

# The life cycle of *Phaeocystis*: state of knowledge and presumptive role in ecology

Véronique Rousseau ·  
Marie-Josèphe Chrétiennot-Dinet ·  
Anita Jacobsen · Peter Verity · Stuart Whipple

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**Abstract** Despite numerous investigations, the number and role of morphotypes involved in the life cycle of *Phaeocystis* species remain under debate. This is partly due to the application of different methodologies such as light, transmission, scanning electron microscopy and flow cytometry on specific samples. This heterogeneity of approaches results in the incomplete morphometric description of the different cell types existing within one species according to relevant criteria and the indetermination of the ploidy level of each observed stage. We review here the different morphotypes observed within each of the six *Phaeocystis* species recognized up to now. Four different cell types have been observed. In common to all six species is the occurrence of a

scaly flagellate producing star-forming filaments (all species except *P. jahnii*) or not (*P. globosa* and *P. jahnii*). In three colony-forming species, *P. globosa*, *P. pouchetii* and *P. antarctica*, three morphotypes are observed: a flagellate with scales and filaments, a colonial cell, and a flagellate devoid of scales and filaments. In the non-colony-forming species, *P. scrobiculata* and *P. cordata*, only flagellates with scales and filaments have been observed. While suspected in *P. pouchetii* and *P. antarctica*, a haploid–diploid life cycle has only been evidenced for *P. globosa*. The two main prominent features of this cycle are that sexuality is prevalent in colony bloom formation and termination and that two types of vegetative reproduction exist. The ecological relevance of alternating haploid and diploid stages is not clearly apparent on the basis of existing ecological studies.

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V. Rousseau (✉)  
Ecologie des Systèmes Aquatiques, ULB, CP 221,  
Boulevard du Triomphe, 1050 Brussels, Belgium  
e-mail: vrousso@ulb.ac.be

M.-J. Chrétiennot-Dinet  
Observatoire Biologique de Banyuls, UMR 7621,  
Lab. Arago, BP 44, 66651 Banyuls-sur-Mer, France

A. Jacobsen  
Department of Biology, University of Bergen,  
PO Box 7800, 5020 Bergen, Norway

P. Verity · S. Whipple  
Skidaway Institute of Oceanography,  
10 Ocean Science Circle, Savannah, GA, 31411, USA

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## Introduction

The genus *Phaeocystis* is a worldwide colony-blooming species that has a significant role in biogeochemical cycles (Schoemann et al. 2005) including the global sulphur cycle (Liss et al. 1994). Despite numerous investigations devoted

to its ecophysiology and the role and impact of colonies in ecosystem processes, knowledge of some major biological features of the genus is still limited. Such is the case for the *Phaeocystis* life cycle and its controlling mechanisms that, 50 years after Kornmann's (1955) classic paper, remain under debate. Problems of taxonomic confusion, lack of fine morphometric description of the different cell types within one species, and inadequacy of cell nomenclature have precluded a complete understanding of the *Phaeocystis* life cycle.

Since early description of the genus *Phaeocystis* by Lagerheim in 1893, the number of inclusive species has long been a matter of discussion (e.g. Kornmann 1955; Kashkin 1963; Parke et al. 1971; Sournia 1988; Medlin et al. 1994). This is mainly because the criteria used to distinguish *Phaeocystis* species were based on phenotypic characters such as the morphometry of the colonial stage, and/or physiological and biochemical properties (Jahnke and Baumann 1987; Baumann et al. 1994; Vaultot et al. 1994). Six species are now recognized based on small subunit (SSU) rDNA sequence analysis and morphological characterization. These are: *P. antarctica* Karsten, *P. globosa* Scherffel, *P. pouchetii* (Hariot) Lagerheim, *P. jahnii* Zingone, *P. scrobiculata* Moestrup and *P. cordata* Zingone et Chrétiennot-Dinet (Moestrup 1979; Medlin et al. 1994; Zingone et al. 1999; Edvardsen et al. 2000; Lange et al. 2002). Colonial forms have been reported for the first four species. It is now considered that probably more than six *Phaeocystis* species exist (Lange et al. 2002; Medlin and Zingone this issue).

