

Role of plankton communities in sea–air variations in pCO₂ in the SW Atlantic Ocean

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ABSTRACT: The influence of the plankton community structure on carbon dynamics was studied in the surface waters of the Argentinean continental shelf (SW Atlantic Ocean) in summer and fall 2002, 2003 and 2004. The horizontal changes in plankton community respiration (R), net community production (NCP) and gross primary production (GPP) were (1) compared with the difference in the partial pressure of CO₂ (pCO₂) between the sea surface and the atmosphere (Δ pCO₂), (2) compared with oxygen saturation and (3) related to the microscopic phytoplankton assemblages. This area, which has recently been shown to be a CO₂ sink, had an average surface oxygen saturation of 108.1%, indicating that net photosynthesis could have played a dominant role in the CO₂ dynamics. At most stations, the production:respiration (GPP:R) ratio was greater than 1, indicating that planktonic communities were autotrophic; the average GPP:R ratio for the whole study was 2.99. Phytoplankton biomass (chlorophyll *a*) and NCP showed an inverse relationship with Δ pCO₂ and a direct relationship with %O₂ saturation when phytoplankton assemblages were dominated by diatoms (30% of the stations). This was not the case when small ($\leq 5 \mu\text{m}$) flagellates were the most abundant organisms. Although NCP was mostly positive for both groups of stations (i.e. diatom-dominated or small flagellate-dominated), other physical and biological processes are thought to modify the CO₂ dynamics when small flagellates are the prevailing phytoplankton group.

KEY WORDS: Gross primary production · Net primary production · Respiration · Phytoplankton composition · pCO₂ · Oxygen saturation · SW Atlantic · Continental shelf

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INTRODUCTION

Oceans play a key role in modulating CO₂ dynamics, storing nearly 48% of the anthropogenic CO₂ emitted into the atmosphere (Sabine et al. 2004, Takahashi 2004). Although some latitudinal differences have been observed in natural CO₂ concentrations (Taylor & Orr 2000), the seasonal and geographical variations in

the partial pressure of CO₂ (pCO₂) in surface water are much greater than those of atmospheric pCO₂ (Takahashi et al. 2002). The flux of CO₂ between the ocean and the atmosphere, which strongly depends on the difference between seawater and atmospheric pCO₂ (Δ pCO₂), will therefore ultimately be a function of seawater pCO₂: the lower the seawater pCO₂ with respect to atmospheric pCO₂, the more negative the Δ pCO₂.

Seawater $p\text{CO}_2$ depends on physical factors and biogeochemical processes (Takahashi et al. 1993). The main factors controlling seawater $p\text{CO}_2$ are temperature, affecting CO_2 solubility and acid constants; winds, influencing the gas transfer velocity; carbonate dissolution in deep water, eventually neutralizing the effect of CO_2 on ocean acidity; calcification, producing a net $p\text{CO}_2$ increase; and organic carbon production (photosynthesis) and consumption (respiration), decreasing and increasing seawater $p\text{CO}_2$, respectively. Organic carbon production and export to the deep ocean are partly mediated by biological activity (the so-called 'biological pump', Eppley & Peterson 1979). Measuring seawater $p\text{CO}_2$ and dissolved O_2 simultaneously can help to identify the biological processes controlling $p\text{CO}_2$ (Bender et al. 2000, Carrillo et al. 2004). For instance, a $p\text{CO}_2$ undersaturation together with an O_2 supersaturation relative to atmospheric concentrations of both gases has been shown to be related to active photosynthesis (Carrillo et al. 2004). The opposite could indicate net respiration by the plankton community.

The biological effects on seawater $p\text{CO}_2$ vary according to the characteristics of the plankton community. Marine autotrophic production provides the organic material to support the producers' own metabolic requirements as well as those of planktonic consumers and decomposers. Ocean areas where autotrophic production (P) exceeds respiration (R) ($P:R > 1$) contribute to biological CO_2 drawdown, while heterotrophic areas ($P:R < 1$) contribute to CO_2 production. Moreover, this ratio is expected to vary seasonally, geographically, with water column depth and with the dominant trophic pathway. In herbivorous food webs (Legendre & Rassoulzadegan 1995), often observed in nitrate-rich areas and where production and grazing are uncoupled, high carbon export out of the surface layer and $P:R > 1$ are expected. In contrast, $P:R$ is expected to be less than 1 in microbial loops, which are characterized by high recycling rates and ammonium-based production as well as by a dominance of autotrophic and heterotrophic bacteria grazed by zooflagellates. Consequently, herbivorous food webs should significantly contribute to a CO_2 sink while systems dominated by microbial loops would add CO_2 to the atmosphere (Legendre & Rassoulzadegan 1996).

Duarte & Agustí (1998) calculated that 80% of the ocean's surface, comprising different biogeochemical regimes and different time scales (from daily to annual), is heterotrophic. It has been suggested that autotrophic coastal and shelf areas produce the organic matter needed to fuel the excess respiration in the open ocean (Bauer & Druffel 1998, del Giorgio & Duarte 2002). Takahashi et al. (2002) indicated that the

southern Atlantic Ocean, between 40° and 60° S, is expected to be a CO_2 sink. In fact, Bianchi et al. (2005) used $\Delta p\text{CO}_2$ data collected between 2000 and 2004 to show that during summer and fall the continental shelf of southern South America was an intense CO_2 sink. The transition between source and sink regions closely followed the location of tidal fronts, suggesting a link between the vertical stratification of the water column and the regional CO_2 balance. These fronts typically have one nearshore homogenized side and one deep well-stratified side. Phytoplankton is influenced by the frontal environment. Thus, on the nearshore side, bottom friction contributes to the intense mixing of the water column, which limits the light availability for phytoplankton photosynthesis. On the other hand, the stratification in offshore waters allows phytoplankton to grow and draw down CO_2 .

The SW Atlantic shelf has been classified as a 'Class 1 large marine ecosystem' (primary productivity $> 300 \text{ g C m}^{-2} \text{ yr}^{-1}$, Bisbal 1995). There is very little local data available on primary production, community respiration, community composition and distribution in this extensive area (Lange 1985, Lutz & Carreto 1991, Carreto et al. 1995). In addition, high zooplankton abundances have been described (Sabatini et al. 2004). This region is also a very rich fishing ground (Castello & Castello 2003) as well as an area with a high abundance of upper trophic level organisms (Campagna et al. 2000).

The aim of the present study was to determine whether there is a relationship between the plankton community composition and (1) its activity (production and respiration), (2) the distribution of $\Delta p\text{CO}_2$ levels and (3) the distribution of O_2 saturation levels in the surface waters of the SW Atlantic Ocean. For this, a series of *in vitro* O_2 production and respiration rate measurements were performed for different plankton assemblages in the studied area during 3 consecutive summers and falls (from 2002 to 2004).

MATERIALS AND METHODS

Study area. The SW Atlantic coast constitutes the largest continental shelf in the Southern Hemisphere (Bisbal 1995); its main characteristics have been described by Acha et al. (2004), Bianchi et al. (2005) and references therein. Briefly, the Argentinean shelf covers a 10^6 km^2 area, extending from approximately 41° S to Cape Horn (near 55° S). We set the southern limit of this study at 57° S, as in Acha et al. (2004). Since temperature shows strong seasonal variability, salinity is frequently used to classify the water masses (see the detailed description in Bianchi et al. 2005). Surface N–NE circulation over the southern Patagon-

ian shelf is mainly dominated by local westerly and south-westerly winds. The propagation of strong tidal currents, freshwater inputs from several Patagonian rivers (Glorioso & Flather 1995, Piola & Rivas 1997, Glorioso 2000) and the low salinity water outflowing from the Magellan Strait (Piola & Rivas 1997) influence the circulation on the Patagonian continental shelf.

