PERGAMON

Deep-Sea Research II 49 (2002) 769–786

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Phytoplanktonic DOC and POC production in the Bransfield and Gerlache Straits as derived from kinetic experiments of ^{14}C incorporation

Xosé Anxelu G. Morán*, Marta Estrada

Departament de Biologia Marina i Oceanografia, Institut de Ciències del Mar, CSIC, Pg. Joan de Borbó, s/n, E-08039 Barcelona, Spain

Received 13 May 1999; received in revised form 4 April 2000; accepted 16 May 2001

Abstract

The production rates of DOC and POC by phytoplankton during the FRUELA 95 cruise were estimated by means of time-course experiments of ^{14}C-bicarbonate incorporation. A three-compartment carbon exchange model was used to avoid the artifacts that may appear in end-point experiments due to heterotrophic removal of recently released DOC. The study area was classified into three regions with different ecological characteristics: Bransfield Strait, Gerlache Strait and the Gerlache–Bransfield Confluence (GB Confluence). Percent extracellular release (PER) for all stations ranged from 3% to 47%, with an average of 24%. In surface (5 m depth) waters, POC and DOC production rates were higher in Gerlache Strait than in the GB Confluence and Bransfield Strait. PER values followed an opposite trend, with an average of 26% in Bransfield Strait, 17% in the GB Confluence and 13% in Gerlache Strait. In Gerlache Strait, PER at 10 m depth was significantly higher than at the surface. With pooled data from all experiments, there was a positive relationship between DOC and POC production rates (log–log), but the slope significantly smaller than 1.0 indicated an inverse trend between PER and primary production rate. Phytoplanktonically produced DOC appeared to meet carbon requirements of heterotrophic prokaryotes in the whole area. A positive relationship between prokaryotic heterotrophic production and DOC production rate was found only in Bransfield Strait. These differences are discussed in relationship with the ecological characteristics of the different regions

1. Introduction

A growing deal of information on primary production in Antarctic waters is becoming available (e.g., Bodungen et al., 1986; El-Sayed, 1988; Holm-Hansen and Mitchell, 1991; Arístegui et al., 1996). It is commonly assumed that most of the carbon fixed is incorporated to algal biomass and thus, most frequently, the release of dissolved organic matter during phytoplankton growth has been considered as a marginal contribution to total primary production rates and has been disregarded. Although it is widely accepted that release of dissolved organic carbon (DOC) represents less than 20% of total primary production (Baines and Pace, 1991; Jackson, 1993; Hansell and Carlson, 1998), there are reports of considerably higher values (e.g., Joiris et al., 1982; Chróst

*Corresponding author. Present address: Instituto Español de Oceanográfía, Centro Oceanográfico de Xixón, Camín de L'Arbeyal, s/n E-33212 Xixón, Spain. Tel.: +34-985-308672; fax: +34-985-326277.

E-mail address: xelu.moran@gi.ieo.es (X.A.G. Morán).

0967-0645/01/$ - see front matter
PII: S0967-0645(01)00123-0

and Faust, 1983), and much controversy remains about the importance of DOC release by healthy cells (Bjørnsen, 1988).

Dissolved compounds released by phytoplankton are important as a readily assimilable substrate for heterotrophic bacterioplankton, as has been emphasized in many studies (e.g., Wiebe and Smith, 1977; Lancelot, 1979; Jensen, 1983; Cole et al., 1988: Leboulanger et al., 1997). Apart of its ecological importance, this fact has methodological implications for the measurement of the rate of DOC release by algae. Concurrent bacterial assimilation of algal released products may produce underestimation of DOC release rates in endpoint measurements of ^{14}C incorporation into organic molecules (Riemann and Søndergaard, 1984). This may explain part of the high variability in reported DOC release values, which range from 0% to ~80% of total primary production (Malinsky-Rushansky and Legrand, 1996). To avoid these potential artifacts, time-course experiments of ^{14}C incorporation into the dissolved fraction have been recommended (Lancelot, 1979; Smith, 1982; Smith and Platt, 1984).

Many studies have shown strong positive correlations between phytoplanktonic and heterotrophic bacterial biomass and production in different systems, including Antarctic waters (Bird and Karl, 1991; Kähler et al., 1997). Although most of these works have considered only particulate primary production, one of the generally accepted explanations is that organic matter released by phytoplankton may be an important substrate for bacterial growth (Larsson and Hagström, 1982; Cole et al. 1988; Williams, 1990; Wood and Van Valen, 1990), especially in regions like the Southern Ocean, where allochthonous inputs of DOM are negligible (Bird and Karl, 1991). In systems other than cold waters it has been shown that as much as 25% of bacterial carbon requirements may be satisfied by DOC released by phytoplankton (Lignell, 1990), while up to more than 50% of the primary production is potentially consumed by bacterioplankton (Cole et al., 1982; Bell et al., 1983; Søndergaard et al., 1985). The lack of relationship between phytoplankton and heterotrophic bacteria reported in some cases has been attributed to particulate primary production or chlorophyll *a* being poor predictors of the DOC actually available to bacteria (Pace and Cole, 1996). Knowledge of the production rate of DOC by phytoplankton, in comparison with other potential sources of DOC, should therefore give insight into the ecological relationships between autotrophic and heterotrophic components of the microbial food web.

The term "bacteria" commonly refers not only to true bacteria but also to archaea. However, as archaea represent a relevant contribution to the abundance and activity of the whole community of heterotrophic prokaryotes in the Southern Ocean (Pedrós-Alió et al., 2002), the terms "prokaryotes" and "prokaryotic production "will be used hereinafter.

One of the goals of the FRUELA project was the determination of the carbon fluxes among the main planktonic components of the Bransfield and Gerlache Strait ecosystems, and the carbon transfers among them. Our research, based on experiments carried out during the FRUELA 95 cruise, aimed to (i) estimate algal particulate and dissolved production rates by means of time-course experiments of ^{14}C uptake, and (ii) test the relationships existing between different variables of phytoplankton and prokaryotic plankton biomass and production, with special emphasis on ascertaining the potential role of phytoplanktonic DOC production in supplying the carbon required for the growth of heterotrophic prokaryotes.

2. Material and methods

2.1. Study area

Experiments were carried out in the Gerlache and Bransfield Straits during the FRUELA 95 cruise on board the R/V *Hespérides*, from 4 December 1995 to 4 January 1996. The stations were divided into three different groups (Fig. 1), named roughly after their geographic location, according to the dominant phytoplankton assemblages found and their primary productivity (Varela et al., 2002).

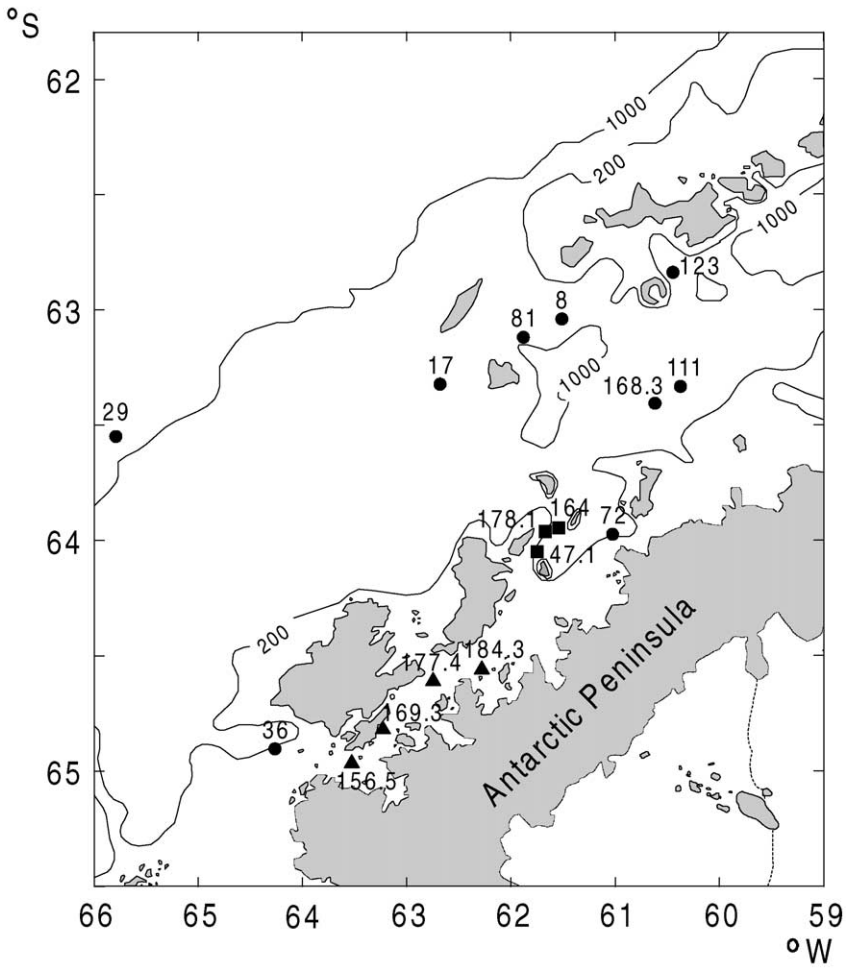

Fig. 1. Map of the studied area showing the positions of the sampled stations in Gerlache Strait (circles), the GB Confluence (squares) and Bransfield Strait (triangles). Stations 17 and 29, located in the Bellingshausen Sea, were grouped with Bransfield Strait stations.

2.2. Chlorophyll a determination

Chlorophyll *a* (Chl *a*) was estimated fluorometrically with a Turner Designs fluorometer. Samples of 50–100 ml were filtered onto Whatman GF/F filters and frozen. Pigments were extracted in acetone (90%) for 24 h in the dark, at 4°C, before measuring fluorescence.

