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Temporal changes in effects of ambient UV radiation on natural communities of Antarctic marine protists

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ABSTRACT: The effects of ambient solar UV radiation (280 to 400 nm) were determined using 3 natural marine protist communities incubated in 650 l tanks (minicosms) for 13 to 14 d over the summer of 2002–2003 at Davis Station, Antarctica. Minicosms were exposed to ambient light that was variously attenuated to give treatments of photosynthetically active radiation (PAR, ≥385 nm wavelength), PAR + UV-A radiation (315 to 385 nm), and PAR + UV-A + 4 different treatments of UV-B radiation (280 to 315 nm) that simulated a range of equivalent depths (ED) in the water column from 4.43 to 7.15 m. Results showed a seasonal progression in the response of microbial communities to UV radiation exposure. The first experiment in November showed that the microbial community was significantly inhibited in the PAR + UV-A-exposed treatment but this inhibition declined with increasing addition of UV-B radiation. The second experiment in December showed that UV-A or UV-B radiation had few significant effects. Like in Expt 1, some taxa were inhibited by PAR + UV-A or promoted by UV-B, but most were inhibited at the highest UV-B irradiances (≤4.43 m ED). The last experiment in January showed UV-B induced inhibition of all but one of the dominant taxa. The seasonal transition in UV wavelengths responsible for inhibition of protists may be due to ozone reduction, the light history of protists, and/or changes in species composition. The increasing UV-B-induced inhibition we observed over the summer corresponded to a decline in ozone concentrations over Davis. This recurrent decline in ozone over Antarctica between January and April coincides with blooms of diatoms that appear to have low UV-B tolerance but are responsible for ~47% of annual primary production in Antarctic waters.

KEY WORDS: Antarctic · Marine protists · UV-A · UV-B · Ozone · Diatoms · Flagellates · Dinoflagellates

INTRODUCTION

Up to 70% reduction of the stratospheric ozone layer over Antarctica can occur in the austral spring (Kerr 1998). This reduction has enhanced UV-B radiation reaching the Earth's surface and has increased Antarctic erythemal irradiances up to 130% in spring (Madronich et al. 1998). In addition, depletion of ozone persists until February, leading to a 50 to 100% increase in UV-B radiation around the summer solstice (Jones & Shanklin 1995). Thus, UV-B radiation is enhanced throughout the period of greatest biological production in Antarctic waters. While current predictions suggest a gradual recovery of ozone concentrations by around the year 2050 (Taalas et al. 2000), the record loss of ozone over Antarctica in 2006 (see www.nasa.gov/vision/earth/lookingatearth/ozone_record.html) highlights the need for continuing research into the harmful effects of UV-B radiation.

UV-B radiation is predicted to have pervasive effects on marine plankton. Laboratory and field studies on marine protists indicate that UV-B radiation directly damages organisms at the molecular level, reducing the growth, production and survival of species with a low tolerance to UV-B exposure (see reviews by Tevini 1993, Vincent & Neale 2000, Davidson 2006). However,

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due to the differing effectiveness of mechanisms to tolerate UV-B exposure, interspecific variation in UV-B-induced damage is reportedly high (e.g. Karentz et al. 1991). This has led to the suggestion that exposure to UV-B radiation may cause changes in the composition and abundance of marine protists with ramifications for trophodynamics and biogeochemical cycles (Laurion et al. 1998, Mostajir et al. 2000, Davidson & Belbin 2002, Sommaruga 2003).

Remarkably few studies have addressed the effects of UV-B radiation on community-level interactions among marine microbes and fewer still have been performed in Antarctic waters (Davidson 2006). Some studies have shown that UV-B radiation has the potential to change the structure and function of Antarctic microbial communities (Smith et al. 1992, Davidson et al. 1996, Davidson & van der Heijden 2000, Davidson & Belbin 2002). However, as the results of community-level studies vary with environment, location and the composition of the community (Smith et al. 1992, Bothwell et al. 1993, Sommaruga et al. 1999, Davidson & Belbin 2002), the effects of enhanced UV-B irradiances on natural communities of Antarctic marine protists remain unclear.

In this study, we examined UV radiation effects on 3 natural marine protist communities that occurred in inshore waters over the 2002–2003 summer at Davis Station, East Antarctica (68° 43.2′ S, 77° 56.4′ E). Each community was exposed to ambient solar radiation with differently attenuated UV radiation. Responses of the 3 communities to the different experimental irradiances were characterised and compared over the summer.

MATERIALS AND METHODS

Three experiments of 13 to 14 d duration were performed between November 2002 and January 2003 in six 650 l polythene tanks ('minicosms') housed in a temperature-controlled shipping container. All minicosms were cleaned with Decon 90 (Decon Laboratories), followed by 10% AR grade HCl and rinsed with MilliQ water prior to each experiment. Following cleaning, the minicosms were filled with seawater and allowed to drain. Seawater was pumped to the minicosms from 2 m depth at a distance of 60 m offshore using a Teflon double diaphragm pump fitted to Teflon-lined hosing that had 200 µm mesh over the intake to exclude metazooplankton. All 6 minicosms tanks were then filled simultaneously to insure they contained the same initial microbial community and the inocula were allowed to equilibrate in the dark for 12 to 15 h before initial sampling. The content of each minicosm was gently mixed by a basal paddle rotating at 3 rpm. Water temperature in the minicosms was regulated by the refrigeration of the shipping container.

Each of the 6 minicosms was exposed to ambient Antarctic sunlight with differently attenuated UV radiation. Sunlight entered the shipping container through acrylic domes in the roof that transmitted 85 to 95% of ambient sunlight between 290 and 700 nm (Fig. 1). Sunlight was conducted from the dome to the top of each minicosm tank by anodised aluminium tubes that reflected ≥96% of incident light irrespective of wavelength. UV-attenuating screens were then used to expose the microbial community in each minicosm tank to UV radiation treatments that simulated different equivalent depths (ED) in the water column (see Table 1). ED was calculated using Beer's Law ($I/I_0 = e^{-kz}$), where I_0 and I are respectively the erythemal irradiances on the roof of the shipping container and 1 cm beneath water surface in the minicosm, $k = 0.4$ for erythemal UV radiation in ice edge water of low turbidity (Davidson & van der Heijden 2000), and z = ED. The transmittance of each screen was measured using a GBC 916 UV/VIS spectrophotometer (Fig. 1). The control treatment was screened with polycarbonate and was predominantly exposed to photosynthetically active radiation (PAR) (>385 nm), equating to an ED ≥12.24 m. A Mylar D screen (DuPont Mylar®, 0.075 mm thickness) transmitted UV-A + PAR (315 to 750 nm) at ED of ≥9.43 m. Borosilicate glass of 9, 5 and 3 mm thicknesses (low UV-B and intermediate UV-B1 and B2, respectively) attenuated UV-B wavelengths to simulate ambient sunlight at EDs of ≥7.15, ≥5.38 and ≥4.97 m, respectively. UV transmissive acrylic transmitted ambient light at ED ≤4.43 m (high UV-B).

Ozone and light. Satellite measurements of total column ozone concentration (spatial resolution ~50 ×

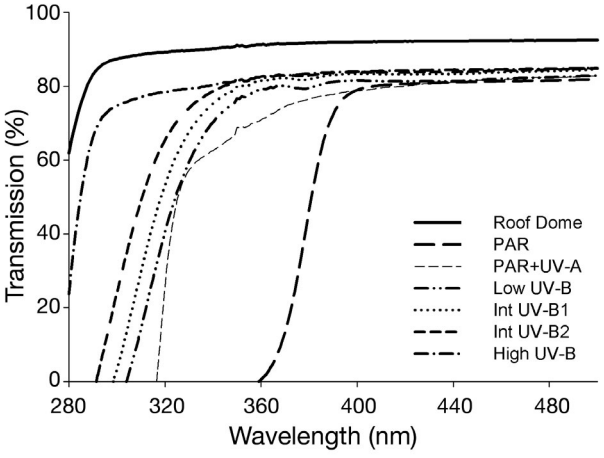

Fig. 1. Percentage transmission of ambient light through the UV transmissive acrylic roof domes and into the minicosms screened by polycarbonate (PAR control), Mylar (PAR + UV-A radiation), borosilicate glass (9, 5 and 3 mm = low UV-B and intermediate [Int] UV-B1 and UV-B2, respectively), and UV transmissive acrylic (high UV-B radiation)

50 km) over Davis Station were obtained from the Total Ozone Mapping Spectrometer (TOMS) website (http://toms.gsfc.nasa.gov/ozone/ozone_v8.html) for each day that minicosm experiments were performed.

Throughout the experiments, erythemal UV radiation and PAR measurements were obtained using a Solar Light Company 501A Biometer and a LI-COR LI-190SA Quantum sensor mounted on the roof of the minicosm container. The Biometer and LI-COR were sampled every second and the average irradiance logged at 10 min intervals.

