Deep-Sea Research II 57 (2010) 877–886

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Role of microbial and phytoplanktonic communities in the control of seawater viscosity off East Antarctica (30-80° E)

Laurent Seuront [a,b,*], Sophie C. Leterme [a,b], Justin R. Seymour [a,d], James G. Mitchell [a], Daniel Ashcroft [a], Warwick Noble [a], Paul G. Thomson [c,e], Andrew T. Davidson [c,e], Rick van den Enden [c,e], Fiona J. Scott [c,e], Simon W. Wright [c,e], Mathilde Schapira [a], Coraline Chapperon [a], Nardi Cribb [a]

[a] School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide SA 5001, Australia
[b] South Australian Research and Development Institute, Aquatic Sciences, West Beach SA 5022, Australia
[c] Australian Antarctic Division, Channel Highway, Kingston 7050, Tasmania, Australia
[d] Department of Civil and Environmental Engineering, Massachussets Institute of Technology, Cambridge, USA
[e] Antarctic Climate and Ecosystems Cooperative research Centre, Private Bag 80, Hobart, Tasmania 7001, Australia

ARTICLE INFO

Article history:
Received 22 September 2008
Accepted 22 September 2008
Available online 24 November 2009

Keywords:
Phytoplankton
Bacteria
Seawater viscosity
Biologically increased seawater viscosity
Southern Ocean
East Antarctica

ABSTRACT

Despite the long-standing belief that seawater viscosity is driven by temperature and salinity, biologically increased seawater viscosity has repeatedly been reported in relation to phytoplankton exudates in shallow, productive coastal waters. Here, seawater viscosity was investigated in relation to microbial and phytoplanktonic communities off the coast of East Antarctica along latitudinal transects located between 30°E and 80°E in sub-surface waters and at the deep chlorophyll maximum (DCM). The physical component of seawater viscosity observed along each transects ranged from 1.80 to 1.95 cP, while the actual seawater viscosity ranged from 1.85 to 3.69 cP. This resulted in biologically increased seawater viscosity reaching up to 84.9% in sub-surface waters and 77.6% at the DCM. Significant positive correlations were found between elevated seawater viscosity and (i) bacterial abundance in sub-surface waters and (ii) chlorophyll *a* concentration and the abundance of flow cytometrically-defined auto- and heterotrophic protists at the DCM. Among the 12 groups and 108 species of protists identified under light microscopy, dinoflagellates and more specifically *Alexandrium tamarense* and *Prorocentrum* sp. were the main contributors to the patterns observed for elevated seawater viscosity. Our observations, which generalised the link previously identified between seawater viscosity and phytoplankton composition and standing stock to the Southern Ocean, are the first demonstration of increases in seawater viscosity linked to marine bacterial communities, and suggest that the microbially-increased viscosity might quantitatively be at least as important as the one related to phytoplankton secretion.

1. Introduction

Seawater dynamic viscosity η (cP) is traditionally considered to be controlled by temperature (Miyake and Koizumi, 1948). The dynamic viscosity more than doubles from tropical (30 °C) to polar (0 °C) waters (Dorsey, 1968). In addition, because changes in temperature have a much greater impact on dynamic viscosity of seawater than on its density ρ (kg m^{-3}), which increases less than 1% over a 30 °C decrease in temperature, the kinematic viscosity ν (i.e. $\nu=\eta/\rho$, , cm^2 s^{-1}) typically changes with η. This is critical for microscopic planktonic organisms as the spatial scales influenced by the physical effects of viscosity depend on the natural range of temperatures they may experience in the ocean. Specifically, changes in seawater dynamic viscosity (hereafter referred to as seawater viscosity) directly affect diffusion, the drag experienced by swimming organisms, the Reynolds number and the minimum scale of turbulent velocity and nutrient gradients, i.e. the so-called Kolmogorov and Batchelor length scales. Consequently variation in viscosity may directly affect the ecological processes of exchange dynamics at the surface of plankton and other suspended particles, aggregation and sedimentation rates, motility and the related encounter and ingestion rates. In this context, and considering that these small scale processes control matter transfer through the food chain and hence influence processes such as climate and fisheries productivity up to the global scale (Kolber et al., 2001; Rivkin and Legendre, 2001), seawater viscosity could modulate ocean production and global climate.

A few studies have been devoted to assess the physiological and the mechanical effects of temperature-controlled viscosity on

* Corresponding author at. School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide SA 5001, Australia.
E-mail address: Laurent.Seuront@flinders.edu.au (L. Seuront).

0967-0645/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2008.09.018

bacteria (Berg and Turner, 1979; Atsuni et al., 1996), zooplankton (Podolsky and Emlet, 1993; Podolsky, 1994; Bolton and Havenhand, 1997, 1998, 2005; Hagiwara et al., 1998; de Araujo et al., 2001), mussels (Riisgård and Larsen, 2007) and fish (Johnson et al., 1998; Weiser and Kauffman, 1998; Fuiman and Batty, 1997; von Herbing and Keating, 2003). Much is still, however, to be done to understand how seawater viscosity impacts oceanic processes at different latitudes, and more specifically relates to biological factors. While a drastic 30 °C decrease in temperature induces a 2- to 3-fold change in seawater viscosity, similar changes are generated by the mucous materials produced during phytoplankton blooms (Jenkinson, 1986, 1993a; Jenkinson and Biddanda, 1995; Seuront et al., 2006, 2007; Seuront and Vincent, 2008). More specifically, positive correlation has been found between seawater viscosity and chlorophyll *a* concentration during blooms of the colony-forming Prymnesiophyceae *Phaeocystis* sp. in the German Bight and the North Sea (Jenkinson, 1993a; Jenkinson and Biddanda, 1995). In contrast, studies conducted over the course of a *Phaeocystis globosa* bloom in the eastern English Channel showed the existence of positive and negative correlations between chlorophyll concentration and seawater viscosity respectively before and after the disruption of colonies by turbulent mixing (Seuront et al., 2006, 2007). These results showed that the viscous properties of seawater are mainly driven by extracellular materials associated with *Phaeocystis* colony formation, maintenance and disruption rather than by cell composition and standing stock (Seuront et al., 2006, 2007). Despite the acknowledged ability of marine heterotrophic bacteria to secrete viscous polysaccharides under certain growth conditions (Grobben et al., 1998) and contribute to the production of transparent exopolymer particles, TEP (Stoderegger and Herndl, 1998, 1999; Passow, 2002; Sugimoto et al., 2007), to our knowledge their potential contribution to seawater viscosity has never been investigated.

Phaeocystis antarctica cells and colonies have repeatedly been reported in Antarctic waters, with cell concentration ranging from 10^6 to 10^8 cells l^{-1} in summer; see Schoeman et al. (2005) for a review. However, to our knowledge, no attempt has been made to assess the relative effects of temperature and phytoplankton composition and abundance on seawater viscosity in Antarctic waters in general and over the Antarctic shelf, slope and rise of East Antarctica in particular. The Antarctic margin of the Southern Ocean south of the Polar Front is, however, host to an important marine ecosystem that supports substantial fisheries and is a significant component of the global carbon cycle. Given the hypothesised mechanical hindrance of grazing by increased viscosity (Schnack et al., 1985; Weisse et al., 1994; Schoemann et al., 2005), and the related consequences on secondary production and carbon export and cycling, it is then critical to identify the relative role of physics (i.e. temperature) and biology (i.e. phytoplankton composition and abundance, and heterotrophic bacteria abundance and activity) on seawater viscosity in the area.

In this context, the aims of this study were (i) to provide baseline information on the relative contribution of physics and biology on seawater viscosity, (ii) to relate seawater viscosity to phytoplankton composition and abundance, and (iii) to assess the potential link between seawater viscosity and bacterial abundance and metabolic activity.

