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Species Succession in Fast Ice Algal Communities: A Response to UV-B Radiation?

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ABSTRACT. In fast ice communities around the margin of Antarctica most of the algal biomass is concentrated in the lowest few centimetres of the sea ice. Much of the taxonomic variation in these communities can be explained by their exposure to differing UV-B irradiances. A light spectral perturbation experiment carried out at Cape Evans, McMurdo Sound in 1996, caused a significant change to the species composition of communities exposed to additional UV-B but similar PAR. These community differences can also be seen in undisturbed environments. Communities beneath snow-free ice, which are exposed to high UV-B fluxes, are dominated by *Berkelaya adeliense* and *Thalassiosira australis*. Communities beneath ice with a heavy snow cover, which are exposed to only low UV-B fluxes, are dominated by *Entomeneis kjellmannii* and *Nitzschia stellata*.

Key Words: algae, Antarctica, diatoms, sea ice, UV-B, succession

Introduction

Sea ice does not comprise a single microalgal habitat. Rather, it is a heterogeneous and structured set of habitats with differing microalgal communities occurring at the top, the bottom and at intermediate depths (Horner 1985; McConville and Wetherbee 1983). In the fast ice bordering coastal regions of Antarctica most of the algal biomass is concentrated in a dense yellow-brown band at the ice-water interface (Palmisano and Sullivan 1983; McMinn and Ashworth, 1998). Here, in late spring, algal biomass typically reaches values greater than 100 mg chl *a* m^{-2} (Watanabe and Satoh 1987; McMinn and Ashworth, 1998) with values greater than 300 mg chl *a* m^{-2} having also been recorded (Palmisano and Sullivan 1983). Although over a hundred algal species have been documented from sea ice, the greater proportion of this biodiversity is limited to the pack ice (Garrison and Buck 1985, 1987). Algal biodiversity in fast ice is typically low with the species composition commonly dominated by only two species, *Entomeneis kjellmannii* (Cleve) Thomas and *Nitzschia stellata* Manguin (McMinn 1996). Species occurring at lower abundances include *Pleurosigma directum* Grunow, *Navicula galciei* Van Heurck, *Nitzschia lecointei* Van Heurck and several small phytoflagellates. In areas beneath snow-free fast ice a different community has been observed to develop. This community is dominated by hanging strands, up to 60 cm long, of the tube-forming diatom *Berkelaya adeliense* Medlin and *Thalassiosira australis* Peragallo (Watanabe 1988; McConville and Wetherbee 1983).

Biomass concentrations in the bottom fast ice community usually start to increase in September and reach a maximum in mid November (Watanabe and Satoh 1987; McMinn and Ashworth 1998). Basal melting from this time on results in a relatively rapid decline of the bottom sea ice algal community. These bottom communities are then replaced by surface meltpool communities comprised largely of

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Gymnodinium sp. and *Navicula glaciei* (Stoecker *et al.* 1992; Robinson *et al.* 1997; Watanabe and Satoh 1987; McConville and Wetherbee 1983).

Since the discovery of the spring ozone hole over Antarctica by Farman *et al.* (1985), there has been global concern about the effects of the increasing levels of UV-B radiation on the Antarctic marine ecosystem (El Sayed *et al.* 1990). Most of this concern has focused on the effects on phytoplankton and particularly the vernal phytoplankton blooms associated with the retreating marginal ice edge zone (Davidson and Marchant 1994; Smith *et al.* 1992). During these blooms, which occur when the ozone hole is at it's deepest, phytoplankton are retained near the surface above a shallow pycnocline allowing them to be exposed to the effects of UV-B radiation, which only penetrates to a maximum of 50 m (Smith *et al.* 1992). More recently, it has become apparent that sea ice algae are also potentially at risk from the additional UV-B arising from the ozone hole (Ryan and Beaglehole 1994; McMinn *et al.* 1994). Sea ice algal blooms occur synchronously with the development of the ozone hole in late spring, sea ice transparency is also at a maximum at this time (Trodahl and Buckley 1990) and the algal cells are positioned at the location of maximum under ice irradiance and are unable to move away. Ryan (1992) and Ryan & Beaglehole (1994) identified a decline in productivity in sea ice algae at McMurdo Sound of approximately 5% associated with increased springtime UV-B fluxes.

