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Exposure of natural Antarctic marine microbial assemblages to ambient UV radiation: effects on the marine microbial community

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ABSTRACT: The effect of ambient solar UV radiation on natural protist (phytoplankton and protozoan) assemblages from Antarctic coastal waters was determined. Subsamples of the community were exposed to UV radiation attenuated to equivalent water column depths (ED) of 1.0, 2.0, 3.0, 3.6 and ≥20 m for periods of between 8 h and 1 wk. Total concentrations of phytoplankton in treatments exposed at 3.0 and 3.6 m ED were similar to those in control treatments. However, exposure of phytoplankton at ≤2.0 m ED for ≥1 d reduced overall cell size, concentration and biomass. Following UV exposure, some species of phytoplankton died, some flourished and others were unaffected. In contrast, the total concentrations of protozoans at ≤2.0 m ED for ≥1 d were commonly higher than in controls, and 2- to 3-fold higher than at 3.0 and 3.6 m ED. Significant negative correlation was observed between the total concentrations of phytoplankton and protozoa, showing that UV-induced mortality of phytoplankton resulted, directly or indirectly, in an increase in the concentrations of protozoans. Our results showed that UV radiation can change the biomass and species composition of marine microbial communities, altering size and availability of food for higher trophic levels and changing their trophic structure. Thus, increased UVB as a result of ozone depletion is likely to change food web structure and function and may influence biogeochemical cycles.

KEY WORDS: Antarctica · UVB radiation · Marine ecology · Phytoplankton · Protozoa · Bacteria

INTRODUCTION

Stratospheric ozone concentrations over Antarctica during spring commonly fall below 50% and may decline below 30% of pre-ozone-hole values (Kerr 1998). Depletion of ozone persists until February, leading to a 50 to 100% increase in UVB (280 to 320 nm) around the summer solstice (Frederick & Lubin 1994, Jones & Shanklin 1995). Thus, UVB radiation is enhanced throughout the period of greatest biological production in Antarctic waters. Ozone depletion currently enhances Antarctic erythemal UV around 130%, and this enhancement is predicted to exceed 100% between the years 2010 and 2020, and continue to exceed 50% from 2040 to 2050 (Taalas et al. 2000).

Concern regarding the effect of UVB on the Antarctic biota has led to extensive literature on the photobiology of Antarctic organisms, most of which has focused on the impact of UVB on phytoplankton (e.g. reviews by Karentz 1994, Davidson 1998, Vernet 2000). The evidence that UVB radiation can damage plankton is overwhelming, reducing production, growth and survival (Karentz 1989, Karentz et al. 1991). Furthermore, large interspecific differences have been reported in the tolerance of phytoplankton to UVB exposure, which can result in UV-induced changes in species composition of mixed algal cultures and natural phytoplankton assemblages (Smith et al. 1992, Davidson et al. 1996, Vernet 2000 and references therein). The sea ice and marginal ice zone support much of the primary production in the Southern Ocean, and blooms coincide with ozone depletion during spring and early summer (Smith & Nelson 1986,

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Voytek 1989). These environments are penetrated by biologically significant doses of UVB radiation (Smith et al. 1992, Ryan & Beaglehole 1994). Thus, enhanced UVB irradiances coincide with the seasonal bloom of plankton in environments that are susceptible to UVB radiation.

Studies of the effect of UVB radiation on Antarctic marine microbial communities have been performed using a single species or communities of phytoplankton. However, phytoplankton production supports planktonic microbial communities of viruses, bacteria and protozoa, through which most of the organic matter in pelagic ecosystems are channelled (Azam 1998). Like phytoplankton, these organisms can be damaged or killed by solar UVB radiation but can also exhibit large species-specific differences in their sensitivity to UV exposure (for reviews see Jeffrey et al. 2000, Mostajir et al. 2000, Vernet 2000). UV-induced changes in their production, growth, survival and species composition are likely to cause changes in the trophodynamics of microbial communities. Bothwell et al. (1994) showed that studies using a single trophic level could not predict the effect of UVB on an ecosystem due to UVB-induced changes in trophic-level interactions. Yet to date, few studies have examined the effect of UV on natural marine assemblages, their findings vary greatly, and none have been performed in Antarctic waters (Keller et al. 1997a,b, Wickham & Carstens 1998, Mostajir et al. 1999).

In this study we show that ambient Antarctic UV radiation can change the species composition and trophic structure of natural microbial communities from near-shore waters off Davis Station, Antarctica.

MATERIALS AND METHODS

The study was conducted at Davis Station between 8 and 18 January 1998. The influence of UV radiation on the natural protist community was determined using aliquots of the same samples used to determine the previously published effect of UV on the bacterioplankton. For detailed methods of sample acquisition, preparation and incubation see Davidson & van der Heijden (2000).

Light measurement. Light measurements were made using an SR9910 Macam double grating spectroradiometer. Wavelengths between 280 and 400 nm were scanned at 1 nm wave-steps every 5 min during the *in vivo* exposure of protist assemblages to Antarctic solar radiation. The downwelling irradiance at each wavelength was multiplied by the percentage transmittance of WhirlPak (Nasco) bags and screens. The spectral irradiance of each light treatment was then erythemally weighted and compared with coincident measurements of erythemal UV collected using a 501B Solar Light UV-Biometer by the Australian Radiation Protection and Nuclear Safety Agency. Erythema was used due to its similarity to plant and DNA action spectra, ease of cross-calibration with Biometer data and the fact that the experiments examined interactive responses of an entire plankton community for which more specific physiological weighting functions were not applicable. Equivalent water column depths (ED) received by the plankton assemblages in each light treatment were calculated using Beer's Law (Kirk 1983) and the attenuation of surface irradiation by each screen.

Plankton sampling and exposure. Approximately 100 l of natural plankton assemblage was obtained from 2 km offshore, at 10 m depth beneath 1.7 m of snow-covered sea ice, on 7 January 1998. The seawater was filtered through a 200 µm mesh into a sterile, acid-cleaned, polythene-lined 200 l stainless steel drum. Three replicate 1 l subsamples of the microbial assemblage were obtained to determine the concentration of each protist taxon at the beginning of the experiment (T_0). A further 132 replicate subsamples of around 350 ml were transferred to 500 ml, sterile, UV-transmissive WhirlPak bags.

WhirlPak bags were exposed to ambient solar UV radiation in out-door incubation tanks. Thirty bags were placed beneath different thicknesses of borosilicate glass that attenuated UV to ED of 1.0, 2.0, 3.0 and 3.6 m (Fig. 1). Samples were exposed to UV for periods of 8 h and 1, 2, 4 and 7 d, at the end of which 6 replicate WhirlPak bags from each light treatment were transferred beneath UV stabilised polycarbonate screening, which removed wavelengths <375 nm (≥20 m ED), and the samples were allowed to grow (post-UV incubation). The total duration of UV exposure plus post-UV incubation for all bags was 10 d. A further 12 bags were held beneath UV-stabilised polycarbonate (≥20 m) for 10 d (T_{10} controls). At the end of the 10 d period, incubated samples were prepared for analysis of the microbial community.

Plankton sample analyses. Following post-UV incubation, the 6 replicate WhirlPaks for each light treatment and exposure time were randomly paired and the pairs pooled. A known volume (approximately half) of the sample was transferred to a glass 1 l bottle and fixed with 1 ml of acid Lugol's iodine. Fixation with Lugol's iodine can result in significant loss of ciliate and flagellate cells (Klein Breteler 1985, Ohman & Snyder 1991); however, other fixatives such as formalin, formaldehyde and glutaraldehyde can also cause cell loss (Sherr & Sherr 1993). Samples were allowed to sediment for ≥48 h, the supernatant was removed by aspiration, and the concentrated samples (~20 ml) were stored at 4°C prior to analysis.

