

Effects of UV radiation on phytoplankton

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Introduction

It is now widely documented that reduced ozone will result in increased levels of ultraviolet (UV) radiation, especially UV-B (280-320nm), incident at the surface of the earth [Watson, 1988; Anderson et al., 1991; Schoeberl and Hartmann, 1991; Frederick and Alberts, 1991; WMO, 1991; Madronich, 1993; Kerr and McElroy, 1993], and there is considerable and increasing evidence that these higher levels of UV-B radiation may be detrimental to various forms of marine life in the upper layers of the ocean. With respect to aquatic ecosystems, we also know that this biologically-damaging mid-ultraviolet radiation can penetrate to ecologically-significant depths in marine and freshwater systems [Jerlov, 1950; Lenoble, 1956; Smith and Baker, 1979; Smith and Baker, 1980; Smith and Baker, 1981; Kirk et al., 1994]. This knowledge, plus the dramatic decline in stratospheric ozone over the Antarctic continent each spring, now known to be caused by anthropogenically released chemicals [Solomon, 1990; Booth et al., 1994], has resulted in increased UV-environmental research and a number of summary reports. The United Nations Environmental Program (UNEP) has provided recent updates with respect to the effects of ozone depletion on aquatic ecosystems [Hader, Worrest, Kumar in UNEP 1989, 1991, Hader, Worrest, Kumar and Smith UNEP 1994] and the Scientific Committee on Problems of the Environment (SCOPE) has provided [SCOPE, 1992] a summary of the effects of increased UV radiation on biological systems. SCOPE has also reported [SCOPE, 1993] on the effects of increased UV on the biosphere. In addition, several books have recently been published reviewing various aspects of environmental UV photobiology [Young et al., 1993], UV effects on humans, animals and plants [Tevini, 1993], the biological effects of UV radiation in Antarctica [Weiler and Penhale, 1994], and UV research in freshwater ecosystems [Williamson and Zagarese, 1994]. Several other reviews are relevant [NAS, 1984; Caldwell et al., 1986; Worrest, 1986; NOAA, 1987; Smith, 1989; Smith and Baker, 1989; Voytek, 1990; Hader, 1993; Acevedo and Nolan, 1993; Holm-Hansen et al., 1993; Vincent and Roy, 1993; Biggs and Joyner, 1994; Williamson and Zagarese, 1994; Karentz, 1994; Cullen and Neale, 1993; Cullen and Neale, 1994]. As Hader et al. have summarized [UNEP, 1989; UNEP, 1991], "UV-B radiation in aquatic systems: 1) affects adaptive strategies (e.g., motility, orientation); 2) impairs important physiological functions (e.g., photosynthesis and enzymatic reactions); and 3) threatens marine organisms during their developmental stages (e.g., the young of finfish, shrimp larvae, crab larvae)". Possible consequences to aquatic systems include: reduced biomass production; changes in

species composition and biodiversity; and alterations of aquatic ecosystems and biogeochemical cycles associated with the above changes. Within the past four years, our knowledge with respect to the environmental effects of ozone-related increased levels of UV-B has increased significantly, and numerous efforts have been directed toward process-oriented studies of UV responses in plants and animals. Consensus is building toward the view that current levels of UV play a major role as an ecological determinant, influencing both survival and distribution, and are thus deserving of increased study independent of ozone-related UV-B increases. This review outlines U.S. research subsequent to 1991 and emphasizes studies concerned with phytoplankton.

Context for Quantitative Analysis

The task is to describe the effects of ultraviolet radiation on a biological process, such as photosynthesis. For a particular location, this requires a description of potential photosynthesis as modified by an inhibition function:

$$P = \int \int \int B(z, t) \cdot P_{pt}^B(\lambda, z, t) \cdot f(E_{B_c}(\lambda, z, t)) \cdot d\lambda \cdot dz \cdot dt(1)$$

where P is daily photosynthesis ($gC \cdot m^{-2}$), B is the concentration of chlorophyll-a ($gChla \cdot m^{-3}$), P_{pt}^B is chlorophyll-normalized photosynthesis in the absence of inhibition ($gC \cdot gChla^{-1} \cdot h^{-1} \cdot nm^{-1}$), and the dimensionless inhibition term is a function of E_{B_c} , spectral irradiance ($W \cdot m^{-2}$), weighted by a wavelength-dependent (λ, nm) biological weighting function, $\epsilon(\lambda)$, discussed below. In principle, one can calculate the effects of ultraviolet radiation on aquatic photosynthesis by evaluating Eq.(1) with and without UV wavelengths, or under different degrees of ozone depletion. Common simplifications are to ignore variation of chlorophyll with depth (z) and time (t) and to represent P_{pt}^B as a function of photosynthetically available radiation (PAR; 400-700 nm), regardless of spectral quality (units: $gC \cdot gChla^{-1} \cdot h^{-1}$).

A great deal of information is required to assign parameters and functional relationships to Eq.(1), and at present it serves better as a context for discussing UV and phytoplankton than as a tool for quantitative analysis. To evaluate the equation, one must specify: 1) Absolute spectral irradiance, $E(\lambda)$ ($W \cdot m^{-2} \cdot nm^{-1}$) as a function of depth and time; 2) Photosynthesis as a function of irradiance in the absence of inhibition, P_{pt}^B vs. $E(\lambda, z, t)$; 3) A biological weighting function (BWF), $\epsilon(\lambda)$, to convert absolute spectral irradiance to biological effective irradiance, $E_{B_c}(W \cdot m^{-2})_c$; 4) A time-dependent function relating inhibition of photosynthesis to E_{B_c} ; and 5) An appreciation of how vertical mixing (hence, variable irradiance exposures of phytoplankton) influences 2) and 4).

It would be quite an accomplishment to evaluate Eq.(1) for one day at one location. To obtain estimates of the effects of ozone

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Paper number 95RG00801.
8755-1209/95/95RG-00801\$15.00

depletion on annual marine photosynthesis in large regions of the ocean, variable biomass and changes in populations and their physiological characteristics would also have to be incorporated. Such a detailed calculation is beyond our reach at this time, but as we show below, many aspects of the problem have been studied, and rough estimates of UV effects have been obtained.

Components of Quantitative Models

Absolute Spectral Irradiance

Bio-Optical Models. The absolute in-water spectral irradiance, $E(\lambda, z, t)$, is an essential component in the modeling and/or measurement of UV effects on phytoplankton. Bio-optical models can be used to predict the penetration of spectral irradiance in the water column. They take as input the spectral irradiance above the air-water interface, compute the transmittance through this interface, and permit the estimation of biologically effective irradiance as a function of depth in natural waters (see Smith 1989 for a review). The inherent optical properties of water are a key element in these models. Recently Kirk [Kirk, 1994; Kirk et al., 1994] has reviewed the optics of UV-B radiation in natural waters and showed that the fundamental optical properties of water in the UV region of the spectrum are still a matter of controversy. He points out that the absorption coefficient for pure water at 310nm, $a(310\text{nm})$, as determined by Quickenden & Irvin (1980) and Boivin et al. (1986) is about an order of magnitude lower than that estimated by Smith & Baker (1981). Kirk suggests that earlier reported higher absorption coefficients can be attributed to dissolved oxygen and trace organic materials which are notoriously difficult to remove completely from water. From an ecological perspective the important issue is our ability to know the optical properties of the clearest natural water in order to construct accurate analytical models of spectral attenuation. Since dissolved oxygen and trace organic materials are usually present in natural waters, the higher absorption values published for clear natural waters should be appropriate for ecological studies, but the potential for lower absorption as determined in laboratory studies should not be overlooked.