2.3. ^{14}C measurements

Time-course incorporation of carbon into the dissolved and particulate fractions was measured by the ^{14}C-technique (Steemann-Nielsen, 1952). Water for incubations was collected from surface (5 m depth), and at some stations also from 10–15 m depth, in 12-l Niskin bottles attached to a rosette sampler. Aliquots (70 ml) were introduced in sterile polystyrene tissue culture bottles (Corning). The bottles were inoculated with 0.3–0.7 MBq (8.4–19 μCi) of ^{14}C-bicarbonate and incubated under constant light conditions. Surface samples were incubated under 90–100 μmol photons $m^{-2} s^{-1}$ except for samples from stations 8, 17 and 29, which were incubated under 50 μmol photons $m^{-2} s^{-1}$. In both cases saturation was

achieved. Samples from 10–15 m depth were incubated under 9 μmol photons $m^{-2} s^{-1}$ to match the decreased irradiance at these depths (on average 7% ± 4% of surface values, Figueroa, 2002). Incubations were made in controlled-temperature baths fixed at in situ temperature (±0.5°C). Part of the bottles (dark bottles) was covered with aluminium foil.

We used Whatman GF/F filters for separating the particulate and dissolved fractions of primary production. Recently, it has been shown (Karl et al., 1998; Morán et al., 1999) that POC production is variably overestimated (and DOC subestimated) by using GF/F filters, as a consequence of DOC adsorption to glass fibers. Four dark bottles (time-zero bottles) were processed immediately at the beginning of the experiment, in the same way as the dark bottles of the subsequent sampling times. In these samplings, aliquots of 5 ml were taken from two light and two dark bottles for determination of total labelled organic carbon (TOC), and the remaining 65 ml were filtered on GF/F filters for determination of total labelled POC. Aliquots of 5 ml from the remaining two light and two dark bottles also were filtered on GF/F filters and the filtrate collected for determination of labelled DOC. The remaining 65 ml were filtered on Nuclepore polycarbonate 0.8- or 2-μm filters (data not shown). Filtration through GF/F filters for DOC sampling was made by gravity. In the other cases, filtration pressure did not exceed 100 mm Hg. Filters were treated with concentrated HCl fumes for ca. 12 h before addition of 4.5 ml of ReadySafe liquid scintillation cocktail. Liquid samples (with labelled TOC or DOC) were acidified with 1 ml HCl 6 M and left open in an orbital shaker for 12 h before addition of 15 ml of scintillation cocktail. Radioactivity was measured in a Beckman LS6000LL liquid scintillation counter. The time-zero values were subtracted from all subsequent samples for correction of abiotic incorporation. Dark bottle values after time-zero blank subtraction were on average 4% ± 1% (SE) of the light bottle values for POC measurements, 24% ± 4% of those for DOC and 16% ± 3% of those for TOC, and did not increase appreciably during the experiments. These dark bottle values were not subtracted, following the recommendation of Watanabe (1980). In each experiment, the radioactivity of the ^{14}C-bicarbonate solution added to the incubation bottles was determined in 20-μl aliquots.

2.4. Carbon exchange model and compartmental analysis

A simple 3-compartment carbon exchange model for obtaining steady-state rates of production of POC and DOC was used (Fig. 2). The equations defining the rates of change of carbon in the compartments are:

$$dC_1/dt = -k(2,1)C_1 + k(1,2)C_2 - k(3,1)C_1, \quad (1)$$

$$dC_2/dt = k(2,1)C_1 - k(1,2)C_2 + k(2,3)C_3, \quad (2)$$

$$dC_3/dt = k(3,1)C_1 - k(2,3)C_3, \quad (3)$$

where C_i is the carbon concentration in pool i, and $k(i,j)$ is the fractional rate constant of flux from C_j to C_i $k(2,1)$ is the constant of particulate carbon production and would reflect only photosynthetically produced carbon. $k(1,2)$ is considered the constant of respiration of synthesized POC, inferred from its influence on $PO^{14}C$ kinetics. $k(3,1)$ is the constant of DOC

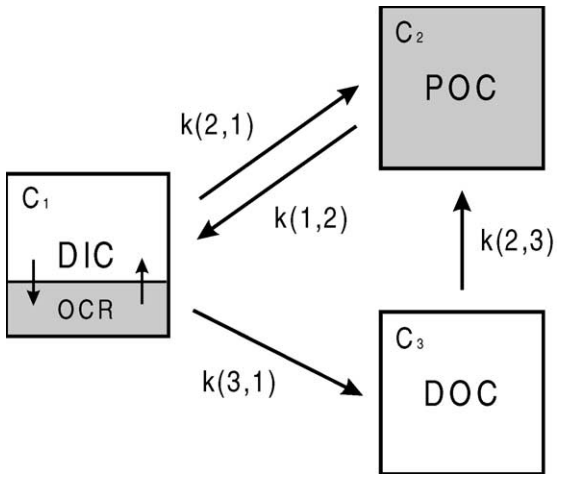

Fig. 2. Carbon exchange model fitted to experimental data. The shaded compartments are intracellular pools. OCR represents the phytoplanktonic pool of organic carbon products fated for release, which is assumed to be in isotopic equilibrium with DIC.

production. No distinction is possible between active excretion by phytoplankton and other sources of labelled DOC release, such as cell lysis. $k(2,3)$ is the constant of heterotrophic assimilation of recently released DOC. The inverse of the rate constant $k(2,3)$ is the turnover time of the photosynthetically produced DOC pool (Lancelot, 1979).

The performance of alternative 3-compartment carbon exchange models (see Discussion) was first evaluated by the residual sum of squares (RSS) after fitting to data, as a measure of the remaining unexplained variance. The model which minimized the average RSS for all experiments was chosen. Least-squares non-linear fitting of the model to actual measurements of $DO^{14}C$ and $PO^{14}C$ was made with software especially designed for such compartmental analysis (SAAM II, SAAM Institute, Washington). Data were weighted by the inverse of the standard deviation of duplicates. These analyses yielded estimates of the rate constants of flux between compartments ($k(i,j)$, in units h^{-1}) and of their variance and total remaining unexplained variance. Once the model was fitted to a set of data, it was possible to derive the DOC and POC production rates ($mg\,C\,m^{-3}\,h^{-1}$) from the estimates of the rate constants and the concentration of dissolved inorganic carbon (DIC) at each sampling site (Álvarez et al., 2002). No isotopic discrimination factor was considered for the conversion of dpm to carbon units. Percent extracellular release (PER) was calculated as the ratio of DOC production rate to the sum of POC and DOC production rates.

In order to detect potential errors in the measurement of radioactivity in the liquid samples, a 2-compartment model for obtaining direct estimation of TOC production rates was fitted to $TC^{14}C$ values. The equations describing the fluxes between DIC and TOC are as follows:

$$dC_1/dt = -k(2,1)C_1 + k(1,2)C_2, \quad (4)$$

$$dC_2/dt = k(2,1)C_1 - k(1,2)C_2, \quad (5)$$

where C_1 represents carbon content in the DIC pool and C_2 carbon content in the TOC pool. This model accounts for losses of synthesized organic carbon during the incubation time, which are described by the rate constant $k(1,2)$. These results were compared with the sum of POC and DOC production rates calculated in the 3-compartment model described above.

To compare DOC and POC production rates derived from compartmental analysis with those that would have been obtained from end-point experiments (Table 2), end-point production rates were obtained by simply dividing the final content of labelled DOC and POC in the water by the incubation time.

Statistical procedures other than time-course fitting were made with the JMP statistical package. Data were log-transformed (base 10) for attaining normality and homogeneity of variances. All linear regressions were made according to model I (Ricker, 1973), except when stated. The coefficient of determination given is the adjusted (R^2_{adj}).

2.5. Prokaryotic heterotrophic production and abundance

The production of heterotrophic prokaryotes was estimated with the ^{3}H-leucine incorporation method (Smith and Azam, 1992). For more details on methodology and conversion factors see Pedrós-Alió et al. (2002). Prokaryotic abundance was measured according to the methodology of Vaqué et al. (2002).

3. Results

In total, 24 experiments were made at stations located in the Gerlache and Bransfield Straits. Fitting failed in two experiments due to insufficient data points; rate constants for the remaining 22 are given in Table 1.

