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Phaeocystis blooms in the global ocean and their controlling mechanisms: a review

Véronique Schoemann[a,*], Sylvie Becquevort[a], Jacqueline Stefels[b], Véronique Rousseau[a], Christiane Lancelot[a]

[a]*Ecologie des Systèmes Aquatiques, Université Libre de Bruxelles, Campus de la Plaine, C.P. 221, Bd du Triomphe, B1050 Bruxelles, Belgium*
[b]*University of Groningen, Department of Marine Biology, PO Box 14, 9750 AA Haren, The Netherlands*

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Abstract

Phaeocystis is a genus of marine phytoplankton with a world-wide distribution. It has a polymorphic life cycle alternating free-living cells and colonies but develops massive blooms under the colony form in nutrient (major)-enriched areas (mostly nitrates) of the global ocean. Among the 6 species, only 3 (*P. pouchetii, P. antarctica, P. globosa)* have been reported as blooming species. However, information is lacking on the present-day contribution of *Phaeocystis*-dominated ecosystems to regional and global marine production as well as to global C and S cycles and on how these might change in the future. As a first step in this direction, this review aims to synthesise knowledge on the physiology, growth and fate of *Phaeocystis* in the global ocean, and to select relevant parameters for implementing mechanistic models describing *Phaeocystis* blooms in the global ocean. Missing information concerning the regulation of the most important bottom-up and top-down processes is also identified. The synthesis of published data suggests that it is possible to derive a single unique parameterisation to describe some bottom-up processes for global modelling without consideration of species and location. Most important among these are the temperature-dependence of the maximum growth rates that characterises all three blooming species, and their high adaptation to environmental light. Other processes seem to be more species-(e.g. colony matrix synthesis) or site-related (top-down controls, e.g. grazing parameters). This review also points out that some crucial processes are still poorly described and need further research. For instance, increased knowledge of iron uptake kinetics and iron quotas is of prime importance given the very large recurrent blooms of *P. antarctica* colonies reported in the HNLC waters of the Southern Ocean.

Keywords: *Phaeocystis*; Food webs; Algal blooms; Biogeochemistry; Ecophysiology; Distribution records

1. Introduction

The eurythermal and euryhaline genus *Phaeocystis* is one of the most widespread marine haptophytes, with species sharing the ability to produce

* Corresponding author.
E-mail address: vschoem@ulb.ac.be (V. Schoemann).

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nearly monospecific blooms of gelatinous colonies in several coastal and oceanic waters. *Phaeocystis* is exceptional not only because of the high carbon biomass reached by its blooms (up to 10 mg C l^{-1}) but mainly because of its unique physiology which impacts food-web structures, hence global biogeochemical cycles and climate regulation (Lancelot et al., 1994). Of particular importance is the existence of a complex polymorphic life cycle exhibiting phase alternation between different types of free-living cells (vegetative non-motile, vegetative flagellate and microzoospore) of 3–9 μm in diameter and gelatinous colonies usually reaching several mm (Rousseau et al., 1994; Peperzak et al., 2000) up to 3 cm (Chen et al., 2002). These colonies, constituted by thousands of cells embedded in a polysaccharidic matrix, are considered to be responsible for the success of *Phaeocystis* in marine systems and for the subsequent changes in ecological and biogeochemical properties (Lancelot and Rousseau, 1994; Hamm, 2000).

Phaeocystis plays a key role as an intermediary in the transfer of carbon as well as sulphur between ocean and atmosphere and vice versa. This makes *Phaeocystis* an ideal model organism to study the role of marine phytoplankters in global biogeochemical cycles and climate regulation. The high productivity associated with its blooms and its ubiquity makes *Phaeocystis* an important contributor to the ocean carbon cycle (e.g. Smith et al., 1991; DiTullio et al., 2000). In addition, *Phaeocystis* produces dimethylsulfoniopropionate (DMSP) and converts it enzymatically into dimethylsulfide (DMS) and acrylate (Stefels and Van Boekel, 1993; Stefels et al., 1995). The oxidation products of the volatile sulphur compound DMS are known to have an impact on the chemical quality of the atmosphere (as a major precursor of the background acidity of the atmosphere in the absence of direct human perturbation; Fletcher, 1989; Davison and Hewitt, 1992) and on global climate regulation (as a contributor to cloud condensation nuclei that affect the earth's radiative budget; Charlson et al., 1987; Ayers and Gillett, 2000). Model calculations have shown that especially in the Southern Hemisphere the contribution of DMS to the total atmospheric non-sea salt sulphate burden is 70% (Gondwe et al., 2003). This implies that DMS has a major impact on cloud albedo and thus on climate. *Phaeocystis* blooms are well known for their high DMS concentrations: 5 to 50 nM DMS are commonly found (e.g. Liss et al., 1994), which is a factor of 10 to 100 times higher than in open ocean areas. Because these blooms have a world-wide distribution, they are regarded as important sources of DMS.

Phaeocystis-dominated ecosystems are generally associated with commercially important stocks of crustaceans, molluscs, fishes and mammals. *Phaeocystis* could have negative effects on higher trophic levels in the marine ecosystem and consequently influence human activities such as fisheries and fish farming, and also coastal tourism through the odorous foams on beaches during the wane of a bloom (Lancelot et al., 1987). Dense blooms have been responsible for causing net-clogging (Savage, 1930), fish mortality (Savage, 1930; Hurley, 1982; Rogers and Lockwood, 1990; Huang et al., 1999) and alteration of fish taste (Levasseur et al., 1994). *Phaeocystis* was shown to be detrimental to shell fish growth and reproduction (Pieters et al., 1980; Davidson and Marchant, 1992b; Prins et al., 1994; Smaal and Twisk, 1997). Moreover, some toxins have been obtained from *Phaeocystis* (He et al., 1999; Stabell et al., 1999; Hansen et al., 2003).

That *Phaeocystis* constitutes a key organism in driving global biogeochemical cycles, climate regulation and fisheries yield is no longer questionable. However, the present-day contribution of *Phaeocystis*-dominated ecosystems to regional and global marine production as well as to global C and S cycles and how these might change in the future has not been sufficiently evaluated. As a first step in this direction, this review paper intends to synthesise knowledge on the physiology, growth and fate of *Phaeocystis* in the global ocean and to select parameters for implementing mechanistic models. The aim of this paper is also to identify missing information on bottom-up and top-down controls of the *Phaeocystis* blooms. Because most of the success of *Phaeocystis* in marine systems has been attributed to its ability to form large gelatinous colonies and because only three among the six species identified—*P. globosa, P. pouchetii, P. antarctica, P. scrobiculata, P. cordata, P. jahnii* (e.g. review by Zingone et al., 1999)—have been reported to form colony blooms, our review will mainly focus on *P. globosa, P. pouchetii* and *P. antarctica.*

2. Biogeographical distribution

2.1. Global species distribution

Fig. 1 synthesises the global distribution of *Phaeocystis* records of occurrence. *Phaeocystis* species have been revised according to criteria described in Baumann et al. (1994), Vaulot et al. (1994) and Zingone et al. (1999). The genus *Phaeocystis* has a world-wide distribution (Fig. 1) and occurs as different species in very contrasting marine systems. Cells in free-living forms are cosmopolitan in distribution and are an important component of the haptophycean assemblage, which dominates oceanic nanophytoplankton in many areas (e.g. Thomsen et al., 1994). They very seldom form blooms (Lancelot et al., 1998). It is generally under the colony form that, in particular, *P. globosa*, *P. pouchetii* and *P. antarctica* are producing blooms in major nutrient-enriched areas (Lancelot et al., 1998) either naturally (e.g. Ross Sea, Greenland Sea; Barents Sea) or due to anthropogenic inputs (e.g. Southern Bight of the North Sea; Arabian Gulf). Recently, recorded blooms of *P. globosa* in the southeast coast of China were also ascribed to a globally abnormal climate and a very strong El Niño event (Huang et al., 1999; Chen et al., 2002). As a general trend *P. globosa* blooms in temperate and tropical waters while *P. pouchetii* and *P. antarctica* are better adapted to the cold temperatures prevailing in Arctic and Antarctic waters, respectively. The temperature tolerance range of *P. pouchetii* overlaps, however, with that of *P. globosa* (Baumann et al., 1994) such that *P. pouchetii* is sometimes recorded in temperate waters (Philippart et al., 2000).

