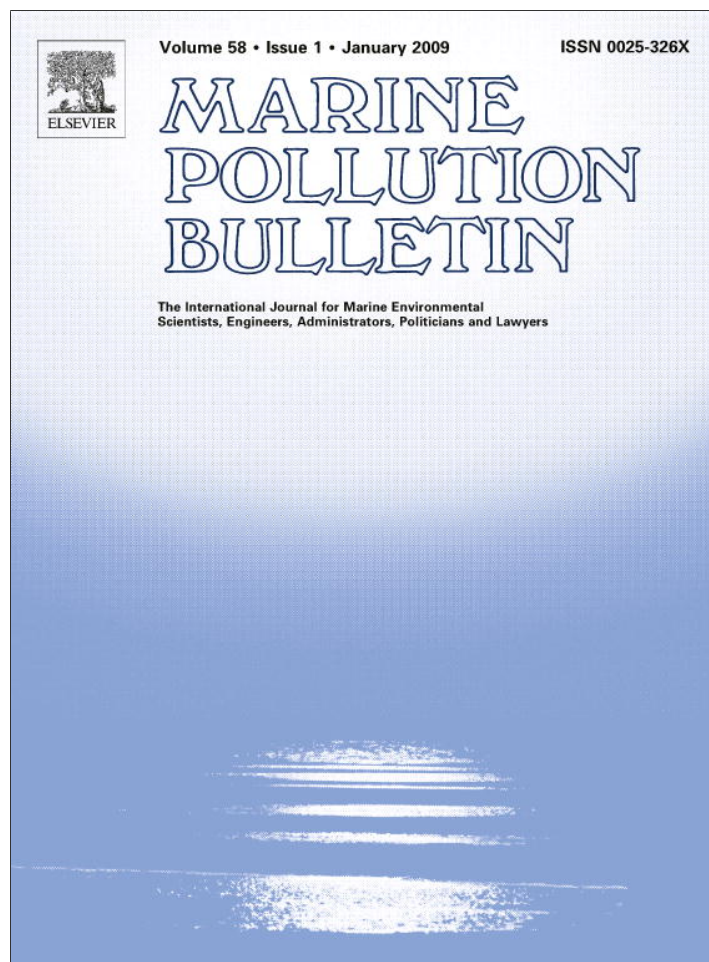


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Impact of the *Phaeocystis globosa* spring bloom on the intertidal benthic compartment in the eastern English Channel: A synthesis

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ABSTRACT

From 1999 to 2005, studies carried out in the frame of regional and national French programs aimed to determine whether the *Phaeocystis globosa* bloom affected the intertidal benthic communities of the French coast of the eastern English Channel in terms of composition and/or functioning. Study sites were chosen to cover most of the typical shore types encountered on this coast (a rocky shore, an exposed sandy beach and a small estuary). Both the presence of active *Phaeocystis* cells and their degradation product (foam) did have a significant impact on the studied shores. The primary production and growth rates of the kelp *Saccharina latissima* decreased during the bloom because of a shortage of light and nutrient for the macroalgae. On sandy sediments, the benthic metabolism (community respiration and community primary production), as well as the nitrification rate, were enhanced during foam deposits, in relation with the presence of bacteria and active pelagic cells within the decaying colonies. In estuarine sediments, the most impressive impact was the formation of a crust at the sediment surface due to drying foam. This led to anoxic conditions in the surface sediment and resulted in a high mortality among the benthic community. Some organisms also tended to migrate upward and were then directly accessible to the higher trophic level represented by birds. *Phaeocystis* then created a shortcut in the estuarine trophic network. Most of these modifications lasted shortly and all the systems considered came back to their regular properties and activities a few weeks after the end of the bloom, except for the most impacted estuarine area.

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1. Introduction

Because of their interface position, coastal ecosystems are highly productive environments (e.g. Gazeau et al., 2004). They are characterised by intense physical and chemical gradients, and human activities have been proved to impact on their functioning, especially through eutrophication (Cloern, 2001; Gray et al., 2002). Within coastal environments, the intertidal zones constitute favourable areas for exchanges with the adjacent terrestrial systems and coastal water masses. Thus, their functioning is mainly

driven by these exchanges of matter and energy and they constitute highly variable systems, both in space and time. In particular, exchanges between the sediment and the water column, especially during phytoplanktonic blooms, often enhanced by eutrophication, have been reported to drastically affect the biogeochemical processes in surficial sediments (e.g. Boon et al., 1998, 1999; Grenz et al., 2000).

Phaeocystis globosa is one of the three *Phaeocystis* species that have been reported to form blooms (for a review, see Schoeman et al., 2005). *Phaeocystis globosa* is a temperate species found on the coast of the eastern English Channel, southern North Sea and the south coast of China. Though not being toxic, *P. globosa* is considered to be responsible for harmful algal blooms (HAB; Veldhuis

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and Wassmann, 2005). Its life cycle is characterized by different forms of solitary cells alternating with colonial stages (Whipple et al., 2005 and references therein). These colonies are constituted of cells packed within a matrix and are surrounded by a “skin” (Hamm et al., 1999) which protects the cells from minute organisms (Hamm, 2000). During the colonial phase, one of the most spectacular manifestations of the bloom, because visible to the naked eye, can be observed on the seashore, consisting in large accumulations of mucilaginous aggregates (foam; Fig. 1). This foam formation occurs under specific windy conditions (Lancelot, 1995) and the amount of foam deposited on the beach is directly dependent on the wind speed and direction that control foam formation and deposit on the beach, respectively. The intensity of the bloom in the eastern English Channel and in Belgian coastal waters appeared to be related to the North Atlantic Oscillation (NAO) and nutrient loads by rivers (Seuront and Souissi, 2002; Breton et al., 2006; Gypens et al., 2007), and the differences in blooms amplitude between the two areas have been assigned to differences in the turbulence regime (Schapira et al., 2006).

Though the effect of the *P. globosa* bloom within the water column has been widely studied regarding for instance seawater properties (Seuront et al., 2006) or interactions with planktonic organisms (e.g. Ruardij et al., 2005), few studies concerned its effect on benthic organisms and/or processes. Accumulation of colonies on the sediment and their incorporation into the food web have been described (Cadée, 1996), as well as the occurrence of meiofauna feeding on the foam (Armonies, 1989) and the efficiency of filtration and absorption of the different life stages by benthic organisms (Smaal and Twisk, 1997). Although the intertidal zone is potentially the most impacted area because of foam accumulations, no study had been devoted to this specific system before the late nineties. However, foam deposits might constitute huge organic matter inputs into the sediment and might then interfere with both the living biota and the sediment biogeochemical pro-



Fig. 1. Accumulations of mucilaginous aggregates (foam) of *P. globosa* on the beach of Wimereux during the 2002 spring bloom.

cesses. Furthermore, the high turbidity levels encountered during the spring bloom (Seuront et al., 2006 and references therein) might interfere with the photosynthetic activity of the benthic autotrophic organisms.