3.1. End-point vs. kinetic experiments

A comparison between the results obtained with time-course experiments and subsequent compartmental analysis with those that would have been obtained from end-point measurements is shown in Table 2. In general, estimated POC production rates changed little regardless of

Table 1
Fitted rate constants of flux between compartments[a]

Region	Station	Depth (m)	$k(2,1)$	$k(1,2)$	$k(3,1)$	$k(2,3)$
			h^{-1}			
B	8	5	5.98×10^{-5}	0.012	1.83×10^{-5}	0
B[b]	17	10	9.07×10^{-5}	0.188	5.94×10^{-5}	0.447
B[b]	29	5	4.52×10^{-4}	0	1.15×10^{-4}	0
B	72	5	1.20×10^{-4}	0	9.86×10^{-5}	0.507
B	81	5	8.33×10^{-5}	0	3.79×10^{-5}	0
B	111	5	8.32×10^{-5}	0	1.60×10^{-5}	0
B	123	5	4.57×10^{-5}	0.053	2.84×10^{-5}	0.106
B	140	5	1.46×10^{-4}	0.081	4.59×10^{-5}	0.195
B	34.1[c]	5	3.38×10^{-4}	0.064	1.61×10^{-4}	0.124
B	36	5	1.67×10^{-4}	0.298	3.89×10^{-5}	0
B	168.3	5	3.53×10^{-4}	0	5.31×10^{-5}	0
G	156.5	5	6.09×10^{-4}	0.062	5.47×10^{-5}	0
G	169.3	5	4.18×10^{-4}	0	1.03×10^{-4}	0.231
G	169.3	10	1.48×10^{-4}	0.086	4.12×10^{-5}	0
G	177.4	5	5.37×10^{-4}	0.047	1.55×10^{-4}	0
G	177.4	10	1.59×10^{-4}	0.042	5.83×10^{-5}	0
G	184.3	5	1.47×10^{-3}	0	4.36×10^{-5}	0
G	184.3	10	2.33×10^{-5}	0	2.10×10^{-5}	0.521
GB	47.1	5	4.19×10^{-4}	0	5.01×10^{-5}	0
GB	164	5	1.22×10^{-4}	0	2.53×10^{-5}	0
GB	178.3	5	6.68×10^{-5}	0.041	2.18×10^{-5}	0.497
GB	178.3	10	3.31×10^{-5}	0.079	9.58×10^{-6}	0.125

[a] B, Bransfield Strait; G, Gerlache Strait; GB, Gerlache–Bransfield Confluence.
[b] Station located in the Bellingshausen Sea, but considered within the Bransfield Strait region.
[c] Incubation time for Station 34.1 was 12.15 h, so it was excluded in the remaining analysis.

the methodology used (kinetic or end-point). The average ratio of POC_k (POC production rate obtained from kinetic analysis) to $POC_{e\text{-}p}$ (POC production rate obtained from end-point measurements) was 1.00.

Estimated DOC production rates were very different depending on the methodology. In 8 out of 21 experiments, time-course data were clearly non-linear and, as expected, introduction of a correction for heterotrophic uptake of $DO^{14}C$ resulted in higher DOC production rates. Overall, estimated DOC production rates were 43% lower when derived from end-point than when obtained from kinetic experiments (ratio $DOC_k/DOC_{e\text{-}p} = 1.75$), but in individual cases they could be up to 4 times lower. Accordingly, estimated average percent extracellular release (PER) decreased from 24% to 18%. Given the better performance of kinetic experiments, as discussed below, only these results will be considered in the following sections.

3.2. POC and DOC kinetics

The time-course of appearance of labelled POC and DOC in the different experiments followed two different patterns: linear and non-linear (asymptotic). Two examples are shown in Fig. 3, corresponding to stations 72 (Fig. 3A) and 177.4 (Fig. 3B). In Fig. 3A, both $PO^{14}C$ and $DO^{14}C$ fitted curves show non-linearity. The estimated rate constant for heterotrophic removal of recently labelled DOC was $k(2,3) = 0.51\ h^{-1}$. This labelled DOC taken up by prokaryotes appears as part of the total labelled POC pool. In contrast, Fig. 3B shows a slight non-linearity only for the $PO^{14}C$, but shows no indication of removal of labelled DOC; accordingly, the fitted $k(2,3)$ was 0.

Table 2
Rates of POC and DOC production (POC-pr, DOC-pr), percentage extracellular release (PER), $POC_k/POC_{e\text{-}p}$ and $DOC_k/DOC_{e\text{-}p}$ ratios and difference in PER obtained with kinetic and end-point experiments[a]

Region	Station	Depth (m)	Date	Kinetic (k)			End-point(e-p)					
				POC-pr	DOC-pr	PER (%)	POC-pr	DOC-pr	PER (%)	$POC_k/POC_{e\text{-}p}$	$DOC_k/DOC_{e\text{-}p}$	$PER_k-PER_{e\text{-}p}$ (%)
				$mg\,C\,m^{-3}\,h^{-1}$			$mg\,C\,m^{-3}\,h^{-1}$					
B	8	5	04.12.95	1.62	0.50	23	1.47	0.38	20	1.10	1.31	3
B[b]	17	10	06.12.95	2.41	1.58	40	2.45	0.49	17	0.98	3.20	23
B[b]	29	5	08.12.95	11.63	2.95	20	13.43	2.64	16	0.87	1.12	4
B	72	5	13.12.95	3.20	2.62	45	4.95	0.95	16	0.65	2.76	29
B	81	5	14.12.95	2.22	1.01	31	2.22	0.25	10	1.00	4.00	21
B	111	5	16.12.95	2.19	0.42	16	2.18	0.88	29	1.00	0.48	−13
B	123	5	17.12.95	1.21	0.75	38	1.29	0.40	24	0.94	1.88	15
B	140	5	18.12.95	3.94	1.24	24	3.53	0.86	20	1.12	1.43	4
B	36	5	20.12.95	4.41	1.03	19	2.82	1.50	35	1.56	0.68	−16
B	168.3	5	26.12.95	9.50	1.43	13	10.17	1.47	13	0.93	0.97	0
G	156.5	5	21.12.95	15.74	1.41	8	14.16	1.53	10	1.11	0.93	−1
G	169.3	5	28.12.95	11.15	2.75	20	11.58	3.13	21	0.96	0.88	−1
		10		3.96	1.11	22	3.13	1.05	25	1.26	1.06	−3
G	177.4	5	30.12.95	14.04	4.05	22	12.83	5.16	29	1.09	0.78	−6
		10		4.21	1.54	27	3.89	1.76	31	1.08	0.88	−4
G	184.3	5	04.01.96	37.43	1.11	3	37.32	1.12	3	1.00	0.99	0
		10		0.62	0.56	47	0.95	0.09	9	0.65	6.10	39
GB	47.1	5	11.12.95	11.04	1.32	11	11.42	1.12	9	0.97	1.17	2
GB	164	5	23.12.95	3.22	0.67	17	3.79	0.78	17	0.85	0.86	0
GB	178.3	5	02.01.96	1.73	0.56	25	2.09	0.13	6	0.83	4.19	19
		10		0.86	0.25	22	0.78	0.22	22	1.10	1.13	0
Mean				6.97	1.37	24	6.98	1.23	18	1.00	1.75	5
SE				1.83	0.21	3	1.82	0.26	2	0.04	0.32	3

[a] Region initials as in Table 1.
[b] Station located in the Bellingshausen Sea, but considered within the Bransfield Strait region.

In the experiments in which DOC labelling presented an asymptotic curve (and therefore a non-zero value of $k(2,3)$ was obtained, as in Fig. 3A), the turnover time of the photosynthetically produced DOC pool could be calculated as the inverse of the $k(2,3)$ rate constant (Lancelot, 1979). These estimated turnover times ranged from 1.9 to 9.4 h (average of 4.8 ± 3.1 h).

A good agreement was found between the sum of DOC and POC production rates estimated from the chosen 3-compartment model and the TOC production rate obtained from the 2-compartment model (Fig. 4), although the sum of POC and DOC production rates were on average 9% higher than the direct measurements total organic carbon production.

3.3. POC and DOC production rates

POC production rates (POC-pr) (Table 2) ranged from 0.62 to $37.43\,mg\,C\,m^{-3}\,h^{-1}$ (average of $6.97\,mg\,C\,m^{-3}\,h^{-1}$). The rate constant of respiration of synthesized POC ($k(1,2)$) during the incubation was lower than $0.10\,h^{-1}$ for most stations. DOC production rates (DOC-pr) ranged from 0.25 to $4.05\,mg\,C\,m^{-3}\,h^{-1}$ (average of $1.37\,mg\,C\,m^{-3}\,h^{-1}$). PER for all experiments ranged from 3% to 47%, with an average of $24\% \pm 3\%$ (SE).

A good agreement was found between the rate of TOC production and the sum of DOC and POC production rates estimated separately. The slope of the regression did not differ significantly from 1 ($p = 0.117$; $n = 19$), although the sum of POC and

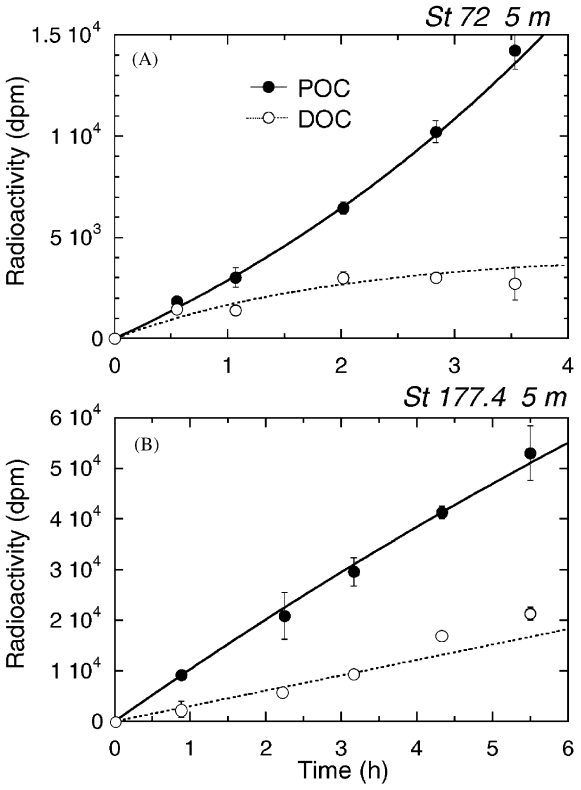

Fig. 3. PO^{14}C and DO^{14}C time-series for the experiments carried out at stations 72 (A) and 177.4 (B). Curves fitted are derived from the 3-compartment model of Fig. 2. Vertical bars are standard deviations of duplicates.

