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SEASONAL PRODUCTION AND BACTERIAL UTILIZATION OF DOC IN THE ROSS SEA, ANTARCTICA

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Heterotrophic picoplankton, including *Bacteria* and *Archaea,* form a major, often dominant component of the euphotic zone biomass throughout much of the world ocean. In Antarctic waters however, the bacterial biomass is a much smaller fraction of the total plankton stock, at least during the Austral summer. In the Ross Sea during the 1996–1997 growing season, bacterial abundance reached a peak of 2-3 x 10^9 cells liter^{-1}, comparable to peak levels in the fertile regions of the world ocean, but bacterial biomass was a paltry 5% of the phytoplankton stock. Bacterial production ranged from <1 to 22% of the daily primary production, averaging 6% during October–April. Bacterial abundance and production were significantly correlated with the accumulation of semilabile dissolved organic carbon (DOC) over the growing season, indicating the importance of this carbon pool as a source of bacterial nutrition. Bacterial production increased prior to any increase in temperature. The semilabile DOC is entirely consumed by the end of the growing season. A microbial carbon budget based on these observations suggests that ca. 30% of the total annual primary production is metabolized by bacteria. Bacterioplankton biomass accumulation and production rates are regulated by the amount of labile dissolved organic carbon produced on seasonal timescales in the upper 150 m of the Ross Sea. This relationship argues for the predominance of bottom-up control of bacterial standing stocks in these waters, possibly in contrast to other Antarctic coastal regions.

INTRODUCTION

Heterotrophic bacterioplankton metabolize daily a mass of carbon equivalent to about half of the co-occurring primary production [*Cole et al.*, 1988; *Ducklow and Carlson*, 1992]. Intensive bacterial activity results in levels of bacterial biomass roughly equal to phytoplankton and zooplankton biomass in most of the temperate and tropical world oceans and the Arctic Ocean (Table 1). The extensive marginal ice zones of Antarctic coastal seas present an interesting exception to this general pattern, however. The seasonal retreat of the sea ice triggers massive phytoplankton blooms in the Ross and Weddell Seas and along the Antarctic Peninsula [*Smith and Nelson*, 1985; *Moline and Prezelin*, 1996; *Smith and Gordon*, 1997; *Smith et al.*, 1998a; *Smith et al.*, 2000b]. The *Phaeocystis antarctica* bloom in the Ross Sea may represent the largest and most extensive accumulation of open water plankton biomass on the planet [*Arrigo and McClain*, 1994]. Yet in spite of these spectacular accumulations of organic matter, bacterioplankton form a small fraction of the total biomass during ice edge blooms (Table 1), presenting a paradox: if bacterial growth is generally controlled by resource supply (i.e., by *bottom-up* forces, *sensu* [*Billen et al.*, 1990; *Ducklow*, 1992; *Church and Ducklow*, 2000]), what limits their growth in the presence of the largest plankton blooms on the planet?

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TABLE 1. Bacterioplankton abundance (10^9 cells L^{-1}) in the euphotic zone of selected ocean sites, and the mean ratio of bacterial to phytoplankton biomass.

Region	Peak Abund.	Proportion of Phyto. Biomass	Reference
		Global Open Oceans	
North Atlantic	3.1	0.2	[*Ducklow*, 1999]
Sargasso Sea	1.1	2.7	"
North Pacific Gyre	1.3	3.6	"
Subarctic North Pacific	3.4	0.9	"
Arabian Sea	2.9	1.2	"
Equatorial Pacific	1.1	0.8	"
		Arctic	
Arctic Ocean	1.0	0.1–> 1	[*Rich et al.*, 1998]
Chukchi Sea, AK	0.9	0.02–0.3	[*Yager et al.*, 2001]
		Antarctica	
Antarctic Polar Front Zone	0.7	0.2	(unpublished data)
Ross Sea	3	0.05	This paper
Gerlache Strait	0.8	0.02	[*Bird and Karl*, 1999]
Prydz Bay, E. Antarctica	0.8	0.07	[*Leakey et al.*, 1996]
Weddell Sea	0.8	0.12	[*Cota et al.*, 1990]
McMurdo Sound	0.3	<0.10	[*Rivkin*, 1991]

The inhibition of bacterioplankton growth in high latitude seas has been attributed to temperature limitation alone [*Sorokin*, 1971], low temperature—organic matter co-limitation [*Wiebe et al.*, 1992; *Pomeroy and Wiebe*, 2001], organic matter limitation arising from unique foodweb structure [*Carlson et al.*, 1998], iron limitation [*Pakulski et al.*, 1996] or intense grazing by nanoflagellate bacteriovores [*Bird and Karl*, 1999]. In this chapter I present additional evidence supporting the hypothesis that bacterial biomass accumulation and production are limited by dissolved organic carbon availability, even during massive phytoplankton blooms. I also construct a carbon budget for microbial utilization of labile and semilabile dissolved organic carbon (see Carlson and Hansell, this volume) during the growing season (October–April) in the Ross Sea.

Our group participated on four process study cruises in the central Ross Sea over the seasonal cycle (P1, 17 Oct.–06 Nov., 1996; P2, 12 Jan.–09 Feb., P3, 12 Apr.–02 May and P4, 12 Nov.–12 Dec., 1997) in the US JGOFS Antarctic Environment and Southern Ocean Process Study (AESOPS; [*Smith et al.*, 2000a]) to examine the temporal evolution of the bacterial response to the *Phaeocystis* bloom, and the physical and biological controls acting to limit bacterial accumulation. Cruises P1–P3 represent a time series of observations within a single growing season. Our data sets are also supplemented by extensive data collected during 14 Nov.–06 Dec. 1994 and 19 Dec. 1995–12 Jan. 1996 in the same region [*Carlson et al.*, 1998; *Ducklow et al.*, 2001]. The P4, 1994 and 1995–96 data add information on interannual variability, and to the extent that trends and relationships are comparable between years, help to construct an annual composite for the full growing season. Measurements of bacterial abundance, biomass, ^{3}H-thymidine and ^{3}H-leucine incorporation (indices of bacterial productivity), dissolved organic carbon (DOC), and hydrographic properties followed standard protocols [*Knap et al.*, 1994]. Most properties were measured throughout the full water column, 300–700 m depth, on repeated oceanographic transects along latitude 76.5° South, from near the Victoria Land coast to 175° East longitude. Here I use a data set of simultaneous measurements of temperature, DOC, chlorophyll *a* and the bacterial abundance and rates that were merged after acquisition from the US JGOFS database (http://usjgofs.whoi.edu/jg/dir/jgofs/southern/). Primary production and other fluxes were obtained from the same source, but are not necessarily synoptic with the bacterial data.

