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EFFECTS OF SOLAR ULTRAVIOLET RADIATION ON EPILITHIC METABOLISM, PIGMENT AND COMMUNITY COMPOSITION IN A CLEAR-WATER BOREAL LAKE.

by

Elise Marie Watkins 

A thesis submitted to the faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

Stratospheric ozone depletion, climate change and acidification will increase the exposure of aquatic ecosystems to ultraviolet radiation (UVR: 280-400 nm). The objective of this study was to determine the ecological effects of ambient UVR exposure on epilithon (algal communities attached to rocky substrata) relative to an artificially reduced UVR environment. UVR exposure was altered in the littoral zone of a boreal lake by selectively filtering segments of the solar spectrum with large acrylic sheets. This 130 day study took place at the Experimental Lakes Area, northwestern Ontario, in 1998. Epilithon were monitored for changes in productivity, biomass, pigment, nutrient and taxonomic composition. UVR decreased epilithic photosynthetic rates, increased carbon and nitrogen content, and consequently increased food quality. UVR effects on algal metabolism were dependent on seasonal trends. Epilithic respiration rates and chlorophyll *a* concentrations were not significantly different among treatments. There was evidence for UV-induced taxonomic shifts in epilithon.

"May the few who ignite sound fuel a change in the night.
May the few who fuel change ignite sound into light."

-Ember Swift

"Rage, rage against the dying of the light."

-Dylan Thomas

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Effects of solar ultraviolet radiation on epilithic metabolism, pigment and community composition in a clear-water boreal lake** submitted by **Elise Marie Watkins** in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

David W. Schindler, Supervisor

Vincent L. St. Louis

Lee Foote

Date: July 10, 2000

I dedicate my efforts to the women in my life who have traced memories of beauty into my spirit. Thank you for teaching me about love and strength and for giving me support to follow my heart.

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INTRODUCTION

Effects of solar ultraviolet radiation on aquatic ecosystems

Stratospheric ozone depletion, climatic warming, and acidification are three of the major human stressors in boreal regions (Schindler 1998a). These stressors act synergistically to elevate the exposure of aquatic ecosystems to ultraviolet radiation (UVR; 280-400 nm) (Schindler 1996a). Algae can act as valuable indicators of anthropogenic activities that alter the UV environment within aquatic ecosystems. UVB inhibits phytoplankton photosynthetic rates (Hader et al. 1998; Hermann et al. 1996; Karentz et al. 1994; Helbling et al. 1992; Smith et al. 1992) and growth rates (Jokiel and York 1984). Benthic algae have shown lower growth rates (Bothwell et al. 1993), reduced biomass accrual (Bothwell et al. 1993, 1994; Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998; McNamara and Hill 2000), and lower ^{14}C assimilation (Nadeau et al. 1999; McNamara and Hill 2000) in response to UVR. UVR-induced changes in species composition have also been reported for periphyton (algae attached to a substrate) (Bothwell et al. 1993; Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998). UVR damages algal DNA, and disrupts the electron transport chain and photosystem II reaction centers (Karentz et al. 1994; Hader et al. 1998). Algal inorganic nutrient uptake (Dohler and Biermann 1987; Dohler 1985; Dohler 1992; Hessen et al.1995), protein synthesis (Gerber and Hader 1992; Behrenfeld et al. 1995; Buma et al. 1996) and fatty acid production (Wang and Chai 1994; Hessen et al. 1997) are also reduced by exposure to UVR.

Outline, objectives, and hypotheses of the study

I examined the effects of ambient UVR on periphyton in the littoral zone of a clear water boreal lake by exposing epilithon (algal communities, and associated bacteria, fungi, viruses and zoobenthos, attached to solid and relatively inert surfaces (Turner et al. 1983)) to three UV regimes; PAR (photosynthetically active radiation; 400 to 700 nm) only, PAR + UVA (320 to 700 nm), and PAR + UVA + UVB (280 to 700 nm). Acrylic solar filters controlled the wavelengths of solar radiation penetrating the water column to the epilithon. Filters that allowed the natural flow of lake water beneath them were used to maintain the complexity and realism of whole ecosystems that mesocosms often lack (Schindler 1998b). A long-term (130 days) experimental design was chosen to determine whether epilithon exposed to UVR and PAR only would become similar once UVR no longer affected growth. My objectives were to determine if reduced ambient UVA (320 to 400 nm) and UVB (280 to 320 nm) exposure on epilithon affects epilithic photosynthetic and respiration rates, biomass, and community composition, pigment concentrations and stoichiometry by testing the following five predictions:

1. Photosynthetic rates will be lower in epilithon exposed to UVR than in epilithon protected from UVR exposure.
2. Respiration rates will be higher in epilithon exposed to UVR than in epilithon protected from UVR due to increased metabolic stress (Odum 1985).
3. Algal biomass will be lower in epilithon exposed to UVR due to depressed growth rates.

4. Epilithic algae will show differential responses to UVR leading to taxonomic shifts among treatments. As UVR intensity decreases through the summer and autumn, community composition will converge because UVR is no longer a significant factor affecting growth.
5. UVR will affect carbon: nitrogen: phosphorus ratios via a combination of reduced nutrient uptake and metabolic losses of carbon from increased respiration rates.

Complexity of solar ultraviolet radiation impacts on aquatic ecosystems

Many investigations have studied the effects of UVR on a single species or trophic level. However, UVR effects on periphyton may be transferred to higher trophic levels through altered primary production or food quality. UVR can suppress algal abundance or promote the growth of less edible, thick-walled taxa, thereby reducing food availability for herbivores (van Donk and Hessen 1995; Xiong et al. 1996). Algae containing high concentrations of UV-absorbing pigments may also grow in response to increased levels of UVR (Leavitt et al. 1997; Vinebrooke and Leavitt 1996; Donkor and Hader 1995), consequently increasing their susceptibility to visual predators. The nutritional quality of algae, which may be altered by UV-induced disruption of nutrient uptake mechanisms, also affects the growth of grazers (van Donk et al. 1997; Gulati and DeMott 1997; Sterner et al. 1993; Soderstrom 1988).

UVR alters trophic level interactions through direct effects on invertebrate and vertebrate grazers. UVR has negative effects on zooplankton (Williamson 1995; Williamson et al. 1994), benthic invertebrates (Bothwell et al. 1994; Donahue and Schindler 1998), amphibians (Blaustein et al. 1997) and fish (Williamson et al. 1999).

These direct declines in grazer abundance can offset UV-induced inhibition of periphyton growth (Bothwell et al. 1994). Assessing the impacts of UVR on aquatic ecosystems is complex with differential and interacting effects among trophic levels.

Investigations of the biological effects of UVR in aquatic ecosystems have often been limited to short-term experiments ranging from hours to days (for examples see McNamara and Hill 2000; Nadeau et al. 1999; Wang and Chai 1994; Buma et al. 1996; Hessen et al. 1997; Smith et al. 1992; Buhlmann et al. 1987). More recently, investigations have attempted to incorporate the complexity of UVR impacts on aquatic ecosystems over the long-term. For example, Vinebrooke and Leavitt (1996, 1998, and 1999a) have done many 30-day mesocosm experiments investigating the effects of UVR on periphyton in alpine lakes. Bothwell et al. (1993) found that over 2-3 weeks, periphytic diatoms had lower growth rates when exposed to UVR than when exposed to PAR only. However, after 5 weeks of growth, diatom biomass accrual was reduced in the PAR only treatment due to differential trophic level sensitivities to UVR (Bothwell et al. 1994). Because length of UVR exposure interacts with multi-trophic level responses, short-term and single trophic level investigations are inadequate to explain whole ecosystem responses to UVR.

The ecological impacts of UVA and UVB can differ. UVA radiation constitutes a larger proportion of the solar spectrum than UVB, and has been shown to have greater detrimental effects on the physiological processes of algae than UVB (Karentz et al. 1994). Bothwell et al. (1994) found that UVA suppressed periphyton growth more than UVB, but UVB was more harmful to herbivorous chironomids than UVA. UVA, however, may also act as a stimulant in the photorepair of UVB

damaged DNA in algal cells (Williamson 1995). Because UVA irradiance is more abundant than UVB, organisms may use UVA as an indicator of the presence of damaging levels of UVB (Williamson 1995). Stratospheric ozone selectively absorbs UVB; therefore, decreases in stratospheric ozone will elevate the ratio of UVB to UVA. Differential effects of UVA and UVB further complicate the modeling of UVR impacts on aquatic ecosystems.

Relevance of study: Cumulative effects of stratospheric ozone depletion, climate change, and acidification on boreal aquatic ecosystems

Stratospheric ozone depletion caused increased transmission of shorter ultraviolet wavelengths (UVB) to the earth's surface (Madronich et al. 1998). Incident UV-B radiation has increased by 4.0 to 5.0 % per decade in Canada's boreal region because of stratospheric ozone depletion (Madronich et al. 1998; Kerr and McElroy 1993). Boreal freshwater ecosystems are particularly vulnerable to increases in UVR due to interactions with other anthropogenic stressors. Acidification, which is the primary stressor of boreal lakes (Schindler 1988), and climate warming, which has been documented in the boreal region of Canada at the Experimental Lakes Area (ELA), northwestern Ontario, Canada, over a 20 year period from 1970-1990 (Schindler et al. 1996b), both reduce the amount of dissolved organic carbon (DOC), the primary attenuator of visible and ultraviolet solar radiation in lakes (Scully and Lean 1994; Schindler et al. 1997). DOC prevents organisms from being exposed to harmful intensities of UVR and it limits the depth at which photosynthesis can occur.

Climate change may create a warmer, drier climate within the boreal region as shown at the ELA. Although it is unknown whether this trend was induced by

increased emissions of greenhouse gases or whether it was part of a natural cycle, the consequences of the warming period provided insight to what the implications of climate warming due to increased emissions would be on boreal regions. During the documented warming period at the ELA, annual air temperature increased by 1.6°C and precipitation decreased by 25% (Schindler et al. 1996a). As a result, evapotranspiration increased by 35%, and once-permanent streams became intermittent. A warmer, drier climate reduced inputs and increased the time for in-lake removal of DOC (Schindler et al. 1997). DOC in unperturbed reference lakes declined by an average of 15-20% in the ELA lakes during the warming trend, allowing increases of 22-63% in the depth of UV-B penetration (Schindler 1996a).

Acidification, caused by anthropogenic emissions of sulphur and nitrogen oxides, is probably the most harmful of the human stressors to small boreal lakes (Schindler 1988). During the twentieth century, sulfur oxide emissions from factories in the Midwestern United States and from smelters in the Sudbury, Ontario region led to the acidification of thousands of boreal lakes (Schindler 1998a). For some lakes, recovery from acidification has been limited or not at all, while others are still acidifying(Schindler 1998a). Acid deposition will continue to be a problem, as full implementation of U.S. emission reductions to 14.4 million metric tons is not expected until 2010. Lakes acidified experimentally (Schindler et al. 1996a) and anthropogenically (Yan et al. 1996) show a rapid decline in DOC concentration. The inhibitory effects of UVR on aquatic ecosystems will be more damaging in acidified lakes than in pristine lakes as a result of depressed DOC concentrations. Donahue et al. (1998) determined that the 1% UVB penetration depth increased by more than

900% in experimentally acidified L302S as a result of an 80% decline in DOC and acid-induced changes in DOC optical properties. Together, stratospheric ozone depletion, acidification and climate change will increase the exposure of boreal freshwaters to UVR (Schindler 1999), thereby potentially damaging entire lake communities.

METHODS

Study Area

This study was conducted at the ELA, in the boreal region in northwestern Ontario (49°40'N, 93°44'W). The ELA has been described elsewhere (Armstrong and Schindler 1971, Brunskill and Schindler 1971). The experiment was conducted in Lake 224 (L224). Lake 224, which has been physically, chemically, and biologically monitored since 1974, is a headwater lake with a maximum depth of 27 m, a surface area of 25.9 ha (Brunskill and Schindler 1971), low DOC concentrations (2.5-3.5 mg L^{-1}) and high UV penetration (1% of incident UV-B at ~2 m) (Schindler et al. 1996b).

Experimental Design

To determine whether blocking UVR would alter epilithic communities, large plastic optical filters (2.4 m by 1.2 m) were set up in L224 to shield epilithon at a depth of 0.5 m. The filters allowed ~95% of visible light to pass through, while absorbing portions of the UVR spectrum. Three types of filters were used to create three UVR treatments (Figure 1):

1) PAR (photosynthetically active radiation; 400-700 nm) only (OP-3 acrylic sheets; 3.0 mm thick; 50% transmission at 398 nm). (Treatment referred to as "PAR" from this point on).
2) PAR +UVA (320-700 nm) (Mylar-D acrylic sheets; Du Pont; 0.1mm thick, 50% transmission at 318 nm). (Treatment referred to as "PAR + UVA" from this point on).

3) PAR +UVA +UVB (280-700 nm) (OP4 acrylic sheets; CYPRO; 3.0 mm thick; 70-90% transmittance throughout the UVA and UVB spectra). (Treatment referred to as "PAR + UVA + UVB" from this point on).

The filters were secured approximately 0.3 m above the lake bottom with PVC tubing frames on rock surfaces of low slope (<10%). The three UV treatments were randomly placed within three blocks along the north shore of L224. A southern exposure was chosen to ensure that shoreline shading was not a factor. Each block was chosen to be as similar to each other as possible and represented an area of epilithon that fit three filters. The experiment commenced in early June 1998 and ran until mid-October for a total of 130 days.

Unglazed ceramic tiles (114.5 cm^2) were placed under the optical filters to provide an artificial substrate for epilithon to colonize. The tiles were placed at least 30 cm inside the edge of the filters to minimize exposure to light that did not passed through the solar filters first. The tiles were washed overnight in a weak acid bath (1% HCl) before the experiment began to ensure they were clean and uncolonized. Epilithic algal metabolism, biovolume, community composition, pigment concentrations and nutrient composition were measured from samples collected from the tiles. Samples were collected every 2 weeks from June to August, 1998 and every 3 weeks in September and October, 1998 for a total of 8 sample periods. Each block was sampled on a separate day in random order within the same week. The blocks are treated as replicates for statistical and graphical purposes. Sampling dates for block averages are depicted as the middle date of the three sampling days within each sample period.

