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Constraining bacterial production, conversion efficiency and respiration in the Ross Sea, Antarctica, January–February, 1997

Hugh W. Ducklow[a,*], Mary-Lynn Dickson[b], David L. Kirchman[c], Grieg Steward[d,e], Joe Orchardo[b], John Marra[f], Farooq Azam[e]

[a]*The College of William and Mary School of Marine Science, P.O. Box 1346, Gloucester Point, VA 23062, USA*
[b]*University of Rhode Island Graduate School of Oceanography, Narragansett, RI 02882, USA*
[c]*The University of Delaware College of Marine Studies, Lewes, DE 19958, USA*
[d]*Monterey Bay Aquarium Research Institute, Moss landing, CA 95039, USA*
[e]*Scripps Institution of Oceanography, La Jolla, CA 92093, USA*
[f]*Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY 10964, USA*

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Abstract

Bacteria consume dissolved organic carbon at rates averaging about 50% of primary production across a wide spectrum of marine ecosystems. However, total utilization rates are poorly constrained due to a lack of data on conversion efficiencies and/or bacterial respiration rates. We estimated total community dark respiration rates (DCR) from in vitro oxygen utilization and estimated bacterial production from ^{3}H-leucine incorporation during January–February 1997 in the Ross Sea, Antarctica. Bacterial respiration rates (BR) were estimated by assuming that BR was less than some fraction of DCR, and by choosing values for the bacterial growth efficiency. By comparing these derived bacterial respiration rates with the DCR we were able to constrain conversion efficiency and bacterial production within various bounds. Bacterial biomass was 10% of phytoplankton stocks, and we considered that bacterial respiration was a similar fraction of the total respiration. To meet this constraint bacterial production rates likely averaged about 5–10% of the net community production, and conversion efficiencies had to be in the range of 35–45%, similar to independent discrete measurements made during the summer season on this cruise. Dark respiration rates are an absolute constraint on the estimates of bacterial carbon demand. A low value of the leucine conversion factor (1.5 kgC mol^{-1}) was required to meet this strong constraint.

* Corresponding author. Fax: 1-804-684-7180.
E-mail address: duck@vims.edu (H.W. Ducklow).

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1. Introduction

Bacterial production (BP) is generally assumed to be equivalent to about 25–30% of simultaneously estimated phytoplankton primary production (PP) rates across a wide range of marine and freshwater ecosystems of varying trophic status (Cole et al., 1988; Ducklow and Carlson, 1992). This generalization may not hold up for open ocean systems as more data become available (Ducklow, 2000). In recent studies, BP appears to be a smaller fraction of PP. For example, it averages about 10% of PP in the subarctic North Pacific (Kirchman et al., 1993) and Antarctic South Atlantic (Kuparinen and Bjørnsen, 1992), 15% of PP in the equatorial Pacific (Kirchman et al., 1995) and 10–15% in the Sargasso Sea (Carlson et al., 1996), HNLC and oligotrophic regimes differing widely in temperature, overall nutrient status and productivity. Precise and accurate estimates of BP (and PP) are still beset by complicated technical as well as conceptual difficulties, but the weight of observations suggests oceanic BP is a lower fraction of PP than in nearshore systems (Ducklow, 1999).

There is conflicting information about the magnitude of bacterial productivity in cold waters (e.g., Pomeroy and Deibel, 1986; Rivkin et al., 1996; Rich et al., 1997). In general though, bacterial stocks and BP are low in Antarctic coastal waters (Karl et al., 1991; Karl, 1993; Carlson et al., 1998). The mechanisms apparently inhibiting bacterial activity and biomass accumulation are not clear. Organic matter limitation (Carlson et al., 1998; Church et al., 2000), especially at low temperatures (Pomeroy et al., 1991), has been advanced to explain low BP during polar and other cold water phytoplankton blooms. Billen and Becquevort (1991) suggested that bacterial activity is merely out of phase with phytoplankton growth due to the production of high molecular weight DOM, and Karl (1993) concluded that there was a rise in the relative importance of BP following the collapse of the phytoplankton blooms (Karl, 1993). For example, Cota et al. (1990) showed that BP averaged 76% of PP in the Weddell Sea in March 1986. Whether or not bacteria–phytoplankton covariation is unique in the Antarctic or just an extreme version of temperate plankton dynamics remains to be established.

We hypothesize that BP is usually a lower fraction of PP in oceanic and Antarctic waters of necessity because bacterial conversion efficiencies are usually low (del Giorgio and Cole, 1998). Unless fluxes of labile dissolved organic matter (LDOM) have greatly departed from near steady-state conditions, BP is constrained to be low, even if the fluxes themselves are large relative to PP. The nonsteady state case may happen, for example, during the decline of a bloom, when heterotrophic grazers and bacteria are decomposing accumulated phytoplankton biomass or accumulated DOM (Azam et al., 1991). In this article we examine this question by placing constraints on bacterial respiration, as a fraction of measured total dark plankton community respiration in the Ross Sea, January–February 1997.

We have carried out extensive investigations of bacterial and phytoplankton dynamics in the Ross Sea, Antarctica over four Austral summers, including extended coverage of the full growing season in 1996–1997. Here, we present synoptic data on BP, net community oxygen production (NCP) and total dark respiration (DCR),

when the annual *Phaeocystis* bloom was declining and BP was relatively high. Bacterial respiration (BR) per se was not measured systematically, although Carlson et al. (1999) derived estimates for several discrete samples. Bacterial respiration on ambient organic matter is difficult to measure directly, and such determinations involve extensive sample manipulation and long incubations. We have a large data set for BP, and seek to constrain the magnitude of BR through a series of assumptions about plankton processes, using the BP and community DCR observations. In this way we can examine whether BP is limited as a fraction of PP by the DOM supply or for other reasons.