SEASONAL EVOLUTION AND RELATIONSHIP AMONG BACTERIA, DOC AND PHYTOPLANKTON STOCKS

In spite of persistently cold temperatures reaching an annual maximum of about 1.5°C in January–February, bacterial abundance in surface waters of the Ross Sea

reached ~ 3 x 10^9 cells L^{-1}, similar to, or greater than in coastal and oceanic waters at lower latitudes and elsewhere in Antarctica (Table 1; Figure 1a). However, phytoplankton stocks reached much greater levels than seen elsewhere [*Smith et al.*, 2000b], and the relative amount of bacterial biomass seldom exceeded about 5% of the phytoplankton stocks [*Ducklow et al.*, 2000; *Ducklow et al.*, 2001]. Similarly, in spite of huge accumulations of plankton biomass, relatively small amounts of the primary production accumulated in the DOC pool [*Carlson et al.*, 1998]. DOC accumulation above background wintertime concentrations persisting in deep water (40–42 μMol C L^{-1}) is defined as ΔDOC and peaked at about 25 μMol C L^{-1} in 1996–97, but the January–February mean was only 11.7 ± 5.0 μMol C L^{-1} (upper 50 m, n = 20 stations, range 1–24 μMol C L^{-1}; [*Carlson et al.*, 2000]). DOC accumulates to 20–30 μMol C L^{-1} or more above background in other ocean regions where the primary production is lower than in the Ross Sea [*Carlson et al.*, 1998]. The comparison is not straightforward, however, due to varying turnover times of the semilabile DOC in different regions. In the Ross Sea, ΔDOC accumulates and is consumed within a single growing season, whereas some portion of it persists for several years in subtropical and tropical seas [*Carlson et al.*, 2000; *Carlson*, 2001]. Both ΔDOC and bacterial abundance were well correlated with temperature over the full growing season (Figures 1bc). Here I interpret the positive relationship with temperature as a reflection of the enrichment of the upper water column with the products of primary production (biomass, detritus and DOM) as the growing season proceeds, rather than as evidence for a direct effect of temperature on microbial processes [*Ducklow et al.*, 1999]. Bacterial abundance was also correlated with ΔDOC, suggesting a dependence of bacterial growth on this pool of semilabile carbon over the seasonal time scale (Figure 1d). To look more closely at the relationship between bacterial stocks and ΔDOC accumulation and removal, I separated the growing season and the course of the bloom into two phases (Figure 2). I defined the seasonal progression of bacteria and DOC in the context of the annual cycle of primary production and phytoplankton biomass accumulation [*Smith et al.*, 2000b] to include a pre-bloom, early-bloom phase including the P1 and P4 cruises (Oct. 1996 and Nov.–Dec. 1997), and a peak to post-bloom period, encompassing the P2 and P3 cruises (Jan.–April, 1997). Note again that cruises P1–P3 define a single growing season, while the P4 cruise was in the following year. Semilabile DOC accumulated during the early phase, then reached a peak and declined in the later phase. A simple relationship of bacterial accumulation with ΔDOC is complicated by covariance with temperature and Chlorophyll a. These relationships are examined below.

The Pre-bloom and Early Bloom Period

Relationships between bacteria, ΔDOC and chlorophyll *a* during specific time periods (cruises) are shown in Figures 3–5. Bacterial stocks in the surface layer (upper 50 m) were correlated with the ΔDOC concentration (Figure 1d) as well as with Chl a (data not shown) from the early spring, pre-bloom condition until after the peak of the annual bloom, between October, 1996 and February, 1997, but the relationships varied among individual cruises. In the October pre-bloom period, bacterial abundance, Chl a and ΔDOC were all low and uniform (Figures 3ac), until after the bloom began in mid-November (Figure 3bd). Note that during this period, ΔDOC had accumulated only to about 5 μM, about 20% of its peak accumulation in the

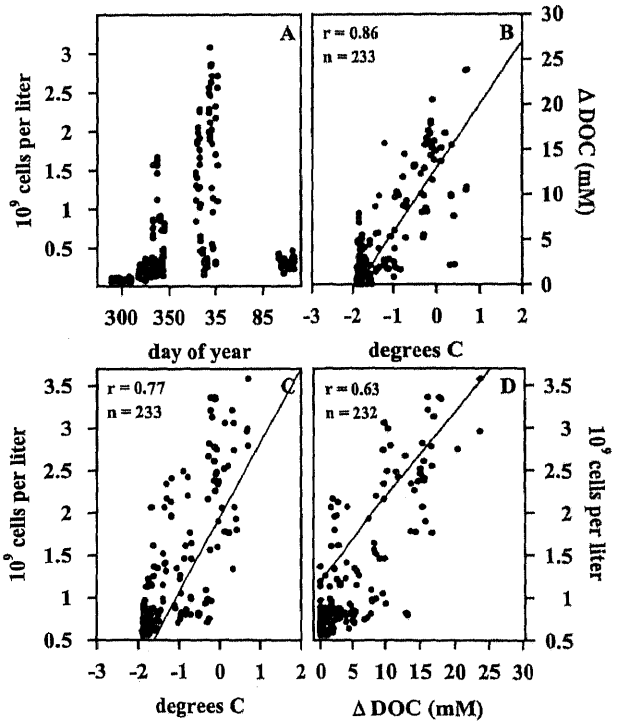

Fig. 1. A: Time course of bacteria abundance in the central Ross Sea, October, 1996–April, 1997 and November–December, 1997. B-D: Relationships in the upper 50 m of the central Ross Sea: B: between accumulated semilabile dissolved organic carbon (ΔDOC) and temperature; C: bacterial abundance and temperature; D: abundance and ΔDOC. The lines are Model II regression fits.

