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Ultraviolet radiation sensitivity of photosynthesis in phytoplankton from an estuarine environment

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Abstract

We have studied temporal variation in the sensitivity of phytoplankton photosynthesis to inhibition by ultraviolet radiation (UV; 280–400 nm) using biological weighting functions (BWFs) that quantify the biological effect of different wavelengths of UV. Variations in irradiance-dependent BWFs were evaluated for natural phytoplankton assemblages from the Rhode River, a shallow subestuary of the Chesapeake Bay, Maryland, from October 1994 to July 1996. Phytoplankton assemblages were sensitive to UV throughout the year. Rhode River assemblages are inhibited more strongly in the UV-B (280–320 nm), particularly below 300 nm, but there is a significant influence well into the UV-A (320–400 nm). There was no inhibition of phytoplankton photosynthesis by photosynthetically available radiation (400–700 nm), but there was significant seasonal variation in the saturated rate of photosynthesis (P_s^B) and in the light saturation parameter (E_s). There was little variation in seasonal average BWFs through the year, but there was considerable variation in BWFs during each season. Individual BWFs varied both in absolute values of the weightings (reciprocal [mW m^{-2}]) and in the spectral shape or relative effect of UV-B versus UV-A, which may be due to changes in species composition, light, temperature, and nutrient availability. Comparison of the most sensitive assemblage (spring) with the least sensitive assemblage (winter) indicates that these BWFs are close to the upper and lower bounds in sensitivity for irradiance-dependent BWFs from all natural and cultured phytoplankton populations. The average, absolute spectral weightings for inhibition of photosynthesis in assemblages from the Rhode River are similar to an average BWF for Antarctic assemblages.

Ultraviolet radiation (UV; 280–400 nm) has deleterious effects on aquatic organisms that are manifested at genetic, physiological, and biochemical levels. These effects occur in habitats ranging from tropical environments, where UV radiation is naturally high, to polar environments, where the levels of UV radiation can become elevated during springtime ozone-depletion events. Stratospheric ozone loss results in a wavelength-dependent shift of incident UV-B (280–320 nm; however, there is no significant surface irradiance for wavelengths below 290 nm) because of the penetration of shorter wavelengths, which are more energetic and more biologically harmful (Lubin et al. 1992). In comparison, UV-A (320–400 nm) and photosynthetically available radiation (PAR; 400–700 nm) remain essentially unaffected by ozone depletion.

Assessments of the effects of variable UV-B have to be made in the context of the full UV spectrum, because both UV-B and UV-A can affect physiological processes and contribute to changes in community structure (Bothwell et al. 1994). Phytoplankton are constrained to photic environments where they are exposed to PAR and UV, possibly requiring a tradeoff between absorption of adequate PAR for photosynthesis and increased exposure to damaging UV. The inhibition of phytoplankton photosynthesis by UV is one effect of major ecological significance, although it is not the only type of damage that can occur (Vincent and Neale 2000 and references therein). Numerous studies have shown that UV-B and UV-A inhibit photosynthesis in natural populations (Helbling et al. 1992; Smith et al. 1992; Behrenfeld et al. 1993; Neale et al. 1994) and cultures (Cullen and Lesser 1991; Cullen et al. 1992; Neale et al. 1998*a*).

To identify the physiological and ecological processes that dominate phytoplankton responses to UV and to assess what portion of responses is associated with ozone-dependent changes in UV-B requires the development of wavelength-dependent weighting functions. Biological weighting functions (BWFs) describe the effectiveness of radiation of different wavelengths to produce a biological response such as inhibition of photosynthesis. A wavelength-dependent description of UV effects on photosynthesis (the BWF/P-I model) has been developed that describes photosynthesis as a function of PAR and photoinhibition as a function of both PAR and UV (Cullen et al. 1992; Neale et al. 1994). Two versions of the BWF/P-I model (the *E* and *H* models) are in use contingent on whether inhibition of photosynthesis is dependent on the rate of exposure (*E*, irradiance) or cumulative exposure (*H*). The irradiance-dependent model (the *E* model) applies when active repair counterbalances the effect of UV damage and photosynthesis attains a steady state during exposure, as has been observed for cultures of temperate phytoplankton (Lesser et al. 1994). Experimental exposures used for estimating a BWF are polychromatic—i.e., shorter

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Table 1. Dates and sites of collections of water samples for determination of biological weighting functions (BWFs) and the dominant phytoplankton species present. Sample sites are described in Gallegos et al. (1992). Sta. 4B is located in the Rhode River, ~4 km upriver from the mouth on the Chesapeake Bay. ''Dock'' refers to a sample taken at the same channel position as Sta. 4B but ~20 m from shore at the end of the SERC pier; Sta. 1A is located 1.4 km east of the mouth of the Rhode River to the Chesapeake Bay; the Bay Bridge is located on the Chesapeake Bay ~20 km north of the Rhode River mouth. ''Int.'' refers to integrated (whole water-column) samples, and ''Surf.'' refers to samples taken of surface water only.

Date	Sampling site	Dominant diatom	Dominant dinoflagellate	Other dominant flagellates
13 Oct 94	4B Int.	*Cyclotella glomerata*		*Cryptomonas* sp.
03 Nov 94	4B Int.	*C. glomerata*		
21 Nov 94	4B Int.	*Skeletonema costatum*		
11 Jan 95	Dock Int.		*Katodinium rotundatum*	
07 Mar 95	4B Int.	*Chaetoceros* sp.	*K. rotundatum*	*Cryptomonas* sp.
06 Apr 95	4B Int.	*Chaetoceros* sp.	*K. rotundatum*	*Cryptomonas* sp.
18 Apr 95	4B Int.	*Cerataulina pelagica*	*Prorocentrum minimum*	*Cryptomonas* sp.
03 May 95	4B Int.	*Thalassiosira pseudonana*	*P. minimum*	
16 May 95	4B Int.	*T. pseudonana*	*Gymnodinium* sp.	*Chrysochromulina* sp.
31 May 95	Dock Int.		*Gyrodinium uncatenum*	
01 Jun 95	Dock Int.		*G. uncatenum*	
12 Jul 95	Bay Bridge Surf.	*Chaetoceros debilis*	*K. rotundatum*	*Chrysochromulina* sp.
18 Jul 95	4B Int.	*Chaetoceros* sp.	*P. minimum*	*Chroomonas* sp.
27 Jul 95	4B Int.		*P. minimum*	
02 Aug 95	1A Surf.		*Scrippsiella trochoidea*	
08 Aug 95	4B Surf.		*S. trochoidea*	
22 Aug 95	4B Surf.	*Chaetoceros* sp.	*Gymnodinium* sp.	
13 Sep 95	4B Surf.		*Polykrikos hartmanni*	
25 Oct 95	4B Int.	*S. costatum*		*Cryptomonas* sp.
20 Nov 95	Dock Int.	*S. costatum*		
13 Dec 95	4B Int.		*K. rotundatum*	*Apedinella radians*
27 Mar 96	Dock Surf.		*K. rotundatum*	
03 Jul 96	Dock Int.		*P. minimum*	

wavelengths of UV-A then UV-B are added to a constant background of PAR, as occurs during environmental exposure (Rundel 1986). It is critical for BWFs to have both high resolution and spectral accuracy in the UV-B region. Solar spectral irradiance drops by three orders of magnitude or more in the 290–320 nm region because of absorption by stratospheric ozone. Small changes in absolute energy levels may represent large effects when weighted by a BWF and may substantially change predictions of UV-B–induced photoinhibition.

