

44

ECOPHYSIOLOGY OF PHYTO- AND BACTERIOPLANKTON GROWTH
IN THE PRYDZ BAY AREA DURING THE AUSTRAL SUMMER 1987

Part II : Bacterioplankton activity

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KEYWORDS

Heterotrophic bacteria, growth rates, thymidine incorporation, Southern Ocean, Prydz Bay.

ABSTRACT

In order to assess the quantitative role of heterotrophic bacterial activity in the cycling of primary produced organic matter, measurements of bacterial biomass, growth and mortality rates were carried out in the Prydz Bay area in February - March 1987. These measurements, along with data from other authors collected in the same area allow to reconcile contradictory opinions published in the literature concerning the significance of the microbial loop in the Antarctic ecosystem in comparison with temperate marine systems:

(i) A similar significant part of primary production is utilized by planktonic heterotrophic bacteria.

(ii) A much longer delay in the response of bacteria to phytoplankton development exists in Antarctica.

These results are discussed in the light of the ecological structure of the Antarctic Ecosystem.

INTRODUCTION

In most marine ecosystems, a significant fraction of primary production is channelled into the pool of dissolved organic matter and utilized by planktonic bacteria instead of being grazed by herbivores (Pomeroy, 1974; Williams, 1981; Joiris et al, 1982; Azam *et al*, 1983). This microbial loop has not been intensively studied in the Antarctic seas and its role in the overall function of the ecosystem is still a matter of controversy. Although several authors (Hodson *et al*, 1981; Hanson *et al*, 1983) reported measurements of microbial activities in the Antarctic Ocean of the same order of magnitude as those observed in temperate areas, others (Kris *et al*, 1969;

Sorokin, 1971; Pomeroy and Deibel, 1986) claimed that a dramatic decrease of bacterial activity occurs at temperature below 2°C, leaving a larger part of primary production available for grazing by herbivores.

We developed a general methodology for measuring and understanding the control of bacterial activity in aquatic environments. Our approach is based on the direct measurement of some basic processes involved in bacterial dynamics (Billen and Fontigny, 1987; Billen *et al.*, 1988). Our purpose was to check the applicability of this approach to Antarctic waters and to try to resolve the present controversy regarding the role of bacterial activity in Antarctic waters.

METHODS

Measurements were carried out on board of the MV Nella Dan in the Prydz Bay area during voyage 7 of the Australian National Antarctic Research Expeditions, from 14th February to 23th March 1987.

Bacterial Biomass determination

Bacterial biomass was determined by epifluorescence microscopy after acridine orange staining according to the procedure of Hobbie *et al.* (1977). Biovolumes were visually estimated by comparison with a calibrated grid. Except in few instances of very high bacterial densities, where larger cells were observed, the bacterial volume was generally between 0.020 and 0.07 μm^3 . Biomass was calculated from biovolume, using a conversion factor of $1.2 \cdot 10^{-7} \mu\text{gC}/\mu\text{m}^3$ (Watson *et al.*, 1977).

Thymidine incorporation and bacterial growth rate measurements

Thymidine incorporation into cold TCA insoluble material was measured following the procedure of Fuhrman and Azam (1982). Thymidine incorporation rate was converted into bacterial production by using a conversion factor of $5 \cdot 10^3$ cells/nmol thymidine. This factor was determined for our own site by

following both cell number increase and thymidine incorporation in 0.2μ filter sterilized surface water reinoculated with 2μ filtered water and incubated at 2-4°C. Carbon production rate was calculated from cell production, taking into account the mean cell volume determined microscopically and the same biomass/biovolume ratio as used for biomass calculations.

Specific growth rates (μ) were determined as the ratio between bacterial production and biomass. Note that this ratio is independent on the conversion factor chosen for converting cell numbers into biomass.

Bacterial mortality

The rate of bacterial mortality was estimated according to a procedure modified from that developed by Servais *et al.* (1985). A sample was incubated for about 24 h. at *in situ* temperature with 25 nmole/l (methyl- H^3)-thymidine. It was then put for 10-20 h. in a dialysis bag in a flow of seawater, in order to eliminate the unincorporated thymidine. The disappearance of radioactivity from the DNA of the bacteria was then followed for about 50 h. A linear decrease was observed in semilog plot, the slope of which give the first order specific mortality coefficient (kd).

RESULTS and DISCUSSION

Bacterial biomass - chlorophyll a relationship.