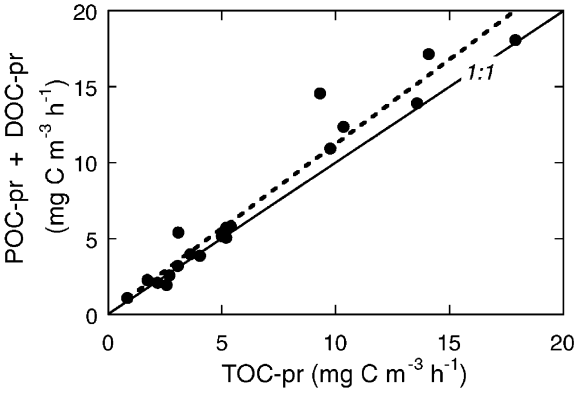

Fig. 4. Relationship between the sum of POC and DOC production rates and TOC production rate calculated from the 2-compartment model explained in the text. The regression line shown is: POC-pr + DOC-pr = 0.15 + 1.11 TOC-pr ($R^2 = 0.94$; $n = 19$).

DOC production rates was 11% higher than total primary production (Fig. 4).

Mean values of surface POC and DOC production rates and PER for the three regions considered are shown in Fig. 5. The experiments made in Gerlache Strait with water from 10 m depth were considered separately. Both POC and DOC production rates were highest in Gerlache Strait, at the surface, with an average of 19.51 and 2.33 mg C m^{-3} h^{-1}, respectively. In the Gerlache–Bransfield Confluence, average production rates were 5.33 mg C m^{-3} h^{-1} for POC and 0.85 mg C m^{-3} h^{-1} for DOC. In Bransfield Strait, POC was 4.44 mg C m^{-3} h^{-1} and DOC was 1.33 mg C m^{-3} h^{-1}. At 10 m depth (only Gerlache Strait stations considered) POC production rate was the lowest (2.93 mg C m^{-3} h^{-1}), with a DOC production rate of 1.07 mgC m^{-3} h^{-1}. One-way ANOVA across regions only showed difference for POC production rate ($p = 0.006$), with Gerlache Strait values being significantly greater than the

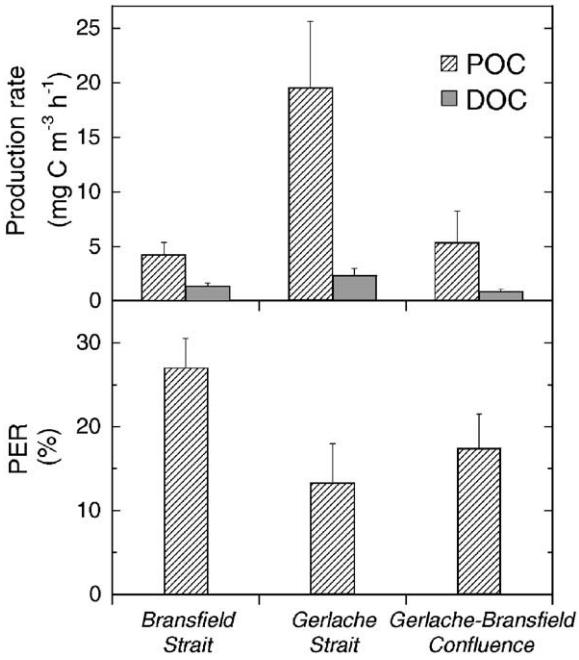

Fig. 5. Average POC and DOC production rates and PER at surface (5 m depth) for the three regions. Bransfield Strait stations were dominated by small flagellates, Gerlache Strait stations by diatoms and GB Confluence stations by Cryptophyceae. Vertical bars are standard errors.

rest (Tukey–Kramer test). Minimum mean PER values (13%) were found in surface waters of Gerlache Strait, with the highest mean PER (32%) corresponding to 10 m depth samples from the same region. This increase was due to a relatively higher decrease in the POC production rate with depth as compared to DOC production rate. Mean values for surface waters of Bransfield Strait and the Gerlache–Bransfield Confluence (GB Confluence) were 26% and 17%, respectively. Differences in PER among regions were not significant.

Chlorophyll *a*-specific production rates or P/B ratios for the particulate fraction (POC^B-pr) ranged between 0.41 and 3.92 mg C (mg Chl $a)^{-1}\,h^{-1}$ (see Table 3 for Chl *a* values). Considering regional averages, POC^B production rate was highest in Gerlache Strait at the surface (2.29 ± 0.77 mg C (mg Chl $a)^{-1}\,h^{-1}$ and lowest in Gerlache Strait at 10 m depth (0.92 ± 0.50 mg C (mg Chl $a)^{-1}\,h^{-1}$). Chlorophyll *a*-specific DOC production rates (DOC^B-pr) varied between 0.06 and 1.60 mg C (mg Chl $a)^{-1}\,h^{-1}$ and were highest in Bransfield Strait (0.69 ± 0.22 mg C (mg Chl $a)^{-1}\,h^{-1}$) and lowest in the GB Confluence (0.25 ± 11 mg C (mg Chl $a)^{-1}\,h^{-1}$). However, these differences among regions were not significant (one-way ANOVA, $p = 0.095$ for POC^B-pr; $p = 0.058$ for DOC^B-pr).

POC and DOC production rates and Chl *a* concentration were all significantly correlated (Table 4). The best linear regression model for DOC-pr included only POC-pr as the independent variable (Fig. 6):

$$\log \text{DOC-pr} = -0.24 + 0.45 \log \text{POC-pr},$$
$$R^2_{\text{adj}} = 0.44,\ p = 0.0007,\ n = 21. \quad (6)$$

Table 3
Concentration of chlorophyll *a* (Chl *a*), prokaryotic heterotrophic production (PHP) and abundance of heterotrophic prokaryotes (PN) in the experiments. PCR/DOC is the ratio of prokaryote carbon requirements (assuming a growth efficiency of 20%) to DOC production rate[a,b]

Region	Station	Depth (m)	Chl *a* (mg m^{-3})	PHP (mg C m^{-3} h^{-1})	PN (cells ml^{-1})	PCR/DOC
B	8	5	0.68	0.005	6.81×10^{-5}	0.05
B[c]	17	10	0.99	0.015	4.21×10^{-5}	0.05
B[c]	29	5	3.13	0.033	2.75×10^{-5}	0.06
B	72	5	3.56	0.014	5.46×10^{-5}	0.03
B	81	5	1.40	–[e]	6.60×10^{-5}	–
B	111	5	1.47	0.004	–	0.05
B	123	5	0.75	0.009	5.20×10^{-5}	0.06
B	140	5	2.43	0.011	4.71×10^{-5}	0.04
B	36	5	1.47	0.015	3.94×10^{-5}	0.08
B	168.3	5	2.43	0.008	3.12×10^{-5}	0.03
		15	2.53	0.017	3.70×10^{-5}	–
G	156.5	5	8.52	0.061	2.57×10^{-5}	0.22
		15	3.99	0.047	1.85×10^{-5}	–
G	169.3	5	6.30	0.042	6.29×10^{-5}	0.08
		10	4.26	0.041	5.96×10^{-5}	0.19
G	177.4	5	4.10	0.041	4.19×10^{-5}	0.05
		10	2.97	0.041	5.17×10^{-5}	0.13
G	184.3	5	17.79	0.059	7.13×10^{-5}	0.27
		10	1.51	0.087	7.63×10^{-5}	0.78
GB	47.1	5	6.82	0.036	7.68×10^{-5}	0.14
GB	164	5	3.67	0.017	–	0.13
GB	178.3	5	1.52	0.079	6.85×10^{-5}	0.70
		10	1.35	0.092	7.04×10^{-5}	1.84

[a] Region initials as in Table 1.
[b] Incubation time for Station 34.1 was 12.15 h, so it was excluded in the remaining analysis.
[c] Station located in the Bellingshausen Sea, but considered within the Bransfield Strait region.
[e] –: not available.

Table 4
Pearson correlation coefficients between different variables of phytoplanktonic and prokaryotic biomass and production[a]

Variables	POC-pr	DOC-pr	Chl *a*	POC^B-pr	PHP	PN	PNP $cell^{-1}$
POC-pr	1.00						
DOC-pr	0.68***	1.00					
Chl *a*	0.84***[b]	0.49*	1.00				
POC^B-pr	0.62**[b]	0.53*	0.08	1.00			
PHP	0.15	0.07	0.47*	−0.38	1.00		
PN	−0.41	−0.50*	−0.14	−0.63**	0.15	1.00	
PNP $cell^{-1}$	0.25	0.08	0.50*	−0.25	0.90***[b]	−0.31	1.00

[a] Number of observations was between 18 and 22. *$0.01<p<0.05$; **$0.001<p<0.01$; * * *$p<0.001$. Abbreviations are explained in the text.
[b] Null correlation > 0.

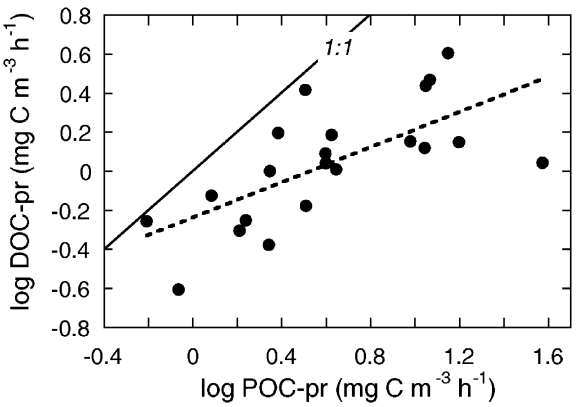

Fig. 6. Relationship between DOC and POC production rates for all experiments. The regression is given in the text. The 1 : 1 line is also shown.

