

## CHAPTER 3

### Phytoplankton blooms in response to nutrient enrichment

Véronique Rousseau<sup>1</sup>, Youngje Park<sup>2</sup>, Kevin Ruddick<sup>2</sup>, Wim Vyverman<sup>3</sup>,  
Jean-Yves Parent<sup>1</sup> and Christiane Lancelot<sup>1</sup>

<sup>1</sup> Université Libre de Bruxelles (ULB), Ecologie des Systèmes Aquatiques (ESA), CP221,  
boulevard du Triomphe, B-1050 Brussels, Belgium

<sup>2</sup> Management Unit of the North Sea Mathematical Models (MUMM), Royal Belgian  
Institute for Natural Sciences, Gulledelle 100, B-1200 Brussels, Belgium

<sup>3</sup> Universiteit Gent (UG), Protistologie en Aquatische Ecologie, Krijgslaan 281 S8,  
B-9000 Gent, Belgium

---

#### 3.1. Phytoplankton blooms in the eutrophied Belgian Coastal Zone

Delivery of continental nutrients to coastal waters generally results in phytoplankton blooms characterized by high biomass levels. Such is the case in the Belgian Coastal Zone (BCZ) where satellite images recurrently detect high Chl *a* concentrations (Fig. 3.1) particularly in the coastal waters influenced by the nutrient-enriched freshwater of the Scheldt and coastal tributaries (see Fig. 2.13 in Brion *et al.*, 2008). These phytoplankton blooms are particularly significant in April and May, when Chl *a* concentrations higher than 10 and locally 25 mg m<sup>-3</sup> are reached in Belgian and Dutch nearshore waters (Fig. 3.1). Phytoplankton blooms start in average in March, in the clearest Southwestern coastal waters (Fig. 3.1; Borges & Frankignoulle, 2002; Muylaert *et al.*, 2006), and propagate in April-May in the almost entire BCZ and adjacent waters (Fig. 3.1). During summer and fall, moderate Chl *a* concentrations, *i.e.* 3-10 mg m<sup>-3</sup>, are still detected but are restricted to the very nearshore region (Fig. 3.1), presumably due to the local influence of nutrient enrichment at that time of the year.

Satellite time series Chl *a* data retrieved for stations 230, 330 and 435 along an in-offshore transect (Fig. 3.1) reproduce well the phytoplankton bloom dynamics in the BCZ, highlighting a major spring bloom at all 3 stations but significant summer blooms at the coastal station 230 only (Fig. 3.2). The time series data show the transient nature of the phytoplankton blooms as well as a significant interannual variability in their magnitude and timing (Fig. 3.2).

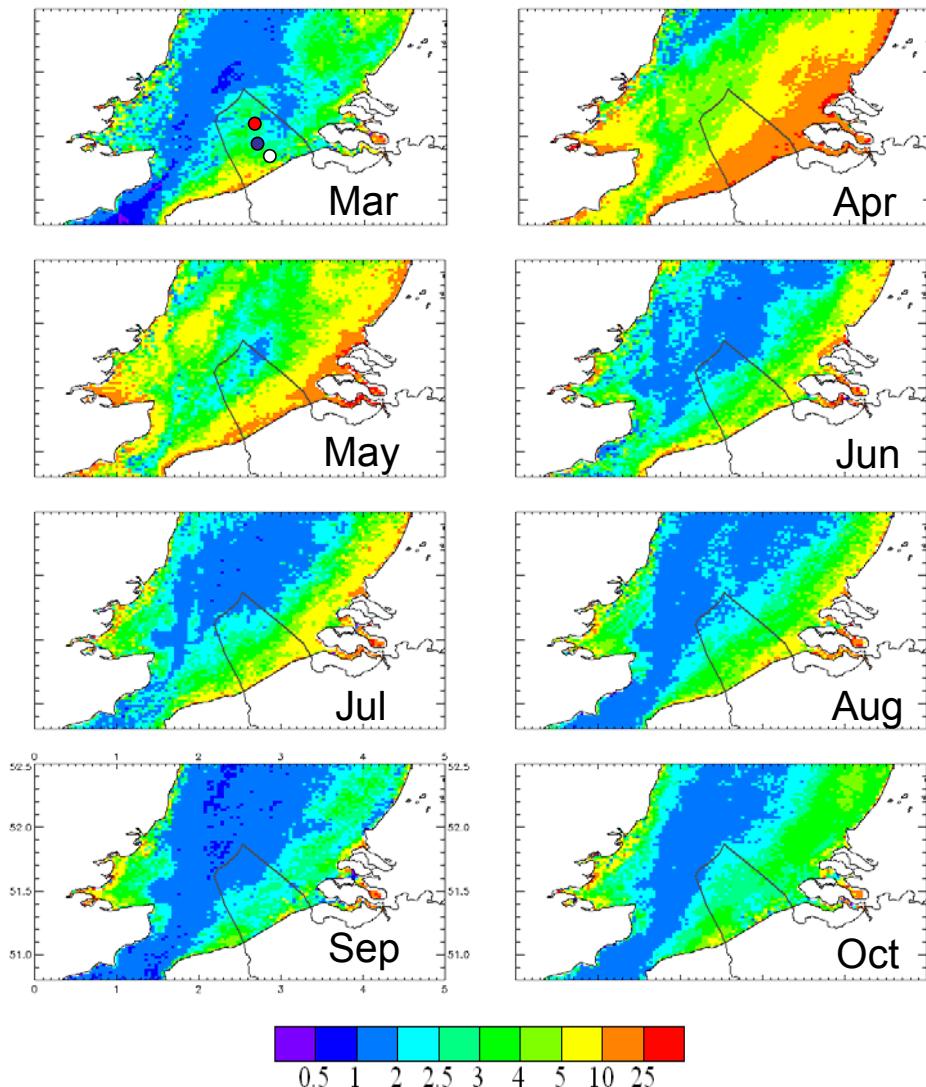


Figure 3.1. Monthly means of MERIS chl a concentration ( $\text{mg m}^{-3}$ ) for the period 2003-2007 derived from the MERIS sensor using processor version 5.02 and 5.04 with data quality screened by use of the product confidence flag. The Belgian continental shelf is indicated by solid black lines. White, blue and red dots indicate stations 230, 330 and 435 respectively. Data provided by the European Space Agency in the framework of Envisat AOID 3443 and processed in the BELCOLOUR-2 project.