The level of photoinhibition will be modified by many factors that influence the extent of exposure and the sensitivity (BWF) of the phytoplankton. High irradiance will enhance photoinhibition when the damage incurred exceeds the capacity of photoprotective and repair processes (Neale 1987). Phytoplankton encountering shallow mixing conditions (Neale et al. 1998*c*) or forming surface blooms will be exposed to high irradiance. Photoinhibition will extend deeper in water bodies with low attenuation coefficients and greater penetration of UV radiation.

Photoprotective and repair processes are particularly important in preventing and reversing the damage to photosynthesis by UV (Lesser et al. 1994; Neale et al. 1994). The induction of photoprotective mechanisms could change the absolute weights and shapes of BWFs by the presence of pigments or UV-screening compounds that absorb in the wavelength range causing the damage (Neale et al. 1994). A specific decrease in the weighting function in the region of absorbance of these compounds would indicate a photoprotective function, as was found for mycosporine-like amino acids (MAAs) in *Gymnodinium sanguineum* (Neale et al. 1998*a*). Carotenoids also act in a photoprotective function against high irradiance (Demers et al. 1991). Organisms have varying abilities to reverse the effects of UV radiation (Karentz et al. 1991; Lesser et al. 1996). Repair may be ongoing (Lesser et al. 1994), may mostly occur after UV exposure (A. T. Banaszak et al. unpubl. data), or may be largely absent (Neale et al. 1998*b*). During exposure to polychromatic UV + PAR, a range of potential repair processes (Neale et al. 1994) is stimulated by longer wavelengths, thus counteracting the damaging effects of UV radiation (Hirosawa and Miyachi 1983; Samuelsson et al. 1985; Neale 1987). Low temperatures have also been hypothesized to enhance the effects of photoinhibition, most likely because of slower rates of repair (Neale et al. 1994; Lesser et al. 1996). Low nutrient levels may increase the photoinhibitory effect on UV-exposed assemblages by limiting both photoprotective and repair processes (Cullen and Lesser 1991; Behrenfeld et al. 1994; Lesser et al. 1994; E. Litchman and P. J. Neale unpubl. data). Thus, the relative importance of repair versus protection will vary depending on specific conditions and the physiological characteristics of the assemblage.

Most studies of the effects of UV radiation on phytoplankton photosynthesis have concentrated on Antarctica, because of the annually occurring, springtime ozone hole. Relatively little is known about the responses of marine phytoplankton in temperate regions with near-normal ozone levels, particularly over the full seasonal cycle. In particular, there has

Table 2. Notation

$a_{det}(\lambda)$	m^{-1}	Detrital particulate (tripton) absorption coefficient
$a_{part}(\lambda)$	m^{-1}	Total particulate absorption coefficient
$a^*_{phy}(\lambda)$	m^2 mg Chl^{-1}	Phytoplankton absorbance normalized to chlorophyll
E^*_{inh}	Dimensionless	Biologically effective fluence rate for the inhibition of photosynthesis
$\varepsilon(\lambda)$	$(mW\ m^{-2})^{-1}$	Biological weightings for inhibition of photosynthesis as a function of UV irradiance
E_{PAR}	W m^{-2}	Photosynthetically available radiation (400–700 nm)
E_s	W m^{-2}	Characteristic irradiance (E_{PAR}) for saturation of photosynthesis
λ	nm	Wavelength
P^B	mg C mg Chl^{-1} h^{-1}	Photosynthesis normalized to chlorophyll *a*
P^B_s	mg C mg Chl^{-1} h^{-1}	Maximum rate of photosynthesis in the absence of inhibition
UV, E_{UV}	mW m^{-2} nm^{-1}	Ultraviolet radiation (280–400 nm) Incident solar UV (290–400 nm)
UV-A	mW m^{-2} nm^{-1}	UV radiation between 320 and 400 nm
UV-B	mW m^{-2} nm^{-1}	UV radiation between 280 and 320 nm

been little study of shallow estuarine waters, the phytoplankton dynamics of which are receiving increased attention because of the rising frequency of harmful algal blooms. Some studies of other planktonic systems indicate that there is less sensitivity to inhibition by UV radiation during the summer months, compared with the spring or fall, but BWFs were not determined (Hobson and Hartley 1983; Gala and Giesy 1991). Furgal and Smith (1997) measured inhibition in freshwater phytoplankton by natural solar UV-B and under controlled conditions, using fluorescent lamps. Although solar effects did vary throughout the year, UV inhibition under the artificial irradiance was fairly constant.

The objective of this study was to determine the spectral dependence of photoinhibition in estuarine phytoplankton and to evaluate how the absolute sensitivities of phytoplankton to UV radiation might change seasonally. Direct measurements on natural phytoplankton populations are used to assess the variability in sensitivity and to determine whether a generalized BWF is suitable to characterize phytoplankton photosynthetic response to UV radiation.

Materials and methods

Sample collection—Integrated water-column samples were collected by use of a Labline 2L teflon sampler at ~1100 h on each of the dates indicated in Table 1. The majority of the samples were collected from the Rhode River, which is a turbid, eutrophic (Gallegos 1992) subestuary on the western shore of the Chesapeake Bay in Maryland. The primary sampling site (Sta. 4B) is located in an estuary segment with a mean depth of 1.6 m (Jordan et al. 1991). Two additional locations were sampled. One station (1A) is located 1.4 km east of the mouth of the Rhode River, and the other sample (Bay Bridge) was obtained on the eastern shore of the bay close to the Chesapeake Bay Bridge. The water samples were immediately transferred into an opaque plastic bottle and maintained in the dark for <1 h at ambient water temperature until determination of photosynthesis-irradiance (P-E) curves in the laboratory. The temperature profile of the water column was measured at the time of sampling by use of a Hydrolab temperature profiler, and Secchi depth was measured with a 20-cm solid white disk. Additional samples for optical measurements were taken in 1999. At these stations (Rhode River only), spectral irradiance (2-nm bandwidth) was measured by use of a Satlantic OCP 200 radiometer with filter center wavelengths of 325, 340, and 380 nm and 10 wavelengths (10-nm bandwidth) in the visible range.

Photosynthesis measurements—Within 1 h of collection of the water samples, photosynthesis as a function of UV and PAR was measured by use of uptake of ^{14}C-bicarbonate and a modification of the ''photoinhibitron'' experimental system, as described by Cullen and Neale (1997). An aliquot was also used to simultaneously measure photosynthesis as a function of PAR by use of a modification of the ''photosynthetron'' method (Lewis and Smith 1983) to obtain robust estimates of P^B_s and E_s (*see* Table 2 for notation). The photoinhibitron and the photosynthetron incubations were maintained at ambient water temperatures by use of recirculating water baths. During the summer months, a 2.5-kW xenon arc lamp was used as the light source for the photoinhibitron experiments, whereas during other times of the year, a 1-kW xenon arc lamp was sufficient to saturate photosynthesis. The light-source beam was reflected upward by a mirror through a recirculated heat trap onto quartz-bottom vials containing the phytoplankton suspension inoculated with ^{14}C-bicarbonate. The illuminated region was divided into eight polychromatic sections by use of 5 × 5 cm Schott series WG long-pass filters with nominal cutoffs (50% T) of 280, 295, 305, 320, 335, 345, and 360 nm and a Schott GG 400-nm long-pass filter as a control (essentially no UV radiation). Each of the eight sections was further divided into nine positions modified by insertion of neutral-density nickel screens, resulting in 72 different combinations of spectral composition and irradiance.