Sampling. The SW Atlantic Ocean was studied on 9 occasions from January 2002 to April 2004 on board the Argentinean icebreaker 'Almirante Irizar' (Fig. 1, Table 1). An integrated sampling system developed at the Laboratoire de Biogéochimie et Chimie Marines (Poisson et al. 1993) allowed the continuous acquisition (sampling interval ~10 s), averaging (to intervals of 10 min) and recording of meteorological, atmospheric and seawater data. An automated SAB600AGMA CR2M weather station provided information on photosynthetically active radiation (PAR). The partial pressure of atmospheric CO₂ (pCO₂) was determined on air obtained from an intake placed on

Table 1. Dates of the transects on which production and respiration measurements were performed during the 2002 to 2004 cruises on board 'Almirante Irizar' in SW Atlantic Ocean. The only outer shelf sampling during fall was in 2004

Location	Date
2002	
Outer shelf	Jan 31–Feb 2
Coastal	Mar 23–26
Outer shelf–Coastal	Apr 10–13
Coastal	May 3–5
2003	
Outer shelf–Coastal	Feb 7–10
Coastal	May 15–18
2004	
Outer shelf	Feb 27–March 1
Outer shelf	March 13–16
Coastal	April 14–17

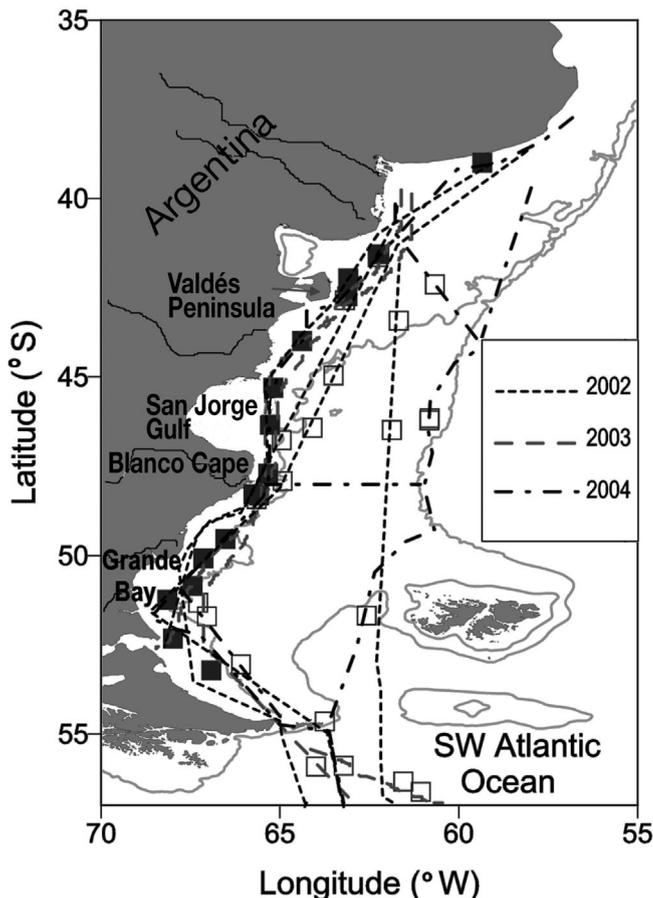


Fig. 1. Tracks of 2002 to 2004 cruises on board icebreaker 'Almirante Irizar', showing stations where NCP and R were measured; (□) offshore stations, (■) coastal stations

the bow of the ship by means of a flow-through equilibrator and an infrared (IR) analyzer (Siemens, Type Ultramat 5F). The analyzer was calibrated every 6 h with 3 gas standards containing 270.0, 361.0 and 489.9 ppm mole fraction of CO₂. pCO₂ was corrected for warming effects using temperature data obtained from high-accuracy sensors placed in the equilibrator and in the seawater intake. In addition, several variables were measured on surface seawater. Seawater was obtained from a pumping system placed at 9 m depth on the ship's exterior. A 550 µm stainless steel filter was used to eliminate large zooplankton. Microscopic *in situ* observations of the water samples showed that the pumping system did not break delicate planktonic organisms. Seawater pCO₂ was measured on the IR analyzer described above. Data were corrected for atmospheric pressure variations, drift and moisture effects as in Bianchi et al. (2005). The standard deviation of water pCO₂ was about 1 µatm (Metzl et al. 1995). The differences between ocean and atmosphere pCO₂ (ΔpCO_2) were later computed. Other variables that were measured continuously on the seawater from the same system included temperature (Sea-Bird SBE 38 sensor), salinity (Sea-Bird SBE 37) and *in vivo* fluorescence (Turner Designs Model 10 fluorometer).

Discrete samples were collected every 3 h from the water pumping system (N = 274). They were used for several analyses:

Dissolved oxygen. Dissolved oxygen concentrations were measured on duplicate 125 ml samples following the Winkler method and using an automatic potentiometer Mettler DL21 titrator. The average coefficient of variation for replicate samples was 0.4. These data were further compared to oxygen saturations in terms of percentage. Dissolved oxygen saturations were cal-

culated as in García & Gordon (1992) using the solubility coefficients of Benson & Krause (1984) and the temperature and salinity data obtained from the continuous sampling system.

Chlorophyll a. For chlorophyll *a* (chl *a*) determination, 2 to 4 l of seawater were filtered through Whatman GF/F filters and frozen at -20°C until analysis. This was done at the Instituto Antártico Argentino within 1 mo of the end of the cruise. Chl *a* samples extracted with 90% acetone were left for 24 h, read for absorbance in a Beckman DU 650 spectrophotometer, and corrected for phaeopigments. The final concentrations, which have an average precision of $\pm 0.05\text{ mg m}^{-3}$, were calculated as in Strickland & Parsons (1972).

Microscopic analysis. Quantitative plankton samples were taken directly from the pumping system, fixed with acid Lugol's solution and kept in cool and dark conditions. Living samples were examined on board. Cell counting was done at the phycology laboratory of La Plata University using an inverted light microscope (Iroscope SI-PH) following the traditional Utermöhl method (Lund et al. 1958). Further taxonomic observations were done on qualitative Lugol's-fixed samples collected with a $20\text{ }\mu\text{m}$ mesh net. Specimens were examined at $400\times$ magnification and photographed using a Wild M20 microscope equipped with a camera; they were also examined with a scanning electron microscope (JEOL JSMT 100 and JEOL JSM6360 LV at the SEM service, Museo de La Plata). Although many samples were examined alive, flagellates generally lose their flagella when fixatives are added and could thus be confused with other round-shaped organisms. Therefore, in the present work, small flagellates and small ($\leq 5\text{ }\mu\text{m}$) round-shaped organisms with or without flagella were counted as a single group of 'small flagellates.' Abundances were converted into phytoplankton carbon according to published conversions and data on species biovolume measured under the microscope (Montagnes et al. 1994, Hillebrand et al. 1999, Menden-Deuer & Lessard 2000).