Detailed Methods

Epilithic metabolism

Rates of epilithic net photosynthesis and respiration were measured *in situ* on the ceramic tiles under the optical filters by measuring the changes in dissolved inorganic carbon (DIC) that occurred in the water overlying samples of epilithon. Two colonized tiles were placed for 1.5-2.0 hours in each of 3 transparent and 3 dark chambers (0.69 L) (made with OP4 and 0% transmittance black plexiglas, respectively) filled with lake water (Turner et al. 1983) to measure photosynthesis and respiration, respectively. All incubations were done at the same time to expose the epilithic communities to the same solar radiation intensities. Water samples (10 ml) were collected with syringes before incubation from above the colonized tiles and after incubation from each chamber. Concentrations of DIC were determined using an infrared gas analyzer (Turner et al. 1983). The coefficient of variation of the method was approximately 1% at 100 μmol C/L. The same tiles were used to measure metabolism (both respiration and photosynthesis) on each sampling date. Changes in DIC were adjusted for the ratio of water volume to area of epilithon enclosed and then expressed as an areal rate (μmol C m^{-2} h^{-1}). The rates measured reflect the activities of the entire epilithic association (Turner et al. 1995).

Gross photosynthesis was estimated by summing the rates of net photosynthesis and the absolute value of dark respiration. This overestimated gross photosynthesis because respiration in the dark is greater than respiration in the light (Turner et al., 1995). In calculating dark respiration: gross photosynthesis ratios

(R_{dark}:P_{gross}), the bias had less effect on the value as it is included in both the denominator and the numerator.

Epilithic algal biovolume, community composition and nutrient composition

Epilithon were collected for taxonomic, chlorophyll, carbon, nitrogen, phosphorus, and pigment analyses from three tiles from under each solar filter on each sampling date. Each tile was removed from under the filters and sampled only once. Epilithon was scraped from the tiles using toothbrushes. Composite suspensions were created by combining the three epilithon samples collected from under each optical filter (total area of 3 tiles = 343.5 cm^2). Each composite suspension from under each optical filter was considered one replicate. Three replicates were collected for each treatment (one from each block) in every sampling period. Each composite suspension was diluted to 1000 ml and three 10 ml sub-samples were taken to analyze carbon/nitrogen, phosphorus, and pigment content (one sub-sample for each analysis). Each 10 ml sub-sample was filtered (Turner et al. 1987), frozen, and analyzed according to Stainton et al. (1971) (carbon, nitrogen, and phosphorus) and Vinebrooke and Leavitt (1999a) (pigment analyses, see below).

Two 20 ml sub-samples from each composite suspension replicate were preserved for taxonomic analysis and biovolume estimation using acid Lugol's solution at a concentration of 4% of final volume. These sub-samples were sonicated to break apart detrital clumps. After sonication, 2 ml was taken from each 20 ml replicate of each treatment on each date and combined to create a composite sample. Only 4 dates were analyzed for taxonomy and biovolume estimates (one from each month the experiment was run). Algae were classified to species (genus when not

possible) and enumerated by cells/cm^2 and cellular volume ($\mu m^3/cm^2$) for each taxa (analyses by David Findlay, Freshwater Institute, Winnipeg, MB). The Shannon-Weiner index (H') was calculated as a measure of taxonomic diversity using biovolume estimates.

Pigment Analyses

The frozen filters from pigment sub-samples were freeze dried for 72 hrs and extracted for 24 hrs in the dark at 4°C using a solution of 80% acetone: 15% methanol: 5% water. The extracted solutions were filtered through 0.2 μm nylon filters and dried under nitrogen gas. The dried extracts were then frozen and stored in the dark. Dried extracts were dissolved in a known volume of injection solvent (70% acetone: 25% ion-pairing reagent: 5% methanol). Dissolved pigments were separated using a Hewlett Packard (HP) Model HPLC (Vinebrooke and Leavitt 1999a). Epilithic sub-samples were too dilute to reliably estimate pigment content except for chlorophyll *a*. Caution should be used with interpretations involving scytonemin, a photoprotective pigment, because the pigment values were too dilute to determine accurate measures.

PAR, UV irradiance, and underwater attenuation

PAR and UVR were measured daily at a meteorological site approximately 3 km from L224. Par was measured with a Li190SA Li-Cor quantum cosign sensor and incident UVR was measured daily with broadband UV-A (320-400 nm) and UV-B (300-320 nm) BW-20, Vital Tecnologies sensors, both attached to a Li1000 Li-Cor data logger. Broadband voltage UVR measures were calibrated to W/m^2 by simultaneously logging broadband data with Li-Cor sensors and interval data with a

Li-Cor Model LI-1800UM Spectroradiometer. Daily voltage data were converted to W/m^2 using a regression equation calculated by fitting simultaneously recorded volt and W/m^2 data. Underwater PAR, UV-A and UV-B were monitored three times throughout the summer in L224 at my study site with a submersible Li-Cor Model LI-1800UM Spectroradiometer. UVR attenuation was calculated using DOC data collected 5 times throughout the summer from L224 and Scully and Lean's (1994) attenuation model.

Statistical Analyses

One-way repeated measures analyses of variance (RM-ANOVA) of epilithic photosynthetic rates, respiration rates, pigment concentrations (chlorophyll *a*, lutein-zeoxanthin, and scytonemin) and particulates (carbon, nitrogen and phosphorus) were used to test for the effects of UVR on epilithon productivity and community structure. There are three treatment levels (No UVR, PAR + UVA and PAR + UVA + UVB) and eight levels of time (eight sample periods). Scheffe's Post Hoc tests were performed to determine which treatments differed from each other in RM-ANOVAs. All data were $\log_{10}$-transformed to account for inequality of variances (Sokal and Rohlf 1969). All statistical analyses were performed using SPSS 9.0. There were two sample periods in which only two blocks could be tested, hence only two replicates were produced on these sample dates. Analyses were conducted with missing values resulting in N=2 for nutrient, stoichiometry and pigment analyses. Two sets of three sub-samples were analyzed for photosynthetic and respiration rates (N=6).

RESULTS

Surface UV Irradiation and UV attenuation

Calculated 1% attenuation depths of UVA and UVB, using Scully and Lean's (1994) attenuation model, based on a mean [DOC] of 3.34 mg/L, were 2.44 m and 1.2 m, respectively (Figure 2). Based on this attenuation model, the percent transmission of UVB at 0.3 and 0.5 m was 30.9% and 14.2%, respectively. Measured attenuation using a Li-Cor Model LI-1800UM Spectroradiometer up to 1.0 m are shown for comparison. Measured UVB % transmission at 0.3 and 0.5 m was 36.2% and 23.7%, respectively.

Incident mean UVA and UVB flux during the metabolic incubations ranges from 34.5 to 15.3 W/m^2 (UVA) and 1.7 to 0.68 W/m^2 (UVB) (Figure 3). UVR is highest in June and July and declines in September and October.

Epilithic Metabolism

Net photosynthesis and respiration increased throughout the summer and declined in the fall (Figure 4). There is a significant effect of time on metabolic rates (Table 1, $p<0.001$).

Overall, rates of net photosynthesis were 37-46% lower in epilithon exposed to UVR (PAR + UVA and PAR + UVA + UVB) than in epilithon in PAR treatment (Figure 5a; Table 1, $p=0.025$). UVA was responsible for the decline in photosynthetic rates (Scheffe's tests; PAR > PAR + UVA = PAR + UVA + UVB).

The effects of UVR on epilithon varied seasonally (significant Time x UVR interaction; Table 1, $p<0.001$). Photosynthetic rates were lower in UV-exposed epilithon in July and August (high UVR) and they converged in September and

October (low UVR) (Figure 5a). The magnitude of difference of net photosynthetic rates between the PAR and UVR treatments increased as a function of the amount of surface UVB irradiation during the incubation period (Figure 6a, Mean r^2=0.5579). This suggests that UVR intensity may be responsible for the significant Time x UVR interaction. The first sample period in June does not fit these trends possibly because the signal to noise ratio was insufficient to detect a signal. This may be because colonization began only two weeks prior to this sample date.

There were no significant differences in respiration rates among UVR treatments (Figure 5b; Table 1, p=0.641). There was a significant Time x UVR interaction (Table 1, p=0.035), indicating differential effects of the UVR treatment over time. The magnitude of difference of respiration rates between the PAR treatment and the PAR + UVA treatment positively correlates with UVR intensity (Figure 6b; r^2=0.5049).

Dark respiration: gross photosynthesis (R_{dark}:P_{gross}) ratios in all UVR treatments were higher early in the colonization process and declined throughout the ice-free season (Figure 7; Table 1, p<0.001). R_{dark}:P_{gross} stabilizes at 0.48 in mid-summer and becomes lower and more variable in September and October. The percent of estimated gross photosynthesis used for respiration was lower in the PAR treatment than epilithon exposed to UVR in July and August, though overall there were no significant differences between treatments (Table 1).

Epilithic Algal Biovolume

Total algal biovolume ($\mu m^3/cm^2$) increased in all treatments until August and declined in Septemeber (Figure 8). Epilithon in the PAR treatment exhibited a larger

increase in algal biovolume than epilithon exposed to UVR. However, these data must be treated with caution, because replicates were not possible (see methods).

Mean photosynthetic rates standardized by total algal biovolume (P/B) were higher in the PAR treatment than in epilithon exposed to UVR in July (Appendix Figure 1). However, in August P/B was much higher in epilithon exposed to PAR + UVA + UVB, than epilithon exposed to the PAR + UVA and PAR treatments, indicating that increasing algal biovolume may decrease photosynthetic efficiency.

Mean respiration rates standardized by total algal biovolume (R/B) declined over time in the PAR treatment (Appendix Figure 2). These results suggest that respiration does not increase as a function of biovolume. Epilithon exposed to UVR showed no trends in R/B ratios.

Epilithic Community Composition

These data must be treated with caution because replicates in taxonomic analyses were not possible (see methods). The epilithic communities were dominated by diatoms (primarily *Achnanthes minutissima* and *Rhopalodia gibba*) and cyanophytes (primarily *Phormidium sp.* and *Calithrix sp.*) (Table 2, Figure 9; see Appendix Figures 3, 4).

Diatoms were the most important contributors to algal biovolume in all UVR treatments (Figure 9). Diatom biovolume was higher in the PAR treatment than in epilithon exposed to both levels of UVR in August and September (Figure 9a). Chlorophytes were second in importance in terms of biovolume in June and July in the PAR treatment (primarily *Bulbochaete sp.*), however diatoms and cyanophytes began to dominate in August and September. Chlorophytes (dominated by *Mougeotia*

sp. and *Oedogonium sp.*) and cyanophytes were second in importance throughout all sampling dates in the PAR + UVA + UVB treatment (Figures 9b,c).

The numbers of chlorophyte, diatom, and cyanophyte taxa were similar in all three UVR treatments (Appendix Figure 3). Overall, diatom taxa were more abundant than chlorophytes and cyanophytes in June and July. Diatom taxa declined over time (Appendix Figure 3a). Cyanophyte taxa increased over time in all treatments (Appendix Figure 3c). Cell numbers were also similar for all taxonomic groups among the three treatments (Appendix Figure 4). Cyanophytes were most important in terms of cell number in all the UV treatments (Appendix Figure 4c).

Average cell biovolume estimates were similar in all three treatments (Appendix Figure 5). Diatom cell biovolume increased over time. Overall, chlorophytes had a larger biovolume per cell than the other taxa, particularly in the PAR + UVA + UVB treatment in July. This may be due to a few large cells appearing in the samples.

Epilithic diversity and species richness were largest in June; two weeks after the tiles began colonizing (Table 3). Species diversity and richness were similar across all treatments on all sampling dates. Community colonization was similar in all three treatments on June 16 (Table 2). However, UVR appears to affect community succession. Chlorophytes were more abundant in PAR + UVA + UVB treatments, in July, August and September (Table 2b). *Mougeotia sp.* was the most abundant chlorophyte in the PAR + UVA + UVB treatment in July and September (approximately 20% of total biovolume from that treatment on those dates). *Achnanthes minutissima* was an important diatom component in all treatments on all

dates (Table 2a). *Rhopilodia gibba* dominated diatom biovolume in the PAR treatment in August and September (Table 2a). This species was primarily responsible for diatoms dominating the biovolume in the epilithon in PAR treatments in August and September (Figure 9a). *Phormidium sp.* was slightly more abundant in PAR treatments in July, August, and September (Table 2c). *Calathrix sp.* first appeared in PAR treatments in August, however in September, it appears in all UV treatments (Table 2c).

Nutrient Concentrations in Epilithon

Epilithic carbon: phosphorus (C:P) and nitrogen: phosphorus (N:P) increased significantly over time in all treatments while carbon: nitrogen (C:N) ratios decreased significantly over time in all treatments (Table 4, $p<0.05$; Figure 10). C:P and N:P ratios were lower in epilithon exposed to UVR (Table 4, $p= 0.054$ and 0.033 respectively; Figure 10a, b). C:N ratios were similar in all three treatments (Table 4, $p=0.293$; Figure 10c). These results correspond with the consistently higher carbon and nitrogen content in PAR treatments than in UV exposed treatments (Table 5) on all but the first and last sample dates (Appendix Figures 6, 7). Although concentrations of cellular carbon, nitrogen, and phosphorus were higher in the PAR treatments (Table 5), RM-ANOVA show no significant differences among treatments (Table 6).

Pigment Concentrations

Epilithic chlorophyll *a* significantly increased over time in all treatments (Table 7, $p<0.001$; Figure 11). RM-ANOVA showed that the three treatments did not affect chlorophyll *a* concentration (Table 7, $p=0.440$). The large variability in the

results diminishes the sensitivity in detecting UV dependent changes in chlorophyll *a*. Scytonemin did not show a trend over time (Table 7, p=0.206) and there was no significant difference in scytonemin concentration among the three UV treatments (Table 7, p=0.137). There was, however, a slightly higher concentration of scytonemin in epilithon exposed to PAR + UVA + UVB than in PAR + UVA and PAR only treatments from mid-July until mid-August (Figure 12).

DISCUSSION

Epilithic Metabolism

Ambient UVR suppressed net photosynthetic rates of epilithic periphyton by 37- 46% (PAR + UVA and PAR + UVA + UVB treatments) for the first 90 days of this 130 day study in L224. Few studies have investigated how epilithic carbon metabolism is affected by long-term exposure to ambient UVR. My results corroborate the findings of others demonstrating that current UVR has a detrimental effect on algal productivity. Short-term exposure to UVR depressed benthic algal ^{14}C uptake rates (Nadeau et al. 1999; McNamara and Hill 2000). Similarly, Bothwell et al. (1993) found that short-term daily exposure to UVB led to a 30-40% reduction of periphytic diatom growth rates and restricted diatom biomass accrual in shallow (depth of 1 cm) experimental flumes. Vinebrooke and Leavitt (1996) also discovered a decline of 50% in biomass accrual when periphyton was exposed to ambient levels of UVR for 30 days in a clear water alpine lake. Kim and Watanabe (1994) found that diatoms, which initially exhibited reduced photosynthetic rates in response to prolonged UVA exposure, acclimitized after 6 days to show similar photosynthetic rates to PAR treatments. In my study, UV-induced reductions in algal productivity under prolonged UV exposure were long lasting.

