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Mike J. Behrenfeld for the degree of Master of Science in General Science presented on August 14, 1989.

Title: Primary Production in the Southeast Pacific Ocean: Effect of Enhanced Ultraviolet-B Radiation.

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Abstract approved: _____
John T. Hardy

Anthropogenic releases of trace gases into the atmosphere are causing a decrease in stratospheric ozone concentrations and a subsequent increase in solar ultraviolet-B (UV-B)(280-320 nm) radiation reaching the earth's surface. The objective of this study was to determine the acute effects of enhanced UV-B radiation on the primary production of natural marine phytoplankton assemblages sampled over a wide latitudinal gradient and incubated under ambient levels of photosynthetically active radiation (PAR). Samples were collected approximately every 2 to 4° latitude in the southeast Pacific. Primary production was measured using the carbon-14 light and dark bottle technique. Fluorescent sunlamps were used to enhance the dose of UV-B radiation above ambient. Samples were maintained at ambient surface water temperature in a flow-through incubation tank. Enhanced UV-B radiation caused a significant mean decrease of 34% in surface water primary production. Decreases in primary production increased with

and with increasing assimilation efficiencies. Results indicate that predicted increases in ambient solar UV-B radiation resulting from stratospheric ozone depletion could result in mean annual decreases of near-surface oceanic primary production of less than 1% near the equator to more than 32% at high southern latitudes.

Primary Productivity in the Southeast Pacific Ocean: Effects of Enhanced Ultraviolet-B Radiation

by

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CONTRIBUTIONS OF AUTHORS

NAME	CONTRIBUTION
Jack Hardy	Major Professor -- Data analysis advice and provided financial support.
Hermann Gucinski	Committee Member -- Data analysis advice, technical assistance, and cruise preparation.
Andy Wones	Technical assistance and data analysis advice

PRIMARY PRODUCTIVITY IN THE SOUTHEAST PACIFIC OCEAN: EFFECT OF ENHANCED ULTRAVIOLET-B RADIATION

INTRODUCTION

The stratospheric ozone layer, at an altitude between 10 and 50 km, protects the earth from damaging solar ultraviolet radiation between 280 and 320 nm, ultraviolet-B (UV-B). However, anthropogenic releases of chlorofluorocarbons, nitrous oxide, bromine-containing halons, and solvents such as methyl chloroform and carbon tetrachloride are causing a decrease in stratospheric ozone and a subsequent increase in the level of UV-B radiation reaching the earth's surface. Models predict that by the year 2060 global mean stratospheric ozone concentrations will be depleted 2% from 1969 levels (Hoffman and Gibbs 1988), with the greatest depletions occurring at high latitudes. By 2060, stratospheric ozone depletions of 14.4% and 16% (averaged over seasons) are expected for the high latitudes in the northern and southern hemispheres, respectively (Watson 1988; EPA 1988). Since the biological effectiveness (cellular damage) of UV-B radiation increases with decreasing wavelength, a 16% decrease in stratospheric ozone would result in an approximate 32% - 47% increase in biologically effective radiation (Setlow 1974; NAS 1979; EPA 1988). Enhanced UV-B radiation at the earth's surface presents a potential hazard to biological processes,

including marine primary productivity in the ocean's surface layer.

Ultraviolet-B radiation effectively penetrates the upper 2 meters of productive coastal waters before being reduced to 1% of the surface intensity. In clear oceanic water, however, a pathlength of nearly 30 meters may be required for the same reduction to 1% of surface intensity (Jerlov 1976; Baker and Smith 1982). The ocean's surface layers are an important site for photosynthesis, for the development of early life stages in many fish and mollusks, and for the growth of zooplankton populations upon which fish depend (Zaitzev 1971). Detrimental effects of enhanced UV-B radiation, including increased larval mortality, decreased fecundity, and an increased frequency of morphological abnormalities, have been demonstrated for many surface layer organisms (Thomson 1986; Worrest et al. 1981; Worrest et al. 1978; Karanas et al. 1981; Karanas et al. 1979; Damkaer et al. 1981; Damkaer and Dey 1983; Hunter et al. 1982).

Phytoplankton exhibit decreased photosynthetic rates (Wolniakowski 1979; Paerl et al. 1985), changes in species composition (Worrest et al. 1978; Worrest et al 1981), decreased community chlorophyll-a concentrations (Worrest et al. 1978), and decreased reproductive rates (Wolniakowski 1979) when irradiated with levels of UV-B radiation that would result from predicted stratospheric ozone depletion. Estimates suggest that with a 16% decrease in stratospheric

ozone, about 20% of the near surface phytoplankton species in a given ecosystem would experience a 50% decrease in photosynthesis due to enhanced levels of UV-B (Worrest et al. 1981). In mid-northern latitudes, an estimated 6.5% decrease in total primary production, integrated over the entire water column, would accompany a 32% increase in UV-B irradiance at the waters surface (Thomson et al. 1980). In summer, at temperate northern latitudes, even current levels of UV-B radiation can reduce photosynthesis in marine phytoplankton (Paerl et al. 1985; Lorenzen 1979). A decrease in total primary production is a significant threat since it would likely decrease fisheries yield (Nixon 1988).

Photorepair mechanisms, which are activated by ultraviolet A (320 - 380 nm) and photosynthetically active (PAR) (400 - 750 nm) radiation, decrease the effect of UV-B radiation on photosynthesis. Such repair mechanisms occur throughout the plant kingdom (Halldal 1967; Jagger 1985; Paerl et al. 1985; Beggs et al. 1986). Production of UV-B radiation absorbing compounds may also be an important means of mitigating the effect of UV-B radiation on photosynthesis (Halldal 1967; Paerl et al. 1985).

A large degree of uncertainty exists with all estimates of the ecological effects resulting from stratospheric ozone depletion. It is difficult, if not impossible, to extrapolate results from short term, in-situ experiments to accurate estimates of changes that will occur in entire ecosystems.

Experiments with enhanced UV-B radiation have generally used low intensities of UV-A and PAR radiation (the wavelengths which activate photorepair mechanisms) and would, therefore, overestimate the effects of UV-B radiation. Experiments with intensities of UV-B radiation far above what might occur from ozone depletion are also difficult to interpret.

The objective of this study was to determine the acute effects of enhanced UV-B radiation on the primary production of natural marine phytoplankton assemblages sampled over a wide latitudinal gradient and incubated under ambient levels of PAR.

Materials and Methods

General Methods

Phytoplankton samples were taken over a wide latitudinal and longitudinal gradient (10°N latitude to 60°S latitude, 105°W longitude to 130°W longitude) between February and April, 1989 (Fig. 1). Samples were exposed to ambient solar radiation and ambient solar radiation plus enhanced UV-B radiation during half day and full day incubations. Primary productivity was assessed using the carbon-14 light and dark bottle technique (Parsons et al. 1984). During the cruise, 18 primary productivity experiments were completed. Measurements of ambient solar radiation, in the wavelength range between 300 and 760 nm, were made at each station location.

