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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.

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⁻¹); Lh_t and Lh_{t+1} 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_t 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 CO₂ 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 (O₂, NH₄⁺) 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 μ 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 CO₂ 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 km² of intertidal area) characterised by a
164 relatively low river discharge (100 m³.s⁻¹ in winter and 60 m³.s⁻¹ 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 ± 2 ,
196 $n = 5$; Fig. 3A) than for individuals in regular conditions (28 ± 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 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 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 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 ¹ 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 CO₂ 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 O₂ 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

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333 Mer du Nord") coordinated by IFREMER and the CNRS and (ii) the "Contrat de Plan Etat-
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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

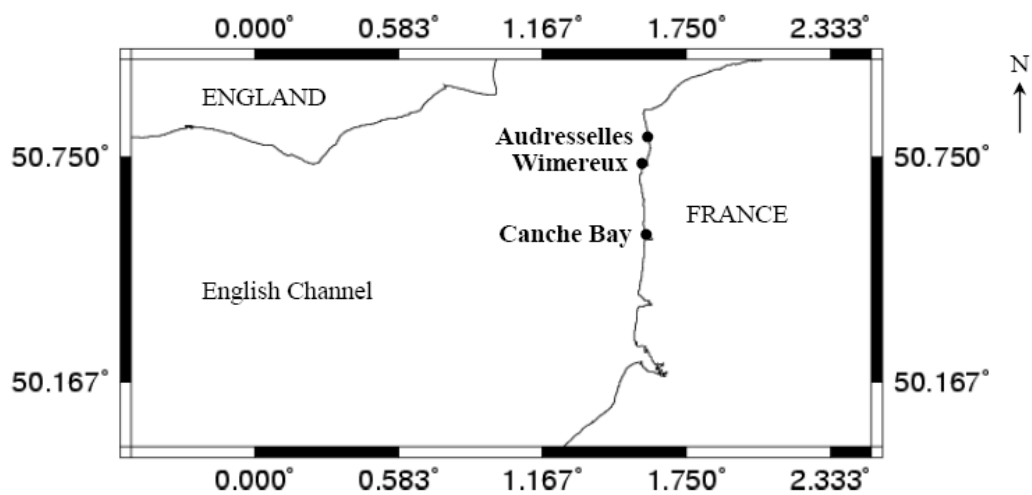
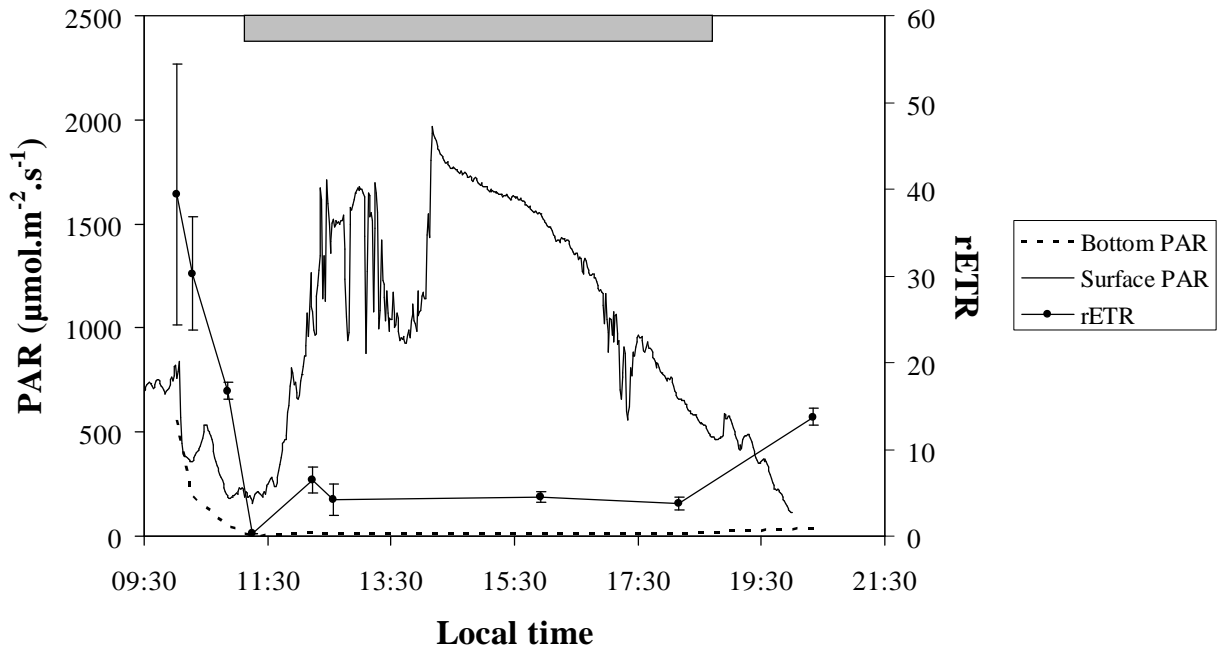


