

## 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.

**Keywords:** Intertidal; *Phaeocystis globosa*; Benthic fluxes; *Saccharina latissima*; Bacteria; Macrozoobenthos

51

## 52 **1. Introduction**

53           Because of their interface position, coastal ecosystems are highly productive  
54 environments (e.g. Gazeau et al., 2004). They are characterised by intense physical and  
55 chemical gradients, and human activities have been proved to impact on their functioning,  
56 especially through eutrophication (Cloern, 2001; Gray et al., 2002). Within coastal  
57 environments, the intertidal zones constitute favourable areas for exchanges with the adjacent  
58 terrestrial systems and coastal water masses. Thus, their functioning is mainly driven by these  
59 exchanges of matter and energy and they constitute highly variable systems, both in space and  
60 time. In particular, exchanges between the sediment and the water column, especially during  
61 phytoplanktonic blooms, often enhanced by eutrophication, have been reported to drastically  
62 affect the biogeochemical processes in surficial sediments (e.g. Boon et al., 1998; Boon et al;  
63 1999; Grenz et al., 2000).

64           *Phaeocystis globosa* is one of the three *Phaeocystis* species that have been reported to  
65 form blooms (for a review, see Schoeman et al., 2005). *P. globosa* is a temperate species  
66 found on the coast of the eastern English Channel, southern North Sea and the south coast of  
67 China. Though not being toxic, *P. globosa* is considered to be responsible for harmful algal  
68 blooms (HAB; Veldhuis and Wassmann, 2005). Its life cycle is characterized by different  
69 forms of solitary cells alternating with colonial stages (Whipple et al., 2005 and references  
70 therein). These colonies are constituted of cells packed within a matrix and are surrounded by  
71 a "skin" (Hamm et al., 1999) which protects the cells from minute organisms (Hamm, 2000).  
72 During the colonial phase, one of the most spectacular manifestations of the bloom, because  
73 visible to the naked eye, can be observed on the seashore, consisting in large accumulations of  
74 mucilaginous aggregates (foam; Fig.1). This foam formation occurs under specific windy  
75 conditions (Lancelot, 1995) and the amount of foam deposited on the beach is directly  
76 dependent on the wind speed and direction that control foam formation and deposit on the

77 beach, respectively. The intensity of the bloom in the eastern English Channel and in Belgian  
78 coastal waters appeared to be related to the North Atlantic Oscillation (NAO) and nutrient  
79 loads by rivers (Seuront and Souissi, 2002; Breton et al., 2006; Gypens et al., 2007), and the  
80 differences in blooms amplitude between the two areas have been assigned to differences in  
81 the turbulence regime (Schapira et al., 2006).

82         Though the effect of the *P. globosa* bloom within the water column has been widely  
83 studied regarding for instance seawater properties (Seuront et al., 2006) or interactions with  
84 planktonic organisms (e.g. Ruardij et al., 2005), few studies concerned its effect on benthic  
85 organisms and/or processes. Accumulation of colonies on the sediment and their  
86 incorporation into the food web have been described (Cadée, 1996), as well as the occurrence  
87 of meiofauna feeding on the foam (Armonies, 1989) and the efficiency of filtration and  
88 absorption of the different life stages by benthic organisms (Smaal and Twisk, 1997).  
89 Although the intertidal zone is potentially the most impacted area because of foam  
90 accumulations, no study had been devoted to this specific system before the late nineties.  
91 However, foam deposits might constitute huge organic matter inputs into the sediment and  
92 might then interfere with both the living biota and the sediment biogeochemical processes.  
93 Furthermore, the high turbidity levels encountered during the spring bloom (Seuront et al.,  
94 2006 and references therein) might interfere with the photosynthetic activity of the benthic  
95 autotrophic organisms.

96         From 1999 to 2005, studies aimed to determine whether the *Phaeocystis* bloom  
97 affected the intertidal benthic communities of the French coast of the eastern English Channel  
98 in terms of composition and/or functioning. The eastern English Channel is an epicontinental  
99 sea that constitutes a transition zone between the Atlantic Ocean and the North Sea. It is  
100 characterized by a semi diurnal megatidal regime, the tidal magnitude reaching 9 m in spring  
101 tides in estuaries. In the area, the shoreline exhibits a complex morphology composed of  
102 sandy beaches, cliffs, estuaries, wetlands and polders (Battiau-Queney et al., 2001; Dauvin, in

103 press). Thus, the study sites were selected along the coast to cover most of the shore types that  
104 might be impacted during the *Phaeocystis* bloom (i.e. a rocky shore, an exposed sandy beach  
105 and a small estuary).

106 While the consequences of the bloom in the subtidal area are described in Denis and  
107 Desroy (this volume), the present paper synthesises the results that were obtained in the  
108 different intertidal environments regarding benthic metabolism and fluxes and the  
109 macrozoobenthic communities composition.

110

## 111 **2. Materials and Methods**

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

115

### 116 *2.1. Macroalgal photosynthetic activity and growth rate in the rocky shore*

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

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

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

131

$$132 \quad GR = 100 [(Lh_{t+1}-Lh_t)/L_t] / TL \quad (1)$$

133

134 with GR the growth rate (%.d<sup>-1</sup>); Lh<sub>t</sub> and Lh<sub>t+1</sub> the length between the hole and the junction  
135 between the frond and the stipe (cm) measured at time t and t+1, respectively; L<sub>t</sub> the total  
136 length measured at time t (cm); TL the time lag between t and t+1 (d). Due to storm events  
137 and human activities (fishing), the number of individuals at the end of the experiment was 34.

138

## 139 *2.2. Benthic metabolism, oxygen and nutrient fluxes, scanning electron microscopy of* 140 *foam in the exposed sandy beach*

141 The study site located in Wimereux was a typical exposed sandy beach characterised  
142 by medium size sand. A survey of benthic metabolism under emersed conditions (community  
143 primary production and community respiration measured as CO<sub>2</sub> fluxes following Migné et  
144 al., 2002) was performed from March 2000 to September 2005 (Spilmont et al., 2005; Hubas  
145 et al., 2007). During the period, seven additional measurements were carried out on  
146 *Phaeocystis* foam deposits (one in 2001, two in 2002, 2003 and 2004). The bacterial biomass  
147 within the first cm of sediment was concurrently estimated together with bacterial production  
148 and growth efficiency during the 2004-2005 survey.

149 Benthic fluxes at the water-sediment interface (O<sub>2</sub>, NH<sub>4</sub><sup>+</sup>) were estimated in 2004 and  
150 2005 on sediment cores incubated in the laboratory, by measuring changes in concentrations  
151 in the overlying water and by measuring solute concentrations in the interstitial water (Rauch  
152 et al., in press).

