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Seasonal changes in phytoplankton and bacterioplankton distribution at the ice-water interface in the Antarctic neritic area

D. Delille[1], M. Fiala[1], C. Rosiers[2]

[1]Observatoire Océanologique de Banyuls, Laboratoire Arago, Université P. et M. Curie, URA CNRS 117, F-66650 Banyuls-sur-Mer, France

[2]Université Claude Bernard (Lyon 1), Bât. 405, 43 Bd du 11 Novembre 1918, F-69622 Villeurbanne Cedex, France

ABSTRACT: To determine the relationship between phytoplankton and bacteria biomass near the ice-water interface in the Antartic, the seasonal distributions of phytoplankton and bacteria populations were investigated on the continental shelf of Terre Adélie during the ice coverage period. An under-ice surface station was sampled weekly from March 1991 to January 1992 for the bottom ice and for surface, 0.5 and 2 m depth seawater. Seawater chlorophyll *a* values ranged from 0.9 mg m^{-3} in summer to 0.01 mg m^{-3} in winter. Values 50 times higher were recorded in the overlying ice. Bacterial abundance ranged from 0.5×10^{11} cells m^{-3} in July to 6.0×10^{11} cells m^{-3} after the ice break-up. Values reaching up to 2.5×10^{12} cells m^{-3} were recorded in sea ice. Bacterial biomass and chlorophyll *a* concentrations were significantly correlated in both sea ice and underlying seawater. Bacterial biomass represents between 1 and 10% of total microbial biomass in sea ice and from 10% (summer) to up to 90% (winter) of the living community in the underlying seawater.

KEY WORDS: Phytoplankton · Bacterioplankton · POC · Seasonal variations · Sea ice · Antarctica

INTRODUCTION

Seasonal changes in critical parameters should not be disregarded if accurate carbon budgets are to be constructed (Platt et al. 1992). An intense temporal variability occurs in Antarctic seawaters, representing perhaps the most extreme seasonality observed anywhere in the world ocean (Karl 1993). Few investigators have examined the distribution of both bacteria and phytoplankton over an annual cycle. During interannual investigations, Ducklow & Shiah (1993) report low covariation of phytoplankton with bacteria in Chesapeake Bay, USA. Accordingly, the 3 yr survey of Hoch & Kirchman (1993) did not show a significant correlation between chlorophyll *a* (chl *a*) concentration and bacterial abundance in a temperate estuary. As a general trend, a number of other investigators working in subtropical (Hopkinson et al. 1989), temperate (Velimirov & Walenta-Simon 1992, Ducklow et al. 1993) and subpolar (Delille 1990, Wiebe et al. 1993) coastal marine systems have reported no direct relationship between seasonal changes in bacterial biomass and phytoplankton.

The pathways that mediate the transfer of nutrients between the primary producers and bacteria in seawater are extremely complex and include numerous feedback mechanisms. Heterotrophic bacteria are largely reliant on phytoplankton for their energy supply, either directly through excretion of dissolved organic matter (Lancelot & Billen 1984, Kuosa & Kivi 1989, Suttle et al. 1991) or indirectly after decomposition of dead phytoplankton cells (Riemann & Sondergaard 1986). On the other hand, it is generally assumed that most of the primary production in pelagic ecosystems is sustained by a continuous and rapid recycling of the growth-limiting inorganic nutrients (Azam et al. 1983, Berman et al. 1987). Depending on food web structure, bacteria may be either a link in food webs, supporting metazoan production, or largely a sink, where bacterial production is respired by microorganisms (Ducklow et al. 1986,

Pomeroy & Deibel 1986, Wylie & Currie 1991, Vaqué et al. 1992). Estimates of ratios of phytoplankton primary production to community respiration suggest that many parts of the ocean margins are net heterotrophic in all but the coldest season (Smith & Mackenzie 1987). Seasonal changes in growth rates and respiratory demands of aerobic heterotrophic bacteria, which dominate total community respiration, can induce change from general heterotrophy to autotrophy (Hopkinson 1985, Griffith et al. 1990, Wiebe et al. 1993). Furthermore, Wiebe et al. (1993) proposed that temperature-substrate interactions underlie seasonal cycles of bacterial activity. It is therefore of considerable interest to study seasonal cycles under an ice-covered system where temperature can be considered as relatively constant. The purpose of the present article is to examine the relationship between phytoplankton and bacteria biomass on the continental shelf of the Terre Adélie area, Antartica, during the ice-covered period. The study comprises some of the first composite information on the seasonal dynamics of phytoplankton and bacterial communities occurring in such areas.

