

Ultraviolet-B Radiation Effects on Natural Phytoplankton Assemblages of Central San Francisco Bay

VICTORIA E. HOGUE*, FRANCES P. WILKERSON, and RICHARD C. DUGDALE

Romberg Tiburon Center, San Francisco State University, 3152 Paradise Drive, Tiburon, California 94920

ABSTRACT: Since the discovery of a depletion of the stratospheric ozone layer over Antarctica in 1979, scientific attention has been directed towards the effects of increased doses of ultraviolet radiation on phytoplankton in other ecosystems. Little is known about the effects of ultraviolet-B (280–320 nm) radiation (UVBR) on temperate estuarine phytoplankton. Freshly collected phytoplankton samples from Central San Francisco Bay were exposed to ambient UVBR in quartz bottles and monitored for biomass and nutrient uptake rates for comparison with phytoplankton dispensed into bottles made of polycarbonate that effectively filtered out the UVBR to evaluate response to natural UVBR exposure. Short-term (10–12 h) exposure experiments were carried out monthly from October 1998 to October 1999. No significant effect of UVBR on chlorophyll *a* concentrations was found but a clear deleterious effect of UVBR on nutrient uptake was observed.

Introduction

Depletion of the stratospheric ozone layer over the Antarctic in 1979 and its subsequent increase in size and depth (Hader 1994) led to research into the effects of increased doses of ultraviolet radiation on marine phytoplankton; in particular ultraviolet-B radiation (UVBR) that occurs between 280 and 320 nm and is greatly reduced by the stratospheric ozone layer as the radiation travels through the atmosphere to the surface of the earth (Moore et al. 1996). Solar ultraviolet radiation at present and enhanced levels have direct and indirect detrimental effects on phytoplankton and primary production (Smith et al. 1992; Behrenfeld et al. 1994; Helbling et al. 1995; Davidson et al. 1996; Holm-Hansen 1997) with resultant effects on higher trophic levels (Bothwell et al. 1994; Ferreyra et al. 1997; Keller et al. 1997a,b; Laurion et al. 1998; Wangberg et al. 1999). Few studies have examined the effect of UVBR on temperate estuarine phytoplankton.

Because of their photosynthetic requirements, phytoplankton dwell in the upper layers of the water column where they are most susceptible to ultraviolet radiation (Hader 1994). Earlier studies of UVBR effects on natural phytoplankton assemblages were directed towards Antarctica where the ozone hole is greatest and UVBR exposure more intense. Remotely sensed data have indicated that the decrease in the stratospheric ozone concentration may be more global such that larger doses of

UVBR are reaching temperate regions (Hader 1994), motivating studies of temperate estuarine or coastal waters (Ferreyra et al. 1997; Halac et al. 1997; Keller et al. 1997a,b; Laurion et al. 1998; Mostajir et al. 1999).

Many studies of UVBR effect on temperate estuarine or coastal ecosystems have employed large-scale enclosures or mesocosms (Demers et al. 1997). A month long mesocosm study conducted in the lower Narragansett Bay, Rhode Island, using 13,000-l mesocosms (Keller et al. 1997a) showed no significant difference in phytoplankton cell counts or chlorophyll concentrations in treatments exposed to higher levels of UVBR compared to treatments either exposed to ambient UVBR or those in which the UVBR was filtered out. There were also no significant differences in copepod and ichthyoplankton abundances between UVBR and non-UVBR treatments. In a different 3-month long experiment using the 13,000-l mesocosms, Keller et al. (1997b) did find a significant decrease in phytoplankton biomass in the upper 2.25 m of the water column in a UVBR-enhanced treatment during the first 8 d of the experiment. After day 8, copepod abundance decreased enabling the phytoplankton biomass to increase. They attributed these changes to a reduction in either grazing due to a change in the nutritional quality of the food or copepod fecundity, both of which could have been due to enhanced levels of UVBR but were not clearly demonstrated. Upon conclusion of both studies, catastrophic cascading trophic interactions were thought unlikely in this coastal estuarine environment (Keller et al. 1997a,b).

In another mesocosm study, Wangberg et al.

* Corresponding author; tele: 415/338-3735; fax: 415/435-7120; e-mail: vhogue@sfsu.edu

(1999) investigated the effects of UVBR in the Gullmar fjord off the Swedish west coast in the spring and summer seasons, using mesocosms of 3.5-m depth and a diameter of 1.5 m. In the spring, dinoflagellates and diatoms dominated the phytoplankton community and phytoplankton activity was enhanced by UVBR. During the summer, diatom abundance and total algal biomass decreased under UVBR stress. The positive effect seen in the spring may have been a result of a negative effect of UVBR on secondary producers causing a reduction in grazing pressure (Wangberg et al. 1999). The UVBR-enhanced photolytic activities that degrade high molecular weight dissolved organic matter into a more biodegradable substrate for bacteria may have also contributed by increasing the regeneration of inorganic nutrients supplied to the phytoplankton (Wangberg et al. 1999). An experiment in a mesotrophic lake in Ontario, Canada, using 20,000-l mesocosms reported higher chlorophyll *a* concentrations in UVBR-enhanced treatments as opposed to those exposed to ambient or no UVBR (Laurion et al. 1998). The phytoplankton showed no evidence of deterioration or impairment due to grazing. Laurion et al. (1998) concluded that the shallow water column and frequent occurrence of diurnal stratification in the lake preselected for UVBR resistant species. The large amount of suspended particulates could have also provided an ultraviolet screen.

The objective of this study was to determine whether UVBR has a negative effect on the natural phytoplankton assemblages in Central San Francisco Bay. Phytoplankton biomass and ammonium and nitrate uptake were measured in samples collected monthly from October 1998 to October 1999 and either exposed to ambient UVBR in quartz bottles or screened from UVBR in polycarbonate bottles. There are no published data of nutrient uptake for this region. Besides providing information concerning phytoplankton response to UVBR, this data also provides information on nutrient uptake rates and ambient nutrient and chlorophyll *a* concentrations over an annual cycle for Central San Francisco Bay for comparison with other estuaries.

Materials and Methods

STUDY SITE

San Francisco Bay is a prominent estuary along the California coast characterized by spatial and temporal variations of both physical and biological processes (Ambler et al. 1985; Cloern et al. 1985; Nichols and Thompson 1985; Jassby and Powell 1994). The San Francisco Bay experiences a landward flow of salt water from the Pacific Ocean that

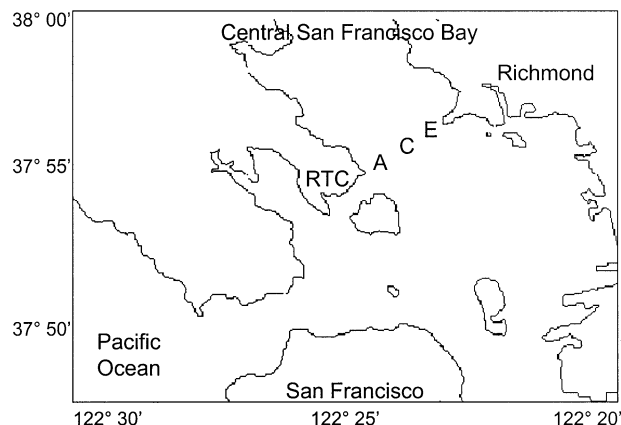


Fig. 1. Map of the study site and Station A, C, and E within Central San Francisco Bay. RTC = Romberg Tiburon Center.

extends northward through the Central Bay up through San Pablo Bay and Suisun Bay to the north, as well as into the southern reaches of the bay (Conomos et al. 1985; Fig. 1). The Sacramento-San Joaquin River system extending from the northern Delta region provides the major source of freshwater inflow to Suisun Bay. Much of this inflow is due to winter runoff, which exhibits a seasonal as well interannual variability (Cloern et al. 1985; Cloern and Nichols 1985; Conomos et al. 1985; Jassby and Powell 1994). The effects of freshwater inflow are greater in the northern reaches of the bay at the mouths of the rivers (Jassby et al. 1996; Kimmerer 2002). This varying degree of influence allows the northern, central, and southern regions of the bay to be distinctly characterized and hydrologically different (Cloern et al. 1985; Cloern and Nichols 1985; Conomos et al. 1985). Surface water samples were taken from three stations (Stations A = 37°53.42'N, 122°26.50'W, C = 37°53.83'N, 122°25.50'W, and E = 37°54.25'N, 122°24.58'W) in Central San Francisco Bay (where waters are more oceanic in properties than either the northern or southern regions) on monthly cruises conducted from October 1998 to October 1999 aboard the R/V *Questuary*. These stations were of different depths (A = 20 m, C = 10 m, E = 5 m) along a cross-bay transect that spanned from Tiburon across the bay to Richmond (Fig. 1).

