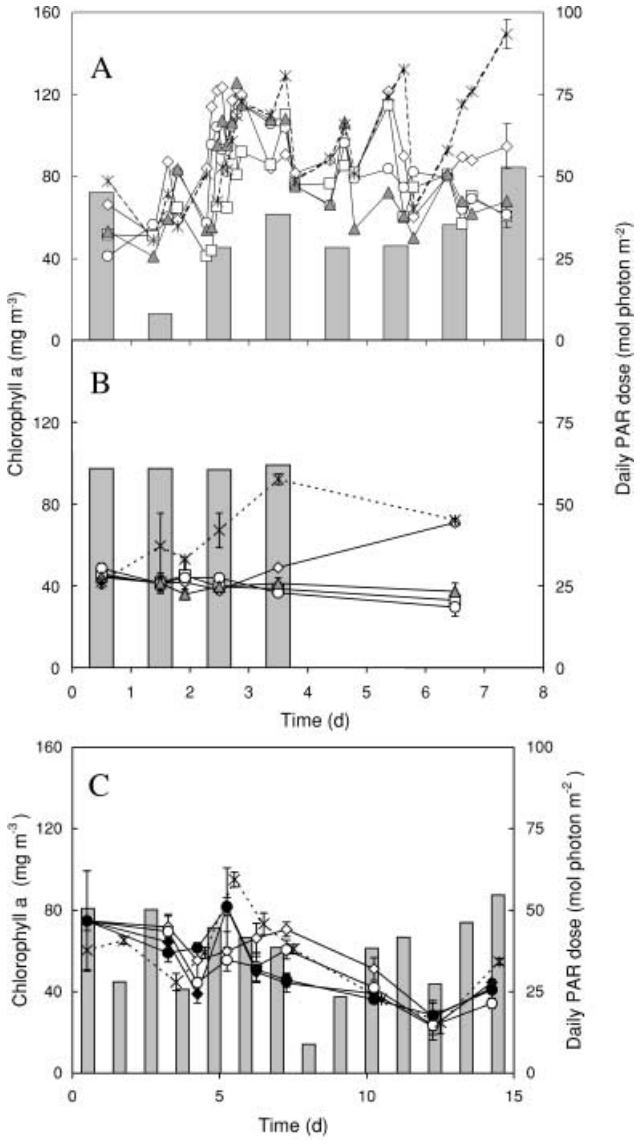

Fig. 4 Changes in chlorophyll a concentration during **A** Expt I of 1995, **B** Expt III of 1995, and **C** 1996. Treatments and symbols for **A** and **B** are PAR (*open diamonds*), PAR+UV-A (*open squares*), PAR+UV-A+UV-B (*open circles*), PAR+UV-A+enhanced UV-B (*filled triangles*), estuarine water (*stars*). *Error bars* indicate SDs based on n=5 for Expt I and n=3 for Expt III. Treatments and symbols for **C** are PAR, continuous mixing (*open diamonds*); PAR+UV-A+UV-B, continuous mixing (*open circles*); PAR, intermittent mixing (*filled diamonds*), PAR+UV-A+UV-B intermittent mixing (*filled circles*); estuarine water (*stars*). *Solid bars* indicate the daily photon dose of PAR (mol m^{-2}) during the experiments

