The impact of turbulence and phytoplankton dynamics on foam formation, seawater viscosity and chlorophyll concentration in the eastern English Channel

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Abstract

The space-time dynamics of chlorophyll *a* concentration and seawater excess viscosity has been investigated in the hydrographically contrasting inshore and offshore water masses of the eastern English Channel. This was done during the phytoplankton spring bloom dominated by *Phaeocystis globosa* before and after the very large-scale formation of foam induced by an increase in wind-driven turbulence and the related wave breakings. The results suggest that the dynamics of chlorophyll *a* concentration and seawater excess viscosity are differentially controlled by the formation of foam through the intensity of the spring bloom and wind-generated turbulence.

1. Introduction

The cosmopolitan genus *Phaeocystis* is well known for producing nearly monospecific dense blooms that may impact heavily on ecosystem structure and function in many areas of the marine environment (see e.g. Schoemann et al. (2005) for a review). *Phaeocystis* is a remarkable producer of dimethylsulphide (Stefels 2000), a significant greenhouse gas (Ayers & Gillet 2000), and may remove atmospheric carbon very efficiently because colonies have high C/N and C/P ratios (Arrigo et al. 1999). *Phaeocystis* is considered to be a nuisance alga through the production of toxins (e.g. Stabell et al. 1999, Hansen et al. 2003), the induction of anoxia and the subsequent massive mortality of fish associated with sinking colonies (Rogers & Lockwood 1990). *Phaeocystis* is also associated with the widely acknowledged formation of thick brown jelly layers and/or 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, Seuront et al. 2006).

Blooms of the colony-forming *Phaeocystis globosa* are a recurring phenomenon in the coastal zones of the North Sea (Gieskes et al. 2007) and the eastern English Channel (Seuront et al. 2006, Seuront & Vincent 2008, in press, Schapira et al. 2008, in press). At times, this species dominates the phytoplankton community, contributing over 90% of the total phytoplankton abundance in the southern North Sea (Lancelot & Mathot 1987) and 73% in the eastern English Channel (Seuront et al. 2006, Seuront & Vincent 2008). *P. globosa* also forms large colonies where cells are embedded in a mucopolysaccharide matrix generated during colony formation by swarming cells (Van Rijssel et al. 2000). *Phaeocystis* sp. blooms were even referred to as 'foul water' or 'baccy juice' (Orton 1923).

Descriptions of bulk-phase seawater during phytoplankton blooms are suggestive of changes in seawater rheological properties induced by phytoplankton mucus secretion (Jenkinson 1986, 1993, Jenkinson & Biddanda 1995, Seuront et al. 2006, 2007). A positive correlation has even been found between seawater viscosity and chlorophyll *a* concentration during *Phaeocystis* blooms in the German Bight and the North Sea (Jenkinson 1993, Jenkinson & Biddanda 1995). In the coastal waters of the eastern English Channel, seawater viscosity has been shown to increase significantly over the course of a *P. globosa* bloom, and positive and negative correlations between chlorophyll *a* concentration and seawater viscosity were identified respectively before and after the formation of foam (Seuront et al. 2006, 2007).

However, the inshore and offshore water masses of the eastern English Channel have very distinct hydrological properties that are likely to influence the dynamics of chlorophyll *a* concentration and seawater viscosity. The inshore water mass is influenced more by the freshwater run-off distributed from the Bay of the Seine to the Strait of Dover, and separated from the offshore waters by a tidally controlled frontal area (Brylinski & Lagadeuc 1990). Compared to these more offshore waters, this coastal flow is characterized by low salinity, high turbidity, and is rich in phytoplankton and zooplankton (Brylinski et al. 1984). Offshore waters are directly influenced by oligotrophic Atlantic Water inputs, and a fivefold decrease in chlorophyll *a* concentration typically occurs between inshore and offshore waters during bloom conditions (Schapira et al. 2008). These differences prompted the present investigation, which was designed to investigate the consequences of foam formation on (i) the viscous properties of bulk-phase seawater and (ii) the relationship between seawater viscosity and chlorophyll *a* concentration in the hydrologically distinct inshore and offshore water masses of the eastern English Channel.