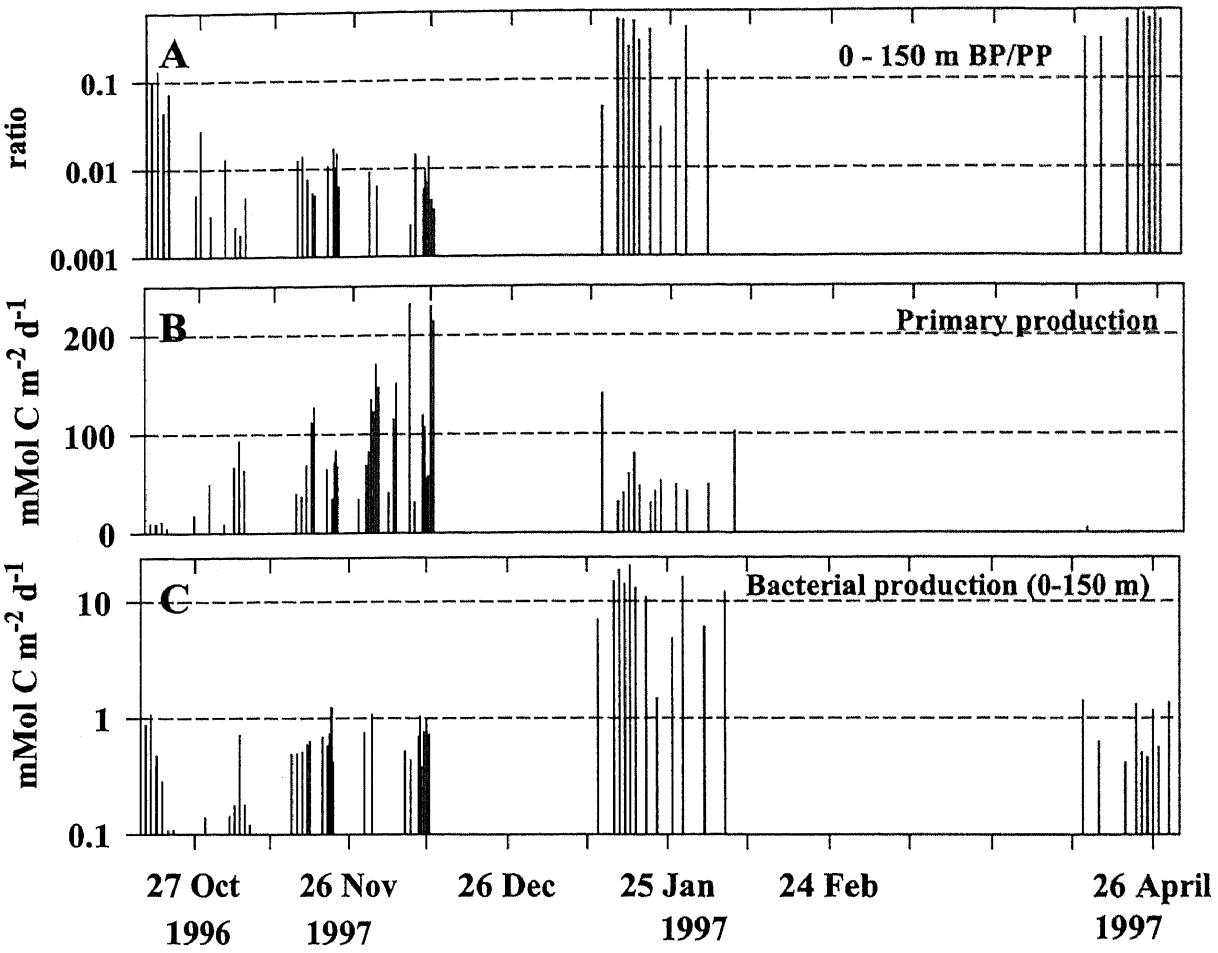

Fig. 2. Annual cycles of: A) the ratio of bacterial to primary production (BP:PP); B) primary and C) bacterial production in the Ross Sea, 1996–1997. The October, January and April data are from one continuous growing season; the November, 1997 data are from the next year.

later period (cf. Figure 1bd), Chl a remained low, and bacteria had also not yet reached their annual maximum. In contrast, during the early bloom period in 1994, Chl *a* reached 9–10 μg L^{-1} while bacterial abundance was slightly lower than in 1997 (data not shown; [*Ducklow et al.*, 2001]). ΔDOC reflected the greater Chl *a* levels, or the more advanced state of the bloom in 1994, reaching 10–15 μM [*Carlson et al.*, 1998; *Carlson et al.*, 2000].

In spite of substantial interannual variability [*Smith et al.*, 2000b; *Ducklow et al.*, 2001], one can characterize the November–December period as the period when phytoplankton grow rapidly (0.5–1 d^{-1}) and reach near-peak productivity at seasonally maximum irradiance levels [*Smith et al.*, 2000b]. As observed by several investigators, the bacterial response lags the phytoplankton bloom by a few weeks or more, reaching maximum levels later in the growing season [*Billen and Becquevort*, 1991; *Lochte et al.*, 1997; *Bird and Karl*, 1999; *Ducklow et al.*, 2001]. Thus leucine incorporation rates remained relatively low, and were not correlated with Chl *a* or ΔDOC in November–December, 1997 (Figure 5ac) when primary production was maximal [*Smith et al.*, 2000b]. Leucine incorporation was correlated with Chl *a* during the early-midbloom period in 1994, possibly reflecting the more advanced stage of the bloom that year [*Ducklow et al.*, 2001].

Late Bloom and Post-bloom Periods

The *Phaeocystis* bloom in the Ross Sea begins early (November) and peaks in Jan.–Feb [*Smith et al.*, 2000b]. Chl *a* concentrations in the upper 50 m were slightly

greater in January and early February, 1997, days 14–37, during the continuation of the 1996–97 growing season (Figure 4a). Bacterial abundance and ΔDOC levels reached their annual maxima, after the peak of the phytoplankton bloom [*Ducklow et al.*, 2001]. Leucine incorporation was correlated with both Chl and ΔDOC in January–February (Figure 5b).

By April, 1997, the phytoplankton bloom had dissipated (Figure 4b and *Smith et al.*, 2000b), and the ΔDOC concentration in the surface layer had returned to 0–5 μM (Figure 4d), slightly greater than the background level [*Carlson et al.*, 2000]. Bacterial abundance was still moderately high (5 x 10^8 cells L^{-1}; Figure 4bd). Bacterial production however, was barely measurable, as was primary production (Figure 2; [*Smith et al.*, 2000b; *Ducklow et al.*, 2001]). Thus by the end of the growing season in April, the ΔDOC was almost entirely consumed by bacterial metabolism, in contrast to lower latitudes, where some fraction of the ΔDOC is more resistant and survives for one or more years [*Carlson et al.*, 2000; *Carlson*, 2001].

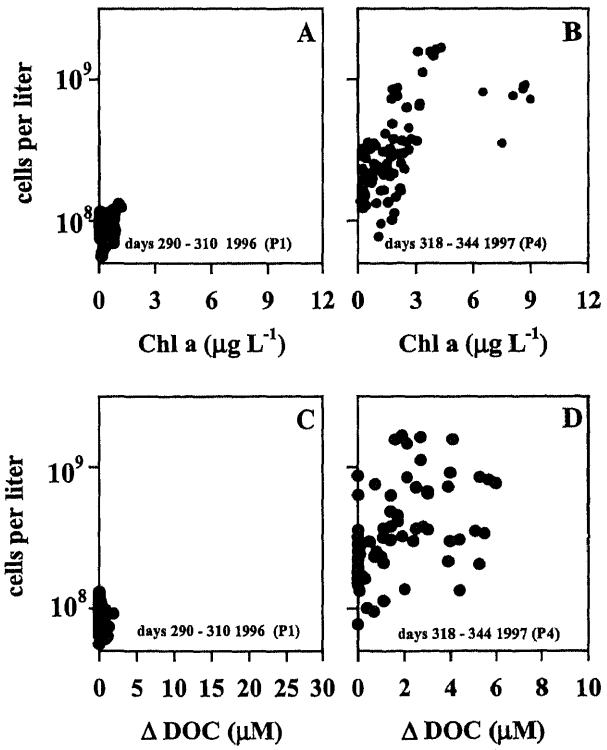

Fig. 3. Relationships between bacterial abundance and Chlorophyll *a* in A: October–November, 1996; B: November–December, 1997; and between bacterial abundance and ΔDOC in C: October–November, 1996 and D: November–December, 1997.

