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Ultraviolet radiation negatively affects growth but not food quality of arctic diatoms

Eva Leu[1]
Department of Biology, University of Oslo, P.O. Box 1066, N-0316 Oslo, Norway; Norwegian Polar Institute, N-9296 Tromsø, Norway

Stig Falk-Petersen
Norwegian Polar Institute, N-9296 Tromsø, Norway; Norwegian Colloge of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway

Dag O. Hessen
Department of Biology, University of Oslo, P.O. Box 1066, N-0316 Oslo, Norway

Abstract

We studied the short-term effects of ultraviolet radiation (UV radiation, 280–400 nm) on the fatty acid composition and cellular stoichiometry of three dominant arctic diatom species (*Thalassiosira antarctica* var. *borealis, Chaetoceros socialis, Bacterosira bathyomphala*) in laboratory experiments. Photosynthetic efficiency during UV irradiation was inhibited 90%, which led to a substantial reduction in biomass. In contrast to results of previous studies, the percentage of total polyunsaturated fatty acids (PUFAs) did not decrease during UV exposure. Instead, the two major PUFAs, 16:4(n-1) and 20:5(n-3), of *B. bathyomphala* increased, and the PUFA content of *T. antarctica* and *C. socialis* did not change significantly. However, the monounsaturated fatty acid 16:1(n-7) content in all three species substantially decreased during UV radiation. Since high concentrations of 16:1(n-7) are usually associated with exponential growth under favorable conditions, UV radiation probably did not affect a specific type of fatty acid directly; the fatty acid profile rather reflected a general deterioration in the algal physiological state. The nutritional quality of the fatty acids did not decrease during UV exposure; the C : P and N : P ratios decreased by 50% in all species, whereas the C : N ratios increased slightly in two species. Our results indicate that UV radiation has strong negative effects on photosynthesis and biomass production, but not on food quality with regard to PUFAs and stoichiometry.

In high latitudes, the stratospheric ozone layer changes seasonally and reaches a minimum in early spring. The ozone layer in polar regions has increasingly been depleted for more than two decades because of the release of chlorofluorocarbons (CFCs). The effective bans on CFCs set forth by the Montreal Protocol will not protect the stratospheric ozone layer in the decades to come, partly owing to the long life of CFCs in the atmosphere and partly because several countries have refused to sign any treaties pertaining to CFCs. Ozone degradation is also enhanced by decreased stratospheric temperatures, caused in part by tropospheric warming and by ultraviolet (UV) radiation (280–400 nm) in concert. The greatest risk for ozone depletion in polar regions is therefore during springtime. In early spring 2005, the ozone levels above the Arctic were the lowest ever recorded, which caused unusually high levels of UVB radiation (280–320 nm).

UV radiation affects phytoplankton in many ways (for an overview, *see*, e.g., Vincent and Neale 2000). Apart from inhibiting photosynthesis, it damages deoxyribonucleic acid (DNA), affects community structure because of interspecific differences in UV sensitivity, and changes cell wall morphology and cellular stoichiometry, i.e., the relative abundances of the elements carbon (C), nitrogen (N), and phosphorus (P). Changes in the polyunsaturated fatty acids (PUFAs) and in the cellular stoichiometry affect the nutritional quality and the digestibility by zooplankton. Both these properties show a considerable plasticity in primary producers, they are substantially influenced by abiotic factors, and they are instrumental for animal nutrition. Since phytoplankton lie at the base of the food web, changes in their nutritional quality have consequences for the entire ecosystem.

PUFAs are essential metabolites, i.e., they cannot be synthesized de novo in sufficient amounts by consumers but have to be taken up via their food (Sargent et al. 1995). PUFAs have important functions in regulating membrane fluidity, and, hence, they ensure the functioning of vital physiological processes. Some experimental studies have furthermore proven a positive correlation between long-chain PUFAs and the reproductive success of marine copepods (e.g., Arendt et al. 2005). High amounts of PUFAs and a high lipid content often characterize organisms in arctic ecosystems; these attributes are adaptations necessary to cope with low temperatures and extreme seasonality.

A few studies have shown the effect of UVB radiation on PUFAs in phytoplankton (Goes et al. 1994; Wang and

[1] Corresponding author (leu@npolar.no).

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Chai 1994; Skerratt et al. 1998). Despite considerable differences, the results all suggested a detrimental effect of UV radiation on the relative abundance of PUFAs either due to photo-oxidation of double bonds or a negative effect on PUFA synthesis. Interspecific differences in the reactions of phytoplankton species exposed to UVB radiation were observed by both Wang and Chai (1994) and Skerratt et al. (1998), but the exposure usually reduced the PUFA content.

The nutritional quality of phytoplankton is also affected by changes in cellular stoichiometry. The C, N, and P ratios are considerably more variable in autotrophs than in consumers, and C : P and C : N ratios are typically far lower in consumers. Hence, a mismatch between food ratios and consumer demands might lead to reduced growth because of an inadequate availability of N or P relative to C, i.e., an excess of C (Anderson and Hessen 1995; Sterner and Elser 2002). A key determinant of the phytoplankton C : P ratio is irradiance, notably photosynthetic active radiation (PAR, 400–700 nm) (Urabe and Sterner 1996; Hessen et al. 2002) because high PAR causes a disproportionately high uptake of C relative to P. UV radiation affects the cellular stoichiometry of autotrophs in different ways. The C : N ratios of phytoplankton are only moderately or not at all affected (Fauchot et al. 2000; Mousseau et al. 2000), probably owing to a simultaneous inhibition of photosynthetic carbon fixation and nitrogen uptake. C : P ratios, however, decrease during UV exposure compared to controls (Xenopoulos et al. 2002; Tank et al. 2003; Leu et al. 2006*a*) because of either enhanced C and N uptake in the UV-shielded controls or increased P uptake during UV irradiation.

Since nutrient limitation also reduces the amount of PUFAs (Reitan et al. 1994), even interactions between the two indicators of food quality, PUFAs and cellular stoichiometry, are likely. The overall impact of UV radiation on phytoplankton food quality is thus not very clear.

In the high Arctic, organisms are commonly exposed to rapid fluctuations in UV radiation caused by shifts in meteorological conditions, mixing regimes in the water column, or shifts in ice cover. Here, we investigated the short-term effects of UV radiation on PUFAs and the cellular stoichiometry of three dominant diatom species in the Arctic (*Thalassiosira antarctica* var. *borealis, Chaetoceros socialis, Bacterosira bathyomphala*). In addition, we measured the photosynthetic efficiency during UV exposure and after recovery to determine the extent of inhibition and the recovery potential of photosynthetic carbon fixation.

