

BENEFICIAL AND DETRIMENTAL EFFECTS OF UV ON AQUATIC ORGANISMS: IMPLICATIONS OF SPECTRAL VARIATION

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Abstract. Solar ultraviolet radiation (UVR) may have beneficial as well as detrimental effects on living systems. For example, UV-B radiation (280–320 nm) is generally damaging, while UV-A radiation (320–400 nm) may cause damage or stimulate beneficial photorepair of UV-B damage. The nature of both direct and indirect effects of UVR in nature depends on both the photon flux density and the spectral composition of the radiation incident on aquatic organisms across environmental UVR gradients in space (depth, transparency, elevation) and time (diel, seasonal, interannual). Here we use the common and widespread freshwater cladoceran *Daphnia pulex* as a model organism to demonstrate the potential importance of these wavelength-specific effects of UVR to the ecology of aquatic organisms. UVR-exposure experiments are used to manipulate both natural solar and artificial UVR sources to examine the beneficial as well as detrimental effects of different wavelengths of UVR. Changes in the spectral composition of solar radiation are also examined along several natural environmental gradients including diel gradients, depth gradients, and dissolved organic carbon (DOC) gradients. The implications of variation in the spectral composition of UVR for aquatic organisms are discussed.

The first biological weighting function (BWF) for a freshwater cladoceran is presented here. It demonstrates that the shortest UV-B wavelengths in sunlight are potentially the most damaging per photon. However, due to the greater photon flux density of longer wavelength UVR in sunlight, the net potential damage to *Daphnia* in nature is greatest for the longer wavelength UV-B and shorter wavelength UV-A radiation in the 305–322 nm range. Overall the contribution of UV-B to the total mortality response of *Daphnia* exposed to full-spectrum solar radiation for 7 h on a sunny summer day is 64% while UV-A contributes 36%. The BWF for *Daphnia* is used with the transmission spectrum for Mylar D to demonstrate that Mylar D cuts out only about half of the damaging UVR in sunlight. Following exposure to damaging UV-B, *Daphnia* exhibits a dramatic increase in survival in the presence of longer wavelength UV-A and visible radiation due to the stimulation of photoenzymatic repair. We present data that demonstrate the importance of both atmospheric ozone and DOC in creating strong environmental gradients in the intensity (irradiance) and spectral composition of solar UVR in nature. The light-absorbing component of DOC, chromophoric dissolved organic matter (CDOM), is particularly important in creating depth refugia from damaging UV-B in freshwater ecosystems. CDOM may also cause intense variations in the ratio of potentially beneficial UV-A to detrimental UV-B radiation to which aquatic organisms are exposed. In addition to changes in atmospheric ozone, future changes in CDOM related to climate change or other environmental disturbances may substantially alter the underwater exposure of a variety of aquatic organisms to different wavelengths of solar UVR.

Key words: biological weighting function; *Daphnia pulex*; dissolved organic carbon; environmental gradients; lake optics; ozone depletion; spectral composition of solar radiation; ultraviolet radiation; UV-A and UV-B, relative damage to aquatic organisms; zooplankton, tolerance of UV radiation.

INTRODUCTION

Solar radiation influences living organisms in many different ways depending on its spectral composition. Longer wavelengths are required for vision in animals and photosynthesis in plants, while shorter wavelength

UV-B radiation (280–320 nm) is damaging to living organisms. Ozone selectively absorbs the shorter wavelength UV-B radiation, leading to essentially no sunlight below 290 nm reaching the earth's surface. In recent decades biologically damaging UV-B has been increasing at temperate as well as polar latitudes in response to stratospheric ozone depletion (Kerr and McElroy 1993, Madronich 1994). Recent modeling efforts indicate that ozone depletion will continue well

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into the new century, and recovery will be aggravated by increases in greenhouse gases (Shindell et al. 1998). In aquatic habitats chromophoric dissolved organic matter (CDOM, the light-absorbing component of dissolved organic carbon) strongly and selectively absorbs ultraviolet radiation (UVR), providing organisms with an additional level of protection from UVR damage (Scully and Lean 1994, Morris et al. 1995). CDOM quantity and quality are in turn altered by disturbances such as climate change and acidification of inland waters, which may further elevate levels of potentially damaging UVR for organisms in underwater habitats (Schindler et al. 1996, Williamson et al. 1996, Yan et al. 1996). Photobleaching by sunlight may also substantially increase water transparency to UVR (Morris and Hargreaves 1997).

One of the most striking pieces of evidence that UV radiation has been an important selective force in ecological communities is the widespread presence of behavioral, physiological, and molecular mechanisms to avoid, reduce, or repair UVR damage (Williamson and Zagarese 1994, Zagarese and Williamson 1994, Roy 2000). In spite of the prevalence of numerous UVR defenses, the detrimental effects of UVR have been documented in a wide variety of organisms in both terrestrial and aquatic ecosystems ranging from bacteria, protists, and plants to both invertebrate and vertebrate animals (Young et al. 1993, Williamson et al. 1994, Häder and Worrest 1997). While shorter wavelength UV-B is generally damaging, longer wavelength UV-A radiation (320–400 nm) may be either detrimental or beneficial. For example, UV-A radiation may cause substantial inhibition of growth or survival in bacteria (Sommaruga et al. 1997), phytoplankton (Smith et al. 1992, Prézélin et al. 1994), protozoa (Ochs and Eddy 1998), zooplankton (Williamson et al. 1994), and fish (Williamson et al. 1997). On the other hand, UV-A may have beneficial effects by stimulating photoenzymatic repair (Sutherland 1981, Mitchell and Karantz 1993, Quesada et al. 1995). Photoenzymatic repair (PER, also referred to as “photoreactivation,” or “photorepair”) is a light-mediated molecular process that repairs UV-B-damaged DNA. Fish larvae benefit from PER as well as from UV-A receptors in their retinas that enhance their foraging efficiency on zooplankton prey (Loew et al. 1993, Browman et al. 1994). Blue light may stimulate the production of photoprotective compounds in plants (Adamse et al. 1994). UV-A inhibits photosynthesis (Neale 2000) but is also photosynthetically active since most light-harvesting pigments also absorb in the UV-A region (Vernet et al. 1989). The lack of good quantitative information on the contrasting detrimental and beneficial effects of the different wavelengths of solar radiation in nature makes it difficult to predict the net response of organisms to changing environmental UVR.

In order to understand how natural communities respond to environmental variations in UVR, information

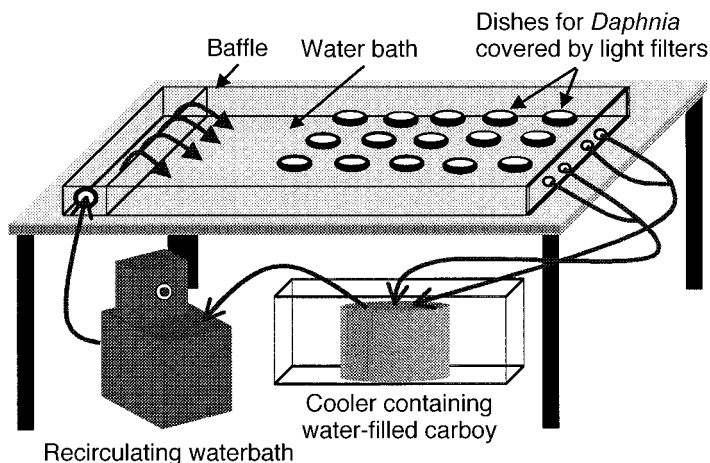
on how organisms respond to the different wavelengths is essential (Smith et al. 1980, Caldwell et al. 1986, Cullen and Neale 1997). Two primary approaches have been used in the past to examine the response of living organisms to different wavelengths of UVR. Monochromatic approaches expose organisms to a narrow wavelength band of UVR and use the response to develop an action spectrum (Setlow 1974, Storz and Paul 1998). Polychromatic approaches on the other hand expose organisms to full-spectrum radiation and progressively remove the shorter wavelengths in multiple treatments to develop biological weighting functions (Neale 2000). The polychromatic approach is generally considered to be more ecologically relevant (Caldwell et al. 1986), and is the approach that we use here.

