JOURNAL OF PLANKTON RESEARCH | VOLUME 27 | NUMBER 7 | PAGES 635–646 | 2005

Spatial distribution of transparent exopolymer particles in the Bransfield Strait, Antarctica

A. CORZO[1]*, S. RODRÍGUEZ-GÁLVEZ[2], L. LUBIAN[2], P. SANGRÁ[3], A. MARTÍNEZ[3] AND J. A. MORILLO[1]

[1]DEPARTAMENTO DE BIOLOGÍA, FACULTAD DE CIENCIAS DEL MAR Y AMBIENTALES, UNIVERSIDAD DE CÁDIZ, POLÍGONO RÍO SAN PEDRO, 11510-PUERTO REAL, CADIZ, ANDALUCIA, SPAIN, [2]INSTITUTO DE CIENCIAS MARINAS DE ANDALUCÍA (CSIC), POLÍGONO RÍO SAN PEDRO, 11510-PUERTO REAL, CADIZ, ANDALUSIA, SPAIN AND [3]DEPARTAMENTO DE FÍSICA, CAMPUS UNIVERSITARIO DE TAFIRA, EDIFICIO DE CIENCIAS BÁSICAS, 35017-LAS PALMAS DE GRAN CANARIA, ISLAS CANARIAS, SPAIN

*CORRESPONDING AUTHOR: alfonso.corzo@uca.es

Received February 20, 2005; accepted in principle May 20, 2005; accepted for publication May 31, 2005; published online June 22, 2005

Communicating editor: K.J. Flynn

Transparent exopolymer particles (TEP) are recognized to play an important role in the flux of exported carbon to the deep ocean. However, there is little information on how TEP standing stocks are affected by different hydrographic conditions and other relevant ecological factors in situ. This lack of knowledge is particularly serious for the Southern Ocean. During Austral summer 1999, the Strait of Bransfield presented high mesoscale variability. Two fronts were present, the Bransfield hydrographic front and a slope front along the South Shetland Islands and several mesoscale anticyclonic eddies and/or frontal meanders. The spatial distributions of biological properties were largely affected by this complex hydrography. Chlorophyll a (Chl a) (0.05–4.81 μg L^{-1}), TEP (from undetectable to 346 μg GXeq L^{-1}) and heterotrophic bacteria (HB) (1.7–9.4 × 10^5 cells mL^{-1}) were positively correlated despite the wide hydrographic heterogeneity of the Bransfield Strait. Higher abundances of autotrophic biomass, and correspondly higher TEP and heterotrophic bacteria (HB), were found in the more stratified waters. TEP spatial distribution was mostly related to the abundance of autotrophic biomass although local high TEP concentrations were not matched by similarly high values of Chl a in some areas where diatoms were relatively abundant.

INTRODUCTION

Transparent exopolymer particles (TEP) are formed mainly by coagulation of dissolved organic compounds (Passow, 2000). These compounds are mainly polysaccharides produced and released as dissolved organic carbon (DOC) by phytoplankton (Alldredge *et al.*, 1993; Passow and Alldredge, 1994). Although heterotrophic bacteria (HB) are known to produce exopolymers, their contribution to TEP abundance in the ocean is unknown.

TEP are considered to play an important role in the vertical carbon flux to the deep ocean. TEP, due to their high stickiness, might increase the aggregation rate of particles and therefore their mean size and the sedimentation rate of particulated organic carbon (POC) to the deep ocean (Passow *et al.*, 2001). TEP and derived aggregates like 'marine snow' are colonized by attached bacteria, which find a microenvironment rich in substrates in the otherwise poor water column. These aggregates, including the microbial community inhabiting them, can be a direct source of carbon for higher trophic levels like microzooplancton or euphausiids (Grossart *et al.*, 1998; Passow and Alldredge, 1999; Ling and Alldredge, 2003). However, there are contrasting results regarding the capacity of copepods of using TEP as carbon source (Prieto *et al.*, 2001; Ling and Alldredge, 2003).

The importance of TEP, both in carbon exported from the mixed layer and as a potential pathway of reintroduction of DOC into marine trophic web, is generally recognised. However, our knowledge on the occurrence and abundance of TEP in different aquatic systems is poor (Passow, 2002a). Very little is known about what ecological factors in the marine ecosystem

doi:10.1093/plankt/fbi038, available online at www.plankt.oxfordjournals.org

control, either TEP seasonal variability or TEP spatial distribution. In particular, there is lack of knowledge about how TEP standing stocks relates with the hydrographic and hydrodynamic structure of the ocean. Given the acknowledged role of TEP in the sedimentation of carbon from the photic layer, we need more field studies to extend our data base about how different hydrographic conditions like degree of mixing and the presence of different frontal systems might affect TEP abundances in nature. In Antarctic waters, there is even less information available on TEP abundances, their spatial distribution and on what ecological factors might be involved in their regulation (Passow *et al.*, 1995; Hong *et al.*, 1997; Passow, 2002a).

In this study we present for the first time the spatial distribution of the concentration of TEP, both vertically and horizontally in the hydrographically heterogeneous region of the Bransfield Strait, Antarctica. The variability in the observed pattern in TEP concentration was related to different hydrographic conditions, changes in standing stocks of chlorophyll *a* (Chl *a*), taxonomic changes in the phytoplankton community as inferred from differences in silicate utilization, nitrate concentration and abundance of HB.

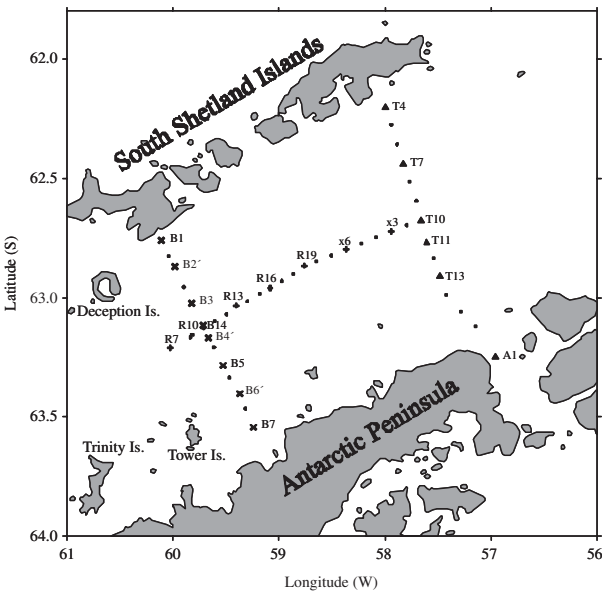

Fig. 1. Map of the study region. Three transects were done in the Strait of Bransfield during the oceanographic cruise CIEMAR, carried out on board of B.I.O. Hesperides (Spain) from 13 December 1999 to 3 January 2000. Transects were designated as East transect, West transect and Central transect. Named stations were sampled for physical and biological variables, the rest were sampled only for physical variables and *in situ* fluorescence.

METHOD

Study site and sampling

The Bransfield Strait, Antarctica, is a complex hydrographic area. It is generally accepted that Transitional Zonal Water with Bellingshausen Sea influence (TBW) is localized in the northern part of the strait and that Transitional Zonal Water with Weddell Sea influence (TWW) is localized in the southern part (García *et al.*, 2002a). TBW, which flows into the Bransfield basin from the Bellingshausen Basin, is a relatively warm and low-salinity water mass, while TWW is a cooler and saltier eastward inflow from the Weddell Sea. The contact between both water masses creates the Bransfield Front in the southeast–northwest direction (García *et al.*, 1994; García *et al.*, 2002a; Gomis *et al.*, 2002). In addition to the hydrographic front, a slope front develops in the northern part of the Bransfield Strait, also in a southwest–northeast direction along the slope of the South Shetland Islands.

Seawater samples were collected during the oceanographic cruise CIEMAR carried out from 13 December 1999 to 3 January 2000 on board of B.I.O. Hesperides. CIEMAR survey was performed in the Passage of Drake, Strait of Bransfield and Strait of Gerlache. Here, we will present mainly the results from the Bransfield Strait (Fig. 1). Samples were obtained from 5, 10, 25, 50, 75, 100 m and the fluorescence maximum depth by mean of a rosette system of 24 oceanographic Niskin bottles of 12 L, operated through a General Oceanic MKIIIC CTD that also provided continuous vertical hydrographic information in real time (temperature, salinity and fluorescence).

