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Natural UVB exposure changes the species composition of Antarctic phytoplankton in mixed culture

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ABSTRACT: Numerous investigators have demonstrated marked interspecific differences in tolerance of Antarctic marine phytoplankton to UVB exposure. Consequent changes in species composition have been proposed but as yet not demonstrated. We conducted competition experiments in which mixed cultures of Antarctic marine diatoms and colonial and flagellate stages in the life cycle of the haptophyte *Phaeocystis antarctica* were exposed to natural Antarctic solar irradiance. Results demonstrated UVB-induced changes in species composition favouring the colonial stage of *P. antarctica* following 2 d exposure or less. These data indicate the potential for altered trophodynamics and carbon flux in Antarctic waters as a result of ozone depletion. Our results also show the limited predictive value of results obtained using UVB exposures above those likely to be experienced in the natural environment.

KEY WORDS: UVB radiation · Antarctic phytoplankton · Species composition

INTRODUCTION

Stratospheric ozone concentrations over Antarctica presently fall to less than 30% of pre-ozone-hole values during spring (Weiler & Penhale 1994). Springtime UVB irradiance is at least as high as that at the summer solstice (Lubin et al. 1989). Melting sea-ice forms a shallow pycnocline in the marginal ice zone (MIZ) which may confine phytoplankton to depths of 20 m or less for up to 6 d (Mitchell & Holm-Hansen 1991, Veth 1991). Phytoplankton blooms in the high light, high nutrient environment of the MIZ contribute 25 to 67% of phytoplanktonic production in the Southern Ocean (Smith & Nelson 1986).

Survival, growth and photosynthesis of phytoplankton in the MIZ are reduced by UVB exposure (Smith et al. 1992) as they coincide with the springtime ozone depletion (Helbling et al. 1994). It has been suggested that exposure of phytoplankton to increased UVB radiation is likely to alter species composition (Calkins & Thordardottir 1980, Karentz 1991, Smith et al. 1992, Davidson et al. 1994). Such changes have been reported from experimental microcosms in temperate environments using artificially increased UVB irradiance (Worrest et al. 1978, 1981). Interspecific differences in the tolerance of Antarctic phytoplankton to UVB have been reported (Karentz et al. 1991a, Marchant et al. 1991). However, direct evidence of changes in species composition has not been reported for the Southern Ocean.

Species specific investigations of the tolerance of phytoplankton to UVB irradiance are important in predicting the effect of ozone depletion (Karentz 1991, Davidson et al. 1994). However, such studies do not include the competitive interactions between phytoplankton species during UVB exposure. Here we report that exposure of mixed cultures of Antarctic phytoplankton to natural and attenuated Antarctic UV irradiance produced changes in phytoplankton species composition.

MATERIALS AND METHODS

Unialgal strains of the diatoms *Chaetoceros simplex* Ostenfeld, *Fragilariopsis lecointei* V. H., *Fragilariopsis*

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curta (V. H.) Hasle, *Thalassiosira tumida* (Jan.) Hasle, *Proboscia (Rhizosolenia) alata* (Brightwell) Sundström and the haptophyte *Phaeocystis antarctica* Karsten were isolated from Prydz Bay, Antarctica. Cultures were maintained under cool white fluorescent light at a photosynthetically active radiation (PAR) intensity of 5.11 W m^{-2} and at 0°C with an 18:6 h light:dark cycle. Exponentially growing cultures of the 6 species (that of *P. antarctica* containing approximately equal concentrations of the flagellate and colonial life stages) were diluted 1:5, culture:fresh culture medium, 5 and 2 d before starting the experiment. Organisms in 10 ml subsamples of each monospecific culture were fixed with buffered Lugol's solution and the cell concentration estimated using the Utermöhl sedimentation technique over 15 replicate randomly chosen fields using an inverted microscope. Aliquots of each culture were mixed to give approximately equal cell concentrations of each species and both *P. antarctica* life stages. Three 10 ml subsamples were removed to determine cell concentrations (as above) of each species at time 0. Nine subsamples, each of 500 ml, were then transferred to polythene bags (WhirlPak, Nasco) which transmit light above 220 nm. Three replicate bags were each exposed to one of 3 light treatments; unscreened (PAR, UVA and UVB treatment), Mylar screened (which transmitted wavelengths above 320 nm: PAR + UVA treatment), and polycarbonate screened (which transmitted wavelengths above 370 nm: PAR treatment) (Davidson & Marchant 1994).