2.2. Phaeocystis distribution and maximal records

2.2.1. Quantitative indicators

Existing records often report *Phaeocystis* blooms as colony or/and total cell (free-living+colony cells) numbers, usually obtained from tedious microscopic observations. With the exception of the preserving procedure described in Rousseau et al. (1990), which is a mixture of lugol, gluteraldehyde and iodine, most of conventional chemical agents used to preserve samples for microscopic observations, cause the disintegration of the colony matrix and prevent an accurate distinction between individual and colony cells. The flagellate cells are difficult to identify by the usual inverted microscopy. For an accurate identification, transmission or scanning electron microscopy or the use of oligonucleotide probe is needed

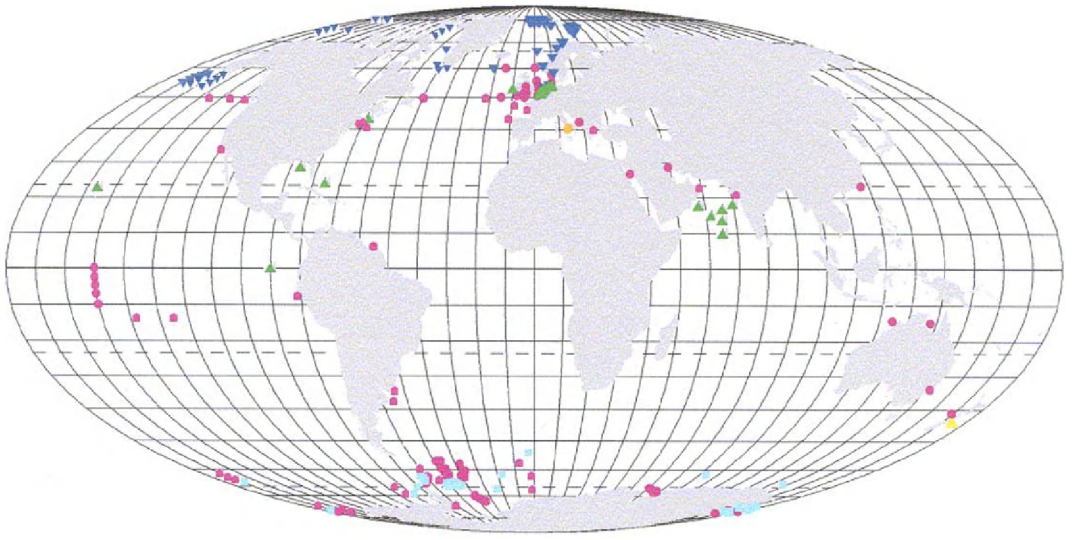


Fig. 1. Geographical distribution of the genus *Phaeocystis*. Some of the species identifications in previous records were revised according to Baumann et al. (1994). *P. pouchetii* is indicated by dark blue triangles, *P. globosa* by green triangles, *P. antarctica* by light blue squares, *P. scrobiculata* by a yellow triangle, *P. jahnii* and *P. cordata*, which have the same location, by an orange circle. The unidentified or unclear species of *Phaeocystis* are represented by pink circles.

(Zingone et al., 1999; Moon-Van der Staay et al., 2000).

Conversion factors for estimating carbon biomass from cell density have been determined for *P. globosa* and *P. antarctica* (Table 1). These are based on average cell biovolume and conventional conversion factors (Eppley et al., 1970; Edler, 1979). A set of species-specific biometric equations were also determined to estimate the carbon biomass *of P. globosa* (Rousseau et al., 1990) and *P. antarctica* (Mathot et al., 2000) colonies, based on colony size measurement (Table 1). This method considers *Phaeocystis* colonies as the sum of colonial cells and mucus associated with the colony matrix. It uses two relationships to relate, respectively, the number of colonial cells and mucus carbon content to the colony size. Comparison of coefficients (Table 1) indicates that the mucus contribution to the carbon-biomass of *P. antarctica* colonies is relatively small compared to *P. globosa*. An alternative method for estimating the carbon biomass of *P. globosa* has been suggested by Van Rijssel et al. (1997), based on the observed hollow inner structure of the colonies. These authors estimated the carbon biomass of *P. globosa* colonies as the sum of colonial cells and a constant amount of mucus surrounding the cell (Table 1). Comparison of estimates obtained by the two methods shows significant carbon biomass differences for very small and very large colonies but not for colony sizes predominantly observed in the field (Table 1). For *P. pouchetii* colonies, no specific biomass estimation has been made so far.

There have also been some attempts to quantify *Phaeocystis* from its pigment signature (Wright et al., 1996). The accessory pigment 19′-hexanoyloxyfucoxanthin (19′-HF) has been reported as typical for haptophytes, with *Phaeocystis* as so-called 'type 4' haptophytes, which also contain chlorophyll-c3 and 19′-butanoyloxyfucoxanthin. The content relative to the more common fucoxanthin (FUCO) has been suggested as a proxy to estimate *Phaeocystis* abundance (Jeffrey and Wright, 1994; Jeffrey, 1997). This approach has been challenged by recent observations indicating the apparent lack or extremely low concentration of 19′-HF in some strains (Table 2; Llewellyn and Gibb, 2000) as well as a distinct variation in pigment pattern for colony and free-living cells (Buma et al., 1991). In general, the 19′-HF content of *P. globosa* cells is much lower, if not absent, compared to the two polar species. Furthermore there are now several studies reporting significant variation in the relative abundance of 19′-HF and FUCO to chlorophyll-a in response to changing environmental factors (Van Leeuwe and Stefels, 1998; Llewellyn and Gibb, 2000; Schluter et al., 2000). Especially variations in light and iron conditions may result in fluctuations of the 19′-HF:FUCO ratios of several orders of magnitude (Van Leeuwe and Stefels, 1998; Schluter et al., 2000).

Table 1
Morphological characteristics and carbon to biomass conversion factor of the bloom-forming species (adapted from Jahnke and Baumann, 1987; Rousseau et al., 1990; Baumann et al., 1994; Riegger and Robinson, 1997; Mathot et al., 2000; Peperzak et al., 2000; Chen et al., 2002)

	P. globosa	*P. antarctica*	*P. pouchetii*
Flagellated cells:			
Size	3–8 μm	2–6 μm	4–7 μm
Carbon, pgC/cell	10.80±3.47	3.33	ND
Colonies:			
Size, min-max	25 μm to 3 cm	25 μm to 1.4 mm	25 μm to 1.5–2 mm
Shape	Spherical and derived forms	Spherical and derived forms	<100μm : spherical >100μm : cloud-like
Cells distribution	Cells evenly in the periphery	Cells evenly in the periphery	Cells only in the curves of the lobes, in group of 4
Cell number/colony (N) V is the volume of the colony	log N=0.51 log V+3.67 V in mm^3	$N=(V/417)^{0.60}$ V in μm^3	–
Carbon, pg/colony cell (mucus excluded)	14.15±5.34	13.60	ND
Carbon, pg/colony cell (mucus included)	57–122	ND	ND
Carbon, ngC/mm^3-mucus	335	213	ND

ND=Not determined.

Table 2
Ratios of marker pigments to chlorophyll-a in the three main *Phaeocystis* species

	Conditions	FUCO	19′-HF	19′-HF:FUCO	References
P. antarctica Cultures					
	I=110 μE	0.59	0.11	0.186	Van Leeuwe and
	I=25 μE	0.64	0.018	0.028	Stefels, 1998[a]
	I=110 μE, Fe-deficient	0.18	0.90	5	
	I=25 μE, Fe-deficient	0.46	0.82	1.783	
	I=variable, max. 400 μE	0.01–0.02	0.3–0.4	20–30	Stefels, unpubl. data
	I=variable, max. 400 μE, Fe deficient	0.007–0.016	0.75		
	24 h light, 100 μE	0.03	0.36	12	Vaulot et al., 1994
Flagellates	I=170 μE	0.66	0.05–0.12	0.075–0.182	Buma et al., 1991
Colonies	I=170 μE	0.24	0.12–0.17		
Field	Southern Ocean[b]	0.40	0.506	1.265	Wright et al., 1996
	East Antarctica– shelf break; 8 depths[c]	0.9–2.1	0.8–1.3	0.381–1.44	Wright and Van den Enden, 2000
	Gerlache and Bransfield Straits[b]	0.011	0.916	83	Rodriguez et al., 2002
P. globosa Cultures					
	I=100 μE	0.62	0.03	0.05	Vaulot et al., 1994
	I=170 μE	0.34	0–0.02	0–588	Buma et al., 1991
Field	North Sea coastal bloom; secchi disk:<3m	0.7	0–0.03	0–0.043	Buma et al., 1991
Phaeocystis sp. Cultures					
	I=~100 μE, Exponential growth	0.500	0.075	0.15	Llewellyn and Gibb, 2000
	I=~100 μE, 'death' phase	0.515	0.156	0.30	
	I=23/4 μE[d]	0.45	0.03	0.066	Schluter et al., 2000
	I=230/94 μE	0.32	0.15	0.469	
	I=554/269 μE	0.23	0.22	0.956	
	I=98 μE green	0.41	0.11	0.268	
	I=88 μE blue	0.18	0.32	1.778	

19′-HF=19′-hexanoyloxyfucoxanthin, FUCO=fucoxanthin. Light conditions (I) are given in μmol photons.m^{-2}.s^{-1} (abbreviated as μE) and are applied in a light-dark cycle, unless stated otherwise.

[a] Recalculated data.

[b] CHEMTAX output ratios.

[c] CHEMTAX calculated range of pigment ratios of type 4 haptophytes with increasing depth, as presented in Fig. 2 of Wright and Van den Enden (2000).

[d] Measured with a 4 π and a 2 π collector respectively; blue and green light measured with a 2 π collector.

Together these results indicate that 19′-HF cannot be used safely as a proxy for *Phaeocystis* abundance in the global ocean.

