Microbial ecology of sea ice at a coastal Antarctic site: community composition, biomass and temporal change

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ABSTRACT: The coastal sea ice in the vicinity of Davis Station, Antarctica (68° 35' S, 77° 58' E), supported a diverse microbial community which varied in composition and biomass in response to increasing insolation and temperature during the austral summer To understand more fully the fate of photosynthetically fixed carbon in sea ice, we examined the dynamics of community composition, biomass and production in autotrophs, heterotrophic protozoa and bacteria. The microbial community inhabiting the bottom few centimeters of land fast ice differed markedly from the interior communities in taxonomic composition and biomass and in the timing and fate of production. Total microbial biomass integrated throughout the ice depth declined during the season from a mean of 1150 mg C m^{-2} on 17 November to 628 mg C m^{-2} by 22 December. This largely reflected a decrease in the biomass of the bottom ice community which was dominated by the diatom *Entomoneis* spp. In contrast, the biomass of the interior ice community increased during summer and was dominated by autotrophic forms <20 μm in length with a small dinoflagellate, *Gymnodinium* sp., becoming particularly abundant. Heterotrophic protozoa, composed of mainly nanoflagellate, euglenoid and dinoflagellate taxa, contributed between 16 and 19% of the total integrated microbial biomass in the interior ice and between 1 and 11% in the bottom ice. The biomass of heterotrophic protozoa increased throughout the ice depth during summer and estimated taxon-specific net growth rates ranged between 0.168 d^{-1} for a heterotrophic euglenoid and 0.05 d^{-1} for the heterotrophic nanoflagellate population over a 23 d period. Bacterial biomass varied by several orders of magnitude between ice depths mainly due to the occurrence of an abundant population of large epiphytic bacteria attached to *Entomoneis* spp. in the bottom ice. However, bacterial biomass contributed a similar proportion of between 4 and 16% of the total microbial biomass in both interior and bottom ice. The biomass of unattached bacteria increased throughout the ice depth during summer and exhibited an estimated net growth rate of 0.05 d^{-1} These data are used to quantify autotrophic production in bottom and interior communities, to estimate the flux of carbon to heterotrophs and to illustrate the complexity of the trophic interactions in coastal sea ice.

KEY WORDS: Sea ice · Antarctica · Micro-organisms · Carbon Biomass

INTRODUCTION

The magnitude of the oceanic sink for carbon dioxide derived from fossil fuels may be influenced by modulation of the air-sea flux of carbon dioxide by biological activity (Watson et al. 1991). In the Southern Ocean, microbial production associated with sea ice significantly contributes to overall production and

therefore to the biological carbon pump. The most comprehensively studied area is McMurdo Sound, where sea ice autotrophs are estimated to contribute approximately 23% of the annual net primary production (Knox 1990). Similarly, sea ice autotrophs have been estimated to contribute 22 to 24% of the total primary production over the vast area of ocean that marks the maximum extent of Antarctic sea ice (Legendre et al. 1992). Therefore, determining the magnitude and fate of the sea ice primary production is a prerequisite

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to understanding the flux of carbon in the surface waters of the Southern Ocean.

In marine planktonic and benthic food chains a substantial part of the carbon flow is channeled through heterotrophic micro-organisms. Studies of the bacterial component of sea ice communities suggest they consume a significant proportion of the primary production in Antarctic sea ice (Kottmeier et al. 1987, Grossmann & Dieckmann 1994, Helmke & Weyland 1995). In addition, heterotrophic protozoa are now viewed as a dominant biotic control of both phytoplankton (Gifford 1988, Paranjape 1990, Burkill et al. 1993, 1995) and bacterioplankton (McManus & Fuhrman 1988, Sherr et al. 1989).

A wide variety of heterotrophic protozoa have been found in Antarctic sea ice (Fenchel & Lee 1972, Lipps & Krebs 1974, Corliss & Snyder 1986, Spindler & Dieckmann 1986, Garrison & Buck 1989, Stoecker et al. 1993) and the proportion of the protist biomass that they comprise ranges from less than 1% to greater than 93% (Garrison & Buck 1989, 1991, Mathot et al. 1991, Stoecker et al. 1993). There have been no direct measurements of the consumption of primary and bacterial production by heterotrophic protozoa in sea ice but several studies suggest that grazing may be a significant factor controlling the development and fate of ice assemblages. For instance, extrapolation of rates reported in the literature for warm water species suggest that in sea ice, consumption by heterotrophic protozoa may exceed the levels of primary production (Garrison & Buck 1991). An increase in the proportion of heterotrophic to autotrophic protists (Stoecker et al. 1993) and increasing ammonium concentrations (Arrigo et al. 1993a) during spring and early summer in sea ice in McMurdo Sound is further evidence for an active heterotrophic protozoan component.

In the Southern Ocean the extent of sea ice ranges with season from less than 5×10^6 km^2 to around 20×10^6 km^2 (Zwally et al. 1983). The nature of the microbial communities that inhabit sea ice varies in response to the physical processes that form, evolve and deteriorate the ice (reviewed in Palmisano & Garrison 1993, Ackley & Sullivan 1994). The major division in sea ice structure and therefore sea ice microbial communities is the distinction between drifting pack ice and the land fast ice. In both pack and fast ice, internal microbial assemblages occur throughout the ice depth but are characterized by relatively low biomass. The bulk of the microbial biomass and production in sea ice is concentrated in characteristic microhabitats. In pack ice, microbial biomass is concentrated in surface and freeboard layers. In contrast, highest biomass and production occurs in fast ice at the base of the ice sheet in bottom and platelet microhabitats. The majority of Antarctic sea ice is pack ice and as a result surface layer and freeboard communities are thought to contribute the majority of the sea ice carbon production in the Southern Ocean (Legendre et al. 1992). However, Ackley & Sullivan (1994) observed that although fast ice occupies only 1 to 5% of the total ice cover around Antarctica, standing crops of algae are 3 orders of magnitude greater than those reported for the ice communities of pack ice and therefore the organic carbon contained in and produced by fast ice communities may be of a similar magnitude to that of the vast expanses of pack ice.

In this paper we describe the seasonal progression in composition, biomass and production of sea ice microbial assemblages including autotrophs, bacteria and heterotrophic protozoa, at a nearshore location in East Antarctica. Land fast ice forms annually in this area and is composed mainly of congelation ice (Scott et al. 1994) consisting of large (~1 cm) columnar crystals. Previously, several studies based at Australian Antarctic stations have examined the composition and production of the bottom ice algal community in East Antarctica (Bunt 1960, McConville & Wetherbee 1983, McConville et al. 1985, Perrin et al. 1987). This work has been expanded upon in the present study to include the whole ice depth and to determine the role that the heterotrophic components of the microbial community play in the fate of sea ice primary production.

METHODS

Sample collection. Sampling was undertaken from mid November 1993 to mid January 1994 at a nearshore location in the vicinity of the Australian Antarctic station of Davis (68° 35' S, 77° 58' E) (Fig. 1). Prior to summer breakout of the land fast sea ice on 23 December 1993, sampling was carried out on 3 occasions at a fixed site (O'Gorman Rocks) approximately 1 km northwest of Davis where the water depth is 22 m. To determine the fate of the microbial community after sea ice breakout, samples were also obtained from pack ice 2 km northwest of O'Gorman Rocks. A floe was chosen, approximately 400 m^2 in area, which had ice depth and snow cover comparable to the O'Gorman Rocks sampling site.

Ice samples were obtained using a SIPRE corer of 76 mm diameter. Samples were taken from the same 20 m^2 area of land fast ice throughout the season before breakout. On each date 3 replicate cores almost 2 m in length were drilled by hand within a 1 m radius. Loss of the delicate bottom ice communities may occur when sampling with a SIPRE corer (Welch et al. 1988). However, use of an underwater video camera lowered through an adjacent hole in the ice verified that the
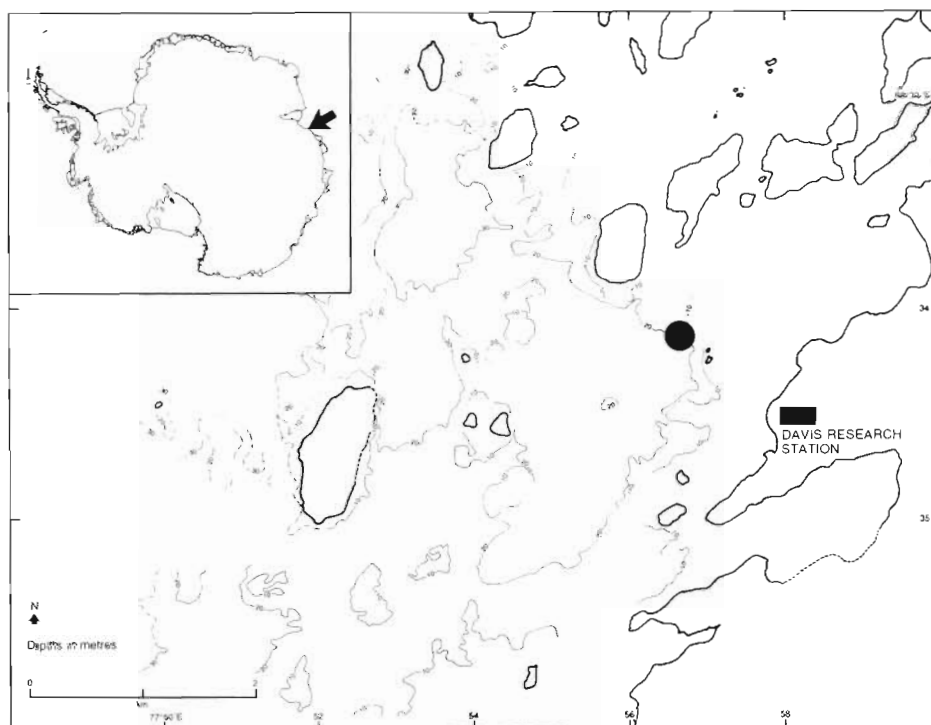
Fig. 1 Map of study area showing the location of the sampling site (●) on fast ice at O'Gorman Rocks offshore from the Australian Antarctic station of Davis

bottom ice community remained intact when coring was carried out with care.