153 For the scanning electron microscopy observation, samples were fixed with  
154 lugol/glutaraldehyde solutions (0.2% v/v final concentration) and filtered through

155 polycarbonate membrane ( Millipore, 2 $\mu$ m). They were then rinsed 3 times in MilliQ water  
156 (Millipore), dehydrated in a graded ethanol series (30, 50, 70, 80, 90 and 100%, Fisher  
157 Scientific, P.A.) and critical point dried in liquid CO<sub>2</sub> using critical point drying  
158 apparatus(Bal-Tec CPD 030). Filters were mounted on a aluminium stubs, sputter-coated with  
159 Au/Pd (Polaron SC7620) and observed at 15kV with a SEM LEO 438 VP.

160

### 161 *2.3. Macrozoobenthos, oxygen and nutrient fluxes and waders frequentation in the* 162 *estuary*

163 The Canche Bay is a small estuary (ca. 6.3 km<sup>2</sup> of intertidal area) characterised by a  
164 relatively low river discharge (100 m<sup>3</sup>.s<sup>-1</sup> in winter and 60 m<sup>3</sup>.s<sup>-1</sup> in summer). Four intertidal  
165 sites were studied for macrozoobenthos (abundance, species richness and diversity), sediment  
166 organic matter content, sediment pigments contents (chlorophyll *a* and phaeopigments) and  
167 oxygen microprofiles from April to December 2001 (Desroy and Denis, 2004). One sandy  
168 and one muddy station were studied both in the northern and the southern part of the Bay  
169 (medium to fine sands and mud in the north; muddy fine sands and mud in the south). Data on  
170 macrofauna were also collected using a multilevel core sampler (Luczak and Menu,  
171 submitted) that provided complementary information on the vertical distribution of the  
172 macrofauna within the sediment. This device allowed the sampled core to be sliced in sub-  
173 samples corresponding to five layers in the sediment (0-1 cm; 1-2.5 cm; 2.5-5 cm; 5-10 cm  
174 and 10-20 cm). Sediment oxygen demand and total fluxes of dissolved inorganic nitrogen  
175 fluxes at the sediment/water interface were also estimated in the northern part of the Bay in  
176 March and May 2003 (Rauch and Denis, in press).

177 The number of waders staging in the estuary was based on the results of counts  
178 performed every ten days (at least one count per ten days period) in 2001. For the 1998-2000  
179 period, data come primarily from the Groupe Ornithologique et Naturaliste du Nord-Pas-de-  
180 Calais (G.O.N.) database. Counts were made by a combination of experienced volunteers and

181 professionals. High water counts were used, when birds concentrate on roosts. When several  
182 counts were performed in a ten days period, the highest count for each species was used  
183 (Yates and Goss-Custard, 1991).

184

### 185 **3. Results and discussion**

#### 186 *3.1. Shortage of light and nutrients for Saccharina latissima*

187 The results obtained during the *in situ* measurements of the photosynthetic activity and  
188 growth rate of *Saccharina latissima* are exhibited on Figs 3 and 4. During the late phase of the  
189 bloom (early May), almost no light reached the bottom as soon as the study site was  
190 submerged, with an average light extinction of 99% (average PAR of  $11 \pm 7 \mu\text{mol.m}^{-2}.\text{s}^{-1}$   
191 during immersion,  $n = 5$ ; Fig. 3A) whereas light kept reaching the algae all along the  
192 immersion period during the experiment conducted after the bloom (early June; 79% average  
193 light extinction,  $118 \pm 88 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  during immersion,  $n=6$ ; Fig. 3B). Thus, the  
194 photosynthetic activity of *S. latissima* during immersion, estimated through the measurement  
195 of rETR, was much lower when measurements were performed during the bloom ( $4 \pm 2$ ,  
196  $n = 5$ ; Fig. 3A) than for individuals in regular conditions ( $28 \pm 17$ ,  $n = 6$ ; Fig. 3B). As a  
197 consequence, the average growth rate of *S. latissima* decreased during the bloom (down to  
198  $0.61 \pm 0.02\%.\text{d}^{-1}$ ; Fig. 4), though March-April is usually a period of intense growth for the  
199 species. Towards the end of the bloom, the growth rate became higher ( $1.37 \pm 0.05\%.\text{d}^{-1}$ ) and  
200 then the algae came back to their regular growth cycle (limited growth rate throughout  
201 summer). The time course of the carbon content (Fig 5A in Gevaert et al., 2001) exhibited a  
202 typical trend for the species (directly linked to the growth cycle), being the lowest in March  
203 ( $23.9 \pm 0.5\%$  DW) and the highest in September ( $31.4 \pm 0.6\%$  DW). However, the time  
204 course of the nitrogen content (Fig. 5B in Gevaert et al., 2001) was characterised by a  
205 decrease from March ( $3.4 \pm 0.1\%$  DW) to June ( $2.2 \pm 0.1\%$  DW), that matched with the  
206 *Phaeocystis* bloom period for the year of the study (1999 in Gevaert et al., 2001). The

207 nitrogen being taken up from the medium by *S. latissima* as  $\text{NO}_3^-$ , it can be assumed that the  
208 seawater was depleted in nitrate during this period and led the algae to use their internal N  
209 stock. The growth of *Phaeocystis globosa* is known to be mainly sustained by the massive use  
210 of  $\text{NO}_3^-$  (Schapira et al., 2006), with concentrations in the seawater almost decreasing down to  
211  $0 \mu\text{mol.l}^{-1}$  in March-April (Gentilhomme and Lizon, 1998); this suggests that *P. globosa* and  
212 *S. latissima* compete for the same nitrogen source.

213 During the bloom it appeared that *S. latissima* was limited both in light and nitrate, as  
214 a consequence of (i) the turbidity induced by the presence of *Phaeocystis* cells and and (ii) a  
215 competition for  $\text{NO}_3^-$ . After the bloom, the algae recovered its regular photosynthetic activity  
216 and growth rate. This testifies to the plasticity of this species to adapt to environmental  
217 variations, as also previously underlined at the day scale (Gevaert et al., 2003).

218

219

220 *3.2. Enhancement of the benthic metabolism due to foam deposits in the exposed sandy*  
221 *beach*

222 Figure 5 shows the results obtained during emersion in terms of gross community  
223 production (GCP) and community respiration (CR), both on bare sediment and on sediment  
224 covered by foam deposits. CR was always higher on foam deposits than on bare sediment and  
225 the highest CR ever measured on this study site was on foam deposits on May 17 in 2001  
226 ( $11.95 \text{ mgC.m}^{-2}.\text{h}^{-1}$ ). By compiling data obtained by Spilmont et al. (2005) and Hubas et al.  
227 (2007), there was a significant positive correlation between sediment bacterial biomass and  
228 benthic community respiration during emersion ( $r = 0.547$ ,  $n = 41$ ,  $p < 0.01$ ; Fig. 6). As  
229 mentioned by these authors the community respiration in this sandy beach was dominated by  
230 bacterial respiration all along the year; the organic matter input made up of *Phaeocystis* foam  
231 would constitute a substratum for autochthonous bacterial populations and would also bring



232 allochthonous bacteria within the matrix, bacterial abundance and production also being linked  
233 to the bloom within the water column (Becquevort et al., 1998; Lamy et al., 2006).

