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Biologically induced modification of seawater viscosity in the Eastern English Channel during a *Phaeocystis globosa* spring bloom

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Abstract

To identify the potential relationship between *Pheaocystis globosa* bloom conditions and seawater properties, a hydrobiological survey was performed in the inshore waters of the Eastern English Channel over the course of the phytoplankton spring bloom. Chlorophyll concentration, auto- and hetero/mixotrophic composition of protists and standing stock, and seawater viscosity were measured weekly from March to June 2004. The decline of the bloom is characterized by a massive foam formation in the turbulent surf zone. Before foam formation, seawater viscosity significantly increased, showing a significant positive correlation with chlorophyll concentration. In contrast, after foam formation this correlation was negative, seawater viscosity kept increasing despite a sharp decrease in chlorophyll concentrations. No significant correlation has been found between seawater viscosity and the composition of the phytoplankton assemblages observed during the survey. However, significant positive correlations have been found between seawater viscosity and both the size and the abundance of *P. globosa* colonies. From the correlation patterns observed between chlorophyll concentration and seawater viscosity, we suggest that the rheological properties of seawater are mainly driven by extracellular materials associated with colony formation and maintenance rather than by cell composition and standing stock.

Keywords: Seawater viscosity; Phytoplankton; Rheology; *Phaeocystis globosa*; Spring bloom dynamics; Eastern English Channel

1. Introduction

Navier–Stokes equations, as well as any subsequent models of marine turbulence (Baumert et al., 2005), implicitly assume the seawater medium to be Newtonian, that is without elasticity and with viscosity independent of shear stress (Jenkinson, 1986). Under this assumption seawater viscosity is mainly controlled by its temperature and salinity (Miyake and Koizumi, 1948). In the ocean, viscosity has therefore mainly been thought as controlled by the temperature gradient. However, more recently non-Newtownian or rhelogical properties in seawater have been resolved where the 'apparent viscosity' of the fluid is altered by the presence of biologically

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derived polymeric materials (Jenkinson, 1986, 1993a). Examples of non-Newtownian fluids include suspensions such as coal–water or coal–oil slurries, food products, inks, glues, soaps and polymer solutions (Irvine and Capobianchi, 1998). In the marine environment the presence of small particles and polymeric materials (Koike et al., 1990; Alldredge et al., 1993; Long and Azam, 1996) has led to the proposal that the seawater medium may more accurately be considered as a 'hydrogel' or 'organic matter continuum' (Chin et al., 1998; Azam, 1998). It has early been suggested that mucus sheaths as well as more dispersed polymers excreted by algae represent increased viscosity that may be used by phytoplankton to manage flow fields (Margalef, 1978; Sournia, 1982). Further studies have indicated changes in the bulk-phase seawater rheological properties in relation to phytoplankton blooms. Phytoplankton produce polymeric substances and fibres which have the potential to modify the physical environment by increasing measured viscosity and elasticity (Jenkinson, 1986, 1993a,b; Ramus and Kenney, 1989; Jenkinson and Biddanda, 1995) and to damp turbulence at high shear rates (Hoyt and Soli, 1965; Ramus et al., 1989).

Viscosity controls most hydrodynamic processes at microscales, which is the scale where the most ecologically relevant processes of viral infection (Furhman, 1999), nutrient uptake (Karp-Boss et al., 1996; Blackburn et al., 1998), aggregate formation (Kiørboe, 2001), light harvesting (Kirk, 1994), predator–prey interactions (Gerritsen and Strickler, 1977) and behavior (Seuront et al., 2004) occur. Specifically, changes in viscosity affect the drag experienced by swimming organisms, the Reynolds number (e.g. Vogel, 1994) and the minimum scale of turbulent velocity and nutrient gradients, i.e. the so-called Kolmogorov and Batchelor length scales (Mann and Lazier, 1996). Consequently variation in viscosity may directly affect the ecological processes of exchange dynamics at the surface of plankton and other suspended particles (Mitchell et al., 1985; Csanady, 1986; Jenkinson, 1986; Lazier and Mann, 1989; Karp-Boss et al., 1996), aggregation of particles (Alldredge and Gotschalk, 1989; Jackson, 1990), sinking of phytoplankton blooms (Smetacek and Pollehne, 1986; Andreassen and Wassman, 1998; Peperzak et al., 2003), matter transfer through the food chain (Decho, 1990), predator–prey and sexual partner encounter rates (Gerritsen and Strickler, 1977; Kiørboe and Saiz, 1995), motility and swimming speed of microorganisms (Mitchell, 1991), ingestion rate of the trochophore larvae of serpulid polychaete (Bolton and Havenhand, 1997) and respiration and excretion in the gills of fishes (Jenkinson, 1989, 1993a). In this context, and considering that the consequences of these small-scale interactions influence processes such as climate and fisheries productivity up to the global scale (Kolber et al., 2001; Rivkin and Legendre, 2001), viscosity is likely to modulate ocean production and global climate. In order to understand biomodification of flow, dispersion, particle sinking, and aggregation/disaggregation processes, much has still, however, to be done to investigate how seawater viscosity varies in relation to biological factors.

In the Eastern English Channel and the Southern Bight of the North Sea, the spring phytoplankton bloom is dominated by the Prymnesiophyceae *Phaeocystis globosa*. Beside the intensity of the blooms (Seuront and Souissi, 2002), the genus *Phaoecystis* sp. is also known for the formation of large colonies where cells are embedded in a mucopolysaccharide matrix generated during colony formation by swarming cells (Guillard and Hellebust, 1971). During intense phytoplankton blooms, the water is so gelatinous that it resembles fresh white of egg (Dreyfuss, 1962) or surface slicks occur, damping ripples (Carlson, 1987; Seuront, pers. obs.), and leads to clogging of plankton and fishing nets (Thompson, 1885; Gran 1902; van Breemen, 1905; Ostenfeld, 1904; Delsman, 1914; Savage, 1930; Chang, 1984). In England, *Phaeocystis* sp. blooms were even referred to as 'foul water' or 'baccy juice' (Chadwick, 1885; Thompson, 1885; Orton, 1923). During bloom conditions it has been recently shown (Breton et al., 1999; Gasparini et al., 2000) that *P. globasa* colonies are not grazed by the small sized copepods (mainly *Temora longicornis*), which dominate the Southern Bight of the North Sea and the Eastern English Channel in spring. *P. globasa* also appears to be an unsuitable food for *Macoma balthica* (Kammermans, 1994) and is responsible for a reduction in the clearance rates of *Mytilus edulis* (Smaal and Twisk, 1997). The reasons for these observed trophic effects are not known but colony size (e.g. Weisse et al., 1994), repellant substances and toxic peculiarities (e.g. acrylic acid, DMSP; Sieburth, 1960; Estep et al., 1990; Eilertsen and Raa, 1995; Aanesen et al., 1998; Stabell et al., 1999) or mechanical hindrance (e.g. clogging of feeding appendages; Schnack et al., 1985) have all been suggested. During the bloom decline, the sedimentation of colonies (Cadée, 1996; Andreassen and Wassman, 1998; Svensen, 2002) leads to a massive mortality of benthic invertebrates via anoxia (Rogers and Lockwood, 1990; Peperzak, 2002). At

that time, colonies have also been observed to be washed ashore and to form thick brown jelly layers (Grøntved, 1960; Al-Hasan et al., 1990). Subsequent descriptions (Jenkinson, 1993b; Jenkinson and Biddanda, 1995) of the bulk phase water during blooms suggest changes in its rheological properties. A better known phenomenon is the accumulation of foam formed in the turbulent surf zone of beaches along the North Sea and the Eastern English Channel (Lancelot et al., 1987; Weisse et al., 1994; Rousseau, 2000; Peperzak, 2002), and may be followed by a disappearance of the above mentioned rheological properties.