MATERIALS AND METHODS

Study site and sampling strategy. The study was conducted from March 1991 to January 1992 in Terre Adélie (66° 40' S, 140° 01' E). Samples were collected weekly at the under-ice Stn B (10 m deep) located in the vicinity of the Pointe Géologie Archipelago (Fig. 1).

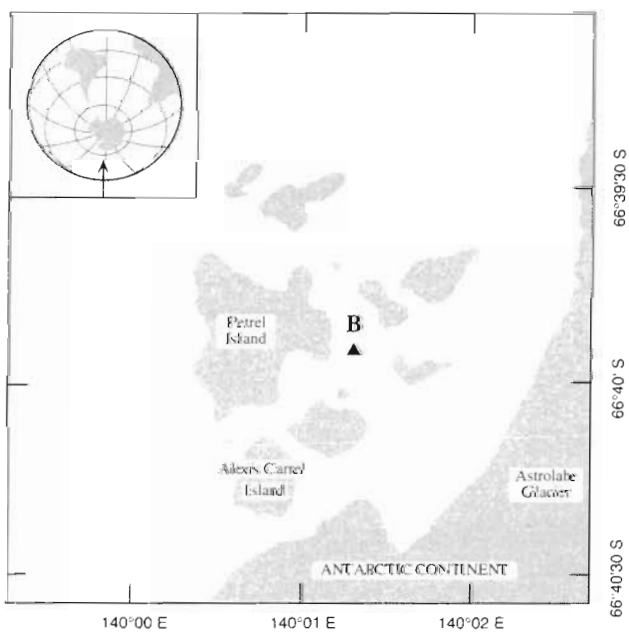

Fig. 1. The Pointe Géologie Archipelago (Terre Adélie), showing the location of the study station (B)

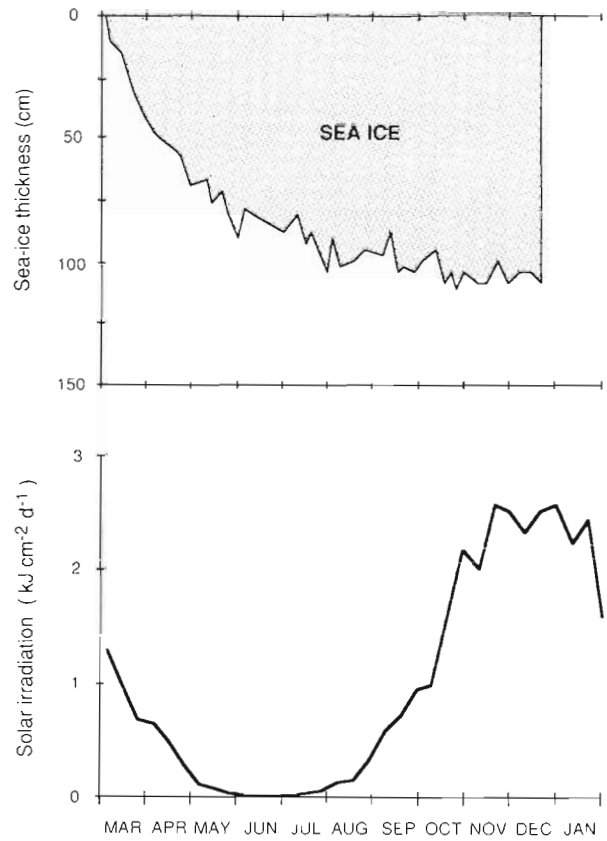

Fig. 2. Seasonal changes in ice coverage and global irradiation recorded at Stn B

Ice cores were collected using 10 cm (internal diameter) ice-coring augers. The bottom part (last 10 cm) of the cores was cut with a sterile blade and stored in a sterile glass box before melting in a known quantity of sterile aged seawater. After drilling of the ice cover, subsurface seawater samples were collected with sterile glass bottles at 0, 0.5 and 2 m depth. All samples were analysed in the laboratory within 15 min.

Chlorophyll biomass. Seawater was filtered through Whatman GF/F glass fiber filters under gentle vacuum (<5 mm Hg). Measurements of chlorophylls and phaeopigments were carried out using the spectrofluorometric method developed by Neveux & Panouse (1987). Chlorophylls and derived pigments were extracted with 90% acetone and their concentrations measured using a spectrofluorometer (Perkin Elmer MPF 66) at 6 coupled wavelengths. Each coupled wavelength corresponded to the fluorescence excitation and emission of each analysed pigment: chl *a*, chl *b*, chl *c*, and phaeophytins (phaeo) *a*, *b* and *c*. A solid sample of phaeophytin *a* in polymethylmethacrylate was used as a reference.

The C biomass of phytoplankton was estimated from chlorophyll measurements using a C/chl *a* factor of 60 according to Neori & Holm-Hansen (1982).

