Uncoupled distributions of transparent exopolymer particles (TEP) and dissolved carbohydrates in the Southern Ocean

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A B S T R A C T

Transparent exopolymer particles (TEP) are formed by the assembly of dissolved precursors, mainly monosaccharides (DMCHO and DPCHO) that are released by microorganisms. Although TEP formation plays a significant role in carbon export to deep waters and can affect gas exchange at the sea surface, simultaneous measurements of TEP and their precursors in natural waters have been scanty reported. In this study, we described the spatial (vertical and regional) distribution of TEP, DMCHO and DPCHO in a region located around the Antarctic Peninsula, assessed their contribution to the total organic carbon pool, and explored their relationships with phytoplankton (with chlorophyll a (chl a) as a proxy) and bacteria. TEP concentration ranged from undetectable values to 48.9 µg XG eq L−1 with a mean value of 15.4 µg XG eq L−1 (11.6 µg TEP-C L−1). DMCHO and DPCHO showed average values of 4.3 µmol C L−1 and 8.6 µmol C L−1, respectively. We did not find simple relationships between the concentrations of TEP and dissolved carbohydrates, but a negative correlation between DMCHO and DPCHO was observed. Chl a was the best regressor of TEP concentration in waters within the upper mixed layer, while bacterial production was the best regressor of TEP concentration below the mixed layer, underlining the direct link between these particles and bacterial activity in deep waters.

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1. Introduction

Transparent exopolymer particles (TEP) are large, sticky particles, formed by acidic polysaccharides, and stainable with Alcian Blue (Alldredge et al., 1993). They are predominantly formed by self-assembly of dissolved precursors, mostly dissolved polysaccharides released by microorganisms (Passow, 2000; Passow and Alldredge, 1994). TEP are significant, in one hand, as components of the sedimentary flux in marine ecosystems as they represent an interstitial matrix in coagulation processes to form marine snow, a sedimentary flume (Azetsu-Scott and Passow, 2004; Mari, 2008). The TEP content in marine aggregates and their conformation, added to other environmental variables, determine their ultimate fate in the water column (sinking vs. floating), with consequences for carbon cycling.

Traditionally, phytoplankton cells have been considered as the major source of TEP and precursors in marine ecosystems (Passow, 2002a; Passow and Alldredge, 1994). Particularly, exponentially-growing diatoms can excrete significant amounts of precursors (Alldredge et al., 1993; Passow, 2002a) or TEP directly via sloughing and lysis of senescent colonies (Hong et al., 1997). Other organisms, such as macroalgae (Ramaiah et al., 2001; Thornton, 2004), or zooplankton (Passow and Alldredge, 1999; Prieto et al., 2001) have also been reported as secondary sources of TEP. However, the interaction between bacterioplankton and TEP remains poorly explored and appears to be more complex than hitherto thought. The abiotic polymerization of dissolved precursors and the subsequent sedimentation of TEP could represent a loss of dissolved organic carbon from the euphotic zone (Engel, 2004). In contrast, bacteria can promote TEP formation through several processes, such as the release of bacterial capsular material (Radic et al., 2006; Stoderegger and Herndl, 1998; Stoderegger and Herndl, 1999); induction of self-coagulation of precursors enhancing collisions due to bacterial motility (Johnson and Kepkay, 1992; Sugimoto et al., 2007); and/or acting as nuclei attracting negatively charged polysaccharides (Van Loosdrecht et al., 1989).

Most studies on TEP have described their formation and dynamics either under experimental conditions (Passow, 2000; Passow, 2002a; Sugimoto et al., 2007) or during phytoplankton blooms (Hong et al.,...
1997; Huertas et al., 2005; Ramaiah et al., 2001). However, the published studies describing simultaneously TEP and dissolved polysaccharides in the field are particularly scarce (Bhaskar and Bhosle, 2006; Hung et al., 2003a). In particular, in the Southern Ocean (Corzo et al., 2005; Passow et al., 1995), where sedimentary carbon fluxes affect the air–sea exchange of CO₂ on a global scale (Marinov et al., 2006) little is known about TEP distribution.

In this study, we described the distribution of TEP and dissolved carbohydrates (DMCHO and DPCHO) along a region located around the Antarctic Peninsula (Southern Ocean), explored the link between these pools in the field, and evaluated the significance of phytoplankton and bacteria as drivers of TEP and dissolved carbohydrate distributions.