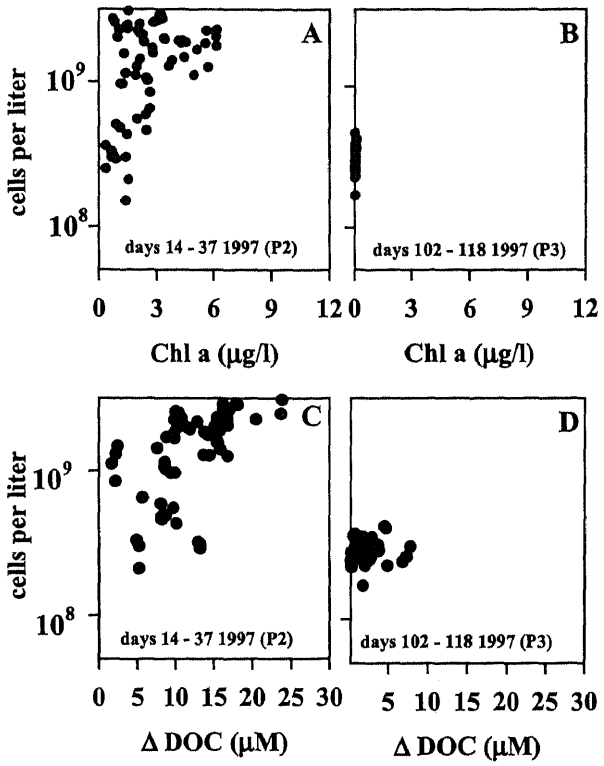

Fig. 4. Relationships between bacterial abundance and Chlorophyll *a* in A: January–February, 1997; B: April, 1997; and between bacterial abundance and ΔDOC in C: January–February, 1997, and D: April, 1997.

Interpretation of Trends and Relationships Among Plankton Variables

During the two principal phases of the *Phaeocystis* bloom in the Ross Sea, different relationships between bacterial abundance or activity and Chl *a* and ΔDOC were observed. There were no statistically significant relationships during the very earliest and latest stages (Figures 3ac, 4bd), but there were significant relationships expressed during the October–December (P1–P4) and January–April (P2–P3) periods. To assess the combined effects of several factors on the bacterial accumulation I used the linear multiple correlation model:

$$Y\ (\text{abundance}) = a + b_1X_1(\text{temperature}) + b_2X_2\ (\Delta\text{DOC}) + b_3X_3\ (\text{Chl}) \quad (1)$$

where ***a*** is the intercept and the ***b***'s are the partial regression coefficients [*Sokal and Rohlf*, 1981]. The equations for cruises P1,2,3 and for cruises P1 through P4 are very similar (Table 2), suggesting that the P4

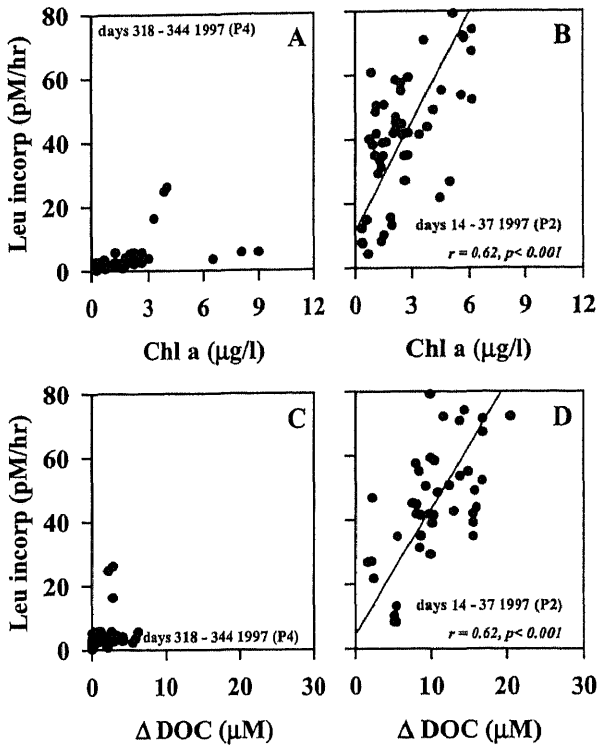

Fig. 5. Relationships between bacterial leucine incorporation rate and Chlorophyll *a* in A: November–December, 1997; B: January–February, 1997; and between leucine incorporation rate and ΔDOC in C: November–December, 1997, and D: January–February, 1997.

(Nov.–Dec. 1997) cruise period can be included in the 1996–97 growing season for purposes of analyzing a full temporal succession. In both P2 and P4, temperature (and/or unspecified factors covarying with it) had the strongest influence on bacterial stocks, as indicated by the relative sizes of the partial regression coefficients ($X_{1,2,3}$ in Table 2). However these relationships differed during the two phases of the growing season (Table 3). Only Chl a was significantly correlated with bacterial abundance during the early bloom period (Oct.–Dec.; P1, P4 cruises, Table 3a). Lack of correlation with ΔDOC suggests that bacteria depended mostly on the recent products of photosynthesis in the early period. In the later, peak to post-bloom period (Jan.–April; P2, P3 cruises), bacterial abundance was significantly related to all three factors (Table 3b). This multiple relationship suggests that bacterial growth was dependent on accumulated DOC as well as the recent products of photosynthesis and foodweb interactions (see below). The dependence of changes in abundance was assessed by computing first- and second-order partial correlation coefficients (Table 4). Besides the relationship between abundance and temperature with Chl held constant (r12.4), the strongest relationships are those between abundance and ΔDOC, with temperature (r13.2) or temperature and Chl (r13.24) held constant, suggesting a dependence of bacterial growth on ΔDOC over the full growing season.

During mid to late Austral spring, (Nov.–Dec. 1997, P4 cruise), ΔDOC changed little, but bacterial biomass

TABLE 2. Multiple regression results for bacterial abundance, temperature, ΔDOC and Chl over the full 1996–1997 growing season. Cruise P4 (Nov.–Dec., 1997) is included in the analysis to add this period to the analysis of the 1996–97 growing season.