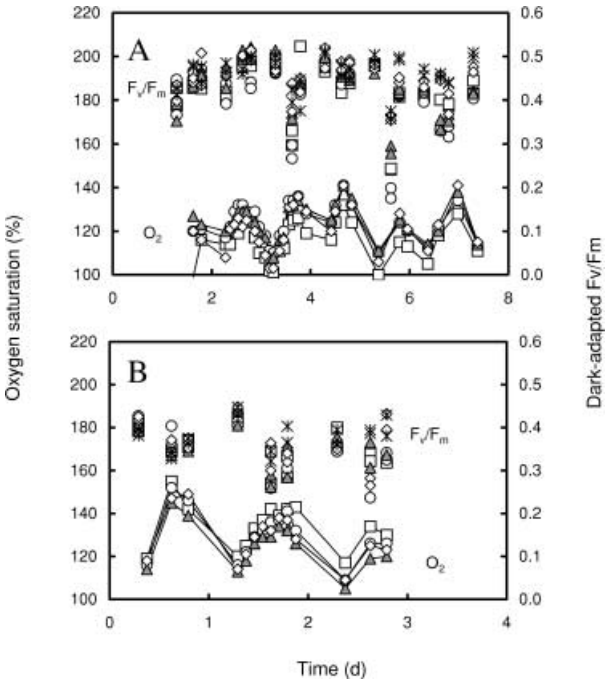

Fig. 5 Diurnal changes in dissolved oxygen concentration and the ratio of variable-to-maximum fluorescence (F_v/F_m) for **A** Expt I of 1995 and **B** Expt III of 1995. Oxygen was measured directly in the water column of the mesocosms and is *plotted with lines connecting the symbols*. F_v/F_m was measured after 10 min of dark adaptation and is plotted as *symbols without lines*. For assignment of symbols to treatments see legend to Fig. 4

A third experiment was started on 26 June 1995 and was run for 6 days. The period of the experiment coincided with the onset of constant, clear weather conditions, and the mean PAR daily doses were higher at 61 mol photon m^{-2} (Fig. 4b). Chlorophyll a concentrations were low at the time of filling and decreased slightly in all four mesocosms during the first 2 days of the experiment (Fig. 4b). Chlorophyll a in the PAR mesocosm was slightly but significantly higher on the third day. In contrast, concentrations of phytoplankton outside the mesocosms increased greatly during Expt III (significant at P<0.05, one-way ANOVA). At this stage it was realised that exposure even to high doses of both natural and artificial UV-B was unlikely to affect the phytoplankton biomass. As a further test, the remainder of Expt III was conducted in the absence of vertical mixing, by switching off the water pumps. After 3 days without mixing, the compartments were thoroughly mixed and final samples were taken. The chlorophyll a concentration had increased in the PAR mesocosm, from 49 mg m^{-3} to 70 mg m^{-3}, but had decreased further to an average of 33 mg m^{-3} in the mesocosms exposed to UV.

Following these results, only two spectral treatments were used in 1996 (PAR and PAR+UV-A+UV-B), and each treatment was mixed either constantly with a submerged pump, or intermittently by means of a paddle. The mesocosms were run for a period of 14 days, during which the daily PAR dose varied from 9 to 55 mol photon m^{-2}. The chlorophyll a concentration at the time of filling the mesocosms was 75 mg m^{-3}. Similar developments were observed throughout the experiment for all four compartments and the natural estuarine water (Fig. 4c). Concentrations decreased in all four treatments during the first 4 days. A maximum was observed in the intermittently paddled mesocosms on the fifth day, followed by a steep drop, and slow decline throughout the rest of the run. The constantly mixed compartments increased slowly during days 4–7, with the PAR-only treat-

ment having a significantly higher concentration by day 7. Thereafter chlorophyll a declined until by day 12 all four treatments had similar concentrations, differing at the end by <10 mg chlorophyll a m^{-3}.

Photosynthesis and respiration

Measurements of the diurnal course of oxygen concentration in the water column (Fig. 1, Fig. 5a, b) provided information on the relative dimensions of photoautotrophic and heterotrophic activity. Continuous measurements of oxygen in the estuary close to Zingst typically show supersaturation of oxygen (>120%) during the spring growth period when nutrients concentrations are high, followed by periods of low oxygen concentration (50–80%) during July and August when phytoplankton blooms crash due to high water temperatures and low nutrient availability. Oxygen concentrations in the mesocosms generally remained >100% saturation during Expt I in 1995 (Fig. 5a). Daytime maxima of 140% were recorded on days 4 and 6, and nocturnal minima of 100% were recorded on the third and fifth nights. The trends in oxygen concentration were similar in all mesocosms except the PAR+UV-A treatment, for which lower values were recorded, but these differences were minor, and were not repeated during Expt II (data not shown). Daily irradiances were higher during the third experiment, and this is reflected in higher oxygen concentrations in all four mesocosms (Fig. 5b). A daytime maximum value during this experiment of 155% was recorded during the first full photoperiod, with maxima of 140% and 135% occurring on the following days. Nocturnal oxygen concentrations remained >100% during this experiment. The diurnal curves were similar for all compartments during the first 2 days of the experiment, but deviated slightly on the last day. Final oxygen values were highest in the PAR+UV-A treatment, and lowest in the enhanced UV-B treatment.