Both monochromatic and polychromatic approaches confirm that per photon, biological damage increases with decreasing wavelength in the UVR range. However, at the same time, fewer photons of this shorter wavelength solar UVR reach Earth's surface, due in large part to absorption by atmospheric ozone. This tradeoff between higher photon-specific damage and decreasing photon flux density with decreasing wavelength leaves open the central question of which wavelengths of sunlight actually contribute the most to UVR damage in nature. This is an especially important consideration in aquatic systems where CDOM creates intense gradients in the spectral composition of sunlight and in the ratio of beneficial to detrimental wavelengths of UVR.

Here we use *Daphnia pulicaria* as a model organism to look specifically at what wavelengths of solar radiation are most damaging. We also examine the potentially beneficial effects of longer wavelength UV-A in stimulating photorepair of UV damage. *Daphnia* was chosen as the experimental organism because it forms a particularly important link in many pelagic freshwater food webs. It is an important food item in the diet of planktivorous fish, and it exerts strong grazing pressures on phytoplankton and bacteria. In addition, *Daphnia*, like many aquatic organisms ranging from phytoplankton to fish, has the ability to photorepair UVR damage. There are clear ecological analogues to *Daphnia* in other ecosystems that are exposed to UVR such as the phytophagous insects in terrestrial and lotic ecosystems, and copepods in marine ecosystems.

Data are also presented here on the variability of both the intensity (irradiance) of UV-A and UV-B as well as the ratio of UV-A to UV-B radiation along several common environmental gradients (CDOM gradients, depth gradients, diel gradients). Although there is variation in the wavelength-specific effects of UVR among organisms and ecosystems, the general principles demonstrated here with *Daphnia* apply to other organisms—UVR can have both beneficial and detrimental effects in nature, and the net effect will depend on the spectral composition as well as the response of the organisms exposed.

FIG. 1. Diagram of the solar phototron used to expose *Daphnia* to different wavelengths of natural sunlight.



Most organisms respond to damaging UVR through some combination of behavioral avoidance, photoprotection, and molecular repair (Worrest 1982, Zagarese and Williamson 1994). Here we look only at the two latter responses, photoprotection and molecular repair, the sum of which we define as "UV tolerance." More specifically we use two novel instruments to examine the effects of the quality (spectral composition) as well as the quantity (irradiance) of UVR on *Daphnia pulex* in a series of experiments under both natural and artificial solar-radiation regimes using polychromatic approaches. First we use a solar phototron with long-wave pass cutoff filters and natural sunlight to examine wavelength-specific responses to solar radiation and develop a biological weighting function (BWF) for *Daphnia*. From this BWF we determine which wavelengths of sunlight cause the most net damage during a midday exposure to UVR, as well as the total biologically weighted exposure (H^*), which is essentially the UVR dose. Second, we use a UV-lamp phototron that permits us to both manipulate UVR irradiance and to separate the effects of potentially beneficial longer wavelength radiation from the damaging shorter wavelength UV radiation. We use this latter approach to assess the importance of both the level of damaging radiation and the effectiveness of photoenzymatic repair (PER) in determining net damage from UVR. Understanding the importance of PER is critical because in the presence of PER the principle of reciprocity (where response is dose dependent rather than dose-rate dependent [Luckiesh 1930]) is invalid and one must then be very cautious about applying weighting functions to diverse radiation regimes (Cullen and Neale 1997). Lastly we examine and discuss natural environmental variations in UV-A, UV-B, and UV-A:UV-B ratios in aquatic ecosystems and the implications of these gradients in UVR for the ecology of organisms such as *Daphnia*.

METHODS

Solar-phototron experiment: What wavelengths are damaging?

Daphnia pulex were collected from Dutch Springs in Bethlehem, Pennsylvania, USA, a UV-transparent lake (1% of surface UV 320-nm radiation penetrates to ~8 m in summer) with a maximum depth of 30 m. The *Daphnia* were exposed to various wavelengths of natural sunlight in the solar phototron (Fig. 1) in order to assess the wavelength-specific nature of their response to net UV radiation (UVR) damage. The *Daphnia* were collected with a 202- μ m mesh net and brought back to the laboratory where they were fed and acclimated to the experimental temperature of 20°C overnight.

The following morning 10 adult *Daphnia* (egg bearers, or individuals the size of egg bearers) were placed in each of five replicate dishes for each of five light-filter treatments. The dishes were shallow (1.7 cm deep, 4.8 cm inside diameter, ~30 mL capacity) to reduce potential shading effects, and painted black on the outside to remove all solar radiation except that which came down through the filter that was placed on top of the dish as a cover. Quartz disks and Schott long-wave pass cutoff filters (50-mm diameter) (Schott Group, Mainz, Germany) with four different wavelength cutoffs were used to manipulate the wavelengths of sunlight to which the organisms in each treatment were exposed. The Schott filters had sharp cutoffs with 50% transmittance at 304, 326, 370, and 404 nm. The quartz treatment permitted exposure to essentially full solar radiation. We found that solar irradiance decreased much more rapidly below 293 nm (an order of magnitude per nanometer) and thus used 293 as the nominal "cutoff" for the quartz treatments. The resulting cumulative energy spectra to which the organisms were exposed are given in Fig. 2.

The dishes with filter covers were suspended on a

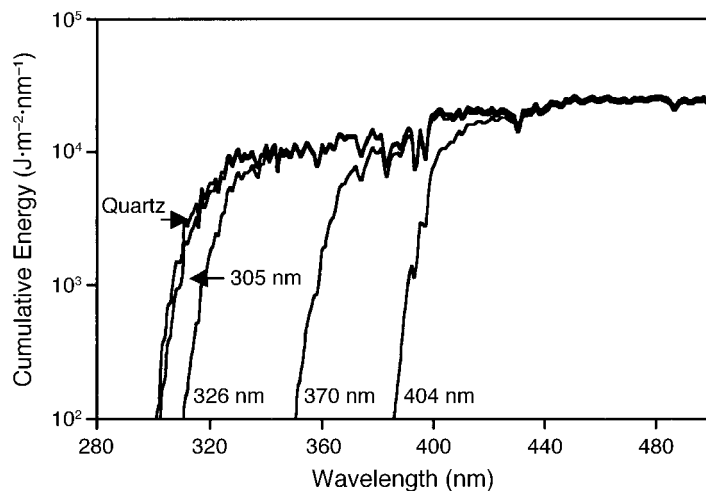


FIG. 2. Solar energy spectra for quartz and Schott long pass cutoff filter treatments. From left to right, the spectra are for quartz, 305-, 326-, 370-, and 404-nm filter treatments. Data are from the 7-h experimental period for the solar phototron experiment on 10 July 1998. See *Methods* for details.

rack in a large flat tray with water circulating underneath and on all sides from a temperature-controlled water bath (Fig. 1) to maintain the experimental temperature at 20°C. The incubation period lasted 7 h beginning at 0930 and ending at 1630 Eastern daylight time EDT on 10 July 1998. The day was very sunny with only occasional short periods of passing clouds. At the end of the experiment the dishes were transferred to an incubator with a 12:12 light:dark cycle (two 40-W cool-white fluorescent bulbs). Mortality in each dish was scored 42 h after the end of the exposure period.

