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Response of Southern Ocean phytoplankton and bacterioplankton production to short-term experimental warming

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Abstract

We examined the potential response of Southern Ocean pelagic ecosystems to warming through changes in total primary production (particulate plus dissolved = PPP + DPP) and bacterial production (BP), determined simultaneously at ambient temperature (-1.4 to 0.4°C) and at 2°C in eight experiments performed near the Antarctic Peninsula in late spring 2002. Short (<6 h) time course experiments of radiocarbon uptake and photosynthesis–irradiance relationships consistently showed that a significant amount of photosynthate appeared as dissolved substances, with a mean 35% extracellular release (PER). Whereas PPP remained virtually unchanged (0.7 mg C m^{-3} h^{-1}), DPP increased significantly at 2°C from 0.5 to 0.9 mg C m^{-3} h^{-1}. The corresponding increase in PER (54% on average) was significantly and positively correlated with the temperature difference among treatments, suggesting that an increase in DPP could be expected with a temperature rise in the Southern Ocean. BP, estimated via [^{3}H]leucine incorporation, tended to increase at 2°C only at low absolute values, and this increment was inversely related to PPP. However, our results show that the estimated bacterial carbon demand (BCD) was generally well below concurrent DPP at both treatments (mean BCD:DPP ratios of 0.60 and 0.27 at ambient temperature and 2°C, respectively), indicating that temperature-related extra inputs of organic substrates were not fully and immediately processed by bacteria. To the extent that these results reflect general ecophysiological trends, warming of Southern Ocean surface waters could produce changes in plankton-mediated biogeochemical processes leading to a greater importance of dissolved organic matter fluxes.

The crucial role of the oceans in the Earth's climatic system has motivated efforts aimed at evaluating the effects of global warming on the structure and functioning of pelagic ecosystems and their associated biogeochemical fluxes (Sarmiento et al. 2004). One of the strongest evidences of recent warming has been found in the Southern Ocean (Gille 2002), and according to coupled ocean–atmospheric models, this ocean basin will continue to suffer a major temperature rise in the next decades (IPCC 2001). Because of its geographic location, future changes in the Southern Ocean will affect the other three major basins. The Southern Ocean is also one of the largest sinks of anthropogenic CO_2 on Earth, and large increases in phytoplanktonic biomass and production have been recently predicted as a consequence of temperature-mediated major changes in stratification and growth season length (Sarmiento et al. 2004).

Macronutrients are not used fully in many parts of the Southern Ocean (e.g., Tréguer and Jacques 1992), the largest high nutrient–low chlorophyll region of the world. Factors such as ambient suboptimal temperatures for phytoplankton growth, intense vertical mixing, predation pressure, and limitation by silica or iron in certain areas have been suggested as possible explanations (*see* review by Boyd 2002). In fact, enhanced photosynthetic rates of polar phytoplankton have been observed in response to increasing temperatures with other factors kept constant (Neori and Holm-Hansen 1982; Jacques 1983; Reay et al. 2001). Experiments on photosynthesis–irradiance (P-E) relationships have also shown significant increases of the light-limited (α^{B}) and light-saturated (P^{B}_{m}) photosynthetic parameters on warming (Tilzer et al. 1986). However, these studies have generally considered only the production of organic matter retained within the cells or particulate primary production (PPP), although a significant amount of photosynthate might be released in dissolved form (Vernet et al. 1998; Morán et al. 2002; Mei et al. 2003). Previous work on the contribution of dissolved primary

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production (DPP) to total rates in Antarctic waters indicates that percent extracellular release (PER) varies from 5% to ~50% (Morán et al. 2001*a*; Morán and Estrada 2002), not different from measurements in lower latitude regions. The effect of temperature on photosynthate partitioning by Southern Ocean phytoplankton remains largely unknown; as far as we know, the only two previous studies have focused mostly on PPP (Tilzer and Dubinsky 1987) and on a single species (Thomas et al. 1992).

Heterotrophic bacteria are the major consumers of oceanic dissolved organic matter; therefore, they are potential users of the mostly labile DPP (Amon et al. 2001). Several studies have documented this trophic link in Antarctic waters with divergent conclusions about the time scale and degree of bacterial dependence on DPP (Fiala and Delille 1992; Bird and Karl 1999; Morán et al. 2002). Such differences are partly because of seasonal changes (Stewart and Fritsen 2004). Apart from its direct effects on enzymatic rates, temperature could indirectly control bacterial dynamics through changes in substrate supply (e.g., Pomeroy and Wiebe 2001). Researchers do not agree on the relative importance of potential factors limiting bacterial growth in polar seas (Carlson et al. 1998; Church et al. 2000; Pomeroy and Wiebe 2001), but according to recent studies, DPP could fulfill bacterial requirements of organic substrates or bacterial carbon demand (BCD) in offshore waters of the Southern Ocean (Morán et al. 2001*a*, 2002). If a temperature rise induced changes in the relative contribution of PPP and DPP, the entire Antarctic microbial food web would be affected (Pomeroy and Wiebe 2001), eventually modifying the fate of the organic matter produced.

A major drawback of experimental work addressing the potential effects of the on-going climatic change on plankton-mediated biogeochemical fluxes is the temporal scale for the changes. Although extremely rapid compared with past geological times, planktonic assemblages will presumably respond to increased temperatures by long-term strategies such as extended growth periods or shifts in community composition (e.g., Karl et al. 2001), which are out of the scope of experimental approaches amenable during an oceanographic cruise. We report here on the short-term effect of experimental warming on phytoplankton and bacterioplankton carbon fluxes. Time scale limitations notwithstanding, this type of perturbation experimental analysis can highlight future directions of change, or at least provide testable hypotheses for time series records. On the basis of our results, important changes in the biogenic fluxes of Antarctic pelagic ecosystems could be expected in response to global warming.