pH measurements also showed a marked diurnal change, with highest values during late afternoon and lowest values at dawn. The maximum pH value during Expt I of 1995 was 9.7 observed during the second day, and the lowest nocturnal value was 9.3 during the first night. The daytime pH fell slowly after day 3 to 9.4 on the last day, indicating an excess of respiratory processes over photosynthesis during this period. In contrast, pH values rose continually during the other two experiments, from 9.4 to 9.7 in Expt II, and from 9.0 to 9.4 in Expt III, indicating a net excess of photosynthesis due to the improved irradiance conditions. Diurnal trends of pH followed very closely the same patterns and range of values in all four experimental treatments.

Recording the ratio of dark-adapted variable-to-maximum fluorescence of PS II enabled us to examine changes related exclusively to the autotrophic community. As with chlorophyll a concentration and oxygen changes, the dynamics in F_v/F_m were very similar for all mesocosms and for freshly collected water from the estuary (Fig. 5a, b). Initial values of F_v/F_m for Expt I were in the range 0.35–0.45, which is low for most phytoplankton species but is typical of situations when cyanobacteria are present as the dominant component of the autotrophic community. The yield increased after 3 days, reaching values of 0.46–0.51, then declined for the remainder of the experiment. Noticeable decreases in the midday F_v/F_m were seen on days 3 and 5, due probably to short exposures of the mesocosms to full sunlight during the period before collection of the samples. There was no evidence for differences in F_v/F_m between the four spectral treatments during Expt I or Expt II. Dark-adapted yields for Expt III were in general lower than those of Expt I or II, with few values >0.4 recorded (Fig. 5b). Due to the absence of clouds, there was a pronounced diurnal course to the yield measurements, with the early morning values and late afternoon values highest and midday values lower and more variable between replicates. Consistent differences between spectral treatments could not be resolved.

Optical properties of the phytoplankton

The phytoplankton of the Darss-Zingst estuary during both 1995 and 1996 was dominated by coccoid cyanobacteria (colonial *Aphanothece* and *Gomphosphaeria*, unicellular *Synechococcus*), and small chlorophytes (chiefly *Scenedesmus*, *Selenastrum* and *Tetrastrum*). Differences in the in vivo absorption spectra between the algae contained in the mesocosms, and the estuarine water outside, became apparent after the first day of incubation. The most prominent difference was a reduction in the area of phycocyanin absorption compared to that of chlorophyll a. This reduction in the 620:680 nm absorption ratio occurred consistently in three of the 1995 mesocosm experiments, but differences between the spectral treatments did not become apparent. The results are shown for the longest of the three experiments (Fig. 6a). In 1996, the phycocyanin:chlorophyll a ratio remained close to 0.3 throughout the 12 days of observation, but differed at all times from that of the estuarine water, which rose from 0.3 at the start to 0.5 after 7 days (Fig. 6b). Again, no consistent differences were caused either by the spectral treatment or the mixing regime.

The analysis of in vivo absorption spectra was most useful in the red region of the spectra, where interference from non-algal absorption was lowest, but the fluorescence excitation spectra gave information on pigment activity throughout the whole of the photosynthetically active range. This enabled comparisons to be made between the contribution of the green algal accessory pigments such as chlorophyll b and carotenoids absorbing at 475 nm, and other pigments such as chlorophyll a and phycocyanin. A plot of the 475:440 nm excitation ratio versus the 620:440 nm ratio revealed slight differences between the mesocosms and the estuarine water column, but no differences within the mesocosm treatments