2. Materials and methods

2.1. Study site

All sampling was carried out aboard the RVIB *Nathaniel B Palmer* during the US JGOFS AESOPS Process-2 cruise, 12 January–06 February 1997 in the southern Ross Sea. All stations except Sei and Emperor (Table 1) were on or near on the main AESOPS transect along 76.5°S, which we occupied annually from 1994 to 1997 (Carlson et al., 1998; Smith et al., 1998; Ducklow et al., 1999). The data presented here consist of euphotic zone rate processes and bacterial biomass integrated to the depth of 1% surface irradiance, measured at the main AESOPS productivity stations (Table 1). Some of the data considered here appear in other AESOPS papers in this volume (Smith et al., 2000). In this analysis, each station is regarded as an independent unit for analysis, without regard to spatial or temporal and variability. Thus, we have a data set consisting of $n = 10$ integrated euphotic zone samples.

2.2. Sampling and sample preparation

Samples for bacterial measurements were collected using the JGOFS CTD/Niskin rosette system with epoxy-coated springs to minimize trace metal contamination (Price et al., 1986; Kirchman et al., 1995; Ducklow et al., 2000). Samples for net oxygen production (NCP) and dark community respiration (DCR) measurements were collected using the Moss Landing Trace Metal Clean Go-Flo Rosette system. Bacterial samples were collected at fixed hydrographic depths along with other samples. Care was taken to avoid trace DOM and metal contamination during subsampling from the Niskin bottles. NCP and DCR samples were collected from standard light depths (85, 50, 25, 10, 5 and 1% of I_0) determined at each station by previous in situ irradiance measurements.

2.3. Rate measurements

Bacterial production was estimated from incorporation rates of ^{3}H-leucine (Leu) using the microcentrifugation technique (Smith and Azam, 1992) as previously

Table 1
Station data and surface hydrography for the US JGOFS AESOPS Process-2 Cruise, Ross Sea, 12 January–06 February 1997

Station	Date	South latitude	East longitude	1% I_0 (m)	Temperature (°C)	NO_3 (μg-at L^{-1})	Chl *a* (μg L^{-1})	Bact (10^9 cells L^{-1})
1 (Minke 1)	13 January	− 76.51	168.96	46	0.46	9.4	2.0	1.3
5 (Big O 1)	17 January	− 76.49	176.99	20	− 0.02	9.5	7.0	2.3
8 (Orca 1)	19 January	− 76.49	− 178.03	29	− 0.27	14.3	3.0	0.5
9 (Emperor)	21 January	− 78.04	− 176.02	36	− 0.43	9.2	1.4	0.4
11 (Sei)	24 January	− 74.00	176.98	33	− 0.32	22.9	1.9	0.1
13 (Minke 2)	27 January	− 76.50	168.99	34	0.18	9.4	1.8	2.4
17 (Big O 2)	30 January	− 76.50	176.00	27	− 0.27	11.1	3.9	2.9
20 (Orca 2)	01 February	− 76.50	− 178.02	36	− 0.44	19.6	1.4	0.5
25 (Big O 3)	04 February	− 76.50	175.00	28	− 0.26	13.4	1.7	2.3
27 (Pack Ice)	06 February	− 76.17	163.35	28	− 1.04	5.7	0.8	2.7

described (Ducklow et al., 2000). Briefly, triplicate 1.7 ml samples were inoculated in clean 2-ml plastic microcentrifuge tubes with 20 nM (final conc.) Leu. This concentration was tested for rate saturation on earlier cruises in the summer, ice-free season. All samples were incubated in dark refrigerated baths within 0.5°C of the in situ temperatures (Table 1) for 6–24 h depending on depth and anticipated activity. Samples were extracted and washed in 5% TCA and 80% ethanol and counted in Ultima Gold (Packard) LSC cocktail.

Bacterial abundance and biovolume were determined as previously described (Ducklow et al., 1999) using epifluorescence video microscopy and digital image analysis. Carbon biomass was calculated using 107 fgC μm^{-3} (Carlson et al., 1999). Use of a larger value would increase the BP estimates, which would make it more difficult to satisfy the respiration constraints (see below). Phytoplankton biomass was estimated using a Phytoplankton-C : Chl ratio of 50 (Smith et al., 2000).

Net community production is equivalent to gross O_2 production minus the oxygen consumed by autotrophic and heterotrophic respiration and the Mehler reaction. Net O_2 production and dark respiration rates were measured from the change in the O_2 concentration following in situ incubation (Bender et al., 1999). Samples were incubated in quartz bottles having a nominal volume of 100 ml. Quadruplicate initial samples were fixed with Winkler reagents after being drawn from a Go-Flo bottle and quadruplicate samples were incubated for 24 h. Net O_2 production samples were incubated in situ, while respiration rates were obtained by incubating samples in the dark in an environmental chamber that maintained ambient surface seawater temperature. Initial and incubated samples were titrated together once the final samples reached thermal equilibrium, approximately 6 h after being fixed. Samples were titrated to a potentiometric endpoint using a high precision, automated titrator configured with a 5 ml ABU burette and a TIM controller (Radiometer America, Westlake, OH). Net O_2 production and respiration rates were calculated from the difference in the $[O_2]$ between final and initial samples. Analytical precision, expressed as standard deviations (S.D.), is 0.04% for iodate standards and 0.07% for replicate samples.

Primary production was also determined by standard in situ 14C incubations as described in Smith et al. (2000).