After removal of the snow layer, 5 sections were cut from each core as follows: the top 10 cm (Horizon A), a middle ice section of 10 cm (Horizon B), two 10 cm sections 25 to 5 cm from the bottom (Horizons C and D), and the bottom 5 cm of ice (Horizon E). This subsampling regime was chosen to distinguish interior ice communities from a distinctive bottom ice community. Temperature was measured for each horizon using a digital thermometer and each section was then placed in a plastic bag and returned to the laboratory in a cool box for further processing.

Sea ice processing. Core horizons were quartered vertically to provide subsamples for the measurement of chlorophyll a (chl a) and fixation in acid Lugol's iodine, glutaraldehyde and formaldehyde solutions. A dilution technique was employed to reduce osmotic changes and cell loss that occur as sea ice melts (Garrison & Buck 1986). Subsamples were weighed, prior to melting in a known volume of filtered sea water, to determine an accurate dilution factor of between 1:4 and 1:5 ice to filtered seawater. Fixatives were added to the filtered seawater to produce final concentrations of 1% Lugol's iodine, 0.3% glutaraldehyde and 2% formaldehyde. After melting in the dark at 4°C for 12 h, samples were analysed for the quantification of microbial biomass as outlined below.

Microbial biomass. Chl a concentration was determined from 250 to 500 ml samples which were filtered onto GF/F filters under low vacuum and analysed spectrophotometrically following Parsons et al. (1984).

The biomass of the microbial community was estimated from microscopical measurements of taxon specific abundance and cell volume. Bacteria and cells less than 20 μm in length were enumerated by epifluorescence microscopy (Hobbie et al. 1977, Porter & Feig 1980). For bacterial enumeration, 5 to 10 ml of glutaraldehyde fixed sample from each ice horizon was stained with 5 μg ml^{-1} final concentration 4',6-diamidino-2-phenylindole (DAPI), concentrated onto a 0.2 μm pore size black polycarbonate filter, and examined at 1250× magnification under UV illumination. Bacteria were identified by their blue fluorescence and counted from 25 fields of view. For other cells less than 20 μm, 10 to 30 ml of glutaraldehyde fixed sample from each replicate ice horizon was similarly stained with DAPI, concentrated onto a 2.0 μm pore size standard polycarbonate filter, and examined at 1250× magnification. Cells were identified by their blue fluorescence under UV illumination and grouped into taxonomic categories based on size, shape and morphology. Heterotrophs were distinguished from autotrophs by the absence of chl a autofluorescence observed under blue light illumination. Cells were counted from 28 fields of view. Cells >20 μm were enumerated from settled samples analysed by inverted microscopy (Utermöhl 1958). For each ice horizon, 25 to 50 ml of sample fixed in Lugol's iodine was concentrated by settling for 48 h and observed at 200 to 400× magnification. Cells were

counted from the whole or a representative portion of the settling chamber. Cells were identified to species level where possible from Lugol's samples. To distinguish heterotrophs from autotrophs, cells were concurrently examined by epifluorescence microscopy using samples fixed in formaldehyde and glutaraldehyde.

Cell volumes were determined by image analysis using a Seescan Solitaire Plus system (Seescan plc, Cambridge, UK). Processing of images was restricted to the function 'High Pass' which attempts to reduce gradual shading across an image due to lighting variations or shadows. To aid thresholding of cell borders the function 'Interactive Threshold' allowed the operator to choose the greyshade values of the threshold. In addition, it was possible to include or exclude areas of the image by drawing around them manually. Cell volumes (v) were calculated from measurements of the area (A) and perimeter (P) using the following equations (Fry & Davies 1985):

$$v = (d^2\pi/4)(l - d) + \pi d^3/6$$

where length (l) and width (d) are:

$$l = P/2 + (1 - \pi/2)d$$
$$d = [P - \sqrt{(P^2 - 4\pi A)}]/\pi$$

This calculation assumes that cell shape approximates a cylinder with hemispherical ends and therefore that cell depth is equal to cell width. Taxa with cell shapes that deviated obviously from this assumption required the measurement of a combination of cell profiles to determine cell volume accurately.

For bacteria the volumes of 31 cells from each replicate ice horizon were measured. For all other taxa up to 20 cells were measured for each sampling date. Mean cell volumes calculated from $\log_{10}$-transformed data were converted to cell carbon using the following conversion factors: bacteria: 0.40 pg C μm^{-3} (Bjørnsen & Kuparinen 1991); heterotrophic nanoflagellates: 0.22 pg C μm^{-3} (Børsheim & Bratbak 1987); ciliates: 0.19 pg C μm^{-3} (Putt & Stoecker 1989); and 0.14 pg C μm^{-3} for heterotrophic dinoflagellates (as quoted in Lessard 1991). All autotrophic and other heterotrophic cell volumes were converted to carbon biomass using the equation:

$$\text{Cell carbon (pg)} = 0.109 [\text{live cell volume } (\mu m^3)]^{0.991}$$
(Montagnes et al. 1994)

where live volume is 1.33 × preserved volume for cells fixed in Lugol's iodine (Montagnes et al. 1994) and 1.41 × preserved volume for cells fixed in glutaraldehyde (Verity et al. 1992).

Photosynthetic rate experiments. A modification of the NaH^{14}CO$_3$ method (Steemann-Nielsen 1952) was used on 2 occasions to estimate the photosynthetic rate of the bottom ice community during the sampling period. Modifications of the method were aimed at preserving the complex sea ice microenvironment and were based upon the method employed by Grossi et al. (1987). On 29 November and 16 December, 3 and 4 cores respectively were collected and the bottom 5 cm subsampled for each experiment. For each core, a subsample of approximately 50 ml of bottom ice was placed in 1 transparent and 1 darkened 125 ml polycarbonate (Nalgene) bottle. A measured volume of filtered (0.2 μm) sea water was then added to fill the bottles and samples were inoculated with NaH^{14}CO$_3$ (Amersham International plc, Little Chalfont, UK) to a final concentration of 0.08 μCi ml^{-1}. Incubation bottles were secured to a perspex rack and positioned *in situ* against the bottom ice surface at least 1.5 m away from the ice hole which was sealed with a polystyrene plug. Sampling was timed to allow dawn-to-dawn 24 h incubations. Samples were then returned in a cool box and allowed to melt within approximately 1 h in the dark prior to filtration. From each 125 ml sample two 50 ml aliquots were filtered onto 25 mm GF/F filters under low vacuum; one filter was used for analysis of the chl a concentration and the other prepared for liquid scintillation counting. These filters were placed in scintillation vials and 2 ml of 5% glacial acetic acid in methanol added to each. Vials were evaporated to dryness to remove unincorporated ^{14}C, and 1 ml of distilled water and 10 ml of scintillation fluid (Optiphase Hi-Safe II, Wallac UK Ltd, Milton Keynes) added prior to scintillation counting. For the determination of photosynthetically fixed dissolved organic carbon a 5 ml subsample of the filtrate was acidified with 0.1 N HCl to pH 2 and shaken for 12 h. Three 1 ml subsamples were then radioassayed. The external standards ratio method was used to convert counts per minute (CPM) to disintegrations per minute (DPM). Values for dissolved inorganic carbon from a depth of 5 m at the time of sampling (Robinson et al. pers. comm.) were used to calculate the amount of ^{14}C fixed. The total amount of carbon fixed was calculated from the sum of the GF/F filter retained and dissolved organic carbon measurements after correction for dark ^{14}C incorporation.

RESULTS

Sea ice in the vicinity of Davis supported a diverse microbial community which varied in composition and magnitude in response to environmental change.

Environment

During November 1993 land fast sea ice extended 10 to 15 km from shore in the vicinity of Davis Station. The

ice gradually decreased as summer progressed, with a complete breakout occurring on 23 December. After this period the extent of drifting pack ice varied irregularly from 0 to approximately 90% cover. Increasing insolation, air temperatures and water temperatures were accompanied by a gradual increase in ice temperature and an alteration of ice temperature profile (Table 1). The fast ice consisted of a typically light snow covered area with ice depths that decreased only slightly during the period from a thickness of almost 2 m (Table 1). Although no systematic ice structural analysis was carried out, ice appeared to be comprised mainly of a columnar structure with regularly spaced vertical brine channels (Weeks & Ackley 1982). Video examination confirmed the lack of the unconsolidated platelet layer that is often observed under the fast ice of McMurdo Sound. Under-ice video observations also revealed dark green discoloration due to an abundant algal community. In contrast to the fast ice, the pack ice exhibited obvious signs of melting, including a raised freeboard and slush-like layers below the snow cover.