Phytoplankton blooms

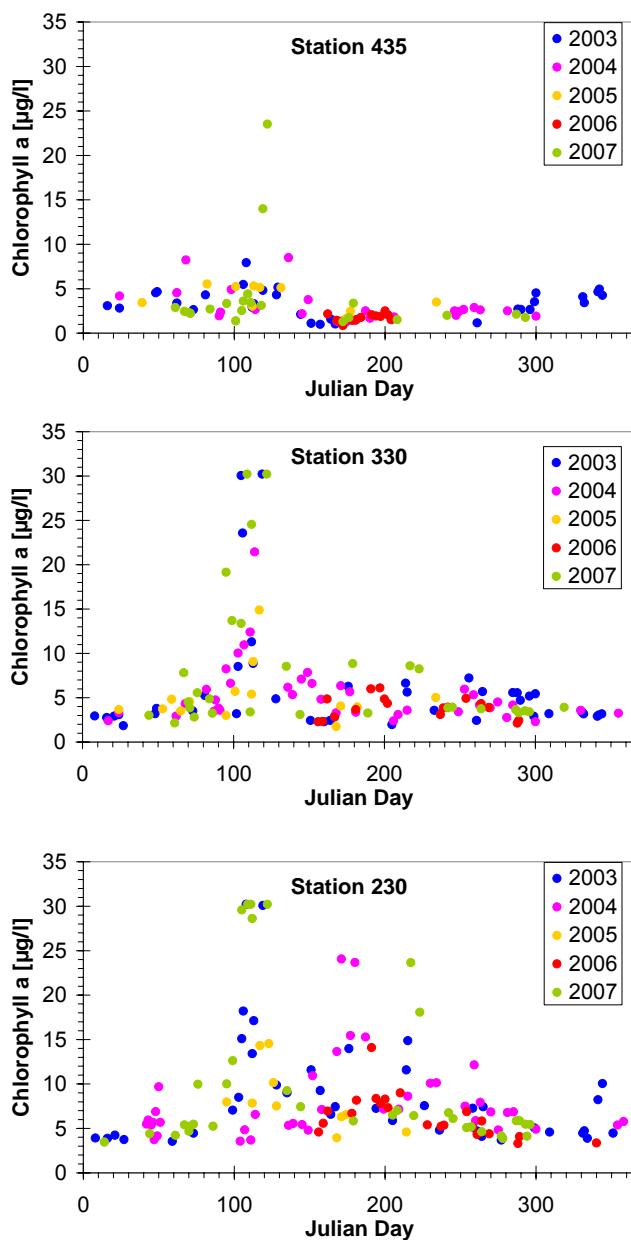


Figure 3.2. Time series of MERIS chlorophyll a concentration for the period 2003-2007, except September 2005-June 2006. Location of stations 230, 330 and 435 is shown in Figure 3.1. Satellite data source and processing as in Figure 3.1.

### 3.2. *Phaeocystis* and diatom blooms in the BCZ

Analysis of phytoplankton composition indicates that two major taxa, the diatoms and the colonial haptophyte *Phaeocystis globosa*, are contributing to the bulk Chl a. Other phytoplankton groups such as cyanobacteria, euglenophytes, cryptophytes, chlorophytes or dinoflagellates are also present but as very minor contributors (Muylaert et al., 2006). The phenology of diatoms and *Phaeocystis* blooms has been intensively investigated during 13 years (1988-2000) at station 330 (see location in Fig. 3.1), chosen because it represents the average physico-chemical conditions prevailing in the BCZ (Rousseau, 2000). This phytoplankton time series data show that diatoms are present during the whole vegetative season while *Phaeocystis* colonies occur only as a single spring event lasting between 4 and 13 weeks (Fig. 3.3; Breton et al., 2006).

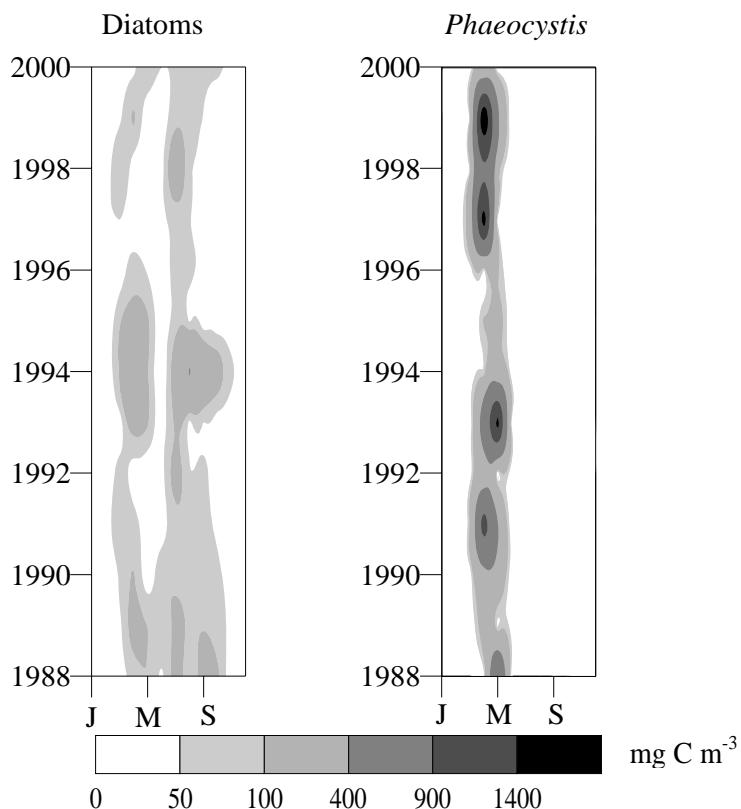


Figure 3.3. Seasonal pattern of diatom and *Phaeocystis* colony biomass ( $\text{mg C m}^{-3}$ ) at station 330 from 1988 to 2000 (JMS: January, May, September). From Breton et al. (2006). Copyright (2008) by the American Society of Limnology and Oceanography, Inc.