Following the incubations, measurements were made concurrently on the roof of the container and within the minicosms in order to model the light climate in each experimental treatment. The model accounted for varying solar zenith angle and attenuation due to the dome, reflective tubing, treatment screen, water depth and chlorophyll biomass (see Appendix 1 for model description in AME Supplementary Material available online at: www.int-res.com/articles/suppl/a052p131_app.pdf). This model was then applied to the average 10 min erythemal irradiance from the container roof giving the cumulative erythemal UV-B dose for each treatment. We used erythemal UV irradiance because the action spectrum is similar to that for whole plants and DNA. Our experiments examined the interactive responses of entire communities of marine microbes for which more specific physiological weighting functions were not applicable (Davidson & van der Heijden 2000, Davidson & Belbin 2002).

Minicosm incubations and sampling. The seawater incubated in Expts 1 and 2 (26 November and 14 December, respectively) was collected from holes drilled through approximately 1.8 m of land-fast sea ice. Seawater for Expt 3 (6 January) was collected after land-fast ice had disappeared from the site. Initial samples (Time 0) were obtained from each minicosm tank following equilibration and further samples were obtained after 1, 2, 4, 7 and 14 d incubation in Expt 1 or finally on Day 13 in Expts 2 and 3. On each sample day ~25 l of seawater from each minicosm was transferred into MilliQ-rinsed, black polythene carboys via a Teflon sample line. The carboys were transferred to the laboratory and subsampled for chl *a*, particulate organic carbon (POC), and species identification and enumeration. Total sample volumes removed during each experiment did not exceed 20% of the initial seawater volume in each minicosm.

Chl *a*. A known volume of between 0.25 and 1 l of seawater from each minicosm was filtered through 13 mm GF/F filters and stored at −80°C at Davis Station. These were transferred to liquid nitrogen during transport to Australia and stored at −135°C in an ultralow freezer (Sanyo) until analysed within 7 mo. Pigments were extracted by sonication in 1.8 ml of MeOH, to which 176 µg of apo-8′-β-carotenal (Fluka) was added as an internal standard. The extract was filtered through a 0.45 µm inline filter, and pigments were identified by HPLC using the methods of Zapata et al. (2000). Hardware included a 626 LC pump (Waters), a Waters Symmetry C8 column (250 × 4.6 mm, 5 µm bead size), a Waters 996 photodiode array and F1000 fluorescence detectors (Hitachi). Millenium 32 (version 3.05.01) and Waters Empower build 1154 software was used for acquisition and processing of data. Pigments were identified by comparison with authentic pigment spectra obtained from the Scientific Committee on Oceanic Research (SCOR) reference cultures (Jeffrey & Wright 1997), and by comparison of retention times of a mixture of standard pigments that was analysed daily. Pigments were quantified following the internal standard method of Mantoura & Repeta (1997) after isolation of individual pigments from SCOR cultures and spectrophotometric quantification in standard solvents (Jeffrey & Wright 1997).

Organic C and N. All glassware and filters were muffle furnaced at 500°C for 8 h prior to use. Forceps and other plastic ware were soaked in 10% Decon 90 detergent for >2 d and thoroughly rinsed in MilliQ water. Within 1 h of sample collection, a known volume of sample (between 0.35 and 1 l) was filtered through a muffled 25 mm GF/F filter (Whatman) until the filter clogged.

The 25 mm GF/F filter was used to determine concentrations of POC and particulate organic nitrogen (PON). Filters were folded in half, sample inward and frozen (see 'Chl *a*' above) prior to analysis. A muffled glass cap on the end of a syringe was used to punch a 2.69 mm diameter subsample from each filter. These were exposed to HCl fumes in a desiccator for ≥12 h to remove inorganic carbon, dried for ≥12 h at 60°C and transferred into ultra lightweight pressed tin capsules (Elemental Analysis). The capsules were then crushed and the concentration of POC and PON determined using a Carlo Erba Elemental Analyser at the University of Tasmania.

Protists. Subsamples were taken from the 20 l carboys for the identification and enumeration of protist species by microscopy. Subsamples of up to 1 l were concentrated over 47 mm, 0.8 µm polycarbonate filters. After resuspension, cells were observed at 400× magnification under Nomarski optics and blue epifluorescense (filter set 487909 with 450 to 490 nm exciter filter, 510 chromatic beam splitter and 520 nm barrier filter) using a Zeiss Axiovert inverted microscope to determine their trophic status based on the presence or absence of chlorophyll. Subsamples of 960 ml were fixed to a final concentration of 1% glutaraldehyde for 20 min, followed by the addition of 2 ml of Lugol's iodine. Protists were allowed to sediment for at least 3 d and the supernatant was then removed by aspira-

tion. The resulting concentrated samples of ~100 ml were stored in the dark at 4°C until counted within 6 mo. Subsamples of 3 to 10 ml were settled in 10 ml chambers and counts performed over 20 randomly selected fields of view at 400× and 1000× magnification by inverted microscopy using Nomarski optics. Mean concentrations and standard errors of each protistan taxa/group were calculated using concentrations obtained from the replicate, microscopic fields of view (n = 20) in each light treatment at each sampling time.

The dimensions of ≥20 cells of each protistan taxa were measured by light microscopy. Protist biovolumes were calculated from the formulae of Hillebrand et al. (1999). Species biovolumes were multiplied by 1.33 to compensate for shrinkage caused by Lugol's fixation (Dehairs et al. 1992). Cellular carbon was calculated using the following conversions: 0.19 pg C μm^{-3} for ciliates (Putt & Stoecker 1989), 0.183 pg C μm^{-3} for heterotrophic dinoflagellates (Caron et al. 1995), and pg C = $0.109 \times (\text{cell volume})^{0.991}$ for all other autotrophic and heterotrophic cells (Montagnes et al. 1994).

Samples were prepared for scanning electron microscopy (SEM) to aid identification of the protistan community composition. Samples were post-fixed with OsO_4 vapour for 30 min, sedimented onto polylysine-coated coverslips and dehydrated over a graded methanol series. The coverslips were then immersed in hexamethylsilizane (HMDS) for 5 min, air-dried, attached to SEM stubs, sputter-coated with gold and examined using a Phillips Electroscan Environmental SEM with Environmental SEM System 2020 Version 3.2 software.

Statistical analysis. ***Exploratory analysis:*** Acclimation to light climate, involving changes in microbial abundance and composition, takes time to be expressed as changes in community composition. As illustrated by the concentrations of POC and chl *a* (see Fig. 4), differences in the abundance of microbes were seldom significant over shorter incubation periods. Consequently, statistics were performed on communities following the maximum duration of exponential increase in concentration, namely after 14, 13, and 7 d for Expts 1, 2 and 3, respectively.

Concentrations of protistan taxa ranged over 3 orders of magnitude and were relativised prior to analysis using the formula (Field et al. 1982):

$$Y_{ie} = 100X_{ij}/\Sigma_{j=1}^{n}X_{ij}$$

where Y_{ie} is the transformed score, X_{ij} is the concentration of the ith species in the jth sample and $\Sigma_{j=1}^{n}X_{ij}$ is the sum of X_{ij} over all samples. This transformation ensured that each taxon or group contributed equally to the analysis. Species totalling <2% of the total carbon biomass were grouped to overcome the confounding effect of low concentrations and high variance.

Cluster analysis was performed using a statistical program called PATN (Belbin 1993) to examine relationships between protist communities in each experiment. The Bray-Curtis measure of association was used to generate quantitative estimates of the taxonomic resemblance between each of the light treatments. These associations were subjected to flexible hierarchical clustering by unweighted pair-group using arithmetic average (UPGMA) to produce dendrograms. Each dendrogram structure was examined to determine arbitrary levels of dissimilarity that conveniently summarised the UV-induced changes in protist composition and abundance.

Confirmatory analyses: Multivariate analysis of variance (MANOVA) and post hoc analysis using Tukey's test was performed to determine the significance of UV-induced changes in relativised cell concentrations of the dominant protist taxa.

RESULTS

Seawater temperatures

Initial temperatures of seawater for Expts 1, 2 and 3 were –1.3, –1.0 and 0.6°C, respectively. Water temperatures in the minicosms averaged 0.8, 1.2 and 0.2°C warmer than ambient but differed by ≤0.24, 0.52 and 0.44°C during Expts 1, 2 and 3, respectively.