2. Material and methods

2.1. Sampling experiment

Sampling was undertaken during austral summer, January-February 28, 2006 off East Antarctica in the area between 30°E and 80°E. The cruise track consisted of 11 meridional transects separated by 5° of longitude with sampling transects alternating with transects where underway data were collected. Detailed biological oceanographic sampling was performed along transect 1 (30°E), 3 (40°E), 5 (50°E), 7 (60°E), 9 (70°E) and 11 (80°E). Between 12 and 18 stations were sampled per transect, using a SeaBird SBE9plus CTD system with dual temperature and conductivity sensors and a single SBE43 dissolved-oxygen sensor, mounted on a SeaBird 24-bottle rosette frame together with a SBE32 24 position pylon and 22 × 10-litre General Oceanics Niskin bottles. At selected stations (Fig. 1A) along each of these transects, samples were obtained for seawater viscosity measurements from a depth of 10 m (subsurface waters) and from the depth of the Deep Chlorophyll Maximum (DCM). On each occasion water from the same Niskin bottle was sampled for salinity, dissolved oxygen, nutrients (phosphate, nitrate+nitrite, silicate and ammonia; Westwood et al., 2010), phytoplankton pigments and community composition (Wright et al., 2010), protist species composition (Davidson et al., 2010)), bacterial concentration and metabolic activity (Thomson et al., 2010) and viral concentration (Thomson et al., 2010).

2.2. Chlorophyll a concentration

Water samples from Niskin bottles, or a clean seawater line, were filtered from 1-2 L seawater onto 13-mm GF/F filters using vacuum < 0.5 atm. The filters were blotted dry and frozen in 1.5-ml cryotubes in liquid nitrogen until analysis. The pigments were extracted by shaking (Biospec Products Mini-beadbeater, 20 sec, 4800 cycles/min) in 300 μL dimethylformamide, following addition of 140 ng apo-8'-carotenal (Fluka) internal standard in 50 μL methanol. Chlorophyll *a* concentrations ($\mu g\, l^{-1}$) were subsequently estimated as detailed in Wright et al. (2010).

2.3. Bacterial abundance

Fresh sea water samples were stained with 2.5 μM of SYTO13 (Molecular Probes) (Gasol and Morán (1999)) and SYTOX Green (Molecular Probes) (Lebaron et al., 1998) to estimate concentrations of total bacteria and bacteria with compromised cell membranes (CCM bacteria), respectively. Fresh samples were also stained with $1\ \mu L\, mL^{-1}$ of 1% (w/v) 6-carboxyfluorecein diacetate (6-CFDA, Polysciences) in acetone to estimate concentrations of bacteria with high esterase activity (Est+ bacteria); see Davidson et al. (2004) for more details. A known concentration of Fluoresbrite 2 μm microspheres (Polysciences) was added to each bacterial sample. Samples were then incubated in the dark for 20 min at 0 ± 0.5 °C of the ambient sea water at the sample site.

Concentrations of stained bacteria and fluorescent microspheres were quantified using a FACScan (Becton Dickinson) flow cytometer. Samples were analysed for 3 min on low flow rate using settings in Table 1 and MilliQ water as the sheath fluid. Numbers of SYTO13 and SYTOX Green stained cells and microspheres were determined in bivariate plots of side scatter (SSC) versus green fluorescence (FL1). Concentrations of Est+ bacteria and microspheres were determined in bivariate plots of FL1 versus red fluorescence (FL3). Numbers of microspheres in each analysis were used to determine the sample volume analysed, allowing the calculation of concentrations of stained bacteria.

2.4. Auto- and heterotrophic protists

A 1:10 working solution of Lysotracker® Green was prepared daily by diluting the 1 mM commercial stock with 0.22 μm

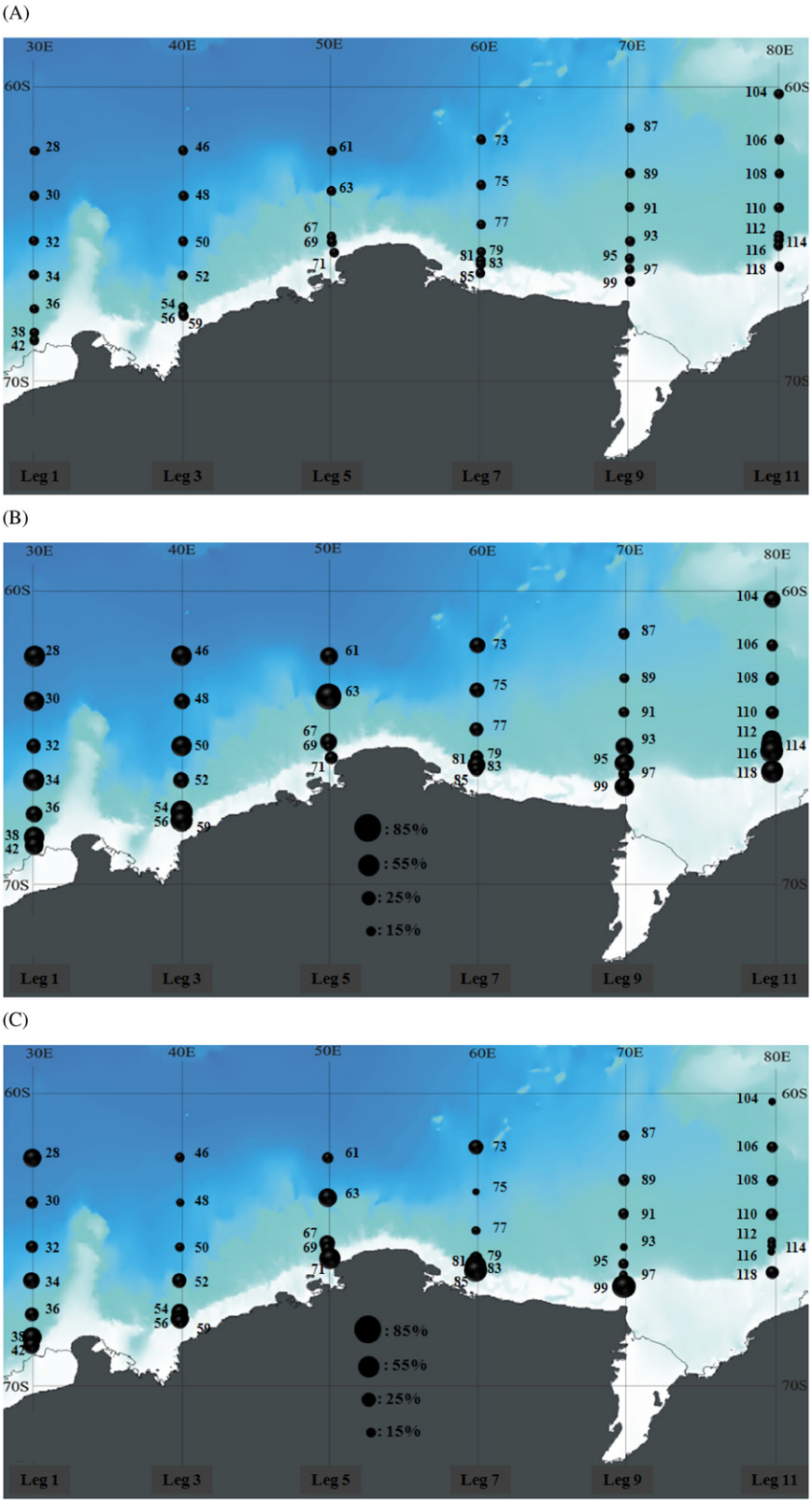

Fig. 1. BROKE-West survey area between 30°E and 80°E showing (A) transect legs and CTD sites where seawater viscosity was investigated, and seawater elevated viscosity η measured in subsurface waters (B) and at the Deep Chlorophyll Maximum (C). The circle area is proportional to seawater elevated viscosity.

filtered seawater. Five ml seawater samples were stained with the working solution to a final stain concentration of 75 nM, mixed and incubated in the dark and on ice for 10 min. Following incubation, 1-ml stained sub-samples were transferred to sterile 5-ml Falcon tubes. A known concentration of 2.5 μm Molecular Probes green PeakFlow beads was added and samples were run in the flow cytometer for 10 min on high flow rate using 0.22-μm filtered seawater sheath fluid. Microautotrophic and

Table 1
Descriptive statistics of the viscosity components of seawater along the 6 latitudinal transects. η_m: measured viscosity ($\eta_m=\eta_{T,S}+\eta_{Bio}$, where $\eta_{T,S}$ and η_{Bio} are the physically-controlled and biologically-controlled viscosity components (cP); DCM: Deep-Chlorophyll Maximum; η: relative excess viscosity (%); SD: standard deviation; Min and Max: minimum and maximum values, respectively.