In this context, the objectives of this article are (i) to investigate seawater viscosity in relation to the dynamics of the *P. globasa* spring bloom occurring in the Eastern English Channel before and after foam formation, (ii) to clarify potential causal relationship between seawater viscosity and the composition of auto- and hetero/mixotrophic protists and standing stocks and (iii) to discuss the implications of variation in seawater viscosity on the physical and biological marine environment.

2. Materials and methods

2.1. Study area

The Eastern English Channel is characterized by its tidal range, between 3 and 9 m, and a residual circulation parallel to the coast, with nearshore coastal waters drifting from the English Channel into the North Sea. Coastal waters are influenced by freshwater run-off from the Seine estuary to the Straits of Dover. This "Coastal Flow" (Brylinski et al. 1991) is separated from offshore waters by a tidally maintained frontal area (Brylinski and Lagadeuc, 1990). This inshore water mass is characterised by its low salinity, turbidity (Dupont et al., 1991), phytoplankton richness (Brylinski et al., 1984) and productivity (Brunet et al., 1992, 1993), when compared to the oceanic offshore waters.

2.2. Sampling strategy

Sampling site was located at the inshore station (50°40′75 N, 1°31′17 E) of the SOMLIT network (Service d'Observation du Milieu Littoral; Fig. 1). This sampling site was chosen as the physical and hydrological properties encountered here are representative of the inshore masses of the Eastern English Channel (Brunet et al., 1992; Seuront, 1999). Sampling was conducted

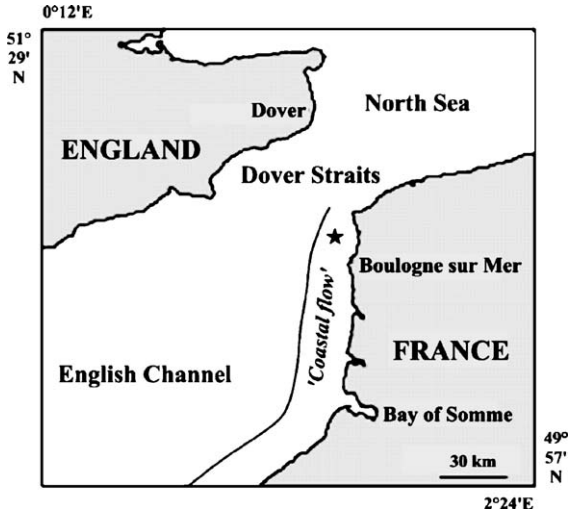

Fig. 1. Study area and location of the sampling station (★) in the inshore waters of the Eastern English Channel.

weekly at high tide, before, during and after the *P. globosa* bloom in the Eastern English Channel from February to June 2004.

Water temperature (°C) and salinity (PSU) profiles from surface to bottom were measured using a Seabird SBE 19 or Seabird SBE 25 Sealogger CTD at each sampling date. The maximal depth never exceeded 25 m. Water samples were taken from sub-surface, intermediate and bottom waters using 5-l Niskin bottles, and repeated 5 times. Chlorophyll *a* concentrations and seawater viscosity were systematically estimated from the same water samples.

The composition and standing stock of auto-, hetero- and mixotrophic protists has been investigated only from sub-surface samples because previous experiments conducted from our inshore sampling site always showed the water column to be well mixed (Lizon et al., 1995; Gentilhomme and Lizon, 1998; Seuront et al., 1996, 1999, 2002; Seuront and Lagadeuc, 1998). In addition, the aim of this paper is to investigate the potential biomodification of seawater viscosity related to the dynamics of the *P. globosa* spring bloom. We thus avoided any possible confusing results which could have resulted from benthic and tychoplanktonic phytoplankton resuspended in the bottom layer of the water column (Dupont et al., 1991; Huault et al., 1994), as their proportion is highly variable at different time scales (MacIntyre and Cullen, 1996; Wolfstein et al., 2000) and strongly depends on the energy dissipation rates of the environment (e.g. spring-neap cycle, season, wind stress; Grabemann and Krause, 2001).

2.3. Chlorophyll a analysis

Chlorophyll concentrations were estimated from 500 ml water samples following Suzuki and Ishimaru (1990). Samples were vacuum filtered on Whatman GF/F glass-fibre filters (porosity 0.45 μm). Chlorophyllous pigments were extracted by direct immersion of the filters in 5 ml *N*,*N*-dimethylformamide, and the extractions were made in the dark at −20 °C. Concentrations of chlorophyll *a* in the extracts were determined following Strickland and Parsons (1972) using a Turner 450 fluorometer previously calibrated with chlorophyll *a* extracted from *Anacystis nidulans* (Sigman Chemicals).

2.4. Protists

The study of auto- and hetero/mixotrophic protists ranging in size from nano- to microplankton was carried out to assess whether particular species were associated with *P. globosa* blooming and thus to investigate their potential contribution, if any, to seawater viscosity fluctuations. One litre samples for micro- and nanoplankton analyses were preserved in the field with acid lugol's solution (2% final concentration) and enumeration was carried out using the Utermöhl (1958) settling method. Ten to 20 ml sub-samples were allowed to settle in Hydro-bios counting chambers and settled slides were observed by inverted microscopy (Olympus; magnification ×320, ×400). Organisms were identified and measured (length and width) using an ocular micrometer. Total ciliated protozoans were enumerated. No taxonomic data are available for May 7.

2.5. Seawater excess viscosity

Viscosity measurements were conducted in the laboratory using a controlled-stress portable Visco-Lab400 viscometer (Cambridge Applied Systems Inc., Boston) from 10 ml water samples stored in the dark in a bucket maintained at in situ temperature. Viscosity was estimated from 3 ml water samples 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. As the force driving the piston is constant, 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 it will take the piston to move through the chamber and the less viscous the fluid, the more rapidly the piston will travel. As viscosity is influenced by the temperature and the salinity, the measured viscosity η_{m} (cP) can be thought as the sum of a temperature- and salinity-controlled viscosity component $\eta_{T,S}$ (cP) and a biologically controlled viscosity component η_{φ} (cP):

$$\eta_{\mathrm{m}} = \eta_{T,S} + \eta_{\varphi}. \tag{1}$$

The physically controlled component $\eta_{T,S}$, was estimated in the laboratory from viscocity measurements conducted on particle-free seawater after filtration through 0.2 μm pore-size filters seawater from the same samples. The biologically induced excess viscosity η_{φ} (cP) was subsequently estimated from each water sample as $\eta_{\varphi}=\eta_{\mathrm{m}}-\eta_{T,S}$. The related relative excess viscosity η is thus given by:

$$\eta = (\eta_{\mathrm{m}}-\eta_{T,S})/\eta_{T,S}. \tag{2}$$

Before each viscosity measurement, temperature and salinity of the water sample were measured using a Hydrolab probe, and the viscometer chamber was carefully rinsed with deionised water between each viscosity measurement. No viscosity measurements were done on February 12 and 16.