In-water irradiance measurement. While there are relatively few instruments developed specifically for the measurement of in-water UV, the past few years has seen significant advancement in this area. Smith [Smith et al., 1992b] developed a new light and ultraviolet submersible spectroradiometer (LUVSS), capable of measuring full spectral irradiance and underwater radiance. The LUVSS instrument has 0.2 nm resolution from 250 to 350 nm and 0.8 nm resolution from 350 to 750 nm and is deployed by a remote operating vehicle that allows accurate in-water data to be obtained independent of ship perturbation effects. Also within the past few years, several commercial instruments have been developed specifically for, or adapted to, in-water UV measurement. Kirk and co-workers [Kirk et al., 1994] carried out a comparison of several commercial instruments and evaluated various instrument results against an atmospheric model to test spectral fidelity. This intercalibration, which was done among several research groups and several instruments, is an important precedent for future research on UV effects.

Atmospheric Models. Atmospheric models play an important role, both for providing computed input to in-water models and for testing and extrapolating above-surface UV data. The Antarctic ozone hole has motivated the development of a number of improved atmospheric models, suitable for polar regions, where low sun elevation (long pathlength) conditions prevail. This work

includes [Lubin and Frederick, 1990; Lubin and Frederick, 1991; Lubin et al., 1992; Stamnes et al., 1988; Stamnes et al., 1990; Stamnes et al., 1990; Tsay and Stamnes, 1992; Smith et al., 1992a; Madronich, 1993]. These models permit: relatively accurate space/time extrapolation of satellite or ground measurements; quantitative estimates of the effects of ozone depletion on spectral solar UV and visible irradiance at the earth; and accurate estimation of column ozone concentrations above ground stations that record relatively high resolution spectra.

Photosynthesis vs. Irradiance

Models of photosynthesis vs. irradiance, or P vs. I, are central to the estimation of aquatic photosynthesis from observed distributions of chlorophyll and light [Ryther and Yentsch, 1957; Talling, 1957]. Since the advent of remote sensing from space, they have been used and modified extensively, because they are necessary components of algorithms to calculate primary productivity from ocean color [Smith et al., 1987; Bidigare et al., 1992b; Platt and Sathyendranath, 1993; Morel, 1991]. The inhibition of photosynthesis by UV and excess PAR is well recognized [Neale, 1987], and the effects of excess PAR have been incorporated into models of P vs. I [Platt et al., 1980; Neale and Richerson, 1987]. However, near-surface inhibition of photosynthesis is generally ignored in water-column models, because photoinhibition in situ is difficult to generalize on the basis of experimental measurements [Marra, 1978; Neale, 1987; Henley, 1993], and because decreases in productivity associated with photoinhibition are relatively small compared with the variability encountered in remotely-sensed data. When interest is turned to UV and its effects on photosynthesis, however, the photoinhibition term is of paramount importance.

The effects of UV have recently been incorporated explicitly into a model of photosynthesis vs. irradiance [Cullen et al., 1992]:

$$P^B = P^B_s \cdot \left(1 - e^{(-E_{PAR}/E_k)}\right) \cdot \left(\frac{1}{1 + E^*_{inh}}\right) \quad (2)$$

where E_{PAR} is PAR ($W \cdot m^{-2}$), P^B is the rate of photosynthesis normalized to chlorophyll, P^B_s is the maximum attainable rate in the absence of photoinhibition, and $E_k (W \cdot m^{-2}, PAR)$ is a saturation parameter for photosynthesis. The product, $P^B_s \cdot \left(1 - e^{(-E_{PAR}/E_k)}\right)$, is equivalent to P_{pt} , the potential productivity in Eq (1). It is essentially the same as in many models. The inhibition term, $\left(\frac{1}{1 + E^*_{inh}}\right)$, is one possible form of $f(E_{B_c}(\lambda, z, t))$ in Eq. (1), where E^*_{inh} (dimensionless) is biologically weighted UV irradiance, plus wavelength-independent biologically weighted PAR. Descriptions of P vs. I and its inhibition by UV could take other forms, but all, either implicitly or explicitly, would have to conform to Eq. (1): $P = P_{pt} \cdot f(E_{B_c})$. Years of work have gone into describing P_{pt} , but as we show below, it is a major task to quantify biologically weighted irradiance, E_{B_c} , and the functional form of its relationship with P/P_{pt} .

Biological Weighting Function

A biological weighting function, or action spectrum, takes account of the wavelength-dependency of biological action; it is a critical parameter in the assessment of the potential biological effects of O_3 -related enhanced ultraviolet radiation [NAS, 1979; NAS, 1982; NAS, 1984; Coohill, 1989]. A number of authors [Rundel, 1983; Caldwell, 1968; Caldwell et al., 1986] have shown that an accurate knowledge of $\epsilon(\lambda)$ is essential in order to make

quantitative estimates of biologically effective irradiance. Biological weighting functions have traditionally been determined by evaluating biological responsiveness to monochromatic radiation with the objective of identifying potential chromophore targets and elucidating photobiological mechanisms [Cochill, 1991]. Caldwell and co-workers (1986) reviewed evidence suggesting that weighting functions determined using polychromatic radiation and intact organisms may have more ecological relevance with respect to assessing the ozone reduction problem. Work during the 80's [Smith and Baker, 1982; Rundel, 1983; Caldwell et al., 1986] provided biological weighting functions for plant damage by UV that showed relatively strong dependence on UV-B but also showed a significant contribution from the UV-A (320-400nm) region.

The last few years have seen significant progress in determining biological weighting functions for the inhibition of photosynthesis by phytoplankton. Recent work by Cullen and co-workers [Cullen et al., 1992; Lesser et al., 1994] used principal component analysis of experimental results to estimate biological weighting functions which describe the effects of polychromatic radiation on cells with a relatively high resolution, smoothly-varying spectral response. Their work provides $\epsilon(\lambda)$ functions for the inhibition of phytoplankton photosynthesis by ultraviolet radiation, with results in absolute units ($[W \cdot m^{-2}]^{-1}$). Other recent estimates, using relatively coarse broadband spectroscopy, of $\epsilon(\lambda)$ of natural populations include the work by Mitchell and co-workers (1990), by Helbling et al. (1992), and by Behrenfeld et al. (1993a,b). Figure 1 compares several recently published action spectra, all normalized to 1.0 at 300nm. There is now broad agreement among these several workers that the biological weighting, while highest in the UV-B, also contains a significant UV-A component. Although it did not employ completely natural irradiance, the experimental approach of Cullen et al. provides a practical advantage toward assessing the effects of ultraviolet radiation and ozone depletion, because it generates weightings in absolute units, permitting direct comparison of biological effectiveness between experiments [Lesser et al., 1994], including more accurate comparison of biological effects produced by artificial sources with different spectral distributions and those due to actual and/or predicted natural radiation. It also provides for the development of quantitative models for the prediction of future impacts of ozone depletion [Cullen and Neale, 1994]. There is a need for accuracy because relatively small changes in $\epsilon(\lambda)$ can lead to large changes in biologically effective irradiance.