Concentration of TEP

TEP concentration was measured according to the dye-binding assay (Passow and Alldredge, 1995a). Seawater subsamples of 50 mL were filtered on 0.4 μm polycarbonate filters (Poretic) under low constant pressure (<100 mm Hg). Immediately after filtration, 500 μL of freshly made alcian blue solution (0.03 g alcian blue dissolved in 150 mL of 0.06% acetic acid, prefiltered through 0.22 μm) was added to the particulate fraction retained on the polycarbonate filter and allowed to react for 2 s. The excess of dye was immediately washed out by successive filtration of two aliquots of 1 mL distilled water filtered through 0.22 μm. At that stage, filters were kept frozen (–20°C) until further processing in the laboratory 1 month later. Alcian blue was released from the particulate fraction by soaking each filter in 3 mL of 80% sulfuric acid for 2 h at continuous agitation at room temperature. Finally the concentration of alcian blue was determined by spectrophotometry at 787 nm. To account for the binding capacity of the polycarbonate filter several blanks were processed as described above. All samples were analysed in triplicate. TEP

values are expressed as xanthan gum weight equivalent calculated by means of a calibration curve according to Passow and Alldredge (Passow and Alldredge, 1995a). Although the carbon content of TEP is species dependent, TEP abundance can be roughly expressed in C units using the conversion factor μg C TEP L^{-1} = 0.70 μg GXeq L^{-1} (Engel and Passow, 2001; Passow, 2002a).

Abundance of heterotrophic bacteria

Fresh bacterioplankton samples from each depth were stained with SYTO-13 and analysed on board immediately after collection by flow cytometry following del Giorgio *et al.* (del Giorgio *et al.*, 1996). Briefly, 2.5 mL of a solution of SYTO-13 (Molecular Probes) dissolved in dimethyl sulfoxide was added to 500 mL of seawater to obtain a final concentration of 2.5 mM of SYTO-13. After vigorous shaking the samples were incubated for 10 min at room temperature in the dark. After this time, 10 mL of a yellow-green autofluorescent microspheres solution (FluoSpheres carboxylated-modified microspheres, 1.0 mm) of known concentration was added to each stained sample. After shaking, the samples were immediately analysed by a FACScalibur flow cytometer (Becton Dickinson). These beads served as an internal standard for instrument performance and, since they were added in known concentration, allowed the calculation of the volume of sample processed and therefore the abundance of bacteria per unit of volume. MilliQ water was used as sheath fluid. The flow rate of sample through the flow chamber was set at low rate (12 ± 3 μL min^{-1}) and calibrated several times during the cruise. This flow rate and the mean concentration of bacteria found in this study determined a conveniently low particle passage rate generally lower than 300 events s^{-1}. Data were acquired with the software CellQuest as Flow Cytometry Standard files and later analysed with CellQuest and Attractor software (Becton Dickinson).

Chlorophyll

Chl *a* was determined fluorimetrically following the method of Yentsch and Menzel (Yentsch and Menzel, 1963) as modified by Holm-Hansen *et al.* (Holm-Hansen *et al.*, 1965). Samples (1 L) were filtered through Whatman GF/F filters and extracted overnight in 5 mL 90% acetone at 4°C in dark. Fluorescence was measured before and after acidification with a fluorometer (Turner Designs 10) calibrated with pure Chl *a* (Sigma) following UNESCO (UNESCO, 1994) recommendations.

Inorganic nutrients

Samples for inorganic nutrients (nitrate, nitrite, phosphate and silicate) were stored frozen (–20°C) until analysis by means of a Traacs 800 Bran Luebbe auto analyser following standard protocols (Grasshoff *et al.*, 1983).

RESULTS

Hydrography and distribution of Chl *a*

During the CIEMAR cruise in 1999, surface waters of most part of the Bransfield Strait had temperatures and salinities typical of TBW, at least in the upper 100 m of the water column (Fig. 2). The Hydrographic Bransfield Front was only clearly detected in the East transect between stations T11 and T13, and it was not detected in the West and Central transects in surface. TBW waters were stratified while TWW waters, located south of the front, were vertically more homogeneous with essentially the same temperature and salinity in the upper 250 m. The Bransfield slope front was located between station T4 and T6 in the East transect and B2 and B3 in the West transect, close to the South Shetland slope (Fig. 2). The Central transect revealed the presence of three successive warm and relatively fresh structures between stations R10 and R8, x8 and x5 and x3 and T10 (Fig. 2). These structures could correspond with warm-core anticyclonic eddies and/or frontal meanders related to the hydrographic front.

The concentration of Chl *a* ranged from 0.05 to 4.81 μg L^{-1} (0.98 ± 0.82) in the Strait of Bransfield. The vertical distribution of Chl *a* differed considerably among different areas (Fig. 3). The homogeneity in the physical properties of the TWW water mass was reflected in the uniformity of the vertical distribution of Chl *a* at the southern side of the Eastern transect (Fig. 3). In comparison, TBW waters showed a higher degree of thermohaline stratification. Chl *a* accumulated mainly in the upper 20–30 m of the water column, with a chlorophyll maximum at about 10 m (Figs 2 and 3). Chl *a* concentration tended to decrease along the Central transect in the northeast direction, although a second maximum was found around station X6 (Fig. 3). Although in general *in situ* fluorescence matched the distribution of Chl *a*, its higher spatial resolution revealed a third maximum further to the East (Fig. 2).

TEP

TEP concentration ranged from undetectable to 345.9 μgGXeq L^{-1} for the whole area of study with a mean value of 56.77 ± 54.50 μg GXeq L^{-1}. TEP concentration generally decreased with depth, except that occasional maxima were found at the chlorophyll maximum or close to it. The horizontal distribution of TEP was highly heterogeneous in Bransfield Strait (Fig. 4).