2.2.2. Geographical distribution of maximal Phaeocystis cell abundance

We have mapped *Phaeocystis* distribution based on reports of *Phaeocystis* cell abundance (http://www.nioz.nl/projects/ironages). Most *Phaeocystis* records in the literature are in this form. As a first approximation, cell abundance> 10^6 l^{-1} indicates the presence of colony forms. Estimate of carbon biomass of *Phaeocystis* cells can be calculated based on species-specific carbon cell content of Table 1. However, such calculation underestimates significantly *Phaeocystis* carbon biomass when colonies are present because of the absence of detailed information on number and sizes of the colonies, which prevents estimation of the mucus carbon contribution. Still, coarse estimates of carbon biomass of *P. globosa* colonies are possible by using the conversion factor of Van Rijssel et al. (1997; Table 1).

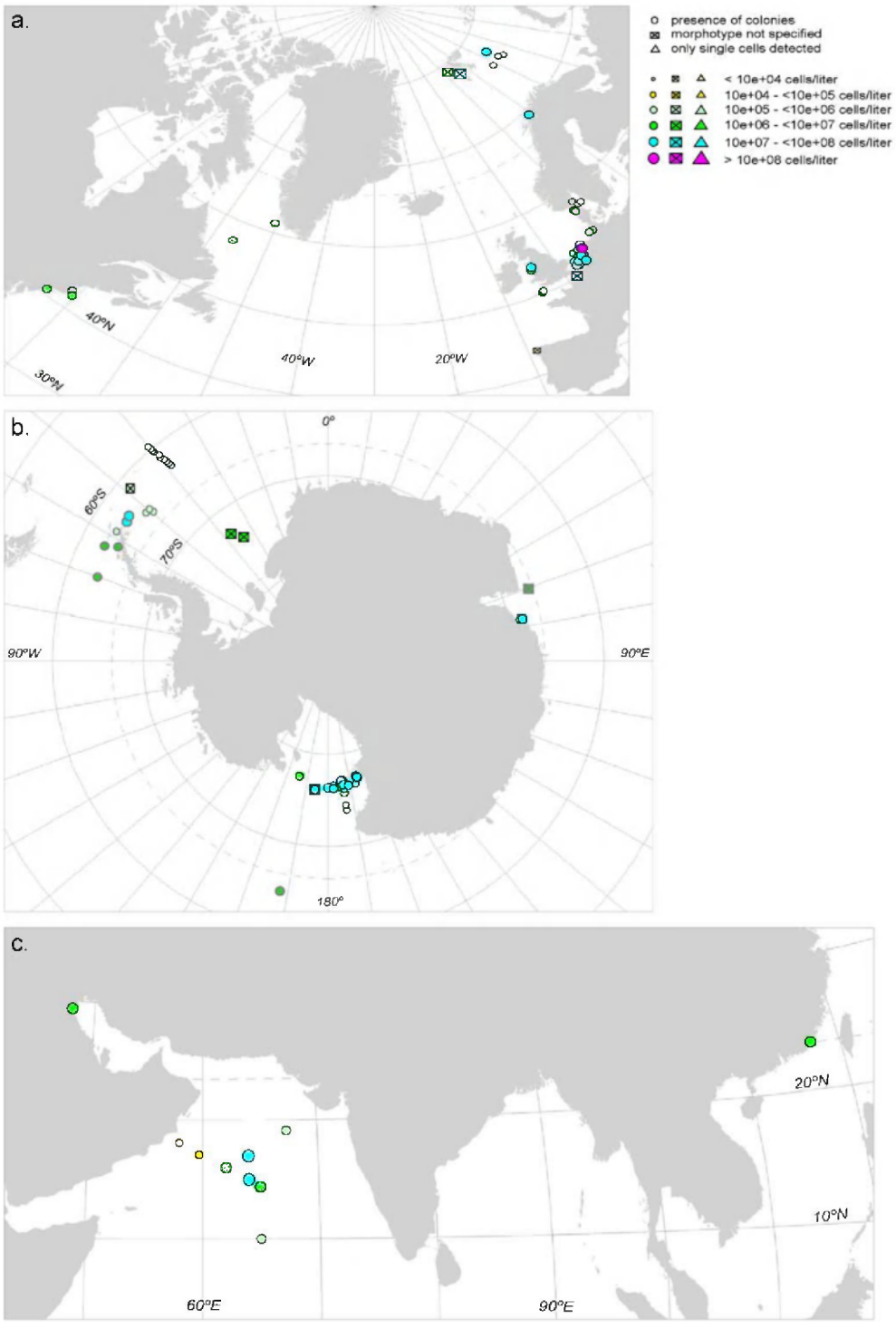


Fig. 2. Detailed geographical distribution and the recorded maximum abundance of: (a) *P. pouchetii and P. globosa* in spring (late April to early May) in the Arctic and mid-Northern latitudes; (b) *P. antarctica* in summer (December to March) in the Southern Ocean; (c) *P. globosa* in tropical waters (see http://www.nioz.nl/projects/ironages for timing, maximum abundance recorded and references).

Detailed geographical distribution and the maximum abundance of *Phaeocystis* cells recorded (http://www.nioz.nl/projects/ironages) are mapped in Fig. 2 for the areas where *Phaeocystis* is recurrently blooming, i.e. the Arctic and mid-northern latitudes (Fig. 2a), the Antarctic (Fig. 2b) and the tropical waters (Fig. 2c). *Phaeocystis* is generally blooming in late April–May in the Arctic fjords and later in July in the Arctic oceanic waters (http://www.nioz.nl/projects/ironages). In the North Sea, it blooms between early April and early June. Blooms were observed between October and February 1998 in the south-eastern waters of China (Huang et al., 1999) and in July–August in the Arabian Sea (http://www.nioz.nl/projects/ironages). Recurrent blooms occur between late November and early January in the Antarctic waters.

As a general trend, maximum abundance of ca. 10^7 cells l^{-1} was reached in all areas of *P. globosa, P. pouchetii, P. antarctica* colony occurrence. To date, a maximum abundance of ca. 20×10^7 *Phaeocystis* cells l^{-1} corresponding to a maximum of ca. 35 μg Chl-a l^{-1} was recorded in the North Sea Dutch coastal area during a bloom of *P. globosa* colonies in May 1985 (Cadée and Hegeman, 1986). Using the conversion factors of Table 1 this maximum corresponded to ca. 10 mg C l^{-1}. In the tropical waters, a similar maximum abundance was observed along the coast of southeast China in early December 1997 (Huang et al., 1999) and maximum records of ca. 6×10^7 cells l^{-1} were observed in the central Arabian Sea in July and August 1996 (http://www.nioz.nl/projects/ironages). The largest blooms of *P. antarctica* colonies were observed in the Ross Sea in December (ca. 3×10^7 cells l^{-1}; http://www.nioz.nl/projects/ironages) and in Prydz Bay (ca. 6×10^7 cells l^{-1}; http://www.nioz.nl/projects/ironages). A maximum of 1.2×10^7 cells l^{-1} *P. pouchetii* was reported in late May 1986 in the Konsfjorden (Eilertsen et al., 1989).

3. Growth physiology and stoichiometry

3.1. Growth-temperature dependence

Fig. 3 plots maximum daily specific growth rates μ (i.e. growth rate measured under non-limiting conditions of light and nutrients) of all colony-forming species and forms (cell vs colony) as a function of temperature T. The examination of Fig. 3 suggests that *P. antarctica* is particularly well adapted to low temperatures, being more competitive than *P. pouchetii* and *P. globosa* between −2 and +2 °C. Contrary to the other two species, *P. antarctica* ceased to grow above 10 °C (Buma et al., 1991). Even if there is an overlap between the temperature growth range of *P. pouchetii* and *P. globosa*, *P. pouchetii* appears to be better adapted to temperatures below 5 °C.

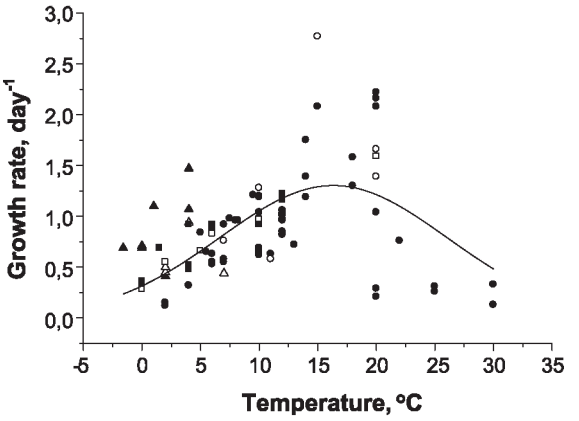


Fig. 3. Relationship between *Phaeocystis* specific growth rate μ and temperature (μ=ln2*υ, with υ=division rate). The closed and the open symbols represent colony cells and solitary cells data, respectively. Squares, circles and triangles represent data for *P. pouchetii*, *P. globosa* and *P. antarctica*, respectively.

For global modelling purposes, it is, however, possible to fit the data of all species and forms with the following relationship:

$$\mu = \mu_{max} * EXP\lfloor -(T - Topt)^2 / dT^2 \rfloor \quad (1)$$

which is defined by three parameters: the optimal temperature T_{opt}, the maximum specific growth μ_{max} at T_{opt} and the temperature interval dT, given in Table 3.