## Phytoplankton blooms

Contrary to diatoms which constitute the major phytoplankton group in well balanced N:P:Si enriched waters, the spring proliferation of *Phaeocystis* colonies is the eutrophication-related event in the BCZ and the Southern Bight of the North Sea. When blooming, *Phaeocystis* cell density can reach 50-120  $10^6$  cells  $L^{-1}$  and represent some 70 % of the spring net primary production (Rousseau *et al.*, 2000). These high biomasses are related to the ability of *Phaeocystis* to rapidly form gelatinous colonies containing several thousands of cells (Fig. 3.4), whose size makes them unpalatable for mesozooplankton (Daro *et al.*, 2008). Ungrazed colonies are responsible for the deposit of thick layers of odorous foam on the beaches resulting from food chain disruption (Fig. 3.4; Lancelot, 1995). These undesirable colony blooms are not recent as demonstrated by model reconstruction of Seine and Scheldt watersheds, showing that *Phaeocystis* colonies were already blooming in pristine time (Lancelot *et al.*, 2008). At that time, *Phaeocystis* colonies were present under grazable forms efficiently transferred to higher trophic levels.

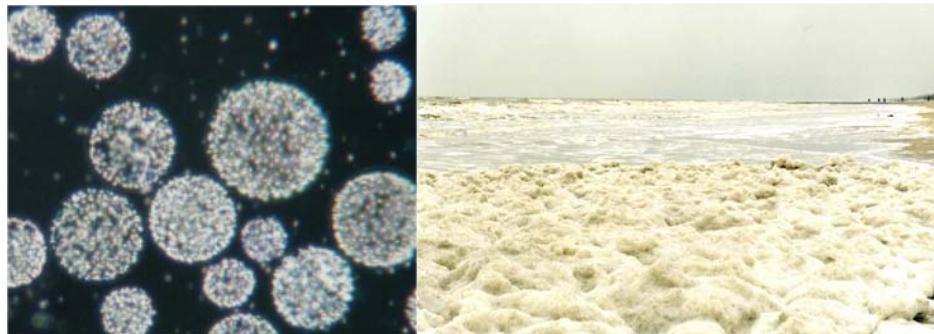


Figure 3.4. Eutrophication-related event in the BCZ; *Phaeocystis globosa* spherical colonies (left); foam accumulation on the beach of Oostend in May 1998 (right).

### 3.2.1. Present-day variability of the magnitude of diatoms and *Phaeocystis* blooms

Diatom and *Phaeocystis* blooms at station 330 present significant interannual fluctuations in their magnitude with most of the years dominated by *Phaeocystis* but a few by diatoms (Fig. 3.3). This year to year variability results from the combined effects of hydro-climatic variability and human activities via the Scheldt nutrient loads (Fig. 3.5; Breton *et al.*, 2006). Hydro-climatic variability is driven by the North Atlantic Oscillation (NAO) which governs meteorological conditions, *i.e.* local wind dominance and rainfall, over the Northwestern Europe (Hurrell, 1995). Wind and rainfall, in turn, determine the hydrodynamical features of the BCZ with a higher propagation of English Channel waters and higher Scheldt water and nutrient discharge under southwesterly wind dominance and high rainfall in the Scheldt watershed (Fig. 3.5). Wind direction also influences the spreading of the Scheldt plume at station 330 with lower freshwater influence under southwesterly wind dominance (Fig. 3.5). On this

Rousseau et al.

basis, Breton et al. (2006) demonstrated that diatom biomass variability at station 330 is mostly related to a change in hydrodynamics, i.e. the balance between English Channel Water Inflow and Scheldt freshwater inputs in the BCZ, while *Phaeocystis* bloom variability results from the NAO modulation of Scheldt freshwater and nutrient discharge on the one hand, and their spreading in the BCZ on the other hand (Fig. 3.5).

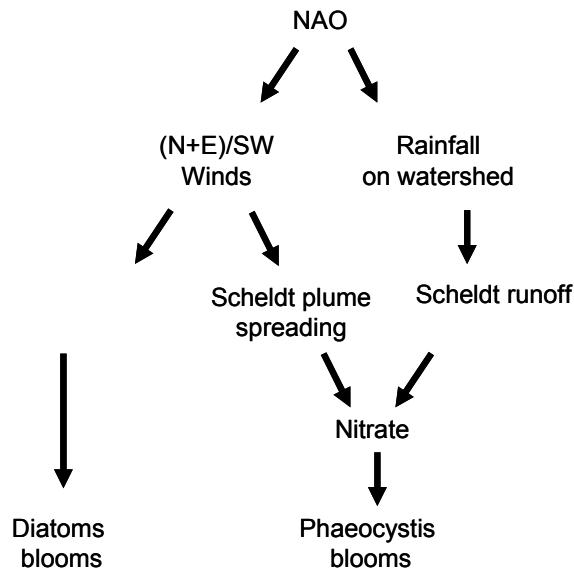


Figure 3.5. Mechanisms linking NAO, meteorological, hydrodynamical, physico-chemical characteristics and diatom and *Phaeocystis* spring blooms at station 330. Redrawn from Breton et al. (2006). (N+E)/SW represents the ratio between northern and eastern to southwesterly winds.