The decline in net photosynthetic rates found in this study can be primarily attributed to UVA. Other investigators have found that UVA was predominantly responsible for photosynthetic inhibition in phytoplankton (Maske 1984, Buhlmann et al. 1987) and inhibited algal growth rates (Kim and Watanabe 1994; Jokiel and York 1984). UVA decreased light ^{14}C uptake rates to just above dark uptake rates in

Antarctic cyanobacterial mats (Nadeau et al. 1999). However, UV-induced damage to phytoplankton becomes more severe with decreasing wavelengths (Cullen 1992; Smith et al. 1992) by inactivating photosystems, disrupting electron transport, and destroying pigments and membranes (Karentz et al. 1994). UVB contains more energy per photon than UVA, therefore it is more deleterious per photon; however, UVA is a larger portion of the solar spectrum than UVB, causing the majority of UV photosynthetic inhibition (Karentz et al. 1994; Cullen et al. 1992).

Epilithic dark respiration rates were not different in the PAR and UVR exposed treatments. These results do not support the hypothesis that respiration increases as a functional response to increased stress within the community (Odum 1985). I hypothesized that dark respiration rates would be higher in epilithon exposed to UVR due to increased ATP expenditure to prevent or repair UVR damage. There is little information about the relationship of epilithic respiration to UVR stress, however, in the following year at the same study location, Weidman (2000) found that epilithic dark respiration rates increased significantly in response to UVR after 28 days of growth at a depth of 0.54m. The epilithic community studied by Weidman (2000) was dominated by chlorophytes, whereas diatoms dominated the epilithon in my study. Further, Donahue (2000) suggested that filamentous chlorophytes may exhibit an increased photorespiratory capacity as a photoprotective mechanism to reduce the UV-induced formation of reactive oxygen species. Our results may be showing differential community responses to UVR.

Although differences in respiration were not detected among treatments, there may be evidence that respiration was higher in epilithon exposed to UVR. R_{dark}:P_{gross}

ratios were higher in UVR treatments than in PAR treatments after 4, 6 and 8 weeks of colonization. Weidman (2000) also found significantly higher R_{dark}:P_{gross} ratios in chlorophyte-dominated epilithon exposed to ambient UVR. Not detecting significant differences in R_{dark}:P_{gross} may be an artifact of the estimation of P_{gross} (sum of P_{net} + R_{dark}). R_{dark} is assumed to be equal to respiration in the light, i.e. respiration is independent of irradiance (which may be incorrect when UVR is the manipulated factor). However, R_{dark} is actually greater than respiration in the light (Graham and Turner 1987). Therefore, calculated P_{gross} is probably an overestimation of actual P_{gross} (Graham and Turner 1987).

Epilithic Chlorophyll *a*, Biovolume, and Cellular Carbon Accrual

There were no significant differences in concentrations of chlorophyll *a* among the three UV treatments in this experiment. Most evidence suggests that UVR inhibits algal productivity by the destruction of photosynthetic pigments, such as chlorophyll, or damage to chloroplasts (Xenopoulos et al. 2000). Previous studies have attributed the UV-induced reduction of periphytic chlorophyll *a* concentrations to inhibited periphyton development (Bothwell et al. 1993, 1994; Vinebrooke and Leavitt, 1996; Francoeur and Lowe, 1998). It is also possible that chlorophyll *a* declines with increased UVR due to pigment bleaching or photoacclimation (Falkowski and LaRoche 1991). The chlorophyll *a* content of algae standardized by dry weight varies considerably with nutrient availability and temperature (Healy 1975). In this study, no change of chlorophyll *a* between treatments, while

photosynthetic rates declined in UVR treatments, indicates that damaged or reduced chlorophyll was not the cause of reduced photosynthesis.

It is possible that chlorophyll *a* concentrations were not different among treatments because UV intensity was not as great in this study as in previous studies. Bothwell et al. (1993) found that UVB restricted chlorophyll accrual in shallow (depth of 1 cm) experimental flumes. - Francoeur and Lowe (1998) detected a substantial decline in chlorophyll *a* concentrations in epilithon (6 cm deep) exposed to UVR in a mesotrophic, glacial lake. Vinebrooke and Leavitt (1996) also found a decline in chlorophyll *a* when periphyton was exposed to ambient levels of UVR in a clear water alpine lake. Alpine and shallow aquatic habitats both have higher intensities of UVR than deeper (30 to 50 cm), higher DOC (i.e., boreal) lakes (Vinebrooke and Leavitt 1996, Schindler et al. 1996a).

Biovolume estimates were lower in epilithon exposed to UVR in August and September. These results combined with consistently lower levels of epilithic carbon content in the UV exposed treatments support the hypothesis that algal growth is inhibited by UVR. McNamara and Hill (2000) also found that epilithic biovolume significantly declined in response to artificially increased UVB in shallow (1.5 cm deep) experimental streams. Biovolume was also lower in periphyton exposed to ambient UVR in an alpine lake (Vinebrooke and Leavitt 1996). Biovolume estimates in my study do not corroborate the chlorophyll *a* measures. Biovolume may be a more sensitive measure to UV damage than chlorophyll *a* because effects were seen when chlorophyll *a* did not detect change

Chlorophyll *a* concentrations, cellular carbon and biovolume estimates did not increase with similar magnitude as the photosynthetic responses in the PAR treatments. If standing biomass (estimated here by cellular carbon, chlorophyll *a* and biovolume) is related to production, the biomass of the epilithon exposed to UV would decline with photosynthetic rates. A possible explanation for the inconsistency between photosynthesis and biomass in the PAR treatment could be the uncoupling of photosynthesis from growth. However, the uncoupling of net primary productivity with population growth in algae is usually a cellular manifestation of stress (Berman-Frank and Dubinsky 1999). Therefore, it is likely that metabolic responses to UVR stress are more sensitive than chlorophyll *a* or biovolume estimates, causing an inconsistency in the measures.

It is unlikely that epilithic biomass was affected by different grazing pressures among the three UV treatments in this study because preliminary results (unpublished data) revealed that chironomids were almost negiligible on the tiles, and few other grazers were observed during sampling. Donahue (2000) also found that L224 had low densities of chironomids. Bothwell et al. (1994) showed that long term exposure to UVR could indirectly stimulate algal biomass accrual by selectively inhibiting benthic herbivores. Vinebrooke and Leavitt (1996) and Francoeur and Lowe (1998) observed negligible effects of grazers on UV-exposed and UV-protected epilithon. However, it is possible that the importance of herbivores in L224 was underestimated in my experiments, because herbivory may be lower on ceramic tiles than on natural substrata (Aloi 1990).

UV-related changes in algal community structure

There is evidence for UV-induced taxonomic shifts among treatments. Diatoms were the most dominant algal group in the PAR treatment in August and September, whereas they were reduced in the UVR treatments. These data support recent findings that diatoms appear to be indicators of low UV conditions (Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998). Leavitt et al. (1999) found that as UV increased 8-fold following acidification of L302S, pigments corresponding with diatoms declined 50%. Vinebrooke and Leavitt (1999b) found that a decrease in diatoms accounted for the decline in benthic algal biomass associated with increasing elevation in a survey of 20 mountain lakes and ponds. As a result of higher incident UVR and lower DOC concentrations, the inhibitory effects of UVR on periphyton may be more damaging in high elevation and acidified lakes than in pristine, lower altitude lakes.. Similar taxonomic trends are seen in response to UV in my experiments as in response to increasing elevation or acidification, therefore, it is possible that taxonomic shifts attributed to changes in pH or altitude may be related at least partly to interspecific UVR adaptations.

Certain diatoms are susceptible to UVR because of their relatively small size (Garcia-Pichel 1994) and low concentration of UV-absorbing pigments (Karentz et al. 1991). Vinebrooke and Leavitt (1996) and Bothwell et al. (1993) both attribute UV-induced decreases in diatom abundance to a decline in *Achnanthes minutissima* (a small diatom). I observed a relatively constant biovolume of *A. minutissima* in L224 in all treatments, while other diatoms changed in response to UVR, which suggests that this species was not sensitive to UVR at my study site. Francoeur and Lowe

(1998) and McNamara and Hill (2000) found that *A. minutissima* increased in periphyton exposed to UVR.

Rhopalodia gibba accounted for the higher diatom biomass in the PAR treatment in this experiment and in the study done by Francoeur and Lowe (1998). This diatom contains cyanobacterial endosymbionts capable of fixing atmospheric nitrogen (Stevensen et al. 1996). UVR may have greater effects on benthic communities in low nitrogen habitats, because the dominant species (nitrogen fixers) are highly UVR sensitive (Francoeur and Lowe 1998). However, nitrogen was not a limiting nutrient in L224, because the epilimnetic sediments regenerate nitrogen (Hendzel et al. 1994). Future studies will be required to determine how UV affects nitrogen assimilation in algal assemblages.

Chlorophytes made up a larger proportion of the algal assemblages in treatments exposed to UVR than in PAR treatments. *Mougeotia sp.* (a filamentous chlorophyte) was responsible for this trend in July and September. Turner et al. (1991, 1995) found that green algae (particularly *Mougeotia sp.*) are abundant in acidified lakes. It is possible that under natural conditions, *Mougeotia sp.* is competitively excluded, but once high UV conditions occur (i.e. due to reduced DOC during acidification), the diatoms are suppressed, allowing the slower-growing *Mougeotia sp.* to dominate. Filamentous green algae were found to be 15 times more abundant in experimental streams exposed to photon flux densities of 450 $\mu E/m^2/s$ than in those exposed to 50 $\mu E/m^2/s$ (DeNicola and McIntire 1990, Steinman and McIntire 1986). Donahue (2000) found that filamentous chlorophytes dominated the shallowest, highest UV and PAR exposure sites in a survey at ELA. Therefore,

Mougeotia sp. may have a competitive advantage over other taxa in high UV conditions.

Although algal taxonomic composition diverged as a result of different UV regimes, species richness and diversity remained relatively unchanged. Vinebrooke and Leavitt (1996) found that species richness was lower in epilithon exposed to UV after 30 days. I found low species richness in July (~30 days after the start of my experiment), however this did not persist. It is possible that epilithic communities exposed to UVR had lower species richness than PAR treatments for the initial stages of succession because the UV exposed communities were slower to reach maturity.

In September, the taxonomic composition in the three UV treatments remained different. Therefore, it appears that algal communities do not converge when UV effects on growth dissipate. I hypothesized that the taxonomic communities would diverge due to differing UV sensitivities during the high UV season and then converge in the autumn when UV became an insignificant factor determining growth. Perhaps community dominance was determined earlier in the growing season, and once fixed, remained stable as UV flux declined.

Limitations of artificial substrata

Preliminary results (unpublished data) revealed that the epilithic community on the ceramic tiles did not represent the natural communities. Tuchman and Stevenson (1980) also found that there was less heterogeneity in the algal communities on ceramic tiles compared to natural rock substrate. Ceramic tiles lack the surface irregularities of natural rock substrata (Aloi 1990). Differences between

natural and clay tile substrates affect algal composition, population size and behaviour of herbivores (reviewed by Aloi 1990). Metabolic rates reported in my study likely did not represent the natural community. Net photosynthetic rates during the early phase of growth in June are much lower than naturally occurring biofilms in L224 (Turner unpublished data). The initial low rate is probably an artifact of the need for colonization of the tiles. Caution must be used in extrapolating the results of this experiment to whole lake ecosystems.

Food Quality

Carbon: phosphorus (C:P) and nitrogen: phosphorus (N:P) ratios were both lower in epilithon exposed to UVR, consequently increasing stoiciometric food quality (Sterner et al. 1993). A higher food quality in epilithon exposed to UVR is counter-intuitive because algal nutrient uptake (Dohler and Biermann 1987; Dohler 1992; Hessen et al. 1995), protein synthesis (Gerber and Hader 1992; Behrenfeld et al. 1995; Buma et al. 1996), and fatty acid production (Wang and Chai 1994, Hessen et al. 1997) have been inhibited by UVR elsewhere. McNamara and Hill (2000) found that artificially increased UVB did not affect cellular nitrogen and phosphorus content in stream periphyton. Weidman (2000) also found that UVR did not change carbon, phosphorus and nitrogen content in epilithon at depths of 0.54 m and greater in L224. The lower carbon uptake rates of epilithon exposed to UVR in this study may have driven C:P ratios down, because the phosphorus content did not differ among treatments. However, McNamara and Hill (2000) did not find that depressed ^{14}C uptake rates corresponded with lower nutrient levels in the periphyton they examined.

There was more cellular nitrogen in the PAR treatment than in UVR exposed treatments in this study, suggesting that nitrogen uptake was inhibited in algae exposed to UVR. ^{15}Nitrogen uptake was reduced in diatoms under UVB irradiance (Dohler 1985; Dohler and Biermann 1987; Dohler 1992). Ammonium and nitrate uptakes were also inhibited in algae exposed to UVB (Behrenfeld et al. 1995). The stoichiometric trends in my experiment may reflect different taxonomic groups present in the epilithon exposed to varying UV treatments. *Rhopilodia gibba*, which contains N-fixing symbionts, was more abundant in epilithon with higher N:P ratios (PAR treatment). Sterner and Hessen (1994) show that high N:P ratios are the outcome of N-fixing dominated algal communities. Research has been limited to pelagic stoichiometric studies. UV may explain the variation in the C:N:P ratios in periphyton (Frost et al. in progress), however future studies are required.

Lower C:P and N:P ratios were found in epilithon exposed to UVR than in the PAR treatment, suggesting that shallow regions of the littoral zone, which are subject to higher intensities of UVR and hydrodynamic energy, may be a beneficial habitat for herbivores to graze from. Food quality shifts in epilithon could have serious implications for benthic grazers (Vos et al. 2000; Sterner et al. 1997). *Daphnia spp.* grazing on nutrient limited algae exhibited reduced growth rates and fecundity (Sterner et al. 1993; Gulati and DeMott 1997; van Donk et al. 1997). Mayfly growth rates have also been reduced by low nitrogen content in food (Soderstrom 1988). There may be a trade-off for grazers to obtain optimal growth if higher food quality exists in harsh, intensely irradiated habitats.