Comparative descriptions of cell types existing within one species using morphometric criteria, i.e., presence/absence of body scales, flagella, haptonema and star-forming filaments, and ploidy levels have been made (e.g. Zingone et al. 1999; Peperzak et al. 2000a). However, a complete study of all morphotypes occurring within one species is still missing (Lancelot and Rousseau 2002). Our current knowledge of *Phaeocystis* cell types relies on composite independent investigations combining light (LM), transmission (TEM) and scanning electron microscopy (SEM) as well as flow cytometry. Each of these methodologies provides part of the information needed for a

complete identification of the morphotype. LM is useful for observations of cell shape, size, number, presence of flagella, and swimming activity. SEM and TEM with higher resolution and magnification are needed for morphological and ultrastructural details of the cell covering, appendages and organelles. Flow cytometry is required for determining the ploidy levels of each cell type. In addition, it is essential that sample preservation and fixation procedures be fully described because such procedures may lead to methodological biases. Use of fixatives can indeed cause cell shrinkage, loss of appendages (Peperzak et al. 2000a; Wassmann et al. 2005) or colony disintegration, releasing colonial cells into the medium, and therefore lead to possible misinterpretation (Wassmann et al. 2005). This mixed approach results in a confuse nomenclature of the various cell types, i.e. solitary flagellates and nonflagellates, free-living single cells, colonial flagellates, motile free-living cells, swimmers, zooids, microflagellates and microzoospores. These terms are often used loosely, and this can lead to misinterpretation of life cycle events.

The number and role of cell types involved in the life cycle of the six *Phaeocystis* species, and whether these are the same within each species, are still among the main questions not yet resolved (Lancelot and Rousseau 2002). Of particular interest is the identification of the stage persisting between two colony bloom events, as well as the nature of colony-forming cells. The persistence of *Phaeocystis* as a flagellate between two colony blooms has been suggested (Kornmann 1955; Parke et al. 1971; Veldhuis et al. 1986; Verity et al. 1988b), but the type of flagellate was never described from field observations due to its low cell density and possible confusion with other nanoplanktonic species. On the other hand, senescent colonies or aggregates have also been proposed as over-wintering forms of *P. globosa* (Cadée 1991). Still unknown are factors responsible for the transition between life stages. The ecological significance of the different life cycle stages, flagellates and colonies, has recently been discussed by Verity and Medlin (2003). Further investigation is however needed to discriminate between the different flagellates that have been identified within some species.

In this paper, we review and synthesize the available information gained from field and culture observations on the different morphotypes occurring within each of the six *Phaeocystis* species, focusing on cell morphology and ploidy level. We also present unpublished data on the morphology of *P. globosa* and *P. antarctica* cells. The role of the different morphotypes within the life cycle will be addressed based on field and culture observations on their occurrence. Finally, the ecological relevance of the free-living and colonial stages will be discussed based on knowledge of physiology and trophic significance of the various morphotypes. Because it is the best-known species, *P. globosa* will be used as a model.

### Morphotypes among *Phaeocystis* species

This section reviews the different cell types reported for the six *Phaeocystis* species which are considered here according to their revised taxonomic status as recommended by Baumann et al. (1994), Medlin et al. (1994) and Vaultot et al. (1994). This is particularly relevant for the species *globosa*, which has long been referred to as *pouchetii* in the previous literature (e.g., Parke et al. 1971; Kayser 1970; Admiraal and Venekamp 1986; Veldhuis et al. 1991; Davidson and Marchant 1992a). The seasonal distribution of the different cell types in the natural environment will also be considered in order to assess their role in the life cycle.

#### Morphotypes of *P. globosa*

A careful analysis of the literature published since the first description of *P. globosa* cells by Scherffel (1899, 1900) suggests that four morphotypes exist: diploid colonial cells, diploid flagellates, and two types of haploid flagellates.