Materials and methods

Cultures and experimental setup—The experiments were carried out with unialgal cultures of the diatom species *Thalassiosira antarctica* var. *borealis, Bacterosira bathyomphala*, and *Chaetoceros socialis*. Monocultures were isolated at the Norwegian College of Fishery Sciences in Tromsø, Norway, from germinating resting spores contained in bottom (60 m) surface sediments collected in May 2001 in subarctic Austnesfjorden (Lofoten). The diatoms were cultured prior to the start of the experiment in f/2 medium (Guillard 1975) at 3°C and an irradiance of 170 μmol m^{-2} s^{-1}, provided by fluorescent tubes (OSRAM Lumilux de luxe 36W/950 daylight) under a 16 h:8 h light : dark (LD) cycle. Photosynthetically active radiation (PAR) was measured with a 4π sensor (QSL-100, Biospherical Instruments). During the experiment, irradiation was provided by three daylight fluorescent tubes (same as above) and two Q-Panel UVA-340 fluorescent tubes (Q-Panel Lab Products) mounted above the algal cultures. The UV spectrum of these light tubes closely resembles the solar spectrum between 280 and 350 nm (Bischof et al. 1998). The entire setup was covered with aluminium foil to provide a light field as homogeneous as possible. During the 56-h experiment, the diatoms were kept in quartz Erlenmeyer flasks and were exposed to UV radiation for 8 h daily on three consecutive days, starting 3 h after initiation of the light period. Two different treatments of four replicates each were applied: (1) PAR: no UV; shielded from UV radiation by an Ultraphan 400 foil (Digefra) and (2) UV: PAR + UV; covered with cellulose acetate foil (Tamboer & Co Chemie B.V.) to correct for the ~10% absorption of Ultraphan 400 in the PAR spectrum. Transmission spectra of the two different foils are shown in Fig. 1.

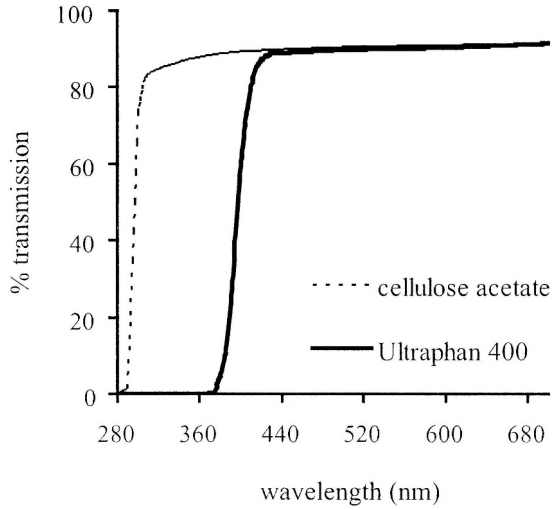

Fig. 1. Transmission spectra of cellulose acetate and Ultraphan 400 foil.

Intensities of the applied UVA (320–400 nm) and UVB (280–320 nm) radiation were measured with an IL 1400A radiometer (International Lights) equipped with an SUL 033 sensor (UVA) or an SPS 300 sensor (UVB). Since the SUL 033 sensor has no sharp cutoff at 320 nm, we used Mylar foil for measuring UVA intensities. The experiments were carried out with a maximum of two species at the same time, with two treatments of four replicates each, i.e., the experimental bench was set up with 16 algal cultures. Irradiance was measured at all 16 positions (UVA: 11.3 ± 0.6 W m^{-2}; UVB: 1.0 ± 0.06 W m^{-2}; mean ± standard deviation [SD]). The UVB irradiance was similar to noon values measured at the sea surface (in air) on a clear day in

May at 79°N (Svalbard); the UVA irradiance under such conditions is usually twice as high as the irradiance used in our study. Unweighted daily doses of UVB applied in this study (29 kJ m^{-2}) corresponded to the average ambient daily dose in May 2004 at Svalbard. The applied daily dose of UVA (324 kJ m^{-2}) was only about 25% of the corresponding field measurement (1200 kJ m^{-2}). Therefore, the applied UV should have been within a realistic range. The PAR was considerably lower (200 μmol m^{-2} s^{-1}) than under natural conditions. To ensure an exposure as equal as possible for all replicate cultures, the positions of the 16 flasks were exchanged randomly every day. The volume of algal culture in each quartz flask was 400 mL; the daily dilution at the end of the UV exposure was 0.25. Samples for determination of fatty acid composition, chlorophyll *a* (Chl *a*) concentration, and cellular stoichiometry were taken prior to the start of the UV irradiation period on the first day and at the end of the irradiation period on day 3. Samples for Chl *a* and fatty acid determinations were also taken immediately after the end of the daily UV irradiation on days 1 and 2.

Parameters analyzed—Algal biomass was analyzed as the concentrations of Chl *a* (daily) and particulate carbon (beginning and end of the experiment). For determination of Chl *a* concentrations, 5-mL samples were filtered on a glass-fiber GF/C filter and stored at −20°C until analysis, usually on the following day. The cells were extracted in 10 mL 90% acetone (v/v) for 4 h at room temperature in the dark. Chl *a* concentrations were then determined with a TD-700 fluorometer (Turner Designs).

To judge the effect of UV radiation on photosynthetic activity, the optimal quantum yield of photosystem II (PSII) was determined by measuring variable chlorophyll fluorescence of photosystem II with a pulse-amplitude modulation fluorometer (Water-PAM, Walz) coupled to a PC with WinControl software (Walz). In the middle of the daily UV irradiation period, the algal cultures were shaken, and a 3-mL aliquot was sampled. Fluorescence was measured in round quartz cuvettes at 0°C, according to a procedure modified after Hanelt (1998). Optimum quantum yield was calculated as the ratio of variable to maximum fluorescence (F_v/F_m) of dark-adapted algae. After application of a 5-s far-red pulse, the samples were kept in the dark in the cuvette for 3 min. The initial fluorescence F_0 (when all reaction centers of PSII are open) was measured by applying weak, red-light pulses, and F_m (when all PSII centers are closed) was determined under a strong, saturating light pulse (0.6 s). F_v was then calculated by $F_v = F_m - F_0$. Optimal quantum yield was also measured on the following morning, immediately before turning on the UV lights again, to determine the maximum recovery.

The nutritional quality of the phytoplankton was determined by measuring the elemental stoichiometry and fatty acid composition. For particulate C, N, and P analyses, samples (50 mL for CHN and 100 mL for P) were filtered on precombusted (3 h, 500°C) GF/C filters. For particulate P analysis, the filters were prewashed with HCl (0.1 mol L^{-1}), and the filters carrying the sample were placed in 15 mL distilled water acidified with 150 μL of 4 mol L^{-1} H_2SO_4 and oxidized with peroxodisulfate (0.15 g $K_2S_2O_8$) and autoclaved (121°C, 1 h). All samples were frozen (−20°C) until analysis. Particulate C and N were analyzed on a Thermo Finnigan FlashEA 1112 elemental analyzer. Particulate P was analyzed spectrophotometrically using the standard ammonium-molybdate method (Hessen et al. 2002).