2. Material and methods

2.1. Field site

This study was conducted in the eastern English Channel, from stations C and L of the SOMLIT network (Service d'Observation du Milieu Littoral). These stations, located in the inshore and offshore waters of the eastern English Channel (Figure 1) were chosen, since their physical and hydrological properties are representative of the inshore and offshore water masses of the eastern English Channel and are not influenced by the tidally-controlled frontal structure separating inshore from offshore waters. These two stations were investigated before and after a massive foam formation that occurred in the turbulent surf zone along the eastern English Channel on 29 and 30 April 2002 (Figure 2). The inshore station was sampled on 16 April 2002 and 8 May 2002, the offshore station on 17 April 2002 and 9 May 2002. Inshore and offshore samples were taken from an anchor station aboard the NO 'Côtes de la Manche' (CNRS–INSU) for 12 h (c. 1 tidal cycle) during a spring tide period.

2.2. Sampling

Every hour, water temperature [°C] and salinity profiles from surface to bottom were measured using a Seabird SBE 25 Sealogger CTD. Every 5 min, current speed and direction were measured at 5, 10 and 15 m with Anderaa current meters. Every 30 min, wind speed and direction data were collected with an on-board anemometer. Every hour in April and May, water samples were taken with Niskin bottles at 1 m depth. The seawater viscosity and chlorophyll *a* concentration of each water sample were measured.

Chlorophyll concentrations were estimated from 500 ml water samples filtered through GF/F glass-fibre filters (porosity 0.45 μm), following Suzuki & Ishimaru (1990). Chlorophyll *a* was extracted by direct immersion of the filters in 5 ml of N,N-dimethylformamide, and actual extractions were made in the dark at −20°C during 4 hours. Concentrations of chlorophyll *a* in the extracts were determined following Strickland & Parsons (1972) using a Turner 450 fluorometer previously calibrated with chlorophyll *a* extracted from *Anacystis nidulans* (Sigma Chemicals).

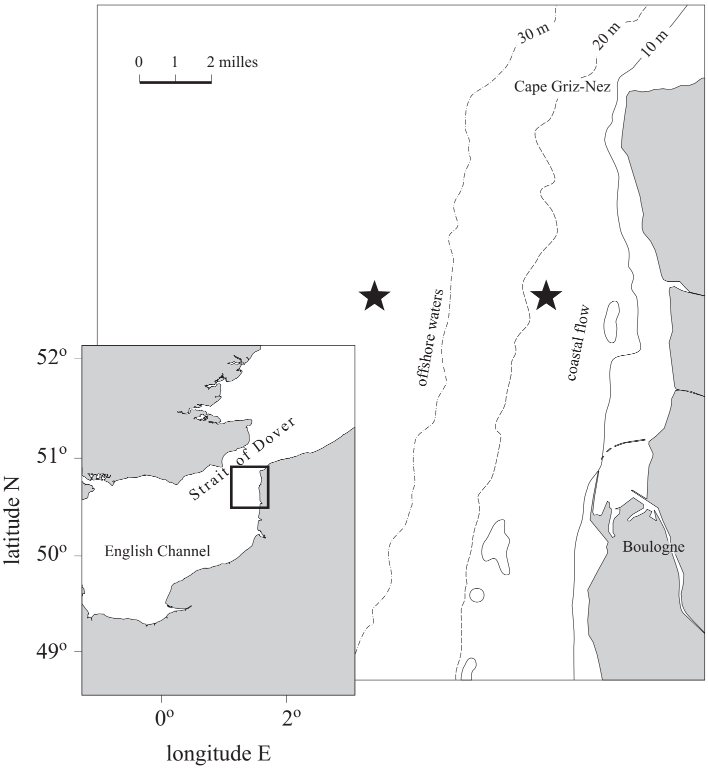

Figure 1. Study area and location of the sampling stations (★) in the inshore and offshore waters of the eastern English Channel

Figure 2. Foam formation in the turbulent surf zone and on beaches along the French coast of the eastern English Channel at Le Portel (50°42′33″N, 1°34′22″E) on 29 April 2002 (a–b) and at Audresselles (50°46′55″N, 1°36′33″E) on 30 April 2002 (c–d)

