Dissolved and suspended organic carbon in the Atlantic sector of the Southern Ocean. Stock dynamics in upper ocean waters


ABSTRACT: Dissolved and suspended organic carbon (DOC and POC) distributions were studied in the undersampled Atlantic sector of the Southern Ocean during Cruise HE052 of the 'Bio Hespérides' in December 1998. The coastal waters of the ice edge, the Gerlache Strait, and the open-ocean waters of the Weddell Sea and the Drake Passage were sampled. The high correlation between chlorophyll a (chl a), DOC and POC suggest that a considerable fraction (estimated at 15 to 30%) of the organic matter available in the upper mixed layer of the different study regions is the product of synthesis and early degradation of planktonic primary production. Relatively low renewal times (≤2 wk) of this material, except in the Polar Front Zone (>5 wk), were deduced from measured primary/bacterial production rates. Maximum contributions of this potentially bioactive organic carbon pool (TOC_B) to the total organic carbon (TOC) were observed in the highly productive waters of the ice edge (24%) and Gerlache Strait (30%) regions, where high chl a levels and shallow upper mixed layers (due to marked salinity gradients) occurred. DOC represented 42 and 56% of TOC_B in these regions, respectively. In contrast, TOC_B comprised ≤20% of TOC in the less productive open-ocean waters of the Weddell Sea and Drake Passage, where DOC made up ≥65% of TOC_B. The Subantarctic Zone constituted an exception, with high chl a levels and a shallow upper mixed layer (due to marked temperature gradients): 29% of the organic carbon in the upper mixed layer was TOC_B, 68% of which was in the dissolved fraction. Accumulation of DOC in the study regions points to a reduction in bacterial activity through mechanisms other than substrate limitation.

KEY WORDS: Dissolved and suspended organic carbon · Primary and bacterial production · Carbon renewal time · Drake Passage · Southern Ocean

INTRODUCTION

Nearly all the organic carbon in the oceans originates from phytoplankton primary production (Kirchman et al. 1993). This phytoorganic material can be subsequently mineralised in situ, transferred through the food web, transported by horizontal circulation, or carried to deep waters by fast-sinking particles, vertical migration of zooplankton and downward mixing of dissolved (DOC) and suspended (POC) organic carbon (Copin-Montégut & Avril 1993, Carlson et al. 1994). Up to the late 1980s new production estimates in the oceans were based on the assumption of a steady-state balance between the downward flux of sinking particulate organic matter and the upward flux of inorganic nutrients at the base of the photic layer (Eppley & Peterson 1979). During the 1990s, special attention was paid to dissolved organic matter (DOM) because of its contribution to the recycling and export of primary
production (e.g. Toggweiler 1989, Bronk et al. 1994). Accordingly, before the late 1980s most papers dealing with organic matter only presented POC, whereas during the 1990s they focused only on DOC. However, the key role of the POC pool in DOM studies — linked to DOM recycling and export processes, particularly in autotrophic systems — has only been considered in some recent DOM works (Carlson et al. 1998, Bodineau et al. 1999, Doval et al. 1999, Hung et al. 2000).

The present study focuses on DOC and POC cycling in the undersampled Atlantic Sector of the Southern Ocean, covering a wide variety of contrasting hydrographic conditions during December 1998. The Southern Ocean is the world largest high-nutrient/low-chlorophyll region and a known sink for atmospheric CO₂ (Le Fèvre & Tréguer 1998). Nowadays, the Southern Ocean is viewed as a mosaic of subsystems, some of which are highly productive whereas others are dominated by long periods of heterotrophy. According to the mechanism that controls nitrogen uptake, and hence phytoplankton production, 4 subsystems have been identified by Tréguer & Jacques (1992): the highly productive Coastal and Continental Shelf Zone (CCSZ), Seasonal Ice Zone (SIZ) and Polar Front Zone (PFZ), and the less-productive Permanently Open Ocean Zone (POOZ). We sampled all of these during Cruise HE052 of the ‘Bio Hespérides’. From south to north, we occupied the coastal zone of the Gerlache Strait, the Weddell Sea ice edge and open waters, and the Antarctic, Polar Front and Subantarctic Zones across the Drake Passage (see Fig. 1). Enhanced primary production regions associated with melting ice and with the frontal structures of the Antarctic Circumpolar Current (ACC) were sampled. In addition, the Weddell-Scotia Confluence (WSC) was visited, where eastward-flowing ACC and Weddell Sea waters mix with continental shelf waters from the Weddell Sea (Withworth et al. 1994).

The role of DOM in the Southern Ocean has been the subject of several recent studies, covering wide latitudinal ranges in the Atlantic (6°W: Kähler et al. 1997), Indian (62°E: Wiebinga & de Baar 1998), Australian (140°E: Ogawa et al. 1999) and Pacific (170°W and 170°E: Doval & Hansell 2000) sectors of the ACC. We occupied the World Ocean Circulation Experiment (WOCE) Line SR1b in the Drake Passage (53 to 58°W), recording for the first time DOC and POC stocks across this region, where the ACC enters into the Atlantic Sector of the Southern Ocean. Total organic nitrogen and phosphorus have also been recently measured by UV photo-oxidation along the same WOCE Line (Sanders & Jickells 2000), allowing comparison with our data. In our study, we examined the relative contribution of the dissolved (Ø < 0.8 µm) and particulate (Ø > 0.8 µm) fractions to the organic carbon pool retained in surface ocean waters. In addition, we analysed the potential reactivity of DOC and POC in the upper ocean waters of the contrasting hydrographic regions visited during the cruise. A novel approach for determining the quality (‘refractory’, ‘labile’) of the DOC and POC pools, based on observed covariance between chlorophyll a (chl a), DOC and POC profiles, was used. The calculations were complemented with measurements of primary and bacterial production rates, allowing a rough estimation of carbon renewal times.