Irradiance measurements—Spectral irradiance [$E(\lambda)$, mW m^{-2} nm^{-1}] in each of the 72 treatments of the ''photoinhibitron'' was measured by use of a calibrated 1,024-channel diode-array spectroradiometer system (EG & G) consisting of a quartz fiber-optic probe fitted with a diffuser appropriate for measuring UV and PAR coupled to a spectrograph with gratings suitable for UV and PAR regions (Acton Research) (Cullen and Lesser 1991). The spectroradiometer was calibrated by scanning a mercury arc lamp for wavelength offset and a 1-kW quartz halogen lamp (Eppley) traceable to the National Institute of Standards and Technology for intensity. For measuring UV (E_{UV}), the lower-wavelength limit for significant irradiance in the treatments was 282 nm, and the

upper-wavelength limit was 395 nm for the grating configuration. E_{PAR} was calculated by use of the measured spectral irradiance from 400 to 700 nm. Correction for stray light at wavelengths <310 nm was made by use of a Schott WG 345 nm long-pass filter (Cullen and Lesser 1991). Quantitative characterization of the 72 spectral treatments was obtained by use of principal component analysis (PCA) of spectra of E_{UV} normalized to E_{PAR}, as described by Cullen and Neale (1997). Spectral components common to all 72 treatments were calculated for each experiment. When PCA was used, the large number of original wavelengths could be adequately represented by two or three components (Neale et al. 1994). Irradiance measurements in the ''photosynthetron'' were made with a quantum scalar (4π) sensor (Biospherical Instruments QSL-100).

Generation of biological weighting functions—Cullen et al. (1992) developed an irradiance-dependent analytical model (BWF_E/P-I) in which photosynthesis is described as a function of PAR and photoinhibition is dependent on biologically weighted UV irradiance and PAR (Cullen and Neale 1997) such that

$$P^B = P_s^B \tanh(E_{PAR}/E_s)\left(\frac{1}{1 + E^*_{inh}}\right), \quad (1)$$

where P_s^B is the maximum attainable rate of photosynthesis in the absence of photoinhibition, E_{PAR} is PAR expressed as irradiance in energy units (W m^{-2}), and E_s is a saturation parameter for photosynthesis (c.f. Jassby and Platt 1976). P^B is the product of potential photosynthesis $[P_s^B \tanh(E_{PAR}/E_s)]$ and inhibition $[1/(1 + E^*_{inh})]$ and is the rate of photosynthesis normalized to chlorophyll (mg C mg Chl^{-1} h^{-1}). The inhibition term is a function of E_{UV}, expressed as biologically weighted exposure, E^*_{inh} (dimensionless), where

$$E^*_{inh} = \sum_{\lambda=282\text{ nm}}^{395\text{ nm}} \varepsilon(\lambda) \times E(\lambda) \times \Delta\lambda \quad (2)$$

and $\varepsilon(\lambda)$ is the wavelength-dependent biological effectiveness for inhibition of photosynthesis by UV $(\text{mW m}^{-2})^{-1}$. Although a parameter for E_{PAR}-dependent inhibition (i.e., ε_{PAR}) can be included in Eq. 2, it was not needed. The BWF/P-I model (Eq. 1) is similar to that described by Cullen and Neale (1997), except that potential photosynthesis is described by a hyperbolic tangent P-E function (Jassby and Platt 1976), which gave higher R^2 values for the model than did fitting to an exponential function. The parameters of the BWF/P-I model were determined statistically from results of the ^{14}C incorporation under a broad range of UVB:UVA:PAR spectral ratios and absolute intensities of PAR, by use of the PCA approach (Cullen et al. 1992; Neale et al. 1994; Cullen and Neale 1997). Briefly, Eq. 2 is transformed to express E^*_{inh} in terms of spectral components, so that fitting the BWF requires estimation of only three or four coefficients (h_o, the mean treatment effect over the whole irradiance spectrum; h_i, the component effect where i corresponds to components 1, 2, or 3) to account for most of the variation in P^B. This method does not sacrifice spectral resolution and requires no a priori assumptions about spectral slope, as is the case for the Rundel approach (Rundel 1986). In most cases, the best fit to the data required a two-component model, and, in rare instances, a three-component model was used. No further significant increase in R^2 was obtained by incorporating more components. The fitted model for the photoinhibitron measurements had an average $R^2 = 0.93$ (minimum = 0.80, maximum = 0.97). An average BWF was computed for each season, with 95% confidence intervals calculated from the standard errors of individual BWFs by use of propagation of errors (Bevington 1969).

Independent measures of P_s^B and E_s were also obtained from detailed (PAR only) P-E curves. Aliquots (1 ml) were incubated in 7-ml scintillation vials by use of 38 different light levels. Irradiance was provided by 250-W halogen bulbs attenuated by use of neutral density screens and measured by use of a quantum scalar sensor (QSL-100) mounted inside a scintillation vial. Quantum scalar irradiance (μmol photons m^{-2} s^{-1}) was converted to E_{PAR} (W m^{-2}) by application of a conversion factor (4.9 μmol J^{-1}) determined from measured spectral irradiance. The photosynthetic parameters (P_s^B and E_s) were estimated as in Eq. 1 (i.e., with $E^*_{inh} = 0$). Curves were fitted with both the hyperbolic tangent function and the exponential function. As for the photoinhibitron data, the hyperbolic tangent function consistently gave better fits than the exponential function.

Cellular absorption and chlorophyll concentrations—Triplicate aliquots of phytoplankton samples were concentrated onto glass-fiber filters (Whatman GF/F) and scanned against a wetted blank filter in a Cary IV spectrophotometer from 280 to 750 nm, to estimate particulate-absorption coefficients. After scanning a fresh filter for total absorbance (a_{part}), the filters were then extracted into 100% methanol overnight, rinsed, and rescanned, to determine detrital absorbance (a_{det}). The phytoplankton absorption coefficient (a^*_{phy}) was estimated from the difference $a_{part} - a_{det}$ normalized to the chlorophyll concentration. Particulate absorbance of samples collected in 1994 was estimated by illuminating the filters with a 1-kW xenon arc source and measuring the spectral transmission by use of the quartz fiber optic coupled to a diode array spectrograph, as described earlier for UV spectral characterization. Because we were interested mainly in the correlation of absorbance and other optical parameters, we did not correct for pathlength amplification (β). Chlorophyll *a* concentrations in phytoplankton samples were determined in triplicate aliquots, which were filtered onto glass-fiber filters (Whatman GF/F), extracted into 10 ml of 90% acetone at −4°C for 24 h, and measured fluorometrically in a Turner Designs fluorometer. The fluorometer was calibrated annually with spinach Chl *a* (Sigma).

MAA concentrations—The extraction and analysis of MAAs by reverse-phase, isocratic, high-performance liquid chromatography (HPLC) were performed according to the procedures in Dunlap and Chalker (1986) with modifications. Approximately 50 ml of sample water was filtered onto glass-fiber filters (Whatman GF/F), extracted overnight into 100% HPLC-grade methanol at 4°C, centrifuged, and the supernatant used for MAA analysis. MAAs were separated on a Brownlee RP-8 column (Spheri-5, 4.6 mm ID × 250 mm), protected with an RP-8 guard column (Spheri-5,

4.6 mm ID × 30 mm). The mobile phase, which consisted of 25% methanol (v:v), 0.1% glacial acetic acid (v:v) in water, was run at a flow rate of 0.7 ml min^{-1}. Identities of peaks were resolved by the wavelength of maximal absorbance with confirmation by primary and secondary standards by use of a diode array UV absorbance detector (Beckman Gold System). All MAA concentrations were normalized to Chl *a*, and concentrations are expressed in nmol (nmol chlorophyll)$^{-1}$.

Incident irradiance—Total incident irradiance (cal cm^{-2} d^{-1}) was measured with an Eppley pyroheliometer, and spectral solar UV-B (minute averages) was measured over the spectral range of 290–325 nm by use of a multifilter radiometer with either 8 5-nm bandwidth filters (Correll et al. 1992) or 18 2-nm bandwidth filters (Early et al. 1998).

