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

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ABSTRACT

Transparent exopolymer particles (TEP) are formed by the assembly of dissolved precursors, mainly mono and polysaccharides (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 scantly 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.



## 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 major pathway for the vertical export of carbon in the ocean (Alldredge et al., 1993; Passow, 2002b; Passow et al., 2001). On the other hand, TEP can migrate upward to the sea surface microlayer (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.,

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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 $CO_2$ 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 (coinciding 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 rossette 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 (Myklestad 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%.

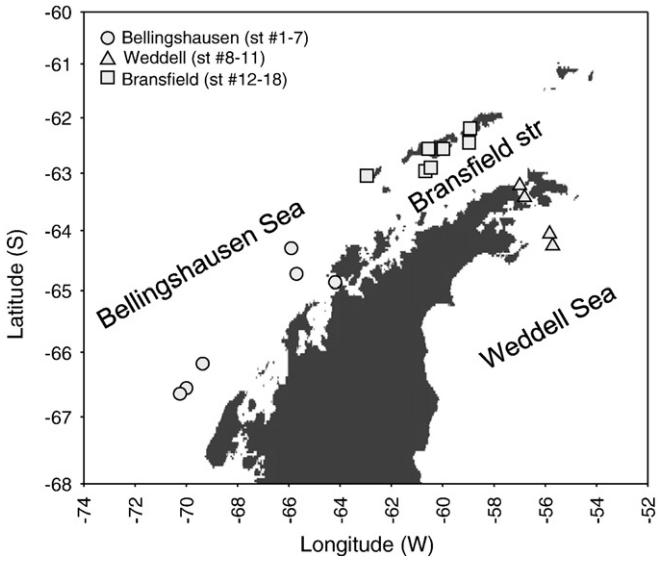


**Fig. 1.** Location of the stations sampled during ICEPOS 2005 cruise. The three study areas are represented using different symbols. Triangles: the Bellingshausen Sea stations (station nos. 1 to 7) Squares: the Weddell Sea stations (station nos. 8 to 11). Circles: the Bransfield Strait stations (station nos. 12 to 18).

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 Wenhao Chen (Univ. of Miami), were used to assess the accuracy of the measurements.

TEP concentration was determined colorimetrically following Passow and Alldredge (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 0.75 µgC µg XG eq $L^{-1}$ proposed by Engel and Passow (2001). The detection limit of the method was 2.2 µg XG eq $L^{-1}$ and the coefficient of variation was 13%.

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 $^{3}$H-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 Giorgio, 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