Materials and methods

Experiments were carried out at eight stations located in the vicinity of the Antarctic Peninsula (~62–66°S; Fig. 1) on board of R/V *Hespérides* during the TÉMPANO cruise from 03 Nov to 16 Dec 2002. Its general objective was to quantify the control exerted by temperature on metabolic processes and the structure of planktonic communities in

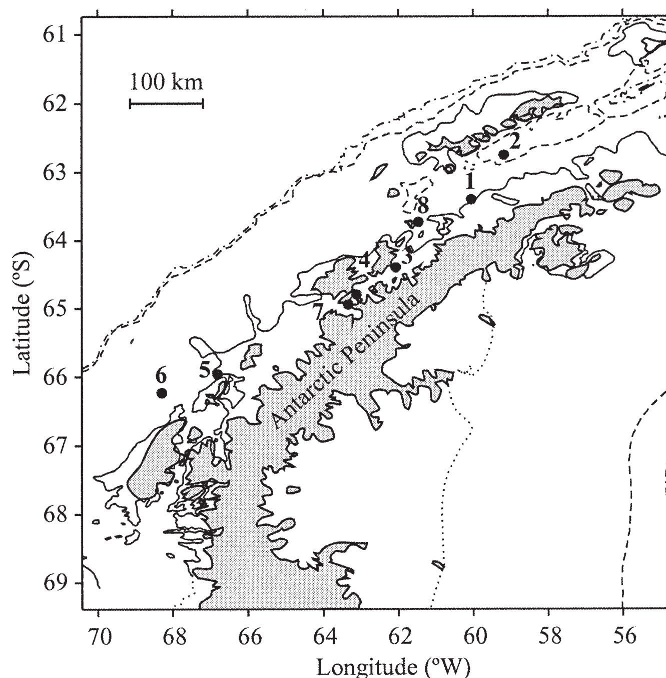

Fig. 1. Map of the Antarctic Peninsula showing the position of the sampling stations for the experiments detailed in Table 1. Continuous contour line, 200 m; dashed contour line, 1,000 m; dash-dot contour line, 2,000 m; dotted line, permanent ice.

the Southern Ocean. Samples from the upper mixed layer, usually at the depth of maximum fluorescence (Table 1), were taken between 10:00 h and 11:00 h local time, except in experiment 2 (14:35 h), with 12-liter Niskin bottles (General Oceanics) mounted on a rosette attached to a Neil Brown Mark III CTD profiler. Incubations started within 1 h. For each experiment, samples were incubated at two temperatures: that found in situ (Table 1), hereafter referred to as "ambient," and 2°C. Temperature was kept constant (±0.3°C) with the use of thermostatic baths. The variability of ambient temperature allowed us to test the effect of a temperature rise over ambient values ranging from 1.5°C to 2.4°C.

Chlorophyll *a* (Chl *a*) was measured fluorometrically after overnight pigment extraction at 4°C in 90% acetone. The abundance of heterotrophic bacteria (BN) was determined by flow cytometry according to standard protocols (Morán et al. 2001*a*), and the composition of phytoplankton assemblages was assessed with an inverted microscope with the Utermöhl technique.

Time course experiments of carbon uptake—Time course experiments of organic carbon production were conducted in the laboratory under constant irradiance (~80 μmol quanta m^{-2} s^{-1}). At each temperature treatment, 10 clear and 10 dark (covered with aluminum foil) Corning tissue culture flasks were filled with 70 mL of water and inoculated with 7.40×10^5 Bq $NaH^{14}CO_3$. Incubations lasted 5–6 h and two clear and two dark flasks were taken at intervals of 0.5 to 1.8 h for determination of the amount

Table 1. Date and depth of the experiments, ambient temperature, standing-stocks, and production rates of phytoplankton and heterotrophic bacteria (BN).

Experiment No.	Date	Depth (m)	Temperature (°C)	Chl *a* ($mg\ m^{-3}$)	TPP ($mg\ C\ m^{-3}\ h^{-1}$)	BN ($cells\ mL^{-1}$)	BP ($\times 10^{-3}\ mg\ C\ m^{-3}\ h^{-1}$)
1	30 Nov 02	6	−0.5	0.71	0.32	4.72×10^5	1.02
2	03 Dec 02	43	−0.6	1.45	1.20	7.90×10^4	1.92
3	05 Dec 02	23	0.2	1.80	1.88	3.82×10^5	4.96
4	07 Dec 02	40	0.4	0.55	0.60	3.50×10^5	1.97
5	09 Dec 02	32	−1.4	1.12	1.14	2.41×10^5	5.22
6	11 Dec 02	34	−1.4	0.75	0.67	2.86×10^5	3.39
7	14 Dec 02	15	−0.4	1.31	1.25	2.45×10^5	4.35
8	16 Dec 02	35	0.4	1.74	2.62	3.91×10^5	4.52

of ^{14}C incorporated into total organic carbon (TOC), dissolved organic carbon (DOC), and particulate organic carbon (POC). A subsample of 5 mL from each flask was used for analysis of $TO^{14}C$, whereas the $PO^{14}C$ fraction (60 mL) was separated by filtration through membrane filters of 0.22-μm pore size, as described in detail elsewhere (Morán et al. 2001*a*). To correct for time 0 uptake of ^{14}C, two dark bottles were processed in the same manner at the beginning of the experiment. Filters were placed into vials and exposed overnight to concentrated HCl fumes to eliminate inorganic ^{14}C from the samples. For liquid samples, 1 mL of 1 mol L^{-1} HCl was added to the vials, and these were placed in an orbital shaker for a minimum of 12 h. Finally, 4.5 mL (filters) or 10 mL (liquid samples) of Ultima Gold XR liquid scintillation cocktail were added to the vials and radioactivity (dpm) was measured on board with a LKB Winspectral 1414 liquid scintillation counter. Despite the low volume used for $TO^{14}C$ determinations, original counts from the light flasks (354 ± 46 dpm) were consistently higher than those from the dark flasks (108 ± 10 dpm) throughout the experiments (3.1-fold higher on average). Hence, we are confident that the dissimilar subsample volumes used for $PO^{14}C$ and $TO^{14}C$ determinations did not affect the precision of estimated primary production rates. These were obtained by means of compartmental analysis with SAAMII software. More details can be found in Morán et al. (2001*a*). The rate of DPP was obtained as the rate of total primary production (TPP) minus that of PPP. Percent extracellular release (PER) was calculated as 100 × DPP/TPP.

