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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

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ABSTRACT: Oxygen consumption and production and carbon fixation by micro-organisms were measured simultaneously in coastal surface waters near the Antarctic Peninsula. Although there was a good qualitative agreement between the oxygen and carbon measurements, total daily water-column integrated carbon incorporation measured by radiocarbon uptake in the particulate fraction underestimated net community production measured by the oxygen method by 29 to 54% (using a photosynthetic quotient of 1.5). Unaccounted-for exudation of dissolved organic carbon during the ^{14}C uptake experiments may explain this discrepancy. Respiratory carbon losses by micro-organisms (largely phytoplankton) ranged between 10 and 50% of gross production, the highest values corresponding to the more productive stations. These estimates are, however, slightly conservative, since they refer to the upper 30 m of the water column, corresponding approximately to the euphotic zone in this region. Our results show that microbial respiration is an important part of the carbon flux of coastal Antarctic plankton. Unless it is considered in carbon flux models, the contribution of higher trophic levels to the carbon fluxes in marine food webs may be seriously overestimated.

KEY WORDS: Primary production · Microbial respiration · Carbon and oxygen fluxes · Coastal Antarctic waters

INTRODUCTION

Coastal waters near the Antarctic Peninsula support highly productive ecosystems where extensive phytoplankton blooms develop throughout the austral spring and summer (Holm-Hansen & Mitchell 1991, Comiso et al. 1993, Sullivan et al. 1993). These areas may therefore represent key sites where the 'biological pump' (Volk & Hoffert 1985, Longhurst & Harrison 1989) transports organic carbon below the mixed layer, and consequently sequesters atmospheric CO_2. However, Huntley et al. (1991) have suggested that air-breathing top predators might return as much as 20 to 25% of the photosynthetically fixed carbon to the atmosphere, causing these ecosystems to be inefficient as a carbon sink. Moloney (1992; see also Huntley et al. 1992) questioned Huntley et al.'s (1992) conclusions, arguing, among other things, that phytoplankton respiration was not accounted for in their food web model. Therefore, Huntley et al.'s (1992) calculations began with net production rather than total production, increasing the apparent contribution of all heterotrophs to the carbon flux.

Huntley et al. (1992) may have ignored phytoplankton respiration in their model because there were at that time no reliable direct measurements from coastal Antarctic waters. Furthermore, published respiration data for the Antarctic Ocean as a whole are few and

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contradictory. Williams (1984), in a review paper, cites (unpublished) values of community respiration from Pomeroy and coworkers, ranging from 0 to 0.5 µmol O_2 l^{-1} d^{-1} for the Antarctic. These figures contrast with the higher oxygen consumption rates (0.5 to 3.69 µmol O_2 l^{-1} d^{-1}) obtained by Robinson & Williams (1993) from the upper 100 m of the water column, between the Falkland Islands and South Georgia, near the Antarctic Convergence. The latter data agree, however, with oxygen consumption measurements obtained in the Arctic Ocean by Harrison (1986) and, more recently, in coastal Antarctic waters by Arístegui & Montero (1995).

Phytoplankton respiratory losses in the Antarctic have also been estimated by ^{14}C cell-labelling experiments. However, results obtained with this method are controversial, since phytoplankton and microheterotrophs are capable of fixing carbon in the dark (Li & Dickie 1991, Geider 1992, Li et al. 1993). This might partly explain the variability in the few published results. Tilzer & Dubinsky (1987) estimated carbon respiratory losses lower than 10% of the gross production in the eastern region of the Bransfield Strait. In contrast, Lancelot et al. (1991) found respiration to account for 50% of gross production in the case of the phytoplankton of the marginal ice zone of the Weddell and Scotia Seas.

In the present study we have directly measured the relationship between plankton community respiration and gross oxygen production in the upper layers of selected stations of coastal Antarctic ecosystems. We have also simultaneously estimated ^{14}C uptake by phytoplankton. Our aim was to assess the contribution of microbial communities to the respiratory flux of inorganic carbon in surface waters of near-shore Antarctic regions, where top predators have been considered to be responsible for a major leak in the biological carbon pump (Huntley et al. 1991).

MATERIAL AND METHODS

Station locations. Data were collected during the cruise 'BIOANTAR 93' on board the 'BIO Hesperides', during February 1993. *In situ* incubations were carried out at 4 stations, which represented different hydrological and biological conditions of Antarctic coastal waters. These stations were (Table 1): S1, in shelf waters of the Antarctic Peninsula, in the Bransfield Strait; S2, in the Gerlache Strait; S3, in Hanusse Bay, near the polar circle, at the marginal ice zone; and S4, in the interior bay of Deception Island, Bransfield Strait. Conditions at these stations varied from waters with moderate chlorophyll [~1 mg chlorophyll *a* (chl *a*) m^{-3}] and a deep (>100 m) mixed layer (S1), to the highly stratified waters of S4, where phytoplankton was blooming (>7 mg chl *a* m^{-3}).

Table 1. Station locations, depths and sampling dates in February 1994

Station	Latitude (S)	Longitude (W)	Depth (m)	Date
S1	63° 48' 55"	61° 12' 10"	656	5 Feb
S2	64° 13' 10"	61° 19' 18"	540	10 Feb
S3	66° 44' 22"	67° 34' 10"	611	12 Feb
S4	62° 57' 10"	60° 37' 53"	156	14 Feb

Hydrographic and optical measurements. At each station, temperature, salinity and density were recorded through the water column with a Neil Brown Mark III CTD system. Temperature and conductivity from the CTD sensors were calibrated against readings of reversing thermometers and salinity analyses (Autosal 2000) of discrete samples. Water samples between the surface and 60 m were collected in 12 l Niskin bottles attached to a rosette frame. Photosynthetically active radiation (PAR) was measured through the water column with a 4π light sensor (Biospherical Co., San Diego, CA, USA). The depth of the euphotic zone (Z_{EZ}) was taken as extending to the depth at which scalar PAR fell to 1% of surface values.

Nutrients and chlorophyll. Samples of nitrate (nitrate + nitrite) and ammonia were immediately analyzed on board after being collected. All the analyses were done in triplicate, using conventional chemical techniques (Parsons et al. 1984).

Chl *a* was estimated fluorometrically by means of a Turner Designs fluorometer, previously calibrated with pure chl *a* (Sigma Co., St. Louis, MO, USA), following the recommendations of Yentsch & Menzel (1963) and Holm-Hansen et al. (1965). Sample aliquots of 50 to 250 ml were filtered through GF/F filters and also through 2 µm polycarbonate membrane filters. Pigments were extracted in cold acetone (90%) for 24 h, and fluorescence was measured before and after acidification, allowing the separate estimation of chl *a*-like pigments and phaeopigments.