234 Gross community production was always detected on foam deposits, except on May  
235 17 in 2001. Furthermore, GCP was often higher on deposits than on bare sediment (on May 6  
236 and 21 in 2002 and on May 5 and June 9 in 2004; Fig. 5) and was as high as  $23.13 \text{ mgC}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$   
237 <sup>1</sup> on foam on June 06 in 2004. This suggested that active phytoplanktonic cells were deposited  
238 within the foam. This hypothesis was corroborated by high assimilation numbers typical of  
239 phytoplanktonic cells calculated by Spilmont et al. (2005) and Hubas et al. (2007). The  
240 scanning electron microscopy photograph of a foam sample taken during the deposit in spring  
241 2004 (Fig. 7), brought a new evidence of phytoplanktonic cells trapped within the foam (a  
242 *Phaeocystis* cell and a diatom are visible). Bacteria responsible for the high respiration rates  
243 were also visible on this picture.

244 As for air-sediment CO<sub>2</sub> fluxes, the sediment oxygen demand (SOD) and ammonium  
245 release increased at the water-sediment interface during the spring bloom of *Phaeocystis*  
246 *globosa*, whereas these processes remained limited during the rest of the year (Fig. 8). The  
247 increase in SOD obviously appeared to be a direct response to the organic matter input and  
248 was correlated to bacterial abundances. The concomitant release of nitrates described by  
249 Rauch et al. (in press) was not only a diffusive flux from the sediment to the water column but  
250 was also linked to high nitrification rates coupled with lower denitrification rates in surficial  
251 sediments.

252 As mentioned by Spilmont et al. (2005) and Rauch et al. (in press), both the phase of  
253 the bloom and the meteorological conditions control the response of the sedimentary  
254 processes. During the early stage of the bloom (exponential growth of both solitary cells and  
255 healthy colonies), low community primary production and respiration were measured, but  
256 calm condition might allow phytoplanktonic cells to settle and lead to an increase in primary  
257 production at the air-sediment interface (Hubas et al., 2007). Nutrients being rapidly

258 consumed in the water column during this phase, the diffusive nutrient fluxes increased.  
259 During the late stage of the bloom (decaying colonies), windy conditions are favourable for  
260 foam accumulations to be brought to the beach and to settle at low tide. Thus, both relatively  
261 high community production and high respiration rates are expected. Nutrient cycling is also  
262 affected during this stage, the nitrification and denitrification processes then being uncoupled  
263 (Rauch and Denis, in press).

264

### 265 *3.3. Benthic fluxes and macrozoobenthic community modifications in the Canche Bay*

266 The results obtained on benthic fluxes in the Canche Bay gave the same conclusions as  
267 those previously described for Wimereux, i.e. an increase in the sediment oxygen demand and  
268 a high dissolved inorganic nitrogen release during the bloom, these modifications being  
269 reversible a short time after the bloom (Rauch and Denis, in press). In a previous analysis of  
270 the macrozoobenthic community at four sampling stations in this study site, Desroy and Denis  
271 (2004) had the opportunity to compare both low-impacted and high-impacted areas  
272 (respectively the south side and the north side of the Bay) during the 2001 bloom. The authors  
273 reported values of usual community descriptors (density, specific richness and diversity)  
274 exhibiting a rapid and significant reduction during the late phase of the *Phaeocystis* bloom in  
275 the impacted area (see their Figs. 7 and 8). These modifications, in terms of quantity and  
276 quality of macrozoobenthos, were linked to the development of anoxic conditions, sometimes  
277 being as extreme as the formation of an encrusting foam avoiding O<sub>2</sub> to penetrate further than  
278 1 mm (see their Fig. 5), when foam deposits were combined with high temperatures. These  
279 anoxic conditions led either to the direct death of some organisms, or to an upward migration  
280 of some individuals. The results obtained with the multilevel corer showed that the  
281 macrofauna tended to migrate upward during the first fortnight of May (Fig. 9) together with  
282 a decreasing number of species in all the layers (Fig. 10), especially in the northern sandy  
283 sediment where the encrusting foam was encountered. In these conditions, preys are directly

284 accessible for birds, without the need to dig them out. Interestingly enough, waders have been  
285 observed feeding on the macrofauna lying on the sediment during anoxic conditions (authors  
286 pers.obs). It appears that the upward migration of the macrofauna perfectly matched with the  
287 second annual peak of abundance of waders in the Canche Bay during refuelling on their  
288 migration route (Fig. 11). Following the diagram proposed by Zwarts and Wanink (1993), in  
289 regular conditions the harvestable fraction of benthic prey for waders depends on the fraction  
290 being profitable within preys that are available. In this context, small preys are usually  
291 ignored for an optimisation of the ratio between the energy needed to handle them and the  
292 energy they bring. In our study, since the remaining living macrofauna was lying on the  
293 sediment or very close to the surface, all preys (i.e. small and large ones) were profitable since  
294 waders did not have to spend much energy to feed on them. In this context, *Phaeocystis* did  
295 temporally and locally modify the energy flow through the estuarine ecosystem. As  
296 underlined by Desroy and Denis (2004), the macrozoobenthic communities recovered slowly  
297 from the disturbance, especially the north mud site which still exhibited very low species  
298 richness and density six months after the bloom.

299

## 300 **Conclusion**

301 *Phaeocystis* is considered to play a key role in global biogeochemical cycles, climatic  
302 regulation and fisheries yield (Schoeman et al., 2005). However, this statement was mainly (if  
303 not only) derived from studies on its impact on the physical, chemical and biological  
304 properties of the water column. In this synthesis, we strengthened this theory through results  
305 obtained on the intertidal benthic compartment. As exhibited in Table 1, both *Phaeocystis*  
306 active cells and their degradation product (foam) did have a significant impact on the studied  
307 shores. *Phaeocystis* actually modified the nitrogen cycle within the sediment and thus the N  
308 fluxes from the sediment, and also appeared to compete with macroalgae for nitrates.  
309 Furthermore, throughout the *Phaeocystis* bloom, the rates of macroalgae primary production