Relationship between Exposure and Effect

A quantitative evaluation of possible UV-related damage to an organism requires experimental data assessing UV effects versus quantified exposure to biologically weighted irradiance, for comparison with current or predicted natural irradiance levels. Commonly, the effects of UV are reported as a function of cumulative exposure (here referred to as dose), in an analysis called a survival or dose-response curve.

Reciprocity. Calculation of dose requires the time-integration of the biological effective irradiance (Eq. 1) over an appropriate interval (hourly, daily, yearly, etc.) to get the biological effective exposure:

$$E_{TB}(Z) [J \cdot m^{-2}]_{\epsilon(\lambda)} = \int E_B(t, z) [J \cdot m^{-2} \cdot s^{-1}]_{\epsilon(\lambda)} \cdot dt [s]. \quad (3)$$

The exposure, via Eq. 1, is weighted by the appropriate relative biological weighting function and the units reflect the arbitrary normalization associated with this weighting. Alternatively, the

BWFs have been determined on an absolute basis with biologically effective exposure expressed as the dimensionless E_{inh}^* [Cullen et al., 1992; Lesser et al., 1994]. In either case, the biological effective exposure is a time integral of an appropriately weighted irradiance and this raises the classic assumption of reciprocity (that the effect is a function solely of cumulative exposure independent of irradiance). Reciprocity fails if, for equal weighted exposures, a short exposure to a highly damaging irradiance causes a different effect than a long exposure to a less damaging irradiance.

The question of reciprocity thus impacts the discussion of radiation amplification factors (see below), interpretation of experimental results, and models for assessing and predicting UV-B effects. Equally important, the time-dependent reciprocity issue almost guarantees a problem with non-linearity if carried across a sufficient range of scale. Laboratory studies [Cullen and Lesser, 1991; Lesser et al., 1994] show that the photoinhibition of photosynthesis, when plotted against cumulative dose of UV-B, is a monotonic, nonlinear function of UV dose for any one time scale. For equal doses, however, a relatively short exposure to high UV-B irradiance is more damaging to photosynthesis than a longer exposure to lower irradiance (i.e., reciprocity fails). These results are consistent with a mechanistic model of photoinhibition as a balance between damage and recovery processes, processes that utilize different parts of the solar spectrum and are likely to operate on different time scales [Neale, 1987]. These workers conclude that for their system, UV inhibition is best modeled as a function of biologically weighted irradiance, but as pointed out by Cullen and Neale (1994), the kinetics of UV-induced photoinhibition must be resolved for natural phytoplankton in a number of environments.

For example, consistent with reciprocity, Behrenfeld and co-workers (1993a,b) combining their own plus earlier [Smith et al., 1980] results of exclusion/inclusion experiments under ambient solar radiation, and using their weighted exponential BWF, found a common linear dose-response curve for all three studies. Their results, which represent data from a wide range of oceanic regimes, describe the cumulative inhibition of carbon fixation by ultraviolet radiation (UVR) as a function of total dose and suggest that reciprocity holds for their experimental conditions (4-8 hr incubations and ambient solar irradiance). Since their dose-response curve is linear with no apparent threshold, they conclude that is likely that any increase in UVR will cause additional photodamage. It is important to recognize that, as Behrenfeld and co-workers acknowledge, these studies assessed UV-B, but not UV-A, effects so that possible nonlinearity based on measurements under different UV-A exposures might not have been readily apparent.

The question of reciprocity in UV-induced photoinhibition of natural phytoplankton has not been resolved: reciprocity failed when Helbling et al. (1994; discussed in more detail below) compared inhibition of photosynthesis in Antarctic phytoplankton exposed to fixed vs. variable irradiance regimes. Unless reciprocity can be justifiably assumed for the full range of time scales under consideration, quantitative generalizations of UV effects require a description of biological effects vs biologically weighted incident irradiance and a description of the time-dependence of the function. The assessment of time-dependence is extremely important [Vincent and Roy, 1993]. For example, if the biological effect is a function of cumulative exposure, independent of dose (i.e., reciprocity is satisfied), then one can predict UV effects under variable irradiance through the day, even under the influence of vertical mixing (cf. Smith and Baker, 1982). Likewise,