Seawater viscosity measurements were conducted using a portable ViscoPro 2000 viscometer (Cambridge Applied Systems Inc., Boston) following the procedure detailed in Seuront et al. (2007). The measured viscosity η_m [cP] is the sum of a physically controlled viscosity component $\eta_{T,S}$ [cP] and a biologically controlled viscosity component η_{Bio} [cP]:

$$\eta_m = \eta_{T,S} + \eta_{Bio}. \tag{1}$$

η_m was measured after screening each water sample through a 200 μm mesh to avoid bias in the viscosity measurement due to large or colonial organisms (Seuront et al. 2007). The physically controlled component $\eta_{T,S}$ was estimated from viscosity measurements conducted on sub-samples passed through 0.20 μm pore size filters. The biologically induced excess viscosity η_{Bio} [cP] was subsequently defined for each water sample as $\eta_{Bio} = \eta_m - \eta_{T,S}$. The relative excess viscosity η [%] was then calculated as

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

Temperature and salinity were measured using a multiparameter analyser (Consort C533).

2.3. Hydrodynamic analysis

In the absence of any vertical gradient of density, the dynamic stability of the water column was calculated using the total shear S defined as $S = \sqrt{(\Delta u/\Delta z)^2 + (\Delta v/\Delta z)^2}$, where Δu and Δv are the vertical gradients in the cross-channel u and along-channel v components of the tidal flow over a distance Δz.

The dissipation rates of wind-generated (ε_{wind} [$\mathrm{m}^2\ \mathrm{s}^{-3}$]) and tide-generated ($\varepsilon_{tide}$, [$\mathrm{m}^2\ \mathrm{s}^{-3}$]) turbulent kinetic energies were respectively estimated as (MacKenzie & Leggett 1991)

$$\varepsilon_{tide} = (6 \times 10^{-3})u^3/h \tag{3}$$

and (MacKenzie & Leggett 1993):

$$\varepsilon_{wind} = (5.82 \times 10^{-9})W^3/z, \tag{4}$$

where u is the M_2 depth-averaged tidal velocity [$\mathrm{m\ s}^{-1}$], W the wind speed [$\mathrm{m\ s}^{-1}$], h the depth of the water column [m] and z the sampling depth [m].

3. Results

3.1. Structure of the water column

No vertical stratification was observed in the temperature and salinity profiles, indicating a well-mixed water column over the course of the survey in both inshore and offshore waters. Before and after the formation of foam, vertically averaged temperature was not significantly different between inshore and offshore waters (Wilcoxon-Mann-Whitney U-test, $p > 0.05$). In contrast, salinity was always significantly higher offshore than inshore (U-test, $p < 0.01$).

3.2. Hydrodynamic conditions

Current speeds ranged from 0.25 to 1.35 $\mathrm{m\ s}^{-1}$ at 5 m, 0.30 to 1.28 $\mathrm{m\ s}^{-1}$ at 10 m and 0.20 to 1.30 $\mathrm{m\ s}^{-1}$ at 15 m in inshore waters, and from 0.10 to 0.95 $\mathrm{m\ s}^{-1}$ at 5 m, 0.14 to 0.82 $\mathrm{m\ s}^{-1}$ at 10 m and 0.12 to 0.90 $\mathrm{m\ s}^{-1}$ at 15 m in offshore waters. No significant differences were observed between the current speeds measured on 16 April and 8 May in inshore waters (Wilcoxon-Mann-Whitney U-test, $p > 0.05$) and on 17 April and 9 May in offshore waters ($p > 0.05$), nor were any significant differences detected between current speeds at any of the three depths investigated in inshore or offshore waters (Kruskal-Wallis H-test, $p > 0.05$). The related shear activity S varied between 6×10^{-4} and $7 \times 10^{-4}\ \mathrm{s}^{-1}$ in inshore waters, and between 4×10^{-4} and $5 \times 10^{-4}\ \mathrm{s}^{-1}$ in offshore waters. The vertically averaged tide-generated dissipation rates ε_{tide} were also higher inshore than offshore