310 on rocky shores decreased, whereas the rates of gross community production and community  
311 primary production were enhanced on the sandy shore, then leading to changes in the carbon  
312 fluxes from the benthos to the air and the water column. The macrozoobenthos quality  
313 (diversity) and quantity (abundances) decreased during foam accumulation, some of these  
314 changes leading to energetic shortcuts within the estuarine trophic network (i.e. from  
315 macrozoobenthos to birds). However, most of these modifications lasted shortly. Indeed, all  
316 the systems and organisms came back to their regular activity or presented their initial  
317 properties a few weeks after the end of the bloom. The only notable exception was one of the  
318 benthic communities from muddy sediments studied in the Canche Bay which did not recover  
319 more than 6 months after the end of the bloom. Nevertheless, this represented a very singular  
320 case since this site was particularly impacted that year (2001). This last remark points out the  
321 fact that the intensity of the *Phaeocystis* bloom remains locally unpredictable in time and  
322 highly variable in space (see Fig. 1). For example, although the abundance of the species has  
323 been stated to be related to the NAO (Seuront and Souissi, 2002; Breton et al., 2006), the  
324 abundance and accumulation of foam is very dependant on local hydrodynamic and  
325 topographic conditions. Thus, the surface covered by foam is not predictable and remains  
326 difficult to estimate at a large spatial scale due to its short residence time (the foam is wiped  
327 out during each rising tide); the calculation of an accurate impact of this deposit on carbon  
328 and nitrogen fluxes remains very hazardous.

329

### 330 **Aknowledgements**

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475

476

477 **Figure captions**

478 Figure 1. Accumulations of mucilaginous aggregates (foam) of *Phaeocystis globosa* on the  
479 beach of Wimereux during the 2002 spring bloom.

480

481 Figure 2. Location of the study sites along the French coast of the Eastern English Channel.

482

483 Figure 3. Photosynthetic activity of *Saccharina latissima* in spring 2001. The photosynthetic  
484 activity was measured as the relative electron transfer rate (rETR, dots) and  
485 photosynthetically active radiations (PAR,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , dashed line) reaching the algae  
486 (bottom PAR) were measured simultaneously. The surface PAR was measured throughout the  
487 experiments (dark line). The grey bars symbolise the periods of immersion.

488

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

492

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

498

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

503

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

507

508 Figure 8. Average Sediment Oxygen Demands and ammonium releases ( $\mu\text{mol.m}^{-2}.\text{h}^{-1}$ ;  $\pm$  SD;  
509 n=4) at the sediment-water interface during the year 2004. Black diamonds represent values  
510 recorded in the absence of *Phaeocystis globosa*, whereas open squares are measurements  
511 performed during the spring 2004 *Phaeocystis globosa* bloom (late March-early May).

512

513 Figure 9. Time course of the average burying depth (cm) of the macrofauna at the four  
514 sampling stations surveyed in the Canche Bay in 2001. The grey bars symbolise the period of  
515 maximal foam accumulation on the sediment. The north site was highly impacted, the south  
516 site was low impacted.

517

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

523

524 Figure 11. Total number of waders counted within the Canche Bay for ten day periods (3 per  
525 each month of the year) for the period 1998-2001 (grey bars, mean  $\pm$  s.d.) and for the year  
526 2001 (dashed bars).

527

528

529 **Table captions**

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

533

534



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Figure 1

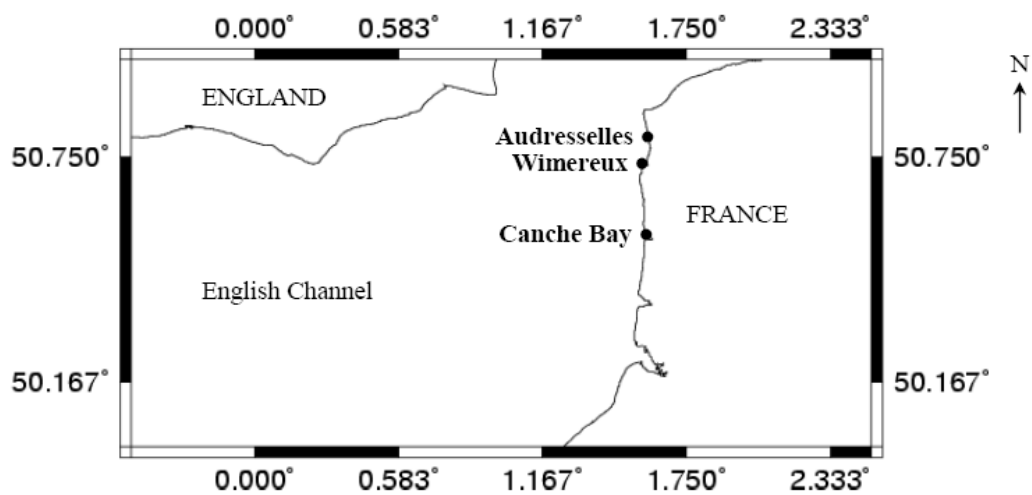
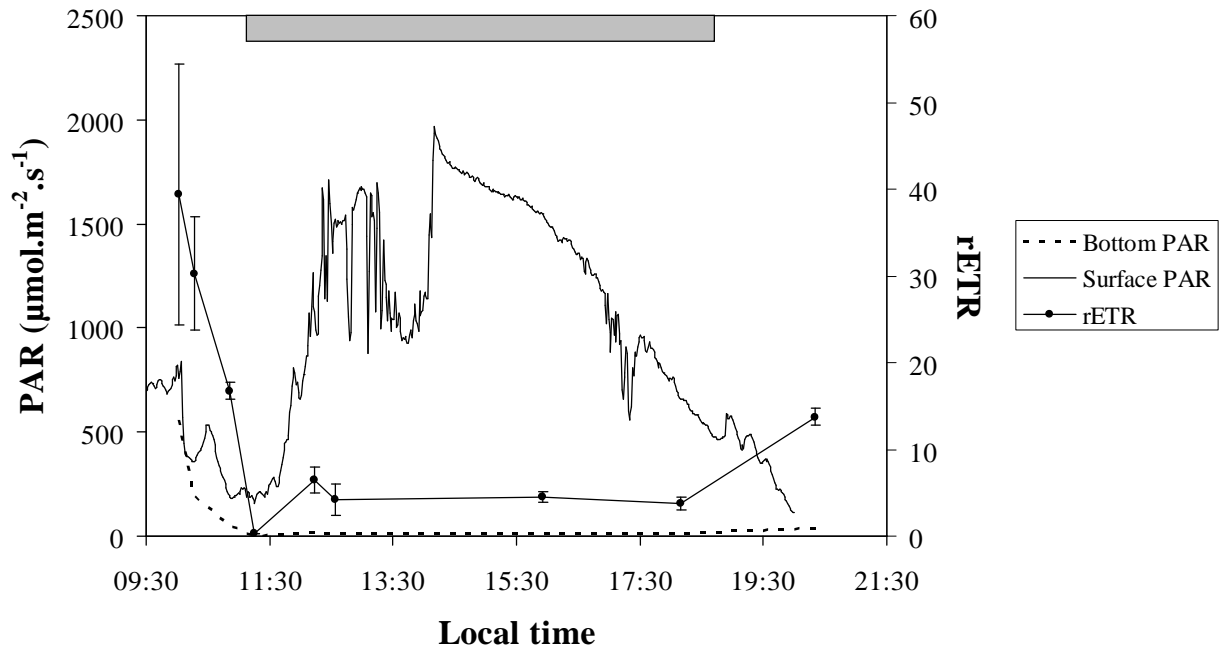