	Transect											
	1		**3**		**5**		**7**		**9**		**11**	
	10 m	DCM	10 m	DCM	10 m	DCM	10 m	DCM	10 m	DCM	10 m	DCM
$\eta_{T,S}$(cP)												
Mean	1.88	1.94	1.85	1.93	1.86	1.93	1.87	1.94	1.85	1.90	1.89	1.89
SD	0.13	0.11	0.05	0.08	0.07	0.10	0.10	0.07	0.08	0.11	0.11	0.08
Min	1.82	1.93	1.80	1.93	1.82	1.91	1.82	1.93	1.83	1.84	1.82	1.83
Max	1.93	1.94	1.90	1.94	1.91	1.95	1.93	1.95	1.87	1.95	1.96	1.94
η_m(cP)												
Mean	2.74	2.32	2.65	2.44	2.61	2.65	2.39	2.53	2.35	2.35	2.67	2.16
SD	0.21	0.24	0.40	0.29	0.44	0.29	0.15	0.51	0.29	0.45	0.37	0.08
Min	2.39	2.12	1.99	2.10	2.05	2.27	2.26	1.94	2.06	2.06	2.22	2.03
Max	2.95	2.81	3.08	2.81	3.44	3.14	2.63	3.42	2.72	3.37	3.14	2.31
η_{Bio}(cP)												
Mean	0.86	0.38	0.80	0.51	0.75	0.72	0.52	0.59	0.50	0.45	0.82	0.27
SD	0.21	0.24	0.40	0.29	0.44	0.29	0.15	0.51	0.29	0.45	0.37	0.08
Min	0.51	0.18	0.14	0.17	0.19	0.34	0.39	0.13	0.21	0.16	0.37	0.14
Max	1.07	0.87	1.23	0.88	1.58	1.21	0.76	1.48	0.87	1.47	1.29	0.42
η(%)												
Mean	45.7	35.8	43.5	26.3	40.1	37.2	27.9	35.2	26.9	23.6	41.4	14.3
SD	11.6	14.2	21.1	15.0	23.8	15.5	7.5	26.2	16.4	24.1	19.0	5.2
Min	27.2	20.7	7.6	8.8	10.2	17.6	21.0	6.6	11.5	8.6	17.4	7.5
Max	57.1	58.8	66.3	45.8	84.9	62.9	40.7	76.5	47.0	77.6	66.0	22.2

heterotrophic protists were discriminated and enumerated by flow cytometry on a scatter plot of green fluorescence versus red fluorescence from their high red and green fluorescence, respectively; see Thomson et al. (2010) for a thorough assessment of the quality and sensitivity of the method. Due to cell diameter restrictions of the FACScan sample probe, only protists smaller than 50 μm were discriminated by flow cytometry. As a consequence, further information on the auto- and heterotrophic protist community composition were obtained through water samples preserved in Lugol's iodine solution (2% final concentration) and enumerated under light microscope; see Davidson et al. (2010) for further details.

2.5. Viscosity measurement

Viscosity measurements were conducted using a portable ViscoLab400 viscometer (Cambridge Applied Systems Inc., Boston) from 10 ml sub-samples following Seuront et al. (2006, 2007). Viscosity was measured in triplicate from 3-ml water subsamples poured into a small chamber, where a low mass stainless steel piston is magnetically forced back and forth, with a 230-μm piston-cylinder gap size. The force driving the piston is constant, and the time required for the piston to move back and forth into the measurement chamber is proportional to the viscosity of the fluid. The more viscous the fluid the longer the length of time it takes for the piston to move through the chamber, and *vice versa*. As viscosity is influenced by temperature and salinity (Miyake and Koizumi, 1948), the measured viscosity η_m (cP) can be thought of as the sum of a physically-controlled viscosity component $\eta_{T,S}$ (cP) and a biologically-controlled viscosity component η_{Bio} (cP):

$$\eta_m = \eta_{T,S} + \eta_{Bio} \quad (1)$$

As the piston-cylinder gap is only 230 μm, any organism or colony of organisms larger than 230 μm would still be destroyed in the measurement chamber and result in a biased increase in seawater viscosity (Seuront et al., 2007), each water sample was carefully screened through a 200-μm mesh before measurements. For each triplicate sample, 10 successive viscosity measurements (η_m) were taken. The physically-controlled component $\eta_{T,S}$ was estimated from viscosity measurements conducted on subsamples after passing through 0.20-μm pore-size filters. The biologically-induced elevated viscosity η_{Bio} (cP) was subsequently defined from each water sample as:

$$\eta_{Bio} = \eta_m - \eta_{T,S} \quad (2)$$

The relative elevated viscosity η (%) is finally given as (Seuront et al., 2006, 2007):

$$\eta = (\eta_m - \eta_{T,S})/\eta_{T,S} \quad (3)$$

Between each viscosity measurement, the viscometer chamber was carefully rinsed first with deionised water and then with bulk phase seawater filtered through 0.2-μm pore-size filters to avoid any potential contamination of the next sample by viscous compounds.

2.6. Statistical analysis

As the number of viscosity measurements per station was low ($N \leq 30$) non-parametric statistics were used throughout this work. Multiple comparisons between transects and stations were performed using the Kruskal-Wallis test (KW test), and a subsequent multiple comparison procedure based on the Tukey test (Zar, 1996) was used to determine which transects were significantly different from each other. Correlation analysis between variables were conducted using the Spearman's rank correlation coefficient ρ.

The presence of monotonous trends along each transect was tested by calculating Kendall's coefficient of rank correlation, τ, between biological parameters and the latitudinal coordinates of each station. Correlation between variables was investigated using Kendall's coefficient of rank correlation, τ. Kendall's coefficient of correlation was used in preference to Spearman's

coefficient of correlation ρ because Spearman's ρ gives greater weight to pairs of ranks that are further apart, while Kendall's τ weights each disagreement in rank equally; see Sokal and Rohlf (1995) for further information.

Spatial patterns in seawater elevated viscosity were related to multivariate protist community structure using the BIOENV procedure (PRIMER-E version 5; Clarke and Warwick, 2001). This procedure (Clarke and Ainsworth, 1983) was used to identify the protist groups and species that best explained variation in seawater elevated viscosity. A square-root transformation was used prior to the analysis to stabilise variance (Clarke, 1993). Combinations of the protist groups and species were considered at increasing levels of complexity, i.e. k variables at a time (k=1, 2, 3), to yield the best matches of biotic and abiotic similarity matrices for each k, as measured by Spearman's rank correlation ρ. This method then selects the protist groups and species that best explain the seawater elevated viscosity pattern by maximizing a Spearman's rank correlation between their respective similarity matrices. The best three explanatory variables were taken into account to determine which combination of protist groups and species induces the changes observed in seawater elevated viscosity.

3. Results

The physical and biological properties that are relevant to the distribution of seawater viscosity of the survey regions have been extensively described in this volume; these include the physical oceanography, circulation and water mass properties of the region (Williams et al., 2010; Meijers et al., 2010), and their contribution to the distribution patterns observed for chlorophyll *a* concentration (Williams et al., 2010), phytoplankton community structure and stocks (Wright et al., 2010), protist species composition and abundance , and marine microbes (Thomson et al., 2010). As a consequence, to avoid redundancy, we only present here the results of the viscosity measurements and the related correlative and multivariate analyses.