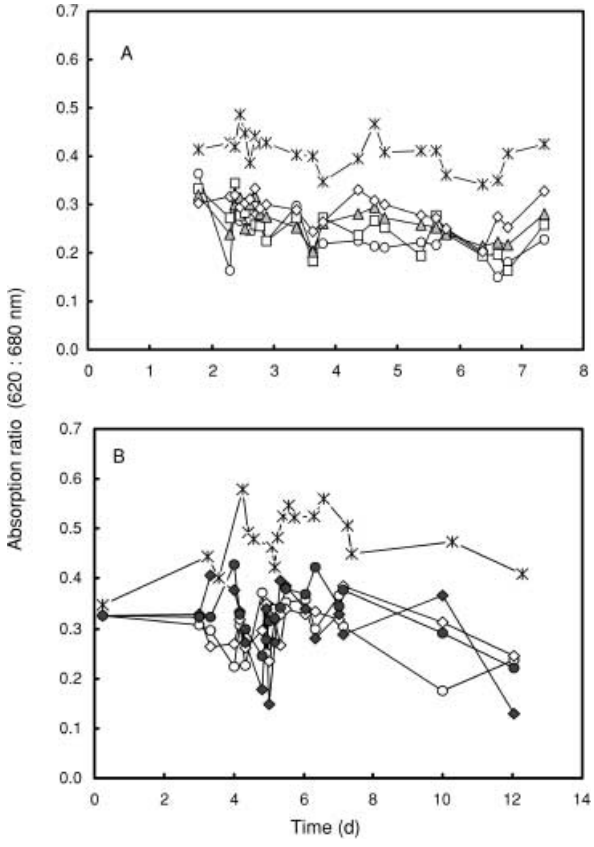

Fig. 6A, B Development of pigmentation differences within the phytoplankton assemblage with time, as shown by the ratio of in vivo absorption at 620 nm to that at 680 nm. Changes in the 620:680 nm ratio are shown for Expt I in 1995 **(A)** and 1996 **(B)**. See legend to Fig. 4 for the symbols and treatments applying to each year

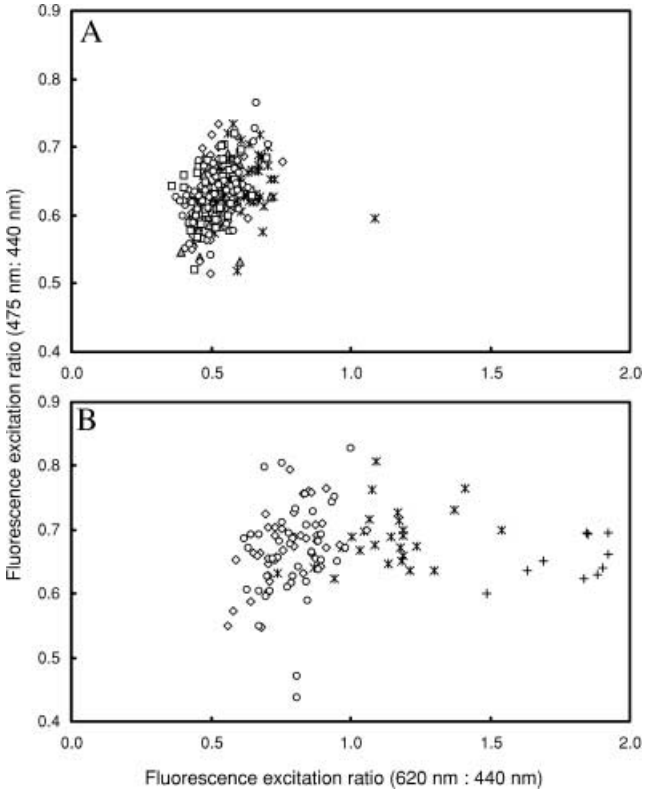

Fig. 7 Differences in fluorescence excitation spectra shown as changes in the ratios of 475:440 nm excitation versus 620:440 nm excitation for pooled data (all days) from the 7 days of Expt I in 1995 **(A)** and 12 days of the experiment in 1996 **(B)**. Treatments and symbols for **A** are as in Fig. 4a, and those for **B** are PAR, continuous mixing (*open diamonds*), PAR+UV-A+UV-B, continuous mixing (*open circles*), estuarine water (*stars*), and shaded land-based mesocosms (*crosses*)

(Fig. 7a). All mesocosm experiments in 1995 showed a tendency towards a lower 620:440 nm ratio, but with little change in the 475:440 nm ratio. This was more pronounced in 1996 (Fig. 7b), where a clear separation of the estuarine water from the mesocosms was observed. In 1996, two land-based mesocosms were additionally shaded to 20% of the incident PAR. Algae in these shaded mesocosms reacted within 2 days by greatly increasing the 620:440 nm ratio, but without a change in the 475:440 nm ratio (Fig. 7b).