The slope was significantly lower than 1.0 ($p = 0.0001$), the expected finding if PER were constant with increasing POC production rate (Baines and Pace, 1991). Using a model II regression (Ricker, 1973), the new slope (0.66) was, also significantly <1.0 (95% confidence limits: 0.47–0.93, Ricker, 1975). Inclusion of Chl *a* did not improve the percentage of variance explained. However, Chl *a* alone explained 70% of the variance in POC production rate:

$$\log \text{POC-pr} = 0.18 + 1.06 \log \text{Chl}\,a,$$
$$R^2_{\text{adj}} = 0.70,\ p < 0.00005,\ n = 21. \quad (7)$$

In this case, the regression slope was not significantly different from 1.0. No significant relationship was found between POC^B and DOC^B production rates.

3.4. Relationship between prokaryotic production and primary production

Prokaryotic heterotrophic production (PHP) ranged over one order of magnitude (Table 3), with the highest values in Gerlache Strait and the Gerlache–Bransfield Confluence (averages of 0.052 and 0.056 mg C m^{-3} h^{-1}, respectively). Bransfield Strait data were considerably lower (average of 0.013 mg C m^{-3} h^{-1}). At the stations where experiments were made at two different depths, PHP at 10 m was equal to or higher than that at the surface. As can be seen in Table 3, prokaryotic abundance (PN) varied noticeably less than PHP between stations or regions. No significant correlation was found between PN and PHP either for all stations or within regions.

Relationships between PHP and PN as dependent variables and Chl *a*, POC-pr and DOC-pr as independent variables were explored (see Table 4 for the correlation coefficients). With the entire data set, the best model for PHP included both Chl *a* and POC-pr, but it explained only 32% of the variance. The corresponding regression equation was

$$\log \text{PHP} = -1.71 - 0.68 \log \text{POC-pr} + 1.24 \log \text{Chl}\,a,$$
$$R^2_{\text{adj}} = 0.32,\ p = 0.0146,\ n = 20. \quad (8)$$

However, when the regression was performed only with Bransfield Strait data, the best model

had DOC as the sole independent variable and presented a positive regression slope (Fig. 7A):

$$\log \mathrm{PHP} = -2.03 + 0.83 \log \mathrm{DOC\text{-}pr},$$
$$R^2_{\mathrm{adj}} = 0.73,\ p = 0.0021,\ n = 9. \quad (9)$$

The regressions with Gerlache Strait and the GB Confluence data alone showed negative slopes with either POC-pr or DOC-pr as independent variables, but none of them were significant.

Similar results were obtained when PHP was expressed on a per cell basis. PHP cell^{-1} was only positively correlated with DOC production rate in Bransfield Strait (Fig. 7B):

$$\log \mathrm{PHP\ cell^{-1}} = -7.68 + 1.07 \log \mathrm{DOC\text{-}pr},$$
$$R^2_{\mathrm{adj}} = 0.59,\ p = 0.0152,\ n = 8. \quad (10)$$

Prokaryotic abundance presented a marginally significant ($p = 0.028$) negative relationship with DOC production when all data were considered. In Bransfield Strait, a significant negative relationship was found when PN was regressed to POC-pr, DOC-pr or Chl *a*. The best model with these variables included only POC-pr:

$$\log \mathrm{PN} = 5.84 - 0.35 \log \mathrm{POC\text{-}pr},$$
$$R^2_{\mathrm{adj}} = 0.70,\ p = 0.003,\ n = 9. \quad (11)$$

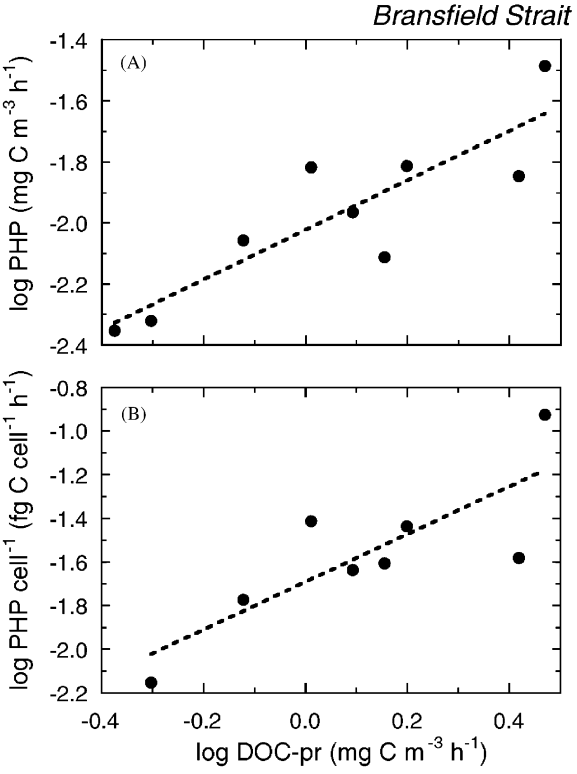

Fig. 7. Relationships between prokaryotic heterotrophic production (PHP), total (A) and cell-specific (B), and DOC production rate for the experiments made in Bransfield Strait. The regressions are given in the text.

4. Discussion

4.1. End point vs. kinetic experiments

When the kinetics of DOC labelling were non-linear, end-point DOC production rates differed notably from rates derived from kinetic experiments (Table 3). In these situations, the error in the calculated rate increases with the incubation length. The measurement of radioactivity in the dissolved phase after a fixed-length incubation can only provide an estimate of the net content of labelled DOC in the water (Riemann and Søndergaard, 1984). End-point experiments are thus subjected to potential errors due to processes like simultaneous heterotrophic removal of recently released DOC, a process acknowledged as important by many authors (e.g., Wiebe and Smith, 1977; Lancelot, 1979; Riemann and Søndergaard, 1984; Lignell, 1990). The total incubation time of $\sim$5 h used in our experiments (Table 2) proved long enough in some cases for the appearance of asymptotic curves (38% of the experiments) while in others DOC labelling remained linear. The fact that different labelling patterns were found even in neighbouring stations makes it difficult to foresee the possible adequacy of end-point incubations. In addition, even in the case of linear DOC labelling, fitting of time-course data will give a more accurate estimate of the production rate than a single end-point, given the relatively high variance of DO^{14}C data.

With respect to POC production, there was virtually no difference between rates obtained with both methodologies (Table 3), indicating that the widespread assumption of linearity was approximately fulfilled in our experiments, which

generally showed respiration rates lower than 10% of the size of the POC pool per hour.

4.2. POC and DOC kinetics

In our experiments, no lag-phase was observed in the appearance of labelled DOC; this is the expected result if isotopic equilibrium is achieved rapidly in relationship with the time scale of the studied phenomena. Both types of kinetics, with and without lag-phase, have been found in previous time-course experiments (e.g., Lancelot, 1979). The question of isotopic equilibrium within the intracellular pool of recently synthesized organic compounds is controversial (Wiebe and Smith, 1977; Larsson and Hagström, 1979; Mague et al., 1980; Smith, 1982; Smith et al., 1986), with proposed times needed for attaining isotopic equilibrium ranging from 0 (Søndergaard et al., 1985) to several days (Jensen et al., 1985). Nevertheless, growing evidence gives support to a rapidly reached internal isotopic equilibrium (see Lignell (1990) and references therein).

In the carbon-exchange model chosen, released DOC is derived from a so-called OCR (organic carbon fated for release) pool, which is located inside the cell, although it is subsumed within the DIC pool in our model (Fig. 2). This representation, supported by the absence of a lag-phase for labelled DOC appearance, is equivalent to assuming quasi-instantaneous isotopic equilibrium with the external DIC pool of the intracellular phytoplanktonic pool of labelled substrates fated for release (Mague et al., 1980; Smith and Platt, 1984; Sundh, 1989). The rationale is that if isotopic equilibrium is attained relatively rapidly, $DO^{14}C$ release is better described, regarding goodness of fit, as coming from the $DI^{14}C$ pool, although it is obvious that labelled C must previously pass through the phytoplanktonic compartment. In a similar way, respired carbon in our model is supposed to equilibrate instantaneously with the added $DI^{14}C$, as considered in Smith and Platt (1984). Another controversial topic is the extent to which results from ^{14}C incubations lie closer to gross or net production (Williams and Lefèvre, 1996; Williams et al., 1996). In our model, accounting for respiration of recently labelled POC and heterotrophic removal of labelled DOC would approximate the calculated POC or DOC production rates to gross rates (Lancelot, 1979; Coveney, 1982).

4.3. POC and DOC production rates

Phytoplankton biomass and rates of particulate primary production for the whole region (Tables 2 and 3) are in the range of previously reported values (e.g., Bodungen, 1986; Bodungen et al., 1986; Arístegui et al., 1996), except for the station 184.3 in Gerlache Strait, which showed very high values ($18\,\mathrm{mg\,Chl}\ a\,\mathrm{m}^{-3}$ and $37\,\mathrm{mg\,C\,m}^{-3}\,\mathrm{h}^{-1}$). Primary production was highest in the Gerlache Strait region, followed by the GB Confluence and Bransfield Strait, in agreement with the pattern described by Varela et al. (2002).

The rates of particulate production per unit Chl a (POC^B-pr) or P/B ratios found in our experiments agree with those previously reported for the Southern Ocean (Sakshaug and Holm-Hansen, 1986; Tilzer and Dubinsky,1987; Holm-Hansen and Mitchell, 1991; Lorenzo et al., 2002), but were higher than those of Varela et al. (2002). This discrepancy may be due to the different sampling times and methodology. Varela et al. used simulated in situ, 24-h incubations, thus including dark respiration. As our experiments were carried out under saturating irradiances, we compared our POC^B values to assimilation numbers (P^B_m) obtained from photosynthesis–irradiance relationships. The average POC^B-pr for all stations ($1.85 \pm 0.99\,\mathrm{mg\,C\,(mg\,Chl}\ a)^{-1}\,\mathrm{h}^{-1}$) was similar to the average assimilation number reported in Figueiras et al. (1994). The average POC^B-pr for Gerlache Strait ($2.29\,\mathrm{mg\,C\,(mg\,Chl}\ a)^{-1}\,\mathrm{h}^{-1}$) was close to the lower part of the range of maximum values given by Bodungen (1986) as characteristic of bloom conditions.

