Effects of ultraviolet-B radiation on simultaneous carbon and nitrogen transport rates by estuarine phytoplankton during a week-long mesocosm study

Laure Mousseau1•, Michel Gosselin1, Maurice Levasseur2, Serge Demers1, Juliette Fauchot1, Suzanne Roy1, Piedad Zulema Villegas1, Behzad Mostajir1

1Institut des sciences de la mer de Rimouski (ISMER), Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada
2Institut Maurice-Lamontagne, Ministère des Pêches et des Océans, CP 1000, Mont-Joli, Québec G5L 324, Canada

ABSTRACT: The effect of UV-B radiation on photosynthesis and nitrogen uptake by an estuarine phytoplankton community was investigated during a week-long experiment, conducted in 8 mesocosms under varying conditions of UV-B radiation: reduced UV-B, natural radiation, and 2 levels of enhanced UV-B. Twice a day, dissolved inorganic carbon and total dissolved nitrogen (15N) transport rates were estimated simultaneously from in situ incubations. Irrespective of the treatment, phytoplankton biomass (chlorophyll a) and primary production increased over the first 3 d. Subsequently, nitrate and silicate depletion resulted in a decrease in algal biomass and productivity. Enhanced UV-B radiation was deleterious to chlorophyll a specific transport rates of C and N when compared to reduced and natural UV-B. The C:N transport ratios, as well as the POC:PON ratios, were generally not affected by enhanced or reduced UV-B. In the enhanced UV-B treatments, carbon transport rates were often significantly higher in the afternoon than in the morning, suggesting that phytoplankton exposed to UV-B developed photoprotective mechanisms against UV radiation on a daily basis. A shift in the algal community assemblage from diatoms (>10 μm) to small flagellates (5–10 μm) was observed during the study. Small flagellates were less sensitive to the UV-B treatments than diatoms, whose abundance decreased under reduced and enhanced UV-B. Results from this study suggest that UV-B exposure on a daily basis could change the chlorophyll a specific transport rates of C and N and alter the structure of the phytoplankton community.

KEY WORDS: Mesocosms · Nitrogen transport · Photoinhibition · Photosynthesis · Phytoplankton · St. Lawrence Estuary · UV-B radiation

INTRODUCTION

The recent decline of the stratospheric ozone concentrations has resulted in a major increase in ultraviolet-B radiation (UV-B: 280–320 nm) reaching the Earth’s surface (Kerr & McElroy 1993), causing concern about the influence of UV-B radiation on living organisms. The impact of such changes in ambient solar radiation on planktonic communities is poorly known, and furthermore, since these variations are occurring rapidly, little is known about the time scale that would be required to develop adaptive responses. Until recently, attention has focused mainly on the Antarctic ecosystems where the ozone hole, and hence the relative increase in UV-B radiation, has been most pronounced. However, several studies have shown that ozone depletion was also occurring in temperate and arctic latitudes, leading to a corresponding increase in UV-B radiation (Kerr & McElroy 1993, Fioletov & Evans 1997, Fioletov et al. 1997, Rex et al. 1997, Tarasick & Fioletov 1997).

During photosynthesis, solar radiation is transformed into chemical energy (e.g. ATP) which is then made available to other metabolic processes (Falkowski & Stone 1975, Turpin & Bruce 1990). For this reason, a tight coupling exists between photosynthesis and nitrogen incorporation by phytoplankton (Döhler 1985, Turpin & Bruce 1990, Behrenfeld et al. 1995, Goes et al. 1995). As already demonstrated, damaging effects of UV radiation on photosynthetic electron transport (Meilis et al. 1992, Schofield et al. 1995, Nilawati et al. 1997) as well as on photosynthetic production of ATP (Vosjan et al. 1990) and NADPH could alter the amount of energy available for nitrogen metabolism (Döhler et al. 1987, Behrenfeld et al. 1995, Döhler & Buchmann 1995). Recently, Goes et al. (1994, 1995, 1996) demonstrated that the inhibition of photosynthesis by UV-B is accompanied by changes in the biosynthesis rates and composition of several biochemical compounds (fatty acids, monosaccharides and amino acids) in phytoplankton. These changes may alter the nutritive value of phytoplankton for upper trophic level organisms.

