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*Minireview*

# Ultraviolet radiation, ozone depletion, and marine photosynthesis

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**Abstract**

Concerns about stratospheric ozone depletion have stimulated interest in the effects of UVB radiation (280–320 nm) on marine phytoplankton. Research has shown that phytoplankton photosynthesis can be severely inhibited by surface irradiance and that much of the effect is due to UV radiation. Quantitative generalization of these results requires a biological weighting function (BWF) to quantify UV exposure appropriately. Different methods have been employed to infer the general shape of the BWF for photoinhibition in natural phytoplankton, and recently, detailed BWFs have been determined for phytoplankton cultures and natural samples. Results show that although UVB photons are more damaging than UVA (320–400 nm), the greater fluxes of UVA in the ocean cause more UV inhibition. Models can be used to analyze the sensitivity of water column productivity to UVB and ozone depletion. Assumptions about linearity and time-dependence strongly influence the extrapolation of results. Laboratory measurements suggest that UV inhibition can reach a steady-state consistent with a balance between damage and recovery processes, leading to a non-linear relationship between weighted fluence rate and inhibition. More testing for natural phytoplankton is required, however. The relationship between photoinhibition of photosynthesis and decreases in growth rate is poorly understood, so long-term effects of ozone depletion are hard to predict. However, the wide variety of sensitivities between species suggests that some changes in species composition are likely. Predicted effects of ozone depletion on marine photosynthesis cannot be equated to changes in carbon flux between the atmosphere and ocean. Nonetheless, properly designed studies on the effects of UVB can help identify which physiological and ecological processes are most likely to dominate the responses of marine ecosystems to ozone depletion.

*Abbreviations:* BWF – biological weighting function; BWF/P-I – photosynthesis versus photosynthetically available irradiance as influenced by biologically-weighted UV; Chl – chlorophyll *a*; DOM – dissolved organic matter; $E_{PAR}$ – irradiance in energy units (PAR); $E_s$ – saturation parameter for PAR in the BWF/P-I model; $E^*_{inh}$ – biologically-weighted dimensionless fluence rate for photoinhibition of photosynthesis by UV and PAR; $\varepsilon$ – biological weighting coefficient; $\overline{\varepsilon}_{PAR}$ – biological weighting coefficient for damage to photosynthesis by $E_{PAR}$; k($\lambda$) – diffuse attenuation coefficient for wavelength $\lambda$; MAAs – mycosporine-like amino acids; PAR – photosynthetically available radiation; $P^B$ – rate of photosynthesis normalized to Chl; $P^B_s$ – maximum attainable rate of photosynthesis in the absence of photoinhibition; UVA – ultraviolet A (320–400 nm); UVB – ultraviolet B (280–320 nm)

## 1. Introduction

Depletion of stratospheric ozone, particularly in the Antarctic, has stimulated concerted efforts to predict the effects of increased ultraviolet radiation on biological systems. The justification for heightened interest is clear: continuing reduction of stratospheric ozone can permit more middle ultraviolet radiation (UVB[1]; 280–320 nm) to reach the earth's surface, and UVB is known to harm many biological processes.

A great deal has been learned about biological effects of UVB, and aspects of the subject have been regularly reviewed (e.g., Smith and Baker 1989, Häder and Worrest 1991, United Nations Environment Programme 1991, Vincent and Roy 1993). Let us consider here the possible influence of UVB and ozone depletion on marine primary production and biogeochemical cycling. This entails discussing the spectral dependence and kinetics of photosynthesis and photoinhibition, the contribution of UVB-induced photoinhibition to reduced phytoplankton growth rates relative to other UVB-sensitive physiological processes, and the degree to which reduced phytoplankton growth rates near the surface might alter the fluxes of carbon in the ocean.

Damage by UVB and protection from that damage are described at the molecular level by Strid and Anderson (1994). The focus here is on the difficult oceanographic problem of quantifying the net effects of UVB on phytoplankton in the natural environment. Characterization of photosynthetic responses is of central importance. Uncertainties include:

1. the magnitude of photoinhibition of photosynthesis in situ, and how much worse it would be under ozone depletion;
2. the adaptability of individual phytoplankton to enhanced UVB fluence and the extent to which UVB-induced damage can be prevented or repaired;
3. the relative sensitivities of different phytoplankton taxa to UVB, and the degree to which ozone depletion might alter planktonic community structure; and
4. the quantitative relationship between reduced photosynthesis near the sea-surface and the fluxes of carbon in the ocean.

The objectives of this review are to describe different methods for assessing the effects of UVB on marine photosynthesis, to examine critical assumptions that strongly influence quantitative predictions, and to suggest what else should be considered when the results of short-term experiments are used to predict long-term and large-scale changes in marine systems.

[1] The terms UVB and UVA are traditional designations for parts of the UV spectrum, but photobiological processes do not respect such arbitrary boundaries. Although we discuss effects of UVB and UVA as potentially distinct phenomena, it should be emphasized that quantitative descriptions of these wavelength-dependent processes transcend pre-existing definitions, because there can be important variation within spectral regions and significant effects from adjacent regions.

## 2. Effects of UV on the photosynthesis of natural phytoplankton

Neither the complex variability of spectral irradiance and other environmental factors in the upper water column, nor the genetic diversity of natural phytoplankton communities can be reproduced in the laboratory. Thus, direct measurements on natural phytoplankton will always be essential to estimating marine photosynthesis and how it might change under the influence of ozone depletion. Experimental measurements require unnatural confinement of phytoplankton, however, and it is sometimes difficult to relate measured rates to the actual rates in situ (Harris 1978, Marra 1978, Cullen and Neale 1993). It is therefore useful to consider the influence of UVB on the *measurement* of primary production prior to discussing the effects of UVB on primary production in situ. Other biological effects of UV will be discussed after photosynthesis is examined in detail.

### *UV and the measurement of primary productivity*

The uptake of carbon by marine phytoplankton is commonly estimated by putting seawater in bottles, inoculating it with $^{14}C$ bicarbonate, incubating samples at the depths from which they were obtained, and measuring the incorpo-

ration of $^{14}C$ into particulate matter over periods from several hours to a day. Alternatively, samples can be incubated on a ship under solar or artificial irradiance attenuated by neutral density screens, sometimes used in conjunction with colored filters (Jitts et al. 1976, Lohrenz et al. 1992). A consequence of these methods is that incubated phytoplankton are exposed to less UV radiation than is natural for the sampling depth, because conventional glass or plastic containers attenuate UV, and also because most artificial light sources are deficient in UV.