Figure 2

A

May 9 2001



B

June 5 2001

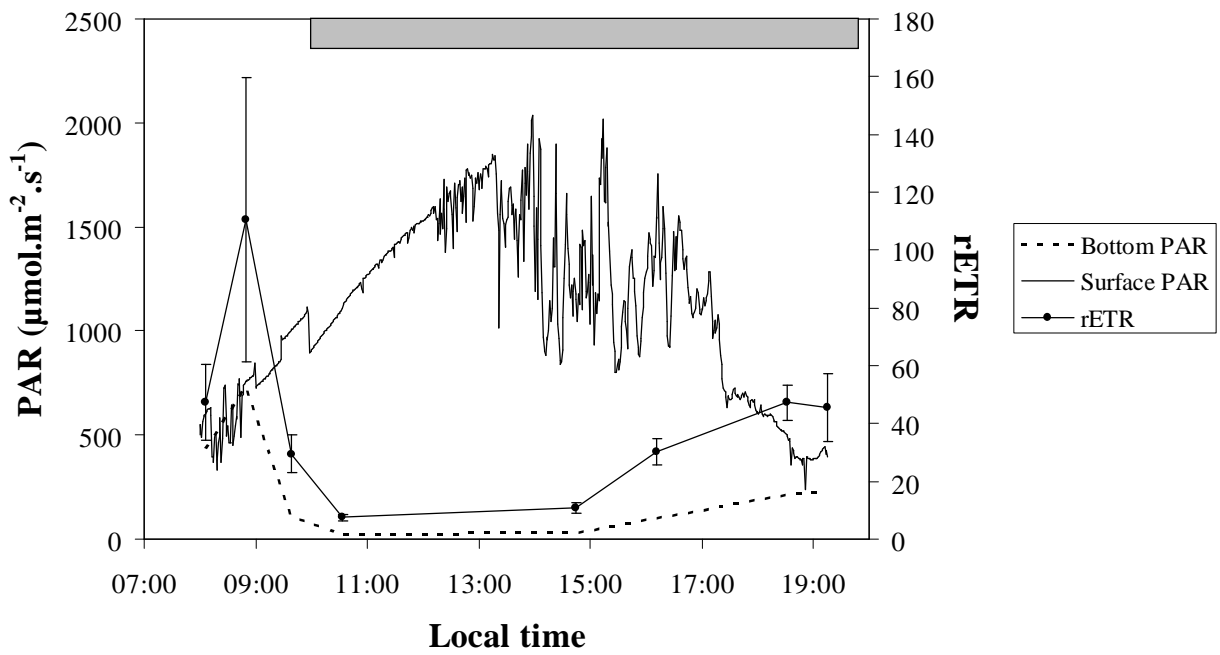


Figure 3