Photosynthesis–irradiance relationships—Photosynthesis–irradiance (P-E) experiments were performed in parallel to time course experiments with water from the same stations and depths, with an additional experiment at Sta. 6. At each treatment, 12 Corning tissue culture flasks (11 clear + 1 dark wrapped in aluminum foil) were filled with 70 mL of sample water, inoculated with 7.40×10^5 Bq $NaH^{14}CO_3$, and placed in closed linear incubators with running water connected to thermostatic baths. One set of flasks was incubated at ambient temperature and the other at 2°C, except at Sta. 6, in which only the ambient temperature incubation was performed because of a failure of the thermostatic bath. The incubators were illuminated with tungsten-halogen lamps. Irradiance at each flask position was measured with a spherical PAR sensor (Illuminova). After placement of neutral-density filters at specific positions, values ranged from ~3 to ~1,200 μmol quanta $m^{-2}\ s^{-1}$. This irradiance gradient was checked after each experiment. At the end of the incubation (2.5–3 h), a subsample of 5 mL from each flask was used for analysis of $TO^{14}C$, and the rest (65 mL) was filtered through 0.22-μm filters for $PO^{14}C$ determination. Processing of samples was as described in the previous section. Because no photoinhibition was detected, the model of Webb et al. (1974) was used for obtaining the photosynthetic parameters. These are the maximum or light-saturated Chl *a*–normalized photosynthetic rate P^B_m (mg C [mg Chl *a*]$^{-1}$ h^{-1}), the initial slope of the P-E relationship α^B (mg C [mg Chl *a*]$^{-1}$ h^{-1} [μmol quanta $m^{-2}\ s^{-1}$]$^{-1}$), and the saturation irradiance E_k, defined as $E_k = P^B_m/\alpha^B$. Following Morán and Estrada (2001), we also estimated a light-saturated Chl *a*–normalized DPP rate (hereafter DPP P^B_m).

Bacterial activity and production—Activity and production of heterotrophic bacteria was determined by [^{3}H]leucine incorporation (Kirchman et al. 1985). Aliquots of 1.2 mL were dispensed into 2-mL microcentrifuge tubes with a step pipette. Control tubes received 133 μL of 50% trichloroacetic acid (TCA) and were vortexed. Next, 48 μL of a 1 μmol L^{-1} solution of [^{3}H]leucine was added to the tubes, providing a final concentration of 40 nmol L^{-1} (which was previously found to be saturating in these waters, e.g., Pedrós-Alió et al. 2002). At least four replicates and two killed controls were incubated per sample. After vortexing, tubes were placed in whirl-pack plastic bags and incubated for 2 to 4 h. Incubations were stopped with 133 μL of 50% TCA and vortexing. Next, tubes were spun in a microcentrifuge for 10 min at 16,000 × g. Liquid was aspirated with a Pasteur pipette connected to a vacuum pump, taking care not to leave any droplets, especially around the cap. Pellets were rinsed with 1.5 mL of 5% TCA, vortexed, and spun again. Supernatant was sucked again, and 0.5 mL of scintillation cocktail were added. The tubes were counted within standard 20-mL scintillation vials in an LKB Winspectral 1414 liquid scintillation counter on board. Counts were repeated after 48 h of adding cocktail. These second sets of counts were less variable and had lower blanks than the initial counts. Samples were incubated at ambient temperature and at 2°C under the same irradiance of the time course carbon uptake experiments. An additional sample was incubated at

Table 2. Rates of particulate (PPP) and dissolved (DPP) primary production and percent extracellular release (PER) obtained from time course experiments at ambient temperature and at 2°C.

	PPP (mg C m^{-3} h^{-1})		DPP (mg C m^{-3} h^{-1})		PER (%)	
Experiment No.	Ambient	2°C	Ambient	2°C	Ambient	2°C
1	0.26	0.28	0.07	0.26	21	48
2	0.69	0.66	0.51	1.26	42	66
3	1.16	1.12	0.72	0.80	38	42
4	0.35	0.33	0.24	0.46	41	59
5	0.94	0.88	0.20	0.87	18	50
6	0.44	0.35	0.23	0.34	34	50
7	1.10	0.88	0.15	0.88	12	50
8	0.70	0.98	1.91	2.40	73	71
Mean	0.70	0.68	0.50	0.91	35	54
SE	0.12	0.12	0.21	0.24	7	3

ambient temperature in the dark to check for changes resulting from irradiance conditions (Morán et al. 2001*b*). Bacterial production (BP) was estimated with a previously used leucine (Leu)-to-C conversion factor obtained in a summer survey in the same area (0.81 kg C [mol Leu]$^{-1}$, Pedrós-Alió et al. 2002).

Unless otherwise indicated, the number of data pairs was eight.

Results

Selected properties of the water samples used for the experiments are shown in Table 1. Sample temperatures were always below 0.5°C and reached the lowest values (−1.4°C) at the southernmost Stas. 5 and 6. A deep, well-mixed water column was encountered at most stations, with temperature differences between the surface and 100 m depth averaging 0.5 ± 0.2°C. However, Stas. 5, 6, and 7 had lower salinity values at the surface (<34) than the rest of the stations (34.1–34.4) because of ice melting. Chl *a* at the surface was highly correlated with integrated Chl *a* values (Pearson's correlation coefficient, $r = 0.91$, $p < 0.001$). Mean (±SE) concentration in the experiments was not as high as expected for the season (1.18 ± 0.17 mg Chl *a* m^{-3}) and is probably indicative of initial stages of bloom development. Dominant taxa were nanoflagellates (10^5–10^6 cells L^{-1}), with high abundance of a cryptomonad at some stations (especially those corresponding to experiments 1, 2, 3, 7, and 8), followed by mostly pennate diatoms (up to 10^4–10^5 cells L^{-1}) and dinoflagellates (up to 10^2–10^3 cells L^{-1}).