Sample Collection

Phytoplankton samples from surface and subsurface waters were used in 16 of 18 primary productivity experiments. For the other 2 experiments, only surface samples were used. Surface samples were taken using a bucket lowered over the side, forward of all ship effluent. Subsurface samples were taken from 20 to 40 m depth, depending on the depth of the mixed layer, using a polyvinylchloride Niskin bottle. A 10

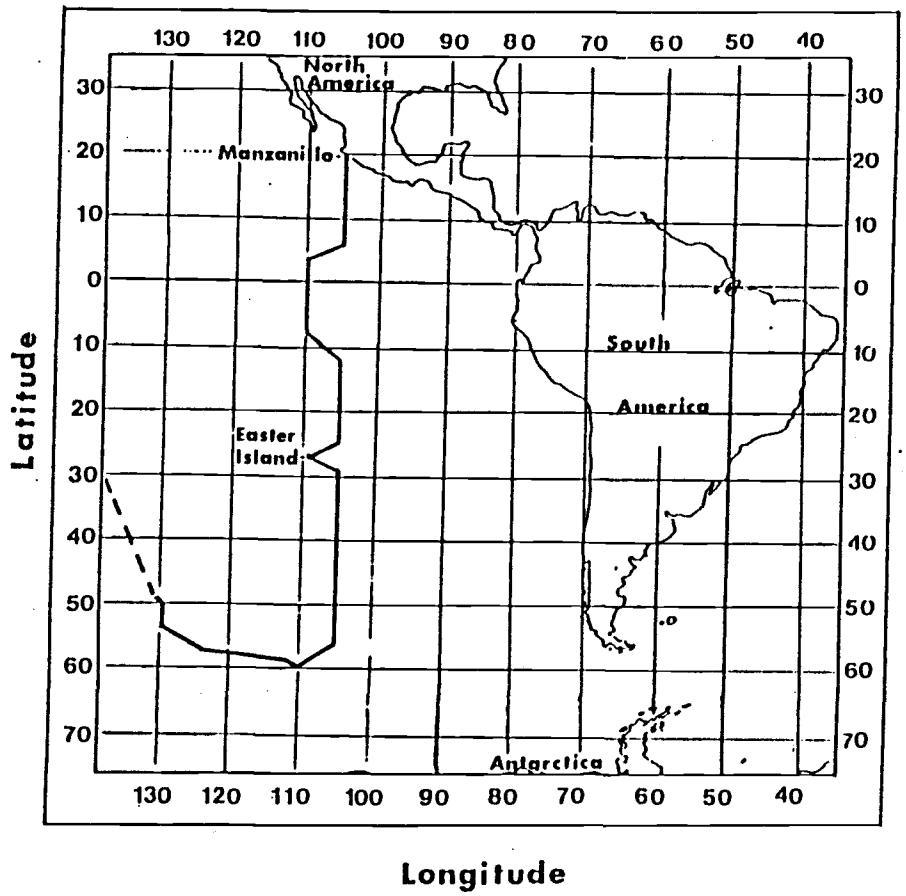

Figure 1: Cruise track in the southeast pacific (solid line).

gallon polyethylene cooler was rinsed 3 times with sample water, filled, and then taken to the lab to fill the sample bottles. Chlorophyll-a concentration was determined on board using the fluorometric technique (Parsons et al. 1984).

Productivity Sample Preparation and Exposure

Five hundred ml teflon FEP bottles were used for the incubations. Teflon FEP bottles were chosen because they transmit UV-B, are considerably less expensive than quartz, are easy to clean, are unbreakable, and do not absorb or leach chemicals. Prior to the first experiment, the teflon bottles were washed with Micro glassware cleaning solution, rinsed three times, filled with distilled water, and allowed to soak for 24 h. After soaking, the bottles were rinsed with 0.25 N HCl and then rinsed three times with distilled water. Before each experiment, the bottles were rinsed once with 0.25 N HCl, three times with distilled water, and then three times with sample water. Once the bottles were cleaned, they were filled to the neck with sample water and placed in a dark container. For each depth sampled, four transparent bottles (two for the enhanced UV-B treatment and two for the ambient UV-B treatment) and two dark bottles were filled.

Immediately before incubation, the samples were inoculated with 10 μCi of $NaH^{14}CO_3$ from a 2 ml pre-prepared ampule (New England Nuclear, specific activity: 8.4 mCi/mmole)

and then stored in a dark container.

When all the inoculations were complete, the phytoplankton sample bottles were exposed to unshaded solar radiation or unshaded solar radiation plus enhanced UV-B radiation in a specially designed on-deck incubator (Fig. 2). A continuous flow-through of surface water was employed to keep the samples at ambient surface temperature throughout the incubation. To keep the phytoplankton suspended, the sample bottles were placed horizontally in the tank on three rows of rollers and rotated at 7 rpm. The bottom of the exposure tank was made of UV-B transparent acrylic (Acrylite OP-4, CYRO Industries). Three ultraviolet fluorescent bulbs (UVB 313, Q-Panel Co.) were located underneath the tank and used to enhance the level of UV-B radiation above ambient. Under the row of sample bottles receiving enhanced UV-B radiation, a sheet of 0.13 mm cellulose acetate filtered out lamp radiation below 290 nm. Under another row of sample bottles, a sheet of 0.13 mm mylar film filtered out UV-B radiation from the lamps. Dark bottles were placed in the center row to separate the enhanced UV-B and the ambient UV-B treatments. To account for photodegradation, filters were replaced before initiating each experiment. Window screen was placed between the tank and the UV-B radiation lamps to serve as a neutral density filter, allowing for adjustment of the UV-B radiation intensity to the desired level.

Incubations were started either at sunrise or at

approximately local apparent noon. The duration of the incubations were for a half day in high productivity waters or for a full day in low productivity waters, as determined by the result from the previous station. To simulate the natural daily cycle, the UV-B radiation bulbs were turned on one hour after sunrise for morning incubations; while, for the afternoon incubations, the UV-B bulbs were turned on immediately and then turned off one hour before sunset. During full day incubations, the UV-B bulbs were turned on one hour after sunrise and off one hour before sunset.

Productivity Measurements

Immediately after the incubation period, the sample bottles were removed, placed in a dark container, and taken to the laboratory. Each sample was then filtered through a 0.45 μm polycarbonate filter (Millipore) at a pressure of 70 kPa. The low vacuum was maintained to prevent cell damage and subsequent loss of incorporated ^{14}C. Following filtration, the filters were placed in small plastic petri dishes and fumed over concentrated HCl for 3 min to remove any inorganic carbon. Each filter was then placed in a scintillation vial along with 10 ml of Aquasol (DuPont, Aquasol Universal LSC Cocktail). The radioactivity in the vials, in disintegrations per minute (DPM), was determined using a liquid scintillation counter (Beckman, model 1701). The samples were counted for

10 minutes or until a 2% standard deviation between replicate counts was reached. Total primary production in the bottles was determined using the relation:

$$\text{Primary Productivity} = \frac{(RS - RB) * W}{R * N} \qquad (1)$$

where R is the total activity (DPM) of the bicarbonate added ($2.22 * 10^7$ DPM); N is the number of hours incubated; RS is the sample count (DPM) corrected for quenching; RB is the dark bottle count (DPM) corrected for quenching; and W is the mass of total carbon dioxide present in $mgC*m^{-3}$. W was determined using the expression:

$$W = 12{,}000 * TC \qquad (2)$$

where TC = total carbon dioxide = 0.96 * carbonate alkalinity at each station.

Calculation of UV-B and PAR Intensities

Irradiance intensities of wavelengths between 300 and 700 nm were measured using a Licor LI-1800UW submersible spectroradiometer. The radiometer was calibrated by measuring the spectrum of a lamp traceable to the U.S. National Bureau of Standards (Model NBS F46). At each station where primary productivity experiments were performed, the intensity of ambient solar radiation was measured at approximately local apparent noon. The intensity of UV-B radiation inside the

sample bottles, resulting from the florescent bulbs, was determined at night by inverting the radiometer over a half bottle submersed in the water-filled on-deck incubator.

The intensity of wavelengths below 300 nm were approximated by a linear regression of the intensities measured for wavelengths between 300 and 304 nm. The irradiance measurements were then corrected for instrument calibration using the expression:

$$IRR_t = IRR_m/(NBS_m/NBS_t) \quad (3)$$

where IRR_t is the true irradiance ($W*m^{-2}$); IRR_m is the irradiance intensity measured by the Licor LI-1800UW (mV); NBS_m is the Licor LI-1800UW irradiance measurement of the NBS F46 bulb (mV); and NBS_t is the true irradiance values for the NBS F46 bulb ($W*m^{-2}$). The UV-B irradiance values at each wavelength were multiplied by the DNA weighting factors (Setlow 1974) (normalized to 300 nm) and then summed over all wavelengths to give the total biologically effective UV-B intensity at the time of the scan ($W*m^{-2}$).