Microbial abundance. Phytoplankton samples were preserved in Lugol's solution (Parsons et al. 1984) and stored in the dark. Subsamples were settled in 50 ml chambers and cells counted with an inverted microscope. Heteroflagellates were counted by epifluorescence microscopy following the protocol of Haas (1982). Samples were fixed in glutaraldehyde (6%) and stained with proflavine before being filtered through 0.2 µm dark polycarbonate membrane filters. Bacteria were enumerated in DAPI-stained preparations (Porter & Feig 1980) by epifluorescence microscopy.

Photosynthetic carbon fixation rates. Primary production was determined by the ^{14}C method (Steeman-

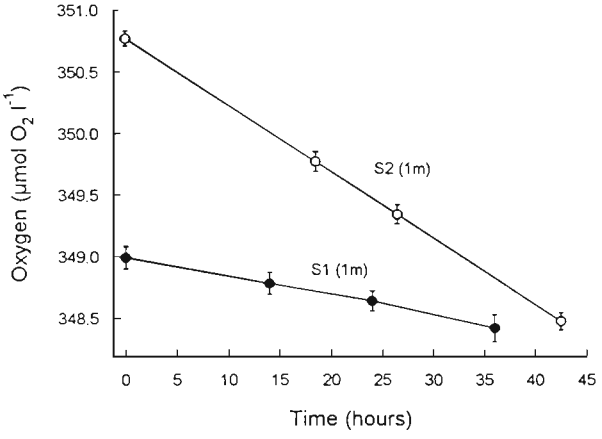

Fig. 1 Time-series measurements of dissolved oxygen concentration in water samples incubated inside replicate dark bottles at Stns S1 and S2 (1 m depth). Each measurement corresponds to the mean value of 4 replicates. Vertical bars indicate ±1 SD

Nielsen 1952). At each *in situ* station, water was collected before dawn from depths between 0 and 60 m. Eight duplicate samples were incubated during daylight (12 to 14 h) in 100 ml polycarbonate bottles hanging on a drifter array at the depths from which they had been collected. Dark samples were incubated on board, in thermostatized baths reproducing *in situ* temperatures. Each of the bottles was spiked with 8 to 15 µCi of ^{14}C-bicarbonate, the greater amount being added to samples with lower phytoplankton abundance. Following each incubation, samples were filtered on GF/F filters and acidified with 1 ml HCl (10%) for 18 h to drive off inorganic carbon. After this, filters were immersed in 6 ml of Aquasol II (NEN) for 24 h, and the incorporated ^{14}C beta-emission measured in a liquid scintillation counter using an external standard as a reference. At the beginning of each incubation a sample was filtered and used as a blank reference. In order to measure the radioactivity added to the samples, a 100 µl aliquot of the ^{14}C-bicarbonate solution was mixed with 1 ml of Protosol (NEN) and 5 ml of Aquasol II, and measured in the same scintillation counter.

Community production and community respiration. Net community production, community respiration and gross production were determined by the oxygen method (Strickland 1960). Each water sample (the same used for the ^{14}C experiments) was gently mixed and distributed with a silicone tube to 16 borosilicate bottles (100 ml nominal volume): 6 initial, 6 light and 4 dark. Bottles were filled and samples fixed in a controlled-temperature room at −1 ± 1°C. Light bottles were incubated *in situ* along with the ^{14}C bottles. Dark bottles were incubated on board in refrigerated baths (±0.1°C) at *in situ* sea temperature for 24 h. Dissolved oxygen was measured with the Winkler technique, following the recommendations of Carrit & Carpenter (1966), Bryan et al. (1976) and Grasshoff et al. (1983). The entire contents of the bottle were titrated in about 3 min. The titration was controlled by an automated system, with colorimetric end-point detection (Williams & Jenkinson 1982). The precision achieved in replicates corresponded to a coefficient of variation of better than 0.08%. Time-series incubations were performed to confirm that the respiration rate was constant throughout the experiments (Fig. 1). Net community production was estimated as the difference between the light and initial bottles; community respiration as the difference between the initial and dark bottles; and gross production as the difference between the light and dark bottles.

RESULTS

Hydrography, nutrients, chlorophyll and microbial distribution

The 4 stations represent different situations characteristic of coastal Antarctic waters during the austral summer Stn S1 (Antarctic Peninsula shelf) had a deep (>100 m) mixed layer, with a uniform vertical distribution of chlorophyll and nutrients (Table 2, Figs. 2–4). The low percentage of chlorophyll >2 µm indicated dominance by picoplankton. Diatoms were almost absent and larger phytoplankton were mostly represented by small cryptophytes (Table 3). This station exemplifies the region of intense mixing and instability in the Bransfield Strait which results from the confluence of Weddell Sea and Gerlache Strait waters. Development of diatom blooms is inhibited by the deep mixed layer (Sakshaug & Holm-Hansen 1984, Kopczynska & Ligowski 1985).

At Stn S2 (Gerlache Strait), the near-surface stratification of the water column was associated with increased abundance of phytoplankton >2 µm. Cryptophytes, although fewer than at S1, were still abundant, but the growth of small (<30 µm) diatoms near the surface increased the percentage of chlorophyll >2 µm (Tables 2 & 3, Figs. 2–4).

Stn S3 (Hanusse Bay) exemplifies marginal ice zone waters where large diatom blooms develop (Brökel 1985, Kopczynska & Ligowski 1985, Knox 1990, Jacques & Panouse 1991, Lancelot et al. 1993). The temperature profile at this station (Fig. 2) showed an irregular distribution caused by vertical mixing of melting ice. Comparatively low nitrate values (<12 mg-at. m^{-3}) were found in the mixed layer, probably as result of their consumption by the diatom bloom (Table 2; Fig. 3). Large diatoms like *Rhizosolenia* spp. and

Table 2. Depth distributions of nitrate (NO_3^-), ammonia (NH_4^+), chlorophyll *a* collected with GF/F (chl *a*) and polycarbonate membrane (chl *a* >2 µm) filters, net community production (NP), gross production (GP) and community respiration (R) (±1 SD) obtained by the oxygen method, ^{14}C uptake by phytoplankton (^{14}C), and apparent molar photosynthetic quotients [ap PQ(gross-$O_2/^{14}C$)] from the euphotic zone at Stns S1 to S4. NP and ^{14}C measurements refer to daylight incubations (~13 h), R refers to 24 h