Early studies, lacking detailed radiometry, showed that UV was an environmental factor that was inadequately simulated during the measurement of primary productivity: rates measured in UV-transparent containers were lower than when environmental UV was screened by glass (Steemann Nielsen 1964, Ilmavirta and Hakala 1972, Jitts et al. 1976) or Mylar (nominally opaque at $<320$ nm; Lorenzen 1979). Smith et al. (1980) used several different manipulations of UVB during incubations of 6–12 h, for the first time supported with measurements of UV spectral irradiance, to characterize photoinhibition of natural phytoplankton as a function of quantified UV. Photoinhibition, defined as the percent decrease of $P^B$ (rate of carbon uptake normalized to Chl, g C g Chl$^{-1}$ h$^{-1}$) relative to the highest rate in the water column, sometimes exceeded 80% at the surface. It was estimated that 25% of this inhibition was due to wavelengths $<340$ nm, and 50% due to wavelengths $<390$ nm, an assessment that was broadly consistent with earlier published results. Although there was clearly an interest in assessing the ecological consequences of UV radiation, authors were cautious, stating that their results applied to the effects of UV on the measurement of photosynthesis, not to the rate of photosynthesis in situ.

### *Requirements for a general description of UV and photosynthesis*

The presentation by Smith et al. (1980; discussed further by Smith and Baker 1982) marked a turning point in the study of UVB and marine primary productivity. The fact that environmental UVB influences the measurement of primary productivity near the surface was established. However, without some quantitative way to relate biological response to UV exposure, it was not possible to generalize or to predict the variation of UV-induced photoinhibition with depth, water type, or under the influence of ozone depletion. Because Smith and colleagues had measured spectral irradiance, they were able to describe and examine a procedure for modeling the effects of UV on the measurement of marine photosynthesis. First, solar irradiance reaching the sea-surface must be measured or modeled (Green et al. 1980, Baker et al. 1982, Lubin et al. 1992, Smith et al. 1992b). Its propagation below the surface can be conveniently represented with wavelength-dependent diffuse attenuation coefficients [$k(\lambda)$; m$^{-1}$], modeled as a function of water type and chlorophyll concentration (Smith and Baker 1979). Given an estimate of spectral irradiance at a position in the water column, a biological weighting function (BWF) is used to calculate biologically effective exposure, either as a fluence rate or as cumulative exposure (fluence rate × time). For example:

$$\text{Biologically Effective Fluence Rate} = \sum_{\lambda=280}^{400} \varepsilon(\lambda)E(\lambda)\,\Delta\lambda \qquad (1)$$

where $E(\lambda)$ is spectral irradiance (mW m$^{-2}$ nm$^{-1}$) and $\varepsilon(\lambda)$ is relative biological effectiveness of UV at wavelength $\lambda$. The weightings, $\varepsilon(\lambda)$, constitute a biological weighting function, also called an action spectrum. Weightings are usually reported in relative units (dimensionless), but can be specified in absolute units (reciprocal mW m$^{-2}$, Cullen et al. 1992b). The challenge for the phytoplankton ecologist is to determine: (i) appropriate BWFs for photoinhibition of photosynthesis; (ii) the relationship between weighted UV exposure and inhibition (i.e., dependence on fluence rate vs. cumulative exposure, linearity vs. saturation); and (iii) the variability of BWFs in nature. Lacking this information, Smith et al. (1980) assumed that photoinhibition was a function of cumulative weighted exposure (J m$^{-2}$) during incubations of 6–12 h, then examined a subset of their data for consistency with pub-

lished biological weighting functions. It was found that the differences in photoinhibition associated with exclusion and enhancement of UV were consistent with a BWF for inhibition of partial reactions in spinach chloroplasts, which weights both UVB and UVA (Jones and Kok 1966), but not with either Setlow's (1974) DNA weighting function or Caldwell's (1971) spectrum for adverse effects on plants, which weight UVB only.

Heuristically assuming a linear decrease of photosynthesis as a function of weighted UV exposure, and using the Jones and Kok (1966) action spectrum, Smith and Baker (1982) calculated that a 25% reduction in ozone thickness would cause a 35% reduction of photosynthesis at the surface and a 9% reduction for the water column, regardless of absolute productivity. Their tentative prediction was tempered with explicit recognition of fundamental uncertainties associated with the BWF and the assumption of reciprocity (i.e., that inhibition was a function of cumulative exposure, independent of fluence rate). Further, they showed how vertical mixing could influence ecological interpretations of their measurements (see also Kullenberg 1982).

Subsequent studies on natural phytoplankton have partially resolved the principal problems. Along the lines of well-supported recommendations (Rundel 1983, Caldwell et al. 1986), information on spectral sensitivity has been improved by using 4 to 6 different long-pass cut-off filters to manipulate solar UVB and UVA radiation (Maske 1984, Bühlmann et al. 1987), and results have been used to generate coarse action spectra (Mitchell 1990, Helbling et al. 1992, Lubin et al. 1992). Behrenfeld et al. (1993) found that results of UVB-manipulation experiments (filtered sunlamps, Mylar film) were better described by weighting UVB with the DNA weighting function than with the Jones and Kok (1966) action spectrum, in contrast to what was found by Smith et al. (1980). More realistic underwater irradiance regimes have been simulated and quantified by performing UV-exclusion experiments in situ with concurrent measurements of spectral irradiance (Smith et al. 1992a, Helbling et al. 1994, Vernet et al. 1994). The study by Smith et al. (1992a) was further enhanced by comparing measurements made under normal ozone conditions with others made under the influence of the Antarctic ozone hole. Also, the variability of UVB-sensitivity of natural phytoplankton photosynthesis has been partially described with respect to season (Hobson and Hartley 1983), depth (Helbling et al. 1992, Smith et al. 1992a, Behrenfeld et al. 1993), latitude (Helbling et al. 1992, Behrenfeld et al. 1993), UV-absorbing compounds (Helbling et al. 1994, Vernet et al. 1994), dominant taxa (Helbling et al. 1993), and irradiance regime (Helbling et al. 1994, Neale et al. 1994, Vernet et al. 1994). These general statements about natural phytoplankton, though not exhaustively validated, are supported by obervations from several studies:

1. Phytoplankton photosynthesis can be drastically inhibited during incubations of several hours under irradiance characteristic of the sea-surface; rates can be enhanced by more than 100% when UV is excluded. Even though UVB irradiance is more damaging to photosynthesis than UVA on a per-photon basis, environmental UVA irradiance is much greater, thereby causing a large amount of the photoinhibition. Little is known about UVB influence on photosynthesis in lakes, but the relative importance of UVA-induced inhibition is likely to be enhanced (cf. Bühlmann et al. 1987, Kim and Watanabe 1993) because UVB is strongly absorbed by the humic substances that are common in inland waters (Kirk 1983).
2. Phytoplankton from stable, high-irradiance environments (e.g., stratified surface waters) are likely to be less sensitive to photoinhibition by UVB (and longer wavelengths as well) than phytoplankton from low-irradiance regimes. This can be considered as adaptation, keeping in mind that at the community level, adaptation includes replacement of sensitive species.