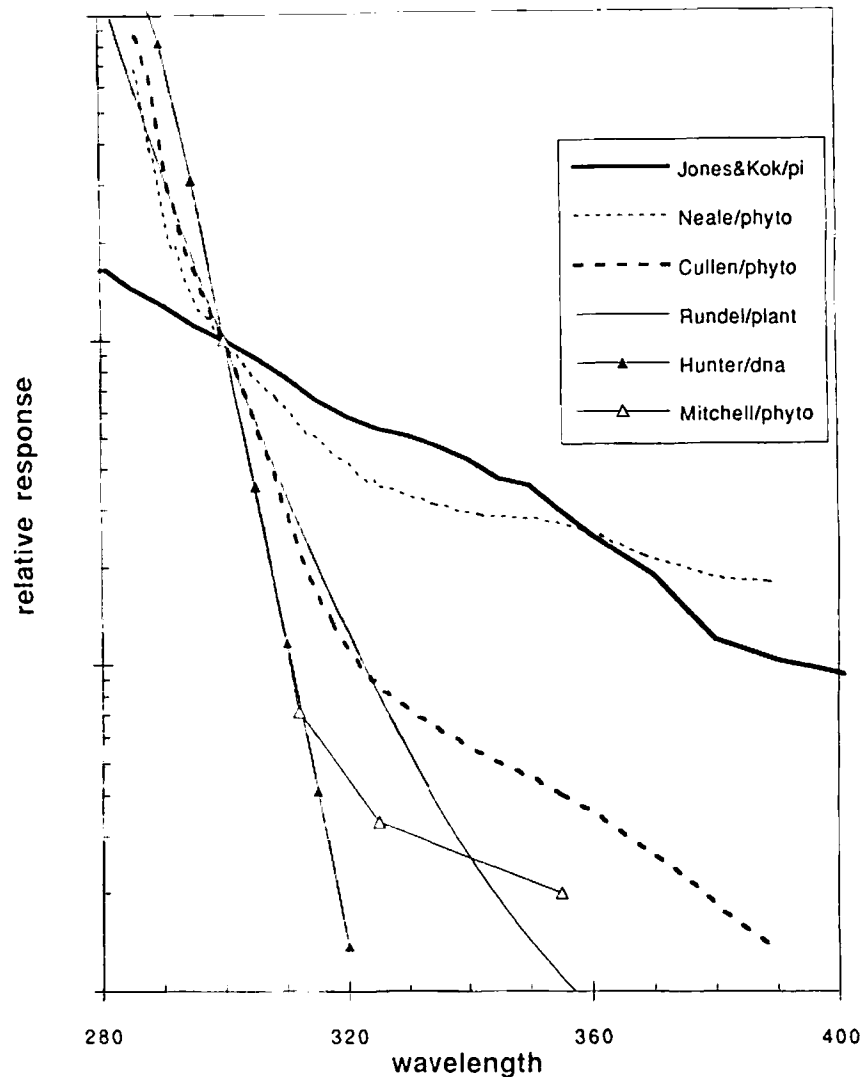


Figure 1. Relative response of biological weighting functions normalized at 300nm versus wavelength. Data from: [Jones and Kok, 1966; Neale et al., 1994; Cullen and Neale, 1993; Rundel, 1983; Hunter et al., 1979; Mitchell, 1990]

modelling is tractable if the effect is a function solely of biologically weighted irradiance (dose rate), regardless of duration [Cullen and Lesser, 1991]. In practice, most researchers have related effects of UV on phytoplankton to cumulative biologically weighted exposure over the course of several hours to a day. Implicitly or explicitly, it has been assumed that cumulative exposure over one day is the relevant quantity for quantifying biologically effective UV. The bottom line (relevant also to the comparisons between laboratory and field results) is that critical issues concerning response-versus-exposure have been identified, but they have yet to be resolved.

Shape of the function. The shape of the inhibition vs. exposure relationship is also important [Vincent and Roy, 1993]. Data from the field on UV-induced photoinhibition have been described with linear [Smith et al., 1980; Behrenfeld et al., 1993a], and sigmoid [Helbling et al., 1992; Smith et al., 1992b] relationships. These shapes influence the amplification factors (see below). The scatter in field measurements, usually dependent upon broad-band exclusion/inclusion techniques, and uncertainties about reciprocity make it difficult to identify the best form. However, laboratory results [Cullen and Lesser, 1991; Cullen et al., 1992; Cullen et al.,

1992] can be characterized with inhibition described as a hyperbolic function of biologically effective irradiance. The same model works for natural phytoplankton from the Antarctic [Neale et al., 1994].

Radiation Amplification Factor (RAF). The concept of an amplification factor, A , such that a 1% decrease in ozone may cause an $A\%$ increase in biological effect, is useful when considering the possible impact of ozone diminution on a biological system. This amplification factor has been subdivided into two components [Nachtwey and Caldwell, 1975; Green et al., 1976; Rundel and Nachtwey, 1978; Rundel, 1983]: (i) the ratio of the proportional change in biological effective irradiance, or dose rate, $\Delta E_{B_e(\lambda)} / E_{B_e(\lambda)}$, to the proportional change in total atmospheric column ozone concentration, or ozone thickness, $\Delta \omega / \omega$; i.e., the radiation amplification factor,

$$R = \left[\frac{\Delta E_{B_e(\lambda)}}{E_{B_e(\lambda)}} \right] / \left[\frac{\Delta \omega}{\omega} \right] \quad (4)$$

and (ii) the ratio of the percentage change in biological effect (e.g., reduction in photosynthesis), $\Delta P / P$, to the proportional change in biologically effective irradiance, $\Delta E_{B_e(\lambda)} / E_{B_e(\lambda)}$; i.e., the biological amplification factor,

$$B = [(\Delta P / P)] / [(\Delta E_{B_{\epsilon(\lambda)}} / E_{B_{\epsilon(\lambda)}})] \quad (5)$$

so that the total amplification factor is

$$A = R \times B = [(\Delta P / P)] / [(\Delta \omega / \omega)]. \quad (6)$$

Radiation amplification factors give the increase of biologically effective irradiance in response to ozone depletion and published values have been reviewed by Madronich et al. [1994]. Biological amplification factors will be exactly 1.0 only when the biological effects are linear functions of weighted exposures and, as discussed above, that is not always the case. The above unitless sensitivity coefficients were developed in the late 70's when ozone reductions were projected to be 5 to 15%. Madronich [Madronich and Granier, 1992; Madronich, 1993; Booth and Madronich, 1994] has pointed out that since the dose versus ozone relationship is nonlinear, the radiation amplification factor, if calculated using Eq.(4), is not constant with ozone concentration over large changes in ozone characteristic of the Antarctic ozone hole. He has proposed a simple power law that provides a more general definition of the dose versus ozone relationship and which results in a sensitivity factor R which is relatively constant for large ozone depletions:

$$\frac{(E_{B_{\epsilon(\lambda)}})_2}{(E_{B_{\epsilon(\lambda)}})_1} = \left(\frac{\omega_2}{\omega_1}\right)^{-R} \quad (7)$$

so,

$$R = - \frac{\ln[(E_{B_{\epsilon(\lambda)}})_2 / (E_{B_{\epsilon(\lambda)}})_1]}{\ln(\omega_2 / \omega_1)}. \quad (8)$$

In dealing with inferences based upon radiation amplification factors, it is important to be aware of how the factor was derived, especially when comparing pre-1990 with more recently published results. It should also be noted that there are very few recent data with respect to the estimation of biological amplification factors except for the nonlinear function of Cullen and coworkers. However, it is not known if their results can be applied directly to the representation of natural populations for time scales greater than one hour, which is necessary for an overall assessment of ozone-related effects.

A reduction in the thickness of the ozone layer leads to an increase in UV-B radiation. This will have a large effect for biological weighting functions which are heavily weighted in the UV-B region (eg., DNA) with $R > 1$. Conversely, biological weighting functions weighted outside the UV-B region, in particular those weighted in the UV-A spectral region, will have smaller direct effects ($R < 1$). Radiation amplification factors, R, for selected biological weighting functions plotted in Fig. 1, calculated using Eq.(8), and averaged over latitude and time, are 0.07 for photoinhibition of chloroplasts [Jones and Kok, 1966], 0.31 for a marine phytoplankton [Cullen and Neale, 1993], 0.51 for plants [Rundel, 1983] and 1.67 for DNA [Hunter et al., 1979] which quantitatively demonstrates that R increases with increased dependence on UV-B.