Stn	Depth (m)	NO_3^- (mg-at. m^{-3})	NH_4^+ (mg-at. m^{-3})	Chl *a* (mg m^{-3})	Chl *a* >2 µm (mg m^{-3})	NP (mg O_2 m^{-3} d^{-1})	R (mg O_2 m^{-3} d^{-1})	GP (mg O_2 m^{-3} d^{-1})	^{14}C (mg C m^{-3} d^{-1})	ap PQ (gross-$O_2/^{14}C$)
S1	1	23.7	0.32	1.03	0.08	104 0 ± 3.1	11.5 ± 3.0	115.5 ± 2.0	13.8	2.9
	10	24.6	0.21	1.10	0.08	100.0 ± 2.1	13.0 ± 2.5	113.0 ± 1.9	12.6	3.2
	15	21.8	0.37	0.93	0.08	97.3 ± 1.7	13.9 ± 1.9	111.2 ± 1.3	12.3	3.2
	20	24.1	0.34	0.93	0.08	85.6 ± 3.0	14.6 ± 1.2	100.0 ± 3.1	9.9	3.5
	30	18.3	0.34	0.91	0.08	55.3 ± 5.1	7.7 ± 5.0	63.0 ± 5.1	6.1	3.4
	40	22.5	0.35	0.88	0.09				4.4	
	60	23.4	0.35	0.30	0.05				0.8	
S2	1	17.4	0.38	1.55	0.41	75.1 ± 3.7	41.5 ± 4.9	116.6 ± 4.4	15.9	2.3
	5	17.8	0.40	1.06	0.43	60.4 ± 7.0	19.2 ± 5.0	79.6 ± 7.2	14.7	1.6
	10	17.1	0.40	0.84	0.31	88.0 ± 7.9	13.0 ± 2.4	101.0 ± 9.4	15.3	2.3
	15	18.8	0.45	0.65	0.28	44.4 ± 3.1	13.0 ± 4.9	57.4 ± 4.9	10.3	1.9
	20	20.0	0.53	0.35	0.21				5.4	
	30	21.0	0.47	0.31	0.18	3.8 ± 3.4	9.1 ± 3.1	12.9 ± 1.5	2.4	1 3
	45	22.6	0.43	0.17	0.10	-4.2 ± 2.6	9.1 ± 2.6	4.9 ± 1.9	0.7	
	60	25.6	0.42	0.15	0.09				0.3	
S3	1	12.0	0.37	3.51	3.87	412.1 ± 2.7	149.8 ± 5.7	1561.9 ± 7.4	73.7	2.5
	5	10.6	0.37	3.78	4.43	433.9 ± 8.2	149.8 ± 7.4	583.7 ± 9.0	106.7	1.8
	10	11.4	0.34	5.04	4.82	327.4 ± 8.0	166.6 ± 8.2	494.0 ± 6.2	34.0	4.5
	15	11.5	0.33	5.43	5.88	173.7 ± 6.7	168.2 ± 6.1	341.9 ± 5.9	30.9	3.1
	20	10.1	0.38	3.83	5.15	79.0 ± 1.6	157.4 ± 4.9	236.4 ± 5.0	27.4	2.1
	30	11.4	0.42	3.51	5.26	10.1 ± 3.3	161.3 ± 10.8	171.3 ± 11.2	29.1	1.1
	45	21.2	0.52	1.01	1.06				0.2	
	60	22.7	0.43	0.05	0.04				0.1	
S4	1	16.8	0.24	7.39	6.83	1021.3 ± 11.4	178.1 ± 1.9	1199.4 ± 15.6	203.0	2.1
	5	18.5	0.21	6.80	6.07	199.0 ± 5.5	129.8 ± 4.3	328.9 ± 6.4	38.3	2.7
	10	16.9	0.24	4.78	2.80	4.3 ± 5.8	118.3 ± 2.8	122.6 ± 8.8	5.7	5.5
	15	20.1	0.26	2.13	1.21				1.2	
	20	21.0	0.31	0.47	0.18	-12.2 ± 1.7	40.8 ± 2.7	28.6 ± 2.5	0.5	
	30	20.7	0.33	0.30	0.13	-20.3 ± 1.7	45.4 ± 2.9	25.1 ± 2.5	0.7	
	45	22.2	0.37	0.17	0.06				0.3	
	60	19.4	0.52	0.11	0.05				0.3	

Chaetoceros sp. were responsible for most of the chlorophyll, which formed a sub-surface maximum below the productivity maximum (compare Figs. 4 & 5). The chlorophyll maximum may have been a result of the progressive sinking of the bloom. Phytoflagellate concentrations were lower than at S1 and S2, but heteroflagellates were more abundant (Table 3).

Stn S4 (Deception Island) represented calm waters with a well-developed warm layer near the surface. This layer contained a prasinophyte-dominated bloom, and the resulting shading restricted the euphotic zone to the first 15 m (Table 2, Figs. 2–4). Blooms of small flagellates are common in Antarctic open-ocean waters (Weber & El-Sayed 1987). Also, they have been ascribed to later successional stages in neritic communities (Brökel 1985, Knox 1990, Jacques & Panouse 1991, Lancelot et al. 1993). However, Schloss & Estrada (1994) have recently suggested that the change of dominance from diatoms to flagellates may be related to the presence of water masses of different origin.

Heteroflagellates and bacteria were more abundant at S4 than at the other stations (Table 3), suggesting that, even during phytoplankton blooms, microbial loop processes were important.

Carbon fixation and oxygen evolution

Vertical profiles of rates of gross production (GP), net community production (NP) and community respiration (R), as well as carbon fixation (^{14}C), are shown in Fig. 5. Both oxygen and carbon units are expressed in mg m^{-3} h^{-1}. In general, there is a good agreement in the shape of the GP and ^{14}C profiles. Moreover, the correlation between the 2 variables is highly significant (r^2 = 0.89, log-log scale) (Fig. 6). However, the

magnitude of both measurements differs considerably, leading to mean apparent photosynthetic quotients (moles $O_2/^{14}C$) greater than 2 (Table 2, Fig. 7).

Integrated carbon uptake rates for the upper 60 m, measured by ^{14}C, lay between 0.3 and 1.5 g C m^{-2} d^{-1}. This 5-fold variability does not seem unusual for coastal waters near the Antarctic Peninsula. Holm-Hansen & Mitchell (1991) reported primary production rates of 0.1 to 3.4 g C m^{-2} d^{-1} for the Gerlache and Bransfield Straits during spring and summer. Furthermore, large interannual variabilities in average pigment concentration (Comiso et al. 1993) and annual mass flux rates (Wefer & Fischer 1991) have been reported for coastal areas, suggesting that time-dependent mechanisms influence phytoplankton distribution and productivity.