EXPERIMENTAL APPROACH

Natural phytoplankton assemblages were exposed for 1 d to ambient UVBR in quartz bottles for comparison with assemblages held in bottles made of polycarbonate that filtered out UVBR. Photosynthetic active radiation (PAR) and UVBR transmission through the quartz and polycarbonate bottles were measured using a LiCor 4π sensor and a UV Process Supply UVX digital radiometer

and showed similar qualities of PAR in both bottle types and elimination of UVBR transmission through the polycarbonate.

Surface water samples were collected aboard the R/V *Questuary* at approximately local noon in 20-L acid-cleaned polycarbonate carboys that were kept in the dark at approximately ambient water surface temperature. Samples were immediately transported to the Romberg Tiburon Center (Fig. 1) and kept dark in an environmental chamber maintained close to or at ambient bay water temperature (approximately 17°C). At dawn the following day, the water was sampled for chlorophyll *a* and inorganic nutrients (nitrate and ammonium). These samples are referred to as $t = 0$, or ambient concentrations. These ambient concentrations were compared to samples taken at the actual time of collection of the water from the bay and showed little to no difference (data not shown). The water was then dispensed into approximately 1-l quartz (ambient UVBR) or polycarbonate (non-UVBR) bottles. Duplicates of each treatment were inoculated with $K^{15}NO_3$ (2.7 μ g-at for quartz bottles, 2.3 μ g-at for polycarbonate bottles) or $^{15}NH_4Cl$ (0.27 μ g-at for quartz bottles, 0.23 μ g-at for polycarbonate bottles) both at 99atom%, equivalent to 5–10% of ambient concentration, i.e., trace enrichments. The bottles were then placed into a bay water-cooled table under 50% mesh screening to simulate collection site in situ temperature and irradiance conditions, and incubated from approximately sunrise to sunset (10–12 h). PAR was measured using a LiCor 4 π sensor that integrated PAR over the entire incubation time while UVBR was measured periodically with a handheld UVBR meter held over the bottles throughout the incubation. Upon completion of the incubation, each bottle was sampled for chlorophyll *a*, inorganic nutrients, and ^{15}N -nitrate or ^{15}N -ammonium uptake.

CHLOROPHYLL *a* ANALYSIS

Chlorophyll *a* concentrations were determined by in vitro fluorometry using a protocol (Venrick and Hayward 1984) adapted from Holm-Hansen et al. (1965). Water samples (50–100 ml) were filtered onto Osmonics, Inc., 25-mm glass microfiber filters (equivalent to Whatmann GF/F filters) under dim light. Each filter was then placed into a borosilicate test tube, which was covered and placed into a $-20^\circ C$ freezer. For analysis, 8 ml of 90% acetone was added to the test tube and frozen filter to allow for a 24-h extraction at $-20^\circ C$. Acetone-extracted fluorescence was measured before and after acid additions with a Turner 111 model fluorometer that was calibrated using commercial-

ly available chlorophyll *a* (Sigma Aldrich Company, St. Louis, Missouri).

NUTRIENT ANALYSIS

Samples for nitrate analysis were frozen in 30-ml polypropylene bottles until analysis using a Technicon Autoanalyzer II according to the procedures of Whitley et al. (1981). Combined nitrate and nitrite concentrations are reported as nitrate. Samples were assayed for ammonium according to the method of Solorzano (1969) using a Hewlett Packard diode array spectrophotometer and 10-cm cell.

^{15}N NITROGEN UPTAKE

The incubations were terminated at sunset by filtration onto precombusted (450°C for 4 h) Osmonics, Inc., 25-mm glass microfiber filters. The filters were kept frozen until analysis when they were dried ($<60^\circ C$ for >24 h) and analyzed for ^{15}N enrichment with a Europa Scientific Roboprep-Tracermass mass spectrometer system (Wilkerson and Dugdale 1992). The transport (ρ) and specific uptake rates (V) were calculated according to Dugdale and Wilkerson (1986).

STATISTICAL ANALYSIS

Using the final chlorophyll *a* values or final inorganic nutrient concentrations measured after the 12-h incubations, a sign test was conducted between UVBR and non-UVBR treatments to evaluate any UVBR effect. A sign test was also used to examine significant differences in nutrient uptake between the two treatments throughout the study.