2.6. Data analysis

The vertical stratification of the water column was calculated using the potential energy E_{p} (J m^{-3}), which corresponds to the amount of energy required to redistribute mass in a complete vertical mixing (Pond and Pickard, 1983):

$$E_{\mathrm{p}} = \frac{1}{H}\int_{-H}^{0}(\rho-\bar{\rho})gz\mathrm{d}z \tag{3}$$

where H, ρ, $\bar{\rho} = \frac{1}{H}\int_{-H}^{0}\rho z\mathrm{d}z$, g and z are the height of the water column, the density, the mean density of the water column, the gravitational acceleration and the depth, respectively.

As the number of viscosity and chlorophyll measurements was low, non-parametric statistics were used throughout this work. Multiple comparisons between depths and sampling dates were conducted using the Kruskal–Wallis test (KW test hereafter) and the Jonckheere test for ordered alternatives (Siegel and Castellan, 1988) was used to identify distinct groups of viscosity measurements.

To detect dates, intensity and duration of any changes in the values of a given parameter, we used the cumulative sums method (Ibanez et al., 1993). The calculation consists of subtracting a reference value

(here the mean of the series) from the data, then these residuals are successively added forming a cumulative function. Successive negative residuals produce a decreasing slope, whereas successive positive residuals create an increasing slope (the value of the slope is proportional to the mean deviation). Values not very different from the mean show no slope.

3. Results

3.1. Environmental conditions

The potential energy E_p was very low ($E_p<0.05$) over the whole survey period, indicating a well-mixed water column. Vertically averaged salinity thus did not exhibit any characteristic pattern, but a stationary behavior fluctuating between 33.80 and 34.54 PSU (34.20±0.22 PSU; $\bar{x}$±S.E.). In contrast, temperature fluctuated from 6.1 °C on March 3 to 17.5 °C on July 8, and exhibited a clear seasonal cycle (Fig. 2). These temperature and salinity values are fully consistent with previous measurements done at the seasonal scale in the inshore waters of the Eastern English Channel (Brunet, 1993; Breton, 2000; Lizon, 1997; Seuront, 1999).

3.2. Chlorophyll concentration

Initiated in March, the phytoplankton bloom reached its peak value on April 30, with values of chlorophyll up to 51.5 μg l^{-1} (Fig. 3A). The bloom is characterized by a significant increasing trend (Kendall's τ, $p<0.05$) in chlorophyll concentration until April 30, followed by a 5-fold decrease observed on May 7 (Fig. 3A). These observations are specified by the cumulative sum analysis that allows the identification of three distinct regimes in chlorophyll concentrations (Fig. 4). We observed a decreasing slope until March 29 which characterized a group of values lower than the mean of the time series, followed by positive and negative slopes between March 29 and April 30 and after April 30, respectively. The beginning of the third regime roughly coincides with the formation of foam in the turbulent surf zone. No significant difference in chlorophyll *a* concentrations has been observed between the three sampling depths over the course of our survey (KW, $p>0.05$). The mean chlorophyll *a* concentrations thus ranged from 0.9 to 49.7 μg l^{-1} (15.0±μg l^{-1}; $\bar{x}$±S.E.) in surface, 1.0 to 47.6 (16.7 ±3.9 μg l^{-1}; $\bar{x}$±S.E.) at intermediate depth, and 1.2 to 57.3 (18.6±4.7 μg l^{-1}; $\bar{x}$±S.E.) at the bottom. In addition, no significant differences have been observed between the three sampling depths at each sampling date (KW test, $p>0.05$). One must finally note that the time courses of chlorophyll concentration and *P. globosa* colony size were similar before the formation of foam. After foam formation, colony size kept increasing while phytoplankton biomass exhibited a sharp decrease (Fig. 3A).

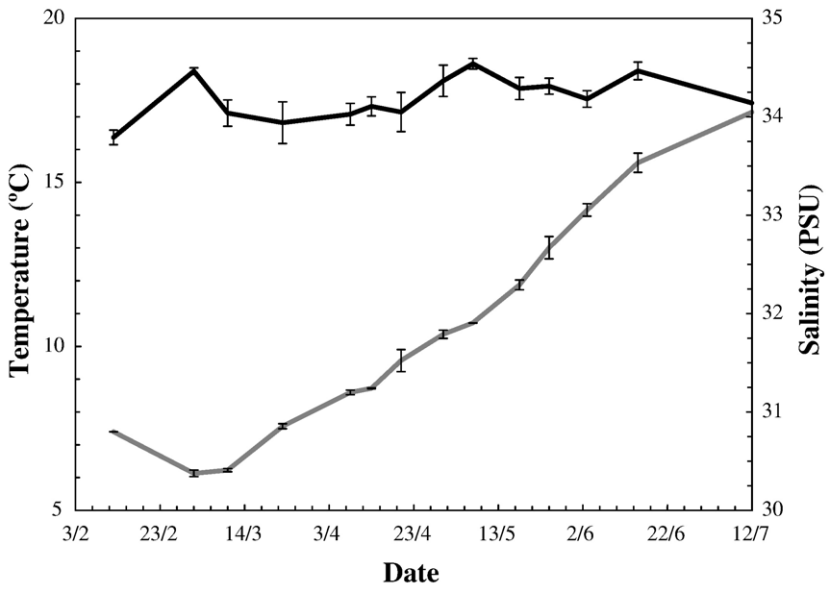

Fig. 2. Time course of depth-averaged temperature (grey) and salinity (black) in the coastal waters of the Eastern English Channel. The error bars indicate the standard deviations of depth-averaged data.

