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Summer community respiration and pelagic metabolism in upper surface Antarctic waters

Susana Agustí[1,*], Maria Paola Satta[2], Maria Paola Mura[2]

[1]Instituto Mediterráneo de Estudios Avanzados (IMEDEA), CSIC-UIB, Miquel Marqués 21, 07190 Esporles, Mallorca, Spain
[2]Centro de Estudios Avanzados de Blanes, CSIC, Camí de Sta Barbara s/n, 17300 Blanes, Girona, Spain

ABSTRACT: Microplanktonic community respiration (*R*) and net community production (NCP) in upper surface waters around the Antarctic Peninsula were studied in the summers of 1993, 1994 and 2000. Data on pelagic community metabolism from upper surface Antarctic waters (N = 27) were collected from the literature and included in the analysis (N = 96). The variability of phytoplankton chl *a* concentration found was high, ranging from 0.06 to 16.75 mg m^{-3} d^{-1}. *R* rates varied from 0.19 to 11.03 mmol O_2 m^{-3} d^{-1} and were not related to chl *a* concentration. The variability in daily NCP rates was higher than that found for *R*, ranging from −6.29 to 35.4 mmol O_2 m^{-3} d^{-1}, and was positively related to chl *a* concentration (R^2 = 0.46). NCP rates were often negative (53% of the observations) in the 1993 survey, indicative of community respiration in excess of primary production. Negative NCP was less frequent during the 1994 and 2000 cruises and in the literature data (18, 7 and 4% of the observations, respectively). A positive and strong relationship (R^2 = 0.92) was observed between NCP and gross primary production (GPP), whereas *R* was independent of GPP. The relationships found imply that changes in GPP play a dominant role in the control of net planktonic metabolism in Antarctic waters, allowing excess carbon to be fixed by phytoplankton during phytoplankton blooms. In contrast, unproductive Antarctic communities (<0.064 g O_2 m^{-3} d^{-1}) tend to be net heterotrophic, thereby representing CO_2 sources, rather than sinks. Since phytoplankton-poor waters extend over most of the Southern Ocean, these results stress the need to evaluate their role in oceanic carbon flow on the basis of a more comprehensive temporal and spatial data set.

KEY WORDS: Antarctic Ocean · Plankton metabolism · Community respiration · Gross primary production · Net community production

INTRODUCTION

The Southern Ocean plays an important role in sequestering atmospheric CO_2 through both physical and biological processes. The Southern Ocean contributes 15% of the oceanic primary production (Huntley et al. 1991), although phytoplankton chlorophyll and production are generally low and show great variability in space and time (Fukuchi 1980, El-Sayed et al. 1983, McMinn & Hodgson 1993, Sullivan et al. 1993, Mura et al. 1995), suggesting that the importance of biota in sequestering atmospheric CO_2 should also be very variable in the Southern Ocean.

The importance of oceanic biota in the net absorption of atmospheric CO_2 depends not only on the extent of carbon fixed by phytoplankton, but also on the fate of this carbon within the food web (Williamson & Holligan 1990, Huntley et al. 1991, Moloney 1992, Duarte & Cebrián 1996). Recent evidence has shown that planktonic microheterotrophs play a more important role in Antarctic waters than previously thought (e.g. Fuhrman & Azam 1980, Delille et al. 1988, Cota et al. 1990, Karl et al. 1991, Delille 1993). The development of an important biomass of microheterotrophic organisms suggests that a significant fraction of the carbon fixed by phytoplankton in surface Antarctic waters may be oxidized to CO_2 by the respiration of microheterotrophic organisms (e.g. Cota et al. 1990, Moloney 1992). The net absorption of CO_2 by Antarctic biota may be, there-

*Email: sagusti@uib.es

fore, much less than that expected from the planktonic primary production alone.

Net community metabolism, the difference between the production of organic matter by photosynthetic organisms and the oxidation of organic matter by respiration in ecosystems, is an important descriptor of the role of biological processes in carbon flow of the ecosystem (Smith & Mackenzie 1987, Smith & Hollibaugh 1993, Duarte & Agustí 1998). There is, however, a paucity of estimates of net planktonic community metabolism in the Southern Ocean (Bouquegneau et al. 1992, Boyd et al. 1995, Arístegui et al. 1996, Serret et al. 2001) that renders the assessment of the role of microplankton as a carbon sink in the Southern Ocean difficult. There is, therefore, a need to increase the empirical basis on the respiration and metabolism of Antarctic planktonic communities, which could be used to examine the patterns and controls on this important component of carbon cycling there.

We examine here the variability of microplanktonic community respiration and resulting net microplankton community metabolism in surface waters around the Antarctic Peninsula during austral summer. We do so based on cruises conducted in January/February 1993 (Bransfield and Gerlache Straits), February 1994 (Bransfield Strait) and January/February 2000 (Bransfield, Gerlache and Antarctic Straits). We test the relative importance of gross production and community respiration as the main drivers of net community metabolism, and test the generality of relationships obtained using a compilation of published estimates on microplankton metabolism in the Southern Ocean.