Results

A seasonal study of variation in sensitivity of Rhode River phytoplankton to photoinhibition by UV radiation was begun during October 1994 (Table 1). For the purposes of analysis, seasons were divided into ''fall'' (23 September–22 December), ''winter'' (23 December–22 March), ''spring'' (23 March–22 June), and ''summer'' (23 June–22 September). The number of replicates in each season was seven, except in winter, when the number of replicates was two. The fall and winter seasons tended to be diatom-dominated populations, whereas during spring, summer, and early fall, dinoflagellates numerically dominated the water column. Other photosynthetic flagellates were present year round in the water samples but were usually less abundant than dinoflagellates or diatoms (Table 1).

Photosynthetic parameters—The photosynthetic parameters (Fig. 1) of the estuarine community varied seasonally. The photosynthetron-based estimates of the light-saturated rate of photosynthesis (P_s^B) and the light saturation parameter (E_s) ($n = 38$) had lower standard errors than fits of the same parameters using the photoinhibitron. Although data from the photoinhibitron has more degrees of freedom ($n = 72$), the design is not optimized for estimates of PAR-dependent photosynthesis. The hyperbolic tangent–based P-E curves were fitted with an R^2 ranging from a minimum of 0.93 to a maximum of 1.00, with an average of 0.98. Documentation of these photosynthetic parameters allowed for an inventory of the physiological state of the community at the time of the determination of the BWF. No PAR photoinhibition was observed up to 400 W m^{-2} PAR. The chlorophyll-specific, light-saturated rate of photosynthesis (P_s^B) varied 20-fold (Fig. 1A) over the seasons, whereas photosynthetic efficiency ($\alpha = P_s^B/E_s$) varied 7-fold (Fig. 1B). Chlorophyll concentrations varied 14-fold (Fig. 1C), with a general trend of low chlorophyll concentrations during winter months and higher chlorophyll concentrations during spring and summer months.

Seasonal variation in biological weighting functions—P-E curves generated by use of the photoinhibitron indicated

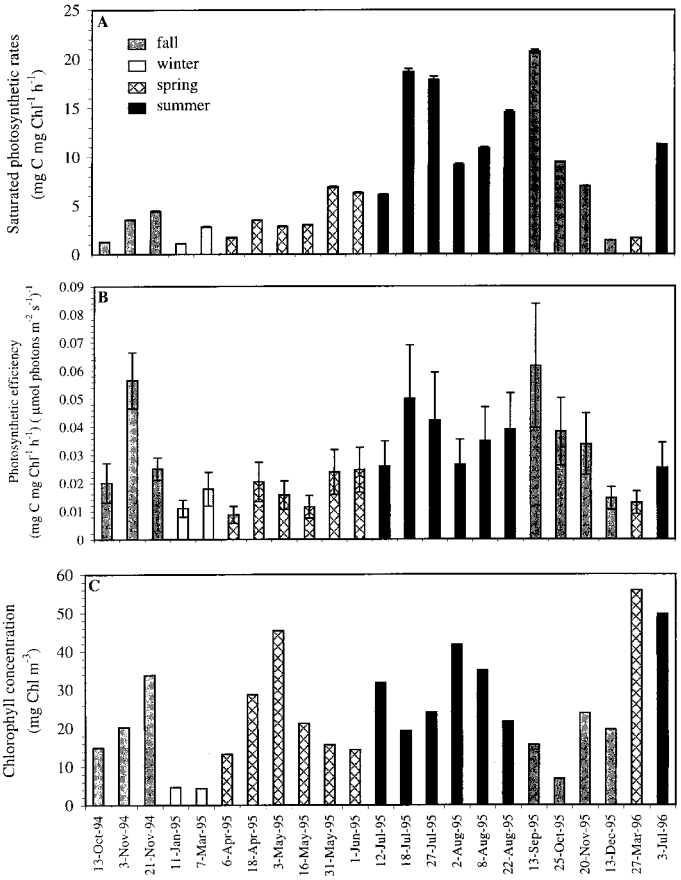

Fig. 1. Seasonal variation in photosynthetic parameters of estuarine phytoplankton from October 1994 to July 1996. Comparison of (A) estimates of the chlorophyll-specific saturated rate of photosynthesis (P_s^B, mg C mg Chl^{-1} h^{-1}); (B) estimates of the chlorophyll-specific photosynthetic efficiency (α, mg C mg Chl^{-1} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$); and (C) chlorophyll concentrations (mg Chl m^{-3}) for each sample used in determining a biological weighting function. Error bars show the standard error of the photosynthetic parameter estimates. Shading corresponds to grouping of dates into fall, winter, spring, or summer seasons.

inhibition of photosynthesis, as determined by ^{14}C uptake, at saturating intensities when samples were exposed to UV radiation. As progressively shorter wavelengths of UV-A then UV-B were added to a constant background of PAR, photoinhibition became progressively more severe (data not shown, but *see* Neale et al. 1998*a* for an example data set).

An irradiance-dependent BWF/P-I model was chosen for UV inhibition of Rhode River phytoplankton. When photosynthetic rates reach steady-state levels rapidly, photoinhibition can be described as a function of irradiance (Neale and Richerson 1987; Cullen and Lesser 1991). On the basis of time courses of Rhode River phytoplankton photosynthesis as inferred from pulsed amplitude–modulated fluorometry (data not shown), steady-state levels were reached within ~20 min of exposure to UV radiation.

When averaged over each season, BWFs for UV inhibition of photosynthesis in Chesapeake Bay phytoplankton do not vary significantly between seasons (Fig. 2). Rhode River assemblages are inhibited more strongly in the UV-B, par-

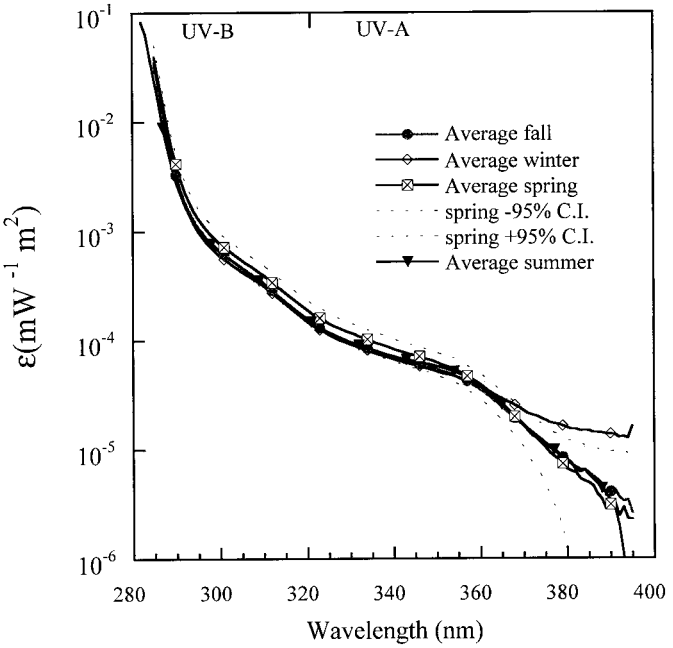

Fig. 2. BWFs for inhibition of photosynthesis by UV radiation in phytoplankton from the Rhode River, Chesapeake Bay. Weighting functions shown are the averages for fall 1994 and 1995 (n = 7), winter 1995 (n = 2), spring 1995 and 1996 (n = 7), and summer 1995 and 1996 (n = 7). Estimated 95% confidence intervals for each average were calculated by propagation of errors from the standard errors of individual BWFs. For clarity, only the 95% confidence interval for the spring average is shown, the 95% confidence intervals for the other averages are similar in width.