For lipid analysis, 100 mL of each replicate was filtered onto GF/C filters prewashed with chloroform : methanol (2 : 1, v/v). Samples were stored in 8 mL chloroform : methanol (2 : 1, v/v) at −80°C until analysis. Total lipids were extracted according to the procedure described in Folch et al. (1957). Afterward, a known amount of the fatty acid 21 : 0 as internal standard was added, and the sample was trans-esterified with 1% sulfuric acid in methanol (Christie 1982). The extract was then cleaned using a silica column (Christie 1982). The percentage of fatty acid methyl esters (FAMEs) was determined using an Agilent 6890 N gas chromatograph equipped with a fused, silica-coated capillary column (50 m × 0.25 mm i.d., Varian Select FAME) with an Agilent 7683 injector and flame ionization detection. Hydrogen was used as carrier gas. A temperature gradient from 60°C to 150°C at 30°C min^{-1} and then to 230°C at 1.5°C min^{-1} was used. Individual components were identified by comparison with two known standards and were quantified using HPChemStation software (Hewlett-Packard). Results are expressed as the percent of the single peak area compared to the total peak area.

Statistical analysis—Effects of UV radiation on fatty acids, photosynthetic yield, and Chl *a* concentration were analyzed by one-way repeated measures analysis of variance (RM-ANOVA) with time as within effect (three levels: days 1–3), and two different treatments (PAR and UV) as between effect. All data were tested for homogeneity of variance using Levene's test, and for sphericity using Mauchley's test. Tukey's honestly significantly different (HSD) was used as a post-hoc test to identify which treatments differed significantly from each other. Variables measured only at the start and the end of the experiment (particulate C, N, P, and ratios calculated from them) were tested using the *t*-test. In cases where the assumptions for parametric statistical analysis were not met, a Mann-Whitney *U*-test was done. All analyses were performed with nontransformed data, using STATISTICA 7 (StatSoft Inc.).

Results

Biomass development—Algal biomass was measured as the Chl *a* and particulate C contents. These two parameters developed differently in the samples exposed to UV radiation. In the control cultures not exposed to UV radiation, the Chl *a* content increased to varying extents, whereas in all cultures exposed to UV radiation, the Chl *a* concentrations decreased significantly during the experiment (Fig. 2). The differences between the treatment and the control increased over time with all three species, as indicated by a significant time × treatment interaction ($p <$

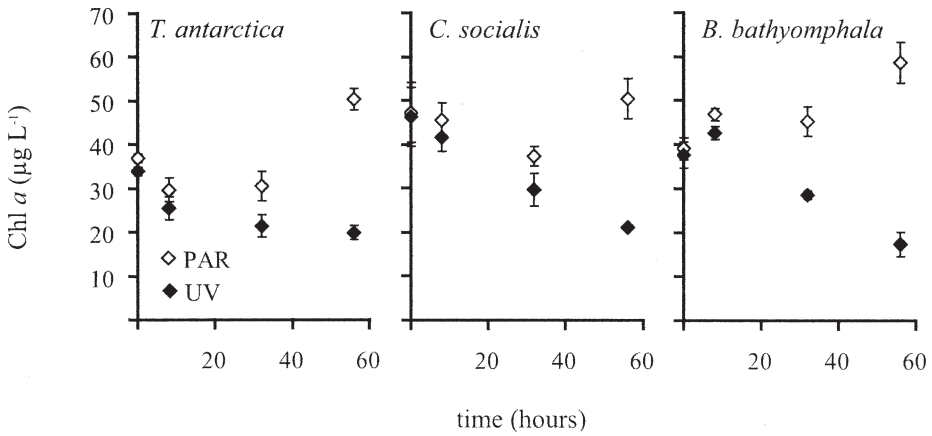

Fig. 2. Chl *a* concentrations in cultures of *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceros socialis* over the course of the experiment. Shown are means ± SD ($n = 4$); values are not corrected for the daily dilution of 0.25.

0.001) in the RM-ANOVA. In the controls of all three species, particulate C concentrations also increased during the 56-h experiment, from 1.5 to around 4 mg L^{-1}, despite the dilution rate of 0.25 d^{-1} (Table 1). In contrast to the results obtained for Chl *a*, the particulate C concentrations of the cultures of two of the species exposed to UV radiation increased slightly (from 1.5 to 1.9 mg L^{-1} in *T. antarctica*, and from 1.5 to 1.8 mg L^{-1} in *C. socialis*); in *B. bathyomphala*, the particulate C concentration decreased from 1.7 to 1.4 mg L^{-1} (Table 1). The average

Table 1. Concentrations and molar ratios of particulate carbon, nitrogen, and phosphorus in *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceros socialis*; shown are means ±SD (n=4; n=3 for t=0 samples of *T. antarctica* and *C. socialis*); t=0 are pre-incubation values, and t-values and significance levels (p) of t-tests between postincubation UV and postincubation PAR samples on day 3 (df=6) are also shown.

Thalassiosira antarctica					
	$t = 0$	PAR	UV	t-value	p
P (µg L^{-1})	64 ± 4	164±11	158±8	0.8	0.460
N (µg L^{-1})	290±64	910±63	419±24	14.4	0.000*
C (µg L^{-1})	1470±139	4057±165	1930±76	23.4	0.000*
C : N	6±1	5.2±0.2	5.4±0.1	−1.5	0.170
C : P	60±9	64±5	32±2	12.6	0.000*
N : P	10±3	12.4±1.3	5.9±0.4	9.6	0.000*
Chaetoceros socialis					
	$t = 0$	PAR	UV	t-value	p
P (µg L^{-1})	91±13	123±18	112±4	1.19	0.280
N (µg L^{-1})	274±63	777±50	311±25	16.76	0.000*
C (µg L^{-1})	1518±347	3935±375	1781±130	–	<0.05*†
C : N	6.5±0.1	5.9±0.2	6.7±0.1	–	<0.05*†
C : P	43±6	84±18	41±4	–	<0.05*†
N : P	6.6±0.9	14.3±2.7	6.1±0.6	5.86	0.000*
Bacterosira bathyomphala					
	$t = 0$	PAR	UV	t-value	p
P (µg L^{-1})	76±4	184±7	141±15	5.33	0.000*
N (µg L^{-1})	389±10	883±15	267±17	54.06	0.000*
C (µg L^{-1})	1747±21	4301±35	1418±71	73.33	0.000*
C : N	5.2±0.1	5.7±0.1	6.2±0.2	−4.46	0.000*
C : P	59±3	60±2	26±4	16.53	0.000*
N : P	11.3±0.7	10.6±0.5	4.2±0.6	16.16	0.000*

* Statistically significant differences between the two treatments.
† No t-test possible because of lack of homogeneity of variances. Shown are p-values from a nonparametric Mann-Whitney U-test.