3.1. Seawater viscosity

The physically-controlled viscosity component $\eta_{T,S}$ due to temperature and salinity only weakly varied along the six latitudinal transects, ranging from 1.80 to 1.96 cP in sub-surface waters and from 1.84 to 1.95 cP at the DCM (Table 1; Fig. 2). In contrast, the actual seawater viscosity η_m ranged from 1.99 to 3.44 cP in sub-surface waters and from 1.94 to 3.42 cP at the DCM (Table 1). This resulted in the biologically-driven viscosity component η_{Bio} ranging from 0.14 to 1.58 cP in sub-surface waters and from 0.13 to 1.48 cP at the DCM (Table 1; Fig. 2). Seawater elevated viscosity η thus ranged from 7.6 to 84.9% in subsurface waters, and from 6.6 to 77.6% at the DCM (Table 1; Fig. 1B, C).

Significant differences were found between transects for each depth (KW test, $p<0.05$). More specifically, sub-surface samples break into two distinct groups of decreasing viscosity including (i) transects 1, 3, 5 and 11, and (ii) transects 7 and 9, respectively. In contrast, DCM samples break into three groups of decreasing viscosity including (i) transects 1, 5, 7 and 11, (ii) transects 3 and 9, and (iii) transect 11, respectively. Seawater elevated viscosity was significantly higher in sub-surface waters than at the DCM for transects 1, 3 and 11 ($p<0.05$), and significantly higher at the DCM than in sub-surface waters for transect 7 ($p<0.05$). In contrast, no significant differences were found in seawater elevated viscosity between the two depths for transects 5 and 9 ($p<0.05$).

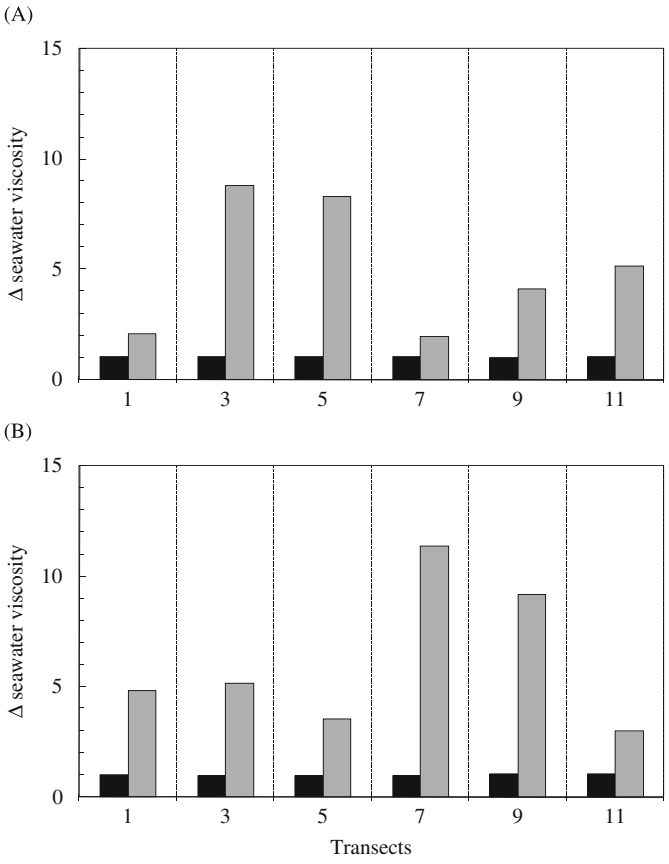

Fig. 2. Maximum changes (defined as the ratio between the observed maximal and minimal values) observed in the physically-controlled viscosity component $\eta_{T,S}$ (black bars) and the biologically-controlled seawater viscosity η_{Bio} (grey bars) along each latitudinal transects in sub-surface waters (A) and at the Deep Chlorophyll maximum (B).

When considered by transect, significant differences were found between stations for each transect (KW test, $p<0.05$). There was also a significant effect of depth on elevated viscosity ($p<0.05$), with significant differences found between the two depths for most stations of each transect ($p<0.05$; Fig. 3). Significantly increasing trends in η towards the continent were observed in sub-surface waters along transects 9 and 11, and at the DCM along transects 3, 5 and 7 (Kendall τ, $p<0.05$). In contrast, elevated seawater viscosity significantly decreased towards the continent in the sub-surface waters of transect 5 ($p<0.05$).

Finally, differences in seawater viscosity across oceanic fronts and between ice and open-water stations were inferred pooling elevated viscosity measurements conducted (i) at stations located north and south of the Southern Boundary and north and south of the Antarctic Circumpolar Current front, and (ii) at stations with no sea-ice present and at stations that had sea-ice present or that had sea-ice up to four days prior to sampling. In both cases, no significant differences were found between the different groups of stations in sub-surface waters and at the DCM (KW test, $p<0.05$).

3.2. Seawater viscosity and microbial community

The abundance of total bacteria, bacteria with high esterase activity (Est+ bacteria) and bacteria with compromised cell membranes (CCM bacteria) ranged from 2.81×10^4 to 69.29×10^4 ml^{-1}, $0.33\times\times10^4$ to 12.36×10^4 ml^{-1}, and 1.29×10^4 to $19.13\times1.29\times10^4$ ml^{-1} over the survey region (Table 2). More specifically, significant differences in the abundance of total

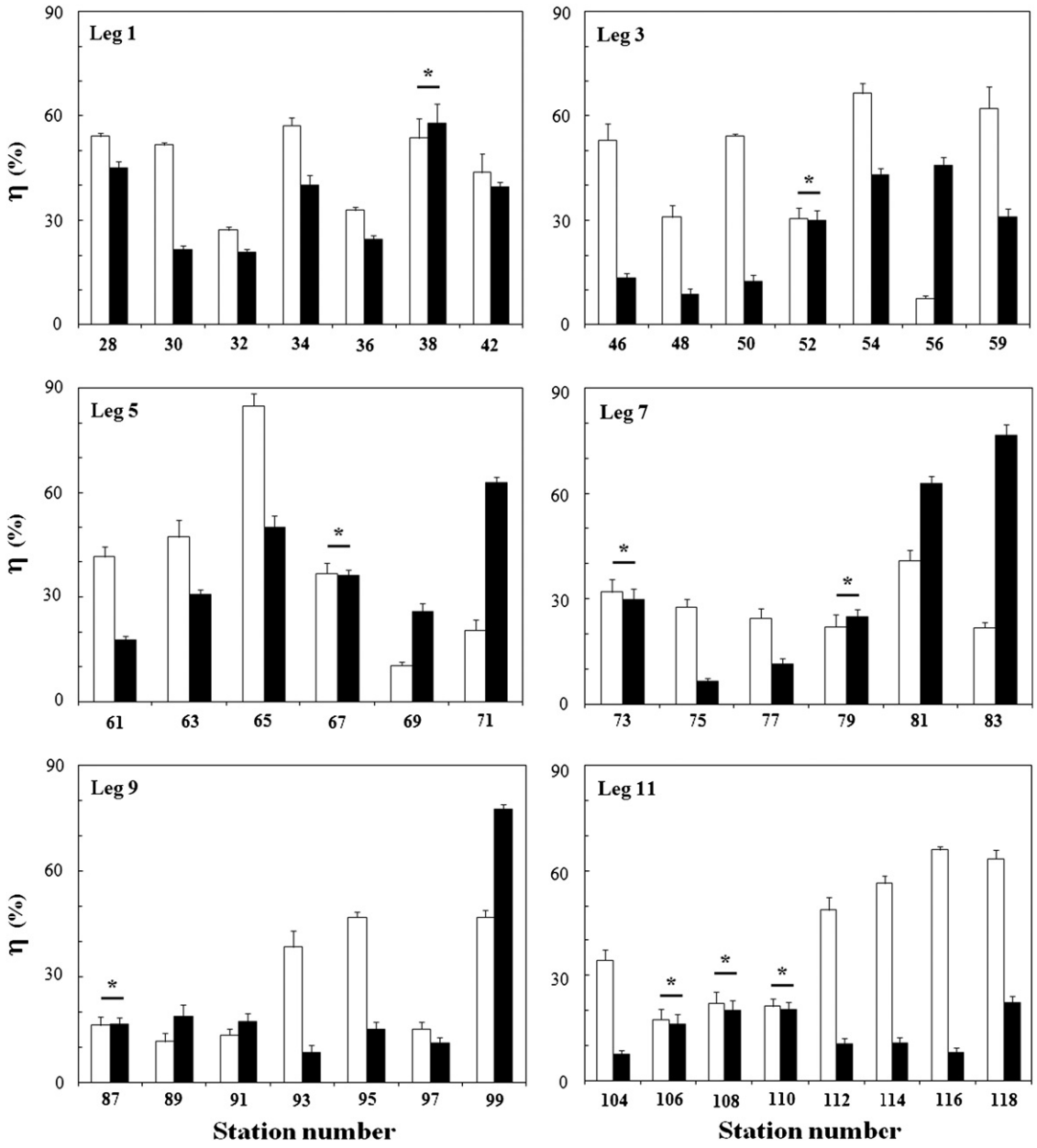

Fig. 3. Elevated seawater viscosity η (%) shown for sub-surface waters (white bars) and the deep-chlorophyll maximum (DCM; black bars) along each latitudinal transect. The error bars are the standard deviations. The stations are numbered in ascending order relative to their respective latitudes. *: stations where sub-surface and DCM elevated seawater viscosities were not significantly different ($p > 0.05$).