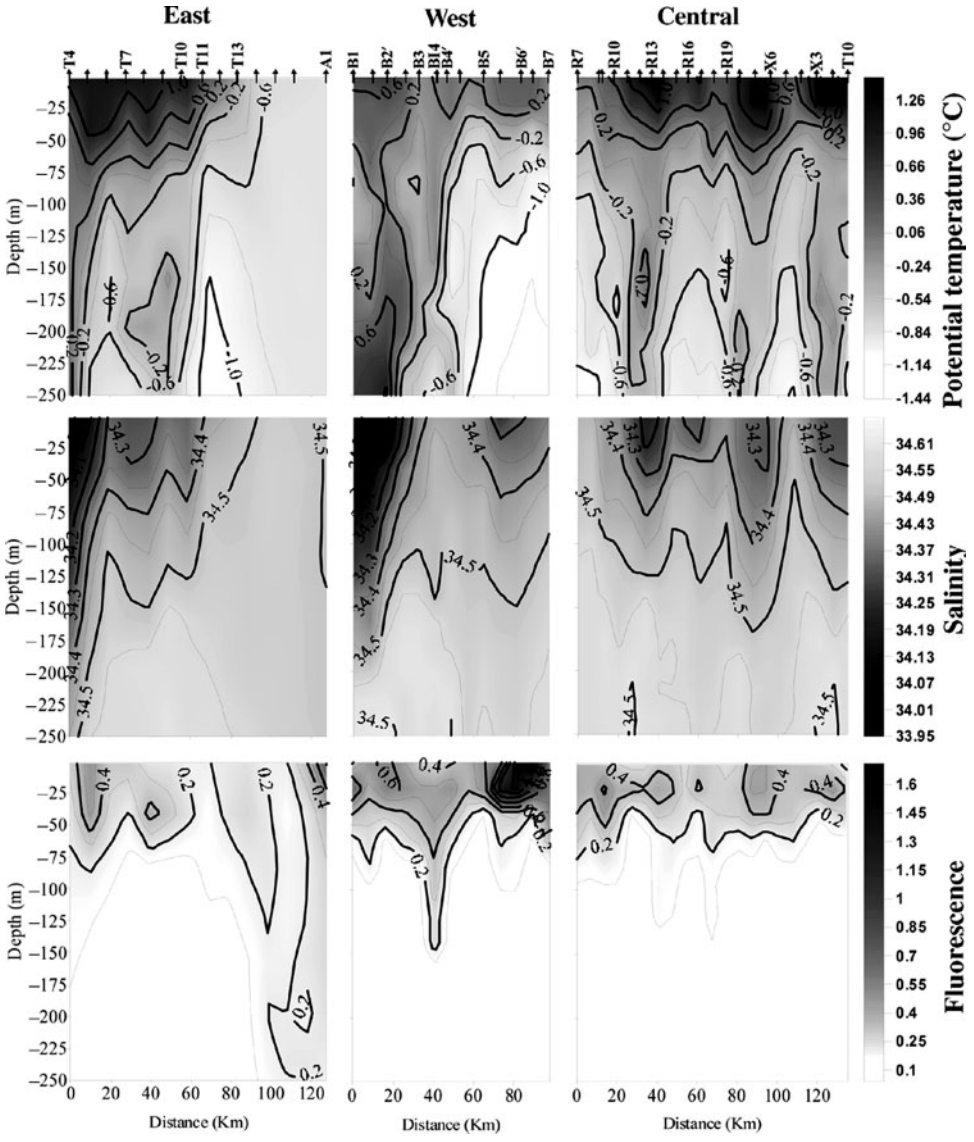

Fig. 2. Temperature, salinity and fluorescence values for the upper 100 m across East, West and Central transects in Bransfield Strait.

This horizontal heterogeneity was mainly associated with the presence of two more conspicuous hydrographic singularities of Bransfield Strait, the hydrographic and the slope fronts (García *et al.*, 1994). In the East and West Bransfield transects, TEP were more abundant in the northern side of the slope front, close to Livingston Island (Fig. 4). In this area TEP concentration, like Chl *a*, accumulated in the upper layer as a consequence of a higher degree of thermohaline stratification (Figs 2, 3 and 4). The hydrographic front was clearly visible in the Eastern transect between stations T11 and T13 (Fig. 2). Its position was particularly well marked by a maximum in TEP concentration on the upper layer in the northern side at station T11 (Fig. 4). TEP vertical distribution was relatively uniform in the TWW water as previously described for Chl *a*; however, the relatively high values of Chl *a* (Fig. 3) were not matched by correspondingly high TEP concentrations in this area (Fig. 4).

The distribution pattern of TEP along the Central transect differed from that of Chl *a* (Fig. 4). Contrary to Chl *a*, TEP concentration in the southwest side was relatively low. A large abundance of TEP was detected in stations R19 and X6 with maximum concentrations at 10 and 25 m, respectively. Although as mentioned in the previous section Chl *a* presented a maximum at station X6, it was of less importance in relative terms.

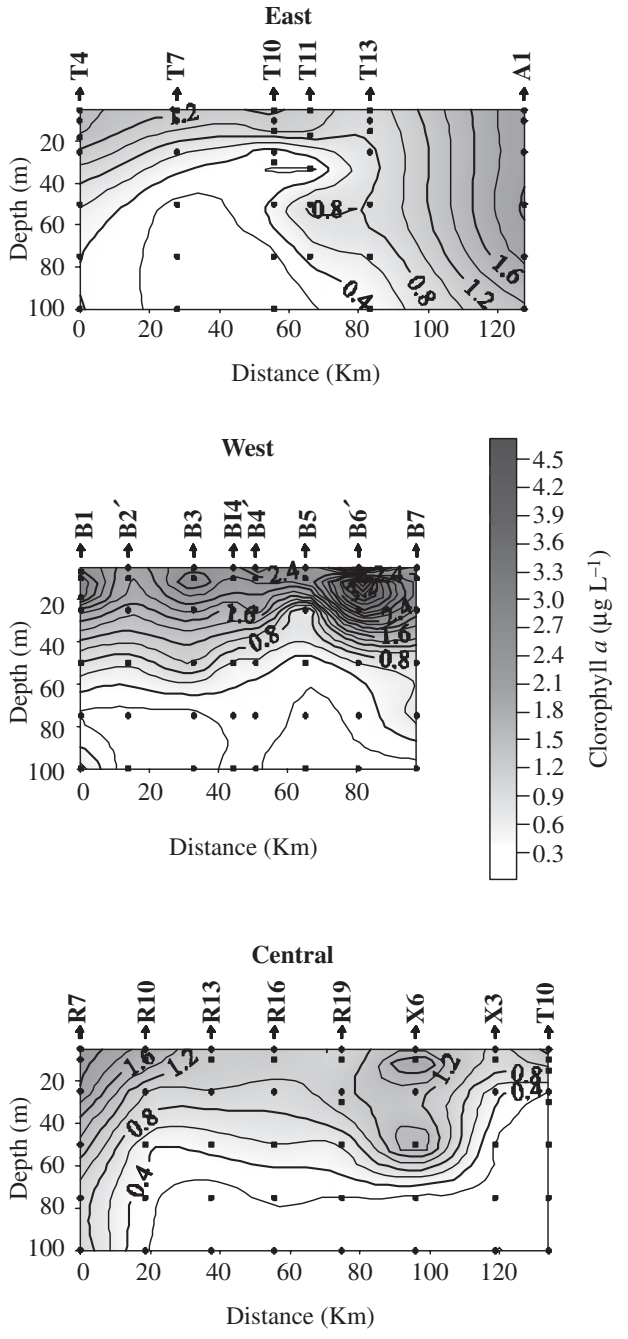

Fig. 3. Chlorophyll *a* (Chl *a*) concentration (µg L^{-1}) for East, West and Central transects.

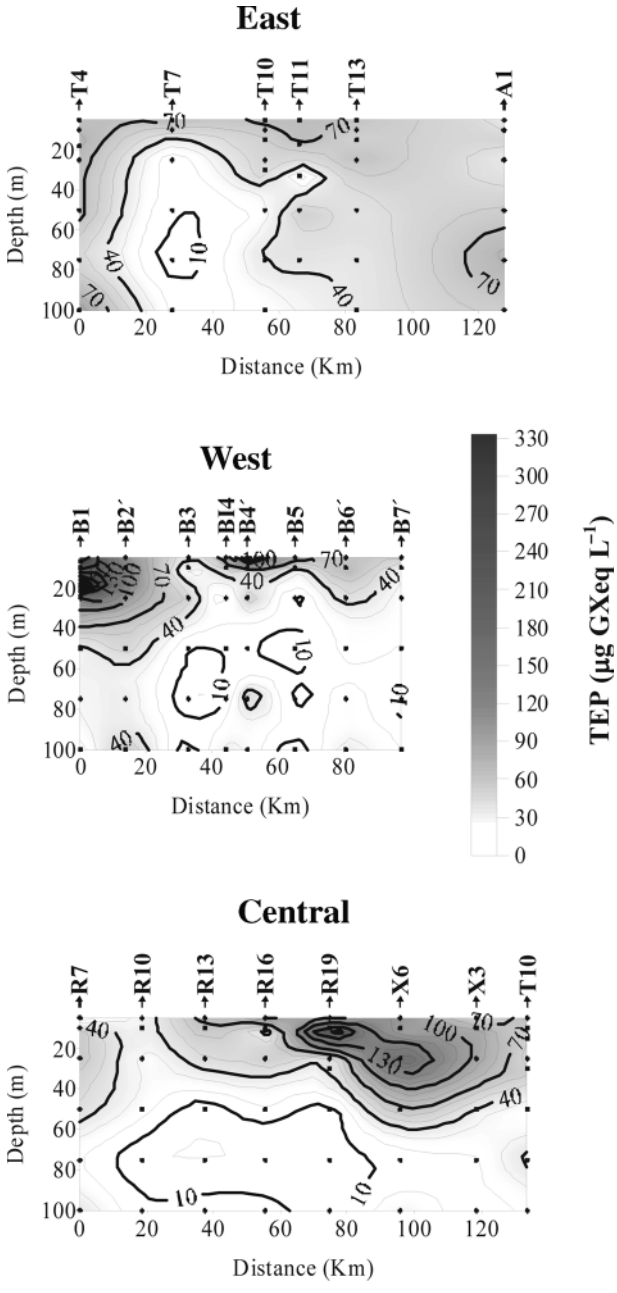

Fig. 4. TEP concentration (µg GXeq L^{-1}) for East, West and Central transects. TEP abundance can be transformed to C units using the conversion factor µg C TEP L^{-1} = 0.70 µg GXeq L^{-1} (Engel and Passow, 2001; Passow, 2002a).