#### Colonial cells

Colonial cells have 2–4 parietal chloroplasts, are deprived of body scales, haptonema, and flagella and are embedded in a mucilaginous matrix (Scherffel 1899; Kornmann 1955). They possess on their flagellar pole two short appendages, the

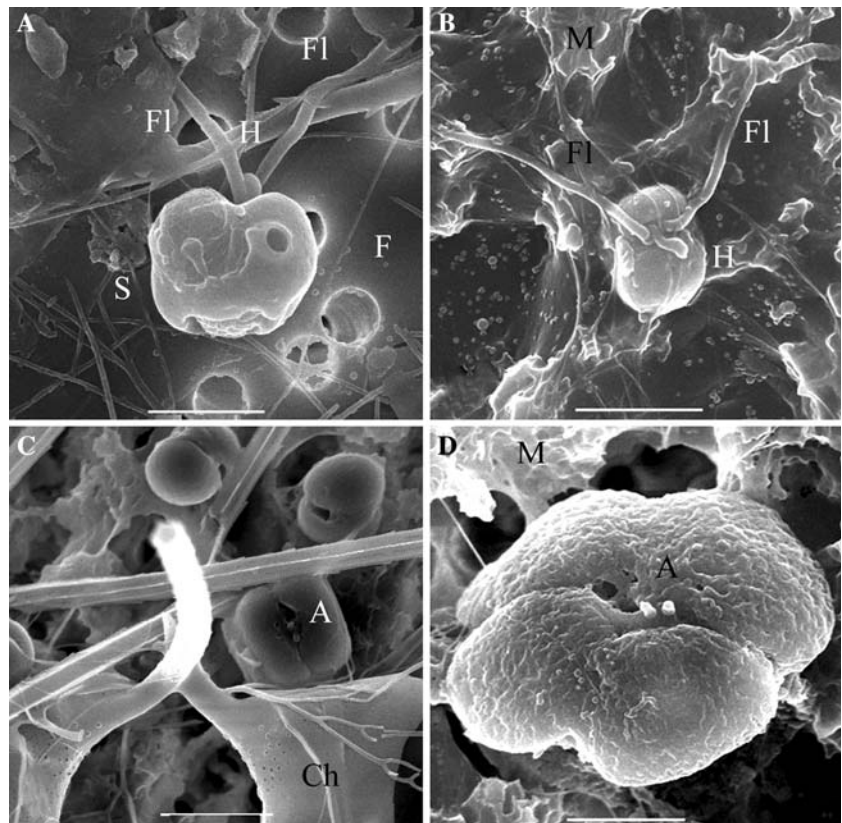
role and nature of which being presently unknown (Fig. 1; Rousseau et al. submitted). Reported size ranges for live colonial cells are 4.5–8.0  $\mu\text{m}$  (Kornmann 1955) and 5.8–10.4  $\mu\text{m}$  (Rousseau et al. submitted) while they are 5.6–8.3  $\mu\text{m}$  (Peperzak et al. 2000a) and 4.6–7.8  $\mu\text{m}$  (Rousseau et al. submitted) for Lugol and Lugol-glutaraldehyde fixed cells. These cells are diploid (Cariou et al. 1994; Vaultot et al. 1994). They are evenly distributed in the colony 15–20  $\mu\text{m}$  beneath a thin skin, and are weakly interconnected with dilute gel (Kornmann 1955; van Rijssel et al. 1997; Hamm et al. 1999). The colony skin is strong and semipermeable with pore size 1.0–4.4 nm in diameter, and presents plastic and elastic properties (Hamm et al. 1999). Diameter of colonies typically ranges from 10  $\mu\text{m}$  to 8–9 mm (Kornmann 1955; Jahnke and Baumann 1987; Rousseau et al. 1990), but may occasionally reach 20–30 mm (Kayser 1970; Gieskes and Kraay 1975; Chen et al. 2002). Colonies are originally spherical but deviate into nonspherical shapes when growing larger or when subjected to hydrodynamical stress (Kornmann 1955; Bätje and Michaelis 1986; Rousseau et al. 1994).