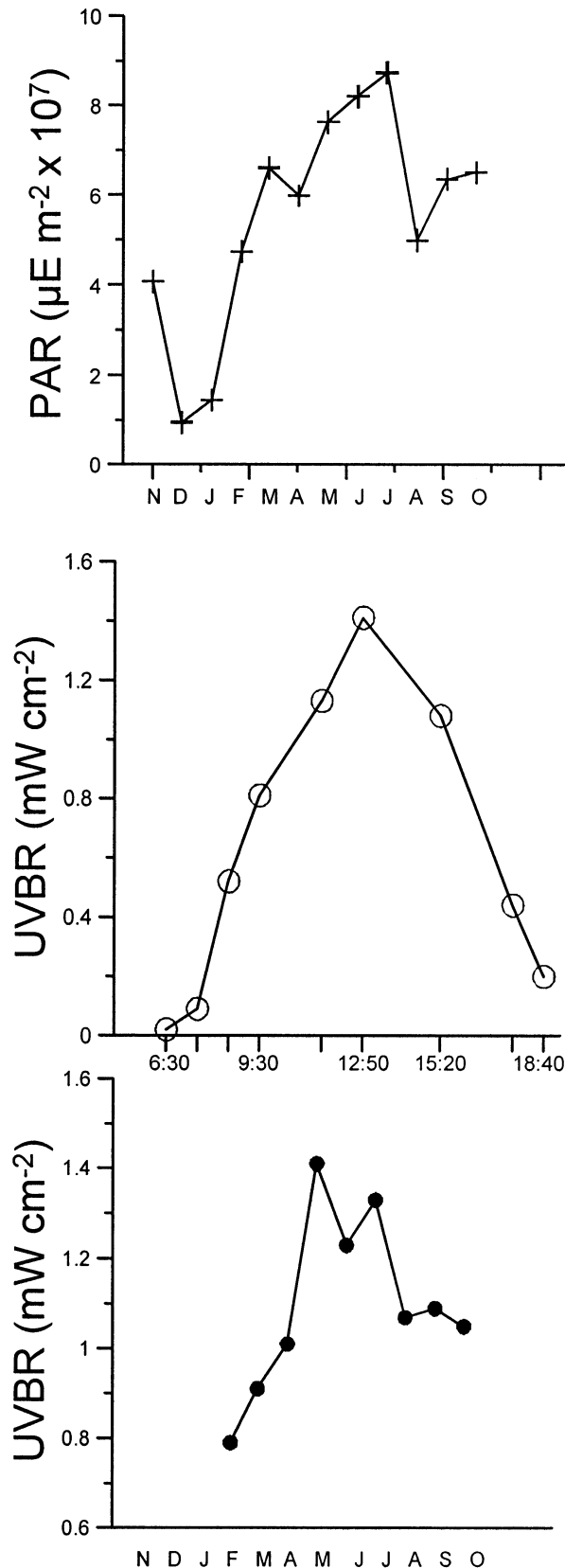
Results

IRRADIANCE CONDITIONS

The total PAR that the natural phytoplankton assemblages were exposed to from dawn to dusk of the ^{15}N incubations ranged from $0.93 \times 10^7 \mu E m^{-2}$ in December 1999 to $8.7 \times 10^7 \mu E m^{-2}$ in July 1999 (Fig. 2), with many of the incubations exposed to PAR greater than $5.0 \times 10^7 \mu E m^{-2}$. Hourly UVBR measurements peaked at approximately local noon so daily values were taken at this time. The highest values measured were May, June, and July (1.41, 1.28, and 1.33 $mW cm^{-2}$, respectively) with a minimum of 0.79 $mW cm^{-2}$ in February 1999. These UVBR measurements are consistent with others made in Central San Francisco Bay (Spekman et al. 2000).

AMBIENT CHLOROPHYLL *a* AND INORGANIC NUTRIENT CONCENTRATIONS AT THE STUDY SITE

Monthly chlorophyll *a* measurements in Central San Francisco Bay from October 1998 to October 1999 showed seasonal increases in the fall and spring (blooms) with little cross-bay variability be-



tween Stations A, C, and E (Fig. 3). Higher chlorophyll *a* concentrations were observed during October 1998 ($4.7\text{--}5.7 \mu\text{g l}^{-1}$), April 1999 ($4.7\text{--}7.5 \mu\text{g l}^{-1}$), and October 1999 ($4.5\text{--}6.8 \mu\text{g l}^{-1}$). During the rest of the year, chlorophyll *a* concentrations were approximately $2 \mu\text{g l}^{-1}$ in the winter months and $3 \mu\text{g l}^{-1}$ in the summer months. Station C tended to show slightly higher chlorophyll *a* concentration values than did Station A or E.

Nitrate concentrations showed a similar homogeneity between stations and ranged from a minimum of $10 \mu\text{M}$ in October 1999 to a maximum of $36 \mu\text{M}$ in February (Fig. 3). Surface ammonium concentrations were similar at Stations A, C, and E and ranged from approximately $2 \mu\text{M}$ in April 1999 to almost $10 \mu\text{M}$ in February 1999. Lower concentrations of ammonium and nitrate tended to occur in the months when chlorophyll *a* concentrations were higher.

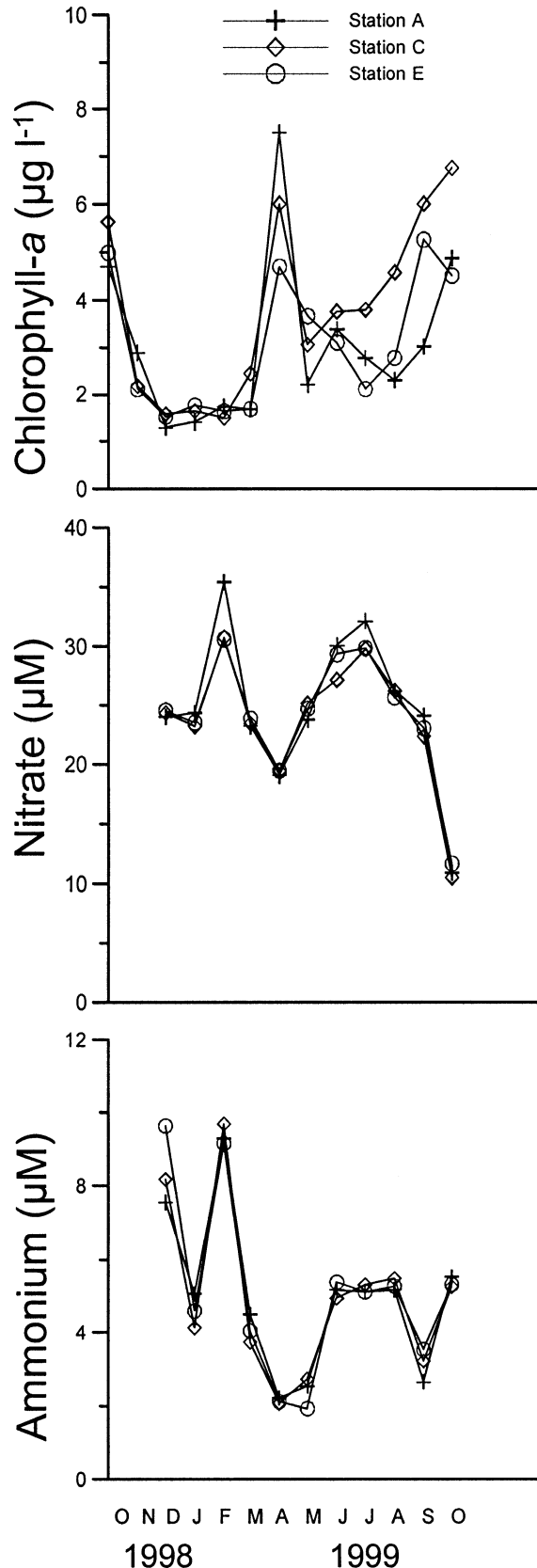
CHLOROPHYLL *a* AND NUTRIENT CONCENTRATIONS IN TREATMENTS

The final chlorophyll *a* values (Fig. 4) measured in UVBR and non-UVBR treatments showed elevated chlorophyll *a* concentrations compared to ambient concentrations measured at $t = 0$ (Fig. 3) for all experiments indicating phytoplankton growth during the 10–12 h incubation periods. This increase in biomass was more obvious during the bloom periods: October 1998, April 1999, and October 1999. There was little difference in final chlorophyll *a* values in bottles exposed to ambient UVBR versus those protected from UVBR. Statistical analysis of the final chlorophyll *a* concentrations by sign test showed no significant difference between UVBR treatments over the wide range of ambient chlorophyll *a* and phytoplankton growth conditions that were encountered (Table 1).

Final nitrate concentrations measured after phytoplankton had been incubated in UVBR transparent (quartz) or UVBR blocking (polycarbonate) conditions showed little difference (Fig. 5). These final nitrate concentrations were, in most cases, less than the ambient ($t = 0$) values even after allowing for the addition of the isotopic nutrients to enable uptake to be measured, indicating nitrate drawdown during the 10–12 h incubation period. This nitrate drawdown was not significant between the two different treatments. Ammonium concen-

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Fig. 2. Integrated photosynthetically active radiation (PAR) during the 10–12 h incubations ($\mu\text{E m}^{-2}$), a typical daily trend of ultraviolet-B radiation (UVBR; mW cm^{-2}) measured in May 1999, and discrete measurements of UVBR at approximately local noon.



treatments were significantly higher in treatments exposed to UVBR (Fig. 6) indicating UVBR had a negative impact on the phytoplankton ability to draw down and assimilate ammonium (Table 1).