Both vertical (Fig. 1) and geographical (Fig. 2) distributions of bacterial biomass observed in Prydz Bay in February-March 1987 suggest a close control by phytoplankton. Much higher biomasses exist above the pycnocline than below and the highest values in the upper layer are found in the areas characterized by a shallow mixed layer, which were shown above to be able of sustaining higher phytoplankton biomasses.

This correlation between bacterial and phytoplankton biomasses is classical in most temperate aquatic environments (Bird and Kalf, 1984). Several authors, however, did not found it back in the Southern Ocean. Thus, Mullins and Priddle (1987) observed only low bacterial biomasses, without any

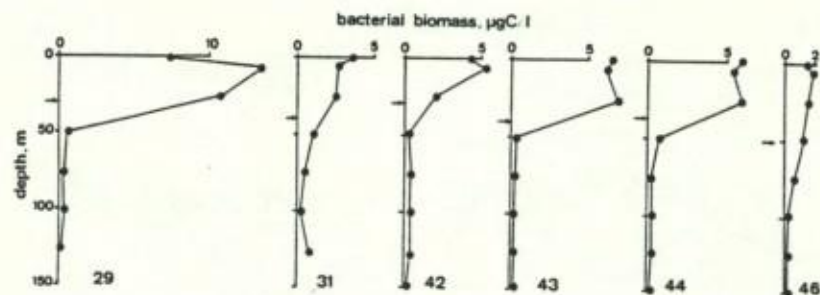


Figure 1. Vertical distribution of bacterial biomass observed in Prydz Bay in Febr.-March 1987. The arrow indicate the depth of the pycnocline.

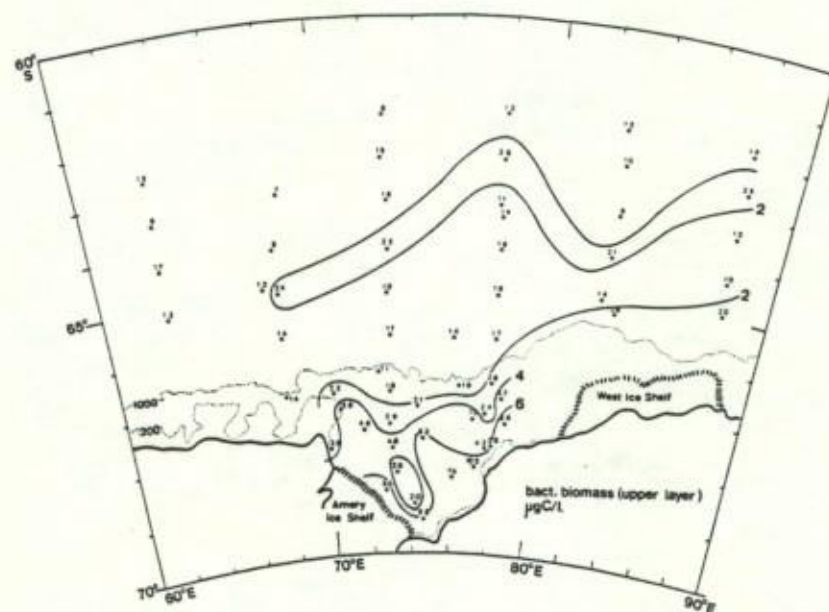


Figure 2. Geographical distribution of bacterial biomass observed in the upper mixed layer in Prydz Bay in February-March 1987.

relationship with phytoplankton in the Bransfield Strait in end-January. So did Davidson (1984) in mid-December off Prydz Bay. Similarly, the data collected in Prydz Bay by our Belgian colleagues on board of the Marion Dufresne in mid-January (Joiris *et al.*, this volume) do not show any significant relationship between the low bacterial biomass and the comparatively high chlorophyll *a* concentrations (Fig. 3). Our data in February, for their part, shows a clear relationship with chlorophyll *a*, with much higher bacterial biomass (Fig. 3). In March, phytoplankton biomasses are much lower, but bacteria remain at high concentrations, in good agreement with the data collected in beginning February by Painting *et al.* (1985) in the same area (Fig. 3).