Near noon solar radiation scans and a model of the diurnal change in UV-B radiation (Green et al. 1980), corresponding to the date and latitude of each primary production experiment, were used to approximate the total dose of UV-B radiation received in the sample bottles during the incubations for each station over the latitudinal gradient.

Thus:

$$\text{Total Dose} = 0.72 * \sum_{x=i}^{i'} \sin[(x-7) * (-3\pi/10)] * I_n/2 + I_n/2 \quad (4)$$

where i and i' are the starting and ending time of the incubation, respectively. I_n is the UV-B irradiance at local apparent noon ($mW*m^{-2}$), determined by:

$$I_n = (2 * I_s)/\sin[(\pi*(t-7)/4.5) + 1] \quad (5)$$

where t is the time of the scan; and I_s is the UV-B intensity at the time of the scan ($mW*m^{-2}$).

Data Analysis

Latitudinal changes in primary production and chlorophyll-a concentrations were also compared. Differences between the photosynthetic rates of the ambient samples and the samples exposed to enhanced UV-B radiation were tested for significance using the paired t-test (Devore and Peck 1986). Correlations between the change in primary production due to UV-B enhancement and total primary production as well as assimilation efficiency were examined using linear regression analysis (Statgraphics, 1987). The percent change between samples receiving ambient and enhanced UV-B radiation was compared to the total enhanced dose of UV-B radiation. The change in primary production in response to enhanced doses of UV-B radiation was examined using probit analysis (Finney 1971).

RESULTS

Physical

The temperature, salinity, and total daily dose of UV-B radiation and PAR corresponding to the location and date of the primary productivity experiments are found in Table 1. The total daily dose of PAR and UV-B radiation (DNA_{300}) is shown in figure 3. The variability in estimates of UV-B radiation and PAR was greatest at high latitudes due to heavy overcast conditions with only occasional clearing.

The total dose of ambient UV-B radiation in the bottles during the incubations was 37 $J*m^{-2}$ to 2293 $J*m^{-2}$ (DNA_{300}), which was slightly less than surface intensities due to attenuation by the teflon bottles (Fig. 4). The total dose of UV-B radiation in the enhanced UV-B radiation treatment, which was dependent on the number of hours incubated, the irradiance from the bulbs, and the intensity of solar UV-B radiation, was 577 $J*m^{-2}$ to 3986 $J*m^{-2}$ (DNA_{300}) (Fig. 4).

Chlorophyll-a concentration

Three distinct latitudinal regions of phytoplankton biomass (estimated from chlorophyll-a concentrations) were observed (Fig. 5). A high concentration of chlorophyll-a occurred between 8°N latitude and 16°S latitude (0.37 to

Table 1. Chlorophyll-a concentration, temperature, salinity, photosynthetic rates, enhanced doses of UV-B radiation, and ambient intensities of solar radiation corresponding to each station location. (S=surface samples; D=deep samples)

DATE	STATION NUMBER	LOCATION	CHL-A ($mg \cdot m^{-3}$)		WATER TEMP.(C°)		SALINITY (0/00)		SURFACE DAILY DOSE ($J \cdot m^{-2}$)			UV-B DOSE ENH. ($J \cdot m^{-2}$ DNA_{300})		PHOTOSYNTHETIC RATE ($mgC \cdot m^{-3} \cdot h^{-1}$)			
														S		D	
			S	D	S	D	S	D	PAR	UV-A	UV-B (DNA_{300})	S	D	AMBIENT UV-B	ENHANCED UV-B	AMBIENT UV-B	ENHANCED UV-B
02/18/89	1-4	8 N, 105 W	0.22	0.36	26.0	15.0	34.31	34.26	9.46E+06	9.83E+05	3331.9	639.9	69.3	0.336	0.147	0.391	0.420
02/20/89	2-7	2 N, 110 W	0.14	0.37	26.0	17.5	34.52		9.95E+06	1.07E+06	3869.6	938.5		0.033	0.026		
02/21/89	3-9	0 N, 110 W	0.25	0.28	27.0	20.0	33.97	34.50	1.07E+07	1.23E+06	4801.4	1199.8	142.6	0.093	0.025	0.021	0.019
02/22/89	4-12	4 S, 110 W	0.11	0.29	26.0	24.0	34.87	34.92	1.00E+07	1.09E+06	4505.5	746.6	88.7	0.542	0.315	0.050	0.069
02/23/89	5-13	6 S, 110 W	0.11	0.16	26.5	24.0	35.01	35.01	9.78E+06	1.09E+06	4556.3	978.5	116.3	0.711	0.634	0.486	0.512
02/25/89	6-16	12 S, 105 W	0.20	0.19	25.5	22.5	35.90	35.90	1.02E+07	1.14E+06	4404.1	1002.5	119.1	0.807	0.562	0.071	0.066
02/26/89	7-18	16 S, 105 W	0.18	0.19	24.5	23.0	36.15	36.16	1.10E+07	1.19E+06	4286.3	1082.5	128.6	0.315	0.215	0.086	0.081
02/27/89	8-20	20 S, 105 W	0.02	0.03	25.0	22.5	34.99	35.05	7.38E+06	9.08E+05	3687.6	999.8	118.8	0.080	0.078	0.011	0.012
03/06/89	9-26	32 S, 105 W	0.03	0.04	23.5	18.0	35.23	35.22	8.29E+06	8.85E+05	2591.4	989.2	989.2	0.034	0.028	0.000	0.000
03/10/89	10-31	44 S, 105 W	0.07	0.07	12.0	12.0	34.03	34.03	7.25E+06	8.08E+05	3027.5	1999.7	1999.7	0.063	0.028	0.012	0.006
03/11/89	11-32	46 S, 105 W	0.09	0.08	10.0	10.0	34.17	34.17	2.67E+06	3.33E+05	423.8	2079.7	2079.7	0.356	0.154	0.190	0.110
03/12/89	12-34	52 S, 105 W	0.26	0.26	8.0	8.0	34.20	34.23	1.68E+06	2.09E+05	335.6	1106.5	1106.5	0.188	0.071	0.115	0.076
03/16/89	13-37	60 S, 109 W	0.24	0.21	4.0	4.0	34.00	34.01	4.83E+06	4.43E+05	281.1	1866.4	1866.4	0.248	0.125	0.077	0.071
03/18/89	14-38	58 S, 112 W	0.16	0.16	5.0	5.0	34.00	34.00	1.14E+06	1.51E+05	124.4	1082.5	1082.5	0.239	0.140	0.128	0.074
03/22/89	15-42	56 S, 125 W	0.23	0.26	6.0	6.0	34.23	34.23	7.22E+06	7.96E+05	667.4	472.7	472.7	0.092	0.095	0.060	0.043
03/23/89	16-43	52 S, 128 W	0.30	0.29	7.0	7.0	34.31	34.31	3.61E+06	3.81E+05	353.5	812.4	812.4	0.168	0.160	0.126	0.098
03/24/89	17	50 S, 128 W			8.0	8.0	34.31		3.94E+06	4.20E+05	373.5	610.5		0.030	0.019		
03/25/89	18-44	49 S, 130 W	0.19	0.19	9.0	9.0	34.30	34.30	4.11E+06	4.39E+05	383.5	1033.1	1033.1	0.173	0.130	0.070	0.058