Epilithic scytonemin concentrations in response to UVR

Scytonemin had a higher prevalence in the PAR + UVA + UVB treatment in L224, although not significantly. Epilithon exposed to PAR + UVA had similar scytonemin concentrations to the PAR treatment. These results suggest that UVB is the primary stimulant of scytonemin production in L224 epilithon. Although my analyses had limited sensitivity, results suggest some areas for future research. Among the many photo-adaptive mechanisms to limit UVR damage, algae produce photoprotective pigments, such as scytonemin, carotenoids, and mycosporine-like amino acids that absorb ultraviolet radiation to prevent cellular damage (Carreto et al. 1990; Karentz et al. 1994). The production of scytonemin, a pigment that absorbs wavelengths from 280-450 nm (McNamara and Hill 2000), is a physiological response to solar radiation within the ultraviolet region (Garcia-Pichel and Castenholz 1991). Leavitt et al. (1997) found that scytonemin concentration in sediment cores increased with maximum depth of UVR penetration in the recently acidified L302S at the ELA, which suggests that scytonemin is useful as a marker of increased depth of UV penetration in lakes. Donahue (2000) also found that scytonemin dominance in epilithic communities increased with UVR exposure in a lake survey at the ELA. The shallowest communities had the largest concentrations of scytonemin in his survey, suggesting that deeper communities need less protection from damaging UVR.

Conclusions

This study, considered together with research conducted in shallower (Bothwell et al. 1993 and 1994; McNamara and Hill 2000) and higher latitude

(Vinebrooke and Leavitt 1996) habitats, suggests that the epilithic community is a valuable indicator of changes to the UVR environment of aquatic ecosystems. The results of this study are consistent with the hypothesis that UVR reduces epilithic photosynthetic rates. Primary production was predominantly reduced by UVA in L224. Further work is necessary, however, to fully understand how epilithic respiration rates are affected by UV-induced algal cellular damage and pigment production, microinvertebrate constituents of the epilithon, and taxonomic shifts within the community.

In this study, there is evidence that UVR induced taxonomic shifts in the epilithic algae. Epilithic communities did not converge once UV declined due to seasonal trends, lending support to the argument that communities are most susceptible to UVR during early stages of colonization. Biovolume estimates and cellular carbon content support the hypothesis that epilithic algal accrual is negatively affected by UVR. There is evidence that epilithic C:N:P ratios are affected by UVR in my study, indicating future research is necessary to determine the effect of UVR on the elemental composition of epilithic biofilms and its consequences on food quality. Future studies should incorporate trophic level interactions and consider the effects of long-term exposure to UVR.

Table 1. Results of RM-ANOVA of the effects of ultraviolet radiation (UVR) and time on epilithic net photosynthesis (n=6), dark respiration rates (n=6) and R_{dark}:P_{gross} ratios (n=2). Data given are F-values.

Source	df	Photosynthetic rates	Respiration rates	R_{dark}:P_{gross}
UVR	2	4.793*	0.458	0.482
Time	7	49.031**	13.494**	10.635**
Time x UVR	14	4.237**	1.901*	1.288

*$p < 0.05$, **$p < 0.001$

Table 2. Biovolume ($\mu m^3/cm^2$) of the most prevalent species in diatoms (A), chlorophytes (B), cyanophytes (C) in each treatment on 4 sample periods. Numbers represent composite samples from 3 replicates.

A	Treatment		
Diatoms	**PAR**	**PAR + UVA**	**PAR + UVA + UVB**
16-Jun-98			
Achnanthes minutissima	5.12	4.00	4.46
Rhopalodia gibba	0.00	0.00	0.00
Nitzschia filiformis	2.06	0.47	0.00
14-Jul-98			
Achnanthes minutissima	13.38	20.53	13.75
Rhopalodia gibba	0.00	10.31	0.00
Nitzschia filiformis	0.60	0.70	1.03
25-Aug-98			
Achnanthes minutissima	14.63	11.00	7.22
Rhopalodia gibba	69.58	35.25	5.15
Nitzschia filiformis	12.06	0.00	0.00
15-Sep-98			
Achnanthes minutissima	8.53	14.93	5.41
Rhopalodia gibba	44.70	14.03	23.39
Nitzschia filiformis	0.00	0.00	0.00

B	Treatment		
Chlorophytes	**PAR**	**PAR + UVA**	**PAR + UVA + UVB**
16-Jun-98			
Mougeotia sp.	2.32	0.00	0.00
Bulbochaete sp.	1.30	1.23	1.07
Oedogonium sp.	0.00	0.00	1.05
14-Jul-98			
Mougeotia sp.	0.00	6.68	19.33
Bulbochaete sp.	8.45	0.00	0.00
Oedogonium sp.	0.00	3.13	0.00
25-Aug-98			
Mougeotia sp.	0.00	5.56	0.00
Bulbochaete sp.	0.00	0.00	0.00
Oedogonium sp.	0.00	7.10	4.64
15-Sep-98			
Mougeotia sp.	0.00	0.00	21.65
Bulbochaete sp.	0.00	0.00	0.00
Oedogonium sp.	5.02	0.00	0.00

C	Treatment		
Cyanophytes	**PAR**	**PAR + UVA**	**PAR + UVA + UVB**
16-Jun-98			
Phormidium sp.	2.67	3.24	3.25
Calithrix sp.	0.00	0.00	0.00
14-Jul-98			
Phormidium sp.	6.60	4.02	4.76
Calithrix sp.	0.00	0.00	0.00
25-Aug-98			
Phormidium sp.	13.78	11.66	9.98
Calithrix sp.	10.44	0.00	0.00
15-Sep-98			
Phormidium sp.	17.97	6.18	6.89
Calithrix sp.	11.44	11.60	1.50

Table 3. Diversity (H') and species richness of epilithon in three UVR treatments on 4 sample periods. Numbers represent composite samples from 3 replicates.

Date	Diversity (H')			Species Richness		
	PAR	PAR+UVA	PAR+UVA +UVB	PAR	PAR+UVA	PAR+UVA +UVB
16- Jun-98	2.89	2.98	2.92	22	28	23
14-Jul-98	2.38	2.70	2.39	19	15	13
25-Aug-98	2.72	2.78	2.57	14	16	14
15-Sep-98	2.40	2.56	2.86	13	14	17

Table 4. Results of RM-ANOVA of the effects of ultraviolet radiation (UVR) and time on epilithic carbon: phosphorus (C:P), carbon: nitrogen (C:N), and nitrogen: phosphorus (N:P) ratios (n=2). Data given are F-values.

Source	df	C:P	C:N	N:P
UVR	2	9.017	1.903	13.086*
Time	7	2.568*	4.781*	4.545*
Time x UVR	14	0.757	0.964	0.928

*$p < 0.05$, **$p < 0.001$

Table 5. Seasonal mean (n=3) epilithic carbon, nitrogen, and phosphorus ($\mu g/cm^2$) (n=19) collected in 7 sample periods (first sample period excluded) in three UVR treatments (± standard error).

Treatment	Carbon	Nitrogen	Phosphorus
PAR	283.77 ± 29.77	18.20 ± 1.72	0.83 ± 0.09
PAR + UVA	226.92 ± 31.57	15.38 ± 1.95	0.71 ± 0.10
PAR + UVA + UVB	202.25 ± 19.95	13.97 ± 1.39	0.77 ± 0.07

Table 6. Results of RM-ANOVA of the effects of ultraviolet radiation (UVR) and time on epilithic carbon, nitrogen, and phosphorus concentrations (n=2). Data given are F-values.

Source	df	Carbon	Nitrogen	Phosphorus
UVR	2	2.664	3.223	0.653
Time	7	12.266**	14.912**	5.231*
Time x UVR	14	0.640	0.756	1.522

*$p < 0.05$, **$p < 0.001$

Table 7. Results of RM-ANOVA of the effects of ultraviolet radiation (UVR) and time on epilithic chlorophyll *a* and scytonemin pigment concentrations (n=2). Data given are F-values.

Source	df	Chlorophyll *a*	Scytonemin
UVR	2	1.271	6.315
Time	7	18.915**	1.631
Time x UVR	14	2.327	0.791

**$p < 0.001$

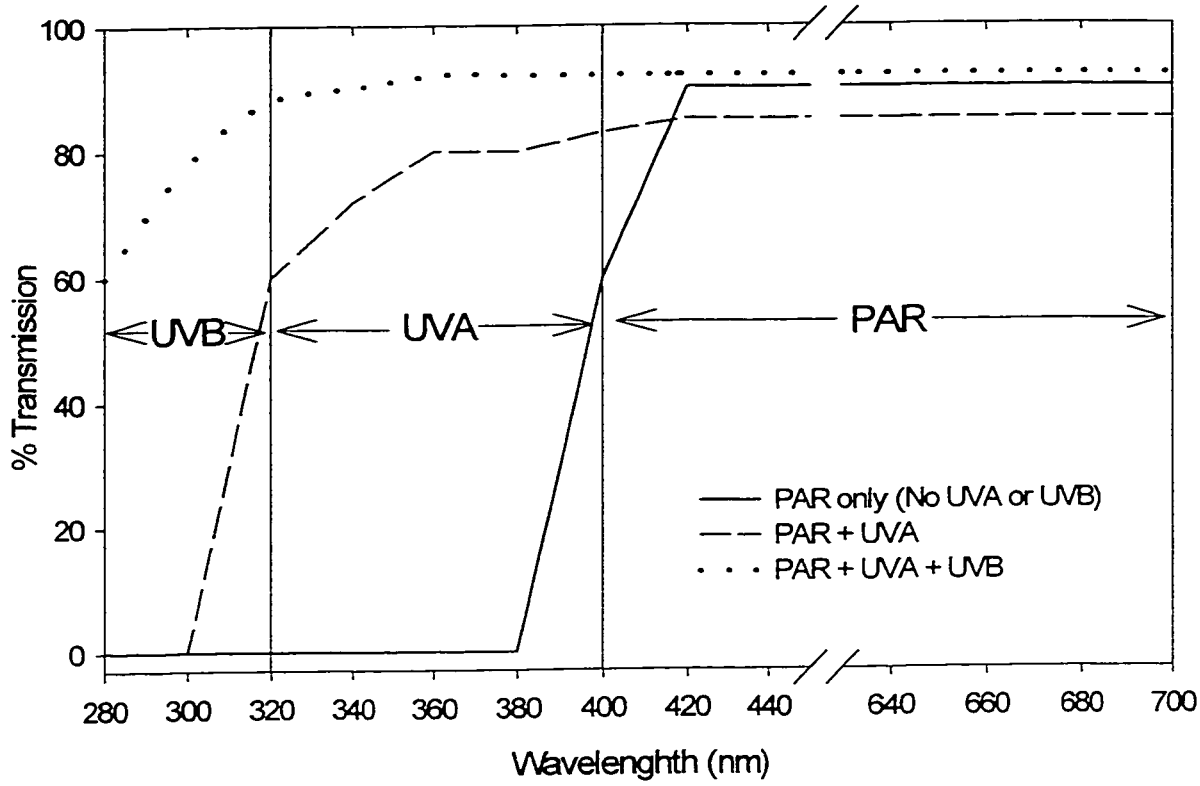

Figure 1. Transmission spectra of acrylic solar filters used for the PAR (photosynthetically active radiation), PAR + UVA, and PAR + UVA + UVB treatments.

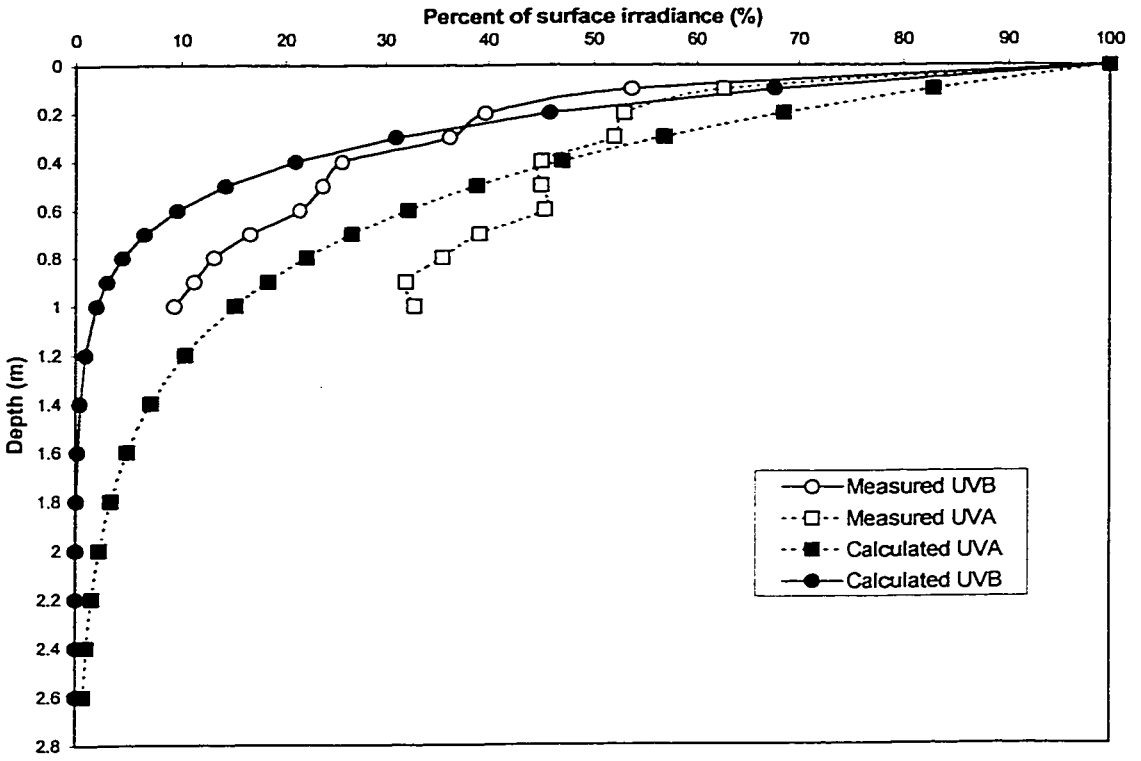

Figure 2. Percent transmission of UVA and UVB in L224 calculated using Scully and Lean's (1994) attenuation model with mean [DOC] for 1998 (3.34 mg/L), and measured with a Li-Cor 1800UM Spectroradiometer.