Mixed phytoplankton populations were incubated for 8 d at Davis Station, Antarctica (68° 35' S, 78° E) at a depth of 0.2 m between 10 and 18 December 1992 in an outdoor tank through which sea water was circulated. Thus, the phytoplankton were exposed to near-surface natural light irradiance. Integrated irradiances were measured using an IL 1700 research radiometer equipped with UVA and erythemal UVB sensors (Davidson & Marchant 1994) which were calibrated to solar irradiances using the sensor response curve and a Macam spectroradiometer and erythemal UVB biometer respectively. Sensors were positioned beside phytoplankton at 0.2 m depth and the UVA and UVB irradiance integrated during incubation.

A subsample of 10 ml was removed from each replicate treatment at 2 d intervals for 8 d and the concentration of each species determined (as above). The cell concentrations of each species after each period of irradiation were used to estimate a single exponential growth rate for each replicate. This provided independent estimates of growth rate, with estimated variances for each species under each of the 3 UV treatments. Exponential ($\log_e$) growth rate estimates were obtained as the slope parameters of a generalised linear model (GLM) (see Chambers & Hastie 1993), using the S-Plus statistical package with Gaussian errors, a log-link function, and weighted by the inverse of the square of the empirical standard error for each cell concentration determination.

The growth rate of cells of each species in the culture became the dependent variable in a fully crossed 2-way analysis of deviance (similar to an ANOVA, but allowing the inverse variances of the estimated growth rates to be used as weights) using a GLM with a Gaussian error model. Thus, growth rates of low variance received higher weight in statistical analysis than those with high variance. Growth rates across all species and by each species were compared between light treatments and presented as a box and whisker plot and interaction profile (see Fig. 1A, B). The flagellate and colonial life stages of *Phaeocystis antarctica* were considered to be functionally separate taxa due to the widely accepted physiological differences between these stages (e.g. Marchant et al. 1991, Davidson & Marchant 1992b).

The size of 100 live cells of each species was measured and the mean cell volume calculated. Variation in the dimensions of cells fixed with Lugol's iodine from each light treatment were within 1 standard deviation of the live cell dimensions. The cell concentrations in replicates of each light treatment at each incubation time were pooled and the mean and standard error computed. Using the equations of Eppley et al. (1970) and the cell volume, carbon contributed by each species was then calculated. The carbon contributed by colonial stage *Phaeocystis antarctica* was likely to be an underestimate as colony matrix was not considered in the calculation.

To investigate the minimum duration of UV exposure required to cause changes in phytoplankton species composition, a 10 ml subsample was removed from each replicate of all light treatments after 2, 4, 6 and 8 d incubation and inoculated into 40 ml of sterile *f*/2 medium in 50 ml polystyrene culture flasks. Flasks were returned to culture maintenance conditions and grown for a further 9 d then thoroughly mixed and a 10 ml subsample removed and counted (as above). This procedure of subculturing samples after the various durations of exposure allowed expression and amplification of changes in phytoplankton species composition, while avoiding the effects of nutrient limitation in culture. For each incubation time and light treatment, the mean proportion of the phytoplankton population contributed by each species following the 9 d amplification was calculated over 3 replicates. For these proportional data, error bars indicate ±1 standard error, calculated by arcsine square root transformation (after Zar 1984).