The UVR exposure in each light-filter treatment was estimated from measured solar-irradiance data, the transmission spectra of the filters, and a solar-radiation model. Solar irradiance was measured continuously throughout the 7 h exposure period at 1–2 s intervals with a carefully leveled profiling ultraviolet radiometer (PUV 501B, Biospherical Instruments, San Diego, California, USA; 1997 solar calibration coefficients in air) placed within a few meters of the solar phototron. The PUV is a medium-bandwidth radiometer that measures photosynthetically active radiation (PAR, 400–700 nm) as well as UVR in four bandwidths (305, 320, 340, and 380 nm). The UVR bands have a bandwidth of 8–10 nm measured as the full width at half maximum response (FWHM, the range between the two wavelengths at which response is 50% of the peak response). The UV irradiance data (in units of $\mu\text{W}\cdot\text{cm}^{-2}\cdot\text{nm}^{-1}$) were integrated over the 7-h exposure period to estimate total energy exposure (in units of $\text{J}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$) at each PUV wavelength. These integrated data were in turn used to generate a solar energy exposure spectrum (280–500 nm, at 1-nm intervals) by fitting a solar spectrum to them. The shape of the solar spectrum was generated using a solar radiation model (Biospherical Instruments: RT Basic radiative transfer model) that quantifies the propagation of different wavelengths of solar radiation through the atmosphere to permit estimation of the shape of the solar spectrum on a given

date and location. A previously developed protocol for fitting full-spectrum data to medium-bandwidth instrument data was used (Kirk et al. 1994, Morris and Hargreaves 1997). The transmission spectra of the filters in each treatment were multiplied by the solar energy exposure spectrum to produce the wavelength-specific energy spectra for each filter treatment with 1-nm resolution (Fig. 2).

Biological weighting function (BWF) approach and model

The basic concept behind a biological weighting function is that the impact of solar radiation depends on its spectral composition: different wavelengths have different effects. A BWF is used to estimate the effects of different wavelengths on a given organism or process by generating a function that provides a weighting coefficient for each individual wavelength. Either a general shape is assumed for the function, or multivariate statistical approaches are used to generate more complex functions. Here the data from the solar-phototron experiment were used to develop a BWF for net damage (combination of damage and repair) in *Daphnia pulex*. We fit a simple exponential function to the *Daphnia* mortality data following a modification of previously described methods (Rundel 1983, Cullen and Neale 1997, Kouwenberg et al. 1999b). This approach is based on the concept that there are two factors that determine the impact of UVR on a living organism—the amount of radiation at each wavelength, and the effectiveness of the energy of the photons at each wavelength. Thus the model expresses net biologically weighted or effective exposure (H^* , unitless) as a function of total cumulative energy exposure at each wavelength ($H(\lambda)$, in joules per square meter per nanometer) and the biological weighting coefficient for each wavelength ($\epsilon_H(\lambda)$, in $[\text{joules per square meter}]^{-1}$), integrated over the wavelength range of interest. We chose the 280–500 nm wavelength range as being comprehensive

to any potentially damaging effects of solar radiation to zooplankton:

$$H^* = \sum_{\lambda=280}^{500} \varepsilon_H(\lambda) \times H(\lambda) \times \Delta\lambda. \quad (1)$$

When the values of $\varepsilon_H(\lambda)$ are plotted against wavelength they comprise what is known as a "biological weighting function." They are estimated from the following model:

$$\varepsilon_H(\lambda) = C \times e^{-(m_1 + m_2(\lambda - 300))} + m_c \quad (2)$$

where m_1 is the natural log of the weight at 300 nm, m_2 is the slope of the BWF, C is a proportionality constant ($[\text{J}/\text{m}^2]^{-1}$), here equal to 1, and m_c is a constant that accounts for wavelength-independent effects. Biologically effective exposure at a given wavelength (H^*_λ ; nm^{-1}) is equal to the product of the energy exposure at each wavelength and the biological weighting coefficient for that wavelength:

$$H^*_\lambda = \varepsilon_H(\lambda) \times H(\lambda). \quad (3)$$

When H^*_λ is integrated over the full wavelength range (Eq. 1) the result is H^* .

The model that we used for estimating mortality due to H^* was based on the standard exponential equation for population growth where N_0 was the starting number of individuals and N_t was the number of survivors at the end of the experimental time period:

$$N_t = N_0 e^{-H^*}. \quad (4)$$

When modified to express the results as percentage mortality as was done here, this becomes

$$100 \times (1 - N_t \times N_0^{-1}) = 100 \times (1 - e^{-H^*}). \quad (5)$$

These relationships assume that the natural log of survivorship is inversely proportional to total biologically weighted UVR exposure (H^*), and that reciprocity holds. Total biologically weighted or effective exposure is roughly the same thing as dose except that the term "dose" is usually reserved for that exposure which is actually absorbed. The "reciprocity principle" states that the response to a given UVR dose is independent of dose rate (Luckiesh 1930, Cullen and Neale 1997). So for example, if reciprocity holds, an organism will respond in a similar way to a given UVR dose whether that dose is received in a single sunny day, or over a period of several cloudy days.

The BWF was estimated numerically given Eqs. 1–4 using a Marquardt nonlinear least-squares algorithm (SAS Institute 1996). The fitting procedure determined the best fit values for m_1 , m_2 , and m_c given spectral exposure and observed mortality (as discussed in *Solar-phototron experiment. . .*, above). Each replicate dish was considered an independent observation ($n = 25$). The 95% confidence interval for the ε_H estimates derived from Eq. 2 were determined from the variance and covariance of the fitted m_1 , m_2 , and m_c using propagation of errors (Bevington 1969).

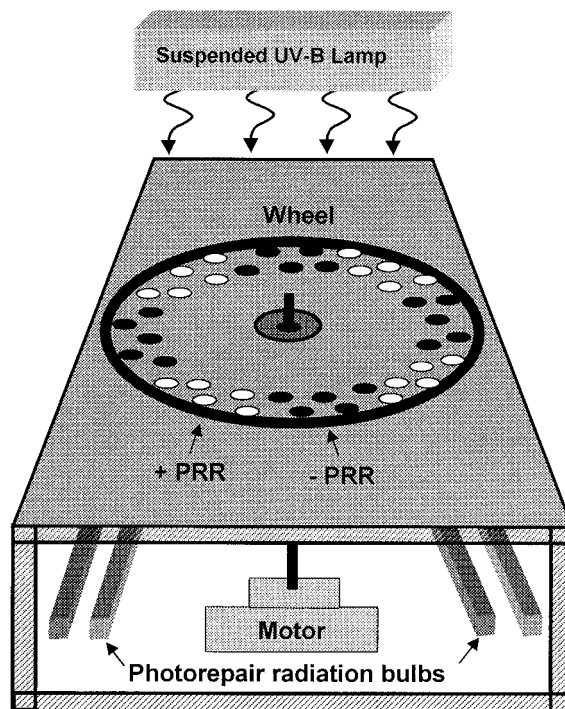


FIG. 3. Diagram of UV-lamp phototron used to expose *Daphnia* to different intensities of damaging UV-B radiation and to manipulate the longer-wavelength photorepair radiation (PRR). Positions on the wheel where dishes are exposed or unexposed to PRR are indicated.

UV lamp phototron experiments: What is the importance of UV damage and photorepair?

The UV-lamp phototron (Fig. 3) is a novel instrument designed to expose organisms to damaging UV-B radiation in the presence or absence of beneficial longer wavelength photoreactivating radiation (PRR). The standard exposure period is 12 h, after which the survival (or growth rate for rapidly reproducing organisms) is monitored until the dark controls drop below 90% survival or for a total of 5 d at 20°C (=endpoint). Percentage survival (or growth rate) at the endpoint is used to measure UV tolerance and its two components: PER (photoenzymatic repair) and DRPP (dark repair and photoprotection). We define "UV tolerance" as the percentage survival at the endpoint in the treatment with both UV-B and PRR (+PRR treatment). In the absence of PRR (–PRR treatment), there is little or no PER so that organism survival following UV-B exposure will be a function of dark repair processes and photoprotective ability, giving us an estimate of what we define here as DRPP. It is important to recognize that substantial photoprotection may be present, and dark repair may be going on even if there is no survival in the absence of PRR (i.e., zero DRPP as defined here). We are using percentage survival at a given UV exposure level as the operational definition of DRPP to measure the consequences of the dark repair and pho-

toprotection rather than directly measuring the physiological and molecular repair processes. PER in turn is measured as the difference in survival in the treatments with (+PRR) and without (-PRR) photorepair radiation. The design of the phototron also permits the investigator to manipulate both the wavelength and the intensity (irradiance) of exposure to both UV-B and PRR in any one experiment.