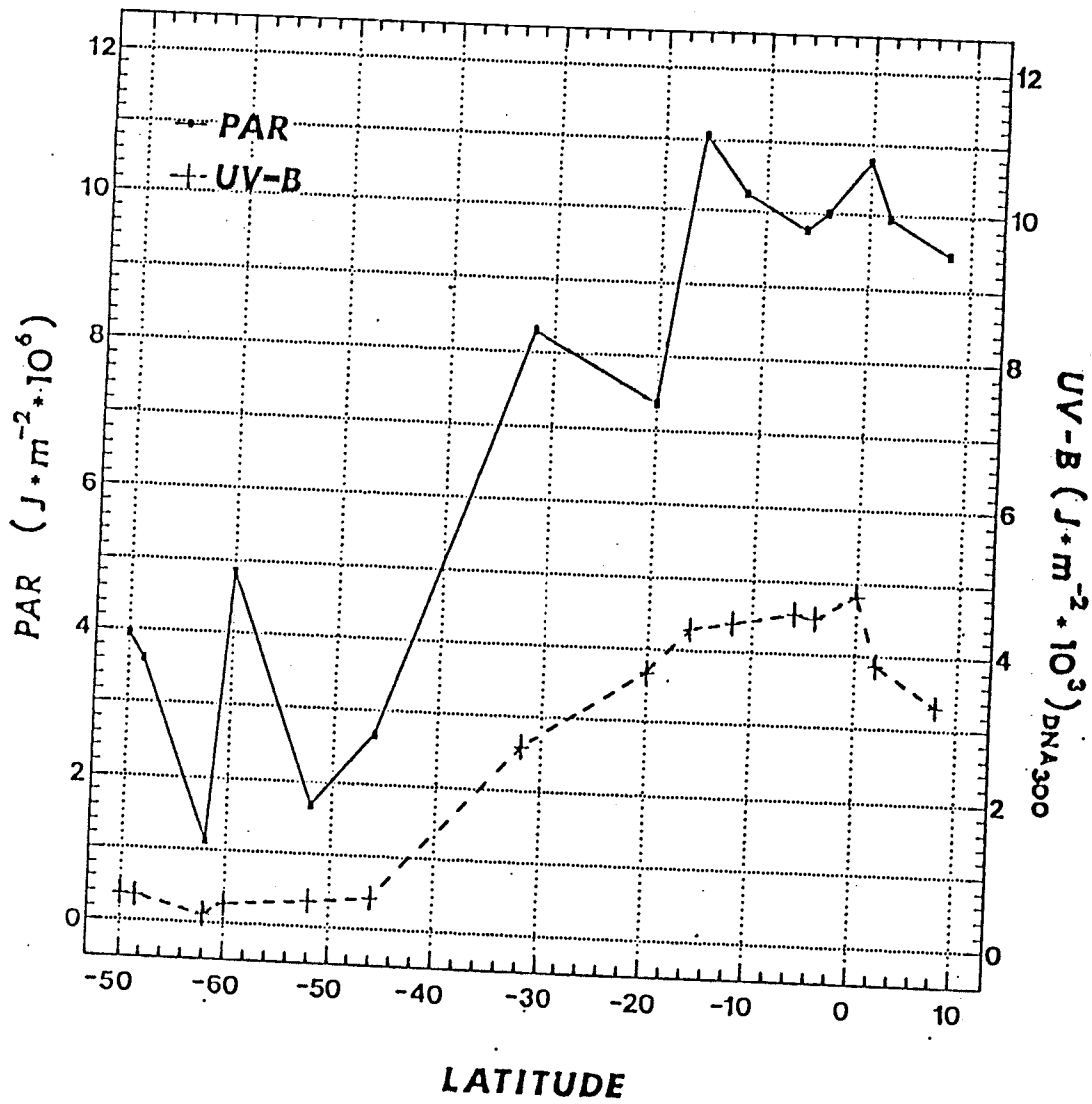

Figure 3: Estimated total daily UV-B radiation and PAR derived from noon measurements at each station. UV-B radiation has been weighted using the DNA_{300} action spectrum values. Negative values correspond to southern latitudes.

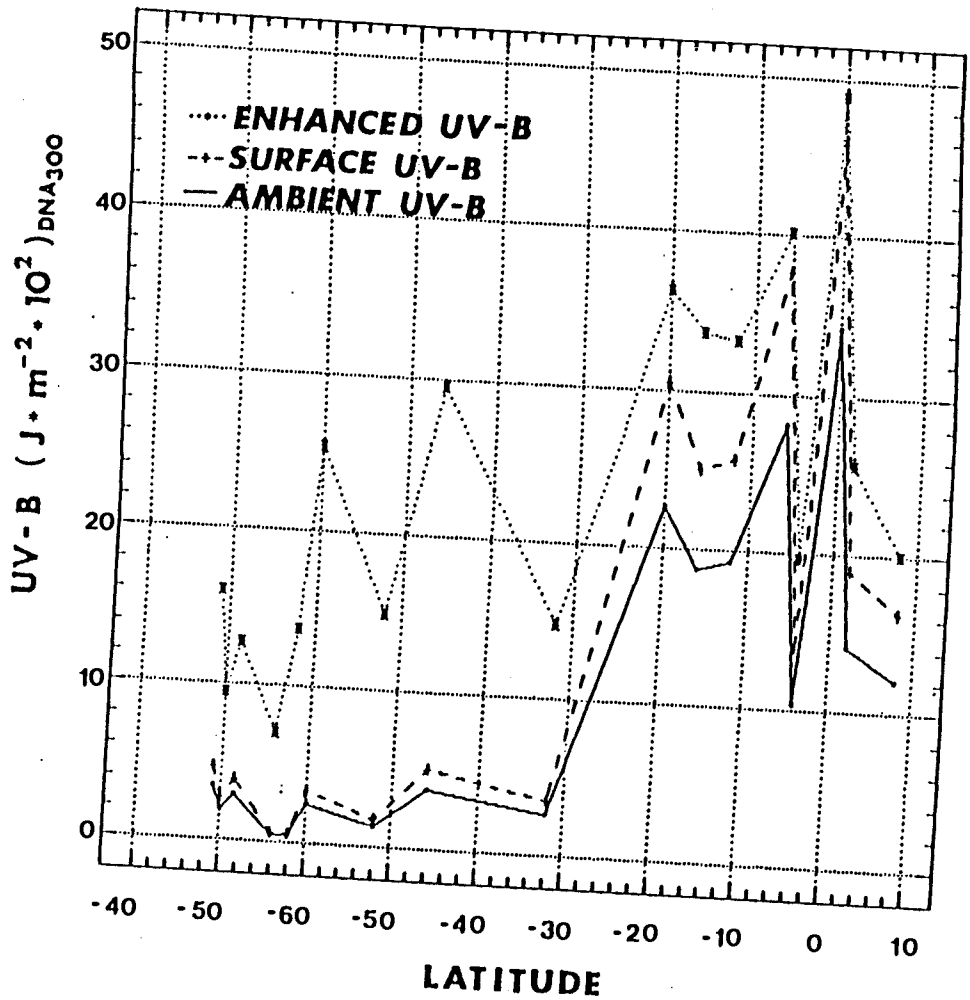

Figure 4: Comparison of the estimated UV-B radiation dose that occurred in the enhanced sample bottles, the ambient sample bottles, and at the surface of the ocean at the location of each experiment. Negative values correspond to southern latitudes.

0.11 $mg*m^{-3}$), corresponding to the nutrient enriched south equatorial current.

A region of low chlorophyll-a concentration was found between 20°S and 46°S (0.02 to 0.09 $mg*m^{-3}$), corresponding to the easterly currents of the south pacific gyre. Between 49°S and 60°S, near the Antarctic convergence, the concentration of chlorophyll-a was again high (0.16 to 0.26 $mg*m^{-3}$). The concentration of chlorophyll-a in the south equatorial current was considerably greater at 40 m than at the surface, while at the other stations the concentrations near the surface, at 20 m, and at 40 m were not significantly different (Fig. 5).