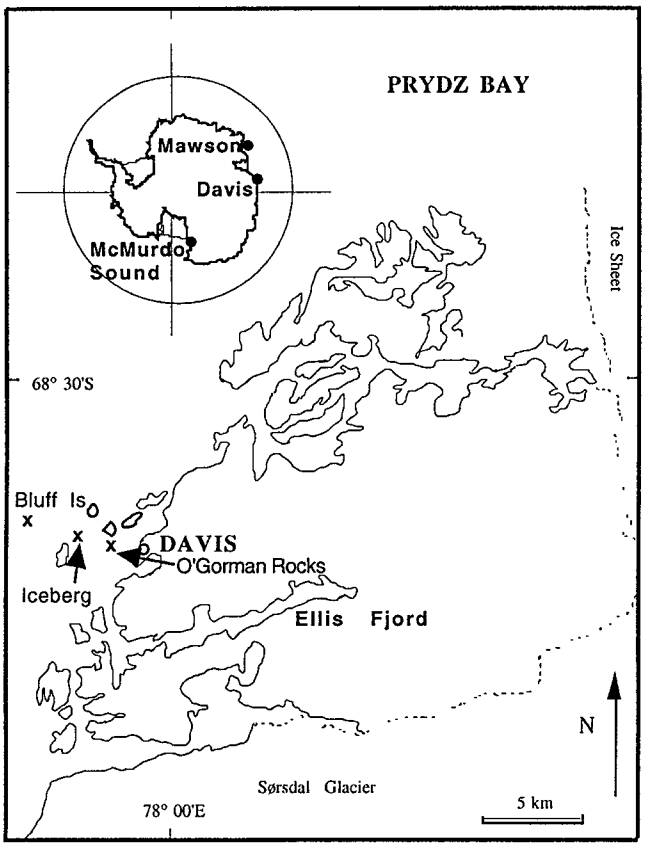

Fig. 1. Location of sampling sites in the Vestfold Hills. Additional locations, ie Mawson and McMurdo Sound, are located on inset map.

Methods

The *in situ* spectral perturbation experiment was conducted on 2.15 m thick annual fast ice with a 10 cm snow cover off Inaccessible Island, McMurdo Sound, between 1st and 15th of November 1996. Two 5 m by 5 m quadrants were cleared of snow and one covered with UV-B absorbing mylar. The snow cover was retained on a further two 5 m by 5 m quadrants but one was additionally covered with mylar. The diameter of the blocks was selected so that algal communities at the centre of each block would not be effected by differing light conditions outside the block. Three replicate ice cores were taken with a 7.5 cm diameter SIPRE corer at the beginning of the experiment and from the centre of each quadrant at the end of the experiment. The bottom 20 cm of each ice core was removed and melted into filtered sea water. These were then filtered on to Whatman GF/F filters and frozen for later fluorometric chlorophyll analysis at the Crary Laboratory at McMurdo Sound Station. Samples for microscope analysis were taken at the same time and preserved with gluteralderhyde. Species composition was based on a count of 400 cells on a Zeiss Axioskop microscope using Nomarski optics.

Field ice algal community samples were also collected from Ellis Fjord, Bluff Is, O'Gorman Rocks, Iceberg and Mawson in 1995 (Fig. 1). An additional sample is included from Ellis Fjord from 1992. The sea ice at the Bluff Is site was 1.05 m thick with a 10 cm snow cover. At O'Gorman Rocks the sea ice was 1.65 m thick with a 5 cm snow cover, although this

reduced to less the 2 cm thick by 22/11/95. The Iceberg site was an area of snow-free ice, 1.05 m thick, in the lee of an iceberg. It was covered by a thin, short lasting snow cover after blizzards. The Ellis Fjord site is a persistently snow-free area with ice 1.8 m thick. The sea ice at Mawson was 1.75 m thick with a 5 cm cover of snow. Sea ice samples were melted in filtered sea water and examined on a Zeiss Axioskop microscope with Nomarski optics.