The UV-lamp phototron consists of a UV-B lamp (Spectronics XX15B) suspended 24 cm above the surface of a rotating black acrylic wheel that has 40 open holes in it in which 1.8 cm deep, 4.6 cm inside diameter, ~30 mL capacity quartz petri dishes are placed (Fig. 3). The UV-B lamp is covered with a fresh sheet of cellulose acetate at the start of each 12-h exposure to cut out the wavelengths of UV-B shorter than ~295 nm and thus better simulate natural solar radiation. Each dish is surrounded by a 2.5-cm-tall black collar of polyvinyl chloride to minimize exposure to stray radiation. Quartz lids cover the dishes. Stainless-steel mesh screens are placed on top of the dishes to manipulate the intensity of UV-B exposure. The wheel covers an enclosed box that contains the lamps that emit PRR consisting of visible, UV-A, and a small amount of UV-B radiation. The PRR bulbs are two 40-W cool-white fluorescent bulbs and two 40-W Q-Panel 340 bulbs located 32 cm below the bottom of the dishes. A black skirt around the acrylic wheel prevents stray PRR from escaping the box. By adding black disks to cover the holes under the dishes the presence or absence of the PRR from below can be manipulated. The box is ventilated with a high-rpm thermostatically regulated fan to prevent heat build up. The wheel rotates the specimens horizontally at 2 rpm to provide uniform exposure of all dishes and simulate the variable intensities of UVR that occur with mixing in the surface waters of lakes. The entire apparatus is placed inside a growth chamber at a constant temperature of 20°C.

The spectral composition of the damaging radiation from above and repair radiation from below the wheel were measured at 1-nm resolution with a custom-made spectral radiometer. Measurements were made at 14 different positions of the rotating wheel for the UV-B lamp radiation and 8 different positions of the rotating wheel for the repair radiation. Values were integrated over these different positions to account for the rotation of the wheel in order to estimate spectral exposures. In addition, a laboratory spectrophotometer was used to measure and account for the degradation of the cellulose acetate over a 12-h period of exposure to the UV-B lamp. The resulting energy spectra from the UV-B and PRR lamps were compared with the solar energy spectrum from the solar-phototron experiment (Fig. 4). The spectral radiometer that was used to make these measurements was custom made by Patrick J. Neale. It consists of a scanning monochromator (model SP 300i, Acton Research Corporation, Acton, Massachusetts, USA) with a UV-sensitive PMT (1P28 photo-

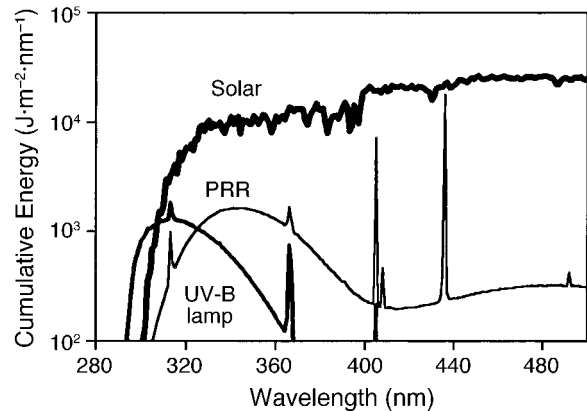


FIG. 4. Energy spectra for the photorepair radiation (PRR; thin line) and UV-B (medium line) sources integrated over a 12-h exposure period in the UV-lamp phototron compared to the energy spectrum for the 7-h sunlight exposure under quartz in the solar phototron (thick line).

multiplier tube) connected to a 3-m fiber-optic cable and a cosine-corrected flat diffuser collector. The response was calibrated for wavelength using a mercury lamp and for irradiance using a 1000-W NIST-traceable standard lamp (National Institute of Standards and Technology [U.S. Department of Commerce], Gaithersburg, Maryland, USA).

For the current experiments five 2–3 d old (immature) *Daphnia pulicaria* from a laboratory culture (originating from Dutch Springs) were placed in each of five replicate dishes in eight different treatments—four levels of UV-B exposure in the presence and absence of PRR. The experiment was run in December 1999. Preceding the experiment the *Daphnia* culture was kept at 20°C and a 12:12 L:D cycle from two 40-W cool-white fluorescent bulbs and fed *Cryptomonas reflexa*. The treatment levels were 11, 26, 34, and 55 kJ/m² of UVR (280–400 nm) from the UV-B lamp. Each treatment level had five dishes exposed to PRR and five not exposed to PRR. The exposure period in the phototron was 12 h. Survival was recorded under a dissecting microscope in each dish every day for five days following the start of the exposure period. The endpoint data from day 5 were corrected for dark control survival (96%) with a modification of Abbott's equation (Newman 1995, Williamson et al. 1999), arcsine square root transformed, and a two-way ANOVA performed on the transformed data where UV exposure level and PRR level were the two factors.

Environmental variation in UV radiation

Selective absorption of short wavelength UVR by ozone in the atmosphere and by dissolved organic carbon (DOC) in aquatic ecosystems creates strong gradients in UVR in nature. Some of the more obvious patterns are the diel and annual variations in UVR related to changes in sun angle, and the decrease in UVR with increase in depth in the water column of aquatic

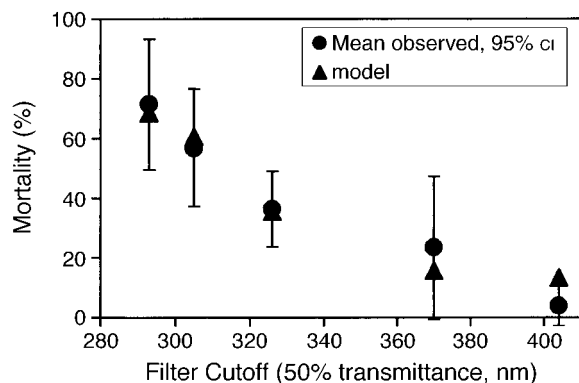


FIG. 5. Percentage mortality of *Daphnia pulicaria* 42 h after the end of the 7-h exposure in the solar phototron, with filter cutoff allowing 50% transmittance. Observed mortality is given as means with 95% confidence intervals. Modeled mortality is based on the biological weighting function fit by iteration to the observed mortality data. Full-spectrum (quartz) treatment is plotted at 293 nm, as below this wavelength solar irradiance declines by an order of magnitude per nanometer.

ecosystems. Perhaps more interesting and less widely recognized is the fact that this selective absorption of shorter wavelength UVR will lead to wide variations in the ratio of longer wavelength (often beneficial) UV-A radiation compared to the shorter wavelength (usually damaging) UV-B radiation. Here we present data on UV-A (380 nm), UV-B (320 nm), and UV-A:UV-B ratios in lake ecosystems.

Our UV group in the Department of Earth and Environmental Sciences at Lehigh University (Bethlehem, Pennsylvania, USA) has been collecting vertical profiles of underwater UVR since 1993 with Biospherical PUV-501 and PUV-501B submersible profiling ultraviolet radiometers. We have also had a ground-based ultraviolet (GUV) radiometer installed in a weather station at our field research site at Lake Lacawac in north-eastern Pennsylvania (USA) since 1993. These instruments record UV irradiance for 305, 320, 340, and 380 nm, as well as photosynthetically active radiation (PAR; 400–700 nm). Diffuse attenuation coefficients (K_d) are obtained for the water column of lakes from the slope of the linear regression of the natural logarithm of down-welling irradiance (E_d) vs. depth over depth intervals where the relationship is linear. Past intercomparisons and optical modeling have shown that although the PUV and GUV have a moderate bandwidth (8–10 nm FWHM), K_d measured with these instruments compare favorably with those measured with spectral radiometers of 1–2 nm bandwidths. Thus they can be used to estimate irradiance over the entire UVR spectrum within a few percent (Kirk et al. 1994, Laurion et al. 1997). Here we use data from our UV archives to illustrate the nature of environmental gradients in UV-A (380 nm) and UV-B (320 nm) as a function of depth in the water column of optically different

lakes. We also present data on variation in the UV-A:UV-B ratio as a function of depth in the water column, as a function of time of day (sun angle), and as a function of DOC concentration among lakes sampled in a broad survey of lakes in both the northern and southern hemispheres (Morris et al. 1995).