### 3.2.2. Present-day interannual variability of succession, timing and duration of diatoms and *Phaeocystis* blooms

A hierarchical classification of phytoplankton observed at station 330 identified a recurrent successional pattern of three diatom communities and *Phaeocystis* (Fig. 3.6; Rousseau et al., 2002; Rousseau et al., in preparation). These assemblages of euryhalin and eurytherm species are typical of the non-stratified Southern Bight of the North Sea. The phytoplankton spring succession is invariably initiated in late winter-early spring by benthopelagic diatom species *Paralia sulcata*, *Thalassionema nitzschiooides*, *Asterionellopsis glacialis*, *Plagiogramma brockmannii*, *Thalassiosira spp.* and *Skeletonema costatum*. This first assemblage is progressively replaced by a community of *Chaetoceros* and then large-sized diatoms, mainly *Guinardia delicatula*, *G. striata* and *Rhizosolenia shrubsolei* and *Phaeocystis* colonies. In the late phase of the spring bloom, *Phaeocystis*, *G. delicatula*, *G. striata* and *R. shrubsolei* are the more often co-occurring before completely disappearing in late spring-early

## Phytoplankton blooms

summer (Fig. 3.6). Later in summer, the large diatoms constitutes the bulk of phytoplankton with *Chaetoceros* and small diatoms succeeding in summer or/and in fall, in a reverse sequence of the spring succession. The presence of *Pseudonitzschia* spp. has also been reported during late spring (Muylaert *et al.*, 2006). A different timing of this succession is observed in the different parts of the BCZ with early spring diatoms blooming one month earlier in the Southwestern than in the Northeastern part (Muylaert *et al.*, 2006).

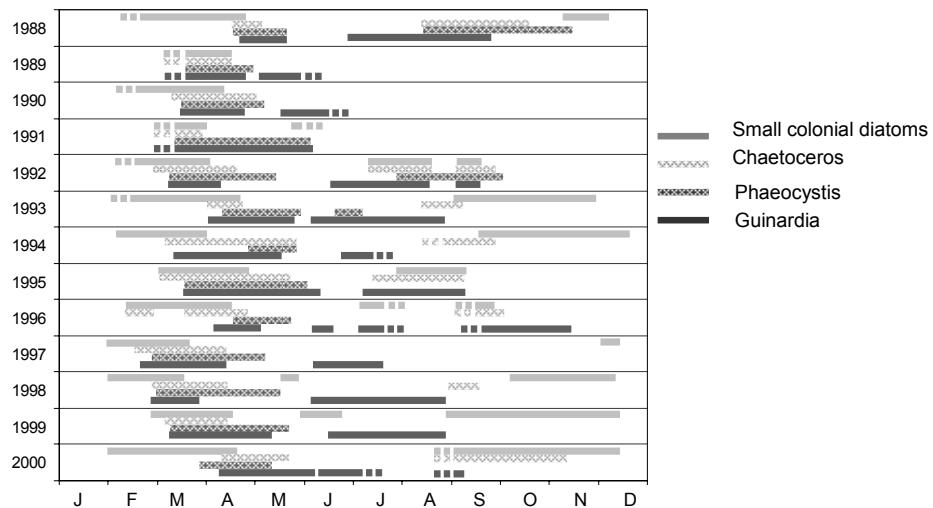


Figure 3.6. Successional pattern of diatoms and *Phaeocystis* between 1988 and 2000. The three diatom communities were identified on based on a hierarchical classification (Rousseau *et al.*, in preparation).

While the phytoplankton succession is remarkably repeated, the onset time and duration of the phytoplankton communities are variable from year to year (Fig. 3.6). The onset of the spring succession varies indeed from early February to early March, being driven by a light threshold of  $12 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  in the water column which is primarily determined by the load of suspended matter of the coastal waters (Rousseau, 2000). The onset time of *Phaeocystis* is invariably associated to that of *Chaetoceros*, taking place between early-March and mid-April (Fig. 3.6).

The control of the successional phytoplankton pattern is multifactorial and consists in a complex interaction between autecological properties of species (regulation of growth by temperature, light and nutrients), potential allelopathic effects and grazing. The ecological preference of the three diatom communities and *Phaeocystis* identified at station 330 are surprisingly similar. The environmental conditions prevailing during their respective growth period encompass indeed a wide and overlapping range of salinity, temperature, nutrients and light (Rousseau *et al.*, in preparation). A better adaptation to low water column irradiance (Meyer *et al.*, 2000; Rousseau, 2000) and temperature

Rousseau et al.

(Lancelot et al., 1998) prevailing in late winter-early spring could however not be excluded to explain the initiation of the diatom-*Phaeocystis* succession by the small colonial diatom community. Once initiated, the diatom succession is shaped by the adaptation of the diatom communities to ambient dissolved silicate (Rousseau et al., 2002). A higher sensitivity of the *Guinardia-Rhizosolenia* community to the grazing by the dinoflagellate *Noctiluca* could well explain phytoplankton disappearance from the water column during summer (Daro et al., 2008).

### 3.3. Understanding the *Phaeocystis* phenomenon

#### 3.3.1 The taxonomy and biology of *Phaeocystis*

The genus *Phaeocystis* sp. belongs to the class of Haptophyceae (synonym Prymnesiophyceae Hibberd), order Phaeocystales Medlin, family of Phaeocystaceae Lagerheim (Edvardsen et al., 2000). Up to now, six species have been formally described within this genus, among which four form colonies (Zingone et al., 1999). Recent molecular and morphological data suggest however that the number of species in the genus is underestimated (Medlin & Zingone, 2007). The *Phaeocystis* species forming large blooms during spring in the Southern Bight of the North Sea has been identified as *P. globosa*. This identification is based on colony morphology, i.e., its globular shape (Sournia, 1990), physiological and biochemical properties (Baumann et al., 1994; Jahnke & Baumann, 1987; Vaulot et al., 1994) and more recently on the SSU rDNA full-length sequence of the strain BCZ99 isolated from the BCZ (Rousseau, Le Gall & Rodriguez, unpublished data).