From 1999 to 2005, studies aimed to determine whether the *Phaeocystis* bloom affected the intertidal benthic communities of the French coast of the eastern English Channel in terms of composition and/or functioning. The eastern English Channel is an epicontinental sea that constitutes a transition zone between the Atlantic Ocean and the North Sea. It is characterized by a semi diurnal megatidal regime, the tidal magnitude reaching 9 m in spring tides in estuaries. In the area, the shoreline exhibits a complex morphology composed of sandy beaches, cliffs, estuaries, wetlands and polders (Battiau-Queney et al., 2001; Dauvin, 2008). Thus, the study sites were selected along the coast to cover most of the shore types that might be impacted during the *Phaeocystis* bloom (i.e. a rocky shore, an exposed sandy beach and a small estuary).

While the consequences of the bloom in the subtidal area are described in Denis and Desroy (2008), the present paper synthesizes the results that were obtained in the different intertidal environments regarding benthic metabolism and fluxes and the macrozoobenthic communities composition.

2. Materials and methods

Three study sites representing the major sediment types of the eastern English Channel were investigated along the French coast (Fig. 2): a rocky shore in Audresselles, an exposed sandy beach in Wimereux and the Canche Bay as an estuary.

2.1. Macroalgal photosynthetic activity and growth rate in the rocky shore

In Audresselles, the photosynthesis and growth rate of the kelp *Saccharina latissima* (formerly *Laminaria saccharina*) were measured in 2001. The photosynthetic activity was measured *in situ*, during the late phase and after the *Phaeocystis* bloom (in early May and early June for the year considered, respectively). A submersible pulse amplitude modulated (Diving PAM, Walz) fluorometer was used to estimate the relative electron transport rate (rETR) following Gevaert et al. (2003). The photosynthetically active radiation (PAR) reaching the algae was measured simultaneously to each rETR measurement, and the surface PAR was continuously recorded during the experiments (Li-Cor SA-190 quantum sensor).

Additionally, 75 individuals (of an initial length between 22.5 cm and 74.1 cm) were marked with coloured thread attached to their stipe in early March. From March to June 2001, during spring tides when algae were accessible by foot (every 15 or 30 days), the total length (from the base on the holdfast to the top

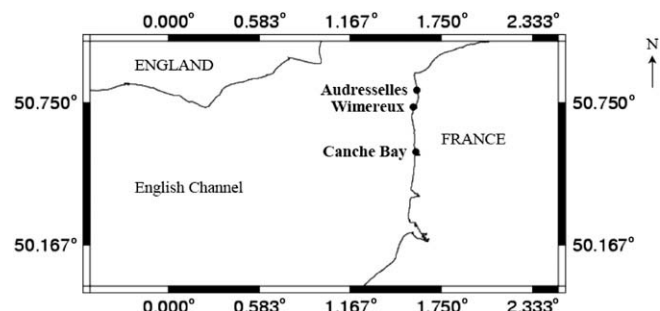


Fig. 2. Location of the study sites along the French coast of the eastern English Channel.

of the frond) of each individual was measured. After each measurement, a hole (1 cm diameter) was pierced in the frond at a distance of 10 cm of the junction between the frond and the stipe. The growth rate was expressed as follow:

$$GR = 100[(Lh_{t+1} - Lh_t)/L_t]/TL \quad (1)$$

with GR the growth rate (%.d⁻¹); Lh_t and Lh_{t+1} the length between the hole and the junction between the frond and the stipe (cm) measured at time *t* and *t*+1, respectively; L_t the total length measured at time *t* (cm); TL the time lag between *t* and *t*+1 (d). Due to storm events and human activities (fishing), the number of individuals at the end of the experiment was 34.

2.2. Benthic metabolism, oxygen and nutrient fluxes, scanning electron microscopy of foam in the exposed sandy beach

The study site located in Wimereux was a typical exposed sandy beach characterised by medium size sand. A survey of benthic metabolism under emersed conditions (community primary production and community respiration measured as CO₂ fluxes following Migné et al., 2002) was performed from March 2000 to September 2005 (Spilmont et al., 2005; Hubas et al., 2007). During the period, seven additional measurements were carried out on *Phaeocystis* foam deposits (one in 2001, two in 2002, 2003 and 2004). The bacterial biomass within the first cm of sediment was concurrently estimated together with bacterial production and growth efficiency during the 2004–2005 survey.

Benthic fluxes at the water-sediment interface (O₂, NH₄⁺) were estimated in 2004 and 2005 on sediment cores incubated in the laboratory, by measuring changes in concentrations in the overlying water and by measuring solute concentrations in the interstitial water (Rauch et al., 2008).

For the scanning electron microscopy observation, samples were fixed with lugol/glutaraldehyde solutions (0.2% v/v final concentration) and filtered through polycarbonate membrane (Millipore, 2 μm). They were then rinsed three times in MilliQ water (Millipore), dehydrated in a graded ethanol series (30%, 50%, 70%, 80%, 90% and 100%, Fisher Scientific, P.A.) and critical point dried in liquid CO₂ using critical point drying apparatus (Bal-Tec CPD 030). Filters were mounted on an aluminium stubs, sputter-coated with Au/Pd (Polaron SC7620) and observed at 15 kV with a SEM LEO 438 VP.