MATERIALS AND METHODS

The study was performed during the cruises BIOANTAR-93 (January 19 to February 21, 1993), BENTART-94 (February 5 to 24, 1994) and ESEPAC-2000 (January 25 to February 17), on board RV 'BIO Hespérides'. During BIOANTAR-93, 27 stations, comprising open ocean and coastal waters, located at the Bransfield and Gerlache Straits were sampled (Fig. 1). During BENTART-94, a time series was performed at 5 stations within the Bransfield Strait, located in Livingston Island (Sur and Falsa bays), in Foster Port (Decepción Island) and 2 stations half way between Decepción and Livingston Islands (Fig. 1). These stations were visited at different frequencies: daily and every 2 d for Sur and Falsa Bays, respectively, and every 3 d for the other 3 stations. During ESEPAC-2000, 7 transects were made around the Antarctic peninsula (Bransfield, Gerlache and Antarctic Straits) to occupy stations encompassing the broadest possible range in productivity in the area. The position of the 14 stations, 2 per transect, sampled was decided on the basis of the *in vivo* fluorescence of chlorophyll (Turner Designs fluorometer) of surface waters (5 m), monitored in real time during the transects using a continuous surface-water sampling system coupled to a fluorometer and a salinity-temperature probe.

Surface water samples (between 1 and 5 m) were collected with Niskin bottles fitted on a CTD-rosette sampler system. Subsurface water (15 m depth) samples were also collected at 3 of the 27 stations sampled during BIOANTAR-93. During BIOANTAR-93, where the oceanographic study was more extensive, the different

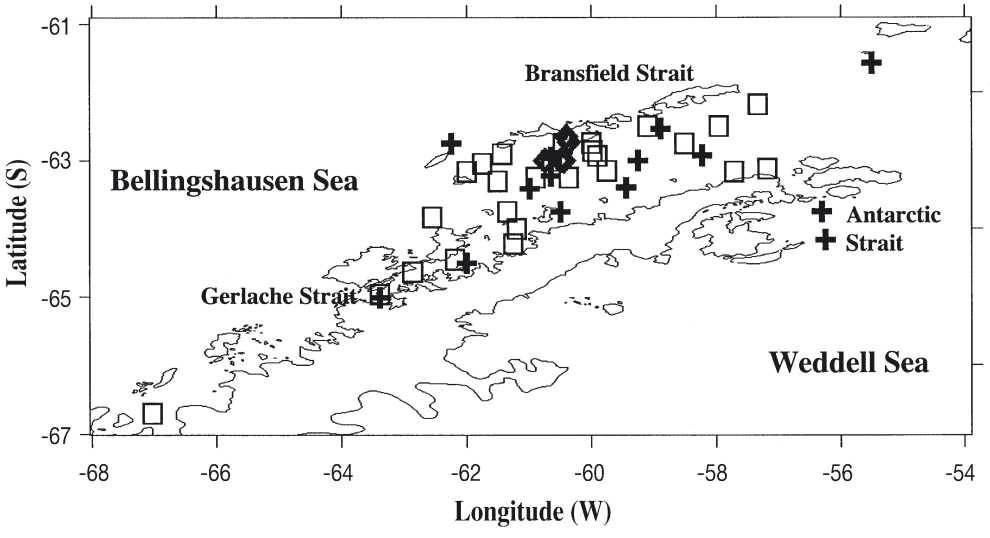

Fig. 1. Location of stations studied during the 3 summer cruises (□, BIOANTAR-93; ◇, BENTART-94; +, ESEPAC-2000) conducted around the Antarctic Peninsula

water masses from the Bellingshausen and Weddell seas, which varied in their characteristic water temperature and salinity (2.75°C, 33‰ and −0.75°C, 34.5 ‰, respectively), were identified in the area. The confluence of the water masses from the Bellingshausen and Weddell seas generated a front located at the NW of the Bransfield Strait (Mura et al. 1995).

Chl *a* concentration was determined fluorometrically by filtering a variable volume of water (between 50 and 250 ml, depending on plankton abundance) on Whatman GF/F filters, homogenized and extracted in 90% acetone for ca. 1 h in the dark and refrigerated conditions. The fluorescence of the extracts was measured in a Turner Design fluorometer (Parsons et al. 1984).