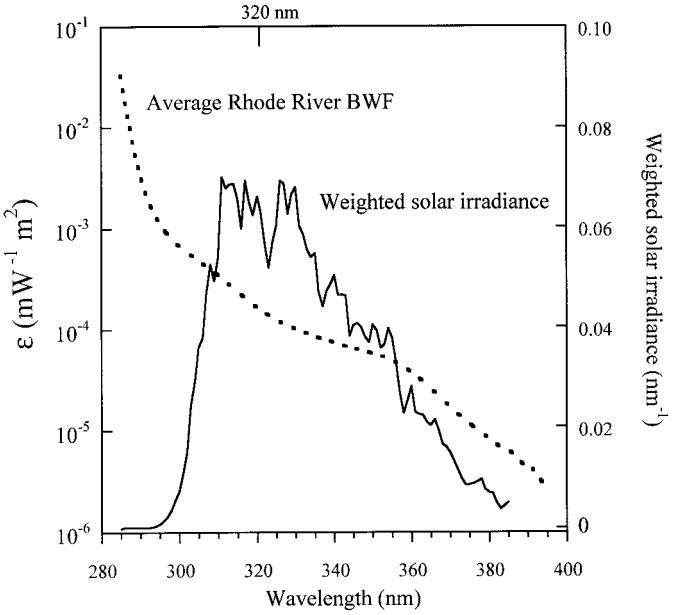

Fig. 3. Weighted solar irradiance determined by use of the product of a BWF with solar irradiance. The BWF is the average (n = 23) estimated for inhibition of photosynthesis by UV radiation for phytoplankton from the Rhode River, Chesapeake Bay. The spectral irradiance used for the weighting is a near-summer-solstice, noontime measurement (mW m^{-2} nm^{-1}) taken at Table Mountain, Colorado (40°N) with a total column ozone of 290 Dobson units (Early et al. 1998) and smoothed to 1-nm effective bandwidth.

ticularly below 300 nm, but there is a significant influence well into the UV-A. When the average BWF (n = 23) for Rhode River phytoplankton was used to weight a near summer solstice a spectral-irradiance curve recorded at a similar latitude (Table Mountain, Colorado, 40°N), effective irradiance was highest in the range from 310 to 330 nm (Fig. 3). There was considerable variation in the BWFs during each season. Figure 4 shows the least sensitive (11 January 1995) and most sensitive (6 April 1995) BWFs obtained for the Rhode River; these BWFs are significantly different from each other (95% confidence intervals not shown for clarity). There are differences in the sensitivity or offset between the two BWFs, and there is variation in the spectral shape or relative effects of UV-A versus UV-B in these assemblages. Other BWFs for the Rhode River are distributed fairly evenly between the minimum and maximum BWFs, as shown by the variation in weightings at 310 nm [ε(310)] as a function of time (Fig. 5A). The photoprotective properties of the phytoplankton also do not show any seasonal trends. Figure 5B shows the variation in MAA content that ranged from undetectable to ~6 nmol (nmol Chl)$^{-1}$. The mean ratio of phytoplankton particulate absorbance (a^*_{phy}) at 310–665 nm is 1.5 (data not shown), consistent with the presence of moderate concentrations of UV-absorbing compounds.

Environmental variation—Although there was little seasonal variation in ε(310), there was seasonal variation in several other basic environmental parameters. Temperature is highly variable in this shallow-water environment, ranging from <5°C in the winter to >30°C in the summer (Fig. 5C). A general indication of water transparency was provided by Secchi depth, which was ~0.5 m during the late spring and summer but was usually >1.0 m during the fall and winter. To better understand spectrally specific changes in water transparency, we examined the relationship between particulate absorbance and attenuation coefficient. This could be done using a more recent (1999) data set of particulate absorbance (measured as described) and spectral attenuation (K_d) at 325 and 340 nm and for PAR, measured in the Rhode River by use of a Satlantic OCP 200 profiling spectroradiometer (C. L. Gallegos et al. unpubl. data). In this data set (not shown), we focused on 340 nm as a general indicator of UV transparency. Both total [a_{part}(340)] and detrital [a_{det}(340)] particulate absorbance are correlated with K_d at 340 nm, but the strongest association is with detrital absorbance (R^2 = 0.67). This indicates that detritus and detrital correlates (e.g., dissolved organic matter) are the dominant factors influencing variations in UV attenuation of these shallow (1.5 m average in the Rhode River) waters (Kirk 1994).

The a_{det}(340) of samples used for the BWF measurements suggest a general seasonal cycle of UV water transparency with lowest attenuation (highest transparency) in the winter and greatest attenuation in the summer (Fig. 5D), consistent with the Secchi depths. The sample from the deeper-water (7 m) Bay Bridge station (12 July 1995) is an exception to this pattern. Here, a_{det}(340) was comparatively low (0.8 m^{-1}),

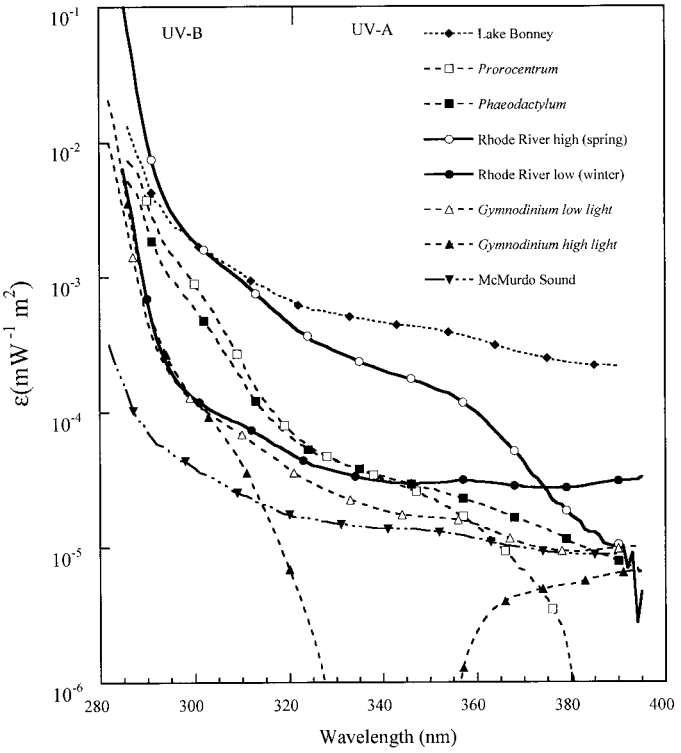

Fig. 4. Comparison of absolute spectral weights for UV inhibition of photosynthesis in natural phytoplankton assemblages from the Rhode River with high (spring) and low (winter) sensitivity with published irradiance-dependent BWFs. The published BWFs are for a natural phytoplankton assemblage from Lake Bonney, Antarctica (Neale et al. 1994); a laboratory culture of the dinoflagellate *Prorocentrum micans* (Cullen et al. 1992); a laboratory culture of the diatom *Phaeodactylum* sp. (Cullen et al. 1992); low- and high-light-acclimated laboratory cultures of the dinoflagellate, *G. sanguineum* (Neale et al. 1998a), and a natural diatom-dominated assemblage from McMurdo Sound, Antarctica maintained in outdoor culture (Neale et al. 1994).

even though the Secchi depth was shallow (0.75 m). This suggests that our empirical relationship between $a_{det}(340)$ and K_d only holds in shallow waters. The seasonal cycle of water transparency inferred from $a_{det}(340)$ is the reverse of the seasonal variation in solar irradiance, particularly in the UV. The seasonal variation of UV in the water column is less than the seasonal variation in incident irradiance (Table 3). A similar analysis based on the correlation of $a_{det}(340)$ and K_d for PAR in the Rhode River indicates that changes in water transparency had less impact on the seasonal variation of PAR (Table 3). Seasonal variation of nutrient availability is well established for the Rhode River (Gallegos et al. 1992; Jordan et al. 1992). In particular, nitrate is usually abundant in the late fall through early spring but low the rest of the year (except for episodic watershed events). Nutrients were not measured for the samples used for BWF analysis, but routine measurements of the Rhode River during the period indicate that nitrate was low (<1 μM) during the whole sample period, except for the winter 1995 and early spring 1996 (27 March) samples (T. Jordan pers. comm.).