Respiration rates, expressed either in volume units or integrated over the water column, were also very variable (up to 1 order of magnitude) among stations (Table 2). The lower values are similar to the upper range of rates given by Williams (1984) for the Antarctic Ocean. However, Robinson & Williams (1993) reported respiration rates near the Antarctic Convergence which are more similar to our data (see also Arístegui & Montero 1995).

Daily (~13 h) oxygen and carbon balances for the upper 30 m are shown in Table 4. This depth approximately coincided with the mean euphotic zone depth (34 ± 17 m), calculated as the 1% surface light penetration depth from several stations in the studied area, including the 4 *in situ* ones. Oxygen was transformed to carbon using a molar PQ (photosynthetic quotient) of 1.5 and an RQ (respiratory quotient) of 1. We assumed that nitrate was the main source of nitrogen consumption by phytoplankton, since ammonia concentration in the water column was low compared with nitrate concentration (Fig. 3). According to this, total daily water-column integrated carbon incorporation measured by radiocarbon uptake in the particulate fraction underestimated net community production measured by the oxygen method by 29 to 54%.

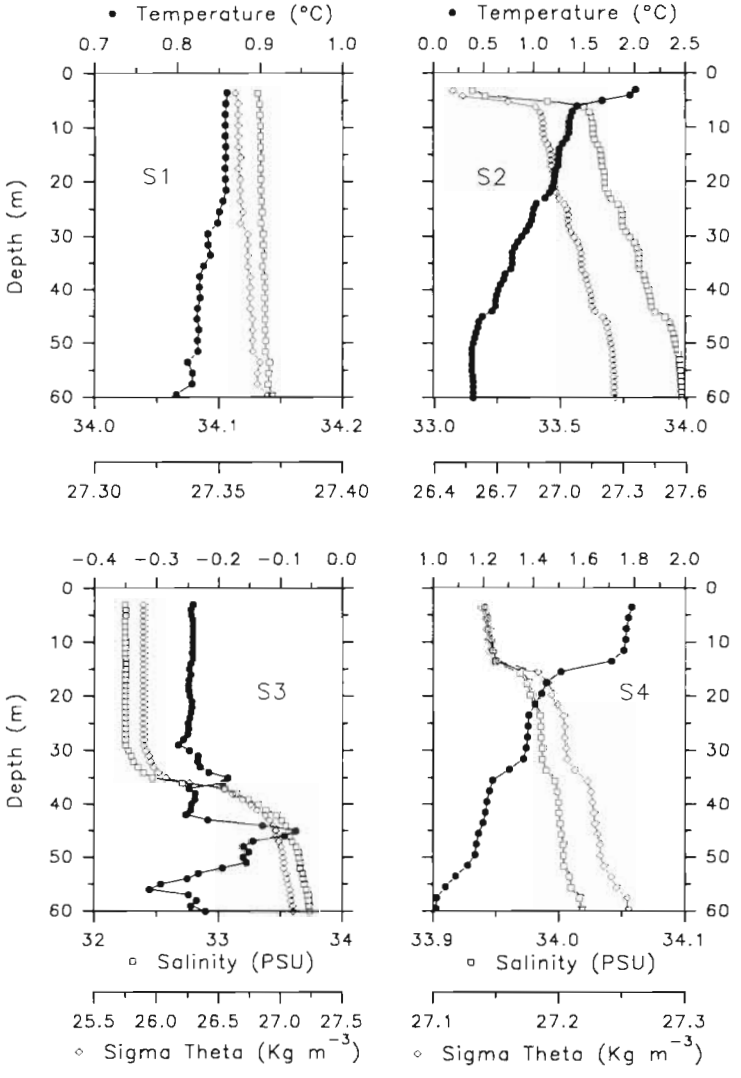

Fig. 2. Vertical profiles of temperature (°C), salinity (PSU) and sigma theta (kg m^{-3}) at Stns S1 to S4

DISCUSSION

Daily primary production

The stations selected for this study demonstrate the wide variability that exists in the hydrography and biology of coastal ecosystems in the vicinity of the Antarctic Peninsula. This variability underlines the importance of adequate sampling to overcome errors in the estimation of productivity in the area. The stations are located in one of the most productive areas of the Antarctic Ocean, where extensive phytoplankton blooms have been reported (Comiso et al. 1993). However, daily productivities may range over more than 1 order of magnitude on scales of tens of kilometers (Holm-Hansen & Mitchell 1991). Overall, our ^{14}C fixation values are in the same range as those reported for other Antarctic coastal areas (see Walsh 1989 for references), and Stn S3 (at the marginal ice zone) showed integrated productivity greater than 1 g C m^{-2} d^{-1} (Table 4), comparable to that of the most productive coastal regions (Holm-Hansen & Mitchell 1991).

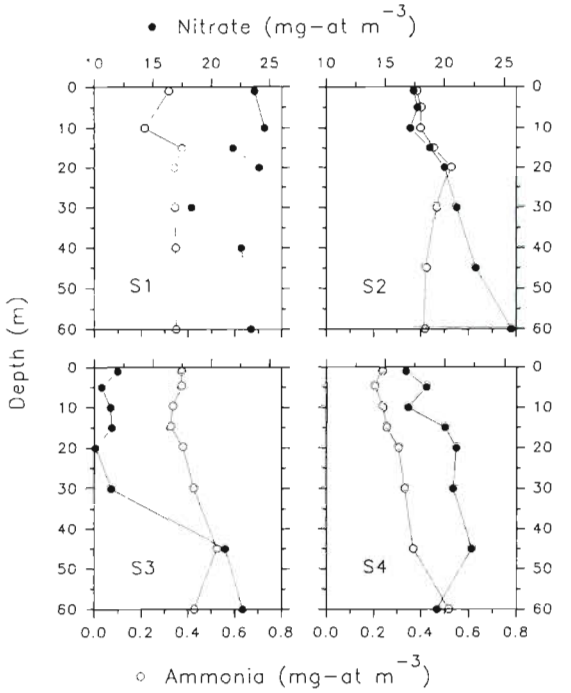

Fig. 3. Vertical profiles of nitrate (mg-at. m^{-3}) and ammonia (mg-at. m^{-3}) at Stns S1 to S4