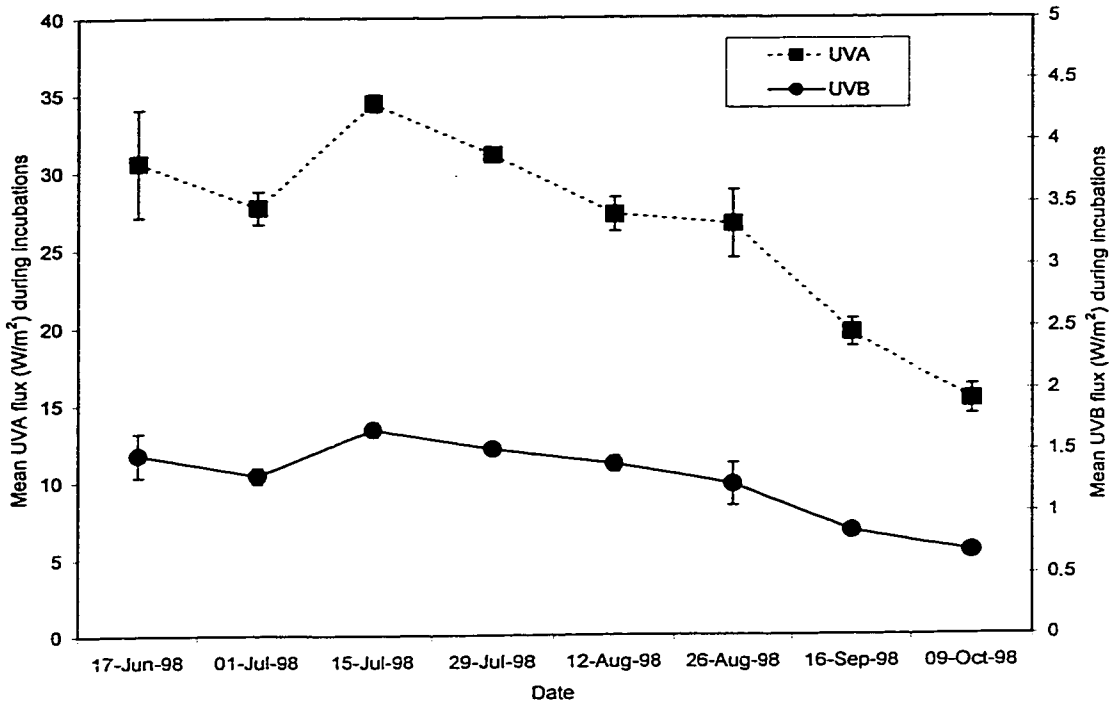

Figure 3. Mean (± standard error) UVA (primary axis) and UVB (secondary axis) flux during metabolic incubations over eight sample periods (n=3).

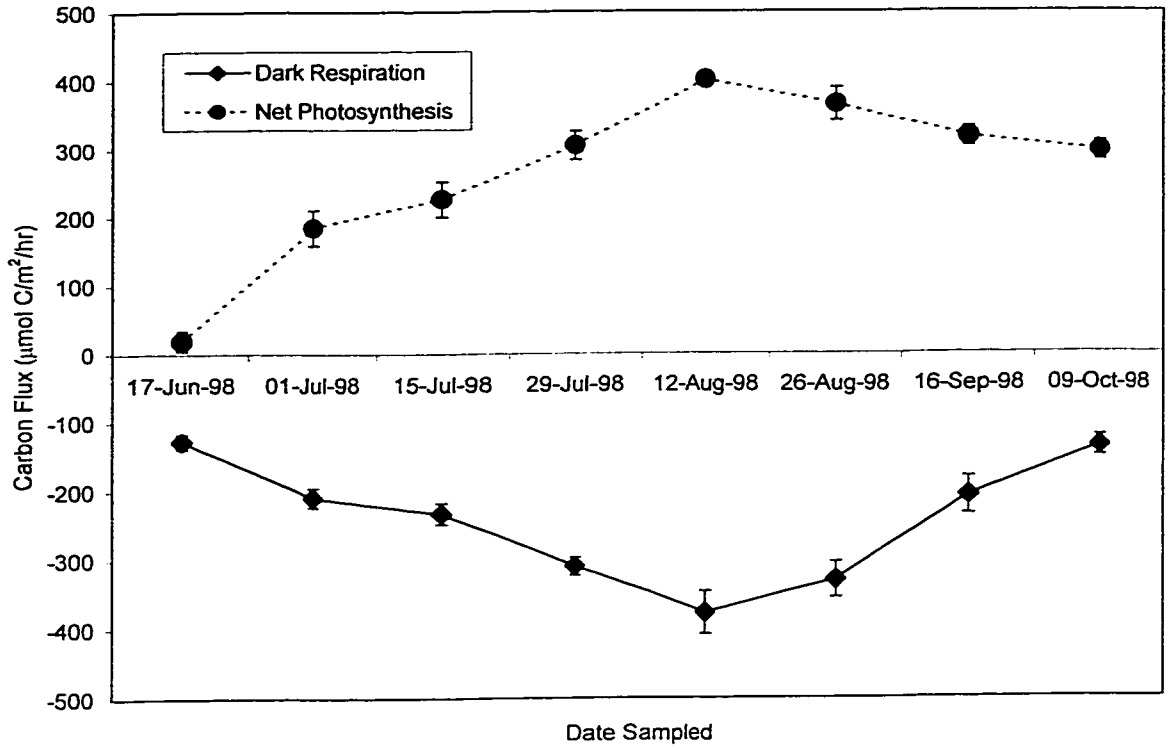

Figure 4. Mean (± standard error) seasonal trends of photosynthetic and respiration rates (µmol C/ m^2/hr) for all treatments (n=9) over eight sample periods. Negative values given for respiration to differentiate the two metabolic measures.

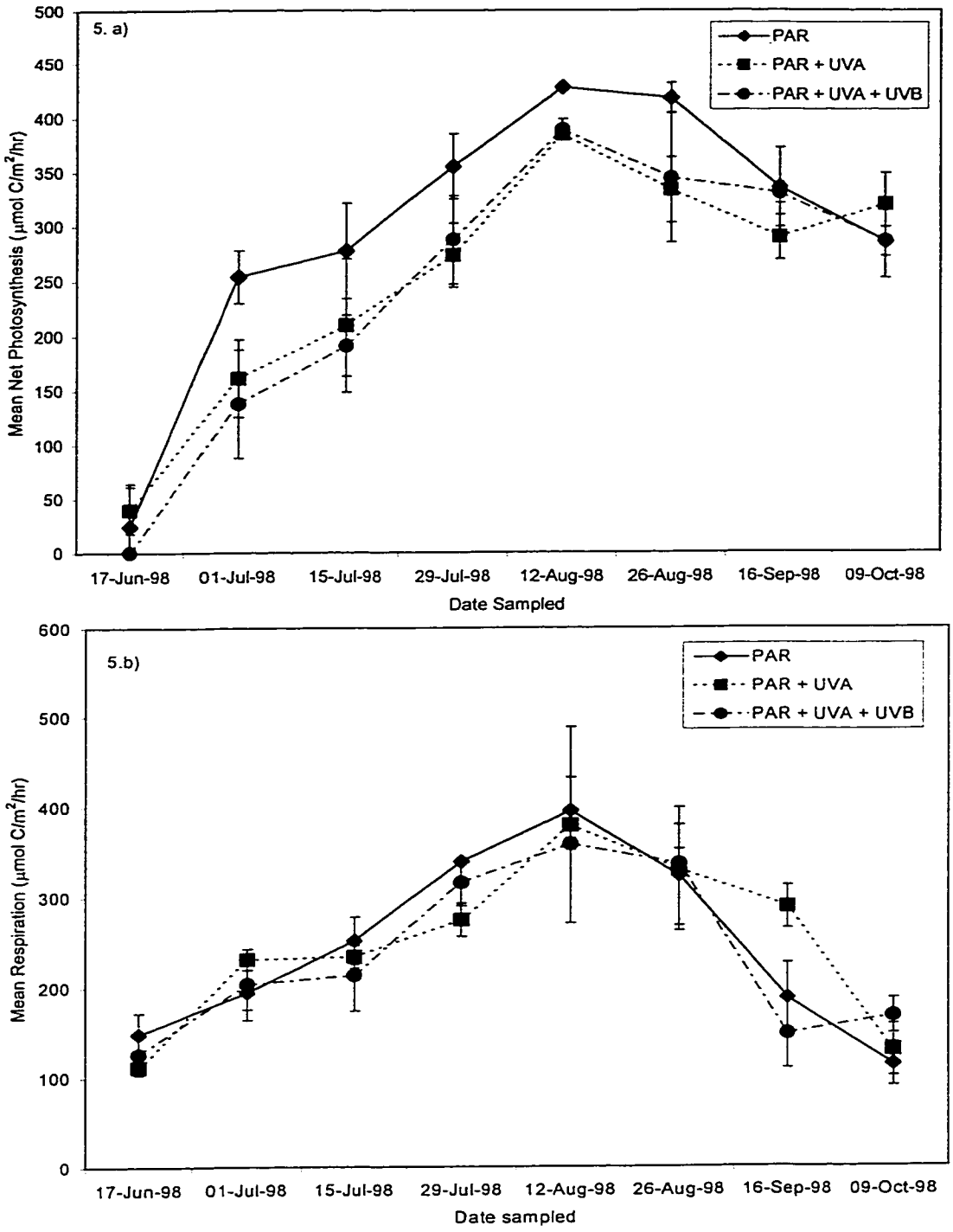

Figure 5. The mean (n=3) (± standard error) net photosynthetic rates (µmol C/ m^2/ hr) (a) and absolute value respiration rates (µmol C/ m^2/ hr) (b) for epilithon exposed to three UV treatments over eight sample periods.

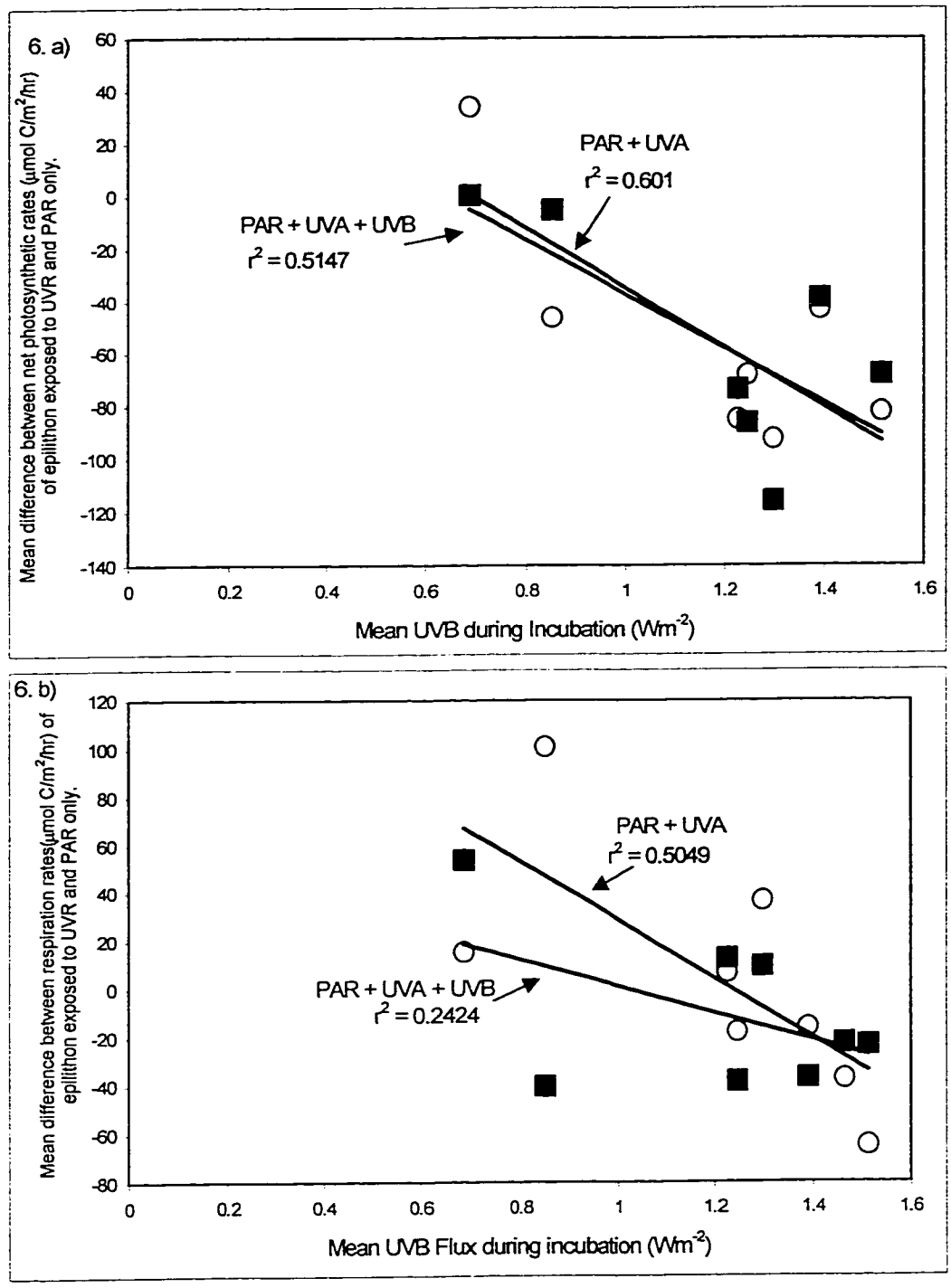

Figure 6. The mean difference of net photosynthetic rates (µmol C/ m²/ hr) (a) and respiration rates (µmol C/ m²/ hr) (b) between epilithon exposed to UVR and PAR only against UVB intensity during metabolic incubations. ○ = (PAR + UVA) –PAR treatments, ■ = (PAR + UVA + UVB) – PAR treatments.

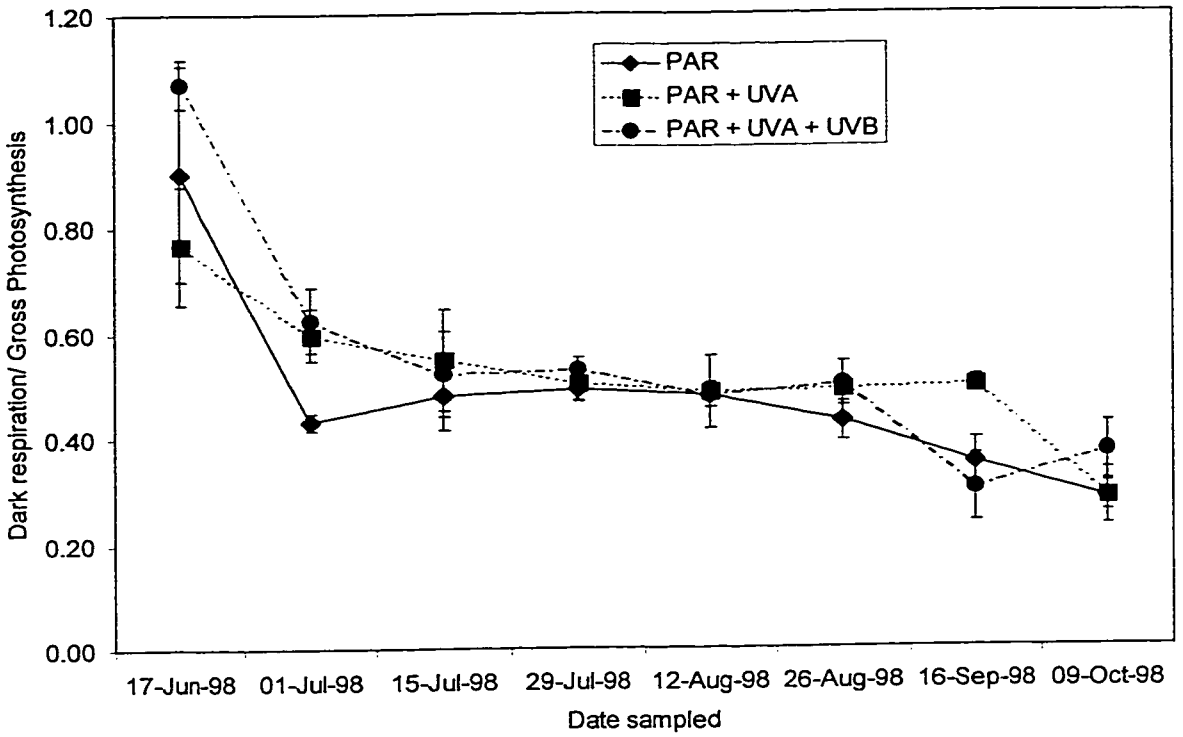

Figure 7. Mean (± standard error) dark respiration to gross photosynthesis ratios (n=3) for epilithon exposed to three UV treatments over eight sample periods.