Table 1. Cumulative integrated UVA and UVB irradiance during 8 d natural irradiation measured using an International Light research radiometer and light sensors

Irradiation (d)	Cum. integr. UVA (J m^{-2})	Cum. integr. erythemal UVB (J m^{-2})
0	0	0
2	9.75×10^5	6.48×10^3
4	18.43×10^5	12.26×10^3
6	28.51×10^5	19.74×10^3
8	36.59×10^5	25.18×10^3

RESULTS AND DISCUSSION

Weather conditions were intermittently sunny during the 8 d of exposure to natural Antarctic solar radiation. However, integrated UVA and UVB irradiances varied little during between-sample intervals (Table 1). Mean integrated UVA and UVB irradiance for each 2 d incubation period was $9.15 \pm 0.93 \times 10^5$ and $6.30 \pm 0.90 \times 10^3$ J m^{-2} respectively.

The analysis of deviance shows significant differences with species, light treatment and their interaction (Table 2). That species specific growth rates are significantly different is not surprising. The distributions of growth rates across species for the different UV treatments are shown in Fig. 1A. Although the main effect due to UV treatment is significant (Table 2), the effects are not substantial, and the statistical significance arises largely because of a few cases where growth rate estimates with low variances have received a high weight in the analysis. The unweighted means and medians of the growth rates across species are not significantly different between light treatments. Similarly, no significant difference was found in total calculated cell carbon concentration between light treatments (Fig. 2A). Thus, the overall growth and production by the community was maintained irrespective of light treatment.

In contrast, the interaction term is highly significant (Table 2). The changes in growth rates for at least some species under the different UV treatments demonstrates that, over time, the species composition, in terms of cell concentration, will differ under the different UV regimes. Differences between the PAR and PAR + UVA light treatments, though significant [$p(\chi^2 < 0.01)$], were only slight. Exposure to UVB caused substantial changes in the growth rates (Fig. 1B) which were statistically highly significant [$p(\chi^2 < 0.000005)$].

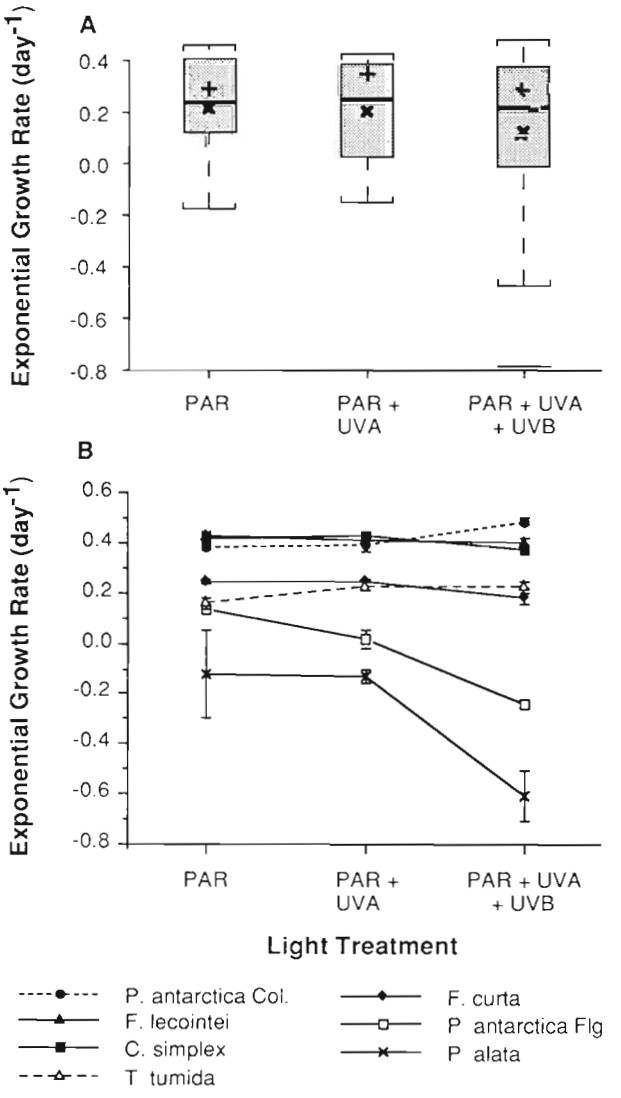

Fig. 1. Analysis of exponential growth rate (d^{-1}) during 8 d exposure to natural irradiation. (A) Box and whisker plot showing similar growth rate across all species and comparing between light treatments and (B) interaction profile showing UVB-dependent changes in the growth rate of each species between light treatments with the standard error over 3 replicates. Box and whisker plot shows mean weighted (+), unweighted (x) and median (–) growth rates for all species between light treatments. Boxes enclose the interquartile range, whiskers extending to the standardised range and '—' represents an outlier