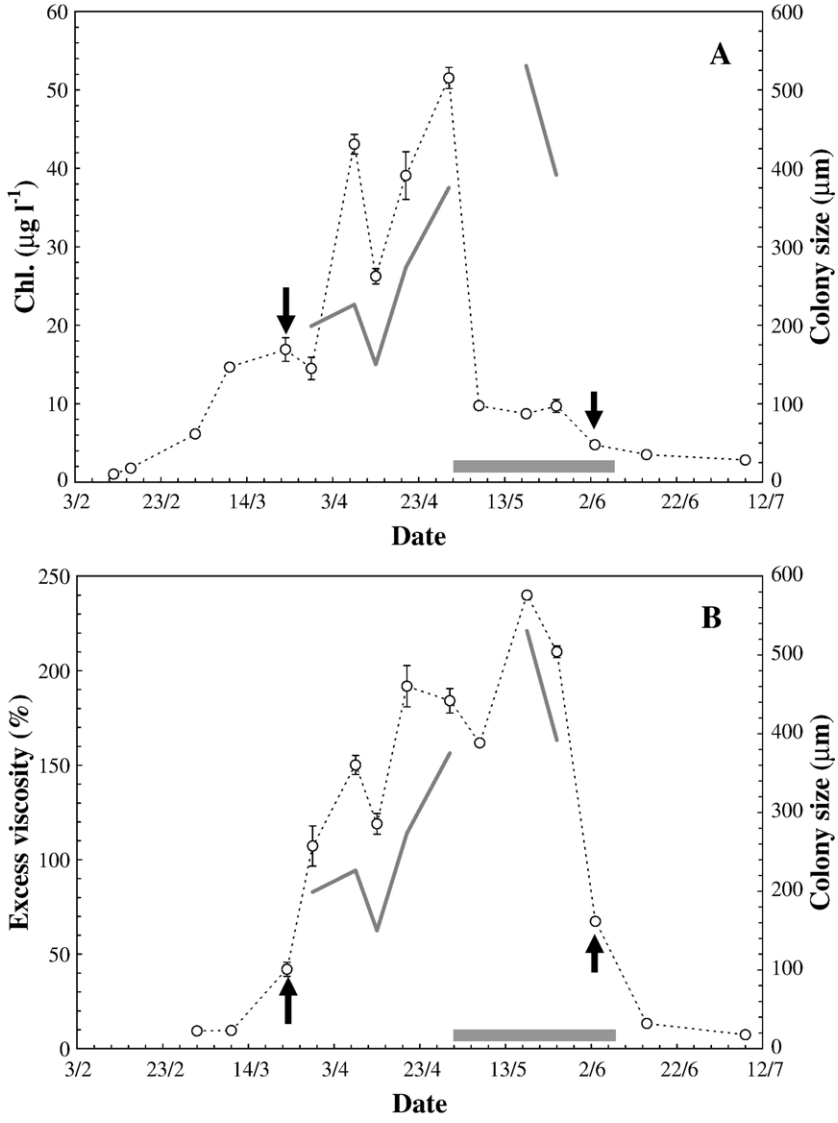

Fig. 3. Time course of chlorophyll concentration (µg l^{-1}; A) and seawater excess viscosity (%; B), shown together with *P. globosa* colony size, in the coastal waters of the Eastern English Channel. The grey bar indicates the period of foam formation, and the black arrows indicate the appearance and disappearance of *P. globosa* in the phytoplankton assemblage. The error bars are the standard deviations of the 15 chlorophyll concentration and viscosity measurements.

3.3. Seawater excess viscosity

The relative excess viscosity η ranged from 8.8% to 259% (117.1±21.7%; $\bar{x}$±S.E.). The time course of the excess viscosity is characterized by a significant increasing trend ($p<0.05$) until May 18 (Fig. 3B), and a sharp decrease on May 7. Examination of the related cumulative sums led to identify three distinct regimes. As observed for chlorophyll concentrations a decreasing slope is observed until March 29 and is followed by positive and negative slopes between March 20 and May 25 and after May 25, respectively. Here the beginning of the third regime is clearly asynchronous with the formation of foam (Fig. 3). No significant difference in excess viscosity has been observed between the three sampling depths over the course of our survey (KW, $p>0.05$). The mean excess viscosity η thus ranged from 9.2% to 274.1% (112.9±20.7%; $\bar{x}$±S.E.) in surface, 9.3% to 238% (115.6±20.0%; $\bar{x}$±S.E.) at intermediate depth, and 9.7% to 234.8% (123.1±21.4%; $\bar{x}$±S.E.) at the bottom. Examination of the differences between the excess viscosity measured at three different depth for

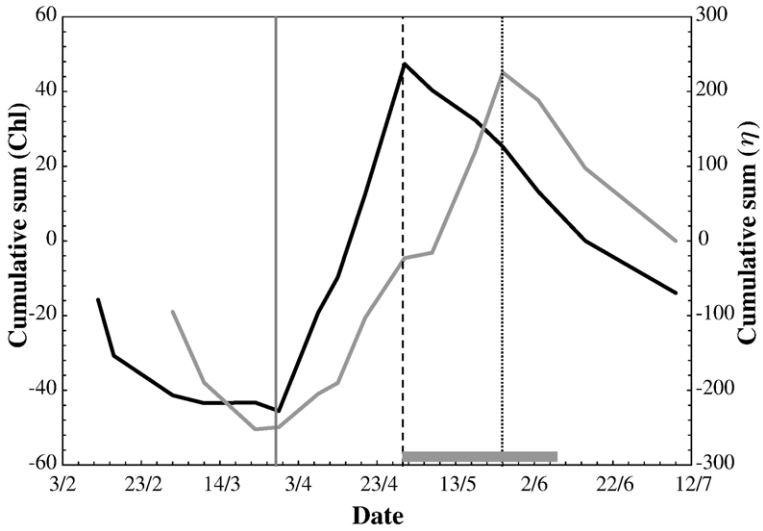

Fig. 4. Cumulative sum estimated for chlorophyll concentration (black) and seawater excess viscosity (grey). The continuous, dashed and dotted lines identified the two and three different regimes observed in the time course of chlorophyll concentration and seawater excess viscosity, respectively. The grey bar indicates the period of foam formation.

each sampling date (i.e. March 2, 10, 23 and 29, April 8, 13, 20 and 30, May 7, 18 and 25, June 3 and 15, and July 8) nevertheless showed that significantly higher excess viscosity has been observed in the bottom layer on March 23 and 29, and April 13, 20 and 30 (Jonckheere test, $p<0.05$). On May 18 and 25 excess viscosity was significantly higher in surface ($p<0.05$). No significant differences were observed between the three different depths investigated on February 12 and 16, April 8, May 7, and June 6 and 15 (KW test, $p>0.05$). The time course of seawater viscosity and *P. globosa* colony size were similar over the whole survey (Fig. 3B).