In this study, we describe the effects of reduced and enhanced UV-B radiation on simultaneous carbon and total nitrogen transport rates by an assemblage of estuarine phytoplankton. For 7 d, carbon and nitrogen transport rates were simultaneously measured twice a day (morning, A.M., and afternoon, P.M.) in order to evaluate short-term (<1 d) UV damage (photoinhibition, depressed nitrogen transport) and long-term (>1 d) potential for repair in the phytoplankton community. It is hypothesized that the impact of UV-B radiation on total nitrogen uptake is closely linked to that of carbon uptake, i.e. a decrease in photosynthetic rates should result in a decrease in total nitrogen uptake.

MATERIALS AND METHODS

Experimental setup. Mesocosm experiments were conducted from 17 to 23 July 1996 at the Pointe-au-Père aquaculture research station (University of Québec; 68.2°W, 48.35°N). Four land-based stainless steel tanks (1.30 m diameter, 2.55 m depth; 3200 l) were each divided into 2 polyethylene mesocosms (1500 l) and filled on 16 July (from 18:00 to 23:00 h) with filtered (240 μm) seawater (salinity of 24) from the Lower St. Lawrence Estuary. The temperature in each mesocosm was maintained close to in situ temperatures (between 8 and 10°C) by circulating estuarine water within the tank double-wall. In order to maintain a homogeneous water mass, a complete turnover of each mesocosm volume was done in 1 h using Little Giant pumps. A constant water level in the mesocosms was maintained by adding seawater between the double-walled tank and mesocosm walls (not inside mesocosms) after each sampling.

In order to assess the effects of UV-B radiation on the planktonic community transferred to mesocosms, 4 experimental designs were set up with different UV-B exposures: natural solar radiation (NUV-B), reduced UV-B (WUV-B), low UV-B enhancement (LUV-B) and high UV-B enhancement (HUV-B). For the WUV-B treatment, the tanks were covered with a 0.13 mm Mylar D sheet which eliminates radiation between 280 and 312 nm. This sheet cuts 91% of incident UV-B, 28% of incident ultraviolet-A radiation (UV-A, 320-400 nm) and 13% of incident photosynthetically available radiation (PAR, 400 to 700 nm) on a sunny summer day at noon (Nozais et al. 1999). Two or 3 UV-B lamps (model XX15B, Spectronics Corporation) were used for LUV-B and HUV-B treatments, respectively. To eliminate UV-C radiation (<280 nm), the emission spectrum from the lamps was filtered with an aged (1 h at 1 cm from the lamps) 0.13 mm cellulose acetate sheet (Cadillac Plastics) which was changed every day. Lamps were pre-burned for 100 h before the beginning of the experiment and were switched on 1 h before use each day in order to attain a constant emission spectrum and UV-B intensity during the experiment. The lamps, positioned 40 cm above the water surface, were switched on from 09:00 to 17:30 h every day. Similar shading conditions were created over NUV-B, LUV-B and HUV-B tanks by using wooden lamp replicates (Belzile et al. 1998). No wooden lamp replicate was installed over the WUV-B mesocosms because the Mylar sheet was already reducing incident irradiance.

Vertical profiles of PAR and UV irradiance in the water column of each mesocosm were measured with a PUV-500 radiometer (Biospherical Instruments). This radiometer measures the cosine-corrected down-
wellirradiance in the visible (PAR) and at 4 discrete
wavebands in the UV range (305, 320, 340 and
380 nm). The irradiance values measured at 305 nm
were multiplied by 2.6 to offset the underestimation
resulting from the lamp calibration method, as sug-
gested by Kirk et al. (1994). UV enhancements pro-
vided by the lamps just below the water surface at 305,
320, 340 and 380 nm averaged 5.62, 4.97, 2.08 and
0.09 μW cm⁻² nm⁻¹ for LUV-B and 8.22, 7.28, 3.04 and
0.13 μW cm⁻² nm⁻¹ for HUV-B (Belzile et al. 1998). Inci-
dent irradiance (PAR, UV-A, UV-B) was recorded
every 1 min with an IL-1700 radiometer (International Light) equipped with SUD033/PAR/QNSD1/W (PAR),
SUD033/UV-A/W (UV-A) and SUD240/SPS300/T/W
(UV-B) broadband and flat sensors. Only ca 40% of the
incident irradiance reached the surface of the meso-
coms, due to the shading created by the tank walls,
the lamps and the lamp dummies. UV-B radiation was
rapidly attenuated within the mesocosms (mean
depths of 1% surface irradiance at 305, 320, 340 and
380 nm were 0.9, 0.93, 1.1 and 1.6 m, respectively)
while 4% of the surface PAR reached the bottom of the
tanks. The NUV-B treatment served as the control.
Additional details on the experimental setup and light
measurements are given in Belzile et al. (1998).