Non-motile free-living cells from colonial origin have also been reported in *P. globosa* cultures. These cells are morphologically similar to colonial cells: same size range, lack of flagella, haptonema (Kornmann 1955; Rousseau et al. 1990; 1994; Peperzak 1993; Peperzak et al. 2000a; Dutz and Koski 2006), body scales (Peperzak et al. 2000a), thread-like filaments and stars (Peperzak et al. 2000a; Dutz and Koski 2006) and were assumed to have the same ploidy level, i.e., diploidy (Peperzak et al. 2000a). On this basis, non-motile free-living and colonial cells should not be considered anymore as distinct morphotypes (Peperzak et al. 2000a; Dutz and Koski 2006).

#### Haploid flagellates

The fine structure of the flagellate stage of *P. globosa* was first described as *P. pouchetii* from TEM by Parke et al. (1971). These cells have been reported as swimmers (Scherffel 1900), microzoospores (Kornmann 1955), small and large zooids (Parke et al. 1971), microflagellates

**Fig. 1** SEM photographs of *P. globosa* cells observed in the Belgian coastal waters. Small-sized flagellates with stars and filaments but no scales observed (**A**) in February during the pre-bloom period; bar = 3  $\mu\text{m}$  and (**B**) in May still embedded within the colony mucus at the end of the colonial stage; bar = 2  $\mu\text{m}$ ; colonial cells with the typical short appendages observed (**C**) in the early stage of the bloom within *Chaetoceros* setae; bar = 4  $\mu\text{m}$  and (**D**) at the end of the bloom just before formation of haploid flagellates; bar = 2.4  $\mu\text{m}$ . H: haptonema; Fl: flagella; S: star; F: filament; M: mucus; A: short appendage; Ch: *Chaetoceros* cell“



(Veldhuis et al. 1986) and micro- and mesoflagellates (Peperzak et al. 2000a). They have a rounded shape, and are smaller than colonial cells, with a diameter of 3–5  $\mu\text{m}$  (Kornmann 1955); 3–6  $\mu\text{m}$  (Parke et al. 1971) and 3.6–5.8  $\mu\text{m}$  (Rousseau et al. submitted) for live cells observed under LM. Their small size has long been used for distinguishing them from other *P. globosa* cell types (e.g. Veldhuis et al. 1986) before Vaultot et al. (1994), using flow cytometry, demonstrated they were the haploid stage of *P. globosa*.

These flagellates are capable of rapid vegetative reproduction (Kornmann 1955; Parke et al. 1971; Rousseau et al. 1994; Vaultot et al. 1994) and swim very actively (Kornmann 1955; Parke et al. 1971). They possess two equal heterodynamic flagella, 10–15  $\mu\text{m}$  in length, and a short haptonema (3–4  $\mu\text{m}$ ) characterized by a distal swelling. They present an anterior depression and two golden-brown plastids (Parke et al. 1971). The cell body is covered by two types of organic scales showing a pattern of radiating ridges, visible on both sides (Parke et al. 1971;

Peperzak et al. 2000a). Two types of haploid flagellates were distinguished by Parke et al. (1971). One type, 3–6  $\mu\text{m}$  in size, possesses two superficial, bright vesicles located on the body surface (Parke et al. 1971). These vesicles release filaments, 20  $\mu\text{m}$  in length, 0.05  $\mu\text{m}$  in diameter, and made of alpha-chitin (Chrétiennot-Dinet et al. 1997), which form a highly characteristic pentagonal star (Parke et al. 1971). The function of these filaments is unknown. It has been hypothesized that they could act as anchors for attachment to solid structures before colony initiation (Chrétiennot-Dinet 1999), or alternatively have a role in defense against grazers (Peperzak et al. 2000a; Dutz and Koski 2006). The other haploid flagellate, 3–5  $\mu\text{m}$  in size, lacks the vesicles and filaments (Parke et al. 1971; Peperzak et al. 2000a). Such a difference in size and ability to produce filaments has also been observed in field samples for cells described as zoids (Manton and Leadbeater 1974 cited in Peperzak et al. 2000a) or meso- and microflagellates (Peperzak et al. 2000a).