bacteria, Est+ bacteria and CCM bacteria were found between transects for each depth (KW test, $p < 0.05$). Total bacteria break into two groups of decreasing abundance including (i) transects 1, 3, 5 and 11 and (ii) transects 7 and 9. In contrast, Est+ and CCM bacteria break into three distinct groups of decreasing abundance including (i) transects 1, 3 and 5, (ii) transect 9 and (iii) transect 7. No significant differences between depth were found along each transect for the abundance of each category of bacteria considered ($p < 0.05$), except for the CCM bacteria that were more abundant at the DCM for transect 3. Est+ bacteria were consistently less abundant than CCM bacteria, with Est+/CCM ratio ranging from 0.41 to 0.89 in sub-surface waters and from 0.32 to 0.56 at the DCM. The reader is referred to for further information on the impact of physical oceanography, circulation and water mass properties on the dynamics of microbial communities.

Correlation analyses revealed highly significant positive correlation ($p < 0.01$) between seawater elevated viscosity η and the abundance of total bacteria, bacteria with high esterase activity (Est+ bacteria), and significant positive correlation ($p < 0.05$) with the abundance of bacteria with compromised cell membranes (CCM bacteria; Table 3) in sub-surface waters. In contrast, at the DCM no significant correlations were found between seawater elevated viscosity η and the abundance of total, Est+ and CCM bacteria ($p > 0.05$; Table 3).

3.3. Seawater viscosity, chlorophyll a concentration and protist community

Chlorophyll *a* concentration (Table 2) significantly differed between transects for each depth (KW test, $p < 0.05$). Chlorophyll *a* concentrations were significantly lower for transect 3 than for transects 1, 5, 7, 9 and 11. Except for transect 3, chlorophyll *a* concentrations were consistently higher at the DCM than in

Table 2
Descriptive statistics of chlorophyll *a* concentration (Chl. *a*), the abundance of flow cytometrically-defined total bacteria, bacteria with high esterase activity (Est+bacteria), bacteria with compromised cell membranes (CCM bacteria), microautotrophic protists (Microautotrophs) and microheterotrophic protists (Microheterotrophs). DCM: Deep-Chlorophyll Maximum; SD: standard deviation; Min and Max: minimum and maximum values, respectively.

	Transect											
	1		3		5		7		9		11	
	10m	DCM	10m	DCM	10m	DCM	10m	DCM	10m	DCM	10m	DCM
Chl.*a*($\mu g\ l^{-1}$)												
Mean	0.70	0.82	0.44	0.47	0.61	1.09	1.18	1.31	0.66	0.77	0.49	0.72
SD	0.33	0.12	0.21	0.09	0.17	0.25	0.54	0.53	0.36	0.35	0.10	0.11
Min	0.10	0.31	0.10	0.18	0.26	0.46	0.21	0.30	0.17	0.30	0.19	0.44
Max	2.63	1.23	1.67	0.78	1.38	2.10	3.35	3.61	2.83	2.83	1.11	1.20
Total bacteria ($\times 10^4\ ml^{-1}$)												
Mean	18.48	23.51	22.97	25.72	24.24	29.56	6.55	7.88	8.22	9.33	39.82	36.78
SD	2.11	3.58	2.34	1.23	6.57	8.27	0.46	1.38	1.87	1.99	2.34	1.92
Min	9.69	13.03	11.44	3.17	8.65	12.42	3.99	4.68	2.81	4.21	13.81	18.74
Max	19.92	35.77	24.77	12.36	24.24	60.61	7.32	15.31	17.91	17.91	69.29	63.91
Est+bacteira ($\times 10^4\ ml^{-1}$)												
Mean	4.52	4.72	5.63	6.82	5.39	4.20	1.43	1.39	2.88	2.73	–	–
SD	1.07	1.12	1.14	1.23	1.81	1.06	0.47	0.42	0.62	0.55	–	–
Min	2.54	1.79	2.55	3.17	1.03	1.65	0.38	0.33	1.25	1.49	–	–
Max	4.52	8.40	9.76	12.36	5.39	7.82	3.67	2.95	5.59	5.59	–	–
CCM bacteira ($\times 10^4\ ml^{-1}$)												
Mean	10.20	10.91	7.43	13.32	11.06	11.72	3.48	3.61	4.81	5.16	–	–
SD	3.02	2.31	0.90	1.24	2.36	2.14	0.59	0.49	0.83	0.71	–	–
Min	3.05	4.61	4.47	8.74	4.25	6.41	1.29	1.72	1.36	2.56	–	–
Max	10.85	18.04	11.35	19.13	11.06	17.67	6.16	5.59	7.63	7.60	–	–
Microautorophs ($\times 10^4\ ml^{-1}$)												
Mean	31.90	34.38	36.71	32.79	21.78	20.12	42.96	41.90	25.71	16.41	–	–
SD	11.63	11.49	7.64	7.78	3.39	4.18	9.27	14.81	6.57	4.85	–	–
Min	18.41	8.40	9.06	7.97	11.71	12.44	17.70	25.51	12.79	6.83	–	–
Max	66.62	52.35	59.65	54.89	25.24	32.41	78.34	86.29	25.71	16.41	–	–
Microheterotrophs ($\times 10^4\ ml^{-1}$)												
Mean	2.33	1.76	1.19	1.20	1.44	2.03	1.90	2.47	1.56	1.09	–	–
SD	0.40	0.59	0.25	0.25	0.29	0.43	0.26	0.67	0.49	0.37	–	–
Min	1.32	0.13	0.37	0.58	0.58	0.80	0.94	1.51	0.35	0.25	–	–
Max	3.29	2.82	2.17	2.14	1.75	3.10	2.47	4.47	1.56	1.09	–	–

Table 3
Spearman correlation analysis between seawater excess viscosity η, the abundance of total bacteria, bacteria with compromised cell membranes (CCM bacteria), and bacteria with high esterase activity (Est+bacteria), Chlorophyll *a* concentration (Chl. *a*) and the abundance of auto- and heterotrophic protists. * and ** are the 5% and 1% significance levels, respectively.

	Seawater excess viscosity	
	Sub-surface	DCM
Total Bacteria	0.57**	0.15
CCM bacteria	0.33*	−0.03
Est+bacteria	0.74**	−0.03
Chl.*a*	0.11	0.76**
Microautorophs	−0.08	0.60**
Microheterotrophs	−0.04	0.56**

sub-surface waters ($p < 0.05$). A similar pattern of variation was observed for both microautotrophic and microheterotrophic protists (Table 2), that were both significantly correlated with chlorophyll a concentrations; see Thomson et al. (2010) for further details on the links between water mass properties and planktonic communities.

Elevated seawater viscosity did not exhibit any significant correlation with chlorophyll *a* concentration and the abundance of auto- and heterotrophic protists in subsurface waters ($p > 0.05$; Table 3). These correlations became, however, highly significantly positive at the DCM ($p < 0.01$; Table 3). None of the 12 groups and 108 species of protists observed over the survey region exhibited significant correlation with elevated seawater viscosity in subsurface waters and at the DCM ($p > 0.05$).