**MATERIALS AND METHODS**

The sampling program was carried out during Cruise HE052 within the framework of the Research Project ‘Diversidad, Heterotrofia, Autotrofia y Relaciones entre Microorganismos Antárticos (DHARMA)’, conducted in December 1998 aboard the ‘Bio Hespérides’. The cruise consisted of a hydrographic transect from the ice edge (Stn 1; 63°S) across the Weddell Sea and Drake Passage to the north of the Subantarctic Front (Stn 32; 55°S). We occupied WOCE Line SR1b across the Drake Passage (Stns 12 to 32). In addition, Stns 47 (ice edge), 49 (Western Gerlache Strait) and 58 (Eastern Gerlache Strait) were also visited (Fig. 1) to study the diel variation of DOC/POC stocks and primary/bacterial production rates. We will include the data from these stations because they are representative for the highly productive ice edge and coastal zones and complement the database generated in Sampling Line SR1b. However, we will not go deeply into the diel cycles, since these will be the subject of a forthcoming paper.

**Thermohaline parameters.** Full-depth conductivity-temperature-depth profiles were obtained at each station with a Mark IIIC probe attached to a rosette sampler fitted with 24 Niskin bottles of 10 l with internal closure (General Oceanics). The gear was also equipped with a Sea Tech fluorometer. Temperature and salinity were used to characterise water masses and to define the surface layer thickness and stability by means of the squared Brunt-Väisälä frequency (N²) in the different hydrographic regions occupied during the cruise. Following Millard et al. (1990), N² can be calculated as:

\[
N^2 = \frac{g}{\rho} \left( \frac{\Delta \rho}{\Delta z} \right)
\]

where g is gravity acceleration and \( \rho \) and \( \Delta \rho/\Delta z \) are mean density and density gradient over the depth interval \( \Delta z (= 5 \text{ m}) \), respectively. The pycnocline is defined as the depth of the N² maximum, separating the surface layer (where chl a, POC and DOC accumulates) from the waters below. The relative contribution
the water column. Chl \(a\) profiles in the upper 100 m were estimated fluorometrically with a Turner Designs 10000R fluorometer (Yentsch & Menzel 1963). Samples (100 ml) were collected on 25 mm \(\varnothing\) GF/F filters, frozen at \(-70^\circ\text{C}\) and left for 12 h in 90% acetone for pigment extraction. The fluorometer was calibrated with natural samples collected on the same cruise and measured spectrophotometrically.

DOC and POC concentrations were determined in the upper 250 m and the whole-water column, respectively. The DOC and POC fractions were separated with GF/F filters (equivalent pore size 0.8 \(\mu\)m). Seawater for the analysis of POC and suspended organic nitrogen (PON) was drawn from the Niskin bottles in 2 l polycarbonate flasks (representative for particles <200 \(\mu\)m). It was immediately filtered with an oil-less vacuum filtration system (filtration pressure <0.3 kg cm\(^{-2}\)) to collect the particulate material in 25 mm \(\varnothing\) GF/F filters (previously precombusted at 450°C, 4 h). The filters were dried on silica gel and frozen at \(-20^\circ\text{C}\) until analysis in the laboratory. Measurements were carried out with a Perkin Elmer 2400 CHN analyser. Acetanilide was used to calibrate the system. The analytical error of the method is \(\pm 0.1 \mu\)M C for POC and \(\pm 0.04 \mu\)M N for PON.

Filtered DOC samples were collected into precombusted 10 ml glass ampoules. After acidification with H\(_3\)PO\(_4\) to pH < 2, the ampoules were heat-sealed and stored in the dark at 4°C, until analysed in the laboratory. After decarbonation of the sample by vigorous stirring, 200 \(\mu\)l were injected into the vertical furnace of a ‘Shimadzu TOC-5000’, filled with a conditioned 0.5% Pt-coated Al\(_2\)O\(_3\) catalyst at 680°C. The system was standardised daily with potassium hydrogen phthalate. The concentration of DOC was determined by subtracting the system blank area from the average peak area and dividing by the slope of the standard curve. The system blank — obtained by frequent injection (every 4 to 6 samples) of UV-Milli-Q water — was equivalent to 10 \(\mu\)M C. Precision of the measurements was about \(\pm 1 \mu\)M C. The accuracy of our DOC measurements was tested daily with reference materials provided by J. Sharp (University of Delaware) and D. A. Hansell (BBSR, Bermuda). We obtained an average concentration of 45.1 ± 0.7 \(\mu\)M C (n = 50) for the ‘deep ocean’ reference material (Sargasso Sea deep water, 2600 m) and 0.4 ± 0.7 \(\mu\)M C (n = 44) for the ‘blank’
reference laboratories are 44.0 ± 1.5 and 0.0 ± 1.5 µM C, respectively.