Inorganic nutrients

Nitrate concentration ranged between 20.8 and 34.6 µM in the upper 100 m of water column (Table I). In general, nitrate spatial distribution was almost the mirror image of Chl *a* distribution (Fig. 5). Phosphate (2.17 ± 0.024 µM) also mirrored the spatial distribution of autotrophic biomass although less precisely than nitrate (results not shown). Nitrate and phosphate concentrations were linearly and significantly correlated ($r = 0.665$, $P < 0.001$ $n = 108$). The general spatial distribution of silicate (74.04 ± 32.44 µM) and nitrite (0.22 ± 0.006 µM) at the three transects were not related neither to Chl *a* standing stocks nor TEP spatial distribution (results not shown). However, low silicate levels

Table I: Average concentration of chlorophyll a (μg L^{-1}), TEP (μg GXeq L^{-1}) and abundance of heterotrophic bacteria (cell $mL^{-1} \times 10^5$) for the upper 100 m of the water column of Bransfield Strait

	Average	SD	CV	Range	*n*
Chl *a*	0.983	0.83	84.4	0.05–4.81	128
TEP	56.77	54.50	96.0	0–346	136
Bacteria	3.61	1.15	31.9	1.70–9.41	128
Nitrate	27.43	2.10	7.7	20.8–34.7	121
Phosphate	2.17	0.15	6.9	1.7–2.6	120
Silicate	74.28	5.47	7.4	61.9–85.8	123
Nitrite	0.22	0.08	36.4	0.08–0.59	122

Standard deviation (SD), coefficient of variation (CV, %), minimum and maximum values (Range) and number of samples (*n*) are also provided. Transparent exopolymer particles (TEP) abundance can be roughly expressed in C units using the conversion factor μg C TEP L^{-1} = 0.70 μgGXeq L^{-1} (Engel and Passow, 2001; Passow, 2002a).

were occasionally associated with high TEP concentration at some stations, like for instance B1 and X6 (Fig. 4).

Heterotrophic bacteria

The abundance of HB ranged from 1.7 to 9.41 × 10^5 cells mL^{-1}. Bacterial abundance generally decreased with depth although a subsurface maximum was frequent at 25 m. The horizontal distribution was largely heterogeneous resembling that of Chl *a*, although there were important differences as well. The Bransfield hydrographic front in the East transect separated the TBW water mass, containing relatively large abundances of HB, Chl *a* and TEP at the surface, from the TWW zone. This water mass had very low abundances of HB, similar Chl *a* concentrations and lower TEP concentrations (Fig. 6). The correspondence of HB abundance with standing stocks of Chl *a* and TEP concentration in the West transect was only partial. The peak in HB abundance on the north side was matched by high concentrations of TEP but not by correspondingly high Chl *a* concentrations. However, the opposite was observed in the southern HB maximum, it was paralleled by relatively high standing stocks of Chl *a*, but TEP concentration was very low (Fig. 6). In the Central transect, the abundance of HB presented two maxima (Fig. 6). Both were displaced to the East respect to the Chl *a* maxima and were coincident with anticyclonic eddies or meanders of warm and fresher water (Figs 2 and 3).

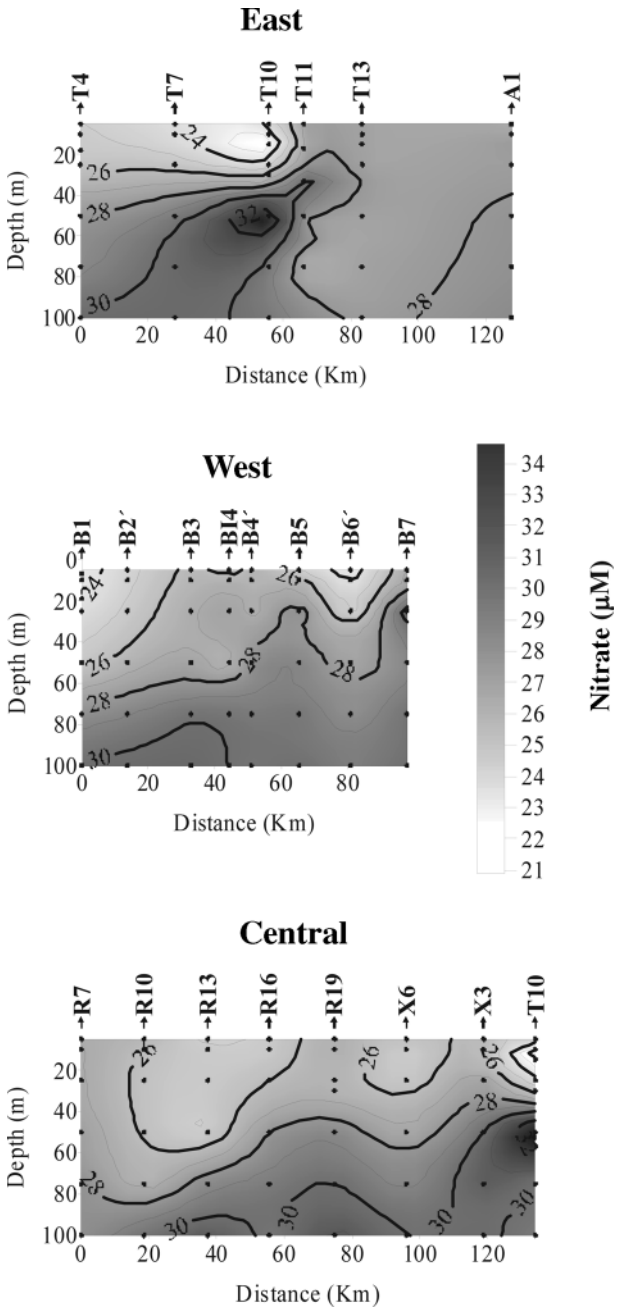

Fig. 5. Nitrate concentration (μmol L^{-1}) for East, West and Central transects.

DISCUSSION

Autotrophic biomass and hydrography

The Bransfield Strait like the Southern Ocean is a High Nutrient Low Chlorophyll (HNLC) area, is characterized by the coincidence in the photic layer of high concentrations of macronutrients and relatively low

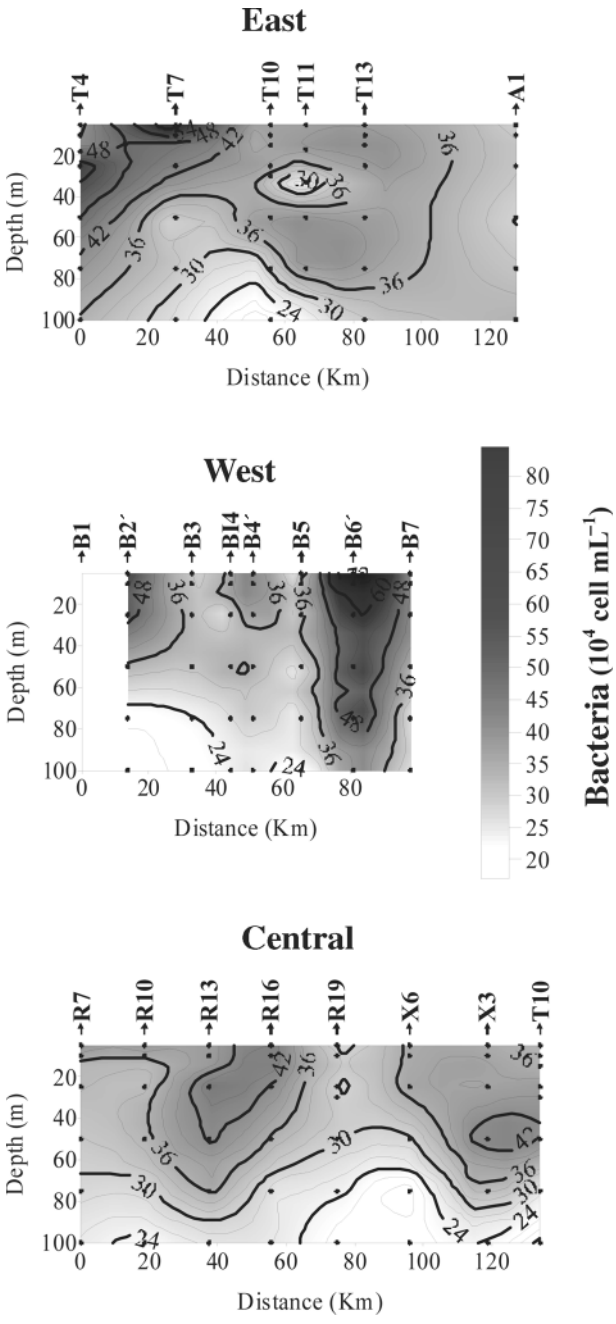

Fig. 6. Abundance of heterotrophic bacteria ($\times 10^4$ cells mL^{-1}) for East, West and Central transects.