2.4. Data analysis and presentation

In this paper, bacterial production was estimated from the rate of Leu incorporation using the approach of Simon and Azam (1989) in which the leucine incorporation rate (pM h^{-1}) is multiplied by 1.5–3 kg C produced mol^{-1} Leu incorporated, yielding production rates in gC L^{-1} h^{-1}. The lower bound assumes no isotope dilution for Leu (Simon and Azam, 1989). The other parameters that determine the 1.5–3 value for the conversion factor are well constrained (i.e. % protein of total C and % Leu in protein are relatively constant, Kirchman et al., 1985; Simon and Azam, 1989; Ducklow et al., 1999), making 1.5 kg C mol^{-1} an acceptable term for estimating the minimum value for BP. In general, most reports of Leu-derived BP in the literature employ 3 kg C mol^{-1} and we started with that value in our analysis. But all BP

estimates reported herein use 1.5 kg C mol^{-1}. Volumetric BP estimates were multiplied by 24 to obtain daily rates and summed over the euphotic zone by trapezoidal integration from the surface to the value at the 1% I_0 depth (Table 1). This latter value was determined by linear interpolation between surrounding samples if necessary. Surface values were assumed to be equal to the value measured at the shallowest depth sampled (usually 1–2 m). Potential diel variability of BP was not considered, and daily BP was obtained by extrapolation of shorter-term measurements to 24 h rates.

Net rates of 24-h oxygen production and dark respiration (mmol O_2 m^{-3} d^{-1}) were converted to carbon flux using photosynthetic (PQ) and respiratory quotients (RQ) of 1.4 and 1.1, respectively (Williams and Robertson, 1991). Euphotic zone rates were determined via trapezoidal integration to the bottom sample depths given in Table 1.

2.5. Constraining bacterial production and respiration

Our approach is similar to that followed earlier by Christian and Karl (1994) and Caron et al. (1995) in which upper and lower bounds were set on bacterial conversion factors and other parameters in order to evaluate contribution of bacterioplankton to the planktonic foodweb. The relationships among carbon flows and measurements are shown in Fig. 1. In the equations below, the measured quantity is in boldface, and the parameters to be varied are in *italics*:

The total bacterial carbon demand, BCD, is the sum of bacterial production, BP, and respiration, BR:

$$\mathrm{BCD} = \mathbf{BP} + \mathrm{BR}. \tag{1}$$

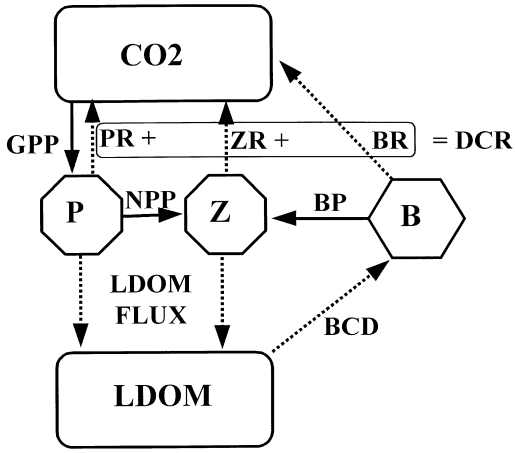

Fig. 1. Measured (solid lines) and unmeasured (dashed lines) carbon flows in the water column and in experimental bottles analyzed to estimate bacterial respiration (BR) and growth efficiency (BGE). P, phytoplankton, Z, zooplankton, B, bacteria. LDOCM, labile dissolved organic matter, PR, ZR and BR, phytoplankton, zooplankton and bacterial respiration, respectively, sum to the measured total dark community respiration, DCR. The measured gross primary production, GPP is the sum of the DCR and measured net community production, NCP (not depicted).

Here our main aim is to set bounds for the bacterial contribution, BR, to the total measured dark community respiration, DCR, and thus bounds on the total bacterial carbon demand (BCD). By knowing the limits to the BCD, we can suggest values for the efficiency at which the bacterioplankton converted carbon into biomass (bacterial growth efficiency, BGE):

$$BGE = \mathbf{BP}/\mathrm{BCD}. \tag{2}$$

We can derive BR by rearranging Eqs. (1) and (2), substituting for BCD:

$$\mathrm{BR} = (\mathbf{BP}/BGE) - \mathbf{BP} \tag{3}$$

and assuming a range of values for BGE. Carlson et al. (1999) estimated that BGE was 33 and 38% for single discrete depths at two stations on this cruise (see Discussion). We seek to extend and generalize those estimates for the entire euphotic zone during this cruise. Our reasoning is that the bacterial respiration *must* be less than the total measured dark community respiration, DCR. This mass balance argument must be true in each and every bottle in which dark oxygen utilization was measured because bacteria contributed to the observed oxygen utilization and so cannot exceed the total:

$$\mathrm{BR} < \mathbf{DCR} \quad \text{at each station.} \tag{4}$$

Since we know that bacterial respiration is not the only contributor to **DCR**, we also can choose to identify some fraction g of **DCR** as the constraining quantity:

$$\mathrm{BR} < g{*}\mathbf{DCR}. \tag{4A}$$

To understand the consequences of constraining the BR and BCD, we also estimate DOC supply to the bacteria. The LDOM supply rate is scaled to the gross primary production (GPP) by a factor $\boldsymbol{f}$.

$$\text{LDOM flux} = f * \mathbf{GPP}. \tag{5}$$

We assume the flux of labile DOC (LDOC; see Discussion) from various planktonic sources into the LDOC pools is balanced by bacterial demand in the Ross Sea over time scales of days–weeks (Carlson et al., 1998):

$$\mathrm{BCD} \approx f * \mathbf{GPP} \quad \text{at each station.} \tag{6}$$

We seek to impose a minimum value of the total LDOM flux, relative to the GPP, as a means for referencing the estimated flux to the observations. The LDOM flux could be larger than the primary production, as for example when the standing stocks of POC are decaying (i.e., $\boldsymbol{f} > 1$). Note that the LDOC flux cannot be referenced to the O_2-NCP, as this quantity could be negative (although it is not in this data set).