It will be shown below that, though much progress has been made, studies of UVB and natural marine phytoplankton have yet to resolve fundamental uncertainties about the dependence of photoinhibition on cumulative exposure vs. fluence rate and the appropriate BWFs for natural phytoplankton.

## 3. Laboratory observations on UV and phytoplankton photosynthesis

Just as it is essential to measure photosynthesis of phytoplankton in the real world, it is extremely important to study the photosynthesis and growth of phytoplankton and other plants in the laboratory, where environmental conditions can be defined and easily manipulated, where individual species can be studied, and where physiological and biochemical measurements can be performed without the limitations of working at sea – extremely low levels of biomass, significant contamination from detritus and heterotrophs, generally unknown preconditioning, variable species composition and inherently uncontrollable environmental conditions. Indeed, laboratory studies have much to contribute to the evaluation of UV effects on marine photosynthesis.

### *UV effects on photosynthesis: Cumulative exposure* vs. *fluence rate*

Photosynthesis is usually described as a function of irradiance, and its inhibition as a function of irradiance and time (Neale 1987), yet the majority of studies and models of the effects of UV on marine photosynthesis describe photoinhibition as a function of cumulative UV exposure (J $m^{-2}$, weighted appropriately; e.g., Smith et al. 1980, 1992a, Behrenfeld et al. 1993, Vernet et al. 1994). Reciprocity is therefore assumed, i.e., photoinhibition is a function of cumulative exposure, independent of fluence rate. This assumption has important consequences in general models of photoinhibition (Cullen and Lesser 1991, Vincent and Roy 1993, Fig. 1).

The assumption of reciprocity has been doubted for some time with respect to marine photosynthesis (Smith and Baker 1982), and even though reciprocity is readily tested for biological responses to UV (Redford and Myers 1951, Trocine et al. 1981, Cullen and Lesser 1991, Blakefield and Calkins 1992), it has only recently been examined for UV-induced photoinhibition of photosynthesis in natural populations of marine phytoplankton. The experiment, a comparison of static incubations vs. simulated vertical mixing (Helbling et al. 1994), clearly showed a failure of reciprocity, but the kinetics of UV-photoinhibition were not resolved. A laboratory study on a marine diatom also showed reciprocity failure: for time scales of 0.5 to 4 h, photoinhibition of photosynthesis by supplemental UVB radiation was well described as a nonlinear function of UVB irradiance, not cumulative exposure (Cullen and Lesser 1991). Considering that reciprocity can hold for one plant and not another (e.g., a comparison of seagrasses, Trocine et al. 1981), it is imperative to resolve the kinetics of UV-induced photoinhibition for natural marine phytoplankton in a number of environments.

Particularly when results will be applied to general models, the shape of the inhibition vs. exposure relationship is also important to resolve (Vincent and Roy 1993). Data on UV-induced photoinhibition in the field have been described with linear (Smith et al. 1980, Smith et al. 1992a, Behrenfeld et al. 1993) and sigmoid (Helbling et al. 1992, Smith et al. 1992a, Helbling et al. 1994) relationships. The scatter inherent in such measurements, combined with uncertainties about appropriate biological weighting for UV exposures and the possibility of reciprocity failure, precludes choosing a 'correct' form on an objective basis. A laboratory study (Cullen and Lesser 1991) indicated that relative photoinhibition under constant PAR was well described as a saturating function of supplemental UVB irradiance, as if photoinhibition was a balance between damage and recovery processes (cf. Neale 1987, Strid and Anderson 1994). Experiments with a more ecologically relevant (Rundel 1983, Caldwell et al. 1986), broad range of UV and PAR exposures over 45 min were consistent with the same saturating relationship for two phytoplankton cultures (Cullen et al. 1992b), and for natural phytoplankton from the Antarctic (Neale et al. 1994).

### *Biological weighting functions for inhibition by UV*

The BWF, or action spectrum, has been repeatedly identified as essential to predicting the biological impact of ozone depletion (Smith et

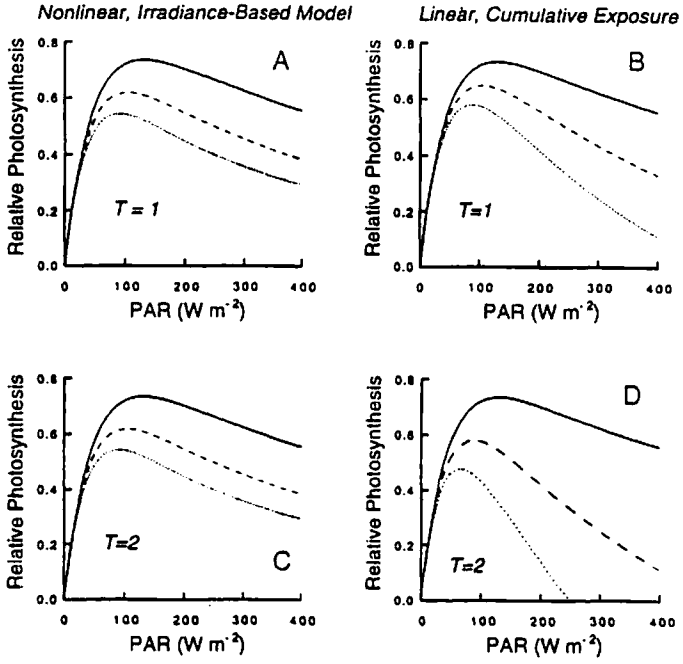


*Fig. 1.* Models of UV-induced photoinhibition: relative photosynthesis vs. PAR for different ratios of biologically-effective UV to PAR. Solid curve represents PAR only, dashed curve is for an arbitrary, but environmentally-realistic amount of UV relative to PAR, and the dotted curve is for doubled UV:PAR. (A) Non-linear, irradiance based model, consistent with photoinhibition as a balance between damage and recovery processes (Neale 1987, Cullen et al. 1992b), and (B) a linear model, dependent on cumulative exposure, consistent with the assumption of reciprocity. The two models are matched for photosynthesis vs. PAR and for relative inhibition at the lower UV exposure at 250 W $m^{-2}$ PAR. For the irradiance-based model, predictions for doubling the duration are the same (C), whereas for the linear model of UV-inhibition as a function of cumulative exposure (D), inhibition is doubled. One could also model UV-photoinhibition with a non-linear model based on cumulative exposure, consistent with target theory (cf. Garcia-Pichel et al. 1993, Vincent and Roy 1993).

al. 1980, Caldwell et al. 1986, Coohill 1989, Lubin et al. 1992). Until recently, however, no action spectrum for UV-induced photoinhibition in marine phytoplankton had been determined. Because photoinhibition is the net result of primary damage (principally by shorter wavelengths) and recovery processes (stimulated by UVA and PAR; Hirosawa and Miyachi 1983, Samuelsson et al. 1985), it is not ecologically relevant to infer biological weightings from a series of individual narrow-band exposures in the UV. Rather, photosynthesis should be determined under irradiance treatments containing progressively greater amounts of UVA, then UVB, added to a constant background of PAR (polychromatic approach; Caldwell et al. 1986). If the absolute intensity of different spectral treatments is varied experimentally (Cullen et al. 1992b), complex interactions between UV and PAR can also be revealed.