RESULTS

Solar-phototron experiment

Mortality was highest (averaging 71%) in *Daphnia* exposed to full-spectrum solar radiation for 7 h in the quartz treatment of the solar phototron experiment (Fig. 5). When the shorter wavelength UV-B (<305 nm) was removed, the average mortality decreased to 57%, and when most of the UV-B (<326 nm) was removed mortality further decreased to an average of 36%. When the medium and short wavelength UV-A (<370 nm) was also removed the mortality declined to 23% (Fig. 5). When essentially all of the ultraviolet radiation (UVR) was removed in the 404-nm treatment the mortality averaged only 4%.

Biological weighting function

The biological weighting function (BWF) for *Daphnia* demonstrates a strongly increasing energy-specific effect with decreasing wavelength (Fig. 6). The shortest wavelength UV-B radiation in sunlight is on the order of a thousand times more damaging to *Daphnia* than is the longest wavelength UV-A per unit energy. The photon-specific effect is similar to the energy-specific effect (but not shown here). However, incident solar energy also shows a strong decrease with decreasing wavelength within the UV-B range (Fig. 7). In order to estimate which wavelengths of sunlight are most damaging to *Daphnia*, the BWF (which gives us energy-specific damage rates) was multiplied by the solar energy spectrum (which tells us how much energy sunlight has at each wavelength). The result is biologically

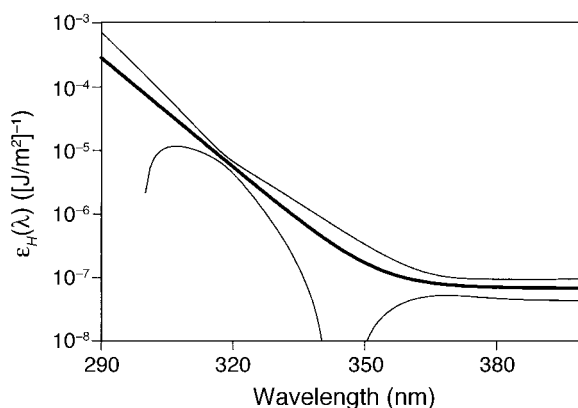
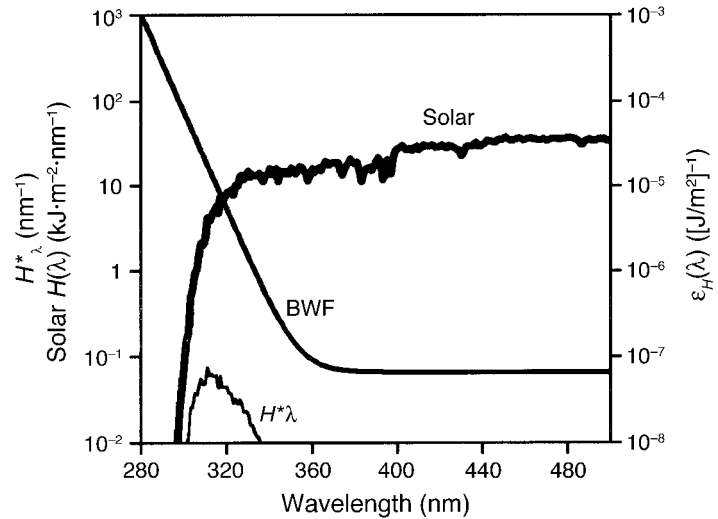


FIG. 6. Biological weighting function (BWF) for *Daphnia pulicaria* (thick line). Thin lines represent ± 1 SE error above and below the BWF. The BWF equation (Eq. 2) here is $\epsilon_H(\lambda) = 7.5 \times 10^{-5}(e^{-0.132(\lambda-300)} + 6.6 \times 10^{-8})$.

FIG. 7. Biologically effective exposure (H^*_λ ; thin line) as estimated from the 7-h solar phototron exposure under quartz (thick line) and the biological weighting function, BWF (medium line). $H(\lambda)$ is wavelength; $\epsilon_H(\lambda)$ is the biological weighting coefficient for each wavelength.



effective exposure at each wavelength (H^*_λ , Fig. 7). This shows us that the most biologically damaging radiation (for *Daphnia* under these conditions) is in the 305–322 nm range (bandwidth measured as the full width at half maximum response, FWHM; i.e., the range between two wavelengths at which response is 50% of the peak response). The BWF also indicates the relative contribution of UV-B and UV-A exposure to mortality for the solar phototron. Overall UV-B contributed 64% of the total response to UV in the full-spectrum quartz treatment while UV-A contributed 36%.

Nonlinear fitting of the parameters of the BWF for *Daphnia* resulted in values of 9.49 ± 0.97 (mean \pm 1 SE) for m_1 , 0.132 ± 0.053 for m_2 , and $6.6 \pm 2.6 \times 10^{-8}$ for m_c (see Eq. 2). The r^2 for the fit of the model was 0.72, but 23% of the variance was replicate variance. In terms of the between-treatment variance (the only

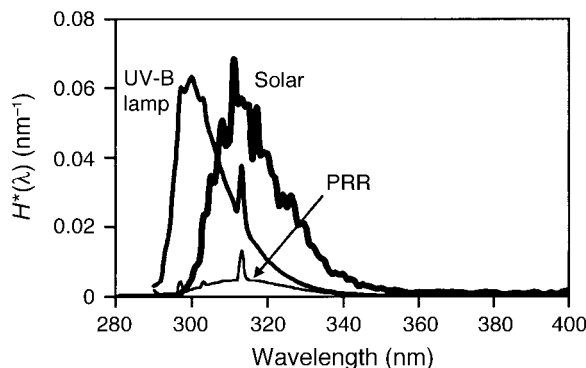


FIG. 8. Biologically effective exposure (H^*_λ) estimates for the solar phototron quartz treatment (thick line), the UV-B lamp (medium line) and the photorepair radiation (PRR) lamps (thin line) in the UV-lamp phototron. These H^*_λ values were estimated by multiplying the biological weighting function for *Daphnia* in Fig. 6 by the lamp and solar spectra in Fig. 4.

variance that can be explained by the model) the model accounted for 94% of the variance. The statistical variation among replicates (Fig. 5) does leave the exact shape of the BWF uncertain. The standard errors estimated through propagation of errors are particularly high below 305 nm and between 335–355 nm, wavelengths that contribute little to effective solar exposure (Fig. 6). However, the BWF is fairly well constrained over the 305 to 335 nm band (centered on 320 nm), which contributes the most to solar exposure. The fit required addition of a “constant” weight (m_c), which dominates the BWF at wavelengths > 370 nm. This constant provides a simple approximation of the net effect of exposure to long wavelength UV-A and visible light.

The weighting function probably does have some wavelength dependence at longer UV-A and visible wavelengths but the slope is much shallower than in the UV-B and short wavelength UV-A. If we assume that the variance is similar among treatments and calculate a pooled variance over all treatments (sample variance as estimated by one-way ANOVA of percentage survival as a function of spectral treatment, with 20 degrees of freedom), then the standard error of the mean in each treatment is $\pm 3\%$ survival. The response to the long wavelength UV-A and visible light (370-nm cutoff) treatment is then significant but the response to the visible-only treatment remains statistically indistinguishable from zero.

We also used the *Daphnia* BWF to compare the biologically effective UV exposures (H^* values) in the solar phototron to those in our UV-lamp phototron to assess how the biologically effective exposures in the UV-lamp phototron compared to more natural solar radiation. To do this we multiplied the BWF (Fig. 6) by each energy spectrum in the UV-lamp phototron (Fig. 4). For the 7-h solar exposure on 10 July the value of H^* was 1.00 (area under the solar curve in Fig. 8, 280–

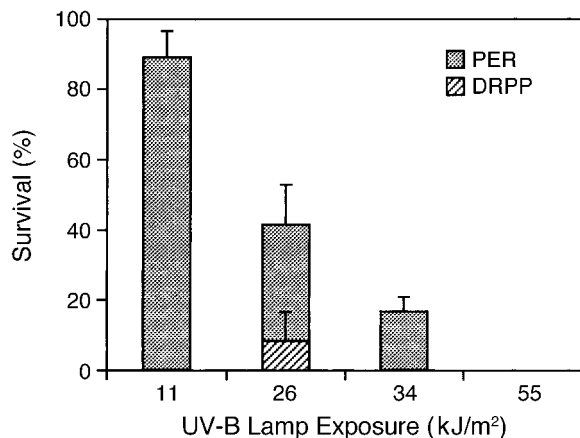


FIG. 9. Contribution of photoenzymatic repair (PER) vs. dark repair and photoprotection (DRPP) to overall UVR tolerance of *Daphnia pulicaria*. DRPP and tolerance are both expressed as percentage survival (means and 1 SE), while PER is the difference between these two. The data are endpoint data on day 5 following a single 12-h exposure to damaging ultraviolet radiation (UVR) in the UV-lamp phototron in the presence and absence of photorepair radiation (PRR).