**Primary and bacterial production rates.** Daily depth-integrated primary production (PP, mg C m⁻² d⁻¹) rates were calculated according to Figueiras et al. (1999), taking into account the spectral irradiance (using Eq. 3) because of the absence of light inhibition:

\[
PP = D \cdot \int_{0}^{Z_C} \text{chl}a(z) \cdot P_{m}^{R}(z) \cdot \left[1 - \exp \left( \frac{E_{PUR}(z)}{E_{bch}^{R}(z)} \right) \right] \cdot dz
\]

(3)

where \( D \) is daylength, \( P_{m}^{R} \) is the chl-specific light-saturated rate of photosynthesis (mg C mg⁻¹ chl h⁻¹), and \( E_{bch}^{R} \) (µmol photons m⁻³ s⁻¹) is the light-saturation parameter for photosynthetically usable radiation (PUR) by phytoplankton. Both parameters were calculated from photosynthesis-irradiance (P-E) curves obtained in lineal incubators and fitted to the model of Webb et al. (1974). As a function of depth of the photic layer, 3 to 5 depths were sampled at each station from the surface down to a depth of 1% incident light. Each incubator housed 14 subsamples collected in 75 ml tissue-culture Corning flasks inoculated with 3.70 × 10⁵ Bq (10 µCi) of 14C-labeled bicarbonate. The samples were maintained at sea temperature by circulating water refrigerated with a Neslab digital temperature controller. Incubators were illuminated at the front by Osram tungsten-halogen lamps and the photosynthetically available irradiance \( E_{PAR}(z) \) was measured using a Li-Cor cosine-corrected sensor (LI 190SA). The light quality did not vary among incubators. Samples were incubated for 2 to 3 h. \( E_{PUR}(z) \) (µmol photons m⁻³ s⁻¹) is the photosynthetic radiation usable by phytoplankton, and it was estimated according to Dubinsky (1980):

\[
E_{PUR}(z) = \int_{400}^{700} d\lambda \cdot a_{ph}(z, \lambda) \cdot E(z, \lambda)
\]

(4)

where \( a_{ph}(z, \lambda) \) is the phytoplankton spectral absorption coefficient, and \( E(z, \lambda) \) is the spectral irradiance at each depth determined from combining underwater measurements taken with a Li-1800UW spectroradiometer and incident irradiance at the sea surface measured on deck at 1 min intervals with a LI-190SA sensor. A 24 h average \( E_{PUR}(z) \) was considered to remove from PP estimates the short time variability caused by clouds. Therefore \( D = 24 \) h. For more details see Figueiras et al. (1999).

The production rate of heterotrophic bacteria (BHP) (assumed to include activities of bacteria and archaea) was estimated by the radioactive ³H-leucine incorporation method (Kirchman 1993) in 1.2 ml samples incubated in Eppendorf vials (Smith & Azam 1992). Forty nM leucine was added to 4 vials and 2 TCA-killed samples were used as controls. This leucine concentration was found to be saturating in previous concentration-dependent incorporation experiments performed in these waters. The Eppendorf vials were incubated in the dark at temperatures within ±0.5°C of \textit{in situ} temperature; the incubations lasted from 2 to 5 h in accordance with results of linearity experiments. After incubation, the samples were precipitated with 50% TCA. On board, we processed the samples by centrifugation and counted the incorporated radioactivity with a Beckman scintillation counter.

Leucine incorporation rates were converted to carbon production rates by empirical conversion factors. Seawater cultures were established from around 20 l of seawater that were filtered using a peristaltic pump. GF/A- and GF/F-filtered seawater was generated, mixed in equal parts, and dispensed into 2 l bottles. The bottles were incubated in the dark for 8 to 10 d at nearly \textit{in situ} temperature in duplicate bottles. Prokaryote counts were done daily by flow cytometry. Subsamples of 1.2 ml were fixed with 1% paraformaldehyde + 0.05% glutaraldehyde (final concentrations) and left in the dark for 10 min prior to transfer to liquid nitrogen. They were subsequently transferred to a freezer (–70°C). Back in the laboratory, samples were unfrozen, stained for 10 min with 2.5 µM Syto13 (Molecular Probes) and run through a FACScanibur flow cytometer (Becton & Dickinson), with a laser emitting at 488 nm. Samples were run at low speed (approximately 22 µl min⁻¹) until 10000 events were acquired in log mode. We added 10 µl per sample of a 10⁶ ml⁻¹ suspension of yellow-green 0.92 µm-diameter Polysciences latex beads as an internal standard. Prokaryotes were detected by their signature in a plot of side-scatter (SSC) versus green fluorescence (FL1), as described by Gasol & del Giorgio (2000). The relationship between yellow fluorescence and bacterial size presented in Gasol & del Giorgio’s study was used to derive bacterial biomass from abundance data; we used the integrative method (Riemann et al. 1987), comparing total biomass produced and total leucine incorporated to derive the leucine conversion factors. These factors ranged between 1.5 and 2.6 kg C mol⁻¹ leu.