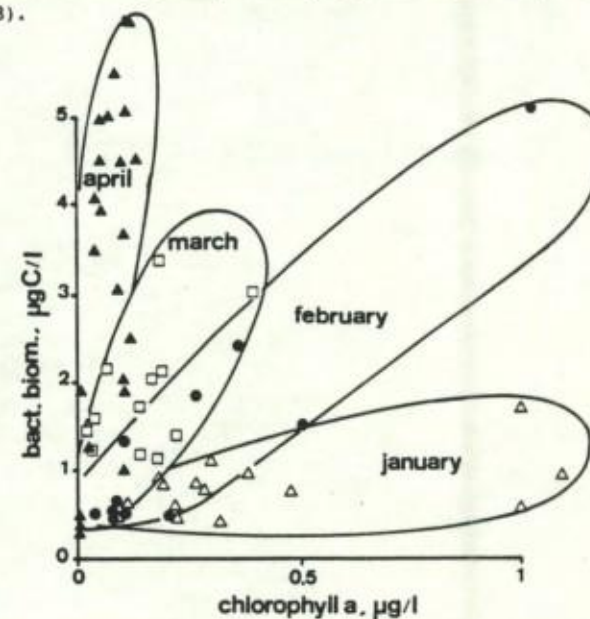


Figure 3. Relationship observed between bacterial biomass and chlorophyll *a* concentration in Prydz Bay at different times of the ice-free period. (Δ) January, Joiris *et al.*, this volume; ($\bullet$) February and ($\square$) March, own observations; ($\blacktriangle$) early April, Painting *et al.*, 1985.

Put together, all these apparently contradictory data are easily reconciled: they indicate the existence of a delayed relationship between

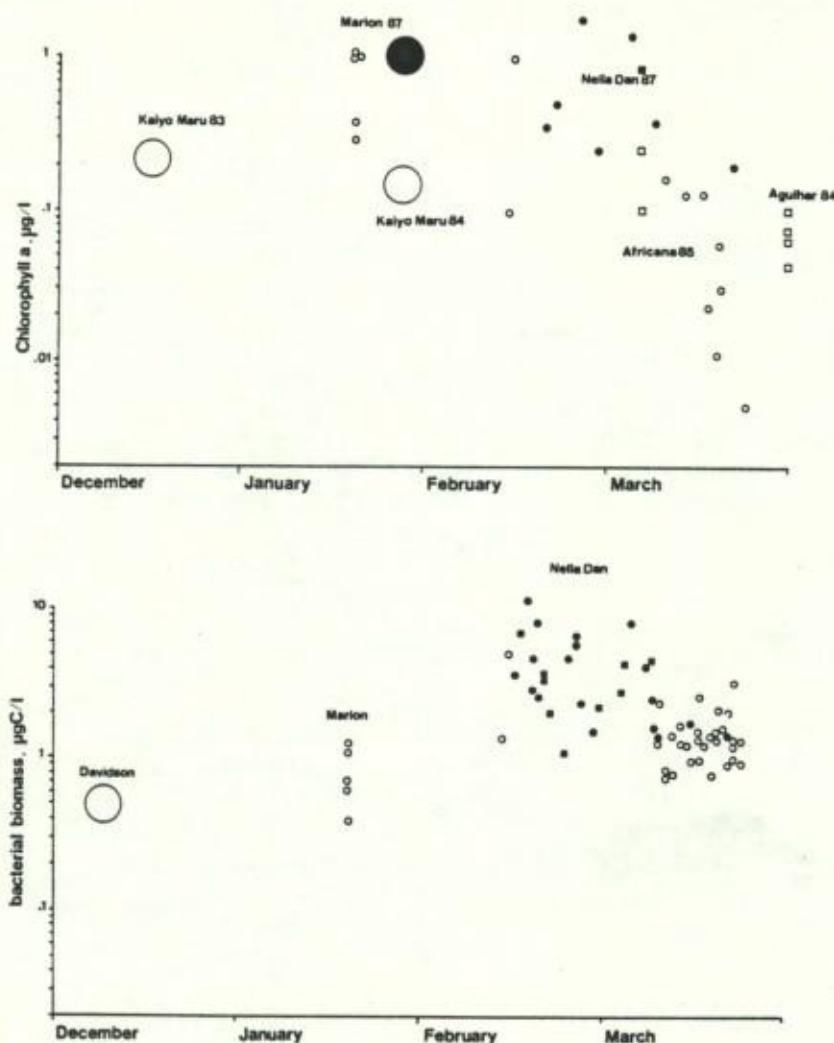


Figure 4. Seasonal variations of chlorophyll a and bacterial biomass in the inshore (closed symbols) and offshore (open symbols) zones of Prydz Bay. Data from our own observations and from Joiris *et al* (this volume), Hecq and Goffart (this volume), Davidson (1985), Fukui *et al* (1986), Painting *et al* (1985), Miller (1986).

phytoplankton and bacteria. Such a delay was already described in the North Sea (Billen & Fontigny, 1987; Billen *et al*, 1988), where the peak of bacterioplankton follows the phytoplankton spring bloom by about 10 days. The data summarized in figure 4 shows that the delay between phytoplanktonic and bacterial peak is of about 1 month in Antarctica, the former occurring in early February, the latter in early March.