These flagellates were observed in senescent cultures, swimming inside spherical colonies of various sizes, and were associated with colony disappearance (Kornmann 1955). In the natural environment and in mesocosms, large numbers of these flagellates were repeatedly reported, at the decline of *P. globosa* colony blooms, either inside spherical colonies (Scherffel 1899, 1900; Cadée 1991; Peperzak et al. 1998, 2000a), or released into the medium leaving ghost colonies or as free-living flagellates (Jones and Haq 1963; Admiraal and Venekamp 1986; Veldhuis et al. 1986; Verity et al. 1988b; Escaravage et al. 1995). These small-sized flagellates were observed invariably associated with the presence of chitinous filaments and stars, a feature specific to the haploid stage of *P. globosa* Scherffel (Vaulot et al. 1994; Zingone et al. 1999). Released from colonies at the end of the bloom, these flagellates were recorded at different periods of the year in the water column of the Channel and the Southern Bight of the North Sea, at cell densities varying from  $80 \times 10^3$  cells L<sup>-1</sup> to  $220 \times 10^3$  cells L<sup>-1</sup> (Fig. 1; Rousseau and Chrétiennot-Dinet, unpublished data). They apparently represent the life stage persisting between two blooms of colonial cells, as suggested by Kornmann (1955) and Parke et al. (1971).

#### Diploid flagellates

The third morphotype of *P. globosa* is a flagellate of the same size range as colonial cells when observed live, i.e., 4.5–8.0  $\mu\text{m}$  (Kornmann 1955), 6–7  $\mu\text{m}$  (Peperzak et al. 2000a) and 6.1–9.3  $\mu\text{m}$  (Rousseau et al. submitted) containing two flagella and one haptonema but lacking scales, filaments and stars (Rousseau et al. submitted). This flagellate has been reported as an asexual swarmer by Kornmann (1955), as a large flagellate by Cariou et al. (1994) and Rousseau et al. (1994), and as a macroflagellate by Peperzak et al. (2000a). It typically appears in cultures within 24 h when colonial cells are released mechanically from the colony (Kornmann 1955; Rousseau et al. 1990; Cariou et al. 1994). This flagellate is diploid as no ploidy change was found during the transformation of colonial cells into flagellates (Cariou et al. 1994; Rousseau et al. 1994).

These flagellates are able to rapidly form new colonies within a day after adhesion to a surface (Kornmann 1955; Kayser 1970; Cariou et al. 1994; Rousseau et al. 1994). Inanimate particles (Rousseau et al. 1994), walls of culture vessels (Kayser 1970; Cariou et al. 1994), and diatoms (Weisse et al. 1986; Boalch 1987; Rousseau et al. 1994) have been observed as adhesion sites. This property of attachment to surfaces, specific to this life stage, led to the assumption that a benthic stage, acting as an overwintering form, exists in the natural environment (Kayser 1970). It is not clear if this flagellate is able to mitotically divide. Its rapid transformation into a colony suggests it is short-lived (Kornmann 1955; Rousseau et al. 1994), but vegetative multiplication was also reported by Kayser (1970). The short lifespan of this morphotype could well explain why it is observed only occasionally in the field (Kornmann 1955; Peperzak et al. 2000a; Rousseau et al. submitted).

Such flagellates were occasionally observed inside colonies in cultures by Kornmann (1955) who considered them as a distinct cell types, the macrozoospores, and in the natural environment (Peperzak et al. 2000a).

#### Morphotypes of *P. pouchetii*

At the present time, two *P. pouchetii* cell types have been confirmed based on EM observations and cytometric analysis: a diploid colonial cell and a diploid flagellate (Jacobsen 2002). However, other reports suggest that a larger flagellate could exist within the *P. pouchetii* life cycle (Sukhanova and Flint 2001; Wassmann et al. 2005).