Sampling and biochemical analyses. Twice a day
(09:00 and 13:00 h), water was sampled 15 cm below
the water surface to estimate nutrient concentrations
(NO₃⁻+NO₂⁻, NO₂⁻, NH₄⁺, urea, Si(OH)₄) and carbon and
nitrogen transport rates. Water for nutrient analysis
was filtered onto pre-combusted Whatman GF/F fil-
ters. Analyses were performed either immediately for
ammonium using the method of Solórzano (1969) de-
scribed in Parsons et al. (1984), or within 1 mo on the
frozen filtrate with a Perstorp FS III Autoanalyzer (Alp-
kem, O.I. Analytical) for nitrate, nitrite and silicate and a
Technicon Autoanalyzer for urea (Price & Harrison
1987).

Carbon and nitrogen uptake rates were estimated
using the tracer method of Dugdale & Wilkerson
(1986). For each sampling time, 3 polyethylene bags
(Whirlpak) containing 250 ml water were inoculated
with trace additions of both ¹³C (NaH¹³CO₃) and ¹⁵N
isotopes (³²Kr¹⁵NO₃, ¹⁵N-urea or (¹⁵NH₄)₂SO₄). Final con-
centrations were 0.1 mM (¹³C), 0.1 μM (¹⁵NO₃ or ¹⁵NH₄) and
0.05 μM (¹⁵N-urea). Samples were then incubated in the middle of the corresponding mesocosm, just
below the water surface. After a 4 h incubation, each
sample was filtered on a precombusted Whatman
GF/F filter. Analyses were performed on desiccated fil-
ters (24 h at 60°C) with a tracermass spectrometer
(Europa Scientific) which measures the abundance of
¹³C and ¹⁵N, and the particulate organic carbon (POC)
and nitrogen (PON). Carbon and nitrogen specific
transport rates were calculated according to Eq. (2) in
Dugdale & Wilkerson (1986) using a concentration of
the label (in atom%) in the particulate fraction at time
0 of 1.11% for ¹³C and 0.365% for ¹⁵N. They were mul-
tplied by POC or PON concentration to obtain carbon
and nitrogen transport rates. The temporal variations
of nitrate, ammonium and urea uptake rates are de-
described in detail in Fauchot et al. (2000). In the pre-
sent study, nitrate, ammonium and urea transport rates
were summed to obtain total nitrogen transport rates.
On the afternoon of Day 3, the ¹³C concentration added
to the samples was uncertain and the absolute ¹³C
transport rate was not reliable. However, as this uncer-
tainty was identical in all mesocosms, the relative
transport rate could still be computed.

Water for chlorophyll a (chl a) determination was
sampled 5 or 6 times a day (09:00, 13:00, 17:00, 21:00,
01:00, and 05:00 h) for the first 4 d, then 3 times a day
day thereafter (09:00, 13:00 and 17:00 h). Samples were fil-
tered onto Whatman GF/F filters which were kept
frozen until 24 h extraction in 90% acetone at 4°C.
Concentrations were then determined fluorometrically
(Parsons et al. 1984). Enumeration and identification
of phytoplankton cells >3 μm were made on samples
collected at 09:00 h on Days 1, 2, 4, 5 and 7 (Villegas
1999) using the Utermöhl technique (Lund et al. 1958). Sam-
plest were kept in acidic Lugol (Thordsen 1978) until
analysis.

Statistical procedure. To compare the biological
effects of UV-B radiation, 1-way analyses of variance
(ANOVA) were performed for each sampling time with
UV-B treatment as the grouping factor. A multiple
comparison test of means (Least Significant Difference
(09:00, 13:00, 17:00, 21:00, 01:00, and 05:00 h) for the first 4 d, then 3 times a day
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Statistical procedure. To compare the biological
effects of UV-B radiation, 1-way analyses of variance
(ANOVA) were performed for each sampling time with
UV-B treatment as the grouping factor. A multiple
comparison test of means (Least Significant Difference
test) was used when significant differences were found
between treatments (Zar 1984). This test identifies
which treatment differs significantly among the 4
experimental conditions.