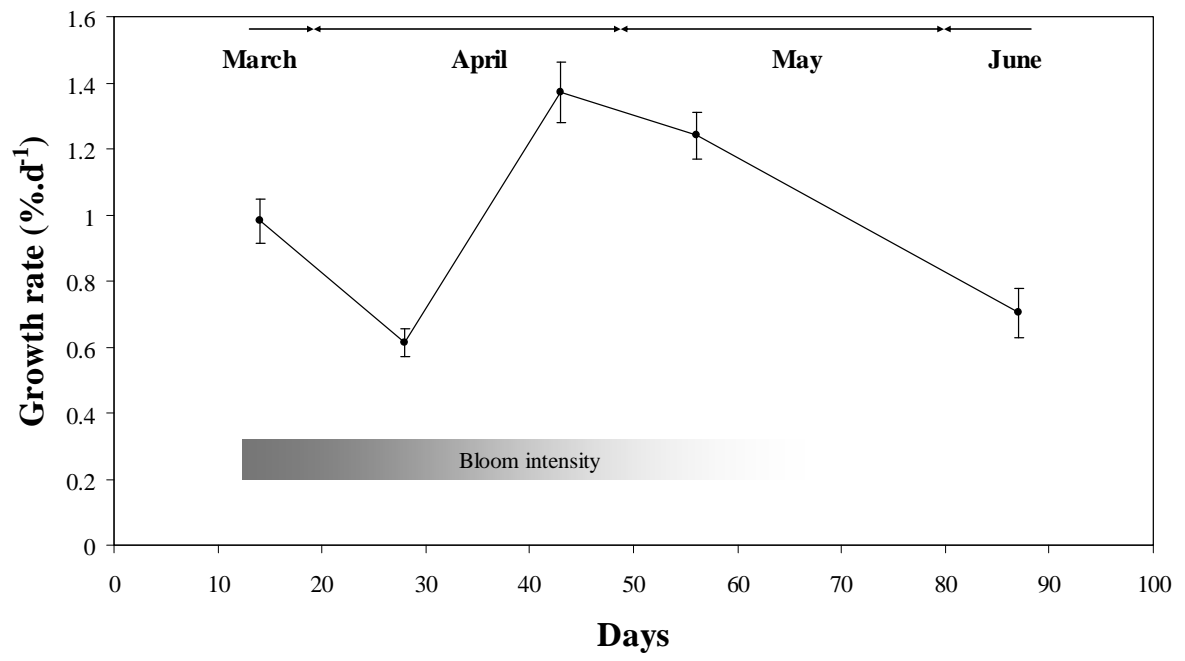


Figure 4

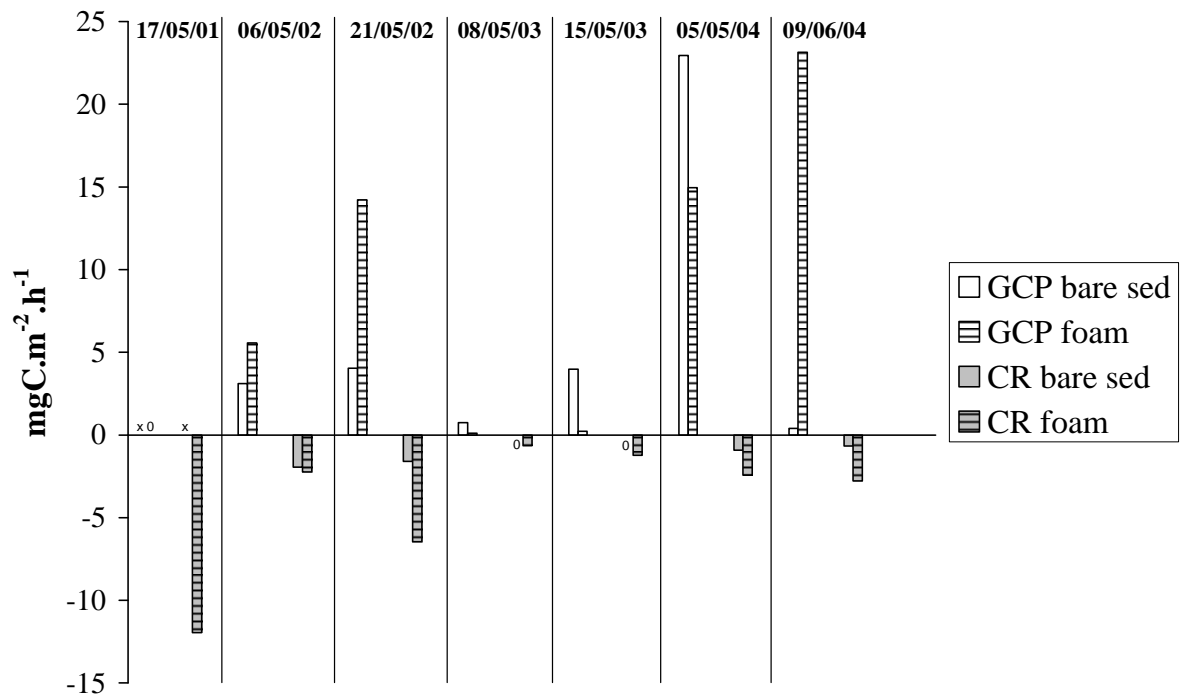


Figure 5.