^{15}N -NITRATE UPTAKE RATES IN TREATMENTS

Biomass specific nitrate uptake throughout the study was typically below 0.002 h^{-1} except during the spring and fall bloom months when uptake rates were higher (Fig. 7), as were also transport rates of nitrate (ρNO_3 , uptake rates on a per-volume-of-water-sampled basis) that increased from minimal values of $0.004\text{--}0.01 \mu\text{mol l}^{-1} \text{ h}^{-1}$ in the winter and summer months to $0.06\text{--}0.08 \mu\text{mol l}^{-1} \text{ h}^{-1}$ in the bloom periods of April and May 1999 and September and October 1999 (Fig. 8) as a result of both increased phytoplankton uptake and biomass (Figs. 7 and 3). There was little variability in nitrate uptake between Stations A, C, and E but sufficiently different maximum values that the data was not combined.

Biomass specific uptake rates of ^{15}N -labeled nitrate (VNO_3) by the natural phytoplankton assemblages of the Central San Francisco Bay appeared to show little to no difference between UVBR treatments except in the bloom periods of April and May 1999 and September and October 1999 when nitrate uptake appeared to be less in bottles exposed to ambient UVBR (Fig. 7). VNO_3 in the Central San Francisco Bay ranged from minimum values of 0.001 h^{-1} in October 1998 under both UVBR treatments to maximum rates of 0.01 h^{-1} in April 1999 with a VNO_3 at Station A of 0.108 h^{-1} under non-UVBR conditions compared to 0.0059 h^{-1} in the ambient UVBR treatment. Station C also showed a negative effect of UVBR in April 1999; $\text{VNO}_3 = 0.008 \text{ h}^{-1}$ under non-UVBR conditions and 0.005 h^{-1} with ambient UVBR. Station E showed uptake rates of 0.0053 h^{-1} and 0.0043 h^{-1} for non-UVBR and ambient UVBR treatments, respectively, indicating little difference between treatments but still maintaining a trend towards lower specific nitrate uptake rates when exposed to ambient UVBR conditions (Fig. 7). Even though differences between treatments were slight in some cases, statistical analysis by sign test showed a significant difference between UVBR and non-UVBR incubations (Table 2). UVBR had a significant neg-

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Fig. 3. Concentrations of ambient chlorophyll *a* ($\mu\text{g l}^{-1}$), ammonium (μM), and nitrate (μM) at Stations A, C, and E in Central San Francisco Bay. Nutrient data was not available from October 1998 or November 1998.

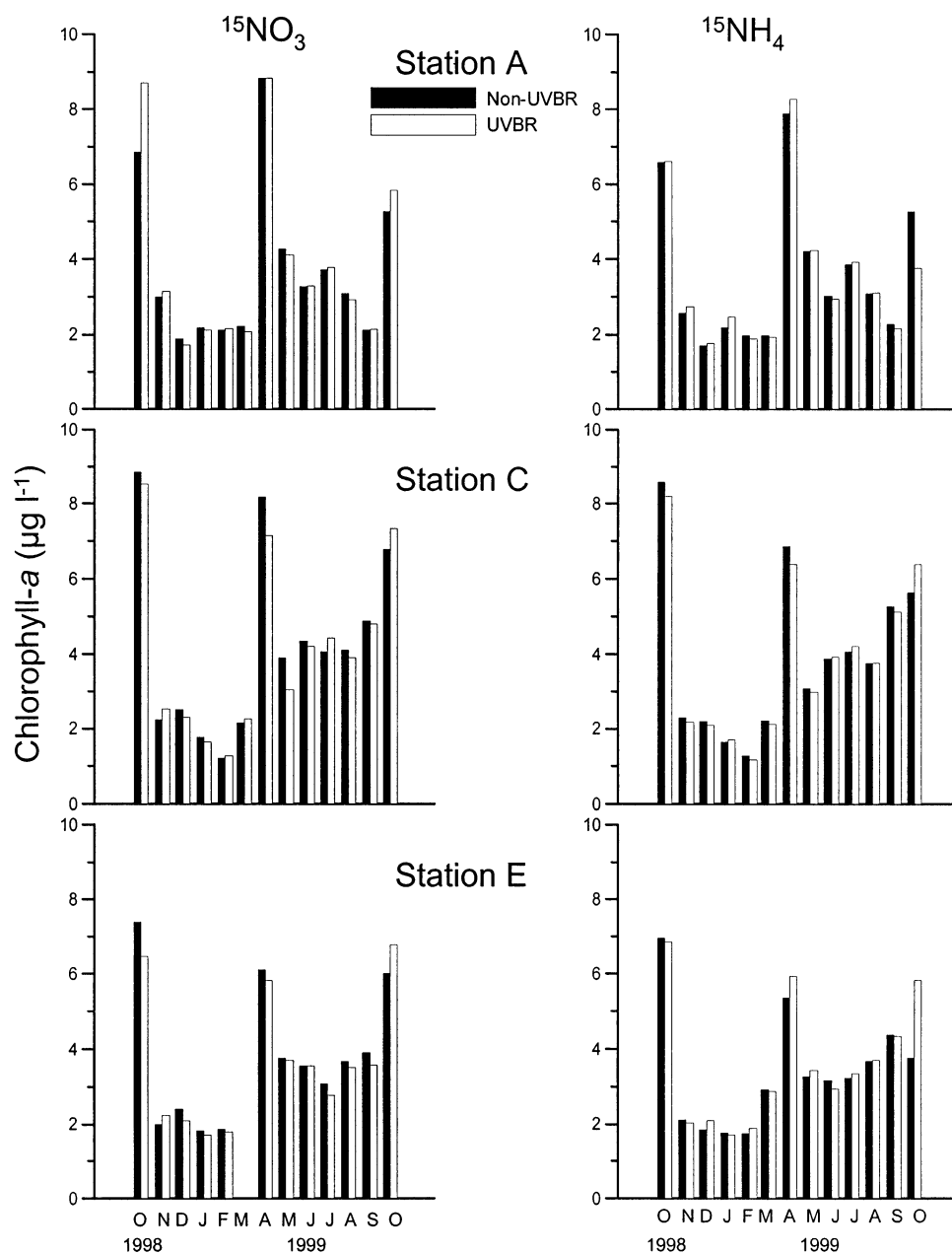


Fig. 4. Final chlorophyll *a* concentrations ($\mu\text{g l}^{-1}$) in the non-UVBR (polycarbonate) and ambient UVBR (quartz) treatments for Stations A, C, and E after 10–12 h incubations with either $^{15}\text{NO}_3$ or $^{15}\text{NH}_4$. Data was not collected at Station E in March 1999.

TABLE 1. Statistical analysis using a sign test to assess significance between chlorophyll *a*, nitrate, and ammonium concentrations for ambient UVBR (quartz; -n) versus non-UVBR (polycarbonate; +n) treatments. * indicates statistically significant.