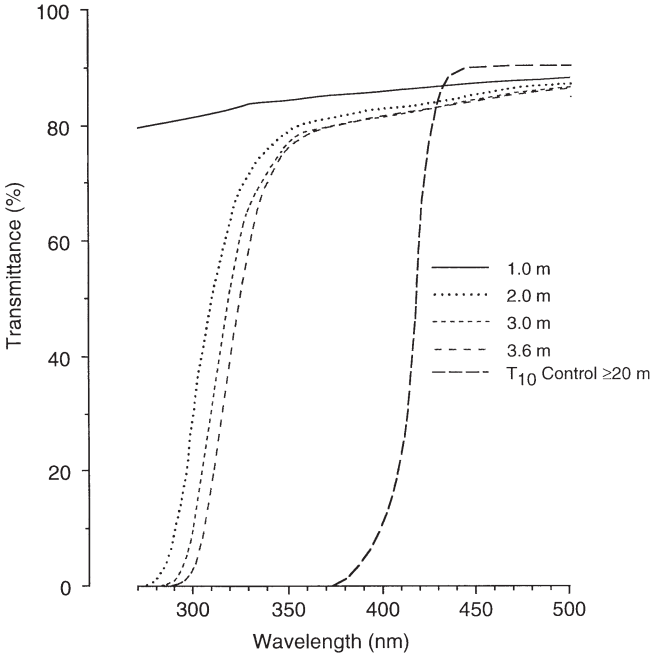

Fig. 1. Percentage transmittance of UV-attenuating screens between 270 and 500 nm wavelength and their equivalent depth in the water column. T_{10} control ≥20 m is the polycarbonate-screened treatment that received no UV <375 nm. Equivalent water column depths of 1.0, 2.0, 3.0 and 3.6 m were obtained using polythene and 3.3, 5.5 and 9.0 mm thick borosilicate glass, respectively

Concentrated samples were sedimented in Utermöhl cylinders and observed using Nomarski optics on a Zeiss Axiovert inverted microscope equipped with blue light epifluorescence at 400 or 1000× magnification. Cells were counted over 5 randomly chosen microscope fields for each of the 3 independent replicate samples at each exposure time and light treatment. Protozoa were identified by the absence of chlorophyll autofluorescence under blue light excitation, and by the absence of chloroplasts and starch under transmitted light. To aid identification of protist species, samples of concentrate were also pipetted onto formvar-coated copper grids, fixed for 60 s with 2% OsO_4 vapour, rinsed gently with distilled water, air dried and shadow cast with chromium metal. Shadow-cast preparations were then examined using a Phillips CM 100 transmission electron microscope.

The mean and standard error of cell concentrations were then calculated for each phytoplankton and protozoan taxon. Concentrations of protists were compared with concentrations at T_0 to quantify growth or mortality of each taxon during exposure to experimental irradiances and T_{10} control treatments to quantify changes in concentration due to UV irradiance and exposure duration.

Between 50 and 100 cells of each protist species were measured using an ocular micrometer at 400 or 1000× magnification, and cell volumes were calculated. The cell volumes of each species were multiplied by 1.33 to compensate for cell shrinkage as a result of Lugol's fixation (Dehairs et al. 1992). Cell carbon concentrations were calculated using the cell volume of each protist taxon and the following conversion statistics: 0.19 pg C μm^{-3} for ciliates (Putt & Stoeker 1989); 0.183 pg C μm^{-3} for heterotrophic dinoflagellates (Caron et al. 1995); 0.22 pg C μm^{-3} for heterotrophic nanoflagellates (HNAN) (Børsheim & Bratak 1987); and pg C = 0.109 × (live cell volume)$^{0.991}$ for all other autotrophic and heterotrophic cells (Montagnes et al. 1994). The means and standard errors of the cell volumes of all phytoplankton and protozoa in each light treatment were also calculated and converted to equivalent spherical diameter (ESD).

Statistical analyses. ***Exploratory analysis:*** A statistical program named PATN (Belbin 1993) was used to examine the relationships between protist communities in each of the 375 replicate field counts independent of light treatment. The concentrations of protist taxa ranged over 4 orders of magnitude so the counts were relativised prior to analysis using the formula $Y_{ij} = 100X_{ij}/\sum_{j=1}^{n} X_{ij}$ (Field et al. 1982), where Y_{ij} is transformed score, X_{ij} is concentration of the ith species in the jth sample, and $\sum_{j=1}^{n} X_{ij}$ is the sum of X_{ij} over all samples. Transformation ensured, *a priori*, that each taxonomic group could make an equal contribution.

The taxonomic composition of incubated samples (UV-exposed and T_{10} controls) was examined by cluster analysis. The Bray & Curtis (1957) measure of association was used to generate a quantitative estimate of the taxonomic resemblance between each pair of the 375 microscope-field counts of protist taxa. These values were then subjected to flexible hierarchical clustering by unweighted pair-group using arithmetic average (UPGMA) (Belbin et al. 1992). After examination of the dendrogram structure, 7 descriptive groups were identified at an arbitrary dissimilarity of 0.54. The difference in species compositions and probabilities of UV-induced changes in concentration between the 7 cluster groups were examined using box and whisker plots and *F*-statistics. The light treatments to which microscope-field counts were exposed in each cluster group were also examined. The frequency of each treatment (ED and durations of exposure) was then determined for each of the 7 cluster groups.

Confirmatory analyses: Multivariate analysis of variance (MANOVA) was performed to determine the statistical significance of UV-induced changes in protist assemblage using 12 protist taxa and relativised cell concentration (see above).

RESULTS

Erythemal UV

The erythemal downwelling solar irradiance varied greatly during the experiment. Diurnal changes accounted for most of the variation, but cloud contributed significantly to attenuation of erythemal irradiance during Days 3, 4, 6 and 7 of the experiment. Days 1, 2 and 5 remained largely cloud free. The increase in cumulative erythemal dose was approximately linear with increasing exposure time (Table 1). Ozone measurements at the nearby Chinese Antarctic station of Zhongshan showed that total column ozone ranged from around 140 DU in September and October to 380 DU during November during the 1997-98 summer, but column ozone during the experiment was around 300 DU. Thus, there was little enhancement of UVB radiation during the experiment due to ozone depletion overhead (Xiangdong et al. 1999).

Total protists

This section examines UV-induced changes in the total concentration and biomass of phytoplankton and protozoa. Changes in the concentration of individual phytoplankton and protozoan taxa are then considered. Other than at T_0, concentrations of cells and cell carbon were obtained from samples that were exposed to UV and post-UV incubated (exposure + post-UV incubation = 10 d).

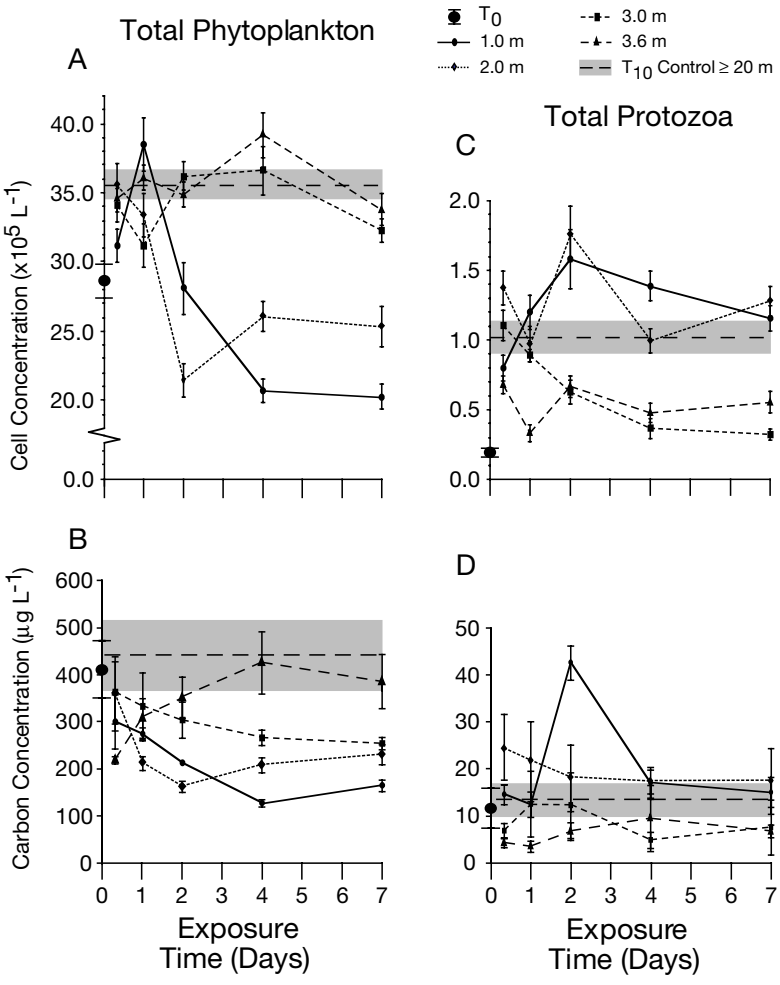

Fig. 2. Total concentrations of (A) phytoplankton cells and their calculated cell carbon (B), and (C) protozoan cells and their calculated cell carbon (D) following exposure to ambient solar irradiances at equivalent water column depths of 1.0, 2.0, 3.0 and T_{10} control ≥20 m treatments for durations between 8 h and 7 d and post-UV incubation (irradiance + post-UV incubation = 10 d). T_0 is the concentration at the beginning of the experiment. Error bars represent ±1 standard error. The shadowed area represents ±1 standard error for T_{10} controls