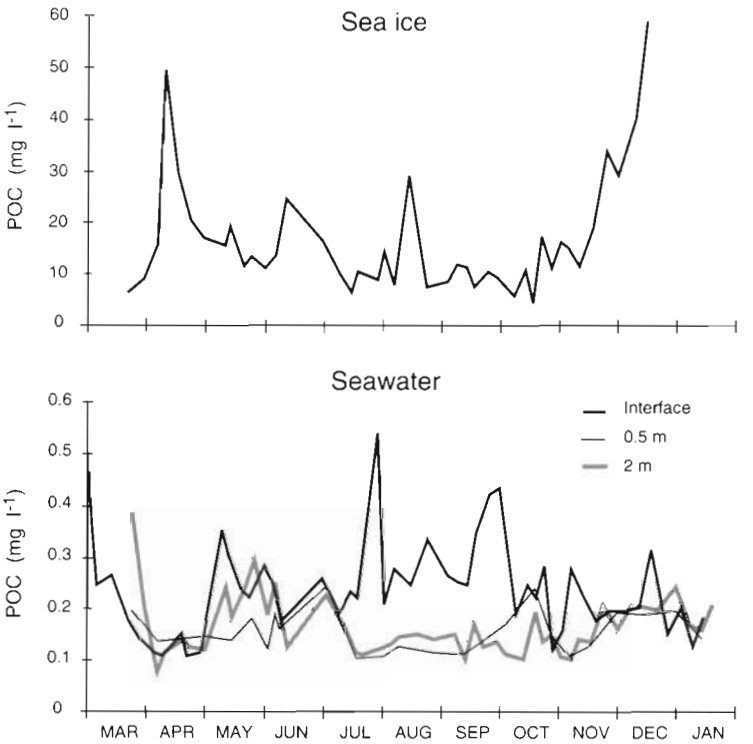

Fig. 3. Comparison of seasonal changes in POC concentrations at the ice bottom and the 3 depths of underlying seawater at Stn B

Particulate organic matter. Seawater samples were filtered directly upon collection using pre-combusted Whatman GF/F filters. Filters were dried in a vacuum desiccator and then stored frozen. Before measurement they were decalcified by treatment with 1 M H_3PO_4 at 60°C for 48 h. Particulate organic carbon (POC) and particulate organic nitrogen (PON) were oxidized in a CHN analyser (Perkin Elmer 2400).

Bacterioplankton biomass. Bacterioplankton abundances were determined through epifluorescence after acridine orange staining (Hobbie et al. 1977; Olympus BHA microscope). Cell volumes were estimated using an ocular micrometer. Bacterial biomass was estimated using a conversion factor of 0.4 pg C μm^{-3} (Bjørnsen & Kuparinen 1991).

RESULTS

Physicochemical data

The study area was free of ice from January to February. The ice thickness increased regularly from a few millimeters in early March to more than 1 m in December (Fig. 2). Water temperature was consistently low, ranging from 0.5°C in summer to −1.7°C in winter (data not shown). Solar irradiation ranged from 6 J cm^{-2} d^{-1} in June–July to more than 2500 J cm^{-2} d^{-1} in December–January.

POC concentrations (Fig. 3) were a hundred times greater in sea ice than in the underlying seawater. Values ranged from about 10 mg C l^{-1} (winter) to more than 50 mg C l^{-1} in sea ice, and from 0.1 to 0.5 mg C l^{-1} in seawater. Four major distinct peaks (April, June, August and December) were observed in the sea ice. In seawater some differences could be observed among the 3 depths. The winter ice-water interface values were 2 to 5 times larger than those observed in subsurface.

POC/PON ratios (Fig. 4) were much less variable in seawater than in sea ice. There were only very small seasonal changes in seawater and the values recorded at the 3 levels generally were relatively similar. In contrast, after 2 months (April–May), corresponding to the ice-formation period during