Station	Chlorophyll <i>a</i>	Nitrate	Ammonium
A	+n = 10, -n = 16 $p < 0.327$	+n = 11, -n = 11 $p < 1$	+n = 3, -n = 19 $p \leq 0.0009^*$
C	+n = 16, -n = 10 $p < 0.327$	+n = 9, -n = 13 $p < 0.523$	+n = 10, -n = 12 $p \leq 0.832$
E	+n = 15, -n = 11 $p < 0.557$	+n = 9, -n = 13 $p < 0.523$	+n = 3, -n = 19 $p < 0.0009^*$
A + C + E	+n = 41, -n = 37 $p < 0.734$	+n = 29, -n = 37 $p < 0.389$	+n = 16, -n = 50 $p < 0.00003^*$

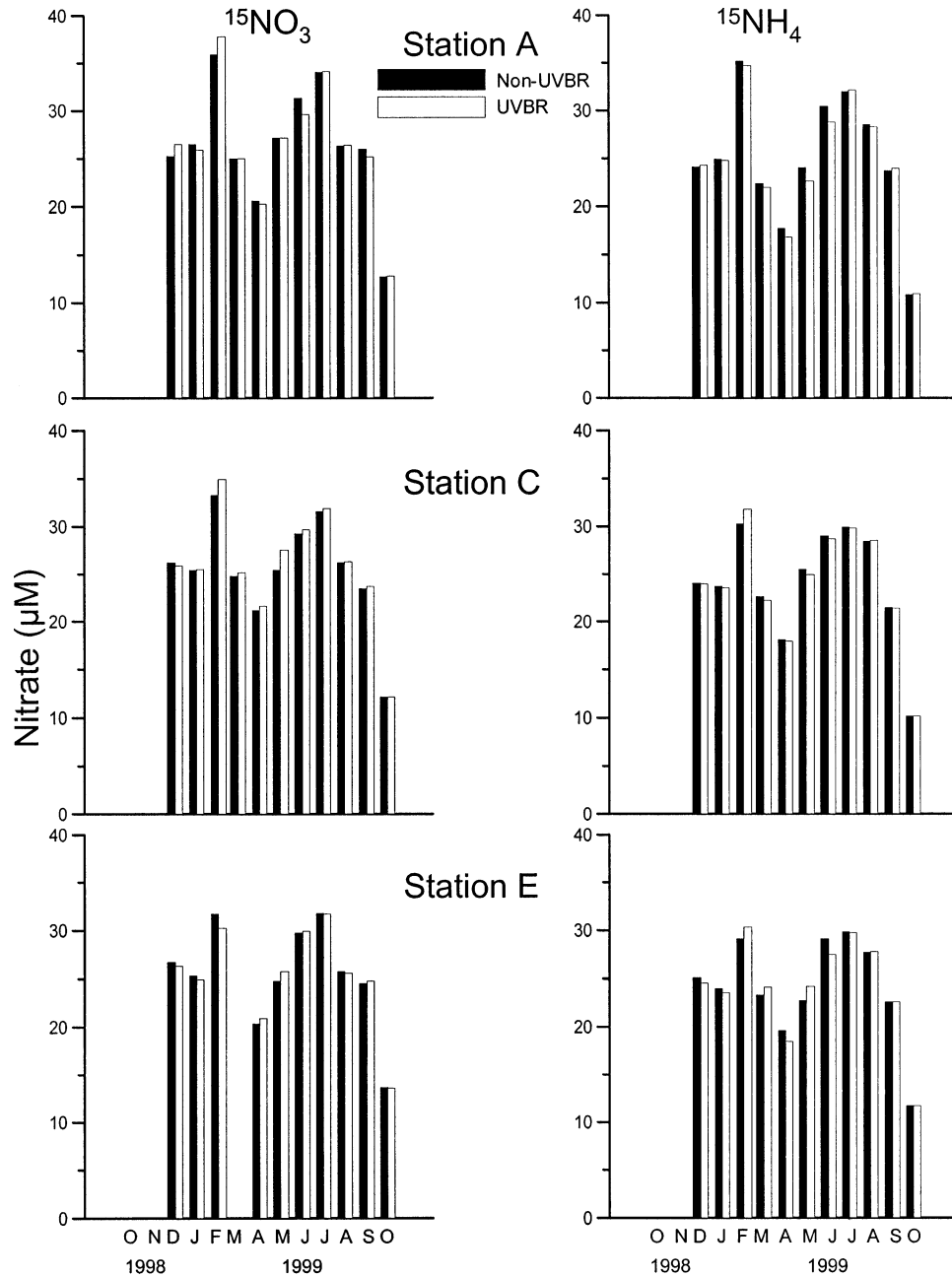


Fig. 5. Final nitrate concentrations (μM) in the non-UVBR (polycarbonate) and ambient UVBR (quartz) treatments for Stations A, C, and E after 10–12 h incubations with either $^{15}\text{NO}_3$ or $^{15}\text{NH}_4$. Data was not collected at Station E in March 1999.

ative effect on the phytoplankton specific nitrate uptake rates over the course of this experiment ($p \leq 0.005$, Table 2). Transport rates (Fig. 8) showed more variability with UVBR treatment than did VNO_3 values (Fig. 7). Higher rates were clear in non-UVBR treatments in April 1999. Sign test analysis gave a significant negative effect of UVBR on phytoplankton transport rates with $p \leq 0.02$.

^{15}N -AMMONIUM UPTAKE RATES IN TREATMENTS

Phytoplankton uptake rates of ^{15}N -ammonium were greater than for ^{15}N -nitrate in most of the incubations (Figs. 7 and 8). The nonbloom month values of VNH_4 at Station A ranged from 0.003 to 0.008 h^{-1} but there were higher rates ranging from 0.007 to 0.02 h^{-1} in the spring and summer seasons. Like VNO_3 , ^{15}N -ammonium specific uptake