Water samples for the measurement of respiration and net community production (NCP) rates were screened through 150 µm mesh to eliminate larger zooplankton and carefully siphoned into 125 ml narrow-mouth Winkler bottles. Microplanktonic community respiration (*R*) and NCP rates were estimated from changes in oxygen concentration after incubation of samples in the dark and light, respectively. Five replicates were used to determinate the initial oxygen concentration and 5 replicate bottles were used for the incubations in the dark and light. The bottles were incubated for 15 to 24 h at *in situ* temperature (temperature range between −0.57 and 2.43°C, 0.85 and 1.73°C, and −0.51 and 3.8°C for 1993, 1994 and 2000, respectively) by flushing the incubators with surface seawater during the 1993 and 2000 cruises, and using a thermostatic incubator during the 1994 cruise. The relatively long incubation times were necessary to obtain reliable estimates of oxygen changes, which may induce possible bottle effects (e.g. Pomeroy et al. 1994). 'Light' bottles from surface water were incubated at 150 µmol photons m^{-2} s^{-1}, close to *in situ* conditions, which averaged, below the water surface, 350 µmol photons m^{-2} s^{-1} during the summer of 1993, and 120 µmol photons m^{-2} s^{-1} during 1994 (Licor 1800-UW spectroradiometer). The 3 subsurface samples from the 1993 survey were incubated at lower irradiances (70 or 40 µmol photons m^{-2} s^{-1}) to reproduce the '*in situ*' irradiance. Examination of production versus irradiance (P-I) curves showed the threshold between light-saturated and light-limited photosynthesis of surface phytoplankton to be between 100 µmol photons m^{-2} s^{-1} in samples of 1993 (Arístegui unpubl. data) and 50 µmol photons m^{-2} s^{-1} in 1994 (Satta unpubl. data). During ESEPAC-2000, 'light' bottles were incubated on deck under natural light conditions, reduced to 50% surface iradiance by using a neutral screen material. Dissolved oxygen concentration was measured using high-precision Winkler titration after Carrit & Carpenter (1966), using a Metrohm-682 Autotritator for the potentiometric (redox electrode) end-point detection (Oudot et al. 1988). Respiration rates were calculated from the difference in oxygen concentration between initial and 'dark' bottles, and NCP was calculated from the difference in oxygen concentration between 'light' bottles and the initial oxygen concentration. The NCP measured in this way was converted to daily (24 h) estimates by considering the length of the day and night periods for each sampling event, except for the ESEPAC-2000 cruise, when 'light' bottles were incubated at the natural photoperiod. Gross primary production (GPP) was calculated as the sum of community respiration rates and net community metabolism.

Additional data of microplankton community respiration and NCP (derived using oxygen evolution) from the Southern Ocean was compiled from the literature to evaluate the generality of our results. This search yielded a total of 27 estimates from surface waters from 4 published studies (Bouquegneau et al. 1992, Boyd et al. 1995, Arístegui et al. 1996, Odate et al. 2002). Only data from open water stations of Bouquegneau et al. (1992) were included in this comparison. Data of hourly NCP of Bouquegneau et al. (1992) were transformed to daily NCP using an estimated daylength duration of 15 h from the reported GPP and dark respiration (i.e. NCP $d^{-1} = 15 \times GPP\ [h^{-1}] - 24 \times R\ [h^{-1}]$). Only data from 1, 5 and 10 m from Arístegui et al. (1996) and 10 m depth from Boyd et al. (1995), and from 0 to 15 m from Odate et al. 2002, were included in the comparison. The data set is available upon request from the corresponding author.

RESULTS

Phytoplankton chl *a* concentration and phytoplankton biomass were highly variable among the surveys. Chl *a* concentration varied between 0.06 mg chl *a* m^{-3} (Gerlache Strait) and 3.63 mg chl *a* m^{-3} (Decepción Island, Bransfield Strait) during BIOANTAR-93, averaging 1.03 mg chl *a* m^{-3} (Table 1). Phytoplankton biomass and community composition during the survey of 1993 reflected the distribution of water masses in the area, with the highest biomasses associated to a frontal structure located to the NW of the Bransfield strait, where phytoplankton biomass was dominated by a nanoflagellate species (Mura et al. 1995). In the 1994 survey, the chl *a* concentration ranged from 0.31 to 3.76 mg chl *a* m^{-3} and averaged 1.43 mg chl *a* m^{-3}, slightly higher than that obtained during the previous survey, with the phytoplankton community dominated by diatoms (*Thalassiosira* sp., Mura & Agustí 1996). The substantial variability in phytoplankton abundance observed within the smaller area sampled

Table 1. Mean (±SE) and range of variation of chl *a* concentration, gross primary production (GPP), community respiration (*R*) and net community production (NCP) values obtained during the 3 surveys