Production—respiration experiments. We collected 46 samples to study phytoplankton production and community respiration (Fig. 1). In 2002 and 2003, samples were incubated in the ship's wet laboratory: samples from stations with low fluorescence signals were incubated for 12 h; when signals were higher in relative terms, incubations were for 6 h to enable the detection of oxygen changes and to avoid the possible nutrient limitation that could result from longer incubations. In 2004, incubations were done on the deck and lasted for 24 h; nutrient data analyzed after the experiments indicated that there was no nutrient limitation for the incubation periods used. For the deter-

mination of net community production (NCP), gross primary production (GPP) and community respiration (R), water from the pumping system was first transferred to a 5 l container in order to reduce replicate variability. We then carefully filled 250 ml borosilicate BOD bottles, allowing approximately 3 bottle volumes of seawater to overflow before closing them. Borosilicate bottles do not transmit UV light, which affects phytoplankton and micrograzers; therefore, we could compare data obtained in 2004 (when incubations were done with natural light) with data from 2002 and 2003, when incubations were done with artificial light. Seawater from the continuous sampling system circulated through the incubator to keep the system at *in situ* temperatures. Temperature varied latitudinally from 19°C in the northern part of the Argentinean continental shelf during summer to 3.5°C in the southern latitudes during fall. Light penetration at the sampling depth (9 m) was measured with a Biospherical PUV radiometer deployed from a launch, about 100 m away from the icebreaker. The depth of the euphotic zone in the area is always $>10\text{ m}$ (Angelescu & Prenszi 1987, in Bisbal 1995) and gets deeper at the limit of the continental shelf. Irradiance in the incubator was measured with a LI-COR quantum-radiometer/photometer Model LI-250 with a microspheric sensor. The irradiance inside the incubator simulated PAR at the sampling depth. In 2002 and 2003, irradiance varied between 40 and $100\text{ }\mu\text{mol photons m}^{-2}\text{ s}^{-1}$. In 2004 (24 h on-deck incubations), bottles were wrapped with neutral filters to reach $\sim 50\%$ of the sea-surface irradiance, corresponding to the irradiance measured at 9 m (sampling depth). The average daily values of surface PAR during 2004 ranged between 45 and $257\text{ }\mu\text{mol photons m}^{-2}\text{ s}^{-1}$, depending on the time of year and cloud conditions. Two to 3 replicates were used to determine the initial oxygen concentration, and there were 3 replicates for each light and each dark incubation. Dissolved oxygen concentrations were measured as described above. The coefficient of variation for replicate samples averaged 2.1%. R was calculated from the difference between the dark incubations and the initial oxygen concentrations while NCP was calculated from the difference between the initial and light-incubated oxygen concentrations. For 2002 and 2003, both R and NCP were converted to daily estimates by multiplying hourly estimates by 24. The day length for each sampling date and latitude was considered for NCP calculations following Agustí et al. (2004) as $\text{NCP d}^{-1} = \text{DL} \times \text{GPP} [\text{h}^{-1}] - 24 \times \text{R} [\text{h}^{-1}]$, where DL = length of the day. Gross primary production (GPP) was computed as $\text{R} + \text{NCP}$.

Data treatment and analysis. To remove the temperature effect, the observed seawater pCO_2 values were

normalized to seasonal temperature averages as in Takahashi et al. (2002). Average sea-surface temperatures for the summer and fall of 2002 to 2004 were calculated after dividing the area into grids of 4° latitude \times 5° longitude. In this study, $Tc\Delta pCO_2$ refers to the difference between seawater pCO_2 and the atmospheric pCO_2 after the effect of temperature was removed from seawater pCO_2 . A 1-way ANOVA was used to determine significant differences among years. In addition, the whole data set was classified according to the season (summer: January to March; fall: April to May) and the sampling area (coastal: depth <60 m; outer shelf waters: depth >60 m). It should be noted that the outer shelf waters were sampled in fall only in 2004 (see Table 1 legend). Stations were further classified according to the dominant phytoplankton group into diatom-, small flagellate- or dinoflagellate-dominated stations. After converting cell numbers to carbon (see above), a group was considered dominant when its carbon content represented more than 50% of the total phytoplankton carbon.

Data were log transformed to satisfy the assumptions of the analysis. Since some production values were negative, a constant value was added to shift its minimum log value to 0, i.e. $\log(\text{data} + \text{constant}) = 0$. Averages and standard errors of means (SE) were calculated. A major axis Model II regression analysis was carried out to describe the relation between either $Tc\Delta pCO_2$ or $\%O_2$ and biomass (as chl *a*) or NCP. Confidence intervals for the regressions were calculated according to Ricker (1973).

RESULTS

ΔpCO_2 and oxygen saturation

The observed range of atmospheric pCO_2 was 10.6 μatm , while the sea pCO_2 was about 268 μatm (ranging between -139 and 129 μatm). Average areal ΔpCO_2 in the SW Atlantic Ocean over all years and seasons was -23 μatm , leading to a net CO_2 sink during the summer–fall period (Fig. 2A). The average sea-surface temperatures were not significantly different between seasons (11.8°C , SE = 3.4 and 10.7°C , SE = 3.9 for summer and fall, respectively; $p = 0.21$). The $Tc\Delta pCO_2$ distribution (Fig. 2B) showed a similar pattern before and after removing the temperature effect on seawater pCO_2 . The average areal $Tc\Delta pCO_2$ remained negative (-21 μatm). The distribution of $\%O_2$ saturation followed a similar regional pattern (Fig. 2C). The regional average was 108.1% (range = 86 to 116%), and the stations with the highest oxygen supersaturation and the lowest $Tc\Delta pCO_2$ (-110 μatm) corresponded to offshore waters.

Chlorophyll *a* and phytoplankton groups

Fig. 2D shows discrete-sampled spectrophotometric chl *a* data obtained in the area from 2002 to 2004. To avoid distortion, chl *a* values >15 mg chl a m^{-3} are indicated on the map but were not used to construct the figure. Average surface chl *a* for summer and fall were 1.45 (SE = 2.10) and 1.21 (SE = 1.08) mg m^{-3} , respectively. Maximum chl *a* concentrations were consistently found on the offshore side of the tidal fronts off Valdés Peninsula (42°S), San Jorge Gulf (close to 46°S), its southern tip (Blanco Cape) and Grande Bay (close to 52°S) (Fig. 2D). The highest value measured on the Patagonian shelf during the whole study period was 19.2 mg chl a m^{-3} , which was found in a wide area off Grande Bay on 9 February 2003. Almost half of this high biomass was from phytoplankton >10 μm (data not shown) and was associated with oxygen supersaturation (105%) and low temperature-corrected seawater pCO_2 (-118.5 μatm). Values around 4 mg chl a m^{-3} were found during March 2002 and values up to 5 mg chl a m^{-3} were measured during the 2004 survey in some coastal locations at 45.7°S , this time corresponding to the <5 μm phytoplankton fraction (data not shown). In general, all 2004 samples were dominated by small flagellates. The high chl *a* concentration found in Grande Bay in 2003 was associated with a massive bloom of the centric diatom *Chaetoceros debilis*, with more than 2×10^6 cells l^{-1} , accompanied by a high number ($>3 \times 10^6$ cells l^{-1}) of 6 to 10 μm flagellates. In front of Blanco Cape (around 48°S , Fig.1), the high phytoplankton biomass ($>3 \times 10^6$ cells l^{-1}) was due to the presence of small (<5 μm) flagellates. This had been previously observed in the 2002 transects, although with smaller numbers both in summer ($>1 \times 10^6$ cells l^{-1}) and in fall ($>0.7 \times 10^6$ cells l^{-1}). For the San Jorge Gulf area, once again small phytoplankton (<5 μm) organisms dominated the phytoplankton assemblages in summer and fall 2002 as well as in summer 2003. Dinoflagellates dominated the plankton assemblages at 1 station only. A detailed description of the phytoplankton species composition will be presented elsewhere (Almandoz et al. 2007).

At stations where diatoms represented more than 50% of the phytoplankton carbon, a significant linear correlation was observed between chl *a* and both $Tc\Delta pCO_2$ and $\%O_2$ saturation (Fig. 3A,B), although this correlation was weaker in the latter case ($r^2 = 0.62$, $p < 0.05$ and $r^2 = 0.31$, $p < 0.05$, respectively). In contrast, no significant relation was found between chl *a* and $Tc\Delta pCO_2$ or $\%O_2$ saturation at the stations dominated by small flagellates ($r^2 = 0.02$, $p = 0.53$ for chl *a* vs. $Tc\Delta pCO_2$ and $r^2 = 0.08$, $p = 0.15$ for chl *a* vs. $\%O_2$ saturation; Fig. 3C,D).