Bacterial production

Rates of secondary production, as measured by thymidine incorporation, were low at the beginning of Expt I but increased in all mesocosms as well as in the natural estuarine water as the experiment progressed (Fig. 8). The mean secondary production rate for all compartments of 14.3 µg carbon l^{-1} h^{-1} is within the range 5–35 µg carbon l^{-1} h^{-1} which has been recorded at this location from 1991–1993 (Klinkenberg and Schumann 1995). The uptake rate recorded in the PAR mesocosm after 7 days was 4 times higher than the original

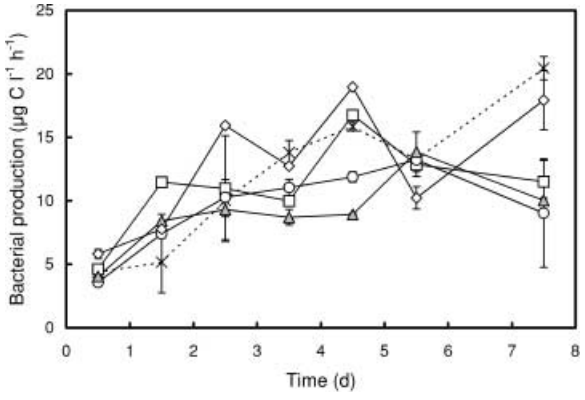

Fig. 8 Bacterial secondary production as measured by the thymidine uptake method during Expt I of 1995. Symbols and treatments are described in the legend of Fig. 4a

rate. Thymidine incorporation was highest in the PAR mesocosm between days 2–4, and on the last day, but was lower than the others on day 5. The enhanced UV-B treatment exhibited the lowest uptake rates on days 2–4, but this difference had disappeared by the end of the experiment. Bacterial production rates in the estuary out-

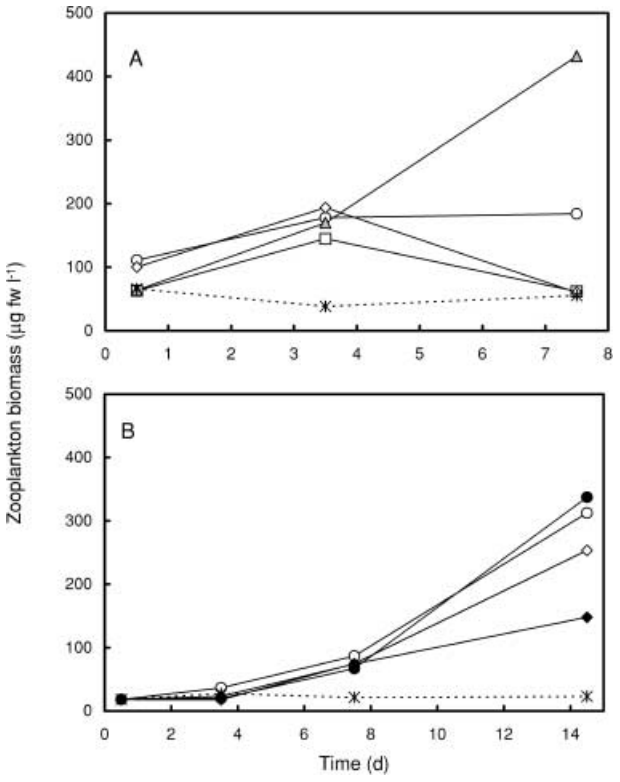

Fig. 9 Changes in the zooplankton biomass during mesocosm Expt I in 1995 **(A)** and in 1996 **(B)**. Biomass was calculated as the sum of copepod and rotifer fresh weights. Symbols and treatments are described in the legend of Fig. 4a

side of the compartments also increased continuously throughout the period of the experiment.

Bacterial cell counts were generally low, with a mean of 2×10^6 cells ml^{-1} and fell outside of the range of values usual for this location ($10–15\times10^6$ cells ml^{-1}). As the bacterial biomass was highest in all compartments at the beginning of the experiment and declined over the course of 7 days, the biomass-specific activity of the bacteria must also have increased as the incubations progressed. Variability in bacterial counts both within a day, and between days, was high, thus no solid conclusions could be drawn about effects of the treatments on bacterial abundance.