Figure 2

A

May 9 2001



B

June 5 2001

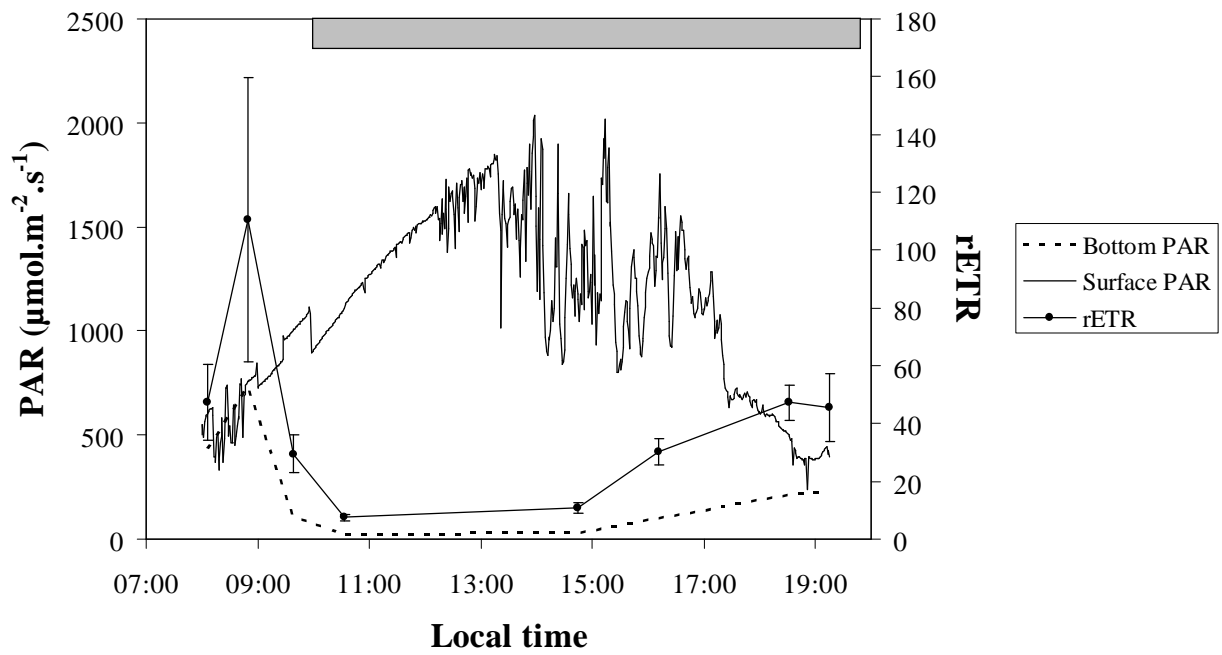


Figure 3



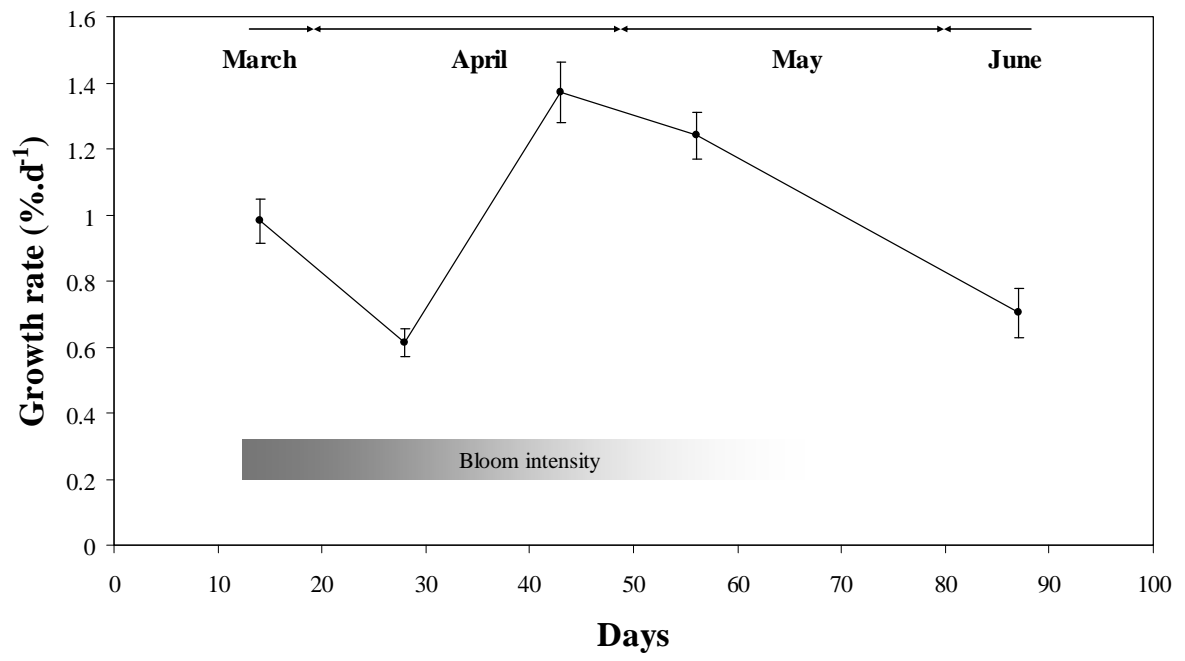