Light treatments

Ozone concentrations over Davis decreased over the summer (Fig. 2). During our experiments, total column ozone declined from 363–316 Dobson units (DU) in late November to 341–306 DU in December and 313–288 DU in January. Downwelling PAR varied during Expt 1 due to cloud cover but reached irradiances of >350 mol m^{-2} s^{-1} on cloud-free days in each experiment

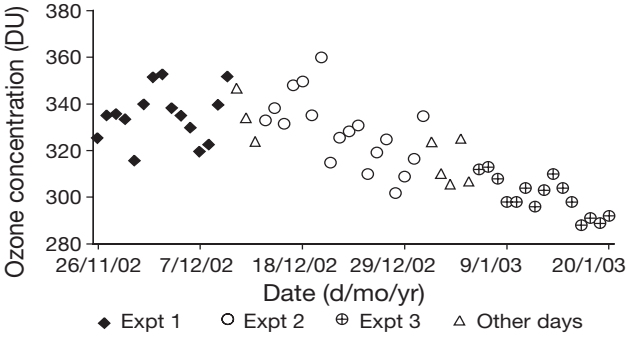

Fig. 2. Stratospheric ozone concentrations (Dobson units [DU]) over Davis Station (data from http://toms.gsfc.nasa.gov/ozone/ozone_v8.html)

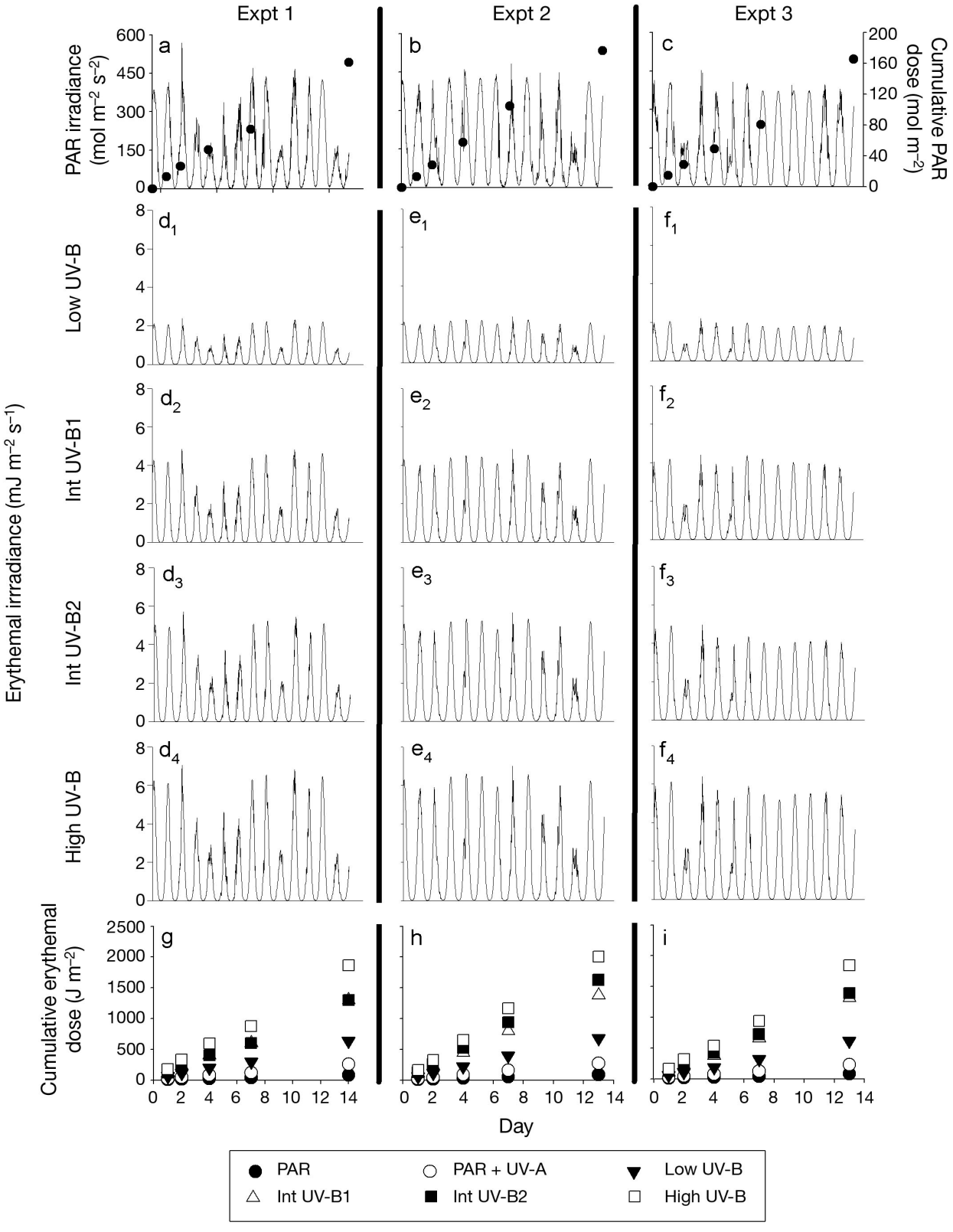

Fig. 3. (a–c) PAR irradiance (solid line) and cumulative PAR dose (●), (d_{1-4} to f_{1-4}) erythemal UV irradiance in Low, Intermediate and High UV-B treatments (Note: peak erythemal UV irradiance in the PAR and PAR+UV-A treatments was ≤5 and 9%, respectively, that of the High UV-B treatment [data not shown]), and (g–i) cumulative erythemal UV dose in each light treatment during Expts 1, 2 and 3, respectively. Int: intermediate

Table 1. Light treatment, UV-attenuating screen, attenuation of downwelling PAR and erythemal UV radiation and equivalent water column depth experienced by marine microbes beneath each light treatment. I_0 and I are the erythemal irradiances at the surface. Int: intermediate

Light treatment	Screen material	Attenuation of PAR I/I_0	Attenuation of erythemal UV I/I_0	Equivalent depth (m)
PAR	Polycarbonate	0.440	0.007	12.24
PAR + UV-A	Mylar	0.421	0.024	9.43
Low UV-B	9 mm glass	0.421	0.058	7.15
Int UV-B1	5 mm glass	0.411	0.116	5.38
Int UV-B2	3 mm glass	0.416	0.138	4.97
High UVB	Acrylic	0.484	0.170	4.43

(Fig. 3a–c). Daily doses of PAR were ~7% higher during Expt 2 (December), which spanned the summer solstice, than in Expts 1 (November) and 3 (January). Cumulative PAR doses reached 164, 178 and 166 mol quanta m^{-2} in Expts 1, 2 and 3 (Fig. 3a–c) but varied little among light treatments in each experiment (± ≤5 mol quanta m^{-2}).

Downwelling erythemal UV radiation showed similar daily patterns to that of downwelling PAR (Fig. 3d–f). The increase in cumulative erythemally

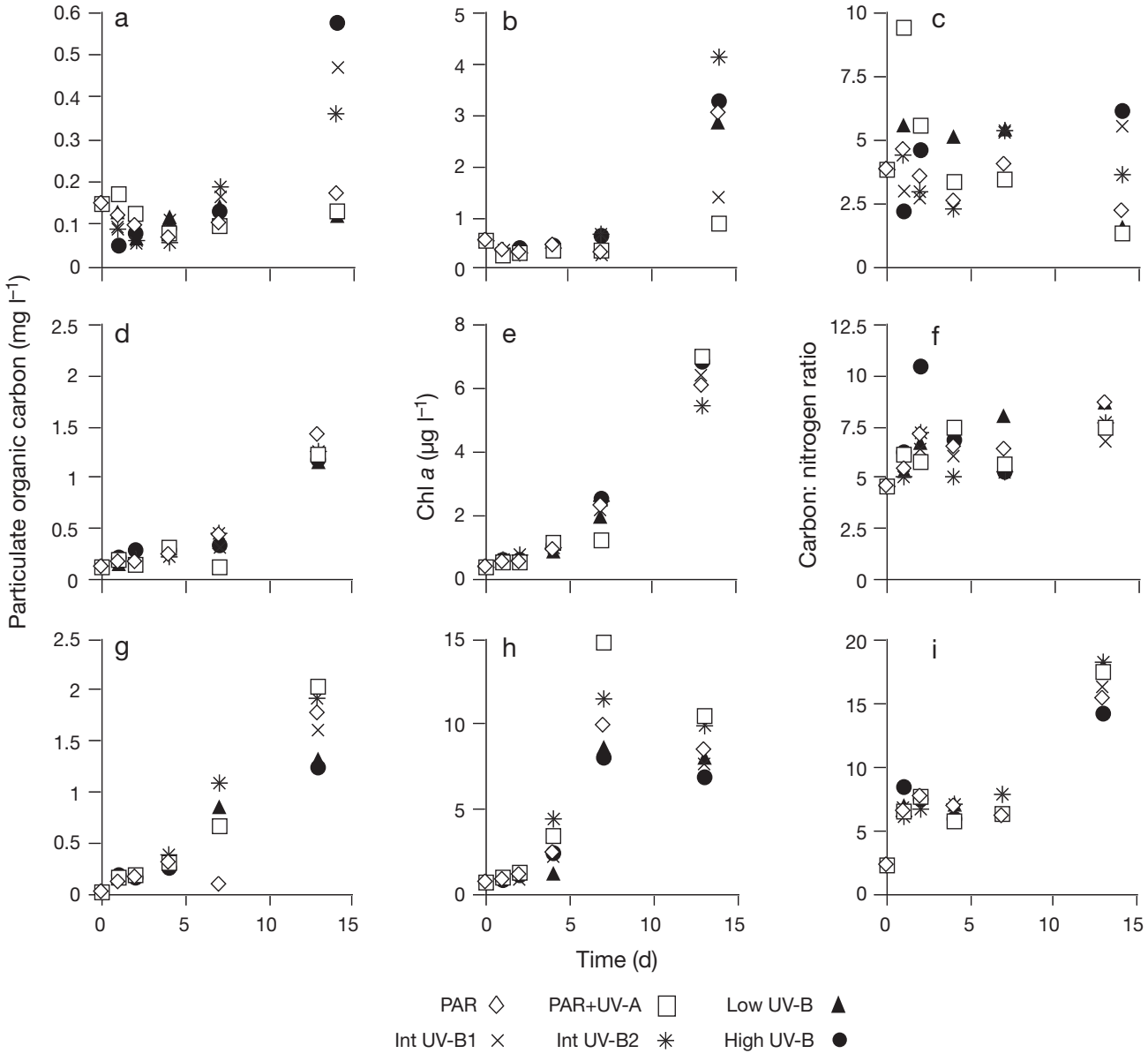

Fig. 4. (a,d,g) Particulate organic carbon (POC) concentration, (b,e,h) chlorophyll *a* concentration and (c,f,i) C:N ratios for each light treatment in Expts 1 (a–c), 2 (d–f) and 3 (g–i). Int: intermediate