2. Methods

2.1. Sampling

Sampling was carried out around the Antarctic Peninsula (Southern Ocean) during the ICEPOS 2005 cruise aboard R/V Hespérides in February 2005. We selected 18 sampling stations and 5–6 depths, from surface to below fluorescence-maximum-depth waters (coincident with deep chlorophyll maxima, generally 100–200 m), from Eastern Bellingshausen Sea (station nos. 1 to 7) to Western Weddell Sea (station nos. 8 to 11) including Bransfield and Gerlache straits (station nos. 12 to 18) (Fig. 1). Seawater was collected using a Sea Bird rosette sampler (24 Niskin bottles, 12 L each) attached to a conductivity–temperature–depth (CTD) system. The mixed layer depth (MLD) was estimated considering a gradient of temperature higher than 0.1 °C m⁻¹ after visualizing vertical temperature profiles obtained with the CTD system.

2.2. Chemical and biological analyses

Samples for dissolved mono- (DMCHO) and polysaccharides (DPCHO) were filtered through pre-combusted glass-fiber filters (Whatman GF/F) and stored in sterile polypropylene flasks at −80 °C until analysis. DMCHO and DPCHO were analyzed following the ferricyanide reaction before (DMCHO) or after hydrolysis (DPCHO) by oxidation of the free reduced sugars (Myllestad et al., 1997). Reagents were calibrated using a standard curve made of d-glucose, and triplicate reagent blanks in MilliQ water were subtracted daily. The detection limit of the method was 0.4 µmol C L⁻¹, and the coefficient of variation between samples was 7%.

Samples for dissolved organic carbon (DOC) analyses were collected after filtration through pre-combusted Whatman GF/F filters into pre-combusted 10 mL glass ampoules, acidified with phosphoric acid (final pH ~2), sealed and stored at 4 °C until analysis. DOC was analysed by High-Temperature Catalytic Oxidation on a Shimadzu TOC-5000A. Standards of 44–45 µmol C L⁻¹ and 2 µmol C L⁻¹, provided by D.A. Hansell and Wennhao Chen (Univ. of Miami), were used to assess the accuracy of the measurements.

TEP concentration was determined colorimetrically following Passow and Allredge (1995). Unfiltered seawater samples (250 mL) were fixed with formalin (1% final concentration) and stored in dark conditions until analysis. The fixation with formalin does not interfere with the stained procedure (Passow et al., 1995). Then, samples were filtered onto 0.4 µm polycarbonate filters (Isopore), stained with Alcian Blue solution, soaked in 80% sulphuric acid for 3 h and measured spectrophotometrically at 787 nm, using empty, stained filters as blanks. Alcian Blue absorption was calibrated using a xantan gum solution (SIGMA) that was processed by tissue grinder and measured by weight. Despite the use of xantan gum solution as TEP calibration standard appears to yield high variability in TEP determinations (Hung et al., 2003a), it was selected for comparative reasons, in particular with previous work in the Southern Ocean. TEP concentration was therefore expressed in µg Gum Xanthan (XG) equivalents per litre and in carbon units using the conversion factor of 20 fgC cell⁻¹ proposed by Banse (1977).

Subsamples of 50 ml were filtered through Whatman GF/F filters for fluorometric analysis of Chl a concentration (Parsons et al., 1984). Phytoplankton carbon content was estimated from Chl a concentration using a conversion factor of 40 µgC µg Chl a⁻¹ proposed by Banse (1977).

Bacterial production (BP) was measured through the incorporation of ³H-leucine using the microcentrifugation technique proposed by Smith and Azam (1992).

Bacterial Abundance (BA) was determined by flow cytometry (Del Giorgio et al., 1996; Gasol and Del Giorgo, 2000). More details on the procedure can be found elsewhere (Ortega- Retuerta et al., 2008). Bacterial abundance was converted into carbon units using the conversion factor of 20 fgC cell⁻¹ (Lee and Fuhrman, 1987).

2.3. Statistical analyses

To explore the potential controlling factors on TEP distributions, we tested the relationship between TEP, precursors, bacterial abundance and production and chl a concentration using regression and correlation analyses. We considered either all data together or separated in two depth layers, within and below the mixed layer. Data were log-transformed when necessary to comply with the assumptions of regression analyses.