*P. globosa* is characterized by a heteromorphic life cycle which alternates colonies of diploid cells and nano-sized haploid free-living cells (Rousseau et al., 2007). The ability of both haploid and diploid morphotypes to divide by mitosis supports the existence of a haploid-diploid life cycle in *P. globosa* (Rousseau et al., 2007). In the natural environment, haploid flagellates persist in the water column between blooms of diploid colonial cells, suggesting that colony bloom initiation and termination involve sexual processes (Fig. 3.7). The vegetative reproduction of the diploid stage occurs through two distinct pathways: (i) the mitotic division of colonial cells within the colony, i.e. colony growth, and (ii) the formation of new colonies from diploid short-living flagellates originating from the transformation of colonial cells when released in the ambient water (Fig. 3.7). However, the significance of this latter process in the natural environment is probably reduced (Rousseau et al., 2007).

The factors responsible for the transition between *P. globosa* life cycle stages are still not understood. The vernal growth of diatoms and a sufficient light intensity have been suggested to induce colony formation from haploid flagellates (Kornmann, 1955; Peperzak, 1993; Rousseau et al., 1994). Alternatively, a possible allelopathic relationship between small *Phaeocystis* colonies and *Chaetoceros* spp. cannot be excluded (section 3.2.2). The formation of haploid flagellates at the end of a *P. globosa* colony bloom has

been related to nutrient depletion (Verity *et al.* 1988; Escaravage *et al.*, 1995), light limitation associated to the sinking of healthy colonies in low light conditions (Peperzak *et al.*, 1998).

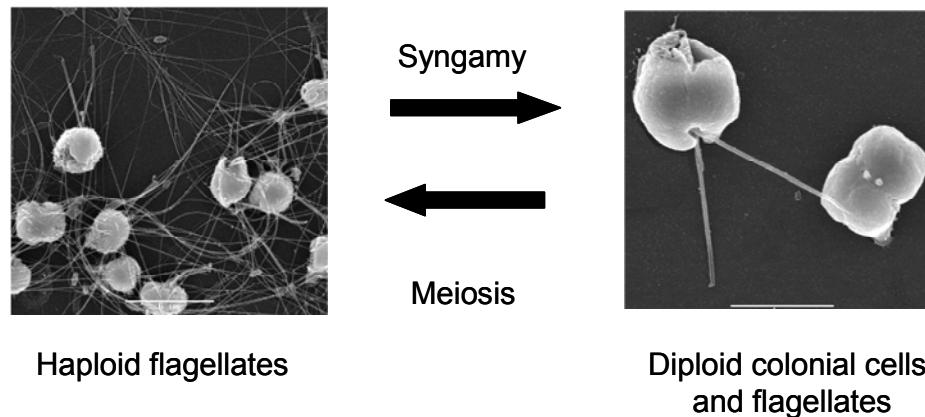


Figure 3.7. The haploid-diploid life cycle of *P. globosa* illustrated with electron microscope photographs of morphotypes present in strain BCZ99 isolated from the BCZ. The haploid flagellates in the size range 3.6-5.8 µm, possess stars, filaments and a cell coverage of scales. Colonial cells and diploid flagellates have the same size range, i.e. 5.8-10.4 µm, and lack the stars, filaments and scales. Colonial cells bear two short appendages on their apical side while diploid flagellates have two flagella and a haptoneema. Photographs: Francois Lantoine (Observatoire biologique de Banyuls sur Mer, France).

### 3.3.2. The physiology and ecology of *Phaeocystis* colonies

The success of *P. globosa* as blooming species has been related to the specific physiology and ecology of its colonial stage (Lancelot & Rousseau, 1994; Lancelot *et al.*, 2002). The colony matrix composed of exopolysaccharide embedding the cells acts as energy and nutrient storage (Lancelot & Rousseau, 1994), allowing higher growth rates to colonial cells (Veldhuis *et al.*, 2005). The higher energetic supply also confers a competitive advantage to *Phaeocystis* colonies to utilize nitrate as nitrogen source (Riegman *et al.*, 1992; Lancelot & Rousseau, 1994). Besides, the ability to use organically-bound phosphorus owing to phosphatase provides *Phaeocystis* colonies with an additional competitive advantage when phosphate is depleted (van Boekel & Veldhuis, 1990; van Boekel, 1991; Lancelot *et al.*, 2007).

In addition, the colonial form precludes an efficient top-down control of its biomass. *P. globosa* colonies with a size higher than 400 µm (Weisse *et al.*, 1994) are indeed generally not, or insignificantly, grazed by mesozooplankton, in particular by *Temora longicornis*, the dominant spring copepod species (Daro *et al.*, 2008). As a consequence, most of *Phaeocystis*-derived production escapes the linear food chain and is mainly remineralised in the water column by intense bacterial activity (Rousseau *et al.*, 2000). Part of this production is

Rousseau et al.

however resuming the classical food-web through mesozooplankton feeding activity on protozoa, leading to complex planktonic food-webs with low trophic efficiency (Hansen et al., 1993; Rousseau et al., 2000; Daro et al., 2008). Moreover, the colony skin constitutes a physical barrier, protecting cells against grazers, virus and bacterial infection (Hamm, 2000; Brussaard et al., 2005). High acrylate accumulation inside the *Phaeocystis* colonies could in addition have antimicrobial effects (Noordkamp et al., 2000).

### 3.4. Linking *Phaeocystis* colony blooms to nutrient enrichment of the BCZ

As in many other coastal regions, eutrophication in the BCZ appears as a shift in the phytoplankton community composition with the spring proliferation of a non-siliceous species, *P. globosa*. This shift results from unbalanced delivery of nutrients compared to phytoplankton N:P:Si requirements (e.g. Billen et al., 1991). The nowadays nutrient enrichment of the BCZ is characterized by a large excess of dissolved inorganic nitrogen, mainly nitrate, compared to phosphate and silicate (Brion et al., 2008). Their peculiar biological and eco-physiological properties (section 3.3.2) make *Phaeocystis* colonies particularly well adapted to take benefit from the excess nitrate in the low phosphate conditions characterizing the coastal waters of the BCZ (Lancelot et al., 1998; 2002). This is evidenced by the positive relationship existing between *Phaeocystis* colonial cell abundance and nitrates (Fig. 3.8; Lancelot et al., 1998; Breton et al., 2006). The control of phytoplankton blooms by anthropogenic nutrient emissions is however not direct due to the complex interaction between hydro-meteorological and human-induced variability of the ecosystem (section 3.2.1; Breton et al., 2006).