weighted UV radiation doses was approximately linear during each experiment (Fig. 3g–i). In all 3 experiments, the PAR-exposed treatment (12.24 m ED) received 84 ± 5 J m^{-2} or 4.4 % of erythemal UV dose in the high UV-B treatment, while the PAR + UV-A treatment (9.43 m ED) received 253 ± 23 J m^{-2} or 13.3 % of the high UV-B dose. Cumulative erythemal UV-B doses reached 2003.3 J m^{-2} in the high UV-B treatment by the end of Expt 2 (Fig. 3h), but only 1864 and 1841 J m^{-2} in Expts 1 and 3, respectively. Average daily erythemal UV-B dose rates increased ~15 % between Expts 1 and 2 (November and December). Daily erythemal dose rates then declined ~14 % in the PAR and PAR + UV-A-exposed treatments between Expts 2 and 3. Doses in treatments that were also exposed to UV-B declined only ~9 % (Fig. 3).

Measurements to model the transmission of PAR and erythemal UV radiation showed that at least 41 % of the downwelling PAR was transmitted to each of the tanks irrespective of the UV-attenuating screen (Table 1). Erythemal UV radiation was attenuated between 83 % in the high UV treatment and 99.3 % in the PAR-exposed treatment (Table 1).

POC, chl *a* biomass, and C:N ratios

Concentrations of POC and chl *a* showed that the microbial community grew exponentially in all 3 experiments (Fig. 4). Expt 1 had an extended lag phase (7 d) (Fig. 4a,b), while Expts 2 and 3 grew exponen-

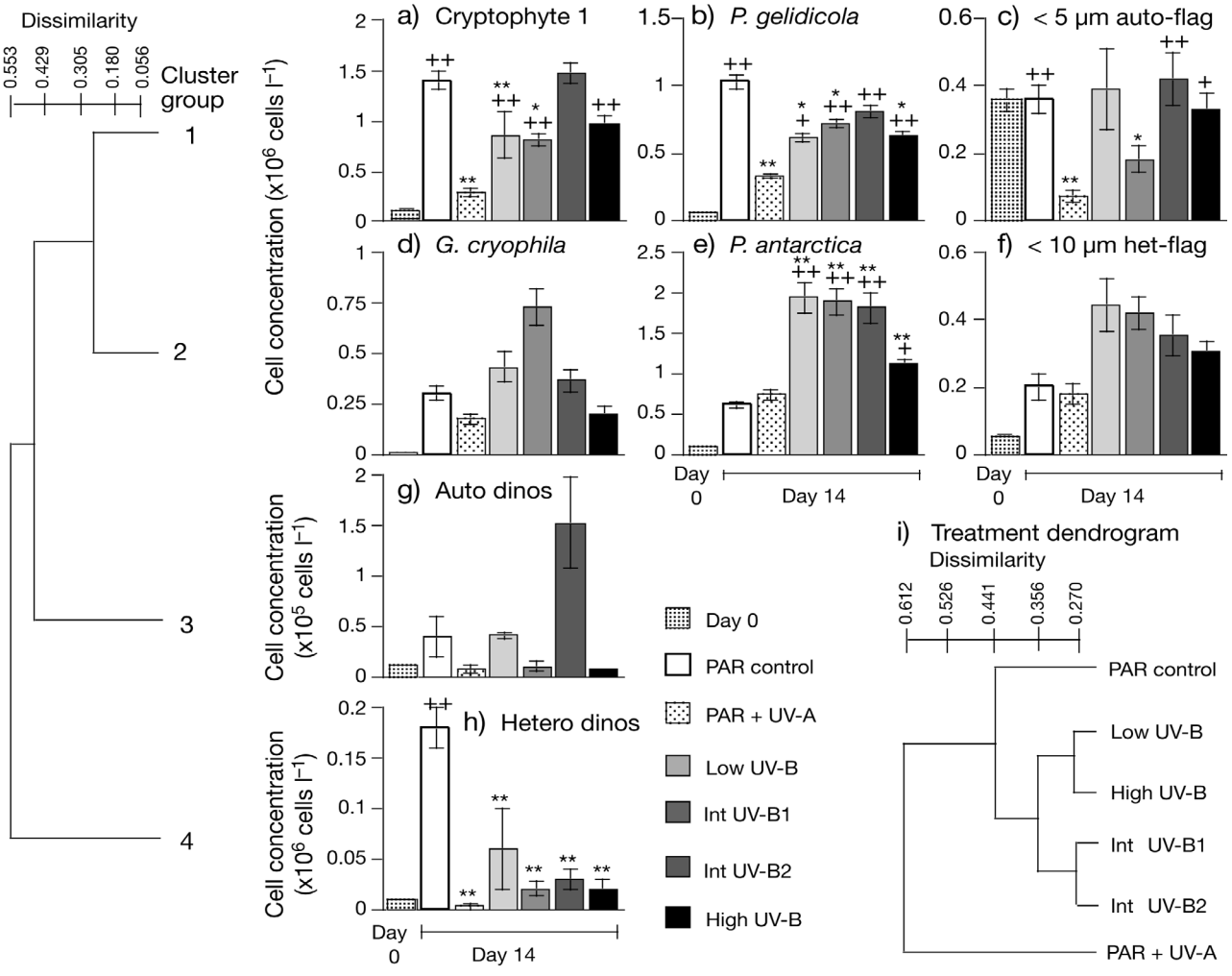

Fig. 5. Four cluster groups that conveniently summarised changes in protist concentrations in Expt 1 (November 2002) following 14 d incubation under different light treatments. (a–h) Concentrations of taxa following 0 and 14 d exposure; (i) cluster grouping of light treatments based on protist composition. Error bars are ±1 SE. Probability (p) of difference from PAR treatment (Table 2) of 0.005 < p < 0.05 denoted by * and p < 0.005 by **. Probability of difference from PAR + UV-A of 0.005 < p < 0.05 denoted by + and p < 0.005 by ++. Cryptophyte 1: see 'Expt 1' under 'Results'; *P. gelidicola*: *Pyramimonas gelidicola*; auto-flag: autotrophic flagellates; *G. cryophila*: *Geminigera cryophila*; *P. antarctica*: *Phaeocystis antarctica*; het-flag: heterotrophic flagellates; Auto dinos: autotrophic dinoflagellates; hetero dinos: Heterotrophic dinoflagellates

tially from early in the incubation (Fig. 4d,e,g,h). In Expts 1 and 2, microbial biomass (POC and chl *a*) increased throughout the incubation and C:N ratios remained relatively low (<9:1, Fig. 4c,f). In Expt 3, concentrations of chl *a* decreased following 7 d of incubation, and C:N ratios increased from an average of 7:1 to 17:1 following 14 d of incubation (Fig. 4h,i).

Protist community composition

The flagellate life stage of the haptophyte *Phaeocystis antarctica* was abundant in all 3 experiments. While the response of most taxa or groups to different UV radiation wavelengths changed through the season, *P. antarctica* showed a high tolerance of exposure to UV-B radiation throughout the summer.

For each of the 3 experiments, cluster analysis was used to examine similarities in responses of dominant protistan taxa/groups to experimental irradiance (taxonomic associations) and among light treatments (treatment associations). Differences in concentrations of protists that led to associations amongst taxa in cluster analysis were not necessarily significant in confirmatory analysis by MANOVA.

Expt 1

The protistan community incubated during Expt 1 was obtained from beneath land-fast ice and was dominated by auto- and heterotrophic flagellates together comprising 98% of the protistan biomass. All abundant taxa were inhibited by exposure to PAR or PAR + UV-A (≥9.43 m ED, Fig. 5). However, to varying degrees, each showed mitigation of this inhibition by exposure to UV-B radiation.

Taxonomic associations. Four groups were discriminated at a dissimilarity of 0.205 that conveniently summarised the responses of protist taxa to light treatment.