Table 2A. P1–P4 Regression Statistics

Multiple R	0.871				
R Square	0.758				
Adjusted R Square	0.754				
Standard Error	3.714				
Observations	205				
Analysis of Variance	df	Sum of Squares	Mean Square	F	Significance F
Regression	3	8688.36	2896.12	209.95	1.14E-61
Residual	201	2772.70	13.79		
Total	204	11461.06			
	Coefficients	Standard Error	t Statistic	P-value	
Intercept	5.73	1.30	4.42	0.000	
x1 temperature	2.57	0.67	3.82	0.000	
x2 DDOC	0.68	0.09	7.96	1.16E-13	
x3 Chl	0.87	0.17	5.10	7.62E-07	

TABLE 3. Multiple regression results for bacterial abundance, temperature, ΔDOC and Chl over the full 1996–1997 growing season. Cruise P4 (Nov.–Dec., 1997) is included in the analysis (Table 2A) to add this period to the analysis of the 1996–97 growing season, and removed from the analysis in Table 2B.

Table 3A. P1, -P4 Early bloom Regression Statistics

Multiple R	0.712				
R Square	0.507				
Adjusted R Square	0.494				
Standard Error	2.526				
Observations	112				
Analysis of Variance	df	Sum of Squares	Mean Square	F	Significance F
Regression	3	711.11	237.039	37.13	0.00000
Residual	108	689.37	6.383		
Total	111	1400.49			
	Coefficients	Standard Error	t Statistic	P-value	
Intercept	4.832	2.711	1.782	0.077	
x1temperature	1.983	1.451	1.366	0.174	
x2ΔDOC	0.371	0.230	1.607	0.110	
x3Chl	0.967	0.216	4.477	0.00002	

Table 3B. P2, P3 Late Bloom =10-Statistics

Multiple R	0.844				
R Square	0.712				
Adjusted R Square	0.702				
Standard Error	4.800				
Observations	93				
Analysis of Variance	df	Sum of Squares	Mean Square	F	Significance F
Regression	3	5082.95	1694.31	73.52	0.00000
Residual	89	2050.96	23.04		
Total	92	7133.91			
	Coefficients	Standard Error	t Statistic	P-value	
Intercept	5.319	1.873	2.839	0.005	
X1 temperature	2.383	0.949	2.509	0.013	
X2 ΔDOC	0.661	0.130	5.073	0.000	
X3 Chl	1.125	0.381	2.953	0.004	

reached near-peak levels (Fig. 3d) and the small increase in ΔDOC was associated with a relatively large change in abundance. Bacteria appeared to be more sensitive to changes in Chl *a* than ΔDOC in the spring (Table 3a). I suggest this is because they were sustained primarily on freshly produced, more labile DOC compounds in the early spring, then switched to utilization of the semilabile, bulk DOC pool later, in the Austral summer. Thus bacteria depended primarily on freshly—produced DOC when primary production was highest, and on accumulated, semilabile DOC later in the season, when the bloom was in decline. During October, there was no ΔDOC and bacteria must have been sustained primarily on fluxes of more labile DOC, which were probably low because PP was so low (Figure 2). In the period between February and April, ΔDOC declined from 25 to nearly 0 μM, suggesting bacterial reliance the semilabile DOC in the postbloom period.

The oceanic bulk DOC pool can be separated functionally into three biologically-distinct components: labile compounds, with turnover times of hours-days, semilabile material, turning over on seasonal to interannual scales, and a highly refractory pool, with a lifetime on the order of the oceanic circulation (millennia) [*Carlson*, 2001; *Kirchman et al.*, 2001]. Labile compounds are released by phytoplankton and during trophic interactions subsequent to phytoplankton ingestion by grazers, or mortality and appear to support the majority

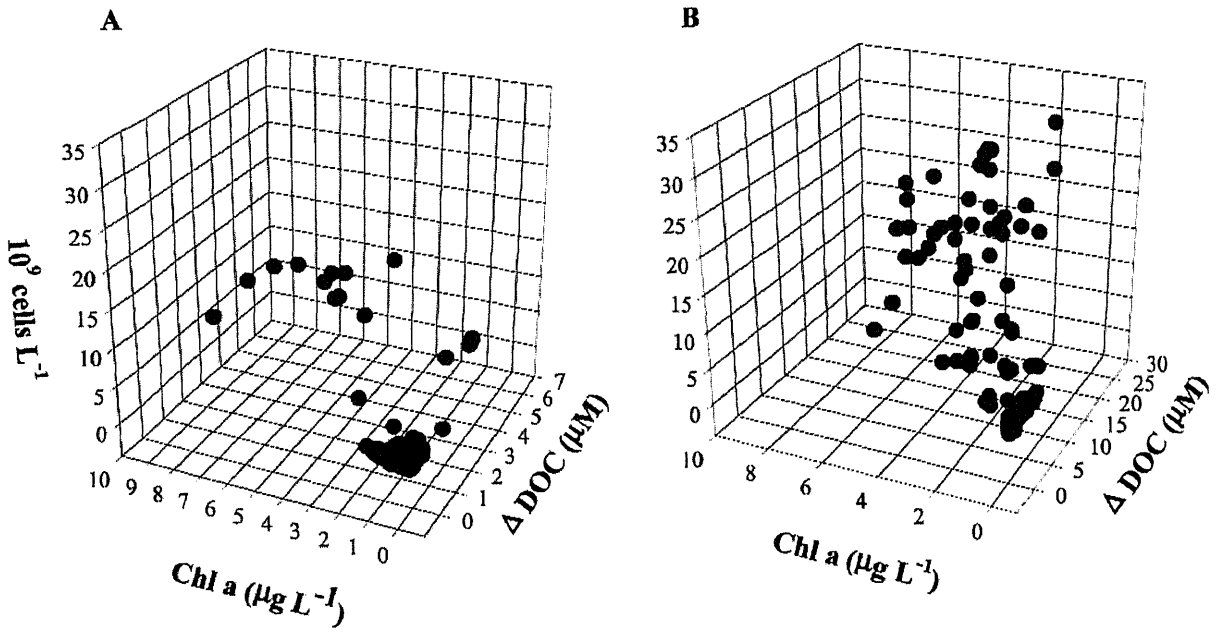

Fig. 6. Multivariate relationships among bacterial abundance, Chl a and ΔDOC in A: October–December, and B: January–April.

of bacterial carbon requirements in open ocean systems. For example, labile DOC supported the observed annual bacterial production in the Sargasso Sea at the BATS site off Bermuda and in the subarctic North Pacific Ocean [*Anderson and Ducklow*, 2001]. In the central equatorial Pacific [*Anderson and Ducklow*, 2001] and during the North Atlantic Bloom Experiment near 47°N, 20°W in May, 1989 (H. W. Ducklow and T. R Anderson, manuscript submitted) labile DOC flux was insufficient to fully support observed bacterial production. In the Ross Sea, one of the few locations for which we have extended observations spanning the growth season (other than Hawaii and Bermuda), there appear to be periods when labile DOC meets most of the bacterial demand, and periods when semilabile DOC supplements the labile fraction in supporting bacterial production. Reasons for this variability in bacterial diets are discussed briefly below.