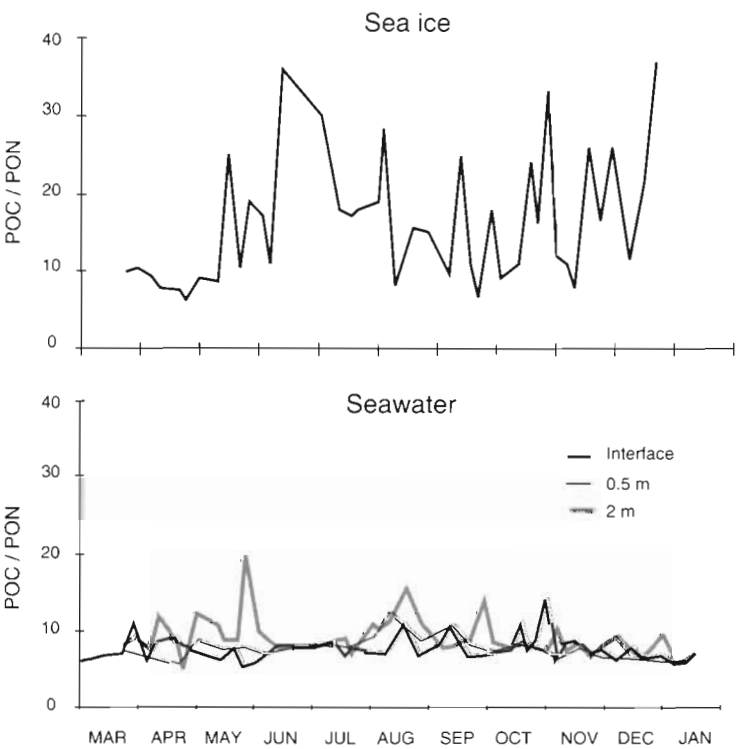

Fig. 4. Comparison of seasonal changes in C/N ratio at the ice bottom and the 3 depths of underlying seawater at Stn B

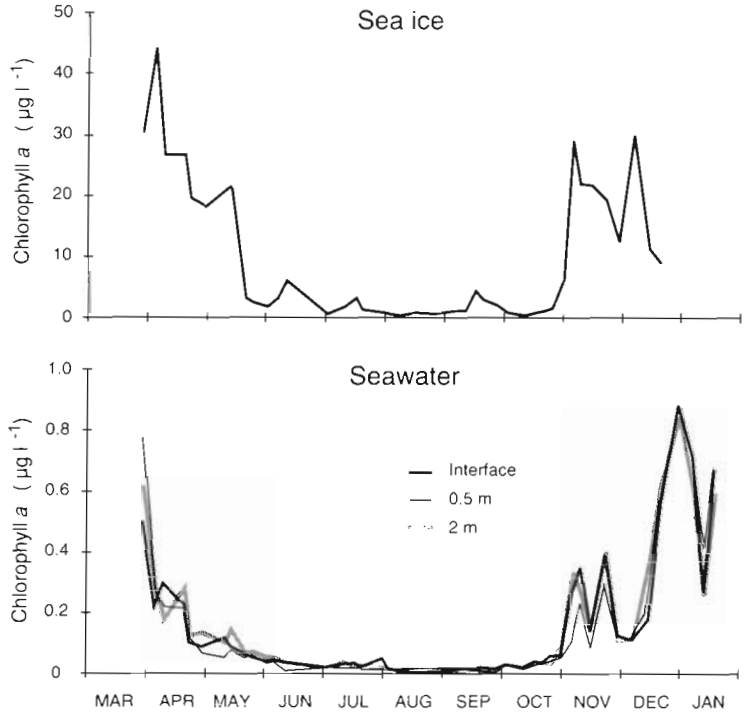

Fig. 5. Comparison of seasonal changes in chl *a* concentrations at the ice bottom and the 3 depths of underlying seawater at Stn B

which POC/PON ratios in sea ice were very close to values observed in seawater (ca 10), several very sharp increases, with values greater than 30 (July, October, December), occurred in the sea ice.

Phytoplankton

During winter, seawater chl *a* was very low, ranging between 0.01 and 0.05 µg l^{-1}. Concentrations increased dramatically during austral summer to a maximum value of 0.9 µg l^{-1}. The observed increase began in November and was made up of a succession of short pulses of limited duration (Fig. 5). Chl *a* changes recorded in sea ice paralleled those observed in the corresponding seawater samples but were 2 orders of magnitude larger. In winter bottom ice samples, the phytoplankton biomass was always greater than 0.5 µg chl *a* l^{-1}. The maximal values occurred in April during early ice formation (44 µg chl *a* l^{-1}) and in November–December just before ice melting (Fig. 5).

In both seawater and sea ice the chl *b* concentration was negligible. Chl *c* was present in larger amounts, and the mean chl *c* / chl *a* ratio ranged between 0.3 in seawater and 0.48 in sea ice. Diatoms appeared to be dominant, as has been reported in previous work conducted in summer (Fiala & Delille 1992).

The evolution of phaeopigments was inverse to that of chl *a*. During winter the mean ratio of phaeopigments to chl *a* [phaeo *a* / (chl *a* + phaeo *a*)] ranged from 0.3 to 0.5 in sea ice while it was consistently greater than 0.6 in the underlying seawater (Fig. 6). During the summer phytoplankton bloom this ratio was lower and averaged 0.3 in both sea ice and seawater.