The density of adult zooplankton at the start of the experiments was low, as water was filtered during filling of the mesocosms. Populations of copepods and rotifers quickly became re-established and, in the absence of fish predation, final numbers were considerably higher than in the estuary. The dominant rotifer species in 1995 were various *Keratella* species, with minor contributions of *Filinia longis*, whereas in 1996 *Synchaeta tremula* was the first to reappear followed by *Filinia longis*, *Keratella* species and *Brachionus urceolata*. The copepod population was dominated by *Eurytemora affinatus* in various developmental stages.

In the first of the 1995 experiments, zooplankton biomass had approximately doubled by the third day, with only minor differences between treatments (Fig. 9a). After 7 days the biomass was greatest in the enhanced UV-B treatment with 432 µg fresh weight (fw) l^{-1} followed by PAR+UV-A+UV-B with 183 µg fw l^{-1}. Zooplankton densities in the mesocosms screened from UV-B declined between day 3 and day 7 to values of 60 and 61 µg fw l^{-1}, respectively. A similar effect was found in 1996 (Fig. 9b). Again, zooplankton concentrations increased as the experiments progressed and final biomasses were highest in the two mesocosms subject to unfiltered solar radiation.

Discussion

The irradiance regime used in the 1995 mesocosm experiments, with mean surface UV-B increased to more than twice the natural midday solar value, and biologically effective doses increased up to 5 times (Forster and Schubert in press), were deliberately chosen in order to identify responses of the pelagic community which were most sensitive to the UV-B stressor. The exposure regime used in the enhanced UV-B treatment was equivalent to that which would occur if the ozone column was reduced from its normal summertime value of 330 Dobson units (DU) to a value <150 DU (Forster and Schubert in press). We consider this an extreme treatment, and one which is far in excess of predicted losses to the ozone column for this location and time of year (Frederick 1997). The irradiance stress on the planktonic community was further enhanced by the 1 m depth of the mesocosms, as many areas of the Darss-Zingst estuary are deeper than this (the mean depth of the estuary is 2.0 m).

Creating a realistic increase in the surface UV-B to levels which will result from the expected ozone depletion of 10–20% can only be achieved with a modulated lamp system coupled to accurate surface measurements of biologically effective UV-B. Such systems have been designed for terrestrial experiments (Mepsted et al. 1996) and have recently been implemented by aquatic ecologists (Underwood et al. 1999).

In view of the large enhancements of UV-B that we used during the 1995 experiments, which were replicated 3 times within a 3-week period during the post-bloom, low nutrient phase of plankton development, it was surprising that no lasting effects were found. The structure and function of the estuarine planktonic community seemed to be resilient to enhanced UV-B for periods of up to 8 days, and did not react to the gradient of UV stress caused by the four spectral treatments within each experiment. The most noticeable effect on phytoplankton biomass was caused by the complete screening of all UV, which resulted in an increase in chlorophyll a by the end of two of the three experiments. However, this effect could not be repeated in the following year. The results of other outdoor mesocosm experiments in an alpine lake (Halac et al. 1997), in a mesotrophic lake (Laurion et al. 1998) and in a Swedish fjord (Wängberg et al. 1999)

have also shown phytoplankton biomass not to be affected by screening or enhancing UV-B. Keller et al. (1997) exposed their estuarine mesocosms to higher UV-B enhancements than we did (DNA-effective dose 10 times higher than ambient), and observed a UV-B-mediated decrease in phytoplankton biomass near the surface of their stratified compartments.

The close correlations that we often observed (e.g. during the first 6 days of Expt I) between the concentration of chlorophyll a in the mesocosms and in the estuary water nearby suggest that the same forcing functions were acting in all cases, and that differences in UV spectral composition were not important. Changes in total photon availability, nutrient supply and temperature should all control the development of the phytoplankton population, with additional modification of the standing crop by grazing pressure. It was noticeable in Expt III of 1995 that concentrations of chlorophyll a in the mesocosms diverged markedly from that of the estuarine water. In this case, the phytoplankton within the mesocosms may additionally have responded to the much higher daily photon dose during this experiment with a decrease in their cellular chlorophyll a concentration.