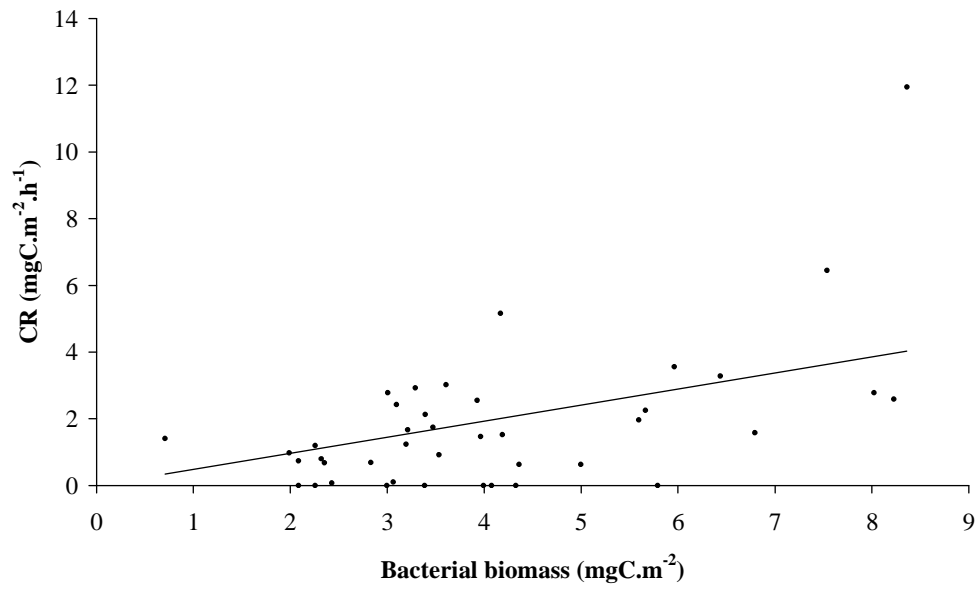


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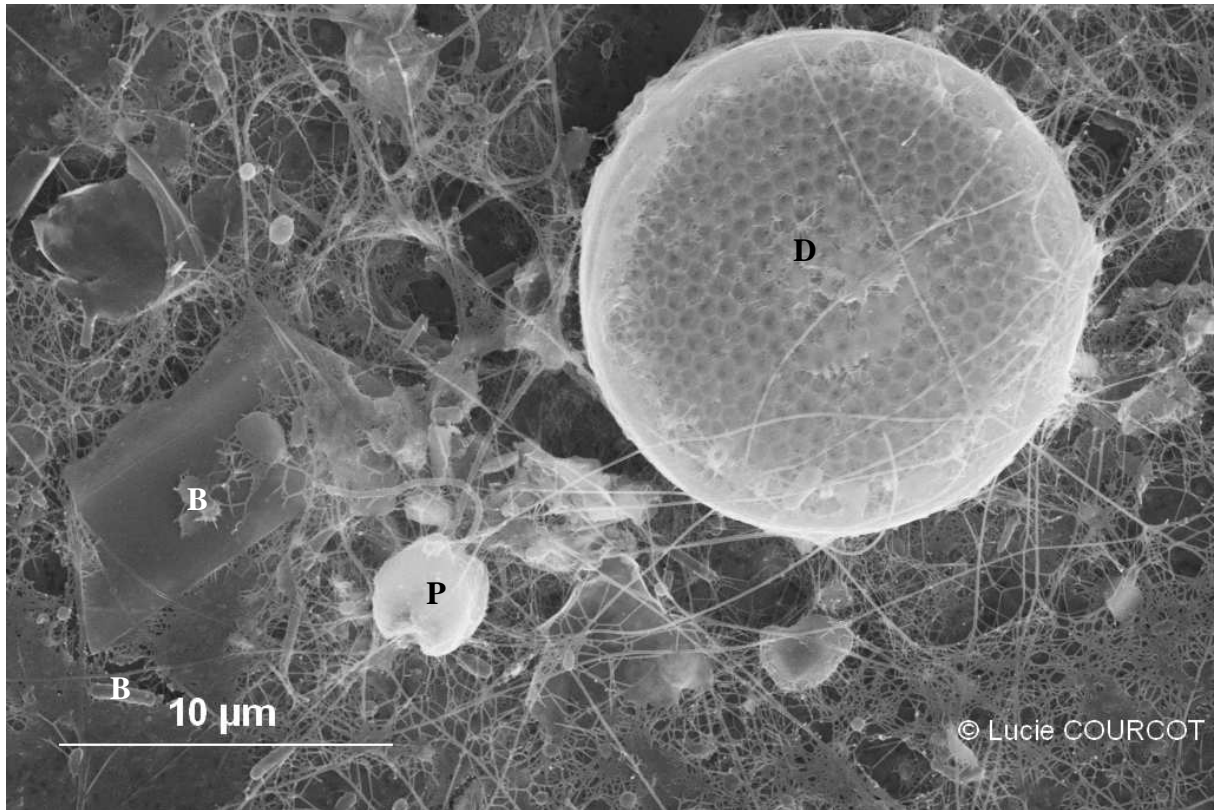