Although BGE values > 0.5 are shown in some model solutions below, we state at the outset that BGE $\geqslant 0.5$ is unlikely in most natural populations growing on ambient substrates (del Giorgio and Cole, 1998). The approach then, is to find values of *BGE*, f and g that allow the derived BR and BCD values to meet the constraints diagrammed in Fig. 1 at each station listed in Table 1. Parameter values meeting the constraints under various degrees of rigor were explored by applying Eqs. (1)–(6) to

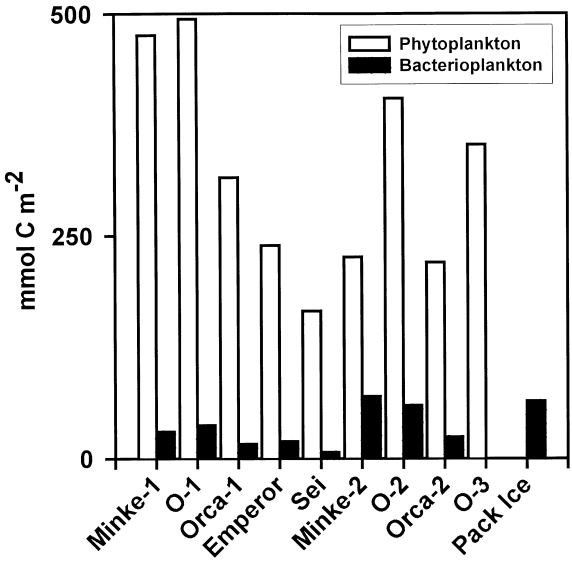

Fig. 2. Standing stocks of particulate organic carbon, phytoplankton and bacterioplankton in the euphotic zone at principal stations during the Process-2 cruise. Phytoplankton stock estimated from C : Chl = 50.

the data shown in Figs. 2 and 3. All calculations were performed in simple spreadsheet models. In all cases we assumed that *BGE*, *f* and *g* were uniform across all stations. Obviously, conclusions could vary greatly if these parameters were adjusted to provide a match at each station.

3. Results

This data set was chosen for analysis because net oxygen production and bacterial rates under 80–100% ice cover and low irradiances on the Process—1 and − 3 cruises (October 1996 and March 1997; Table 2) were nearly all at limits of analytical detection. Oxygen – based rates were not measured on the Process-4 cruise (November 1997). In mid-January the study area along 76.5°S was ice-free, open water. Only the "pack ice" station 27 near the Victoria Land coast (Table 1) was covered with unconsolidated ice floes. Surface waters (upper 10 m) were − 0.5 to + 0.5°C with lower nitrate concentrations depleted by ca. 10–20 μg-at L^{-1} from early spring levels of ca 30. Surface chlorophyll *a* values were moderate to low (1–4 μg L^{-1}) and bacterial abundance was generally high ($1–2 \times 10^9$ L^{-1}), suggesting the declining phase of the *Phaeocystis* bloom in the southern Ross Sea. This condition can be placed in a seasonal context through comparison with other recent Ross Sea cruise data (Table 2). Primary production and Chl *a* standing stocks were lower than during the same November–December peak bloom period in 1994–1995, whereas bacterial biomass and production were greater, and the ratio of BP–PP was ca. 0.1

Table 2
Bacterial and phytoplankton standing stocks and productivity in the Ross Sea, 1996–1997

Cruise	Dates	Depth[a] (m)	Bact biomass[b] (mmol C m^{-2})	Mean abund. (10^9 cells l^{-1})	Bact prod[c] (mmol C m^{-2} d^{-1})	Chl a[b] (mg m^{-2})	PP[d] (mmol C m^{-2} d^{-1})	BP : PP	N
AESOPS P-1	18 Oct–7 Nov 96	142	5	0.1	0.3	20	30	0.04	11
AESOPS P-2	**12 Jan–6 Feb 97**	**43**	**36**	**1.5**	**5.4**	**83**	**57**	**0.11**	**13**
AESOPS P-3	16–29 April 97	226	23	0.3	1.1	5	2	0.81	11

[a]Euphotic zone depth to 0.1% I_0.
[b]based on 107 fgC $cell^{-1}$ (Carlson et al., 1999); C : Chl = 50.
[c]All BP estimates from leucine incorporation rate multiplied by 1.5 kg C mol^{-1} (Simon and Azam, 1989 and see text for choice of this value).
[d]PP estimates in this Table from on-deck ^{14}C incubations (Smith and Gordon, 1997).

(both integrated to the 0.1% I_0 depth, Table 2). Thus, at the time of the Process-2 cruise bacterial activity was probably near its annual maximum both in absolute and relative terms (excluding the high BP/PP ratios in Austral autumn–winter when PP is vanishingly low or nonexistent (e.g., P3 cruise in Table 2).

Nonetheless, bacterial biomass was low (Fig. 2). Bacterial stocks in the euphotic zone (1% I_0) averaged 11% of the phytoplankton. This small biomass was highly active relative to its size. Bacterial production at the main productivity stations averaged 13% of the O_2-based NCP to 1% I_0 (Fig. 3; range 2–26%).