Time course experiments—Differences between TOC and POC fixation were generally evident from the first sampling time through the whole incubation period. The corresponding production rates obtained after compartmental model fitting are shown in Tables 1 and 2. At ambient temperature, they were strongly correlated with Chl *a*, as expected ($r = 0.91$, $p < 0.01$ for TPP; $r = 0.76$, $p < 0.05$ for PPP). Chl *a*–normalized rates (mean ± SE) for TPP and PPP were 0.97 ± 0.10 and 0.60 ± 0.06 mg C (mg Chl *a*)$^{-1}$ h^{-1}, respectively, similar to values obtained previously in Antarctic waters during spring–summer (e.g., Jacques 1983; Basterretxea and Arístegui 1999; Morán et al. 2001*a*). Ambient PER (PER_{amb}) ranged from 12% to 73% (Table 2) and tended to increase with temperature, although the correlation was not significant ($r = 0.65$, $p = 0.08$).

Ambient TPP and PPP rates (TPP_{amb} and PPP_{amb}, respectively) were highly correlated with those at 2°C ($TPP_{2°C}$ and $PPP_{2°C}$; $r = 0.96$, $p < 0.001$; $r = 0.91$, $p < 0.01$, respectively), but marked differences were observed in the temperature response of both fractions (Fig. 2A). On average, $TPP_{2°C}$ was 36% ± 9% higher than TPP_{amb}, whereas $PPP_{2°C}$ and PPP_{amb} were essentially identical (0.68 and 0.70 mg C m^{-3} h^{-1}, respectively). Consequently, DPP rates, calculated as the difference between TPP and PPP, increased from an ambient 0.50 ± 0.21 to 0.91 ± 0.24 mg C m^{-3} h^{-1} at 2°C (Table 2). Paired *t*-tests confirmed that differences were significant for TPP ($p = 0.009$) and DPP ($p = 0.005$) but not for PPP ($p = 0.69$). $PER_{2°C}$ values were also significantly higher than PER_{amb} (paired *t*-test, $p = 0.005$), with about half of the photosynthate retained within the cells and half released extracellularly in the 2°C treatment (54% ± 3%; Table 2). A significant relationship was found between the corresponding increases in PER ($\Delta PER = PER_{2°C} - PER_{amb}$) and temperature ($r = 0.81$, $p < 0.05$; Fig. 2B).

Photosynthesis–irradiance relationships—Coefficients of determination of the fitted P-E curves were >0.90 on most occasions. In spite of the different light sources used (cool fluorescent in time course experiments and tungsten-halogen lamps in P-E experiments), both methods of estimating primary production yielded comparable results. Maximum rates of PPP derived from P-E relationships (P^B_m × Chl *a*) and PPP rates obtained in time course experiments were significantly correlated ($r = 0.68$, $p < 0.01$, $n = 15$) and not significantly different (paired *t*-test, $P = 0.23$, $n = 15$). However, slightly higher P^B_m values compared with the corresponding Chl *a*–normalized PPP rates were likely due to the use of an irradiance level below E_k in the time course experiments.

Mean (±SE) values of photosynthetic parameters for each treatment are shown in Table 3. Maximum Chl *a*–normalized photosynthetic rates (P^B_m) and initial slopes (α^B)

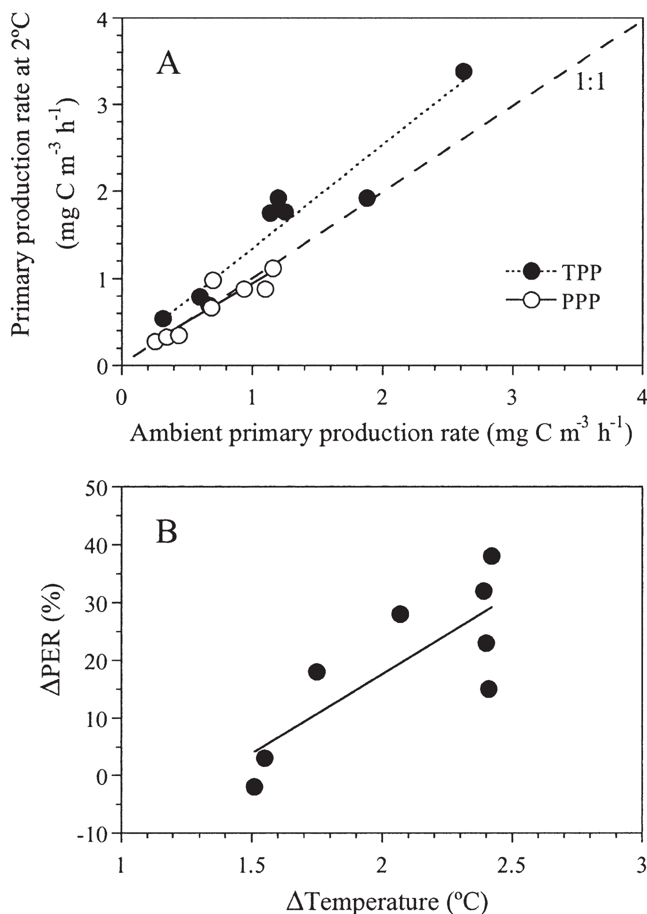

Fig. 2. (A) Relationship between particulate (PPP) and total (TPP) primary production rates in both temperature treatments. Fitted lines are model I (ordinary least squares) linear regressions: $PPP_{2^\circ C} = 0.06 + 0.89PPP_{amb}$, $r^2 = 0.83$, $p = 0.002$, $n = 8$; $TPP_{2^\circ C} = 0.15 + 1.19TPP_{amb}$, $r^2 = 0.92$, $p < 0.001$, $n = 8$. (B) Relationship between the difference in temperature between treatments (2°C–ambient) and the corresponding difference in PER ($PER_{2^\circ C} - PER_{amb}$) at each experiment. Fitted line is model I linear regression: $\Delta PER = -37.7 + 27.7\Delta Temperature$, $r^2 = 0.66$, $p = 0.015$, $n = 8$.

of the P-E relationships for TPP were significantly higher than for PPP in both treatments (paired *t*-tests, $p < 0.05$, $n = 7$), indicating a significant contribution of extracellular release to TPP along the experimental range of irradiance and further supporting the results of the time course experiments. Differences in the light saturation parameter (E_k) were not significant, likely because of the concurrent increase in P^B_m and α^B from ambient temperature to 2°C. A significant correlation was found between α^B and P^B_m with all data pooled ($r = 0.66$, $P < 0.001$, $n = 33$; Fig. 3).