TABLE 4. Partial correlation coefficients for the regression equation $X_1=a+b_2X_2+b_3X_3+b_4X_4$* for the 1996–97 season (cruises P1–P3).

Coefficient	Value
r12.3	0.477
r12.4	0.545
r13.2	0.555
r13.4	0.359
r14.2	0.132
r14.3	0.372
r13.24	0.56
r14.23	0.168
r12.34	0.332

*X1, abundance; X2, 3, 4 temperature, ΔDOC and Chl, respectively.

The difference in the strength of the bacterial response to variations in ΔDOC was likely due to variations in the labile DOC supply, these differences could also be due in part to changes in the composition and quality of the semilabile DOC itself, slightly warmer temperatures or somewhat greater predation pressure later in the season. The exact reason is not known; here I emphasize that there are differences in the relationships between abundance and semilabile DOC. I use this line of reasoning below to construct a carbon budget for bacterial utilization of labile and semilabile DOC (ΔDOC) during the 1996–97 growing season.

A BUDGET FOR BACTERIAL CARBON UTILIZATION IN THE ROSS SEA

Relatively small amounts of DOC are produced during the intense spring-summer *Phaeocystis* blooms in the Ross Sea. The labile DOC production is difficult to measure directly by chemical analysis because we do not

TABLE 5. A. BP in 0–150 m layer supported on newly produced DOC or utilization of ΔDOC.

Day	ΔDOC[a]	int PP	int BP	(BP: PP)	BCD[b]	DOC Prod	DOC Prod/PP
(period)	Mol C m^{-2}	Mol C m^{-2} $period^{-1}$		—	Mol C m^{-2} $period^{-1}$		—
291	0.02	0	0	0	0	0.02	—
33 (291–33)	1.14	10.07	0.35	0.03	1.17	2.29[c]	0.23
118 (33–118)	0.19	3.88	0.51	0.13	1.68	0.73[d]	0.19
291–118	—	13.96	0.86	0.06	2.85	3.04	0.22

[a] Table 3 of Carlson et al., (2000).
[b] BCD in surface = BP/BGE where BGE = 0.3.
[c] DOC production = BCD + ΔDOC accumulation.
[d] DOC Production = BCD – previously produced ΔDOC.

know all the individual compounds produced [*Williams*, 2000]. One can estimate the mean levels of labile DOC produced by calculating the DOC metabolized by the bacteria from the measured bacterial production (BP) and some estimate of the bacterial growth efficiency (BGE). This quantity is known as the bacterial carbon demand (BCD),

$$BCD = BP / BGE \quad (2)$$

Bacterial production was estimated from leucine incorporation rates using a conservative conversion factor (1.5 kgC produced $mole^{-1}$ leucine incorporated, [*Simon and Azam*, 1989]). This value was justified for the Ross Sea on the basis of concurrent measurements of BP and dark respiration [*Ducklow et al.*, 2001] and it yielded BP estimates which were consistent with empirically-estimated values [*Ducklow*, 1999; *Ducklow et al.*, 1999]. BGE was estimated directly during deck incubations with measurements of changes in DOC and bacterial CO_2 production [*Carlson et al.*, 1999]. BGE was 10% early in the growing season but reached 30% by the late spring [*Carlson et al.*, 1999]. Here I use the 30% value as it yields conservative estimates of DOC utilization. Using the seasonal increase from 10% to 30% [*Carlson*, 2001] does not greatly change the overall budget, because periods when the BGE was lower, and total carbon demand greater for a given BP, were periods when the BP was low, and vice-versa. These trends tend to offset each other. The budget is constructed for the upper 150 m.

Total, or gross DOC production, ΣDOC, includes the labile DOC utilized by bacteria on short time scales and the semilabile DOC (ΔDOC; [*Carlson et al.*, 1998] their figure 5) which accumulated in the upper water column:

$$\Sigma DOC = \Delta DOC + BCD \quad (3)$$

The observed net changes in ΔDOC, cumulative BP, BCD and primary production (PP) are presented in Table 5. The progression of biogeochemical change over the growing season is broken into the two phases of the bloom already identified (prebloom—early bloom, days 291–33; peak bloom—post bloom, days 33–118), and following [*Carlson et al.*, 2000]. Over the full growing season, BP was low, averaging just 6% of the total PP, but reached 13% of PP during the declining phase of the bloom. At a 30% BGE the BCD was 20% of the total PP for the growing season. That is, about 20% of the total PP was channeled through bacterial metabolism. The BCD includes utilization of both labile and semilabile DOC, plus any particulate matter that was utilized directly by bacteria without first entering the bulk DOC pools.

Total DOC production was estimated by calculating a net DOC accumulation rate between October and February and adding to it an estimate of the total DOC metabolized by the bacteria over the growth season [*Carlson et al.*, 1998]. Between days 291–33, ΔDOC increased from 0.02 to 1.14 Mol C m^{-2}, and then declined to 0.19 by day 118. Thus there was net production of ΔDOC until February, followed by a net loss back nearly to the original low value by the end of April. The gross production of DOC between days 291–33 was (1.14–0.02) + (1.17) = 2.29 Mol C m^{-2}. During the declining phase of the bloom, ΔDOC also decreased, so the BCD includes utilization of the previously accumulated DOC (1.14–0.19 = 0.95), plus additional labile DOC production, and so the total DOC production for the period was equal to the BCD of 1.68–0.95 = 0.79 Mol C m^{-2}. Over the entire growing season, the total DOC production was the total BCD, 2.85 plus the remaining 0.19 Mol C m^{-2}, which was 22% of the total PP.

The relative importance of labile and semilabile DOC for bacteria changed during the growing season (Table 5B). In the first phase of the bloom, days 291–33, the

Table 5. B. Contributions from carbon sources to BCD. Values summed from Table 1A.

Interval	labile DOC	semilabile ΔDOC
	Mol C m^{-2} pd^{-1}	
291–33	1.17	0
33–118	0.73[a]	0.95[b]
291–118	1.90	0.95

[a] BCD of 1.68–0.95 from above.
[b] ΔDOC loss of 1.14–0.19 in above.

Proportional contributions (sum = 1.0)		
Interval	labile DOC	Semilabile DOC (ΔDOC)
291–33	1.00	0
33–118	0.43	0.57
291–118	0.67	0.33

semilabile DOC which increased from 0.02 to 1.14 Mol m^{-2}, did not contribute to the observed BCD. I assume that bacterial production during this period was supported entirely by DOC which was produced and metabolized over a time scale of days. However, during the later phase, days 33–118 (i.e., 02 January–28 April), (1.14–0.19)/1.68 = 57% of the BCD was met by semilabile DOC. With this accounting one can see that bacterial production was a small fraction of the total PP because only 22% of the PP entered the DOC pools available for bacterial metabolism. At a BGE of ~30%, BP was necessarily limited by the carbon supply to <10% of the PP, even though nearly all the DOC produced was labile over the seasonal time scale.