3. Results

The three sampled areas showed distinctive physical properties. The stations located in the Bellingshausen Sea were characterized by relatively high temperatures within the upper MLD (mean value 1.27 °C) and low salinity (mean value 33.5 PSU), and shallow mixed layers (from 20 to 50 m). By contrast, the stations located in the Antarctic Strait and Weddell Sea, areas surrounded by ice platelets, showed lower temperatures (mean value −0.70 °C), higher salinity (mean value 34.2 PSU) and mixed vertical profiles. The stations located in the Bransfield strait were more variable, with a mean temperature of 1.41 °C and salinity of 33.9 PSU, and vertical profiles...
ranging from homogenous (stations 13 and 15, located in coastal areas) to deep mixed layers (from 70 to 100 m).

Chl \(a\) concentration ranged from 0.01 µg L\(^{-1}\) to 5.36 µg L\(^{-1}\), with the lowest concentration in the Bellingshausen Sea and the highest concentration in the Weddell Sea. Phytoplankton C showed an average value of 61.9 µg C L\(^{-1}\). BA ranged from 0.6 to 17.6×10\(^5\) cells mL\(^{-1}\) (equivalent to 1.1 µg C L\(^{-1}\) to 35 µg C L\(^{-1}\)) and BP ranged three orders of magnitude from 0.2 to 183.8 ng C L\(^{-1}\) h\(^{-1}\).

DMCHO concentration ranged from undetectable to 12.6 µmol C L\(^{-1}\) (mean 4.3 µmol C L\(^{-1}\)), and DPCHO ranged from undetectable to 21.0 µmol C L\(^{-1}\), with an average concentration of 8.6 µmol C L\(^{-1}\) (Table 1). DMCHO concentrations were higher in the Bellingshausen Sea and Bransfield strait than in the Weddell Sea, where a mean value of 2.8 µmol C L\(^{-1}\) was observed. However, DPCHO concentrations did not differ significantly within the different areas. On the other hand, similar average DMCHO concentrations were observed over the upper several 200 m, while the concentration of DPCHO was slightly higher in waters of the upper mixed layer relative to waters below the MLD. The vertical profiles of DMCHO and DPCHO did not show a consistent pattern across the different stations or areas (Fig. 2). DMCHO and DPCHO were negatively correlated (\(r = -0.380, p<0.001, n = 84\), Fig. 3). Together, dissolved carbohydrates (DMCHO + DPCHO) accounted for 23% of the

Table 1
Mean ± standard deviation and ranges of dissolved monosaccharides (DMCHO, µmol C L\(^{-1}\)), dissolved polysaccharides (DPCHO, µmol C L\(^{-1}\)), transparent exopolymer particles (TEP, µg XG eq L\(^{-1}\)), carbon content of TEP (µg TEP-C L\(^{-1}\)), TEP/chl \(a\) (µg XG eq µg chl \(a\) L\(^{-1}\)), TEP/BA (µg XG eq cell\(^{-1}\)) determined in the three geographical areas.

<table>
<thead>
<tr>
<th></th>
<th>All data</th>
<th>Bellingshausen Sea</th>
<th>Weddell Sea</th>
<th>Bransfield Strait</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (ranges)</td>
<td>Mean (ranges)</td>
<td>Mean (ranges)</td>
<td>Mean (ranges)</td>
</tr>
<tr>
<td>DMCHO</td>
<td>4.3±2.8 (bdl–12.6)</td>
<td>4.5±2.7 (bdl–12.3)</td>
<td>2.8±1.9 (bdl–6.9)</td>
<td>4.7±3.1 (bdl–12.6)</td>
</tr>
<tr>
<td>DPCHO</td>
<td>8.6±5.3 (bdl–21.0)</td>
<td>8.8±5.0 (bdl–21.0)</td>
<td>9.5±4.8 (2.0–21.0)</td>
<td>7.9±6.0 (bdl–20.6)</td>
</tr>
<tr>
<td>TEP/C</td>
<td>11.5±7.9 (bdl–36.7)</td>
<td>10.8±7.1 (bdl–25.3)</td>
<td>12.2±9.4 (bdl–36.7)</td>
<td>10.8±7.3 (bdl–25.3)</td>
</tr>
<tr>
<td>TEP/chl (a)</td>
<td>40.9±157.8 (bdl–1402)</td>
<td>84.2±57.5 (bdl–1402)</td>
<td>3.8±7.4 (1.2–28.4)</td>
<td>15.0±10.4 (3.0–18.0)</td>
</tr>
<tr>
<td>TEP/BA</td>
<td>31.3±37.6 (1.0–244.9)</td>
<td>47.4±51.9 (2.5–244.9)</td>
<td>17.5±13.3 (1.0–41.2)</td>
<td>18.4±11.5 (4.5–52.8)</td>
</tr>
</tbody>
</table>

bdl = below detection limit.