Table 1. Depth of ice horizons (cm) and seasonal variation in ice temperature (°C) and hours of sunshine during the sampling period 17 November 1993 to 3 January 1994. Ice depth is accurate to within 1–2 cm. Temperatures are mean values of 3 measurements. Hours of sunshine is the mean of the 5 days centred on that date. ND: not determined

	Date: Day:	17 Nov 93 1	9 Dec 93 23	22 Dec 93 36	3 Jan 94 47
Snow					
	Depth	10	5–10	2.5	2.0
	Temperature	ND	−0.4	−0.2	ND
Ice horizons					
A	Depth	0–10	0–10	0–10	0–10
	Temperature	−6.1	−1.3	−1.2	−0.3
B	Depth	80–90	80–90	82–92	80–95
	Temperature	−5.6	−3.3	−2.1	−1.8
C	Depth	165–175	167–177	160–170	145–155
	Temperature	−3.0	−2.3	−1.9	−1.2
D	Depth	175–185	177–187	170–180	155–165
	Temperature	−2.5	−2.0	ND	−1.2
E	Depth	185–190	187–192	180–185	165–170
	Temperature	−2.0	−1.6	−1.2	−1.2
Ice/water interface					
	Temperature	−1.9	−1.3	−0.9	−1.2
Sunshine (h d^{-1})		6.46	21.8	21.9	ND

Community composition

Land fast ice

In the land fast ice a major distinction in composition and biomass occurred between the bottom (Horizon E) and interior (Horizons A, B, C and D) ice. An abundant diatom community dominated by *Entomoneis* spp. inhabited the bottom few centimeters of fast ice. The maximum recorded biomass of *Entomoneis* spp. was 34 g C m^{-3} on 17 November which contributed 96% of total microbial biomass in that sample (Table 2A). Although proportionately less significant than *Entomoneis* spp., other diatoms were abundant. For instance, *Pleurosigma* sp., *Nitzschia stellata* and a number of epiphytic species (of the genera *Nitzschia* and *Synedropsis*) occurred at a maximum biomass of 309, 34 and 58 mg C m^{-3} respectively (Table 2A). Photosynthetic dinoflagellates including *Gymnodinium* spp.2, *Exuviaella antarctica* and *Gyrodinium* sp. were also common in the bottom ice community (Table 2A). Athecate dinoflagellates are difficult to identify once fixed and the cells grouped under *Gymnodinium* spp.2 in Table 2A were of a wide size range and may have

included different species and/or different life history stages. The biomass of *Gymnodinium* spp.2 reached a maximum of 2.5 g C m^{-3} in the bottom ice, accounting for 36% of the total microbial biomass in that sample (Table 2A). The motile form of *Phaeocystis* sp. and the cryptomonad *Gemingera cryophila* made up the greatest biomass amongst autotrophs of less than 20 µm length in Horizon E (Table 2A).

In contrast to the bottom ice, the autotrophic community of the interior ice was dominated by autotrophic forms less than 20 µm in length which generally made up greater than 51% of the biomass in Horizons A, B, C and D (Table 2A, Fig 2). A small dinoflagellate, *Gymnodinium* sp.1, was particularly abundant. This species closely resembled a small dinoflagellate species described from samples collected in McMurdo Sound by Stoecker et al. (1992). Both vegetative and hypnozygote stages were abundant and occurred throughout the ice. Highest numbers of vegetative cells occurred in Horizon B with a maximum value of 193 mg C m^{-3} accounting for 50% of total biomass (Table 2A). Pennate diatoms, particularly *Navicula* sp. and a number of species of the genera *Nitzschia* and *Synedropsis*, were abundant in the internal ice (Table 2A). However, diatoms generally accounted for less than 25% of the total biomass in these horizons (Fig. 2).

Table 2. Summary of taxonomy and mean cell size of (A) autotrophic and (B) heterotrophic components of the microbial community. For each division maximum biomass encountered during the sampling period is given along with date and depth of occurrence and percentage of total microbial biomass that this contributed. Note: this value does not necessarily represent the maximum contribution to biomass observed for each species

(A) Autotrophic component

Taxa identified in each category	Mean cell volume (μm^3)	Sample biomass (mg C m^{-3})	Maximum recorded Date and horizon of occurrence	% of total biomass
Autotrophs ≤20 µm				
1 Flagellates ≤5 µm	17	59	22 Dec 93 (E)	2
2 Chlorophyceae including Phaeocystis sp.	146	211	22 Dec 93 (E)	3
3 Cryptophyceae including Geminigera cryophila	193	131	9 Dec 93 (E)	1
4 Diatomophyceae	60	7	22 Dec 93 (E)	2
5 Gymnodinium sp.1 hypnozygote	307	193	9 Dec 93 (B)	51
	956	99	22 Dec 93 (A)	45
Autotrophs >20 µm				
Chlorophyceae				
1. Unidentified spp.	1620[a]	56	9 Dec 93 (E)	1
Diatomophyceae				
Centrales				
2. Unidentified spp.1	18000	2	3 Jan 94 (A)	1
3. Unidentified spp.2	41600	78	3 Jan 94 (A)	29
4. Unidentified spp.3	254000	123	3 Jan 94 (A)	45
5. Corethron criophilum	194000	17	3 Jan 94 (A)	6
Pennales				
6. Epiphytic diatoms including Synedropsis spp.1	135	58	17 Nov 93 (E)	1
7. Entomoneis spp.	9520[a]	33906	17 Nov 93 (E)	96
8. Navicula sp.	401	18	22 Dec 93 (B)	8
9. N. kerguelensis	2530	22	9 Dec 93 (B)	5
10. N. prolongatoides	397	2	9 Dec 93 (E)	<1
11. N. stellata	1550	34	17 Nov 93 (E)	1
12. Nitzschia spp.2	165	2	9 Dec 93 (E)	<1
13. Nitzschia spp.3	3530	71	9 Dec 93 (B)	15
14. Pinnularia sp.	9240	1	22 Dec 93 (D)	<1
15. Pleurosigma sp.	29000	309	9 Dec 93 (E)	26
16. Synedropsis spp.2 S. hyperboreoides	138	2	22 Dec 93 (B)	1
17. Synedropsis spp.3	208	13	3 Jan 94 (B)	5
18. Pennale sp.	2930	172	3 Jan 94 (B)	43
19. Tropidoneis sp.	3530	1	22 Dec 93 (B)	<1
Dinophyceae				
20. Gymnodinium spp.2	3420[b]	2453	22 Dec 93 (E)	36
21. Gyrodinium sp.	670	3	9 Dec 93 (E)	<1
22. Exuviaella antarctica	1250[a]	228	22 Dec 93 (E)	7
Ciliophora				
23. Mesodinium rubrum	4770	7	9 Dec 93 (E)	<1