Table 2. Two-way analysis of deviance showing the significance of UV effects on the growth of Antarctic phytoplankton species

Factor	df	Deviance	Residual df	Residual deviance	Probability χ^2
Null			62	2809.445	
Species	6	2620.609	56	188.836	0.00000000
UV treatment	2	11.630	54	177.206	0.00298
Species:UV interaction	12	134.048	42	43.158	0.00000000

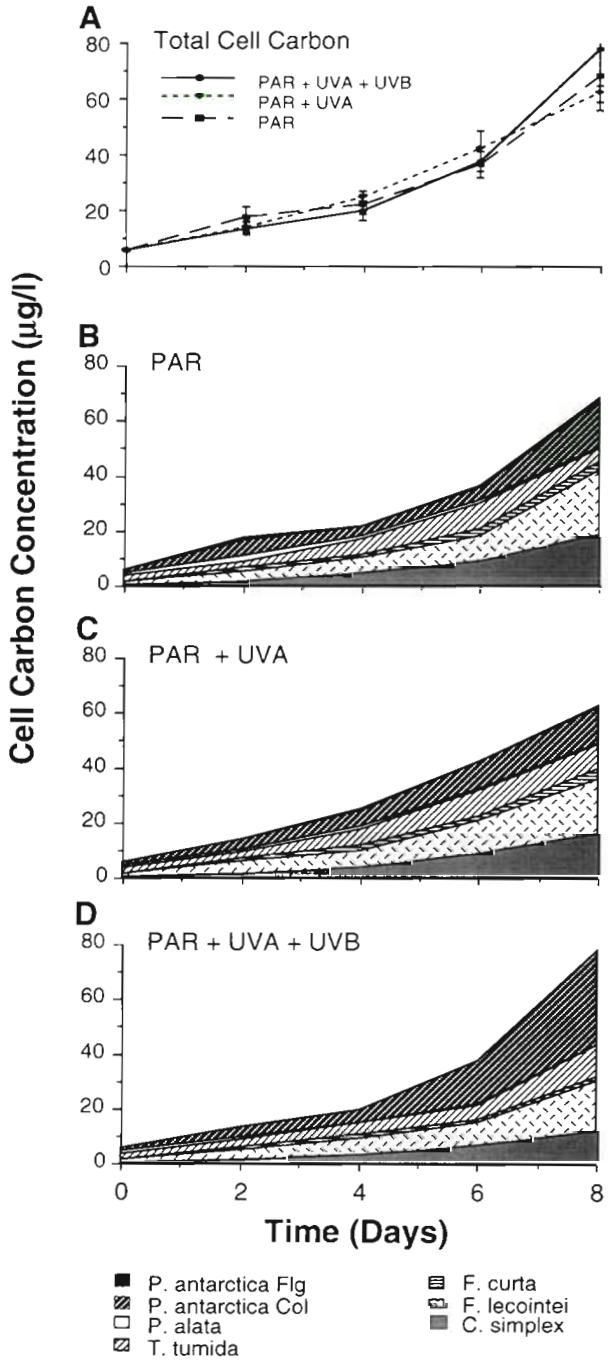

Fig. 2. Calculated cell carbon concentration of Antarctic phytoplankton during 8 d of natural irradiation showing (A) total cell carbon across all species, and contributions by each species exposed to (B) PAR, (C) PAR + UVA and (D) PAR + UVA + UVB. *P. antarctica* Col and Flg indicate the colonial and flagellate life stage respectively. Error bars indicate standard error of the mean over 3 replicates

The growth rate of diatoms and the flagellate stage of *Phaeocystis antarctica* exposed to UVB either did not change significantly or declined. Only the colonial stage of *P. antarctica* showed a substantial promotion of growth as a result of exposure to UVB. The proportion of cell carbon contributed by diatoms and the flagellate stage of *P. antarctica* exposed to UVB also fell (Fig. 2B–D) but were replaced by colonial stage *P. antarctica*. Thus, Antarctic near-surface UVB irradiance alters phytoplankton species composition in culture.