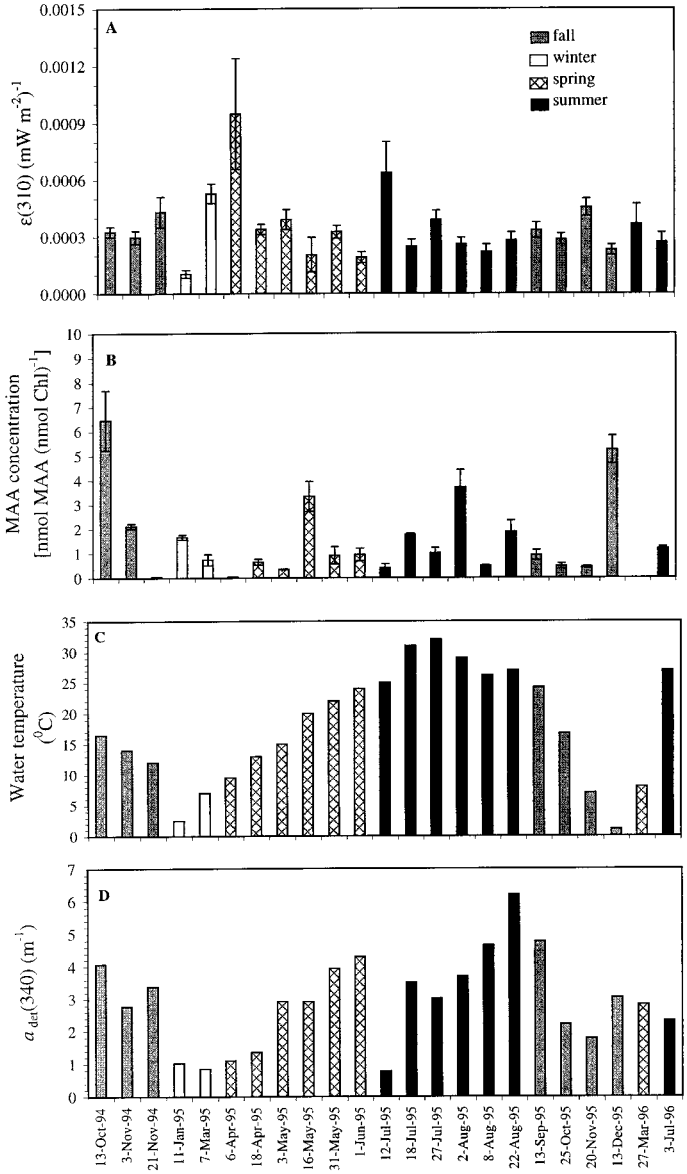

Fig. 5. Seasonal variation in (A) spectral weighting function for inhibition of photosynthesis at 310 nm [$\varepsilon(310)$, (mW m^{-2})$^{-1}$], (B) total concentration of MAAs (nmol [nmol Chl]$^{-1}$), (C) water temperature (°C), and (D) detrital particulate absorbance ($a_{det}(340)$, m^{-1}). The error bars show the standard error (n = 3) of MAA concentrations and the 95% confidence intervals of ε[310].

Impact of UV on primary production—The main objective of this study was to understand the seasonal variation of BWFs, and the optical data necessary to make a comprehensive assessment of in situ effects were not measured. Nevertheless, a first-order sensitivity analysis was performed to ascertain the potential for UV impacts on Rhode River primary production. The details of this calculation can be obtained from P. Neale. The sensitivity analysis used observations of surface spectral irradiance (noon, 4-week period around summer solstice 1999; c.f. Fig. 3), optical penetration (weekly profiles summer 1999), and BWFs (this study) to

Table 3. Seasonal variation of incident and in situ irradiance in the Rhode River. Irradiance was averaged for the 1 week period prior to sampling (Table 1), from which a seasonal average was calculated grouping samples as in Fig. 5. Average irradiance over the water column was estimated by use of the formula $E_0(1 - e^{-kz})/kz$, where E_0 is incident irradiance, k is the attenuation coefficient, and depth (z) is 1.5 m. Integrated daily irradiance (cal cm^{-2} d^{-1}) measured with an Eppley pyroheliometer was converted to mol photons m^{-2} d^{-1} of PAR by use of the factor 9.6×10^{-6} mol photons cal^{-1}. The attenuation coefficient for PAR (K_{dPAR}) was estimated from a_{det} (340) on the basis of regression analysis of 1999 data ($R^2 = 0.47$). Incident UV-B for the 1-h period centered around solar noon in the 320–325-nm wavelength range (mW m^{-2}) was measured with a Smithsonian multifilter (SR8 or SR18) spectroradiometer. The attenuation coefficient for 325 nm [(K_d(325)] was estimated by application of the average ratio of $K_d(325) : K_d(340)(1.3)$ to K(340), estimated from regression with a_{def}(340) in 1999 data ($R^2 = 0.67$). The last column is the ratio between the maximum and minimum value in each row.

	Winter	Spring	Summer	Fall	Max/ Min
Incident					
PAR (mol m^{-2} d^{-1})	21.5	33.9	42.2	21.3	2.0
UV (320–325 nm) (mW m^{-2})	401.0	877.6	879.1	612.1	2.2
In situ					
PAR (mol m^{-2} d^{-1})	8.0	11.6	13.2	6.8	2.0
UV (320–325 nm) (mW m^{-2})	39.0	70.3	62.8	44.4	1.6

calculate depth-integrated primary production to 1.6 m. According to this analysis, midday primary production in the presence of UV is 3%–33% lower than PAR-only production, depending on conditions. Variation in sensitivity and optical properties (UV and PAR transparency) contributed about equally to the variation in inhibition by UV. Optical variation may be even more important on short timescales, because time series (1-h resolution) of optical properties in the Rhode River have revealed many-fold changes in transparency over the course of a few hours (Gallegos and Neale; unpublished data).

Discussion

We have determined 23 BWFs for inhibition of phytoplankton photosynthesis, which constitute the first annual survey of BWFs for phytoplankton (estuarine or otherwise) in marine waters. Phytoplankton assemblages in the Rhode River were sensitive to UV radiation throughout the year, and both UV-A and UV-B contributed to inhibition, at least by surface irradiance. There was no significant inhibition of photosynthesis by PAR. There was little variation in seasonal average BWFs through the year, but individual BWFs were quite variable. Between the least and most sensitive BWFs for the Rhode River, there are differences in both the absolute magnitude and in the relative effect of UV-B versus UV-A (Fig. 4). The weighting at 310 nm varied by approximately one order of magnitude (Fig. 5A).

Comparison with other biological weighting functions—The range of variation observed in the Rhode River is comparable to the overall variation in other irradiance-dependent (*E* model) BWFs for natural assemblages and cultures (Fig. 4). This variation is seen both in marked differences in the offset or magnitude of the BWF over all wavelengths as well as differences in the shapes of the BWFs. The highest sensitivity BWF observed to date (using the *E* model) is for a cryptomonad-dominated assemblage from the extreme shade environment of a permanently ice-covered lake in Antarctica (Lake Bonney; Neale et al. 1994). The BWF of the most-sensitive spring assemblage from the Rhode River was comparable to the Lake Bonney BWF in the UV-B and short-wavelength UV-A. A lower sensitivity group consists of laboratory cultures of diatoms and dinoflagellates (Cullen et al. 1992; Neale et al. 1998*a*), and a natural, diatom-dominated assemblage from McMurdo Sound, Antarctica maintained in outdoor culture (Neale et al. 1994). The BWF of the low sensitivity, winter assemblage of phytoplankton from the Rhode River was comparable to this group.