standing stocks of Chl *a*. The concentration of Chl *a* was similar to those reported previously in the same area (Holm-Hansen and Mitchell, 1991; Basterretxea and Arístegui, 1999; Varela *et al.*, 2002). In general, our results have also shown that the high levels of autotrophic biomass in Bransfield were always associated with relatively warm and low-salinity water masses. Meltwater stabilization of the water column, together with a higher temperature, could contribute to the development of phytoplankton blooms in Bransfield Strait (Mitchell and Holm-Hansen, 1991). Clearly, the vertical and the horizontal distributions of autotrophic biomass were largely affected by the major hydrographic features of the Strait, the slope and the Bransfield hydrographic fronts (García *et al.*, 1994). The presence of mesoscale anticicyclonic eddies and/or frontal meanders in the central axis of the Strait was an additional source of horizontal heterogeneity for seston.

The presence of the slope front seems to create a relatively narrow band of waters, rich in autotrophic biomass, between the coasts of the South Shetland Islands and the front (Fig. 3). This high autotrophic biomass could be associated with the advection of rich waters form Bellighasusen Sea and Gerlache Strait (Basterretxea and Arístegui, 1999) and also with the existence of a shallower mixed layer than the critical depth in the stratified side of the front (Sverdrup, 1953; Mann and Lazier, 1991). During December 1999, the hydrographic front was only clearly detected in the East transect, where it separated two well-differentiated water masses in terms of temperature and salinity (Fig. 2), biological properties (Figs 3, 4 and 6) and inorganic nutrients (Fig. 5). North of the front, as a result of a higher degree of vertical stratification, autotrophic biomass accumulated in the upper layer that got progressively thinner as the hydrographic front was approached from the north because the warm and less saline TBW slipped over the denser TWW (Fig. 3). In contrast, in the south side of the front, TWW did not show any vertical stratification in the whole water column. Correspondingly, autotrophic biomass was uniformly distributed in the upper 100 m.

The Bransfield hydrographic front was neither detected in surface in the West, nor in the Central transect. According to the temperature and salinity measurements, TWW water did not reach southwest of Bransfield. This might be due to the entrance of a water mass from the Gerlache Strait, which is also warmer and less saline. We found high abundances of autotrophic biomass associated with warm and less saline water in the southern extreme of West transect, between Tower and Astrolabe Islands, and coincident with a stratified water column around station B6. The role of the Gerlache Strait as a source of high-Chl *a* waters for the Bransfield Strait have been previously recognized (Lipski, 1985; Basterretxea and Arístegui, 1999). In fact, the decreasing west–east gradient frequently observed in the chlorophyll abundance in the Bransfield Strait (Fig. 3) has been interpreted as an indication that an important part of this biomass could have originated in adjacent areas like the Gerlache Strait and the Bellingshausen Sea and had been transported along the

Bransfield Strait in a west–east direction (Holm-Hansen and Mitchell, 1991; Karl *et al.*, 1991; Basterretxea and Arístegui, 1999).

TEP and autotrophic biomass

The available information on TEP concentration and dynamic in Antarctic waters is very scarce (Table II, see also a recent review by Passow, 2002a). Previous available information dealt with production of TEP by *Phaeocystis antarctica* (Hong *et al.*, 1997) and temporal variability of TEP concentration in surface (2–6 m) coastal waters off Bonaparte Point, Anvers Island (Passow *et al.*, 1995). TEP concentration in the Strait of Bransfield was highly variable (Table I, Fig. 4). Similar ranges and degree of variability were also observed in Drake Passage and Straits of Gerlache (Table II). Mean TEP concentrations in Drake Passage and in the Straits of Bransfield and Gerlache were lower than those reported for coastal waters off Anvers Island and one order of magnitude lower than those reported during a bloom of *P. antarctica* in the Ross Sea (Hong *et al.*, 1997). The capacity of different *Phaeocystis* species to produce and release large amount of carbohydrate that might be precursors for TEP formation is well known (Guillard and Hellebust, 1971; Eberlein *et al.*, 1985; Passow and Wassmann, 1994; Hong *et al.*, 1997). During the cruise CIEMAR in 1999 we did not detect blooms of *Phaeocystis* in Bransfield Strait, nor in adjoining areas like Southern Drake Passage or Gerlache Strait, despite the acknowledged importance of this species for the ocean carbon flux in the Antarctic (Smith *et al.*, 1991; Smith *et al.*, 1996). The TEP concentrations in the Strait of Bransfield were sometime undetectable or frequently in the low ranges of those reported for different location around the world (Passow, 2002a), even if they are compared with oligotrophic areas in lower latitudes such as the North East Atlantic (Engel and Passow, 2001) or the relatively oligotrophic Gulf of Cádiz in South Iberian Peninsula (García *et al.*, 2002b) and one order of magnitude lower than those of more eutrophic environments like Otsuchi Bay in Japan, where part of TEP production was due to exudates released by the macroalga *Undaria pinnatifida* (Ramaiah *et al.*, 2001).

TEP vertical and horizontal distributions in the Bransfield Strait paralleled the Chl *a* distribution in general. The abundance of TEP was higher in the photic layer than below, and TEP tended to be more abundant in areas where Chl *a* was also more abundant. This has been the commonly observed pattern in the TEP spatial distribution in the relatively few available field studies (Passow and Alldredge, 1995a,b; Hong *et al.*, 1997; García *et al.*, 2002b; Passow, 2002a). However, no direct correlation was found in some cases, for example in the Adriatic Sea (Shuster and Herndl, 1995), and in coastal

Table II: Comparative data of TEP and Chl a for several geographic locations

Location	Comments	TEP	TEP range	Chl *a*	HB	TEP : Chl *a*	TEP : HB	Reference
Monterrey Bay	Summer	—	50–191	—	—	—	—	Passow and Alldredge, 1995a
Santa Barbara Channel	Winter, summer, 0–75 m	—	29–252	10.1–10	—	27.8	—	Passow and Alldredge, 1995a
Anvers Island, Antarctica	Summer, coastal samples	—	15–>500	—	—	—	—	Passow *et al.*, 1995
Ross Sea, Antarctica	Phaecystis bloom, summer, 0–150 m	308	0–2800	3.61	—	89.9	—	Hong *et al.*, 1997
Otsuchi Bay, Japan	Spring bloom	1344	24–2,321	<1–12	3.1–9.9	206.8	—	Ramaiah *et al.*, 2001
Gulf of Cadiz, Mediterranean Sea	Summer, 0–100 m	118	<25–609	0.05–6.9	—	281.5	—	Garcia *et al.* 2002
Bransfield Strait, Antarctica	Summer, 0–100 m	50	0–346	0.98	3.61	51.0	13.8	This study
Gerlache Strait	Summer, 0–100 m	38	0–283	1.16	2.82	32.7	13.5	Rodríguez-Gálvez *et al.*, unpublished
Drake Passage	Summer, 0–100 m	35	0–157	1.17	3.47	29.9	10.1	Rodríguez-Gálvez *et al.*, unpublished

Mean Transparent exopolymer particles (TEP; μg GXeq L^{-1}), mean Chlorophyll *a* (Chl *a*; μg L^{-1}), TEP : Chl *a* [μg GXeq (μg Chl *a*)$^{-1}$], hetotrophic bacteria (HB; cell $mL^{-1} \times 10^5$), TEP : HB [picog Gxeq (10^5 cells)$^{-1}$]. For comparison of TEP : Chl *a* ratios between different studies, when mean TEP and/or Chl *a* values were not provided in the cited reference () they were calculated by us, assuming a normal distribution for both variables, as the mean value of the range {minimum + [(maximum – minimum)/2]}.