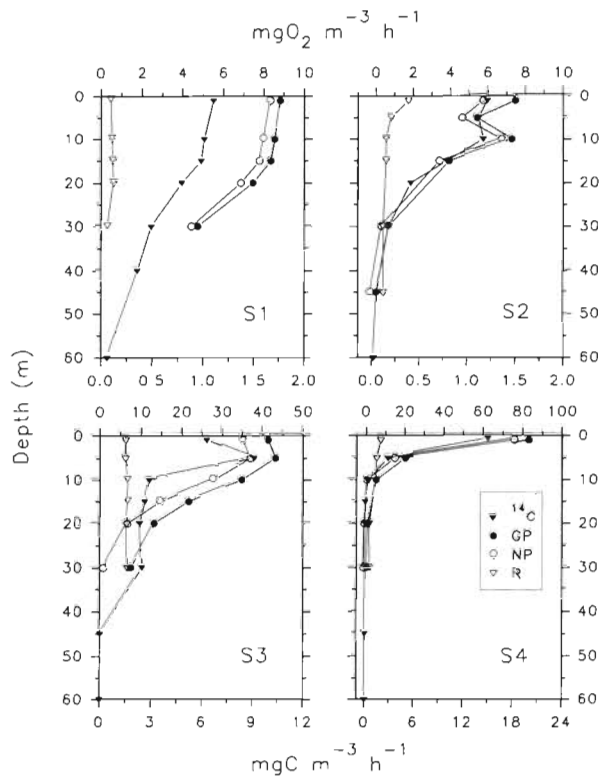

Fig. 5. Vertical profiles of gross production (GP), net community production (NP) and community respiration (R) obtained by the oxygen method (in mg O_2 m^{-3} h^{-1}), and ^{14}C uptake by phytoplankton (in mg C m^{-3} h^{-1}) at Stns S1 to S4

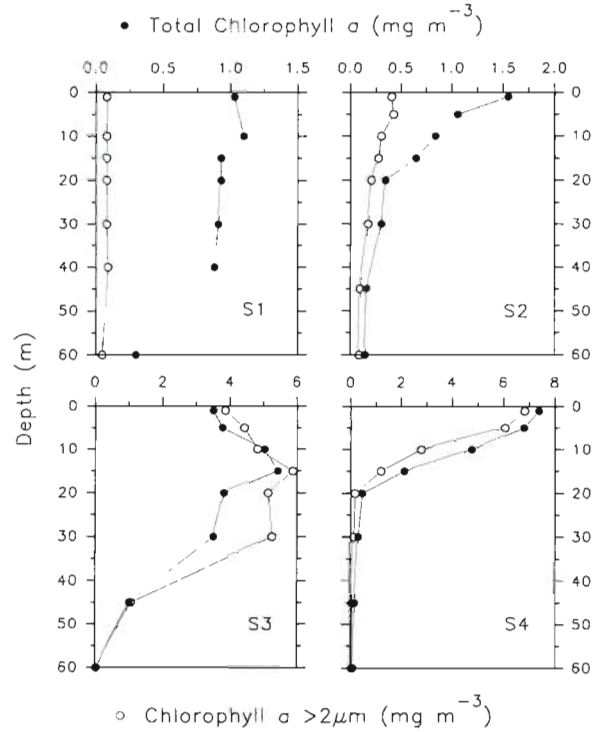

Fig. 4. Vertical profiles of chlorophyll *a* (mg m^{-3}) collected with GF/F filters (total chlorophyll) and polycarbonate membrane filters (chlorophyll >2 μm) at Stns S1 to S4

Apparent photosynthetic quotients

The comparison of the ^{14}C and oxygen data shows, however, that our ^{14}C measurements of carbon uptake underestimated both gross and net production calculated from oxygen changes. Apparent molar PQ(gross-O_2/^{14}C) and PQ(net-O_2/^{14}C) values calculated from our results (Table 2, Fig. 7), were on average higher than the theoretical upper PQ boundaries calculated by Williams & Robertson (1991) for conventional photosynthetic products. The latter authors attribute high PQ values to unshared systematic errors in the O_2 and ^{14}C methods. Analytical errors in the ^{14}C method, however, are more likely to be the cause of high PQ values, since in the O_2 method the enhancement of light-induced respiration in light bottles (the most significant error of the method) leads to an underestimation of gross production. Williams (1993) pointed out the recycling of respiratory ^{12}C within the cell and the respiration of freshly fixed ^{14}C as two of the main reasons accounting for an upward shift in the apparent PQ values. In this context, Li & Harrison (1982) found that non-linearity of ^{14}C uptake in Arctic plankton, caused by catabolic loss of radiocarbon, might lead to an underestimation of true gross production by 40% after 24 h.

Table 3. Depth distributions of cell abundances of the most representative phytoplankton groups (diatoms, prasinophytes and cryptophytes), heterotrophic flagellates and bacteria at Stns S1 to S4

Station	Depth (m)	Diatoms (cells ml^{-1})	Cryptophytes (cells ml^{-1})	Prasinophytes (cells ml^{-1})	Heteroflagellates (cells ml^{-1})	Bacteria ($\times 10^2$ cells ml^{-1})
S1	1	7	2580	100	1300	2350
	10	14	1320	–	1650	
	15	16	2180	–	1000	3350
	20	2	2330	–	1400	2150
	30	–	2090	–	700	
	40	–	1000	–	700	3150
	60	–	1000	–	1700	
S2	1	16	640	10	2750	1650
	5	150	800	10	2000	1900
	10	37	190	1	1800	2700
	15	771	140	–	2100	2250
	20	70	160	–	1850	2100
	30	26	15	–	1850	
	45	11	42	–	800	
	60	7	15	–	800	2200
S3	1	470	60	2	1500	1500
	5	550	60	1	2600	2300
	10	900	47	1	1600	2500
	15				2450	2200
	20	900	20	–	1500	2350
	30	960	6	–	1750	2600
	45	54	–	–	1100	2750
	60	15	–	–	700	2100
S4	1	9	100	5000	4500	3700
	5	43	161	1300	3750	5300
	10	20	161	1000	4200	4700
	15	66	161	540	4000	5100
	20	17	100	–	5000	6500
	30	15	53	–	3700	4000
	45	–	31	–	2500	3000
	60	–	107	–	2500	5500

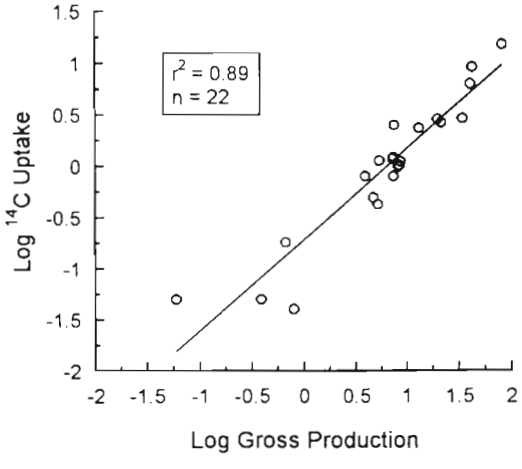

Fig. 6. Relationship between gross production obtained by the oxygen method (in mg O_2 m^{-3} h^{-1}) and ^{14}C uptake (in mg C m^{-3} h^{-1}). Data are log-transformed; line of best fit is shown (r^2 = 0.89, n = 22)