2.3. Macrozoobenthos, oxygen and nutrient fluxes and waders frequentation in the estuary

The Canche Bay is a small estuary (ca. 6.3 km² of intertidal area) characterised by a relatively low river discharge (100 m³ s⁻¹ in winter and 60 m³ s⁻¹ in summer). Four intertidal sites were studied for macrozoobenthos (abundance, species richness and diversity), sediment organic matter content, sediment pigments contents (chlorophyll *a* and phaeopigments) and oxygen microprofiles from April to December 2001 (Desroy and Denis, 2004). One sandy and one muddy station were studied both in the northern and the southern part of

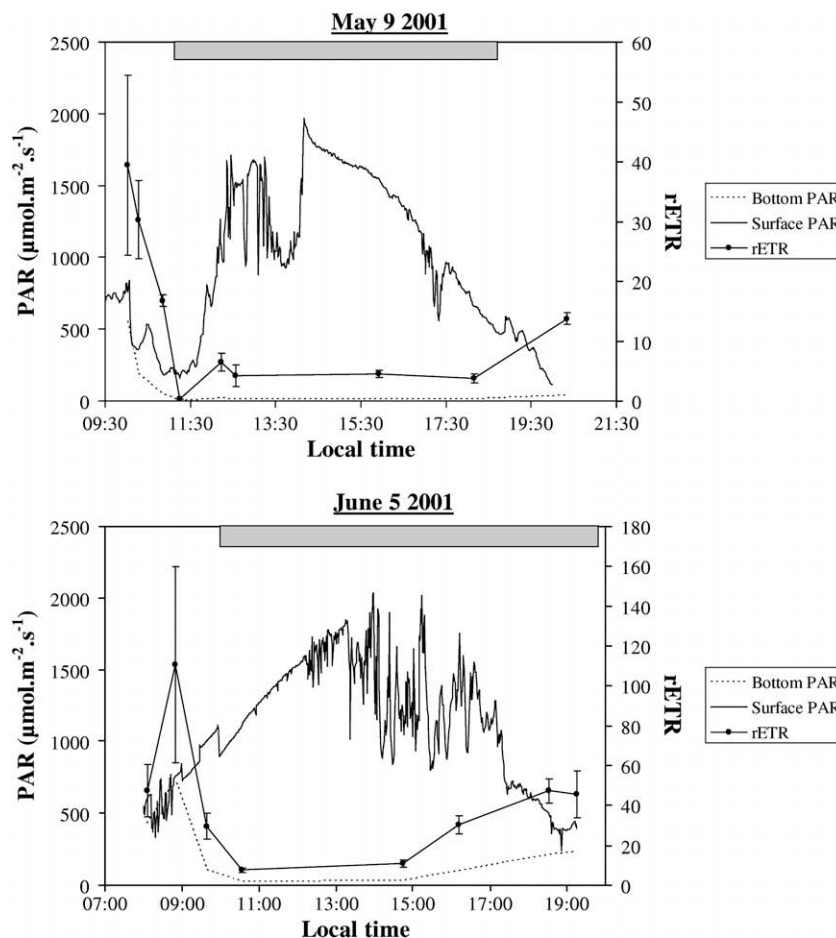


Fig. 3. Photosynthetic activity of *S. latissima* in spring 2001. The photosynthetic activity was measured as the relative electron transfer rate (rETR, dots, mean ± s.d.) and photosynthetically active radiations (PAR, μmol m⁻² s⁻¹, dashed line) reaching the algae (bottom PAR) were measured simultaneously. The surface PAR was measured throughout the experiments (dark line). The grey bars symbolise the periods of immersion.

the Bay (medium to fine sands and mud in the north; muddy fine sands and mud in the south). Data on macrofauna were also collected using a multilevel core sampler (Luczak and Menu, submitted for publication) that provided complementary information on the vertical distribution of the macrofauna within the sediment. This device allowed the sampled core to be sliced in sub-samples corresponding to five layers in the sediment (0–1 cm; 1–2.5 cm; 2.5–5 cm; 5–10 cm and 10–20 cm). The changing in the burying depth was tested using a non-parametric multivariate analysis of variance (Permanova; Anderson, 2001).

Sediment oxygen demand and total fluxes of dissolved inorganic nitrogen fluxes at the sediment/water interface were also estimated in the northern part of the Bay in March and May 2003 (Rauch and Denis, 2008).

The number of waders staging in the estuary was based on the results of counts performed every ten days (at least one count per ten days period) in 2001. For the 1998–2000 periods, data come primarily from the Groupe Ornithologique et Naturaliste du Nord-Pas-de-Calais (G.O.N.) database. Counts were made by a combination of experienced volunteers and professionals. High water counts were used, when birds concentrate on roosts. When several counts were performed in a ten days period, the highest count for each species was used (Yates and Goss-Custard, 1991).

3. Results and discussion

3.1. Shortage of light and nutrients for *Saccharina latissima*

The results obtained during the *in situ* measurements of the photosynthetic activity and growth rate of *Saccharina latissima* are exhibited on Fig. 3 and 4. During the late phase of the bloom (early May), almost no light reached the bottom as soon as the study site was submerged, with an average light extinction of 99% (average PAR of $11 \pm 7 \mu\text{mol m}^{-2} \text{s}^{-1}$ during immersion, mean \pm s.d., $n = 5$; Fig. 3A) whereas light kept reaching the algae all along the immersion period during the experiment conducted after the bloom (early June; 79% average light extinction, $118 \pm 88 \mu\text{mol m}^{-2} \text{s}^{-1}$ during immersion, mean \pm s.d., $n = 6$; Fig. 3B). Thus, the photosynthetic activity of *S. latissima* during immersion, estimated through the measurement of rETR, was much lower when measurements were performed during the bloom (4 ± 2 , mean \pm s.d., $n = 5$; Fig. 3A) than for individuals in regular conditions (28 ± 17 , mean \pm s.d., $n = 6$; Fig. 3B). As a consequence, the average growth rate of *S. latissima* decreased during the bloom (down to $0.61 \pm 0.02\% \cdot \text{d}^{-1}$, mean \pm s.d.; Fig. 4), though March–April is usually a period of intense growth for the species. Towards the end of the bloom, the growth rate became higher

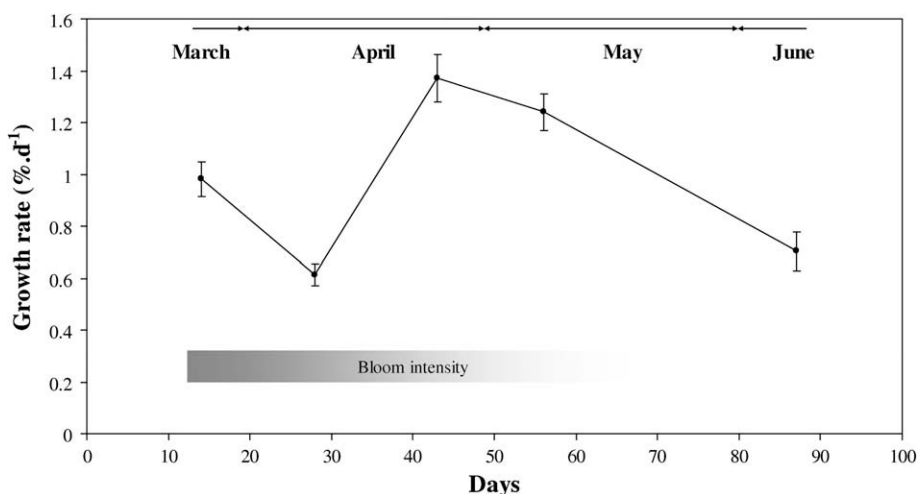


Fig. 4. Growth rate(C) of *S. latissima* measured from March to June 2001, expressed in $\% \cdot \text{d}^{-1}$ (mean \pm s.d.). The grey bar roughly represents the bloom intensity (the darker, the higher the chlorophyll concentration in the water column).