(B) Heterotrophic component

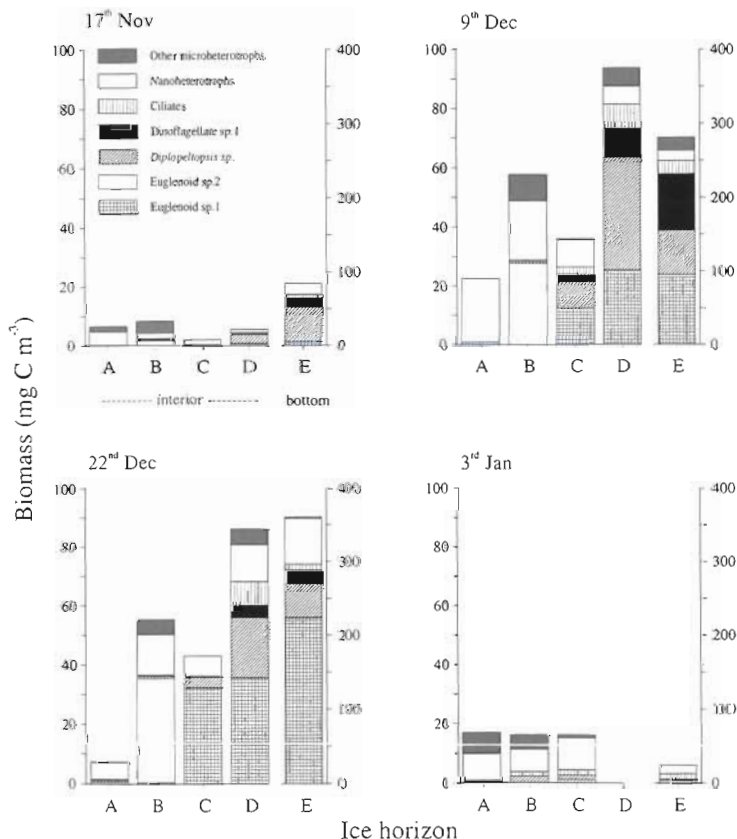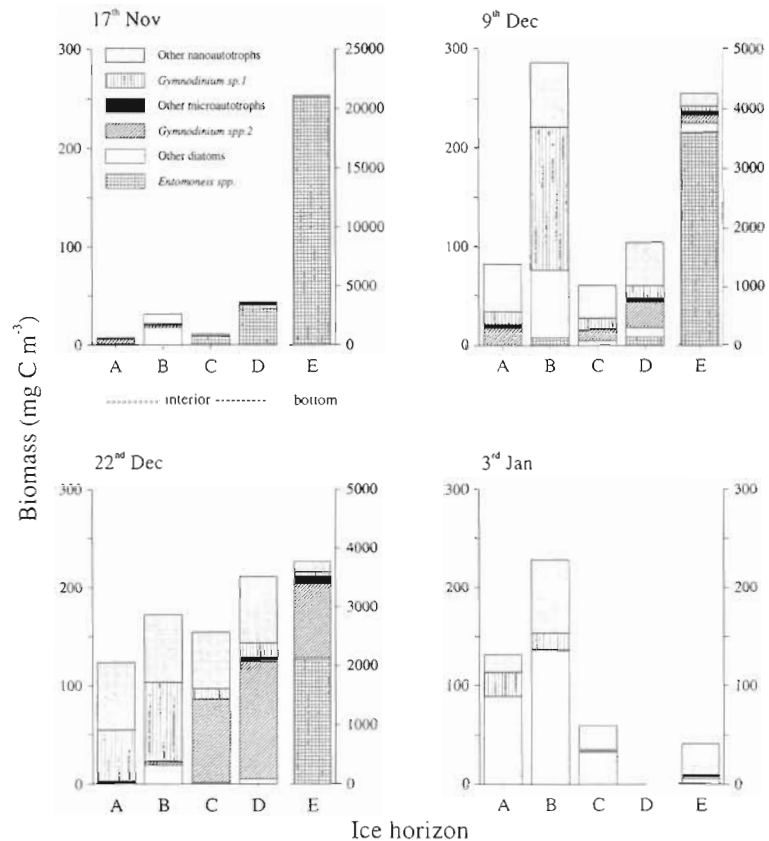| Taxa identified in each category	Mean cell volume (μm^3)	Sample biomass (mg C m^{-3})	Maximum recorded Date and horizon of occurrence	% of total biomass
Bacteria				
1. Unattached	0.13	193	22 Dec 93 (E)	<1
2. Epiphytic	0.42	1415	22 Dec 93 (E)	33
Heterotrophs ≤20 µm				
1. Flagellates ≤5 µm	15	9	22 Dec 93 (E)	<1
2. Flagellates including Cryothecomonas spp.	159	89	22 Dec 93 (E)	3
Heterotrophs >20 µm				
Ciliophora				
1 Choreotrich spp.1	2480	1	9 Dec 93 (E)	<1
2. Hypotrich spp.1	21700	15	22 Dec 93 (E)	<1
3. Hypotrich spp.2	6590	5	9 Dec 93 (E)	<1
4. Hypotrich spp.3	5060	5	9 Dec 93 (E)	<1
5. Rhabdoaskenasia sp.	616	1	9 Dec 93 (E)	<1
6. Unknown spp.1	280000	29	9 Dec 93 (E)	3
7 Unknown spp.2	899	3	9 Dec 93 (E)	<1
Dinophyceae				
8. Dinoflagellate sp.1	5110[a]	100	9 Dec 93 (E)	9
9. Diplopeltopsis sp.	26900[a]	112	22 Dec 93 (E)	2
10. Protoperidinium sp.1	28700	16	22 Dec 93 (D)	8
11. Protoperidinium sp.2	195000	48	9 Dec 93 (E)	4
Euglenophyceae				
12. Euglenoid sp.1	3780[a]	477	22 Dec 93 (E)	7
13 Euglenoid sp.2	5560	60	22 Dec 93 (B)	20
14. Euglenoid sp.3	3330	3	9 Dec 93 (B)	3

[a] Separate mean values used to calculate species biomass for each sampling date
[b] Grouped mean of 3 separate size classes used for calculations of biomass

Fig. 2. Mean (n = 3) biomass of 6 major categories of autotrophic taxa recorded from 5 ice horizons in cores sampled on 17 November 1993, 9 and 22 December 1993 and 3 January 1994. Details of ice horizon depth are given in Table 1. Note the different scales for Horizon E

Abundant and diverse communities of heterotrophic protozoa inhabited all horizons of the land fast ice (Table 2B, Fig. 3). The dominant heterotrophic taxa occurring in the bottom few centimeters of ice were a species of euglenoid, and 2 dinoflagellates (Fig. 3). Euglenoid sp.1 was characterized by typical squirming movements, a ridged pellicle, 2 emergent flagella of equal length and a possible ingestion organelle (Larsen & Patterson 1991). The carbon biomass of Euglenoid sp.1 reached a maximum on 22 December, accounting for 7% of the total microbial biomass in one sample (Table 2B) and almost 70% of the mean heterotrophic biomass on that date (Fig. 3). Two dinoflagellates, Diplopeltopsis sp. and Dinoflagellate sp.1, each made up 25% of the mean heterotrophic protozoan biomass on occa-

sion. Identification of Diplopeltopsis sp. was based upon the description of thecate structure in Antarctic forms of this genus by Balech (1975). The athecate Dinoflagellate sp.1 was similar to a species described by Buck et al. (1990), in that no flagella or sulcus and cingulum were present and the cells possessed a shallow groove approximately 10 μm long on the cell surface. However, cells were smaller and none contained a food vacuole or any evidence of ingested particles. Instead, identification of Dinoflagellate sp.1 was based upon the presence of condensed chromosomes and a lack of chlorophyll autofluoresence.

Internal assemblages were also largely made up of heterotrophic flagellates, including nanoflagellates, euglenoids and dinoflagellates (Fig. 3). Euglenoid sp.2 was of larger

Fig. 3. Mean (n = 3) biomass of 7 major categories of heterotrophic protozoan taxa recorded from 5 ice horizons in cores sampled on 17 November 1993, 9 and 22 December 1993 and 3 January 1994. Details of ice horizon depth are given in Table 1. Note the different scales for Horizon E

cell volume than Euglenoid sp.1 (Table 2B). It possessed a ridged pellicle, 2 flagella of unequal length and an obvious ingestion organelle. Ingested cells, particularly those of the small autotrophic *Gymnodinium* sp.1, were often observed. Euglenoid sp.2 occurred throughout the ice depth but was most abundant in Horizon B where it formed greater than 50% of the average heterotrophic protozoan biomass during December (Fig. 3). Heterotrophic cells of less than 20 μm in length were also abundant and contributed up to 100% of the heterotrophic biomass in Horizon A.

Although identification of ciliates is uncertain without silver staining procedures, a diverse assemblage of heterotrophic ciliates was found in the land fast sea ice (Table 2B). However, distribution was sporadic and biomass relatively low. Ciliate variety and abundance was highest in the bottom ice where Hypotrich spp.1 and a large unidentified form (Unknown spp.1) contributed most to biomass (Fig. 3).

Bacteria occurred throughout the ice depth. However, biomass varied by several orders of magnitude between horizons ranging from less than 5 mg C m^{-3} in Horizon A to greater than 1400 mg C m^{-3} in the bottom ice (Fig. 4, Table 2B). The much higher bacterial biomass found in the bottom ice was attributable to epiphytic bacteria attached to both living and dead *Entomoneis* spp. cells. Like *Entomoneis* spp. these bacteria were most abundant in the bottom ice contributing up to 93% of bacterial (Fig. 4) and 33% of total biomass (Table 2B). Unattached bacteria were considerably

smaller than epiphytic forms having a mean cell volume of 0.13 μm^3 compared to 0.42 μm^3. The maximum biomass of unattached bacteria of 193 mg C m^{-3} (Table 2B) recorded in the bottom ice was also considerably lower than that of epiphytic forms.

Pack ice

The composition and vertical distribution of the microbial community in the pack ice sampled on 3 January differed from that observed in land fast ice. Maximum biomass was found in Horizons A and B, where diatoms were the main component (Fig. 2). Large diatoms including *Corethron criophilum*, *Chaetoceros* sp., *Rhizosolenia* sp., *Eucampia* sp. and a variety of centric taxa dominated the biomass of Horizon A (Table 2A). The pennate diatoms *Pennale* sp. and *Synedropsis* spp.3 made up the bulk of the biomass in the Horizon B, contributing a maximum of 172 and 13 mg C m^{-3} respectively (Table 2A, Fig. 2). In contrast, the community that inhabited the bottom few centimeters of ice was composed largely of small autotrophic flagellates and contained no cells of *Entomoneis* spp.

Consistent with the autotrophic community, the abundance of heterotrophic protozoa was relatively low in the ice floe samples (Fig. 3). Small flagellates accounted for the highest proportion of biomass often exceeding 50% at all ice depths (Fig 3). Interestingly, ciliate biomass was proportionately higher in the ice floe with hypotrich species making up the bulk of the ciliate biomass. No distinction between epiphytic and unattached bacteria occurred in the pack ice due to the absence of *Entomoneis* spp. However, the mean cell volumes of unattached bacteria found in the pack ice were significantly (analysis of variance, ANOVA, p < 0.001) larger than those of the land fast ice. Estimation of the bacterial biomass in the interior of the pack ice also exceeded that found in the fast ice reaching maximum mean values of almost 50 mg C m^{-3} in Horizon B (Fig. 4).