Table 1. Cumulative erythemal UV dose (kW m^{-2}) at the surface and 1.0, 2.0, 3.0, 3.6 and ≥20 m equivalent water column depths for each attenuated UV treatment for at each sample time

Time	Depth (m)					
	Surface	1.0	2.0	3.0	3.6	≥20
8 h	3.46	2.18	1.47	1.04	0.77	0.00
1 d	5.56	3.52	2.40	1.72	1.29	0.00
2 d	8.82	5.57	3.83	2.75	2.09	0.00
4 d	13.0	8.66	6.05	4.42	3.40	0.00
7 d	22.2	14.1	9.96	7.33	5.67	0.00

Phytoplankton

The total concentration of phytoplankton after T_{10} control incubations was around 25% higher than that at T_0, indicating that phytoplankton grew in control treatments. Total phytoplankton concentrations exposed at 3.0 and 3.6 m ED remained similar to those in control treatments irrespective of the duration of exposure to UV and post-UV incubation (Fig. 2A). In contrast, phytoplankton concentrations following exposure to UV at ≤2.0 m ED for ≥2 d and post-UV incubation were around 40% lower than T_{10} controls and 15% lower than at T_0 (Fig. 2A). Concentrations of phytoplankton in treatments exposed to UV for ≤1 d

seldom differed significantly from T_{10} controls, indicating that brief exposure to UV did not inhibit overall growth of phytoplankton during irradiance and post-UV incubation.

Phytoplankton biomass in T_{10} control treatments did not differ significantly from that at T_0 (Fig. 2B). Therefore, while the concentration of phytoplankton increased in T_{10} controls (see above), the biomass did not. Carbon concentrations in treatments exposed for ≥2 d at 3.6 m ED and post-UV incubated were similar to concentrations at T_0 and in T_{10} controls. However, in comparison with the T_{10} controls, phytoplankton biomass at 3.0 m ED declined around 30% and 50 to 70% at ≤2.0 ED (Fig. 2B). The rate of decline in biomass generally increased with increasing UV irradiance.

Protozoa

Concentrations of protozoa were approximately 5-fold higher in T_{10} control treatments than at T_0, showing substantial growth of microheterotrophs in the absence of short wavelength solar UV radiation (Fig. 2C). Protozoa also grew in all UV-exposed treatments as their concentrations were significantly higher than at T_0. Their concentrations were generally highest in treatments that were exposed at ≤2.0 m ED. Concentrations of protozoa peaked at around 1.65×10^5 cells l^{-1} following exposure for 2 d at ≤2.0 m ED and post-UV incubation, approximately 3 times that at low irradiances and 30% higher than T_{10} controls. Concentrations decreased following longer exposures (4 to 7 d) and were similar to those of T_{10} control treatments. Exposure to low UV irradiances (3.0 and 3.6 m ED) for 1 to 2 d caused protozoan concentrations following post-UV incubation to decrease to around half that in T_{10} controls. Longer exposures to UV (≥4 d) did not significantly change their concentrations.

While total protozoan cell concentration changed substantially between T_0 and the T_{10} control treatments, their biomass did not. Mean protozoan biomass following exposure at ≤2.0 m ED and post-UV incubation was commonly greater than in T_{10} control treatments. Their biomass following exposure at 3.0 and 3.6 m ED was less than T_{10} controls and occasionally less than at T_0 (Fig. 2D). Protozoan carbon concentrations in treatments exposed to UV at ≤2.0 m ED were commonly 2 to 4 times higher than at 3.0 and 3.6 m ED. However, protozoan biomass generally showed high variance due to the occurrence of infrequent large taxa such as dinoflagellates, tintinnids and other ciliates (data not shown) that greatly altered the carbon concentration between replicate fields.

Least squares regression analysis showed a significant negative correlation between total heterotroph and autotroph cell concentrations ($0.002 < r < 0.005$) (Fig. 3). The high variance of calculated carbon biomass confounded any significant correlation between auto- and heterotrophic biomass. No significant correlation existed between the cell concentration or biomass of bacteria (Davidson & van der Heijden 2000) and phytoplankton or protozoa.

Cell size

No significant change in ESD of phytoplankton occurred between T_0 (12.72 µm) and the T_{10} control treatments (12.04 µm) (Fig. 4). At low UV irradiance (3.6 m ED) the ESD of phytoplankton increased with increasing exposure duration and did not differ significantly from the diameter in T_{10} control treatments following exposures ≥2 d and post-UV incubation. At higher UV irradiances (≤3.0 m ED), ESD of phytoplankton were initially similar to that of T_{10} controls but declined with increasing exposure duration and were significantly (around 2 µm) less than the ESD of T_0 and T_{10} controls following ≥2 d exposure and post-UV incubation.

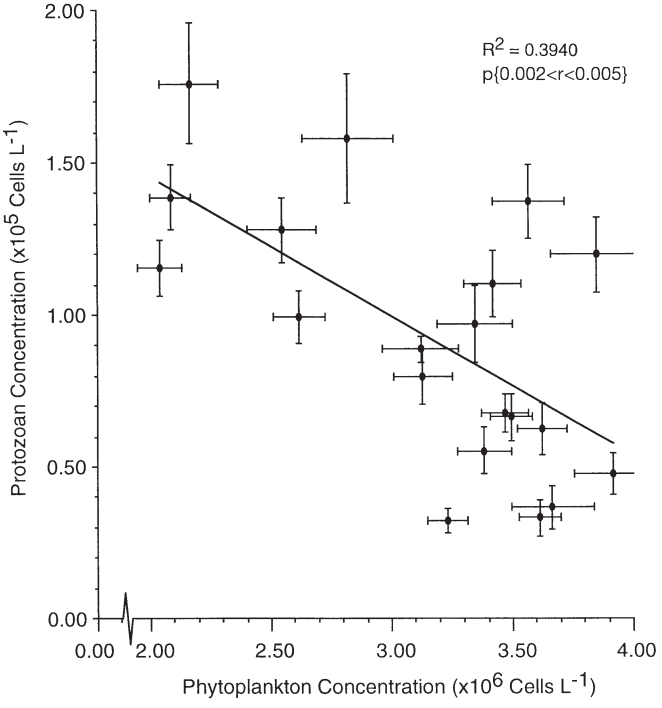

Fig. 3. Least squares regression analysis of phytoplankton and protozoan concentrations exposed to ambient solar irradiances at equivalent water column depths of 1.0, 2.0, 3.0 m and T_{10} control ≥20 m treatments for durations between 8 h and 7 d and post-UV incubation (irradiance + post-UV incubation = 10 d). R^2 is the correlation coefficient of the regression and p is the probability of the correlation coefficient (2-tailed, df = 18). Error bars represent ±1 standard error