The polychromatic approach was used in controlled experiments to measure the action spectrum for inhibition of photosynthetic gas exchange in the terrestrial plant *Rumex patientia* (Rundel 1983, Caldwell et al. 1986). Similar procedures were employed to estimate spectral weightings for photoinhibition of natural phytoplankton during simulated in situ and in situ incubations using solar irradiance attenuated by different long-pass optical filters (Maske 1984, Mitchell 1990, Helbling et al. 1992, Smith et al. 1992a). The usual trade-offs for working in the field applied: natural phytoplankton assemblages were characterized, but spectral resolution of the weighting functions were limited to two to seven points and possible influences of variable ir-

radiance during incubations could not be assessed. Only Smith et al. (1992a) had access to contemporaneous, high-resolution data on solar irradiance and spectral diffuse attenuation in the water column. They used only two optical filters, though, and reported spectral sensitivity with the equivalent of a two-band action spectrum: UVB and UVA.

*An integrated model of photosynthesis and UV-photoinhibition*

Recently, techniques have been developed to measure the BWF for photoinhibition of photosynthesis as part of a more general model of photosynthesis vs. PAR and UV (Cullen et al. 1992b). The BWF/P-I model describes photosynthesis as a function of PAR and photoinhibition as a function of PAR and biologically-weighted UV:

$$P^B = P_S^B(1 - e^{(-E_{PAR}/E_S)})\left(\frac{1}{1 + E^*_{inh}}\right) \qquad (2)$$

where $E_{PAR}$ is PAR (W m$^{-2}$), $P^B$ is the rate of photosynthesis normalized to chlorophyll, $P_s^B$ is the maximum attainable rate in the absence of photoinhibition, and $E_s$ (W m$^{-2}$, PAR) is a saturation parameter for photosynthesis, comparable to the more commonly used $I_k$ (Talling 1957, Platt et al. 1980). Similar to other models (Platt et al. 1980, Neale 1987), $P^B$ is the product of a term for potential photosynthesis, $P^B(1 - \exp(-E_{PAR}/E_s))$, and one for inhibition, $1/(1 + E^*_{inh})$. The inhibition term is new because it is a function of both UV and PAR as expressed using the form of Eq. (1):

$$E^*_{inh} = \bar{\varepsilon}_{PAR}E_{PAR} + \sum_{\lambda=280\text{ nm}}^{400\text{ nm}} \varepsilon(\lambda)E(\lambda)\,\Delta\lambda \qquad (3)$$

This formulation ignores spectral dependence of photoinhibition within PAR (e.g., Jones and Kok 1966) and instead represents the sensitivity of photosynthesis to inhibition by PAR with a single relative biological efficiency for damage, $\bar{\varepsilon}_{PAR}$ (reciprocal W m$^{-2}$); the errors associated with this assumption could be estimated by accounting for differences between absorbed and incident PAR. The dimensionless parameter $E^*_{inh}$ thus quantifies biologically effective fluence rate for both UV and PAR. As discussed above, the nonlinear form, $1/(1 + E^*_{inh})$, is consistent with photoinhibition being a dynamic balance between damage and recovery (Neale 1987).

The BWF/P-I model (Eq. (2)) predicts $P^B$ versus $E_{PAR}$ as a function of biologically-effective fluence rate per unit $E_{PAR}$. Thus, the model can be used to calculate photosynthesis at the surface, where the ratio of UV to $E_{PAR}$ changes as a function of ozone depletion and other atmospheric properties, and photosynthesis versus depth in a water column, where both $E_{PAR}$ and the ratio of UV to $E_{PAR}$ change as a function of water transparency. Parameters of the BWF/P-I model, including high-resolution spectral weightings, are determined statistically from results of carbon-incorporation experiments on up to 72 small samples (2–3 ml) incubated under a broad range of both UVB:UVA:PAR spectral ratios and absolute intensities of PAR (Cullen et al. 1992b, Cullen and Neale 1993, Neale et al. 1994). The first BWFs from laboratory experiments on cultures of a marine diatom and dinoflagellate differed only slightly, and both were similar in shape to the weighting function for inhibition of photosynthetic gas exchange in *Rumex patientia* (Rundel 1983, Caldwell et al. 1986). These laboratory-derived weighting functions are also consistent with broad-band action spectra describing experiments on natural phytoplankton (Mitchell 1990, Helbling et al. 1992, Fig. 2A). Relatively steep slopes near 300 nm agree with recent measurements on marine phytoplankton during exposures to solar irradiance with varying amounts of UVB (Behrenfeld et al. 1993, see also Worrest 1983): relative inhibition of photosynthesis in those experiments was better predicted by weighting UVB with a DNA weighting function (Setlow 1974) than with the action spectrum for in vitro chloroplast photoinhibition (Jones and Kok 1966), which has a much more gradual slope in the UVB. If one is interested in ozone-related changes of photoinhibition relative to the total, however, the effects of UVA and PAR must also be quantified. The shallow slopes in the UVA for the photoinhibition BWFs in Fig. 2 suggest that the percent increase of photoinhibition associated with ozone depletion is likely to be much less

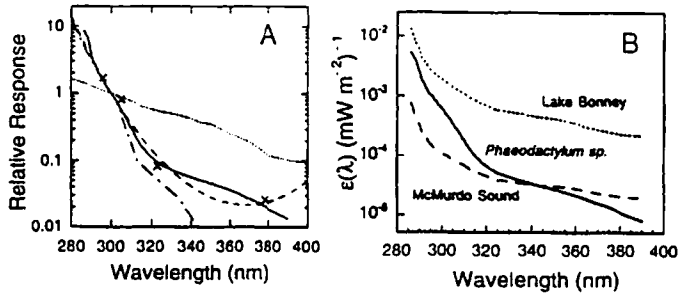


*Fig. 2.* Biological weighting functions for harmful effects of UV. (A) in relative units, normalized to 1.0 at 300 nm: (— - —) damage to DNA in alfalfa seedlings (Quaite et al. 1992); (· · ·) inhibition of photosynthetic electron transport in vitro (Jones and Kok 1966); (---) the differential spectrum for inhibition of photosynthesis in *Rumex patientia* (Rundel 1983, Caldwell et al. 1986); (—) inhibition of photosynthesis for the marine diatom *Phaeodactylum* sp. (Cullen et al. 1992b); and (×) broad-band action spectrum estimates from experiments on inhibition of photosynthesis in Antarctic phytoplankton (Helbling et al. 1992). (B) Weightings from BWF/P-I experiments ($\varepsilon(\lambda)$, reciprocal mW $m^{-2}$). Because BWF/P-I weightings are in absolute units, the laboratory-derived BWF (*Phaeodactylum*, —) can be compared without normalization to weightings for natural phytoplankton from the Antarctic: (· · ·) phytoplankton from ice-covered Lake Bonney, and (---) phytoplankton from McMurdo Sound cultured under conditions similar to the marginal ice zone (Neale et al. 1994).

than for damage to DNA (cf. Quaite et al. 1992).

