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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.

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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 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%.

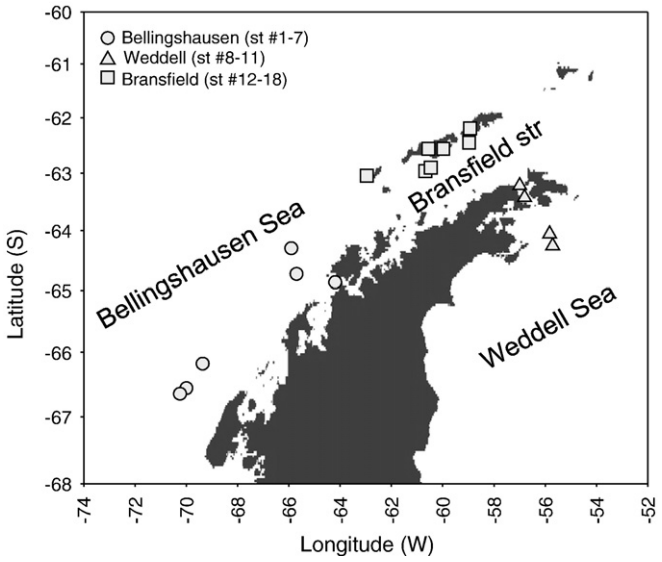

Fig. 1. Location of the stations sampled during ICEPOS 2005 cruise. The three study areas are represented using different symbols. Triangles: the Bellingshausen Sea stations (station nos. 1 to 7) Squares: the Weddell Sea stations (station nos. 8 to 11). Circles: the Bransfield Strait stations (station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

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^{-1}), TEP/BA (fg XG $cell^{-1}$) determined in the three geographical areas.

	All data	n	Bellingshausen Sea	n	Weddell Sea	n	Bransfield Strait	n
	Mean (ranges)		Mean (ranges)		Mean (ranges)		Mean (ranges)	
DMCHO	4.3 ± 2.8 (bdl–12.6)	87	4.5 ± 2.7 (bdl–12.3)	36	2.8 ± 1.9 (bdl–6.9)	17	4.7 ± 3.1 (bdl–12.6)	34
DPCHO	8.6 ± 5.3 (bdl–21.0)	92	8.8 ± 5.0 (bdl–21.0)	35	9.5 ± 4.8 (2.0–21.0)	22	7.9 ± 6.0 (bdl–20.6)	35
TEP	15.4 ± 10.0 (bdl–48.9)	94	14.3 ± 9.5 (bdl–33.8)	34	16.3 ± 12.5 (bdl–48.9)	18	15.8 ± 8.9 (bdl–35.8)	36
TEP-C	11.6 ± 7.9 (bdl–36.7)	94	10.8 ± 7.1 (bdl–25.3)	34	12.2 ± 9.4 (bdl–36.7)	24	10.8 ± 7.3 (bdl–25.3)	36
TEP/chl *a*	40.9 ± 157.8 (bdl–1492)	86	84.2 ± 257.5 (bdl–1492)	34	9.8 ± 7.4 (1.2–28.4)	24	15.0 ± 20.4 (3.0–18.0)	28
TEP/BA	31.3 ± 37.6 (1.0–244.9)	75	47.4 ± 51.9 (2.5–244.9)	34	17.5 ± 13.3 (1.0–41.2)	18	18.4 ± 11.5 (4.5–52.8)	23

bdl = below detection limit.

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 μgC 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 showed 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