The potential role played by protist community composition on the observed elevated seawater viscosity η was specified by the BIOENV procedure that revealed that dinoflagellates best explained the patterns of elevated seawater viscosity ($r_{spearman}=0.260$, $p < 0.05$; Spearman's rank correlation coefficient). More specifically, among the 17 species identified within the dinoflagellates group, two species (*Alexandrium tamarense* and *Prorocentrum* sp.) best explained the seawater elevated viscosity spatial patterns ($r_{spearman}=0.324$, $p < 0.01$). This result was confirmed by a BIOENV procedure conducted on the 108 species identified over the study region which showed that the two species that best explained the spatial patterns of seawater elevated viscosity were also *Alexandrium tamarense and Prorocentrum* sp. ($r_{spearman}=0.324$, $p < 0.01$).

4. Discussion

4.1. Elevated viscosity and phytoplankton composition and standing stock

The positive correlation between elevated seawater viscosity and chlorophyll *a* concentration at the DCM is consistent with

observations conducted during the growth phase of intense *Phaeocystis globosa* blooms in the coastal waters of the English Channel (Seuront et al., 2006, 2007; Seuront and Vincent, 2008). This is also consistent with the observed increase in transparent exopolymer particles (TEP) production during the growth phase of a *P. globosa* bloom (Mari et al., 2005). Biologically-increased seawater viscosity has previously been specifically related to the secretion of extracellular polymers by phytoplankton cells, through the identification of significant positive correlations between seawater viscosity and chlorophyll concentration (Jenkinson, 1993a; Jenkinson and Biddanda, 1995; Seuront et al., 2006, 2007; Seuront and Vincent, 2008). Significant negative correlations between elevated seawater viscosity and chlorophyll *a* concentration have also been identified during the wane of a *P. globosa* bloom, when the physical disruption of the colonial matrix by turbulent mixing leads to the release of *P. globosa* cells and other phytoplankton cells from the mucilaginous materials (Seuront et al., 2007; Seuront and Vincent, 2008). In contrast to previous observations that have related the temporal patterns of biologically-controlled seawater viscosity to the presence and abundance of *P. globosa* (Seuront et al., 2006, 2007; Seuront and Vincent, 2008), no significant correlation was found between elevated seawater viscosity and the abundance of single celled or colonial *Phaeocystis antarctica* off East Antarctica. The contribution of dinoflagellates to the carbon biomass of phytoplankton assemblages was relatively low (Davidson et al., 2010). This group (and in particular *Alexandrium tamarense* and *Prorocentrum* sp.), however, appears to be the main contributor to the biologically-driven increase in seawater viscosity. This is consistent with the previously reported viscous properties of dinoflagellate species such as *Gyrodinium aureolum* and *Noctiluca scintillans* (Jenkinson, 1993b; Jenkinson and Biddanda, 1995), the reported production of exudates by *Alexandrium tamarense* and *Prorocentrum* sp. (Ogata and Kodama, 1986; Taylor, 1987; Hansen, 1989), the observation of sticky mucus layer embedding resting cysts of *Alexandrium* species in the water column (Persson, 2006), and the scarcity of the Prymnesiophyceae *Phaeocystis antarctica* (Davidson et al., 2010).

4.2. Microbial versus phytoplanktonic control of seawater viscosity

The positive correlations found between elevated seawater viscosity and bacteria abundance in sub-surface waters and between elevated seawater viscosity and chlorophyll *a* concentration at the DCM (Table 3) suggest a distinct control of seawater viscosity in these two waters masses. More specifically, the positive correlation found between elevated seawater viscosity and bacteria abundance in the phytoplankton depleted surface waters is consistent with previous observations of correlations between heterotrophic bacterial abundance and the amount of viscous transparent exopolymeric (TEP) material in seawater (Corzo et al., 2005). The relationship between bacteria and TEP is, however, quite complex (Passow and Alldredge, 1994) and appears to vary according to environmental conditions (Grossart 1999), with bacteria apparently responsible for both the production and dissolution of TEP. Bacteria are often found attached to, or embedded within, TEP (Passow and Alldredge, 1994; Mari and Kiørboe, 1996) and may in some instances be important agents in TEP degradation (Mari and Kiørboe, 1996). Indeed polymeric materials may be an important source of organic carbon for marine bacteria and microbial transformation and exploitation of organic polymers has been predicted to play an important role in the oceanic carbon cycle (Azam, 1998; Bhaskar and Bhosle, 2005). Alternatively, bacterial activity can also lead to increased TEP production. Levels of TEP production by diatoms have been shown to increase in the presence of bacteria (Grossart, 1999), and it is possible that in some circumstances the intense enzymatic dissolution of POC by bacteria attached to organic aggregates (Smith et al., 1992) could lead to TEP accumulation. Bacteria also secrete viscous polysaccharides under certain growth conditions (Grobben et al., 1998) and marine bacteria have been directly implicated in the production of TEP (Stoderegger and Herndl, 1998, 1999; Passow, 2002; Sugimoto et al., 2007). Indeed marine bacteria may be an important source of TEP production in the absence of phytoplankton (Ramaiah et al., 2001). Our observations are the first demonstration of increases in seawater viscosity linked to marine bacterial communities, but are consistent with previous observations linking bacterial abundance and activity to the production and distribution of polymeric materials in seawater. These observations, in conjunction with previous evidence (Stoderegger and Herndl, 1999; Passow, 2002; Sugimoto et al., 2007) indicate that, like phytoplankton, bacteria may modify the viscosity of seawater by producing polymeric materials. Additionally, changes in polymeric materials in seawater may influence bacterial growth (Azam et al., 1983; Azam, 1998) and related changes in the viscosity of seawater can also influence the ecology and morphology of marine bacteria (Atsuni et al., 1996).

The present work is then the first report supporting microbially-increased seawater viscosity. In addition, except for transect 1, the elevated seawater viscosity reported here in surface waters is significantly higher or similar to that observed at the DCM. This suggests that the microbially-increased viscosity might quantitatively be at least as important as that related to phytoplankton secretion. The lack of any significant differences between the abundance of bacteria in sub-surface waters and at the DCM further suggests that the increase in seawater viscosity in sub-surface waters might be related to the level of activity of the microbial community. This hypothesis is not supported by significant differences in the relative abundance of Est+ and CCM bacteria in sub-surface waters and at the DCM. However, the method employed to assess bacteria abundance and activity intrinsically considers free-living bacteria, and as such underestimate the fraction of attached-bacteria which are likely to be more abundant in the particle-rich DCM (e.g., Middelboe et al., 1995; Unanue et al., 1997). Further studies investigating the link between bacterial abundance and activity and seawater viscosity should then take care in identifying the relative abundance and contribution to seawater viscosity of free-living and attached-bacteria.

4.3. Biologically-increased seawater viscosity: eastern Antarctic waters versus temperate waters

The elevated seawater viscosity observed in the present work ranged from 3 to 89% (Table 1). These values are consistent with recent estimates ranging from 1 to 362% (Seuront et al., 2006, 2007; Seuront and Vincent, 2008). Taking into account the temperature differences encountered in the present work off East Antarctica over the duration of our survey (-1.6 to 1.26 °C) and in the eastern English Channel over the duration of the phytoplankton spring bloom (February to July, 6-18 °C), the corresponding physically-controlled viscosity component $\eta_{T,S}$ ranged from 1.80 to 1.95 cP, and from 1.15 to 1.57 cP, respectively. This converts into actual viscosity η_m ranging from 1.85 to 3.69 cP off East Antarctica, and from 1.23 to 4.58 cP in the eastern English Channel. Because of the limited temperature changes observed in Antarctic waters over the survey region, most of the variability in seawater viscosity is induced by the modifications observed in the biologically-controlled viscosity component η_{Bio}. In contrast, in the eastern English Channel, the actual seawater viscosity

η_m results from the interplay between the decreasing $\eta_{T,S}$ with summer heating and the complex dynamics of η_{Bio} driven by the concentration and the composition of the phytoplankton community. Further work would then be needed to assess the impact of the temporal dynamic of a phytoplankton bloom on seawater viscosity in Antarctic waters and also the potential contribution of the microbial community to the observed viscosity fluctuations in temperate waters.