3.4. Protists' composition and standing stocks

P. globosa cells reached a concentration bounded between 0.8×10^6 cell l^{-1} and $5.5\times$cell l^{-1} between March 29 and April 30, i.e. between 40.4% and 73.2% of the total phytoplankton abundance, and so can be regarded as the major contributor in terms of cell numbers to the spring bloom observed in the Eastern English Channel (Fig. 5A, B). Nanoflagellates represent the second dominant group reaching 1.3×10^6 and $9.4\times$cell l^{-1} (i.e. representing more than 50% of total phytoplankton cell numbers) before and after *P. globosa* bloom, respectively. Diatoms varied from 6% to 70% of total phytoplankton abundance throughout the study period. Observed phytoplankton dynamics revealed the succession of three distinct phytoplankton assemblages, in accordance with previous works done at the seasonal scale in Belgian coastal waters and in the Southern North Sea (Lancelot et al., 1991, 1998; Rousseau et al., 2000; Rousseau et al., 2002). These assemblages correspond to (i) a pre-bloom assemblage (February) dominated by *Thalassiosira rotula* and *Asterionellopsis glacialis*; (ii) a bloom assemblage dominated by *Chaetoceros* sp., *Guinardia delicatula* and *Pseudonitzschia pseudodelicatissima* and (iii) a post-bloom assemblage characterized by *Guinardia flaccida*, *G. delicatula* and *Cerataulina pelagica*. Diatom abundance exhibited two maxima, the first reached a concentration of 1.7×10^6 cell l^{-1} on April 8, which coincided with the one reported for *P. globosa*, while the second occurred on June 15 with a concentration of 2.8×10^6 cell l^{-1}. The first peak is mainly due to diatoms in chain-forming colonies such as *Chaetoceros* sp. (12 μm length), *G. delicatula* (30 μm length) and the pennate *P. pseudodelicatissima* (35 μm length) that reached 1.1×10^6, 1.2×10^5 and 1.1×10^5 cell l^{-1}, respectively. In addition, microscopic examination highlighted the particular embedding of *P. pseudodelicatissima* and *Chaetoceros* sp. into *P. globosa* colonies. The second peak was strongly dominated by *Chaetoceros* sp. that reached 2.1×10^6 cell l^{-1}. Cryptophyceans (7 μm) were at times abundant before and after the *P. globosa* bloom, reaching 20% of total phytoplankton abundance (Fig. 5B). Dinoflagellates and ciliated protozoans were far less abundant with maximum abundance values respectively never exceeding 6.0×10^5 and 1.6×10^4 cell l^{-1}, corresponding to a maximum relative abundance smaller than 15%.

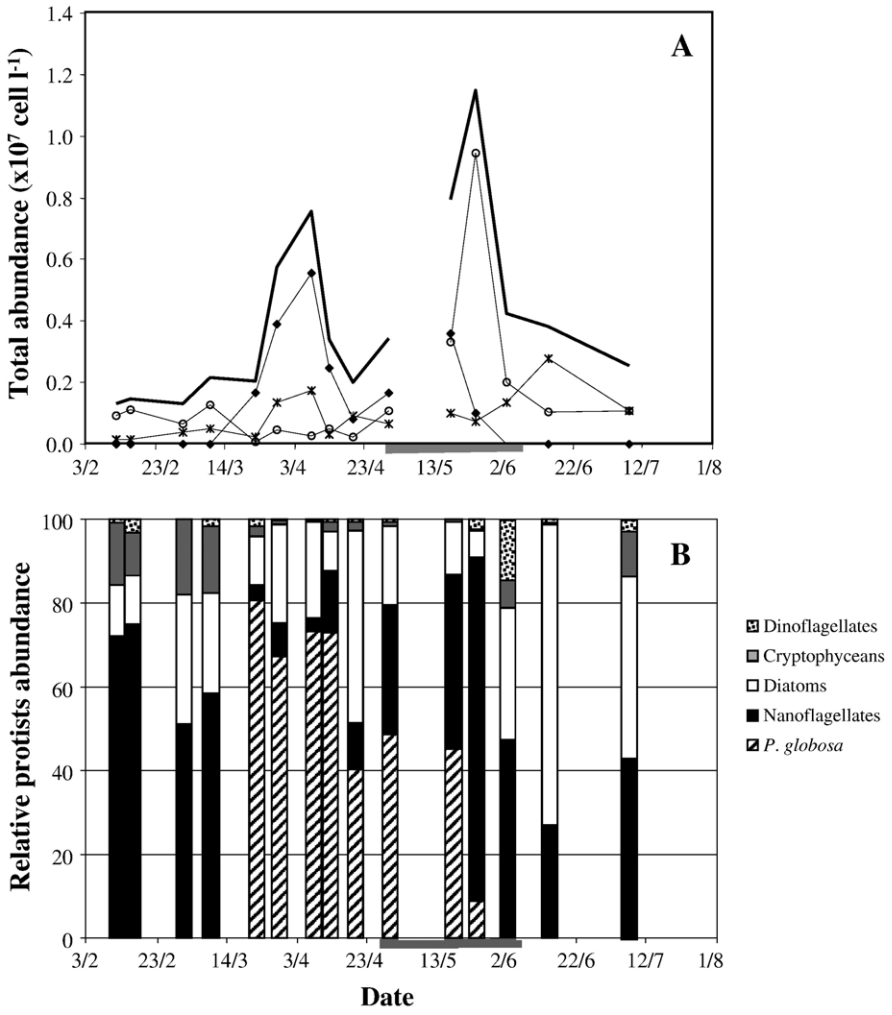

Fig. 5. Time course of total phytoplankton (–), *P. globosa* (♦), nanoflagellates (○) and diatoms (×) abundance (cell l^{-1}, A) and relative protists abundance (%, B) in the coastal waters of the Eastern English Channel. The grey bar indicates the period of foam formation.

3.5. Correlation analyses

Chlorophyll concentration and relative excess viscosity η were not significantly correlated over the course of the survey ($p > 0.05$). This result is specified by the two different correlation patterns observed at each sampling date between the 15 measurements of chlorophyll concentrations and seawater viscosity in relation with the foam formation and the presence of *P. globosa* cells in the phytoplankton populations (Fig. 6A). Before and after the formation of foam, chlorophyll concentration and excess viscosity were then always positively and negatively correlated, suggesting a coupling/decoupling dynamic between phytoplankton biomass and seawater viscosity. This is confirmed by the clear increase in the values of the excess viscosity, b_η, predicted by the linear regression $\eta = a_\eta[\mathrm{Chl}] + b_\eta$ in the absence of chlorophyll (Fig. 6B).

4. Discussion

We have provided evidence that seawater viscosity was at different times either positively or negatively correlated with chlorophyll concentration during the phases of the spring *P. globosa* bloom preceding and following the formation of organic matter, transformed into foam in the turbulent surf zone. We will propose hereafter a mechanistic explanation of the observed coupling/decoupling dynamics between phytoplankton biomass and excess viscosity based on the bloom dynamics of the swarming Prymnesiophyceae *P. globosa*. It has been previously shown that the