Figure 4

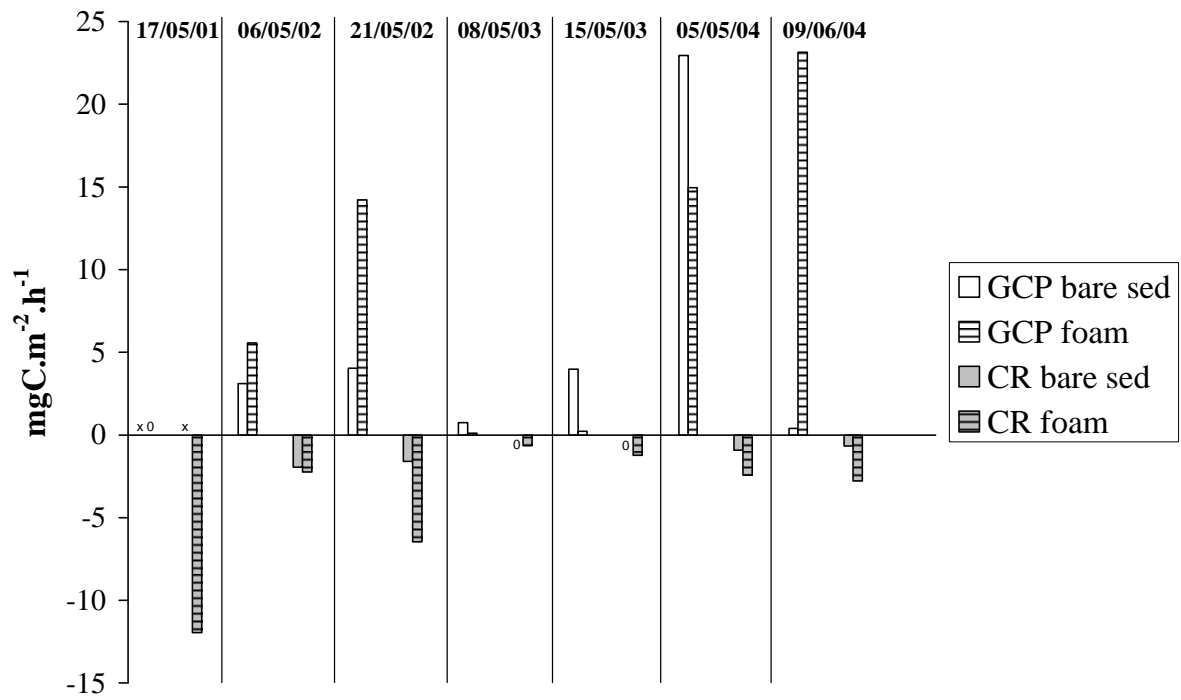


Figure 5.

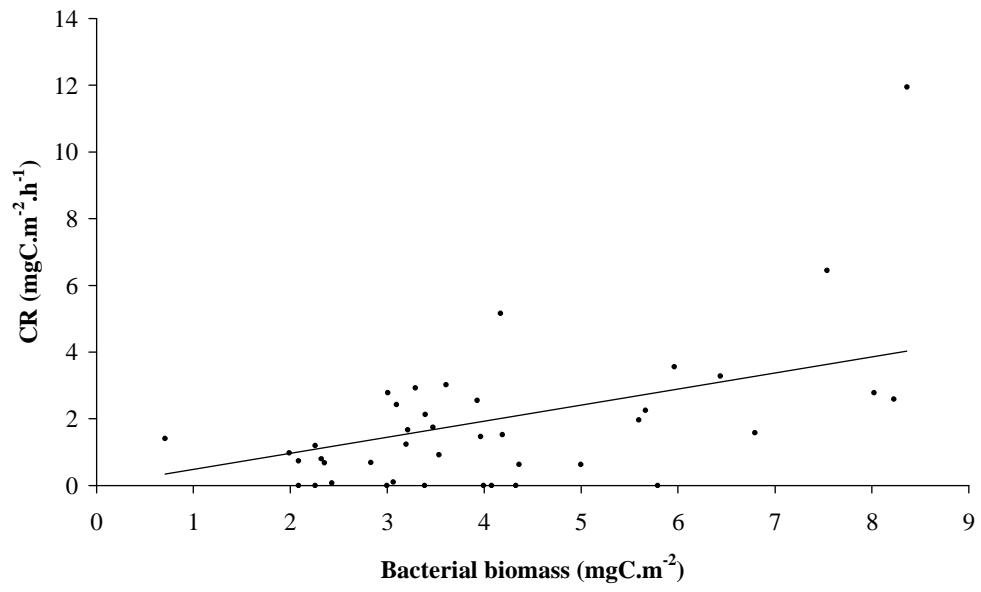


Figure 6.