Cluster group 1 was composed of protists whose concentrations were lowest in treatments exposed to PAR + UV-A radiation. This group comprised the following: an unidentified, tear-shaped cryptophyte reported by Scott & van den Hoff (2005), hereafter called Cryptophyte 1; *Pyramimonas gelidicola*; and <5 µm autotrophic flagellates, including chrysophytes, prasinophytes and haptophytes. Cryptophyte 1 and *P. gelidicola* increased significantly in concentration from Day 0 to Day 14 in all treatments (Fig. 5a,b; Tukey's test $p \leq 0.008$). Concentrations of the <5 µm autotrophic flagellates decreased significantly from Day 0 to Day 14 in the PAR + UV-A and UV-B1 treatments (Fig. 5c) but did not change in other light treatments. Among treatments on Day 14, concentrations of Cryptophyte 1 and *P. gelidicola* were significantly lower in the PAR + UV-A-exposed treatment than in all other light treatments (Table 2, Fig. 5a,b). Concentrations of <5 µm autotrophic flagellates were also lower under PAR + UV-A radiation, but this difference was only significant for treatments exposed to PAR and high UV-B radiation (12.24 and ≤4.97 m ED, respectively; Fig. 5c, Table 2).

Table 2. Significant differences between abundances of protist taxa in treatments exposed to PAR + UV-A radiation or PAR (control) and all other light treatments following 14 d exposure in Expt 1 (November 2002) (ANOVA, $F_{0.05(2),\ 5,\ 482} = 7.62$, $p < 0.0001$; p by Tukey's test). Crypto 1: cryptophyte sp. 1 (see 'Expt 1' under 'Results'); *P. gelid*: *Pyramimonas gelidicola*; auto-flag: autotrophic flagellates; *P. antar*: *Phaeocystis antarctica*. No significant difference where no data are given

Equivalent depth (ED) and light treatment	Crypto 1	*P. gelid*	<5 µm auto-flag	*P. antar*	Heterotrophic dinoflagellates
PAR + UV-A comparison					
ED 12.24 m PAR control	<0.001	<0.001	0.001		<0.001
ED 7.15 m PAR + UV-A + Low UV-B	0.001	0.003		<0.001	
ED 5.38 m PAR + UV-A1 + UV-B 1	<0.001	<0.001		<0.001	
ED 4.97 m PAR + UV-A + UV-B2	<0.001	<0.001	0.005	<0.001	
ED 4.43 m PAR + UV-A + High UV-B	<0.001	<0.001	0.002	0.010	
PAR control comparison					
ED 9.43 m PAR + UV-A	<0.001	<0.001	0.001		<0.001
ED 7.15 m PAR + UV-A + Low UV-B	<0.001	0.002	0.028	<0.001	<0.001
ED 5.38 m PAR + UV-A + UV-B1	0.023	0.035	0.016	<0.001	<0.001
ED 4.97 m PAR + UV-A + UV-B2				<0.001	<0.001
ED 4.43 m PAR + UV-A + High UV-B		0.022		<0.001	<0.001

Cluster group 2 was composed of protists with lowest abundances in treatments exposed to both PAR and PAR + UV-A radiation (≤9.43 m ED). This group comprised *Geminigera cryophila*, *Phaeocystis antarctica,* and the <10 µm heterotrophic flagellates (mostly the choanoflagellates *Bicosta* spp. and *Diaphanoeca multiannulata*). Abundances of *G. cryophila* and *P. antarctica* increased significantly in all treatments during the 14 d of incubation (Fig. 5d,e; Tukey's test $p \leq 0.0001$). Abundances of the <10 µm heterotrophic flagellates also increased from Day 0 to Day 14; however, these increases were not significant. Among treatments on Day 14, results showed lower abundances of these taxa in treatments exposed to PAR and PAR + UV-A radiation, indicating that inhibition of their abundance was mitigated by exposure to low to intermediate UV-B irradiance. This effect was only statistically significant for *P. antarctica*, the most abundant flagellate (Table 2). Though not significant, high UV-B irradiances (≤4.43 m ED) also appeared to inhibit abundances of members of Cluster group 2 (Fig. 5d–f).

Cluster group 3 contained only autotrophic dinoflagellates, including *Polarella glacialis* and 2 unidentified gymnodiniod species. We found that abundances of the autotrophic dinoflagellates did not change significantly between Days 0 and 14 and there were no significant differences between light treatments (Fig. 5g). Cluster group 4 contained only heterotrophic dinoflagellates, including *Gyrodinium lachryma*, *Protoperidium charcoti*, *Prorocentrum antarcticum,* and a 20 µm long, armoured *Gymnodinium* sp. Abundances increased significantly in most treatments (Tukey's test $p < 0.02$) between Days 0 and 14, but decreased significantly in the PAR + UV-A-exposed treatment (Fig. 5h; Tukeys test $p < 0.0001$). Among treatments on Day 14, abundances of heterotrophic dinoflagellates were significantly lower in all PAR + UVR-exposed treatments than the PAR-exposed control (Table 2).

Treatment associations. Cluster analysis of light treatments based on the abundance of protist taxa or groups in Expt 1 showed that the PAR + UV-A-exposed treatment was the most dissimilar (0.612) from other light treatments (Fig. 5i). This agrees with the finding that abundances of dominant protist taxa were lowest in this treatment (in Cluster group 1 above), as were concentrations of chl *a* and POC (Fig. 4a,b). The treatments exposed to PAR alone were the second most dissimilar (0.441), reflecting low concentrations of abundant protist taxa in this treatment.

UV-B-exposed treatments were more similar (0.356), with subgroupings of low and high versus intermediate UV-B exposures at a dissimilarity of 0.270. This reflects the higher concentrations of protists in UV-B-exposed treatments than those exposed to PAR or PAR + UV-A radiation. Amongst the UV-B-exposed treatments, concentrations of some taxa (Cryptophyte 1, *Pyramimonas gelidicola*, *Geminigera cryphila* and autotrophic dinoflagellates) were lower in treatments exposed to the low (7.15 m ED) and high (4.43 m ED) UV-B than at intermediate UV-B irradiances (4.97 and 5.38 m ED).

Expt 2

The microbial community incubated for Expt 2 was again obtained from beneath fast ice and was similar in composition to that in Expt 1. Auto- and heterotrophic flagellates again dominated but comprised 70% of the total protistan biomass. Despite the similarity of the protist community to that in Expt 1, confirmatory statistical analysis found few significant differences in the abundance of each protist taxa amongst light treatments.

Taxonomic associations. Three cluster groups conveniently discriminated between protist taxa in Expt 2 (Fig. 6). Group 1 contained 5 of the 8 major taxa, namely Cryptophyte 1, *Geminigera cryophila*, *Pyramimonas gelidicola*, <5 µm autotrophic flagellates, and autotrophic dinoflagellates (Fig. 6a–e). With the exception of *P. gelidicola,* abundances of these taxa increased significantly after 13 d of incubation (Tukey's test $p \leq 0.0001$). In contrast with the first experiment, the abundance of these taxa by Day 13 was commonly highest in the PAR + UV-A or PAR + UV-A + low UV-B treatments (9.43 and 7.15 m ED, respectively). Though seldom significant, concentration of taxa in this group were lowest in treatments exposed to PAR (>12.24 m ED) or intermediate to high UV-B irradiances (≤5.38 m ED). Only autotrophic dinoflagellates showed significant differences in concentration among light treatments, with concentrations in the high UV-B-exposed treatment being lower than others exposed to UV radiation ($\leq 1.71 \times 10^6$ cells l^{-1}; Tukey's test $p < 0.001$) and to PAR (2.72×10^6 cells l^{-1}; Tukey's test $p < 0.001$).

Cluster 2, containing all diatoms, showed a similar response to that of Cluster group 1 (Fig. 6f) and it is likely that this group was differentiated largely on the basis of their abundance (10-fold lower than any other taxa). No significant light-induced differences were found in the concentrations of diatoms but their concentrations were lowest at the highest UV-B irradiance (4.43 m ED).

Cluster group 3 was composed of *Phaeocystis antarctica* and heterotrophic flagellates and ciliates (Fig. 6g,h) whose concentrations increased with increasing UV-B irradiance, although not signifi-