400 nm). To extend these data to a full-day equivalent, we assumed that H^* follows the same trend as 320 nm from dawn to dusk (Fig. 12B). This was necessary because different wavelengths follow different trends over the diel cycle. The result was that this 7-h period represents 77% of the solar radiation in a full day of UV exposure at this time of year, giving a value of $H^* = 1.30$ for a full day of solar UVR under quartz.

We estimated that during a 12-h exposure to the full-strength UV-lamp phototron, *Daphnia* receives UVR damage equivalent to 86% of that received on a sunny day near summer solstice. In the UV-lamp phototron the biologically effective exposure for a 12-h exposure to one UV-B lamp gives a value of $H^* = 0.94$ (Fig. 8, UV-B lamp curve, 280–400 nm). The repair radiation from within the phototron box also produces a small amount of damaging radiation ($H^* = 0.18$, Fig. 8 PRR curve, 280–400 nm) that, when added to the UV-B, gives an H^* value of 1.12, which is 86% of 1.3.

UV-lamp phototron experiments

The experiments with the UV-lamp phototron showed a clear effect of UV exposure level ($P < 0.001$) as well as an effect of the addition of longer wavelength photorepair radiation ($P < 0.001$) on the survival of juvenile *Daphnia* exposed to damaging UVR. The UVR tolerance of *Daphnia* (expressed as percentage survival) decreased from 89% at 11 kJ/m², to zero in the fully exposed treatments (55 kJ/m², Fig. 9). Photoenzymatic repair (PER) was by far the most important component of the observed UVR tolerance at all exposure levels. In the absence of photorepair radiation (–PRR treatments), the DRPP (dark repair and photoprotection) alone resulted in little or no survival: only 2 out of 100

individuals survived in all four of the –PRR treatments.

Environmental variation in UV radiation

Here we present data on environmental gradients in both UVR irradiance and ratio of UV-A (380 nm) to UV-B (320 nm) radiation. These wavelengths were chosen based on the availability of our extensive PUV (profiling ultraviolet) and GUV (ground-based UV) radiometer data and the knowledge that solar radiation in the 320-nm range is the most biologically effective in causing damage to *Daphnia* (Fig. 7). For ease of understanding these wavelengths are referred to here as “UV-A” and “UV-B,” respectively.

Underwater UVR varies greatly in aquatic ecosystems as a function of the quality and quantity of dissolved organic carbon, DOC. For example in lakes with low DOC the 320-nm UV-B may penetrate to depths of 8 m or more, while in lakes with even moderate DOC concentrations most UV-B is absorbed within <1 m of the surface (Fig. 10). Thus a major portion of the mixed layer in low-DOC lakes may be exposed to levels of damaging UV-B that are 10% or more of surface levels while in lakes with higher DOC a substantial refuge from damaging UVR exists within the lower portion of the mixed layer (Fig. 10).

Within a lake UV-A radiation penetrates substantially deeper than does UV-B (Fig. 10). At the same time, the ratio of beneficial UV-A to damaging UV-B radiation remains very low (<10) throughout the high UVR mixed layer of low-DOC lakes, but increases to much higher levels within the top meter of moderate-DOC lakes (Fig. 11). This means that lakes with higher levels of DOC not only have less of the damaging UV-B radiation, but also proportionally more beneficial UV-A.

The variation in UV-A:UV-B ratios is even more evident across lakes with a range of DOC concentrations. For example, at a depth of 1 m across a range of lakes that we sampled as part of a previous study (Morris et al. 1995), UV-A:UV-B ratios vary over a thousandfold (Fig. 12A). UV-A:UV-B ratios can also vary with changes in sun angle due to the increased cross section of ozone when the sun is lower in the sky. The variation in the UV-A:UV-B ratio with sun angle is not as extreme as it is with changes in DOC underwater, but it can vary from on the order of 2.5 near midday to 10 or more at dawn and dusk (Fig. 12B). This same sort of variation would be expected with changes in sun angle and ozone cross section during different times of the year or at different latitudes.

DISCUSSION

The above experiments provide the first biological weighting function (BWF) and estimate of biologically effective exposure for a freshwater cladoceran. They demonstrate the potential importance of the spectral composition of sunlight to the ecology of *Daphnia pul-*

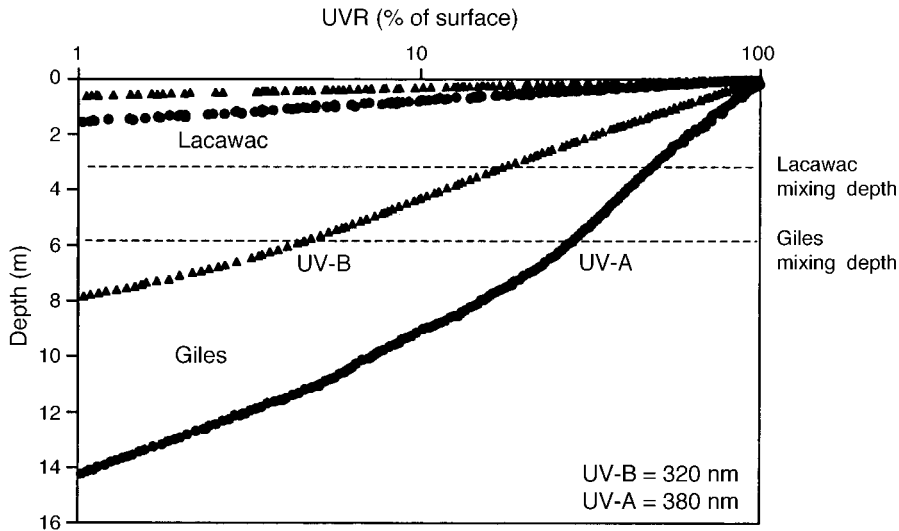


FIG. 10. UV-A (380 nm) and UV-B (320 nm) radiation vs. depth in two northeast Pennsylvania (USA) lakes with differing dissolved organic carbon (DOC) concentrations. Lake Giles has a DOC concentration of ~1.2 mg/L, while Lake Lacawac has a DOC concentration of ~4.7 mg/L. Mixing depths represent the shallowest depth at which the thermal gradient is <1°C/m depth. Data are from June 1999.

icaria, a widespread and important grazer in pelagic freshwater food webs. These experiments also demonstrate the tradeoff between the greater energy-specific damage of short wavelength ultraviolet radiation (UVR) and the greater photon flux density of the longer wavelengths of UVR. For this population of *D. pulex* the implication is that the most important wavelengths of sunlight in terms of net damage are those in the 305–322 nm range. The BWF for *Daphnia* falls between those previously obtained for UV-induced mortality in eggs of another planktonic crustacean, the marine copepod *Calanus finmarchicus*, and cod (*Gadus morhua*) (Kouwenberg et al. 1999a, b), but was more similar in slope to that of the copepod (Fig. 13). A major difference was that *Daphnia* did exhibit some sensitivity to UV-A.

The experiments with the UV-lamp phototron dem-

onstrate the key importance of longer wavelength UV-A and visible light in stimulating photoenzymatic repair of UVR damage. Interestingly, longer wavelength UV-A may actually have a net negative effect at very high irradiance levels (Fig. 6). However, this effect is orders of magnitude less than that for shorter wavelength UV-B. The lack of a negative effect of UV-A in the UV-lamp phototron is attributable to the lower levels of UV-A in the phototron compared to solar radiation (Fig. 4). These contrasting effects of different wavelengths and irradiance levels of UVR combined with the intense gradients in both beneficial and damaging UVR in the natural environment suggest the need for more careful attention to the importance of the full spectral composition of sunlight in studies of UVR effects.