It was noted that the *Berkelaya adeliense/ Thalassiosira australis* strand community was readily detached by sampling and so is likely to be under-represented in counts of ice core material. During sampling of these communities large numbers of algal filaments could usually be seen floating in water samples, presumably detached from the underside of the ice.

Field PAR light measurements were taken with a Biosphaerical QSP-200 radiometer attached to an under ice arm that enabled light measurements to be made 2 m away from the initial Jiffey Drill hole.

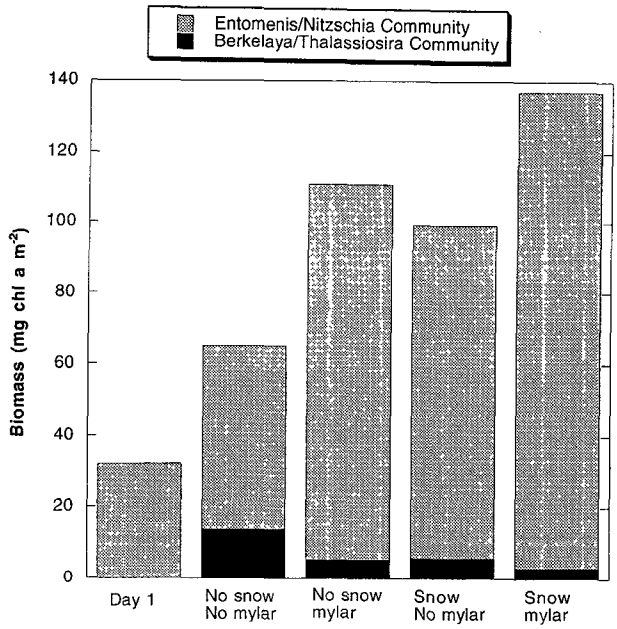

Fig. 2. Percentage of the *Berkelaya adeliense* community in quadrants with differing snow and mylar covers. Results from the light pertebation experiment at Cape Evans, 1996.

Results

Light Perturbation

There was a significant difference in the accumulation of algal biomass on the underside of the sea ice between the different quadrants over the 14 days of the *in situ* light perturbation experiment (Fig. 2). Biomass increased from 32.17 mg chl *a* m^{-2} on 1st November to 99.18 mg chl *a* m^{-2} in the control on 14th November, a net growth rate of 0.08 d^{-1}. However, there is a significant difference in growth rate between the two quadrants from which the snow cover had been removed. The mylar-covered quadrant experienced an accumulation of biomass more than 40% higher than the uncovered quadrant. The mylar-covered quadrant experienced an accumulation of biomass more than 40% higher than the uncovered quadrant. At the same time there was a significant shift in species composition in the quadrant exposed to higher UV-B levels (Fig. 2). On November 1st the algal assemblage was comprised dominantly of *Nitzschia stellata* and *Entomeneis kjellmannii* with minor *Navicula glaciei* and *Nitzschia lecontei* as epiphytes. *Berkelya adeliense* was completely absent. By the 14th November the species composition in the control quadrant had varied little but there was a small increase in the proportion *B. adeliense* to 4.0%. In the snow-cleared quadrants, however, the *B. adeliense* component had increased to 3.8% in the mylar-covered quadrant but to 21.5% in the mylar-free quadrant (Table 1, Fig. 2). The quadrant with both a snow and mylar cover had the lowest proportion, ie 2.6%, of *B. adeliense*.