Antarctic waters dominated by cryptomonads (Passow *et al.*, 1995). Although the horizontal distribution of TEP in the Strait of Bransfield followed the general distribution of primary producers, there were exceptions. TEP and autotrophic biomass showed opposite trends at both sides of the slope front. North to the front, both autotrophic biomass and TEP decreased in the southwest–northeast direction. In contrast, an inverse pattern was observed in the Central transect. Chl *a* concentration tended to decrease along the transect in the southwest–northeast direction in accordance with previous studies in the area (Holm-Hansen and Mitchell, 1991; Karl *et al.*, 1991; Basterretxea and Arístegui, 1999), but TEP concentration increased along the transect (Fig. 4). The simplest interpretation is an increase in TEP abundances as phytoplankton blooms, transported in the southwest–northeast direction by the Bransfield Current, enter the senescence stage along the Central transect. TEP abundances are usually higher in the senenscent phase of phytoplankton blooms in cultures (Corzo *et al.*, 2000), mesocosms (Passow and Alldredge, 1995b; Engel *et al.*, 2002; Prieto *et al.*, 2002) and field studies (Passow *et al.*, 1994; Mari and Kiørboe, 1996). The time lag between the Chl *a* maximum and the peak in TEP concentration is likely responsible for the ocurrence of the TEP maximum downstream of those of Chl *a*. Similar observations were reported by García *et al.* (García *et al.*, 2002b) in Gulf of Cádiz. These differences between both sides of the slope front suggest a different origin for the water masses being transported on each side of the front or at least a different timing in the coupling between autotrophic biomass and TEP across the front.

In aquatic environments, the relationship between TEP and Chl *a* concentrations is necessarily complex because there are many processes involved. Unfortunately our understanding of all of them is uneven and scarce in some cases. The standing stocks of TEP might be affected by phytoplankton species composition (Passow and Alldredge, 1994; Waite *et al.*, 1995; Passow, 2002b), growth rate (Waite *et al.*, 1995), nutrient availability (Obernosterer and Herndl, 1995; Corzo *et al.*, 2000) and aggregation rate (Passow, 2002a). Consumption by microheterotrophs of TEP precursors, bacterial degradation of TEP (Mari and Kiørboe, 1996; Passow, 2002a) and grazing by protozoans, copepods and euphasiids (Decho and Moriarty, 1990; Shimeta, 1993; Tranvik *et al.*, 1993; Grossart *et al.*, 1998; Passow and Alldredge, 1999) might affect TEP abundance as well. Changes in the intensity of some of these processes have been documented during the development and senescence of blooms in nature (Passow *et al.*, 1994; Mari and Kiørboe, 1996; Mari and Burd, 1998) and experimental mesocosmos (Alldredge and Jackson, 1995; Dam and Drapeau, 1995; Passow and Alldredge, 1995b; Prieto *et al.*, 2002). Below, we examine the relationship between TEP and autotrophic biomass through the TEP : Chl *a* ratio and the slope of the regression equation between both variables.

Mean TEP : Chl *a* ratio [51 μg GXeq (μg Chl *a*)$^{-1}$] in Bransfield Strait is among the lower published values (Table II). TEP and Chl *a* concentrations in the upper 100 m were significantly correlated in Bransfield Strait (Table III, Fig. 7). In most studies, where the relationship between TEP and Chl *a* has been examined, the

Table III: Regression equations among several variables in Bransfield Strait

Dependent variable	Intercept (SE)	Slope (SE)	Independent variable	r^2	Sample size	*P*
log TEP	1.63 (0.03)	0.32 (0.07)	log Chl *a*	.17	128	<.01
log TEP	10.14 (1.34)	–5.97 (0.94	log NO_3^-	.28	121	<.01
log TEP	–4.10 (1.41)	1.02 (0.25)	log HB	.13	128	<.01
log Chl *a*	12.93 (1.60)	–9.13 (1.10)	log NO_3^-	.38	120	<.01
log HB	5.57 (0.01)	0.14 (0.02)	log Chl *a*	.28	128	<.01

Chl *a*, Chlorophyll *a*; HB, heterotrophic bacteria; TEP, transparent exopolymer particles.

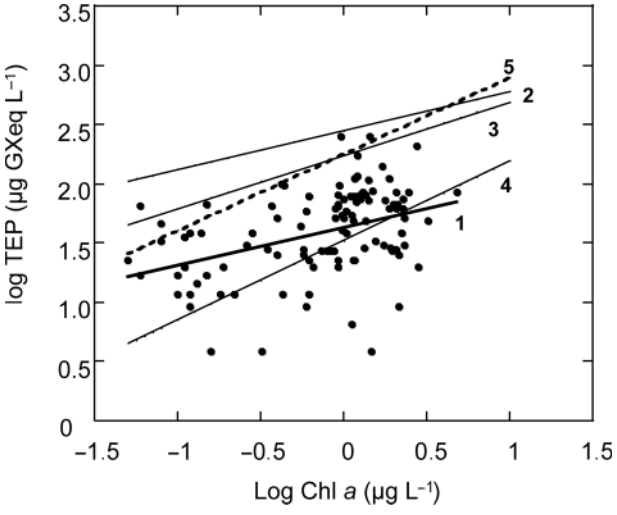

Fig. 7. Correlation between TEP concentration and chlorophyll *a* (Chl *a*) standing stocks in the Strait of Bransfield. The best fit for experimental data (line 1) was the equation log TEP = 1.63 + 0.317 log Chl *a* (r^2 = 0.168, n = 128, P < .001). For comparison the regression lines obtained in other field studies are plotted. Line 2, mixed diatom bloom in the Baltic Sea, (Engel, 1998 in Passow, 2002a); line 3, diatom dominated community in the East Sound (Kiørboe, 1996 in Passow, 2002a); line 4, Gerlache Strait, Antarctic (Rodríguez-Gálvez *et al.*, unpublished); line 5, regression line obtained after the calculation of the mean values of constants a (176.25 ± 59.26, nonlog transformed) and b (0.647 ± 0.262) from Table III of Passow (Passow, 2002a) excluding Hong *et al.* (Hong *et al.*, 1997).

best fit was obtained with a potential function of the form TEP = a(Chl a)^b both in mesocosms and nature. The exponent b, the slope of the linear regression when TEP and Chl a are log-transformed, can be used for across system comparisons. The value obtained for the Bransfield Strait (b = 0.317) is the lowest among the available published value as far as we know (Passow, 2002a,b). According to the available information [Table III in (Passow, 2002a)], the value of b is variable, but it is generally >1. However, b was 3.63 in the Ross Sea during a *P. antarctica* bloom (Hong *et al.*, 1997). Because this very high value is outside the general trend found in other studies it has been excluded from the calculation of the mean values of constants a (176.25 ± 59.26) and b (0.647 ± 0.262), from Table III of Passow (Passow, 2002a). Most of results used for this calculation stem from batch cultures or mesocosm studies, and therefore *in situ* measurement were underrepresented. With the available information it seems that b tends to be lower *in situ* as compared with cultures and mesocosms. The slope b in Bransfield, although the lowest, is close to that found in the East Sound and the Baltic Sea (Fig. 7). Moreover, it seems that low b values are not necessarily a specific feature of Antarctic waters because we found a larger slope (0.670) in the Gerlache Strait (Rodríguez-Gálvez *et al.*, unpublished). Since b is generally <1, either the specific production rate of TEP decreases as autotrophic biomass increases or TEP loss processes increase (Passow, 2002a). No other clear pattern is evident in the relationship between TEP and Chl a in across system comparisons with the scarcely available information, probably because the relationship between TEP and autotrophic biomass is more dependent on the growth stage of blooms and on species composition than on differences in the general trophic status of aquatic environments.