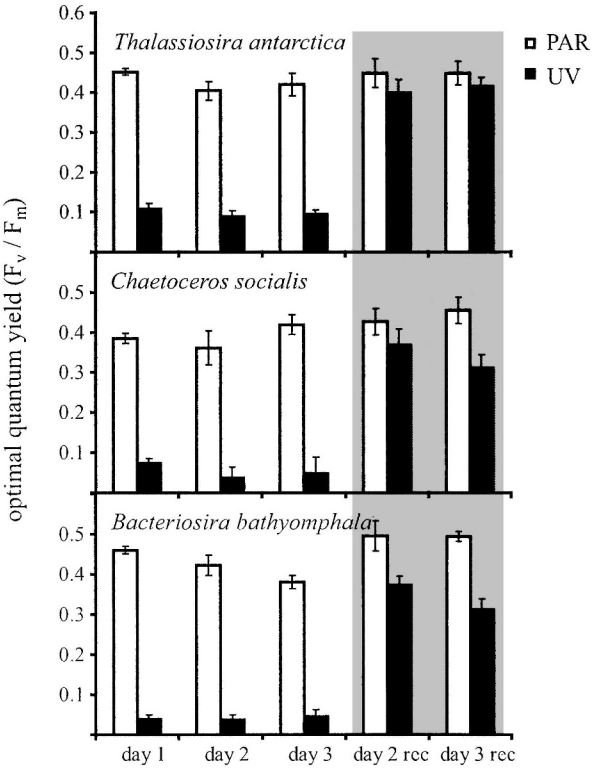

Fig. 3. Optimal quantum yield (F_v/F_m) measured in *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceros socialis* in the middle of the daily UV irradiation period. Recovery measurements were taken in the morning, immediately before the UV lights were switched on. Shown are means ± SD ($n = 4$).

growth rates of the controls calculated from particulate C concentrations were 0.68 ± 0.05 d^{-1} (mean ± SD, $n = 4$) for *T. antarctica*, 0.67 ± 0.11 d^{-1} for *C. socialis*, and 0.63 ± 0.01 d^{-1} for *B. bathyomphala*. UV radiation led to a 50% decrease in the growth rates of *T. antarctica* and *C. socialis* (0.33 ± 0.02 and 0.30 ± 0.13 d^{-1}, respectively), while the growth rate of *B. bathyomphala* decreased to 0.16 ± 0.03 d^{-1}.

Photosynthetic efficiency—UV radiation strongly and negatively affected the optimal quantum yield of PSII (F_v/F_m), but the recovery potential was high. Interspecific differences in sensitivity were detected. The F_v/F_m value of the control samples of all three species was between 0.4 and 0.5 and did not show a clear trend over time (Fig. 3). Photosynthetic efficiency measured in the cultures exposed to UV radiation in the middle of the daily irradiation period decreased by 76–91% (all species: RM-ANOVA, treatment: $p < 0.001$), and *T. antarctica* was least affected. The algal cultures recovered considerably from the exposure to UV, as indicated by the yield measurements taken on the following morning before the start of the next exposure. *T. antarctica* exhibited F_v/F_m values corresponding to 90% of the control, *C. socialis* had values corresponding to 86% and 68% of the control on days 2 and 3, respectively, and *B. bathyomphala* had values corresponding to 75% and 63% of the control on days 2 and 3, respectively. In all cases, however, UV irradiation caused reductions (RM-ANOVA, treatment: $p < 0.05$ for *T. antarctica*, and $p < 0.001$ for *C. socialis* and *B. bathyomphala*). The incomplete recovery of the UV-exposed cultures of *C. socialis* and *B. bathyomphala* pointed to photodamage that could not be fully repaired in the dark and during the UV-free period in the light. The treatment effect after recovery in *T. antarctica* was small, but significant (RM-ANOVA, $p = 0.044$) and constant over time. In other words, the recovery potential of the photosynthetic efficiency of *T. antarctica* seemed to be higher than that of *C. socialis* and *B. bathyomphala*.

Stoichiometry—The effect of UV radiation on the C, N, and P contents of the algal cultures was determined by comparing the contents at the beginning and end of the experiment. The concentrations of C, N, and P increased in the control cultures of all three species, despite a daily dilution rate of 0.25. UV exposure reduced this increase, but pronounced interspecific differences occurred (Table 1). It is important to note that the UV-induced decreases were not equal for the three elements, as reflected in changes of their molar ratios. The C and N concentrations in cultures of *T. antarctica* and *C. socialis* exposed to UV radiation decreased 50% compared to the controls, whereas the P concentrations did not differ from the controls after 3 days (*t*-test, $p = 0.46$, and $p = 0.28$, respectively; Table 1). In all species, exposed or not exposed to UV radiation, the C : N ratios were fairly constant (ratio of 5–6; Fig. 4), indicating that the uptake of C and N is tightly linked. In contrast, the relative P concentrations were more variable and strongly increased as a response to UV radiation. This resulted in significantly lower C : P ratios in cultures exposed to UV (Table 1; Fig. 4). In *T. antarctica* and *B. bathyomphala* cultures exposed to UV, the C : P ratios on day 3 were only 50% of those measured prior to the start of the experiment and in the control on day 3 (Fig. 4). In contrast, the C : P ratios of cultures of *C. socialis* exposed to UV did not change over the course of the experiment, yet the C : P ratio of the control doubled by the end of the experiment. The relative effect for all three species was the same, i.e., a 50% reduction of the C : P ratio caused by UV radiation compared to the control. The same pattern was seen with the N : P ratios (Fig. 4). The treatment effects were statistically significant in all species (*see* Table 1). Despite reduced variability, some statistically significant changes were also found in the C : N ratios in *C. socialis* and *B. bathyomphala*; in both cases, UV radiation raised the C : N ratios relative to the controls.

Fatty acid composition—The fatty acid profiles of the three diatom cultures displayed interspecific differences, but in general reacted similarly to UV radiation (Table 2). PUFAs did not decrease in any of the species exposed to UV radiation (RM-ANOVA, treatment: $p = 0.2$, *T. antarctica*; $p = 0.3$, *C. socialis*; Table 3). In *B. bathyomphala*, the PUFA content was even higher when exposed to UV radiation, but the difference between exposed and unexposed cultures decreased toward the

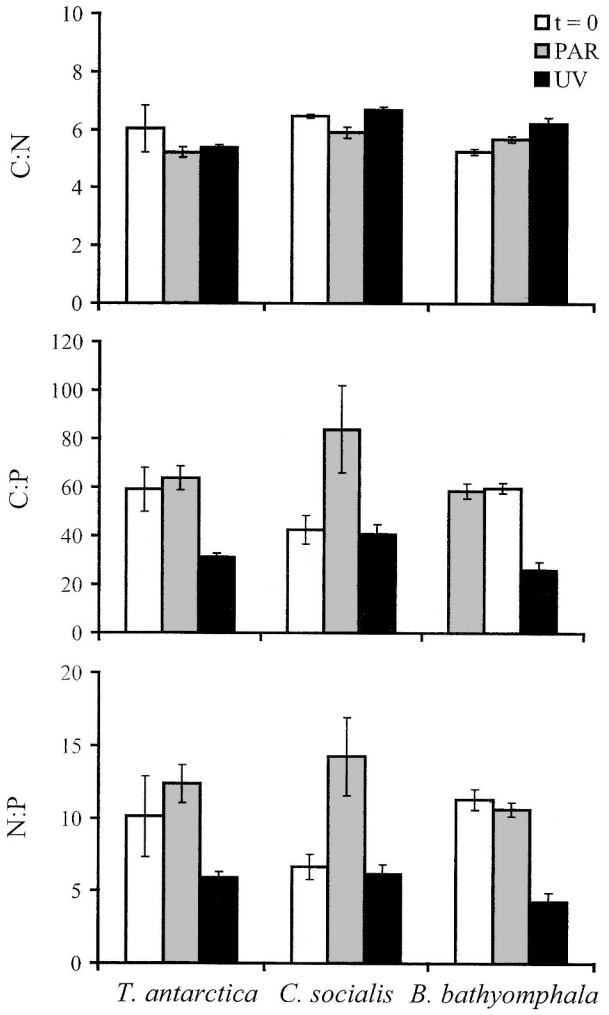

Fig. 4. Molar ratios of cellular C, N, and P in *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceros socialis* measured at the start and the end of the experiment. Shown are means ± SD ($n = 4$).