The range of PER variation (3–47%) obtained in our study agrees with previous work in other regions (Mague et al., 1980; Lancelot and Billen, 1984; Baines and Pace, 1991). Our average PER (24%) was nevertheless higher than the 9–12% given for a station in the same area by Tilzer and Dubinsky (1987). This discrepancy may be

partially due to the fact that these authors used 24-h incubations and did not account for possible simultaneous heterotrophic removal of DOC. In contrast, our PER values are lower than the 40–50% proposed by Karl et al. (1991) from changes in the concentration of nutrient pools. PER values in the 50–70% range have been reported by Passow et al. (1994) and Vernet et al. (1994) for Arctic waters with dominance of *Phaeocystis*. As very different methods and experimental designs have been used to calculate phytoplanktonic DOC production, it is not always possible to compare these values directly. One of the methodological problems hindering comparisons is the use of different filters. In our study, DOC was operationally defined as the fraction passing through Whatman GF/F filters. These glass-fiber filters have been reported to adsorb dissolved organic matter, rendering higher estimates of POC production rates. Maske and Garcia-Mendoza (1994) measured on average 6% higher particulate ^{14}C uptake onto GF/F than onto membrane filters, but more recently Karl et al. (1998) and Morán et al. (1999) consistently recovered a higher amount apparent $PO^{14}C$ onto GF/F filters. In a later experiment in the Southern Ocean, Morán et al. (1999) found 28% more activity onto GF/F filters than onto membrane ones. If, as it looks like, DOC adsorption to glass fiber is a general phenomenon, the values of PER given here should be revised upwards.

In the experiments where simultaneous heterotrophic removal was observed, the turnover time of the phytoplanktonically produced DOC pool was 4.8 ± 3.1 h, similar to the 4.4 ± 1.9 h measured by Lancelot (1979). This low turnover time suggests that excreted compounds were mainly labile low molecular weight molecules (Lancelot, 1984).

The higher PER value with depth at the three Gerlache Strait stations was due to a proportionally higher decrease in POC-pr as compared to DOC-pr, perhaps related to the lower irradiance levels (Zlotnik and Dubinsky, 1989). The incubation irradiance of the 10-m depth samples was 10% of the value used for the surface samples, corresponding to the light limited region of the $P-E$ relationship (Lorenzo et al., 2002).

Our findings emphasize the importance of considering DOC release in carbon flux studies (Peterson, 1980; Williams, 1993; Williams and Lefèvre, 1996). It is clear from Table 2 that measuring incorporation of ^{14}C only in the particulate fraction would underestimate total primary production. This could contribute to explain the high apparent photosynthetic quotient (PQ) values reported on occasions (Williams and Robertson, 1991). Thus, dissolved primary production could help reconcile the ^{14}C vs. oxygen method discrepancies such as those reported by and Arístegui et al. (1996) and Serret et al. (2002) during the same FRUELA 95 cruise.

4.4. Relationship between POC and DOC production

Overall, DOC production rates were more correlated with POC production rates than with Chl *a* or POC^B (Table 4). A strong coupling between rates of POC and DOC production has been frequently found (e.g., Zlotnik and Dubinsky, 1989; Baines and Pace, 1991; Feuillade et al., 1988). The log–log relationship between DOC and POC (Fig. 6) can be explained as the result of a constant relationship between the incremental changes of DOC and POC production rates:

$$d\text{DOC-pr}/\text{DOC-pr} = 0.45\, d\text{POC-pr}/\text{POC-pr}, \quad (12)$$

where 0.45 is the slope of the DOC vs. POC regression line.

These results suggest that the amount of DOC being produced, by algal release or other mechanisms (released $DO^{14}C$ would be indistinguishable from that derived from cell lysis or sloppy feeding), is ultimately constrained by the availability of photosynthate. If we assume that the appearance of extracellular $DO^{14}C$ is mainly due to phytoplankton, the relationship given in (12) would indicate that DOC production is rather a result of active release of products from an internal pool, the size of which is dependent on the photosynthetic rate, than a passive diffusion process (Bjørnsen, 1988), related to the surface to volume ratio, and hence, more correlated to

biomass. A similar conclusion was reached by Baines and Pace's review (1991).

Decreasing PER values with increasing POC production rates (Fig. 8) have been found in many studies (e.g., Williams and Yentsch (1976) and references in Mague et al. (1980)), and sometimes have been disregarded as a methodological artifact (Mague et al., 1980; Williams, 1990) due to errors associated to low radioactivity counts. This is not the case of the experiments shown here, in which counts were always well above initial blanks. Baines and Pace (1991) in their literature review found this to be a general trend in freshwater environments but not in marine systems. However, these authors showed that this relationship appeared within systems, with an average slope of 0.70 for the regression of log DOC-pr on log POC-pr, higher than the slope shown here.

The trend of decreasing PER with increasing photosynthetic rate (either POC or TOC production rate) has often been linked to increasing cell sizes and lower surface to volume ratios (Kiørboe, 1993), which results in low PER for the larger forms of phytoplankton (Sundh, 1989), often with the implicit assumption than passive diffusion is the underlying mechanism (Bjørnsen, 1988). However, this explanation would not agree with the fact that DOC production rate was better related to photosynthetic rate than to biomass (as Chl *a*), as we argue above. The association of the alternative passive diffusion and overflow mechanisms with a respectively decreasing or constant PER along the gradient of productivity, proposed by Williams (1990) on theoretical grounds, may be difficult to prove in nature, where a multiplicity of processes are acting together. Bearing in mind that the significant regressions among variables such as POC and DOC production rates do not imply necessarily causal relationships, other variables such as nutrient concentration, irradiance or water column stability, which usually covary with photosynthetic rate, could be the ultimate cause for the observed changes in PER (Williams, 1990).

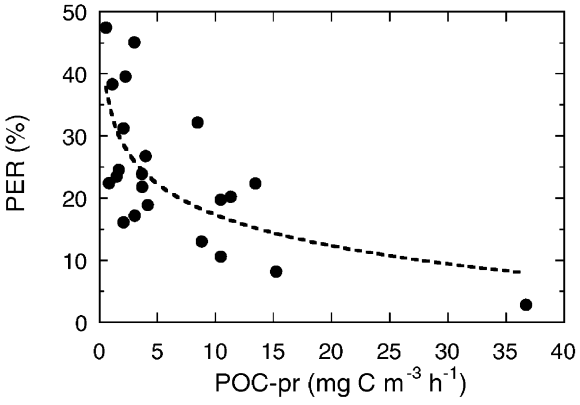

Fig. 8. Relationship between PER and POC production rate for all experiments. The regression line is: PER = 33.9−16.6 log POC-pr; $R^2 = 0.44$.

4.5. *Relationship between prokaryotic production and primary production*

Prokaryotic heterotrophic production in the area (Pedrós-Alió et al., 2002) was in the range of published values (Fuhrman and Azam, 1980; Sullivan et al., 1990), and amounted to an average 5% of DOC production rate and 1% of TOC (POC + DOC) production rate in our experiments with surface water; higher percentages were reached in the 10-m depth samples. Values of PHP between 0.5% and 10% of primary production have been previously found for Antarctic waters by Fuhrman and Azam (1980) and Rivkin (1991). Joint and Pomeroy (1983) found PHP to be <7% of DOC production, and proposed low bacterial growth efficiency (BGE) as a possible explanation. Reported BGE values vary between <10% and almost 100% (e.g. Lignell, 1990; Bjørnsen, 1986; Güde et al., 1991), although recent studies in the sea have tended to support low (<20%) values (del Giorgio et al., 1997; Kähler et al., 1997).

In an attempt to determine the potential importance of DOC released by phytoplankton for PHP, prokaryotic carbon requirements (PCR) were calculated and compared with DOC production using two different BGE. It is implicitly assumed than phytoplanktonic DOC is readily available to prokaryotes, directly or after exoenzymatic hydrolysis. With the widely used value of 50% BGE (Ducklow, 1983), the DOC production rates found in our experiments would be enough to

meet BCR in all cases (data not shown). With a BGE of 20%, phytoplankton alone could provide enough DOC for the growth of heterotrophic prokaryotes in all but one of the experiments (Table 3, ratio BCR/DOC). Considering average phytoplanktonic and prokaryotic production rates in our experiments, 25% of the DOC produced by phytoplankton would pass through heterotrophic prokaryotes if bacterioplankton depended solely on DOC of this origin. This percentage is considerably lower (5%) when only Bransfield Strait stations were considered.

Prokaryotic heterotrophic production was higher at the Gerlache Strait and the GB Confluence stations, where primary production was higher, than in Bransfield Strait, suggesting that overall prokaryotic heterotrophic activity was enhanced by the increased substrate concentrations likely to be associated with higher primary production rates. However, a good correlation between PHP and DOC production rate was found only for Bransfield Strait stations (Fig. 7A), but not for those of Gerlache Strait or the Gerlache–Bransfield Confluence.