	Chl *a* (mg m^{-3})	GPP (mmol O_2 m^{-3} d^{-1})	*R* (mmol O_2 m^{-3} d^{-1})	NCP (mmol O_2 m^{-3} d^{-1})
BIOANTAR-93				
Bransfield Strait (N = 26)				
Mean ± SE	1.03 ± 0.16	4.8 ± 1.47	2.65 ± 0.34	2.23 ± 1.47
Min–max	0.09–3.63	0.5–39.45	0.53–7.05	(–5.08)–35.4
Gerlache Strait (N = 4)				
Mean ± SE	0.64 ± 0.24	3.6 ± 0.97	6.95 ± 1.73	–3.35 ± 1.53
Min–max	0.06–1.21	1.8–5.75	2.55–11.03	(–6.29)–(–0.51)
BENTAR–94				
Livingston Island (N = 17)				
Mean ± SE	1.14 ± 0.14	3.41 ± 0.34	1.97 ± 0.23	1.43 ± 0.38
Min–max	0.31–2.8	1.86–6.59	0.61–3.97	(–1.42)–5.1
Decepción Island (N = 3)				
Mean ± SE	1.57 ± 0.26	3.24 ± 1.19	2.26 ± 0.22	0.98 ± 1.08
Min–max	1.04–1.88	1.2–5.35	1.89–2.65	(–1.02)–2.7
Bransfield Strait (N = 7)				
Mean ± SE	1.85 ± 0.16	6.01 ± 1.26	3.08 ± 0.54	3.53 ± 0.97
Min–max	0.13–3.76	2.8–12.12	0.2–5.9	1.57–8.96
ESEPAC–2000				
Bransfield Strait (N = 10)				
Mean ± SE	3.16 ± 1.5	8.46 ± 2.5	1.89 ± 0.37	6.56 ± 2.3
Min–max	0.38–16.75	3.6–31.18	0.24–4.4	1.57–26.7
Gerlache Strait (N = 2)				
Mean ± SE	2.09 ± 0.48	3.89	5.14	1.09 ± 2.3
Min–max	1.61–2.57	—	—	(–1.25)–3.43
Antarctic Strait (N = 2)				
Mean ± SE	10.49 ± 4.6	32.5 ± 8.4	7.14 ± 1.79	25.38 ± 6.6
Min–max	5.14–15.14	24.1–40.9	5.35–8.93	18.75–32.01

in the summer of 1994 derived from the occurrence of a phytoplankton bloom between February 13 and 16 in the stations visited. The ESEPAC-2000 cruise confirmed high variability in chl *a* concentration in the area. The variability was highest in the Bransfield Strait (Table 1), where the lowest (minimum of 0.06 mg m^{-3} in 1993) and highest (maximum of 16.75 mg m^{-3} in 2000) values of chl *a* concentration were found. High values of chl *a* concentration were also found (15.2 mg chl *a* m^{-3}) in the Antarctic Strait. Phytoplankton chl *a* concentration during the ESEPAC-2000 averaged 3.16 , 10.5, and 2 mg chl *a* m^{-3} in the Bransfield, Antarctic and Gerlache Straits, respectively (Table 1), with phytoplankton biomass dominated by diatoms. The variability in chl *a* concentration observed in this study exceeds that in published reports of microplankton metabolism, where chl *a* concentration ranged between 0.17 and 7.39 mg chl *a* m^{-3} (Table 2).

Microplankton daily respiration rates ranged from 0.52 to 11.03 mmol O_2 m^{-3} d^{-1} during the summer of 1993, with averaged values of 2.65 and 6.95 mmol O_2 m^{-3} d^{-1} for the Bransfield and Gerlache straits, respectively (Table 1). Microplankton respiration rates varied from 0.19 to 5.99 mmol O_2 m^{-3} d^{-1} during the 1994 survey and from 0.24 to 8.9 mmol O_2 m^{-3} d^{-1} during ESEPAC-2000 (Table 1). Community respiration rates were only weakly related to chl *a* concentration, which accounted for <10% of the variability in respiration rates (R^2 = 0.089, $p < 0.01$, n = 89, log-log relationship).Daily NCP rates varied greatly in the 1993 survey (from –6.29 to 35.4 mmol O_2 m^{-3} d^{-1}, Table 1), with a mean (±SE) value of 1.66 ± 1.2 mmol O_2 m^{-3} d^{-1}. The range of NCP observed during February 1994 was much narrower (–1.41 to 8.96 mmol O_2 m^{-3} d^{-1}). The variability in NCP rates during ESEPAC-2000 was also high, varying between –1.25 and 32 mmol O_2 m^{-3} d^{-1}. The communities examined were often heterotrophic, with community respiration rates exceeding primary production. Overall, 20% of the communities examined were heterotrophic, and were more frequently observed during the 1993 survey (53% of the observations) than the 1994 and 2000 surveys (18 and 7% of observations, respectively).

Table 2. Literature data on chl *a* concentration, net community production (NCP), gross production (GP) and respiration (*R*) rates of microplankton communities from Antarctic surface waters. Wedell Sea data are surface water data, from open sea stations, transformed to daily rates assuming a day length of 15 h

	Chl *a* (mg m^{-3})	GPP (mmol O_2 m^{-3} d^{-1})	*R* (mmol O_2 m^{-3} d^{-1})	NCP (mmol O_2 m^{-3} d^{-1})	Source
Weddell Sea (N = 6)					
Mean ± SE	1.57 ± 0.23	7.78 ± 0.84	2.31 ± 0.78	5.47 ± 0.53	Bouquegneau et al.
Min–max	0.9–2.0	5.29–9.03	0.6–4.08	4.51–6.78	(1992)
Bellingshausen Sea (N = 2)					
Mean ± SE	2.33 ± 1.41	6.15 ± 1.85	1.75 ± 1.15	4.4 ± 0.7	Boyd et al.
Min–max	0.92–3.75	4.3–8.0	0.6–2.9	3.7–5.1	(1995)
Antarctic Peninsula (N = 11)					
Mean ± SE	3.35 ± 0.72	10.84 ± 3.25	2.81 ± 0.65	8.02 ± 2.76	Arístegui et al.
Min–max	0.84–7.39	2.49–37.4	0.36–5.57	0.13–31.9	(1996)
Indian Sector (N = 8)					
Mean ± SE	1.12 ± 0.32	2.36 ± 0.49	1.7 ± 0.31	0.65 ± 0.23	Odate et al.
Min–max	0.24–3.09	0.5–5.1	0.8–3.6	(–0.5)–5.1	(2002)