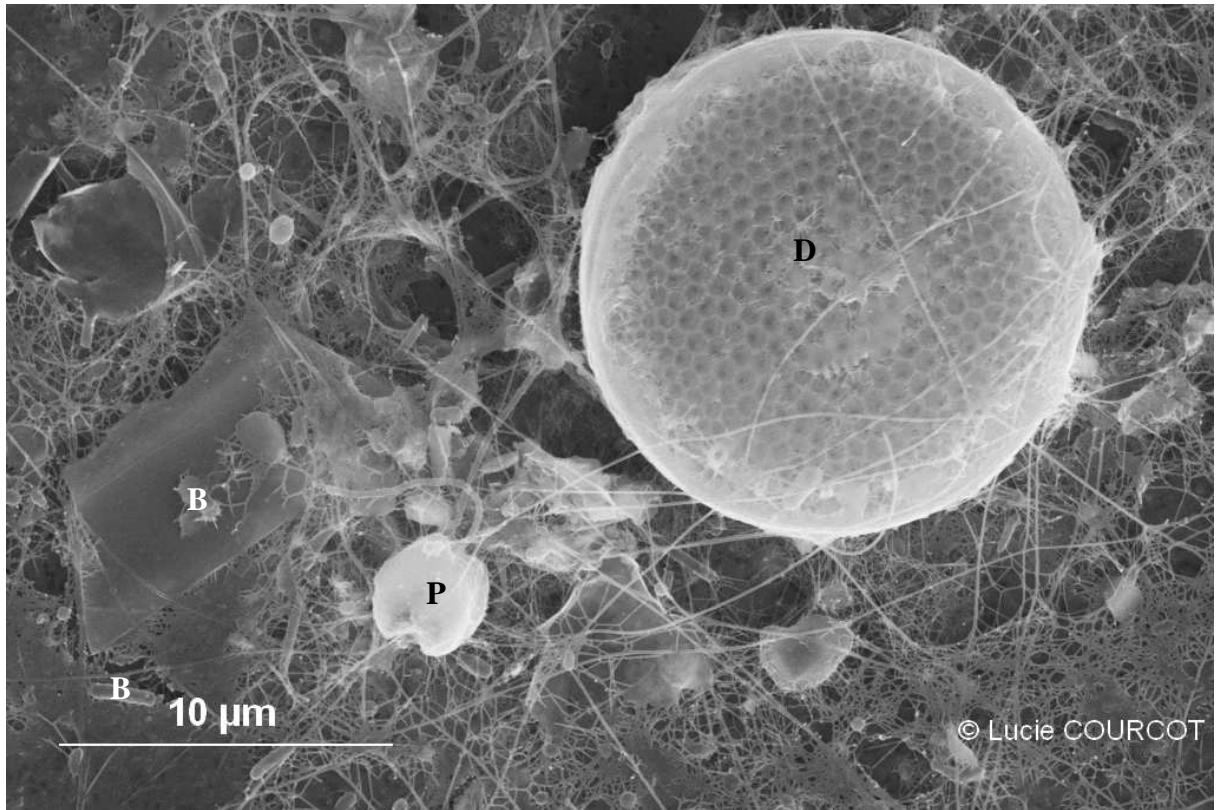


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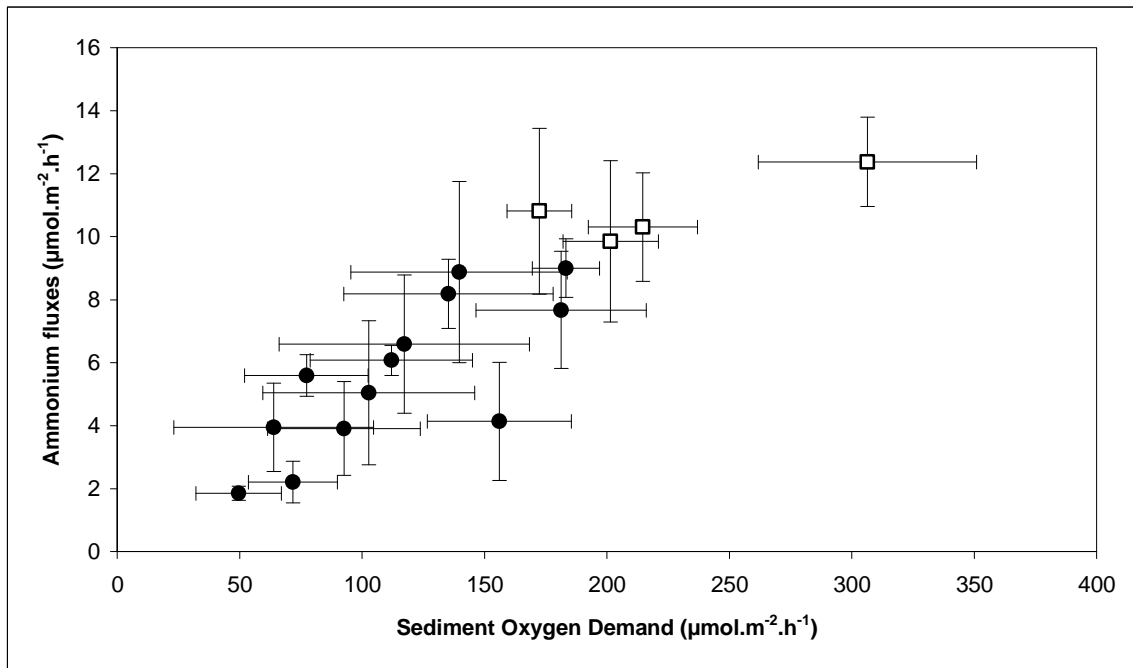


Figure 8.

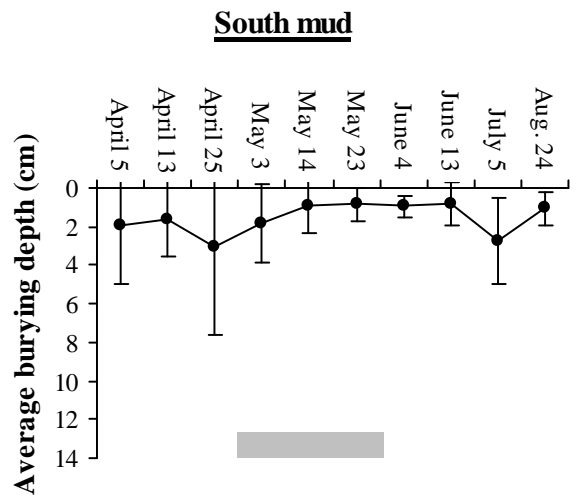
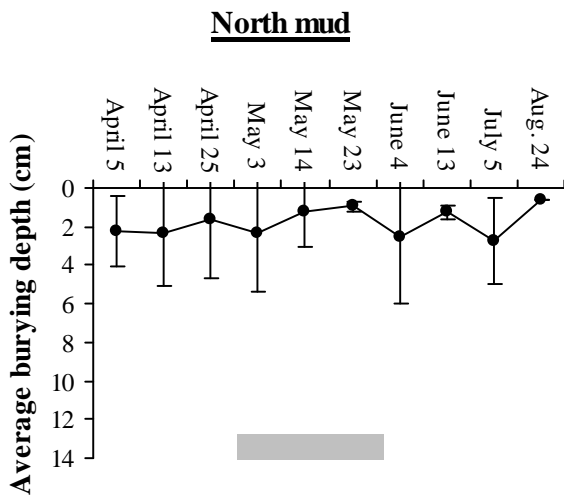
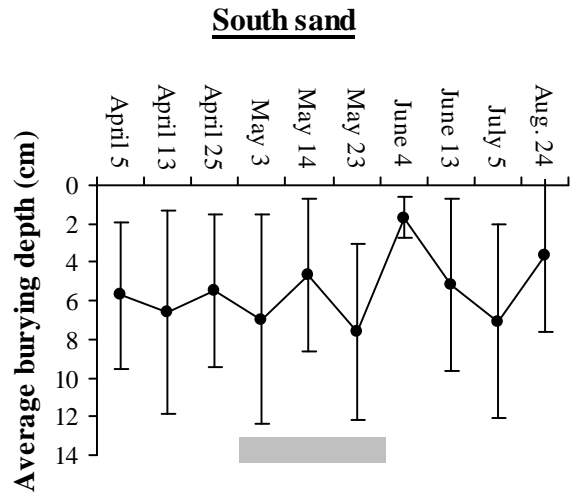
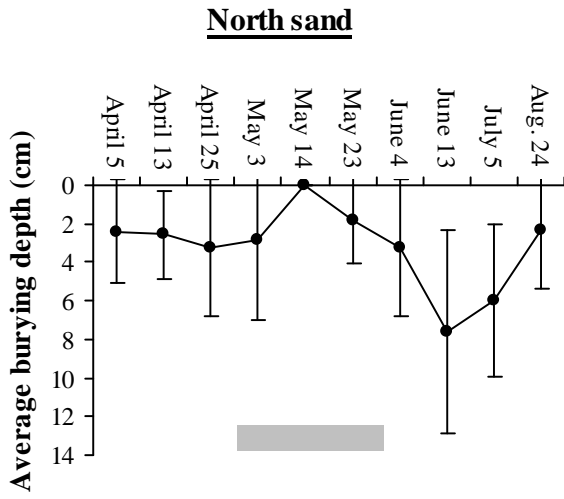


Figure 9.