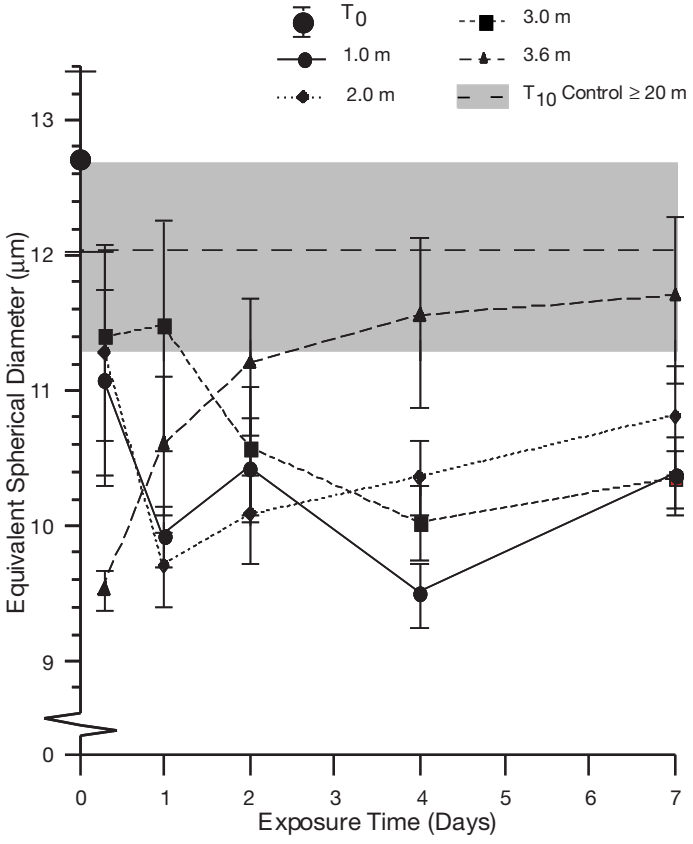

Fig. 4. Equivalent spherical diameter of phytoplankton exposed to ambient solar irradiances at equivalent water column depths of 1.0, 2.0, 3.0 m and T_{10} control ≥20 m treatments for durations between 8 h and 7 d and post-UV incubation (irradiance + post-UV incubation = 10 d). Error bars represent ±1 standard error. The shadowed area represents ±1 standard error for T_{10} controls

UV-induced changes in protozoan cell size were also examined. The size of protozoa in control treatments was significantly lower than that at T_0. However, due to the lower concentration of protozoa and the occurrence of infrequent large cells, estimates of their ESD in UV-exposed treatments had high variance and seldom differed significantly from T_0 or control concentrations (data not shown).

Protist species composition

Phytoplankton

Fragilariopsis curta (Van Heurck) Krieger and *F. cylindrus* (Grunow) Krieger constituted around 70% of the total phytoplankton abundance. While *F. curta* constituted >90% of cells observed in valve view in all light treatments, these species were commonly observed in girdle view and the species could not be separated. Hence they are referred to as *F. curta/cylindrus*.

Some phytoplankton taxa occurred at low concentrations in this study or could not be reliably identified by light microscopy and were therefore grouped. Other diatom spp. contain diatoms that occurred at low abundance, mostly comprising *Nitzschia prolongatoides* Hasle, *Cylindrotheca closterium* (Ehrenb.) W. Smith, *Chaetoceros dichaeta* Ehrenb., *Chaetoceros bulbosum* (Ehrenb.) Heid. and *Pinnularia quadrataria* var *constricta* (Østr.) Heid. Autotrophic nanoflagellates could not reliably be identified by light microscopy but were mostly *Pyramimonas gelidicola* McFadden, Moestrup and Wetherbee, *Geminigera cryophila* (Taylor & Lee) Hill, an unknown Chrysophyte, and mixotrophic *Chrysochromulina* sp. Autotrophic dinoflagellates were mostly gymnodiniod species.

T_0 and T_{10} control treatments

The phytoplankton community at T_0 was dominated by *Fragilariopsis curta/cylindrus* (1.32×10^6 l^{-1}) with *Pseudonitzschia subcurvata* Hasle subdominant (8.85×10^5 l^{-1}) (Fig. 5). *Fragilariopsis pseudonana* (Hasle) Krieger, autotrophic nanoflagellates and *Thalassiosira ambigua* Kozlova were significant contributors to the phytoplankon assemblage (2.31×10^5 l^{-1}, 1.83×10^5 l^{-1} and 1.29×10^5 l^{-1} respectively) while *Navicula glaciei* Van Heurck, *Chaetoceros simplex* Ostenfeld, diatom spp. and autotrophic dinoflagellates were minor components (6.76×10^4 to 1.05×10^4 cells l^{-1}).

Changes in the phytoplankton species composition were observed between T_0 and the T_{10} control treatments. Concentrations of *Fragilariopsis curta/cylindrus* increased by around 50% and continued to numerically dominate the community, while concentrations of autotrophic nanoflagellates and *Navicula glaciei* increased 5- and 16-fold, respectively (Fig. 5A,E,H). *Chaetoceros simplex*, other diatom spp. and autotrophic dinoflagellates showed little growth (Fig. 5F,G,I) but concentrations of *Pseudonitzschia subcurvata*, *Fragilariopsis pseudonana*, and *Thalassiosira ambigua* declined 83, 61 and 29%, respectively (Fig. 5B–D).

UV-exposed treatments

UV-induced mortality of *Fragilariopsis curta/cylindrus* was responsible for most of the decline in phytoplankton concentrations at high UV irradiances.

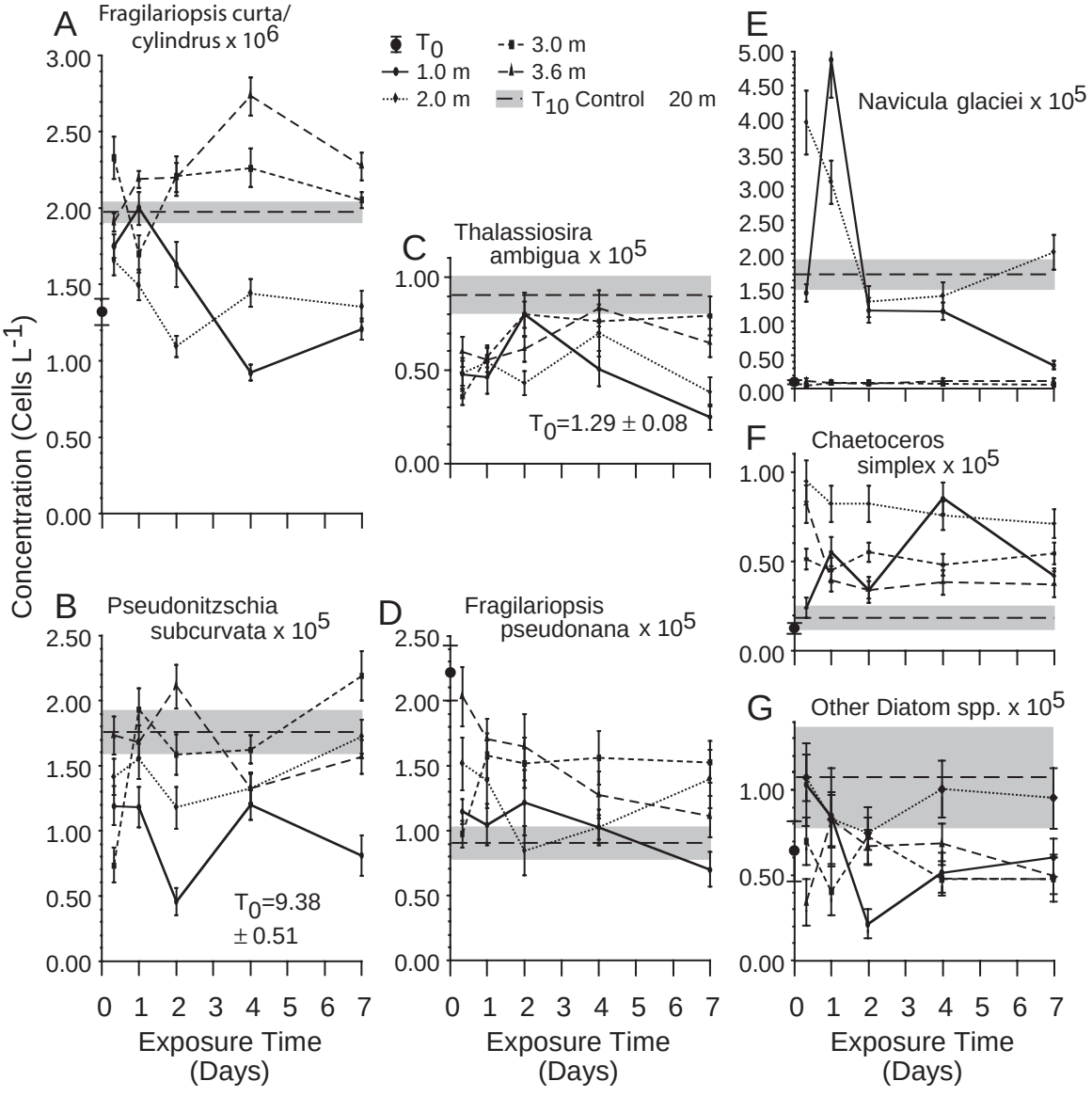

Fig. 5. (Above and following page.) Concentrations of phytoplankton (A to I) and protozoa (J to L) following exposure to ambient solar irradiances at equivalent water column depths of 1.0, 2.0, 3.0, 3.6 m and T_{10} control ≥20 m treatments for durations between 8 h and 7 d and post-UV incubation (irradiance + post-UV incubation = 10 d). Error bars represent ±1 standard error. The shadowed area represents ±1 standard error for T_{10} controls. Note different exponents of individual taxa