Although higher values of total and particulate α^B and P^B_m were generally found at 2°C (Table 3) than at ambient temperature, differences were not significant because of the small number of samples and only marginally significant for P^B_m and TPP data (paired *t*-test, $P = 0.06$, $n = 7$). Similar to time course results, the mean increase in P^B_m for TPP at 2°C, compared with ambient values, was double that for PPP (28% vs. 16%, respectively). The light-saturated Chl *a*–normalized DPP rate is also shown in Table 3. The corresponding increase in DPP P^B_m at 2°C (from 0.73 to 1.04 mg C [mg Chl *a*]$^{-1}$ h^{-1}) was not significant (paired *t*-test, $P = 0.16$, $n = 7$).

Bacterial activity and production—Incorporation rates of leucine by heterotrophic bacteria were uniformly low, ranging from 1.3 to 6.4 pmol Leu L^{-1} h^{-1}. Incubating the samples under light or dark conditions at ambient temperature had no clear effects on incorporation rates (Fig. 4A). Indeed, both estimates were correlated ($r = 0.81$, $p < 0.05$) and not significantly different (paired *t*-test, $p = 0.36$, $n = 8$). However, this was not the case for the samples incubated at 2°C in the light, which did not display any relationship with ambient values ($p = 0.30$), although a relative increase was observed at lower rates (Fig. 4B).

In spite of the apparent lack of consistent response of bacterial activity to temperature increases (Fig. 4B), the difference in BP between treatments ($\Delta BP = BP_{2^\circ C} - BP_{amb}$) was positive (i.e., BP increased at 2°C) at low levels of phytoplankton productivity (PPP) and became negative at higher levels (Fig. 5), with an overall correlation coefficient between ΔBP and PPP of −0.73 ($p < 0.05$).

Total carbon demand by bacteria (BCD) was calculated as BP divided by bacterial growth efficiency (BGE), which was in turn estimated with the empirical relationship

Table 3. Mean (±SE) photosynthetic parameters after P-E curve model fitting to total (TPP) and particulate (PPP) primary production data for treatments at ambient temperature and 2°C. Estimates of P^B_m for the dissolved fraction (DPP) and corresponding PER values (see the text for details) are also given. The significance of the differences between TPP and PPP parameters within treatments is also indicated (* $p < 0.005$; n.s., nonsignificant).

Temperature	Fraction	P^B_m (mg C mg Chl a^{-1} h^{-1})	α^B (mg C [mg Chl a]$^{-1}$ h^{-1} [μmol quanta m^{-2} s^{-1}] $^{-1}$)	E_k (μmol quanta m^{-2} s^{-1})	$PER_{P\text{-}E}$ (%)
Ambient	PPP	0.67 ± 0.09	0.0042 ± 0.0006	180 ± 39	47 ± 7
	TPP	1.40 ± 0.28*	0.0085 ± 0.0015*	187 ± 35 n.s.	
	DPP	0.73 ± 0.26			
2°C	PPP	0.74 ± 0.06	0.0069 ± 0.0015	127 ± 19	51 ± 6
	TPP	1.78 ± 0.35*	0.0111 ± 0.0021*	173 ± 31 n.s.	
	DPP	1.04 ± 0.32			

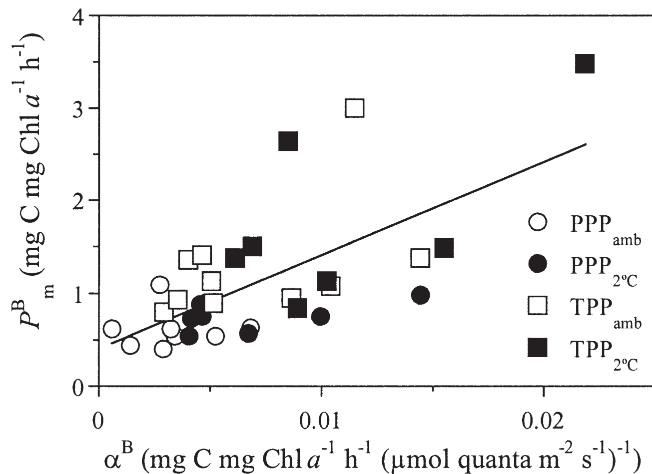

Fig. 3. Relationship between the initial slope of the P-E relationship (α^B) and the maximum Chl *a*–normalized photosynthetic rate (P^B_m) for TPP and PPP in both treatments. Fitted line is model I linear regression: $P^B_m = 0.41 + 100.13\alpha^B$, $r^2 = 0.43$, $p < 0.001$, $n = 33$.

obtained by del Giorgio and Cole (1998) from a dataset on bacterial respiration and production: BGE = 0.037 + 0.65BP/(1.8 + BP). We recently proposed a definition of bacterioplankton–phytoplankton coupling that implied