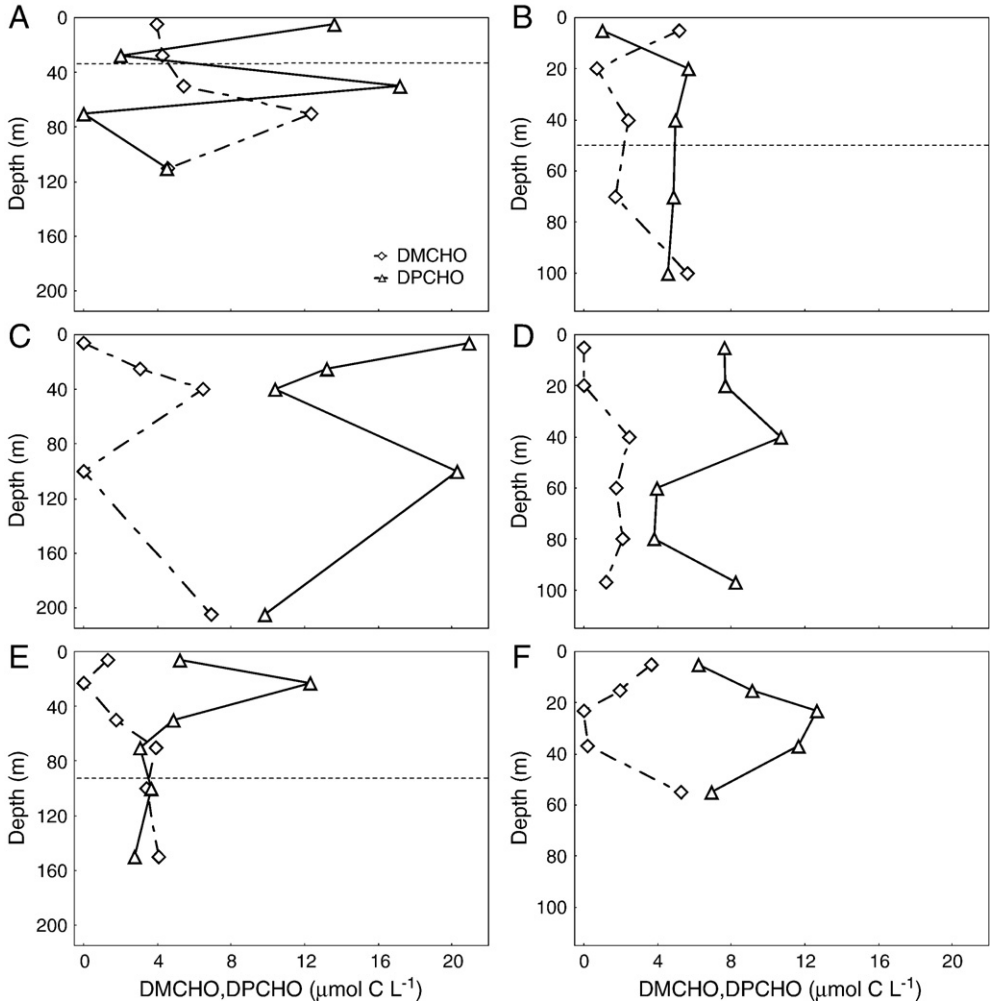

Fig. 2. Representative vertical profiles of DMCHO and DPCHO (μmol C L^{-1}) in deep (left column) and shallow (right column) locations situated in the three geographical areas: the Bellingshausen Sea (station nos. 3 and 7, A–B), the Weddell Sea (station nos. 10 and 8, C–D) and the Bransfield Strait (station 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.

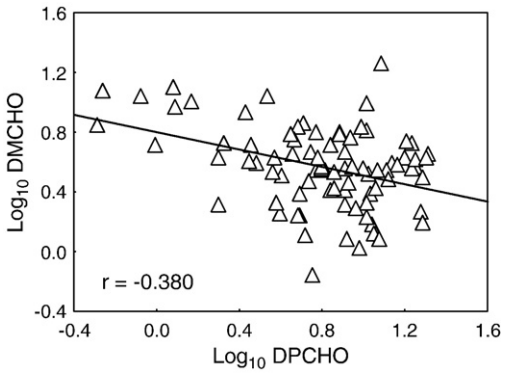

Fig. 3. Scatterplot between DPCHO and DMCHO (log–log). r = correlation coefficient.

total DOC pool. This percentage was very consistent across the different geographical areas studied (Fig. 4A) and over and below the MLD (24% and 20% respectively).