A fuller accounting of the amount of PP passing through bacteria has to include the remaining water column below the upper 150 m. In the Ross Sea, water depths over the shelf vary from 300–700 m, so here I describe a carbon budget for the 150–300 m layer, the upper portion of the 'twilight zone'. Including deeper depths would increase the total slightly. BP was nearly uniform and always low below 300 m [*Ducklow et al.*, 2001]. Below 150 m, DOC did not accumulate [*Carlson et al.*, 2000] but there was measurable bacterial production. In the early spring (ca day 291–337) rates of BP were homogeneous throughout the water column [*Ducklow et al.*, 2001], and the depth-integrated BP was 0.08 Mol m^{-2} in the 150–300 m layer. During days 33–118, BP was strongly concentrated in the upper 150 m (0.51 Mol m^{-2}), and totaled 0.16 Mol m^{-2} in the 150–300 m layer between. BP below the euphotic zone is sustained by decomposition of the particle flux [*Cho and Azam*, 1988; *Simon et al.*, 1992; *Hoppe et al.*, 1993; *Nagata et al.*, 2000], downward mixing and advection of DOC from the surface layer [*Carlson et al.*, 1994] and DOC fluxes from zooplankton. The latter sources are difficult to quantify; here I use the POC exports through 100 m, estimated from ^{234}Th disequilibria [*Cochran et al.*, 2000] as a way of scaling carbon supply into the upper twilight zone. Between days 291–33, the POC flux was 1.9 Mol m^{-2}, which was 19% of the PP over the same period. The POC flux was 2 Mol m^{-2} from days 33–118, or 51% of the PP. Over the whole growing season, the POC flux/PP (e-ratio) was 28%. There are few direct estimates of the BGE for bacteria growing on decomposing POC, but it is likely to be lower than on labile DOM. [*Osinga et al.*, 1997] found that *Phaeocystis* debris was utilized with a BGE of 1–20% in Dutch coastal waters. Using a conservative estimate of 15%, BCD for the lower layer is 0.24/0.15 = 1.6 Mol C m^{-2} for the full growing season, which was 41% of the delivery rate of POC below 100 m. Slightly less than half the POC flux leaving the upper 100 m may have been metabolized by bacteria between 150–300 m. Over the full growing season, and throughout the entire water column, accounting for DOC utilization as well as decomposition of the POC flux, bacteria metabolized 32% of the total primary production in the Ross Sea in 1996–97. During the decline of the bloom, BCD was especially intense, consuming over 70% of the primary production. This calculation underscores the importance of including the full water column in calculating BP:PP [*Anderson and Ducklow*, 2001].

With the water column fluxes through the DOC pool and into bacteria quantified, one can also estimate the relative importance of three carbon sources for bacterial

nutrition: labile and semilabile DOC and sedimenting particles falling into the upper aphotic (twilight) zone. In the first half of the bloom (days 291–33), labile DOC accounted for all the upper layer BCD and 70% of the total in the 0–300 m water column. During the latter half (declining phase) of the bloom, the three carbon sources contributed approximately equally to the total water column BCD. Over the full growing season, labile DOC supported almost half the total BCD, with semilabile DOC contributing about 20%, and sinking POC, 36%. The ratios and absolute amounts are dependent on assumptions about the values of BGE, still poorly-constrained in most cases.

DISCUSSION

I have focused on the sources of organic carbon supporting bacterial production in the Ross Sea over the full daylight period (the October–April growing season). Other factors undoubtedly influence bacterial growth and accumulation in the region. Bacterial abundance, biomass and incorporation rates in the upper water column were all significantly correlated with temperature (e.g., Fig. 1C). However, nearly the full range of the seasonal variability in bacterial abundance is also observed near the annual minimum temperature of −1.8°C. Bacterial accumulation commences in early November while temperatures are still low, and bacterial stocks attain near-peak levels, and rapid growth rates before substantial warming has occurred [*Ducklow et al.*, 2001]. The strong relationship with temperature may be a consequence of other growth-limiting properties covarying with the seasonal rise in temperature. [*Carlson et al.*, 1998] showed that in 1994-1995 there was a 3-5 fold increase in bacterial biomass and an order of magnitude increase in BP despite almost constant low temperature, and argued for bottom up control (resource limitation) of bacterial growth in the Ross Sea. Bacterial growth experiments conducted in the Ross Sea did not show any significant growth response to temperature increases of 1–2 °C [*Ducklow et al.*, 1999], and bacterial growth rates in cold waters are not significantly different from those achieved in warm waters [*Rivkin et al.*, 1996].

Although correlations between bacterial abundance and chlorophyll *a* or between bacterial and primary production have been used to infer the dependence of bacterial metabolism on photosynthetic organic matter production in the sea and lakes [*Cole et al.*, 1988], such relations are not always found in Antarctic data sets [*Bird and Karl*, 1999], including the Ross Sea (e.g., Figure 5a). This is because the bacterial bloom lags the phytoplankton bloom by about a month, compared to lags of zero to ca. 10 days at lower latitudes [*Billen et al.*, 1990; *Ducklow et al.*, 1993]. This lag period in bacterial response to the phytoplankton bloom may be related to growth limitation by the interactions between low temperature and organic matter [*Wiebe et al.*, 1992; *Pomeroy and Wiebe*, 2001]. The peak bacterial response follows accumulation of semilabile bulk DOC which occurs later in the phytoplankton bloom cycle. In November–December, 1996 (P4), abundance and incorporation rates increased with only a small DOC accumulation. DOC accumulation is not required to trigger increasing BP, so long as a source of labile DOC is available. But maximum levels of abundance and BP were not attained until later, after semilabile DOC began to accumulate.