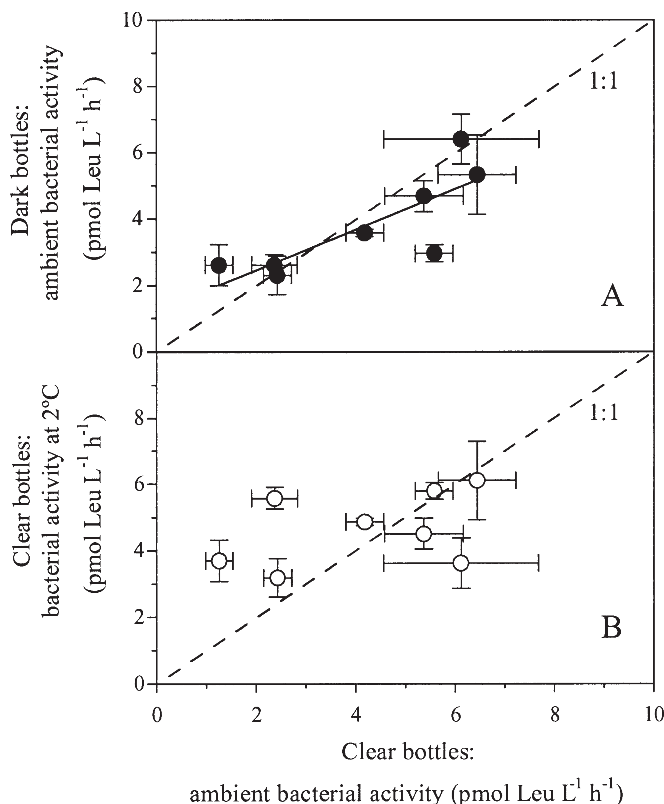

Fig. 4. Relationship between ambient bacterial leucine (Leu) uptake rates in the light and (A) in the dark, and (B) at 2°C in the light. Error bars represent SE. Fitted line in panel A is model I linear regression: dark Leu: 1.23 + 0.61 light Leu, $r^2 = 0.65$, $p < 0.016$, $n = 8$.

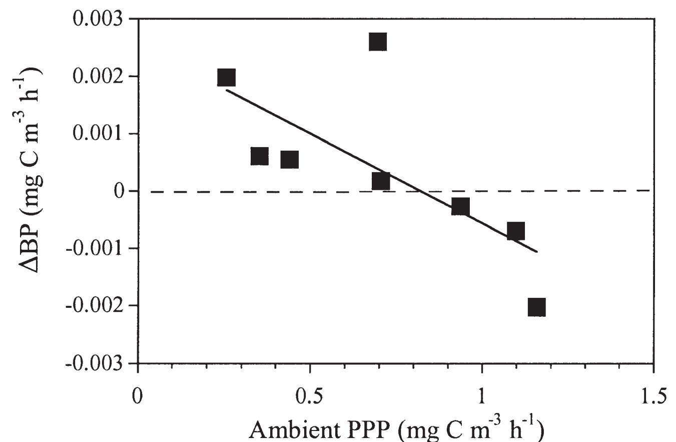

Fig. 5. Relationship between ambient particulate primary production (PPP_{amb}) and between-treatments difference in bacterial production ($\Delta BP = BP_{2°C} - BP_{amb}$) at each experiment. Fitted line is model I linear regression: $\Delta BP = 0.0026 - 0.0031PPP_{amb}$, $r^2 = 0.53$, $p = 0.041$, $n = 8$.

(1) that BCD should be lower than or equal to DPP and (2) the existence of a significant relationship between BCD and DPP (Morán et al. 2002). According to this definition, bacteria were loosely coupled to phytoplankton at ambient temperature because, although DPP_{amb} could provide all carbon needed by bacteria in most experiments (mean ± SE for DPP_{amb}:BCD_{amb}, 0.60 ± 0.15), the positive covariation between BCD_{amb} and DPP_{amb} was not significant ($p = 0.37$). Phytoplankton biomass and production were intermediate between the low values generally found in the open sea and the high values reached during coastal or ice-edge blooms (e.g., Moore and Abbott 2000). From previous work, the degree of coupling is expected to decrease along the productivity range (Morán et al. 2002). Whereas DPP significantly increased by 177% ± 60% (SE) at 2°C, the much smaller increase in BCD (38% ± 27%) was not significant (paired *t*-test, $p = 0.48$; *see also Fig. 6*). DPP_{amb} was lower than BCD_{amb} in only two experiments, whereas $DPP_{2°C}$ was markedly higher than $BCD_{2°C}$, 1.7-fold on average, in all experiments (Fig. 6). Consequently, the mean (±SE) $BCD_{2°C}$:$DPP_{2°C}$ decreased to 0.27 ± 0.06, indicating an excess of DPP produced by phytoplankton over bacterial needs at 2°C.

Discussion

One of the likely consequences of global warming in Antarctic pelagic ecosystems is the occurrence of shifts in community composition, as already reported for other regions (Karl et al. 2001). Moline et al. (2004) have demonstrated a recurrent association between decreased salinities and dominance by cryptophytes rather than diatoms during austral summer, an observation that they attributed to warmer conditions. These longer term changes, as well as the way they could affect the capacity of the biological pump to draw down increased levels of atmospheric CO_2, can only be detected through time series records. Yet warming might also induce changes mediated by the physiology of extant planktonic assemblages (Reay

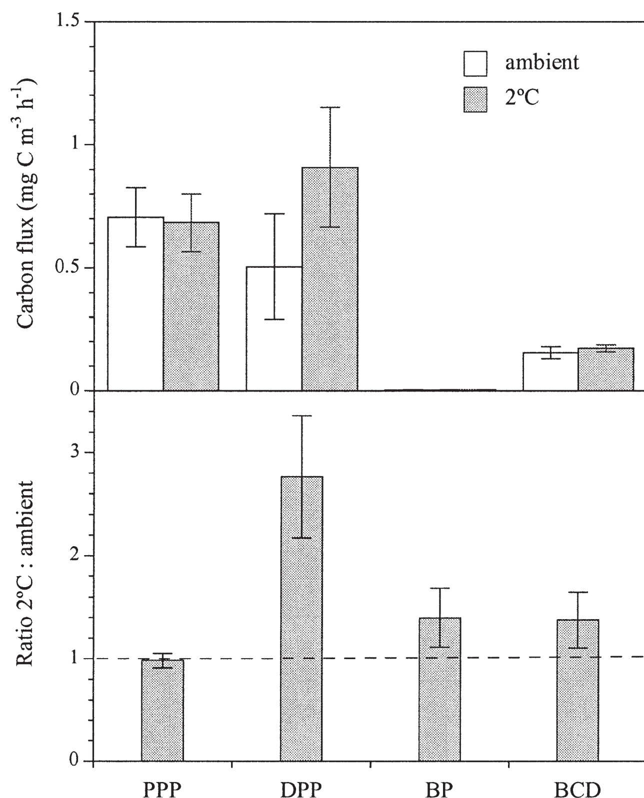

Fig. 6. Mean (±SE) of the estimated carbon fluxes for particulate (PPP) and dissolved (DPP) primary production and bacterial production (BP) and carbon demand (BCD) at ambient temperature and at 2°C. Also shown the ratio between 2°C and ambient temperature values.