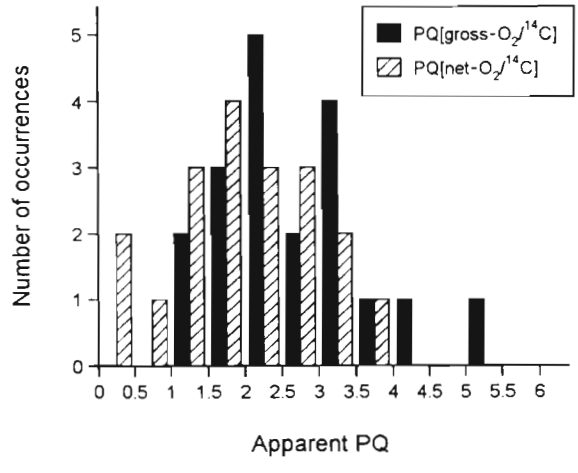

Fig. 7. Frequency distribution of apparent gross and net molar photosynthetic quotients [(gross-O_2/^{14}C), (net-O_2/^{14}C)], calculated from the euphotic zone at Stns S1 to S4

Table 4. Depth integrated values of ^{14}C uptake by phytoplankton, and gross production (GP) and community respiration (R) calculated by the oxygen method. GP, R and ^{14}C measurements refer to daylight incubations (~13 h). Respiratory losses of GP in oxygen (O_2) and carbon (C) units are calculated. A photosynthetic quotient of 1.5 and a respiratory quotient of 1 (mol:mol) were used to transform oxygen to carbon (see text for details). Z_{EZ}: depth of the euphotic zone at each station

Station	Z_{EZ} (m)	Range (m)	^{14}C uptake (mg C m^{-2})	GP (mg O_2 m^{-2})	GP (mg C m^{-2})	R (mg O_2 m^{-2})	R (mg C m^{-2})	R/GP (O_2) (%)	R/GP (C) (%)
S1	58	0-30	316	2760	690	188	71	6.8	10.3
		0-60	419						
S2	35	0-30	279	1571	393	236	89	15.0	22.6
		0-60	308						
S3	30	0-30	1303	8194	2049	2269	851	27.7	41.5
		0-60	1525						
S4	15	0-30	620	4133	1033	1385	520	33.5	50.3
		0-60	631						

An additional source of error in the calculation of apparent PQ may arise from unaccounted-for dissolved organic carbon (DOC) exudated by cells during the incubation period (Williams & Robertson 1991).

In our study no correction was made for either phytoplankton ^{14}C respiratory losses or excretion. Therefore, we are not able to quantify the magnitude of these errors. Phytoplankton excretion could be, however, a primary explanation of the high PQ observed, according to recent results published from polar sea studies.

From changes in the concentration of ambient nutrient pools, Karl et al. (1991b) estimated that at least 40 to 50% of photosynthetically fixed carbon may accumulate as DOC in the euphotic zone of Bransfield and Gerlache Strait waters. This loss could account for the difference found between our estimates of net primary production from O_2 change and net particulate C assimilation from ^{14}C uptake. High concentrations of DOC have been reported for water samples collected from the Bransfield Strait during the austral summer (Bölter & Dawson 1982). Supporting these observations, Davidson & Marchant (1992) reported high concentrations of dissolved organic matter coinciding with a *Phaeocystis* bloom in another coastal Antarctic area. These findings also agree with recent experiments carried out during a spring bloom in the Barent Sea. Passow et al. (1994) and Vernet et al. (1994) observed that an average 50 to 70% of the primary production was released as extracellular carbon by phytoplankton during the ^{14}C uptake experiments.

Pomeroy & Wiebe (1993) showed evidence that bacterial growth and respiratory rate may be limited by substrate availability in low temperature environments. Therefore, a large DOC pool or flux might have important implications on the abundance and metabolism of bacteria in coastal waters near the Antarctic Peninsula. Karl et al. (1991a), however, found that in these areas bacterial population dynamics were uncoupled from photoautotrophic processes during the seasonal bloom. Moreover, bacterial numbers were lower than expected in relation to the chlorophyll concentrations found. Our results (Table 3) show similarly low bacterial numbers for the 4 stations, although we do not know if there were differences in their metabolic activities.

Despite the latter evidence we can not be sure of the causes that produced our observed high PQ. For instance, Tilzer & Dubinsky (1987) calculated lower extracellular losses (between 9 and 12.4% of total 24 h production) by phytoplankton from the Bransfield Strait. A more detailed simultaneous study of carbon (^{14}C and CO_2) and oxygen fluxes in this coastal Antarctic region considering soluble organic material exudated by phytoplankton during ^{14}C uptake experiments is needed in order to clarify this problem.

In any case, there is increasing evidence that particulate ^{14}C assimilation measurements underestimate primary production in Antarctic waters. Minas & Minas (1992) obtained, in open-ocean Antarctic waters, estimates of daily average new production (from observations of nitrate removed from the water column) of the same magnitude as, or even higher than, estimates of production from ^{14}C uptake measurements. Karl et al. (1991a) observed that although microbial biomass was clearly dominated by phytoplankton in the Bransfield and Gerlache Straits during some periods of the year, autotrophic production (by the ^{14}C method) appeared to be only a small portion of total microbial production (by the [^{3}H]-adenine method). This suggests that autotrophic production could have been severely underestimated by the ^{14}C method.

Water column balance

Oxygen fluxes from the upper 30 m (approximately the euphotic zone for these coastal waters) showed

positive net production at all stations. Integrated respiration accounted for 7 to 34% of the GP in oxygen units and 10 to 50% in carbon units (Table 4). These percentages are higher than the estimated value (<10% of GP) derived by Tilzer & Dubinsky (1987) from ^{14}C uptake experiments for phytoplankton in the Bransfield Strait.

The contribution of phytoplankton to microbial respiration in Antarctic coastal waters is not well known, but is certainly high. In most marine ecosystems microheterotrophs contribute a large part of total microbial respiration (Pomeroy & Johannes 1966, 1968, Williams 1981a, b, Harrison 1986, Iriarte et al. 1991). However, in coastal Antarctic waters phytoplankton seem to dominate microbial respiration. Several studies (Lancelot et al. 1991, Estrada et al. 1992, Martínez & Estrada 1992, Arístegui & Montero 1995) have shown that community respiration is closely related to chlorophyll or primary production in Antarctic coastal waters. Our respiration data also show a correlation with total chlorophyll (r^2 = 0.69, log-log scale) and chlorophyll >2 µm (r^2 = 0.87, log-log scale), suggesting that most respiration in the euphotic zone was due to large phytoplankton. This agrees with the conclusions of Karl et al. (1991a) that phytoplankton play the main role in community metabolism in the Bransfield and Gerlache Straits.