The absence of differences in the $K_{(\lambda)}$ between the four compartments suggests that the availability of photosynthetically available irradiance would be very similar in all cases. Taken together with approximately the same concentration of phytoplankton biomass in each compartment would lead one to predict that the daily integral of photosynthesis would also be similar in each treatment. Indeed, the net production of the phytoplankton community was not affected by any of the spectral treatments, as shown by similar diurnal changes in dissolved oxygen concentration and pH in each mesocosm. The relatively large daily fluctuations in oxygen concentration, with peak daytime values well above equilibrium with the atmosphere, and equally large nocturnal decreases, indicate considerable activity of both autotrophic and heterotrophic organisms within the mesocosms. The balance between photosynthetic and respiratory processes seems not to have been sensitive to UV. Daily oxygen production was maximal when incident irradiance was highest, especially at the beginning of Expt III when the lower pH of 9.0 indicated a slightly higher availability of dissolved inorganic carbon than in the other experiments. In another outdoor mesocosm experiment, photosynthetic carbon fixation rates were unaffected by a treatment which enhanced the UV-B fluence rate to twice that of ambient (Wängberg et al. 1999).

The lack of a significant change in the fluorescence parameter F_v/F_m despite the enhancement of UV-B to double the solar dose shows that damage to the photosynthetic reaction centres – a known target of UV-B – did not occur. F_v/F_m was temporarily decreased following periods of high irradiance – this is a consequence of dynamic, photoprotective processes acting to reduce the excitation pressure on PS II. Recovery of F_v/F_m in late afternoon is a good indication that regulation, rather than damage to PS II, had indeed taken place.

Although differences in primary production, and therefore the supply of carbon to the microbial food web and higher trophic levels, were not caused by the spectral treatments, it is still possible that important changes within the phytoplankton community would occur if UV influenced other aspects of physiology such as nutrient uptake, or caused damage to the genetic material. Changes in the species composition can alter the nutritional quality of the food, with cyanobacteria often being considered to be of lower nutritional value, or being less digestible than other algal groups. The phytoplankton communities of many of the Baltic Sea estuaries are dominated by 1- to 5-µm colonial green algae and cyanobacteria, often of similar shape, and whose lack of prominent structural features makes identification to the species level with the light microscope difficult. Optical methods, based for example on differences in refractive index, cell size or pigmentation, are extremely useful for rapidly determining the dominant taxonomic groups in this type of system and enable the processing of many more samples than would be possible with traditional counting methods. We used measurements of in vivo absorption and fluorescence to resolve differences in the pigment composition of the algal assemblages during these experiments.

A clear pattern emerged in all experiments. After enclosure of the estuarine water within the mesocosms, there was always a reduction in the absorption due to the pigment phycocyanin, indicative of cyanobacteria, at around 620 nm. Other regions of the spectrum showed little or no change. Reductions in phycocyanin were also confirmed in the fluorescence excitation spectra. This shift can indicate either a reduction in the quantity of cyanobacteria, or an adjustment of the pigment ratios within the cyanobacterial population, or both. A reduction in the ratio of phycocyanin-to-chlorophyll a has been known to result from photoacclimation to higher irradiance availability, or from nutrient deprivation (Grossman et al. 1993). Land-based mesocosm experiments in 1996 in which PAR was shaded to 20% of incident showed an increase in the phycocyanin:chlorophyll ratio, opposite in direction to that observed in the full solar-exposed mesocosms, and indicating that the total photon irradiance is an important factor controlling the pigment composition.

There were no indications of pigment shifts within the main mesocosm treatments in either 1995 or 1996, clearly indicating that no large displacements of species had occurred. Halac et al. (1997) deployed a 1,000-l mesocosm in an alpine lake and also found no change in phytoplankton species composition after screening UV-B for periods of 1–6 days. In contrast, Cabrera et al. (1997) observed a decrease in the abundance of two diatoms coupled with an increase in the density of the chlorophyte *Ankyra* in mesocosms exposed to full sunlight. Our results do not rule out the possibility that certain individual species may have increased or decreased under the spectral treatments, as single-species shifts were not detectable with our optical methods.