end of the experiment (RM-ANOVA, time × treatment: $p = 0.003$; Table 3). The PUFA content of *T. antarctica* and *C. socialis* increased during the experimental period, irrespective of whether the cultures were exposed to UV radiation or not (RM-ANOVA, time: $p < 0.001$, and $p = 0.005$).The highest PUFA content was found in *B. bathyomphala* (45–50%). The most-abundant PUFAs found in all three species were 20:5(n-3) and 16:4(n-1), which accounted for more than 70% of total PUFAs in *T. antarctica* and *B. bathyomphala*, and 85–90% in *C. socialis*; neither of these PUFAs decreased in content after exposure to UV radiation (Table 2). In fact, 16:4(n-1) was higher in cultures of *B. bathyomphala* exposed to UV, but this difference disappeared on day 3 (RM-ANOVA, time × treatment: $p < 0.001$). The same trends were seen for both of these fatty acids in all three species, but the overall treatment effect was not statistically significant in *T. antarctica* and *C. socialis* (Table 3). Among the less-abundant PUFAs, only one, 18:4(n-3), decreased in content after UV radiation in cultures of *T. antarctica* and *B. bathyomphala* (RM-ANOVA, treatment: $p < 0.001$); this PUFA was not found in *C. socialis*.

In contrast to most of the PUFAs, the monounsaturated fatty acid (MUFA) 16:1(n-7) was most strongly affected by UV radiation, and its content was substantially lower under UV irradiation in all three species (RM-ANOVA, treatment: $p < 0.001$, $p = 0.012$, and $p < 0.001$ for *T. antarctica*, *C. socialis*, and *B. bathyomphala*, respectively). This effect was constant over time in *T. antarctica* and decreased over time in the other two species (RM-ANOVA, time × treatment: $p = 0.459$, $p = 0.016$, $p = 0.002$; Table 3). Since 16:1(n-7) was by far the dominant MUFA in all three species, the negative effect on this fatty acid was also reflected in the overall MUFA content in UV-irradiated cultures; the overall MUFA content was constant in *T. antarctica* but decreased in the other two species (RM-ANOVA, time × treatment: $p = 0.804$, $p < 0.001$, $p < 0.001$ for *T. antarctica*, *C. socialis*, and *B. bathyomphala*, respectively).

Similar to most of the PUFAs, the C18 saturated fatty acid (SFA) was higher in UV-exposed cultures of all species (RM-ANOVA, treatment: $p = 0.047$, $p = 0.009$, $p < 0.001$ for *T. antarctica*, *C. socialis*, and *B. bathyomphala*, respectivly). Only in *B. bathyomphala* was a significant time × treatment interaction found ($p = 0.023$). Likewise, the overall SFAs increased only in *B. bathyomphala* (RM-ANOVA, treatment: $p = 0.009$).

The ratio between the MUFA 16:1(n-7) and the SFA 16:0 increased in cultures of all three species exposed and unexposed to UV radiation from day 1 to day 3 (Fig. 5). In the UV-shielded cultures of *T. antarctica* and *B. bathyomphala*, however, this ratio was higher than the ratio of cultures exposed to UV radiation (RM-ANOVA; time: $p < 0.001$ for all species; treatment: $p = 0.005$, $p = 0.061$, and $p < 0.001$ for *T. antarctica*, *C. socialis*, and *B. bathyomphala*, respectively).

Discussion

UV radiation and PUFAs—Previous laboratory experiments with different phytoplankton species (Goes et al. 1994; Wang and Chai 1994; Skerratt et al. 1998) have illustrated a trend in the general UV-induced reduction of the overall PUFA content of phytoplankton. Skerratt et al. (1998) described a reduction in the PUFA content of two of three investigated species under high UVB intensities (1.6 W m^{-2}) and an increase in the PUFA content of one species under low UVB (0.37 W m^{-2}). Wang and Chai (1994) observed major interspecific differences in the responses of eight different phytoplankton cultures to UVB, ranging from severe reduction to a substantial increase in the algal (n-3) fatty acids during the first four days of their experiment. In particular, the PUFA content of two centric diatoms increased when cultures were exposed to UV radiation. However, the lack of any statistical information in this study impairs further interpretation and comparison of their results. Finally, Goes et al. (1994) found a substantial reduction in the percentage of PUFAs in one marine prasinophyte after 12 h of UV exposure.

In contrast to the results of these previous studies, we did not find a reduction in the PUFA content of the species tested. However, because of the different experimental conditions used, including temperature, applied irradiances, exposure periods, species chosen, and ambient nutrient concentrations, the results cannot be easily compared.

We chose temperatures and (maximum) UV doses similar to those that arctic phytoplankton species encounter during the spring bloom. The conditions in our study were similar to those described by Skerratt et al. (1998), but the temperatures were higher and UV doses were lower in the other two studies (Goes et al. 1994; Wang and Chai 1994).While the PAR : UV ratio used in the present work was clearly lower than that under natural conditions, it was still higher than that in most other studies. High PAR intensities have been shown to reduce the UV-induced decrease in PUFA content (Wang and Chai 1994). We even found that under natural PAR : UV ratios in the Arctic, PAR might have a stronger effect on PUFAs than UV (Leu et al. 2006*b*,*c*). The results from this outdoor experiment and field studies in the high Arctic strongly support the results of our laboratory experiments reported here. In these field studies, ambient and enhanced UV radiation had only a very weak or even no effect on PUFAs, whereas rapidly increasing or naturally high PAR intensities close to the surface yielded a substantial decrease in the relative amount of PUFAs.

In any case, the underlying mechanism of UV damage and the resulting effect on PUFAs have not yet been proven. It is a widely held belief that UV mainly affects PUFAs in aquatic systems through photo-oxidation of double bonds (Hessen et al. 1997; Vincent and Neale 2000; Björn and McKenzie 2002). A correlation between the number of double bonds in a fatty acid and its susceptibility to photo-oxidation has been shown in highly artificial systems (e.g., Cosgrove et al. 1987; for a review, *see* Girotti 2001). But to our knowledge, corresponding effects have not been observed in intact, photosynthetically active cells. There is indeed evidence for oxidative stress in phytoplankton caused by UV radiation. Rijstenbil (2002) showed a major increase of active oxygen production as response to UVB irradiation in *Thalassiosira pseudonana*, yet it remains to be proven that these radicals really cause oxidative damage of PUFAs inside the intact membrane bilayer. The double bonds of fatty acids in galacto-, phospho-, or sulfolipids are not easily accessible to radical species, especially since lipid layers in general have a low permeability for oxygen (F. Jüttner, pers. comm.). In addition, there has been a long evolutionary adaptation for photosynthetic organisms to optimize their scavenging and repair potential and to cope with reactive oxygen species. They must be able to handle excess radiation energy in their chloroplast membranes, which contain the highest percentage of PUFAs. With these considerations, a UV-induced inhibition of PUFA synthesis, as suggested by Goes et al. (1994), seems more plausible, but our results also do not provide indications for this.