The enhanced growth of colonial *Phaeocystis antarctica* when exposed to UVB agrees with earlier findings which demonstrated that exposure of unialgal cultures of this species to *in situ* UVB increased cell size, growth rate and production by the colonial stage (Davidson & Marchant 1994) and may contribute to this species being one of the first to bloom in the ice and surface waters, where it frequently dominates the phytoplankton (Garrison et al. 1987, Fryxell & Kendrick 1988, Davidson & Marchant 1992a). Only *Proboscia alata* exhibited no significant growth in the absence of UV radiation (Fig. 1B). This may reflect the observed sensitivity of the species to mechanical disturbance during subculturing which leads to an extended lag phase in its growth.

Our results differ from those reported by other authors. McMinn et al. (1994) found that sediment cores from fjords in East Antarctica did not exhibit evidence of a significant change in species composition of the diatom community since springtime ozone depletion began. However, it is likely that persistent sea ice, which attenuates UVB by at least 90% (Trodahl & Buckley 1989), provided shielding for these organisms. Bothwell et al. (1995) also criticise other aspects of the conclusions drawn by McMinn et al. (1994). Others (Smith et al. 1992, Karentz 1994, Karentz & Spero 1995) have reported that exposure of diatoms and *Phaeocystis antarctica* to natural UVB did not alter their growth rates or that growth by *P. antarctica* declined.

Our study used natural solar irradiance and selected Antarctic phytoplankton species but did not simulate natural Antarctic conditions. We used a limited species assemblage grown in nutrient enriched media with and without exposure to a near-surface UVB light climate and wavelength structure. The effects of *in situ* UVB radiation on naturally occurring phytoplankton communities could differ from those we observed and the effect of increased UVB flux as a result of ozone depletion on phytoplankton species composition remains to be ascertained. Results obtained by Karentz (1994) for *Phaeocystis antarctica* were highly variable due to the clumped distribution of cells in colonies, changes within or between light treatments were seldom significant and, unlike Smith et al. (1992) and Davidson & Marchant (1994), *P. antarctica* growth was also negative irrespective of light treatment. Differences between the results presented here and those of Smith et al. (1992) may be due to differences in

methodology, the physiological state of cells or our use of cultured material and a multi-species mix. Karentz & Spero (1995) report a strong positive correlation between *P. antarctica* concentration and column ozone concentration in the MIZ of the Bellingshausen Sea. The apparent conflict between their results and those presented here can only be reconciled with further study. Differences in methodology mean the studies are not directly comparable and it remains unclear whether the changes in *P. antarctica* concentration observed by Karentz & Spero (1995) were directly related to changes in the *in situ* UVB climate during their study.

Our results also contrasted with our previous findings. The colonial stage in the life cycle of *Phaeocystis antarctica* produces high concentrations of UV-absorbing compounds (Marchant et al. 1991). These enhanced survival of its colonial stage when exposed to high UVB irradiances (Marchant et al. 1991) but diatoms, which largely lack UV absorbing compounds, survived UVB irradiances 3 to 5 times that which caused mortality in colonial *P. antarctica* (Davidson et al. 1994). Thus, the role of UV-absorbing compounds in alleviating UVB damage is questionable. Many Antarctic marine organisms possess UV-absorbing compounds (Karentz et al. 1991b). However, the presumed protection afforded organisms by such compounds remains largely unquantified. Results presented here show that growth by the colonial stage of *P. antarctica* was promoted under natural UVB exposure. Consequently, the UVB irradiance at which *P. antarctica* died (Marchant et al. 1991) was not indicative of its enhanced growth at sub-lethal natural irradiances. Nor was survival of diatoms up to far higher UVB irradiances than *P. antarctica* (Davidson et al. 1994) indicative of their slowed growth and production at these sub-lethal irradiances as here we show that *P. antarctica* dominates at their expense. The poor predictive value of a species response to high UVB irradiance experiments clearly demonstrates the limited value of extrapolating results of such experiments (Worrest et al. 1978, Karentz et al. 1991a, Marchant et al. 1991, Davidson et al. 1994) to the natural environment.