#### Colonial cells

Diploid colonial cells are in the size range of 5–7  $\mu\text{m}$ , have an anterior longitudinal groove and are deprived of filamentous appendages and scale coverings (Jacobsen 2002). Actively growing colonial cells are typically distributed in groups on lobes of cloud-like colonies (Jahnke and Baumann 1987; Gunkel 1988; Baumann et al. 1994; Rousseau et al. 1994; Jacobsen 2002). *Phaeocystis pouchetii* colonies, which are spherical up to 0.1 mm (Rousseau et al. 1994), have a maximum size

of 1.5–2 mm (Jahnke and Baumann 1987). They are characterized by a delicate mucus which disrupts easily compared to the solid mucilage of *P. globosa* (van Rijssel et al. 1997; Jacobsen 2002; Wassmann et al. 2005). Non-motile free-living cells morphologically similar to colonial cells, i.e., deprived of flagella, haptonema, filamentous appendages, scales, can be found together with the colony stage due to colony disruption (Eilertsen 1989; Jacobsen 2002; Wassmann et al. 2005).

### Flagellates

A filament-bearing flagellate has been described in detail by Jacobsen et al. (1996) and Jacobsen (2002) on the basis of LM and TEM observations. This flagellate, which originates from a colony when brought into culture, is round and has an average diameter of 5  $\mu\text{m}$  when live. It has two golden-brown parietal chloroplasts, two heterodynamic equally long (11  $\mu\text{m}$ ) flagella, and a short non-coiling haptonema (1.5  $\mu\text{m}$ ). The cell body is covered by two types of scales, both with radiating ridges visible on both surfaces. The filaments are coiled inside one or two superficial vesicles, and form five-ray stars when unwound. Contrary to the filament-producing cell of *P. globosa*, this flagellate was assumed to be diploid (Jacobsen 2002). This flagellate was observed during winter, increasing in abundance prior to colonial development, and has been thought to be the precursor of the colonial stage (Jacobsen 2002; Jacobsen and Veldhuis 2005). Such flagellates were observed inside colonies at the end of spring blooms, being subsequently released in the water column (Jacobsen 2002).

From LM observation of field samples, two types of flagellates were reported within the *P. pouchetii* life cycle based on size criteria, i.e., large (6  $\mu\text{m}$ ; Sukhanova and Flint 2001; Wassmann et al. 2005) and small heart-shaped (3–4  $\mu\text{m}$ ; Wassmann et al. 2005) cells. The large flagellates co-occurred with colonies and were abundant, sometimes being dominant over colonial cells in terms of cell density (Sukhanova and Flint 2001; Wassmann et al. 2005). The small flagellates were found free-living (Wassmann et al. 2005) or within decaying colonies before their disappearance (Lagerheim 1896; Wassmann

et al. 2005). They might well correspond to the flagellate described by Jacobsen (2002), with the size difference explained by cell shrinkage due to the use of Lugol-glutaraldehyde as sample fixative. Interestingly, small flagellate formation and their further release into the water column have been shown to originate from colonies assuming a spherical shape (Gunkel 1988; Whipple et al. this issue).

### Morphotypes of *P. antarctica*

Three morphotypes have been observed in *P. antarctica*: colonial cells and two types of flagellates. Two ploidy levels have been recorded.