Primary productivity

Primary production rates in the surface samples exposed to ambient solar radiation ranged from 0.03 mg $C*m^{-3}*h^{-1}$ to 0.81 mg $C*m^{-3}*h^{-1}$. Similar measurements of primary productivity (0.08 mg $C*m^{-3}*h^{-1}$ to 1.08 mg $C*m^{-3}*h^{-1}$) were observed from other experiments conducted at the locations corresponding to our data (Chavez, personal communication). Measurements of primary production in the deep samples were low (mean = 0.12 mg $C*m^{-3}*h^{-1}$) due to suspected phthalate ester contamination from the polyvinylchloride Niskin bottles used for sampling. Evidence for contamination was shown by low surface primary productivity measurements in samples taken with the Niskin bottles as compared to the primary production

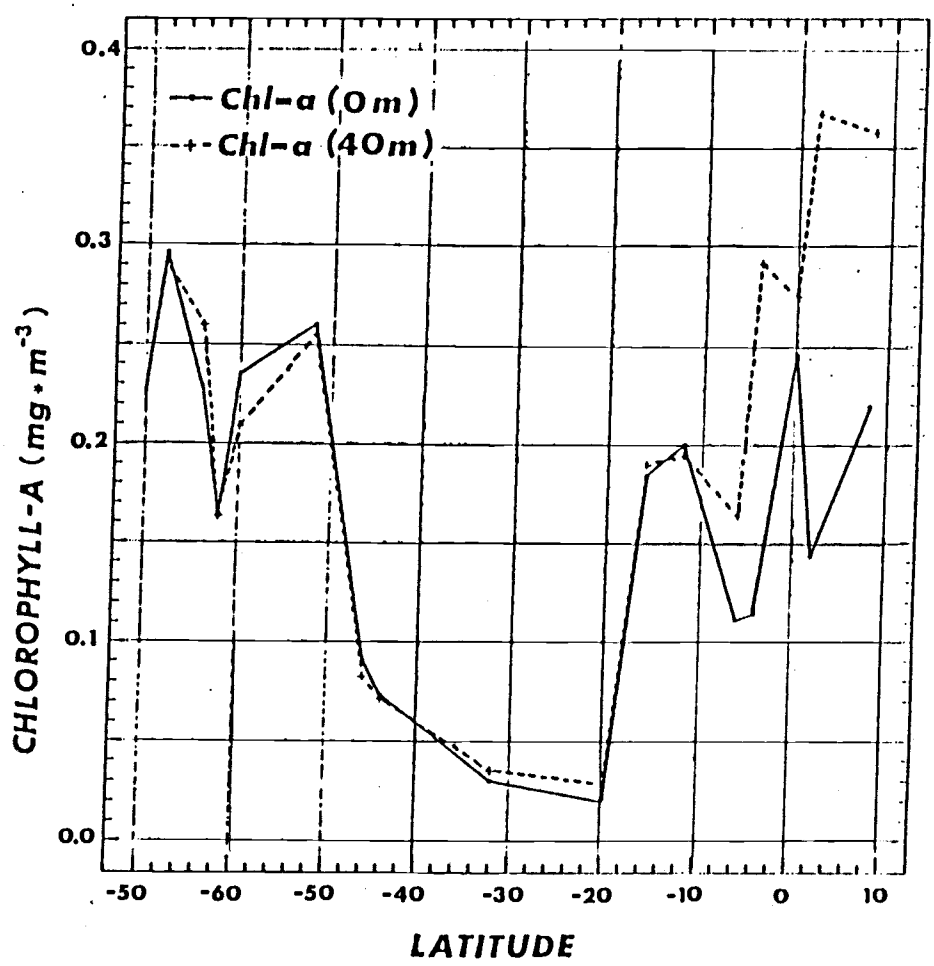

Figure 5: Latitudinal distribution of biomass in mg Chl-a* m^{-3}. Negative values correspond to southern latitudes. surface primary productivity measurements in samples taken

measured for bucket samples from the location. Although the total primary production values do not represent the true production rates for the deep water sampled, the effects of UV-B enhancement were similar in both the deep and surface samples, so the results were combined in figures 8, 9, and 10.

Three distinct regions of primary production occurred and generally followed the same pattern as the chlorophyll-a concentrations (Table 1, Figs. 6 and 7). Although the chlorophyll-a concentrations in the south equatorial region and near the Antarctic convergence were similar, the surface assimilation efficiencies in the south equatorial region were considerably higher (mean = 2.72 mg $C*mg^{-1}$ $Chl\text{-}a*h^{-1}$, s.d. = 2.3) than in the Antarctic convergence region (mean = 0.85 mg $C*mg^{-1}$ $Chl\text{-}a*h^{-1}$, s.d. = 0.38).

Enhanced UV-B radiation caused a significant decrease in the primary production rates in the surface samples (t-test, $p<0.001$, $n = 18$) (Fig. 6). There was no significant (t-test, $0.20>p>0.10$, $n = 16$) difference in primary production in the deep samples in response to enhanced UV-B radiation (Fig. 7). The decrease in primary production ($r=0.92$, $p<0.0001$, $n = 31$) in the ambient bottle was significantly related to the total production (Fig. 8) but not related to the percent decrease in production (Fig. 9). The mean percent decrease in the surface and deep samples was 34% and 26%, respectively. When the primary production was low, the variance in percent

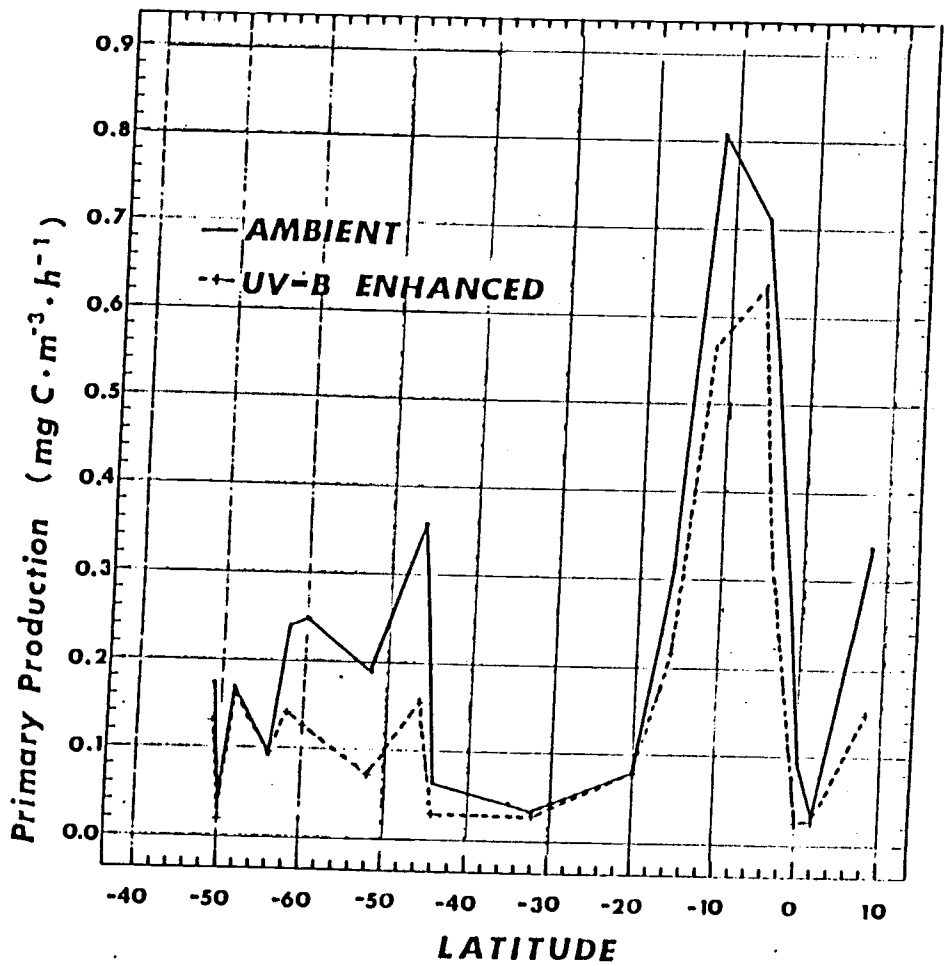

Figure 6: Latitudinal distribution of surface primary production in the ambient and enhanced UV-B radiation bottles. Negative values correspond to southern latitudes.