Changes in atmospheric ozone are likely to alter the

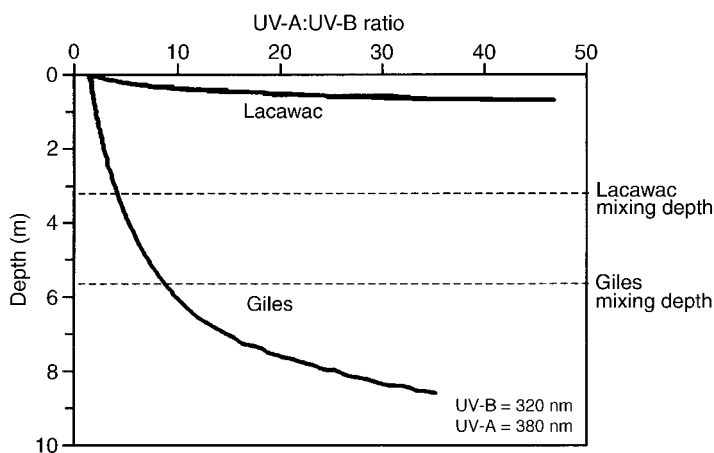


FIG. 11. Ratio of UV-A (380 nm) to UV-B (320 nm) irradiance vs. depth in lakes Lacawac and Giles (Pennsylvania, USA) from the surface to the depth of 1% of the 320-nm surface UV. Mixing depths and dates are as in Fig. 10.

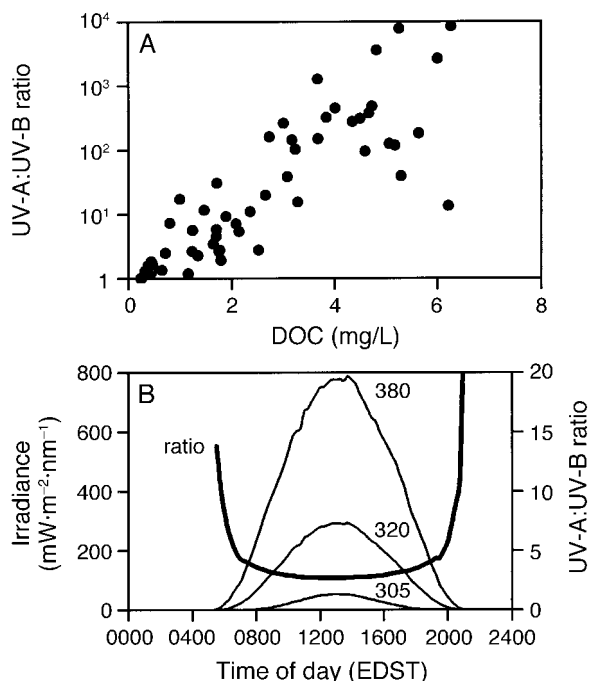


FIG. 12. Variation in ratio of UV-A (380 nm) to UV-B (320 nm) irradiance along (A) environmental gradients in dissolved organic carbon (DOC) and (B) time. (A) Ratio of UV-A to UV-B at 1-m depth vs. DOC concentration in a series of lakes surveyed in North and South America (Morris et al. 1995). The very high ratios are due largely to the fact that so little UV-B remains at 1-m depth in lakes with higher DOC concentrations. (B) Irradiance vs. time of day on 26 June 1999 (Eastern daylight savings time, EDST) for different wavelengths of ultraviolet radiation. The thick line gives the ratio of UV-A to UV-B throughout the day. Data were collected at Lake Lacawac in northeastern Pennsylvania, USA, on a clear day at 15-min intervals with a ground-based UV radiometer (Biospherical GUV).

potential impact of UV-B on *Daphnia* that remain in the surface waters during the day. This can be seen by the fact that the biologically effective exposure curve ($H^{\beta}\lambda$) is constrained by the abrupt decrease in shorter wavelength UV-B in the solar spectrum (Fig. 7). *Daphnia* often avoid the surface waters of lakes due to visual predators or potential damage from UVR (Leech and Williamson 2001). However, up to 20% or more of the population of *Daphnia catawba* may be in the surface mixed layers during July and August in high-UVR lakes such as Lake Giles, Pennsylvania (USA) (Leech and Williamson 2000). High UVR in the surface waters of lakes may also enhance photobleaching of CDOM (chromophoric dissolved organic matter), the light-absorbing DOC (dissolved organic carbon) compounds, with consequent reductions of UVR absorbance and greater penetration of UVR in the water column (Morris and Hargreaves 1997). This creates a positive feedback that may further increase underwater UVR levels, especially in low-DOC lakes (Williamson et al. 1996).

It is important to note that the function of the UV-

lamp phototron is to separate out photoenzymatic repair (PER) and dark repair and photoprotection (DRPP) components of UVR tolerance. The data from the UV-lamp phototron should not be used to estimate UVR damage in nature on an energy basis because the spectral composition of the UVR is very different from that in sunlight (Fig. 4). For example, the ratio of UV-A:UV-B (380:320 nm) in the UV-lamp phototron is 0.3 in the fully exposed +PRR (photoreactivating radiation) treatments, while in natural sunlight (solar phototron quartz treatment) it is 2.2. In nature this ratio generally increases along environmental gradients in DOC or ozone (Figs. 11 and 12). The hazards encountered in extrapolating data from artificial light sources such as UV-B lamps to nature on an energy basis alone are evident from a comparison of the survival in the +PRR and -PRR treatments. In Fig. 9 we plot survival as a function of only the UV-B lamp energy as this is what we manipulated. Survival decreases with increasing energy from the UV-B lamps against a background of UV-A and visible light (Fig. 9). However, survival was much higher in the presence of PRR (i.e., higher energy: add 89 kJ/m² for PRR 280–400 nm to each UV-B lamp energy exposure on the x -axis of Fig. 9), than in the absence of PRR (=UV-B lamp exposure energy on x -axis in Fig. 9). In addition, PER may be somewhat underestimated in the UV-lamp phototron. Other experiments that we have carried out have shown that while PER is substantial with only two PRR lamps in the phototron, the PER response does not saturate until somewhere between four and six PRR lamps (equal numbers of 40-W UV-A 340 nm and cool-white lamps; M. E. Behum and C. E. Williamson, unpublished data). The negative impacts of UVR demonstrated here in both the UV-lamp and solar phototrons are also likely underestimated due to the short-term,

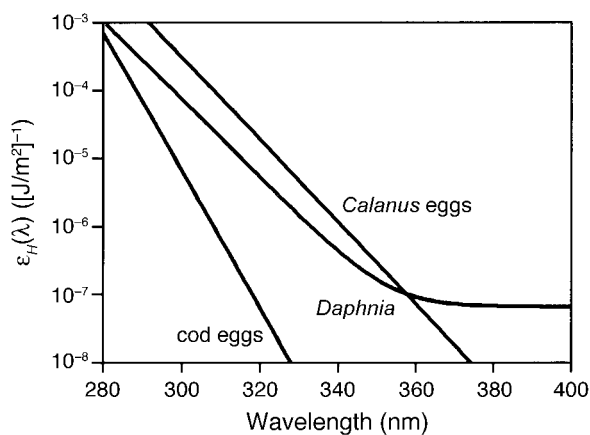


FIG. 13. Biological weighting function for *Daphnia pulicaria* plotted with weighting functions obtained for the eggs of a marine calanoid copepod *Calanus finmarchicus* and eggs of Atlantic cod (*Gadus morhua*) by Kouwenberg et al. (1999a, b).

acute nature of the experiments, as well as the focus on only lethal effects.