Fig. 2. Representative vertical profiles of DMCHO and DPCHO (µmol C L\(^{-1}\)) in deep (left column) and shallow (right column) locations situated in the three geographical areas: the Bellingshausen Sea (station nos. 3 and 7, A–B), the Weddell Sea (station nos. 10 and 8, C–D) and the Bransfield Strait (station nos. 12 and 15, E–F). Note the different depth scales. Horizontal dashed lines in A, B and E represent mixed layer depth. C, D and F represent vertically mixed stations over the sampled depths.
undetectable values to 48.9 µg XG eq L⁻¹ concentrations did not differ significantly between geographical areas studied (Fig. 4A) and over and below the MLD (24% and 20% respectively).

DMCHC and DPCHO concentrations were independent (p > 0.05) of DOC concentration, chl a, BA and BP. In addition, no significant relationships (p > 0.05) between DMCHO and DPCHO, and TEP concentration, were observed (Table 2), neither merging all data nor discriminating between geographical areas or depths.

TEP concentration averaged 15.4 µg XG eq L⁻¹ and ranged from undetectable values to 48.9 µg XG eq L⁻¹ (Table 1). TEP mean concentrations did not differ significantly (p > 0.05) among the different areas (Table 1), but showed their maxima in the deep chlorophyll maximum of Weddell Sea stations (48.9 µg XG eq L⁻¹, station no. 9) and inside Foster Bay in Deception Island (station no. 15, Fig. 5F).

TEP concentrations were generally higher within the upper mixed layer, with a mean value of 17.9 µg XG eq L⁻¹, than below the MLD (8.5 µg XG eq L⁻¹). Vertical profiles generally tracked those of chl a and bacteria, showing a decreasing pattern with depth in the upper mixed layer (11 of 18 stations, Fig. 5A–C), and some exceptional stations with homogeneous profiles or irregular vertical patterns (e.g. station no. 8 in the Antarctic Sound, Fig. 5D, station no. 12 in the Bransfield Strait, Fig. 5E, or station no. 15 in the Deception Island, Fig. 5F). TEP concentration increased slightly in waters below 100 m in 10 of the 18 stations examined (Fig. 5A–C and D).

The highest TEP concentrations were found in the stations with the highest chl a, BP and BA (station no. 9 in the Weddell Sea or station no. 15 at Port Foster in Deception Island), but the highest TEP/chl a, TEP/BA and TEP/BP ratios were located in the Bellingshausen Sea (station nos. 1 to 7) (Fig. 5A). These ratios were also higher below the mixed layer (93.3 µg XG eq µg chl a⁻¹, 4682 µg XG eq µg C h⁻¹ and 0.027 pg XG eq cell⁻¹ respectively) than in the upper layer (10.7 µg XG eq µg chl a⁻¹, 665 µg XG eq µg C h⁻¹ and 0.018 pg XG eq cell⁻¹ respectively). In terms of carbon units, TEP concentrations ranged from 0 to 36.7 µmol C l⁻¹ (Table 1). Unlike the uniformity in the percentage of dissolved carbohydrates to total DOC across geographical areas (Fig. 4A), the percentage of TEP with respect to non-detrital particulate organic carbon (POC) (that is, TEP-C normalized by the sum of TEP-C, phyto-C and bact-C) was particularly higher in the Bellingshausen area than in the two other sites (Fig. 4B).

TEP concentration was significantly related to chl a. The general equation obtained for the TEP-chl a relationship is log₁₀(TEP) = 0.38 log₁₀(chl a) + 1.08 (r² = 0.239, p < 0.001, n = 86). However, this relationship varied considering data over and below the MLD, being stronger within the upper mixed layer, while not significant below the MLD (Table 2). In contrast, significant and positive relationships were found between TEP and BP both within and below the mixed layer (Table 2), and between TEP and BA only within the mixed layer (Table 2). We calculated partial correlation coefficients to explore the relative contribution of each parameter to determine TEP concentration. The results showed that chl a was the best regressor of TEP concentration in waters above the MLD, while BP was the best regressor of TEP concentration below MLD (Table 3).