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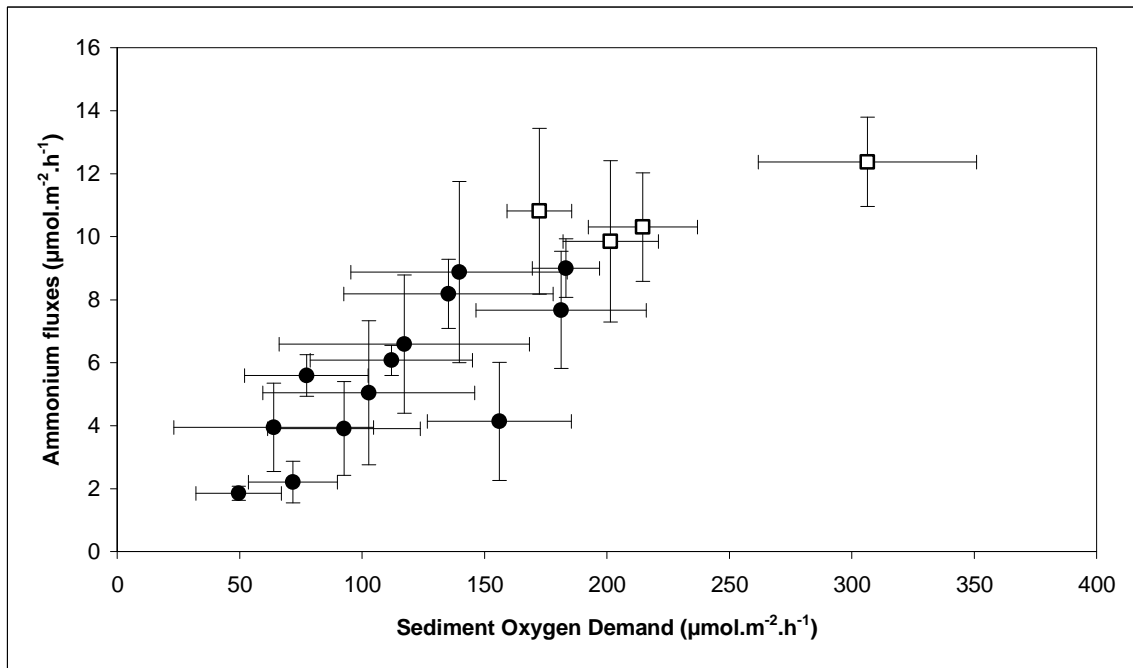