The variability of daily GPP (Fig. 2), the sum of NCP and community respiration, was high, as well as that observed for NCP rates (Fig. 2), contrasting, however, with the lower range of variability found for community respiration (Fig. 2). High gross production was found in Decepción Island (Bransfield Strait) in the summer of 1993 (Table 1), and in the same location and the Antarctic Strait in the summer of 2000 (Table 1). Mean gross production remained relatively similar across surveys (Table 1), despite the fact that NCP and GPP values of the 1993 and 1994 surveys could be overestimated, as NCP was derived from the incubation of light bottles at constant, saturated light conditions.

Community respiration rates of the data collected from the literature varied within the ranges observed in this study (Table 2). Literature data on NCP from Antarctic surface waters also varied greatly between –0.5 and 31.9 mmol O_2 m^{-3} d^{-1}. There was an overall positive relationship between NCP and chl *a* concentration (R^2 = 0.46; Table 3), while NCP was strongly, positively correlated with gross production (R^2 = 0.92; Table 3, Fig. 3). In contrast, community respiration was poorly related to gross production rates (R^2 = 0.11, $p < 0.001$, log-log relationship).

The GPP:*R* ratio (i.e. the ratio of daily gross primary production to community respiration) reflects the degree of coupling between primary production and community respiration (e.g. Odum 1956). The GPP:*R* ratio ranged broadly among the communities investigated, varying from 0.26 to 25, although the median (±SE) GPP:*R* value for the Antarctic waters analyzed was 3.49 ± 0.41 (n = 96). The fact that this value significantly exceeded 1 indicated that gross production exceeded community respiration in the majority of the samples in our combined data set. The GPP:*R* ratio was

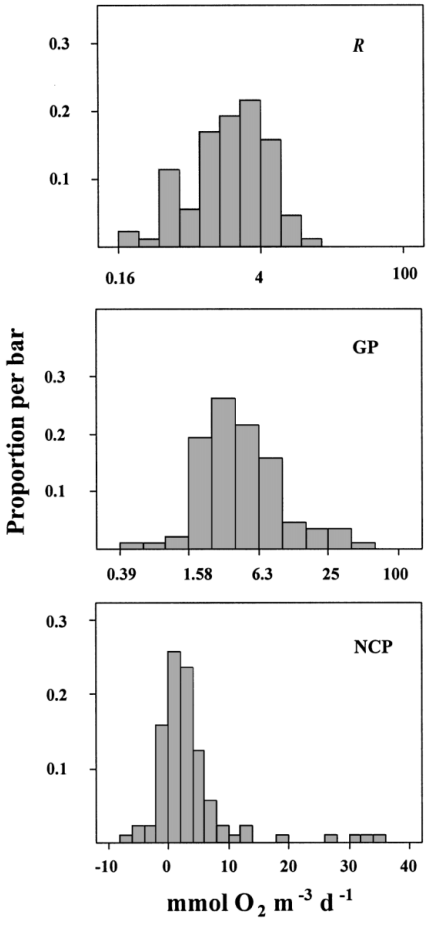

Fig. 2. Distribution of values of microplankton community respiration (log scale, *R*), gross primary production (log scale, GP) and net community production (NCP) from upper surface Antarctic waters obtained during this study (N = 69) and collected from the literature (N = 27)

Table 3. Parameters of the least-squares linear regression equations describing the relationship between Antarctic plankton net community production (NCP, mmol O_2 m^{-3} d^{-1}), chl *a* concentration (chl *a*, mg m^{-3}) gross primary production (GPP, mmol O_2 m^{-3} d^{-1}) and the GPP:*R* ratio (gross production:respiration). All relationships were statistically significant (*F*-test, $p < 0.001$). Standard errors (SE) of the slopes and constants (Cons.) are indicated. Observations (N = 96) comprised data from this study (N = 69) and from the literature (N = 27). Data were log-transformed (indicated as log) when necessary to comply with the assumptions of the analysis

y	*x*	R^2	Slope ± SE	Cons. ± SE
NCP	Chl *a*	0.47	1.91 ± 0.20	−0.01 ± 0.65
NCP	GPP	0.92	0.88 ± 0.02	−1.94 ± 0.25
GPP:*R* (log)	GPP (log)	0.33	1.10 ± 0.09	−0.34 ± 0.06