Other Rhode River BWFs were about evenly distributed between these high- and low-sensitivity extremes (c.f. Fig. 5A), so the average BWF for the Rhode River corresponds to a moderate level of sensitivity. A large number of BWFs have also been determined for Antarctic assemblages, including the McMurdo area (Neale et al. 1994), the Weddell-Scotia Confluence (WSC; Neale et al. 1998*b*), and coastal waters of the Antarctic Peninsula (Neale et al. in press; J. J. Fritz et al. unpubl. data). We sought to determine how the average BWF for these environments resembled that of the Rhode River. However, the Antarctic BWFs include both irradiance (*E* model) and cumulative exposure (*H* model) BWFs; the latter were estimated for WSC phytoplankton (Neale et al. 1998*b*; Neale 2000). We established a common basis for comparing BWFs with these two models by limiting the comparison to effects over the 1-h period used to measure photosynthesis. This procedure requires adjustment for both the units and functional differences between the *H* and *E* models in describing the hyperbolic dependence of inhibition on exposure (Neale et al. in press). Adjusted in this way, average BWFs for the Rhode River and the Antarctic assemblages are quite similar (Fig. 6). Indeed, the similarity is quite striking, considering how different are these two environments. In each case, the average response to UV shows significantly greater sensitivity than is typically shown by laboratory cultures, particularly in the UV-A (c.f. Fig. 4) (Neale and Kieber 2000). It appears that natural phytoplankton are typically constrained in their ability to defend against UV, although more fully acclimated assemblages sometimes occur (e.g., low-sensitivity Rhode River and McMurdo culture BWFs in Fig. 4). The possible causes of BWF variation are considered below in the section, *Seasonal variability of UV response.*

Several other studies of temperate and tropical marine phytoplankton have shown sensitivity of photosynthesis to UV but have not defined BWFs (e.g., Smith et al. 1980; Helbling et al. 1993). The only study that defines a BWF for non-Antarctic marine phytoplankton is that of Behrenfeld et al. (1993). These authors suggested a single BWF was effective in estimating inhibition of photosynthesis by UV-

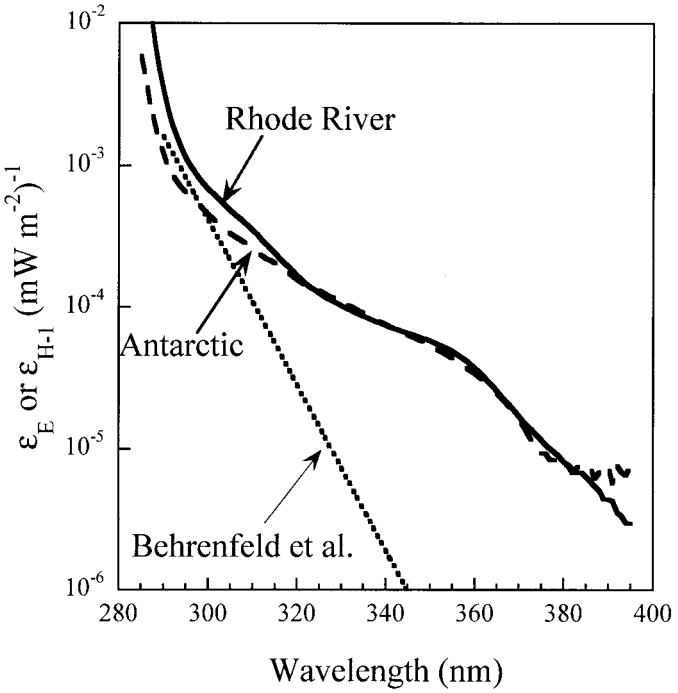

Fig. 6. Average BWFs for the inhibition of photosynthesis by UV for Rhode River and Antarctic phytoplankton (Neale and Kieber 2000) and the generalized BWF defined by Behrenfeld et al. (1993). The Behrenfeld et al. BWF is given as inhibition per unit irradiance in mW m^{-2}, under the assumption of a 1-h exposure. It was calculated as the product of the relative action spectrum (unity at 300 nm), the response coefficient for inhibition by photosynthesis (0.0116 reciprocal [J m^{-2}]) and a constant (3.6) to convert effect per J to effect per mW-h.

B over a range of marine systems (although they did not sample estuaries). A general comparison of the Behrenfeld et al. BWF with Rhode River BWFs is not possible, because this previous study models inhibition as a linear function of cumulative exposure, whereas the BWF/P-I model assumes a hyperbolic dependence on weighted irradiance. A specific comparison can be made over a 1-h incubation period, just as for the WSC BWFs, although we cannot adjust for the linear versus hyperbolic dependence on exposure. If the Behrenfeld et al. BWF is multiplied by 3.6 (to account for the number of Joules in a mW-h), the weight at 300 nm is similar to the $\varepsilon(300)$ of the Rhode River and Antarctic BWFs (Fig. 6). However, average weights for the latter BWFs are one to two orders of magnitude higher than the Behrenfeld et al. BWF in the long-wavelength UV-B and short-wavelength UV-A range, where solar radiation has maximum biological effectiveness (c.f. Fig. 3). Because the WSC BWFs were based on a cumulative exposure model (*H* model), they can be directly compared with the Behrenfeld et al. BWF (Neale et al. 1998*b*). However, a similar result is obtained: the weights are similar at 300 nm and diverge at longer wavelengths (Neale 2000). On the other hand, there does seem to be some constancy in responses to UV by natural phytoplankton assemblages when considering averages over large space- and timescales (Fig. 6), which recalls Behrenfeld et al.'s (1993) conjecture. However, the average BWFs presented here differ considerably from the hypothesized common response. At this point, it is unknown whether the average response in other marine systems will resemble the Rhode River and Antarctic averages. Finally, it is important to note that these average BWFs only apply to a 1-h timescale, and the response of a specific phytoplankton assemblage can diverge quite substantially from these averages.

MAAs and UV sensitivity—Accumulation of MAAs has received much attention as a primary defense against UV in marine organisms. Higher concentrations of MAAs have been correlated with UV photoprotection in dinoflagellates (Banaszak and Trench 1995; Neale et al. 1998*a*). High concentrations of MAAs can decrease sensitivity to UV, as has been shown for *G. sanguineum*, a dinoflagellate of moderate cell size. The shape of the BWF was affected when total MAA content was ~44 nmol (nmol Chl)$^{-1}$ but not when MAA content was 2 nmol (nmol Chl)$^{-1}$ (Neale et al. 1998*a*). In the Rhode River, the average MAA concentration was 1.5 nmol (nmol Chl)$^{-1}$. This suggests that the protective effects of MAAs on photosynthesis in the Rhode River were usually too small to resolve a spectral screening. For two samples from the Rhode River, MAA content was higher [between 5 and 6 nmol (nmol Chl)$^{-1}$]. MAAs may have provided some photoprotection on these dates, but the effect still may have been too small to resolve without replicate BWF determinations, as was even necessary at 44 nmol (nmol Chl)$^{-1}$. On

Table 4. Irradiance-dependent biological weighting functions (BWFs) published to date and the mycosporine-like amino acid (MAA) concentrations of the population used for the determination of the BWF. The high- and low-sensitivity BWFs are diagrammed in Fig. 4.