3.2. Photosynthesis-light adaptation

Literature ^{14}C-based data on the photosynthesis-light dependence of *Phaeocystis* colonies are numerous for both field populations and cultured strains. However, only a few data are useful for deriving photosynthetic parameters due to some bias in the methods used for isolating colonies, the incubation times and temperatures. For instance, the use of a post-incubation filtration procedure to measure ^{14}C fixed by *Phaeocystis* colonies can severely underestimate the

Table 3
Growth-temperature adaptation parameters of *Phaeocystis* obtained from the following fitting equation := μ-μ_{max} * EXP [-(T-Topt)^2/dT^2]

Species	μ_{max}, d^{-1}	T_{opt}, °C	dT, °C	n	r
All species[1]	1.3±0.1	16.3±1.0	13.7±1.6	86	0.58

total carbon photo-assimilated by the whole colonies because significant colony matrix disruption might occur during the filtration procedure. Long-term (12–24 h) ^{14}C-incubations also underestimate photosynthesis due to carbon loss through catabolic processes (Veldhuis and Admiraal, 1985; Lancelot et al., 1986). In addition, a significant dependence of the photosynthetic capacity on temperature has been observed for *P. pouchetii* when cultured under conditions of non-limiting nutrients (Verity et al., 1991). Therefore, among existing data from which photosynthetic parameters could be derived, we selected those obtained for field and cultured *Phaeocystis* with short incubation time (less than 3 h) and for which information on temperature and filtration procedure is given. The derived photosynthetic parameters are gathered in Table 4. It gives for each colony-forming species the range of values obtained for the maximum photosynthetic capacity P_m^B and the light adaptation coefficient E_K (all obtained by fitting data with the equation from Platt et al., 1980). Also it distinguishes between colonies (cells+mucus) and colony cells where possible. Large variation in these parameters is observed within each species and no clear species distinction can be made on the basis of their photosynthetic characteristics (Table 4). In contrast to the findings of Verity et al. (1991), the observed variability of the colony maximum photosynthetic capacity P_m^B cannot be explained by a difference in ambient temperature (Table 4). On the contrary, P_m^B values reported for the *Phaeocystis* colonial cells only show lower intra-specific fluctuations (*P. globosa* and *P. antarctica* in Table 4). Overall the observed lower P_m^B values of *P. antarctica* cells compared to *P. globosa* suggest a similar trend for the temperature dependence of growth (Fig. 3) and P_m^B. Hence most of the observed scattering in *Phaeocystis* colony P_m^B should be attributed to considerable variation in the amount of newly synthesised carbon inside the mucilaginous matrix, which accounts for more than 50% of the total photo-products, and not as cellular carbon (Table 4). Some evidence exists that nutrient limitation would favour the synthesis of the polysaccharidic matrix of *P. globosa* (i.e. enhancement of extracellular polymers synthesis at low nitrates, Lancelot and Mathot, 1987). A similar relationship has not been observed for the Antarctic species although some iron control of P_m^B is suspected in the Ross Sea (Van Hilst and Smith, 2002).

The large fluctuations of E_K parameters suggest a high degree of flexibility adaptation to a large range of ambient light (~5–150 µmole quanta m^{-2} s^{-1}; Table 4). This hypothesis is supported by Fig. 4, which

Table 4
Selected photosynthetic parameters of *P. antarctica, P. pouchetii, P. globosa*

Species	Sample	P_m^B (mgC mgChl-a^{-1} h^{-1})	E_K (µmol m^{-2} s^{-1})	Temperature (°C)	References
P. antarctica					
Colony	F	3.52–8.08	47–144	−1.8	Palmisano et al., 1986
	F	0.23–7.45	11–94	−1.8–0	Van Hilst and Smith, 2002
	C	1.5–4.1	19–57	5	Matrai et al., 1995
	C	0.91–1.86	71–248	0	Van Hilst and Smith, 2002
	C	0.19	73	4	Hong et al., 1997
Colony cells	C	1.2–1.5	22–64	5	Matrai et al., 1995
P. pouchetii					
Colony	F	2.5–22.5	71–191	−1.5–2	Cota et al., 1994
	C	0.8–1.21	4–29	6	Matrai et al., 1995
	C	0.78	29	3	Schoemann et al., 2001
P. globosa					
Colony	F	5.2–6.11	54–108	8–11	Lancelot et al., 1987
Colony cells	F	2.3–2.6	35–53	8–11	Lancelot et al., 1987

F and C refer to the origin of the sample: F=field, C=pure culture.

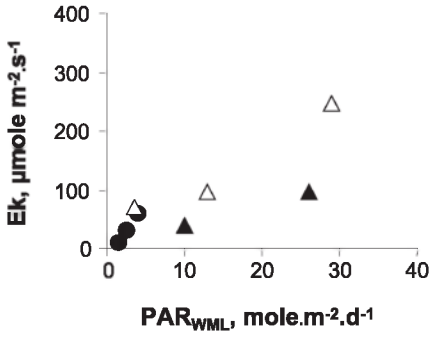


Fig. 4. Relationship between *Phaeocystis* light adaptation parameter E_k and the average daily photosynthetically active light (PAR) in the upper mixed layer. Data for *Phaeocystis globosa* in the North Sea (unpublished data from Lancelot and Rousseau) are represented by closed circles and data for *Phaeocystis antarctica* (Van Hilst and Smith, 2002) in pure cultures and in the Ross Sea are represented by open and closed triangles, respectively.

suggests a positive relationship between the light adaptation coefficient typical of *P. globosa* and *P. antarctica* populations and the average daily light available in the upper mixed layer. In accordance, many reports suggest that the success of *P. antarctica* in deep-mixing waters of the Ross Sea is due to a better adaptation to low light compared to diatoms (e.g. Moisan et al., 1998; Arrigo et al., 1999). This hypothesis has been challenged, however, by a recent comparison of *P. antarctica* and diatom P-E curves in the Ross Sea (Van Hilst and Smith, 2002). It is suggested that the spatial distribution of *Phaeocystis antarctica* and diatoms does not simply result from different photosynthetic responses but more likely reflects a complex interplay of factors, e.g. trace metal limitation, vertical mixing.

3.3. CO_2 limitation

CO_2 is a potentially limiting growth factor for algae (Riebesell et al., 1993). Depending on temperature, salinity and pH, free CO_2 represents approximately 0.5 to 1% of the total inorganic carbon species in the oceans. During bloom situations, the pH increases and the CO_2 concentration can come close to or below the half saturation constant of RubisCO, the central C fixing enzyme in photosynthesis, and thus become growth limiting (see Badger et al., 1998). Algae can have different strategies to overcome a possible limitation of CO_2. One strategy is to actively take up HCO_3^- across the plasma membrane. Another is to catalyse the conversion of HCO_3^- to CO_2 extracellularly by carbonic anhydrase (CA), followed by diffusion of CO_2 across the membrane. There appears to be a high plasticity in the mode of inorganic carbon acquisition in marine algae, with different strategies within one genus and even within one species (e.g. Elzenga et al., 2000). *Phaeocystis* appears to possess an extracellular CA to convert HCO_3^- to CO_2 (Elzenga et al., 2000), which can become beneficial in bloom situations when the pH may increase to 8.7 (Brussaard et al., 1996; Schoemann et al., 1998) and dissolved CO_2 concentrations decrease to 5 µM (Schoemann et al., 1998). In support of this, Tortell et al. (2002) recently observed increased dominance of *Phaeocystis* cells relative to diatoms under low CO_2 conditions and suggested that the CO_2 concentration can potentially influence competition among species.

3.4. Nutrient limitation

Phytoplankton nutrient kinetic parameters reported in the literature are related to both nutrient uptake and nutrient limitation of growth. Nutrient uptake rates depend strongly on the level of limitation, resulting in increasing rates under nutrient limitation. Nutrient uptake rates are generally measured by nutrient enrichment experiments in the field or in culture. They are commonly described by a Michaelis-Menten equation (Eppley et al., 1969) although there is considerable evidence that the control of uptake rates by nutrient concentration is much more complex and confounds such a simple model (e.g. Harrison et al., 1989). The regulation of growth by ambient nutrients is described by a Michaelis Menten-type equation, which relates directly the specific growth rate µ (h^{-1}) to the ambient nutrient concentration. Parameters of this equation are experimentally determined by running chemostats. For a specific nutrient, the half saturation constant (mmol m^{-3}) for uptake (K_{nut}) is higher than that for growth regulation ($K\mu_{nut}$) when growth is limited by this nutrient.

This section reviews the parameters available for nutrient uptake and assimilation of the various species or ecotypes of *Phaeocystis* colonies and free-living cells. Surprisingly, *Phaeocystis* has been very poorly documented. Most of the field studies have been performed with *P. globosa* (Veldhuis et al., 1986;

Lancelot et al., 1987) and *P. pouchetii* species (Smith et al., 1991; Muggli and Smith, 1993). Very little is known about nutrient uptake kinetics of *P. antarctica*. Although nutrient uptake rates have been reported in the Southern Ocean (Smith, 1993; Goeyens et al., 2000), no nutrient kinetic parameters have been determined. Nitrogen and phosphorus are indeed non-limiting nutrients in the Southern Ocean (Smith et al., 1996) due to prevalent iron limitation (Smith and Nelson, 1985). Generally, available data are too scarce to assess the interspecific variability of nitrogen and phosphorus metabolism.