Concentrations of *F. curta/cylindrus* declined following exposures at ≤2.0 m ED for between 8 h and 4 d, after which they remained at or below their T_0 concentration (Fig 5A). Concentrations *F. curta/cylindrus* in samples exposed at 3.0 and 3.6 m ED for ≥2 d exceeded those in the T_{10} control treatments.

Concentrations of *Thalassiosira ambigua* and *Fragilariopsis pseudonana* declined to around 50%, and *Pseudonitzschia subcurvata* to ≤20%, of their T_0 concentrations in all UV-exposed light treatments (Fig. 5C,D,B, respectively). Concentrations of these species seldom differed significantly between light treatments but were commonly lowest at ≤2.0 m ED.

In contrast, the diatoms *Navicula glaciei* Van Heurck and *Chaetoceros simplex* Ostenfeld showed UV-induced enhancement of cell concentrations (Fig. 5E,F). Exposure of *N. glaciei* at ≤2.0 m ED for 8 h to 1 d caused a dramatic increase in concentration (Fig. 5E). At this time, concentrations were around 25 times higher than that at T_0 and in low UV treatments (3.0 and 3.6 m ED) and 2.9 times higher than the T_{10} controls. Following longer exposures to high UV

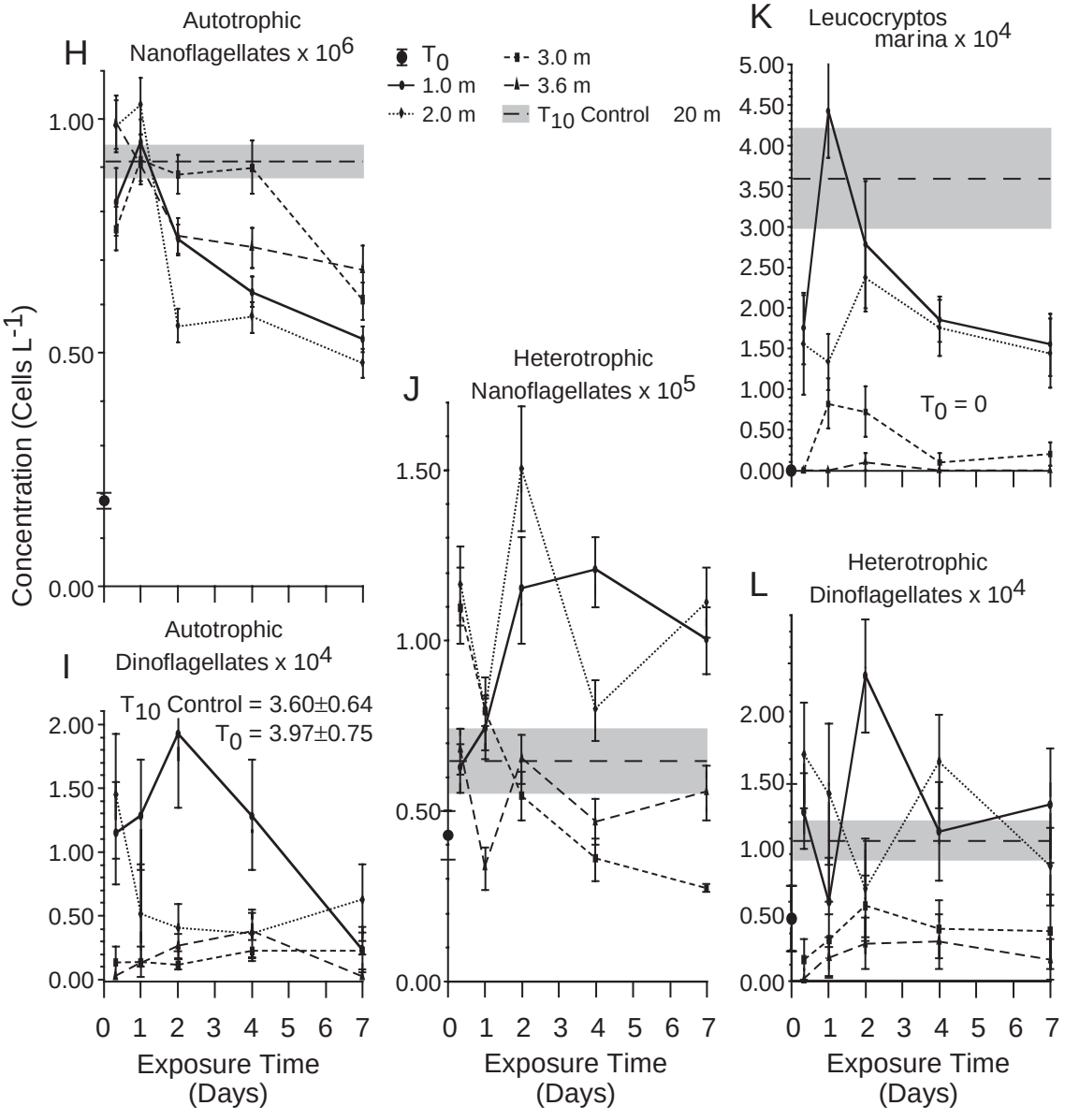

Fig. 5 (continued)

irradiance, *N. glaciei* declined to concentrations that were at or below the T_{10} controls. *N. glaciei* concentrations at 3.0 and 3.6 m ED did not differ significantly from concentrations at T_0.

Concentrations of *Chaetoceros simplex* were, with one exception, significantly higher in UV-exposed treatments than at T_0 and in the T_{10} controls. Concentrations were highest in treatments exposed to UV at 2.0 m ED and generally declined with increasing depth of exposure, irrespective of the duration of exposure and post-UV incubation (Fig. 5F). The exception was at 1.0 m ED, where concentrations peaked after 4 d exposure, but were generally variable and seldom differed significantly from those at 3.0 and 3.6 m ED. Concentrations of other diatoms spp. were variable and seldom differed from the T_{10} control or T_0 concentrations (Fig. 5G).

Concentrations of autotrophic nanoflagellates did not differ significantly from control treatments following exposure to UV for ≤1 d (Fig. 5H). Longer exposures caused a decline in their concentrations; the rate of this decline generally increased with increasing irradiance.

Concentrations of autotrophic dinoflagellates were generally higher at high UV irradiances (Fig. 5I). At 1.0 m ED, their concentrations initially increased with increasing exposure duration, reaching a maximum after 2 d exposure, but declined at longer exposures. Con-

centrations at 2.0 m ED were high following 8 h exposure but declined significantly after exposure for 1 d and did not change following longer exposures. Following exposure at 3.0 and 3.6 m ED, concentrations of autotrophic dinoflagellates were low and seldom changed significantly with increased exposure duration.

Protozoa

Most species of HNAN were not identifiable in fixed samples by light microscopy but included such species as *Telonema subtile* Griessmann, *Thaumatomastix splendida* Thomsen, *Bicosta antennigera* Moestrup and other choanoflagellates species. While ciliates such as tintinnids and *Strombidium* spp. were observed, counts of these taxa were low, and variances were similar to mean concentrations (data not shown). Heterotrophic dinoflagellate species were principally from the genera *Gyrodinium*, *Protoperidinium*, *Amphidinium* and *Prorocentrum*.