In the temperate waters of the North Sea and the English Channel, the intensity of the phytoplankton spring blooms, i.e. up to 60 μg of chlorophyll *a* per litre, the related organic exudation and the numerical dominance of *P. globosa* on the phytoplankton community have been shown to be the main contributors of the increase in seawater viscosity (Seuront et al., 2006, 2007; Seuront and Vincent, 2008). However, other phytoplankton species are also contributing to increased seawater viscosity as an elevated viscosity of up to 12% has been observed in the absence of *P. globosa* in the phytoplankton community (Seuront et al., 2006, 2007). It is then likely that the viscosity increases related to phytoplankton biomass at the DCM are not only driven by the abundance of *A. tamarense* and *Prorocentrum* sp., but the cumulative result of the exudates produced by the whole phytoplankton community.

4.4. On the relevance of biologically-increased seawater viscosity

While this is beyond the scope of the present work, it is also stressed that biologically-increased seawater viscosity may have a variety of implications for a range of physical processes such as eddy diffusivity, the scale of the smallest turbulent eddies or propagation of acoustic waves in seawater. A novel acoustic absorption mechanism has recently been suggested for frequencies above 100 kHz as the result of biologically-increased seawater viscosity (Rhodes, 2008). The predicted additional absorption typically lies in the frequency band of bio-acoustic spectra and high frequency navigational sonars, acoustic Doppler velocimeters, fish-finding sonars and mine-hunting and side-scan sonars. Biologically-increased seawater viscosity therefore might have significant impacts on a range of ecological processes involving marine mammals and anthropogenic activities. This issue, however, has only been theoretically investigated (Rhodes, 2008), and still critically needs to be thoroughly assessed.

5. Conclusions

The potential contribution of phytoplanktonic exudates to increase seawater viscosity has only marginally been considered in the literature. The present work then extends previous investigations conducted in the laboratory or in relation to intense bloom formation to the waters of the Southern Ocean. We also provide the first evidence of the link between bacterial abundance and seawater viscosity, and suggest that the microbially-driven contribution to seawater viscosity might be at least as important as the one related to phytoplankton secretion. The role played by biologically-driven seawater viscosity is potentially far reaching as it may directly affect sedimentation and remineralisation processes, but also predator-prey, male-female and virus-host encounter rates, and as such impact biogeochemical fluxes. Due to the intricate links existing between polymeric materials, seawater viscosity and the dynamics of planktonic organisms (e.g. Azam, 1998), the elucidation of the relative contributions of phytoplanktonic and microbial communities to seawater viscosity, through, e.g., viral lysis, over a wide range of habitats is likely to provide new insights into the structure and function of marine ecosystems.

Acknowledgments

The authors thank the captain and crew of the RSV *Aurora Australis* for their expertise and cooperation throughout the duration of the cruise, and the team of CTD operators and samplers for their assistance in collecting the water samples. This research was supported by the Australian Government's Cooperative Research Centres Programme through the Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC). This work was funded by the Australian Antarctic Division (Projects #2382 to J.G. Mitchell and #2596 to L. Seuront), the Flinders University and the Australian Research Council. (Discovery Projects DP0664681, DP0666420 and DP0772186). Professor Seuront is the recipient of an Australian Professorial Fellowship (project number DP0988554). We are very grateful to Klaus Meiners and Karen Westwood for their constructive comments on an earlier version of this work.

References

Atsuni, T., Maekawa, Y., Yamada, T., Kawagishi, I., Imae, Y., Homma, M., 1996. Effect of Viscosity on Swimming by the Lateral and Polar Flagella of *Vibrio alginolyticus*. Journal of Bacteriology 178, 5024–5026.

Azam, F., 1998. Microbial control of oceanic carbon flux: the plot thickens. Science 280, 694–696.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. Marine Ecology Progress Series 10, 257–263.

Berg, H.C., Turner, L., 1979. Movement of microorganisms in viscous environments. Nature 278, 349–351.

Bhaskar, P.V., Bhosle, N.B., 2005. Microbial extracellular polymeric substances in marine biogeochemical processes. Current Science 88, 45–53.

Bolton, T.F., Havenhand, J.N., 1997. Physiological versus viscosity-induced effects of water temperature on the swimming and sinking velocity of larvae of the serpulid polychaete *Galeolaria caespitosa*. Marine Ecology Progress Series 159, 209–218.

Bolton, T.F., Havenhand, J.N., 1998. Physiological versus viscosity-induced effects of an acute reduction in water temperature on microsphere ingestion by trochophore larvae of the serpulid polychaete *Galeolaria caespitosa*. Journal of Plankton Research 20, 2153–2164.

Bolton, T.F., Havenhand, J.N., 2005. Physiological acclimation to decreased water temperature and relative importance of water viscosity in determining the feeding performance of larvae of a serpulid polychaete. Journal of Plankton Research 27, 875–879.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecolology 18, 117–143.

Clarke, K.R., Ainsworth, M., 1983. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205–219.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition PRIMER-E, Plymouth, UK.

Corzo, A., Rodríguez-Gálvez, S., Lubian2, L., Sangrá, P., Martínez, A., Morillo, J.A., 2005. Spatial distribution of transparent exopolymer particles (TEP) in the Bransfield Strait (Antarctica). Journal of Plankton Research 27, 635–646.

Davidson, A.T., Thompson, P.G., Westwood, K., van den Enden, R., 2004. Estimation of bacterioplankton activity in Tasmanian coastal waters and between Tasmania and Antarctica using stains. Aquatic Microbial Ecology 37, 33–45.

Davidson, A.T., Scott, F.J., Nash, G.V., Wright, S.W., Raymond, B., 2010. Physical and biological control of protistan community composition, distribution and abundance in the seasonal ice zone of the Southern Ocean between 30 and 80E. Deep-Sea Research II 57 (9–10), 828–848.

de Araujo, A.B., Hagiwara, A., Snell, T.W., 2001. Effect of unionized ammonia, viscosity and protozoan contamination on reproduction and enzyme activity of the rotifer *Brachionus rotundiformis*. Hydrobiologia 446/447, 363–368.

Fuiman, L.A., Batty, R.S., 1997. What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. Journal of Experimental Biology 200, 1745–1755.

Gasol, J.M., Morán, X.A.G., 1999. Effects of filtration on bacterial activity and picoplankton community structure as assessed by flow cytometry. Aquatic Microbial Ecology 16, 251–264.

Grobben, G.J., Chin-Joe, I., Kitzen, V.A., Boels, I.C., Boer, F., Sikkema, J., Smith, M.R., de Bont, J.A.M., 1998. Enhancement of Exopolysaccharide Production by *Lactobacillus delbrueckii* subsp. *bulgaricus* NCFB 2772 with a Simplified Defined Medium. Applied and Environmental Microbiology 64, 1333–1337.

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. Aquatic Microbial Ecology 19, 1–11.

Hagiwara, A., Yamamiya, N., de Araujo, A.B., 1998. Effect of water viscosity on the population growth of the rotifer *Brachionus plicatilis* Müller. Hydrobiologia 387/388, 489–494.