Abundance of bacteria

At the beginning of sea-ice formation a large increase in bacterial abundance occurred in ice-bottom-layer assemblages (Fig. 7). The maximal value of 2.5×10^6 cells ml^{-1} was reached in April. A steady decrease in cell number then occurred until September. After the winter minima, a small

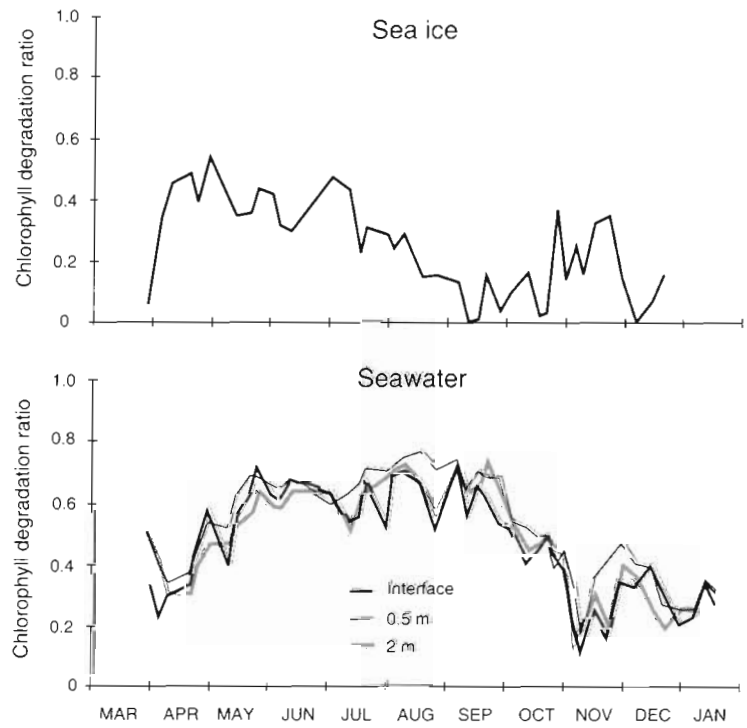

Fig. 6. Comparison of seasonal changes in the degradation ratio [phaeo *a* / (chl *a* + phaeo *a*)] at the ice bottom and the 3 depths of underlying seawater at Stn B

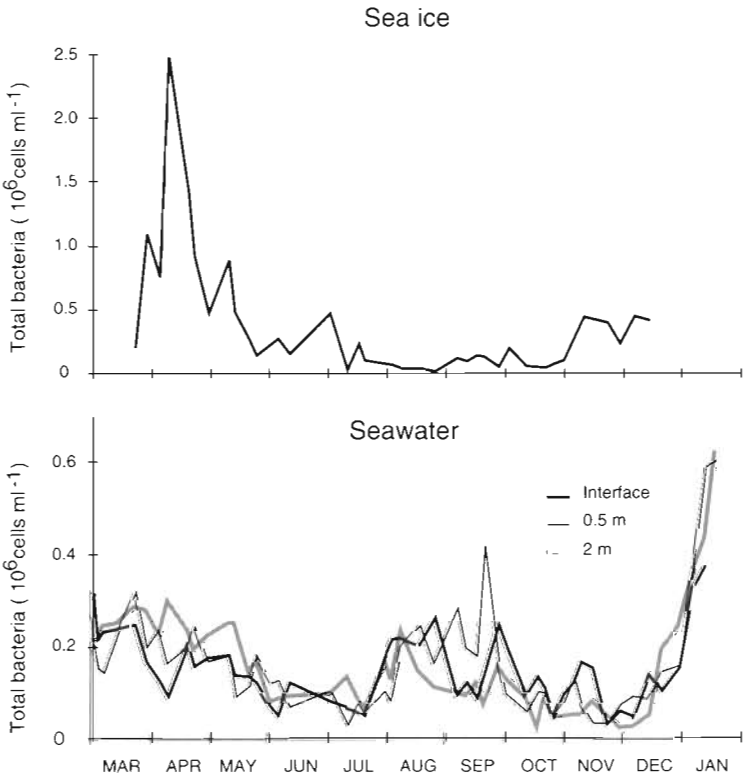

Fig. 7. Comparison of seasonal changes in total bacterial abundance at the ice bottom and the 3 depths of underlying seawater at Stn B

increase was recorded in spring and early summer. In seawater, the data collected for the 3 levels were very similar. A small period of increasing abundance was discernible in winter (August–September), although the most striking feature is the strong increase observed just after ice melting (January). Total bacteria ranged from less than 10^5 cells ml^{-1} in some December samples to more than 0.6×10^6 cells ml^{-1} in post-melt samples.