3.4.1. Nitrogen metabolism

The regulation of *Phaeocystis* growth by nitrogen has only been documented for *P. globosa* colonies. A $K_{\mu NO3}$ of 4 mmol m^{-3} related to specific protein synthesis has been measured in the Belgian coastal waters of the Southern Bight of the North Sea making use of tracer (^{14}C and ^{15}N)-based methods (Lancelot et al., 1986). Available information for *P. pouchetii* is related to the uptake process and indicates a K_{NO3} value of 0.29 mmol m^{-3} for natural populations in the Greenland Sea (Muggli and Smith, 1993).

3.4.2. Phosphorus metabolism

Experimental study of P metabolism has been conducted with *P. globosa* colonies and solitary cells (Veldhuis and Admiraal, 1987; Veldhuis et al., 1991). Both *Phaeocystis* cell types differ in their kinetic parameters for phosphate uptake. From batch experiments, Veldhuis and Admiraal (1987) estimated an apparent $K_{\mu PO4}$ of 0.7 mmol m^{-3} for colonial cells but much smaller for solitary cells. This elevated value should, however, be considered with caution as it was derived from batch cultures inappropriate for the determination of parameters describing the control of growth by nutrients. The determination of uptake kinetics was made under severe P limitation making use of ^{32}P short-term uptake measurements (Veldhuis et al., 1991). Quite similar maximum uptake rates were measured for free-living (0.141 10^{-12} mmol P min^{-1} $cell^{-1}$) and colonial cells (0.158 10^{-12} mmol P min^{-1} $cell^{-1}$) but K_{PO4} of P-limited colonial cells (3.08 mmol m^{-3}) is about 8 times higher than that of free-living cells (0.31 mmol m^{-3}; Veldhuis et al., 1991). The difference in K_{PO4} may be ascribed to a diffusion boundary layer surrounding the mucus matrix, whereby the concentration at the cell surface is lower than the bulk water concentration (Ploug et al., 1999). In addition, *P. globosa* has been shown to be able to grow on organic phosphorus through phosphatasic activity (Admiraal and Veldhuis, 1987; Veldhuis and Admiraal, 1987). A K_s for hydrolysis of organic phosphate (nucleoside monophosphate) of 0.25–0.45 mmol m^{-3}, lower than for phosphate uptake (0.80 mmol m^{-3}), was established in pure culture under PO_4 limitation (Admiraal and Veldhuis, 1987). The ability to grow on organic P has not yet been demonstrated for the *P. pouchetii* and *P. antarctica* species.

3.4.3. Trace metals

Iron and manganese are two essential elements for phytoplankton growth (Sunda, 1988/1989) that have been examined in more detail for *Phaeocystis*. To date there is no estimate of maximum uptake rates and half-saturation constants for uptake and growth available for *Phaeocystis*. Intracellular uptake rates of Fe were estimated to be 1.3 × 10^{-18} mol $cell^{-1}$ h^{-1}, one order of magnitude higher than that of Mn (9.0 × 10^{-20} mol $cell^{-1}$ h^{-1}) for *P. globosa* cultured in media containing excess 40 nM dissolved Fe and 22 nM dissolved Mn (Schoemann et al., 2001).

The colonies of *Phaeocystis* have been shown to accumulate Fe and Mn in their mucus (Davidson and Marchant, 1987; Lubbers et al., 1990; Schoemann et al., 2001). *Phaeocystis* colonies accumulate more Fe than Mn, but the mechanisms differ between the two elements (Schoemann et al., 2001). The accumulation of Mn by the colonies was controlled by photosynthesis of colony cells, whereas the uptake of Fe associated with the mucus was only slightly influenced by photosynthesis (Schoemann et al., 2001). The increased pH and to a smaller extent the increased oxygen concentrations around and inside photosynthesising colonies stimulate the precipitation and accumulation of Mn in the mucus (Davidson and Marchant, 1987; Lubbers et al., 1990; Schoemann et al., 2001). Contrary to Mn, Fe could have been largely complexed by the mucus polysaccharides and rapidly precipitated on the mucus, without being much influenced by the observed pH and oxygen changes (Schoemann et al., 2001). Iron accumulation by *Phaeocystis* colonies is likely to result from adsorption, complexation and precipitation (Schoemann et al., 2001). Mechanisms such as

physiological or photochemical reduction could then make some of the mucous-trapped Fe and Mn bioavailable. Experiments on Mn accumulation by *Phaeocystis* colonies were conducted both on *P. globosa* and *P. pouchetii*, but experiments on Fe accumulation have only been conducted on *P. globosa*. However, the mucus from all colony-forming species should be able to provide sufficient organic ligands for Fe. In areas where Mn and Fe concentrations may become limiting for phytoplankton growth, e.g. the Southern Ocean, this accumulation in the mucus could constitute a supplementary reservoir of these elements to *Phaeocystis* in periods of temporary low availability. This mechanism could render *Phaeocystis* more competitive with respect to other phytoplankton species and therefore play a significant role in structuring the phytoplankton community and hence the associated food web.

3.5. Stoichiometry: elemental ratios and Chl-a:C quotas

3.5.1. C:N :P ratios

Most information on elemental composition and derived stoichiometry of colonies and free-living cells of the three colony-forming *Phaeocystis* proceeds from traditional elemental analysis. Alternate methods based on the ratio of nutrient removal from the water column at the time of a *Phaeocystis* bloom have been used for characterising the elemental composition of *P. antarctica* (Arrigo et al., 2000; Smith and Asper, 2001). While removal ratios could reflect phytoplankton stoichiometry, they could, however, be strongly biased by differential N and P recycling processes due to bacterial or grazing activity. Therefore in this section we only consider stock-based data reported for pure cultures of *Phaeocystis* and assemblages dominated by more than 95% *Phaeocystis* spp. and discuss their inter-and intra-specific variability based on available information on growth conditions (Table 5).

As a general trend, molar C:N ratios of exponentially growing free-living cells of *P. globosa* and *P. antarctica* are in the same range, varying between 4 and 6 (Table 5). No data are available for *P. pouchetii*. Values above the classical Redfield's ratio (C:N=6.6) are reported for cells growing under condition of nutrient limitation with the highest C:N cell ratios recorded under low nutrient but high light, explained by the light-stimulated synthesis of carbon-based storage products (Lancelot et al., 1986). Exponentially growing *Phaeocystis* colonies are characterised by distinct average C:N ratios of, respectively, 6 for *P. globosa* and *P. antarctica*, and 9 for *P. pouchetii*. Deviation of *Phaeocystis* colony C:N from Redfield's ratios must be attributed in particular to the increased production of the mucilaginous matrix (basically polysaccharidic consisting of varying monosaccharides; see the review by Van Rijssel et al., 2000) under conditions of high light but low nutrient concentrations. Recent data nevertheless suggested that extracellular polymers for *P. globosa* and *P. antarctica* are carbohydrate-rich but also contain significant amounts of small nitrogen-containing compounds such as amino sugars (Solomon et al., 2003).

This corresponds with the role of energy reservoir for the *Phaeocystis* matrix as demonstrated for *P. globosa* (Lancelot and Mathot, 1985; Veldhuis and Admiraal, 1985). Accordingly, molar C:N ratios of *P. globosa* and *P. pouchetii* colonies vary between 6–30 and 6–21, respectively, and increase exponentially with the ambient inorganic nitrogen for concentrations below 15 μM (Lancelot et al., 1991; Baumann et al., 1994). Observed variations of C:N in *P. antarctica* are comparatively smaller ranging from 5 to 8, and may be related to iron depletion although this has not been demonstrated.

Data on *Phaeocystis* C:P ratio are limited to *P. globosa* (Table 5) and show large fluctuations—80 to 568-with highest values related to P depletion (Jahnke, 1989). Highly varying P content (0.016–0.52 pmol P $cell^{-1}$) with the lowest value found after PO_4 depletion were also measured for colonial and solitary cells in batch cultures (Veldhuis and Admiraal, 1987).

3.5.2. Fe:C and Mn:C ratios

Intracellular stoichiometric ratios of Fe:C and Mn:C are not known for *Phaeocystis* cells. Schoemann et al. (2001) have given some estimate of colony Fe:C and Mn:C ratios based on measurement of particulate Mn and Fe and C-cell estimate. The latter was obtained by microscopic cell counting and making use of the cell to carbon conversion factor from Van Rijssel et al. (1997). They found an Fe:C ratio of 93.4 μmol mol^{-1} and a Mn:C ratio of 5.4 μmol mol^{-1} for *P. globosa* colonies cultured under non-limiting dissolved Fe and Mn concentrations of

Table 5
C:N and C:P molar ratios reported for colonies and cells of *P. antarctica*, *P. pouchetii*, *P. globosa*

Species	Sample	Growth conditions	C:N	References
P. antarctica				
Colonies	F	exponential growth	5.7–6.4	Smith and Asper, 2001
	F	stationary stage	5.4±0.3	El-Sayed et al., 1983
	F	nutrient-depleted	6.2–7.5	Smith et al., 1998
	E	nutrient-depleted	5.4–7.9	Smith et al., 1998
Cells	C	exponential growth, high light	4–6	Stefels and Van Leeuwe, 1998
	C	stationary phase, high light, N limited	11–12	Stefels and Van Leeuwe, 1998
	C	stationary phase, low light, N limited	8	Stefels and Van Leeuwe, 1998
	C	Fe-limited, high light	4–8	Stefels and Van Leeuwe, 1998
	C	Fe-limited, low light	5–9	Stefels and Van Leeuwe, 1998
	C	late exponential phase	4.9–5.5	Solomon et al., 2003
P. pouchetii				
Colonies	E	exponential growth	6.2–10.9	Verity et al., 1988, 1991
	F	exponential growth	5.73±1.31	Smith, 1993
	C	exponential growth	7.6±1.0	Jahnke, 1989
	E	N-depleted	14.3–20.5	Verity et al., 1991
P. globosa				
Colonies	C	exponential growth	6.9±0.7	Jahnke, 1989
	F	exponential growth	6.5	Lancelot et al., 1986
	F	stationary stage	8	Lancelot et al., 1986
	C	P-deficient	7.6–9.7	Jahnke, 1989
Cells	C	exponential growth	4–4.7	Llewellyn and Gibb, 2000
	C	late exponential phase	4.2–4.9	Solomon et al., 2003
	F	exponential growth	6	Lancelot-Van Beveren, 1980
Species	Sample	Growth condition	C:P	References
P. globosa				
Colonies	C	exponential growth	80	Jahnke, 1989
	C	P-deficient	128–568	Jahnke, 1989

C, For E refers to the origin of sample: C=pure culture, F=field; E=enclosure.