Field Samples

Microalgal samples taken from the ice-water interface at a number of coastal sites around Davis, eastern Antarctica, had species compositions that appeared to be determined by the extent of snow cover. Most sites had a snow cover between 2 and 10 cm thick and had microalgal assemblages dominated by *Entomeneis kjellmannii* and *Nitzschia stellata*. Some sites, however, remained snow-free throughout the year and these had microalgal communities dominated by *Berkelaya adeliense* and *Thalassiosira australis*. Sites with either a thin snow cover or a temporary snow cover had microalgal communities

Table 1. Species distribution in fast ice bottom communities. Samples from Cape Evans and Inaccessible Is were collected in November 1996. Most samples from Davis (Bluff Is, O'Gorman Rocks and Iceberg) were collected in November 1995. One sample from Ellis Fjord was collected in 1992

	PAR (μM photons m^{-2} s^{-1})	*E. Kjellmannii*	*N. Stellata*	*Pleurosigma directum*	*B. Adeliense*	*T. australis*	*N. glaciei*	*Fragilariopsis* spp.	*N. lecointei*	*Gymnodinum* sp.	Other flagellates
Cape Evans 1/11/96	1	63.3	12.7	15.2	0.0	0.0	0.0	8.9	0.0	0.0	0.0
Cape Evans 14/11 control	1	62.3	21.2	8.4	3.7	0.0	2.2	2.1	0.0	0.0	0.0
Cape Evans 14/11 mylar, no snow	4	66.2	13.6	10.3	4.0	0.0	1.0	5.0	0.0	0.0	0.0
Cape Evans 14/11 no snow	4	55.2	18.8	3.9	21.5	0.0	0.5	0.9	0.0	0.0	0.0
Cape Evans 14/11 snow, mylar	1	40.0	34.3	11.6	2.4	0.0	0.0	10.4	0.0	0.0	0.0
Inaccessible Is 2/11/96	3	55.7	24.0	9.2	0.8	0.0	6.7	3.6	0.0	0.0	0.0
Davis, Bluff Is 31/10/96	2	92.0	1.5	2.0	0.0	0.0	1.5	3.0	0.0	0.0	0.0
Davis, Bluff Is 8/11/96	2	96.0	2.0	0.5	0.0	0.0	1.5	0.0	0.0	0.5	0.0
Davis, Bluff Is 22/11/96	2	85.0	14.0	0.0	0.0	0.0	0.5	0.0	0.0	0.5	0.0
Davis, Ellis Fjord 27/10/96	-	0.0	0.0	0.0	61.0	4.0	1.0	0.0	33.0	0.0	0.0
Davis, Ellis Fjord 15/11/96	24	0.0	0.0	0.0	64.0	23.0	4.5	0.0	5.5	0.0	1.0
Davis, Ellis Fjord 25/11/92	-	5.0	0.0	0.0	14.0	32.0	21.5	25.5	0.0	6.0	0.0
Davis, O'Gorman Rocks 31/10/96	1	85.0	0.5	2.5	0.0	0.0	1.5	1.0	8.0	2.0	0.0
Davis, O'Gorman Rocks 8/11/96	15	94.0	0.0	0.0	0.0	0.0	2.5	0.0	3.5	0.0	0.0
Davis, O'Gorman Rocks 22/11/96	10	75.0	4.0	0.0	0.0	0.0	14.0	1.5	0.0	0.0	4.5
Davis, Iceberg 2/11/95	210	14.0	44.5	0.0	15.5	1.0	24.5	0.0	0.5	0.0	0.0
Mawson 5/11/95	-	42.0	47.5	0.0	0.0	0.0	6.5	4.0	0.0	0.0	0.0

comprised of species common to both microalgal assemblages (Table 1). Dominance by *E. kjellmannii* and *N. stellata* at snow-covered coastal sites was also observed near Mawson in 1995 (Table 1).

Similar distribution patterns were also observed at Cape Evans in 1996. Sites examined had snow covers between 5 and 10 cm thick and all were dominated by *Nitzschia stellata* and *Entomeneis kjellmannii*.