Between days 291–33 BP only averaged 3% of PP. I suggest that bacteria respond to the instantaneous production of labile DOC, but the BP is limited because the supply rate was relatively low. Why this is so remains poorly understood [*Carlson et al.*, 1998; *Carlson et al.*, 2000] but may in part be explained by the lack of grazing on the *Phaeocystis* bloom. Grazing by microzooplankton and/or mesozooplankton mobilizes significant DOC release via cell breakage as well as animal metabolism [*Strom et al.*, 1997; *Nagata et al.*, 2000]. Microzooplankton grazing was nearly nonexistent in the Ross Sea [*Caron et al.*, 2000]. There are few measurements of grazing rates on *Phaeocystis* but its large size and colonial morphology is believed to be an antigrazing adaptation [*Lancelot et al.*, 1998]. *Phaeocystis* itself can have either high or very low DOM release rates (Nagata, 2000), and rates are apparently quite low in the Ross Sea, unless nutrients or iron are depleted and limit algal growth [*Smith et al.*, 1998b]. [*Kirchman et al.*, 2001] found very low ambient concentrations and low uptake of dissolved monosaccharides in the Ross Sea in 1996–97, consistent with low DOM release rates. [*Anderson and Ducklow*, 2001] developed a model to estimate BP:PP as a function of DOM release and BGE. Even with 0% release from the *Phaeocystis,* and low to moderate grazing rates, the model would estimate BP:PP of 10–15% at a BGE of 0.3, at least twice as great as observed in the Ross Sea in the early to mid-bloom period.

BP and bacterial abundance reached maximal levels only after DOC accumulated. BP:PP was 13% between days 33–118, with some values in excess of 20% (Figure 2; [*Ducklow et al.*, 2001]). Dissolved neutral (combined) sugars accounted for about 50% of the ΔDOC pool dur-

ing this period [*Kirchman et al.*, 2001]. These compounds apparently resisted bacterial attack enough to allow accumulation to 10–20 μM C before consumption between February and April. I suggest that accumulation of semilabile DOC, and possibly slightly increased temperatures stimulated BP during and following the peak of the bloom. Even at this time however, bacterial utilization was about evenly split between the labile and semilabile pools in the euphotic zone (Table 5b). Later in the Austral summer and autumn, as irradiance levels declined and PP rates fell steeply, BP:PP reached high values while continuing to draw down the ΔDOC. BP:PP was in excess of 1.0 during days 102–118 when the daylight period was just 1–2 hr long [*Ducklow et al.*, 2001]. However the precision of these estimates is low, as both BP and PP were near limits of detection. When we left the study area on May 1, 1997, ΔDOC was 0.19 Mol m^{-2}, leaving a small reservoir to support subsequent BP in the early winter.

Few studies have addressed partitioning of BCD among labile and semilabile DOC pools, and no others exist for polar seas. [*Lancelot et al.*, 1991] modeled plankton and DOC dynamics for an ice edge bloom in the Weddell-Scotia Sea, and included both macromolecular and free monomeric DOC pools, using their HSB model. However, in this formulation, all DOC production feeds the macromolecular pool (corresponding roughly to some fraction of the bulk semilabile pool), which decays directly into the monomeric pool, so in effect, all the BCD is supported by the macromolecular pool. Several other models [*Connolly and Coffin*, 1995; *Anderson and Williams*, 1998; *Levy et al.*, 1998; *Walsh et al.*, 1999; *Vallino*, 2000]; all for non-polar systems) also employ two or more DOM pools of varying lability, but in no case were budgets given for bacterial utilization. Yet is clear from all the models that inclusion of a DOM compartment with low turnover rates (order 0.01 d^{-1}) was necessary to simulate observed seasonality of DOC concentrations.

The other factor primarily responsible for limitation of bacterial accumulation is removal by protozoan grazers and/or viruses. Bacterial accumulation appears to be strongly limited by removal during the diatom bloom in the Gerlache Strait, Antarctica [*Bird and Karl*, 1999]. Peak bacterial abundance there was similar to November levels in the Ross Sea (0.5–1 x 10^9 cells L^1) but the population of nanoflagellates grazers was much larger. In the Gerlache area, the number of bacterial cells per bacteriovore cell was just 85 [*Bird and Karl*, 1999], compared to over 500 in the Ross in Nov.–Dec. 1997 (David Caron, personal communication and US JGOFS database). Intense bacterivory limited bacterial accumulation and slowed the response to the bloom in the Antarctic peninsular region, but in the Ross Sea, grazer populations were lower and bacterial growth and accumulation were primarily limited by bottom-up forces.

What are the mechanisms which allow the semilabile DOC to accumulate from October to January, then disappear relatively quickly before the onset of winter? It is possible that the quality (lability) of the labile DOC released from *Phaeocystis* and foodweb interactions changed as the bloom progressed, forcing the bacteria into partial dependence on the semilabile pool. The progressive shift observed in the bacterial conversion efficiency (see Carlson and Hansell, this volume) is one indication of such a change. Another possibility that remains to be explored is the development of a bacterial assemblage capable of breaking down the ΔDOC. A bacterial assemblage able to use semilabile DOC imported from the surface layer (upper 100 m) exists below 100 m in the Sargasso Sea, but not in the euphotic zone [*Carlson*, 2001]. However, specific bacterial assemblages are selected during phytoplankton blooms [*Kerkhof et al.*, 1999]. Attached bacteria increased in number and size during the *Phaeocystis* bloom in McMurdo Sound, Antarctica [*Putt et al.*, 1994]. There was some evidence for adaptation of the bacterial community to *Phaeocystis*-derived mucopolysaccharides during the *Phaeocystis pouchetti* bloom in the North Sea [*Janse et al.*, 1999] showed that bacterial inocula collected later in the bloom decomposed purified mucopolysaccharides somewhat more rapidly than similar inocula collected earlier. Members of the *Cytophaga-Flavobacterium* group of bacteria are good agents of ΔDOC breakdown because they attack polymeric compounds like those constituting the semilabile fraction of the DOC [*Glockner et al.*, 1999; *Cottrell and Kirchman*, 2000], and are wide-spread in the oceans [*Hugenholtz et al.*, 1998]. Members of this group have been recovered in many Antarctic water, sea ice and sediment samples using traditional bacterial cultivation media [*Helmke and Weyland*, 1995; *Delille*, 1996; *Bowman et al.*, 1997; *Hagström et al.*, 2000]. However, because viable bacteria are very poorly recovered from natural seawater by cultivation, with selection for and against various groups, it is not certain that reliable quantitative occurrence patterns can be derived from such studies. There have been just a few investigations of bacterial community structure in Antarctic seas employing culture-independent methods including fluorescent in situ hybridiza-

tion and cloning of PCR-amplified 16S rRNA genes for various target groups. Notably, [*Simon et al.*, 1999] found that members of the *Cytophaga-Flavobacter* cluster hybridizing to probe CF319a constituted over 70% of the total DAPI cell counts in samples from the marginal ice zone of the Lazerev Sea, Antarctica, during a *Phaeocystis* bloom in January, 1996. They suggested that accumulation of mucilage and other substrates in the *Phaeocystis* bloom fostered a relatively homogeneous bacterial assemblage dominated by members of the *Cytophaga/Flavobacterium* cluster. Careful time series observations of ΔDOM accumulation and molecular probe detection of specific bacteria groups during the course of Antarctic phytoplankton blooms are needed to delve further into the specific ecological and physiological mechanisms of semilabile DOC accumulation and decay.

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