The mean bacterial cell volume (Fig. 8) showed the same trend in seasonal variations in both sea ice and underlying seawater. Values ranged from about 0.05 µm^3 in winter to more than 0.23 µm^3 in autumn and summer in both sea ice and underlying seawater.

Relationship between bacteria and phytoplankton biomasses

Phytoplanktonic carbon represented only a relatively small fraction of total POC (Fig. 9). The relative importance of phytoplankton decreased in winter: 3 sharp increases in the POC/phytoplankton C ratio were found in sea ice (in July, August and October), and a steady increase in these ratios was found in seawater (from April to October).

Comparison between bacterial biomass and chl *a* concentrations reveals significant correlations in both sea ice and underlying seawater ($r^2 = 0.60$, $p < 0.001$, and $r^2 = 0.49$, $p < 0.001$, respectively). Although the mean cell volume of bacteria (0.12 µm^3) was small relative to that of phytoplankton, the estimated bacterial biomass constituted a significant fraction of the total biomass. In sea ice, bacterial carbon accounted for 1% of total biomass in autumn and spring and for 10% in winter (i.e phytoplanktonic C/bacterial C close to 100 and 10, respectively; Fig. 10). In the underlying seawater, phytoplanktonic and bacterial biomass were of the same order of magnitude from April to July. The bacterial communities predominated from August to October while the algae were dominant in summer (November to early January).

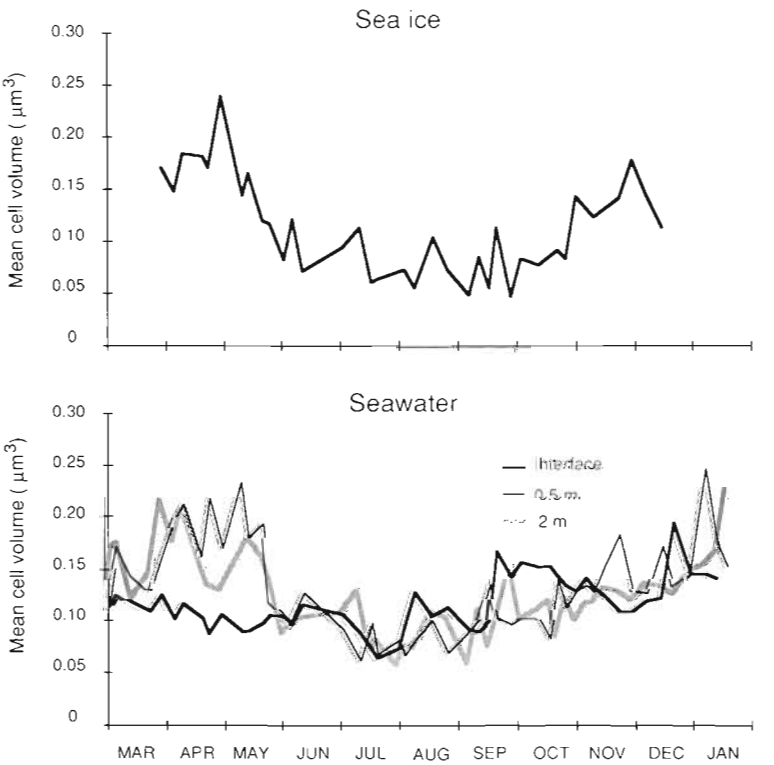

Fig. 8. Comparison of seasonal changes in mean bacterial cell volume at the ice bottom and the 3 depths of underlying seawater at Stn B