Total biomass

Mean values of total carbon biomass of the microbial community within individual horizons of land fast ice spanned 3 orders of magnitude from 16 to nearly 22 000 mg C m^{-3} (Table 3). Variability is a characteristic of the taxonomy, distribution and biomass of sea ice microbial communities. Comparisons were made of mean values based on 3 replicate samples taken simultaneously and close together on each date and from the same site on different sampling dates. We
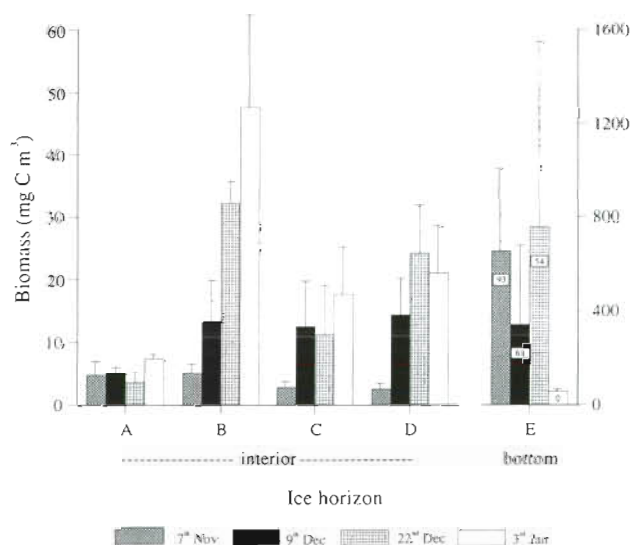

Fig. 4. Mean (n = 3) and standard deviation of bacterial biomass recorded from 5 ice horizons in cores collected on 4 dates during the sampling period. Values in the bars are the mean percentage of total bacterial biomass contributed by epiphytic bacteria in the bottom ice on each sampling date. Note the different scale for Horizon E

Table 3. Vertical distribution and integrated values of total carbon biomass and integrated chl *a* concentration of the sea ice microbial community at Davis Station. Values are means ± standard deviation of 3 replicate cores per sampling date. Ice cores were sampled from a fixed site except for the drifting ice floe sampled on 3 January 1994. See Table 1 for information on ice depth and temperature of each horizon

| | Date: | 17 Nov 93 | 9 Dec 93 | 22 Dec 93 | 3 Jan 94 |
	Day:	1	23	36	47
Biomass (mg C m^{-3})					
Ice horizon	A	16.3 ± 4.1[a]	94.0 ± 14.0[a]	132.0 ± 45.3	152.0 ± 59.2
	B	44.8 ± 8.6	348.5 ± 92.2	253.7 ± 34.1	287.9 ± 53.4
	C	16.2 ± 3.4	104.2 ± 9.1	205.8 ± 55.5	85.2 ± 40.6[a]
	D	51.8 ± 23.3	205.0 ± 47.4	308.1 ± 16.5	
	E	21829.0 ± 8131.5	4869.3 ± 2595.5	4864.4 ± 2595.5	112.6 ± 40.5[a]
Integrated biomass (mg C m^{-2})					
Interior ice		58.2 ± 13.2	391.8 ± 135.0	385.0 ± 124.0	309.4 ± 76.1
% autotrophs		67.0 ± 3.3	76.9 ± 2.8	74.3 ± 3.1	78.3 ± 4.5
% heterotrophic protozoa		19.2 ± 5.4	17.8 ± 2.9	16.0 ± 6.9	5.7 ± 1.3
% bacteria		13.8 ± 2.4	5.3 ± 0.3	9.7 ± 3.8	16.0 ± 5.7
Bottom ice		1091.5 ± 704.2	243.5 ± 202.9	243.2 ± 224.8	5.6 ± 2.9
% autotrophs		95.4 ± 3.4	83.4 ± 9.0	77.3 ± 19.7	33.5 ± 14.1
% heterotrophic protozoa		0.7 ± 0.8	11.1 ± 12.3	6.9 ± 0.6	12.3 ± 4.9
% bacteria		3.9 ± 2.6	5.5 ± 3.3	15.8 ± 19.1	54.2 ± 18.9
Total		1150 ± 713	635 ± 132	628 ± 347	315 ± 75
Integrated chl *a* (mg chl *a* m^{-2})					
Interior ice		3.6 ± 2.5	5.9 ± 1.8	2.9 ± 1.8	5.4 ± 3.3
Bottom ice		69.4 ± 71.4	7.7 ± 10.5	6.2 ± 6.6	0.2 ± 0.0
Total		73.1 ± 69.9	13.6 ± 12.3	9.1 ± 5.4	5.5 ± 3.3
Autotrophic carbon:chl *a*					
Total		15	37	52	44

[a]n = 2

believe our sets of replicate samples fairly represent the microbial communities at this site. A 2-way ANOVA with replication (Sokal & Rohlf 1973) was carried out on the total biomass of autotrophs, heterotrophic protozoa and bacteria measured in each horizon and confirmed that the data illustrated significant seasonal and vertical changes in the community and were not merely a consequence of variation between replicate samples (Table 4) The distinction in taxonomic composition, carbon biomass and chl *a* concentration between the interior Horizons A, B, C and D and the bottom ice of Horizon E justified a division of the 2 communities.

When integrated throughout the respective ice depths, the difference between the total biomass (mg C m^{-2}) of bottom and interior assemblages is less marked, with between 38 and 95% of the total integrated biomass attributable to organisms within the bottom 5 cm of fast ice (Table 3). In the pack ice values measured within interior horizons were comparable to those of the fast ice, ranging from 85 to 288 mg C m^{-3}, however, mean integrated biomass of the bottom ice was more than 40 times lower than for fast ice (Table 3).

Table 4. Spatial and temporal variability of the ice microbial community: summary of results of a 2-way ANOVA with replication (Sokal & Rohlf 1973) on the autotrophic, heterotrophic and bacteria biomass in individual horizons. Values of biomass from only the land fast ice are used. ANOVA was carried out on log$_{10}$-transformed data

Source of variation	df	MS	F
Autotrophs			
Among dates	2	1.41	17.47, $p < 0.001$
Among horizons	4	6.82	84.50, $p < 0.001$
Interaction	8	0.63	7.83, $p < 0.001$
Between replicates	30	0.08	
Total	44		
Heterotrophic protists			
Among dates	2	3.43	30.77, $p < 0.001$
Among horizons	4	2.44	21.95, $p < 0.001$
Interaction	8	0.24	2.11, $p > 0.05$
Between replicates	30	0.11	
Total	44		
Unattached bacteria			
Among dates	2	1.19	17.11, $p < 0.001$
Among horizons	4	1.35	19.34, $p < 0.001$
Interaction	8	0.18	2.63, $p < 0.05$
Between replicates	30	0.07	
Total	44		

Seasonal change

Total microbial biomass integrated throughout the ice depth (interior plus bottom) declined from a mean of 1150 mg C m^{-2} on 17 November to 635 and 628 mg C m^{-2} on 9 and 22 December respectively (Table 3), indicating a seasonal decline in fast-ice community biomass during the study period. Mean integrated microbial biomass within the ice floe samples was lower than that of the fast ice at 315 mg C m^{-2}.

The decline in total microbial biomass observed in the bottom community of fast ice was largely attributable to a decline in autotrophs (Fig. 5). In particular, the mean biomass of *Entomoneis* spp. decreased from over 2×10^4 mg C m^{-3} on 17 November to 2×10^3 mg C m^{-3} on 22 December (Fig. 2). As a result, the mean integrated autotrophic biomass and chl a concentration declined from 1041 to 188 mg C m^{-2} and 69 to 6 mg chl a m^{-2} during the same period. Conversely, the biomass of heterotrophic protozoa in the bottom ice more than trebled, largely due to the increase in biomass of Euglenoid sp.1, Dinoflagellate sp.1 and heterotrophic

nanoflagellates (Fig. 3). Variation in bacterial biomass was dependent on the presence of epiphytic forms that colonised both live and dead cells of *Entomoneis* spp. However, the large decrease in biomass of *Entomoneis* spp. between 17 November and 22 December was not matched by a reduction in bacterial biomass (Fig. 5) and the mean percentage of bacteria increased from 3.9 to 15.8% of the total biomass (Table 3).

In contrast to the bottom ice, an increase in total integrated biomass from 58 mg C m^{-2} on 17 November to 392 mg C m^{-2} in December occurred in the interior ice (Table 3). This was a consequence of increases in both autotrophic and heterotrophic fractions, the relative percentages of which remained almost constant throughout the period (Table 3). An increase in biomass of *Gymnodinium* sp.1 and other nanoautotrophs contributed most to the change in autotrophic biomass in the interior ice (Fig. 2). An increase in all components of the heterotrophic biomass took place between 17 November and 9 December (Fig. 3). Bacterial biomass also increased throughout the interior ice and throughout the sampling period (Figs. 4 & 5).
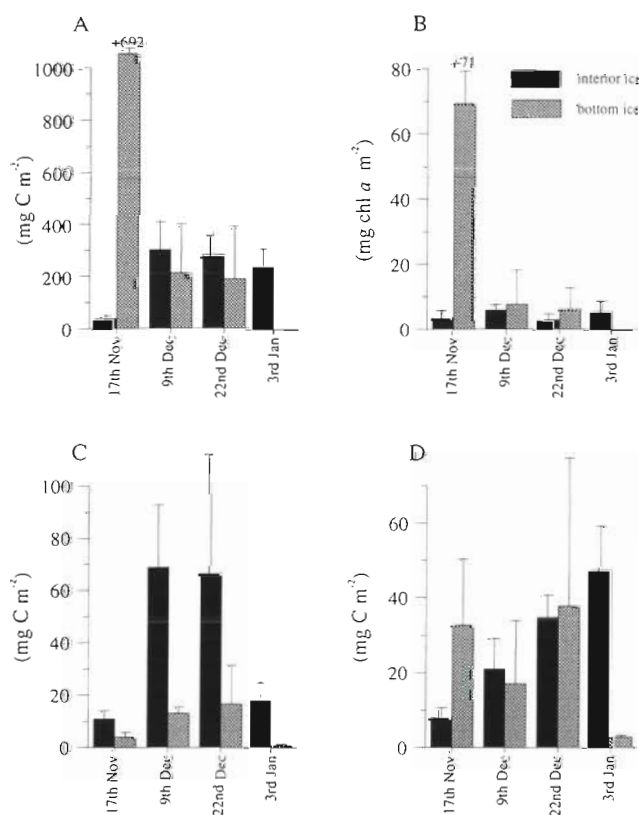
Photosynthetic rate measurements

Photosynthetic rate measurements were carried out on 2 dates midway between the major ice sampling dates. Mean production rates in the bottom ice based on measurements of ^{14}C incorporation were 637 and 94 mg C m^{-3} d^{-1} on 29 November and 16 December respectively. When normalised to the chl a concentration in each sample, ^{14}C incorporation rates gave mean assimilation values on 29 November and 16 December of 18.2 and 8.3 mg C mg^{-1} chl a d^{-1}, respectively (Table 5).