RESULTS

Light measurements

Total daily incident irradiance ranged from 7.1 to 49 E
m⁻², with minimal values between Days 3 and 5 due to
overcast skies (Fig. 1a). Daily incident values of UV-B,
UV-A and PAR varied from 6 to 34 kJ m⁻², 168 to
928 kJ m⁻² and 6.5 to 46 E m⁻², respectively. Under
cloudy skies, the proportion of incident UV-A relative
to the total incident irradiance increased while the rela-
tive value of incident UV-B was less affected by the
cloud cover (Fig. 1b). During the overcast period, the
ratio of total ultraviolet radiation (UV-A + UV-B) to total
incident irradiance was more than 7%. It is also worth
noting that the 2 enhanced UV-B mesocosms received a
higher proportion of UV-B radiation (averaged over the
Sampling day

Fig. 1. Temporal variations of (a) total daily incident radiation (PAR + UV-A + UV-B) and (b) the ratios of daily incident UV-A (left scale) and UV-B (right scale) to total daily incident radiation. Incident irradiance was measured with an IL-1700 radiometer and ratios were calculated from data transformed to E \( m^{-2} \cdot d^{-1} \).

water column) during the overcast period (>50%) than during the sunny period (<20%) as the UV-B provided by the lamps was constant throughout the entire experiment, independent of natural radiation.

Nutrients, chlorophyll \(a\) and phytoplankton composition

Since no effect of the UV-B treatments was apparent on ambient inorganic and organic nitrogen concentrations, a daily average for all tanks was computed. Nitrate concentrations decreased abruptly during the first 3 d of the experiment and then remained nearly undetectable thereafter (Fig. 2a). The pattern for ambient ammonium concentrations in contrast showed no definite trend and varied between 0.1 and 0.3 \( \mu M \) (Fig. 2b). Urea concentrations decreased from 0.8 \( \mu M \) to 0.4 \( \mu M \) throughout the experiment with slightly higher values on Days 4 and 5 (Fig. 2c). Silicate concentrations decreased from 10 \( \mu M \) on Day 1 to ca 1 \( \mu M \) on Day 4 in all treatments (Fig. 2d). These concentrations continued to decrease in the NUV-B, WUV-B and LUV-B treatments but remained more or less constant in the HUV-B mesocosms. During the last 3 d of the experiment, the concentrations of silicate were significantly (\( p < 0.05 \)) higher in the HUV-B mesocosms than in the NUV-B mesocosms (Fig. 2d).

From Days 1 to 3, chl \(a\) biomass increased from ca 5 \( \mu g \cdot l^{-1} \) to ca 19 \( \mu g \cdot l^{-1} \) in all treatments (Fig. 3). Algal biomass started to decrease at the end of Day 4 reaching ca 12 \( \mu g \cdot l^{-1} \) at the end of the experiment. From Days 5 to 7, phytoplankton biomass seemed to be more affected by reduced UV-B than by enhanced or natural UV-B. During the last 2 d, chl \(a\) biomass was significantly (\( p < 0.05 \)) lower under reduced UV-B treatment than that under natural or enhanced treatments.

Phytoplankton including diatoms (mainly 10–15 \( \mu m \) Chaetoceros spp. and 13–18 \( \mu m \) Thalassiosira spp.), dinoflagellates (mainly 8–10 \( \mu m \) Katodinium spp.,

Fig. 2. Temporal variations in (a) nitrate, (b) ammonium, (c) urea and (d) silicate concentrations. Averages between the 8 mesocosms are computed for nitrogen nutrients while silicate concentrations are described for each tank. Average and standard deviation are shown.
10–12 μm Heterocapsa spp. and 5–15 μm Prorocentrum spp.) and flagellates (mainly the 5.5–8.0 μm cryptophyte Plagioselmis spp. and the 6.0–9.0 μm prymnesiophyte Prymnesium spp.) started to increase after Day 2 in the 4 treatments (Fig. 4). Under enhanced and natural UV-B radiation, diatom abundances increased from 0.5 × 10^6 to ca 3.4 × 10^6 cells l^-1 during the first 4 d. On Day 5, their abundances under LUV-B (2.4 × 10^6 cells l^-1) and HUV-B (1.7 × 10^6 cells l^-1) were significantly lower (p < 0.05) than under natural or reduced UV-B (3.4 × 10^6 and 4.2 × 10^6 cells l^-1, respectively). At the end of the experiment, diatoms in the WUV-B, LUV-B and HUV-B treatments were significantly lower in abundance (p < 0.05) than under natural conditions (Fig. 4a). Dinoflagellates, the less abundant group, ranged from 0.1 × 10^6 cells l^-1 on Day 1 to ca 0.9 × 10^6 cells l^-1 on Day 4, and then remained relatively constant until the end of the experiment (Fig. 4b). The abundance of flagellates increased continuously from ca 0.38 × 10^6 cells l^-1 on Day 1 to 5 × 10^6 cells l^-1 on Day 7 in all the mesocosms (Fig. 4c). Throughout the experiment, no statistically significant (p < 0.05) effect of UV-B treatments was observed on dinoflagellate and flagellate abundances. Under enhanced UV-B, the phytoplankton assemblage was dominated by diatoms (>55% of the total abundance) during the first 4 d and by naked flagellates and dinoflagellates (>63% of the total abundance) for the remainder of the experiment. This change in species composition was not distinguishable in the mesocosm under natural UV-B radiation, where diatoms and flagellates represented an equal proportion (ca 50% of the total abundance) of the phytoplankton assemblage during the whole experiment.