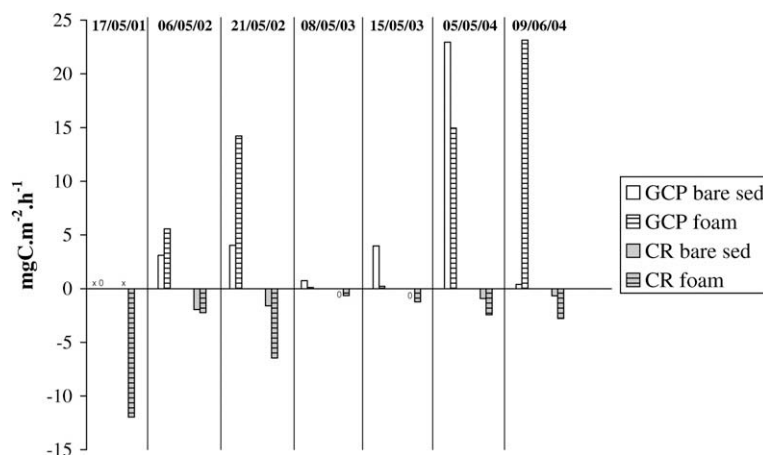


Fig. 5. Gross community production (GCP, positive values in $\text{mgC m}^{-2} \text{h}^{-1}$) and community respiration (CR, negative values in $\text{mgC m}^{-2} \text{h}^{-1}$) measured during emersion in the sandy beach of Wimereux on bare sediment (open bars) and on foam deposits (dashed bars). 0 indicates that no flux was detected and \times indicates that fluxes were not measured. Redrawn from Spilmont et al. (2005) and Hubas et al. (2007).

($1.37 \pm 0.05\% \cdot d^{-1}$, mean \pm s.d.) and then the algae came back to their regular growth cycle (limited growth rate throughout summer). The time course of the carbon content (Fig. 5A in Gevaert et al., 2001) exhibited a typical trend for the species (directly linked to the growth cycle), being the lowest in March ($23.9 \pm 0.5\%$ DW, mean \pm s.d.) and the highest in September ($31.4 \pm 0.6\%$ DW, mean \pm s.d.). However, the time course of the nitrogen content (Fig. 5B in Gevaert et al., 2001) was characterised by a decrease from March ($3.4 \pm 0.1\%$ DW, mean \pm s.d.) to June ($2.2 \pm 0.1\%$ DW, mean \pm s.d.), that matched with the *Phaeocystis* bloom period for the year of the study (1999 in Gevaert et al., 2001). The nitrogen being taken up from the medium by *S. latissima* as NO_3^- , it can be assumed that the seawater was depleted in nitrate during this period and led the algae to use their internal N stock. The growth of *P. globosa* is known to be mainly sustained by the massive use of NO_3^- after an initial use of NO_4^+ (Tungazara et al., 2003; Schapira et al., 2006), with concentrations of NO_3^- in the seawater almost decreasing down to $0 \mu\text{mol l}^{-1}$ in March–April (Gentilhomme and Lizon, 1998); this suggests that *P. globosa* and *S. latissima* compete for the same nitrogen source.

During the bloom it appeared that *S. latissima* was limited both in light and nitrate, as a consequence of (i) the turbidity induced by

the presence of *Phaeocystis* cells and (ii) a competition for NO_3^- . After the bloom, the algae recovered its regular photosynthetic activity and growth rate. This testifies to the plasticity of this species to adapt to environmental variations, as also previously underlined at the day scale (Gevaert et al., 2003).

3.2. Enhancement of the benthic metabolism due to foam deposits in the exposed sandy beach

Fig. 5 shows the results obtained during emersion in terms of gross community production (GCP) and community respiration (CR), both on bare sediment and on sediment covered by foam deposits. CR was always higher on foam deposits than on bare sediment and the highest CR ever measured on this study site was on foam deposits on May 17 in 2001 ($11.95 \text{ mgC m}^{-2} \text{ h}^{-1}$). By compiling data obtained by Spilmont et al. (2005) and Hubas et al. (2007), there was a significant positive correlation between sediment bacterial biomass and benthic community respiration during emersion ($r = 0.547$, $n = 41$, $p < 0.01$; Fig. 6). As mentioned by these authors the community respiration in this sandy beach was dominated by bacterial respiration all along the year; the organic matter input made up of *Phaeocystis* foam would constitute a substratum for autochthonous bacterial populations and would also bring allochthonous bacteria within the matrix, bacterial abundance and production also being linked to the bloom within the water column (Becquevort et al., 1998; Lamy et al., 2006).

Gross community production was always detected on foam deposits, except on May 17 in 2001. Furthermore, GCP was often higher on deposits than on bare sediment (on May 6 and 21 in 2002 and on May 5 and June 9 in 2004; Fig. 5) and was as high as $23.13 \text{ mgC m}^{-2} \text{ h}^{-1}$ on foam on June 06 in 2004. This suggested that active phytoplanktonic cells (i.e. cells still performing photosynthesis) were deposited within the foam. This hypothesis was corroborated by high assimilation numbers typical of phytoplanktonic cells calculated by Spilmont et al. (2005) and Hubas et al. (2007). The scanning electron microscopy photograph of a foam sample taken during the deposit in spring 2004 (Fig. 7), brought a new evidence of phytoplanktonic cells trapped within the foam (a *Phaeocystis* cell and a diatom are visible). Bacteria responsible for the high respiration rates were also visible on this picture.