Fig. 5. Temporal change in the integrated biomass of (A) autotrophs, (B) chl a, (C) heterotrophic protozoa and (D) bacteria in the interior and bottom ice. Values are mean (n = 3) and standard deviation of 3 replicate cores on each sampling date. Note that samples collected on 3 January were from a drifting ice floe, not the fixed land fast site sampled on the other 3 dates

Table 5. Photosynthetic rate estimates (means ± SD) from the measurement of ^{14}C incorporation in bottom ice samples

Date	Chl a (mg m^{-3})	Specific carbon incorporation (mg C mg^{-1} chl a d^{-1})	Production (mg C m^{-3} d^{-1})
29 Nov	36.9 ± 9.0	18.2 ± 4.2	637 ± 117
16 Dec	14.9 ± 15.7	8.3 ± 3.3	94 ± 64

DISCUSSION

Community composition

The coastal sea ice examined in this study provided a habitat for abundant and dynamic microbial communities in both the interior and bottom horizons.

Autotrophs

This and previous studies in the nearshore ice of East Antarctica have demonstrated an active autotrophic community of high biomass inhabiting the bottom few centimeters of fast ice during spring and summer (Hoshiai 1977, McConville & Wetherbee 1983, Mc-Conville et al. 1985, Perrin et al. 1987, Watanabe & Satoh 1987). McConville & Wetherbee (1983) reported a bottom ice community dominated by colonial pennate diatoms in land fast ice near all 3 Australian Antarctic stations of Davis, Casey (66° 17' S, 110° 30' E) and Mawson (67° 36' S, 62° 53' E). Similar communities have been described in the vicinity of the Japanese station of Syowa (69° 00' S, 39° 35' E) (Hoshiai 1977, Watanabe et al. 1990). In all cases, including the present study, the peak standing crop occurs in November and declines thereafter as water and ice temperatures rise and insolation increases, although at Davis the overall ice thickness did not decrease at this time. The reason for the rapid decrease in bottom community biomass is unclear. McConville & Wetherbee (1983) reported that a low salinity layer occurs just below the ice at this time of year and may contribute to the decline. It was established that large numbers of metazoan grazers were present under the ice, but it is unlikely that grazing accounts for the rapid decline in biomass, and here as elsewhere it appears that most of the diatom community becomes detached into the water beneath (see below).

Comprehensive studies of the bottom ice autotrophic communities of annual and multi-year ice have taken place in McMurdo Sound (approximately 78° S, 165° E) (Palmisano & Sullivan 1983, Grossi et al. 1984, Grossi & Sullivan 1985, Lizotte & Sullivan 1992, Arrigo et al. 1993b). The bottom few centimeters of congelation ice contain a spring/summer community of similar taxonomy and biomass to that observed off East Antarctica. However, a layer of platelet ice crystals colonised by pennate diatoms and greatly exceeding in biomass the overlying congelation ice communities often develops in McMurdo Sound (Grossi et al. 1987, Arrigo et al. 1993b) Platelet ice layers form in areas where sea water is supercooled at depth by contact with the continental ice shelf (Foldvik & Kvinge 1977, Dieckmann et al. 1986) and therefore bottom ice platelet layers are unlikely to be found in the relatively shallow coastal regions in the vicinity of land as occurs off Davis and Syowa Stations. Observations using SCUBA equipment (McConville et al. 1985) and our underwater video observations confirmed the lack of a platelet layer in the Davis region.

Diatom communities of various fast ice habitats have been described at lower latitudes close to the shore of Signy Island (60° 42' S, 45° 36' W) and Anvers Island (64° 46' S, 64° 06' W) (Whitaker 1977, Krebs et al. 1987). Particularly high concentrations of chl a of 236 and 3991 mg m^{-2} respectively were attributed to the diatom *Navicula glaciei* at these 2 sites.

Fewer studies have examined the interior assemblages of land fast ice. Similar vertical profiles of chl a to those recorded in this study have been reported for fast ice in McMurdo Sound (Palmisano & Sullivan 1983), close to Syowa Station (Hoshiai 1977) and in fast ice along the ice shelf that forms the eastern coast of the Weddell Sea (Spindler & Dieckmann 1986). In all 3 locations the chl a concentrations found in the interior ice were several orders of magnitude lower than in the bottom few centimeters of ice; although a peak of chl a concentration in the interior ice was observed during winter at Syowa Station and was attributed to the incorporation of an autumnal bottom ice diatom bloom as the ice depth increased (Hoshiai 1977). Stoecker et al. (1992) described an autotrophic community inhabiting the interior of fast ice in McMurdo Sound with a similar taxonomic composition to that found in this study. A small dinoflagellate resembling *Gymnodinium* sp.1 reached an abundance of 2796 cells ml^{-1} of brine and photosynthetic dinoflagellates and their cysts comprised over 80% of the autotrophic biomass in December. Chl a values extrapolated from concentrations in brine samples from the upper 50 cm of fast ice in McMurdo Sound increased during December from 0.07 to 0.88 mg m^{-3} of ice (Stoecker et al. 1992). This is similar to the almost 7-fold increase in integrated biomass of the interior ice communities at Davis during early summer. Hoshiai (1977) also reported the development of a dinoflagellate population in the interior of the fast ice off Syowa in December. This suggests that an actively growing interior ice assemblage dominated by autotrophic dinoflagellate species may be widespread in fast ice around Antarctica.

Heterotrophic protozoa

It is becoming increasingly clear that a wide variety and in some cases a high abundance of heterotrophic protozoa inhabit sea ice. Estimates of the mean total integrated biomass of heterotrophic protists in the land fast ice at O'Gorman Rocks increased from 19 to 97 mg C m^{-2} from November to December. Interior assemblages contributed the major part of the integrated biomass. However, maximum concentrations occurred in the bottom ice with mean values for heterotrophic protozoan biomass approaching 300 mg C m^{-3} during December. In the pack ice of the Weddell Sea estimates of the integrated biomass of heterotrophic protozoa were generally less than half the maximum value

of 75 mg C m^{-2} (Garrison & Close 1993). Maximum concentrations of heterotrophic protozoa were found in the surface layers of pack ice reaching 160 mg C m^{-3} and corresponding with high autotrophic biomass (Garrison & Buck 1991). In brine samples from the upper 50 cm of fast ice of McMurdo Sound the average biomass of non-photosynthetic protists ranged from 0.2 to 27.6 mg C m^{-3} varying with location and date (Stoecker et al. 1993). Brine samples represented an approximately 4-fold concentration of actual ice values at the time of sampling (Stoecker et al. 1992), suggesting similar or lower values than were recorded in Horizon A of ice offshore from Davis. The taxonomic composition of heterotrophic protozoa was similar in the pack ice of the Weddell Sea and the upper fast ice of McMurdo Sound to that found in coastal sea ice examined in East Antarctica in the present study.

Heterotrophic nanoflagellates appear to be major contributors to the biomass in both pack and fast ice. Choanoflagellates were noticeably abundant in the surface layer assemblages of the summer pack ice in the Weddell Sea (Garrison & Buck 1991). The present study and samples collected in the upper ice brine samples from McMurdo Sound (Stoecker et al. 1993) suggest that choanoflagellates are not as important a part of the heterotrophic community in land fast ice. On the other hand, *Cryothecomonas* spp. appear to be ubiquitous in Antarctic sea ice (Garrison & Buck 1989, Thomsen et al. 1991, Garrison & Close 1993, Stoecker et al. 1993, present study).

The presence of heterotrophic euglenoids in sea ice has been recorded previously but they were not regarded as a major component of the heterotrophic biomass (Garrison & Buck 1989). In this study Euglenoid sp.1 and Euglenoid sp.2 at certain times each contributed greater than 50% of the biomass of heterotrophic protozoa in the bottom and interior horizons. Heterotrophic dinoflagellates were found throughout the ice depth and athecate and thecate forms contributed a similar high proportion of the heterotrophic biomass. Heterotrophic dinoflagellates, especially athecate forms, were a common component of the ice community in both the Weddell Sea (Garrison & Buck 1989, Mathot et al. 1991) and fast ice of McMurdo Sound (Stoecker et al. 1993). Pack ice assemblages contained an unusual phagotrophic dinoflagellate that is able to engulf pennate diatoms and produces detrital pellets (Buck et al. 1990). Dinoflagellate sp.1 observed in this study had several characteristics in common with the phagotrophic dinoflagellate described by Buck et al. (1990), but showed no evidence of being phagotrophic (see 'Results') The large phagotrophic dinoflagellate *Polykrikos* sp. commonly found in brine samples from McMurdo Sound (Stoecker et al. 1993) was not observed in this study.