Vertical Mixing

Many mechanisms, such as mixing, provide UV-B protection by reducing radiant energy to which cells are exposed, but they also reduce the energy available for photosynthesis. The several photoprocesses that are simultaneously active within the cell (cf Smith et al., 1992) have different wavelength sensitivities, operate with different time constants, respond differently, and probably

non-linearly, to changing irradiance levels as they are mixed within the water column. Thus physical mixing significantly complicates attempts to resolve the biological balance between damage (usually shorter less penetrating wavelengths) and repair (usually longer more penetrating wavelengths) processes. Early analytic models [Morowitz, 1950; Zepp and Cline, 1977; Smith and Baker, 1982], often overlooked by more recent workers, show that that balance between 'protection' to near surface organisms and 'added exposure' of otherwise deep organisms by vertical mixing is a balance between depth and rate of mixing and optical properties of the water column. Smith [1989] recently reviewed this subject and pointed out that an important consideration, with respect to the dose response of phytoplankton, is the ratio of biological dose to the photosynthetically available radiation, E_B / E_{PAR} , versus biological damage.

If the time scale for a biological response (e.g., UV damage, photoadaptation) is shorter than that for vertical mixing, phytoplankton will exhibit a vertical gradient of this response [Lewis et al., 1984; Cullen and Lewis, 1988]. On the other hand, if mixing occurs with a time scale shorter than that of the biological response, no such gradient will be observed. The rates of various photoprocesses (which are strong functions of wavelength), as compared with that of vertical mixing (which rapidly alters the in-water spectral irradiance), will determine the overall effect on the populations at depth. It is also important to recognize that transient stratification, often associated with phytoplankton 'bloom' events [Riley, 1942; Sverdrup, 1953; Brown et al., 1985], can often coincide with periods of high irradiance, thus maximizing UV exposure.

While it has long been known that vertical mixing is a major complication in attempting to quantify UV-B effects on phytoplankton [Kullenberg, 1982; Smith and Baker, 1982], recent work suggests that linking the rates of the various photoprocesses to a physical mixing model may be more complex than previously thought. Work by Prezelin and co-workers [Prezelin et al., 1986; Prezelin et al., 1992; Prezelin et al., 1994a] shows strong diurnal patterns in the photosynthetic capacity and depth-dependent photosynthesis-irradiance relationships and also strong diurnal effects in UV-inhibition of photosynthesis. They note that the problem is also confounded by wavelength changes in irradiance with depth. Cullen and Lesser [1991] have shown that photoinhibition of phytoplankton production is dependent on irradiance only for time scales longer than the induction period for photoinhibition, i.e., > approximately 1 hr. On shorter time scales relative photoinhibition is time (dose) dependent. They conclude that conventional productivity incubations (typically 2 to 24 hr.) will adequately represent conditions in the water column only if this column is relatively stable over these same periods.

Helbling et al. [1994], using rotating incubator experiments to simulate vertical mixing, studied the effects of UV radiation on Antarctic marine phytoplankton. These workers found that the magnitude and sign of the difference in column integrated production between rotating samples (exposed to varying irradiance levels with a 6 hr time scale) and fixed samples depended upon the mean irradiance level. This demonstrated a failure of reciprocity under the variable irradiance treatment, consistent with a disproportionate amount of inhibition resulting from short periods of high irradiance experienced by the rotating samples.

Methodological Issues

Methodological issues seem to plague UV-effects research, perhaps because results impinge closely on policy concerns, but also

because there are subtle problems associated with the dosimetry involved in accurate quantitative measurements. Considerations associated with the estimation of biological weighting functions, dose response curves, and reciprocity have been discussed above. A continuing critical factor in the methodology of laboratory experiments is that radiation regimes in laboratory experiments cannot easily simulate ambient levels of solar radiation throughout the total spectrum. This is especially true when vertical mixing through an in-water irradiance field is under consideration. As a consequence, while experiments may enhance the UV-B spectral region, the visible portion of the spectrum may be as much as an order of magnitude lower than in nature, possibly limiting the energy necessary for optimum photoreactivation and photorepair [Kaupp and Hunter, 1981; Damkaer and Dey, 1983; Worrest, 1986]. Further, simulation of in-water irradiance is difficult to match, especially with respect to UV dosimetry, and results are very difficult to compare without the application of BFWs, which is seldom done.

Another methodological concern, that there may be a UV-B induced toxicity in polyethylene bags which significantly lowers the rate of CO_2 assimilation, has recently been raised [Holm-Hansen and Helbling, 1993; Holm-Hansen et al., 1993]. This assertion runs counter to previous tests and experience ([El-Sayed et al., 1990; Smith et al., 1992b; Prezelin et al., 1992], Karentz and El Sayed, personal communication). Several additional tests concerning this UV-B toxicity question [Prezelin and Smith, 1993; Prezelin et al., 1994a; Prezelin et al., 1994b; Milot-Roy and Vincent, 1994; Moeller, 1994] show no toxic effects were evident from the use of polyethylene bags. Milot-Roy & Vincent, in agreement with Prezelin & Smith, point out that experimental comparisons using containers of different materials and optical geometries should be undertaken with caution. The careful experiments explicitly aimed at evaluating the use of the operationally more available and easily used polyethylene bags for UV field work [Prezelin et al., 1994b] shows conclusively that these bags can be used for accurate quantitative work and that no toxicity exists.

Extrapolation of Results

A dominant consideration, when concerned with possible ozone-related UV-B effects, is how laboratory and field results can be properly extrapolated to longer time and larger spatial scales. The work of numerous investigators, beginning with Steemann Nielsen [1964] and continuing until today, provides conclusive evidence that exposure to UV-B decreases measured rates of algal productivity. Much of this evidence is based upon comparison of rates of ^{14}C uptake in incubation bottles that transmit, or do not transmit, UV radiation. This subject continues to be explored [Holm-Hansen, 1990; Mitchell, 1990; Vernet, 1990; El-Sayed et al., 1990; Karentz et al., 1994; Holm-Hansen et al., 1993; Vernet et al., 1994; Cullen and Lesser, 1991; Lesser et al., 1994; Gala and Giesy, 1991; Behrenfeld et al., 1992; Behrenfeld et al., 1993a]. Further, there is convincing evidence that UV radiation, at levels currently incident at the surface of the ocean, may have an influence on phytoplankton productivity [Worrest et al., 1978; Worrest et al., 1980; Worrest et al., 1981b; Worrest et al., 1981a; Smith and Baker, 1980; Calkins and Thordardottir, 1980; Worrest, 1982; Worrest, 1983; Jokiel and York Jr, 1982; Jokiel and York, Jr, 1984; Dohler, 1984; Dohler, 1985; Häder, 1984; Häder, 1985; Häder, 1986; Häder, 1987; Smith et al., 1992b; Behrenfeld et al., 1993a]. Consequently, there is now little dispute that UV damages phytoplankton in laboratory and microcosm experi-

ments. On the other hand, extrapolation of this information to natural populations and ecosystems continues to be controversial.