As for air-sediment CO_2 fluxes, the sediment oxygen demand (SOD) and ammonium release increased at the water-sediment

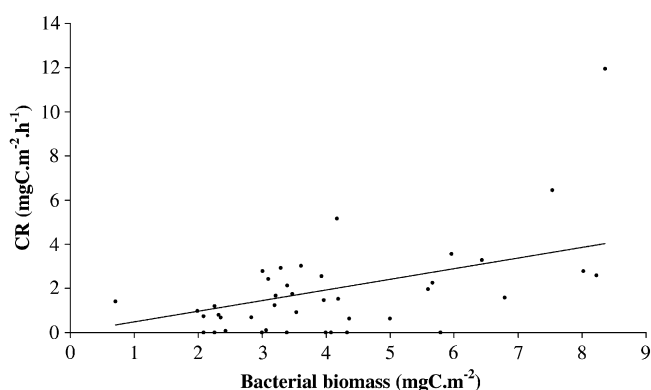


Fig. 6. Sediment bacterial biomass (mgC m^{-2}) plotted against benthic community respiration during emersion (CR, mgC m^{-2}) and linear regression forced through the origin ($CR = 0.48 \times \text{Bacterial biomass}$, $r = 0.547$, $n = 41$, $p < 0.01$). Data compiled from Spilmont et al. (2005) and Hubas et al. (2007).

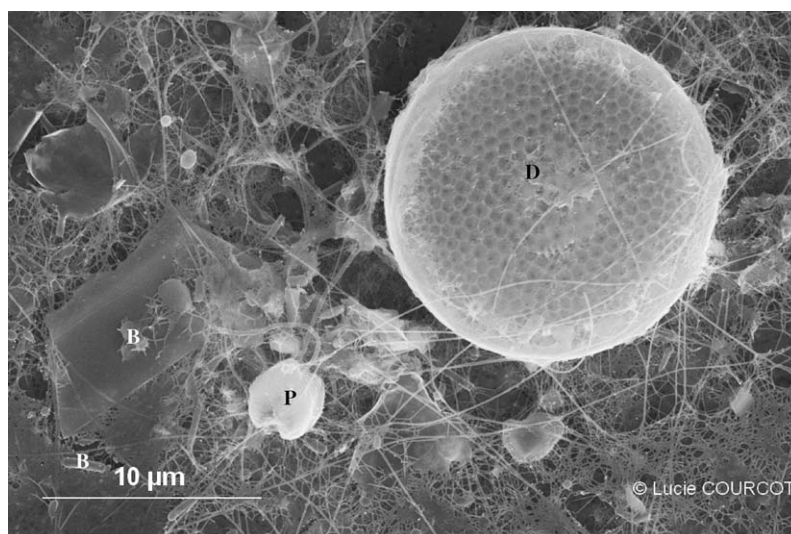


Fig. 7. Scanning electron microscopy photograph of a foam sample (observed at 15 kV with a SEM LEO 438 VP) showing a *P. globosa* solitary flagellate cell (P), a diatom (D) and some bacteria (B).

interface during the spring bloom of *P. globosa*, whereas these processes remained limited during the rest of the year (Fig. 8). The increase in SOD obviously appeared to be a direct response to the organic matter input and was correlated to bacterial abundances. The concomitant release of nitrates described by Rauch et al. (2008) was not only a diffusive flux from the sediment to the water column but was also linked to high nitrification rates coupled with lower denitrification rates in surficial sediments.

As mentioned by Spilmont et al. (2005) and Rauch et al. (2008), both the phase of the bloom and the meteorological conditions control the response of the sedimentary processes. During the early stage of the bloom (exponential growth of both solitary cells

and healthy colonies), low community primary production and respiration were measured, but calm condition might allow phytoplanktonic cells to settle and lead to an increase in primary production at the air-sediment interface (Hubas et al., 2007). Nutrients being rapidly consumed in the water column during this phase, the diffusive nutrient fluxes increased. During the late stage of the bloom (decaying colonies), windy conditions are favourable for foam accumulations to be brought to the beach and to settle at low tide. Thus, both relatively high community production and high respiration rates are expected. Nutrient cycling is also affected during this stage, the nitrification and denitrification processes then being uncoupled (Rauch and Denis, 2008).

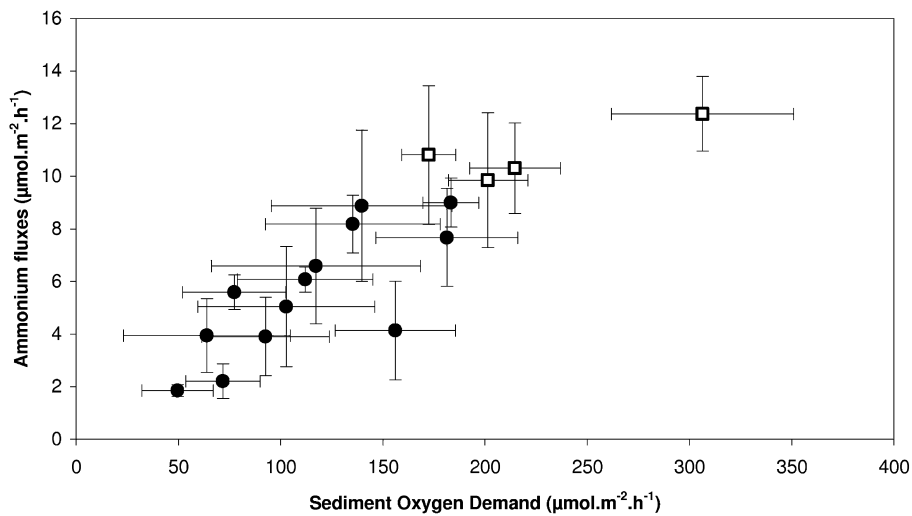


Fig. 8. Average sediment oxygen demands and ammonium releases ($\mu\text{mol m}^{-2} \text{h}^{-1}$; mean \pm s.d.; $n = 4$) at the sediment-water interface during the year 2004. Black diamonds represent values recorded in the absence of *P. globosa*, whereas open squares are measurements performed during the spring 2004 *P. globosa* bloom (late March–early May).