Hansen, P.J., 1989. The red tide dinoflagellate *Alexandrium tamarense:* effects on behaviour and growth of a tintinnid ciliate. Marine Ecology Progress Series 53, 105–116.
Jenkinson, I.R., 1986. Oceanographic implications of non-Newtonian properties found in phytoplankton cultures. Nature 323, 435–437.
Jenkinson, I.R., 1993a. Bulk-phase viscoelastic properties of seawater. Oceanolgica Acta 16, 317–334.
Jenkinson, I.R., 1993b. Viscosity and elasticity of *Gyrodinium aureolum* and *Noctiluca scintillans* exudates in relation to mortality of fish and damping of turbulence. In: Smayda, T.J., Shimizu, Y. (Eds.), Toxic Phytoplankton Blooms in the Sea. Elsevier, Amsterdam, pp. 757–762.
Jenkinson, I.R., Biddanda, B.A., 1995. Bulk-phase viscoelastic properties of seawater: relationship with plankton components. Journal of Plankton Research 17, 2251–2274.
Johnson, T.P., Cullum, A.J., Bennett, A.F., 1998. Partitioning the effects of temperature and kinematic viscosity on the C-start performance of adult fishes. Journal of Experimental Biology 201, 2045–2051.
Kolber, Z.S., Plumley, F.G., Lang, A.S., Beatty, J.T., Blankenship, R.E., VanDover, C.L., Vetriani, C., Koblizek, M., Rathgeber, C., Falkowski, P.G., 2001. Contribution of aerobic photoheterotrophic bacteria to the carbon cycle in the ocean. Science 292, 2492–2495.
Lebaron, P., Catala, P., Parthuisot, N., 1998. Effectiveness of SYTOX Green stain for bacteriql viability assessment. Aquatic Microbial Ecology 64, 2697–2700.
Mari, X., Kiørboe, T., 1996. Abundance, size distribution and bacterial colonization of transparent exopolymer particles (TEP) during spring in the Kattegat. Journal of Plankton Research 18, 969–986.
Mari, X., Rassoulzadegan, F., Brussaard, C.P.D., Wassmann, P., 2005. Dynamics of transparent exopolymeric particles (TEP) production by *Phaeocystis globosa* under N- or P-limitation: a controlling factor of the retention/export balance. Harmful Algae 4, 895–914.
Meijers, A.J.S., Klocker, A., Bindoff, N.L., Williams, G.D., Marsland, S.J., 2010. The circulation and water masses of the Antarctic shelf and continental slope between 30 and 80E. Deep-Sea Research II 57 (9–10), 723–737.
Middelboe, M., Søndergaard, M., Letarte, Y., Borch, N, 1995. H. Attached and free-living bacteria: production and polymer hydrolysis during a diatom bloom. Microbial Ecology 29, 231–248.
Miyake, Y., Koizumi, M., 1948. The measurements of the viscosity coefficient of sea water. Journal of Marine Research 7, 63–66.
Ogata, T., Kodama, M., 1986. Ichthyotoxicity found in cultured media of *Protogonyaulax* spp. Marine Biology 92, 31–34.
Passow, U., 2002. Production of transparent exopolymer particles (TEP) by phyto- and bacterioplankton. Marine Ecology Progress Series 236, 1–12.
Passow, U., Alldredge, A.L., 1994. Distribution, size and bacterial colonization of transparent exopolymer particles (TEP) in the ocean. Marine Ecology Progress Series 113, 185–198.
Persson, A., 2006. Grazing on toxic *Alexandrium fundyense* resting cysts and vegetative cells by the eastern oyster (*Crassostrea virginica*). Harmful Algae 5, 678–684.
Podolsky, R.D., 1994. Temperature and viscosity: physiological versus mechanical effects on suspension feeding. Science 265, 100–103.
Podolsky, R.D., Emlet, R.B., 1993. Separating the effects of temperature and viscosity on swimming and water movement by sand dollar larvae (*Dendraster excentricus*). Journal of Experimental Biology 176, 207–221.
Ramaiah, N., Yoshikawa, T., Furuya, K., 2001. Temporal variations in transparent exopolymer particles (TEP) associated with a diatom spring bloom in a subarctic ria in Japan. Marine Ecology Progress Series 212, 79–88.
Rhodes, C.J., 2008. Excess acoustic absorption due to the biological modification of seawater viscosity. ICES Journal of Marine Science, in press.
Riisgård, H.U., Larsen, P.S., 2007. Viscosity of seawater controls beat frequency of water-pumping cilia and filtration rate of mussels *Mytilus edulis*. Marine Ecology Progress Series 343, 141–150.
Rivkin, R.B., Legendre, L., 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291, 2398–2400.
Schnack, S.B., Smetacek, V., Von Bodungen, B., Stegmann, P., 1985. Utilisation of phytoplankton by copepods in Antarctic waters during spring. In: Gray, J.S., Christiansen, M.E. (Eds.), Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. Wiley, Chichester, pp. 11–17.
Schoemann, V., Becquevort, S., Stefels, J., Rousseau, V., Lancelot, C., 2005. Phaeocystis. blooms in the global ocean and their controlling mechanisms: a review. Journal of Sea Research 53, 43–66.
Seuront, L., Lacheze, C., Doubell, M.J., Seymour, J.R., Van Dongen Vogels, V., Newton, K., Alderkamp, A.C., Mitchell, J.G., 2007. The influence of *Phaeocystis globosa* on microscale spatial patterns of chlorophyll *a* and bulk-phase seawater viscosity. Biogeochemistry 83, 173–188.
Seuront, L., Vincent, D., 2008. Increased seawater viscosity, *Phaeocystis globosa* and *Temora longicornis* feeding and swimming behaviours. Marine Ecology Progress Series, in press.
Seuront, L., Vincent, D., Mitchell, J.G., 2006. Biologically-induced modification of seawater viscosity in the eastern English Channel during a *Phaeocystis globosa* spring bloom. Journal of Marine Systems 61, 118–133.
Sokal, R.R., Rohlf, F.J., 1995. Biometry, The principles and practice of statistics in biological research. Freeman, San Francisco.
Stoderegger, K., Herndl, G.J., 1998. Production and release of bacterial capsular material and its subsequent utilization by marine bacterioplankton. Limnology Oceanography 43, 877–884.
Stoderegger, K., Herndl, G.J., 1999. Production of exopolymer particles by marine bacterioplankton under contrasting turbulence conditions. Marine Ecology Progress Series 189, 9–16.
Sugimoto, K., Fukuda, H., Abdul Baki, M., Koike, I., 2007. Bacterial contributions to formation of transparent exopolymer particles (TEP) and seasonal trends in coastal waters of Sagami Bay. Japan. Aquatic Microbial Ecology 46, 31–41.
Taylor, F.J.R, 1987. Dinoflagcllate Morphology. In: Taylor, F.J.R. (Ed.), The Biology of Dinoflagellates. The Botanical Monographs, Vol. 21. Blackwell, Oxford, pp. 21–91.
Thomson, P.G., Davidson, A.T., van den Enden, R., Pearce, I, Seuront, L. Paterson, J.S., Williams, G., 2010. Distribution and abundance of marine microbes in the Southern Ocean between 30 and 80°E longitude. Deep-Sea Research II 57 (9–10), 815– 827.
Unanue, M., Ayo, B., Azúa, I., Barcina, I., Iriberri, J., 1997. Temporal variability of attached and free-living bacteria in coastal waters. Microbial Ecology 23, 27–39.
von Herbing, I.H., Keating, K., 2003. Temperature-induced changes in viscosity and its effects on swimming speed in larval haddock. In: Browman, H.I., Skiftesvik, A.B. (Eds.), The Big Fish Bang of the 26th Annual larval Fish Conference, pp. 23–34.
Weiser, W., Kauffman, R., 1998. A note on interactions between temperature, viscosity, body size and swimming energetics in fish larvae. Journal of Experimental Biology 201, 1369–1372.
Weisse, T., Tande, K., Verity, P., Hansen, F., Gieskes, W., 1994. The trophic significance of *Phaeocystis* blooms. Journal of Marine System 5, 69–79.
Williams, G.D., Nicol, S, Bindoff, N., Aoki, S., Meijers, A., Marsland, S., Klocker, A., Iijima, Y., 2010. Surface Oceanography of BROKE-West, along the Antarctic Margin of the South-West Indian Ocean (30°-80°E). Deep-Sea Research II 57 (9–10), 738–757.
Wright, S.W., van den Enden, R.L., Pearce, I., 2010. Phytoplankton community structure and stocks in the Southern Ocean (30–80°E) determined by CHEMTAX analysis of HPLC pigment signatures. Deep-Sea Research II 57 (9–10), 758–778.
Zar, J.H., 1996. In: Biostatistical analysis. Prentice Hall, NJ.