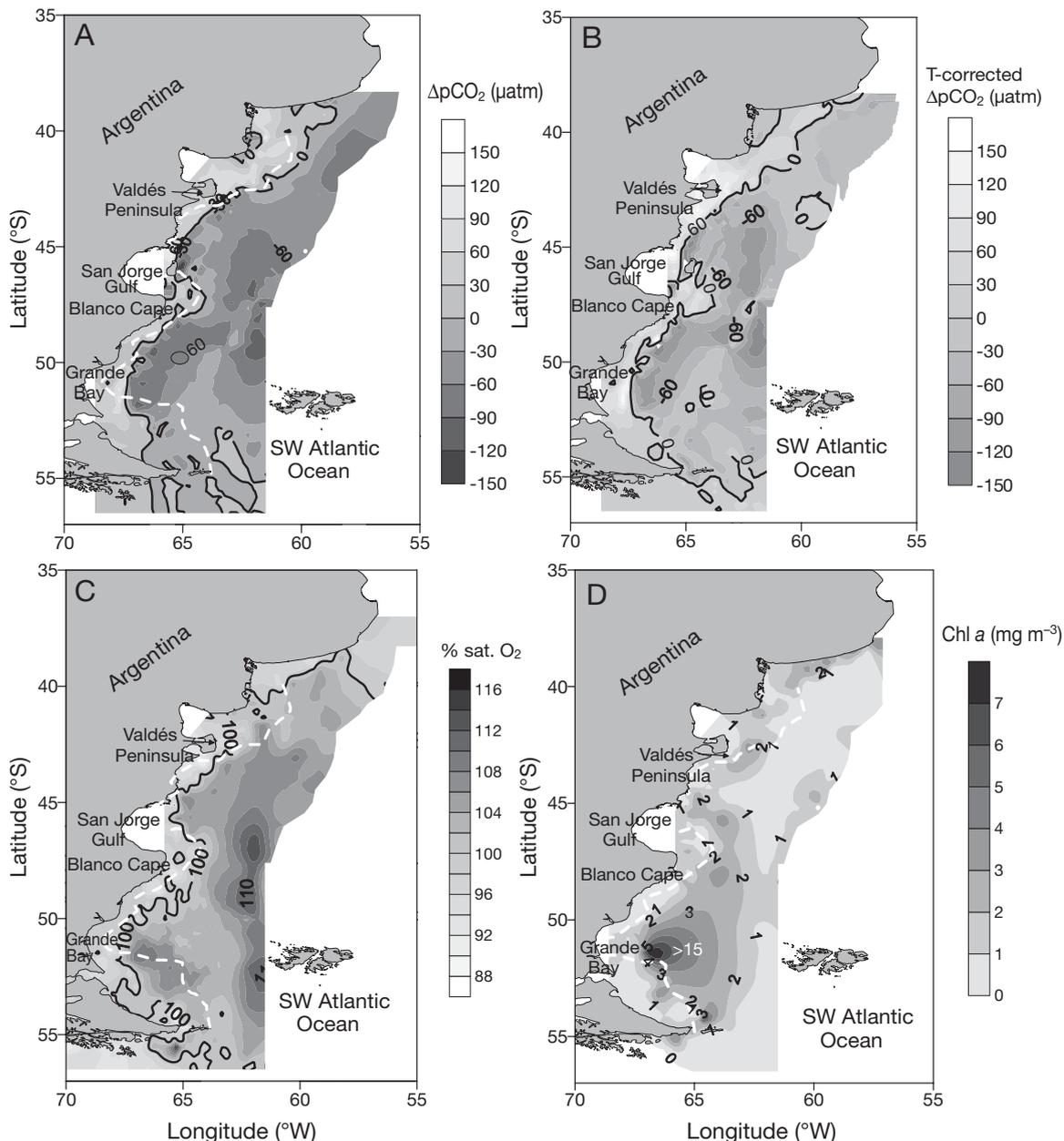


Fig. 2. (A) Average $\Delta p\text{CO}_2$ (μatm) distribution for summer and fall 2002, 2003 and 2004; negative values indicate $p\text{CO}_2$ sink. (B) Average $T_c\Delta p\text{CO}_2$ (μatm) distribution for summer and fall 2002, 2003 and 2004 (i.e. after effect of temperature was removed from seawater $p\text{CO}_2$ values; see 'Materials and methods'). (C) Surface $\% \text{O}_2$ saturation for same years. (D) Surface distribution of discrete chl *a* samples, averaged from 2002 to 2004. In (A), (C) and (D), white dashed line indicates approximate locations of tidal fronts (after Bianchi et al. 2005)

Production and respiration

One-way ANOVAs showed that there were no significant differences in respiration rate, R ($p = 0.29$, $F = 1.29$) or in NCP ($p = 0.23$, $F = 1.59$) among years. Therefore, data from the 3 yr were pooled for all the following analyses. No significant differences were found in R when comparing summer and fall ($p = 0.17$, $F = 1.99$).

R was correlated neither to temperature ($p = 0.28$ for log-transformed R data) nor to chl *a* concentration ($p = 0.18$ for log-transformed data of both series). The average daily respiration rate for all stations was 4.38 ($\text{SE} = 0.60$) $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ (Table 2). The highest R values were obtained for summer 2003 and fall 2002 (Table 2). High R values were mostly found at stations located close to the coast (Fig. 4A). In summer 2002, values of

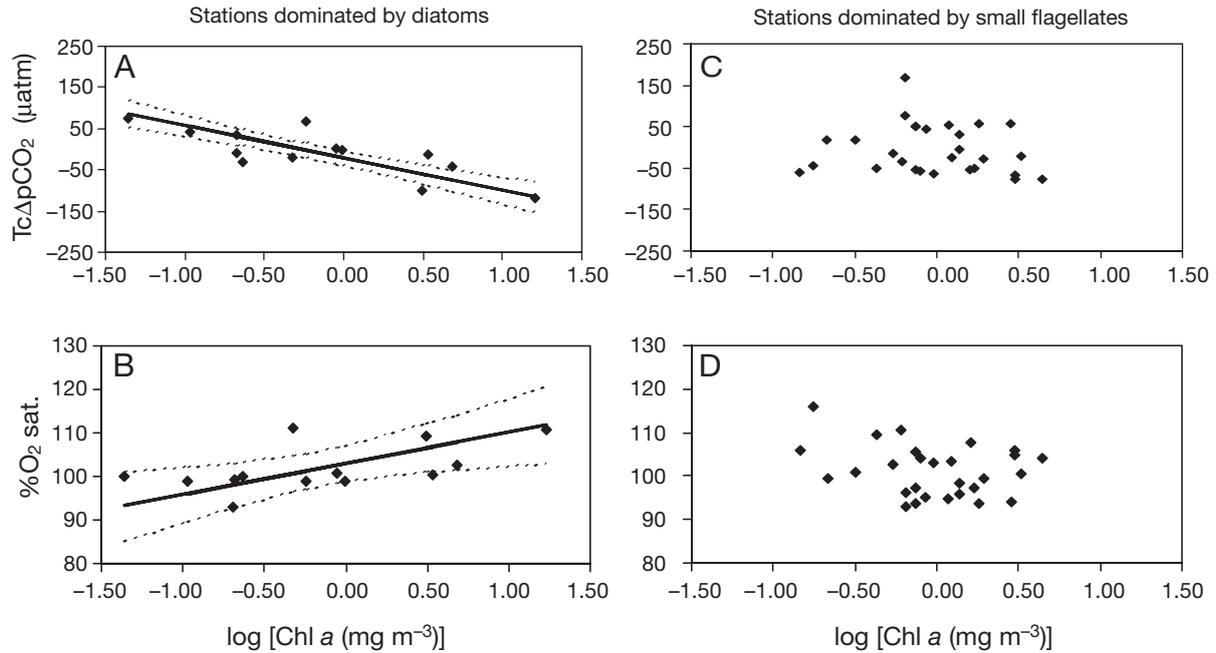


Fig. 3. (A,B) Relationship between chl *a* content and (A) $Tc\Delta pCO_2$ and (B) $\%O_2$ saturation for diatom-dominated stations. (C,D) Relationships between chl *a* content and (C) $Tc\Delta pCO_2$ and (D) $\%O_2$ saturation for small flagellate-dominated stations. Continuous lines: Major Axis Model II regressions; dashed lines: 95% confidence intervals