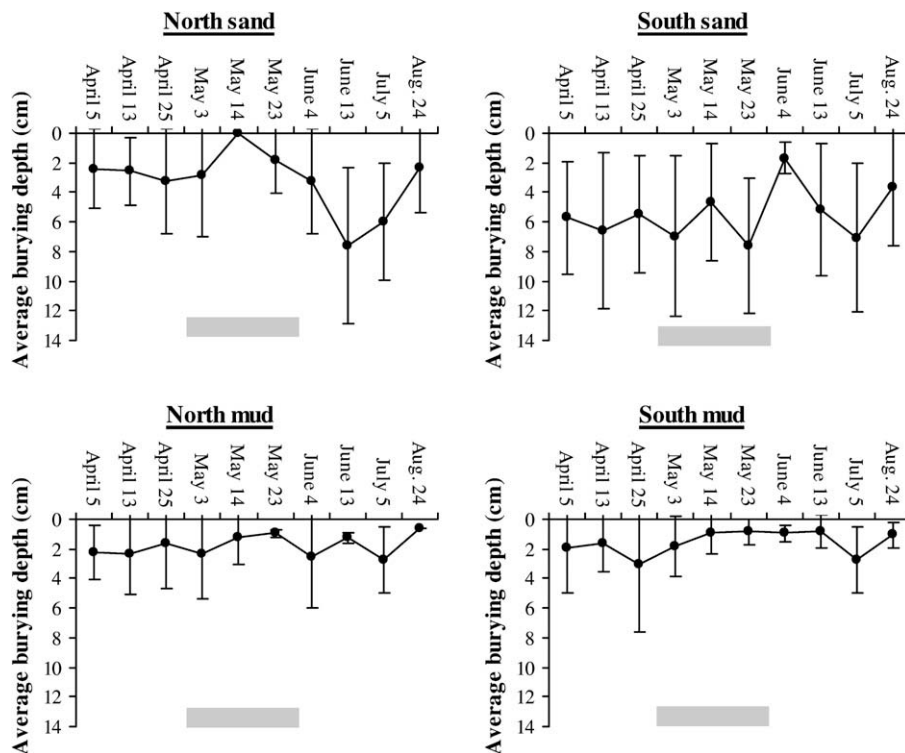


Fig. 9. Time course of the average burying depth (cm; 3 replicates; mean \pm s.d.) of the macrofauna at the four sampling stations surveyed in the Canche Bay in 2001. The grey bars symbolise the period of maximal foam accumulation on the sediment. The north site was highly impacted, the south site was low impacted.

3.3. Benthic fluxes and macrozoobenthic community modifications in the Canche Bay

The results obtained on benthic fluxes in the Canche Bay gave the same conclusions as those previously described for Wimereux, i.e. an increase in the sediment oxygen demand and a high dissolved inorganic nitrogen release during the bloom, these modifications being reversible a short time after the bloom (Rauch and Denis, 2008). In a previous analysis of the macrozoobenthic community at four sampling stations in this study site, Desroy and

Denis (2004) had the opportunity to compare both low-impacted and high-impacted areas (respectively the south side and the north side of the Bay) during the 2001 bloom. The authors reported values of usual community descriptors (density, specific richness and diversity) exhibiting a rapid and significant reduction during the late phase of the *Phaeocystis* bloom in the impacted area (see their Figs. 7 and 8). These modifications, in terms of quantity and quality of macrozoobenthos, were linked to the development of anoxic conditions, sometimes being as extreme as the formation of an encrusting foam avoiding O₂ to penetrate further than 1 mm (see

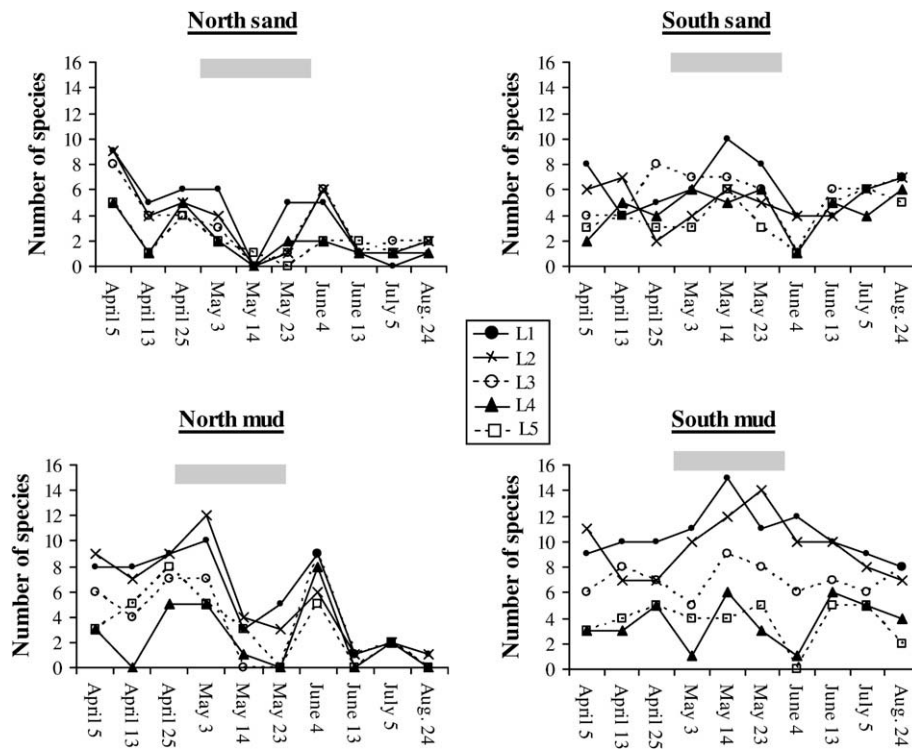


Fig. 10. Time course of the number of species found in each layer sampled using the multilevel corer (layer 1 (L1): 0–1 cm, layer 2 (L2): 1–2.5 cm, layer 3 (L3): 2.5–5 cm, layer 4 (L4): 5–10 cm, layer 5 (L5): 10–20 cm; sum of the 3 replicates) at the four sampling stations surveyed in the Canche Bay for the year 2001. The grey bars symbolise the period of maximal foam accumulation on the sediment. The north site was highly impacted, the south site was low impacted.

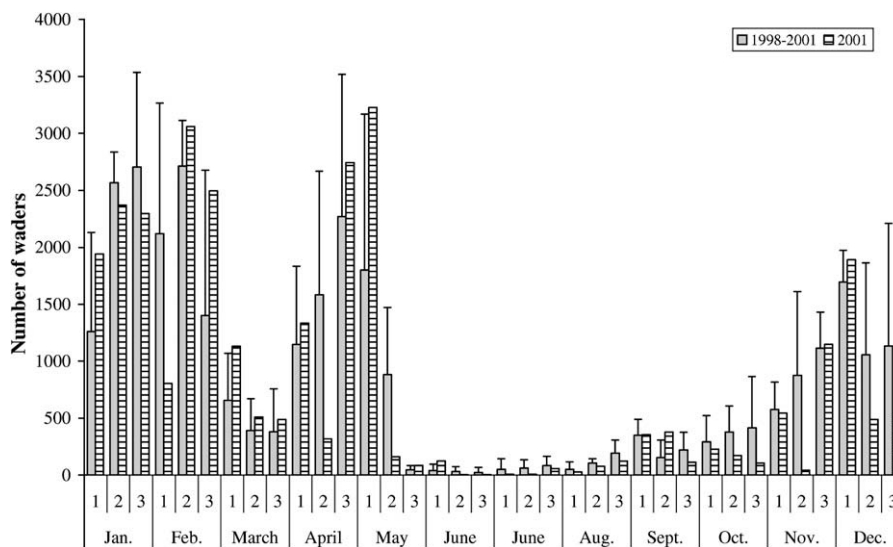


Fig. 11. Total number of waders counted within the Canche Bay for ten day periods (3 per each month of the year) for the period 1998–2001 (grey bars, mean \pm s.d.) and for the year 2001 (dashed bars).