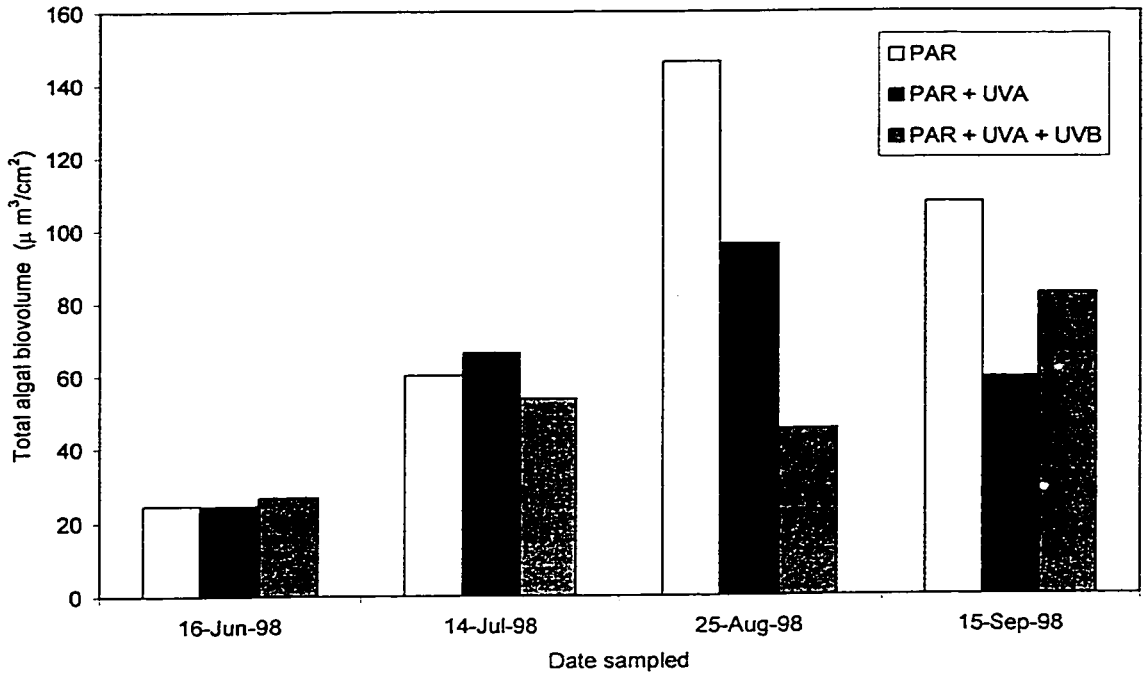

Figure 8. Total algal biovolume ($\mu m^3/cm^2$) of epilithon under three UV treatments on four sample periods. Each bar represents a composite sample of three replicates.

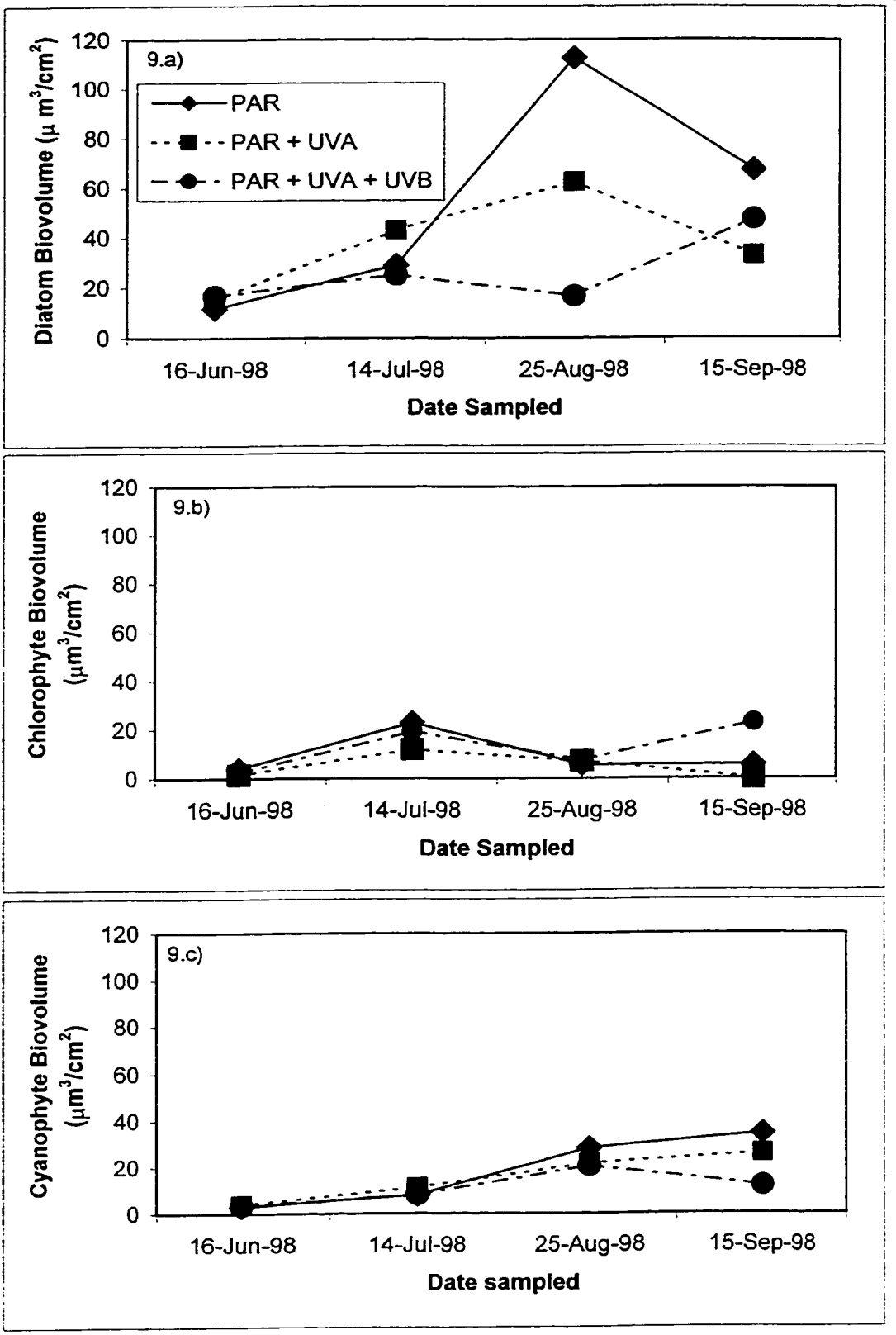

Figure 9. Biovolume ($\mu m^3/cm^2$) of diatoms (a), chlorophytes (b) and cyanophytes (c) of epilithon exposed to three UV treatments on 4 sample periods. Each point represents a composite sample of three replicates.

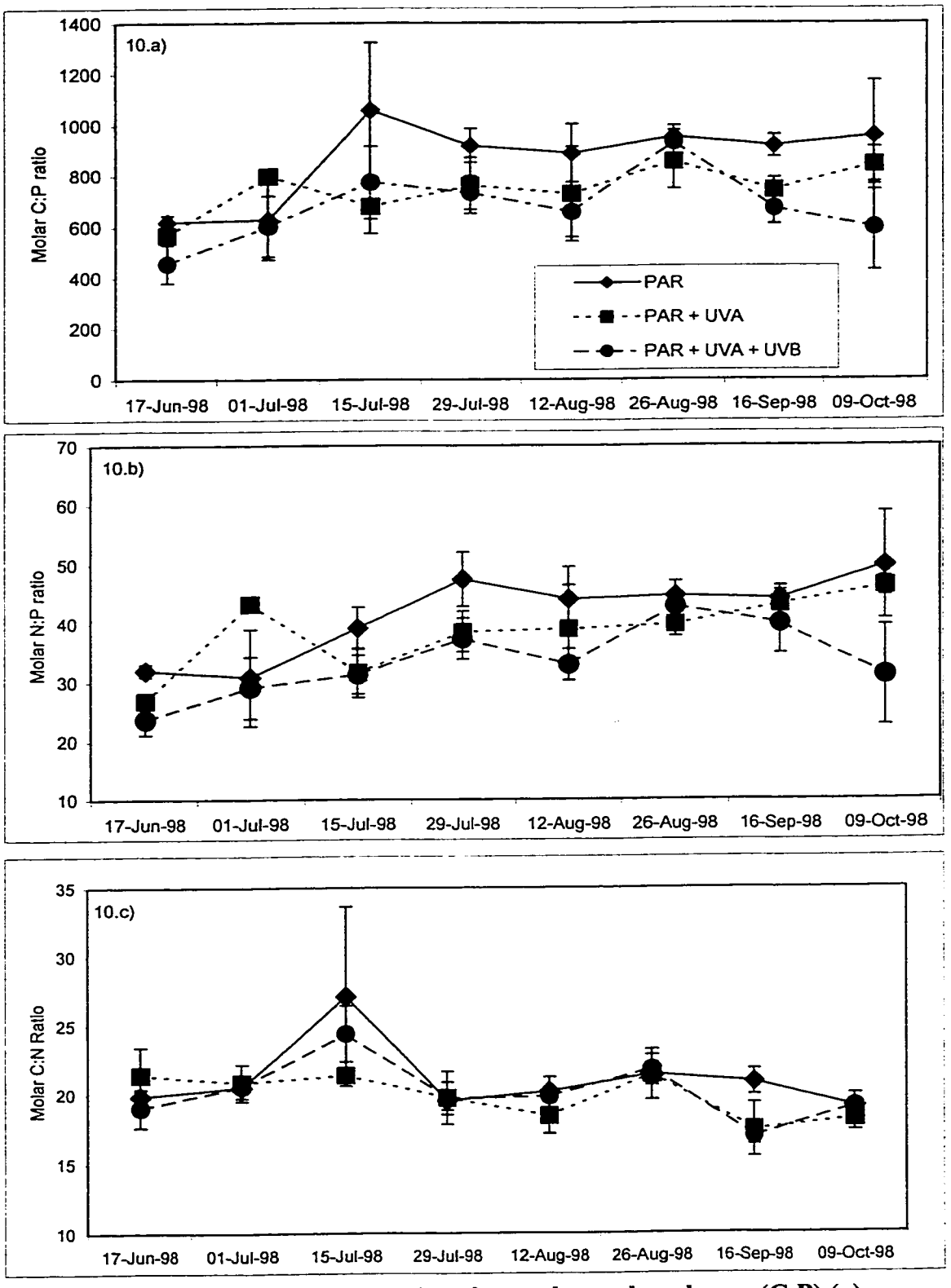

Figure 10. Mean (± standard error) molar carbon: phosphorus (C:P) (a), nitrogen; phosphorus (N:P) (b) and carbon: nitrogen (C:N) (c) epilithic ratios exposed to three UV treatments over eight sample periods (n=3).

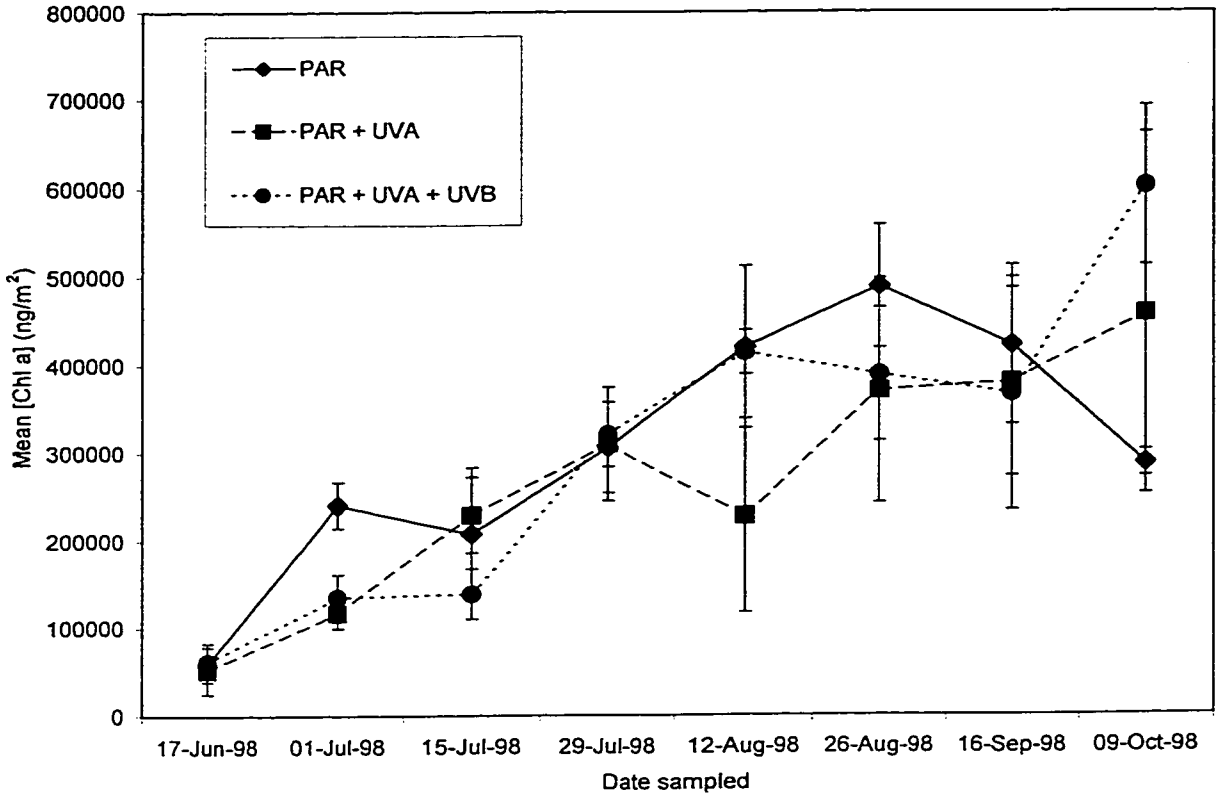

Figure 11. Mean (± standard error) chlorophyll *a* pigment concentrations (ng/m^2) for epilithon exposed to three UV treatments over 8 sample periods (n=3).