2.2. Bacterial growth and mortality rates.

In order to further characterize the dynamics of bacterioplankton populations in Prydz Bay, measurements of the fluxes of production and mortality, which together govern the variations of bacterial biomass, have been carried out.

Bacterial production rates in the upper mixed layer are the highest in the Eastern inshore area ($.100 - .300 \mu\text{gC/l.h}$). In the offshore zone, they range between $.02 - .04 \mu\text{gC/l.h}$. A regular decrease is observed in all areas until the end of March, when production rates have dropped by nearly two orders of magnitude.

The ratio of production rate to bacterial biomass gives the specific growth rate (μ) (Fig. 5). The highest values observed in Antarctica are quite similar to those observed in temperate marine systems (see eg Billen *et al*, 1988), in spite of the low temperatures. They decrease regularly from mid-February to end-March.

Mortality rates, on the other hand, seem much more constant during this period, as also shown in Fig. 5. These values are significantly lower than the specific mortality rate constants found in temperate marine systems (Billen *et al*, 1988), indicating a slower turnover rate of bacterial biomass in the Southern Ocean.

Growth rates are clearly higher than mortality in February, corroborating our conclusion that the bacterial population is actively growing at that time. End-March, specific growth rates are very close to, or lower than mortality rates, indicating a declining bacterial population.

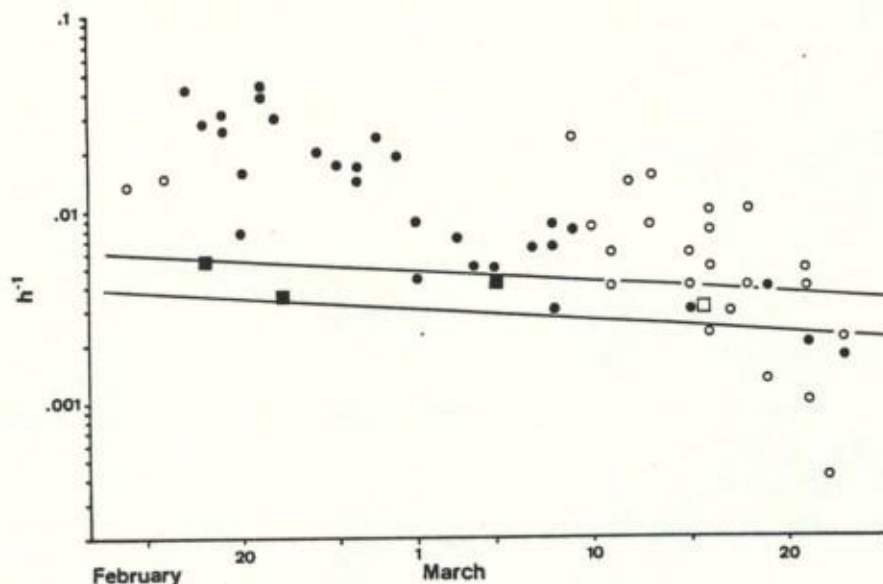


Figure 5. Specific bacterial growth (circles) and mortality rates (squares) observed in the inshore (closed symbols) and offshore (open symbols) zone of Prydz Bay in February-March 1987.

2.3. Quantitative importance of the bacterial loop in organic matter cycling.

Our biomass and production measurements in Prydz Bay, along with those recorded in the literature for the same area, allow a first estimate of the budget of organic matter at the first trophic levels during the ice-free period (i.e. from January to end-March for the inshore area and from December to mid-April for the offshore zone). The figures and hypothesis leading to these estimations are presented in Table I. Except for values in brackets, which are best guess estimates, the figures of bacterial biomass and specific growth rates mentioned in this table are the rounded means of the observations made by ourselves or by other authors and discussed in this paper. Bacterial production figures were then calculated from these data.