(U-test, $p < 0.01$), ranging from 3.8×10^{-6} to 9.1×10^{-5} m^2 s^{-3} in inshore waters and from 1.5×10^{-7} to 1.3×10^{-5} m^2 s^{-3} in offshore waters. This is consistent with the values, previously found at the same location, of the vertical shear activity and turbulent kinetic energy dissipation rates, which are characteristic of strongly mixed tidal flows (Seuront et al. 2002, Seuront 2005). The wind-generated dissipation rates ε_{wind} estimated at 1 m depth ranged from 1.6×10^{-7} to 2.5×10^{-4} m^2 s^{-3} in both inshore and offshore waters. This indicates a significant effect of wind-generated turbulence on sub-surface waters.

3.3. Chlorophyll concentration and seawater viscosity

After the massive formation of foam observed in the turbulent surf zone on 29 and 30 April 2002 (Figure 2), a weekly routine survey from 30 April to 15 June recorded hardly any foam formation at the surface of the offshore waters, whereas foam formation and accumulation did occur consistently in the inshore waters and the turbulent surf zone (L. Seuront, personal observation).

Prior to foam formation, the chlorophyll *a* concentration ranged from 13.2 to 21.4 μg dm^{-3} in inshore waters and from 6.0 to 8.2 μg dm^{-3} in offshore waters. Seawater viscosity ranged between 11.2 and 42.1% inshore and 14.5 and 36.9% offshore. A highly significant threefold decrease in chlorophyll *a* concentrations was observed between the inshore and offshore waters (Figure 3a; U-test, $p < 0.01$). Seawater excess viscosity did not exhibit any significant differences between inshore and offshore waters (Figure 3b; U-test, $p > 0.05$). Seawater excess viscosity and chlorophyll *a* concentration were significantly positively correlated at the inshore ($r = 0.91$, $p < 0.01$) and offshore ($r = 0.97$, $p < 0.01$) stations (Table 1).

Table 1. Relationship between chlorophyll *a* concentration (Chl *a*) and seawater excess viscosity (η); ns – not significant

Date	Site	Depth [m]	Chl *a* vs. η	
16 April 2002	inshore	1	$r = 0.91$	$p < 0.01$
17 April 2002	offshore	1	$r = 0.97$	$p < 0.01$
8 May 2002	inshore	1	$r = -0.73$	ns
9 May 2002	offshore	1	$r = -0.51$	ns

After the formation of foam, the chlorophyll *a* concentration and seawater excess viscosity recorded inshore ranged from 3.2 to 5.5 μg dm^{-3}

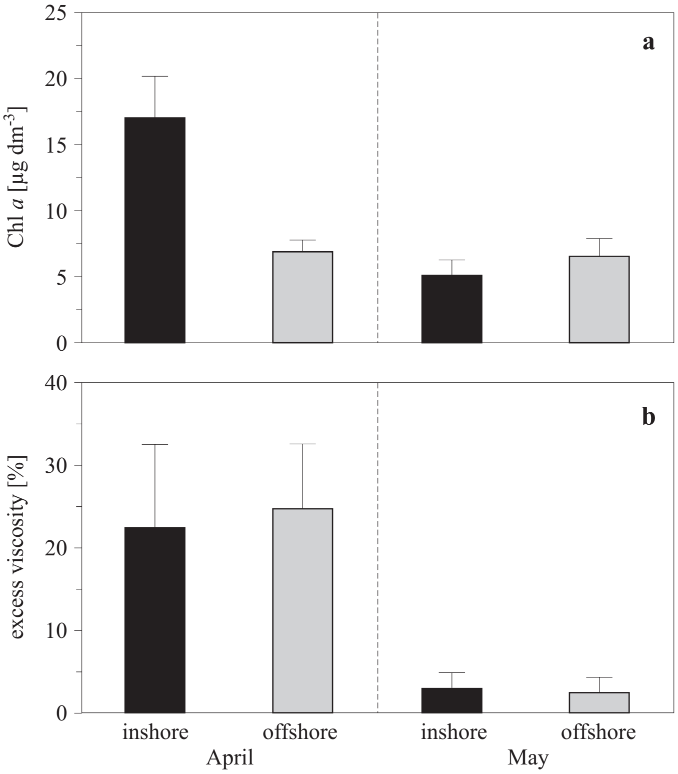

Figure 3. Chlorophyll *a* concentration (a) and seawater excess viscosity (b) in the inshore and offshore waters of the eastern English Channel in April and May