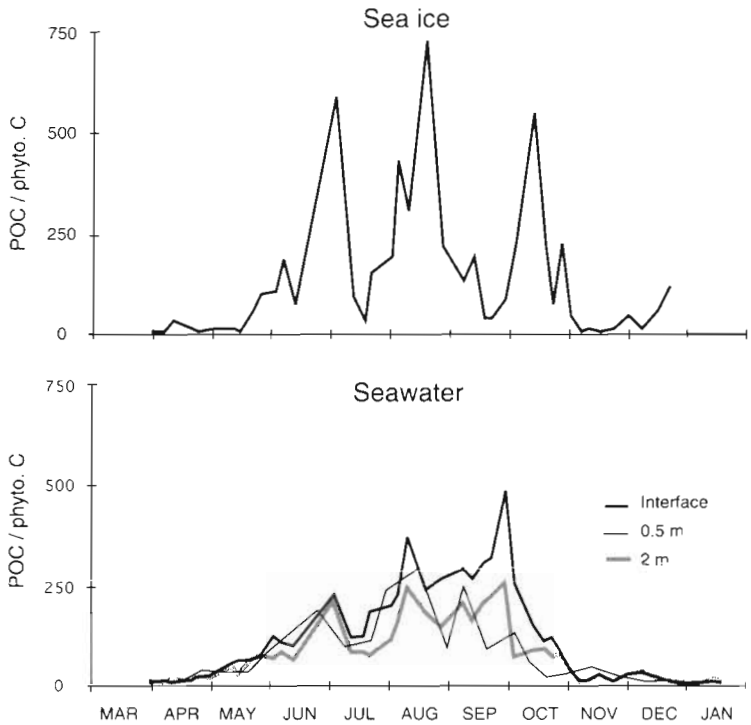

Fig. 9. Comparison of seasonal changes in the POC/phytoplanktonic C ratio recorded at the ice bottom and the 3 depths of underlying seawater at Stn B

DISCUSSION

POC and PON values observed in seawater were of the same order of magnitude as those reported by other authors in the Ross Sea (Smith & Nelson 1985, Fabiano et al. 1993) and in the Pacific sector of the Southern Ocean (Tanoue 1985). C/N ratios were low and corresponded to values observed in phytoplankton or bacterial cultures. They were similar to those measured in the Antarctic Peninsula region (Bodungen et al. 1986) and in the Weddell and Ross Seas (Nelson et al. 1989). In sea ice C/N ratios were markedly higher, indicating a preferential loss of nitrogen during organic matter decomposition processes, as have been previously reported to occur during particle sedimentation (Muller et al. 1986, Fabiano et al. 1993). The POC/phytoplankton C ratios recorded in winter seawater samples were more than 1 order of magnitude higher than the values reported for more offshore Antarctic samples (Bodungen et al. 1986, Nelson et al. 1989, Fabiano et al. 1993). Such high values of this ratio may be expected in environments characterized by nutrient deficiency (Parsons et al. 1977), low temperatures, low light (Smith & Nelson 1985) or self-shading (Smith & Sakshaug 1990), or they may be due to a detrital effect (Treguer et al. 1990). Undoubtedly all these factors operate simultaneously, although the detrital effect may be very important in the coastal area studied (Delille 1993).

The bottom-layer assemblages of the landfast ice in the study area were generally autotrophic. Chl *a* concentrations in ice-bottom assemblages reached levels considerably greater than those found in the underlying seawater. However, seasonal chl *a* maxima were relatively low when compared to some of the relevant published data. In platelet ice, the maximum chl *a* concentration is usually less than 200 mg m^{-3} (Bunt & Lee 1970, Grossi et al. 1987) but seasonal chl *a* maxima ranging from 600 to 2900 mg m^{-3} have been reported in the bottom layer of landfast ice (Palmisano & Sullivan 1983, Watanabe et al. 1990). In contrast, springtime chl *a* concentrations at the ice-water interface which were 1 order of magnitude higher than in bottom ice have been reported in the Arctic (Michel et al. 1993).

Bacterioplankton never constitute a major fraction of the sea ice microbial assemblage. As previously reported (Horner 1985, Grossi et al. 1987, Kottmeier et al. 1987, Garrison & Close 1993), algae appear to dominate the living biomass, suggesting that losses to consumers are low. However, drastic seasonal changes have been found to occur. Microalgae may be physically enriched within newly forming sea ice by the 'scavenging' effects

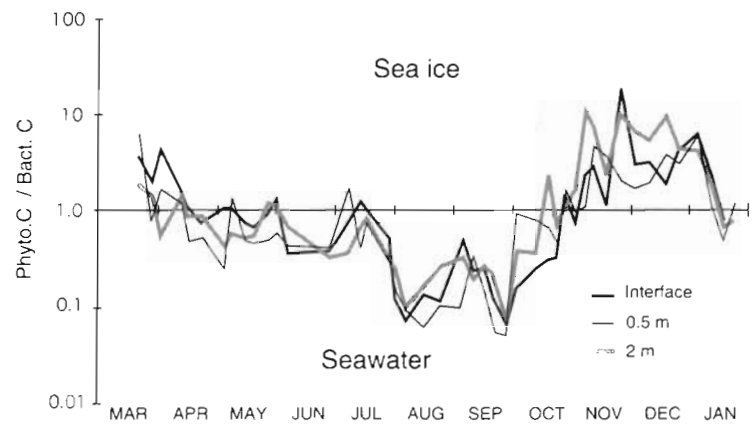

Fig. 10. Comparison of seasonal changes in the phytoplanktonic C/bacterial C ratio recorded at the ice bottom and the 3 depths of underlying seawater at Stn B

of frazil ice crystals (Garrison et al. 1983, 1989); additionally, enrichment of bacterial cells in new ice in conjunction with phytoplanktonic cells has been observed (Grossmann 1994, Grossmann & Dieckmann 1994). Such phenomena could explain the bacterial peak observed in the fall. The proportion of bacterial carbon in the total biomass increased from less than 1% in fall and summer to more than 10% in winter.