**RESULTS AND DISCUSSION**

**Contrasting hydrographic regions occupied during Cruise HE052**

The \textit{quasi}-meridional line from Stns 1 to 32 covered 5 contrasting hydrographic regions (Fig. 1), distinguishable by their distinct thermohaline parameters: the ice edge (IE; Stn 1), the Weddell Zone (WZ; Stns 3–12), the Antarctic Zone (AZ; Stns 14–20), the
The IE, sampled in more detail at Stn 47, displayed surface temperature and salinity values around –1°C and 34.1 respectively (Figs 2a, b & 3a), slightly modified by ice-melting compared with the waters below. Ice-melting contributes chl a and organic matter produced within the ice (Smith & Nelson 1986, Melnikov 1998) and increases water-column stratification, favouring accumulation of materials and enhancing photosynthetic activity (Sullivan et al. 1988, Murphy et al. 1998). A maximum chl a (>3 mg m⁻³) was recorded in the upper mixed layer (Figs 2c & 3b). The pycnocline was at about 50 m and the stability of the surface layer, essentially maintained by haline stratification (χ = 0.7), ranged from 0.2 to 0.4 min⁻² (Fig. 2d). 

Eastward-flowing Weddell Sea waters from the northern limb of the cyclonic Weddell gyre and continental waters from the Weddell Sea mix in the WZ. These waters are characterised by relatively low temperature (<0°C) and high salinity (>34.1) (Fig. 2a, b). The WZ was the least stratified of all the hydrographic regions studied: average $N^2$ at the pycnocline was only 0.13 min⁻² (Fig. 2d). This is due to vigorous vertical mixing (Gordon et al. 1977) and enhanced eastward velocities (García 1996) in this area. A surface chl a maximum (>1 mg m⁻³) was recorded at Stn 11, associated with a brief salinity minimum probably due to continental waters off Elephant Island (Fig. 2c). The surface layer extended to about 100 m and the reduced stability was mainly maintained by the salinity gradient.

The AZ is part of the ACC, which transports Antarctic Surface Water (AASW) from the Pacific Sector of the Southern Ocean across Drake Passage, resulting in a clear-cut difference between the physical characteristics of the IE and WZ. The AZ is characterised by a temperature around 0°C and a salinity of <34.0, with a well-developed temperature minimum embedded in the halocline (Gordon et al. 1977). Water-column stability was relatively high ($N^2$ max. > 0.4 min⁻²; Fig. 2d), a result of the salinity gradient ($\chi > 1$). The pycnocline was at about 100 m. A marked chl a maximum (>1 mg m⁻³) was observed at Stn 14, associated with the well-defined Weddell-Scotia Front (Fig. 2c). The relative stability maximum at Stn 18 (>0.5 min⁻²) was also accompanied by a relative surface chl a maximum (>0.6 mg m⁻³).

The Polar Front (PF), at Stn 22 (58° S), was marked by the northern limit of the 0°C isotherm at 100 m (Fig. 2a) in agreement with Nowlin et al. (1977). The PFZ, a region of transition between AASW and Subantarctic Surface Water (SASW), was characterised by a dramatic latitudinal gradient of temperature (from 1 to 5°C) in the upper 400 m (Fig. 2a). Stratification was relatively weak (average $N^2$ max. = 0.19 min⁻²), evolving from haline ($\chi > 0.8$) to thermal control ($\chi < 0.1$) across the temperature gradient. The upper mixed layer of the PFZ was the deepest (average 133 m) and showed the lowest chl a levels (<0.5 mg m⁻³) of all the hydrographic regions studied.
In the northernmost side of the transect, where temperatures of 5 to 6°C and salinities around 34.0 were observed in the upper 100 m (Fig. 2a,b), the Subantarctic Front was crossed to enter the SAZ (Peterson & Stramma 1991). This zone presented the highest chlₐ levels within Drake Passage (>1.5 mg m⁻³; Fig. 2c). The pycnocline rose to <80 m and the stability of the upper mixed layer increased to 0.30 min⁻², mainly due to the vertical temperature gradient (χ < 0.3; Fig. 2d).

The Gerlache Strait was the sixth study region. The western (Stn 49) and eastern (Stn 58) ends were occupied (Fig. 1), and showed some differences in their temperature and salinity profiles; the surface layer of the western end was slightly cooler and fresher (Fig. 3c,e). Waters from the Bellingshausen and Weddell Seas, modified by the local glaciers, characterised this region (Niiler et al. 1991). The pycnocline was very shallow (from 20 to 50 m), and stratification high (N² max. > 0.7 min⁻²) and controlled by the salinity gradient (χ > 0.9). Average chlₐ levels in the surface layer of Stns 49 and 58 were as high as 5 and 12 mg m⁻³ respectively (Fig. 3d,f).

POC/chlₐ relationships: assessing quality of suspended materials

The POC distributions resembled the chlₐ variability both in the Gerlache Strait (Fig. 3d,f) and along the quasi-meridional hydrographic line from the ice edge to the Subantarctic Zone (Figs 2c & 4a). In general, a POC maximum accompanied each local chlₐ maximum in the upper mixed layer, except for the POC maximum at Stns 24 to 26 in the PFZ which displayed no distinct chlₐ signal.

The linear correlation between POC and chlₐ over the upper 100 m (chlₐ sampling range) for the whole data set (n = 155) was very high (r = 0.92). However, to minimise the effect of water-mass mixing on the covariance between POC and chlₐ, an individual correlation analysis was performed for each hydrographic region (Table 1). The high correlation coefficients indicate a similar origin and fate for both parameters, i.e. that a substantial part of the suspended materials accumulated in the upper mixed layer are the products of synthesis and early degradation of phytoplankton primary production (e.g. Anderson 1995).