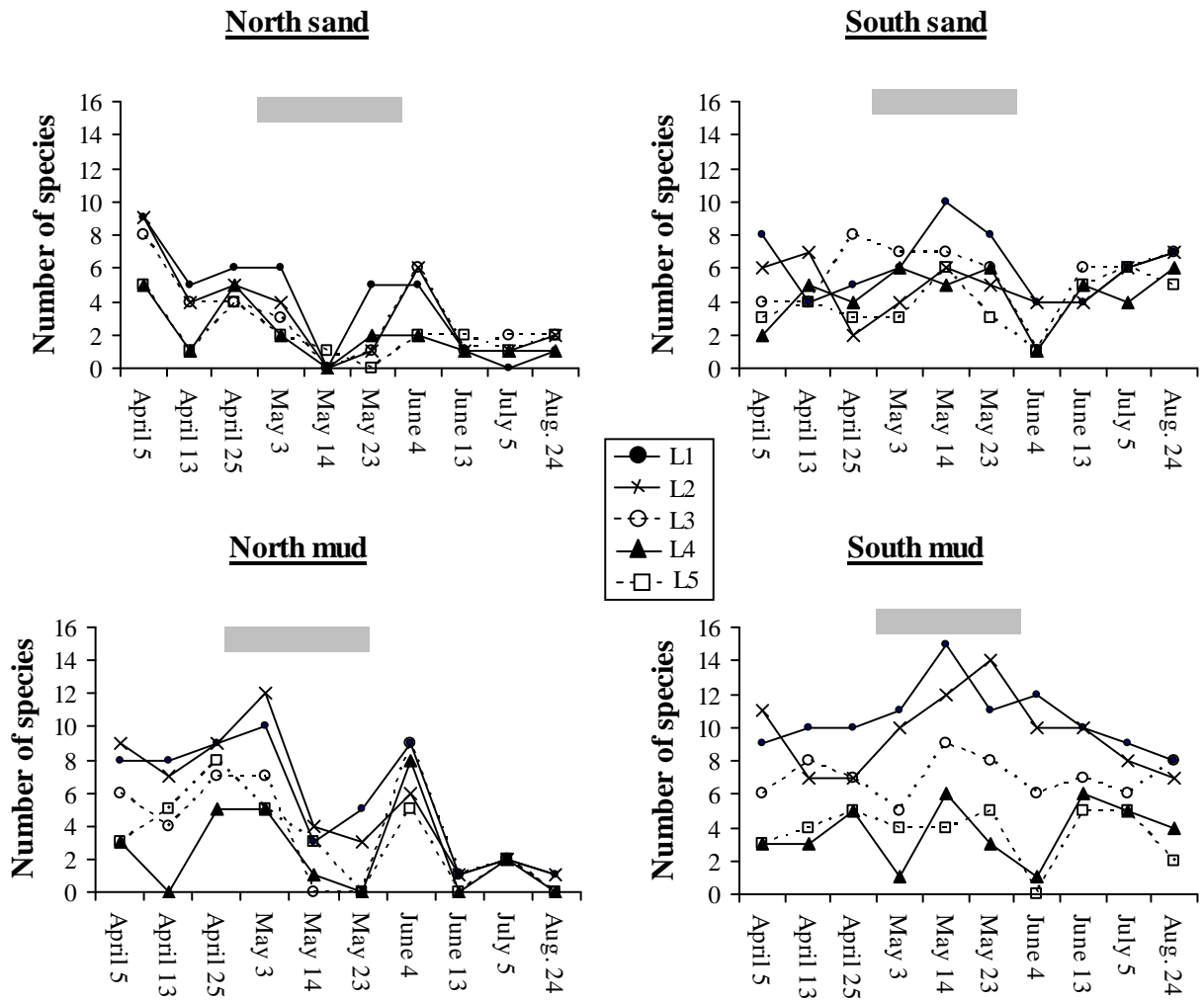


Figure 10.

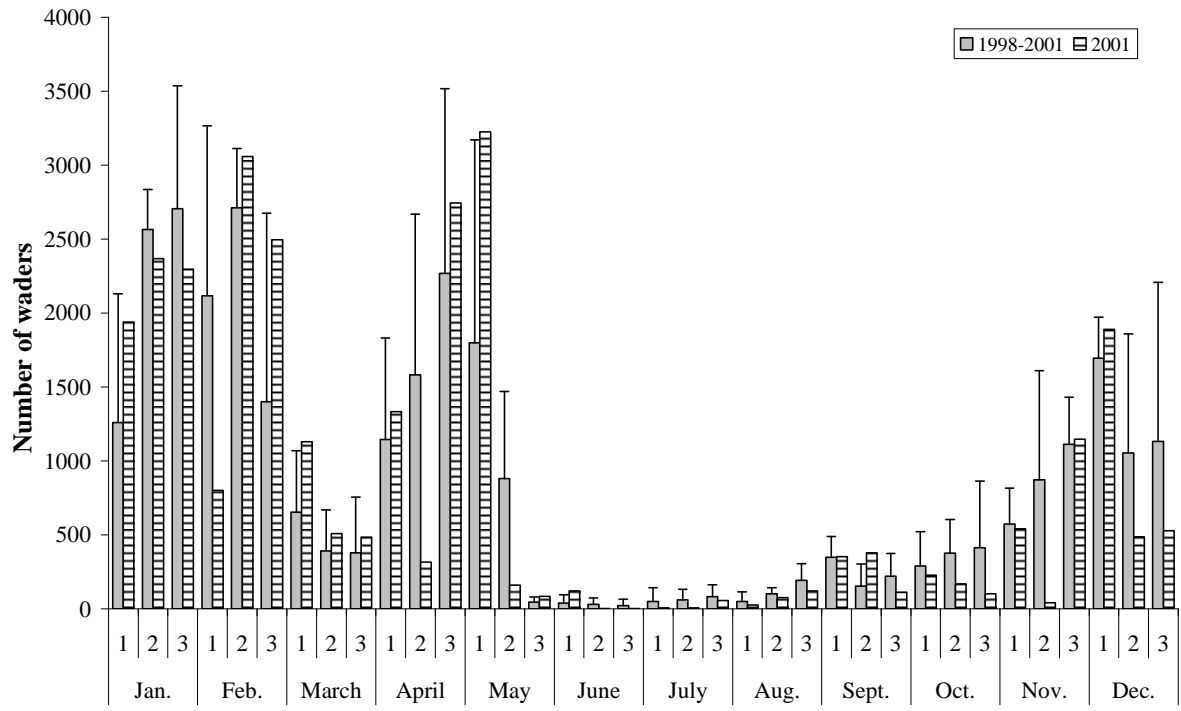


Figure 11.



Table 1

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 $\text{NH}_4^+$ 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 $\text{O}_2$ 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. $\text{NH}_4^+$ 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