Our results also clearly demonstrate the complexity of estimating UVR damage to organisms such as *Daphnia* that have photoenzymatic repair. In the presence of photorepair, the reciprocity principle is not valid and the ability to effectively apply BWFs to dissimilar radiation regimes is compromised (Cullen and Neale 1997). The BWF that we generated is the result of the combination of both damage and repair processes going on during a sunny midday exposure near summer solstice at a latitude of about 40°N. It tells us the wavelengths of solar radiation that cause the greatest net damage (in terms of acute mortality response) in *Daphnia* under these conditions. The presence of PER in *Daphnia* means that reciprocity does not apply. In fact, we have demonstrated the lack of reciprocity in *Daphnia pulicaria* more explicitly in other experiments (Grad et al. 2001). The lack of reciprocity means that this BWF cannot be applied effectively to exposure conditions that differ greatly from this experiment such as would occur over longer exposure periods at deeper depths, during deep-mixing periods in the water column, or on cloudy days. Similarly, the lack of reciprocity and differences in the radiation regimes in our UV-lamp vs. solar experiments also means that our estimates of H^* for the UV-lamp experiments must be interpreted cautiously. For example, even if we use the 48-h survival data for *Daphnia* in the UV-lamp phototron experiment (analogous to the 42-h solar phototron survival data), the BWF overestimates survival at the highest UV-B exposure (33% predicted vs. 4% observed survival), and underestimates it at the lowest UV-B exposure level (69% predicted vs. 96% observed survival). At the intermediate exposures the BWF overestimates survival by 13–15%. Models that parameterize damage and repair processes separately will be necessary to deal with the inability to apply simple BWFs to a wide range of optical environments in the presence of PER. This is one of the major long-term goals of our studies, and one on which one of us has already begun to develop some of the basic model parameters (Neale et al., *in press*).

Knowledge of BWFs is important for the accurate interpretation of experiments that use various UVR filters. For example, many investigators use the sharp cutoff of Mylar D at 316 nm to experimentally estimate UV-B effects in nature. This cutoff goes right through the middle of the biologically effective exposure curve for *Daphnia* (Fig. 7), so Mylar D really only removes a portion of the shorter-wavelength UV-B rather than all of it. Multiplying the transmission spectrum of Mylar D by the solar energy spectrum for a full day (10 July 1998 data from the solar phototron experiment), reveals that Mylar cuts out only about 60% of the UV-B (solar energy at wavelengths <320 nm). Multiplying the transmission spectrum of Mylar D by the biologically effective UVR (H^* , Fig. 7), reveals that Mylar

D only cuts out about half (56%) of the biologically damaging solar UVR. This is an important consideration when interpreting experiments in which UVR-related mortality has been observed in treatments that were both shielded and unshielded from UV-B with Mylar D (Williamson et al. 1994, 1997, Zagarese et al. 1994). Total solar UVR impacts may be grossly underestimated when Mylar D is used to manipulate UVR. The exact percentages that Mylar D cuts out will vary with the shape of the solar spectrum at different times, depths, and geographic locations as well as the shape of the BWF of a given organism. Investigators should also be aware that there are several other types of Mylar that are not made to any particular optical specifications.

The presence of environmental gradients in the ratio of beneficial to detrimental UVR raises several interesting ecological questions. One question of particular interest is the potential importance of a threshold level above which additional UV-A and visible light no longer add to the enhancement of PER (M. E. Behum and C. E. Williamson, *unpublished data*). Does this threshold vary with the level of UV-B damage? Is more UV-A required to stimulate the repair of higher levels of UV-B damage? For example, although the UV-A:UV-B ratios are much lower in the surface waters of low-DOC lakes (Fig. 11), the absolute amounts of both damaging UV-B and beneficial UV-A are much higher (Fig. 10). If there is a threshold UV-A level above which PER does not increase, then UV-B damage will likely increase more rapidly as one approaches the lake surface than if no threshold exists and PER continues to increase towards the surface with increasing UV-A. The BWF experiments for *Daphnia* suggest that at very shallow depths such as those in the very surface waters of lakes, longer wavelength UV-A may reach a level that actually causes net damage.

Another question is how these environmental UVR gradients influence the interactions of *Daphnia* with other abiotic components of aquatic ecosystems. For example, there is a distinct demographic advantage to *Daphnia* that maximize their time spent in the warm surface waters of lakes (Orcutt and Porter 1983, Stich and Lampert 1984). Warmer temperatures speed up rates of growth and reproduction, and reduce the duration of the juvenile life stages that are most vulnerable to starvation and invertebrate predation. High CDOM may lead to shallower thermal stratification and warmer surface-water temperatures in smaller lakes (Fee et al. 1996). In these same lakes the higher CDOM will create a refuge from UVR damage (Figs. 10 and 11). In contrast, the surface waters of low-CDOM lakes are often somewhat cooler and will thus offer less of a demographic advantage to *Daphnia*. In these low-CDOM lakes much of the surface mixed layer may also be exposed to high levels of damaging UV-B that are 10% or more of surface levels (Fig. 10).

Environmental UVR gradients can also alter the in-

teractions of *Daphnia* with other trophic levels via indirect effects. For example, on the one hand photo-inhibition of phytoplankton by UVR may reduce the quality or quantity of *Daphnia*'s food supply (Moeller 1994, De Lange and Van Donk 1997, Hessen et al. 1997). On the other hand UVR may transform recalcitrant DOC to more labile DOC that stimulates the microbial loop and thus enhances *Daphnia*'s food supply (H. J. De Lange, D. P. Morris, and C. E. Williamson, unpublished manuscript).

Environmental UVR gradients may also influence the interaction of *Daphnia* with its predators. For example, larval fish have UV-A receptors that are thought to enhance their ability to forage on zooplankton prey (Loew et al. 1993, Browman et al. 1994). These same photoreceptors may also permit the larval fish to avoid damaging UVR in the surface waters of lakes. This may be particularly important to larvae of fish such as yellow perch, which are positively phototactic during the first months of their lives (Thorpe 1977), yet perish when exposed to only a few days of solar UVR in the surface waters of low-DOC lakes (Williamson et al. 1997). Interestingly, *Daphnia* also has UV photoreceptors (Smith and Macagno 1990), and exhibits a negative phototactic response when exposed to wavelengths of UVR shorter than ~360 nm, but a positive phototaxis to longer wavelengths of sunlight (Storz and Paul 1998, Leech and Williamson 2001). The ability of zooplankton and larval fish to detect and respond to UVR would enable them to use twilight migrations to increase their exposure to beneficial UVR and thus prolong photorepair in UV-B stressed environments (Fig. 12B). Twilight migrations involve upward migrations at dawn and dusk, with often substantial presence maintained in the surface water during the day (Hutchinson 1967). Parallel migration responses in zooplankton and fish would also alter the vertical overlap between predators and their prey during these twilight periods, potentially enhancing predation rates (Williamson 1993).

What are the implications of these results for ecosystem management? Human activities have pronounced effects on both CDOM and atmospheric ozone, the two major regulators of underwater UVR in pelagic ecosystems. On a global scale, stratospheric-ozone depletion has led to an increase in UV-B reaching the earth's surface, with the effect generally increasing with latitude in both northern and southern hemispheres. On a more regional scale, increases in tropospheric ozone from pollution can ameliorate these UV-B increases (Stolarski et al. 1992, Madronich 1998). The effects of damaging UVR are likely to be most pronounced in aquatic ecosystems with DOC concentrations <1–2 mg/L where UVR penetration is particularly high (Williamson et al. 1996). The source of the DOC will also determine its aromaticity and hence absorptivity of the CDOM content (McKnight et al. 1994). Local to regional changes in climate, acid precipitation, or watershed use may alter CDOM levels

and hence UVR in aquatic ecosystems (Schindler et al. 1996, Williamson et al. 1996, Yan et al. 1996). Protection of wetlands and vegetation coverage within the watershed may also be important to maintaining CDOM levels (Engstrom 1987, Engstrom et al. 2000, Williamson et al. 2001). All of these factors will in turn influence the availability of refugia from damaging UV-B, as well as the amounts of potentially beneficial longer wavelength UVR in aquatic ecosystems. Particular attention should be given to protecting high-elevation alpine lakes. With their small and fragile watersheds, short growing seasons, and high exposure to UVR, they are likely to be some of the most sensitive ecosystems to future changes in UVR.

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