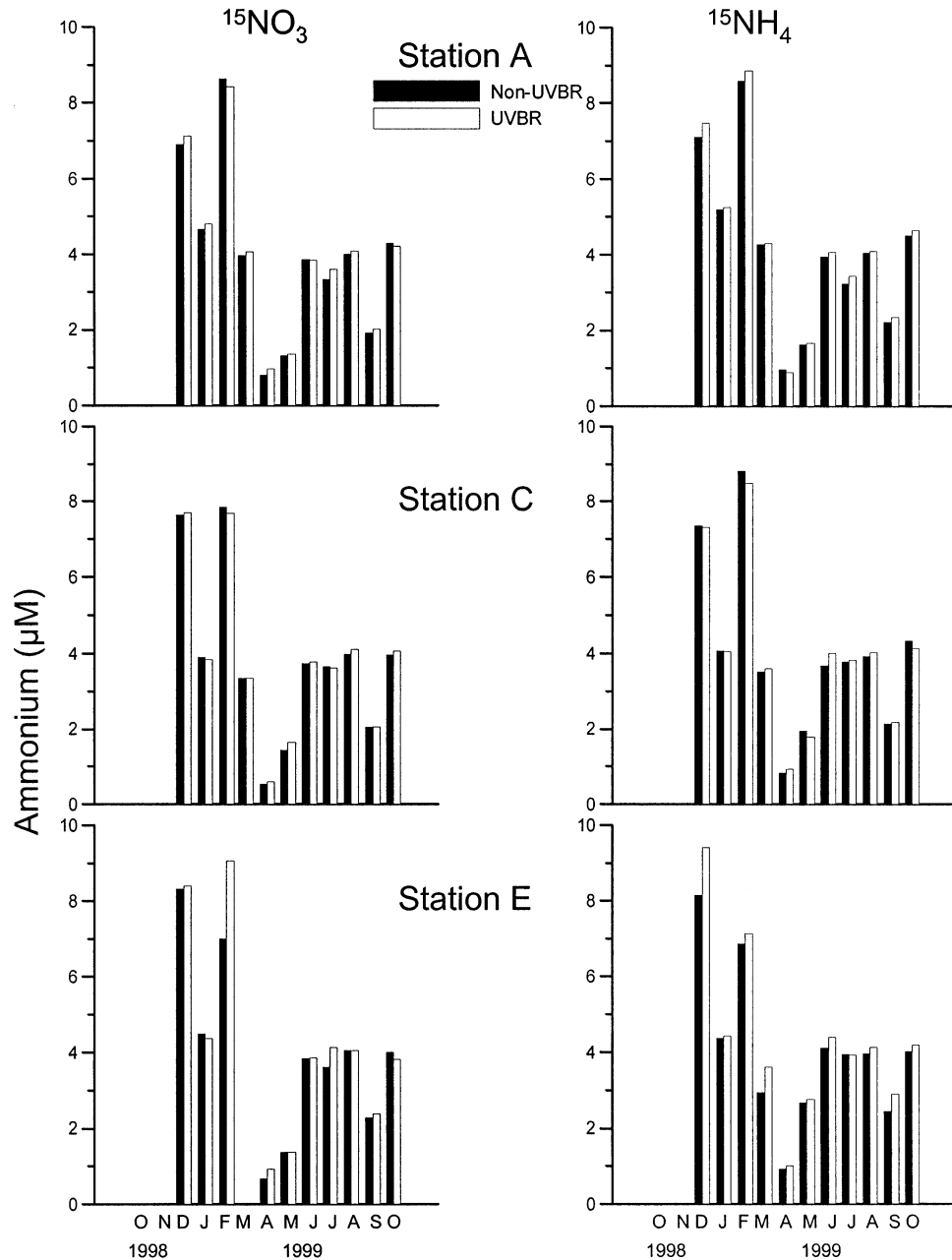


Fig. 6. Final ammonium concentrations (μM) in the non-UVBR (polycarbonate) and ambient UVBR (quartz) treatments for Stations A, C, and E after 10–12 h incubations with either $^{15}\text{NO}_3$ or $^{15}\text{NH}_4$. Data was not collected at Station E in March 1999.

rates (VNH_4) decreased in UVBR treatments (Fig. 7). In October 1998, the VNH_4 at Station A in the non-UVBR treatment was 0.05 h^{-1} compared to 0.02 h^{-1} with ambient UVBR. April 1999 had lower VNH_4 values for both treatments than October 1998 but like October 1998, decreased uptake was measured with UVBR. Stations C and E showed lower VNH_4 with UVBR in April 1999; non-UVBR $\text{VNH}_4 = 0.013 \text{ h}^{-1}$ and ambient UVBR $\text{VNH}_4 = 0.011$ and 0.009 h^{-1} for Stations C and E, re-

spectively (Fig. 8). In September 1999, all stations (A, C, and E) had a VNH_4 of 0.06 h^{-1} in the non-UVBR treatment in comparison to the lower specific ammonium uptake rate of 0.02 h^{-1} in the UVBR exposed treatment. Results of the sign test state a negative effect of UVBR on the specific ammonium uptake rates ($p \leq 0.0003$, Table 2).

The transport rates ρNH_4 for the nonbloom fall and winter months ranged from 0.02 to $0.07 \mu\text{mol l}^{-1} \text{ h}^{-1}$ for all Stations A, C, and E (Fig. 8) and were

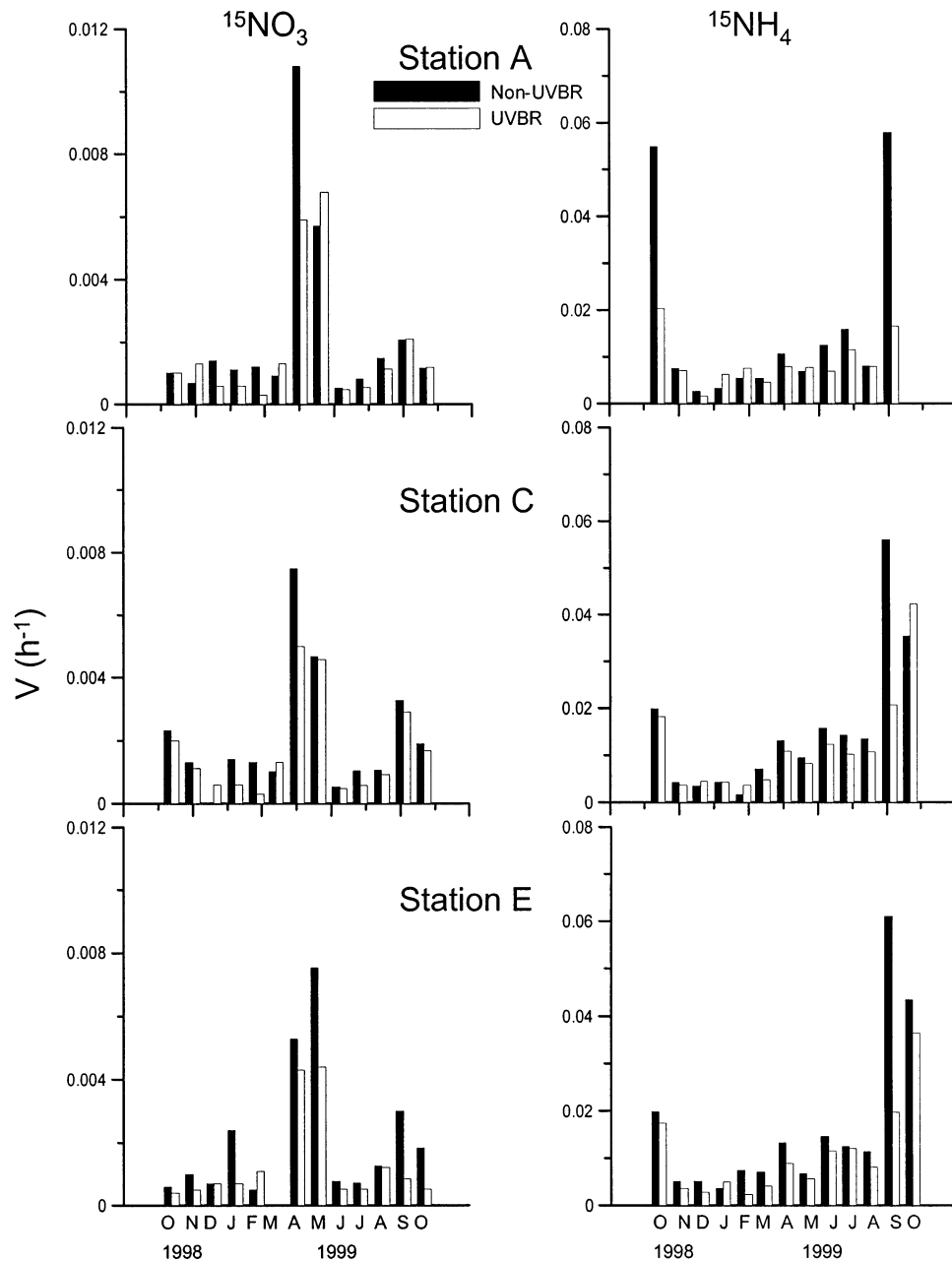


Fig. 7. Specific uptake rates (V , h^{-1}) of $^{15}\text{NO}_3$ incorporation and $^{15}\text{NH}_4$ incorporation by phytoplankton in the non-UVBR (polycarbonate) and ambient UVBR (quartz) treatments for Stations A, C, and E after 10–12 h incubations with either $^{15}\text{NO}_3$ or $^{15}\text{NH}_4$. Data was not collected at Station E in March 1999.

slightly higher in the spring and summer months ($0.05\text{--}0.1 \mu\text{mol l}^{-1} \text{h}^{-1}$). ρNH_4 reached maximum values in October 1998 and September and October 1999 ($0.2 \mu\text{mol l}^{-1} \text{h}^{-1}$) with even higher values in the non-UVBR incubation at Station A in 1998 and Stations C and E in 1999 when transport rates of $0.3 \mu\text{mol l}^{-1} \text{h}^{-1}$ were reached. As with VNH_4 , statistical analysis by sign test showed a highly sig-

nificant negative effect of UVBR on phytoplankton ammonium transport rate ($p \leq 0.00001$, Table 2).