A recent Scientific Committee on Problems of the Environment (SCOPE) workshop [SCOPE, 1993] addressed and summarized issues associated with UV impacts on global ecosystems. The SCOPE report points out that we presently lack the necessary knowledge and appropriate models to make use of laboratory results for quantitative prediction of whole-system performance at the ecosystem level. Currently, little information is available with which to infer long-term ecological consequences from short-term observations. Further, Bothwell and co-workers [Bothwell et al., 1993; Bothwell et al., 1994] recently demonstrated that UV-B could potentially influence trophic structure, via differential predator/prey sensitivity to UV-B, thus emphasizing the need for long-term (multigeneration times) studies on both individual and multiple organism populations in order to assess ecosystem structure. In short, ecosystem level information with respect to enhanced levels of UV-B is limited and in great need of further research, recognizing that a variety of issues influence meaningful extrapolation of current results.

Differential sensitivity and physiological adaptation of phytoplankton to UV exposure

Karentz et al. [1991] [Karentz et al., 1991] studied twelve species of Antarctic diatoms for cell survival characteristics and molecular responses to UV-B radiation and determined the average exposure for cell death. Their studies, which did not simulate natural sunlight conditions and were not intended to do so, showed that: 1) dose responses of population survival to UV exposure varied considerably among species, and there were significant differences as a function of wavelengths available or absent for photorepair; 2) a general relationship was evident between the surface area/volume ratios of cells and the amount of damage induced by UV exposure. Smaller cells, with larger ratios, sustained greater amounts of damage per unit of DNA. However, when they studied growth of diatom species under natural irradiance in the Antarctic [Karentz, 1994], they found that the growth rates were not enhanced when UV was excluded.

The results of Helbling et al. [Helbling et al., 1994], interpreting the distributions and characteristics of Antarctic phytoplankton, did not provide conclusive results with respect to the relative influence of UVR on different size components of phytoplankton photosynthesis. They show that small flagellates are strongly inhibited by UVR but also suggest that these phytoplankton are able to acquire resistance to UV by photoadaptive processes. Further their results suggest that diatoms, most of which were in the larger microplankton size range, were relatively resistant to UVR, consistent with the culture experiments of Karentz [Karentz, 1994]. Since it has long been recognized that differential influence of UV radiation with respect to size of phytoplankton could have major implications for lower food web processes [Bidigare et al., 1988], this issue of differential sensitivity to UVR possibly selecting for size remains an important unresolved question.

Phytoplankton have evolved a variety of protective mechanisms associated with high solar radiation in general and high UV exposure in particular. One mechanism is the synthesis of UV-absorbing compounds. Chalker and Dunlap [Chalker and Dunlap, 1990] summarize a substantial body of literature dealing with UV-B and UV-A absorbing compounds in marine macroalgae. They point out that UV-B absorbing compounds (especially mycosporine-like amino acids, MAAs) have been found in many marine organisms, are frequently related to environmental levels

of UV radiation [Dunlap *et al.*, 1986; Sivalingham *et al.*, 1974], and hence have been proposed as a physiological adaptation to UV exposure. Vernet [1990] showed that Antarctic phytoplankton exposed to ambient levels of UV radiation seem to have the ability to synthesize potentially protective UV-absorbing compounds, and that they may have the capacity to utilize some of the UV radiation in photosynthesis through pigments that absorb below 400nm. El Sayed *et al.* [1990] show changes in photosynthetic pigmentation with elevated UV-B. Carreto *et al.* [Carreto *et al.*, 1990] in laboratory studies have demonstrated that MAA synthesis is stimulated by UVA, adding further evidence for potential physiological adaptation. Karentz *et al.* [1991a] surveyed 57 species (1 fish, 48 invertebrates, and 8 algae) from the vicinity of Palmer Station (Anvers Island, Antarctic Peninsula) for the presence of MAAs. They found that the majority of species examined had absorbance peaks in the range from 315 to 335nm and they identified eight MAAs. They suggest that this widespread occurrence of MAAs found in Antarctic marine organisms may provide some degree of natural biochemical protection from UV exposure during spring ozone depletion. Bidigare *et al.* [Bidigare *et al.*, 1992a] provided further direct chemical confirmation of MAAs in marine phytoplankton from the Southern Ocean. Their work during Icecolors'90 was undertaken to measure directly the effects of ozone diminution and UV radiation on Southern Ocean phytoplankton. Along a north-south transect across the marginal ice zone (MIZ), they found concentrations of diadinoxanthin (a photoprotective carotenoid found in *Phaeocystis* spp. and diatoms) highest in surface waters and decreasing with increasing depth suggesting photoprotective adaptation to potentially harmful irradiance.

Vernet and co-workers [Vernet *et al.*, 1994], studying the response of Antarctic phytoplankton to UVR, found results supporting the hypothesis that UV-absorbing compounds are photoprotective. Making use of the ratio of *in vivo* pigment specific phytoplankton absorption at 330nm and 675 nm, these workers found this ratio to be a good index of the relative absorption of UV with respect to photosynthetic pigment absorption. Their data suggest that synthesis of UV-absorbing compounds may occur as a response to phytoplankton assemblages exposed to relatively high surface irradiance because of shallow mixed depths or relatively clear waters, thus providing photoadaptive protection to enhanced levels of UVR. These findings are in general agreement with the analysis of Helbling *et al.* (1994).

All of the above observations lend credibility to the hypothesis that physiological adaptation to UV exposure is possible in at least some species of phytoplankton. On the other hand, Cullen and Neale (1994) point out that there is little direct evidence indicating the biological functions of UV-absorbing compounds [Mitchell and Karentz, 1993] and then go on to discuss recent results of protection by UV-absorbing compounds in terrestrial plants. While there may be analogies to mechanisms in terrestrial plants, these authors point out that in microalgae, UV absorbing compounds operate over much shorter pathlengths and hence may only provide partial protection to UV-B. It is evident that a wide variety of mechanisms are available for the acclimation of microalgae of UV-B [Marchant, 1994; Vincent and Roy, 1993].

O_3 -related UV-B Effects on Natural Phytoplankton Populations

Ultimately the issue of O_3 -related UV-B increases must be assessed with respect to the direct impact on natural populations. Smith, Prezelin and co-workers [Smith *et al.*, 1992b; Prezelin *et*

al., 1992] directly measured the increase in and penetration of UV-B radiation into Antarctic waters and provided the first conclusive evidence of a direct O_3 -related effect on a natural population. Making use of the extreme change in ozone associated with the hole, which creates a sharp gradient (or "front") in incident UV-B analogous to an atmospheric or oceanographic front [Smith, 1989; Smith and Baker, 1989], they made comparative studies of the impact of UV-B on phytoplankton in the marginal ice zone (MIZ) of the Southern Ocean. The MIZ was selected for their study because it is, like the ozone hole, a spring phenomenon and because the physical conditions of water column stability that give rise to enhanced productivity within the MIZ also promote conditions for maximum exposure of phytoplankton to UV-B. Also, production within the marginal ice zone is estimated to contribute significantly to the overall production of the Southern Ocean and to be a significant element in Antarctic spring-time ecology.