and from 0.4 to 5.1% respectively (Figure 3b). Seawater excess viscosity was not significantly correlated with chlorophyll *a* concentration inshore and offshore (Table 1).

4. Discussion

4.1. Foam formation and turbulence intensity

A link between the amplitude of *Phaeocystis* blooms and foam formation was first suggested by Bätje & Michaelis (1986) and Lancelot et al. (1987) and later quantified by Peperzak (2002). Nevertheless, the mechanisms for foam formation are still unclear. It has been hypothesized that the foam is derived from *Phaeocystis*-related dissolved organic matter (Eberlein et al. 1985) and from the poorly-biodegradable remnants of a *Phaeocystis* colony (Lancelot & Rousseau 1994). These colony remnants accumulate near the bottom of the water column (Peperzak et al. 2003) and may be advected by bottom currents to the coast, where they are beaten to foam in the turbulent surf zone (Peperzak et al. 1998). In the present work, foam formation was related to exceptional wind velocities between 30 and 35 m s^{-1}. The corresponding turbulent kinetic energy at 1 m depth was then of the order of $\varepsilon_{wind} = 2 \times 10^{-4}$ m^2 s^{-3} (eq. (2)). This is consistent with the general hypothesis that the formation of coastal foam is triggered by an increase in wind-induced turbulence (Peperzak 2002).

The critical amount of turbulent energy, ε_c, necessary to induce the observed foam formation is, however, likely to be much higher than ε_{wind}. First of all, in the coastal waters where *Phaeocystis globosa* flourishes, turbulence is driven mainly by tidal currents and is typically between 10^{-7} and 10^{-4} m^2 s^{-3} at the tidal scale (Seuront et al. 2002, Seuront 2005), suggesting that this species is well adapted to highly turbulent environments. Secondly, foam formation has only been observed at the surface of the inshore waters under wave breaking conditions and in the turbulent surf zone, where the dissipation rates related to intermittently breaking waves can be one to two orders of magnitude higher than ε_{wind} (e.g. Melville et al. 2002, Gemmrich & Farmer 2004). More generally, the critical values ε_c could also be highly dependent on the physiological state of the colonies, as senescent colonies, for example, would be more fragile than healthy ones.

4.2. Regulation of chlorophyll concentration, seawater viscosity and foam formation

Prior to foam formation, seawater excess viscosity was significantly positively correlated with chlorophyll concentration. In contrast, after foam formation no significant relationships were found (Table 1). This is congruent with a recent mechanistic explanation (Seuront et al. 2006) suggesting that disruption of the mucilaginous colonial matrix by turbulent mixing leads to decoupling between the viscous and non-viscous contributions of *P. globosa* to the bulk-phase seawater properties. This is also consistent with the dynamics of Transparent Exopolymeric Particles (TEP) produced by *P. globosa* (Mari et al. 2005); these authors found that during the growth phase of *P. globosa*, TEP and chlorophyll *a* concentration were positively correlated, whereas the release of large TEP from the mucilaginous matrix of *P. globosa* colonies following colony disruption led to a negative correlation between TEP and chlorophyll *a* concentration (Mari et al. 2005).