An increase in bacterial production with time was measured during Expt I of 1995 in all mesocosms, which could have been a response to an increased supply of organic substrates from the phytoplankton. Under conditions of high irradiance, high pH and low nutrient availability, phytoplankton increase their exudation of organic materials. Higher grazing pressure at the end of the experiment would also provide bacteria with additional substrate via an increase in the number of damaged and leaking phytoplankton cells. There is ample evidence to show that UV can negatively impact bacterial populations, for example by causing DNA damage (Jeffrey et al. 1996) and decreased metabolic activity (Aas et al. 1996). Sommaruga et al. (1999) observed a reduction in thymidine uptake as well as a reduction in the biomass of non-filamentous bacteria due to the presence of ambient UV in their mesocosm experiments in an alpine lake. We did find some evidence that the increased UV-B treatment reduced bacterial production during days 2–4 of Expt I, but this reduction was not maintained until the end of the experiment. Also, our samples were taken early in the morning which may have given bacterial cells sufficient time to recover from the previous day's UV exposure.

Solar radiation may exert a positive effect on bacterioplankton if photolysis of recalcitrant dissolved humic materials results in an increased availability of low molecular weight, bioavailable compounds or nutrients (Mopper et al. 1991; Bushaw et al. 1996). Bacteria will readily assimilate the products which are formed when high molecular weight cDOM is exposed to UV (Wetzel et al. 1995), but we found no evidence of an increased bacterial production as would be expected if photolysis of DOM by the enhanced UV-B was important. The absence of photochemical "bleaching" of cDOM as shown by absorption measurements during the experiments is also evidence against a large change within the dissolved organic pools of the mesocosms. As with phytoplankton chlorophyll concentration, bacterial production was highest on the last day of the experiment in the PAR mesocosm, which suggests a close coupling between primary and secondary producers.

Populations of the smaller zooplankton such as rotifers and copepodite stages of copepods increased rapidly during the mesocosm experiments, probably due to the absence of predation by fish and larger zooplankton. It was notable that the final population of zooplankton was higher in treatments including UV-B and UV-A. The reason for this is not clear, and reports of beneficial effects of UV on microzooplankton are rare. Responses of arctic ciliates and rotifers to UV-B exclusion with Mylar were variable: some ciliates did increase in concentration in full sunlight, whereas for others concentrations were depressed (Wickham and Carstens 1998). Rotifer numbers in the arctic experiments were unaffected by UV-B, but a strong inhibition of rotifer populations occurred in the UV-B exclusion mesocosms of Cabrera et al. (1997). Exposure to UV-B has previously been shown to reduce the digestibility of *Selenastrum* when fed to *Daphnia*, possibly because of cell wall thickening (Van Donk and Hessen 1995). An improvement in food quality may explain the increase in zooplankton populations in our UV-B-exposed mesocosms, and it is apparent that sublethal doses of UV-B can alter the biochemical composition of phytoplankton (Arts and Rai 1997). However, previous work has mainly indicated that UV-B-irradiated algae are of inferior quality, e.g. have a lower concentration of essential fatty acids (Odmark et al. 1998).

We conclude from these experiments that the structure and function of the post-bloom phytoplanktonic and bacterial communities of the Darss-Zingst estuary are unlikely to be affected either by present day doses or by enhanced doses of UV-B, but that further investigations are necessary to clarify the responses of zooplankton communities to UV-B. The UV-B exposure of planktonic organisms within the mesocosm was controlled by the rate at which they are mixed through the surface layer. For the phytoplankton at least, the short period of exposure in the upper 10 cm of the water column, where UV-B was detectable, was insufficient to cause a reduction in photosynthesis, or a change in the dominant taxonomic groups within the community. The strong attenuation of UV-B by cDOM in the upper layer effectively shields the rest of the water column from damage. Additionally, the presence of photorepair (e.g. replacement of damaged DNA) and photoprotective processes (e.g. induction of UV-absorbing pigments) may also have contributed to the lack of response to UV-B.

We cannot rule out the possibility that certain phytoplankton species were negatively affected by UV-B, or that UV-B sensitivity of the community may be greater at other times of year. For example, low water temperatures during the early spring growth period may reduce the rate of enzymatic repair of UV-B damage. However, solar UV-B is much lower at this time of year, and it is known that cDOM concentrations in the estuary are extremely high at all times of year due to input from both adjacent reed beds and from terrestrial sources. It is therefore unlikely that a period exists when the pelagic organisms of this estuary are at risk from UV-B.

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