More than 20 ciliate taxa have been identified using silver staining techniques from the pack ice of the Weddell Sea (Corliss & Snyder 1986). Stoecker et al. (1993) also reported a diverse ciliate assemblage in the upper 50 cm of fast ice in McMurdo Sound. Ciliates contributed a major part of the biomass of heterotrophic protists in both the Weddell Sea pack ice (Garrison & Buck 1989) and the fast ice of McMurdo Sound (Stoecker et al. 1993). Highest ciliate biomass in the present study occurred in the lower horizons reaching values of 10 mg C m^{-3} and always <10% of heterotrophic protozoan biomass. In the upper ice horizons corresponding to the brine sampled by Stoecker et al. (1993) ciliate biomass rarely exceeded 2 mg C m^{-3} and contributed an even lower proportion of heterotrophic protozoan biomass. Brine volume was calculated to be approximately 25% ice volume in the upper 50 cm of fast ice in McMurdo Sound in late December (Stoecker et al. 1992) which would make estimates of ciliate biomass comparable to those found offshore from Davis. However, in both cases they are considerably lower than values reported from surface layers of pack ice where total ciliate biomass exceeded 100 mg C m^{-3} on occasions (Garrison & Buck 1991). This is despite the fact that the volume to carbon conversion factor used by Garrison & Buck (1989) was less than half that used by Stoecker et al. (1993) and in the present study.

Foraminifera were not found in the sea ice examined in this study or reported to occur in the upper fast ice of McMurdo Sound (Stoecker et al. 1993). This confirms their scarcity in congelation ice.

Bacteria

The mean standing crop of bacteria in sea ice offshore from Davis was 40 to 70 mg C m^{-2} (Fig. 5). This is higher than values reported for McMurdo Sound where a mean standing crop of 9.8 mg C m^{-2} was recorded by Sullivan & Palmisano (1984). However, the cell volume to carbon conversion factor of 0.4 pg C µm^{-3} (Bjørnsen & Kuparinen 1991) used in the present study is 4 times greater than that used by Sullivan & Palmisano (1984) and explains some of the difference. The vertical profile of bacterial biomass in fast ice at O'Gorman Rocks is similar to that described in McMurdo Sound (Sullivan & Palmisano 1984). In both cases the presence of epiphytic bacteria in the bottom ice contributes to the large variation in bacterial biomass between bottom and interior assemblages. McConville & Wetherbee (1983) also reported high concentrations of epiphytic bacteria attached to *Entomoneis* spp. and to the mucilage sheaths of the diatom *Amphipleura* sp. in bottom ice near Casey (66° 17' S,

110° 30' E). At least 65 % of epiphytic bacteria occurred on diatoms of the genus *Amphiprora* (= *Entomoneis* spp. in the present study) in the bottom ice of McMurdo Sound (Grossi et al. 1984). A commensal or mutualistic interaction between the epiphytic bacteria of *Entomoneis* spp. and their host has been suggested by both Sullivan & Palmisano (1984) and Grossi et al. (1984). A similar relationship occurs in the bottom ice of Barrow Strait in the Canadian Arctic where the dominant diatom *Nitzschia frigida* is the preferred host of epiphytic bacteria (Smith et al. 1989). Epiphytic bacteria attached to *Entomoneis* spp. contributed mean percentages of between 54 and 93 % of bacterial biomass in the bottom ice samples in the present study but their biomass was highly variable. An increase in free living bacterial biomass occurred throughout the ice depth between November and December in the fast ice offshore from Davis. Integrated biomass of the interior ice matched that of the bottom ice assemblages at greater than 30 mg C m^{-2} by 22 December, illustrating that an important and active bacterial community exists in the interior of land fast ice.

Production and trophic interactions

Early summer at Davis Station was a period of increasing insolation culminating in a general increase in temperature throughout the depth of sea ice and a reduction in snow cover. These are conditions that would be expected to promote microbial production in sea ice. However, the fate of the bottom and interior ice communities differed markedly during this period.

Primary production of sea ice microalgae has been estimated in a number of ways including incorporation rate of ^{14}C and accumulation of biomass. Comparisons of the 2 methods reveal up to a 10-fold greater estimate when rates of incorporation of ^{14}C are compared to estimates made from the accumulation of biomass in bottom ice communities of McMurdo Sound (Grossi et al. 1987). Possible causes of this discrepancy are loss of biomass to the water column and losses due to grazing by metazoans and protozoans (Grossi et al. 1987). McConville et al. (1985) observed sea ice algal fragments that had fallen out of the ice into the water column at Davis. Using underwater video in the present study, large numbers of amphipods were observed on the underside of the ice. A minimum estimate of the biomass of the bottom community that enters the water column or is grazed can be obtained from the decline in biomass between sampling dates. A decline of 838 mg C m^{-2} occurred between 17 November and 9 December

A more realistic estimate of the carbon biomass produced in the bottom ice can be calculated using mea-

surements of primary production of bottom ice communities. *In situ* incubations of the bottom ice community with ^{14}C, recorded during the middle of the day at Davis, gave a mean hourly assimilation number of 1.3 mg C mg^{-1} chl *a* h^{-1} in December for samples containing 2.7 to 15.6 mg chl *a* m^{-2} (McConville et al. 1985). *In situ* 24 h ^{14}C incubations of intact bottom ice samples in the present study indicated similar daily assimilation numbers of 18.2 and 8.3 mg C mg^{-1} chl *a* d^{-1} on 29 November and 16 December respectively. Assuming the majority of the bottom ice community biomass fell into the water column soon after 17 November then the chl *a* concentration in bottom ice on 9 December may be used as a minimum value to relate assimilation number to production. This would give an estimated production rate of 140 mg C d^{-1} and a total production of 3.089 g C m^{-2} in the bottom ice during the period 17 November to 9 December. Following the same assumptions, estimated production during the period 9 to 22 December would equal a total of 670 mg C m^{-2} at a rate of 51.2 mg C m^{-2} d^{-1}. When combined with the decline in biomass of the bottom ice community this would suggest that a minimum quantity of 4.6 g C m^{-2} of primary production from the bottom ice community entered the water column or was consumed by heterotrophs following the peak of algal biomass in November.

The increase in the total biomass of heterotrophic protozoa in the bottom ice represented a minimum estimate of instantaneous growth rate of 0.054 d^{-1} and 0.018 d^{-1} in the 2 time intervals. These values obviously ignore the probability of migration into or from the bottom ice and the change in population biomass of heterotrophs involved a complex interaction of increase and decrease in different taxa. Alteration in biomass of the bottom ice bacterial population comprised largely of epiphytic forms would be expected to coincide with the decline in biomass of *Entomoneis* spp. However, despite the large variability between replicates and an increase in unattached bacterial biomass during the sampling period, the greater proportion of epiphytic bacteria relative to *Entomoneis* spp. biomass indicates increased colonisation of *Entomoneis* spp. cells by 22 December.

Measurements of ^{14}C incorporation were not carried out for interior fast ice communities in this study. Instead, an estimate of primary production can be made from the accumulation of biomass in the interior ice between sampling dates. This assumes no migration of autotrophic biomass into or from the bottom ice and no grazing loss. Integrated autotrophic biomass increased by 280 mg C m^{-2} in the interior assemblage between 17 November and 9 December representing an intrinsic rate of growth of the autotrophic population of 0.095 d^{-1}. The integrated biomass of hetero-

trophic protozoa and bacteria also increased during this period and, if the same assumptions are made, showed population growth rates of 0.083 and 0.043 d^{-1} respectively. Net autotrophic production (gross production – respiratory losses) can be re-evaluated when growth of the heterotrophic component is taken into account. Among many variables, the incorporation efficiency of carbon by both bacteria and heterotrophic protozoa will depend upon utilisability of the organic matter or food quality (Azam et al. 1983, Caron 1991) Gross growth efficiencies of heterotrophic protozoa may vary between 2 and 82% (Caron & Goldman 1990). In the North Atlantic the transfer efficiency of carbon biomass between phytoplankton and heterotrophic protozoa was estimated at 30 to 100%, increasing with a decrease in the proportion of phytoplankton grazed (Burkill et al. 1993). Estimates of the gross growth efficiency of bacteria are equally variable. Bacterial carbon growth yields of between 40 and 38% have been estimated in cultures established from Weddell and Scotia Sea waters (Bjørnsen & Kuparinen 1991). If the carbon conversion efficiency of heterotrophic protozoa and bacteria was 40% in the present study and autotrophic production was the only food source available, then the autotrophic biomass consumed by these 2 groups would be 146 and 32 mg C m^{-2} respectively. This would raise the value of net primary production from 280 to 457 mg C m^{-2}, representing a growth rate of 0.115 d^{-1}. Continuing this theme, the proportion of interior ice net primary production consumed during this period by heterotrophic protozoa and bacteria can be estimated at 32 and 7% respectively. The slight decrease in mean integrated autotrophic biomass that occurred between 9 and 22 December was due to a decline in the mean autotrophic biomass in Horizon B. In all other interior horizons the autotrophic biomass continued to grow, suggesting that the decline in Horizon B may have been due to grazing losses or migration within the ice

rather than to a decrease in photosynthetic capacity. Although these calculations involve gross extrapolation of the available data, they provide an invaluable estimate of the summer primary production in interior ice and a rare illustration of the importance of both heterotrophic protozoa and bacteria in sea ice.