As judged by the correlation coefficients, the relationship between PHP and DOC production rate in Bransfield Strait was stronger than with Chl *a* or POC production rate. A weak relationship between PHP and these latter variables suggests that POC production or Chl *a* may be poor descriptors of labile carbon production (Pace and Cole, 1996). The existence of a strong coupling between heterotrophic prokaryote production in Bransfield Strait and substrates released by phytoplankton is supported by the positive relationship between PHP cell^{-1} and DOC production rate (Fig. 7B). As suggested in Kähler et al. (1997) prokaryotes appear to rely on labile substrates provided directly by phytoplankton. Although the production rates of algae and prokaryotes were correlated in Bransfield Strait, prokaryotic abundance was negatively correlated with POC-pr (Eq. (11)), which was partially explained by a lack of relationship between PN and PHP, perhaps due to the presence of inactive cells or prokaryotes being controlled by protozoan grazers (Bird and Karl, 1999).

The lack of significant relationships between PHP and DOC or POC production rates in Gerlache Strait and the GB Confluence may have several explanations, apart from the uncertainty derived from the small number of samples. A more oligotrophic situation was found in Bransfield Strait compared with Gerlache Strait, where a bloom of diatoms was present during the cruise. It could be that in Gerlache Strait, where diatoms appeared to be growing actively, prokaryotic growth on newly released DOC compounds had not yet reached its maximum potential rate. A time-lag of the prokaryotic response to the phytoplankton can cause weakness of correlation between prokaryotes and primary producers activity (Bird and Karl, 1991). Temporal shifts in bacterioplankton and phytoplankton activity peaks in Antarctic waters have been reported at a seasonal time scale (Rivkin, 1991; Davidson and Marchant, 1992), with highest rates of production for phytoplankton in summer and for bacterioplankton in winter (Delille and Mallard, 1991), giving rise to an accumulation of DOC produced by phytoplankton during the summer (Azam et al., 1991; Doval et al., 2002). Nevertheless, no evidence of a higher prokaryotic activity was found in the second FRUELA cruise, where PHP had decreased compared to the results reported here (Pedrós-Alió et al., 2002). Competition between phytoplankton and prokaryotes for a limiting substrate other than N or P (Karl et al., 1991) or bacteriostatic effects due to extracellular products (Davidson and Marchant, 1987) have been proposed as possible causes. One likely reason could be the different physiological conditions of the microbial community in the Bransfield and Gerlache Strait areas, which presented very different phytoplankton assemblages. Changes in the phytoplankton assemblages could produce changes in the nature of released products (Hellebust, 1965; Lancelot, 1984), which in turn would affect the responses of heterotrophic prokaryotes (Bell et al., 1974; Riquelme et al., 1989).

Acknowledgements

We thank J.M. Gasol, C. Pedrós-Alió and D. Vaqué and two referees for critical review of the

manuscript. We are also grateful to D. Vaqué and N. Guixa-Boixereu for the measurements of prokaryotic production and the crew of the R/V *Hespérides* for their help during the cruise. X.A.G.M. aknowledges the receipt of a FPI fellowship from the Spanish Ministry of Education. This work was supported by CICYT grant ANT94-1010.

References

Álvarez, M., Ríos, A.F., Rosón, G., 2002. Spatio-temporal variability of air-sea fluxes of carbon dioxide and oxygen in the Bransfield and Gerlache Straits during Austral summer 1995–96. Deep-Sea Research II 49, 643–662.

Arístegui, J., Montero, M.F., Ballesteros, S., Basterretxea, G., van Lenning, K., 1996. Planktonic primary production and microbial respiration measured by ^{14}C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during austral summer: implications for carbon flux studies. Marine Ecology Progress Series 132, 191–201.

Azam, F., Smith, D.C., Hollibaugh, J.T., 1991. The role of microbial loop in Antarctic pelagic ecosystems. Polar Research 10, 239–243.

Baines, S.B., Pace, M.L., 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. Limnology and Oceanography 36, 1078–1090.

Bell, W.H., Lang, J.M., Mitchell, R., 1974. Selective stimulation of marine bacteria by algal extracellular products. Limnology and Oceanography 19, 833–839.

Bell, R.T., Ahlgren, G.M., Ahlgren, I., 1983. Estimating bacterioplankton production by measuring ^{3}H-thymidine incorporation in an eutrophic Swedish lake. Applied and Environmental Microbiology 45, 1709–1721.

Bird, D.F., Karl, D.M., 1991. Spatial atterns of glutamate and thymidine assimilation in Bransfield Strait, Antarctica during and following the austral spring bloom. Deep-Sea Research 38, 1057–1075.

Bird, D.F., Karl, D.M., 1999. Uncoupling of bacteria and phytoplankton during the austral spring bloom in Gerlache Strait, Antarctic Peninsula. Aquatic Microbial Ecology 19, 13–27.

Bjørnsen, P.K., 1986. Bacterioplankton growth yield in continuous plankton cultures. Marine Ecology Progress Series 30, 191–196.

Bjørnsen, P.K., 1988. Phytoplankton exudation of organic matter: why do healthy cells do it? Limnology and Oceanography 33, 151–154.

Bodungen, B., 1986. Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica—implications from sediment trap collections. Polar Biology 6, 153–160.

Bodungen, B.V., Smetacek, V.S., Tilzer, M.M., Zeitzschel, B., 1986. Primary production and sedimentation during spring in the Antarctic Peninsula region. Deep-Sea Research 33, 177–194.

Cole, J.J., Likens, G.E., Stryer, D.L., 1982. Photosynthetically produced dissolved organic carbon: an important carbon source for planktonic bacteria. Limnology and Oceanography 27, 1080–1090.

Cole, J.J., Findlay, S., Pace, M.L., 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Marine Ecology Progress Series 43, 1–10.

Coveney, M.F., 1982. Bacterial uptake of photosynthetic carbon from freshwater phytoplankton. Oikos 38, 8–20.

Chróst, R.H., Faust, M.A., 1983. Organic carbon release by phytoplankton: its composition and utilization by bacterioplankton. Journal of Plankton Research 5, 477–493.

Davidson, A.T., Marchant, H.J., 1987. Binding of manganese by Antarctic *Phaeocystis pouchetii* and the role of bacteria in its release. Marine Biology 95, 481–487.

Davidson, A.T., Marchant, H.J., 1992. Prostist abundance and carbon concentration during a *Phaeocystis*-dominated bloom at an Antarctic coastal site. Polar Biology 12, 387–395.

del Giorgio, P.A., Cole, J.J., Cimbleris, A., 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385, 148–151.

Delille, D., Mallard, L., 1991. Seasonal changes of Antarctic marine bacterioplankton. Kieler Meeresforschungen, Sonderheft 8, 213–218.

Doval, M.D., Álvarez-Salgado, X.A., Castro, C.G., Pérez, F.F., 2002. Dissolved organic carbon distributions in the Bransfield and Gerlache Straits, Antarctica. Deep-Sea Reasearch II 49, 663–674.

Ducklow, H.W., 1983. Production and fate of bacteria in the oceans. BioScience 33, 494–501.

El-Sayed, S.Z., 1988. Biological productivity of the southern ocean: a closer look. Comparative Biochemeistry and Physiology 90B, 489–498.

Feuillade, M., Dufour, P., Feuillade, J., 1988. Organic carbon release by phytoplankton and bacterial assimilation. Schweizische Zeitschrift fuer Hydrologie 50, 115–135.

Figueiras, F.G., Pérez, F.F., Pazos, Y., Ríos, A.F., 1994. Light and productivity of Antarctic phytoplankton during austral summer in an ice edge region in the Weddell–Scotia Sea. Journal of Plankton Research 16, 233–253.

Figueroa, F.L., 2002. Bio-optical characteristics of Gerlache and Bransfield Strait waters during an Antarctic summer cruise. Deep-Sea Reasearch II 49, 675–691.

Fuhrman, J.A., Azam, F., 1980. Bacterial secondary production estimates for coastal waters of British Columbia, Antarctica, and California. Applied and Environmental Microbiology 39, 1085–1095.

Güde, H., Jürgens, K., Parth, G., Walser, R., 1991. Indications for low net productivity of pelagic bacterioplankton. Kieler Meeresforschungen, Sonderheft 8, 309–316.

Hansell, D.A., Carlson, C.A., 1998. Net community production of dissolved organic carbon. Global Biogeochemical Cycles 12, 443–453.

Hellebust, J.A., 1965. Excretion of some organic compounds by marine phytoplankton. Limnology and Oceanography 10, 192–206.

Holm-Hansen, O., Mitchell, B.G., 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Research 38, 961–980.

Jackson, G.A., 1993. The importance of the DOC pool for primary production estimates. ICES Marine Science Symposia 197, 141–148.

Jensen, L.M., 1983. Phytoplankton release of extracellular organic carbon, molecular weight composition, and bacterial assimilation. Marine Ecology Progress Series 11, 39–48.

Jensen, L.M., Jørgensen, N.O.G., Søndergaard, M., 1985. Specific activity. Significance in estimating release rates of extracellular dissolved organic carbon (EOC) by algae. Verhandlungen. Internationale Vereinigung für Theoretische und Angewandte Limnologie 22, 2893–2897.

Joint, I.R., Pomeroy, A.J., 1983. Production of picoplankton and small nanoplankton in the Celtic sea. Marine Biology 77, 19–27.

Joiris, C., Billen, G., Lancelot, C., Daro, M.H., Mommaerts, J.P., Bertels, A., Bossicart, M., Nys, J., 1982. A budget of carbon cycling in the Belgian coastal zone: relative roles of zooplankton, bacterioplankton and benthos in the utilization of primary production. Netherlands Journal of Sea Research 16, 260–275.

Kähler, P., Bjørnsen, P.K., Lochte, K., Antia, A., 1997. Dissolved organic matter and its utilization by bacteria during spring in the Southern Ocean. Deep-Sea Research II 44, 341–353.