The first BWF/P-I experiments on natural phytoplankton (Neale et al. 1994) demonstrate two types of variability that might be expected in nature (Fig. 2B): changes in the slope of the weighting function and changes in the offset (relative sensitivity at all UV wavelengths). Both BWFs on natural phytoplankton would lead to lower predicted effects of ozone depletion as compared to predictions from the laboratory results (Cullen et al. 1992b). Further assessment of environmental variability in BWFs will be essential to evaluating models of UV effects.

## 4. Critical modeling decisions

Assuming for now that subsurface spectral irradiance can be adequately described, and deferring consideration of longer-term effects of UVB on marine phytoplankton, we can identify the fundamental components of a model of marine photosynthesis, UVB, and ozone depletion: (i) a relationship between $P^B$ and PAR; (ii) a BWF for the inhibition of photosynthesis by UV; and (iii) an analytical representation of photoinhibition as a function of biologically-weighted UV irradiance and time. Despite a great deal of effort, we still have insufficient evidence on which to make critical decisions. Only a few BWFs have been measured on marine phytoplankton. The shape of inhibition vs. exposure relationships cannot be specified with confidence on the basis of field measurements, especially when one considers that if spectral shape varies with exposure, an appropriate BWF must be applied first to quantify effective UV. Further, reciprocity of UVB photoinhibition has been incompletely tested on natural phytoplankton. Thus, it would be legitimate at this time to examine a broad range of assumptions in constructing and comparing models of UV and marine photosynthesis.

It is instructive to compare three of many possible models of water-column photosynthesis as influenced by ozone depletion (Fig. 3). We examine here the choice of BWF and the functional form of the relationship between weighted exposure and inhibition. The BWF/P-I model (Fig. 3 A,D) uses Eq. (2), with parameters for a diatom in culture (Cullen et al. 1992b; BWF in Fig. 2). A linear version (Fig. 3 B,E) uses the same weighting function but assumes a linear relationship between weighted UV exposure and photoinhibition (cf. Behrenfeld et al. 1993). A third model uses the linear assumption, but weights UV according to Setlow's (1974) DNA action spectrum (Fig. 3 C,F). The possible effects of ozone depletion are explored by comparing a vertical profile under normal ozone to that under the ozone hole. The vertical variation

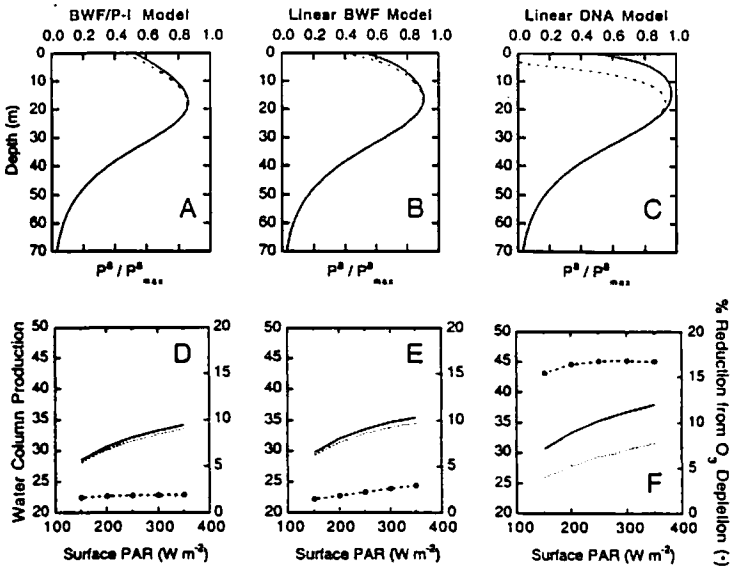


*Fig. 3.* Three different models of water-column primary production as influenced by UV and ozone depletion. (A) Relative $P^B$ vs. depth predicted by the BWF/P-I model using (as described by Cullen et al. 1992b): (i) BWF/P-I parameters for a marine diatom in culture; (ii) surface irradiance from McMurdo Station, Antarctica (PAR = 250 W $m^{-2}$) on days of normal atmospheric ozone (ca. 350 DU, solid curve) and low ozone (ca. 175 DU, dotted curve); and (iii) spectral diffuse attenuation coefficients ($m^{-1}$) at 1 nm intervals for UV (consistent with spectral irradiance measurements presented by Smith et al. 1992a); and (iv) one attenuation coefficient for PAR. (B) Predictions of a model that assumes linearity in the relationship between photoinhibition and UV (weighted with the same BWF as in A). (C) Predictions of a model that assumes a linear relationship between photoinhibition and UV weighted with the Setlow (1974) DNA action spectrum. The results for surface irradiance under normal ozone are matched for all three models. Results for different surface PAR irradiances are presented in (C), (D) and (E) for the BWF/P-I, linear BWF model and linear DNA models, respectively. Solid lines are water column production (relative units, left axes) for normal ozone, dotted lines are for low ozone. Filled circles show the percent reduction of water column productivity associated with ozone depletion (scales on right axes). Uniform chlorophyll concentration with depth is assumed for these calculations.

of predicted photosynthesis is substantially different between models using the BWF vs. DNA weightings. The DNA-effective irradiance, with relatively greater weights on the shorter, more rapidly attenuated wavelengths, decreases more rapidly with depth than irradiance weighted with the diatom BWF. The attenuation coefficients for weighted irradiance are neither constant with depth nor independent of the degree of ozone depletion (data not shown; see also Smith and Baker 1979). Consequently, there is no conversion factor that can equate the weighted exposures for different depths.

More profound differences are seen in model results for ozone depletion: the impact predicted by the DNA model is much more severe. This is partially because of the steeper slope near 300 nm for the DNA BWF, but mostly because the DNA weighting function has no weight in the UVA: the models are matched for the surface under normal ozone, but the BWF model accounts for this inhibition with both UVB and UVA, whereas the DNA model attributes it to UVB, which is strongly affected by ozone depletion. Clearly, biological effectiveness in the UVA must be determined if the relative effects of ozone depletion are to be predicted in this way (cf. Quaite et al. 1992).

Assumptions about linearity also have some influence. For example, if inhibition is 50% for a particular weighted irradiance, the BWF/P-I model predicts 67% inhibition for double that irradiance whereas the linear model predicts 100% inhibition (Fig. 1, Eq. (2)). However, a linear model with the BWF weighting is not dramatically different from the nonlinear BWF/P-I because the range of weighted exposures is not extreme.