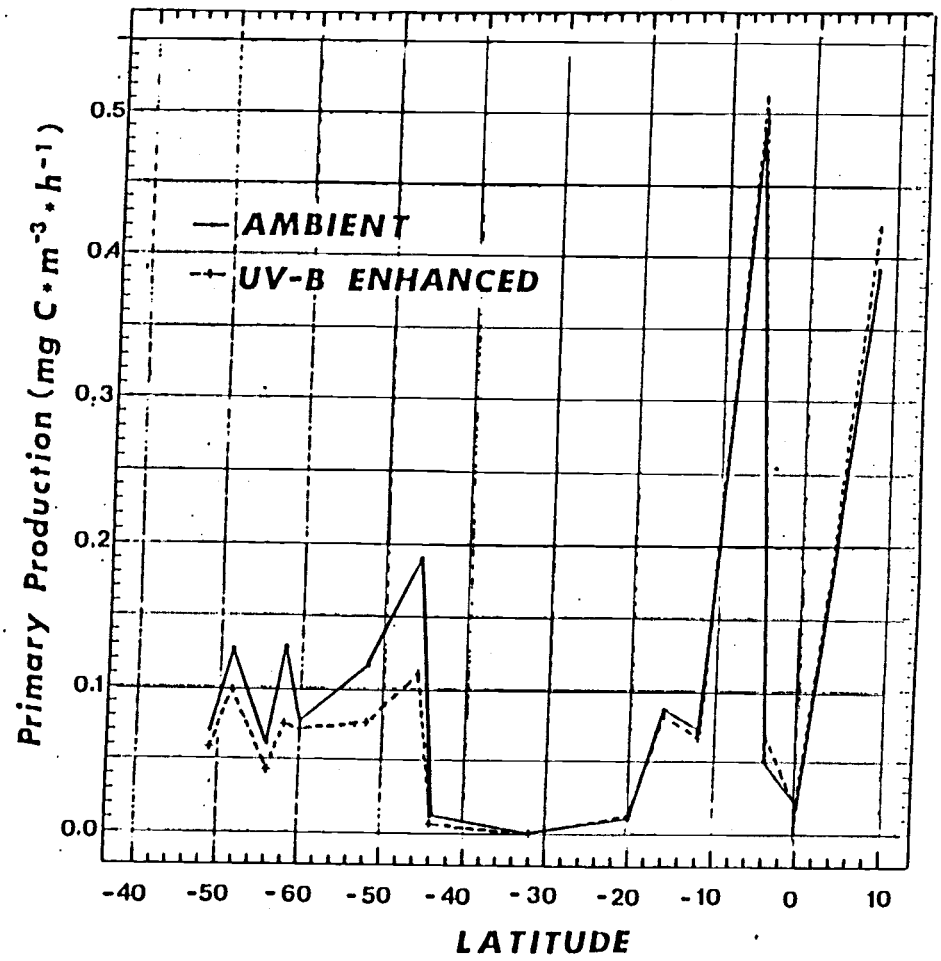

Figure 7: Latitudinal distribution of deep (20 - 40 m) primary production in the ambient bottle and enhanced UV-B radiation bottles. Negative values correspond to southern latitudes.

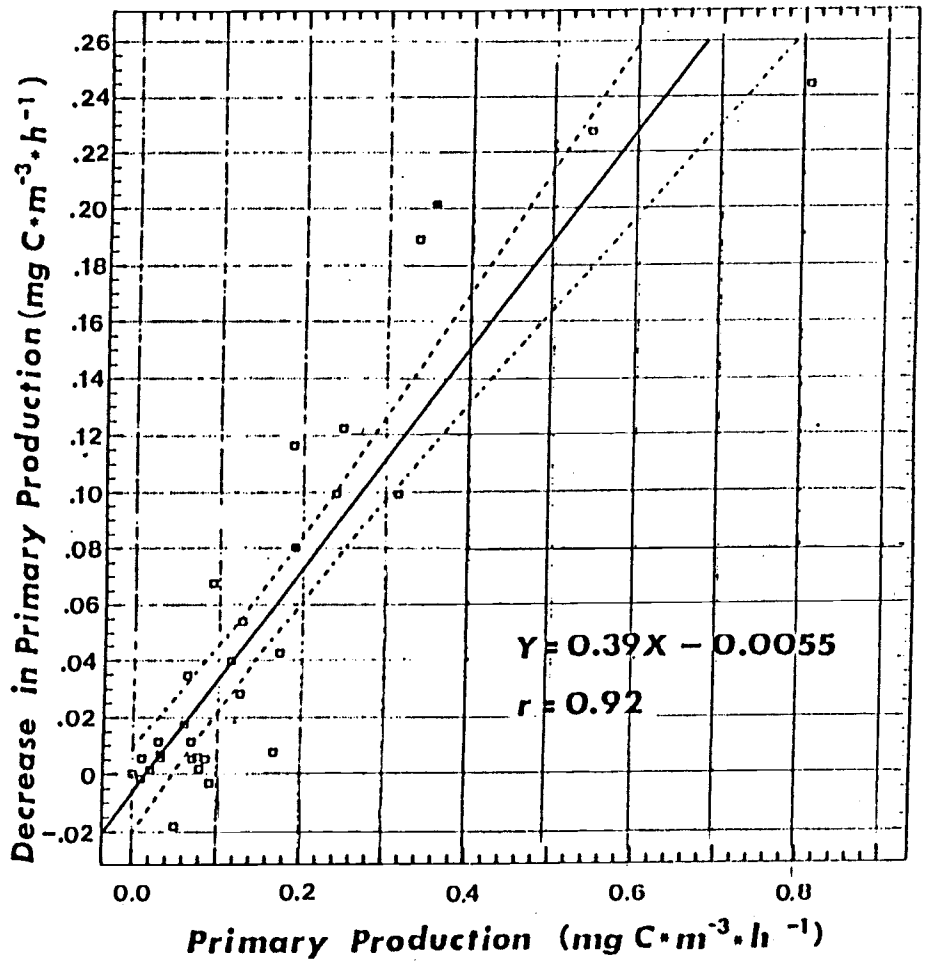

Figure 8: Decrease in primary production from enhanced UV-B radiation in relation to the total primary production. The least squares regression line and the 95% confidence limits are included.