Table 1
Synthesis of the effects of the *Phaeocystis* bloom on the physical and/or biological environment with their consequences on the benthic communities from the different shore types studied

Bloom stage	Early stage		Late stage	
Shore type	Rocky shore	Sandy shore	Sandy shore	Estuarine sediments
<i>Phaeocystis</i> effect on the physical and/or biological environment	Decrease in the light penetration and NH_4^+ availability in the water column	Active cells deposits in calm conditions	Settlement of foam including active phytoplanktonic cells and bacteria	Anoxic conditions due to a limited O_2 penetration into the sediment
Consequences on the benthic communities composition/functioning	Low primary production and low growth rate for underlying macroalgae	Increase in the sediment primary production	Increasing community primary production and respiration. NH_4^+ release	Rapid dramatic decrease in the species richness and density Macrofauna directly accessible to shorebirds. Energy flow modification
Recovery after the bloom	Rapid	Rapid	Rapid	Slow

their Fig. 5), when foam deposits were combined with high temperatures. These anoxic conditions led either to the direct death of some organisms, or to an upward migration of some individuals. The results obtained with the multilevel corer in the northern sandy sediment where the encrusting foam was encountered showed that the macrofauna tended to migrate upward during the first fortnight of May, all the individuals being found on the surface on May 14 (Permanova: $p < 0.05$, Fig. 9). Concurrently a decreasing number of species was observed in all the layers (Fig. 10). In these conditions, preys are directly accessible for birds, without the need to dig them out. Interestingly enough, waders have been observed feeding on the macrofauna lying on the sediment during anoxic conditions (authors pers.obs). It appears that the upward migration of the macrofauna perfectly matched with the second annual peak of abundance of waders in the Canche Bay during refuelling on their migration route (Fig. 11). Following the diagram proposed by Zwarts and Wanink (1993), in regular conditions the harvestable fraction of benthic prey for waders depends on the fraction being profitable within preys that are available. In this context, small preys are usually ignored for an optimisation of the ratio between the energy needed to handle them and the energy they bring. In our study, since the remaining living macrofauna was lying on the sediment or very close to the surface, all preys (i.e. small and large ones) were profitable since waders did not have to spend much energy to feed on them. In this context, *Phaeocystis* did temporally and locally modify the energy flow through the estuarine ecosystem. As underlined by Desroy and Denis (2004), the macrozoobenthic communities recovered slowly from the disturbance, especially the north mud site which still exhibited very low species richness and density six months after the bloom.

4. Conclusion

Phaeocystis is considered to play a key role in global biogeochemical cycles, climatic regulation and fisheries yield (Schoeman et al., 2005). However, this statement was mainly (if not only) derived from studies on its impact on the physical, chemical and biological properties of the water column. In this synthesis, we strengthened this theory through results obtained on the intertidal benthic compartment. As exhibited in Table 1, both *Phaeocystis* active cells and their degradation product (foam) did have a significant impact on the studied shores. *Phaeocystis* actually modified the nitrogen cycle within the sediment and thus the N fluxes from the sediment, and also appeared to compete with macroalgae for nitrates. Furthermore, throughout the *Phaeocystis* bloom, the rates of macroalgae primary production on rocky shores decreased, whereas the rates of gross community production and community primary production were enhanced on the sandy shore, then leading to changes in the carbon fluxes from the benthos to the air and the water column. The macrozoobenthos quality (diversity) and quantity (abundances) decreased during foam accumulation, some

of these changes leading to energetic shortcuts within the estuarine trophic network (i.e. from macrozoobenthos to birds). However, most of these modifications lasted shortly. Indeed, all the systems and organisms came back to their regular activity or presented their initial properties a few weeks after the end of the bloom. The only notable exception was one of the benthic communities from muddy sediments studied in the Canche Bay which did not recover more than 6 months after the end of the bloom. Nevertheless, this represented a very singular case since this site was particularly impacted that year (2001). This last remark points out the fact that the intensity of the *Phaeocystis* bloom remains locally unpredictable in time and highly variable in space (see Fig. 1). For example, although the abundance of the species has been stated to be related to the NAO (Seuront and Souissi, 2002; Breton et al., 2006), the abundance and accumulation of foam is very dependant on local hydrodynamic and topographic conditions. Thus, the surface covered by foam is not predictable and remains difficult to estimate at a large spatial scale due to its short residence time (the foam is wiped out during each rising tide); the calculation of an accurate impact of this deposit on carbon and nitrogen fluxes remains very hazardous.

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References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- Armonies, W., 1989. Occurrence of meiofauna in *Phaeocystis* seafoam. *Marine Ecology Progress Series* 53, 305–309.
- Battiau-Queney, Y., Fanchois, J., Deboudt, P., Lanoy-Ratel, P., 2001. Beach-dune systems in a macrotidal environment along the northern French coast (English Channel and southern North Sea). *Journal of Coastal Research* 34, 580–592.
- Becquevort, S., Rousseau, V., Lancelot, C., 1998. Major and comparable roles of free-living and attached bacteria in the degradation of *Phaeocystis*-derived organic matter in Belgian coastal waters of the North Sea. *Aquatic Microbial Ecology* 14, 39–48.
- Boon, A.R., Duineveld, G.C.A., Berghuis, E.M., van der Weele, J.A., 1998. Relationships between benthic activity and the annual phytoplankton cycle in near-bottom water and sediments in the southern North Sea. *Estuarine, Coastal and Shelf Science* 46, 1–13.
- Boon, A.R., Duineveld, G.C.A., Kok, A., 1999. Benthic organic matter supply and metabolism at depositional and non-depositional areas in the North Sea. *Estuarine, Coastal and Shelf Science* 49, 747–761.
- Breton, E., Rousseau, V., Parent, J.-Y., Ozer, J., Lancelot, C., 2006. Hydroclimatic modulation of diatom/*Phaeocystis* blooms in nutrient-enriched Belgian coastal waters (North Sea). *Limnology and Oceanography* 51, 1401–1409.