The contrasting coefficients (y-intercept, slope) of the linear regressions (Model II; Sokal & Rohlf 1995) computed for the 6 study regions are also presented in Table 1. The POC/chlₐ slopes of the linear regressions varied between 28 ± 3 g C g⁻¹ chlₐ in the Gerlache Strait (maximal average chlₐ in the upper mixed layer) and 113 ± 15 g C g⁻¹ chlₐ in the PFZ (minimum average chlₐ). Despite the possible interference of micro-
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heterotrophs and detritus, the POC/chl $a$ slope has traditionally been considered to provide a good estimate of the phytoplankton POC/chl $a$ ratio (Banse 1974, 1977, Eppley et al. 1977, Nelson et al. 1989). These slopes were within the wide range of POC/chl $a$ ratios reported for Antarctic waters (between 11 and 416 g C g$^{-1}$ chl $a$: El Sayed & Taguchi 1981, Palmisano et al. 1985). There was a clear inverse relationship between the average chl $a$ concentration in the upper mixed layer and the POC/chl $a$ slope. This could be due to an exponential increase in efficiency of POC production, in addition to the higher heterotrophic relative to autotrophic biomass (Gasol et al. 1997) and the higher proportion of detritus (Verity et al. 1996) in regions with lower chl $a$. Since POC and chl $a$ correlate quite well in the various hydrographic regions (Table 1), we can roughly estimate the fraction of the POC pool which covaries with chl $a$ by multiplying the slope of the corresponding regression by the average integrated chl $a$. This will be what we call the ‘bioreactive fraction of POC’ (POCB), which is susceptible to (but does not necessarily undergo) degradation. Our results (Table 1) indicate that >75% of the POC pool in the Atlantic Sector of the Southern Ocean is POCB, exceeding 80% in the chl $a$ rich IE and Gerlache Strait regions.

POC and PON were extremely well related throughout the upper 250 m (POM sampling range); the linear correlation for all samples was high ($r = 0.99$) and the C/N slope of the linear regression (Model II) was $6.0 \pm 0.1$ mol C mol N$^{-1}$. The latitudinal evolution of the POC/PON ratio was characterised by values of ~5.9 mol C mol N$^{-1}$ in the Gerlache Strait, ~6.1 mol C mol N$^{-1}$ throughout the Weddell Sea, and a clear increasing trend in the ACC from 5.9 mol C mol N$^{-1}$ at the WSF to 6.7 mol C mol N$^{-1}$ in the SAZ (Fig. 4b). Therefore, all stations showed average C/N ratios below the Redfield value of 6.7 (Anderson 1995). Nitrogen-rich materials have been traditionally considered as potentially available to organisms (Eppley et al. 1977, Copin-Montégut & Copin-Montégut 1983). These C/N ratios are typical of net autotrophic systems (Holm-Hansen et al. 1989, Nelson et al. 1989), as also suggested by the elevated percentages of POCB (Table 1).

DOC/POC relationships. Refractory versus potentially bioreactive fractions of DOC in upper ocean waters

POC (Fig. 4a) and DOC (Fig. 5) distributions were remarkably parallel throughout the upper 250 m ($r = 0.76$, $n = 90$). Maximum DOC values were observed in the upper mixed layer, with average concentrations ranging from ~47 µM C in the WZ to ~55 µM C in the SAZ.

Table 1. Chlorophyll $a$ (chl $a$)-POC relationships in the 6 regions occupied during Cruise HE052. Average integrated POC and chl $a$ concentrations in the upper mixed layer, slope and $y$-intercept of the POC/chl $a$ linear regressions (Model II: Sokal & Rohlf 1995), correlation coefficient ($r$) and average percentage of POC covarying with chl $a$ (% POC$_b$). IE: ice edge; WZ: Weddell Zone; AZ: Antarctic Zone; PFZ: Polar Front Zone; SAZ: Subantarctic Zone. POC$_b$ = bioreactive POC (= slope $\times$ chl $a$); % POC$_b$ = POC$_b$/POC.

<table>
<thead>
<tr>
<th>Region</th>
<th>POC (µM C)</th>
<th>Chl $a$ (mg m$^{-3}$)</th>
<th>Slope (g C g$^{-1}$ chl $a$)</th>
<th>$y$-intercept (µM C)</th>
<th>$r$</th>
<th>POC$_b$ (µM C)</th>
<th>% POC$_b$</th>
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<tr>
<td>IE</td>
<td>8.0</td>
<td>1.7</td>
<td>47 ± 4</td>
<td>1.4 ± 0.6</td>
<td>0.91</td>
<td>6.5</td>
<td>81</td>
</tr>
<tr>
<td>Gerlache</td>
<td>14.1</td>
<td>5.1</td>
<td>28 ± 2</td>
<td>2.1 ± 1.0</td>
<td>0.88</td>
<td>11.8</td>
<td>83</td>
</tr>
<tr>
<td>WZ</td>
<td>3.4</td>
<td>0.5</td>
<td>62 ± 4</td>
<td>1.0 ± 0.2</td>
<td>0.94</td>
<td>2.5</td>
<td>74</td>
</tr>
<tr>
<td>AZ</td>
<td>4.9</td>
<td>0.6</td>
<td>75 ± 8</td>
<td>1.3 ± 0.4</td>
<td>0.87</td>
<td>3.7</td>
<td>76</td>
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<tr>
<td>PFZ</td>
<td>4.8</td>
<td>0.4</td>
<td>113 ± 15</td>
<td>1.2 ± 0.5</td>
<td>0.82</td>
<td>3.7</td>
<td>77</td>
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<tr>
<td>SAZ</td>
<td>7.9</td>
<td>1.3</td>
<td>55 ± 8</td>
<td>1.8 ± 0.7</td>
<td>0.90</td>
<td>6.0</td>
<td>76</td>
</tr>
</tbody>
</table>