**Temporal variations of carbon transport rates**

The overall pattern of ^13^C transport rates (Fig. 5a) was almost similar for the 4 treatments, with increasing values from Day 1 (ca 30 μg C l^-1 h^-1) to attain a maximum value on Day 4 (ca 80 μg C l^-1 h^-1) and then, rapidly decreasing towards the end of the experiment to values ca 15 μg C l^-1 h^-1. From Days 1 to 4, differences between the treatments were small, except on Day 3 A.M., when rates in the HUV-B treatment were significantly (p < 0.05) lower than the other treatments. From Day 4 onwards, neither enhanced nor reduced UV-B radiation treatments had a deleterious effect on ^13^C transport rates, except on Day 5 when enhanced UV-B treatments significantly (p < 0.05) reduced uptake rates as compared to NUV-B conditions. On Days 2, 6 and 7, transport rates estimated in the afternoon were slightly higher than those in the morning, especially within the LUV-B and HUV-B samples.
In order to estimate the potential ability of a given phytoplankton biomass to fix dissolved inorganic carbon, the chl a specific carbon transport rate was calculated as the ratio of the carbon transport rate per unit of chl a. This ratio remained close to 3.5 μg C μg chl a⁻¹ h⁻¹ for the first 5 d of the experiment except in the WUV-B mesocosms where values ranged between 5 and 6 μg C μg chl a⁻¹ h⁻¹ on Days 1 and 2 (Fig. 5b). Afterwards, the ratio decreased to ca 3 μg C μg chl a⁻¹ h⁻¹ in the NUV-B and WUV-B treatments and to ca 2 μg C μg chl a⁻¹ h⁻¹ in the LUV-B and HUV-B treatments (Fig. 5b). The deleterious effect of enhanced UV-B was clearly visible on Days 5 and 7, when rates in the LUV-B and HUV-B treatments were significantly (p < 0.05) lower than in the other treatments.

The relative chl a specific carbon transport rates with respect to the NUV-B treatment (control) are presented in Fig. 5c. Ratio >1 indicates that photosynthesis was stimulated by the UV-B treatment whereas a ratio <1 indicates that photoinhibition occurred. Values were generally >1 for the WUV-B treatment while those for enhanced UV-B treatments remained below 1 after Day 2 A.M. in the HUV-B treatment, and after Day 3 P.M. in the LUV-B treatment (Fig. 5c).

### Temporal variations of total nitrogen transport rates

In all treatments, total ¹⁵N transport rates peaked on Day 2 P.M., except for WUV-B, and then decreased to values similar to those measured on Day 1 (Fig. 6a). Under HUV-B, ¹⁵N transport rates were significantly lower (p < 0.05) than the other treatments on Days 1, 3 A.M., 4 A.M., 5, 6 P.M. and 7. In the LUV-B mesocosms, ¹⁵N transport rates on Days 4 A.M., 5 P.M., 6 P.M. and 7 A.M. were also significantly lower (p <0.05) than under NUV-B and WUV-B treatments. As compared to natural radiation, reducing UV-B significantly stimulated (p < 0.05) nitrogen metabolism on the morning of Days 2, 5 and 7.

Chl a specific nitrogen transport rates (nitrogen uptake per unit of chl a) varied from 0.01 to 1.3 μg N μg chl a⁻¹ h⁻¹ (Fig. 6b). On Days 1, 2, 6 P.M. and 7, the chl a specific nitrogen transport rates under reduced UV-B were significantly (p < 0.05) higher than those measured in the other treatments.

Relative to the NUV-B sample, chl a specific nitrogen transport rates were generally higher (ratio >1) in the WUV-B treatment and were lower (ratio <1) for HUV-B treated samples (Fig. 6c). Relative values for the LUV-B treatment varied between 0.5 and 1.3, ranging between the values observed in the WUV-B and HUV-B treatments.