Table I. : Tentative budget of organic matter cycling in Prydz Bay during the ice free period.

mixed layer	Eastern Inshore area 30m			Offshore area 50m		
	bact.biom. ($\mu\text{gC/l}$)	μ (h^{-1})	bact.prod. ($\text{mgC/m}^2.\text{d}$)	bact.biom. ($\mu\text{gC/l}$)	μ (h^{-1})	bact.prod. ($\text{mgC/m}^2.\text{d}$)
DEC	-	-	-	.5	(.01)	(6)
JAN	(.5)	(.035)	13	.8	(.02)	19
FEB	4	.03	85	2.5	.014	42
MAR	2	.008	12	1.5	.006	10
APR	-	-	-	1.5	.006	10
bact.prod. ($\text{gC/m}^2.\text{period}$)			3.3	2.5		

In the absence of nutrient limitation, a growth yield of .3 is a reasonable estimate for heterotrophic bacteria (Lancelot & Billen, 1986; Servais *et al.*, 1987). Based on this, the total flux of primary produced organic matter flowing through the bacterial compartment can be estimated to 11 and 8 $\text{gC/m}^2.\text{period}$ for the inshore and the offshore zones respectively. At the present time, we have no estimation of primary production in Prydz Bay for the same periods. From literature data (Treguer and Jacques, 1986; El Sayed, 1984) a reasonable range of 20-60 and 10-20 $\text{gC/m}^2.\text{period}$ can be assumed for the two zones respectively. This would imply that about 20-55% and 40-80% of the organic matter made available by phytoplankton growth is used by microheterotrophs in the inshore and offshore areas respectively.

Thus, the overall importance of the microbial loop does not differ a lot in the Southern Ocean from what has been observed in temperate marine systems, in good agreement with the previous conclusions of Hodson *et al.* (1981) and Hanson *et al.* (1983). However, a much longer delay in the response of bacteria to phytoplankton development has been evidenced by our observations. This long delay could explain the conclusion reached by other authors that bacteria do not play a significant role in the utilization of primary produced organic matter in Antarctic waters, based on observations made mostly at the early stage of the vegetation season.

CONCLUSIONS

Our study of the first trophic levels of the Antarctic ecosystem allow to derive some general conclusions concerning its overall functioning in connection to the apparent paradox of the abundance of higher organisms in the Southern Ocean.

We confirmed that this apparent richness is not caused by an exceptionally high primary production. During summer, when light intensity, photoperiod and nutrient concentrations are at high levels, primary production is mostly controlled by the vertical mixing of the water column. This results in low phytoplanktonic biomass and production in most open sea areas, while very high biomass and production values can be locally and temporarily reached in areas where the water column is stabilized.

Similarly, the "richness" of the Southern Ocean is not to be explained -as suggested by some authors (Pomeroy and Deibel, 1986)- by a generally low activity of heterotrophic microorganisms, leaving most of the primary production available to grazers. The microbial loop quantitatively plays the same role in the Antarctic marine ecosystem as in temperate environments.

The high biomasses of organisms belonging to the Krill-vertebrates food chain is therefore not the result of a particularly high availability of vegetal organic matter. It rather results from two adaptations of higher organisms in Antarctica.

Firstly, their ability to efficiently use, at a large geographical scale, resources of local and temporary nature. Most of the higher organisms, from krill to whale, are indeed characterized by a very high mobility.

Secondly, their ecophysiological K-strategy, in which most resources are devoted to reserve accumulation, aimed to ensure a minimal maintenance during long starvation periods, while reproduction is kept to a very low rate.

These characteristics result in an extreme fragility of the Antarctic ecosystem. Its richness is only apparent: the large stocks, being only slowly replaced, cannot necessarily sustain intensive exploitation.

ACKNOWLEDGEMENTS

The preceding text present results of the Belgian Program "Scientific research on the Antarctic" (Services of the Prime Minister - Science Policy office). The scientific responsibility is assumed by its authors. We are greatly indebted to the Australian Antarctic Division for the kind invitation to take part to the MV Nella Dan Voyage 7 of the 1986-1987 Australian National Antarctic Research Expeditions to Prydz Bay. Collaboration on board with Dr. S. Wright and D. Thomas was greatly appreciated. G. Billen is Research Associate of the FNRS (Fonds National de la Recherche Scientifique).

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