Calculations of water-column photosynthesis further illustrate the contrast between models

(Fig. 3 D–E). For this trial calculation, the BWF/P-I model predicts < 2% reduction of water-column photosynthesis associated with 50% ozone depletion; the linear BWF model predicts a slightly greater effect with more dependence on surface PAR; whereas the linear DNA model predicts > 15% reduction. These calculations are meant to illustrate differences between models, not to describe the responses of Antarctic phytoplankton. For comparison, estimates of decreased water-column productivity associated with the ozone hole, based on results of 6–12 h incubations of natural Antarctic phytoplankton, ranged from a 3.8% inhibition (Helbling et al. 1994) to 6–12% (Smith et al. 1992a). The point of Fig. 3 is that BWFs and linearity of response vs. exposure should be thoroughly examined for natural populations before a model is accepted for general use in a variety of environments.

## 5. More problems: Vertical mixing

Nearly all data on UVB and the photosynthesis of natural phytoplankton comes from incubations of 4–12 h, and incubations at surface irradiance provide much of the information. When photosynthesis is measured during incubations, it is implicitly or explicitly assumed that the process examined in the control containers is occurring in nature as well. This would seem reasonable if the upper water column were stable for the duration of the experiments, but, because of vertical mixing, such is often not the case. When vertical mixing is active, conventional 6–12 h static incubations might be too long, leading to overestimation of inhibition because natural phytoplankton can tolerate short exposures to inhibiting irradiance during mixing (Harris 1978, Marra 1978, Neale 1987).

One approach to assessing the effects of vertical mixing is to compare a vertical profile from static incubations with a series of samples cycled vertically through the water column (e.g., Marra 1978). Variations of this experiment have been performed many times, with mixed results, but only recently have experiments been done with UV-transparent containers. Using a cycling time of 6 h (i.e., changes between 100% surface irradiance to 3% and back in 12 steps over 6 h using neutral density screens), Helbling et al. (1994) found that photosynthesis in cycled bottles, relative to average photosynthesis in static bottles, was inversely correlated with surface irradiance. That is, photoinhibition (which independent measurements suggested was due principally to UV) as a function of cumulative exposure was greater when all the phytoplankton in the simulated mixed layer were exposed to inhibiting irradiance for about an hour as compared the static situation, where only some of the phytoplankton were exposed to inhibiting irradiance, but for the duration of the experiment. As discussed above, these results demonstrate a failure of reciprocity. The relevance to nature depends on rates of vertical mixing, which could be much faster (about 30 min cycling time) or slower, depending on conditions (Denman and Gargett 1983). It is possible, though not common, to estimate rates of vertical mixing during studies of photosynthesis (Lewis et al. 1984, Smith et al. 1992a).

The 'fresh sample' technique is another way to examine photoinhibition and vertical mixing (Neale 1987, Neale et al. 1993). The premise is that if photoinhibition is occurring in situ, it should be detectable as a depression of short-term photosynthetic capacity near the surface, as observed in Lake Titicaca (Vincent et al. 1984, Neale and Richerson 1987) and the equatorial Pacific Ocean (Cullen et al. 1992a) during diurnal stratification of nocturnally-mixed surface layers. Inappropriately long incubation times are indicated when photoinhibition is observed during static incubations but not in the water column. For one example from a station in the tropical Pacific with a mixed layer of 50 m, Cullen and Neale (1993, data of J.J. Cullen and M.R. Lewis) showed that photosynthetic capability in a surface sample was almost completely destroyed during an incubation of 9 h under solar irradiance, even though UVB was excluded by the bottle. Chlorophyll content was reduced more than 50% in a process that tends to occur after chlorophyll-specific photosynthesis has reached a minimum (J.J. Cullen and H.L. MacIntyre, unpublished data). In contrast, short-term measurements on fresh samples from the surface at midday showed little or no reduction

of chlorophyll or photosynthetic capacity, presumably because the vertically-mixed phytoplankton tolerated the short exposures to potentially inhibiting irradiance (Harris 1980). It was concluded that a conventional half-day experiment to determine spectral sensitivity of photosynthesis to UV would be too long, and therefore grossly compromised under these conditions. We will see below that although conventional incubations might be too long to assess photoinhibition in situ, they are also too short to measure other critical biological responses.

## 6. UVB effects on photosynthesis: Contribution to reduced growth

This discussion has been constrained to the topic of aquatic photosynthesis and to time scales of a day or less. A principal goal, however, is to describe ecosystem changes over many years of predicted increases in UVB, superimposed on substantial seasonal variation (Frederick et al. 1989). Even if phytoplankton alone are examined, it is clear that many other physiological processes and longer-term responses must be studied if the potential consequences of ozone depletion are to be resolved.

### *Other harmful effects of UVB compared to photoinhibition of photosynthesis*

Not surprisingly, UVB inhibits or interferes with many processes in phytoplankton besides photosynthesis (reviews: Worrest 1982, Häder and Worrest 1991, Vincent and Roy 1993): damage to DNA reduces survival after short exposures to high fluence rates of UVB (Karentz et al. 1991a); aspects of nitrogen metabolism are altered (Döhler 1985, 1988, Döhler et al. 1987); motility is inhibited (Häder and Häder 1988, Ekelund 1990, 1991); and so are mechanisms for orientation (Häder and Häder 1988, Häder and Liu 1990, Blakefield and Calkins 1992). The harmful effects of UVB are countered by protection and recovery mechanisms (Vincent and Roy 1993). One suggested protection mechanism is the accumulation of UV absorbing compounds (Carreto et al. 1989, 1990a,b, Karentz et al. 1991b, Marchant et al. 1991, Helbling et al. 1994, Larkum and Wood 1993, Vernet et al. 1994). Recovery mechanisms include DNA repair (Karentz et al. 1991a), and degradation and resynthesis of damaged proteins, including photosynthetic proteins (Strid and Anderson 1994). The ultimate result of physiological and behavioral effects is a change in net specific growth rate, and a number of studies have shown that UVB inhibits growth or survival in phytoplankton, with a wide range of relative sensitivities between species (e.g., Calkins and Thordardottir 1980, Worrest et al. 1981, Worrest 1983, Jokiel and York 1984, Ekelund 1990, 1991, Behrenfeld et al. 1992, Smith et al. 1992a, Larkum and Wood 1993) or between strains of a species (Marchant et al. 1991). Differential sensitivities of phytoplankton species are thought to be a major reason for changes in microalgal communities under experimentally altered UVB regimes (Worrest et al. 1978, 1981, Bothwell et al. 1993). However, these studies were not designed to evaluate the contribution of UV-inhibition of photosynthesis as compared to other physiological, behavioral, or ecological processes in reducing net growth rates of phytoplankton species.