Figure 8.

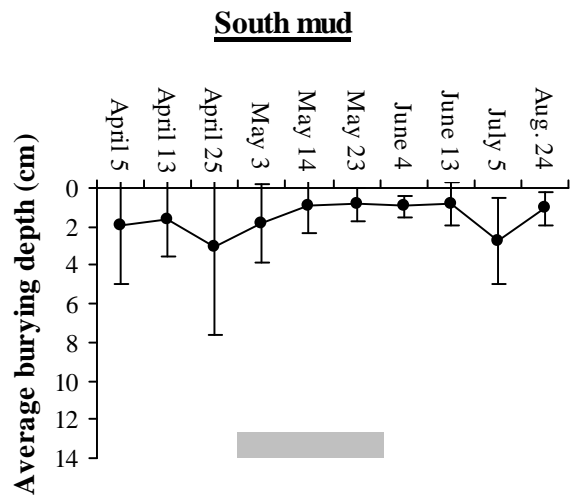
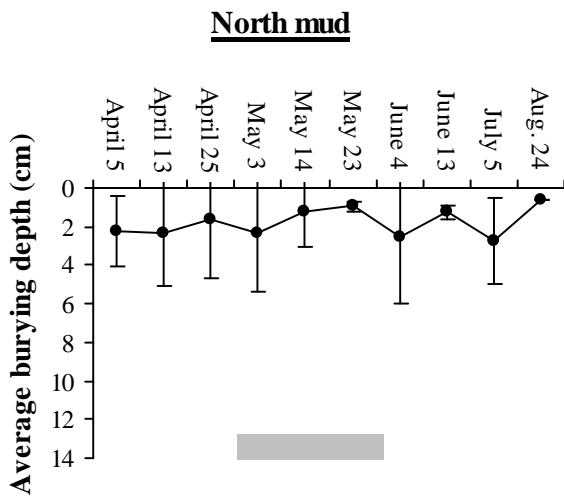
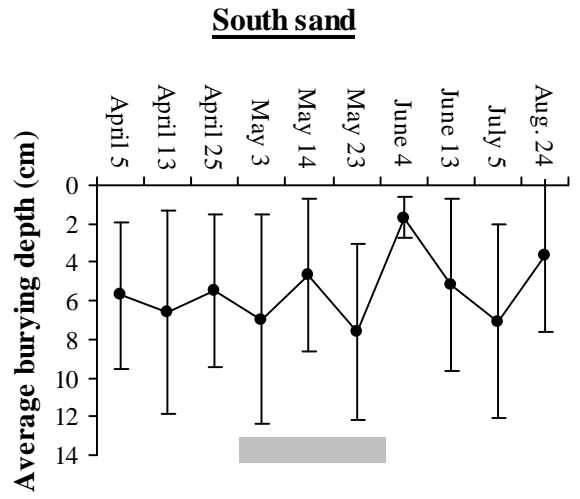
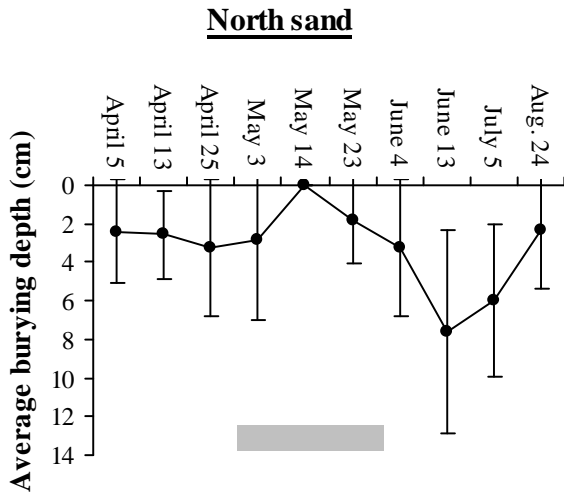