Discussion

The Central San Francisco Bay data collected between October 1998 and October 1999 show the characteristic seasonal cycles of nutrients and phytoplankton that have been observed in the north-

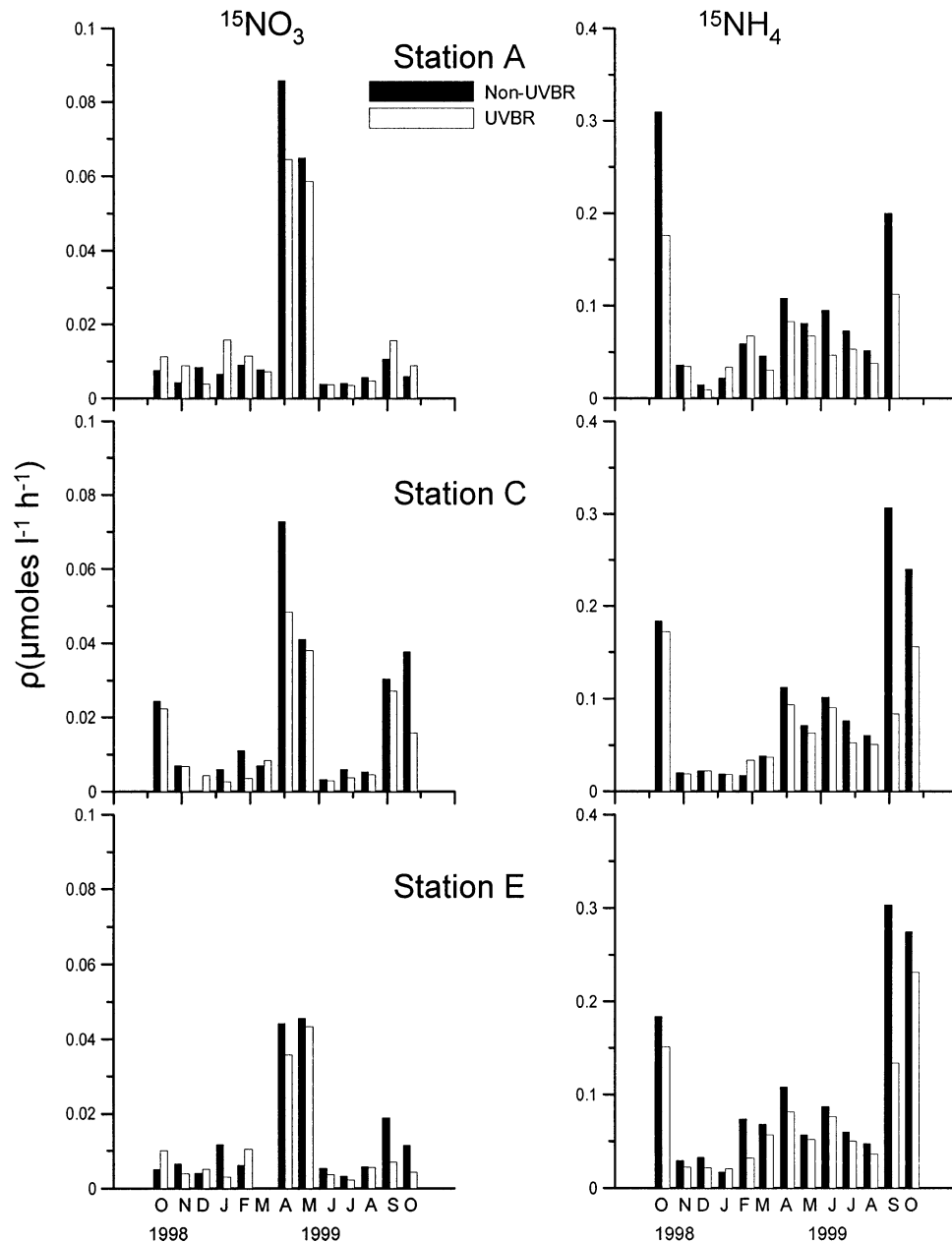


Fig. 8. Transport rate (ρ , $\mu\text{mol l}^{-1} \text{h}^{-1}$) of $^{15}\text{NO}_3$ incorporation and $^{15}\text{NH}_4$ incorporation by phytoplankton in the non-UVBR (polycarbonate) and ambient UVBR (quartz) treatments for Stations A, C, and E after 10–12 h incubations with either $^{15}\text{NO}_3$ or $^{15}\text{NH}_4$. Data was not collected at Station E in March 1999.

ern and southern parts of the bay (Jassby et al. 2002; May et al. 2003). Nutrients are at nonlimiting but variable levels throughout the year with nitrate averaging $25 \mu\text{M}$ and ammonium at $4 \mu\text{M}$. Ambient nutrients showed lower values in spring (April and May 1999) and fall (October 1999) that paralleled the timing of chlorophyll *a* increases ($>4 \mu\text{g l}^{-1}$) or phytoplankton blooms in the Central Bay. The maximum chlorophyll *a* concentration

measured during the April 1999 spring bloom was $8 \mu\text{g l}^{-1}$. These chlorophyll *a* levels are within the range of chlorophyll *a* concentrations measured in the North Bay (Jassby et al. 2002) and in the South Bay (May et al. 2003; $2\text{--}40 \mu\text{g l}^{-1}$). Parameters were measured at the three locations in Central Bay (Fig. 1) in a transect across the bay that showed very similar values. This lack of variability across the bay was surprising considering the different wa-

TABLE 2. Statistical analysis using a sign test to assess significance between specific uptake (V , h^{-1}) and transport (ρ , $\mu\text{mol l}^{-1} \text{h}^{-1}$) rates of nitrate and ammonium for ambient UVBR (quartz; -n) versus non-UVBR (polycarbonate; +n) treatments. * indicates statistically significant.

Station	$V^{15}\text{NO}_3$	$V^{15}\text{NH}_4$	$\rho^{15}\text{NO}_3$	$\rho^{15}\text{NH}_4$
A	+n = 7, -n = 6 $p \leq 1$	+n = 9, -n = 4 $p < 0.267$	+n = 7, -n = 6 $p \leq 1$	+n = 10, -n = 3 $p < 0.092$
C	+n = 11, -n = 2 $p < 0.023^*$	+n = 10, -n = 3 $p < 0.092$	+n = 11, -n = 2 $p < 0.023^*$	+n = 11, -n = 2 $p < 0.023^*$
E	+n = 10, -n = 2 $p < 0.039^*$	+n = 12, -n = 1 $p < 0.003^*$	+n = 9, -n = 4 $p < 0.267$	+n = 12, -n = 1 $p < 0.003^*$
A + C + E	+n = 28, -n = 10 $p < 0.005^*$	+n = 31, -n = 8 $p < 0.0003^*$	+n = 27, -n = 12 $p < 0.024^*$	+n = 33, -n = 6 $p < 0.00001^*$

ter depths of the three stations (Stations A = 20 m, C = 10 m, E = 5 m) and the variability observed across the bay in the southern reaches of San Francisco Bay (Lucas et al. 1999).

There was no clear evidence of either a negative or positive effect of UVBR on phytoplankton biomass (growth measured as chlorophyll *a*) in Central San Francisco Bay following a 10–12 h exposure in which cells in both UVBR and non-UVBR treatments grew. This study did not assess UVBR effects across trophic levels over extended periods of time (>12 h) even though there may be cascading trophic effects due to UVBR stress (Keller et al. 1997b; Mostajir et al. 1999; Wangberg et al. 1999). This lack of significant UVBR effect observed on chlorophyll *a* biomass in Central San Francisco Bay water is consistent with other temperate aquatic ecosystems (Ferriera et al. 1997; Halac et al. 1997; Keller et al. 1997a). Keller et al. (1997a) found an overall lack of UVBR radiation effect on phytoplankton biomass in Narragansett Bay and attributed this to a rapid extinction of UVBR radiation in the highly colored waters in which the 1% PAR level was a mean of 4.3 m. Consistent with Keller et al. (1997a), the depth to which surface irradiance reached the 1% PAR level across the Central San Francisco Bay over the course of this study (October 1998–October 1999) ranged from 1.1 to 5.4 m. The turbid and colored waters of the Central San Francisco Bay reduce UVBR penetration and offer a means of protection. This reduction in light while protecting them from the damaging effects of UVBR also shades the phytoplankton from the light needed to photosynthesize. Despite the lack of water clarity in Central San Francisco Bay, light is not always limiting as a phytoplankton bloom was detected in the fall of 1998 and the fall and spring months of 1999 (Fig. 3) indicating that the phytoplankton were exposed to conditions that allowed them to use ambient levels of light for growth. This increased growth was observed across the entire Central Bay during the fall and spring months.