### Percent change in carbon and nitrogen transport rates

To estimate the effect of UV-B treatments on carbon and nitrogen transport rates, we compared transport rates (p) under reduced and enhanced UV-B against those under natural UV-B (control) by calculating the \(\frac{p_{\text{treatment}} - p_{\text{control}}}{p_{\text{control}}}\) ratio. The percent change for carbon transport rates generally decreased throughout the experiment in each treatment, the variations depending on the treatment and the time of sampling (Fig. 7a, b). In the morning samples, a negative effect appeared from Day 4 to the end of the experiment in all treatments whereas, in the afternoon period, it started on Day 1 under HUV-B treatment and on Day 3...
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Temporal variations in the ratios of carbon to nitrogen transport rates and of POC to PON

Similar trends were observed between the control and treatments for the ratios of carbon to nitrogen transport rates and of POC to PON (Fig. 8a, b). During the first 5 d of the experiment, the ratios of carbon to nitrogen transport rates varied between ca 7 and ca 40 μg-at C (μg-at N⁻¹), with maximum values on Days 1 A.M., 3 A.M., 4 A.M. and 5 P.M. (Fig. 8a). Thereafter, they decreased to reach ca 2 μg-at C μg-at N⁻¹ on Day 7. In the HUV-B and WUV-B treatments, the C:N uptake ratio was significantly (p < 0.05) different from the other treatments on Days 1 A.M. and 7 P.M., respectively.

POC:PON atomic ratios decreased from ca 7 on Day 1 to ca 5 on the afternoon of Day 3. Then, values started to increase up to ca 8.5 on Day 7 (Fig. 8b). During the first 4 d of the experiment, there was no significant difference in the POC:PON ratio between treatments. However later on, this ratio was slightly but significantly (p < 0.05) lower in the HUV-B (Days 5, 6 A.M. and 7 A.M.), LUV-B (Day 7 A.M.) and WUV-B (Day 7) treatments than under NUV-B experimental conditions.

DISCUSSION

Experimental conditions

UV-B radiation reaching the Earth's surface is considered a natural stress for aquatic organisms (Behrenfeld et al. 1994). This study provides the first results of the effects of UV-B radiation on the simultaneous transport rates of dissolved inorganic carbon and total dissolved nitrogen (i.e. nitrate + ammonium + urea) by phytoplankton estimated with stable isotopes (¹³C and ¹⁵N). This study also represents the first such attempt on natural phytoplankton communities, as opposed to those conducted with laboratory cultures under totally artificial illumination conditions. In our study, a natural planktonic community, maintained in large volume mesocosms filled with water from the St. Lawrence Estuary, was subjected to different UV-B radiation regimes. This setup helped overcome constraints induced by laboratory studies (e.g., small volumes and time scales, culture media, artificial solar radiation). Consequently, the results of the present study are expected to more closely resemble field conditions.

Light attenuation in the water column of the mesocosm adequately reproduced that observed in the estuarine water column. In July, 1% of the surface PAR reached a depth of ca 5 m in the St. Lawrence Estuary (Levasseur et al. 1984) whereas in our experiment, the
bottom of the mesocosm received 4% of incident PAR, the 1% depth being estimated at ca 3.1 m (Belzile et al. 1998). Attenuation of UV-B radiation in the mesocosms occurred rapidly, with 1% depth at ca 1 m. In the enhanced treatments, UV-B radiation levels were somewhat higher than those associated with the ozone depletion over Antarctica (see Belzile et al. 1998, Mostajir et al. 1999b).

**Nutrients and phytoplankton composition**

Summer growth of phytoplankton takes place from June to September in the St. Lawrence Estuary, with maximal values of algal biomass and primary production generally in July (Levasseur et al. 1984, Sime-Ngando et al. 1995, Roy et al. 1996). Diatom growth at this time of the year is sustained by the high concentrations of nitrate and silicate. With the exhaustion of nitrate and silicate in the euphotic layer, diatom numbers decrease and flagellates become the dominant algal group (Levasseur et al. 1984). In all treatments examined in this study, changes in phytoplankton community structure and ambient nutrient concentrations did not differ from this general trend (Figs. 2 & 4). However, the response of the algal community (in terms of cell numbers) differed according to the treatment. From Days 5 to 7, reduced UV-B affected chl a biomass while enhanced UV-B influenced phytoplankton productivity, abundance and species composition (Figs. 3, 4 & 5a). At the end of the experiment, diatom (>10 μm) numbers were lower under reduced and enhanced UV-B relative to natural conditions while the abundances of dinoflagellates (5–15 μm) and naked flagellates (5–10 μm) were not affected by the UV-B.
treatments. Since nitrate, ammonium and urea concentrations were similar in all treatments, these changes were not induced by nitrogen nutrients (Fig. 2a–c). Hence, we can reasonably postulate that these effects on community structure of phytoplankton were directly induced by UV-B or indirectly via predation (Mostajir et al. 1999a) and not by a bottom-up control by nutrients (sensu McQueen et al. 1986). Thus, in the HUV-B treatment, where the lowest diatom abundance was reached in spite of silicate availability, the stress induced by UV-B radiation on diatom growth appears to have been strong enough to prevent the consumption of silicate.