Assemblage	Reference	Culture and/or light conditions	MAA [nmol (nmol Chl *a*)$^{-1}$]
High-Sensitivity BWFs			
Lake Bonney cryptomonad assemblage	Neale et al. (1994)	Variable but low light	0?
Rhode River spring assemblage	This study	Variable	0.05 (n = 1)
Low-Sensitivity BWFs			
Rhode River winter assemblage	This study	Variable	1.66 (n = 1)
Gymnodinium sanguineum low-light culture	Neale et al. (1998a)	Static 15 W m^{-2}	2.09 (n = 5)
G. sanguineum high-light culture	Neale et al. (1998a)	Static 76 W m^{-2}	44.35 (n = 5)
McMurdo Sound diatoms (outdoor culture)	Neale et al. (1994)	Variable noon = 125 W m^{-2} average = 37 W m^{-2}	3.91 (n = 6)

the other hand, assemblages with low concentrations of MAAs are characterized by high sensitivity to UV radiation (Table 4). Lake Bonney cryptomonads were not examined for MAAs; however, Vernet et al. (1994) showed that cryptomonads from Antarctica have a low spectral-absorption coefficient at 300 nm compared with PAR, suggesting that these cryptomonads have either no or very low concentrations of MAAs. For *G. sanguineum,* the $\varepsilon(310)$ was low even when MAA concentration was comparable to the average concentration in the Rhode River assemblages. Even though MAA-accumulating phytoplankton are generally more resistant to UV, the MAAs themselves may only be a second level of defense (Lesser 1996*a*,*b*) that affect the spectral shape of the BWF more than the absolute sensitivity, such as was seen in high-light– versus low-light–grown *G. sanguineum* (Neale et al. 1998*a*).

Seasonal variability of UV response—Seasonal variation of environmental parameters is a basic characteristic of most temperate aquatic ecosystems. The Rhode River environment is seasonally variable in temperature, as well as in light and nutrient availability (Fig. 5, Table 3). Rhode River phytoplankton respond to this seasonal variation in several ways. Photosynthetic performance (i.e., P_s^B) is highest during the summer, and phytoplankton biomass is high during spring and summer (Fig. 5). Summer blooms are usually dominated by dinoflagellates, whereas other flagellates are more important in the winter and spring, and diatoms are found yearround (C. Gallegos pers. comm.). The UV sensitivity of phytoplankton has been shown to differ depending on light acclimation status (Neale et al. 1998*a*), nutrient availability (Cullen and Lesser 1991; Behrenfeld et al. 1994; Lesser et al. 1994), and temperature (Roos and Vincent 1998), and there are some systematic differences between sensitivity of algal groups, or at least species (Xiong et al. 1996; E. Litchman and P. J. Neale unpubl. data). As a result, seasonal shifts in UV sensitivity could be expected, and simple measures of UV sensitivity have been seasonally variable in some systems (Hobson and Hartley 1983; Gala and Giesy 1991).

Despite these expectations, seasonally averaged BWFs for inhibition of photosynthesis did not vary in any systematic way. This was not due to an absence of variability per se but a result of the temporal distribution of variability. For $\varepsilon(310)$, the coefficient of variation was 50% over all samples; however, only 8% of variance occurred between seasons (1-way ANOVA). The remaining variance (92%) occurred within seasons (i.e., between samples). Presently, we cannot account for this surprising temporal distribution. It may be that factors that contributed to short-term variability tended to covary in such a way as to minimize shifts in UV response on a seasonal basis. Multiple regression analysis of $\varepsilon(310)$ on temperature, irradiance, and MAAs were attempted to test this hypothesis empirically, but no significant ($P < 0.05$) relationships could be derived. Nutrients were not included in this analysis because they were not measured for the BWF samples. This suggests that our database is presently too small to resolve relationships and/or that variations were caused by other factors that were not measured (e.g., nutrient availability).

We do have some indications from other studies as to how species composition, light, temperature, and nutrient availability can affect sensitivity to UV, but our understanding is not presently advanced enough to formulate a quantitative model of BWF response to multiple factors. Nevertheless, it is instructive to consider conceptually how several factors or factor interactions may have contributed to the variation that we have documented for the Rhode River assemblages. Of the factors listed, probably the least is known about variation in UV sensitivity between species, a detailed analysis of which has not been attempted for our data set. However, we did observe that the samples with the highest sensitivity (early spring 1995) were the ones with the highest proportion of flagellates such as *Cryptomonas* sp., whereas the low-sensitivity (winter 1995) sample was dominated by a dinoflagellate (*Katodinium rotundatum*). The comparative sensitivity of dinoflagellates and cryptomonads is being further investigated in current culture studies. The availability of PAR and water temperature can influence UV sensitivity because they determine the light-acclimation status of phytoplankton (MacIntyre et al. 2000). High light acclimation in algae is correlated with increased antioxidants such as carotenoids and with increased capacity for turnover of damaged molecular complexes (''repair''). Antioxidants can contribute to UV resistance to the extent that reactive oxygen species mediate UV effects (reviewed in Vincent and Neale 2000; Neale and Kieber 2000). Repair processes also lower biological weights by affecting overall sensitivity and possibly by altering the shape of the BWF, depending on the wavelength specificity of the damage and repair processes.

The twofold seasonal increase in available irradiance (Table 3) might seem sufficient to induce a higher degree of light acclimation in summer assemblages, but there is a complication. This is because acclimation is a function of both light availability, which controls the generation of energy carriers (NADPH and ATP), and other factors, like temperature, that determine metabolic rates and thus energy consumption—a concept called excitation pressure (Maxwell et al. 1995) or energy balance (MacIntyre et al. 2000). Maxwell et al. (1995) found that the light intensity needed to induce resistance to inhibition by E_{PAR} was higher for *Chlorella vulgaris* grown at high temperatures than that for cultures grown at low temperatures. In the Rhode River, both irradiance and temperature increase seasonally, but the relative increase in temperature is larger (Fig. 5B, Table 3). It may be that excitation pressure is at a similar level, on average, between seasons but is variable within seasons. However, a more detailed data set is needed to test this hypothesis. Previous studies in the Rhode River have documented brief (i.e., several day) phytoplankton blooms, which are induced by episodic nutrient enrichment (Gallegos 1992; Gallegos et al. 1992), and short-term forcing of photosynthesis is probably a general feature of shallow estuarine environments (MacIntyre et al. 2000).

Another factor that can constrain acclimation to UV exposure is low nutrient availability. Nutrient stress, particularly limited availability of nitrogen, may affect photoprotection because of the requirement of nitrogen for MAA synthesis. Preliminary results indicate that accumulation of MAAs is decreased under conditions of nitrogen limitation (E. Litchman et al. unpubl. data). Rates of repair are also

slower under nitrogen-limited conditions, probably because nitrogen-requiring enzymes are needed for repair (Cullen and Lesser 1991; E. Litchman unpubl. data). Seasonal nitrogen availability is usually lowest when irradiance is highest. Again, there is a possibility that the opposed seasonal phasing of environmental factors may limit seasonal variation in BWFs. Because average responses in the Rhode River phytoplankton resemble those of the Antarctic, and perhaps other systems, a better understanding of what causes the variability in this system may have implications beyond the estimation of effects in shallow estuarine waters.

In summary, we have shown that Rhode River phytoplankton have a moderate sensitivity to UV that mainly varies on short-term rather than seasonal timescales. The BWFs provide an improved basis for assessing the effects of long-term changes in the UV environment on the phytoplankton community, as can occur through changes in incident UV and UV transparency of the water body. Better understanding of the effects of UV variation on estuarine productivity and species composition is dependent on obtaining more information on short-term variation in estuarine optical properties and the kinetics of acclimation to UV radiation by phytoplankton.

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