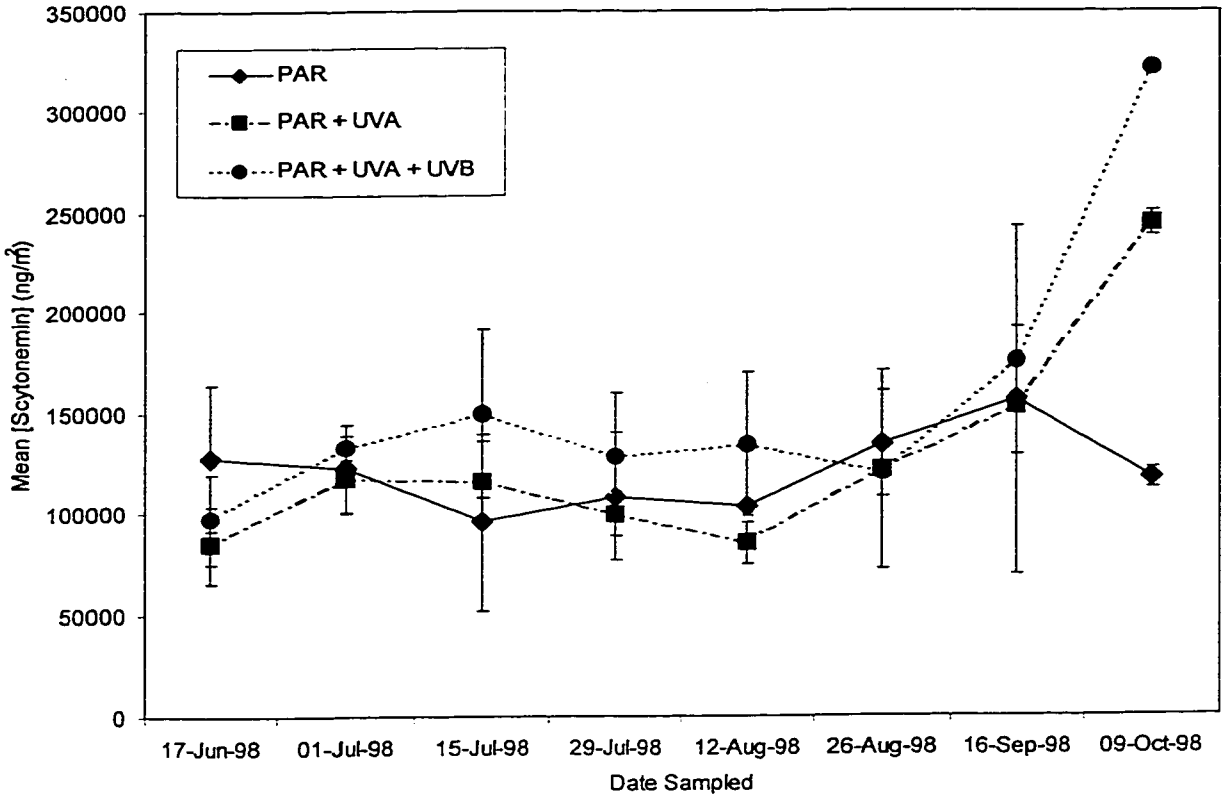

Figure 12. Mean (± standard error) scytonemin pigment concentrations (ng/m^2) for epilithon exposed to three UV treatments over 8 sample periods (n=3).

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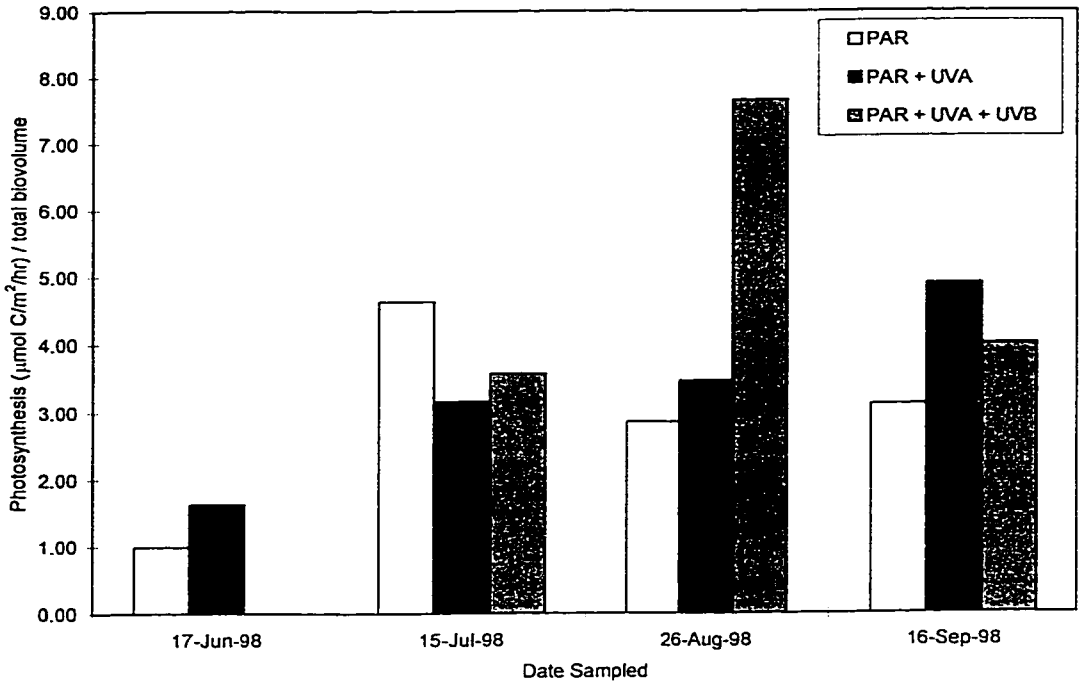
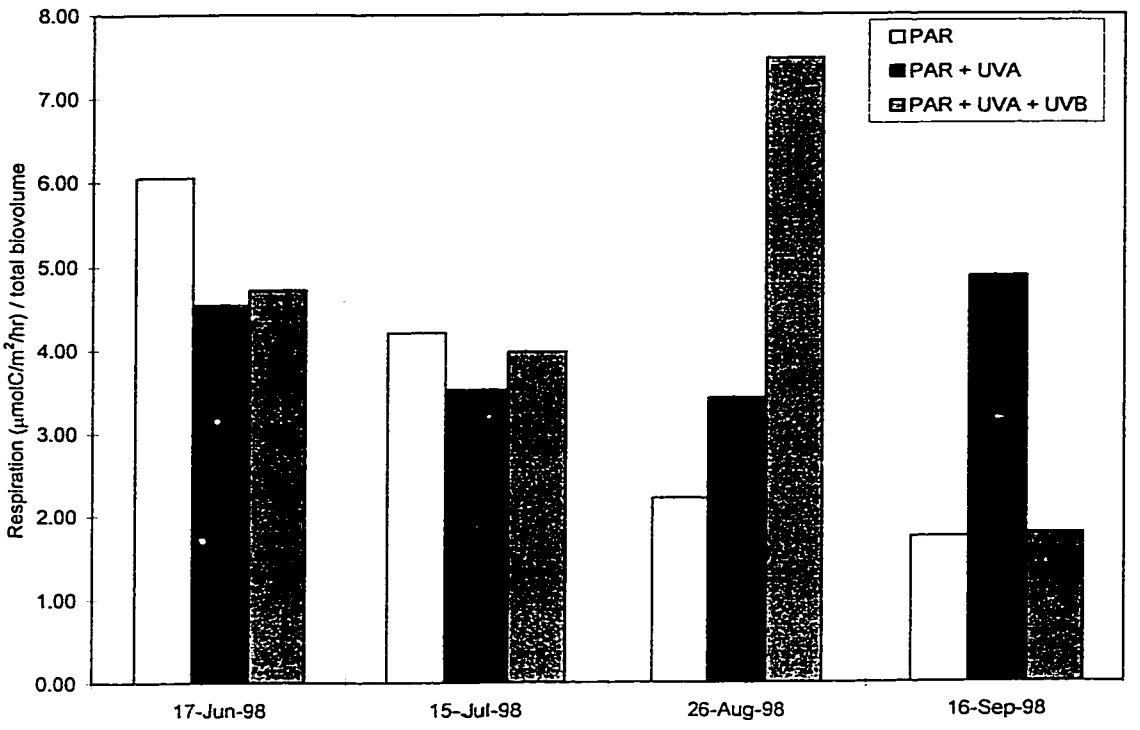
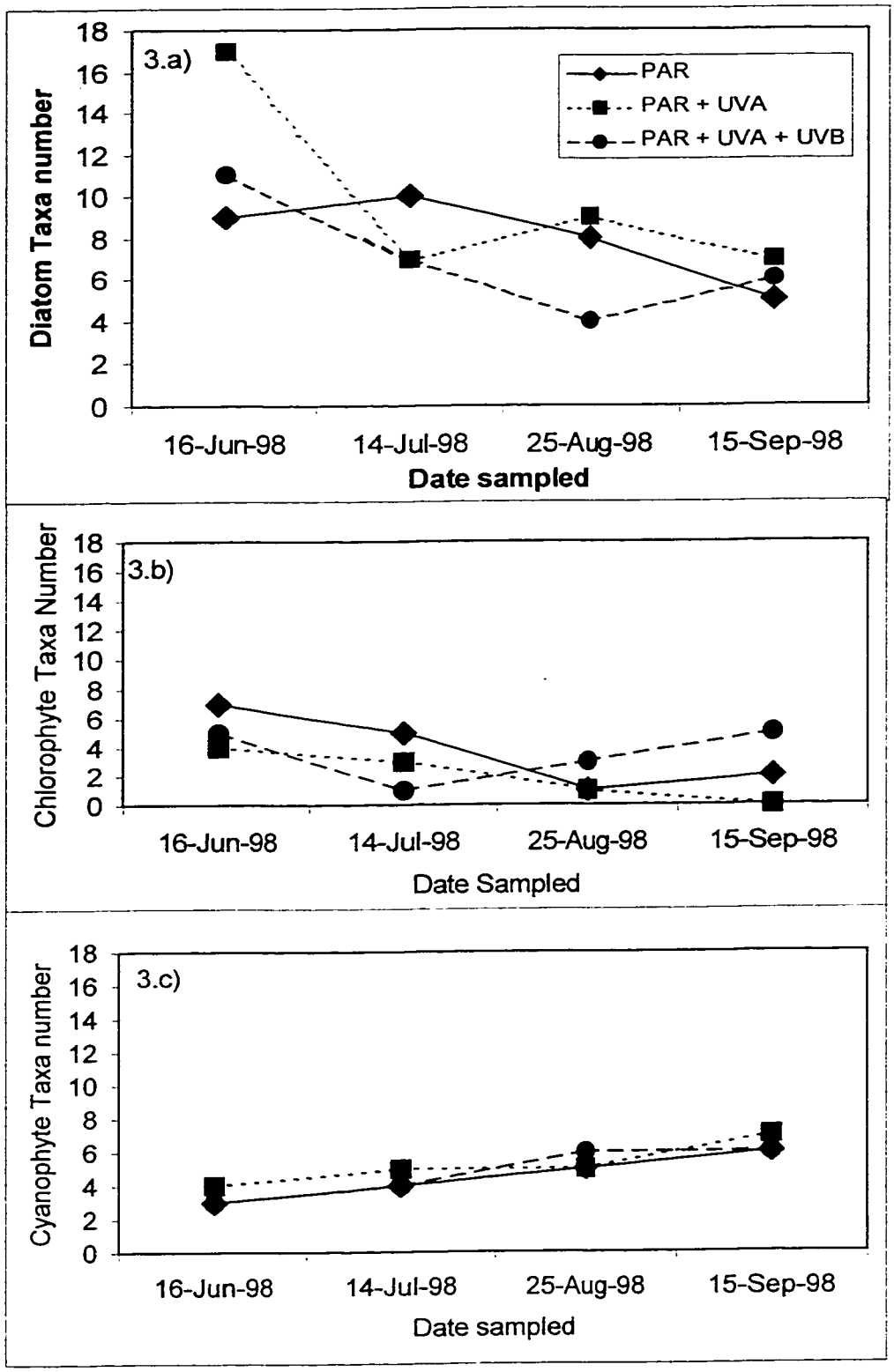
APPENDIX



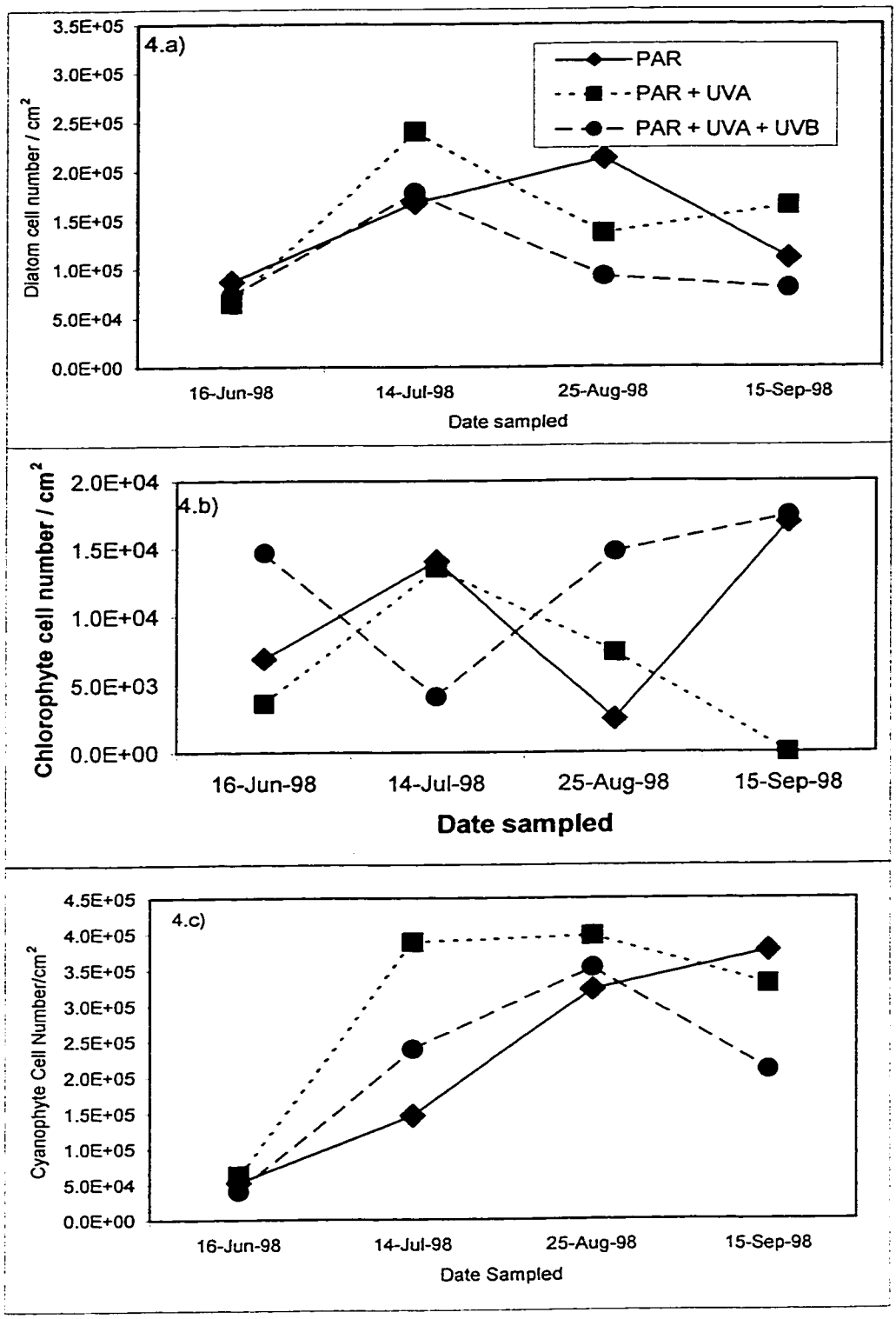
Appendix Figure 1. Photosynthesis (µmol C/ m^2/hr) standardized by biovolume (P/B) (µm^3/cm^2) of epilithon under three UV treatments on four sample periods. Each bar represents a mean photosynthetic rate (n=3) divided by a composite sample of three replicates.