Since phytoplankton sensitivity to UV radiation varies among species and taxonomic groups, increases in surface UV-B radiation resulting from ozone depletion could induce changes in the phytoplankton community structure, as postulated by Jokiel & York (1984), Karentz et al. (1991a), Vincent & Roy (1993) and Santos et al. (1998). During this study, a shift from a community dominated by diatoms (>10 µm) to a community dominated by small naked flagellates (5 to 10 µm) occurred more rapidly under enhanced UV-B than under natural UV-B radiation. This could have major implications for the transfer of carbon as the size of primary producers determines (1) the type and dynamics of trophic pathways and hence the number of trophic levels towards large metazoans and (2) the rate of carbon fixation and its potential sequestration (e.g. Keller et al. 1997, Legendre & Michaud 1998, Mostajir et al. 2000).

Influence of UV-B on carbon transport rates

An extensive literature describes the negative effects of UV-B radiation on photosynthesis (Steeman-Nielsen 1964, Lorenzen 1979, Smith et al. 1980, 1992, Jokiel & York 1984, Maske 1984, Helbling et al. 1992, Behrenfeld et al. 1993, Lesser et al. 1994, Villafañe et al. 1995, Figueroa et al. 1997). In this study, significant changes in phytoplankton productivity were observed throughout the experiment, of which some were associated with a UV-B induced alteration of the phytoplankton assemblage. The chlorophyll a specific carbon transport rate was lower during the last 2 d of the experiment, reflecting the lower photosynthetic performance of the phytoplankton assemblage at the end of the experiment (Fig. 5b). Although this reduction of photosynthetic performance may have resulted from an excess of irradiance or a nutrient limitation in the mesocosms on Days 6 and 7, the lowest values were observed within the enhanced UV-B mesocosms and the highest within the WUV-B mesocosm. As shown by the relative chlorophyll a specific carbon transport rate, the enhancement of UV-B was generally detrimental for photosynthesis while the reduction of UV-B was generally beneficial for photosynthesis (Fig. 5c). Low values of the relative chlorophyll a specific carbon transport rate appeared sooner in HUV-B than in LUV-B, suggesting that both the UV-B dose and the duration of exposure influence the carbon metabolism of the phytoplankton community.

Although carbon productivity was generally highest in the WUV-B treatment, the chlorophyll a concentration was lower than in the other treatments during the last 2 d of the experiment (Figs. 2 & 5b,c). Low algal biomass associated with high primary production per biomass unit may be indicative of a high grazing rate. In support of this hypothesis, Mostajir et al. (1999a) showed higher ciliate abundance (15–35 µm) under reduced UV-B treatment compared to natural conditions during the last 2 d of this experiment. This, in turn, induced a decrease in the abundances of bacteria, heterotrophic flagellates (2–10 µm) and small phytoplankton (<5 µm) due to a higher grazing pressure exerted by the ciliates. Hence, the decrease in chlorophyll a may be explained by increased ciliate grazing on small photosynthetic algae. In contrast to the reduced UV-B treatment, a shift in the trophic structure from a herbivorous food web towards a microbial food web (bacteria, auto- and heterotrophic flagellates) occurred under enhanced UV-B (Mostajir et al. 1999a). Even within a microbial community, UV can alter the balance between autotrophic and heterotrophic processes (Bergeron & Vincent 1997). Hence, changes in UV radiation may not only influence phytoplankton productivity and composition but also the fate of algal biomass.