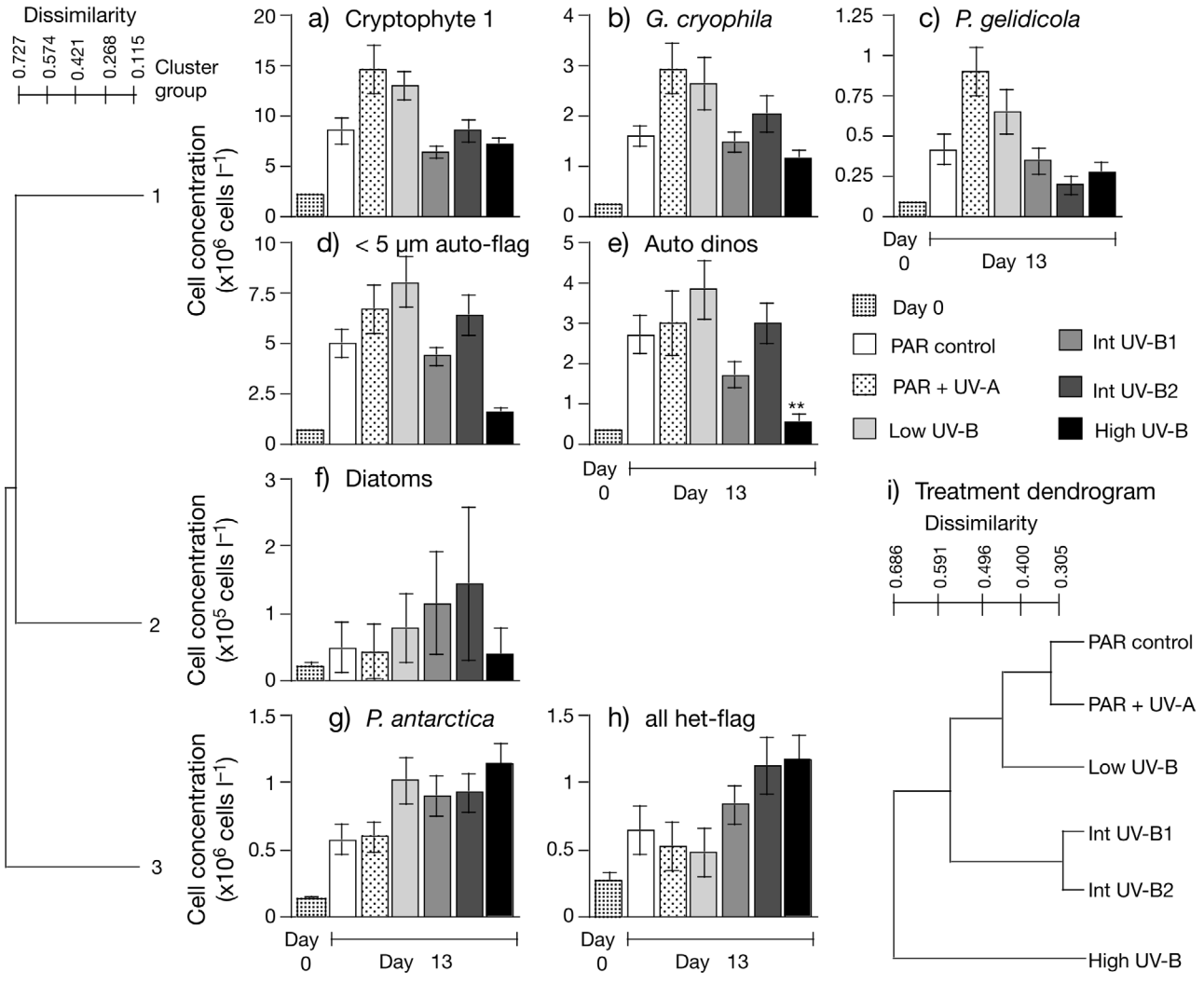

Fig. 6. Three cluster groups that conveniently summarised changes in protist concentration in Expt 2 (December 2002) following 13 d incubation under different light treatments. (a–h) Concentrations of taxa following 0 and 13 d exposure; (i) cluster grouping of light treatments based on protist composition. Error bars are: ±1 SE. Probability (p) of difference from PAR treatment of $p < 0.005$ denoted by **. See Fig. 5 legend for abbreviations

cantly. The heterotrophic flagellate group contained a variety of organisms including heterotrophic dinoflagellates of the same species as occurred in Expt 1: the flagellates *Cryothecomonas armigera* and *Leucocryptos marina,* the ciliates *Rimostrombidium glaciicolum*, *Tintinnopsis* spp. and choanoflagellates (as in 'Expt 1' above).

Treatment associations. The highest UV-B treatment (≤4.43 m ED) was the most dissimilar from other treatments (Fig. 6i), reflecting the lower abundances of protists in this treatment in Cluster groups 1 and 2 (above). Intermediate UV-B exposures (4.97 m and 5.38 m ED) were grouped together, commonly containing intermediate abundances of the main protist taxa. Treatments that received little or no UV-B radiation (≥7.15 m ED) were most similar.

Expt 3

In contrast to the previous experiments, in Expt 3 the incubated seawater was obtained following the disappearance of land-fast ice and diatoms comprised 98% of the protistan biomass. The remaining 2% was comprised of auto- and heterotrophic flagellates.

Taxonomic associations. Six cluster groups were identified that summarised the wavelength-specific responses of the protistan community to ambient solar radiation (Fig. 7). Two of these groups (containing only 'other pennate' diatoms such as *Nitzschia* and *Navicula* spp. or 'other centric' diatoms including *Chaetoceros* and *Thalassiosira* spp. and *Eucampia antarctica*) had high variance, showed no significant differences between light treatments, and are not shown or considered further.

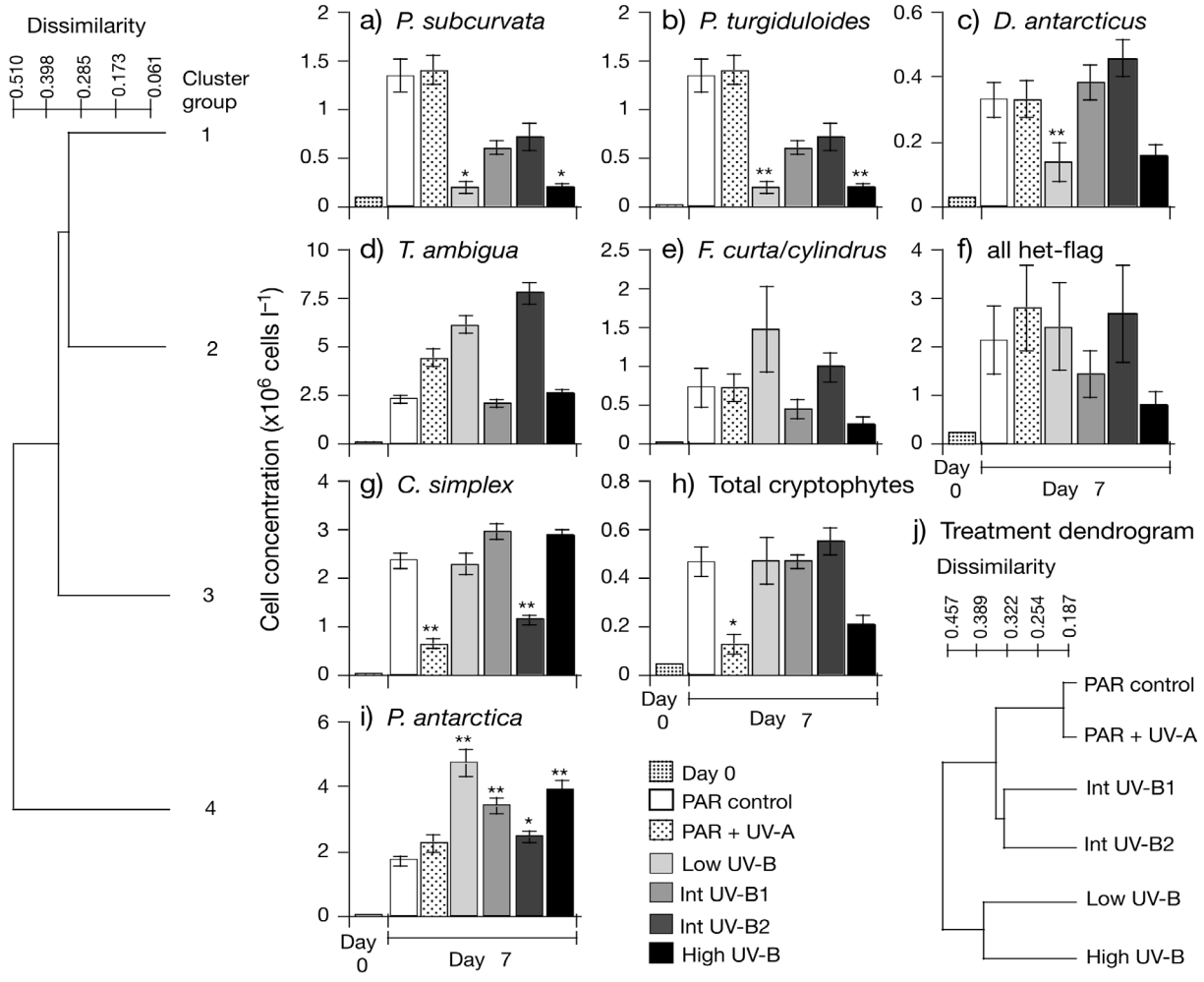

Fig. 7. Four cluster groups that conveniently summarised changes in protist concentration in Expt 3 (January 2003) following 7 d incubation under different light treatments. (a–i) Concentrations of taxa following 0 and 7 d incubation; (j) cluster grouping of light treatments based on protist composition. Error bars are: ±1 SE. Probability (p) of difference from PAR treatment (Table 3) of $0.005 < p < 0.05$ denoted by * and $p < 0.005$ by **. *P. subcurvata*: *Pseudonitzschia subcurvata*; *P. turgiduloides*: *Pseudonitzschia turgiduloides*; *D. antarcticus*: *Dactyliosolen antarcticus*; *T. ambigua*: *Thalassiosira ambigua*; *F. curta/cylindrus*: *Fragilariopsis curta/cylindrus*; het-flag: heterotrophic flagellates; *C. simplex*: *Chaetoceros simplex*; *P. antarctica*: *Phaeocystis antarctica*