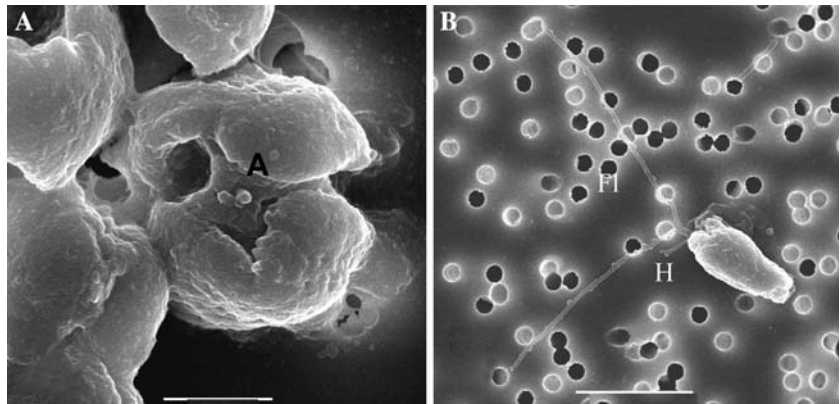
### Colonial cells

The colonial cell of *P. antarctica* has no flagella, no haptonema, no scales, and no vesicles or star-forming filaments (Davidson 1985). This cell has an anterior depression and two short appendages similar to those observed on *P. globosa* colonial cells (Fig. 2; Chrétiennot-Dinet and Rousseau, unpublished). The size range reported for colonial cells of *P. antarctica* is quite large, depending on preservation and fixation procedures. Size range includes: 10  $\mu\text{m}$  for live cells (Moestrup and Larsen 1992), and 3.2–7.9  $\mu\text{m}$  (Mathot et al. 2000), 4.7–5.6  $\mu\text{m}$  (Vaultot et al. 1994), 4–6  $\mu\text{m}$  (this study) for Lugol-glutaraldehyde fixed cells. Colonial cells of *P. antarctica*, assumed to be diploid (Vaultot et al. 1994), are evenly distributed along the periphery of colonies characterized by a solid mucus. Field *P. antarctica* colonies are typically spherical but can include numerous morphs with a maximum size of 9 mm (Baumann et al. 1994; Marchant and Thomsen 1994).

### Flagellates

One *P. antarctica* flagellate bears scales and produces filaments and stars; the other is devoid of scales, filaments and stars. The scale-bearing flagellate was described in detail by Davidson (1985): it has an anterior depression, two chloroplasts with a large central pyrenoid, and bears two flagella and an haptonema. Cell size ranges between 3.5  $\mu\text{m}$  and 7  $\mu\text{m}$  when fixed with

**Fig. 2** SEM photographs of *P. antarctica* (strain CCMP 1871): (A) Colonial cells with four plastids and the two short appendages typical of the colonial cell on the flagellar pole; bar = 2  $\mu\text{m}$ : (B) Flagellates co-occurring with colonies (diploid?) deprived of scales and filaments; bar = 6  $\mu\text{m}$ . H: haptonema; Fl: flagella; A: short appendage



glutaraldehyde and observed with TEM. The two flagella are equally long (6–10  $\mu\text{m}$ ). The haptonema presents a bulbous tip and is 1.5–2  $\mu\text{m}$  long. The body cell is covered by two types of scales with a pattern of radiating ridges visible on both sides. Thread-like material is regularly arranged within circular postero-lateral vesicles. When deployed, the threads have a length of 25  $\mu\text{m}$  and form a pentagonal star.

In the natural environment, such scale-bearing flagellates increase in number at the beginning of the colonial bloom, and decline during the bloom; they are present in large numbers after the bloom (Davidson and Marchant 1992b). Similar flagellates, that have a diameter of 5.2  $\mu\text{m}$  when fixed with glutaraldehyde, two flagella of 14.3  $\mu\text{m}$  in length, and filamentous appendages of 40  $\mu\text{m}$  in length forming a pentagonal star, were found at the ice edge of the Weddell Sea during the austral summer (Buck and Garrison 1983). Flagellates with thread-like material were observed in the Bransfield Strait region during post-bloom period (Kang and Lee 1995). On the other hand, an increase in the abundance of small-sized free-living flagellates (2.4–5.5  $\mu\text{m}$  when fixed with glutaraldehyde) was observed in the Ross Sea in early austral spring just before colony formation occurred (Mathot et al. 2000; Smith et al. 2003). Although no fine morphological description was provided, these small flagellates could well correspond to the flagellates described by Buck and Garrison (1983) and Davidson (1985), the size difference resulting from cell shrinkage and preparation for microscopic observations. Their relative abundance decreased to a minimum, while

colonial cells dominated in late spring before they were observed again inside colonies (Smith et al. 2003) or as free-living cells (Putt et al. 1994) at the end of the bloom.