### 4. Discussion

Previous experimental studies have demonstrated the formation of TEP from acidic polysaccharides (Engel, 2004; Mopper et al., 1995; Passow, 2000). However, this link between TEP and dissolved carbohydrates was not obvious in our study (Table 2). This absence of relationship has been previously reported in field studies (Bhaskar and Bhosle, 2006). It is necessary to consider that the spectrophotometric technique used in this study to determine DMCHO and DPCHO gives bulk measurements of both neutral and acidic dissolved carbohydrates. However, TEP precursors are apparently composed by the more homogenous group of acidic sulfated polysaccharides enriched in deoxy sugars and galactose (Mopper et al., 1995; Zhou et al., 1998). Only under certain conditions where most

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**Table 2**

Results of the regression analyses performed between TEP and different variables (Note all variables were log₁₀ transformed).

<table>
<thead>
<tr>
<th>Dependent Var</th>
<th>Independent Var</th>
<th>Intercept Slope±SE</th>
<th>r²</th>
<th>p level</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEP Over MLD</td>
<td>DTCHO (µmol C l⁻¹)</td>
<td>1.46</td>
<td>−0.28±0.27</td>
<td>0.02</td>
</tr>
<tr>
<td>TEP Over MLD</td>
<td>chl a (µg l⁻¹)</td>
<td>0.98</td>
<td>0.64±0.13</td>
<td>0.27</td>
</tr>
<tr>
<td>TEP Over MLD</td>
<td>BP (µg C l⁻¹ h⁻¹)</td>
<td>0.49</td>
<td>0.43±0.14</td>
<td>0.12</td>
</tr>
<tr>
<td>TEP Over MLD</td>
<td>BA (cell ml⁻¹)</td>
<td>−2.26</td>
<td>0.58±0.22</td>
<td>0.13</td>
</tr>
<tr>
<td>TEP Below MLD</td>
<td>DTCHO (µmol C l⁻¹)</td>
<td>0.64</td>
<td>−0.74±0.56</td>
<td>0.07</td>
</tr>
<tr>
<td>TEP Below MLD</td>
<td>chl a (µg l⁻¹)</td>
<td>0.97</td>
<td>0.18±0.15</td>
<td>0.07</td>
</tr>
<tr>
<td>TEP Below MLD</td>
<td>BP (µg C l⁻¹ h⁻¹)</td>
<td>0.64</td>
<td>0.32±0.10</td>
<td>0.24</td>
</tr>
<tr>
<td>TEP Below MLD</td>
<td>BA (cell ml⁻¹)</td>
<td>−1.08</td>
<td>0.35±0.24</td>
<td>0.08</td>
</tr>
</tbody>
</table>

SE= Standard Error. r²= explained variance. p level = level of significance. ns = not significant.
polysaccharides are TEP precursors, (e.g. under phytoplankton bloom conditions) a significant link between those and TEP may be observed. However, the proportion of TEP precursors within the carbohydrate pool is unknown, but likely variable.

The DMCHO and DPCHO concentrations found in this study are similar to those previously reported for oceanic waters and particularly for Antarctic waters using spectrophotometric techniques (Myklestad et al., 1997; Pakulski and Benner, 1994; Van Oijen et al., 2003; Hung et al., 2003a). However, other studies (Herborg et al., 2001; Kirchmann et al., 2001; Simon and Rosenstock, 2007) have reported lower concentrations in the Ross and Weddell Seas. These lower values have been associated with the use of chromatographic techniques, which generally yield lower concentrations than spectrophotometric methods (Panagiotopoulos and Sempere, 2005). Additionally, we report a significant contribution of carbohydrates to the total DOC pool (23%), higher than the reported in previous studies in the same area (16%, Pakulski and Benner, 1994) but in the range of those published in other areas of the ocean (Hung et al., 2003a).

In this study, we have determined TEP concentration using a standard colorimetric technique (Passow et al., 1995). This is a semi-quantitative technique since the measured concentration of TEP is dependent on factors such as the calibration standard (xantan gum vs alginic acid, Hung et al., 2003a), the composition and structure of extracellular polysaccharides (e.g. sulfated vs. carboxilated, linear vs. branched) or the fixation of samples. Due to all these potential biases, all numerical values of TEP concentrations in natural environments should be taken with caution.

The published literature on dissolved carbohydrate distributions in the ocean have reported variable vertical patterns, from homogeneous concentrations to decreasing concentrations over depth (Pakulski and Benner, 1994; Wang et al., 2006). In this study, we did not find a common vertical pattern for all the stations. However, the negative correlation between DMCHO and DPCHO concentration found in our study is consistent with previous observations (Pakulski and Benner, 1994) and suggests that DMCHO can be derived in part from the degradation of DPCHO.