Table 3. Significant differences between abundances of protist taxa in treatments exposed to PAR (control) and all other light treatments following 7 d exposure in Expt 3 (January 2003) (ANOVA, $F_{0.05(2),62,310} = 19.51 < 0.0001$; p by Tukey's test). *P. subc*: *Pseudonitzschia subcurvata*; *P. turgid*: *Pseudonitzschia turgiduloides*; *D. antar*: *Dactyliosolen antarcticus*; *C. simp*: *Chaetoceros simplex*; total cryptos: total cryptophytes; *P. antar*: *Phaeocystis antarctica*. No significant difference where no data are given

Equivalent depth (ED) and light treatment	*P. subc*	*P. turgid*	*D. antar*	*C. simp*	Total cryptos	*P. antar*
ED 9.43 m PAR + UV-A				<0.001	0.010	
ED 7.15 m PAR + UV-A + Low UV-B	0.002	<0.001	0.001			<0.001
ED 5.38 m PAR + UV-A + UV-B1						<0.001
ED 4.97 m PAR + UV-A + UV-B2				0.001		0.022
ED 4.43 m PAR + UV-A + High UV-B	0.002	<0.001				<0.001

Protist taxa in Cluster group 1 (*Pseudonitzschia subcurvata*, *P. turgiduloides* and *Dactyliosolen antarcticus*) increased significantly in abundance between Days 0 and 7 (Fig. 7a–c; Tukey's test $p \leq 0.0005$). By Day 7, these taxa had lower cell abundances in treatments exposed to high or low UV-B irradiances (Table 3). ANOVA and post hoc analysis showed that abundances in the high and low UV-B treatments were significantly lower than in the PAR-exposed control treatment for both *P. subcurvata* and *P. turgiduloides*. *D. antarcticus* was only significantly lower in the low UV-B treatment (Table 3).

Cluster group 2 contained *Thalassiosira ambigua*, *Fragilariopsis curta/cylindrus* and heterotrophic flagellates (Fig. 7d–f), the abundance of which increased significantly in concentration between Days 0 and 7 (Tukey's test $p \leq 0.0001$). Although not significant, abundances of these taxa at Day 7 were lowest in the high UV-B-exposed treatment, with variable densities in light treatments with lower UV-B doses.

Cell abundances of *Chaetoceros simplex* and total cryptophytes in Cluster group 3 were lowest following exposure to PAR + UV-A radiation (Fig. 7g,h). Of these taxa, only *C. simplex* increased significantly in abundance between Days 0 and 7 (Tukey's test $p < 0.0001$). Abundances of *C. simplex* and total cryptophytes were significantly lower in the PAR + UV-A treatment than the PAR-exposed control (Table 3). However, abundances of *C. simplex* in the intermediate UV-B2 treatment (4.97 m ED) were also significantly lower than in the control treatment.

Abundances of the flagellate *Phaeocystis antarctica*, the sole member of Cluster group 4, increased significantly in concentration between Days 0 and 7 (Fig. 7i; Tukey's test $p < 0.0001$). By Day 7, *P. antarctica* abundances were significantly lower in treatments exposed to PAR and PAR + UV-A than all treatments exposed to PAR + UV-A + UV-B (Table 3).

Treatment associations. After 7 d exposure, abundances of most protist taxa were lowest in the high UV-B-exposed treatment (4.43 m ED, Fig. 7j). The high UV-B treatment was weakly associated (0.389 dissimilarity) with the low UV-B treatment as the latter also contained low abundances of protists (Cluster group 1, Fig. 7a–c,j) and lowest concentrations of chl *a* (Fig. 4h).

Like in Expt 2, treatments exposed to PAR (12.24 m ED) and PAR + UV-A radiation (9.43 m ED) were closely associated. With the exception of Cluster group 3, cell abundances in these treatments were very similar. The relatively low dissimilarity between these treatments and those that also received intermediate UV-B irradiances (4.97 and 5.38 m ED) indicated that intermediate UV-B irradiances seldom significantly affected protist community abundance compared to the control.

DISCUSSION

Despite over 2 decades of intense scientific attention, the crucial question 'What are the effects of solar UV radiation on natural marine protist communities?' remains largely unanswered (Davidson 2006). The methods we used were chosen to maximise the likelihood that the responses of the protists were indicative of those in near-shore waters off Davis Station. We exposed natural communities of Antarctic marine microbes that were similar in composition to those recently reported from this site (Archer et al. 1996, Scott et al. 2000, Davidson & Belbin 2002) to differently attenuated ambient solar radiation. The minicosms we used supported exponential growth of protists for the entire incubation period in Expts 1 and 2 or for 7 d in Expt 3 after which C:N ratios of approximately 16:1 indicated that communities had become nutrient-limited (Healy 1975). Unlike previous field studies in which the light history of the protists was unknown (Davidson 2006), variations in the extent of land-fast ice over summer imposed large changes in the light history that allowed us to consider the effect of *in situ* acclimation on protistan sensitivity to solar wavelengths.

We found taxon-specific differences in the response of protists to solar radiation within each experiment and temporal changes in the sensitivity of protists to solar wavelengths through the season. Due to logistical constraints, we were unable to replicate light treatments (tanks). Thus, we were unable to estimate the natural variability in the response of a protist assemblage to a specific UV climate. However, the large volume in each tank increased the likelihood that our estimate closely approximated that in nature (Zar 1999).

Wavelength-specific responses

PAR and UV-A radiation

Instances of PAR and PAR + UV-A-induced inhibition of protist concentrations were observed throughout the summer. PAR irradiances that exceed saturation of photosynthesis are known to decrease productivity in Antarctic phytoplankton (Smith et al. 1992, Neale et al. 1994) and UV-A exposure can reportedly reduce water column photosynthesis and phytoplankton growth by up to 80% (e.g. Villafañe et al. 1995). Similarly, our study showed cluster groups containing taxa whose abundances were lowest in treatments exposed to PAR in each of the 3 experiments conducted over the summer (Cluster group 2 in November, 1 in December and 4 in January) and in the PAR + UV-A-exposed treatment in Expts 1 and 3 (Cluster groups 1 and 4 in November and 3 in January).

UV-B radiation

Responses of protist taxa to UV-B exposure were variable. Cluster analysis identified groups of taxa whose concentrations were reduced by exposure to UV-B radiation. In some instances, though not significant, inhibition increased with increasing UV-B dose and decreasing ED (Cluster 1 in December). Furthermore, concentrations of many taxa in Expt 3 were significantly lower following exposure to the highest UV-B irradiance treatment (4.43 m ED) than to other light treatments. It is likely that UV-B radiation, while promoting the abundance of some taxa at intermediate irradiances (next paragraph), can result in a large species-specific increase in phytoplankton mortality at higher irradiances. Thus, like previous studies (Smith et al. 1992, Davidson & Marchant 1994, Davidson & Belbin 2002), our results indicate that UV-B can alter the species composition of Antarctic protist assemblages by inhibiting the abundance of taxa with a low tolerance of exposure to UV-B radiation.

Contrary to most available literature (e.g. Karentz et al. 1991, Smith et al. 1992, Vernet 2000, Davidson 2006), we found that UV-B radiation frequently promoted or had little effect on protistan concentrations. Cluster analysis identified groups of taxa whose abundances in UV-B-exposed treatments did not differ significantly from those exposed to PAR (Cluster 1 in November) or were higher in UV-B-exposed treatments than those exposed to PAR or PAR + UV-A radiation (Cluster 2 in November and 3 in December). In addition, many protist taxa were abundant at intermediate UV-B irradiances (4.97 and 5.38 m ED), causing strong dissimilarity between these treatments and those exposed to high and low UV-B radiation in all 3 experiments.

Studies showing that exposure to UV-B wavelengths can increase protistan abundance are rare. Davidson & Marchant (1994) reported that the survival, growth, production and cell size of colonial *Phaeocystis* spp. in UV-B-exposed treatments was higher than those exposed to PAR and PAR + UV-A. Nilawati et al. (1997) also reported that addition of UV-B wavelengths to cultures exposed to PAR + UV-A radiation enhanced rates of photosynthesis by the polar diatom *Pseudo-nitzschia seriata*. However, few studies report beneficial effects of UV-B radiation and none have demonstrated such effects in natural communities of Antarctic marine protists.

The mechanism by which UV-B radiation could benefit protists is uncertain but may involve induction of photoprotective responses that ameliorate damage by PAR or UV-A radiation. Exposure to UV-B radiation can promote synthesis of photoprotective compounds such as mycosporine-like amino acids, antioxidants and carotenoids, or induce enzymatic protein repair mechanisms (reviewed in Banaszak 2003). UV-B-induced increases in photoprotection may also provide protection from damage by PAR or UV-A wavelengths, especially if cells are acclimated to low light beneath land-fast ice (see section 'Seasonal responses'). Our finding that concentrations of some taxa were highest in treatments exposed to intermediate fluxes of UV-B radiation suggests that moderate UV-B irradiances may enhance protection from PAR and/or UV-A. However, at higher UV-B fluxes, the abundance of some taxa declined, perhaps due to accumulation of unrepaired damage and/or the metabolic expense of further increasing their photoprotection (reviewed in Banaszak 2003).