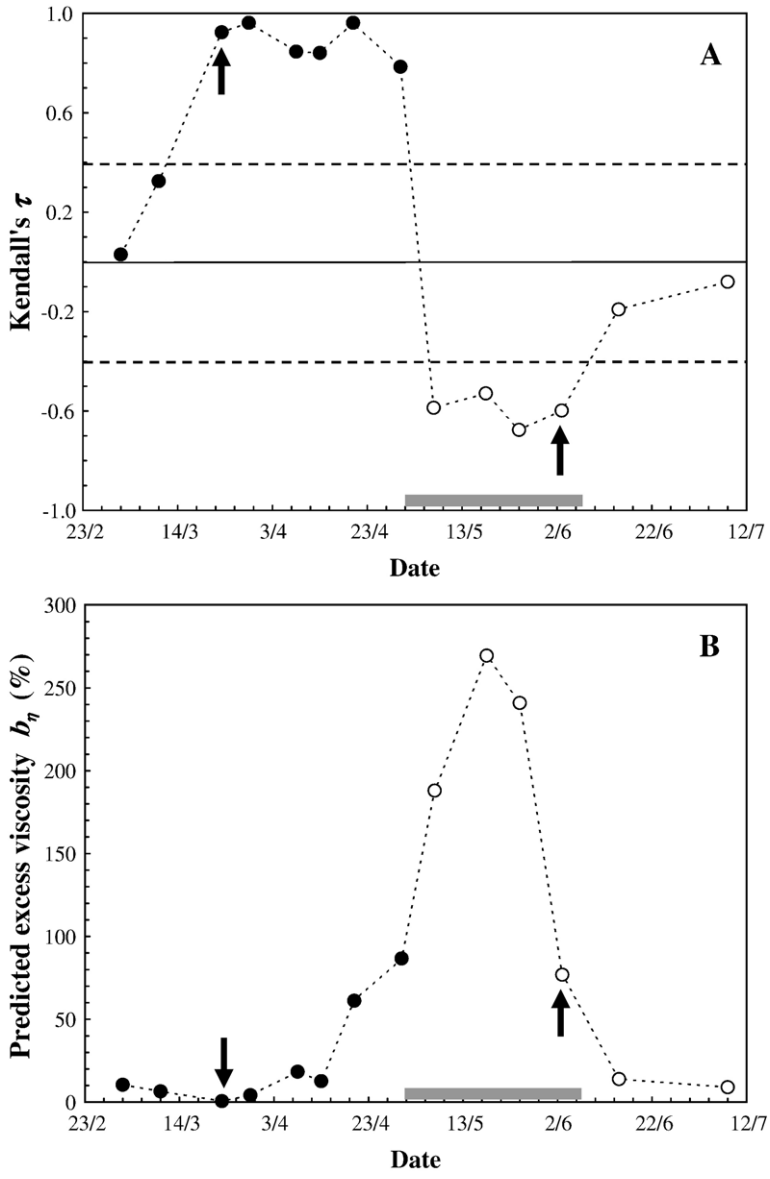

Fig. 6. Plot of the time course of the Kendall's correlation coefficient τ, estimated between the 15 replicate measurements of chlorophyll concentrations and seawater viscosity at each sampling date (A), and the excess viscosity, b_η, predicted by the linear regression $\eta = a_\eta[\mathrm{Chl}] + b_\eta$ in the absence of chlorophyll (B). The dotted lines identified the 95% confidence limits for the Kendall's τ. The open and black dots correspond to the samples taken before and after the initial foam formation, respectively. The grey bar indicates the period of foam formation and the black arrows indicate the appearance and disappearance of *P. globosa* in the phytoplankton assemblage.

phytoplankton exopolymers largely determine the bulk-phase elasticity and excess viscosity of seawater (Jenkinson, 1986, 1993b; Jenkinson and Biddanda, 1995) and can impart to it a yield stress (Jenkinson and Arzul, 1998), although for a given concentration different algae were not all equally active. We will confirm the previous theoretical arguments and experimental findings that phytoplankton concentration alone cannot explain the viscosity of seawater (Jenkinson, 1986, 1993a,b; Jenkinson and Biddanda, 1995; Jenkinson and Arzul, 1998). We shall further show that for *P. globosa*, initiation of colony formation and associated secretion of extracellular materials are the most important prerequisite to induce a modification of seawater viscosity. The potential implications of the observed biomodification of seawater viscosity on plankton ecology are finally briefly discussed in relation to microscale turbulent processes.

4.1. Phytoplankton biomass, taxonomy and seawater viscosity

The absence of a decreasing gradient of chlorophyll from surface to bottom is fully congruent with the absence of stratification observed throughout the whole survey and the strong hydrodynamic conditions characterizing the area, with turbulence intensities ranging between 10^{6} and 10^{-4} cm^2 s^{-3} (Seuront et al., 2002). It also indicates that no active displacement of flagellates occur towards the surface layer. On the other hand, the absence of an increasing gradient of chlorophyll from surface to bottom indicates that no elevated sinking rates, nor tidally driven resuspension processes were taking place during our survey. This fully ensures the relevance of our sub-surface investigation of the composition and standing stock of auto-, hetero- and mixotrophic protists as being representative of the whole water column.

Our results indicate that seawater viscosity does not show a single relationship with phytoplankton concentration in the Eastern English Channel. This is specified considering that (i) excretion of gelatinous mucus (or more generally extracellular polymers and fibres) is a widely acknowledged source of increased viscosity in marine waters, (ii) *P. globosa* dominates the phytoplankton spring blooms in the Eastern English Channel (see Fig. 5), (iii) our survey took place respectively before and after the massive foam formation that occurred along the beaches of the Eastern English Channel, (iv) the differences observed in the viscosity/phytoplankton relationship were recorded before and after the formation of foam and (v) the presence and the absence of significant relationship between seawater viscosity and the abundance of either *P. globosa* or other phytoplankton groups is remarkable. The viscosity patterns observed in the present work, as well as the differential relationships between phytoplankton biomass and seawater viscosity (see Figs. 3 and 6), could be mainly related to the dynamical properties of the mucilaginous colonial matrix of *P. globosa*. However, although the mucilage producer *Chaetoceros* sp. (Rousseau et al., 1994) was often observed, its 10-fold lower abundance compared to *P. globosa* suggests that its contribution to total mucus production was negligible.

4.2. Phytoplankton biomass, foam formation and seawater viscosity

As foam formation is believed to be associated to the disruption of the mucilaginous colonial matrix by turbulent mixing in the surf zone (Lancelot et al., 1987; Rousseau, 2000; Peperzak, 2002), we propose a mechanistic hypothesis for the differential control of seawater viscosity observed before and after foam formation (Fig. 7):

(1) Before the appearance of *P. globosa* cells in the environment, seawater viscosity does not seem to be dependent on chlorophyll concentration (Fig. 7A) as a 2.4-fold increase in chlorophyll concentration is only associated with a negligible increase in seawater excess viscosity from 9.40% to 9.62% (Fig. 3).
(2) At the beginning of the bloom, before colony formation, concentration of individual *Phaeocystis* cells can reach 10^{6} to 10^{7} cell l^{-1} (Peperzak, 2002; Seuront and Souissi, 2002; Stelfox-Widdicombe et al., 2004; present paper). Considering that the dominant diatoms, namely *Chaetoceros* sp., *G. delicatula* and *P. pseudodelicatissima* reached 1.1×10^{5} to 1.1×10^{6} cell l^{-1}, seawater viscosity could thus be purely phytoplankton concentration-dependent (Fig. 7B,C) as previously suggested (Jenkinson and Biddanda, 1995). Alternatively, considering that individual cells can release exopolymeric materials (Cariou et al., 1994; Peperzak et al., 2000; Fig. 7C), the observed density-dependence (Fig. 6A) could be related to the combination of phytoplankton cells and their excreted materials (Fig. 7D). This is illustrated by the excess viscosity increasing with chlorophyll biomass before the formation of *P. globosa* colonies (see Fig. 3B), when *P. globosa* cells where present for the very first time at 1.7×10^{6} cell l^{-1}. Despite the observed positive correlation found between excess viscosity and chlorophyll concentration before foam formation, the seawater viscosity may also be driven by the quantity of extracellular materials rather than by the cell concentration only. This is confirmed by the non-zero values taken by the predicted excess viscosity in the absence of chlorophyll (Fig. 6B).
(3) Once individual cells have developed into a colony (Fig. 7E) the positive correlation between chlorophyll concentration and excess viscosity before foam formation (Figs. 3 and 6A) may then be implicitly induced by the cells embedded into the colony (i.e. *Chaetoceros* sp. and *P. pseudidelicatissima*). Our field observations have indeed revealed that *Chaetoceros* sp. was embedded into young spherical colonies of *P. globosa* while *P. pseudodelicatissima* appeared later, during colony