Fig. 4. Distribution of POC (a) and POC/PON (mol C/mol N) (b) in study area. Black dots in (a) represent sampling depths, numbers in (b) stations. Note that upper 100 m are expanded (×2) compared to the 100 to 250 m depth range.
These DOC levels were within the range found in other recent studies of ACC surface waters: 38 to 55 µM C in the Atlantic sector (Kähler et al. 1997), 52 to 63 µM C in the Indian sector (Wiebinga & de Baar 1998), 45 to 55 µM C in the Australian sector (Ogawa et al. 1999), and 45 to 63 µM C in the Pacific sector of the Southern Ocean (Doval & Hansell 2000). Local DOC maxima have also been found in association with ice-melting areas (Kähler et al. 1997) and with the thermohaline fronts (PF, SAF) of the ACC (Wiebinga & de Baar 1998, Doval & Hansell 2000).

The most striking feature of the DOC distribution in the 100 to 500 m depth range is a significant increase in the concentration to the north of the PF: from <45 to >48 µM C. An equivalent raise was observed in the POC distributions also (Fig. 4a). Finally, DOC in deeper waters (>1000 m) was constant at 44 ± 1 µM C (data not shown). This ‘baseline’ or ‘refractory’ DOC concentration is not significantly different from the most recent deep-sea DOC values reported for the Southern Ocean (Kähler et al. 1997, Carlson et al. 1998, Wiebinga & de Baar 1998, Ogawa et al. 1999, Doval & Hansell 2000).

Table 2. TOC/POCb relationship in the 6 regions occupied during Cruise ’HE052’. Average integrated TOC, DOC and POCB in the upper mixed layer, slope of the TOC/POCb linear regressions (Model II: Sokal & Rohlf 1995) correlation coefficient (r), average bioreactive TOC (TOC\textsubscript{B}), average percentage of bioreactive TOC in the TOC pool (% TOC\textsubscript{B}), average percentage of bioreactive DOC in the TOC pool (% DOCB/TOC\textsubscript{B}) and average percentage of bioreactive DOC in the DOC pool (% DOCB) are shown. TOC\textsubscript{B} = slope \times \text{POC}_{\text{B}}, % \text{TOC}_{\text{B}} = \text{TOC}_{\text{B}}/\text{TOC}; % \text{DOC}_{\text{B}} = \text{DOC}_{\text{B}}/\text{DOC}. Region abbreviations as in Table 1.

<table>
<thead>
<tr>
<th>Region</th>
<th>TOC (µM)</th>
<th>DOC (µM)</th>
<th>POC\textsubscript{B} (µM)</th>
<th>Slope</th>
<th>r</th>
<th>TOC\textsubscript{B} (µM)</th>
<th>% TOC\textsubscript{B}</th>
<th>% DOCB/TOC\textsubscript{B}</th>
<th>% DOCB</th>
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<td>IE</td>
<td>61</td>
<td>53</td>
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<td>2.3 ± 0.3</td>
<td>0.89</td>
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<td>52</td>
<td>11.7</td>
<td>1.7 ± 0.1</td>
<td>0.96</td>
<td>20</td>
<td>30</td>
<td>42</td>
<td>16</td>
</tr>
<tr>
<td>WZ</td>
<td>50</td>
<td>47</td>
<td>2.6</td>
<td>2.9 ± 0.3</td>
<td>0.90</td>
<td>8</td>
<td>15</td>
<td>66</td>
<td>11</td>
</tr>
<tr>
<td>AZ</td>
<td>54</td>
<td>49</td>
<td>3.8</td>
<td>2.9 ± 0.3</td>
<td>0.91</td>
<td>11</td>
<td>20</td>
<td>65</td>
<td>15</td>
</tr>
<tr>
<td>PFZ</td>
<td>53</td>
<td>50</td>
<td>3.6</td>
<td>2.8 ± 0.3</td>
<td>0.89</td>
<td>10</td>
<td>20</td>
<td>65</td>
<td>13</td>
</tr>
<tr>
<td>SAZ</td>
<td>63</td>
<td>55</td>
<td>6.0</td>
<td>3.1 ± 0.3</td>
<td>0.97</td>
<td>18</td>
<td>29</td>
<td>68</td>
<td>22</td>
</tr>
</tbody>
</table>
of the Weddell Sea and Drake Passage (34% POCB, 66% DOCB).

Table 2 also shows that the contribution of DOCB to the TOCB pool tends to increase as the POCB pool decreases, i.e. as chl a levels decline. Therefore, it suggests that TOCB tends to accumulate in dissolved form in regions with reduced phytoplankton biomass, where the POC/chl a ratio is higher and the POCB/POC ratio is lower (Table 1). In this context, it has commonly been observed that POC represents a major fraction of the accumulated materials in surface waters of high chl a regions: 50 to 60% in the Iberian upwelling system (Álvarez-Salgado et al. 1999) and up to 89% during the spring bloom in the Ross Sea (Carlson et al. 1988). In contrast, POC represents <25% of the accumulated organic carbon in the low chl a oligotrophic Mediterranean Sea (Copin-Montégut & Avril 1993, Doval et al. 1999).