- Cadée, G.C., 1996. Accumulation and sedimentation of *Phaeocystis globosa* in the Dutch Wadden Sea. *Journal of Sea Research* 36, 321–327.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210, 223–253.
- Dauvin, J.-C., 2008. The main characteristics, problems, and prospects for western European coastal areas. *Marine Pollution Bulletin*, 57, 22–40.
- Denis, L., Desroy, N., 2008. Consequences of spring phytodetritus sedimentation on the benthic compartment along a depth gradient in the eastern English Channel. *Marine Pollution Bulletin*. doi:10.1016/j.marpolbul.2007.07.019.
- Desroy, N., Denis, L., 2004. Influence of spring phytodetritus sedimentation on intertidal macrozoobenthos in the eastern English Channel. *Marine Ecology Progress Series* 270, 41–53.
- Gazeau, F., Smith, F.V., Gentili, B., Frankignoulle, M., Gattuso, J.-P., 2004. The European coastal zone: characterization and first assessment of ecosystem metabolism. *Estuarine, Coastal and Shelf Science* 60, 673–694.
- Gentilhomme, V., Lizon, F., 1998. Seasonal cycle of nitrogen and phytoplankton biomass in a well-mixed coastal system (eastern English Channel). *Hydrobiologia* 361, 191–199.
- Gevaert, F., Davoult, D., Créach, A., Kling, R., Janquin, M.-A., Seuront, L., Lemoine, Y., 2001. Carbon and nitrogen content of *Laminaria saccharina* in the eastern English Channel: biometrics and seasonal variations. *Journal of the Marine Biological Association of the United Kingdom* 81, 727–734.
- Gevaert, F., Créach, A., Davoult, D., Migné, A., Levavasseur, G., Arzel, P., Holl, A.-C., Lemoine, Y., 2003. *Laminaria saccharina* photosynthesis measured *in situ*: photoinhibition and xanthophyll cycle during a tidal cycle. *Marine Ecology Progress Series* 247, 43–50.
- Gray, J.S., Wu, R.S.S., Or, Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series* 238, 249–279.
- Grenz, C., Cloern, J., Hager, S.W., Cole, B.E., 2000. Dynamics of nutrient cycling and related benthic nutrient and oxygen flux during a spring phytoplankton bloom in South San Francisco Bay (USA). *Marine Ecology Progress Series* 197, 67–80.
- Gypens, N., Lacroix, G., Lancelot, C., 2007. Causes of variability in diatom and *Phaeocystis* blooms in Belgian coastal waters between 1989 and 2003: a model study. *Journal of Sea Research* 57, 19–35.
- Hamm, C.E., 2000. Architecture, ecology and biogeochemistry of *Phaeocystis* colonies. *Journal of Sea Research* 43, 307–315.
- Hamm, C.E., Simson, D.A., Merkel, R., Smetacek, V., 1999. Colonies of *Phaeocystis globosa* are protected by a thin but tough skin. *Marine Ecology Progress Series* 187, 101–111.
- Hubas, C., Lamy, D., Artigas, L.F., Davoult, D., 2007. Seasonal variability of intertidal bacterial metabolism and growth efficiency in an exposed sandy beach during low tide. *Marine Biology* 151, 41–52.
- Lamy, D., Artigas, L.F., Jauzein, C., Lizon, F., Cornille, V., 2006. Coastal bacterial viability and production in the eastern English Channel: a case study during a *Phaeocystis globosa* bloom. *Journal of Sea Research* 56, 227–238.
- Lancelot, C., 1995. The mucilage phenomenon in the continental coastal waters of the North Sea. *Science of the Total Environment* 165, 83–102.
- Luczak, C., Menu, D., submitted for publication. A multilevel core sampler device to directly estimate food supply accessible to waders. *Marine Biology*.
- Migné, A., Davoult, D., Spilmont, N., Menu, D., Boucher, G., Gattuso, J.-P., Rybarczyk, H., 2002. A closed-chamber CO₂-flux method for estimating intertidal primary production and respiration under emersed conditions. *Marine Biology* 140, 865–869.
- Rauch, M., Denis, L., 2008. Spatio-temporal variability in benthic mineralization processes in the eastern English Channel. *Biogeochemistry* 89, 163–180.
- Rauch, M., Denis, L., Dauvin, J.-C., 2008. The effects of *Phaeocystis globosa* bloom on the dynamics of the mineralization processes in intertidal permeable sediment in the eastern English Channel (Wimereux, France). *Marine Pollution Bulletin* 56, 1284–1293.
- Ruardij, P., Veldhuis, M.J.W., Brussaard, C.P.D., 2005. Modeling the bloom dynamics of the polymorphic phytoplankter *Phaeocystis globosa*: impact of grazers and viruses. *Harmful Algae* 4, 941–963.
- Schapira, M., Seuront, L., Gentilhomme, V., 2006. Effects of small-scale turbulence on *Phaeocystis globosa* (Prymnesiophyceae) growth and life cycle. *Journal of Experimental Marine Biology and Ecology* 335, 27–38.
- Schoeman, 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., Souissi, S., 2002. Climatic control of *Phaeocystis* spring bloom in the eastern English Channel (1991–2000). *La Mer* 40, 41–51.
- 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.
- Smaal, A.C., Twisk, F., 1997. Filtration and absorption of *Phaeocystis* cf. *Globosa* by the mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology* 209, 33–46.
- Spilmont, N., Migné, A., Lefebvre, A., Artigas, L.F., Rauch, M., Davoult, D., 2005. Temporal variability of intertidal benthic metabolism under emersed conditions in an exposed sandy beach (Wimereux, eastern English Channel, France). *Journal of Sea Research* 53, 161–167.
- Tungazara, C., Rousseau, V., Brion, N., Lancelot, C., Gichuki, J., Baeyens, W., Goeyens, L., 2003. Contrasting nitrogen uptake by diatom and *Phaeocystis*-dominated phytoplankton assemblages in the North Sea. *Journal of Experimental Marine Biology and Ecology* 292, 19–41.
- Veldhuis, M.J.W., Wassmann, P., 2005. Bloom dynamics and biological control of a high biomass HAB species in European coastal waters: a *Phaeocystis* case study. *Harmful Algae* 4, 805–809.
- Whipple, S.J., Patten, B.C., Verity, P.G., 2005. Life cycle of the marine alga *Phaeocystis*: a conceptual model to summarize literature and guide research. *Journal of Marine Systems* 57, 83–110.
- Yates, M.G., Goss-Custard, J.D., 1991. A comparison between high water and low water counts of shorebirds on the Wash, East England. *Bird Study* 38, 179–187.
- Zwarts, L., Wanink, J.H., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research* 31, 441–476.