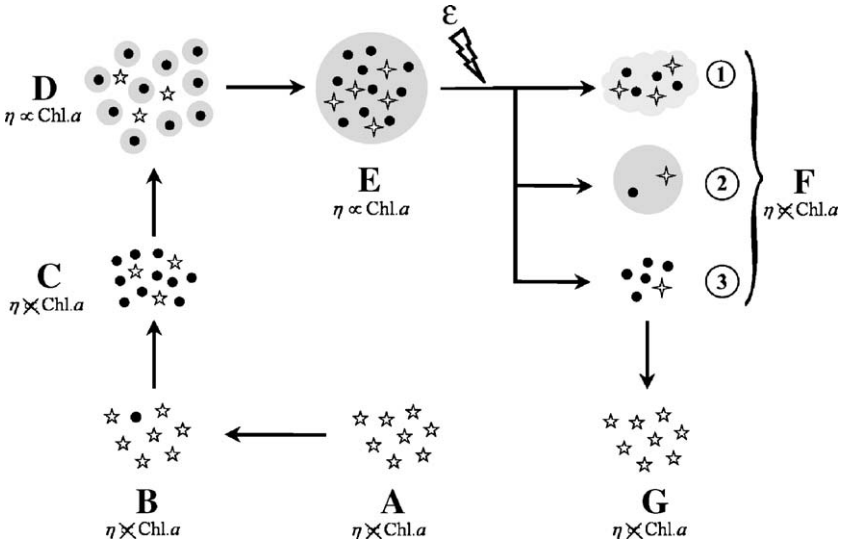

Fig. 7. Mechanism for regulating bulk-phase seawater viscosity during the *Phaeocystis* sp. colony development. Before the apparition of *P. globosa* cells in the environment, seawater viscosity is not dependent on chlorophyll concentration (A, B) as a 2.4-fold increase in chlorophyll concentration is only associated to a negligible increase in seawater excess viscosity. At the beginning of the bloom, before colony formation, seawater viscosity is directly dependent on chlorophyll concentration (C) or indirectly through the solitary cells mucous release (D). Once individual cells have developed into a colony (E) the observed dependence on chlorophyll concentration before foam formation is implicitly induced by the cells embedded into the colony. After foam formation (F, 1), the negative relationship observed between phytoplankton biomass and seawater viscosity suggests a control of viscosity by the extracellular mucous matrix (F, 2) rather than by the released cells (F, 3). After the disappearance of *P. globosa* cells (g) excess viscosity cannot be distinguished from the values observed before the apparition of *P. globosa* cells in the environment despite clear differences in species composition and cell concentrations.

senescence. These results are congruent with previous observations (Rousseau et al., 1994; Riegman and Van Boekel, 1996) highlighting (i) the need for *P. globosa* to have a physical support to initiate colony formation and (ii) the potential colonization of senescent colonies by microorganisms such as diatoms (Lancelot and Rousseau, 1994). This is illustrated by the similar trends observed between both chlorophyll concentration and excess viscosity and the size and number of *P. globosa* colonies (Fig. 3) and the positive correlation between chlorophyll concentration and excess viscosity before foam formation (Fig. 6A). One may also note here that the abundance (i.e. 1.7×10^6 cell l^{-1}) of the large centric chain-forming *G. delicatula* during initial colony formation may also contribute to the observed increase in the correlation between chlorophyll concentration and viscosity.

(4) The disruption of the mucilaginous colonial matrix by turbulent mixing in the surf zone leads to the formation of foam and to the transformation of colonial cells into flagellate cells (Figs. 7F and 5B). The nanoflagellates peak observed on May 25, i.e. when senescent *P. globosa* colonies were observed, is in accordance with the cell release described by many authors (Verity et al., 1988; Cariou et al., 1994; Peperzak et al., 2000). As colony senescence leads to the accumulation of dissolved polymeric materials in the water column, the excess viscosity recorded in May may be mainly driven by extracellular materials. This is strongly supported by the observation after the foam formation of the negative relationship between phytoplankton biomass and excess viscosity (Fig. 6A) and the high values of the predicted excess viscosity in the absence of chlorophyll (Fig. 6B).

(5) After the disappearance of *P. globosa* cells (Fig. 7G), the observed excess viscosity, bounded between 7.12% and 10.05%, cannot be distinguished from the values observed before the appearance of *Phaeocystis* cells in the environment (ca. 9.50%) despite clear differences in species composition and cell concentrations (see Fig. 5). In particular, the maximum concentration observed for *Chaetoceros* sp. (i.e. 2.07×10^6 cell l^{-1}) on June 15 led us to conclude that it does not affect seawater viscosity as a similar excess viscosity was measured on April 8 when diatom concentration was one order of magnitude lower.

One must finally note here that the sharp, 5-fold decrease in chlorophyll concentration observed after the initial foam formation might be related to a loss of phytoplankton biomass entrained within the foam during the emulsion process (Fig. 7F), a process fully similar to the previously observed phytoplankton loss through wind entrainment of wave breaking foam (Cincinelli et al., 2001; Monohan and Dam, 2001). This was clearly illustrated by the disappearance of *Chaetoceros* sp. and *P. pseudodelicatissima* in the samples on April 30 resulting in a strong decrease in diatoms relative abundance, i.e. from 19% to 6% (Fig. 5B). To specify this hypothesis, measurements of the chlorophyll content of freshly formed foam have been punctually made over the whole period of foam formation (Fig. 8). It then appears that during the initial foam formation the foam contained up to 25 μg of chlorophyll per litre. This content consistently decreased to 6.43 μg l^{-1} until *P. globosa* colonies were observed again, and reached 10.6±0.7 μg l^{-1} before decreasing during colony senescence. These results should nevertheless be taken with great caution considering that measuring a litre of foam is strongly case dependent as it can be easily biased by e.g. the density and the freshness of the foam, but also by the intensity of the mixing process. They nevertheless provide a clear indication that a non-negligible fraction of the phytoplankton population can be lost through the foam formation process. Similar observations have been conducted in the laboratory after foam formation through grid-generated turbulence mixing of natural seawater (Seuront, unpubl. data).