Figure 9.

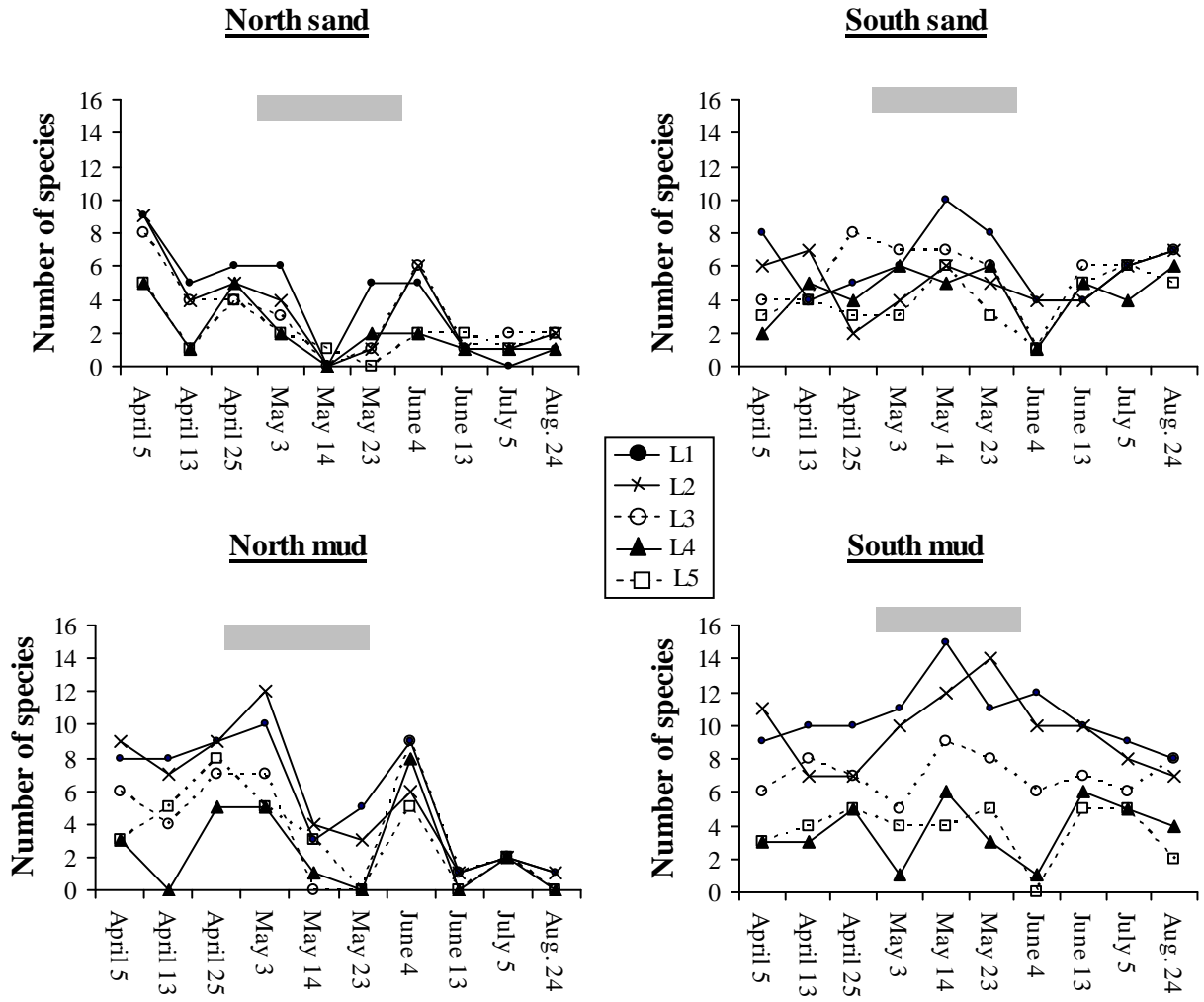


Figure 10.

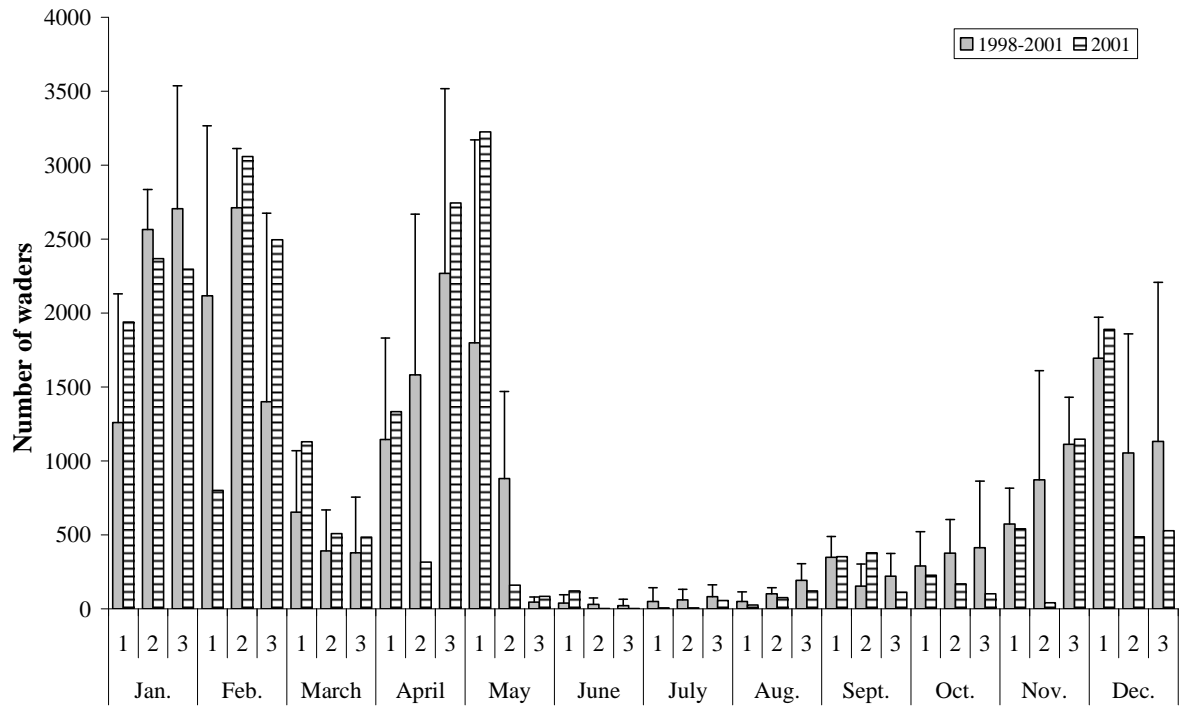


Figure 11.

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 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