Estimates of the specific growth rates (μ) of the major heterotrophic components of the sea ice community were calculated from changes in specific integrated biomass between sampling dates [$\mu = (\ln C_1 - \ln C_2)/(t_2 - t_1)$, where C is biomass at time t] (Table 6). This equation assumes exponential growth, no mortality due to predation and no migration out of or into the ice. Net growth rates of heterotrophic protozoa estimated in the present study ranged between 0.168 d^{-1} for Euglenoid sp.1 and 0.050 d^{-1} for the heterotrophic nanoflagellate population in the period between 17 November and 9 December (Table 6); only the euglenoids continued to show net growth between 9 December and 22 December. When the low temperature (less than –1.9°C) and possible losses due to grazing (particularly for the nanoflagellates) or migration to the water column are considered, these values are tenable.

Previous studies of bacterial growth in bottom ice indicate a faster rate of growth for epiphytic than for unattached forms (Grossi et al. 1984, Kottmeier et al. 1987, Smith et al. 1989). However, these measurements were carried out during the bloom in bottom ice autotrophic production. The sampling period of this study coincided with a decline in the bottom ice autotrophic biomass that may explain the high variability of bottom ice bacterial biomass (Fig. 4). The growth rates (μ) of unattached bacteria integrated throughout the ice depth (0.040 to 0.046 d^{-1}; Table 6) are comparable to growth rates measured in the bottom of congelation ice in McMurdo Sound from net accumulation of biomass (0.03 to 0.09 d^{-1}; Grossi et al. 1984) and thymidine incorporation (0.007 to 0.200 d^{-1}; Kottmeier et al. 1987). Similar estimates of bacterial

Table 6. Temporal change in biomass of individual heterotrophic protist types and bacteria. Biomass values are mean ± SD of integrated biomass of 3 replicate cores. Growth rates are net rate of growth calculated from the change in integrated biomass between sampling dates

|	Biomass (mg C m^{-3})			Growth rate (μ, d^{-1})	
Date:	17 Nov 93	9 Dec 93	22 Dec 93		
Days:	1	23	36	1 to 23	23 to 36
Euglenoid sp.1	0.33 ± 0.07	13.08 ± 7.28	29.44 ± 16.71	0.168	0.062
Euglenoid sp.2	1.38 ± 0.89	23.25 ± 14.82	28.07 ± 24.87	0.128	0.015
Diplopeltopsis sp.	3.06 ± 1.15	11.82 ± 8.47	6.00 ± 2.66	0.061	−0.052
Dinoflagellate sp.1	0.76 ± 0.25	5.96 ± 2.74	1.72 ± 1.41	0.094	−0.095
Nanoflagellates	5.62 ± 0.60	16.79 ± 4.84	11.22 ± 2.17	0.050	−0.031
Unattached bacteria	9.50 ± 3.74	22.86 ± 7.83	41.32 ± 2.71	0.040	0.046
Epiphytic bacteria	31.01 ± 18.85	15.25 ± 16.08	31.10 ± 36.13	−0.032	0.055
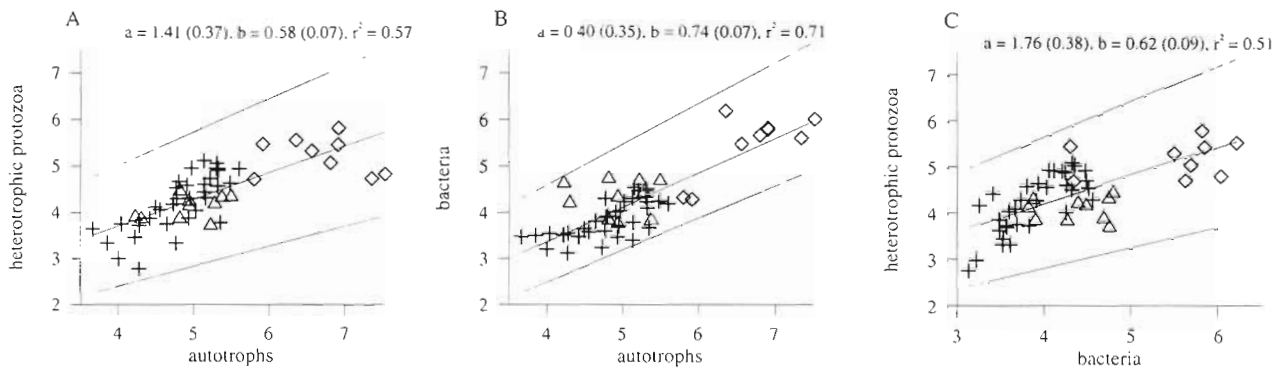
Fig. 6. Relationships between biomass of trophic categories in sea ice offshore from Davis station. Data are $\log_{10}$ biomass (pg C m^{-1}) from each sample collected on all 4 sampling dates. Samples representing values from bottom ice (◊), interior ice (+) and the pack ice (Δ) communities are distinguished. Lines represent least squares linear regression together with 95% confidence intervals. Respective equations are shown

growth rate have been recorded in the bottom community of Arctic sea ice (74° 40' N) (Smith et al. 1989), although growth rates measured by thymidine incorporation in the bottom ice of Frobisher Bay (66° 30' N) were 15 times higher at about 0.75 d^{-1} (Bunch & Harland 1990) than the estimates of Smith et al. (1989) from net accumulation of biomass. Pack ice bacteria also grow at similar rates to those measured in Antarctic bottom ice communities (Kottmeier & Sullivan 1990, Grossmann 1994).

Trophic coupling and carbon flow

The evidence presented indicates that an active population of heterotrophic protozoa and bacteria exists in the land fast ice offshore from Davis. Questions then arise about the trophic interactions that are taking place and the extent to which autotrophic and heterotrophic biomass is coupled. Microbial interactions in the water column can be highly complex (Fenchel 1988) and as suggested by Palmisano & Garrison (1993) the same may be true of sea ice communities. Evidence for close coupling between autotrophic, bacterial and heterotrophic protozoan populations within sea ice is illustrated by the relationship between the total biomass of each component in each sample examined during the summer period (Fig. 6). A schematic summary of the changes in microbial carbon biomass and the estimates of carbon flow within and from the sea ice during the austral summer sampling period is given in Fig. 7.
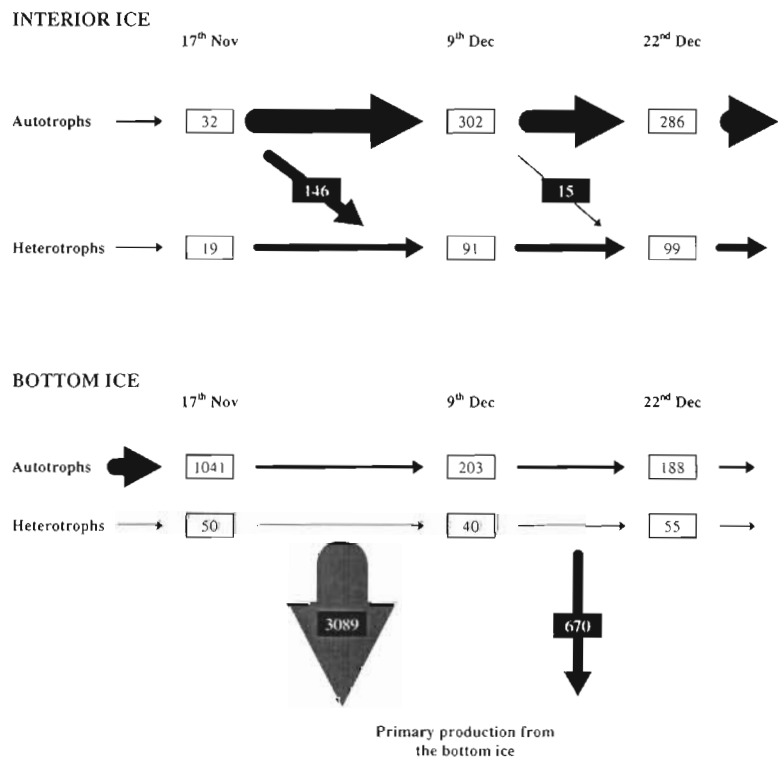

Fig. 7 Schematic summary of changes in microbial carbon biomass and inferred carbon flow within interior and bottom fast ice offshore from Davis station during austral summer 1993/1994. Numbers in white boxes are microscopically determined values of carbon biomass (mg C m^{-2}) and those in black boxes are estimations of autotrophic carbon biomass (mg C m^{-2}) consumed by heterotrophs or lost from the ice. Autotrophic production within interior ice was estimated from accumulation of biomass of autotrophic and heterotrophic components between sampling dates. An incorporation efficiency of 40% was used to estimate consumption of autotrophic production by both heterotrophic protozoa and bacteria. Primary production in bottom ice was estimated from measurements of ^{14}C incorporation. Details of calculations of carbon production and flow are discussed in the text

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