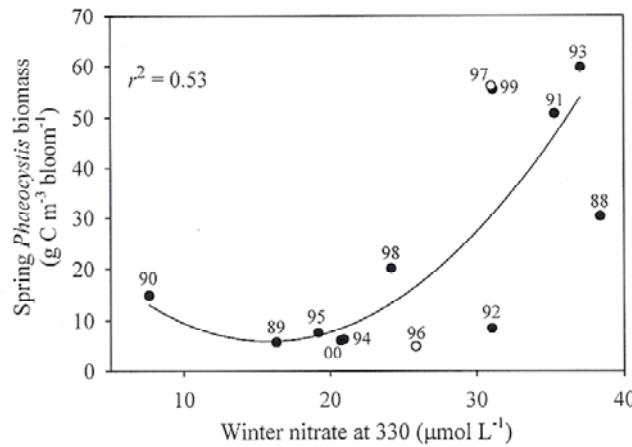


Figure 3.8. Relationship between spring *Phaeocystis* colony biomass and winter nitrate at station 330 between 1988 and 2000. Figures on the graph represent the years. From Breton et al. (2006). Copyright (2008) by the American Society of Limnology and Oceanography, Inc.

### 3.5. Conclusions and perspectives

The eutrophication event in BCZ occurs as high biomasses of the non-siliceous colonial haptophyte *Phaeocystis globosa*. Besides *Phaeocystis*, no other manifestation of eutrophication such as blooms of toxic algae have been recorded in BCZ. Recently however, blooms of the dinoflagellate *Noctiluca scintillans* have been linked to anthropogenic nutrient enrichment (Vasas *et al.*, 2007).

*Phaeocystis* occurs as massive spring blooms of ungrazed gelatinous colonies which are the diploid stage in a haplo-diploid life cycle where nano-sized haploid flagellates persist in water between two colonial events. *Phaeocystis* colonies occur within a recurrent successional pattern of diatom communities and are sustained by nitrate excess left over after the growth of silicate and/or phosphate-limited early spring diatoms in P-regenerated conditions.

Despite substantial progress achieved in understanding the mechanisms behind phytoplankton blooms dynamics in BCZ, some crucial questions still need to be addressed.

- The unique development of *Phaeocystis* colonies during springtime while diatoms persist along the vegetative season requires a better knowledge of factors driving the diatom-*Phaeocystis*-diatom succession as well as the eco-physiology of the different taxa.
- *P. globosa* life cycle must be substantiated by the direct observation of syngamy and meiosis and by identifying the factors inducing these sexual processes. Also, understanding the ecological significance of blooming as diploid cells but persisting as haploid stage throughout the year should be appraised through eco-physiological characterization of haploid and diploid stages.
- The extent of diatoms and *Phaeocystis* blooms is of major interest, particularly in the frame of international policies such as those of the OSPAR convention or the Water Framework Directive which recognize *Phaeocystis* as an indicator species for eutrophication. Remote sensing of ocean colour constitutes for this purpose, a significant and powerful tool for mapping phytoplankton blooms (e.g. Ruddick *et al.*, 2008). Research is in progress to provide more information than just the chlorophyll a concentration and optical remote sensing of phytoplankton functional groups is a key objective. Preliminary work (Astoreca, 2007) suggests that absorption by the chlorophyll c3, indicator of *Phaeocystis* may affect sufficiently reflectance spectra around 467nm to enable detection of at least strong *Phaeocystis* blooms, provided suitable wavelengths are available on satellite sensors.

Rousseau et al.

### 3.6 References

- Astoreca R. 2007. Study and application of the Inherent Optical Properties of coastal waters from the *Phaeocystis*-dominated Southern Bight of the North Sea. PhD Thesis, Université Libre de Bruxelles 137 pp.
- Baumann M.E.M, Lancelot C., Brandini F.P., Sakshaug E. and D.M. John. 1994. The taxonomic identity of the cosmopolitan prymnesiophyte *Phaeocystis*: a morphological and ecophysiological approach. In: Ecology of *Phaeocystis*-dominated ecosystems. Lancelot C. and P. Wassmann (Eds). Journal of Marine Systems 5: 5-22
- Billen G., Lancelot C. and M. Meybeck. 1991. N, P and Si retention along the Aquatic Continuum from Land to Ocean. In: Ocean Margin Processes in Global Change. Mantoura R.F.C., Martin J.-M. and R. Wollast (Eds). John Wiley & Sons, Ltd, P. 19-44
- Borges A.V. and M. Frankignoulle. 2002. Distribution and air-water exchange of carbon dioxide in the Scheldt plume off the Belgian coast. Biogeochemistry 59: 41-67
- Breton E., Brunet C., Sautour B. and J.-M. Brylinski. 2000. Annual variations of phytoplankton biomass in the Eastern English Channel: comparison by pigment signatures and microscopic counts. Journal of Plankton Research 22: 1423-1440
- Breton E., Rousseau V., Parent J.-Y., Ozer J. and C. Lancelot. 2006. Hydroclimatic modulation of diatom/*Phaeocystis* blooms in the nutrient-enriched Belgian coastal waters (North Sea). Limnology and Oceanography 51(3): 1401-1409
- Brion N., Jans S., Chou L. and V. Rousseau. 2008. Nutrient loads to the Belgian Coastal Zone. In: Current Status of Eutrophication in the Belgian Coastal Zone. Rousseau V., Lancelot C. and D. Cox (Eds). Presses Universitaires de Bruxelles, Bruxelles, pp.17-43
- Brussaard C., Riegman R., Noordeloos A., Cadée G., Witte H., Kop A., Nieuwland G., van Duyl F. and R. Bak. 1995. Effects of grazing, sedimentation and phytoplankton cell lysis on the structure of a coastal pelagic food web. Marine Ecology Progress Series 123: 259-271
- Brzezinski M.A. 1985. The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. Journal of Phycology 21: 347-357
- Cadée G.C. and J. Hegeman. 1991. Historical phytoplankton data of the Marsdiep. Hydrobiological Bulletin 24: 111-118
- Daro N., Breton E., Antajan E., Gasparini S. and V. Rousseau 2008. Do *Phaeocystis* colony blooms affect zooplankton in the Belgian coastal zone? In: Current Status of Eutrophication in the Belgian Coastal Zone. V. Rousseau, C. Lancelot and D. Cox (Eds). Presses Universitaires de Bruxelles, Bruxelles, pp. 61-72
- Dutz J., Klein Breteler W.C.M. and G. Kramer. 2005. Inhibition of copepod feeding by exsudates and transparent exopolymer particles (TEP) derived from a *Phaeocystis globosa* dominated phytoplankton community. In: Harmful Algae. Veldhuis M.J.W. and P. Wassmann (Eds). 4: 915-940
- Edvardsen B., Eikrem W., Green J.C., Andersen R.A., Moon-van der Staay S.Y. and L.K. Medlin. 2000. Phylogenetic reconstructions of the Haptophyta inferred from 18S ribosomal DNA sequences and available morphological data. Phycologia. 39 (1): 19-35
- Escaravage V., Peperzak L., Prins T.C., Peeters J.C.H. and J.C.A. Joordens. 1995. The development of a *Phaeocystis* sp. bloom in a mesocosm experiment in relation to nutrients, irradiance and coexisting algae. Ophelia 42: 55-74
- Hamm F.C. 2000. Architecture, ecology and biogeochemistry of *Phaeocystis* colonies. Journal of Sea Research 43: 307-315
- Hansen FCR, Reckermann M, Klein Breteler WCM and Riegman R (1993) *Phaeocystis* blooming enhanced by copepod predation on protozoa: evidence from incubation experiments. Marine Ecology Progress Series 102: 51-57