TEP and inorganic nutrients

Limitation of autotrophic biomass by inorganic macronutrients is unlikely in Antarctic waters, but nutrient consumption by phytoplankton affected the spatial distribution of nitrate, phosphate, silicate and nitrite to different degrees (Castro *et al.*, 2002). TEP concentrations were inversely correlated with nitrate, which explained 28% of observed variability in TEP. The inverse relationship between TEP concentrations and nitrate is interesting because an increase in nitrate availability has been shown to decrease the production of TEP in cultures (Corzo *et al.*, 2000), and nutrient limitation in the final phase of blooms could be responsible of the high TEP concentration at this stage. The suggested mechanism is an increase in the photosynthetic release of organic carbon as a result of the imbalance between N and C assimilation in N-limited phytoplankton (Corzo *et al.*, 2000). Although the N : P ratio in Antarctic waters indicates higher relative availability of phosphate than inorganic nitrogen, it is unlikely that the existence of a strong N-limitation could explain the observed inverse relationship between TEP and nitrate. TEP and nitrate kept strong and inverse relationship with depth and chlorophyll. The analysis of residuals of these correlations showed that when the effects of depth and chlorophyll are removed the relationship between TEP and nitrate was significant ($p < 0.01$), but nitrate explained only about 8 % of observed variability in TEP.

The observation that the general silicate distribution was not similarly controlled by phytoplankton biomass suggests that diatoms were not a significant component of the autotrophic community in Bransfield Strait. Similar observations have been reported previously (Castro *et al.*, 2002; Rodriguez *et al.*, 2002; Varela *et al.*, 2002). However, there were exceptions to this general rule. The local low concentration of silicate observed in the northern part of the West transect is likely associated with the advection of TBW from the Bellingshausen Sea, where a strong silicate depletion in the mixed layer related with a higher importance of diatoms has been documented (Castro *et al.*, 2002; Rodriguez *et al.*, 2002; Varela *et al.*, 2002). A silicate minimum was also observed in station x6 in the Central transect associated with a maximum in Chl a in an anticyclonic eddy or frontal meander of warm and fresher water. Microscopic observation and the analysis of phytoplankton by flow cytometry confirmed that large nanoplankton, integrated mainly by diatoms, was abundant in both zones (Rodríguez-Gálvez *et al.*, in preparation). Diatoms are considered major TEP producers in aquatic environments. High concentrations of TEP have frequently been observed during blooms dominated by diatoms (Passow and Alldredge, 1994; Mari and Kiørboe, 1996; Mari and Burd, 1998; Passow *et al.*, 2001). TEP tended to be higher in areas where silicate was relatively low due to its consumption by diatoms. In both cases relatively high TEP levels were not matched by similarly high Chl a concentrations.

TEP and heterotrophic prokaryotes

The relationship between TEP and heterotrophic prokaryotes is complex because free-living bacteria are able to generate TEP (Stoderegger and Herndl, 1999; Grossart, 1999; Passow, 2002b), but they can also use the dissolved organic compounds that serve as precursors for TEP and TEP themselves as sources of organic carbon (Kiørboe and Hansen, 1993; Mari and Kiørboe, 1996; Ogawa *et al.*, 2001; Passow, 2002a). The bacterial contribution to

the observed TEP concentration *in situ* is unknown (Passow, 2002b), although in principle it could be potentially important, considering the quantitative importance of bacterioplankton. However, since a significant positive correlation is usually found between TEP concentration and Chl *a* both in nonaxenic cultures and mesocosms (Corzo *et al.*, 2000; Passow, 2002b; Prieto *et al.*, 2002) and *in situ* (Passow and Alldredge, 1995a,b; Hong *et al.*, 1997; Passow, 2002a), it is likely that phytoplankton rather than bacteria control the production of TEP in nature. Our results seem to support this general trend. TEP concentrations were significantly correlated with Chl *a* in Bransfield, and although TEP showed a weak but significant positive correlation with bacteria abundances, it is likely that this is due to the stronger dependence of both variables, TEP and bacteria, on Chl *a* concentrations. In principle, if bacterial degradation of dissolved organic compounds, precursors for TEP formation, and/or of already formed TEP were quantitatively important processes, an inverse relationship should exist between bacteria abundance and TEP concentration *in situ*. A positive correlation between bacteria and TEP was also found by Passow *et al.* (Passow *et al.*, 2001), which seems to exclude bacterial degradation of TEP as a dominating process in the surface.

ACKNOWLEDGEMENTS

This work was financially supported by grants: MAT2000-0261-P4-04, REN2002-01281/MAR and REN2001-2650/ANT from Ministerio de Ciencia y Tecnología, Spain. We acknowledge the support and help of the Officers and Crew of BIO-Hesperides during CIEMAR. Authors thank three anonymous referees for their suggestions and corrections.

REFERENCES

Alldredge, A. L. and Jackson, G. A. (1995) Aggregation in marine systems. *Deep-Sea Res. II*, **42**, 1–9.

Alldredge, A. L., Passow, U. and Logan, B. (1993) The existence, abundance, and significance of large transparent exopolymer particles in the ocean. *Deep-Sea Res. I*, **40**, 1131–1140.

Basterretxea, G. and Arístegui, J. (1999) Phytoplankton biomass and production during late Austral spring (1991) and summer (1993) in the Bransfield Strait. *Polar Biol.*, **21**, 11–22.

Castro, G. C., Ríos, A. F., Doval, M. D. *et al.* (2002) Nutrient utilization and chlorophyll distribution in the Atlantic sector of the Southern Ocean during Austral summer 1995–96. *Deep-Sea Res. II*, **49**, 623–641.

Corzo, A., Morillo, J. A. and Rodríguez, S. (2000) Production of transparent exopolymeric particles (TEP) in cultures of Chaetoceros calcitrans under nitrogen limitation. *Aquat. Microb. Ecol.*, **23**, 63–72.

Dam, H. G. and Drapeau, D. T. (1995) Coagulation efficiency, organic-matter glues and the dynamics of particles during a phytoplankton bloom in a mesocosm study. *Deep-Sea Res. II*, **42**, 111–123.

Decho, A. W. and Moriarty, D. J. W. (1990) Bacterial exopolymer utilization by a harpacticoid copepod: a methodology and results. *Limnol. Oceanogr.*, **35**, 1039–1049.

Eberlein, K., Keal, M. T., Hansen, K. D. *et al.* (1985) Dissolved organic substances during a Phaecystis bloom in the German Bight (North Sea). *Mar. Biol.*, **89**, 311–316.

Engel, A., Goldthwait, S., Passow, U. *et al.* (2002) Temporal decoupling of carbon and nitrogen dynamics during the course of a mesocosm diatom bloom. *Limnol. Oceanogr.*, **47**, 753–761.

Engel, A. and Passow, U. (2001) Carbon and nitrogen content of transparent exopolymer particles (TEP) in relation to their alcian blue adsorption. *Mar. Ecol. Prog. Ser.*, **219**, 1–10.

García, M. A., López, O., Sospedra, M. *et al.* (1994) Mesoscale variability in the Bransfield Strait region (Antarctica) during Austral summer. *Ann. Geophys.*, **12**, 887–902.

García, M. A., Castro, C. G., Ríos, A. F. *et al.* (2002a) Water masses and the distribution of physico-chemical properties in the Western Bransfield Strait and Gerlache Strait during Austral summer 1995/96. *Deep-Sea Res.II*, **49**, 585–602.

García, C. M., Prieto, L., Vargas, M. *et al.* (2002b) Hydrodynamics and the spatial distribution of plankton and TEP in the Gulf of CádiZ. (SW Iberian Peninsula). *J. Plankton Res.*, **24**, 817–833.

del Giorgio, P. A., Bird, D. F., Prairie, Y. T. *et al.* (1996) Flow cytometric determination of bacterial abundance in lake plankton with the green nucleid acid stain SYTO 13. *Limnol. Oceanogr.*, **41**, 783–789.

Gomis, D., García, M. A., López, O. *et al.* (2002) Quasi-geostrophic 3D circulation and mass transport in the western Bransfield Strait during Austral summer 1995/96. *Deep-Sea Res.II*, **49**, 603–621.

Grasshoff, K., Ehrhardt, M. and Kremling, K. (1983) *Methods of Sea Water Analysis*. Verlag Chemie, Weinheim.

Grossart, H. P. (1999) Interactions between marine bacteria and axenic diatoms (Cylindrotheca fusiformis, Nitzschia laevis and Thalassiosira weissflogii) incubated under various conditions in the lab. *Aquat. Microb. Ecol.*, **19**, 1–11.

Grossart, H. P., Berman, T., Simon, M. *et al.* (1998) Occurrence and microbial dynamics of macroscopic organic aggregates (lake snow) in Lake Kinneret, Israel, in fall. *Aquat. Microb. Ecol.*, **14**, 59–67.