The two fatty acids most strongly affected by UV radiation in the present study were 16:1(n-7) and 18:0; the 16:1(n-7) content substantially decreased under UV irradiation in all three species, and the 18:0 content increased. High relative amounts of 16:1(n-7) are generally observed during exponential growth, i.e., under favorable conditions. High levels of 18:0, in contrast, are commonly judged as an indication of poor growth conditions (Falk-Petersen et al. 1998; Zhukova et al. 1998; Reuss and Poulsen 2002). The observed changes thus indicate a general deterioration of the physiological status of the UV-irradiated cultures, rather than a specific damage targeted at a certain group of fatty acids.

Hence, while it is reasonable to assume that there is no single response to UV in all species and under all conditions, our data strongly suggest that PUFAs are not a very sensitive parameter with regard to UV stress in arctic diatoms.

UV radiation and stoichiometry—Despite a strong reduction in biomass accumulation, measured as Chl *a* and particulate C, caused by exposure to UV, the C : N ratios of the phytoplankton increased only slightly. These results are in keeping with those of Mousseau et al. (2000), who showed that enhanced UVB radiation inhibited the uptake of both C and N by estuarine phytoplankton similarly, yielding only minor changes in the C : N ratios. The C : P ratios of all three species in our study, however, substantially decreased following UV irradiation. Similar results for phytoplankton and epilithic communities in freshwater ecosystems have been reported by, for example, Xenopoulos et al. (2002) and Tank et al. (2003), but the mechanism behind this observation was not examined. We also did not address this question directly in our experiments, but in at least two of the three species tested, we have indications that the increased C : P ratios are caused by an increased uptake of P. The C : P ratios of *T. antarctica* and *B. bathyomphala* decreased after exposure to UV compared to the ratios measured at the start of the experiment; the relatively higher concentrations of P led to the decrease in the ratios. This increase in P concentrations could reflect an increased demand for P during UV exposure necessary for the higher activity of biosynthesis and repair mechanisms, as suggested by Hessen et al. (1995). We hypothesize that there are physiological costs of maintaining essential membrane and intracellular functions. An increased turnover rate caused by UV-induced damage could possibly enhance the rate of protein biosynthesis, and hence, mRNA (messenger ribonucleic acid) levels, which would lead to an increased demand for P. These costs would affect the fitness, survival, and reproduction rate of the affected organisms, in particular under conditions in which they were unable to satisfy their extra demands (e.g., under nutrient limitation). Several studies have even shown a negative effect of nutrient limitation on PUFA content, especially during P limitation (e.g., Klein Breteler et al. 2005). Although our study design, with nutrients added in surplus, did not allow us to test this directly, the obviously increased demand for P suggested a competitive disadvantage of these diatoms under such conditions.

Table 2. Fatty acid composition (in % of total fatty acids; shown are means±SD of three replicates) of *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceras socialis*. Fatty acids accounting for <1% in all samples are not shown.