Carbon fluxes calculated by Lancelot et al. (1991) in the Scotia and Weddell Seas using a coupled physical-biological model yielded average phytoplankton respiratory losses of 50% of GP, while microheterotrophic respiration (due to bacteria and protozoa) accounted for 25 to 30% of GP. The planktonic food web described by Lancelot et al. (1991), in which 71% of the net primary production is assimilated in the microbial food web, may differ from the hypereutrophic diatom-dominated ecosystems found in Antarctic coastal waters (Huntley et al. 1991, 1992), where phytoplankton and bacterioplankton population dynamics are uncoupled (Karl et al. 1991a). However, it illustrates the importance of phytoplankton respiratory losses to the overall photosynthetically fixed carbon. If we were to conclude that most of the community respiration at high chlorophyll concentrations is due to phytoplankton, then Lancelot et al.'s (1991) calculations on phytoplankton respiratory losses would broadly agree with the values we obtained from our 2 more productive stations (S3 and S4).

Considering that on average 40% of GP is lost by phytoplankton respiration during phytoplankton bloom situations, the carbon flux model proposed by Huntley et al. (1991) for hypereutrophic coastal Antarctic ecosystems should be reconsidered. These authors did not include phytoplankton respiration in their model, and as a result they increased the imputed heterotrophic contribution to the carbon flux budget (Moloney 1992). Recalculations of their data including phytoplankton respiratory losses of 40% of GP would lead to respiratory losses by air-breathing top predators of about 7%. Recent estimations of carbon consumption rates by top predators, derived from animal densities in coastal Antarctic ecosystems (Franeker et al. 1994), suggested that less than 0.5% of primary production is being returned to the atmosphere, even in areas where top predators are abundant. This value is still far lower than the recalculated value obtained after considering phytoplankton respiration. Huntley et al. (1991, 1992) assumed in their model that more than 90% of net primary production was (either directly or indirectly) channeled to macrozooplankton. However, although particle sedimentation in the Antarctic Peninsula area may be largely mediated by krill (Wefer et al. 1982, 1988, Dunbar 1984, Bodungen et al. 1987), sedimentation of intact cells and rapid sinking of diatom resting spores (Bodungen et al. 1986, Liebezeit 1987, Karl et al. 1991b, Leventer 1991) is another important pathway for carbon export not considered in Huntley et al.'s (1991) model. Furthermore, Banse (1995) has recently questioned the gross growth efficiencies used by Huntley et al. (1991) in their carbon flux model. According to Banse (1995), the use of lower growth efficiencies in the model [characteristic of field populations, instead of the higher growth efficiencies of individuals used by Huntley et al. (1991)] would lead to a leaking to the atmosphere of ≤3% of the net primary production by air-breathing top predators.

In summary, our results show that all phytoplankton losses (including exudation and respiration) must be carefully considered to interpret carbon fluxes in coastal Antarctic regions. Microbial respiration represents a considerable loss of photosynthetically fixed carbon in productive ecosystems in the waters around the Antarctic Peninsula. This loss is in all instances much higher than the respiratory loss due to top predators.

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LITERATURE CITED

Arístegui J, Montero MF (1995) Plankton community respiration in Bransfield Strait (Antarctic Ocean) during austral spring. J Plankton Res 17:1647–1659

Banse K (1995) Antarctic marine top predators revisited: homeotherms do not leak much CO_2 to the air. Polar Biol 15:93–104

Bodungen B von, Fisher G, Nothig EM, Wefer G (1987) Sedimentation of krill faeces during spring development of phytoplankton in Bransfield Strait, Antarctica. Mitt Geol Palaeontol Inst Univ Hamburg 62:49–164

Bodungen B von, Smetacek VS, Tilzer MM, Zeitzschel B (1986) Primary production and sedimentation during spring in the Antarctic Peninsula region. Deep Sea Res 33: 177–194

Bölter M, Dawson R (1982) Heterotrophic utilisation of biochemical compounds in Antarctic waters. Neth J Sea Res 16:315–332

Brökel K von (1985) Primary production data from the southeastern Weddell Sea. Polar Biol 4:75–80

Bryan JR, Riley JP, Williams PJLeB (1976) A procedure for making precise measurements of oxygen concentration for productivity and related studies. J Exp Mar Biol Ecol 21:191–197

Carrit DE, Carpenter JH (1966) Comparison and evaluation of currently deployed modifications of the Winkler method for determining dissolved oxygen in seawater: a NASCO Report. J Mar Res 24:287–318

Comiso JC, McClain CR, Sullivan CW, Ryan JP, Leonard CL (1993) Coastal Zone Color Scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. J Geophys Res 98:2419–2451

Davidson AT, Marchant HJ (1992) Protist interactions and carbon dynamics of a *Phaeocystis*-dominated bloom at an Antarctic coastal site. Polar Biol 2:387–395

Dunbar RB (1984) Sediment trap experiments on the Antarctic continental margin. Antarct J US 19:70–71

Estrada M, Martínez R, Mathod S (1992) Respiratory electron transport activity in plankton of the Weddell and Scotia Seas during late spring-early summer: relationships with other biological parameters. Polar Biol 12:35–42

Franeker JA van, Bathmann U, Mathot S (1994) Southern Ocean carbon fluxes: the role of top predators. EOS 75(suppl):177

Geider RJ (1992) Respiration: taxation without representation? In: Falkowsky PG, Woodhead AD (eds) Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York, p 333–360

Grasshoff K, Ehrhardt M, Kremling K (1983) Methods of seawater analysis. Verlag Chemie, Deerfield Beach, FL

Haas L (1982) Improved epifluorescence microscopy for observing planktonic micro-organisms. Ann Inst Oceanogr, Paris 58:261–266

Harrison WG (1986) Respiration and its size dependence in microplankton populations from surface waters of the Canadian Artic. Polar Biol 6:145–152

Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorometric determination of chlorophyll. J Cons Int Explor Mer 30:3–15

Holm-Hansen O, Mitchell BG (1991) Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep Sea Res 38: 961–980

Huntley ME, López MDG, Karl DM (1991) Top predators in the Southern Ocean: a major leak in the biological carbon pump. Science 253:64–66

Huntley ME, López MDG, Karl DM (1992) Response to the comment of Moloney CL. Science 257:259–260

Iriarte A, Daneri G, García VMT, Purdie DA, Crawford DW (1991) Plankton community respiration and its relationship to chlorophyll *a* concentration in marine coastal waters. Oceanol Acta 14:379–388