Alternatively, increased concentrations of phytoplankton may be due to UV-B-induced changes in microbial trophodynamics. Studies by Bothwell et al. (1994), Mostajir et al. (1999), and Sommaruga et al. (1996, 1999) showed that exposure to UV-B radiation can inhibit grazers more than their prey, releasing prey from top-down control and allowing their abundance to increase in UV-B-exposed treatments. Similarly, we found that large heterotrophic dinoflagellates were greatly inhibited by UV radiation in Expt 1. Grazing by heterotrophic dinoflagellates can comprise much of the herbivory in Antarctic waters and some species can consume particles up to 50 µm in length (e.g. Bjørnsen & Kuparinen 1991, Boenigk & Arndt 2002). Thus, the increased abundance of many protist taxa may be due to UV-B-induced changes in trophodynamics.

In contrast with heterotrophic dinoflagellates, concentrations of some heterotrophs either increased or remained unchanged with increasing UV-B dose. Concentrations of heterotrophic flagellates, most of which were bacterivorous choanoflagellates, were higher in treatments exposed to UV-B than other light treatments in Expts 1 and 2. Mortality of protist taxa with low tolerance to UV-B wavelengths may have enhanced concentrations of heterotrophic flagellates by increasing concentrations of food such as dissolved organic carbon and bacteria (Davidson & van der Heijden 2000, Davidson & Belbin 2002). However, our results are inconclusive owing to low concentrations of heterotrophic flagellates and grouping of taxa with dissimilar trophic behaviour.

Seasonal responses

We observed a seasonal transition in light-induced inhibition of protists from PAR or PAR + UV-A radiation in November, to no significant effects in December, and inhibition by PAR + UV-A and PAR + UV-A + high UV-B radiation in January. This is despite the

highest doses of PAR and UV radiation in our study occurring over the summer solstice in December. Seasonal changes in sensitivity of protists to solar wavelengths may be due to light history, changes in species composition and/or declining stratospheric ozone concentrations over summer.

November

The sensitivity of the protist community to PAR and PAR + UV-A radiation in November may be due to their light history. Protists incubated in Expt 1 were obtained from beneath land-fast ice. This ice becomes increasingly opaque over spring and summer as melting creates brine inclusions that scatter and absorb light, with as little as 0.1 to 0.9% of surface PAR and 0.2 to 0.4% of surface UV radiation reaching the underlying water column (SooHoo et al. 1987, Trodahl & Buckley 1989, Lazzara et al. 2007). As a result, phytoplankton beneath land-fast ice are adapted to extremely low light levels, resulting in saturation of photosynthesis at low irradiances (Moisan & Mitchell 1999, Arrigo 2003, Moisan et al. 2006). Sudden exposure to high levels of light saturates the photosystem and generates damaging oxygen radicals such as singlet oxygen, hydrogen peroxide and superoxide, especially at low temperature and under exposure to short-wavelength, high-energy UV radiation (SooHoo et al. 1987, Neale et al. 1994, Roos & Vincent 1998, Thomas & Dieckmann 2002, Buma et al. 2003). Yet, with the exception of heterotrophic dinoflagellates, we found no UV-B-induced inhibition of protistan concentrations in November.

Instead, we found that sudden exposure of natural protist communities from beneath land-fast ice to near-surface solar irradiance resulted in longer-term effects (14 d) caused by PAR and PAR + UV-A radiation. These effects included up to 70% inhibition of chl *a* biomass by UV-A radiation and significantly reduced concentrations of some taxa by both PAR and PAR + UV-A radiation. Similarly, van de Poll et al. (2005) found that light history mediated the sensitivity of *Chaetoceros brevis* to PAR and UV-A exposure. In this case, acclimation to low light decreased the viability of cells exposed to ambient solar irradiances at these wavelengths. Sudden increases in irradiance similar to that seen in our study can occur in nature. High winds can cause the rapid break-out of land-fast ice along the Davis coastline during November and December (Heil et al. 1996, Thomson et al. 2006), exposing the planktonic protist community to such a sudden increase in ambient light. Similar increases in ambient irradiance may occur when pack ice, which covers some 19×10^6 km^2, retreats towards the Antarctic continent in spring and summer.

December

No significant inhibition of protists by PAR or PAR + UV-A radiation occurred in Expt 2. This is despite the persistence of land-fast ice at the sample site, little change in the protistan community composition and only a slight increase in the erythemal UV dose. Taxa that were inhibited in Expt 1 by exposure to PAR and PAR + UV-A radiation (Clusters 2 and 1, respectively) were among the most abundant in these treatments in Expt 2, despite further melting of land-fast ice that would have increased its opacity.

The decline in sensitivity to PAR and PAR + UV-A radiation between Expts 1 and 2 may have been due to the decline in land-fast ice extent and increased ice fracturing between these experiments. Fast ice cover retreated ~9 km between experiments to within 1.5 km of the sample site. Based on the current speeds and directions near Davis Station (Gibson et al. 1997, Gibson 1999), the time taken for cells to be advected from the ice edge to the sample site declined from 15–22 h in Expt 1 to 2–3 h in Expt 2, greatly reducing their acclimation to low light beneath the ice. Furthermore, tide cracks in the near vicinity of the sample site enlarged between Expts 1 and 2 from fractures only centimetres wide to fissures and ice-free areas over a metre wide. Thus, protists in Expt 2 that were derived from beneath land-fast ice surrounding the sample site would also have been acclimated to higher light levels, reducing their sensitivity to sudden exposure to PAR and UV-A radiation.

January

Significant UV-B-induced inhibition of protist concentrations was only observed after the land-fast ice disappeared. The disappearance of sea ice from the sample site prior to the experiment in January eliminated acclimation to the very low light climates below land-fast ice as a factor responsible for inhibition by UV-B radiation. The change in protist species composition from a flagellate-dominated community of November and December to one dominated by diatoms in January coincided with the appearance of significant UV-B-induced inhibition. Tolerance of exposure to UV-B radiation varies greatly between protist species (e.g. Karentz et al. 1991, Sommaruga & Buma 2000, Vernet 2000). Overall, flagellates in our experiments appeared to be more tolerant than diatoms of exposure to UV-B radiation. This is despite the reported sensitivity of smaller cells and some cryptophytes to UV-B-induced damage (Karentz et al. 1991, Hernando & San Román 1999). Tolerance was most pronounced for *Phaeocystis antarctica* as its

abundance was either unaffected or enhanced by exposure to UV-B radiation in all 3 experiments. *P. antarctica* and diatoms comprise most of the phytoplankton biomass in Antarctic waters (Smetacek et al. 2004). Our results, like those of Davidson et al. (1996), indicate that ozone reduction and the consequent enhancement of UV-B irradiances may increase the abundance of *P. antarctica* relative to diatoms.

The decline in stratospheric ozone concentrations over Davis Station in January to 288 DU may also have contributed to significant UV-B-induced inhibition of protists at this time. Thinning summer ozone (TSO) is not a new phenomenon. Ozone concentrations over Halley Bay have fallen below 300 DU in January since the mid-1970s (Solomon 1990, Jones & Shanklin 1995), and records show that TSO is widespread and recurs annually over the Southern Ocean between January and April (see http://toms.gsfc.nasa.gov/index_v8.html).

Ozone reduction enhances UV-B irradiances relative to other wavelengths, increasing the ratios of UV-B to PAR and UV-A radiation (Smith & Baker 1989, Quesada et al. 1995). Limited evidence suggests this alters the balance between UV-B-induced photodamage and PAR- and UV-A-induced repair (Smith et al. 1992, Vincent & Roy 1993, Holm-Hansen et al. 1997). Furthermore, our finding of significant inhibition of protist taxa by UV-B radiation in January agrees with a modelling study by Nunez et al. (2006) that showed changes in the structure and function of a diatom-dominated community at Davis Station below an ozone threshold of 300 DU. However, our use of a broadband sensor to measure erythemal UV radiation precluded our ability to detect changes in the ratio of UV-B radiation to other wavelengths. Sensors that resolve UV-B irradiance and/or the spectral irradiance of the UV-B radiation band would overcome this limitation in future field studies.

Light history, species composition and ozone concentration probably act simultaneously to determine the responses of marine protists that we observed to solar wavelengths. As in most previous studies, we did not include the effects of mixing and we removed the effect of metazoan grazers by filtration through 200 µm mesh. However, as far as practicable, we attempted to simulate the natural environment experienced by Antarctic marine microbes. The light climate is only one of a range of stressors that simultaneously affects the abundance, structure and function of Antarctic marine microbes. While the focus of the scientific community has perhaps moved to other pressing issues (Davidson 2006), ozone depletion attained a new record low for ozone concentrations in spring 2006 (see http://abc.net.au/science/news/stories/2006/1754508.htm?enviro). Global warming is also predicted to increase stratification of surface waters, especially at high latitudes, trapping plankton in near-surface waters and exposing them to higher UV radiation fluxes than those resulting from ozone depletion (Davidson 2006 and references therein). Our results indicate that exposure to near-surface UV-B fluxes can profoundly alter the abundance and composition of protist communities in Antarctic coastal waters with potential ramifications for trophodynamics and carbon flux. However, unlike most prior studies, we found that PAR and UV-A radiation can inhibit the abundance of protists acclimated to low light and that UV-B radiation can ameliorate this inhibition.

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