Foam formation has also been followed by a decrease in chlorophyll *a* concentration and an increase in seawater excess viscosity in the turbulent surf zone (Seuront et al. 2007) and in the inshore waters (Seuront et al. 2006) of the eastern English Channel. This has been related (i) to a significant proportion of cells being entrained within the foam during the emulsion process and (ii) to colony disruption, which increases the amount of polymeric materials in the bulk-phase seawater. The former is consistent with the 3.5-fold decrease in chlorophyll *a* concentration observed in the inshore waters following the formation of foam. It may also be related, however, to increased grazing pressure on *P. globosa* cells released in the bulk-phase seawater (Seuront & Vincent 2008) and/or cell lysis after viral infection (Bratbak et al. 1998, Brussaard et al. 2005). In contrast to previous works (Seuront et al. 2006, 2007, Seuront & Vincent 2008), seven- and tenfold decreases were identified in the seawater excess viscosity in the inshore and offshore waters following foam formation (Figure 3b), which may be due to the bacterial degradation of *P. globosa*-derived polymers (e.g. Janse et al. 1999). In addition, the chlorophyll *a* concentration did not significantly decrease after foam formation in the offshore waters (U-test, $p > 0.05$; Figure 3a). This has enabled both the specification and the generalization of the previous mechanistic hypothesis (Seuront et al. 2006) for the differential control of seawater viscosity before and after foam formation (Figure 4).

Assuming that disruption of the colonial matrix by turbulent mixing leads to the formation of foam and to the release of colonial materials likely to increase the bulk-phase seawater viscosity (Seuront et al. 2006; Figure 4a), the decrease in seawater excess viscosity observed in inshore and offshore waters suggests that the mixing processes were so intense that most intra- and extra-colonial polymeric materials were transformed into foam during the emulsion process (Figure 4b). As *P. globosa* contributes over 73% of the total phytoplankton abundance in the eastern English Channel (Seuront et al. 2006, Seuront & Vincent 2008), the decrease in seawater excess viscosity after foam formation could also be related to the interannual differences in the intensity of the *P. globosa* spring bloom (Figure 4). The chlorophyll *a* concentrations measured here in the inshore and offshore waters before foam formation (i.e. 17.02 ± 3.07 μg dm^{-3} and 6.92 ± 0.74 μg dm^{-3} respectively; Figures 4b, c) were low when compared to the 51.5 and 57.4 μg dm^{-3} reported in the coastal waters (Seuront et al. 2006, Seuront & Vincent 2008; Figure 4a) and in the surf zone (Seuront et al. 2007; Figure 4a) of the eastern English Channel in 2004. Such low concentrations of chlorophyll *a* suggest a less intense bloom which, in turn, leads to the weak production of intra- and extra-colonial polymeric materials (e.g. Van Rijssel et al. 2000). This is consistent with our seawater excess viscosity measurements, which were one order of magnitude smaller than those previously recorded in the inshore waters and the surf zone of the eastern English Channel (Seuront et al. 2006, 2007, Seuront & Vincent