Net community oxygen production (NCP) was positive at all stations, as expected in ice-free conditions and 24 h of daylight. NCP ranged from 25 to 140 mmol C m^{-2} d^{-1} (avg. 63 $\pm$ 37 S.D.). The 24-h dark respiration was greater than the NCP at seven stations and lower at the other three (Fig. 3), ranging from 39 to 209 mmol C m^{-2} d^{-1} (mean 72 $\pm$ 47). Net community production was positive at all stations during this cruise. Primary production estimated from 24 h, in situ C14 incubations ranged 15–90 mmol C m^{-2} d^{-1} (mean 35 $\pm$ 22), or 25–130% of the NCP (mean 55%). Fig. 3 suggests that Stations Minke and "O" in particular had relatively high levels of heterotrophic respiration (since dark respiration exceeded the NCP), but there was no simple relationship between DCR and BP or bacterial biomass (Model 2 regressions of BP, biomass and DCR, $p > 0.05$; $n = 10$, data not shown).

Under the assumption that BP = 3 kg C mol^{-1} Leu incorporated (see Methods), and arbitrarily requiring BR to be less than $g = 0.5$ of DCR (see Discussion for rationale for g values), we found that the BGE must be 0.36 or greater at all stations (rigorous constraints). The derived values for BR are compared to 0.5∗DCR in Fig. 4.

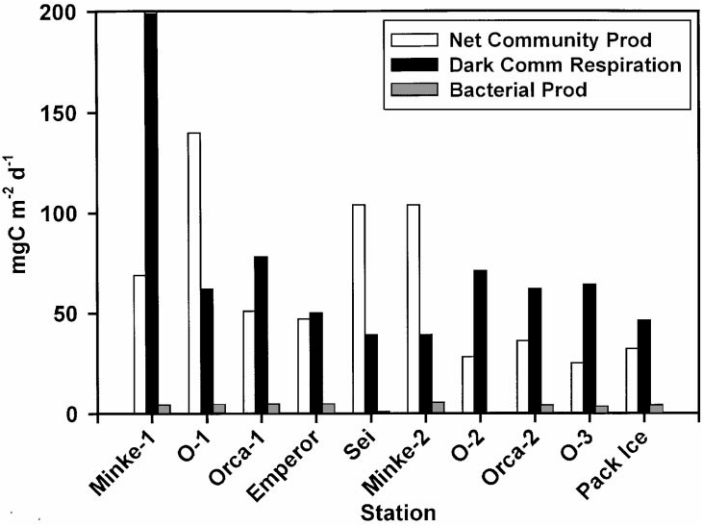

Fig. 3. Measured rates of net community production and dark community respiration determined by oxygen changes in vitro, bacterial production estimated from leucine incorporation (1.5 kg C produced mol^{-1} incorporated; see text for details).

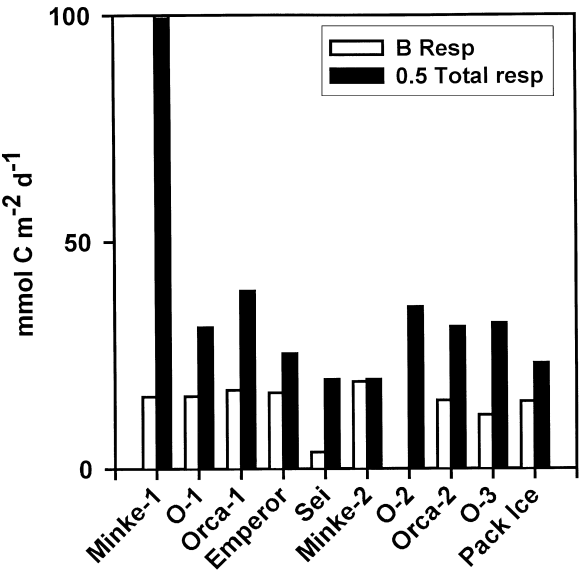

Fig. 4. Estimated bacterial respiration derived from BP estimates by assuming a conversion efficiency of 36%, compared to 50% of the measured total dark respiration rates. Note the equivalence of rates at station Minke-2. These estimates derived with BP = Leu∗3 kg C mol^{-1} (see text for details). Compare to Fig. 6.

It can be seen from the equal heights of the bars at Station Minke-2 that this station sets the value of g for this initial evaluation of the equations. BP was highest and DCR minimal at this station. If BGE is 0.36, the resulting BCD values require that the LDOM flux is at least $0.20 * \text{GPP}$. If f is less than 0.20, BCD will exceed the LDOM flux at least at one station, in this case Station Orca (Fig. 5). Station Orca had low GPP and moderately high BP (Fig. 3). These two values, BGE = 0.36 and the fractional LDOC flux $f = 0.20$ are the lowest values meeting the two constraints when $g = 0.5$, and set a kind of benchmark for considering bacterial carbon flux during this observation period. To be consistent with the observed bulk DOC accumulation of only 15– > 20 μM in the euphotic zone over longer time scales, the excess of DOC release over the BCD cannot be too great, as it is in Fig. 5 at some stations (e.g., Sei and Minke, black bars). Small-scale, short-term variations in DOC, especially of individual compounds, are not excluded by assuming this larger-scale balance. The gray bars show lower DOC release rates for a less rigorous scenario (see next paragraph and Table 3).