	$t = 0$		Day 1		Day 2		Day 3	
	PAR	UV	PAR	UV	PAR	UV	PAR	UV
Thalassiosira antarctica								
14:0	10.2±0.1	11.7±0.4	12.0±0.2	10.7±0.6	12.0±0.4	9.9±0.3	11.1±0.3	9.2±0.3
16:0 pristanic	3.3±0.1	3.8±0.1	2.5±0.1	2.9±0.1	2.0±0.3	2.6±0.1	1.8±0.1	2.3±0.3
16:0	20.0±0.8	23.0±0.4	24.5±2.5	21.5±1.2	22.3±2.0	21.8±1.1	16.3±0.6	16.1±0.4
16:1(n-7)	13.3±0.2	14.7±0.6	18.8±0.8	12.9±0.5	21.1±0.8	15.5±0.9	20.9±0.1	15.9±0.4
16:1(n-5)	5.2±0.4	4.7±1.6	2.8±0.5	4.2±1.0	1.4±0.1	1.7±0.1	0.4±0.0	1.2±0.1
16:2(n-7)	2.1±0.1	2.1±0.3	1.9±0.1	2.3±0.2	1.4±0.1	1.8±0.1	1.7±0.1	2.0±0.1
16:3(n-4)	1.5±0.0	1.2±0.1	1.0±0.1	1.1±0.1	0.9±0.2	1.0±0.2	2.0±0.0	1.3±0.1
16:4(n -1)	10.9±0.5	7.4±0.7	5.6±0.7	8.7±2.1	6.4±0.9	8.1±1.7	11.4±0.8	12.3±1.0
17:0 phytanic	0.0±0.0	0.3±0.6	0.8±0.0	1.0±0.1	0.9±0.3	1.1±0.2	0.6±0.0	1.0±0.1
17:0	4.3±0.1	5.0±0.3	3.7±0.1	4.2±0.3	3.2±0.2	3.9±0.1	2.9±0.0	3.6±0.1
18:0	4.6±0.2	4.8±0.8	3.6±0.4	4.5±0.1	2.1±0.4	4.9±2.6	1.0±0.1	1.8±0.1
18:1(n-9)	0.0±0.0	0.0±0.0	0.0±0.0	0.3±0.5	0.6±0.6	1.3±0.3	0.3±0.0	0.5±0.1
18:4(n-3)	2.3±0.1	1.6±0.2	3.3±0.2	1.8±0.2	4.1±0.4	2.2±0.4	4.8±0.2	3.1±0.1
20:0	1.4±0.0	1.5±0.2	1.1±0.1	1.5±0.1	0.7±0.1	1.4±0.1	0.4±0.0	0.8±0.1
22:0	1.0±0.0	0.8±0.7	1.2±0.3	1.6±0.4	0.7±0.3	1.1±0.2	0.3±0.1	0.6±0.2
20:5(n-3)	15.6±0.6	13.3±1.7	13.3±2.9	14.9±2.9	16.2±2.0	16.3±2.7	19.3±0.2	21.1±1.5
22:6(n-3)	1.8±0.1	1.9±0.3	2.0±0.1	2.5±0.7	2.3±0.6	2.5±0.2	2.9±0.2	3.1±0.2
PUFA	34.9±1.3	28.2±2.8	27.6±4.3	33.0±2.9	31.9±3.2	33.2±4.8	42.8±0.7	46.0±1.6
MUFA	19.1±0.4	20.4±1.7	22.2±1.4	18.5±1.2	23.8±0.6	19.5±0.8	22.4±0.2	18.1±0.6
SFA	42.6±0.9	48.5±3.5	46.8±3.2	44.6±2.0	41.5±2.5	43.6±4.2	32.4±0.6	32.6±0.7
Chaetoceros socialis								
14:0	15.3±0.1	13.5±0.1	14.8±0.9	11.6±1.1	11.9±1.1	11.1±0.4	12.6±0.9	11.1±3.0
16:0 pristanic	2.9±0.6	3.1±0.3	2.6±0.6	2.7±0.3	1.9±0.1	2.1±0.1	1.9±0.2	2.0±0.4
16:0	12.5±1.4	13.6±0.4	14.2±1.5	15.7±2.3	18.3±1.7	21.6±1.9	12.8±2.0	11.7±1.4
16:1(n-7)	14.2±1.6	14.0±0.9	17.6±0.7	13.2±1.1	19.6±1.3	14.9±0.7	20.7±1.3	18.8±1.7
16:1(n-5)	3.0±1.8	2.8±0.6	1.9±1.0	1.6±0.1	1.4±0.2	2.1±1.0	0.7±0.3	2.4±0.9
16:2(n-7)	2.7±0.1	2.6±0.1	2.2±0.1	2.4±0.2	2.0±0.1	1.9±0.0	2.2±0.2	2.2±0.1
16:3(n-4)	1.8±0.1	1.7±0.1	1.2±0.1	1.1±0.1	1.1±0.0	0.9±0.0	1.2±0.1	1.0±0.0
16:4(n-1)	15.5±0.3	14.6±0.6	13.0±1.0	14.2±1.0	10.5±0.1	10.6±0.3	12.4±0.9	12.2±0.3
17:0 phytanic	2.4±0.0	2.3±0.0	2.0±0.1	2.0±0.2	1.3±0.1	1.6±0.1	1.2±0.2	1.8±0.3
17:0	3.5±0.6	3.5±0.2	3.0±0.1	3.6±0.2	3.2±0.1	3.3±0.2	3.2±0.2	3.0±0.3
18:0	2.8±0.1	3.0±0.1	2.9±0.6	3.8±0.9	3.0±0.5	3.9±0.4	1.8±0.4	2.2±0.1
18:1(n-9)	0.5±0.1	0.3±0.3	0.6±0.2	0.7±0.2	0.5±0.2	0.5±0.0	0.7±0.3	0.7±0.2
18:4(n -3)	0.2±0.3	0.3±0.3	1.4±0.2	0.1±0.1	0.9±0.0	0.3±0.0	1.0±0.2	0.5±0.1
20:5(n-3)	18.1±1.4	20.3±1.7	18.4±3.4	23.3±2.0	20.4±3.9	20.2±3.4	24.9±2.4	25.3±1.6
PUFA	39.9±4.2	40.6±1.5	37.2±3.6	42.0±1.8	36.0±3.5	35.2±3.6	42.5±2.2	43.7±0.8
MUFA	19.4±3.0	18.5±1.2	21.3±0.9	16.5±1.1	22.6±1.3	18.7±1.4	23.0±1.1	23.0±2.2
SFA	35.5±0.7	35.5±0.4	36.8±2.4	36.7±2.4	38.3±2.5	42.4±2.5	31.5±2.4	29.5±2.7
Bacterosira bathyomphala								
14:0	4.7±0.4	4.2±0.1	4.5±0.0	4.5±0.1	5.1±0.2	4.2±0.1	5.3±0.1	4.6±0.2
16:0 pristanic	3.1±0.3	2.4±0.2	1.9±0.1	2.6±0.4	1.6±0.5	1.9±0.1	1.5±0.1	1.5±0.1
16:0	16.9±1.9	21.3±3.3	18.2±0.1	19.1±2.3	18.1±0.8	20.6±1.8	13.7±0.3	14.9±0.3
16:1(n-7)	12.3±0.9	10.7±0.6	19.2±0.6	10.7±0.7	25.5±0.6	18.3±0.7	27.4±0.5	23.2±0.9
16:1(n-5)	2.2±1.3	1.7±0.5	1.4±0.5	1.3±0.1	0.5±0.4	1.3±0.1	0.4±0.1	1.0±0.2
16:2(n-7)	4.6±0.5	4.4±0.3	4.2±0.1	5.0±0.0	3.7±0.1	3.4±0.0	4.5±0.1	3.6±0.0
16:3(n-4)	2.8±0.1	2.6±0.2	1.7±0.1	1.5±0.5	1.0±0.0	0.6±0.5	1.2±0.0	0.8±0.1
16:4(n-1)	15.9±0.5	15.1±0.8	14.6±0.0	16.8±0.4	12.0±0.3	14.5±0.3	15.3±0.3	15.4±0.2
17:0	3.1±0.3	2.9±0.1	2.5±0.1	2.9±0.1	2.3±0.1	2.5±0.1	2.5±0.0	2.5±0.0
18:0	3.6±0.8	3.6±0.3	2.4±0.2	3.2±0.2	1.7±0.2	3.4±0.4	0.7±0.1	1.6±0.3
18:1(n-9)	1.1±0.3	1.0±0.1	0.6±0.0	0.6±0.0	0.4±0.0	1.1±0.1	0.3±0.0	0.7±0.1
18:4(n-3)	3.8±0.8	3.8±0.3	4.9±0.2	3.8±0.1	3.9±0.1	3.1±0.0	4.2±0.2	3.5±0.0
18:5(n-3)	0.9±0.0	0.8±0.1	0.7±0.0	1.0±0.1	0.7±0.4	1.1±0.3	0.5±0.1	0.9±0.1
20:0	1.6±0.1	1.5±0.1	1.0±0.0	1.5±0.1	0.7±0.1	1.2±0.1	0.5±0.0	0.9±0.1
22:0	0.4±0.7	1.1±0.2	0.0±0.0	0.9±0.1	0.2±0.3	0.4±0.6	0.1±0.1	0.2±0.3
20:5(n-3)	20.2±1.5	18.8±1.2	18.4±0.2	20.1±0.4	17.5±0.6	16.9±0.3	17.5±0.2	19.2±0.2
22:6(n-3)	1.8±0.1	1.8±0.1	1.5±0.2	2.0±0.2	2.1±0.4	1.8±0.2	2.2±0.2	2.0±0.1
PUFA	49.5±3.9	47.6±3.2	46.6±0.2	50.8±1.6	41.9±0.8	43.3±1.3	45.9±0.3	46.8±0.7

Table 2. (Continued).