40 and 22 nM, respectively. By radiotracer experiments, they also measured total colonial Fe:C and Mn:C uptake ratios of 79.3 μmol mol^{-1} and 6.2 μmol mol^{-1}, respectively.

3.5.3. Chl-a:C ratios

In their review, Baumann et al. (1994) suggested a species-specific cellular Chl-a:C ratio with higher values more typical of *P. antarctica*. Since then, however, theoretical and experimental evidence has shown a strong dependence of phytoplankton Chl-a:C on the light and nutrient growth conditions due to a complex interplay of biochemical processes (Geider et al., 1997). As a general trend the lowest phytoplankton chlorophyll quotas are recorded under growth conditions of high light and low nutrient (Geider et al., 1997). Moreover the impact of nutrient deficiency on Ch-a:C quota might be particularly important for the iron-limited Southern Ocean species as iron is required for synthesising chlorophyll. Indeed, as illustrated in Table 6, a threefold variability of Chl-a:C is observed

Table 6
Iron and light dependence of chlorophyll-a cell quota and ratios to cell-carbon in cultured *P. antarctica* cells

Iron and light conditions	Cellular (pg cell^{-1})	Chl-a:C (mg:g)
I=110 μE, Fe-sufficient	0.27	14
I=25 μE, Fe-sufficient	0.55	31
I=110 μE, Fe-deficient	0.14	10
I=25 μE, Fe-deficient	0.26	13

Data from Van Leeuwe and Stefels (1998) and Stefels and Van Leeuwe (1998).

for *P. antarctica* cells growing under contrasting light and iron conditions. Extremely low Chl-a:C of 10 (mg:g) were observed for iron-deficient *Phaeocystis* cells growing under high light conditions while values around 30 were typical of actively growing cells. Combining these data with those reported previously by Baumann et al. (1994), it is reasonable to consider an average Chl-a:C value of 30 (mg:g) for healthy growing *Phaeocystis* cells valid for all species.

The few Chl-a:C data available for *Phaeocystis* colonies were reviewed by Baumann et al. (1994). These authors concluded that healthy growing *P. globosa* and *P. pouchetii* colonies can be characterised by a similar Chl-a:C basal ratio of 18 (mg:g). The low value compared to the cellular ratios is due to the carbon associated to the polysaccharidic matrix. These authors also reported a high range of variability, between 3 and 18 with the lower values exponentially related to nitrogen deficiency. The decreasing trend is explained by an increased production of the polysaccharidic matrix under conditions of sufficient light and low nutrient (see Baumann et al., 1994).

4. Trophic fate of material derived from *Phaeocystis* colonies

One unresolved question about *Phaeocystis* blooms in the global ocean is to which extent their success is due to their high competitiveness for the resources (adaptation to light fluctuations and/or their ability to use organic P and sequester Fe) or to their resistance to grazing and sinking. In a recent review, Hamm (2000) suggests that the skin-like structure of the colony matrix, demonstrated for *P. globosa* colonies (Hamm et al., 1999), explains their general resistance to loss processes. The latter include colony degradation and cell lysis, viral infection, grazing, sinking, aggregation and sedimentation. The significance of these processes for the different colony-forming species is discussed in this section, as well as the impact on the food-web structure and related carbon cycle.

4.1. Grazing

The knowledge of grazer trophic responses to *Phaeocystis* is essential for understanding the top-down controls of *Phaeocystis* blooms. Literature on *Phaeocystis* grazing is ample but reaches different conclusions about the trophic value for the three colony-forming species, which bloom in different geographical areas. The distribution of *P. pouchetii* and *P. antarctica* blooms usually coincide with the most intensive growth and production of large herbivorous copepods in the polar oceanic waters such as the Barents Sea, the coastal areas of northern Norway Sea, the Labrador Sea, the Bellingshausen Sea (Hansen and Van Boekel, 1991; Head and Harris, 1996; Meyer-Harms et al., 1999). On the contrary, a poor nutritional value is generally documented for *P. globosa* colonies due to a low or inefficient feeding (Verity and Smayda, 1989; Claustre et al., 1990; Hansen et al., 1990b; Schnack-Schiel et al., 1998; Gasparini et al., 2000) and/or egg production rates (Verity and Smayda, 1989; Ianora and Poulet, 1993; Bautista et al., 1994) with consequently drastic decreases in copepod abundance (Bautista et al., 1992).

However, most of the difficulty in interpreting existing data on *Phaeocystis* grazing is due to the large size range of both *Phaeocystis* life forms (~2–8 μm to cm) and potential grazers (~20 μm to cm). Much of the reported resistance of *Phaeocystis* colonies to grazing (see the review by Weisse et al., 1994) could be attributed to a size mismatch or mechanical hindrance due to the presence of the mucilaginous matrix rather than a low nutritional value. This is supported by Table 7, which gives extreme values of ingestion rates sorted by grazers

Table 7
Overview of zooplankton grazing on *Phaeocystis*

Zooplankton	Form	*Phaeocystis* food	Ingestion rate, (% body-C d^{-1})	
		Species	Field	Culture
Krill	Col	*P. pouchetii, antarctica*	1–5	
Copepods>2mm	Col	*P. pouchetii, globosa*	2–72	0.2–36
	SC			0.1–6.7
Copepods<2mm	Col	*P. pouchetii, globosa*	1.7–≤35	0–68
	SC			0–18
Microzooplankton	SC	*P. pouchetii, globosa*	1–126	3–91

Data from Weisse, 1983; Huntley et al., 1987; Tande and Båmstedt, 1987; Verity and Smayda, 1989; Hansen et al., 1990a; Weisse and Scheffel-Möser, 1990; Hansen and Van Boekel, 1991; Hansen et al., 1993; Hansen et al., 1994; Weisse et al., 1994; Metz, 1998; Hansen et al., 2000; Tang et al., 2001. Col=colonies, SC=Single cells.

(from microzooplankton up to krill) and *Phaeocystis* forms (free-living cell vs colony) and species. As a general trend, krill is able to ingest colonies smaller than 500 μm (Hansen et al., 1994) at a maximum observed daily rate of 5% of their body carbon. Krill has also been reported to crunch on larger ones and break them in small pieces, to supply some *Phaeocystis* food to microzooplankton grazers as well (Hansen et al., 1994). Large copepods (mainly *Calanus* spp.) feed efficiently on *Phaeocystis* colonies (Huntley et al., 1987; Tande and Båmstedt, 1987; Eilertsen et al., 1989) with reported maximum ingestion rates of 72% of their body carbon d^{-1} (Table 7). On the contrary, reported ingestion rates of *Phaeocystis* colonies by small copepod species (*Acartia* spp., *Centropages* spp. and *Temora* spp.) are very low (maximum ingestion rates of 6% of their body carbon d^{-1}) indicating that these copepods are not capable of feeding efficiently on *Phaeocystis* colonies. One exception, however, is *Oncaea curvata*, a small copepod present in the polar sea, which was reported to ingest *Phaeocystis* colonies at a much higher daily rate of up to 67% of their body carbon (Metz, 1996, 1998). A heterotrophic dinoflagellate, *Noctiluca scintillans*, has also been reported to ingest small colonies (Jacobsen et al., 1996).

Due to their small size, single *Phaeocystis* cells are not efficiently consumed by mesozooplankton (Breton et al., 1999), but are well consumed by microzooplankton (Table 7) including ciliates and heterotrophic dinoflagellates. The trophic role of ciliates as an intermediate protozoan prey for mesozooplankton has been recently shown to improve the trophic value of *P. globosa* (Tang et al., 2001), suggesting complex interactions among grazers.