TOCB in the study regions was estimated by multiplying the TOC/POCB slope and the corresponding average integrated POCB concentration (Table 2). TOCB concentration was maximum in the Gerlache Strait (20 µM C) and SAZ (18 µM C), where it represented ~30% of the measured TOC. It was also relatively high at the ice edge and decreased in the other study zones. It was minimum in the WZ, with 8 µM C and only 15% of TOC. For comparison: TOCB amounted to 20 and 30% of the organic matter accumulated in the Bransfield and Gerlache Straits respectively during the austral summer of 1995 to 1996 (Doval et al. 2002), and Carlson et al. (1998) reported 15% for the Ross Sea. On the other hand, DOCB (7 ± 2 µM C) represented 15% of the total DOC pool in the upper mixed layer, ranging from 11% in the WZ to 22% in the SAZ. This decrease in DOCB indicates a low accumulation of DOC in the study area, and is in agreement with the most recent studies of DOM in the Southern Ocean (Kähler et al. 1997, Carlson et al. 1998, Ogawa et al. 1999, Doval & Hansell 2000).

**Primary versus bacterial production rates: assessing renewal times of TOCB**

Table 3 summarises the latitudinal evolution of primary production rates (PP), which were maximum in the highly productive IE and Gerlache Strait zones because of their substantial accumulation of chl a (Figs 2c & 3b,d,f) in a relatively shallow upper mixed layer (Fig. 2b). A combination of high chl a and $E_{PUR}$ values produced high PP rates (Eq. 3). This is also the reason behind the relatively high PP (~1.0 g C m$^{-2}$ d$^{-1}$) recorded for the SAZ. PP decreased in open-ocean waters to a minimum of <0.5 g C m$^{-2}$ d$^{-1}$ in the PFZ, mainly due to low chl a values found in a deep (100 to 170 m) upper mixed layer. These rates are in agree-

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**Table 3.** Integrated area-average chlorophyll a (chl a), integrated POCB, TOCB, primary production (PP), bacterial heterotrophic production (BHP), bacterial carbon demand (BCD) assuming a bacterial gross growth efficiency, BGE, of 20%, renewal times of TOCB, $\tau_{20}$ (with BGE of 20%) and $\tau_{10-40}$ (BGE of 10 to 40%), and DOCB/BCD (assuming BGE of 20%) in the upper mixed layer (UML) of the 6 study regions during Cruise ‘HE052’ are shown. $\tau = \text{TOCB/(PP-BCD)}$. Region abbreviations as in Table 1

<table>
<thead>
<tr>
<th>Region</th>
<th>UML (m)</th>
<th>Chl a (mg m$^{-3}$)</th>
<th>POCB (g C m$^{-2}$)</th>
<th>TOCB (g C m$^{-2}$)</th>
<th>PP (g C m$^{-2}$ d$^{-1}$)</th>
<th>BHP (g C m$^{-2}$ d$^{-1}$)</th>
<th>BCD (g C m$^{-2}$ d$^{-1}$)</th>
<th>$\tau_{20}$ (d)</th>
<th>$\tau_{10-40}$ (d)</th>
<th>DOCB/BCD (wk)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IE</td>
<td>55</td>
<td>1.7</td>
<td>4.31</td>
<td>9.87</td>
<td>1.66</td>
<td>0.024</td>
<td>0.120</td>
<td>6</td>
<td>7–6</td>
<td>6</td>
</tr>
<tr>
<td>Gerlache</td>
<td>49</td>
<td>5.1</td>
<td>7.01</td>
<td>12.28</td>
<td>2.05</td>
<td>0.029</td>
<td>0.144</td>
<td>6</td>
<td>7–6</td>
<td>5</td>
</tr>
<tr>
<td>WZ</td>
<td>94</td>
<td>0.5</td>
<td>2.67</td>
<td>7.84</td>
<td>0.69</td>
<td>0.017</td>
<td>0.084</td>
<td>13</td>
<td>15–12</td>
<td>9</td>
</tr>
<tr>
<td>AZ</td>
<td>104</td>
<td>0.6</td>
<td>4.44</td>
<td>12.71</td>
<td>0.91</td>
<td>0.018</td>
<td>0.092</td>
<td>15</td>
<td>17–15</td>
<td>13</td>
</tr>
<tr>
<td>PFZ</td>
<td>133</td>
<td>0.4</td>
<td>5.65</td>
<td>15.65</td>
<td>0.49</td>
<td>0.017</td>
<td>0.087</td>
<td>39</td>
<td>49–35</td>
<td>16</td>
</tr>
<tr>
<td>SAZ</td>
<td>78</td>
<td>1.3</td>
<td>5.39</td>
<td>16.76</td>
<td>1.15</td>
<td>0.025</td>
<td>0.214</td>
<td>16</td>
<td>19–15</td>
<td>8</td>
</tr>
</tbody>
</table>
ment with those found in most studies in the area (Bracher et al. 1999 and references there in, Figueiras et al. 1999, Park et al. 1999). Bacterial production rates (BHP: Table 3) showed the same latitudinal trend as PP rates, representing <4% of PP in all the study regions. BHP/PP ratios ranging between 0.01 and 0.10 have been recently found in the high-latitude areas of the central Arctic Sea (Rich et al. 1997) and the Ross Sea (Carlson et al. 1998). A low BHP/PP ratio (preliminary index for organic carbon processes by marine bacterio-
plankton) points to the likely accumulation of products of phytoplankton photosynthesis.