Table 2. Mean (SE) minimum (Min.) and maximum (Max.) ($N = 46$) chlorophyll *a*, net community production (NCP), dark community respiration (R), and gross primary production (GPP) for the years studied. Data separated according to season (summer or fall); average yearly data are also presented (summer + fall). All values are in $mmol O_2 m^{-3} d^{-1}$. -: no data

Season	N	Chl <i>a</i>		NCP		R		GPP	
		Mean (SE)	Min. Max.	Mean (SE)	Min. Max.	Mean (SE)	Min. Max.	Mean (SE)	Min. Max.
2002									
Summer	5	0.48 (0.14)	0.04 0.89	3.24 (1.85)	-3.48 10.02	4.22 (1.56)	0.86 11.33	7.47 (2.67)	-1.43 13.2
Fall	7	0.52 (0.15)	0.18 0.98	1.14 (1.73)	-3.03 5.88	6.61 (1.28)	2.90 9.68	7.75 (2.16)	1.96 12.52
Summer + fall	12	0.50 (0.10)		2.29 (1.26)		5.31 (1.05)		7.60 (1.50)	
2003									
Summer	10	3.44 (1.45)	0.21 15.90	18.8 (6.07)	-0.47 62.38	7.72 (1.50)	1.17 13.72	26.52 (7.26)	0.70 75.94
Fall	17	1.16 (0.34)	0.11 4.81	2.28 (0.86)	-2.20 10.87	2.32 (0.69)	0.02 7.64	4.60 (0.94)	1.04 12.39
Summer + fall	27	2.15 (0.69)		9.04 (3.02)		4.53 (0.92)		13.57 (3.75)	
2004									
Summer	6	1.75 (0.47)	0.43 3.28	4.59 (1.15)	0.3 6.88	2.29 (0.55)	1.05 4.59	6.88 (1.55)	1.34 11.39
Fall	1	2.85		4.36		3.28		7.64	
Summer + fall	7	2.85		4.56 (0.97)		2.43 (0.49)		6.99 (1.31)	
Total									
Summer	21	2.17 (0.71)		9.87 (3.19)		4.96 (0.95)		15.68 (3.89)	
Fall	25	1.08 (0.26)		1.91 (0.65)		3.19 (0.65)		5.10 (0.82)	
Summer + fall	46	1.67 (0.40)		6.40 (1.75)		4.38 (0.60)		10.77 (2.15)	

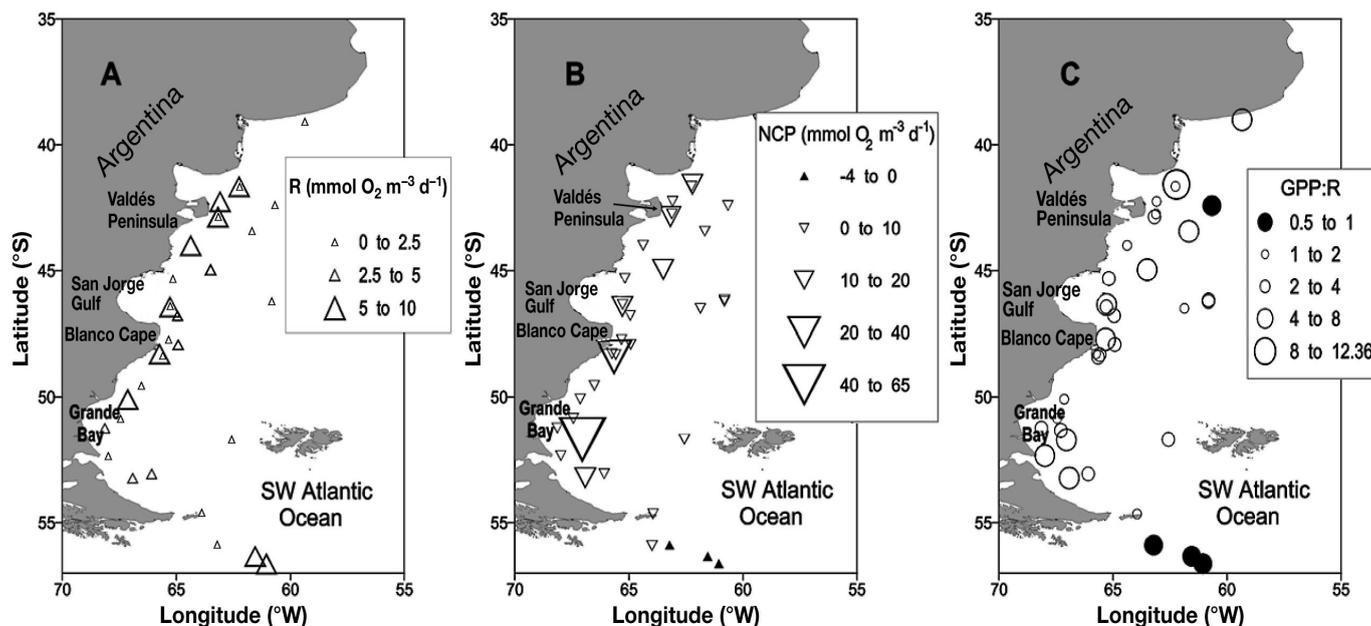


Fig. 4. (A) Dark community respiration (R), (B) net community production (NCP) and (C) production:respiration ratio (GPP:R) measured experimentally in 2002, 2003 and 2004

$R > 5 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ coincided with relatively low (around $10 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) NCP values. In contrast, R values $> 5 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ in summer 2003 were accompanied by the highest average NCP values (Fig. 4A,B).

NCP was higher than R at 61% of the stations. Significant differences were found for NCP when comparing summer and fall data ($p < 0.05$, $F = 6.18$). The highest NCP value ($62.38 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$; Table 2) was measured at 51.7°S , 67.4°W (Fig. 4B) on 9 February 2003 and corresponded to the *Chaetoceros debilis* bloom described in the foregoing subsection. High NCP values were mostly located offshore, on the stratified side of the tidal fronts. Moreover, NCP was significantly correlated with biomass (chl *a*) concentration ($r^2 = 0.61$, $p < 0.001$) (Fig. 5A). NCP represented 59.4% of the GPP for all the data, with 62.9% during summer and 37.5% during autumn. The correlation between NCP and GPP was higher ($r^2 = 0.63$, $p < 0.001$) (Fig. 5B) than that between GPP and R ($r^2 = 0.53$, $p < 0.001$) (Fig. 5C). The distribution of the GPP:R ratio showed values < 1 for 4 outer shelf stations, with 1 of them located north and the other 3 south of the Argentinean shelf, near Drake Passage (Fig. 4C). GPP:R ratios averaged 2.46 for the whole data set with no significant differences between seasons (average GPP:R summer = 3.16, fall = 2.67). The GPP:R ratio was > 1 in 91% of the cases, indicating that gross primary production exceeded community respiration in most incubations (Table 2) regardless of phytoplankton biomass concentrations or stratification conditions.