Several researchers have demonstrated that al-

though total phytoplankton biomass is not affected by UVBR radiation, there may be a species composition change with UVBR exposure, favoring the more resilient species (Dohler et al. 1991; Villafane et al. 1995; Davidson et al. 1996; Wangberg et al. 1999; Nilawati et al. 1997). Although this current study did not identify phytoplankton community composition or specific species, Hogue et al. (2001) reported that larger cells (>5 μm in diameter) tend to dominate in Central San Francisco Bay during periods of increased phytoplankton biomass (i.e., spring bloom season). In another study by Hogue (2000), size fractionated samples of chlorophyll *a* from Central San Francisco Bay water exposed to UVBR over a 4-d period showed the percentage of larger phytoplankton (>5 μm) to increase throughout the first 3 d and in most cases into the fourth day compared to smaller picoplankton. These larger cells (likely diatoms) may be better able to withstand UVBR exposure over time.

To determine the effect of UVBR radiation on an aquatic ecosystem over longer periods of time than accomplished in this current study, much of the research done in more turbid estuarine, coastal, and fresh waters has been conducted over time periods extending from days to weeks and months to examine species composition changes and possible cascading trophic effects due to UVBR radiation stress (Keller et al. 1997b; Mostajir et al. 1999; Wangberg et al. 1999). Since a positive or negative effect of UVBR on one trophic level may have effects on other trophic levels (Bothwell et al. 1994) and the length of time the ecosystem is exposed to UVBR is also a factor, an interdisciplinary study analyzing the response of a variety of trophic levels under UVBR stress over longer periods of time (>12 h) would be needed to clearly assess positive or negative UVBR effects.

In agreement with data concerning chlorophyll *a* concentration changes with UVBR treatments in the Central San Francisco Bay, there was no significant difference in final nitrate concentrations measured in the incubated bay water at the end of

both UVBR treatments (ambient UVBR and non-UVBR). In contrast to nitrate concentrations, significantly more ammonium was taken up by phytoplankton under non-UVBR conditions in comparison to UVBR conditions such that significantly higher ammonium concentrations were measured in the UVBR treatment (Table 1). This study does not take into account any activity or contribution to the nutrient concentration by bacterial processes such as the photochemical release of biologically available nitrogen from dissolved organic matter as well as the potential effects of nitrifying and denitrifying bacteria (Bushaw et al. 1996; Jeffrey et al. 1996; Herndle et al. 1997).

Both depletion data and ^{15}N specific uptake and transport rates showed rates to be greater for ammonium than nitrate (Figs. 5–8) indicating that ammonium was the nitrogen source used most by the natural phytoplankton assemblage of the Central San Francisco Bay most of the year. During the bloom months there was a differential uptake of nitrogen sources; a maximal nitrate uptake in spring ($\text{VNO}_3 = 0.01 \text{ h}^{-1}$), but a maximal ammonium uptake in the fall ($\text{VNH}_4 = 0.06 \text{ h}^{-1}$). The higher nitrate uptake in the spring was accompanied by low ambient ammonium concentrations whereas in the fall, ammonium was greater than $4 \mu\text{M}$ and may have been inhibitory for nitrate uptake. Higher nitrate uptake occurred when ammonium values were $<3 \mu\text{M}$.

Consistent with previous studies (Dohler et al. 1991; Dohler and Hagmeier 1997; Laurion et al. 1998), the ability for phytoplankton in Central San Francisco Bay to assimilate nitrate and ammonium was affected by exposure to ambient levels of UVBR by reducing uptake rates. A decrease in nitrate and ammonium uptake with UVBR exposure was observed in monospecific algal cultures under artificial laboratory conditions (Dohler 1984, 1990, 1992; Dohler et al. 1987; Dohler and Bierman 1997). Their studies with phytoplankton assemblages examined under field conditions showed variable responses in nitrate and ammonium uptake with ambient and increased levels of UVBR (Dohler et al. 1991; Dohler and Hagmeier 1997; Laurion et al. 1998). They reasoned that the changing ambient UVBR experienced by the phytoplankton under natural conditions when they moved across depths and light fields compared to a constant laboratory light regime may be the cause of the different in situ experimental results (Dohler et al. 1991) and that field studies provide a more true assessment of UVBR effects on a phytoplankton community.

Dohler (1997) showed the negative UVBR effect on nitrogen assimilation to be a result of its affect on the glutamine synthetase/glutamate synthase

(GS/GOGAT) enzyme pathway that governs ammonium assimilation. This pathway will affect nitrate assimilation since it also uses ammonium resulting from nitrate reduction (by the nitrate assimilation enzymes). Damage to this pathway coupled with a reduction in the supply of ATP, which can also occur with UVBR stress, can greatly impair the ability of a phytoplankton cell to metabolize different nitrogen sources (Dohler 1997, 1998; Dohler and Hagmeier 1997). The degree of damage to the enzymes varied depending on the phytoplankton species. Lohman et al. (1998) also found an increase of glutamate and a decrease of the glutamine pools indicating a negative influence of UVBR on the glutamine synthetase pathway that provides glutamine from glutamate as ammonium is incorporated. Dohler and Hagmeier (1997) found that ^{15}N -ammonium uptake by natural phytoplankton assemblages that preferentially chose ammonium over nitrate as the nitrogen source was higher and more sensitive to UVBR than ^{15}N -nitrate uptake capabilities, which is consistent with this current study. They again observed an influence on the GS/GOGAT pathway that pointed towards an inhibition of ^{15}N -ammonium assimilation into the phytoplankton cell as a result of UVBR stress.

This study of how field populations of Central San Francisco Bay phytoplankton sampled throughout the year respond to ambient UVBR showed the damaging effects ambient UVBR have on the phytoplankton community. The data showed that chlorophyll *a* biomass was unaffected by short 12-h exposures to UVBR. Ambient UVBR had a significant effect on both nitrate and ammonium assimilation, supporting the culture and non-estuarine phytoplankton studies done primarily by Dohler (Dohler 1997, 1998; Dohler and Hagmeier 1997). The response in this temperate estuary is surprising due to the highly turbid waters that are expected to cause light limitation and, in turn, offer protection from UVBR penetration. These results suggest that at least a portion of the phytoplankton community has not developed adequate avenues of resistance to UVBR stress or repair mechanisms to recover from any damage. This study indicates that at the present time the ambient UVBR in the temperate latitudes of San Francisco Bay is at a level that is deleterious to phytoplankton cells.

ACKNOWLEDGMENTS

We would like to thank Al Marchi for nutrient analyses. Victoria Hogue appreciates the help given by her Masters committee members, Dr. Alissa Arp and Dr. Stephen Bollens. We are also grateful to Dr. William Cochlan, Dr. Steven Obrebski, Christa Speckman, Jay Tustin, and a special thanks to Don, Marie, and Aimee Hogue.

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Received, March 1, 2004
Revised, September 21, 2004
Accepted, November 22, 2004