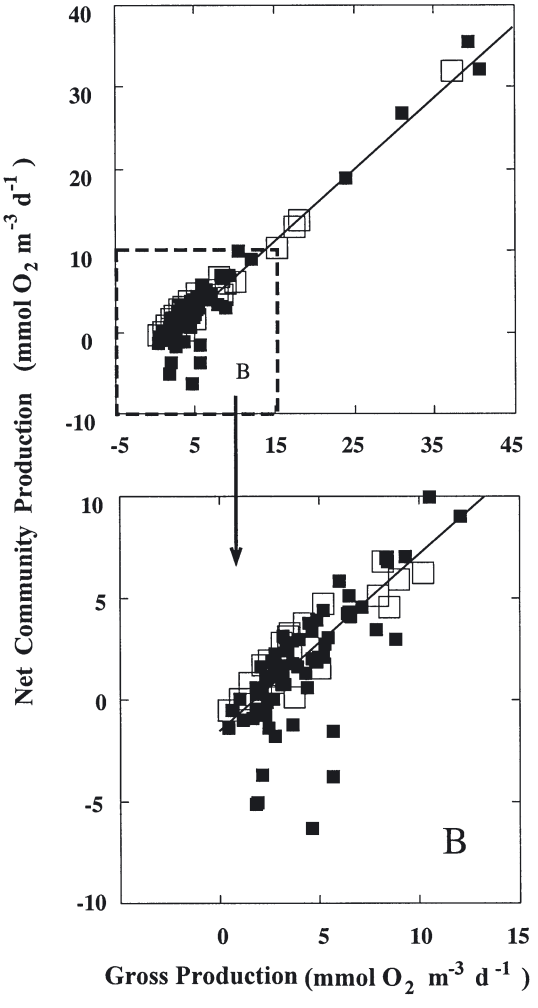

Fig. 3. Relationship between microplankton net community production and gross production for the Antarctic communities studied. ■ and □ symbols correspond to data from this study and the literature, respectively. The solid line represents the fitted regression line (Table 3). Panel B shows the relationship for unproductive waters

positively related to gross production (R^2 = 0.33; Table 3), as expected from the greater variance in GPP relative to *R* and the absence of a significant correlation between them. However, the GPP:*R* ratio tended to be <1, indicative of consumption to exceed production in low productive waters, at low gross production rates.

DISCUSSION

The positive relationships between NCP and chl *a* concentration and, especially, the strong relationship found between NCP and gross production, reveal the variability in phytoplankton chlorophyll and production as the main drivers of the net metabolism of Antarctic microplankton communities. The strong correlation between NCP (i.e. gross production – community respiration) and GPP shown here for Southern Ocean microplankton is, however, not a general feature of marine communities, for variation in community respiration has been shown to determine NCP in different ecosystems (e.g. Smith & Hollibaugh 1993, Satta et al. 1996, Valentini et al. 2000, Williams 2000). However, the variability in community respiration rates in Antarctic waters analyzed was smaller than that observed for gross production, and community respiration remained low when GPP was high. Indeed, there was a tendency for microplankton communities to remain, on average, autotrophic, suggesting that the excess carbon fixed by phytoplankton during phytoplankton blooms allows Antarctic planktonic communities to be, on average, net autotrophic. While increased net carbon uptake may appear to be a necessary consequence of increased primary production, this is often not the case as, unlike the case in the Antarctic waters examined, there is often a close, general relationship between primary production and community respiration in marine ecosystems (e.g. Iriarte et al. 1991, Smith & Hollibaugh 1993, Duarte & Agustí 1998, Williams 1998), resulting in marginal NCP even at high gross production rates. The results described are in agreement with the reduced bacterial and protozoan respiratory rates during periods of high phytoplankton production predicted by the enhanced substrate requirement of bacteria at polar temperatures (Wiebe et al. 1992). This low community respiration relative to gross production during phytoplankton blooms should lead to the export and subsequent burial of the particulate organic matter that is not oxidized within the water column to the sediments. These transferences reduce the availability of excess primary production to support community respiration during periods of low primary production or during winter.

Conversely, the lack of immediate coupling between community respiration and primary production described here implies that community consumption remains high in waters supporting sparse phytoplankton populations. These results are in agreement with reports of a relative uncoupling at large phytoplankton biomass between bacterial and phytoplankton production in Antarctic waters (Karl et al. 1991, Morán et al. 2002). As a consequence, the microplankton communities of these Antarctic phytoplankton-poor waters were found to be net heterotrophic, thereby representing CO_2 sources, rather than sinks. This result is in agreement, however, with the observation that unproductive aquatic ecosystems tend to be net heterotrophic (Duarte & Agustí 1998, Duarte et al. 2001).

The results show a tendency to net autotrophic metabolism in the Antarctic Ocean, as represented by the majority of samples found with a GPP:$R > 1$ (73%), indicating that primary production tended to exceed community respiration. However, for the 27% of communities sampled, respiration exceeded gross production, and they were found to be net heterotrophic. The conclusion that the microplanktonic communities of Antarctic waters tend to be net autotrophic, and therefore act as potential carbon sinks, may be, however, misleading. Our results indicated that there is a high variability in the pelagic net metabolism in the Antarctic Ocean, varying form net-heterotrophic to net-autotrophic depending on the productivity of the waters. Odate et al. (2002) found negative NCP occurring at low phytoplankton concentration and production in the Indian sector of the Antarctic Ocean (Odate et al. 2002). Net heterotrophic metabolism was also found by Bender et al. (2000) at the Ross Sea in summer. El-Sayed (1984) indicated that the occasional large phytoplankton blooms found in the Southern Ocean have obscured the large variability of phytoplankton standing crop and productivity in Antarctic waters. Similarly, many studies (e.g. Boyd et al. 1995, ESEPAC-2000, this study) were designed to examine pelagic metabolism during phytoplankton blooms in Antarctic waters, obscuring the large variability in net metabolism.