DMCHO 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

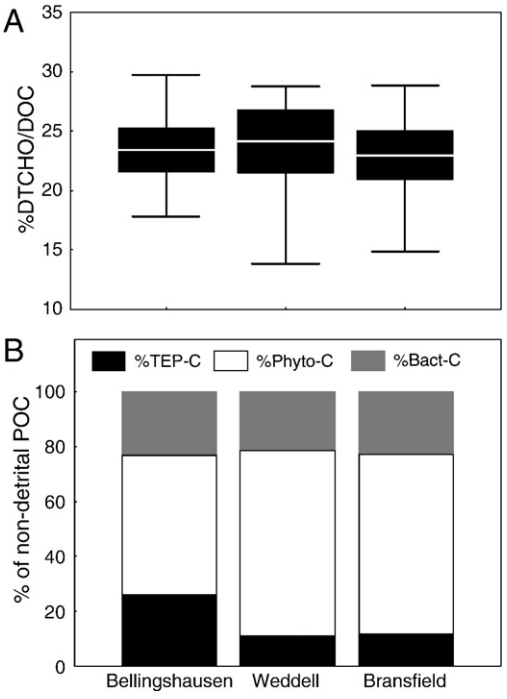

Fig. 4. Mean percentage of DMCHO and DPCHO respect to DOC (A), and relative contribution of TEP-C, phytoplankton-C and bacterial-C (%) to non-detrital particulate organic carbon (B) in the three geographical areas: the Bellingshausen Sea (station nos. 1–7), the Weddell Sea (station nos. 8–11) and the Bransfield Strait (stations nos. 12–18). Boxes = standard errors. Whiskers = not-outlier extremes.

Table 2
Results of the regression analyses performed between TEP and different variables (Note all variables were $\log_{10}$ transformed).

Dependent Var	Independent Var	Intercept	Slope ± SE	r^2	p level
Over MLD					
TEP	DTCHO (μmol C l^{-1})	1.46	−0.28 ± 0.27	0.02	ns
	Chl *a* (μg l^{-1})	0.98	0.64 ± 0.13	0.27	<0.001
	BP (μg C $l^{-1}h^{-1}$)	0.49	0.43 ± 0.14	0.12	<0.01
	BA (cell ml^{-1})	−2.26	0.58 ± 0.22	0.13	<0.05
Below MLD					
TEP	DTCHO (μmol C l^{-1})	0.64	−0.74 ± 0.56	0.07	ns
	Chl *a* (μg l^{-1})	0.97	0.18 ± 0.15	0.07	ns
	BP (μg C $l^{-1}h^{-1}$)	0.64	0.32 ± 0.10	0.24	<0.01
	BA (cell ml^{-1})	−1.08	0.35 ± 0.24	0.08	ns

SE = Standard Error. r^2 = explained variance. p level = level of significance. ns = not significant.

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/BP and TEP/BA ratios were located in the Bellingshausen Sea (station nos. 1 to 7) (Table 1). 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 μg TEP-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-C 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 $\log_{10}(\text{TEP}) = 0.38 \log_{10}(\text{chl } a) + 1.08$ ($r^2 = 0.239$, $p<0.001$, $n = 86$). 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 polysaccharide (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 deoxysugars and galactose (Mopper et al., 1995; Zhou et al., 1998). Only under certain conditions where most