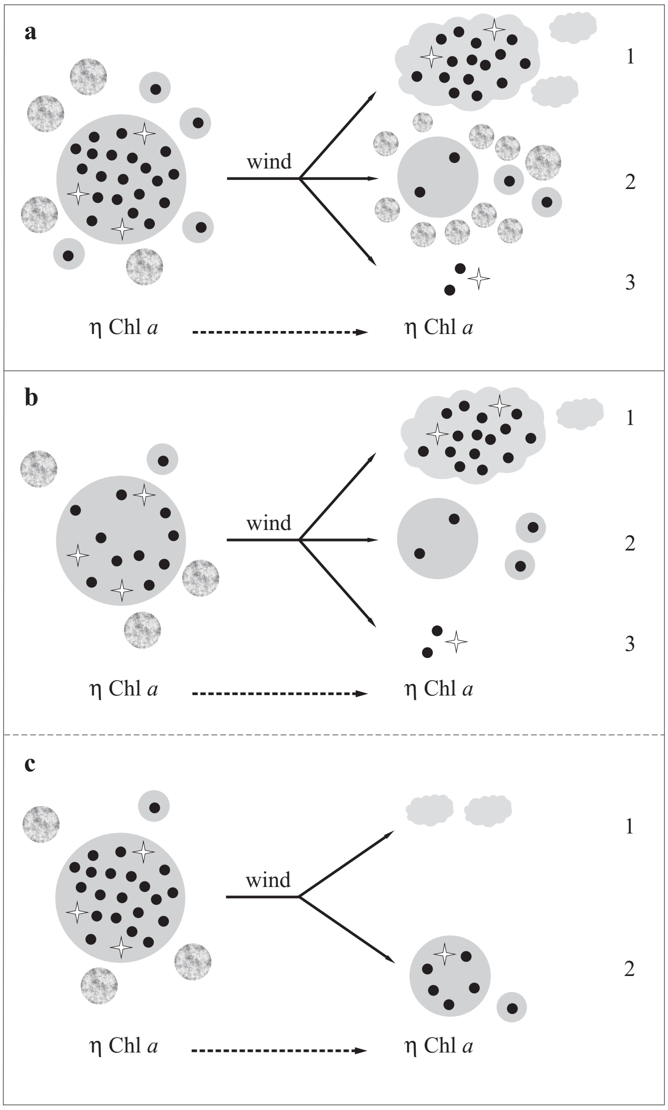

Figure 4. Suggested mechanisms for regulating chlorophyll *a* concentration (Chl *a*), bulk-phase seawater viscosity (η) and foam production during a *Phaeocystis globosa* spring bloom in the eastern English Channel. An increase in wind-generated turbulence leads to decoupling between chlorophyll *a* concentration and seawater excess viscosity related to foam formation. Under intense bloom conditions (a – modified from Seuront et al. 2006), foam formation causes a decrease in chlorophyll *a* concentration and an increase in seawater excess viscosity, as a significant proportion of cells are entrained in the foam during the emulsion process (a1), whereas colony disruption releases intra-colonial exopolymeric materials (a2) and phytoplankton cells (a3) into the bulk-phase seawater. In contrast, under weak bloom conditions (b, c) an increase in (*continued on next page*)

(**Figure 4**, *continued*) wind-generated turbulence still leads to the formation of foam (b1, c1), but to a decrease in seawater viscosity, suggesting that most of the exopolymeric materials have been turned into foam during the emulsion process. However, foam formation is related only to a decrease in chlorophyll *a* concentration in the inshore waters (b2, b3). This suggests that in the offshore waters most of the emulsion process (c1) was due to extra-colonial materials (shaded light grey) present in the water prior to foam formation and that mixing processes were not powerful enough to destroy the colonial matrix (c2). The black dots represent *P. globosa* cells, and the crosses other phytoplankton taxa

2008). The observed decrease in seawater excess viscosity following the formation of foam (see Figure 3b) therefore suggests that the intra-colonial materials released into the bulk-phase seawater following colony disruption were not concentrated enough to influence the bulk-phase seawater viscosity (Figure 4b, c). Finally, as foam formation was observed only under wave breaking conditions, the absence of any decrease in the offshore chlorophyll concentration after foam formation may indicate that mixing intensities induced by breaking waves were not strong enough to destroy the colonial matrix, in which case most of the emulsion process may have been due to the extra-colonial secretion present in the water column before foam formation (Figure 4c).

5. Conclusion

The present work extends previous results, which initially showed a positive correlation between seawater excess viscosity and *Phaeocystis* sp. concentration (Jenkinson 1993, Jenkinson & Biddanda 1995), and also a shift between the positive and the negative correlations before and after the formation of foam (Seuront et al. 2006, 2007). Although the dynamics of both chlorophyll *a* concentration and seawater excess viscosity are still related to the temporal dynamics of the *Phaeocystis globosa* spring bloom, the present work demonstrates that it is differentially controlled by the intensity of the spring bloom and wind-generated/wave breaking turbulence, which both vary in time and space. The general implications of biologically induced seawater viscosity on plankton ecology have been widely discussed (Jenkinson 1986, 1993, Jenkinson & Wyatt 1992, Jenkinson & Biddanda 1995, Seuront et al. 2006, 2007, Seuront & Vincent 2008). However, as seawater viscosity plays a critical role in individual processes, e.g. nutrient uptake, swimming and sinking rates of aquatic microorganisms, the dynamics of turbulent flows and the related aggregation/disaggregation dynamics, failure to consider the physiological and mechanical effects of seawater viscosity is likely to lead to erroneous conclusions about the extent of physiologically-based changes in functional performance.

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