et al. 2001), which is the underlying assumption in perturbation experiments such as those reported here. Although the interaction between changes in community structure and ecophysiological responses is not easy to foresee, we show here that small increases in temperature strongly affect phytoplankton photosynthesis and that changes in organic carbon partitioning might have profound effects in plankton-mediated biogeochemical processes.

Total primary production at ambient temperature was well within the range of the few reports, also including the production of DOC in their measurements (Morán et al. 2001*a*; Morán and Estrada 2002), but with a somewhat different partitioning between the particulate and dissolved fractions. Mean ambient PER was higher (35%) than in offshore waters of the Weddell and Scotia Seas (12%; Morán et al. 2001*a*) characterized by a lower biomass (0.45 mg Chl *a* m^{-3}), but it was also higher than values obtained in the same region later in the growth season (24%; Morán and Estrada 2002), with a mean biomass of 3.64 mg Chl *a* m^{-3}. These differences could be because of a different composition of coastal and offshore phytoplankton assemblages or temporal changes. Vernet et al. (1998) and Mei et al. (2003) found relatively high PER (36–55%) for Arctic phytoplankton, especially during diatom or *Phaeocystis* spp. blooms. Our Chl *a* values (mean 1.18 mg m^{-3}) could represent initial phases of blooming phytoplankton, and temporary increases in PER have been found to be associated with rapid shifts in community composition toward a dominance by larger cells (Morán and Estrada 2001).

Among the several hypotheses aiming to explain the generally low assimilation rates of Antarctic phytoplankton (Bracher et al. 1999) are suboptimal temperatures for growth (Jacques 1983; Reay et al. 2001). The expected increase in TPP with increasing temperature was caused by a significant increase in DPP while PPP either increased only slightly or remained constant (Table 2). Higher increases in PPP observed by other researchers (Neori and Holm-Hansen 1982; Tilzer et al. 1986) were not evident in the narrower ranges of temperature shifts used here. In our study, the relatively high ambient PER became still higher at 2°C (54%), and the magnitude of this increase was in turn positively related to the difference in temperature between treatments (Fig. 2B). Temperature would thus appear to be a crucial factor affecting the partitioning of photosynthate in the Southern Ocean. To our knowledge, the only papers explicitly and extensively dealing with the effect of temperature on primary production partitioning are those of Watanabe (1980), Verity (1981), and Zlotnik and Dubinsky (1989). Whereas Watanabe (1980) found increased PER in natural assemblages growing at suboptimally low and high temperatures, Verity (1981) observed that DPP was independent of temperature after acclimation of a diatom culture. Although the duration of our experiments was shorter than generation times and the measured enhancement of DPP might not be sustained after acclimation, experiments with cultures have also provided evidence of changes in PPP and DPP rates. Interestingly, in the three species (a prymnesiophyte, a cyanobacterium, and a chlorophyte) examined by Zlotnik and Dubinsky (1989), they found significantly higher PER values at temperatures higher than the optimal for each species. However, cultures might not be representative of natural phytoplankton assemblages, and they did not include any cold-adapted species.

Our results demonstrate that photosynthesis was strongly temperature dependent in Southern Ocean waters during late spring, but in contrast to previous reports of an effect only on the particulate fraction (Tilzer and Dubinsky 1987; Thomas et al. 1992), the increase in organic carbon fixation was largely found extracellularly shortly afterwards. This result might help explain the lack of consistent covariations of phytoplankton biomass and water temperature reported in other studies (e.g., Holm-Hansen et al. 2004). It is tempting to relate this inefficient C fixation at higher temperatures to a limitation by iron that would preclude its final assimilation into cellular compounds. The addition of iron to Southern Ocean phytoplankton has been recently demonstrated to enhance not only primary production rates but also POC export (Bishop et al. 2004). If the results of these rapid temperature shifts were to hold in the much slower rates of climatic change predicted by models, a warming of 1–2°C in the next decades (IPCC 2001) might result in significantly higher amounts of photosynthate flowing to the DOC pool. Concurrent with temper-

ature, increased CO_2 levels can also result in enhanced diversion of photosynthate to the dissolved pool (Riebesell 2004).

Ambient photosynthetic parameters α^B and P^B_m calculated for the particulate fraction (PPP) were similar to those found by Bodungen et al. (1986) and Basterretxea and Arístegui (1999) in November and December but lower than other observations later in the growth season (Helbling et al. 1995; Lorenzo et al. 2002). Nevertheless, as pointed out by Tilzer et al. (1986), photosynthetic parameters seem lower and less variable in the Southern Ocean than at lower latitudes, especially regarding the maximum photosynthetic rate, which does not usually exceed 3 mg C (mg Chl *a*)$^{-1}$ h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$ (Helbling et al. 1995; Bracher et al. 1999). Tilzer et al. (1986) reported on a marked temperature dependence of PPP α^B and P^B_m in Antarctic waters. In this study, both parameters tended to increase with higher temperature in a fashion similar to the time course experiments: changes were higher for TPP than for PPP (Table 3), which remained virtually unaltered, although the difference for TPP was only marginally significant. Unexpectedly, no significant differences were observed in the temperature sensitivities of α^B and P^B_m, in contrast to previous studies (Tilzer et al. 1986). Relatively constant E_k values have been repeatedly found in the Southern Ocean upper layers (Figueiras et al. 1998; Basterretxea and Arístegui 1999), hence indicating an "E_k-independent variation" of the P-E relationship (Behrenfeld et al. 2004). The covariation between α^B and P^B_m (Fig. 3), with comparatively smaller variations in E_k (Table 3), as also observed by Tilzer et al. (1986), implies that warming did not alter this photoacclimatization response to the varying light regime characteristic of deeply mixed water columns. However, changes in α^B and P^B_m with temperature might have large implications for the growth of phytoplankton communities adapting to concomitant changes in mixed layer depth (Sarmiento et al. 2004).