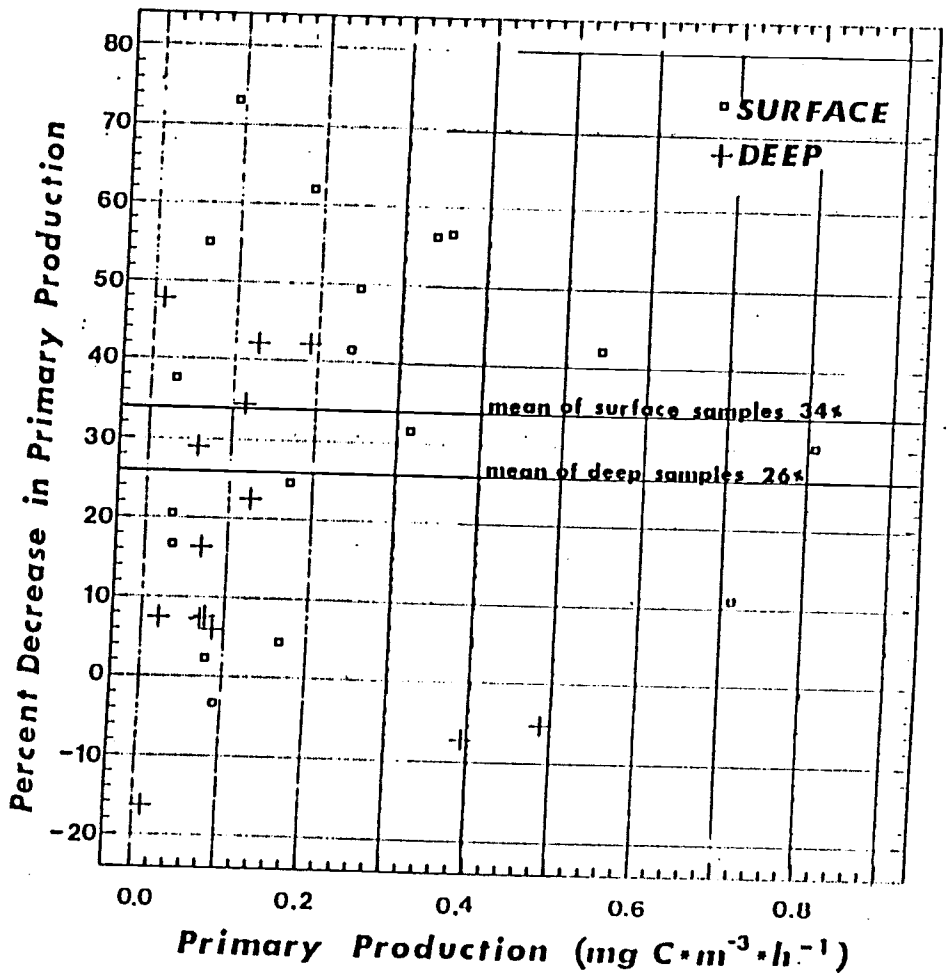

Figure 9: Percent decrease in primary production from enhanced UV-B radiation vs the total primary production in the ambient UV-B radiation treatment.

the primary production was low, the variance in percent

decrease was high, but as the primary production increased the percent decrease converged toward the mean (Fig. 9). The decrease in primary production increased with increasing assimilation efficiency ($r=0.86$, $p<0.0001$, $n = 31$), indicating an increase in sensitivity to UV-B radiation in photosynthetically efficient phytoplankton (Fig. 10).

A sigmoidal relationship was found between the percent decrease in surface primary production and the total enhanced dose of UV-B radiation, suggesting a threshold of sensitivity to UV-B radiation. Three samples, corresponding to stations 4-12, 9-26, and 12-34 (Table 1), indicated high sensitivity to UV-B radiation by having a large percent decrease with a low enhanced dose of UV-B. A significant relationship ($r=0.72$, $p<0.003$, $n = 15$) was found between the percent decrease in primary production and the total dose of enhanced UV-B radiation by eliminating these three sensitive samples, transforming the percent decrease into probit values, and taking the logarithm of the total enhanced dose (Fig. 11). The equation describing the relationship between total enhanced dose of UV-B radiation and the resulting percent decrease in primary production was:

$$P_{probit} = 4.60*D - 9.80 \qquad (6)$$

where D is the logarithm of the total enhanced UV-B dose (DNA_{300} $J*m^{-2}$); and P_{probit} is the resulting probit decrease in primary production.

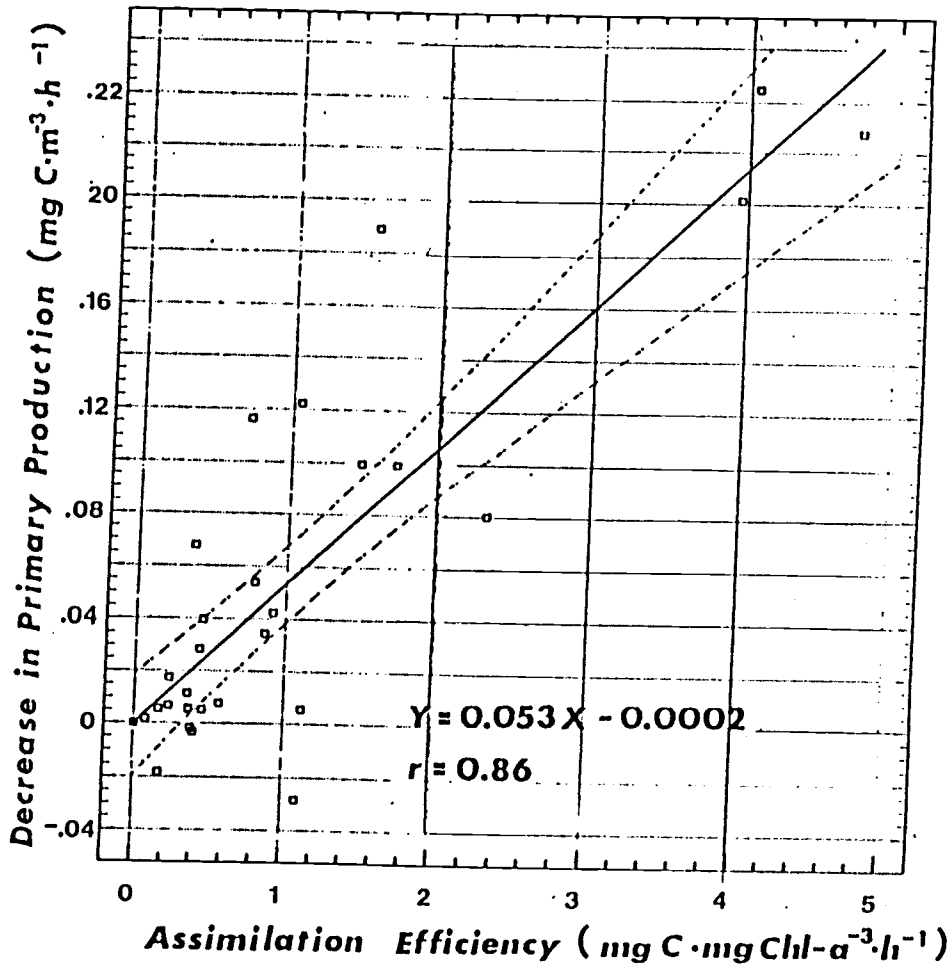

Figure 10: Total decrease in primary production vs assimilation efficiency. Included is the least squares regression line and the 95% confidence interval.