Table 3
Results of partial coefficients obtained in multiple regression between TEP vs. chl a, bacterial production and bacterial abundance over and below the upper mixed layer depth (ns = not significant).

<table>
<thead>
<tr>
<th>Region</th>
<th>Dependent Var</th>
<th>Independent Var</th>
<th>Partial coefficient</th>
<th>p level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Over MLD</td>
<td>TEP</td>
<td>Chl a</td>
<td>0.56</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B Production</td>
<td>0.10</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B Abundance</td>
<td>-0.09</td>
<td>ns</td>
</tr>
<tr>
<td>Below MLD</td>
<td>TEP</td>
<td>Chl a</td>
<td>-0.16</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B Production</td>
<td>0.55</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B Abundance</td>
<td>-0.07</td>
<td>ns</td>
</tr>
</tbody>
</table>

Fig. 5. Vertical profiles of TEP (µg XG eq L⁻¹), chl a (µg L⁻¹), bacterial production (ngC h⁻¹ L⁻¹), and bacterial abundance (× 10⁵ cell mL⁻¹) in the same stations as showed in Fig. 2. Horizontal dashed lines in A, B and E represent mixed layer depth. C, D and F represent vertically mixed stations over the sampled depths.
There is an ample evidence that phytoplankton can release high concentrations of TEP (µg XG eq l\(^{-1}\)) and TEP/chl \(a\) ratios (µg XG eq µg chl \(a\) \(^{-1}\)), and equation of chl \(a\)-TEP relationship (log\(_{10}\) µg l\(^{-1}\) vs log\(_{10}\) µg XG eq l\(^{-1}\)) determined in different studies in the Southern Ocean and other marine areas. (Table 4). In fact, the relationship between phytoplankton and TEP appears to be related to variables such as the species composition (Hung et al., 2003b) or their growth status (Passow, 2002b). In our study, the slope of this relationship for the upper layer (0.64 ± 0.13 µg XG eq µg chl \(a\) \(^{-1}\)) was within the range reported in the literature (0.65 ± 0.26 XG µg XG eq µg chl \(a\) \(^{-1}\), Passow, 2002b) and similar to the reported in the Gerlache Strait (Table 4), and, merging all data (above and below the MLD) was similar to the slope reported by Corzo et al. (2005) in waters of the same area (Table 4).

Contrasting relationships between TEP and bacteria have been found across diverse ocean areas, underlining the complexity of TEP-bacteria link. Some authors (Corzo et al., 2005; Passow et al., 2001; Hung et al., 2003b; Santschi et al., 2003) have reported positive relationships, whereas Passow and Alldredge (1994) and Bhaskar and Bhosle (2006) found negative or no correlations at all. In our study, although a positive relationship was found between TEP and bacterial abundance within the mixed layer, the slope of the relationship was lower than the reported in the Corzo et al. (2005) study (1.02 ± 0.25 µg XG 10\(^{-3}\) cell\(^{-1}\)). The relationship between bacteria and TEP in the mixed layer waters appears to be indirect and mediated by phytoplankton as higher partial coefficient was obtained for the relationship with chl \(a\) (Table 3). However, in waters below the MLD, a significant relationship was found between TEP and TP. This positive relationship can be due to several explanations. First, an active release of TEP (Passow, 2002a; Stodereger and Herndl, 1999) or surface-active bacterial capsules (Hung et al., 2003b) by bacterioplankton. Second, an enhanced bacterial activity attached to TEP (e.g. using hydrolytic enzymes) (Grossart and Simon, 1998; Herndl, 1988; Hung et al., 2003b). Third, a stimulation of the self-assembly of dissolved precursors into TEP driven by bacteria (Sugimoto et al., 2007). Finally, a common response of both bacterial activity and TEP to the presence of dissolved compounds (i.e. dissolved acidic polysaccharide) that are both TEP precursors and labile organic substrate for bacteria (Mari and Kiorboe, 1996).

In this study, we reported significant contributions of the dissolved carbohydrates and TEP to the dissolved and particulate organic carbon pools in this area of the Southern Ocean. However, these parameters were not significantly related in the field, suggesting considerable complexity in TEP dynamics. In the Southern Ocean, TEP appeared to be weakly controlled by phytoplankton in the upper mixed layer but the TEP/chl \(a\) ratios differed among regions. On the other hand, bacterial activity controlling TEP was restricted to waters below the mixed layer, and more experimental studies are required to untangle the complex role of bacteria regulating TEP dynamics in natural environments.

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