Relatively unproductive Antarctic microplankton communities were found to be net heterotrophic, consistent with observations elsewhere (Duarte & Agustí 1998, Duarte et al. 1999, 2001, Odate et al. 2002). The GPP needed to render Antarctic microplankton communities autotrophic (i.e. GPP:R = 1) was found to be 0.064 g O_2 m^{-3} d^{-1} (or 2.05 mmol O_2 m^{-3} d^{-1}), which is close to the threshold of 0.035 g O_2 m^{-3} d^{-1} predicted for open sea ecosystems by Duarte & Agustí (1998). Phytoplankton-poor waters extend, however, over most of the Southern Ocean (cf. Sullivan et al. 1993), suggesting that heterotrophic microplankton communities may be more prevalent in the Southern Ocean than portrayed by the few published reports available to date (Odate et al. 2002). Whether low-chlorophyll areas elsewhere in the Antarctic Ocean are net heterotrophic should be, however, tested once a larger observational basis is available. This assessment will be, however, important to elucidate the role of Antarctic planktonic communities in the global carbon flow.

In coastal waters, organic carbon fixed by other marine primary producers, such as macroalgae (Bouvy & Delille 1988, Fiala & Delille 1992), may represent a source of organic carbon able to support the net heterotrophic planktonic communities. It is, however, more likely that the lag between primary production of organic matter and its comsumption by the community described here allows the accumulation of organic carbon following bloom periods. The subsequent use of this excess carbon by heterotrophic communities should lead to a more balanced equilibrium between primary production and community respiration over temporal and spatial scales greater than those encompassed by our study. The net metabolic balance of a system should be best examined over periods comparable to those over which production and consumption are coupled. The relatively loose coupling between gross production and respiration reported here suggests that the extended time scales over which this processes should be coupled probably result in a spatial offset, because of advective and diffusive transport between net production and consumption of organic carbon. The present empirical basis is, however, insufficient to address both the temporal and spatial offsets between production and respiration in Antarctic waters, which is also prevented by the lack of data on plankton metabolism during the dark winter period. The lack of data on planktonic metabolism during the Austral winter prevents the evaluation of the metabolic balance at the annual scale, and does not allow us to establish whether the excess of organic matter produced during previous periods of high production is enough to maintain the heterotrophic activity during wintertime. This gap in our knowledge must be addressed in future efforts to assess the planktonic metabolic balance in the Southern Ocean.

In summary, the results obtained pointed to a high variability in the net metabolism of Antarctic microplankton communities, largely dominated by variability in GPP. The results suggest the uncoupling between consumption (community respiration) and production in Antarctic waters, where heterotrophic metabolism tends to exceed GPP in unproductive (< 0.064 g O_2 m^{-3} d^{-1}) areas but that allows, however, an important net carbon uptake in productive areas. Although low-chlorophyll waters extend over most of the Southern Ocean, the extrapolation to a larger scale

of the results presented here is required in the assessment of metabolic budgets at temporal and spatial scales, something that cannot be encompassed by the limited observational database for the Southern Ocean.

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LITERATURE CITED

Arístegui J, Montero MF, Ballesteros S, Basterretxea G, Lenning KV (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. Mar Ecol Prog Ser 132:191–201

Bender ML, Dickson ML, Orchardo J (2000) Net and gross production in the Ross Sea as determined by incubation experiments and dissolved O_2 studies. Deep-Sea Res II 47: 3141–3158

Bouquegneau JM, Gieskes WWC, Kraay GW, Larsson AM (1992) Influence of physical and biological processes on the concentration of O_2 and CO_2 in the ice-covered Weddell Sea in the spring of 1988. Polar Biol 12:163–170

Bouvy M, Delille M (1988) Spatial and temporal variations in Antarctic and subAntarctic bacterioplankton. Neth J Sea Res 22: 139–147

Boyd PW, Robinson C, Savidge G, Williams PJleB (1995) Water column and sea-ice primary production during Austral spring in the Bellingshausen Sea. Deep-Sea Res 42: 1177–1200

Carritt DE, Carpenter JH (1966) Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea water. A NASCO Report. J Mar Res 24:286–318

Cota GF, Kottmeier ST, Robinson DH, Smith WOJr, Sullivan CW (1990) Bacterioplankton in the marginal ice zone of the Weddell Sea: biomass, production and metabolic activities during austral autumn. Deep-Sea Res 37: 1145–1167

Delille D (1993) Seasonal changes in the abundance and composition of marine heterotrophic bacterial communities in an Antarctic coastal area. Polar Biol 13:463–470