It has been demonstrated that zooplankton grazing can be taxon-specific. In the laboratory, *Acartia* spp. selected diatoms over *P. pouchetii* (Verity and Smayda, 1989). Selective grazing for diatoms has also been reported for krill (Haberman et al., 2003). The selectivity cannot be entirely attributed to differential sieving efficiency based on particle size, but the food quality could also be a key factor (Haberman et al., 2003). The complexity of trophic relationships in *Phaeocystis* dominated ecosystems was pointed out in a recent paper (Tang et al., 2003). Tang et al. (2003) gave the first empirical evidence that the increase in colony size of *Phaeocystis globosa* was stimulated by dissolved chemicals generated by ambient grazing activities. The *Phaeocystis* colony size increase provided a defensive response against grazers.

4.2. Aggregation and sedimentation

The contribution of *Phaeocystis* sp. to the vertical export (see review by Wassmann, 1994) is still a matter of controversy. Data on specific sinking rates of *Phaeocystis* single cells, colonies and derived aggregates are scarce. A synthesis of the data is shown in Table 8. In accordance to their nanosize, *Phaeocystis* solitary cells have low sinking rates, less than 1 m d^{-1} (Becquevort and Smith, 2001; Peperzak et al., 2003). Specific sinking rates for *Phaeocystis* colonies range between –0.37 and 14 m d^{-1}. Negative sinking rates demonstrated their capacity to regulate their buoyancy. High sinking rates of up to 200 m d^{-1} have been observed only for *Phaeocystis*–derived aggregates. Aggregation has been recognised as an important mechanism enhancing vertical flux (Kiørboe, 1993). Three different mechanisms may contribute to the formation of *Phaeocystis*-derived aggregates: self-aggregation; colonisation by other microorganisms; and self-induction by matrix-derived polysaccharides. The *Phaeocystis* potential aggregation resulting from aggregation between cells or colonies has been reported as inefficient in comparison to diatoms (Riebesell, 1993; Passow and Wassmann, 1994). The most efficient mechanism for building *Phaeocystis*-derived aggregates is via the colonisation of fragile senescent *Phaeocystis* colonies by auto-and heterotrophic microorganisms as reported for *P. globosa* in

Table 8
Overview of *Phaeocystis* sinking rates observed during the wax and wane of *Phaeocystis* blooms

Species	Sinking rates, m d^{-1}	
	Exponential phase	Colonies and aggregates
P. antarctica	0–14	4–>200
P. pouchetii	–	0–160
P. globosa	–0.37–11.5	–

Data from Van Boekel et al., 1992; Osinga et al., 1996; Riegman and Van Boekel, 1996; Asper et al., 1997; Asper and Smith, 1999; Becquevort and Smith, 2001; Svensen et al., 2001; Peperzak et al., 2003.

the North Sea (Rousseau et al., 1994; Becquevort et al., 1998) and in the Arabian Sea (Garrison et al., 1998), and for *P. antarctica* in the Ross Sea (Putt et al., 1994). In addition, the transparent exopolymer particles (TEP) released after disruption of senescent colonies have been reported as a key cement for triggering formation of *P. pouchetii*-derived aggregates in the Scandinavian fjords (Riebesell et al., 1995; Reigstad et al., 2000). We therefore conclude that healthy *Phaeocystis* cells and colonies do not contribute significantly to vertical flux but that the sedimentation of mucous flocs colonised by microorganisms constitutes an efficient pathway by which carbon assimilated during *Phaeocystis* blooms may sink. However, knowledge about factors responsible for *Phaeocystis* colony senescence and disruption is still very limited.

Massive sedimentation of *Phaeocystis* material has been well recorded in polar waters in the Barents Sea (*P. pouchetii*; e.g. Wassmann et al., 1990; Asper and Smith, 1999) and the Ross Sea (*P. antarctica;* e.g. Asper et al., 1997). Recently, DiTullio et al. (2000) reported unexpected results suggesting a rapid export of healthy growing *P. antarctica* in the Ross Sea. In most of these deep-water environments, however, the exported *Phaeocystis*-derived material is largely remineralised in the mesopelagic zone (Von Bodungen et al., 1986; Wassmann, 1994; Sweeney et al., 2000) with little carbon reaching the deep ocean and the sediment. On the other hand, the significance of aggregation and sedimentation for the termination of *P. globosa* in coastal waters of the North Sea is still a matter of debate. Carbon budget calculation over the vegetative period indicates that *Phaeocystis* sedimentation would be of little significance in this shallow coastal sea (Brussaard et al., 1995; Rousseau et al., 2000). This is challenged by observed transient accumulations of colonies on the sediment (Riebesell, 1993; Cadée, 1996; Peperzak et al., 1998) as well as indirect evidence of fresh organic matter deposit to the sediment during the decline of a *Phaeocystis* bloom (Schoemann et al., 1998).

4.3. *Phaeocystis lysis and bacterial remineralisation of Phaeocystis-derived organic matter*

Lysis was identified as the major fate of ungrazed *P. globosa* colonies in the Dutch coastal waters of the North Sea (Van Boekel et al., 1992; Brussaard et al., 1995). Values as high as 0.35 d^{-1} were reported and related to nutrient stress (nitrate depletion; Van Boekel et al., 1992). Lysis can also be the result of viral infection and a strain-specific virus for *P. pouchetii* cell has been isolated (Jacobsen et al., 1996) as well as for *P. globosa* (Veldhuis, pers. comm., 2003). Cell mortality rates by virus infection of up to 0.8 d^{-1} have been calculated for *Phaeocystis pouchetii* (Brussaard et al., 2001). The virus was, however, not able to infect healthy *Phaeocystis* colonies (Bratbak et al., 1998) most probably due to the mechanical protection offered by the skin-like envelope of the colony matrix (Hamm, 2000). It might therefore be suggested that nutrient and/or light stress are the key factors triggering colony senescence and lysis, and subsequent release of *Phaeocystis* free-living cells and dissolved organic matter into the ambient water. When released into the ambient water, *Phaeocystis* cells are vulnerable to viral infection, which in turn provokes cell lysis and subsequent sudden release of dissolved organic matter in the water column. Elevated transient DOC concentrations have often been associated directly with the decline of the bloom in areas where grazing is insignificant (Eberlein et al., 1985; Billen and Fontigny, 1987; Davidson and Marchant, 1992a) suggesting that bacteria are not responding fast enough to the sudden supply of organic matter. In accordance, delays of some 25–31 and 5–12 days have been observed between *Phaeocystis* blooms and bacteria biomass for *P. antarctica* (Davidson and Marchant, 1992a; Putt et al., 1994; Ducklow et al., 1995) and *P. globosa* (Billen et al., 1990; Blight et al., 1995; Brussaard et al., 1996; Becquevort et al., 1998; Rousseau et al., 2000) blooming areas, respectively. Different hypotheses have been proposed to explain this delay. Among these, the low biodegradability of the mucilaginous matrix and the C:N:P imbalance of *Phaeocystis*-derived material are most often invoked. Existing data from biodegradation experiments conducted on *P. globosa* and *P. antarctica* (Table 9) reveal a high biodegradability of *Phaeocystis* material under conditions of non-limiting nutrients. Table 9 also shows that most of the *P. globosa*-derived carbon is degraded in less than 7 days. On the other hand, the significantly lower biodegradability of DOC at the time of *P. antarctica* bloom could be due to iron limitation, although this has not been demonstrated. We might then suggest that the mineralisation of

Table 9
Biodegradable fraction (BDOC) of *Phaeocystis*-derived DOC measured after a period of <7 days or <30 days (bio-assays according to the protocole of Servais et al. (1987)

Species	*Phaeocystis*-material	Sample	BDOC- < 7 d %	BDOC- < 30 d %	References
P. globosa	Colonies derived DOC	C	57	67	Tallier, 1994
	Cells derived DOC	C	81	82	Tallier, 1994
	Colony matrix derived DOC	C	89–93	89–94	Tallier, 1994
				50	Janse et al., 1999
	DOC-bloom period	F	61–87	61–100	Déliat, 2001
P. antarctica	DOC-bloom period	F	7–24	18–39 (15 days)	Carlson et al., 1999

C=culture, F=field during *Phaeocystis* bloom.

Phaeocystis-derived material is under the control of nutrient limitation, N and P in northern European blooms (Thingstad and Billen, 1994) and iron in the Southern Ocean (Pakulski et al., 1996).