Criteria can be relaxed in several ways. Increasing g the fraction of DCR contributed by BR, results in lower BGE values. Decreasing the original BP estimates, for example by using a lower value for the leucine conversion factor, will also allow lower BGE. Finally, the constraining Eqs. (4A) and (5) can be relaxed by acknowledging that all measurements are subject to error, and thus not requiring the constraints to be met at all stations simultaneously. One way to do this is to minimize the sum of the

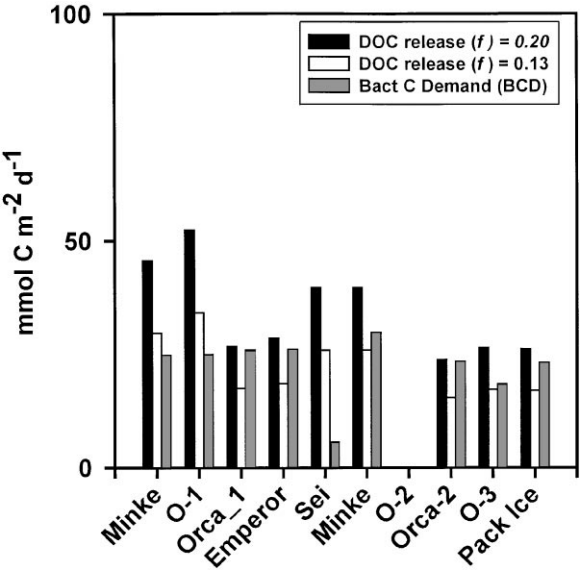

Fig. 5. Estimated DOC release required to meet the bacterial carbon demand (gross BP) derived from a 36% growth efficiency (see Fig. 3). These LDOC release rates are 21 and 13% of the corresponding GPP values at each station. Note equivalence of rates at stations O–3, and Pack Ice. These estimates derived with BP = Leu∗3 kg C mol^{-1} (see text for details).

Table 3
Scenarios for constraining bacterial respiration during the Process-2 cruise

LCF[a]	BR/DCR[b]	Constraints[c]	BGE[d]	LDOM/GPP[e]
3	0.11	Rigorous	0.72	0.10
3	0.11	Relaxed	0.57	0.06
3	0.5	Rigorous	0.36	0.20
3	0.5	Relaxed	0.23	0.13
1.5	0.11	Rigorous	0.56	0.07
1.5	0.11	Relaxed	0.40	0.06
1.5	0.5	Rigorous	0.22	0.17
1.5	0.5	Relaxed	0.13	0.11

[a]Leucine conversion factor (Simon and Azam, 1989).
[b]Fraction of total measured community respiration (Fig. 3) contributed by bacteria.
[c]See text for details.
[d]Bacterial conversion efficiency required to meet specified level for BR/ΣR.
[e]Release rate for labile DOM as a fraction of measured GPP (Table 2) required to meet bacterial carbon demand (BP + BR).

deviations between BR and DCR (i.e. minimize Σ(DCR-BR) summed over all stations, while allowing BR > DCR at some stations). Recognizing variability in the measurements (Fig. 6) indicates that BGE = 0.23 will meet relaxed criteria with $g = 0.5$ and BP = 3 kgC mol^{-1} Leu. This method of evaluating fits to criteria removes the

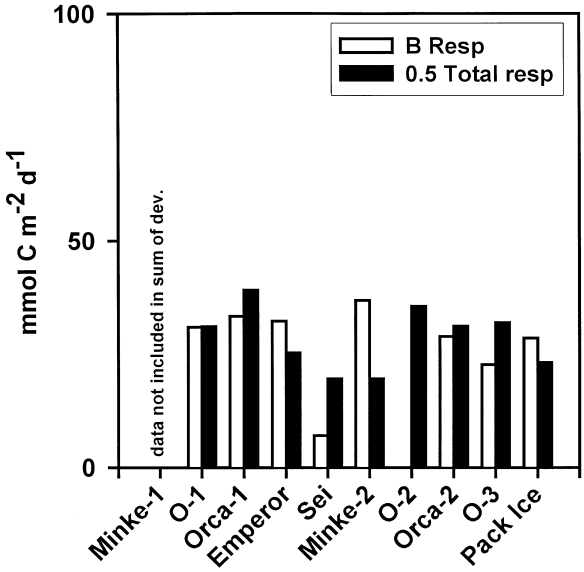

Fig. 6. Bacterial respiration derived assuming conversion efficiency was 23% to meet BR = 50% total respiration and acknowledging error in BP and total R measurements (relaxed criteria). Note similarity of most rates. See text for details.

sensitivity to the station with the lowest DCR value (in this case, Minke-2; Fig. 3). Fig. 6 shows that the derived bacterial respiration values are mostly balanced near the 0.5 * DCR criterion. If we allow BCD > LDOM release at some stations, this same technique yields a minimum LDOM release of 0.13 * NCP (Fig. 5). Table 3 summarizes BCD and LDOM release values for various assumptions and criteria. With our assumptions and criteria, permissible BGE values for this data set range from 0.13–0.72. As we point out below, most of the values in the upper half of this wide range are not likely, even if theoretically possible. The flux of LDOM must be at least 0.06 of the observed GPP, and varies over a relatively narrow range, 0.06–0.20, to meet the bacterial demand for carbon, given various scenarios for BCD, BP derivation, and the bacterial contribution to total respiration. Note that these low values for LDOM release are a consequence of referencing to GPP. Reference to C14 PP would result in higher release rates required to meet the BCD. At some stations f would have to be > 1 (i.e., the release > measured C14-PP) to meet the BCD.

4. Discussion

4.1. Community respiration

Our community respiration (DCR) observations averaged 73 mmol $C\,m^{-2}\,d^{-1}$ ($n = 10$, range 39–209) during the January–February period of the AESOPS Process-2

Table 4
Water column respiration rates in Antarctic waters.