Community metabolism, $\Delta p\text{CO}_2$ and % O_2 saturation

The relationship between NCP and the $\text{Tc}\Delta p\text{CO}_2$ dynamics shows a different pattern for the 2 studied seasons. In summer, most of the NCP data were positive and accompanied by negative $\text{Tc}\Delta p\text{CO}_2$ data (Fig. 6A). Oxygen saturation was frequently $> 100\%$, although all data were very close to the equilibrium (Fig. 6B). During fall (mainly coastal stations), $\text{Tc}\Delta p\text{CO}_2$ was generally > 0 , indicating that even though NCP was positive, the area would not be acting as a CO_2 sink; in addition, waters were not saturated in oxygen for these same NCP positive values (Fig. 6C, D). Comparing production and respiration between diatom- and small flagellate-dominated stations, only R and GPP were significantly different among groups, although this was not the case for the GPP:R ratio (Table 3). The 1-way ANOVA did not show differences for NCP or for chl *a* concentration (Table 3). However, as shown for chl *a* (Fig. 3), the relationships between NCP and both $\text{Tc}\Delta p\text{CO}_2$ and % O_2 saturation were consistently different for both the diatom-dominated (Fig. 7A,B) and the small flagellate-dominated (Fig. 7C,D) communities. A significant linear correlation was observed between NCP and both $\text{Tc}\Delta p\text{CO}_2$ and % O_2 saturation ($r^2 = 0.49$, $p < 0.01$ and $r^2 = 0.52$, $p < 0.01$, respectively) (Fig. 7A,B). In contrast, no significant relation was found between NCP and $\text{Tc}\Delta p\text{CO}_2$ or % O_2 saturation at the stations dominated by small flagellates ($r^2 = 0.13$, $p = 0.06$ for NCP vs. $\text{Tc}\Delta p\text{CO}_2$ and $r^2 = 0.00$, $p = 0.92$ for NCP vs. % O_2 saturation) (Fig. 7C, D). This could indicate that

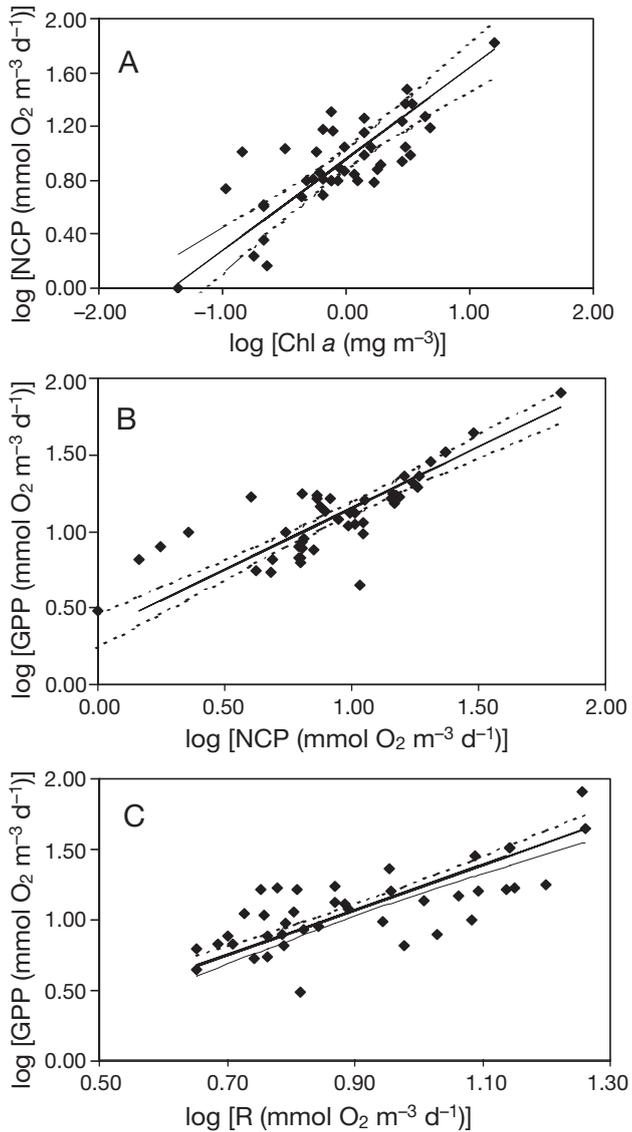


Fig. 5. Model II regressions between (A) chl *a* and net community production (NCP), (B) NCP and gross community production (GPP), and (C) community respiration (R) and GPP. Dashed lines: 95% confidence intervals. Since some production values were negative, a constant value was added to shift its minimum log value to 0 (see last subsection of 'Materials and methods')

the influence of phytoplankton on seawater pCO₂ differs among groups, regardless of total biomass.

DISCUSSION

Bianchi et al. (2005) showed that the SW Atlantic Ocean acts as a CO₂ sink during summer and fall. In that study, the simultaneous presence of the lowest seawater pCO₂ and the highest chl *a* concentrations on the stratified side of tidal fronts led to the conclusion that

the combined physical–biological processes control pCO₂ dynamics in surface waters over almost all the Argentinean shelf. In the present study, TcΔpCO₂ data are complemented by information on %O₂ saturation and phytoplankton production and respiration in relation to the composition and distribution of phytoplankton assemblages for the first time in this area. After removing the effect of temperature on surface water pCO₂, average areal TcΔpCO₂ was still negative and had values similar to ΔpCO₂. This indicates that other factors affect seawater pCO₂. However, thermal stratification and water column structure are essential to phytoplankton photosynthesis, and high phytoplankton concentration is only possible under the appropriate physical environment. Therefore, the temperature effect on water column stratification and biological production are intimately related and probably act jointly to produce the negative ΔpCO₂ that we observed.

The production estimates in this study are representative of the surface mixed layer of the water column, which averages 25 m during summer and fall (Rivas & Piola 2002). The few previous estimates of primary production in the area indicate that overall production on the Patagonian shelf south of 41°S and west of the Malvinas (Falkland) Islands was about 150 to 250 mg C m⁻² d⁻¹. In the slope region from 23°S to the Malvinas (Falkland) Islands, it varied between 250 and 500 mg C m⁻² d⁻¹ (Bisbal 1995). In order to allow a proper comparison, we converted our oxygen-based production data set into carbon using a photosynthetic quotient (PQ = Δ[O₂]/Δ[CO₂]) of 1.4 (based on nitrate assimilation) (Dickson & Orchardo 2001). NCP data (in mmol O₂ m⁻³ d⁻¹) obtained in the present 3 yr study were converted into carbon by multiplying the number of mmol oxygen by 12 to obtain mg of carbon. The estimated average net primary production in the area, without considering the exceptional 2003 bloom in Grande Bay, was 34 ± 7.4 mg C m⁻³ d⁻¹. When that bloom was included, production reached 45.4 ± 9.6 mg C m⁻³ d⁻¹. A rough estimation indicates that in either case, our primary production values are much higher than earlier (1972) estimates of the FAO (Food and Agriculture Organization of the United Nations; see Bisbal 1995). Even assuming that the values reported in Bisbal (1995) result from integrating production only in the upper 25 m, the estimated production would fall between 10 and 25 mg C m⁻³ d⁻¹. However, our data are in agreement with other production estimates for the area based on benthic carbon content (Seiter et al. 2004) and remote sensing (Antoine et al. 1996). They are also similar to values corresponding to other continental shelf areas (de Haas et al. 2002, Verity et al. 2002).