T_0 and T_{10} controls

Concentrations of HNAN and dinoflagellates were low at the beginning of the experiment (T_0), and *Leucocryptos marina* (Braaud) Butcher was not detected (Fig. 5J–L). Protozoa grew in T_{10} control treatments. HNAN increased from 4.28×10^4 to 6.5×10^4 cells l^{-1}, dinoflagellates increased from 0.39×10^4 to 0.89×10^4 cells l^{-1}, and *L. marina* rose from undetectable to concentrations around 3.52×10^4 cells l^{-1}.

UV-exposed treatments

The concentration of heterotrophic taxa generally increased following exposure to increasing UV irradiances, but differences were observed in the timing and extent of UV-induced enhancement (Fig. 5J–L). Concentrations of HNAN exposed to UV at ≥3.0 m ED seldom differed significantly from T_0 or the T_{10} control treatments (Fig. 5J). In contrast, concentrations in treatments exposed at ≤2 m ED for ≥2 d increased 2- to 4-fold.

Leucocryptos marina grew in all UV-exposed treatments; however, only after 1 to 2 d exposure at 1.0 m ED and post-UV incubation did concentrations reach that in T_{10} controls (Fig. 5K). Maximum concentrations occurred after 1 to 2 d exposure in all UV treatments but declining thereafter. Concentrations of *L. marina* exposed at 3.0 and 3.6 m ED were low, seldom changed significantly with exposure duration, and were only 5 to 20% of that in treatments at ≤2.0 m ED.

Counts of the heterotrophic dinoflagellates had large standard errors due to their low concentrations (Fig. 5L). While their concentrations were commonly higher in treatments exposed at ≤2.0 m ED, they seldom differed significantly from T_{10} control treatments. At depths ≥3.0 m their concentrations did not differ significantly from those at T_0 and were around 30% of that in high UV treatments.

Statistical analyses

Statistical analyses were performed to determine patterns and relationships between the UV irradiance (ED), exposure duration and species composition.

Exploratory statistics

Cluster analysis, based solely on the protist species composition of the 375 replicate microscope field counts, distinguished 7 groups at a dissimilarity of 0.54 that conveniently summarised changes in the microbial species composition. Two of these clusters were due to the absence of *Thalassiosira ambigua*, dinoflagellates or *Leucocryptos marina*, had ≤10 field counts per cluster group, and were not considered further (Fig. 6 dotted lines).

We also examined the light treatment (ED and exposure duration) received by microscope field counts contained in each of the cluster groups above. The frequency of each light treatment in each cluster group was calculated, and the frequency distribution of exposure depths and durations were plotted beside each of the cluster groups (Fig. 6A–J).

Dissimilarity of the 5 cluster groups (Fig. 6 numbers 1 to 4, 6 enclosed by squares) showed that there were 3 subgroups. Cluster group 1 comprised control treatments (≥20 m ED) and brief exposures to high UV (Fig. 6A,B). The group was characterised by moderate concentrations of all protist taxa and highest concentrations of autotrophic dinoflagellates and *Leucocryptos marina*. The species composition of this group was more similar to cluster groups 2 to 4, which contained treatments exposed to high (≤2.0 m ED) UV irradiance, than to groups that contained treatments exposed to low (3.0 and 3.6 m ED) UV irradiance due to the high concentrations of protozoan taxa (see Protozoa: T_0 and T_{10} controls).

Cluster groups 2 to 4 contained microscope field counts from treatments exposed to high UV irradiances (≤2.0 m ED) (Fig. 6D,F,H). These groups differed little, with a dissimilarity of 0.03 between cluster groups 2 and 3, and between groups 3 and 4. High UV-irradiance treatments were characterised by high concentrations

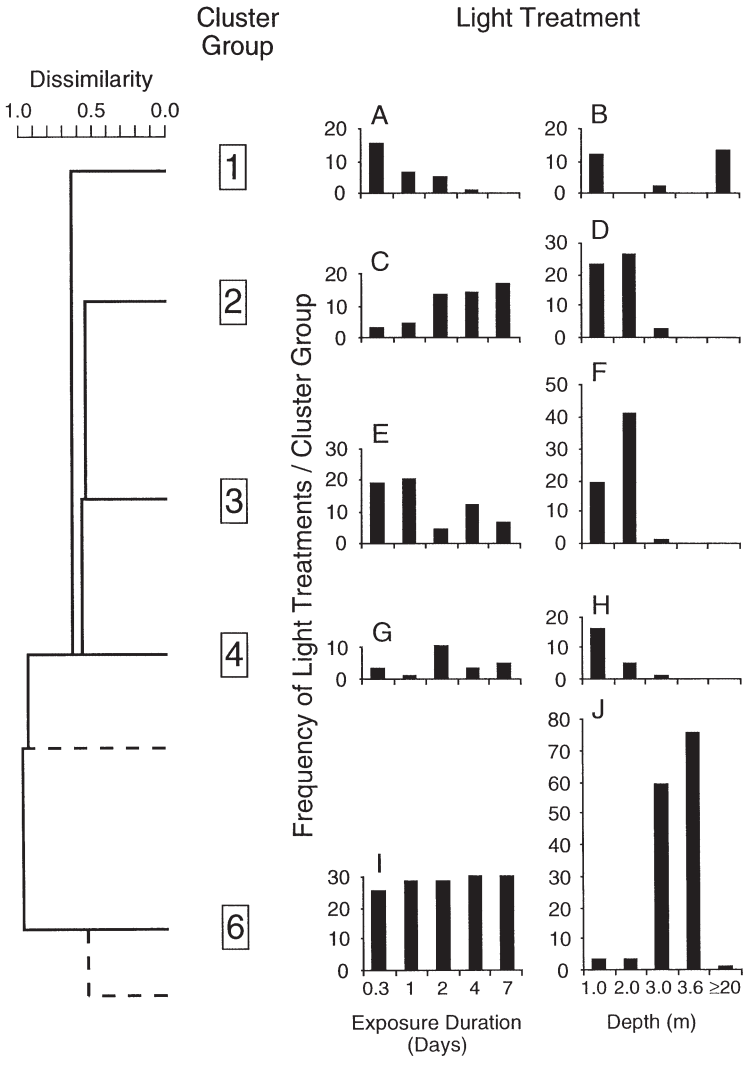

Fig. 6. Seven cluster groups, which conveniently summarised the changes in microbial species composition of individual microscope-field counts, were obtained at a dissimilarity of 0.54. Dotted lines denote cluster groups containing ≤10 replicate field counts that are not considered in detail. The numbers 1 to 4 and 6 enclosed in rectangles denote the 5 remaining cluster groups. The frequency of UV treatments (durations and equivalent depths of UV exposure) received by the microscope fields in each cluster group is presented beside each cluster group (A to J)

of *Navicula glaciei*, other diatom spp., auto- and heterotrophic dinoflagellates *Leucocryptos marina* and HNAN, but low concentrations of *Fragilariopsis curta/cylindrus*, *Pseudonitzschia subcurvata* and *Thalassiosira ambigua*. Subdivision of the high UV-irradiance treatments into cluster groups 2 to 4 generally correlated with the duration of UV exposure, indicating that changes in exposure duration generated different species compositions (Fig. 6C,E,G).

Cluster group 2 contained field counts exposed to high UV (≤2.0 m) for 2 to 7 d (Fig. 6C,D). This group was characterised by the lowest concentrations of *Fragilariopsis curta/cylindrus*, low autotrophic flagellates concentrations and high concentrations of *Chaetoceros simplex* and HNAN. Cluster group 3 mostly contained field counts exposed to high UV (≤2.0 m) for ≤1 d (Fig. 6E,F). This group was characterised by concentrations of the *F. curta/cylindrus*, *Pseudonitzschia subcurvata*, and *Fragilariopsis pseudonana* that were similar to those of group 6 (see below) but had the highest concentrations of *Navicula glaciei* and *C. simplex*, and had higher concentrations of HNAN and *Leucocryptos marina* than at 3.0 and 3.6 m ED, respectively. Cluster group 4 contained 22 field counts, most of which had been exposed at 1 m ED for 2 d but included some other exposure durations (Fig. 6G,H). This group was characterised by low concentrations of the diatoms *F. curta/cylindrus*, *P. subcurvata* and *F. pseudonana*, and high concentrations of heterotrophic dinoflagellates.