Vernet et al. (1994) found that high haptophyte concentrations in Antarctic waters correlated with high *in situ* absorption at 330 nm and low inhibition of photosynthesis when exposed to UVB. At sub-lethal natural UVB irradiances, metabolic processes such as photosynthesis apparently are shielded from damage by UV-absorbing compounds. Other metabolic costs of exposure to UVB are thereby minimised. Thus, at natural UVB irradiances colonial *Phaeocystis antarctica* may be afforded substantial protection by UV-absorbing compounds. High *in situ* absorption (Vernet et al. 1994) also suggests that blooms of *P. antarctica* may confer some UV protection on other organisms in the water column (Marchant et al. 1991), a feature not included in this experiment as colonial *P. antarctica* did not reach sufficient concentrations to attenuate UVB throughout the irradiated cultures.

The duration of UVB exposure required to elicit changes in phytoplankton species composition is critical in determining the potential magnitude of changes in phytoplankton species composition in Antarctic waters. Incubations of only 2 to 6 d may not have allowed expression of these changes in species composition. To express and amplify such changes, samples were removed from natural irradiation, subcultured, returned to culture maintenance conditions (which lack UV) and grown for a further 9 d. Differences in proportional abundance of each species were not greatly increased by exposure times exceeding 2 d (Fig. 3). Thus, 2 d exposure to ambient near-surface UVB irradiance was sufficient to largely determine the UVB-mediated species composition. Exposure to UVA and UVA + UVB increased the proportion of colonial *Phaeocystis antarctica* in culture, mainly at the expense of *Chaetoceros simplex* (Fig. 3A, B). The proportion of total cells contributed by other species differed little between light treatments (Fig. 3C–E). Two days was the shortest natural exposure time investigated; the minimum exposure required to elicit changes in species composition remains unknown.

Results demonstrate that natural Antarctic UVB irradiance can alter phytoplankton species composition and also indicate that ozone depletion and the associated increase in UVB may promote the abundance of *Phaeocystis antarctica* relative to diatoms in Antarctic waters. This species accounts for some 10% of the total biogenic flux of dimethylsulfide (DMS) released to the atmosphere (Gibson et al. 1990). DMS is a principal source of sulfate cloud condensation nuclei and influences oceanic cloud cover (Charlson et al. 1987). *P. antarctica* also plays a pivotal role in determining the structure and function of the planktonic community (Garrison et al. 1987, Fryxell & Kendrick 1988, Davidson & Marchant 1992a). Its blooms produce high concentrations of dissolved organic carbon and slow-sinking mucilaginous particulate organic carbon which promote bacteria and microheterotrophs, but the large mucilaginous colonies of this alga are selectively avoided by many grazers (Davidson & Marchant 1992b). Thus, any UVB-mediated increase in the abundance of *P. antarctica* could effect climate through changes in global albedo (Charlson et al. 1987) and significantly alter rates of vertical carbon flux and the particle size, form and availability of carbon to higher trophic levels (Marchant & Davidson 1991).