Quantitative assessments of the relative sensitivity to UVB of photosynthetic rate vs. growth rate might indicate whether an emphasis on photosynthesis is warranted. Unfortunately, such comparisons are not easy to make. Laboratory experiments with artificial sources of PAR, supplemented by filtered sunlamps (Calkins and Thordardottir 1980, Thomson et al. 1980, Ekelund 1990, 1991, Marchant et al. 1991) indicate that present-day levels of UVB depress the growth rates or kill some phytoplankton species and clearly demonstrate interspecific variability in sensitivity. As with many laboratory studies of photosynthesis, the ratios of UVB:PAR were commonly much higher than near the sea-surface, however, and it is not certain that the same inhibition from UVB would be obtained with more realistic irradiance regimes. Recently, Larkum and Wood (1993) used a filtered xenon arc lamp for exposing different marine plants to simulated solar irradiance ± UVB. They, too, found substantial differences in sensitivities between species of phytoplankton, macroalgae and seagrasses. Cul-

tures were preconditioned to low light conditions in the absence of UVB, and experimental inhibition of photosynthesis was rapid and severe.

Long-term incubations under solar irradiance, attenuated by different long-pass filters (e.g., Jokiel and York 1984, Karentz 1994) are desirable for studying ecological questions, as are manipulations of solar irradiance with filtered sunlamps and Mylar screen (Behrenfeld et al. 1992). However, neither method simulates gradients of underwater irradiance. Also, results can be difficult to interpret. For example, measurements on natural Antarctic phytoplankton have shown very severe UV-photoinhibition during 4–12 h incubations under near-surface irradiance, sometimes exceeding 50% (Helbling et al. 1992, 1994, Smith et al. 1992a, Vernet et al. 1994). Longer-term experiments during the late spring were different: Karentz (1994) demonstrated that specific growth rates of 9 clonal isolates of Antarctic phytoplankton were unaffected by either UVA or UVB during 12-day incubations under Antarctic solar irradiance attenuated by long-pass filters. Reconciliation of these superficially contradictory results will require a deeper appreciation of the residence times of phytoplankton near the surface, the rates and types of adaptation to potentially inhibiting irradiance, and more experiments during which effects on photosynthesis are measured concurrently with effects on growth.

*Ultraviolet radiation as an ecological factor*

Studies of UVB and phytoplankton growth are difficult to generalize in a consistent, quantitative framework, yet the weight of the results indicates that environmental UV can inhibit the growth of many phytoplankton and that sensitivities differ between species and strains. As expected, then, manipulations of UVB have significantly influenced microalgal community structure during controlled experiments (Worrest et al. 1978, 1981, Helbling et al. 1992, Bothwell et al. 1993). Community responses to UVB include altered trophic interactions (Bothwell et al. 1993, Herndl et al. 1993) culminating in results that do not have straightforward explanations, e.g., as the net result of UVB-induced differences in growth rate. Simply, we don't know enough to say what will happen, except that species composition will probably change.

*Acclimation to changes of UVB*

Apart from determining whether inhibition of photosynthesis is the dominant process mediating UV effects on growth, there are additional problems in extrapolating short-term changes in photosynthesis to longer-term effects on growth. If environmental conditions are more-or-less constant over several generation times (i.e., days to weeks), then one can assume a close coupling between photosynthesis and the growth of phytoplankton (Kiefer and Mitchell 1983, Geider et al. 1986). Under such steady conditions, cellular chemical composition changes little, day-to-day, and an energy balance is fulfilled, whereby the carbon-specific rate of photosynthesis equals the gross specific growth rate (Geider et al. 1986). The carbon-specific rate of photosynthesis is a function of both the quantum yield of photosynthesis and the cellular C:Chl ratio, both of which vary with growth irradiance and other environmental factors as a result of photoacclimation (Falkowski and La Roche 1991) and related processes (Prézelin and Matlick 1983, Laws and Chalup 1990, Cullen et al. 1993). Thus, although both short-term $P^B$ and longer-term growth are functions of irradiance, photosynthesis during a short experiment will generally be out of balance with long-term growth so that $P^B$ vs. irradiance is not the same as growth rate vs. irradiance (Myers 1970, Cullen 1990). Over time, adjustments will occur in the photosynthetic machinery to restore the energy balance. Adjustment or 'acclimation' of photosynthesis is fairly well described as a function of changing PAR (Falkowski and La Roche 1991), but only a little is known about responses to changing UVB, and the consequences of those responses in terms of growth rate.

One option for acclimation of phytoplankton to higher UVB exposure is to increase protection from UV irradiance or the damaging photochemistry it might cause. Circumstantial evidence for such protective mechanisms is strong: the cellular content of UV-absorbing compounds can increase with exposure to UVB, UVA or relatively high PAR irradiance (Carreto et al.

1989, 1990b); UVB absorbance in phytoplankton is enhanced in higher-irradiance environments (Vernet et al. 1989; see also Dunlap et al. 1986); and strains of the prymnesiophyte *Phaeocystis* which produce UVB absorbing compounds are less sensitive to UVB than those which do not (Marchant et al. 1991). Likewise, carotenoids can protect plants from UV-induced toxic intermediates, and they are potentially inducible (Vincent and Roy 1993). These, too have been found in enhanced concentrations in surface waters, suggesting a photoprotective role (Smith et al. 1992a). Another defensive mode is enzymatic protection from toxic oxygen species (Strid and Anderson 1994), such as by the production of superoxide dismutase and a peroxidase (cf. Lesser and Shick 1989). Distributions of these enzymes have not been reported in studies of UVB and natural marine phytoplankton encountered during our review.

There is little direct evidence indicating the biological functions of UV-absorbing compounds in phytoplankton (Karentz 1994), but quantitative documentation of protection by UV-absorbing compounds has recently been presented for terrestrial plants. One specific molecular target for UVB induced photoinhibition is suggested to be Photosystem II, and specifically the D1 reaction center protein (see Strid and Anderson 1994 for more details). When *Brassica napus* (oil seed rape) was acclimated to UVB plus visible light, sufficient to induce UV-absorbing compounds, the turnover rate of D1 during subsequent exposure to UVB (an indication of the rate at which the protein is damaged) was decreased about 40% when compared to control plants grown under visible irradiance. Both UVB-adapted and control plants had similar D1 turnover rates under visible light, however, indicating that only damaging UVB was screened in the acclimated plants (Wilson and Greenberg 1993). In microalgae, UV absorbing compounds operate over much shorter optical pathlengths and may only provide partial protection against UVB. Experiments on a terrestrial cyanobacterium indicated that intracellular mycosporine-like amino acids (MAAs) reduced cytoplasmic damage from UVB by 30%, not enough to explain fully the resistance of the adapted cells to UVB (Garcia-Pichel et al. 1993). Clearly, acclimation of microalgae to UVB can involve a wide variety of mechanisms (Marchant 1993, Vincent and Roy 1993).