Jaques G, Panouse M (1991) Biomass and composition of size fractionated phytoplankton in the Weddell-Scotia Confluence area. Polar Biol 11:315–328

Karl DM, Holm-Hansen O, Taylor GT, Tien G, Bird DF (1991a) Microbial biomass and productivity in the western Bransfield Strait, Antarctica during the 1986–1987 austral summer. Deep Sea Res 38:1029–1055

Karl DM, Tilbrook BD, Tien G (1991b) Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antarctica. Deep Sea Res 38:1097–1126

Knox GA (1990) Primary production and consumption in McMurdo Sound, Antarctica. In: Kerry KR, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer-Verlag, Berlin, p 115–128

Kopczynska EE, Ligowski R (1985) Phytoplankton composition and biomass distribution in the southern Drake Passage, the Bransfield Strait and the adjacent waters of the Weddell Sea in December 1983–January 1984 (BIOMAX-SIBEX). Pol Polar Res 6:65–77

Lancelot C, Billen G, Veth C, Becquevort S, Mathot S (1991) Modelling carbon cycling through phytoplankton and microbes in the Scotia-Weddell Sea area during sea ice retreat. Mar Chem 35:305–324

Lancelot C, Mathot S, Veth C, Baar H de (1993) Factors controlling phytoplankton ice-edge blooms in the marginal ice-zone of the northwestern Weddell Sea during ice retreat 1988: field observations and mathematical modelling. Polar Biol 13:377–387

Leventer A (1991) Sediment trap diatom assemblages from the northern Antarctic Peninsula region. Deep Sea Res 38:1127–1143

Li WKW, Dickie PM (1991) Light and dark ^{14}C uptake in dimly lit oligotrophic waters: relation to bacterial activity. J Plankton Res 13(suppl):29–44

Li WKW, Harrison WG (1982) Carbon flow into the end-products of photosynthesis in short and long incubations of a natural phytoplankton population. Mar Biol 72:175–182

Li WKW, Irwin BD, Dickie PM (1993) Dark fixation of ^{14}C: variations related to biomass and productivity of phytoplankton and bacteria. Limnol Oceanogr 38:483–494

Liebezeit G (1987) Particulate carbohydrate fluxes in the Bransfield Strait and the Drake Passage. Mar Chem 20: 255–264

Longhurst AR, Harrison WG (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. Prog Oceanogr 22:47–123

Martinez R, Estrada M (1992) Respiratory electron transport activity of microplankton in the Weddell Sea during early spring: influence of the ice cover and the ice edge. Polar Biol 12:275–282

Minas HJ, Minas M (1992) Net community production in 'High Nutrient–Low Chlorophyll' waters of the tropical and Antarctic Oceans: grazing vs iron hypothesis. Oceanol Acta 15:145–162

Moloney CL (1992) Carbon and the Antarctic marine food web. Science 257:259

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford

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

Pomeroy LR, Johannes RE (1966) Total plankton respiration. Deep Sea Res 13:971–973

Pomeroy LR, Johannes RE (1968) Occurrence and respiration of ultraplankton in the upper 500 m of the ocean. Deep Sea Res 15:381–391

Pomeroy LR, Wiebe WJ (1993) Energy sources for microbial food webs. Mar Microb Food Webs 7:101–118

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25:943–947
Robinson C, Williams PJLeB (1993) Temperature and Antarctic plankton community respiration. J Plankton Res 15: 1035–1051
Sakshaug E, Holm-Hansen O (1984) Factors governing pelagic production in polar oceans. In: Bolis L, Gilles R (eds) Marine phytoplankton and productivity. Springer-Verlag, New York, p 1–17
Schloss I, Estrada M (1994) Phytoplankton composition in the Weddell-Scotia Confluence area during austral spring in relation to hydrography. Polar Biol 14:77–90
Steeman-Nielsen E (1952) The use of radio-active carbon (^{14}C) for measuring organic production in the sea. J Cons Int Explor Mer 18:117–140
Strickland JDH (1960) Measuring the production of marine phytoplankton. Bull Fish Res Bd Can 122:1–172
Sullivan CW, Arrigo KR, McClain CR, Comiso JC, Firestone J (1993) Distributions of phytoplankton blooms in the Southern Ocean. Science 262:1832–1837
Tilzer MM, Dubinsky Z (1987) Effects of temperature and day length on the mass balance of Antarctic phytoplankton. Polar Biol 7:35–42
Vernet M, Matrai PA, Ruel J (1994) Photosynthetic carbon production at the ice edge in the Barents Sea: cellular and extracellular carbon pools. EOS 75(suppl):127
Volk T, Hoffert MI (1985) Ocean carbon pumps, analysis of relative strengths and efficiencies in ocean-driven atmospheric CO_2 changes. Geophys Monogr 32:99–110
Walsh JJ (1989) Arctic carbon sinks: present and future. Global Biogeochem Cycles 3:393–411
Weber LH, El-Sayed SZ (1987) Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. J Plankton Res 9:973–994
Wefer G, Fisher G (1991) Annual primary production and export flux in the Southern Ocean from sediment trap data. Mar Chem 35:597–613
Wefer G, Fisher G, Fütterer D, Gersonde R (1988) Seasonal particle flux in the Bransfield Strait, Antarctica. Deep Sea Res 35:891–898
Wefer G, Suess E, Balzer W, Liebezeit G, Müller PJ, Ungerer CA, Zenk W (1982) Fluxes of biogenic components from sediment trap deployment in circumpolar waters of the Drake Passage. Nature 299:145–147
Williams PJLeB (1981a) Microbial contribution to overall plankton community respiration—studies in enclosures In: Grice GD, Reeve MR (eds) Marine mesocosms: biological and chemical research in experimental ecosystems. Springer-Verlag, Berlin, p 305–321
Williams PJLeB (1981b) Microbial contribution to overall marine plankton metabolism: direct measurements of respiration. Oceanol Acta 4:359–364
Williams PJLeB (1984) A review of measurements of respiration of marine plankton populations. In: Hobbie JA, Williams PJLeB (eds) Heterotrophic activity in the sea. Plenum Press, New York, p 357–389
Williams PJLeB (1993) Chemical and tracer methods of measuring plankton production. ICES Mar Sci Symp 197:20–36
Williams PJLeB, Jenkinson NW (1982) A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. Limnol Oceanogr 27: 576–584
Williams PJLeB, Robertson JE (1991) Overall planktonic oxygen and carbon dioxide metabolisms: the problem of reconciling observations and calculations of photosynthetic quotients. J Plankton Res 13 (suppl):153–169
Yentsch CS, Menzel DW (1963) A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep Sea Res 10:221–231

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