Bacterial cells in sea ice have been reported to be generally larger than those found in the underlying seawater (Delille 1992, Palmisano & Garrison 1993), which may be a reflection of generally higher organic nutrient concentrations in the ice environment (Marra et al. 1982, Sullivan 1985). This was not confirmed for the bottom-layer assemblages in landfast ice that we studied.

More striking features occurred in the underlying seawater. In winter, calculated ratios of bacterial to algal biomass suggested that bacteria constitute the majority of the microbial assemblage present beneath the ice cover. This observation is consistent with data obtained beneath the Ross Ice Shelf (Karl 1993). However, bacterial abundances observed in the seasonally ice-covered station we studied were more than 1 order of magnitude higher than those reported for the seawater located beneath the Ross Ice Shelf, a permanent floating shelf of glacial ice more than 400 m thick which completely prevents photosynthesis all year round (Holm-Hansen et al. 1978, Azam et al. 1979). In the summer situation, despite conditions such as reduced wind disturbance, high solar irradiance and high nutrient levels which could potentially support high phytoplankton growth, the studied coastal waters support relatively low levels of algal biomass. However, chl *a* values were similar to those reported for Antarctic oceanic waters, which typically fall in the range of 0.1 to 1.0 mg m^{-3} (Weber & El-Sayed 1987, Nelson et al. 1989). If the estimated levels of bacterial abundance and biomass are compared to the relevant published data (Hanson et al. 1983, Painting et al. 1985, Delille 1987, 1993, Kottmeier et al. 1987, Rivkin et al. 1989, Karl et al. 1991), it can be seen that these values were fairly low but similar to those in other parts of the Antarctic. The ratios between bacterial and algal biomass are consistent with some of the few field data that are available (Mullins & Priddle 1987, Fiala & Delille 1992) and are in agreement with the general assumption that bacterial microflora constitutes on average about 20% of the total microbial population (Cole et al. 1988). There were no obvious deficits in bacterial cell numbers comparable to those observed in several eutrophic regions of the southern oceans during phytoplanktonic bloom events (Prydz Bay, Lancelot et al. 1989; Weddell-Scotia Sea marginal ice zone, Cota et al. 1990; Southern Bransfield Strait, Karl et al. 1991). However, chl *a* values never reached concentrations of 2.5 µg l^{-1} or greater, as reported during these bloom events.

There is strong evidence for algal-bacterial coupling in sea-ice microbial communities. Grossi et al. (1984) found that numbers of bacteria increased with increasing abundance of algae during a spring bloom in McMurdo Sound, Kottmeier et al. (1987) found that bacterial production paralleled the rate of primary production and Priscu et al. (1990) found a significant correlation between dark CO_2 fixation and chl *a*. Thus, the positive correlation between algal and bacterial biomass observed in sea ice in this study is not surprising and confirms these previous observations. In contrast, the same correlation observed in seawater is more controversial. Although several examples of correlations between bacteria and phytoplankton have been reported (Fuhrman et al. 1980, Bird & Kalff 1984, Cole et al. 1988, Tobiesen 1991), such correlations may depend on the scale of the observations (McManus & Peterson 1988).

In summer, when light is available, the trophic system is classically autotrophic. The parallel increases observed for both bacterial and phytoplankton biomasses in sea ice during fall can be attributed to the harvesting mechanism associated with frazil ice formation (Garrison et al. 1983, 1989, Garrison & Close 1993). As light intensity decreases, the relative importance of bacterial communities increases. Heterotrophic organisms become dominant in winter when solar irradiation is no longer available. Simon et al. (1992) have shown that the ratio of bacterial carbon biomass to phytoplankton carbon biomass dramatically increases with decreasing phytoplankton abundance. As reported in some oligotrophic oceans (Fuhrman et al. 1989, Cho & Azam 1990), bacterial biomass in seawater exceeds that of phytoplankton during the polar night. Assuming that aquatic bacteria have a 50% carbon-based growth efficiency (Suttle et al. 1991), the Antarctic coastal heterotrophic microflora, which exhibit relatively short generation times (Delille et al. 1988, Rivkin et al. 1989), may require a large flux of organic matter. In summer this flux can originate from the primary producers, either directly via phytoplankton exudates or, more likely, indirectly through the action of zooplankton grazing. In winter the accumulated POC, especially in sea ice, will be sufficient to fuel the heterotrophic communities.

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