Location and date	Rate (mmol C m^{-3} d^{-1})	Reference
Antarctic	0–15	Pomeroy, in Williams (1984)
Antarctic Peninsula, Feb. 93	10–130	Aristegui et al. (1996)
Antarctic Convergence[a]	0.3–3.7	Robinson and Williams (1993)
Bellingshausen Sea, Dec. 93[b]	0.5–2.6	Boyd et al. (1995)
Davis Station, Dec–Feb 93–94[a]	1–12	Robinson et al. (1999)
Ross Sea, Jan–Feb 1997[c]	39–209	This study
Ross Sea, Jan–Feb 1997[b]	2–37	This study

[a]Surface values.
[b]Upper 10 m.
[c]Euphotic zone to 1% I_0 (m mol $Cm^{-2}d^{-1}$).

cruise. There are relatively few measurements of community respiration from throughout the global marine environment (del Giorgio and Cole, 1998; Williams, 1998), at least compared to the large collection of primary production measurements made by various means. There are only a very few other respiration measurements in Antarctic waters for comparison (Table 4). The values for surface depths and integrated euphotic zone rates fall within the larger envelope defined in our study.

4.2. Bacterial contribution

We chose two reference values to evaluate the contribution of bacterial respiration to the total community respiration. BR = 50% DCR was chosen as a midrange value, after examining other reports of BR/DCR (see below). Our other choice, BR = 11% DCR, was chosen by assuming that each component of DCR was proportional to its biomass. The bacterial stocks averaged 11% of phytoplankton stocks during the January–February period. Direct determination of bacterial respiration is difficult and may be subject to artifacts of sample preparation and other systematic and site-specific errors (Hopkinson et al., 1989). In general, direct oxygen utilization or (in a few cases) CO_2 production is measured following gentle size fractionation through 0.8–1.0 μm filters (Williams, 1981; Chin-Leo and Benner, 1992; Coffin et al., 1993). BR/DCR has been estimated indirectly by measuring BP, assuming some growth efficiency (BGE) and then comparing the derived BR to DCR (e.g., Robinson et al., 1999). Since our analysis involved a variant on this procedure, we only review the direct determinations of bacterial respiration, recognizing that they are also subject to error.

The bacterial fraction of community respiration varies widely, depending on trophic status, location, season and other factors. del Giorgio and Peters (1993) suggested from analysis of 118 lakes that bacterial respiration varied systematically as a function of chlorophyll content. Bacterial respiration was a maximum of about 50% of DCR when Chl was < 1 μg L^{-1}, declining to 25–30% above Chl = 50 μg L^{-1}. They also indicated bacterial respiration was a larger fraction of DCR in lakes than in marine systems.

BR/DCR ranged 7–93% in the Mississippi River Plume (Chin-Leo and Benner, 1992) and 30–50% in other estuarine and coastal marine systems (Hopkinson et al., 1989; Sand-Jensen et al., 1990) and lakes (Schwaerter et al., 1988). There are few direct bacterial respiration measurements from oceanic regions, largely because rates are too low to measure without extended incubations or sample concentration (e.g., Pomeroy and Johannes, 1968). Fasham et al. (1999) used related observations and a numerical model to estimate system carbon flows at 47°N, 20°W in the North Atlantic. They estimated that bacterial respiration was 39% of DCR for the period 1–21 May 1990.

There are few direct measurements of size-fractionated bacterial respiration rates in Antarctic waters. Robinson et al. (1999) observed that 53% of 10.5 mmol O_2 m^{-3} d^{-1} was < 0.8 μm in a single sample, and that 94% of 4.9 mmol O_2 m^{-3} d^{-1} was < 2 μm in another sample. They also indirectly estimated a bacterial contribution of 5–21%, using thymidine-based BP estimates and assuming a BGE of 0.4. Aristegui et al. (1996) did not partition respiration rates but suggested phytoplankton respiration itself was the major contributor. Karl et al. (1996) also stated that bacterial respiration was a relatively small fraction of DCR west of the Antarctic Peninsula. From these few previous studies it seems likely that bacterial respiration is a small fraction ($< 20\%$) of the total community respiration in Antarctic coastal waters, during the peak to declining phases of phytoplankton blooms, but larger values cannot be ruled out. Carlson et al. (1999) determined CO_2 production rates in < 0.8 μm filtrates in dark gas-tight bags (Kruse, 1993) on the same cruise as our measurements, finding bacterial respiration rates ranging 0.21–0.56 mmol C m^{-3} d^{-1}, or 7–18% of the mean surface DCR rates. This level of BR/DCR also was supported by independent oxygen measurements made in the same bags (J. Orchardo, pers. comm.).

If BR/DCR were uniformly 50% at all stations, BR would have ranged 20–100 mmol C m^{-2} d^{-1} (solid bars in Fig. 4), or 1–2.6 μM O_2 d^{-1} in the surface samples (data not shown). These bacterial respiration values would be equivalent to those measured in a shallow eutrophic fjord in summer (Sand-Jensen et al., 1990), and by Coffin et al. (1993) in coastal Florida in summer. In this context, BR/DCR approaching 50% seems high for the Ross Sea when bacterial biomass was ca. 10% of the (declining) phytoplankton biomass.

4.3. Bacterial conversion efficiency

After setting reference limits for BR/DCR we derived BR from measured BP values (Fig. 3) by assuming various BGE values that allowed BR/DCR to meet the imposed constraints. BGE has been determined directly from measurements of BP and < 1 μm respiration (Chin-Leo and Benner, 1992; Coffin et al., 1993; Daneri et al., 1994); or by comparing BP and total carbon utilization (Kirchman et al., 1991; Zweifel et al., 1993; Carlson et al., 1999). Like BR/DCR, the BGE values range widely (Jahnke and Craven, 1995; del Giorgio and Cole, 1998), from $< 10\%$ (Kirchman et al., 1991) to over 60% in some enriched samples (Coffin et al., 1993). del Giorgio and Cole (1998) conclude that BGE is generally ca. 20% in marine waters, but with large variation. Bjornsen and Kuparinen (1991) estimated that BGE was 40% in the Weddell-Scotia Confluence

(ca. 60°N, 50°W) in December 1988. Carlson et al. (1999) estimated BGE in the dark incubations of Ross Sea water (76.5°S) from DOC utilization and CO_2 production. Their values for BGE ranged from 9% in December, 1995 to 38% on our cruise in January–February 1997. In view of the wide range in the literature, we left BGE as a free parameter in our exercise, and varied it to meet the other constraints we imposed.