Phytoplankton blooms

- Hurrell J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269: 676-679
- Jahnke J. and M. Baumann. 1987. Differentiation between *Phaeocystis pouchetii* (Har.) Lagerheim and *Phaeocystis globosa* Scherffel. Colony shapes and temperature tolerances. *Hydrobiological Bulletin* 21: 141-147
- Kornmann P. 1955. Beobachtungen an *Phaeocystis*-Kulturen. *Helgoländer Wiss. Meeresunt.* 5: 218-233
- Lancelot C. 1995. The mucilage phenomenon in the continental coastal waters of the North Sea. *The Science of the Total Environment*. 165: 83-102
- Lancelot C. and V. Rousseau. 1994. Ecology of *Phaeocystis*: the key role of colony forms. In: *The Haptophyte Algae*. Green J.C. and B.S.C. Leadbeater (Eds). Clarendon Press, Oxford. Pp. 229-245
- Lancelot C., Billen G., Sournia A., Weisse T., Colijn F., Veldhuis M.J.W., Davies A. and P. Wassmann. 1987. *Phaeocystis* blooms and nutrient enrichment in the continental coastal zones of the North Sea. *Ambio* 16 : 38-46
- Lancelot C., Keller M., Rousseau V., Smith W.O.Jr and S. Mathot. 1998. Autoecology of the Marine Haptophyte *Phaeocystis* sp. In: *NATO Advanced Workshop on the physiological ecology of Harmful Algal Blooms*. NATO-ASI Series. Anderson D.A., Cembella A.M., Hallegraef G. (Eds). Springer-Verlag Berlin. Series G: Ecological Science 41: 209-224
- Lancelot C., Rousseau V., Schoemann V. and S. Becquevert. 2002. On the ecological role of the different life forms of *Phaeocystis*. In: *Proceedings of the workshop LIFEHAB: Life histories of microalgal species causing harmful blooms*. Garcés E., Zingone A., Montresor M., Reguera B. and B. Dale (Eds). Calvia, Majorca, Spain, octobre 2001. Research in Enclosed Seas series 12: 71-75
- Lancelot C., Rousseau V., Gypens N., Parent J.-Y., Bissar A., Lemaire J., Breton E., Daro M.-H., Lacroix G., Ruddick K., Ozer J., Spitz Y., Soetaert K., Chrétiennnot-Dinet M.-J., Lantoine F. & F. Rodriguez. 2007. AMORE II : Advanced MOdelling and Rresearch on Eutrophication. Rapport final. Belgian Science Policy publication. D/2007/1191/5
- Long J.D. and M.E. Hay. 2006. When intraspecific exceeds interspecific variance: Effects of phytoplankton morphology and growth phase on copepod feeding and fitness. *Limnology and Oceanography* 51: 988-996
- Medlin L.K. and A. Zingone. 2007. A taxonomic review of the genus *Phaeocystis*. *Biogeochemistry* 83: 3-18
- Meyer A., Tackx M. and N. Daro. 2000. Xanthophyll cycling in *Phaeocystis globosa* and *Thalassiosira* sp.: a possible mechanism for species succession. *Journal of Sea Research* 43: 373-384
- Muylaert K., Gonzales R., Franck M., Lionard M., Van der Zee C., Catrijssse A., Sabbe K., Chou L. and W. Vyverman. 2006. Spatial variation in phytoplankton dynamics in the Belgian coastal zone of the North Sea studied by microscopy, HPLC-CHEMTAX and underway fluorescence recordings. *Journal of Sea Research* 55: 253-265
- Nejstgaard J.C., Tang K.W., Steinke M., Dutz J., Koski M., Antajan E. and J.D. Long. 2007. Zooplankton grazing on *Phaeocystis*: quantitative review and future challenges. *Biogeochemistry*. 83: 147-172
- Noordkamp J.B., Gieskes W.W.C., Gottschal J.C., Forney L.J. and M. Van Rijssel. 2000. Acrylate in *Phaeocystis* colonies does not affect the surrounding bacteria. *Journal of Sea Research* 43: 287-296
- Peperzak L. 1993. Daily irradiance governs growth rate and colony formation of *Phaeocystis* (Prymnesiophyceae). *Journal of Plankton Research* 15: 809-821
- Peperzak L., Colijn F., Gieskes W.W.C. and J.C.H. Peeters. 1998. Development of the diatom-*Phaeocystis* spring bloom in the Dutch coastal zone of the North Sea: the silicon depletion versus the daily irradiance threshold hypothesis. *Journal of Plankton Research* 20 : 517-537

Rousseau et al.