Tidal amplitude on the Patagonian shelf is one of the highest in the World Ocean (Kantha et al. 1995). Tidal and shelf-break fronts show elevated levels of algal

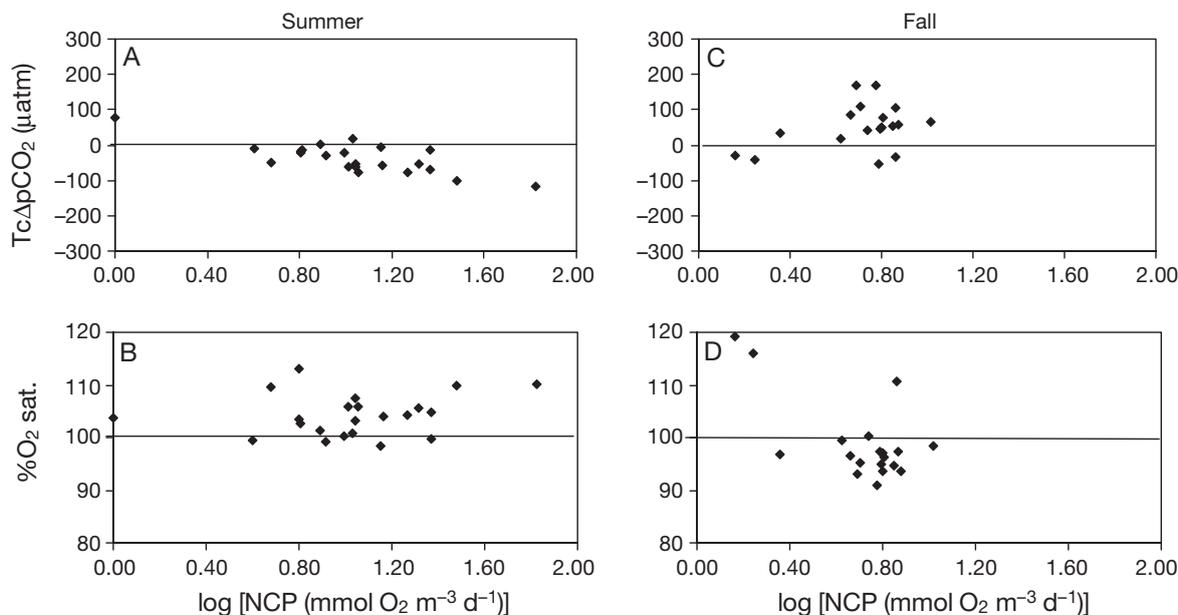


Fig. 6. Relationships between $Tc\Delta pCO_2$ and $\%O_2$ saturation, and microplanktonic net community production (NCP) for (A,B) summer and (C,D) fall. Since some NCP values were negative, a constant value was added to shift its minimum log value to 0

biomass due to either *in situ* growth or aggregation at a frontal convergence (Longhurst 1995), as stated for the frontal areas in the SW Atlantic (Acha et al. 2004). Close to the coastline, river discharges of suspended sediments may limit light availability. In addition to intense mixing, this contributes to explaining the low productivity and low phytoplankton biomass values consistently found near the continent. In this region, low GPP:R ratios and $\%O_2$ saturations were measured both in summer and in fall (Figs. 2C & 4C). However, coastal stations still showed GPP:R > 1. This suggests that plankton production does not compensate for

other processes that convert this area into a CO_2 source (Fig. 2A). Then, seawater pCO_2 in coastal zones could have several origins other than phytoplankton respiration. River input not only limits irradiance for photosynthesis, but also adds inorganic and organic carbon to the coastal Patagonian ecosystem (Depetris 1996). In addition, both benthic respiration (Middelburg et al. 2005) and the remineralization of dissolved organic matter (Broecker & Peng 1982) contribute to seawater pCO_2 in coastal oceans. Conversely, high primary production and negative ΔpCO_2 were generally found in the stratified zones of the frontal regions. High phytoplankton biomass and production (as found off Grande Bay) could be explained by stratification leading to adequate light conditions and to an intense nutrient supply, especially from waters that originated in the subantarctic region. Preliminary results on nutrients in the area (where no nutrient limitation was evident) support this hypothesis (Paparazzo et al. 2004).

Table 3. Average (SE) (N = 45) and significance of 1-way ANOVAs for different variables measured in relation to the dominant phytoplankton group in the studied samples. One station, where phytoplankton carbon was dominated by dinoflagellates, was not included in the analysis. ΔpCO_2 (μatm) is the difference between seawater and atmospheric pCO_2 without correcting for sea-surface temperature (SST). ns = not significant

	— Stations dominated by —		p
	Diatoms (31 % of stations)	Small flagellates (67 % of stations)	
SST ($^{\circ}C$)	10.36 (1.16)	12.16 (0.67)	ns
$\%O_2$ saturation	103.89 (1.92)	101.16 (1.11)	ns
$Tc\Delta pCO_2$ (μatm)	21.67 (23.89)	8.08 (14.11)	ns
ΔpCO_2 (μatm)	-1.85 (13.9)	-3.81 (8.33)	ns
R ($mmol O_2 m^{-3} d^{-1}$)	6.77 (1.23)	3.22 (0.55)	$p < 0.01$
NCP ($mmol O_2 m^{-3} d^{-1}$)	9.51 (5.02)	4.95 (0.94)	ns
GPP ($mmol O_2 m^{-3} d^{-1}$)	17.17 (5.75)	7.93 (1.32)	$p < 0.05$
GPP:R	2.46 (0.67)	3.03 (0.37)	ns
Chl a ($mg m^{-3}$)	2.38 (1.20)	1.33 (0.20)	ns

Phytoplankton concentration along the Argentinean coast has well-defined maxima in spring and fall (Acha et al. 2004). Since the present study did not cover the start of the phytoplankton growth season, it is possible that the low ΔpCO_2 values measured during summer were the result of spring production, later accompanied by episodic

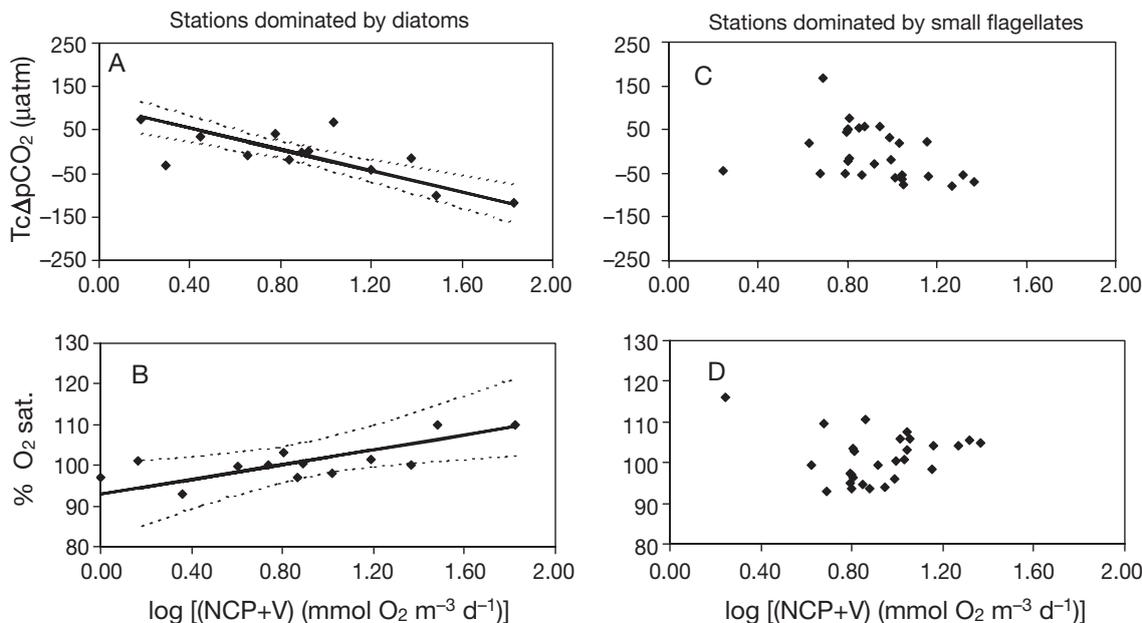


Fig. 7. (A,B) Relationships between microplanktonic net community production (NCP) and (A) $Tc\Delta pCO_2$ and (B) % O_2 saturation for diatom-dominated stations. (C,D) Relationships between NCP and (C) $Tc\Delta pCO_2$ and (D) % O_2 saturation for small flagellate-dominated stations. Continuous lines: Model II regression; dashed lines: 95% confidence intervals. Since some NCP values were negative, a constant value was added to shift its minimum log value to 0

high production events during the summer season. To complete the understanding of the SW Atlantic, spring and winter studies are necessary. Local discrepancies that can be seen between the distribution patterns of both $Tc\Delta pCO_2$ and % O_2 saturation (Fig. 2A,B,C) can be explained by the lower solubility of O_2 compared to CO_2 , since O_2 approaches atmospheric equilibrium concentrations faster than CO_2 (Carrillo et al. 2004). In fact, an intensive latitudinal sampling like the present one has an uncertainty related to the temporal evolution of the water masses. On occasion, low seawater pCO_2 is the result of a previous bloom that was not retained in the surface layer (probably through sedimentation) but that left a residual CO_2 deficiency in surface waters. Such a time lag between primary production and CO_2 exchange has been described for other areas (Borges & Frankignoulle 2001, Anadón & Estrada 2002). A similar situation was found when comparing NCP distribution and % O_2 saturation. In some areas, as in the open waters between 46 and 49° S, high % O_2 saturations were not accompanied by high NCP values. Since incubations were fewer in number than the discrete oxygen sampling, some highly productive areas may have been missed.