Phytoplankton can also acclimate to UV by increasing the capacity of processes which correct UV-induced damage. Systems for repairing DNA have been described (Karentz 1994). Enhanced recovery from UV-induced damage to photosynthetic systems may come from increased protein degradation and resynthesis to replace UV-sensitive proteins almost as fast as they are damaged, the D1 protein for example (Greenberg et al. 1989, Strid and Anderson 1994).

Even though protection and recovery processes may mitigate the decrease in photosynthesis that is induced by chronic episodes of UV-B exposure, there may yet be a significant effect on growth rate. This is because counteracting strategies have a certain energy cost and can ultimately result in redirection of cellular resources from growth to maintenance, i.e., an increase in the 'overhead' of growth. The synthesis of UV-absorbing compounds can impose a metabolic cost for growth in UV depending on the intra- and extra- cellular concentrations and how fast the compounds turn over (Raven 1991). For MAAs, $< 1\%$ of cellular dry biomass can screen some UVB, so they may be 'regarded as a good improvement for a small investment' (Garcia-Pichel et al. 1993). Recovery processes seem to require more overhead: it has been estimated that D1 turnover connected with the damage of the PS II complex would account for up to 10% of the net protein synthesis at maximum growth rate of the cyanobacterium *Anacystis nidulans* if net photosynthetic rates are to remain unaffected by stress from excessive PAR (Raven and Samuelsson 1986). A similar situation might be expected in response to UVB exposure, which is also known to increase D1 turnover rate in plants (Greenberg et al. 1989). The potential importance of protein synthesis was suggested by the observation that for a marine diatom, short-term (0.5 to 4 h) photosynthesis in a nitrogen-limited culture was nine times more sensitive to UVB than in a nutrient-replete culture (Cullen and Lesser 1991).

As results of more studies are compared, uncertainties should be resolved and the degree

to which photoinhibition of photosynthesis contributes to reduced growth will be easier to assess. For now, it seems reasonable to assume that net damage to photosynthetic systems is an important part of UV effects on the growth of phytoplankton. In the future, comparisons will be easier if BWFs for inhibition of growth rate are determined in absolute units for comparison with BWFs for inhibition of photosynthesis. So far, a DNA weighting function has been used to describe changes in growth rate associated with manipulations of UVB (Thomson et al. 1980, Behrenfeld et al. 1992), but the relative sensitivity of UVA has yet to be quantified, even though it has been shown to be important (Jokiel and York 1984).

### 7. Ozone depletion and the biogeochemical cycling of carbon

Accepting for the purpose of discussion that increases in UVB can lead to a decrease in phytoplankton growth rates and marine primary productivity, we can consider what consequences this might have on global carbon cycles. It has been suggested that, since phytoplankton are a sink for $CO_2$, ozone-related reductions in phytoplankton growth will result in equivalent reductions of $CO_2$ going into the ocean (Worrest 1983, Häder and Worrest 1991, United Nations Environment Programme 1991). However, when interpreting experimental data on ozone-related reductions in Antarctic primary production, Smith et al. (1992a) made no direct extrapolation to changes in carbon flux to the ocean. Reasons for such caution merit examination.

A few principles are relevant. First, as discussed at length above and well recognized in all reviews, short-term photoinhibition of photosynthesis might not translate directly into longer-term inhibition of growth rate. Also, net growth is affected by much more than UVB. Consider the influence of ozone depletion on Antarctic phytoplankton communities. Growth experiments on the prymnesiophyte *Phaeocystis* sp. and the diatom *Chaetoceros socialis* showed a much greater UVB-inhibition of growth rate in the prymnesiophyte, yet *Phaeocystis* spp. dominated most phytoplankton communities in the waters influenced by the ozone hole (Smith et al. 1992a; see also Marchant 1993). Clearly, UVB was not the only environmental factor determining the species composition of phytoplankton (Karentz 1991, 1994).

Secondly, the turnover rate of phytoplankton in the ocean is in general more rapid than for land plants, so instead of accumulating as phytoplankton biomass, much marine primary production is consumed and respired in the surface layer on the time-scale of days, releasing $CO_2$ with no net effect on the flux of carbon between the atmosphere and ocean (Platt et al. 1992). The component of marine primary production that does influence the balance between atmospheric and marine $CO_2$ is that which can be transported to the deep ocean, either by sinking or by water motions (new production: Dugdale and Goering 1967, Eppley and Peterson 1979). Quantifying new production involves much more than measuring vegetation density. Moreover, downward biological fluxes of organic carbon are largely balanced by upward fluxes of inorganic carbon, so that new production is not a straightforward measure of the flux of carbon from the atmosphere to the ocean (Eppley and Peterson 1979, Lewis 1992, Platt et al. 1992).

The reader is referred elsewhere for more a comprehensive treatment of the role of photosynthesis in ocean carbon budget (e.g., Chisholm and Morel 1991). For the purpose of this review, we state that marine photosynthesis is only one of several interacting processes which strongly influence marine carbon cycling and that the effects of UVB should be assessed within this context. For example, since the fate of phytoplankton carbon depends heavily on trophic interactions (Michaels and Silver 1988, Marchant 1993), UVB-influenced changes in species composition may be more important to carbon flux than absolute changes in community productivity. Also, since marine dissolved organic matter (DOM), one of the largest carbon reservoirs on the Earth's surface, derives mainly from phytoplankton and can be a significant absorber of UVB in the ocean, UVB effects on the synthesis and excretion of DOM as a component of photosynthesis may have particular interest. Photochemical conversion of DOM is important to the cycling of carbon (Mopper et al. 1991),

and UVB-induced production of reactive transient species might have significant biological consequences (Mopper and Zhou 1990), so studies of photochemistry should be integrated with biological research on the effects of UVB. Though much remains to be learned about the physiological effects of solar UVB on phytoplankton photosynthesis and growth, an appreciation of ecological and chemical interactions should help to provide results with maximum utility for evaluating possible biogeochemical impacts.

## 8. Conclusions

Research on UVB and marine phytoplankton has accelerated rapidly in the past few years, but much of the new information cannot yet be synthesized into a robust assessment of the degree to which present-day UVB influences phytoplankton, and how much worse it will be for a given amount of ozone depletion. We do know that environmental UVB can harm marine phytoplankton, and we can infer from several studies that UVB is a significant ecological factor. We cannot, however, use results from experimental incubations to predict with confidence the ecological consequences of ozone depletion. Such experiments are nonetheless important because they provide quantitative information on sensitivities to UVB, so we can identify which physiological and ecological processes most likely dominate ecosystem responses to enhanced UVB. Comparison of experimental results is critical, and that requires accurate spectral radiometry and the development of appropriate biological weighting functions. As more results are shared and compared, better generalizations will develop and more accurate predictions will be possible.

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