4.3. Biomodification of seawater viscosity: ecological implications

The general implications of biologically induced seawater viscosity on plankton ecology are numerous and have previously been widely addressed (Jenkinson, 1986, 1989, 1993b; Jenkinson and Wyatt, 1992; Jenkinson and Biddanda, 1995). Here, we briefly focus on the potential implications of increased viscosity on structure and functions of the pelagic ecosystems in relation with *P. globosa* blooms. In particular, we suggest that mucus secretion may be regarded as an environmental engineering strategy used by *P. globosa* to dampen turbulence and create a more favorable microhabitat, and to limit the grazing impact of zooplankton.

4.3.1. Phytoplankton dynamics

The basis of this strategy lies in the smoothing effect that organic exudates have in limiting the size of the smallest turbulent eddies, i.e. the so-called Kolmogorov scale l_k, defined as $l_k=(\nu^3/\varepsilon)^{1/4}$ where ν is the kinematic viscosity (m^2 s^{-1}, $\nu=\eta_m/\rho$ where η_m and ρ are the fluid

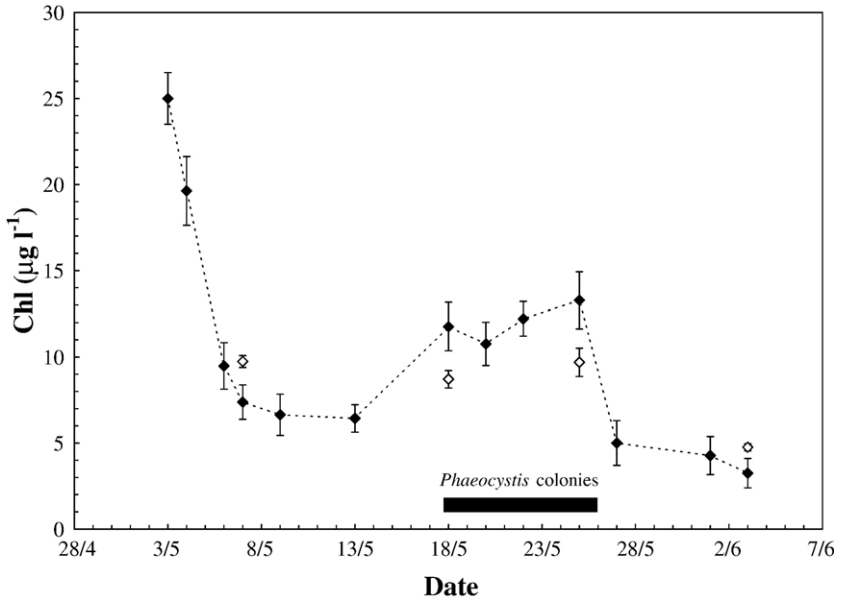

Fig. 8. Time course of chlorophyll content (black rhombs; μg l^{-1} of foam) of freshly formed foam washed ashore over the whole period of foam formation, shown together with bulk-phase seawater chlorophyll concentration (open rhombs; μg l^{-1}). The black bar indicates the period of colony formation. For each date, the error bars are the standard deviations from 5 and 15 measurements of chlorophyll concentrations of freshly formed foam and bulk-phase seawater, respectively.

viscosity and density, respectively) and ε the turbulent energy dissipation rate ($m^2\ s^{-3}$). Mucous secretion may be an environmental engineering strategy that phytoplankton use to dampen turbulence and create a favorable physical habitat (Smayda, 2002). However, in the sea most polymers and suspensions of aggregates are generally dependent on deformation rate. The biologically induced excess viscosity η_φ is then related to the shear γ (s^{-1}) as (Jenkinson, 1986):

$$\eta_\varphi = k\gamma^{-P} \quad (4)$$

where k is a constant, $\gamma=(\varepsilon/\nu)^{0.5}$ with $\nu=10^{-6}$ m s^{-1}, and P has so far been found to lie between 0 and 1.6 (e.g. Jenkinson and Biddanda, 1995), or even as low as −0.2 (Jenkinson et al., 1998). Considering the lack of information related to the value of P for *P. globosa*, the range of P values proposed in the literature and the range of turbulence intensities found in *P. globosa* natural environment (i.e. $\varepsilon=10^{-7}$ to 10^{-4} $m^2\ s^{-3}$, Seuront et al., 2002; Seuront, 2005), any attempt to quantify the non-trivial effect of excess viscosity on the Kolmogorov scale is unreasonable at this time. It can nevertheless be suggested that for a given turbulence intensity, the more viscous the fluid and the larger the Kolmogorov scale is. As a consequence, any nutrients contained within a microzone (e.g. Mitchell et al., 1985; Blackburn et al., 1998) are likely to be more accessible, which may be a valuable strategy when the bulk concentrations are too low for biological uptake and/or to increase the competitivity for nutrient resource. In particular, these differences in characteristic scales and viscosity may provide a phenomenological explanation for the competitive advantage of the colonial form of the genus *Phaeocystis* for nutrients, and under nutrient limitations (Peperzak et al., 1998).

4.3.2. Zooplankton dynamics

It has been recently shown that high concentrations of ambient solitary *P. globosa* cells and other phytoplankton seemed to suppress colony enlargement in *P. globosa*, and that grazers would help reduce this inhibition by removing the solitary cells (Tang, 2003). Such a strategy to regulate colony size development would allow *P. globosa* to defend itself in diverse planktonic systems, and may explain the global success of this species. In addition, phytoplankton polymeric exudates have been repeatedly reported as reducing copepod grazing (e.g. Malej and Harris, 1993; Jenkinson and Wyatt, 1995). As suggested by Jenkinson and Wyatt (1992), the high shear environment related to suspensions of aggregates may be used by *P. globosa* flagellates released from colonies to minimize predation. The reported resistance of *Phaeocystis* colonies to mesozooplankton grazing has also often been attributed to a mechanical hindrance due to increased viscosity, but never demonstrated (Schoemann et al., 2005). In addition to colony formation, the exudates released by *P. globosa* and the subsequent increase in viscosity might then also be considered as a potential antipredator adaptive strategy.

5. Conclusions

While previous studies have punctually investigated the rheological properties of seawater in bloom conditions (Jenkinson, 1986, 1993a,b, Jenkinson and Biddanda, 1995), we specifically investigated here the evolution of bulk-phase seawater viscosity in the inshore waters of the Eastern English Channel over the course of the spring phytoplankton bloom. In particular, we showed that the apparent coupling/decoupling dynamics observed between phytoplankton chlorophyll concentration and seawater viscosity that occurred before and after the formation of foam were rather driven by extracellular materials than by cell concentration only. Additional field and laboratory experiments are needed to ensure the generality and the ecological relevance of the present results, in particular to correlate chlorophyll concentration, abundance and colony size of *P. globosa*, viscosity, and the quality and quantity of the mucilaginous matrix. As discussed above, bulk-phase seawater viscosity still needs to be thoroughly investigated before it can be reliably incorporated into future studies as it represents one of the most fundamental fluid properties likely to affect (i) the essence of a flow per se and thus the outcome of any subsequent modelling approach, and (ii) plankton biology and ecology.

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