- Riegman R., Noordeloos A. and G.C. Cadée, G.C. 1992. *Phaeocystis* blooms of the continental zones of the North Sea. *Marine Biology* 112: 479-484
- Rousseau V. 2000. Dynamics of *Phaeocystis* and diatom blooms in the eutrophicated coastal waters of the Southern Bight of the North Sea. Ph.D. thesis. Université Libre de Bruxelles. 205 pp.
- Rousseau V., Mathot S. and C. Lancelot. 1990. Calculating carbon biomass of *Phaeocystis* sp. from microscopic observations. *Marine Biology* 107: 305-314
- Rousseau V., Vaulot D., Casotti R., Cariou V., Lenz J., Gunkel J. and M. Baumann. 1994. The life cycle of *Phaeocystis* (Prymnesiophyceae): evidence and hypotheses. In: Ecology of *Phaeocystis*-dominated ecosystems. Lancelot C. and P. Wassmann (Eds.) *Journal of Marine Systems* 5: 23-39
- Rousseau V., Becquevert S., Parent J.-Y., Gasparini S., Daro M.-H., Tackx M. and C. Lancelot. 2000. Trophic efficiency of the planktonic food web in a coastal ecosystem dominated by *Phaeocystis* colonies. *Journal of Sea Research* 43: 357-372
- Rousseau V., Leynaert A., Daoud N. and C. Lancelot. 2002. Diatom succession, silification and silicic acid availability in the Belgian coastal waters (Southern North Sea). *Marine Ecology Progress Series* 236: 61-73
- Rousseau V., Breton E., De Wachter B., Beji A., Deconinck M., Huijgh J., Bolsens T., Leroy D., Jans S. and C. Lancelot. 2004. Identification of Belgian maritime zones affected by eutrophication (IZEUT). Towards the establishment of ecological criteria for the implementation of the OSPAR Common Procedure to combat eutrophication. Belgian Science Policy, Brussels, Final report. 77 pp.
- Rousseau V., Chrétiennot-Dinet M.-J., Jacobsen A., Verity P. and S. Whipple. 2007. The life cycle of *Phaeocystis*: state of knowledge and presumptive role in ecology. *Biogeochemistry* 83: 29-47
- Ruddick K., Lacroix G., Lancelot C., Nechad B., Park Y., Peters S. and B. Van Mol. 2008. Optical remote sensing of the North Sea. In V. Barale and M. Gade [eds.], *Remote sensing of the European Seas*. Springer-Verlag, pp. 79-90
- Sournia A. 1990. *Phaeocystis* (Prymnesiophyceae): How many species? *Nova Hedwigia* 47: 211-217
- Smayda T.J. 1997. Bloom dynamics: physiology, behavior, trophic effects. *Limnology and Oceanography* 42: 1132-1136
- Turner J.T., Ianora A., Esposito F., Carotenuto Y. and A. Miraldo. 2002. Zooplankton feeding ecology : does a diet of *Phaeocystis* support good copepod grazing, survival, egg production and egg hatching success. *Journal of Plankton Research* 24(11): 1185-1195
- van Boeckel W.H.M. and M.J.C. Veldhuis. 1990. Regulation of alkaline phosphatase synthesis in *Phaeocystis* sp. *Marine Ecology Progress Series* 61:281-289
- Van der Zee C. and L. Chou. 2005. Seasonal cycling of phosphorus in the Southern North Bight of the North Sea. *Biogeosciences* 2: 27-42
- Vaulot D., Birrien J.-L., Marie D., Casotti R., Veldhuis M.J., Kraay G.W. and M.-J. Chrétiennot-Dinet. 1994. Morphology, ploidy, pigment composition and genome size of cultured strains of *Phaeocystis* (Prymnesiophyceae). *Journal of Phycology* 30: 1022-1035
- Veldhuis M.J.W., Brussaard C.P.D. and A.A.M. Noordeloos. 2005. Living in a *Phaeocystis* colony : a way to be successful algal species. In: *Harmful Algae*. Veldhuis M.J.W and P. Wassmann (Eds). 4: 841-858
- Verity P.G., Villareal T.A. and T.J. Smayda. 1988 Ecological investigations of blooms of colonial *Phaeocystis pouchetii*. II. The role of life cycle phenomena in bloom termination. *Journal of Plankton Research* 749-766
- van Boeckel W.H.M. 1991. Ability of *Phaeocystis* sp. to grow on organic phosphates; direct measurement and prediction with the use of an inhibition constant. *Journal of Plankton Research* 13: 959-970

Phytoplankton blooms

- Vasas V., Lancelot C., Rousseau V. and F. Jordan. 2007. Eutrophication and overfishing in temperate nearshore pelagic food webs : a network perspective. Mar. Ecol. Progr. Ser. 336: 1-14
- Weisse T., Tande K., Verity P., Hansen F. and W.W.C. Gieskes. 1994. The trophic significance of *Phaeocystis* blooms. In: Ecology of *Phaeocystis*-dominated ecosystems. Lancelot C. and P. Wassmann (Eds.). J. Mar.Syst. 5: 67-79
- Zingone A., Chrétiennot-Dinet M.-J., Lange M. and L.K. Medlin. 1999. Morphological and genetic characterization of *Phaeocystis cordata* and *P. Jahnii* (Pymnesiophyceae), two new species from the Mediterranean Sea. J. Phycol. 35: 1322-1337