A rough estimate of the renewal time ($\tau$) of TOC$_B$ in the upper mixed layer can be calculated by:

$$\tau = \frac{POC_B + DOC_B}{PP - BCD} = \frac{POC_B + DOC_B}{BHP - 0.20}$$

(5)

where the bacterial carbon demand (BCD), i.e. the carbon that flows through bacteriaplankton, has been calculated assuming an average bacterial growth efficiency (BGE) of 20% ($\tau_{50}$: Table 3). This lies between the values of 14 and 12 to 38% (Carlson et al. 1998, 1999) and 23 to 30% (Kähler et al. 1997) reported for Antarctic waters, and is very close to the median ocean estimate of 22% (del Giorgio & Cole 1998). The photosynthetic parameters for calculating the daily PP rates are obtained from short $^{14}$C incubations (2 h), so respi-
ration of photo-assimilated $^{14}$C during this short period can be considered negligible (e.g. Williams 1993, Joint et al. 2002). PP roughly represents the gross PP of organic matter, and is the prime source of both POC$_B$ and DOC$_B$ in the upper mixed layer. On the other hand, BCD is the prime sink of DOC$_B$ enabling the bal-
cancing of TOC$_B$ sources and sinks in the upper mixed layer. Since both PP and BHP rate estimates are repre-
sentative for a period of <24 h, sedimentation and hor-
izontal advection are not sinks relevant for consider-
ation in Eq. (4). Therefore, it should be kept in mind that $\tau$ represents the time required to renew the TOC$_B$ pool if the initial conditions of negligible sedimentation and advection are maintained.

Renewal time, $\tau$, was only 1 wk in the highly produc-
tive waters of the IE and the Gerlache Strait, increasing to 2 wk in open-ocean waters of the Weddell Sea and Drake Passage. The PFZ was an exception ($\tau > 5$ wk), because of the combination of a great excess of bio-
active materials in the >100 m upper mixed layer (average 15.7 g C m$^{-2}$) and a very low PP rate (average <0.5 g C m$^{-2}$ d$^{-1}$). The interpretation of our results does not essentially alter when considering a broad range of BGE numbers, from 10 to 40% ($\tau_{10-40}$: Table 3). In the same way, underestimation of PP by 10 and 20% because of the exudation of $^{14}$C during PP incubations; (e.g. Carlson et al. 1998) and overestimation by 0 to 10% due to phytoplankton respiration does not result in significant differences in the estimated $\tau$ values. The whole range of parameters considered produces an error in the $\tau_{50}$ index of between 10 and 25% across the various study regions. The current literature considers as ‘labile’ organic material with turnover times of <10 d (e.g. Kirchman et al. 1991, Normann et al. 1995).

As suggested by the low BHP/PP ratio, the short TOC$_B$ renewal times resulted from the combination of relatively high PP rates and reduced bacterial activity. This suggests a ‘malfunctioning’ of the microbial loop not related to the availability of (1) inorganic macronu-
trients, which are in excess (Levitus et al. 1993) and in forms utilisable by bacteria (Kirchman 2000), or (2) organic carbon (TOC$_B$). The low temperatures of Antarctic waters (Pomeroy & Deibe 1986) (specifically temperature inhibition of the initial steps of POM degradation processes: Lancelot et al. 1989), micro-
zooplankton grazing on bacteria (Bird & Karl 1999) and/or the possible lag time between PP and BHP peaks (Lancelot et al. 1989, Karl et al. 1996) are the most probable reasons for the accumulation of DOC. Iron limitation of bacterial growth also cannot be ruled out (Pakulski et al. 1996). The DOC$_B$/BCD ratio (Table 3), representing the time that heterotrophic bacteria require to process the bioactive DOC in the upper mixed layer, ranges from 5 wk in the Gerlache Strait to 16 wk in the PFZ, assuming an average BGE of 20%. Borsheim (2000) calculated the DOC$_B$/BCD ratio for the Greenland Sea in the Arctic to range from 1 to 13 wk, similar to the range that we calculated for the Antarctic.

**Conclusions**

The correlation between chlorophyll $a$ and dissolved and suspended organic carbon pools across contrast-
ing coastal, ice edge and open-ocean waters of the Atlantic Sector of the Southern Ocean suggests that a considerable fraction (15 to 30%) of the organic carbon in the upper mixed layer consists of the products of synthesis and early degradation of marine primary production. Maximum fractions of these potentially bioactive materials are present in the highly produc-
tive coastal, ice edge and subantarctic regions. A rough calculation of their renewal times (usually ≤2 wk) can be made from measured primary and bacterial production rates. Reduced bacterial activity seems to be related to mechanisms other than sub-
strate (nutrients, organic matter) limitation. The contribu-
tion of DOC to the organic matter accumulated in the upper mixed layer increased from the chl $a$-rich coastal and ice edge regions to the chl $a$-poor open-
cean waters.
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LITERATURE CITED


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