Karl, D.M., Holm-Hansen, O., Taylor, G.T., Tien, G., Bird, D.F., 1991. Microbial biomass and productivity in the western Bransfield Strait Antarctica during the 1986–87 austral summer. Deep-Sea Research 38, 1029–1055.

Karl, D.M., Hebel, D.V., Björkman, K., Letelier, R.M., 1998. The role of dissolved organic matter release in the productivity of the oligotrophic North Pacific Ocean. Limnology and Oceanography 43, 1270–1286.

Kiørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Advances in Marine Biology 29, 1–72.

Lancelot, C., 1979. Gross excretion rates of natural marine phytoplankton and heterotrophic uptake of excreted products in the southern North Sea, as determined by short-term kinetics. Marine Ecology Progress Series 1, 179–186.

Lancelot, C., 1984. Extracellular release of small and large molecules by phytoplankton in the Southern Bight of the North Sea. Estuarine, Coastal and Shelf Science 18, 65–77.

Lancelot, C., Billen, G., 1984. Activity of heterotrophic bacteria and its coupling to primary production during the spring phytoplankton bloom in the southern bight of the North Sea. Limnology and Oceanography 29, 721–730.

Larsson, U., Hagström, Å., 1979. Phytoplankton exudate release as an energy source for the growth of pelagic bacteria. Marine Biology 52, 199–206.

Larsson, U., Hagström, Å., 1982. Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. Marine Biology 67, 57–70.

Leboulanger, C., Oriol, L., Jupin, H., Descolas-Gros, C., 1997. Diel variability of glycolate in the eastern tropical Atlantic Ocean. Deep-Sea Research 44, 2131–2139.

Lignell, R., 1990. Excretion of organic carbon by phytoplankton: its relation to algal biomass, primary productivity and bacterial secondary productivity in the Baltic Sea. Marine Ecology Progress Series 68, 85–99.

Lorenzo, L.M., Arbones, B., Figueiras, F.G., Tilstone, G.H., Figueroa, F.L., 2002. Photosynthesis, primary production and phytoplankton growth rates in Gerlache and Bransfield Straits during Austral summer: cruise FRUELA 95. Deep-Sea Research II 49, 707–721.

Mague, T.H., Friberg, E., Hughes, D.J., Morris, I., 1980. Extracellular release of carbon by marine phytoplankton; a physiological approach. Limnology and Oceanography 25, 262–279.

Malinsky-Rushansky, N.Z., Legrand, C., 1996. Excretion of dissolved organic carbon by phytoplankton of different sizes and subsequent bacterial uptake. Marine Ecology Progress Series 132, 249–255.

Maske, H., Garcia-Mendoza, E., 1994. Adsorption of dissolved organic matter to the inorganic filter substrate and its implications for ^{14}C uptake measurements. Applied and Environmental Microbiology 60, 3887–3889.

Morán, X.A.G., Gasol, J.M., Arin, L., Estrada, M., 1999. A comparison between glass fiber and membrane filters for the estimation of phytoplankton POC and DOC production. Marine Ecology Progress Series 187, 31–41.

Pace, M.L., Cole, J.J., 1996. Regulation of bacteria by sources and predation tested in whole-lake experiments. Limnology and Oceanography 41, 1448–1460.

Passow, U., Wassmann, P., Vernet, M., 1994. A new hypothesis on the fate of extracellular carbon released by phytoplankton in Arctic shelf waters. EOS 75 (Suppl.), 116.

Pedrós-Alió, C., Vaqué, D., Guixa-Boixereu, N., Gasol, J.M., 2002. Prokaryotic plankton biomass and heterotrophic production in western Antarctic waters during the 1995–96 Austral summer. Deep-Sea Research II 49, 805–825.

Peterson, B.J., 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: a history of the productivity problem. Annual Review of Ecology and Systematics 11, 359–385.

Ricker, W.E., 1973. Linear regression in fishery research. Journal of the Fisheries Research Board of Canada 30, 409–434.

Ricker, W.E., 1975. A note concerning Professor Jolicoeur's comments. Journal of the Fisheries Research Board of Canada 32, 1494–1498.

Riemann, B., Søndergaard, M., 1984. Bacterial growth in relation to phytoplankton primary production and extracellular release of organic carbon. In: Hobbie, J.E.,

Williams, P.J.leB. (Eds.), Heterotrophic Activity in the Sea. Plenum Press, New York, pp. 233–248.

Riquelme, C.E., Fukami, K., Ishida, Y., 1989. Growth response of bacteria to extracellular products of bloom algae. Nippon Suisan Gakkaishi 55, 349–355.

Rivkin, R., 1991. Seasonal patterns of planktonic production in McMurdo Sound, Antarctica. American Zoologist 31, 5–16.

Sakshaug, E., Holm-Hansen, O., 1986. Photoadaptation in Antarctic phytoplankton: variations in growth rate, chemical composition and P versus I curves. Journal of Plankton Research 8, 459–473.

Serret, P., Fernández, E., Anadón, R., Varela, M., 2002. Trophic control of biogenic carbon export in Bransfield and Gerlache Straits, Antarctica. Journal of Phytoplankton Research (in press).

Smith, R.E.H., 1982. The estimation of phytoplankton production and excretion by carbon-14. Marine Biology Letters 3, 325–334.

Smith, D.C., Azam, F., 1992. A simple, economical method for measuring bacterial protein synthesis rates in seawater using ^{3}H-leucine. Marine Microbial Food Webs 6, 107–114.

Smith, R.E.H., Platt, T., 1984. Carbon exchange and ^{14}C tracer methods in a nitrogen-limited diatom, *Thalassiosira pseudonana*. Marine Ecology Progress Series 16, 75–87.

Smith, R.E.H., Harrison, W.G., Trwin, B., Platt, T., 1986. Metabolism and carbon exchange in microplankton of the Grand Banks (Newfoundland). Marine Ecology Progress Series 34, 171–183.

Søndergaard, M., Riemann, B., Jørgensen, N.O.G., 1985. Extracellular organic carbon (EOC) released by phytoplankton and bacterial production. Oikos 45, 323–332.

Steemann-Nielsen, E., 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. Journal du Conseil Permanent International de la Mer 18, 117–140.

Sullivan, C.W., Cota, G.F., Krempin, D.W., Smith Jr., W.O., 1990. Distribution and activity of bacterioplankton in the marginal ice zone of the Weddell–Scotia Sea during austral spring. Marine Ecology Progress Series 63, 239–252.

Sundh, I., 1989. Characterization of phytoplanktonextracellular products and their subsequent uptake by heterotrophic organisms in a mesotrophic forest lake. Journal of Plankton Research 11, 463–486.

Tilzer, M.M., Dubinsky, Z., 1987. Effects of temperature and day length in the mass balance of Antarctic phytoplankton. Polar Biology 7, 35–42.

Varela, M., Fernández, E., Serret, P., 2002. Size-fractionated phytoplankton biomass and primary production in the Gerlache and South Bransfield Straits (Antarctic Penninsula) in Austral summer 1995–1996. Deep-Sea Research II 49, 749–768.

Vaqué, D., Guixa-Boixereu, N., Gasol, J.M., Pedrós-Alió, C., 2002. Distribution of microbial bio mass and importance of protists in regulating prokaryotic assemblages in three areas close to the Antarctic Penninsula in spring and summer 1995/96. Deep-Sea Research II 49, 847–867.

Vernet, M., Matrai, P.A., Ruel, J., 1994. Photosynthetic carbon production at the ice edge in the Barents Sea: cellular and extracellular carbon pools. EOS 75 (Suppl.), 127.

Watanabe, Y., 1980. A study of the excretion and extracellular products of natural phytoplankton in Lake Nakanuma. Internationale Revue der Gesamten Hydrobiologie 65, 809–834.

Wiebe, W.J., Smith, D.F., 1977. Direct measurement of dissolved organic carbon release by phytoplankton and incorporation by microheterotrophs. Marine Biology 42, 213–223.

Williams, P.J.leB., 1990. The importance of losses during microbial growth: commentary on the physiology, measurement and ecology of the release of dissolved organic material. Marine Microbial Food Webs 4, 175–206.

Williams, P.J.leB., 1993. Chemical and tracer methods of measuring plankton production. CES Marine Science Symposia 197, 20–36.

Williams, P.J.leB., Lefèvre, D., 1996. Algal ^{14}C and total carbon metabolisms. 1. Models to account for the physiological processes of respiration and recycling. Journal of Plankton Research 18, 1941–1959.

Williams, P.J.leB., Robertson, J.E., 1991. Overall planktonic oxygen and carbon dioxide metabolisms: the problem of reconciling observations and calculations of photosynthetic quotients. Journal of Plankton Research 13, 153–169.

Williams, P.J.leB., Yentsch, C.S., 1976. An examination of photosynthetic production, excretion of photosynthetic products, and heterotrophic utilization of dissolved organic compounds with reference to results from a coastal subtropical sea. Marine Biology 35, 31–40.

Williams, P.J.leB., Robinson, C., Søndergaard, M., Jespersen, A-M., Bentley, T.L., Lefèvre, D., Richardson, K., Riemann, B., 1996. Algal ^{14}C carbon and total carbon metabolisms. 2. Experimental observations with the diatom *Skeletonema costatum*. Journal of Plankton Research 18, 1961–1974.

Wood, A.M., Van Valen, L.M., 1990. Paradox lost? on the release of energy-rich compounds by phytoplankton. Marine Microbial Food Webs 4, 103–116.

Zlotnik, I., Dubinsky, Z., 1989. The effect of light and temperature on DOC excretion by phytoplankton. Limnology and Oceanography 34, 831–839.