In the Argentinean shelf region, plankton communities appeared to be autotrophic. Moreover, the correlation between NCP and GPP was much higher ($r^2 = 0.7$) (Fig. 5B) than between GPP and R (Fig. 5C), in agreement with what has been found in other ocean areas (i.e. the Southern Ocean; Agustí et al. 2004). Although

GPP might be underestimated because of enhanced respiration under illuminated conditions (Dickson & Orchardo 2001) and due to the grazing activity of small (<500 μm) zooplankton and protozoans, NCP oxygen incubation results represent the maximal potential productivity in the absence of physical disturbances. Following the criteria of Duarte & Agustí (1998) and Agustí et al. (2004), the parameters of a power equation ($R = a GPP^b$) relating GPP and R were calculated in order to estimate the GPP value required to balance the seasonal community average R (i.e. $GPP:R = 1$) and render the communities autotrophic. This resulted in a GPP of 8.95 $mmol O_2 m^{-3} d^{-1}$ for summer + fall, 12.65 $mmol O_2 m^{-3} d^{-1}$ for summer and 4.67 $mmol O_2 m^{-3} d^{-1}$ for fall. These estimated GPP values were then compared to the average GPP values obtained experimentally (Table 2). Both the estimated values for summer + fall as well as for summer are well below the seasonal measured GPP averages. However, the estimated fall GPP value needed to render $GPP:R = 1$ was higher than the average value measured in 2003 and higher than some of the fall values found during the 3 yr studied (Table 2). Furthermore, according to the linear relationship between chl *a* and NCP (Fig. 5A) and between NCP and GPP (Fig. 5B), the phytoplankton biomass levels required to reach these GPP values were 0.9 $mg chl a m^{-3}$ for summer + fall, 0.5 $mg chl a m^{-3}$ for summer and 1.67 $mg chl a m^{-3}$ for fall. Again, this last value is higher than the seasonal mean we found in the area (see 'Results'). Less negative

Tc Δ pCO₂ values and lower %O₂ saturations were found during fall (Fig. 6C,D) than during summer (Fig. 6A,B). Increased vertical mixing during fall is probably responsible for the uncoupling between NCP and gas exchanges. Excess fall heterotrophy has to be compensated with organic matter coming from an external source. Since fall sampling has been mainly conducted in the coastal area, terrigenous (allochthonous) inputs (Duarte & Agustí 1998) as well as dissolved organic carbon produced locally (Bauer & Druffel 1998) could account for the excess respiration. In outer shelf waters, respiration could be due to the activity of ciliates, which can be abundant in the area (Thompson 2004), or other microzooplankton. Bacterial respiration, which has not been considered separately in the present study, probably plays a central role in NCP and R uncoupling, as it does in other continental shelf areas (Griffith & Pomeroy 1995).

Communities with NCP >0 should significantly contribute to the CO₂ sink while those with NCP <0 should be a source of this gas from the ocean to the atmosphere (Ducklow & McCallister 2004). Although NCP is similar in both diatom- and small flagellate-dominated stations on average, a linear relationship between Tc Δ pCO₂ and %O₂ saturation with phytoplankton biomass and NCP is only evident when the phytoplankton community is dominated by diatoms (Figs. 3 & 7, Table 3). Such a relationship has been described before for different environments (Anadón et al. 2002, Brown et al. 2002, Tremblay et al. 2002, Sarthou et al. 2005). Diatoms dominate the phytoplankton assemblages in nutrient-rich and frontal areas (Sarthou et al. 2005). The dominance of diatoms during the few high production events favors the establishment of a herbivorous food web (Legendre & Rassoulzadegan 1995) and can lead the area to act as a CO₂ sink. As a consequence, the non-oxidized particulate matter could be exported towards the sea bottom, therefore contributing to the carbon sink. The excess production could be buried in the sediments and/or exported to fuel respiration in the open-ocean interior (Bauer & Druffel 1998).

Diatoms dominated the plankton assemblages in 31 % of the studied stations. In terms of total biomass, these stations represented 47 % of the chl *a* in the area and 49 % in terms of phytoplankton carbon. This means that most stations were dominated by small flagellates and that more than half of the phytoplankton biomass and carbon on the Patagonian shelf was due to this group, for which no relationship was found between their abundance or between measured NCP and either Tc Δ pCO₂ or %O₂ saturation. Moreover, the whole area still behaves as a CO₂ sink: 64 % of the stations dominated by small flagellates showed negative Tc Δ pCO₂ values and 78 % of them had GPP:R ratios >1.

It is thus evident that small flagellates certainly play a significant role in the dynamics of seawater pCO₂ and %O₂ saturation. This type of community, which leads to microbial food webs and microbial loops, is in general much less studied than communities dominated by diatoms. The recycling of nutrients and carbon is enhanced in these communities, and therefore no linear or simple power relation is found regarding Tc Δ pCO₂ or %O₂ saturation. It must be noted that although microscopic examination only allowed us to detect small flagellates and identify diatom taxa, production and respiration experiments consider the whole microplanktonic community. Furthermore, in a climate change scenario (i.e. increases in atmospheric CO₂, sea-surface temperature and stratification, and a decrease in nutrient supply to surface waters), decreases in chlorophyll, primary production and export from the euphotic zone are expected, as well as a shift in phytoplankton taxa, from diatoms to relatively smaller phytoplankton cells (Legendre & Rivkin 2002). In the present study, small flagellates were not further characterized. In addition, we did not consider the effect of grazers >500 μ m. To study the role of biology on CO₂ dynamics, it is essential to consider the complete composition of plankton assemblages. Diatoms are easier to identify than organisms making up the small flagellate group. The identification and comprehension of the physiology and ecology of the small flagellates, as well as those of picoplankton and bacteria, which will be subject of further studies, are the 'black box' that must be opened to understand the relationship between plankton composition and CO₂.

CONCLUSIONS

Over most of the Argentinean continental shelf, the GPP:R ratio was >1, suggesting that phytoplankton production greatly influences the negative average Δ pCO₂ values found in the area. The present study confirms the importance of continental shelves and slopes, which comprise <20 % of the World Ocean area (Bauer & Druffel 1998), in the global carbon cycle. Excess production in this area is a source of biological carbon fueling the vast heterotrophy found in the open ocean (del Giorgio et al. 1997). Our results show that there is a linear relationship of biomass and production with Tc Δ pCO₂ and %O₂ concentrations at stations dominated by diatoms, while no such relationships were found when small flagellates dominated the phytoplankton assemblages. This was the case in 67 % of the stations studied. As shown for other processes in the ocean (i.e. export flux), food web structure and phytoplankton composition affects the CO₂ dynamics. The lack of a linear relation between chl *a* and

Tcp Δ CO₂ in these situations indicates that community composition (i.e. more than just biomass) is an important aspect to be considered in future works as well as in modeling efforts. Changes in environmental conditions leading to the dominance of either group could then have consequences on the biogeochemical cycles and especially on CO₂ dynamics. Knowledge of system controls and feedbacks on the primary production in coastal areas will contribute to our understanding of the system's responses to the anthropogenic-induced climatic changes that are under way.

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