Cluster group 6 contained all microscope field counts exposed at 3.0 and 3.6 m ED, indicating a consistent change in species composition irrespective of exposure duration (Fig. 6I,J). This cluster group was characterised by high concentrations of the diatom species *Fragilariopsis curta/cylindrus*, *Pseudonitzschia subcurvata*, *F. pseudonana* and *Thalassiosira ambigua* and low concentrations of *Leucocryptos marina*, HNAN, and auto- and heterotrophic dinoflagellates.

Confirmatory statistics

MANOVA showed that UV irradiance (ED), exposure duration and the interaction of the two caused highly significant changes in protistan species composition ($p_F < 0.001$) (Table 2). UV irradiance alone caused a significant change in the concentration between protist taxa and within each taxon (parametric and nonparametric $p_F < 0.001$) (Table 2). Exposure duration was responsible for significant changes in the concentration between protist species but also caused significant changes in the concentrations of *Pseudonitzschia subcurvata*, *Navicula glaciei*, *Thalassiosira ambigua*, diatom spp., autotrophic flagellates and *Leucocryptos marina* ($p_F < 0.05$). The interaction effect of irradiance and duration together was significant between species and for each species ($p_F < 0.03$) except diatom spp. and auto- and heterotrophic dinoflagellates (Table 2).

Table 2. Probability obtained by 2-way multivariate analysis of variance (MANOVA) of the relativised concentrations of all protist species showing the non-parametric probability (Wilks' lambda) between species and within (*F*-test) probabilities of changes in concentration of each species resulting from the individual effects (equivalent depth [ED], duration of UV exposure) and their interaction. Summary of all effects gave a non-parametric probability of < 0.0005

Source	ED	Duration	Interaction: ED × Duration
Between species	0.000	0.000	0.000
Fragilariopsis curta/cylindrus	0.000	0.102	0.000
Pseudonitzschia subcurvata	0.000	0.010	0.000
Fragilariopsis pseudonana	0.000	0.221	0.001
Navicula glaciei	0.000	0.000	0.000
Thalassiosira ambigua	0.000	0.002	0.001
Chaetoceros simplex	0.000	0.089	0.000
Diatom spp.	0.000	0.015	0.277
Autotrophic dinoflagellates	0.000	0.654	0.555
Autotrophic flagellates	0.000	0.000	0.000
Leucocryptos marina	0.000	0.000	0.027
Heterotrophic dinoflagellates	0.000	0.639	0.180
Heterotrophic flagellates	0.000	0.689	0.000

DISCUSSION

Natural plankton communities comprise a complex web of trophic interactions; however, scientific attention has focused on the impact of UV on phytoplankton. Remarkably little is known about the effect of UVB on marine microbial communities. The few studies that have examined UV-induced changes to marine communities are from the northern hemisphere. Their findings indicate that the impact of UV radiation on planktonic communities range from insignificant or small in comparison with natural variability (Halac et al. 1997, Keller et al. 1997a,b, Laurion et al. 1998) to major changes in the structure and function of the pelagic food web (Wickham & Carstens 1998, Mostajir et al. 1999, Sommaruga et al. 1999). Our results show that UV can change the trophic structure and species composition of the marine microbial community.

Exposure of microbial assemblages to UV for between 8 h and 7 d was chosen because shallow mixed depth in the marginal ice zone may persist for around 6 d (Mitchell & Holm-Hansen 1991, Veth 1991). Biologically significant UVB irradiances can penetrate to >20 m depth in Antarctic waters (Karentz & Lutze 1990, Smith et al. 1992). Thus, exposure durations used in this experiment were ecologically sustainable. Similar to Davidson et al. (1996), we included post-UV incubation in our experiments. As the total duration of UV exposure plus post-UV incubation was 10 d, samples exposed to UV for different exposure periods necessarily had different recovery periods. However, our experimental design incorporated photoadaptation and photorepair in response of microbial assemblages to UV exposure, allowed expression of UV-induced changes in the microbial species composition (especially following brief UV exposures), and allowed statistical analysis of the results using cell concentrations since they all received the same total period of growth.

Total protists

Phytoplankton and protozoa grew during the experiments. Phytoplankton increased in T_{10} control treatments and samples exposed to UV at 3.0 and 3.6 m ED compared with T_0 concentrations. Protozoan concentrations also increased in all treatments and T_{10} controls, but increases were greatest in control and high UV treatments. However, large overall differences in the concentrations of protists were observed between light treatments.

Phytoplankton

Numerous authors report that the growth, survival and production of phytoplankton are reduced by exposure to UV radiation (for reviews see Davidson 1998, Vernet 2000). We found that exposure to Antarctic solar UV radiation at 3.0 and 3.6 m ED caused no significant inhibition of phytoplankton concentration in comparison with T_{10} controls, but prolonged exposure to high UV irradiances (≥2 d at ≤2.0 m ED) caused substantial mortality of phytoplankton. The extent of phytoplankton mortality was dependent on the irradiance (ED) and exposure duration. Thus, phytoplankton concentrations were determined by UV dose and dose rate. Villafañe et al. (1995) and Davidson et al. (1996) found that community-based acclimation maintained the overall biomass of UV-exposed phytoplankton assemblages. Similar to McMinn (1997), we found that exposure to high UV irradiances reduced phytoplankton biomass over the duration of the experiment. This was probably due to the UV sensitivity of the dominant species in the community we examined, the extent to which the species composition changed to attain an appropriate level of UV tolerance and the time allowed for acclimation of the community composition to UV exposure (Villafañe et al. 1995).

Protozoa

Similar to Chatila et al. (1999) and Mostajir et al. (1999), we found that protozoan concentrations and biomass increased at high UV irradiances. UVB can impair cell orientation, flagella motion and feeding currents, and may cause mortality of many protozoa (e.g. Sommaruga et al. 1996, Ochs 1997, Chatila et al. 1999, Mostajir et al. 1999). However, Chatila et al. (1999) found that the UV tolerance of protozoans increased with increasing nutrient concentrations. In our study, survival and growth of protozoa were enhanced at high UV irradiances and coincided with increased phytoplankton mortality (see below). UV-induced inhibition of protozoa may have occurred at irradiances that were insufficient to cause phytoplankton mortality (see below). Such inhibition may explain why protozoan concentrations were lower at 3.0 and 3.6 m ED than in T_{10} controls and why control treatments were not more closely associated with treatments exposed to low UV irradiances in cluster analysis.

Interactions

A significant negative correlation was found between the total concentrations of phytoplankton and protozoa in UV-exposed treatments. Death of phytoplankton following exposure at ≤2.0 m ED for ≥2 d resulted in a significant decline in the concentrations of calculated phytoplankton cell carbon. Thus, mortality released substantial concentrations of particulate and dissolved organic carbon. Phytoplankton mortality coincided with an increase in protozoan concentrations, due largely to increases in *Leucocryptos marina*, *Thaumatomastix splendida*, *Telonema subtile*, *Bicosta antennigera* and an unknown heterotrophic flagellate. Such taxa reportedly consume detrital matter, nanoplankton, bacteria and dissolved organic carbon (Vørs 1992, Marchant & Scott 1993, Thomsen & Ikavalko 1997, Brandt & Sleigh 2000, M. Sieracki pers. comm.). The negative correlation we observed between the concentrations of phytoplankton and those of protozoa may have been due to UV-induced mortality of phytoplankton that increased the nutrition availability for protozoa, increasing their UV tolerance (Chatila et al. 1999) and supporting their growth. Thus, similar to Chatila et al. (1999) and Mostajir et al. (1999), it is likely that indirect effects of UV on the microbial trophodynamics enhanced the concentrations of protozoa rather than direct enhancement of protozoans by exposure to UV radiation.

Concentrations of bacteria in this study were similar between treatments exposed to high and low UV (Davidson & van der Heijden 2000) despite substantial phytoplankton mortality. Senescence and mortality of phytoplankton can enhance growth of bacterioplankton (e.g. Kirchman 1999), and UVB radiation can photodegrade dissolved organic matter (DOM) to smaller molecules that are more available to bacteria and promote their growth (Herndl et al. 1997, Kaiser & Herndl 1997). UV radiation can also inactivate viruses that are thought to be a major cause of bacterial mortality (Suttle & Chen 1992, Murray & Jackson 1993). However, bactivorous grazers may mediate UV-induced enhancement of bacterioplankton. Protozoan grazing of bacteria is a major route for carbon in the marine ecosystem, returning carbon from the dissolved organic carbon pool to the food chain via the microbial loop (Azam 1998). Bactivory can limit the concentration of bacteria by grazing the new production (e.g. Becquevort et al. 2000). Gustavson et al. (2000) found that enhanced UVB probably increased bacterial activity, but that this was matched by increased rates of bactivory. Together with the increase in protozoan concentrations we observed in high UV treatments, this may explain the absence of any increase in bacterial concentration in our study.