The activity of heterotrophic bacterioplankton in our experiments (Fig. 4) was low as in recent surveys (Morán et al. 2001*a*; Oliver et al. 2004), and adds to a growing body of evidence of a much lower magnitude of BP in the Southern Ocean compared with lower latitudes (Bird and Karl 1991; Morán et al. 2002, Oliver et al. 2004). BP estimates were two to three orders of magnitude lower than primary production rates as a consequence of low leucine incorporation rates rather than the choice of the Leu-to-C conversion factor (Pedrós-Alió et al. 2002). The absence of a significant effect of light versus dark incubations on ambient bacterial activity (Fig. 4A) confirms previous findings in the Weddell and Scotia Seas (Morán et al. 2001*a*). This contrasts with lower latitude oligotrophic ecosystems, in which dark conditions could significantly enhance bacterial incorporation of leucine (Morán et al. 2001*b*). These authors reasoned that the absence of a bacterial response to changes in photosynthesis because of light perturbations would indirectly suggest that bacteria were not substrate limited during the experiments. Unlike the observations of phytoplankton production, we did not find a clear-cut response of bacteria to temperature increase (Fig. 4B). One reason could be the high variability of the bacterial response to temperature observed by Pedrós-Alió et al. (2002) in December in the same region, with Q_{10} (BP ratios over a 10°C temperature increase) values ranging from 2 to 25. These authors also failed to find a consistent response between cell-specific Leu incorporation and temperature. Ducklow et al. (1999) found that bacterial growth was not stimulated during several days in seawater cultures at +2°C compared with −2°C. Although significant positive responses of bacteria to temperature have sometimes been reported (Pomeroy and Wiebe 2001), experimental temperature increases were much higher than those used here. An interesting finding, however, is that bacteria were affected by higher temperatures only at the less productive sites (roughly $<$4 pmol Leu L^{-1} h^{-1} (Fig. 4B) and $<$0.8 mg C m^{-3} h^{-1} of PPP; Fig. 5). These results suggest that only under severe organic nutrient deprivation would bacteria respond to temperature-associated enhancement of DPP by increasing their affinity for substrates (Nedwell 1999).

An assessment of BCD is essential before further consideration of organic substrate as a potentially limiting factor of bacterial growth. The estimation of BCD relies on accurate estimates of BGE, which were not attempted during this study. However, setting an upper limit for BCD could suffice for our purposes. According to the BP-based model of del Giorgio and Cole (1998), the estimated mean BGE would be an extremely low value (2%), and likely an underestimation of the true value in the light of the few experimental determinations in Antarctic waters (9%–38%; Carlson et al. 1999; Ducklow et al. 2000). Any higher BGE, Leu-to-C conversion factor, or both would decrease estimated BCD (e.g., by a factor of eight following Ducklow et al. 2000). Therefore, we can safely conclude that DPP rates exceeded the maximum possible bacterial uptake at ambient temperature. Despite the claimed limitation of bacterial growth by low DPP in Antarctic waters (Bird and Karl 1999; Carlson et al. 1998; Oliver et al. 2004), direct measurements indicate that DPP could completely meet BCD in most instances (Morán et al. 2001*a*; Morán and Estrada 2002). The accumulation of labile DOC during summer (Kähler et al. 1997) would also argue against a widespread limitation of bacterial growth by organic substrate supply, although restricted affinity for organic substrates because of low temperatures (Nedwell 1999) could yield an apparent carbon limitation. Bacteria can also be temporarily carbon limited during the development of phytoplankton blooms (Carlson et al. 1998; Morán and Estrada 2002), with indications that this limitation varies geographically across the Southern Ocean (Church et al. 2000). Yet, if bacteria were severely carbon limited in our experiments, we would expect an increase in the amount of photosynthate processed by bacteria (and hence BCD) whenever DPP was enhanced. However, the 177% mean increase in DPP in the 2°C treatments was followed by a much smaller 38% increase in BCD (Fig. 6). The fine balance between DPP and BCD rates suggested by Carlson et al. (1998) and demonstrated by Morán et al. (2002*a*) for offshore Antarctic ecosystems would then be lost after a rise in temperature, at least temporarily, because

a lagged response could also be expected. Karl et al. (1991) have shown that bacteria take around one month before responding to increased substrate supply associated with phytoplankton blooms. Alternatively, the response of bacteria to warming-related enhanced DPP might have been prevented because of the poor quality of the substrates if the hypothesis of iron limitation of photosynthetic production were applicable to our experiments. In this regard, Oliver et al. (2004) have shown parallel increases of PPP and BP following the addition of iron in Southern Ocean waters, which they attributed to higher DPP absolute rates.

Warming of Southern Ocean surface waters might affect phytoplankton photosynthesis through an absolute increase in CO_2 fixation. This, however, was mostly channeled to extracellular products rather than used to build up algal biomass in our experiments. Temperature rises and its associated increase in DPP did not translate into a straightforward response of heterotrophic bacteria. Although bacterial communities were apparently limited by substrate at low primary productivity sites, this is not a widespread feature of late spring Antarctic ecosystems. Without discarding a possible lagged processing, a low immediate bacterial utilization of temperature-related extra inputs of DOC is expected. The response to temperature investigated here lies at an extreme point within the gradient of possible velocities of change, with that of climate change being on the order of decades. The question is whether polar microbial assemblages, which are shown to be sensitive to small brief warming, will be able to acclimate, and over which timescales, or whether they will be replaced by other communities. These results could prove useful in forming testable hypotheses about the possible directions of change of plankton-mediated carbon fluxes in the Southern Ocean.

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