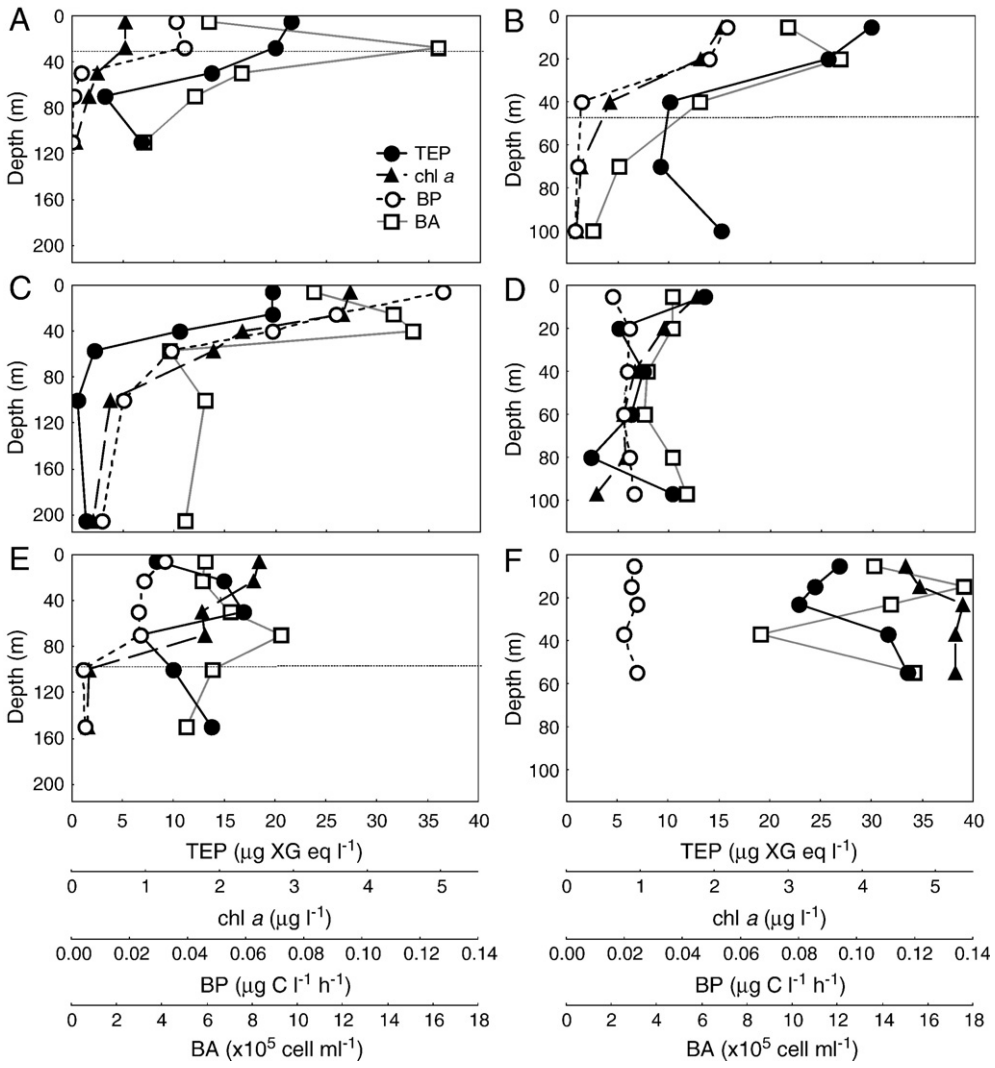

Fig. 5. Vertical profiles of TEP (µg XG eq L^{-1}), chl *a* (µg L^{-1}), bacterial production (ngC h^{-1} L^{-1}), and bacterial abundance ($\times 10^5$ cell mL^{-1}) in the same stations as showed in Fig. 2. Horizontal dashed lines in A, B and E represent mixed layer depth. C, D and F represent vertically mixed stations over the sampled depths.

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).

Region	Dependent Var	Independent Var	Partial coefficient	*p* level
Over MLD	TEP	Chl *a*	0.56	<0.001
		B Production	0.10	ns
		B Abundance	−0.09	ns
Below MLD	TEP	Chl *a*	−0.16	ns
		B Production	0.55	<0.01
		B Abundance	−0.07	ns

Table 4
Average (minimum–maximum) values 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.