In this study, the ratio of UV-B to total incident radiation was altered by the use of an artificial light source. The enhanced UV-B treatments received a higher proportion of UV-B radiation than the other treatments, especially during the cloudy period (Days 3 to 5) when incident irradiance was low. Variations in carbon and nitrogen transport rates were not correlated with these changes in the ratio of UV-B to total incident irradiance. These results contrast from those of Smith et al. (1992) who concluded that inhibition of photosynthesis increased linearly with the ratio of UV-B to total radiation. However, their study was conducted under different conditions in the marginal ice zone of the Bellingshausen Sea in the austral spring when the O2 layer was thinning. During their experiment, the vernal phytoplankton community was dominated by the prymnesiophyte *Phaeocystis* spp. while in our study, the summer algal community was composed of a mixed assemblage of diatoms, dinoflagellates and naked flagellates with different UV sensitivity.
The potential short-term effect of UV-B radiation was estimated by sampling each treatment in the morning and in the afternoon. The carbon transport rate was often slightly higher in the afternoon than in the morning, despite the higher cumulative dose of UV received by the algae. This result indicates that phytoplankton has the ability to develop photoprotective mechanisms against UV irradiance on a daytime scale. Several adaptive strategies have been developed to protect the photosynthetic system from UV radiation (Karentz et al. 1994, Helbling et al. 1996a, Roy 2000). One of them is the synthesis of biological compounds which absorb in the UV wavelengths. Mycosporine-like amino acids (MAAs; Karentz et al. 1991b) and photoprotective pigments are examples of natural UV screens (Vincent & Roy 1993). If their cellular concentrations increase under UV-B stress, photoprotection should be enhanced. In our study, enhanced UV-B induced both the synthesis of MAAs and an increase in total carotenoids relative to total chlorophylls from Days 4 to 7 (K. Walsh & S.R. unpubl.) suggesting progressively increased photoprotection. However, no clear trends were observed between morning and afternoon samples. Other photoprotective measures (e.g. DNA repair) may also be active, which could explain the differences observed here throughout the day.

Influence of UV-B on total nitrogen uptake

As with carbon, UV-B radiation is also known to negatively impact nitrogen transport in phytoplankton (Döhler et al. 1987, Döhler 1992, 1997, Behrenfeld et al. 1995, Lohmann et al. 1998). During our study, reduced and enhanced UV-B treatments generally influenced the chl a specific transport rates of dissolved inorganic carbon and total dissolved nitrogen in approximately the same proportion, as compared to the natural conditions. Hence, the ratios of carbon to total nitrogen transport rates were not significantly affected by the different UV-B treatments. However, the ratio was generally higher than the 6.6 atomic ratio of Redfield et al. (1963) and varied significantly throughout the experiment. A part of this variability seems to be associated with changes in the incident irradiance. Indeed, this ratio was lower during the sunny days (at the beginning and at the end of the experiment) than during the cloudy days in the middle of the experiment. The variability of the ratio of carbon to total nitrogen transport rates may also be partly explained by major changes in the nitrogen sources (from nitrate to ammonium and urea; Fauchot et al. 2000) and the dominant algal groups (from diatoms to flagellates) which occurred during the study. The C:N transport ratio decreased during the 2 sunny day periods; during the first period (Days 1 and 2), a diatom-dominated community was actively using nitrate whereas during the second period (Days 6 and 7), a flagellate-dominated community was using mainly urea (Fauchot et al. 2000). Hence, the imbalance between C and N assimilation could be associated with changes in the incident irradiance, in the nitrogen sources and/or in the composition of the algal community.

As observed for the carbon to nitrogen assimilation ratio, the POC:PON ratio was also not strongly affected by the different UV-B treatments (Fig. 8b). This ratio was however higher than the Redfield atomic ratio (C:N = 6.6:1) during the last 2 d of the experiment, suggesting that the phytoplankton community was nutrient-limited. This increase in the POC:PON ratio may also be related to the resuspension of senescent cells from the earlier diatom bloom period (Days 1 to 3) due to the vertical mixing by the pump.

CONCLUSIONS

The results from this experiment show that enhanced UV-B radiation adversely affects the transport of carbon and nitrogen in phytoplankton when compared to reduced and natural UV-B. Since the rates of carbon and nitrogen uptake were affected in the same proportion by enhanced or reduced UV-B, very little differences in the C:N transport ratio and POC:PON ratio were detected between treatments. Although UV-B radiation impaired phytoplankton, nighttime repair processes possibly took place since nitrogen transport rates did not decline throughout the study. Furthermore, photoprotective mechanisms seemed to develop during the day since afternoon carbon transport rates were slightly higher than morning ones. The enhanced and reduced UV-B treatments also modified the structure of the phytoplankton community. At the end of the experiment, the diatom (>10 µm) abundance was lower under reduced and enhanced UV-B while abundances of dinoflagellates (5–15 µm) and naked flagellates (5–10 µm) were not affected by the UV-B treatments. The effect of UV-B on the phytoplankton community structure and their carbon and nitrogen transport rates may thus have broad implications for estuarine ecosystems and may seriously alter the transfer of matter within the pelagic food web.

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