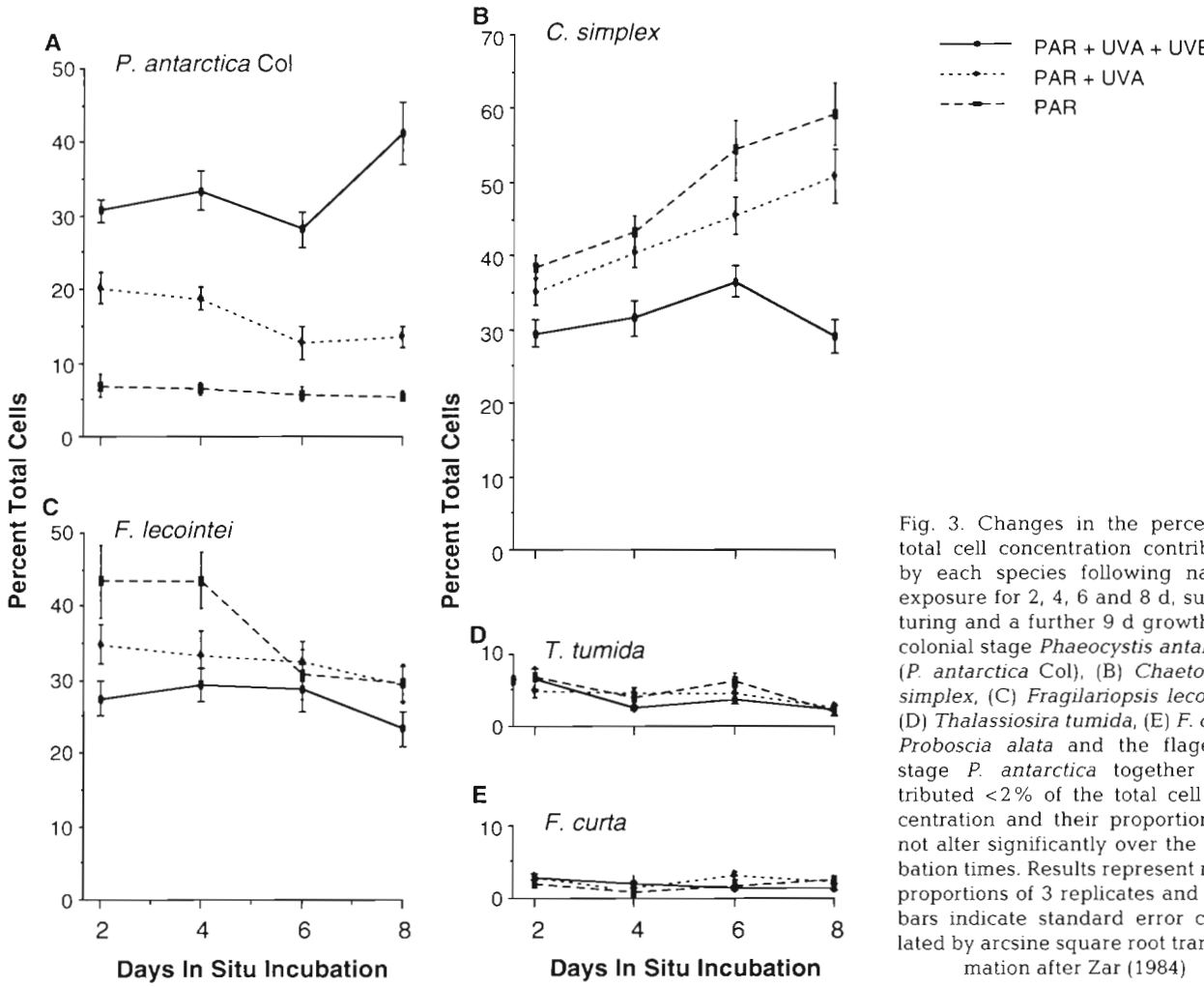

Fig. 3. Changes in the percent of total cell concentration contributed by each species following natural exposure for 2, 4, 6 and 8 d, subculturing and a further 9 d growth. (A) colonial stage *Phaeocystis antarctica* (*P. antarctica* Col), (B) *Chaetoceros simplex*, (C) *Fragilariopsis lecointei*, (D) *Thalassiosira tumida*, (E) *F. curta*. *Proboscia alata* and the flagellate stage *P. antarctica* together contributed <2% of the total cell concentration and their proportion did not alter significantly over the incubation times. Results represent mean proportions of 3 replicates and error bars indicate standard error calculated by arcsine square root transformation after Zar (1984)

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