4.4. DOM release rates

There is a large literature on DOM release by phytoplankton (e.g., Williams, 1990; Wood et al., 1992) and to a lesser extent on DOM release by zooplankton and protozoa (Strom et al., 1997). As with the other processes, however, there are few direct measurements in Antarctic waters. Davidson and Marchant (1992) found that DOC and *Phaeocystis* abundance covaried in time in Prydz Bay, implicating *Phaeocystis* as a major DOC source in Antarctic waters. In contrast, Carlson et al. (1998) observed few changes in [DOC] in space or time during *Phaeocystis* blooms in our study area in 1994–1995, or subsequently on the US JGOFS 1996–1997 cruises (unpubl. data available at: http://usjgofs.whoi.edu/jg/serv/jgofs/southern/nbp97_1/DOC.html). Interestingly, *Phaeocystis* species exhibit the widest range of DOM excretion rates, normalized to production rates, from < 5 to $> 50\%$ (Nagata, 2000). Smith et al. (1998) showed that DOC release by nutrient-depleted *Phaeocystis* assemblages could be very high, but macronutrients are seldom, if ever, depleted in the central Ross Sea (Table 1). There is some evidence that phytoplankton were moderately iron-depleted during Process-2, however (Dickson, unpub. data). Net DOC production is about 10–15% of NCP in the Ross Sea (Carlson et al., 1998; Hansell and Carlson, 1998). During the Jan–Feb. cruise, *net* $DO^{14}C$ release averaged 23% of the total ^{14}C-based production (range 0–77%; J. Marra, unpub. data). The ^{14}C measurements address mainly the direct release of DOC from phytoplankton, rather than total release from all plankton components. Estimating total release including release mediated by grazers and grazer excretion is more difficult. Recently Strom et al. (1997) showed that DOM release from phytoplankton in the presence of grazers was 4–6 times greater than from phytoplankton alone. Using a numerical simulation model of the Scotia-Weddell region, Lancelot et al. (1991) estimated that the cumulative DOC release during ice edge retreat was 42% of the 17.5 gC m^{-2} NPP. About half the release was due to sloppy feeding by zooplankton. However, both mesozooplankton and microzooplankton grazing and biomass are low in the Ross Sea. This latter observation suggests that total DOC release was probably low ($< 30\%$ of the NCP) during our cruise, but sporadic high-release 'events' cannot be ruled out. In any case, the amount of DOC release estimated to balance the bacterial requirement in this study was just 6–20% of the measured GPP.

4.5. Implications and conclusions

Community respiration rates (DCR) determined during the decline of the *Phaeocystis* bloom in the southern Ross Sea in 1997 appear similar to previous estimates from

coastal Antarctic as well as oceanic regions (Table 4, Williams, 1998). Based on the previous literature for the region as well as biomass data, we suggest it is most likely that bacterial respiration contributed somewhat less than half the total respiration, perhaps only 10–20%. Accepting at face value the total community respiration and bacterial production rates we observed (Fig. 3), bacterial conversion efficiency would have had to be at least 40–72% to keep BR within 11% of DCR (Table 3). These values are higher than most recent estimates for Southern Ocean or other systems (del Giorgio and Cole, 1998). If BR was 50% of DCR, the BGE could have been 13–36%, closer to other estimates. If we adopt a lower value for the leucine conversion factor (1.5 kgC mol^{-1}; Simon and Azam, 1989), it is still difficult to obtain low BR estimates without using rather high BGE values (40–56%; Table 3). However, BGE values of 33–38% derived during our cruise (Carlson et al., 1999) are probably not significantly different from the lower end of the BGE range needed to meet a BR/DCR ceiling of 10–20%.

The magnitude of LDOC flux meeting bacterial demands for these scenarios ranges from 15 to 74% of the mean NCP (Table 3), similar to the observed range of ^{14}C DOC release rates measured on the cruise. The total DOM flux integrates a myriad of processes, including phytoplankton exudation, zooplankton sloppy feeding and bacterial hydrolysis (Smith et al., 1992). The latter process may be significant during the declining phase of the *Phaeocystis* bloom when bacteria are commonly attached to *Phaeocystis* colonies (Putt et al., 1994).

In conclusion, this analysis supports findings by Carlson et al. (1999) and extends their application to larger time and space scales. BR could have been a relatively minor part of DCR only if the BGE was at least 33–38%. Further, the average BP could not be much larger than ca. 5 mmol C m^{-2} d^{-1} (Table 3). This level of BP requires a value for the Leu factor toward the lower end of the range given by Simon and Azam (1989). These lower BP values are near the minimum values that can be derived for the measured Leu incorporation rates. Stated another way, higher BP values (derived from larger Leu factors) are only consistent with the community respiration data if BGE is $> 35\%$ and if BR/DCR is $\geqslant 50\%$, an unlikely scenario for the reasons considered here. Although the required levels of BP are low, they are not inconsistent with most generalizations about coastal Antarctic waters (Karl, 1993). Low BP values coupled with relatively high growth efficiency (35–40%) do appear sufficient to balance the low DOM production rates observed in the Ross Sea. Finally, the balance between BCD and LDOC release indicates most of the released DOM was labile on time scales of days–weeks, even at low temperature (Carlson et al., 1998).

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