Delille D, Bouvy M, Cahet G (1988) Short-term variations of bacterioplankton in Antarctic zone: terre adelie area. Microbial Ecol 15:293–309

Duarte CM, Agustí S (1998) The CO_2 balance of unproductive aquatic ecosystems. Science 281:234–236

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. Limnol Oceanogr 41:1758–1766

Duarte CM, Agustí S, del Giorgio PA, Cole JJ (1999) Regional carbon imbalances in the oceans. Science 284:1735b

Duarte CM, Arístegui J, González N, Agustí S, Anadón R (2001) Evidence for a heterotrophic subtropical NE Atlantic. Limnol Oceanogr 46:425–428

El-Sayed SZ (1984) Productivity of the Antarctic waters—a reappraisal. In: Holm-Hansen BL, Gilles R (ed) Marine phytoplankton and productivity. Springer, p 19–34

El-Sayed SZ, Biggs DC, Holm-Hansen O (1983) Phytoplankton Standing crop, primary productivity, and near-surface nitrogenous nutrient fields in the Ross Sea, Antarctica. Deep-Sea Res 30:871–886

Fiala M, Delille D (1992) Variability and interactions of phytoplankton and bacterioplankton in the Antarctic neritic area. Mar Ecol Prog Ser 89:135–146

Fuhrman JA, Azam F (1980) Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica, and California. Appl Environ Microbiol 39: 1085–1095

Fukuchi M (1980) Phytoplankton chlorophyll stocks in the Antarctic Ocean. J Oceanogr Soc Jpn 36:73–84

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

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

Karl DM, Holm-Hansen O, Taylor GT, Tien G, Bird DF (1991) Microbial biomass and productivity in the western Bransfield Strait, Antarctica during the 1986–87 austral summer. Deep-Sea Res 38:1029–1055

McMinn A, Hodgson D (1993) Summer phytoplankton succession in Ellis Fjord, eastern Antarctica. J Plankton Res 15:925–938

Moloney CL (1992) Carbon and the Antarctic Marine Food Web. Science 257:259–260

Morán XAG, Estrada M, Gasol JM, Pedrós-Alió C (2002) Dissolved primary production and the strength of phytoplankton-bacterioplankton coupling in contrasting marine regions Microbial Ecol 44:213–223

Mura MP, Agustí S (1996) Growth rates of diatoms from coastal Antarctic waters estimated by '*in situ*' dialysis incubation. Mar Ecol Prog Ser 144:237–245

Mura MP, Satta MP, Agustí S (1995) Water-mass influences on summer Antarctic phytoplankton biomass and community structure. Polar Biol 15:15–20

Odate T, Furuya K, Fukuchi M (2002) Photosynthetic oxygen production and community respiration in the Indian sector of the Antarctic Ocean during austral summer. Polar Biol 25:859–864

Odum HT (1956) Primary production in flowing waters. Limnol Oceanogr 1:102–117

Oudot C, Gerard R, Morin P, Gningue I (1988) Precise shipboard determination of dissolved oxygen (Winkler procedure) for productivity studies with a commercial system. Limnol Oceanogr 33:146–150

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

Pomeroy LR, Sheldon JE, Sheldon WMJ (1994) Changes in bacterial numbers and leucine assimilation during estimations of microbial respiratory rates in seawater by the precision winkler method. Appl Environ Microbiol 60: 328–332

Satta MP, Agustí S, Mura MP, Vaqué D, Duarte CM (1996) Microplankton respiration and net community metabolism in a bay on the NW Mediterranean coast. Aquat Microb Ecol 10:165–172

Serret P, Fernández E, Anadón R, Varela M (2001) Trophic control of biogenic carbon export in Bransfield and Gerlache Straits, Antarctica. J Plankton Res 23: 1345–1360

Smith SV, Hollibaugh JT (1993) Coastal metabolism and the oceanic organic carbon balance. Rev Geophys 31:75–89
Smith SV, Mackenzie FT (1987) The Ocean as a net heterotrophic system: implications from the carbon biogeochemical cycle. Global Biogeochem Cycles 1:187–198
Sullivan CW, Arrigo KR, McClain CR, Comiso JC, Firestone J (1993) Distributions of phytoplankton blooms in the Southern Ocean. Science 262:1832–1837
Valentini R, Matteucci G, Dolman AJ, Schulze ED and 26 others (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865
Wiebe WJ, Sheldon JR, Pomeroy LR (1992) Bacterial growth in the cold: evidence for an enhanced substrate requirement. Appl Environ Microbiol 58:359–364
Williams PJ le B (1998) The balance of plankton respiration and photosynthesis in the open oceans. Nature 394: 55–57
Williams PJleB (2000) Net production, gross production and respiration: what are the interconnections and what controls what? In: Hanson RB, Ducklow HG, Field JG (eds) The changing ocean carbon cycle. Cambridge University Press, Cambridge, p 37–60
Williamson P, Holligan PM (1990) Ocean productivity and climate change. TREE 5:299–303

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