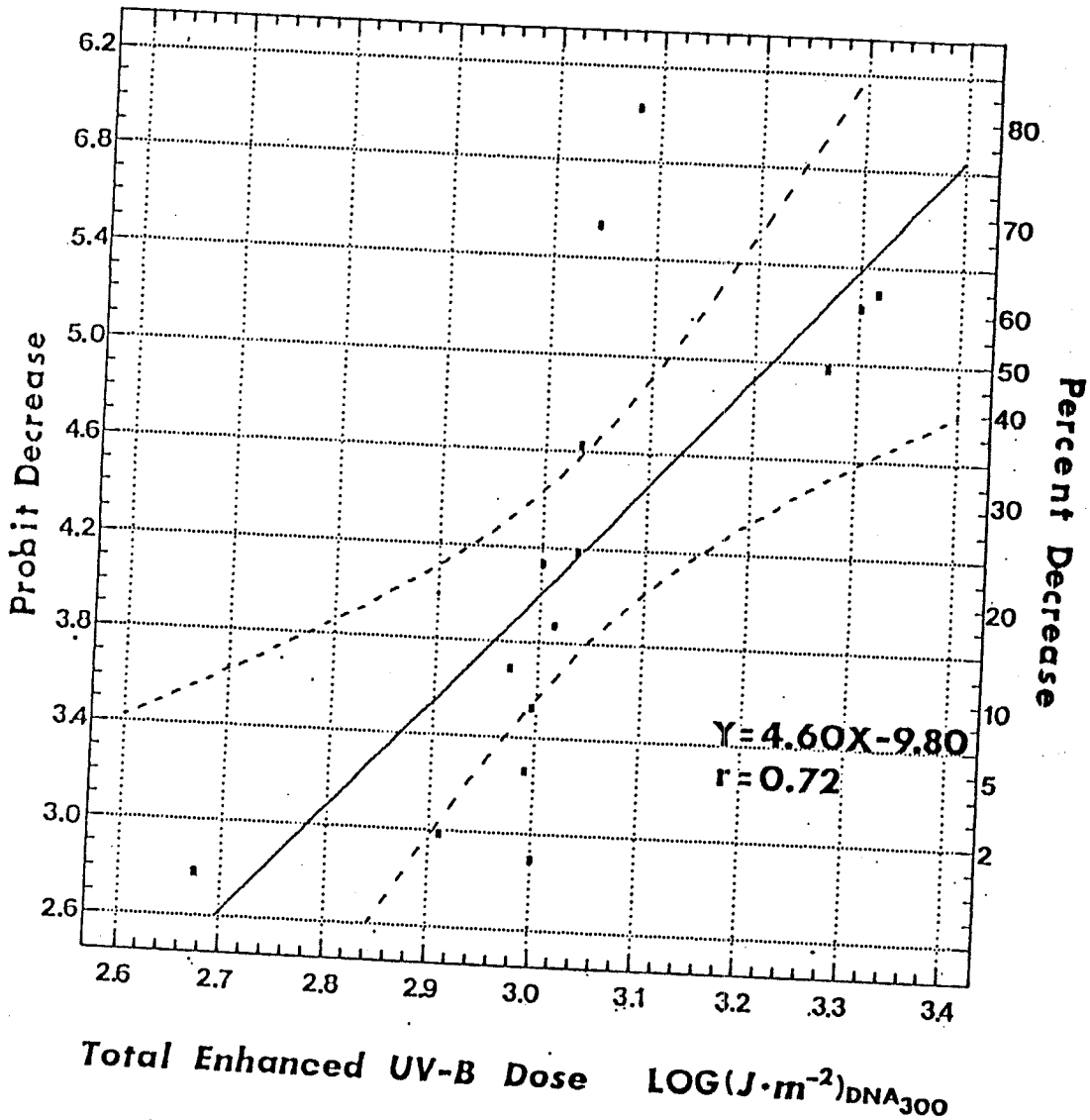

Figure 11: Probit decrease and the corresponding percent decrease vs total UV-B dose enhanced. The least squares regression line and the 95% confidence interval are included.

Discussion

Our results indicate that an increase in the total daily dose of UV-B radiation would cause a significant decrease in surface primary production. The mean percent decrease in primary production was 32% in the surface samples for a mean enhanced dose of UV-B radiation of 1378 $J*m^{-2}$ (DNA_{300}).

When the total ambient primary production was low, a large variance in the percent decrease in primary production occurred in both the surface and deep samples. In regions of low primary production small differences between sample populations, such as species composition, number of zooplankton in the sample, or species specific tolerances to UV-B radiation, may have had a large effect on the measured percent decrease in productivity. Decreased counting precision of the scintillation counter associated with low count may also have contributed to the variability in regions of low productivity. However, when the primary production was high, the percent decrease in primary production was less sensitive to small differences between sample bottles. The linear relationship between the total decrease in primary production and the total ambient primary production supports the conclusion that the percent decrease is independent of the total productivity.

A significant correlation was found between the decrease in primary production and the assimilation efficiency. The

highest assimilation efficiencies, concurrent with the largest decreases in primary production from UV-B enhancement, occurred in the south equatorial region which has optimal growing conditions of high nutrient concentrations, warm temperatures and a high intensity of PAR (Thurman 1988). In regions where conditions are less than optimal for efficient photosynthesis, the decrease in primary production from UV-B enhancement was low. The decreasing effect of UV-B radiation on primary production that accompanied a decrease in assimilation efficiency suggests that phytoplankton, already stressed by other limiting factors, were less vulnerable to the effects of UV-B radiation. If the contamination in the deep samples is considered as an additional stress on photosynthetic efficiency, then the small decrease in primary production associated with the low assimilation efficiencies in the deep samples also suggests a decreased sensitivity to UV-B radiation in stressed phytoplankton. Some experiments using terrestrial plants have also indicated a decreased sensitivity to UV-B radiation in plants already stressed by other limiting factors (Teramura 1986; Fitzwater et al. 1982).

By the year 2060, stratospheric ozone depletions ranging from 2% to 16% over 1969 concentrations are expected in the southern equatorial region and in high southern latitudes, respectively (Watson 1988; EPA 1988). From our measurements of daily UV-B doses, a 2% decrease in stratospheric ozone over the south equatorial region would represent an approximate

daily increase in surface UV-B radiation of 90 $J*m^{-2}$ (DNA_{300}) (EPA 1988). At 45°S, a 16% decrease in stratospheric ozone would result in an approximate daily increase in surface UV-B radiation of 1378 $J*m^{-2}$ (DNA_{300}) (EPA 1988). From equation 6, the percent decrease in surface primary production corresponding to ozone depletions from 2% to 16% would range from less than 1% near the equator to more than 32% in high southern latitudes.

The probit transformation was used in equation 6 to convert a sigmoid relationship to a linear relationship, which could then be easily tested for significance. The sigmoid relationship of the untransformed data suggests the occurrence of a threshold sensitivity to UV-B radiation. The dose of enhanced UV-B at the threshold may be an indication of the dose at which photorepair mechanisms are saturated. The three experimental stations not included in the dose response relation demonstrated large percent decreases in primary production from relatively low enhanced doses of UV-B radiation. A lower threshold existing among the dominant species of those three samples would be one possible explanation for the high sensitivities exhibited. Worrest, et al. (1981) exposed monocultures of seven phytoplankton species to enhanced UV-B radiation and found the sensitivity to be species specific. Their results (Worrest et al. 1981) did not indicate a threshold for the effects of UV-B radiation, which may have been due to the low levels of PAR

used both in growing the stock cultures and during the experiment.

The relationship described by equation 6, between the dose of enhanced UV-B radiation and the resulting percent decrease in primary production, can be used to approximate the effect of stratospheric ozone depletion on oceanic surface primary productivity. However, changes in the spectral composition of UV-B radiation and the distribution of phytoplankton abundance occurring with increasing depth complicate estimates of overall regional and global effects of UV-B radiation.

The results of this study are based on short-term, in-situ experiments which may not represent the long term effects of enhanced UV-B radiation on marine primary production. Caution is advised in extrapolating these results to the effects of stratospheric ozone depletion on overall marine primary production. Wolniakowski (1979) observed a decrease in photoinhibition over time when monocultures of the marine phytoplankton, Dunaliella tertiolecta, were incubated under enhanced levels of UV-B radiation. On the other hand, use of the ^{14}C uptake method may underestimate the effects of enhanced UV-B on marine phytoplankton since it does not account for the possible long-term effects (eg. growth inhibition) that may occur due to DNA damage.

The decrease in primary productivity due to enhanced solar UV-B radiation can be extrapolated to greater depths

because the attenuation of UV-B radiation is reasonably well characterized. To model the overall effect of future ozone depletion on oceanic productivity one must also address the question of exposure of organisms that undergo vertical migration, the temporal scales of these processes, and the presence of adaptive or selective mechanisms that could mitigate or amplify observed effects. A small reduction in marine primary productivity could decrease production at higher levels of the food chain (Nixon 1988) and also lead to releases of CO_2 and atmospheric perturbations of global significance (Viecelli 1984, Gaudry et al. 1987).

The present study demonstrates that a significant decrease in primary production can occur over a wide latitudinal and longitudinal area in response to predicted increases in UV-B radiation reaching the earth's surface. These results are also important because they demonstrate that the significant decreases in primary production found by others in controlled laboratory conditions can occur when natural assemblages of phytoplankton are exposed to enhanced UV-B radiation simulating stratospheric ozone deletion.

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