	$t = 0$		Day 1		Day 2		Day 3	
	PAR	UV	PAR	UV	PAR	UV	PAR	UV
MUFA	16.8±1.3	14.6±0.5	22.1±0.3	13.7±0.6	27.4±0.1	21.6±0.6	28.8±0.4	25.7±0.9
SFA	30.4±3.5	35.4±3.8	29.3±0.2	33.0±2.5	28.7±0.9	33.2±1.7	23.3±0.4	25.3±0.8

UV effects on photosynthetic efficiency and growth—The exposure of the phytoplankton to UV radiation also affected the optimal quantum yield. The 90% reduction indicated a severe photoinhibition of photosynthesis during the 8 h of daily exposure, which led to decreased biomass accumulation. Despite this pronounced effect during exposure, all species showed a substantial recovery during the period between the cycles of UV irradiation. The extent of the recovery in *C. socialis* and *B. bathyomphala* was, however, lower than in *T. antarctica*, and seemed to decrease over time, pointing toward chronic photoinhibition or photodamage (cf. Hanelt 1996). Again, interspecific differences were found; *B. bathyomphala* was most sensitive to UV, followed by *C. socialis*. *T. antarctica* showed a higher recovery potential and no indication for photodamage of the photosynthetic apparatus until day 3. During the periods between the cycles of UV irradiation, the cultures experienced both PAR only (5 h after the end of UV irradiation, and 3 h prior to the start of UV irradiation) and darkness (8 h in between two exposures to PAR only). Judging from the C concentrations in the three cultures at the beginning and at the end of the experiment, the growth rates of *T. antarctica* and *C. socialis* during the PAR-only periods were sufficient to balance the daily dilution of 0.25, whereas biomass of *B. bathyomphala* slightly decreased over the course of the experiment. Despite the strong reduction in biomass accumulation and growth rate caused by UV irradiation, the algal cultures were still metabolically active, as could be seen from the postirradiation recovery of optimal quantum yield

Table 3. Results of RM-ANOVA on fatty acid composition of *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceros socialis*. For those fatty acids that were significantly affected by UV radiation, it is indicated in which of the treatments higher values were found.

	Treatment (df=1)			Time (df=2)		Treatment × time (df=)	
	F	*p*		*F*	*p*	*F*	*p*
Thalassiosira antarctica							
16:0	14.8	0.291		70.3	0.000*	3.3	0.092
16:1(n-7)	258.9	0.000*	UV<PAR	31.5	0.000*	0.9	0.459
18:0	8.1	0.047*	UV>PAR	10.4	0.000*	1.7	0.25
16:4(n-1)	7.0	0.057		32.2	0.000*	1.4	0.298
18:4(n-3)	166.2	0.000*	UV<PAR	48.7	0.000*	1.1	0.384
20:5(n-3)	0.6	0.487		20.8	0.001*	0.5	0.638
22:6(n-3)	1.9	0.241		7.6	0.014*	0.7	0.531
PUFA	2.9	0.164		45.8	0.000*	0.9	0.464
MUFA	73.7	0.001*	UV<PAR	5.0	0.039*	0.2	0.804
SFA	0.0	0.989		62.2	0.000*	1.6	0.264
Chaetoceros socialis							
16:0	2.3	0.205		25.7	0.000*	2.1	0.19
16:1(n-7)	18.3	0.012*	UV<PAR	60.1	0.000*	7.2	0.016*
18:0	22.9	0.009*	UV>PAR	10.0	0.007*	0.2	0.792
16:4(n-1)	0.6	0.489		36.2	0.000*	2.1	0.188
20:5(n-3)	0.7	0.441		9.8	0.007*	2.7	0.128
PUFA	1.7	0.268		11.2	0.005*	1.6	0.265
MUFA	7.4	0.053		63.1	0.000*	25.2	0.000*
SFA	0.4	0.535		20.8	0.001*	2.1	0.187
Bacterosira bathyomphala							
16:0	4.5	0.103		38.2	0.000*	0.9	0.463
16:1(n-7)	592.4	0.000*	UV<PAR	330.4	0.000*	14.2	0.002*
18:0	107.7	0.000*	UV>PAR	79.5	0.000*	6.3	0.023*
16:4(n-1)	141.6	0.000*	UV>PAR	183.2	0.000*	43.6	0.000*
18:4(n-3)	485.3	0.000*	UV<PAR	68.7	0.000*	4.7	0.044*
20:5(n-3)	32.2	0.005*	UV>PAR	53.3	0.000*	23.3	0.000*
22:6(n-3)	0.0	0.894		2.3	0.163	3.5	0.083
PUFA	10.7	0.031*	UV>PAR	157.3	0.000*	13.2	0.003*
MUFA	1358.0	0.000*	UV<PAR	350.0	0.000*	10.9	0.000*
SFA	22.5	0.009*	UV>PAR	58.2	0.000*	1.6	0.269

* Statistically significant ($p<0.05$).

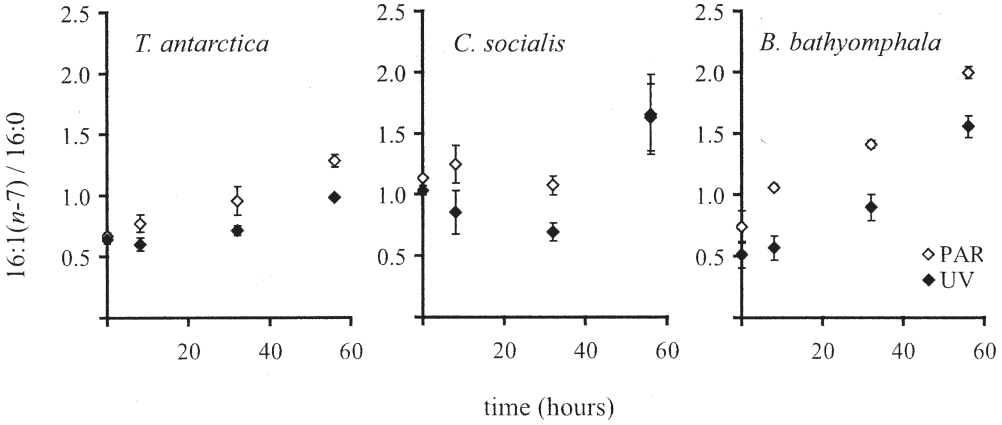

Fig. 5. Temporal development of the 16:1(n-7)/16:0 ratio for *Thalassiosira antarctica*, *Bacterosira bathyomphala*, and *Chaetoceros socialis*. Shown are means ± SD ($n = 3$).

and the development of the particulate C concentrations. Chl *a* concentrations indicated much lower growth rates, especially in cultures exposed to UV radiation. However, Chl *a* concentrations cannot be considered as a robust measure of biomass, in particular in experiments in which cultures are irradiated differently.

While our results confirmed a negative quantitative effect on photosynthetic efficiency and biomass accumulation, we were unable to demonstrate any negative effect of UV radiation on the nutritional quality of diatoms in terms of fatty acid or elemental composition. From a stoichiometric perspective, the UV effect could in fact be seen as a positive impact on nutritional quality owing to a reduction of the C : P ratios (cf. Sterner and Elser 2002). However, this gain in food quality is likely to be offset by a substantial decrease in food quantity because of the inhibition of carbon fixation.

We conclude that changes in fatty acid composition and molar C : N : P ratios might contribute to a better understanding of the mechanisms of UV stress on the general physiology of phytoplankton, but the nature of these changes does not decrease the nutritional quality per se. Given the strong negative effect of UV on photosynthesis and biomass, the absence of an effect on PUFAs is remarkable, and it clearly suggests that PUFAs are not the weak link in the food web in correlation with UV damage.

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