Guillard, R. R. L. and Hellebust, J. A. (1971) Growth and the production of extracellular substances by two strains of Phaeocystis pouchetii. *J. Phycol.*, **7**, 330–338.

Holm-Hansen, O. and Mitchell, B. G. (1991) Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield strait region. *Deep-Sea Res.*, **38**, 961–980.

Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W. *et al.* (1965) Fluorimetric determination of chlorophyll. *J. Cons. Perm. Int. Explor. Mer.*, **30**, 3–15.

Hong, Y., Smith, W. O. and White, A. M. (1997) Studies of transparent exopolymer particles (TEP) produced in the Ross Sea (Antarctica) and by Phaeocystis antarctica (Prymnesiophyceae). *J. Phycol.*, **33**, 368–376.

Karl, D. M., Tilbroook, B. D. and Tien, G. (1991) Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait Antarctica. *Deep-Sea Res.*, **38**, 1097–1126.

Kiørboe, T. and Hansen, J. L. S. (1993) Phytoplankton aggrégate formation: observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material. *J. Plankton Res.*, **15**, 993–1018.

Ling, S. C. and Alldredge, A. L. (2003) Does the marine copepod *Calanus pacificus* consume transparent exopolymer particles (TEP)? *J. Plankton Res.*, **25**, 507–515.

Lipski, M. (1985) Chlorophyll *a* in the Bransfield Strait and the southern part of Drake Passage during BIOMASS-SIBEX (December 1983-January 1984). *Pol. Polar Res.*, **6**, 21–30.

Mann, K. H. and Lazier, J. R. N. (1991) *Dynamics of Marine Ecosystems.* Blackwell, Oxford.

Mari, X. and Burd, A. (1998) Seasonal size spectra of transparent exopolymeric particles (TEP) in a coastal sea and comparison with those predicted using coagulation theory. *Mar. Ecol. Prog. Ser.*, **163**, 63–76.

Mari, X. and Kiørboe, T. (1996) Abundance, size distribution and bacterial colonization of transparent exopolymer particles (TEP) in the Kattegat. *J. Plankton Res.*, **18**, 969–986.

Mitchell, B. G. and Holm-Hansen, O. (1991) Observations and modelling of Antarctic phytoplankton crop in relation to mixing depth. *Deep-Sea Res.*, **38**, 981–1007.

Obernosterer, I. and Herndl, G. J. (1995) Phytoplankton extracellular release and bacterial growth: dependence on the inorganic N : P ratio. *Mar. Ecol. Prog. Ser.*, **116**, 247–257.

Ogawa, H., Amagai, Y., Koike, I. *et al.* (2001) Production of refractory organic matter by bacteria. *Science*, **292**, 917–920.

Passow, U. (2000) Formation of transparent exopolymer particles, TEP, from dissolved precursor material. *Mar. Ecol. Progr. Ser.*, **192**, 1–11.

Passow, U. (2002a) Transparent exopolymer particles (TEP) in aquatic environments. *Prog. Oceanogr.*, **55**, 287–333.

Passow, U. (2002b) Production of transparent exopolymer particles (TEP) by phyto- and bacterioplankton. *Mar. Ecol. Prog. Ser.*, **236**, 1–12.

Passow, U. and Alldredge, A. L. (1994) Distribution, size and bacterial colonization of transparent exopolymer particles (TEP) in the ocean. *Mar. Ecol. Prog. Ser.*, **113**, 185–198.

Passow, U. and Alldredge, A. L. (1995a) A dye-binding assay for the spectrophotometric measurement of transparent exopolymer particles (TEP). *Limnol. Oceanogr.*, **40**, 1326–1335.

Passow, U. and Alldredge, A. L. (1995b) Aggregation of a diatom bloom in a mesocosm: the role of transparent exopolymer particles (TEP). *Deep-Sea Res.II*, **42**, 99–110.

Passow, U. and Alldredge, A. L. (1999) Do transparent exopolymer particles (TEP) inhibit grazing by the euphausiid Euphasia pacifica? *J. Plankton Res.*, **21**, 2203–2217.

Passow, U., Alldredge, A. L. and Logan, B. E. (1994) The role of particulate carbohydrate exudates in the flocculation of diatom blooms. *Deep-Sea Res.I*, **41**, 335–357.

Passow, U., Kozlowski, W. and Vernet, M. (1995) Palmer LTER: temporal variability of transparent exopolymeric particles in Arthur Harbor during the 1994–95 growth season. *Antarct. J.-Review*, **1995**, 265–266.

Passow, U., Shipe, R. F., Murray, A. *et al.* (2001) The origin of transparent exopolymer particles (TEP) and their role in the sedimentation of particulate matter. *Cont. Shelf Res.*, **21**, 327–346.

Passow, U. and Wassmann, P. (1994) On the trophic fate of Phaeocystis pouchetii (Hariot) : IV. The formation of marine snow by P. pouchetii. *Mar. Ecol. Prog. Ser.*, **104**, 153–161.

Prieto, L., Ruiz, J., Echevarría, F. *et al.* (2002) Scales and processes in the aggregation of diatom blooms: high time resolution and wide size range records in a mesocosm study. *Deep-Sea Res.I*, **49**, 1233–1253.

Prieto, L., Sommer, K., Stibor, H. *et al.* (2001) Effects of planktonic copepods on transparent exopolymer particles (TEP) abundance and size spectra. *J. Plankton Res.*, **23**, 515–525.

Ramaiah, N., Yoshikawa, T. and Furuya, K. (2001) Temporal variations in transparent exopolymer particles (TEP) associated with a diatom spring bloom in a subartic ria in Japan. *Mar. Ecol. Prog. Ser.***212**, 79–88.

Rodriguez, F., Varela, M. and Zapata, M. (2002) Phytoplankton assemblages in the Gerlache and Bransfield Straits (Antarctic Peninsula) determined by light microscopy and CEMTAX analysis of HPLC pigment data. *Deep-Sea Res.II*, **49**, 723–747.

Shimeta, J. (1993) Diffusional encounter of submicrometer particles and small cells by suspension feeders. *Limnol. Oceanogr.*, **38**, 456–465.

Shuster, S. and Herndl, G. J. (1995) Formation and significance of transparent exoplymeric particles in the northern Adriatic Sea. *Mar. Ecol. Prog. Ser.*, **124**, 227–236.

Smith, W. O. Jr., Codispoti, L. A., Nelson, D. M. *et al.* (1991) Importance of Phaeocystis blooms in the high-latitude ocean carbon cycle. *Nature*, **350**, 514–516.

Smith, W. O. Jr., Nelson, D. M., DiTullio, G. R. *et al.* (1996) Temporal and spatial patterns in the Ross Sea: phytoplankton biomass, elemental composition, productivity and growth rates. *J. Geophys. Res.*, **101**, 18467–18478.

Stoderegger, K. and Herndl, G. J. (1999) Production of exopolymer particles by marine bacterioplankton under contrasting turbulence conditions. *Mar. Ecol. Prog. Ser.*, **189**, 9–16.

Sverdrup, H. U. (1953) On conditions for the vernal blooming of phytoplankton. *J. Cons. Perm. Int. Exp. Mer.*, **18**, 287–295.

Tranvik, C. J., Sherr, E. B. and Sherr, B. F. (1993) Uptake and utilization of colloidal DOM by heterotrophic flagellates in seawater. *Mar. Ecol. Pro. Ser.*, **92**, 301–309.

UNESCO (1994) Protocols for the Joint Global Ocean Flux Study (JGOFS) core measurements. *Manuals Guides*, **29**, 1–170.

Varela, M., Fernández, E. and Serret, P. (2002) Size-fractionated phytoplankton biomass and primary production in the Gerlache and south Bransfield Straits (Antarctic Peninsula) in Austral summer 1995–1996. *Deep-Sea Res.II*, **49**, 749–768.

Waite, A.M. , Olson, R. J., Dam, H. G. *et al.* (1995) Sugar-containing compounds on the cell surfaces of marine diatoms measured using concanavalin a and flow cytometry. *J. Phycol.*, **31**, 925–933.

Yentsch, C. S. and Menzel, D. W. (1963) A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Res.*, **10**, 221–231.