Their results indicate a minimum of 6 to 12 percent reduction in MIZ primary production associated with O_3 depletion within the ozone hole. Figure 2 shows average values for *in situ* phytoplankton production versus depth in the MIZ of the Southern Ocean. Results show a comparison of productivity inside the ozone hole (stratospheric ozone less than 200 Dobson Units, $1DU = 2.69 \cdot 10^{19} \text{ molecules } O_3 \cdot \text{cm}^{-2}$) with productivity outside the hole (stratospheric ozone levels greater than 300 DU). Higher UV-B levels (inside the hole) are consistently associated with reduced (left hand curve) levels of production. That there is less UV-B inhibition at the surface as compared to deeper has sparked

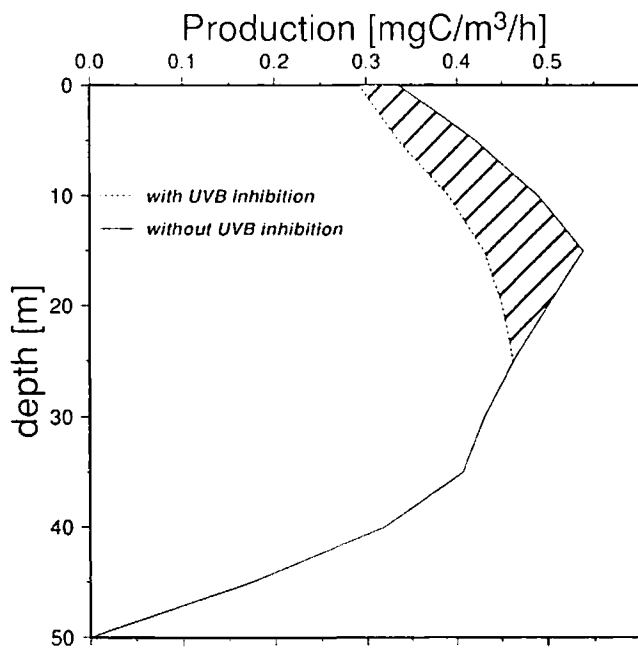


Figure 2. Average values for *in situ* phytoplankton productivity [$\text{mgCm}^{-3}\text{h}^{-1}$] versus depth [m] within the marginal ice zone of the Bellingshausen Sea in austral spring of 1990. Comparison of productivity inside the ozone hole (stratospheric ozone levels less than 200 Dobson Units, DU) with productivity outside the hole (stratospheric ozone levels greater than 300 DU). Higher UV-B levels (inside the ozone hole) are consistently associated with reduced (left-hand curve) levels of production. Integration of these curves shows that higher UV-B levels within the ozone hole lead to a reduced water column production (6 to 12%). Adapted from Science, 1992, 255:952-959).

interest in possible photoregulatory interactions of UVR on phytoplankton. The causes of depth-related variations in UV-B inhibition are consistent with the hypothesis [Smith *et al.*, 1992b; Prezelin *et al.*, 1994a] that the regulation of UV-B damage to cell vitality is initiated through UV-A, but not UV-B, photoreceptors (see Fig. 6, Smith *et al.*, 1992). Under this hypothesis, phytoplankton are cued to short-term (minutes to a few hours) changes in UV-A flux as an index of changing total UVR thus leaving the phytoplankton unable to respond favorably to significant elevations in the magnitude of the ratio of UV-B to UV-A. Alternatively, Cullen has suggested the possibility that relatively less UV-B inhibition was observed at the surface because UV-A treatments were strongly inhibited and leaving proportionally less "target" for the UV-B + UV-A treatment to inhibit. Further studies on photoregulation are needed to clarify this issue. The work by Smith and co-workers was done in stratified waters of the MIZ, where the fixed-depth incubations of 7 to 12 hours should be appropriate for quantifying UV effects. In waters where vertical mixing is active, similar experiments would yield artifactual overestimates of photoinhibition [Marra, 1978; Cullen and Neale, 1993; Cullen and Lewis, 1994]. It is also important to recognize that their research in the MIZ, by making use of UV-B variability associated with the ozone-hole and by comparing phytoplankton UV-B inhibition inside to outside the hole, are in effect making use of a very large-scale human-induced experiment on natural populations and thus their results are largely independent of various modeling assumptions and methodological issues.

Southern Ocean Phytoplankton Productivity and atmospheric CO_2

An important question, on which estimates disagree, and which was first addressed quantitatively by Smith and Prezelin [Smith *et al.*, 1992b], is what is the loss, if any, of primary production in the Southern Ocean due to ozone-related enhanced UV-B and would this loss have any feedback effect on atmospheric CO_2 ? Differences in the spectral properties of field incubators used by various groups to measure UV effects complicates direct comparison of results since, if results are not first normalized with common weighting functions, relatively minor spectral differences in filters can cause quantitative differences in reported results. Prezelin and co-workers [Prezelin *et al.*, 1994b] have normalized and summarized the work of several austral spring data bases of UV-B inhibition of primary production in the Southern Ocean and show that results, once normalized, are in relatively close agreement. They show that in the absence of an ozone hole (>320 DU), the ambient UV-B radiation suppresses daily primary production by at least 4% to 7% in surface waters (2 m) and by about 12% in near surface waters (5-10 m). This is the background influence of UV-B against which ozone-related effects of enhanced UV-B must be compared. Extrapolation of this information in order to estimate effects to the whole Southern Ocean remains controversial.

Holm-Hansen, Helbling and co-workers [Helbling *et al.*, 1992; Helbling *et al.*, 1994] estimate the loss of primary productivity for all the ice-free waters south of the Polar front. As a simplification, they treat all oceanic areas (open ocean, marginal ice zone, shelf and coastal waters) as equivalent, although the various water types in the Antarctic are significantly different in terms of hydrography and productivity [Smith and Sakshaug, 1990; Holm-Hansen *et al.*, 1977] and likely in sensitivity to UV-B. With this simplification and taking into consideration the magnitude of ozone depletion and its space/time variations, they estimate losses in primary productivity due to ozone-related enhanced UV-B to be less than 0.15% for the entire year.

Smith, Prezelin and co-workers [Smith *et al.*, 1992b; Prezelin *et al.*, 1994a; Prezelin *et al.*, 1994b] first focused their attention on the marginal ice zone (MIZ) within the Southern Ocean. For pelagic waters surrounding the MIZ of the Southern Ocean, current estimates of annual primary productivity are about $610 \times 10^{12} \text{ gC} \cdot \text{y}^{-1}$ [Smith and Sakshaug, 1990; El-Sayed and Turner, 1977; Holm-Hansen *et al.*, 1977]. Productivity estimates for the MIZ were derived by W.O. Smith and Nelson [1986] using a simple model of ice-edge bloom genesis to be about $380 \times 10^{12} \text{ gC} \cdot \text{y}^{-1}$ or about a 40% of the total MIZ plus pelagic production south of the Antarctic Convergence. Thus, the MIZ potentially plays a major role in the ecological and biochemical cycles of the Southern Ocean.