5. Concluding remarks

5.1. Blooming success of Phaeocystis colonies

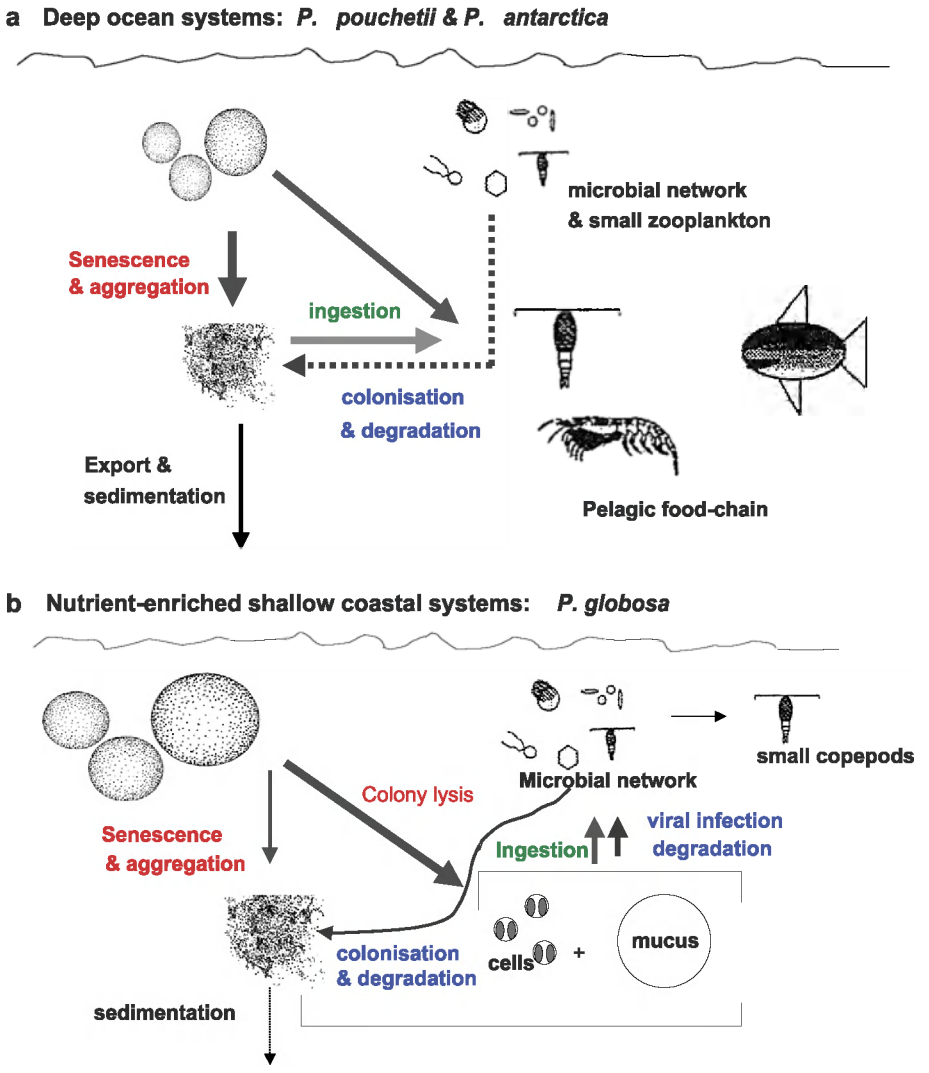
This overview of the bottom-up and top-down controls of *Phaeocystis* colony blooms confirms that most of their success is the consequence of the ability to form gel-like colonies. On the one hand, the colony matrix, by acting as an energy and nutrient (Fe, PO_4) reservoir, could give a competitive advantage to *Phaeocystis* when resources (light and nutrients-mostly PO_4 and dissolved Fe) are scarce or highly fluctuating (Veldhuis et al., 1991; Schoemann et al., 2001). On the other hand, the skin-like structure *of P. globosa* colonies with pore size< 4.4 nm (Hamm et al., 1999) has been suggested to prevent pathogen infection (Jacobsen et al., 1996) of the colonial cells. In addition DMSP produced by *Phaeocystis* cells and accumulating in the colony matrix releases acrylic acid when converted to DMS, which would deter grazers (Sieburth, 1960). In accordance, high acrylate concentrations have been measured inside the *P. globosa* matrix (Noordkamp et al., 2000). However, the repellent properties of *Phaeocystis* colonies have never been investigated. The reported resistance of *Phaeocystis* colonies to mesozooplankton grazing is generally attributed to a size mismatch or mechanical hindrance due to increased viscosity. The latter has often been suggested but never demonstrated.

5.2. Impact on the ecosystem structure and functioning

Schematic representations (adapted from Hamm, 2000) are given in Fig. 5 for extreme structures of *Phaeocystis*-dominated deep-ocean (Fig. 5a) and nutrient-enriched shallow coastal (Fig. 5b) systems. These diagrams suggest species-dependence and geographic variability, which could be attributed to difference in the colony size and structure of the colony matrix and/or the presence/absence of large grazers. In the nutrient-enriched coastal system (Fig. 5b) most of the *Phaeocystis* biomass —often dominated by large colonies of *P. globosa* (North Sea) or *P. antarctica* (Prydz Bay)— escapes grazing by indigenous zooplankton. Ungrazed senescent colonies disrupt and/or aggregate and are remineralised by free-living and attached bacteria. Colonial cells released into the ambient water after colony disruption are ingested by ubiquitous microzooplankton and are vulnerable to virus infection. Hence in *Phaeocystis*-dominated coastal systems most of the carbon photoassimilated by *Phaeocystis* flows through the microbial food network which maintains CO_2 in surface waters.

In ocean systems (e.g. *P. pouchetii* in the Greenland/Barents Sea and *P. antarctica* in the Ross/Weddell Sea), colonies are relatively small and grazed by large copepods and euphausids (Fig. 5a). To our knowledge, ungrazed colonies do not disrupt or sink significantly. Senescent colonies aggregate and sink but most of the exported carbon is remineralised in the mesopelagic waters with little carbon reaching the deep ocean and the sediments.

Interestingly, the structure and functioning of *P. pouchetii*-dominated ecosystem of Scandinavian



fjords lie in between these two extremes with DOC release by ungrazed colonies leading to the production of TEP, which enhances formation of *Phaeocystis*-derived aggregates that are exported to deep waters (Reigstad et al., 2000).

5.3. *Phaeocystis* and global climate change

Phaeocystis blooms have an impact on climate change, not only through the carbon cycle, but also through the production of DMS. With a rough calculation, an indication can be given of the contribution of *Phaeocystis* blooms to the global DMS flux. If we ignore the ongoing uncertainties of transfer velocities of gases through the air-sea interface and assume that *Phaeocystis* blooms cover approximately 6% of the ocean surface for one month and that during this month the mean DMS-concentration is 25 nM and the wind speed is 8 m s^{-1}, then it can be calculated that *Phaeocystis* blooms emit 0.05 Tmol DMS y^{-1} to the atmosphere. With a global flux estimate of 0.5 to 1 Tmol y^{-1} (Kettle and Andreae, 2000), the contribution

of *Phaeocystis* blooms is 5 to 10%. Locally, especially during blooms in the Southern Ocean, when both the DMS concentration and the wind speed are often found to be much higher, the significance of *Phaeocystis* to the DMS flux will increase strongly.

In turn, global climate change will have an impact on the trophic state of ecosystems and their species composition and, as a consequence, on the flux of DMS to the atmosphere. Recent model studies have shown that an increased atmospheric CO_2 concentration may result in increased DMS fluxes over the Southern Ocean by 20 to 30% (Bopp et al., 2003; Gabric et al., 2003). How climate change will affect *Phaeocystis* blooms is yet unknown. Gabric et al. (2003) suggest that *Phaeocystis* will benefit from climate change in the Southern Ocean, but a predicted stabilisation of the mixed layer depth might suggest the contrary. Obviously, more complex ecosystem modelling is needed to improve our understanding of the directional change of the system upon climate change and the consequences for feedback processes.

5.4. Implication for mechanistic modelling and recommendations for further research

This review of mechanisms controlling *Phaeocystis* colony blooms in the global ocean suggests that a unique parameterisation could be derived for describing some processes while others seem to be more species- or site-related. For instance, it is possible to derive one unique temperature-dependent parameterisation that describes *Phaeocystis* cell (colonial and free-living) growth and photosynthesis. Photosynthesis rates still need to be measured for temperatures between 20 and 30 °C. An adaptation to high ambient light (the average daily PAR in the upper mixed layer) has been suggested for all colony forms. However the parameterisation linking E_k to ambient PAR (Fig. 4) derived from *P. globosa* and *P. antarctica* has still to be verified for *P. pouchetii*.

The maximum synthesis rates of the extracellular polysaccharides composing the *Phaeocystis* colony matrix show much variabilility. There is some suggestion that this light-dependent process is co-regulated by nitrate or iron availability although this has not yet been demonstrated. The role of nutrients (N, P, Fe) in colony matrix synthesis has thus to be properly assessed by running P-E experiments for the three colony species and under different conditions of nutrient limitation. Describing the mucus synthesis properly is of prime importance given the suspected role of the colony matrix as a reservoir for energy, PO_4 and Fe. Experiments showing the bioavailability of PO_4 and Fe linked to the colony matrix need to be designed.

In general, little information on nutrient uptake kinetics and stoichiometry is available for *Phaeocystis*. Filling this gap is particularly crucial for iron given that very large blooms of *P. antarctica* colonies, able to outcompete diatoms, have been reported in the HNLC waters of the Southern Ocean (Fig. 2b). Also of importance for nutrient parameterisation is the ability of colony forms to grow on organic phosphate which has still to be demonstrated for *P. pouchetii* and *P. antarctica* colonies.

Clearly, parameterisation of *Phaeocystis* colony grazing is site-specific and relies on the presence of overwintering large zooplankton. On the other hand, parameterisation of *Phaeocystis* colony losses would greatly benefit from an increased understanding of factors causing disruption of ungrazed colonies and their transformation in aggregates colonised by auto- and heterotrophic microorganisms.

There are also too few studies assessing the triggering factors of colony formation and disruption in spite of the importance of *Phaeocystis* colony blooms over the global ocean. Increased understanding of mechanisms controlling transition between the free-living and colony forms for all three blooming species would obviously improve parameterisation of *Phaeocystis* blooms at the scale of the global ocean.

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