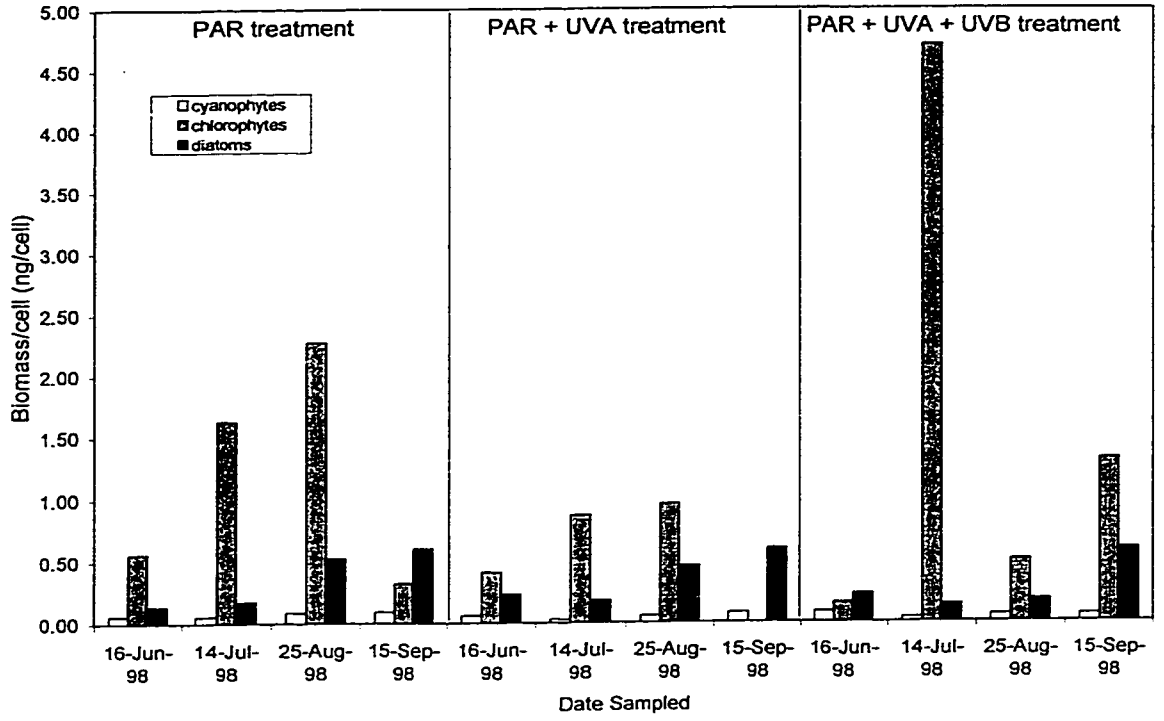
Appendix Figure 2. Respiration (µmol C/ m^2/hr) standardized by biovolume (R/B) (µm^3/cm^2) of epilithon under three UV treatments on four sample periods. Each bar represents a mean photosynthetic rate (n=3) divided by a composite sample of three replicates.



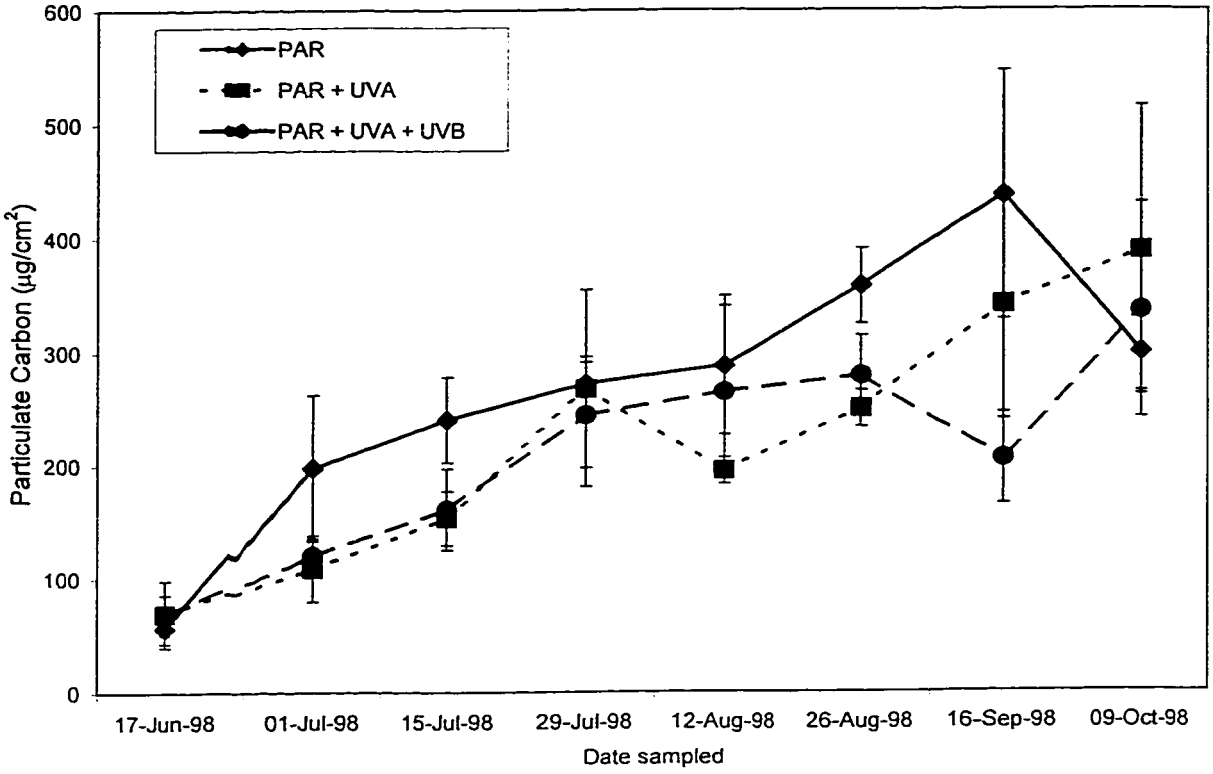
Appendix Figure 3. Taxa number of diatoms (a), chlorophytes (b) and cyanophytes (c) of epilithon exposed to three UV treatments on 4 sample periods. Each point represents a composite sample of three replicates.



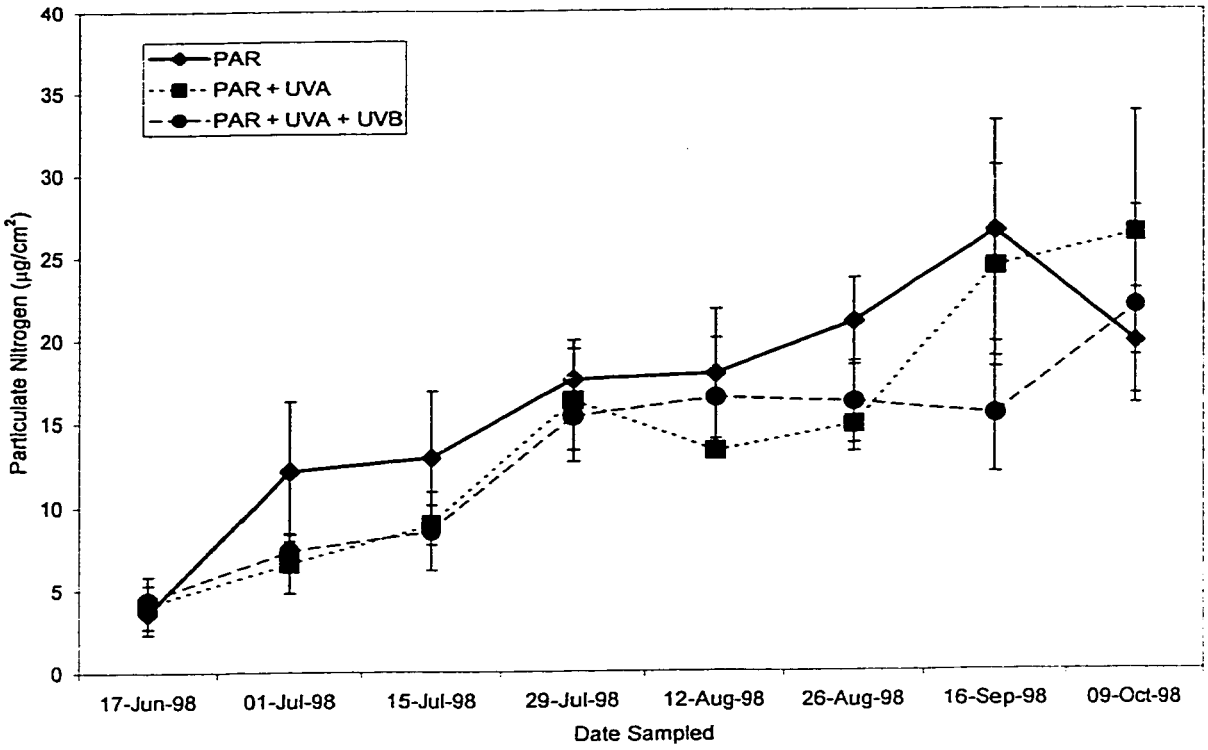
Appendix Figure 4. Cell number of diatoms (a), chlorophytes (b) and cyanophytes (c) of epilithon exposed to three UV treatments on 4 sample periods. Each point represents a composite sample of three replicates.



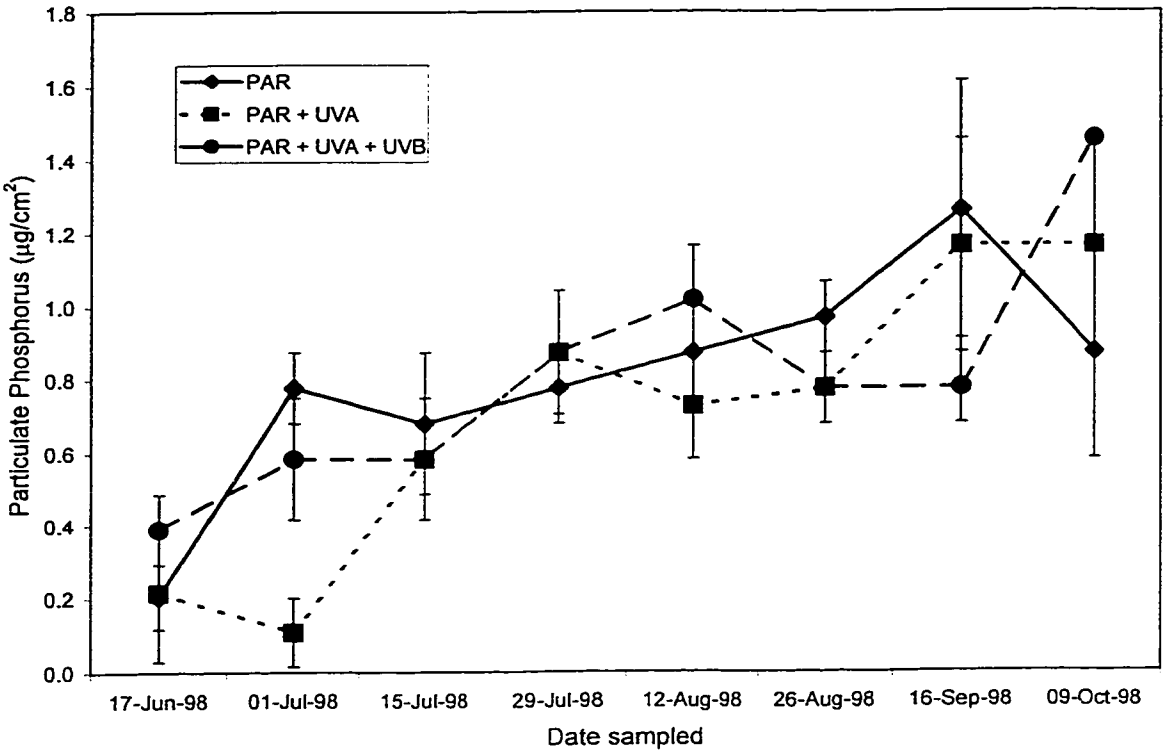
Appendix Figure 5. Biomass/cell (ng/cell) of diatoms, chlorophytes, and cyanophytes in three UV treatments over 4 sample periods. Each point represents a composite sample of three replicates.



Appendix Figure 6. Mean particulate carbon content (µg/cm^2) (n=3) of epilithon over 8 sample periods exposed to three UV treatments. Error bars represent standard error.



Appendix Figure 7. Mean particulate nitrogen content (µg/cm^2) (n=3) of epilithon over 8 sample periods exposed to three UV treatments. Error bars represent standard error.



Appendix Figure 8. Mean particulate phosphorus content ($\mu g/cm^2$) (n=3) of epilithon over 8 sample periods exposed to three UV treatments. Error bars represent standard error.