Smith & Prezelin make an estimate of the impact of reduced ozone on primary production for the MIZ of the Bellingshausen Sea (Fig. 2) based upon a determination of phytoplankton productivity data averaged for inside and outside the O_3 hole. Again, it is important to note, that this simple comparison of production inside vs. outside the O_3 hole avoids complicating assumptions and focuses on the consequences to the phytoplankton community to the increased UV-B inside the hole. Based on these *in situ* data, a yearly estimate of production loss for the MIZ of the Southern Ocean can be made by assuming that the loss they measure is representative of the MIZ and integrating production over the MIZ area and over the 3-month duration of the O_3 hole during Antarctic spring. They estimate (using a 6% loss of water column productivity and conservatively assuming a given location is outside the O_3 hole one-half of the time) that this productivity loss to the MIZ is $7 \times 10^{12} \text{ gC} \cdot \text{y}^{-1}$, corresponding to about 2% of the estimated yearly production of the MIZ. Their assumptions are such that this is a minimum loss estimate and values could be at least two times higher depending upon the specific space-time extent of the O_3 hole. They note that they used short-term ^{14}C studies to assess changes in natural communities of phytoplankton caused by variations in the ozone hole which occurred on time scales from hours to weeks. Thus, because the water column was not actively mixing and fixed-depth incubations of several hours were appropriate, the time scale of their experimental protocol matched that of the processes observed. However, caution must be used when inferring longer-term ecological consequences from short-term observations [Smith and Baker, 1980]. Likewise, in environments where vertical mixing imposes variations of UV on time scales much less than the incubation time, the possibility of artifactual overestimation of UV effects should be considered [Cullen and Neale, 1993].

The interannual variability of primary production of the MIZ has been estimated to be substantial [Smith, Jr. *et al.*, 1988], and such that the maximum productivity is 50% greater than the minimum. This variability associated with the annual advance and retreat of pack ice is thought to be a major physical determinant of space-time changes in the structure and function of polar biota [Ainley *et al.*, 1986; Fraser and Ainley, 1986; Smith and Vidal, 1986; Smith and Nelson, 1986; Walsh and McRoy, 1986; Garrison *et al.*, 1987; Ainley *et al.*, 1988; Smith, 1990]. In particular, this interannual variability is likely to have a significant effect on total annual primary production, although to date these natural changes have not been accurately quantified. Thus, Smith and Prezelin note that their estimate of (2 to 4%) loss to MIZ productivity should be viewed in the context of a presumed natural variability of $\pm 25\%$.

Concern has been expressed [Voytek, 1990] that O_3 -induced phytoplankton loss may trigger a positive feedback with respect to atmospheric CO_2 that would exacerbate the greenhouse effect.

The estimated loss of $7 \times 10^{12} \text{ gC} \cdot \text{y}^{-1}$ is about 3 orders of magnitude smaller than estimates of global phytoplankton production and thus is not likely to be significant in this context. Furthermore, Peng [Peng, 1992] using a global circulation model, found negligible global effect (with respect to CO_2) of turning off all phytoplankton production in the Southern Ocean. On the other hand, the finding that the O_3 -induced loss to a natural community of phytoplankton in the MIZ is measurable, leaves the ecological consequences of the magnitude and timing of this early spring loss as something to be determined.

Summary

There is nearly undisputed evidence that human activities have caused a diminution of stratospheric ozone, especially in the south polar vortex region, and this diminution has led and will continue to lead to increased levels of UV-B incident at the surface of the earth. There is also widespread agreement that ozone-related increases in UV-B has the potential to cause wide-ranging direct and indirect effects on aquatic ecosystems [SCOPE, 1993; Häder et al.,] as enumerated in the introduction. Damage at the molecular, cellular, population and community levels has been demonstrated (at least in phytoplankton). At the ecosystem level there are few, if any, convincing data with respect to effects of ozone-related UV-B increases, considerable uncertainty remains, there is no consensus, and much future work remains.

An important area of convergence concerns the BWF for photoinhibition of photosynthesis. While all results are not in exact agreement, the work of several groups are consistent with the high-resolution work of Cullen and co-workers (Fig. 1) in showing a function heavily weighted in the UV-B but with a significant component in the UV-A region. Thus, ozone-related UV-B increases are an environmentally relevant issue with respect to phytoplankton, but the magnitude of the potential impact is less than what would be inferred by use of a DNA (deoxyribonucleic acid) action spectrum. This convergence on an accurate BWF is an important step toward quantitative predictive modeling of potential UV-B effects on phytoplankton.

Another important area of agreement is that individual phytoplankton species demonstrate differential sensitivity to UV-B as was suggested by early workers [Calkins and Thordardottir, 1980; Worrest, 1983]. Virtually all recent UV-related aquatic research results show, or are consistent with, this hypothesis of differential sensitivity. While there is general agreement on the existence, there is little agreement over the possible consequences, of differential sensitivity. That a community might show variable response to increased UV-B creates a key unpredictable factor: a 'wild card' that could dramatically influence (through altered species composition, food web structure, differential impact on predator/prey components, etc.) ecosystem structure. Alternatively, differential sensitivity could merely be a demonstration of the high level of resilience and community-level adjustment of phytoplankton to increased UV-B levels. The uncertainties associated with the ecological consequences of possible altered species composition on communities and ecosystems impinges on two other important considerations: short-term variability vs. long-term consequences and trophic level interactions.

Smith, Prezelin and co-workers [Smith et al., 1992b] conclusively measured an impact on an Antarctic phytoplankton community within the ozone hole. They also pointed out that the magnitude of this impact was less than the presumed natural variability in southern ocean phytoplankton productivity. While the ecological significance and magnitude of this impact continues to be

debated, the fact remains that chlorofluorocarbons (CFCs) generated primarily in the Northern Hemisphere have been linked to a measurable impact on a Southern Ocean phytoplankton community. Karentz [Karentz, 1991] has observed that the ozone hole has now been in existence for over a decade, thus any potential ecological effects may have already been initiated, yet none have been conclusively documented. She also observed that baseline (pre ozone hole) photobiological data are lacking so that a quantitative assessment of any possible change is difficult. Smith and Baker [Smith and Baker, 1980] pointed out that productivity estimated using short-term incubations (e.g., ^{14}C technique) are inadequate for assessing longer-term processes. At the ecosystem level, the work of Bothwell and co-workers [Bothwell et al., 1993; Bothwell et al., 1994], demonstrates the complexity of trophic-level response to added UV-B and they emphasize the need for long-term (multigeneration times) autecological studies to assess ecosystem structure. Thus while uncertainties persist and the need for process oriented laboratory studies remains, there is a growing consensus that long-term ecosystem studies are required in order to answer ecosystem related questions. It is at the ecosystem level that the greatest interest, uncertainties and challenges remain.

Acknowledgments. Supported by NSF/DPP Grants No. DPP8917076 (RCS) and DPP901844 (JJC), NASA Grants No. NAGW-290-10 (RCS) and NAWG3549 (JJC) and NSERC Canada (JJC).

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(Received November 1, 1994; revised December 27, 1994; accepted January 3, 1995.)