Discussion

The presence of different microalgal communities at the bottom of Antarctic near shore fast ice was initially recognised by McConville & Wetherbee (1983). They recognised an interstitial community dominated by *Entomeneis kjellmannii* and *Nitzschia stellata* and a strand community dominated by *Berkelya adeliense*. Watanabe (1988) documented the occurrence of a strand community (ie *B. adeliense*) beneath ice that was snow-free until the end of October and noted that it was better developed close to cracks in the ice and that an increase in available light was the most likely cause. Other records of *B. adeliense* also show that it is usually associated with a minimum snow cover, and hence high PAR and UV-B levels. These include beneath snow-free ice at both Arrival Heights (Ryan and Beaglehole 1994; Ryan, pers. comm.) and Cape Armitage (Palmisano *et al.* 1985; Grossi *et al.* 1987), McMurdo Sound; at Syowa (Watanabe 1988) and at Casey and Davis (McConville and Wetherbee 1983). McConville & Wetherbee (1983) and McConville *et al.* (1985) did not indicate whether the ice they studied was snow free but as the communities were associated with relatively high under ice irradiances (18-38 μmol photons m^{-2} s^{-1}) it suggests that the ice was snow-free at the time.

The *in situ* light perturbation experiment isolated the effect of UV-B on sea ice microalgae from the effect of higher 400-700 nm irradiances. In the quad-

rants from which the snow cover had been removed, and therefore substantially increasing the PAR, only the quadrant that had no UV-B absorbing mylar showed a significant shift in species composition. Here, the proportion of the *Berkelaya adeliense/Thalassiosira australis* community increased from 0% to 21.5% compared to an increase to only 3.8% in the mylar-covered quadrant. This quadrant also experienced a decline in biomass accumulation of more than 40% relative to the snow-cleared quadrant covered with UV-B absorbing mylar. Mylar transmits approximately 80% of incident radiation (Ryan and Beaglehole 1994; Davidson and Marchant 1994, McMinn, unpublished data) and so the mylar-covered quadrants received roughly 20% less light than the uncovered quadrants but still experienced a much greater biomass accumulation. The low under ice light levels beneath the snow-free quadrants, ie approximately 4 μmol photons m^{-2} s^{-1}, are well below the documented irradiances for sea ice algal photoinhibition (Palmisano *et al.* 1985; McMinn and Ashworth, 1998) and so the differences in growth between the covered and uncovered quadrants actually underestimates the full impact of UV-B on algal growth. Quadrants that retained their snow cover, with or without a mylar covering, showed little change in species composition. In these quadrants the snow cover was sufficient to attenuate both the PAR and UV-B irradiances to levels that did not impact on the species succession. Although the light levels below the snow-covered quadrants were low, ie less than 1 μmol photons m^{-2} s^{-1}, the addition of mylar still caused an increase in biomass accumulation in the covered quadrants.

A similar light perturbation experiment was conducted on a graded snow cover at Cape Armitage, McMurdo Sound by Grossi *et al.* (1987). Initial snow cover in that experiment was 25 cm and they modified that to produce quadrants with a 0, 5, 10, 25 and 100 cm snow cover. Sampling occurred regularly between 9th October and 26th December. A well developed strand community had developed beneath the 0 cm snow cover quadrant by mid December.

Ryan & Beaglehole (1994) also conducted an *in situ* light perturbation experiment at Arrival Heights, McMurdo Sound, but covered a naturally snow-free area of ice with mylar rather than a naturally snow-covered ice area as here. They recorded only a small decrease in productivity as a result of being covered by mylar. The difference between the two studies can be attributed largely to the different microalgal communities being investigated. The UV-B tolerant *Berkelaya adeliense* community was examined by Ryan & Beaglehole (1994) whereas the less UV-B tolerant, *Entomeneis kjellmannii/Nitzschia stellata* community, which was examined herein, showed a far larger response. A community already adapted to high UV levels, such as that beneath snow-free ice, is likely to show only a small response to a decrease in UV. A community adapted to low UV levels, on the other hand, is likely to show a strong response to a large increase in UV.

Light is the most fundamental resource limiting the growth of microalgae and many species, such as those growing in some sea ice environments, show evidence of extreme shade adaption. It has been shown here that different bottom sea ice communities develop under different irradiances. Results of the light pertebation experiment reported herein, however, also suggest that the successional changes observed are not simply responses to changes in the quantity of light but also reflect responses to changes in the quantity of UV-B. Further field work with UV-B absorbing covers should allow these observations to be confirmed.

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