Geographic area	Depth	Conditions	TEP	TEP/chl *a*	TEP-chl *a* relationship	Reference
Southern Ocean						
Antarctic Peninsula	0–200 m	Non-bloom	15.4 (0–48.9)	40.9 (0–1492)	$y=0.38x+1.08$	This study
Anvers Island	Surface		207 (10–407)	123 (12–708)	Not related	Passow (pers. comm.)
Ross Sea	0–150 m	Bloom. Time series	308 (0–2800)	89.1	$y=3.63x+1.01$	Hong et al. (1997)
Bransfield Strait	0–100 m	Non-bloom	57(0–346)	51.0	$y=0.32x+1.63$	Corzo et al. (2005)
Gerlache Strait	0–100 m	Non-bloom	0–283	32.7	$y=0.67x+1.52$	Corzo et al. (2005)
Drake Passage	0–100 m	Non-bloom	0–157	29.9	Data not available	Corzo et al. (2005)
Other Areas						
Mediterranean Sea	0–200 m	Non-bloom	21(5–94)	453(0–12,386)	$y=0.17x+1.43$	Ortega-Retuerta unpubl.
Santa Barbara Channel	0–75 m	Time series	197(1–1216)	197(0–6066)	Not related	Passow (pers. comm.)
Friday Harbor	0–20 m	Time series	83(15–159)	31(5–184)	Not related	Passow (pers. comm.)
Northeast Atlantic	10–50 m	Different bloom stages	28.5(10–110)	49–104	Not related	Engel (2004)
Gulf of Cadiz/Strait of Gibraltar	0–200 m	Different bloom stages	25–205	42–2708	$y=2.14x+0.20$	Prieto et al. (2006)

TEP values obtained in this study are lower than previously reported for the Southern Ocean (Corzo et al., 2005; Hong et al., 1997; Passow et al., 1995) or other oceanic areas (Engel, 2004; Passow, 2002b; Passow and Alldredge, 1995; Prieto et al., 2006) (Table 4). However, those studies were confined to TEP dynamics during phytoplankton blooms or in productive areas, where the concentrations of TEP are expected to be maxima. Indeed, our data is within the ranges of previously published, particularly for Southern Ocean waters (Table 4), considering the TEP/chl *a* ratio. Comparatively higher TEP/chl *a* and TEP/BA ratios were observed in the stations located at the Bellingshausen Sea (Table 1). The TEP/chl *a* ratio is associated with the stage of phytoplankton blooms. In the first stages of a bloom, TEP/chl *a* ratios are usually low, and while the bloom develops nutrient concentrations decline with a subsequent decrease in phytoplankton biomass and, hence, TEP/chl *a* ratios tend to be higher (Corzo et al., 2000). The lowest TEP/chl *a* ratios were observed in the Weddell Sea, an area of recent ice melting, therefore delivering nutrients into the water where phytoplankton were likely on the first growth stages. In fact, Prieto et al. (2006) showed that TEP/chl *a* is associated with nutrient availability. On the other hand, the higher TEP/chl *a* ratio in the Bellinghsausen Sea, as it was not mirrored by higher DMCHO or DPCHO concentrations can also be related to a higher rate of self-assembling of precursors (Passow, 2000).

The contribution of TEP-C in comparison with other significant pools of particulate organic carbon such as phytoplankton-C and bacterial-C is highlighted in our study (18% on average, Fig. 4B). We used standard conversion factors for chlorophyll *a* and bacterial-C, however, even if we consider the highest chorophyll to carbon ratio proposed in the literature (172 μgC μg chl a^{-1}, Buck et al., 1996) TEP-C contribution would be still noticeable (8% on average). The subtle increases of TEP concentration observed in waters below the mixed layer, could be attributed to different reasons as: an elevated TEP excretion by phytoplankton and bacteria, marine snow formation and sedimentation (Passow et al., 2001), or a higher stability of polymer particles far from photochemical cracking (Orellana and Verdugo, 2003). Also, possible shifts in TEP chemical composition could account for differences in staining capacity and, hence, in the apparent concentrations, as TEP colorimetric measurements are considered semi-quantitative. This contribution of TEP-C to the total non-detrital POC, even when all organic carbon in the area is likely derived from autochtonous biological sources, suggest that TEP have a longer residence time than phytoplankton or bacterial cells and therefore could have been accumulated in the water column.

There is an ample evidence that phytoplankton can release high amounts of TEP and dissolved carbohydrates during exponential growth phase or senescence of colonies (Passow and Alldredge, 1994; Passow et al., 1995). However, this evidence is not always supported by significant relationships between chl *a* and TEP standing stocks (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 upper 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 upper 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 BP. This positive relationship can be due to several explanations. First, an active release of TEP (Passow, 2002a; Stoderegger 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 hydrolitic 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 Kiørboe, 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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