Species composition

Cluster analysis, based solely on protist species composition, formed cluster groups that corresponded to the experimental light treatments from which the replicate microscope field counts were obtained. Thus, most of the changes in species composition were due to the light treatment.

Phytoplankton

Changes in phytoplankton species composition were observed between T_0 and the T_{10} control treatments. While the total concentration of phytoplankton increased (see above) and *Fragilariopsis curta/cylindrus* maintained dominance in the T_{10} controls, the relative contribution by many subdominant diatom species declined (e.g. *Pseudonitzschia subcurvata*, *Fragilariopsis pseudonana* and *Thalassiosira ambigua*). These species were replaced by increases in the relative concentrations of autotrophic nanoflagellates, *Navicula glaciei* and other diatom spp. Thus, experimental incubation exerted a species-selective force that was independent of UV exposure. Such changes are likely due to differences between the environment at the collection site (10 m depth beneath 1.7 m of snow-covered sea ice) and near-surface exposure to wavelengths >375 nm.

There is a growing body of evidence that interspecific differences in UV tolerance cause changes in the species composition of natural marine phytoplankton assemblages exposed to UV radiation (Smith et al. 1992, Wängberg et al. 1996, McMinn 1997, Laurion et al. 1998). Similarly, we found that following UV exposure, some species died, some flourished, while others were unaffected. MANOVA showed that the UV irradiance (dose rate) changed the phytoplankton species composition, significantly changing the concentrations of every taxon.

The integrated UV dose also changed the phytoplankton species composition as many phytoplankton taxa showed significant changes in concentrations as a result of exposure duration. However, our results also suggest photoacclimation to UV exposure by some phytoplankton taxa. The concentrations of *Fragilariopsis curta/cylindrus*, *Fragilariopsis pseudonana*, *Pseudonitzschia subcurvata* and *Chaetoceros simplex* differed between UV irradiances (ED), indicating that exposure to high UV irradiances caused inhibition or mortality of these species. However, MANOVA showed that their concentration did not change significantly with changes in exposure duration. Those taxa that survived brief exposures to high UV irradiances (≤2 d at ≤2.0 m ED) also survived prolonged exposures (7 d). UV tolerance mechanisms may have changed the sensitivity of phytoplankton to UV exposure wavelengths (Cullen & Lesser 1991, Karentz et al. 1991, Helbling et al. 1992). Little is known about variation in UV tolerance within phytoplankton species, but our data suggest that selection of UV-tolerant strains may also contribute to persistence of some species in UV-exposed communities.

Attempts have been made to categorise the sensitivity of phytoplankton to UVB radiation on broad taxonomic criteria or cell size (e.g. Karentz et al. 1991, Villafañe et al. 1995, Helbling et al. 1996). Karentz et al. (1991) observed an increase in UV-induced damage with decreasing cell size. In contrast, we observed an overall decrease in the ESD of phytoplankton cells with increased UV irradiance. Thus, small species had a greater UV tolerance than larger species, recovered faster or grew more rapidly during the post-UV incubation. Alternatively, UV-induced changes in the protozoan community may have altered size-selective grazing on the phytoplankton community.

We also found large interspecific differences in UV tolerance within broad taxonomic criteria. Exposure to high UV (≤2.0 m ED) caused concentrations of such diatoms as *Fragilariopsis curta/cylindrus* and *Fragilariopsis pseudonana* to decline, while diatoms of similar cell size such as *Navicula glaciei* and *Chaetoceros simplex* respectively increased in these treatments. Such species-specific variation is likely to defy any attempts to resolve differences in UV tolerance between broad taxonomic criteria. Thus, similar to other studies (Davidson et al. 1996, Wängberg et al. 1996, McMinn 1997, Laurion & Vincent 1998, Mostajir et al. 1999), we could not categorise the UV tolerance of the phytoplankton species based on cell size or taxonomic affinity.

Protozoa

The concentrations of all 3 protozoan taxa increased between T_0 and the T_{10} control treatments. *Leucocryptos marina* greatly increased its contribution to the protozoan community, rising from negligible concentrations at T_0 to become the second most abundant species in T_{10} control and high UV-irradiance treatments.

We found that concentrations of all 3 protozoan taxa were highest following exposure to high UV irradiances. Protozoans reportedly differ greatly in their sensitivity to UV exposure (Sommaruga & Buma 2000). Mostajir et al. (1999) found that changes in the composition and abundance of protozoan species were due to differences in the UV tolerance. However, we found enhanced concentrations of all the protozoan taxa, which correlated with the mortality of the phytoplankton. We proposed (see above) that UV-induced phytoplankton mortality increased nutrition for protozoa, enhancing their UV tolerance (Chatila et al. 1999) and fuelling their growth. However, MANOVA showed that the response of each protozoan taxon differed in relation to the UV treatment.

Concentrations of all protozoan taxa differed significantly between UV irradiances (ED). However, only *Leucocryptos marina* changed significantly in concentration as a result of exposure duration, while concentrations of heterotrophic dinoflagellates did not change significantly in the interaction of irradiance and exposure duration. The reasons for differences between light treatments are unclear but may have been due to: the statistical variance of the counts (especially dinoflagellates); UV-induced changes in species composition within heterotrophic dinoflagellates and HNAN; changes in the quality or quantity of their food due to UV irradiance and duration; or UV-induced inhibition of protozoa growth and survival.

Interactions

Changes in protist species composition during the first 1 to 2 d of UV exposure, when phytoplankton mortality is at its highest, are erratic and difficult to predict. During this apparently chaotic state, UV-tolerant

opportunistic species of phytoplankton and protozoa such as *Navicula glaciei* and *Leucocryptos marina* can greatly increase their contribution to the marine microbial community. However, similar to Davidson et al. (1996), we found that UV-induced changes in the community had largely been determined following exposure for >2 d. Thereafter, the community persisted with relatively little change as a result of increased exposure duration.

In conclusion, our results show that ambient Antarctic UV changed the species composition of natural marine microbial assemblages. The magnitude of these changes appears related to the sensitivity of the individual species that constitute the community and the extent to which these species are key determinants of the community structure and function. The effect of the UV-induced changes on the community were dependent on the UV irradiance, duration of exposure and sensitivity of the component species, resulting in a complex mosaic of changing abundance. Changes were initially chaotic but developed clear patterns of changing community structure and function with increasing exposure duration. UV-induced mortality of phytoplankton was a key determinant of protist abundance and species composition. While we only observed phytoplankton mortality at depths ≤2.0 m following exposure for 1 to 2 d, biologically significant UVB irradiances can penetrate to >20 m depth in Antarctic waters (Karentz & Lutze 1990, Smith et al. 1992) and UVB can cause mortality of phytoplankton to 10 m depth (Karentz 1989). Blooms of marine microbes in the sea ice and marginal ice zone during spring contribute much of the production in the Southern Ocean (Smith & Nelson 1986, Voytek 1989) but coincide with ozone depletion in spring and early summer and occur in environments that are penetrated by UVB radiation (Davidson 1998). Our results show that enhanced UV may significantly affect the species composition of Antarctic protist communities. Such changes could alter size, availability, palatability and nutritional value of food available to higher trophic levels (Vincent & Roy 1993). We also found UV-induced inhibition and mortality of phytoplankton, and previous studies have shown that UVB exposure reduced the rate at which carbon is sequestered by photosynthesis (e.g. Smith et al. 1992, Helbling et al. 1992). Bacterial concentrations in our study did not change, but UV-induced phytoplankton mortality directly or indirectly enhanced the abundance of protozoa. We propose that respiration by these organisms, together with reduced phytoplankton production, could increase concentrations of CO_2 in near-surface waters and reduce vertical carbon flux, exacerbating accumulation of greenhouse CO_2 in the atmosphere.

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