The second *P. antarctica* flagellate type has the same size as the colonial cell, ranging from 6.5  $\mu\text{m}$  (Garrison and Thomsen 1993) to 7.5  $\mu\text{m}$  (Fryxell 1989). This flagellate bears two flagella and a haptonema but lacks scales, filaments and stars (Fig. 2, Garrison and Thomsen 1993; Marchant and Thomsen 1994; Chrétiennot-Dinet and Rousseau, unpublished). This flagellate was formed inside and released from spherical or elongated colonies at the ice edge during austral spring (Fryxell 1989; Garrison and Thomsen 1993; Marchant and Thomsen 1994). Some 5–6 h after formation, it was found attached to the spines and processes of large diatoms (Garrison and Thomsen 1993; Marchant and Thomsen 1994) where it subsequently formed new colonies (Fryxell 1989).

#### Morphotypes of *P. jahnii*

Two cell types have been described for *P. jahnii*: colonial cells and flagellates (Zingone et al. 1999).

#### Colonial cells

*Phaeocystis jahnii* colonial cells possess the two short appendages typical of *P. globosa* and *P. antarctica* colonial cells, have a size of 6–8.5  $\mu\text{m}$  when live and are irregularly distributed in loose, irregular colonies. Non-motile free-living cells of the same size have also been reported (Zingone et al. 1999).

**Table 1** Different morphotypes reported for the six *Phaeocystis* species recognized to date

	Flagellates with scales, threads and stars	Flagellates with scales	Flagellates without scales, threads and stars Same size range as colonial cells	Colonial cells
	<i>P. globosa</i> X (n)	X (n)	X (2n)	X (2n)
	<i>P. pouchetii</i> X (2n)	–	X	X(2n)
	<i>P. antarctica</i> X	–	X	X(2n)
Measured or assumed	<i>P. jahnii</i> –	X	–	X
ploidy levels are indicated	<i>P. cordata</i> X (n)	–	–	–
— not observed	<i>P. scrobiculata</i> X	–	–	–

### Flagellates

The *P. jahnii* flagellate is round, 3.5–5.0  $\mu\text{m}$  in diameter when observed live, and has two to four golden-brown parietal chloroplasts. It bears two unequally long flagella (8.5–12  $\mu\text{m}$  and 5.5–6.5  $\mu\text{m}$ ), a non-coiling haptonema 3.0–4.5  $\mu\text{m}$  in length, and two scale types (Zingone et al. 1999). Filaments were not observed.

### Morphotype of *P. cordata*

*Phaeocystis cordata* has only been described as a flagellated cell (Zingone et al. 1999). Live cells are 3–3.5  $\mu\text{m}$  long and 3–4  $\mu\text{m}$  wide. They have two unequally long flagella of 5.5–7.5  $\mu\text{m}$  and 4.5–6  $\mu\text{m}$  in length, and a non-coiling haptonema 2.2–2.5  $\mu\text{m}$  in length. They possess two scale types, both with faint radiating ridges. These cells produce filaments forming pentagonal figures.

### Morphotype of *P. scrobiculata*

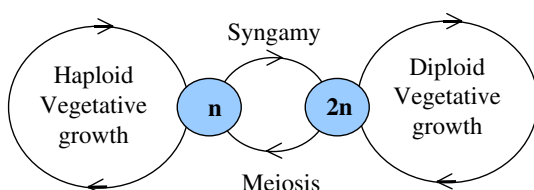
*Phaeocystis scrobiculata*, which has been observed occasionally in field samples and never in cultures, was only reported as a flagellate (Moestrup 1979; Hallegraeff 1983; Estep et al. 1984; Chrétiennot-Dinet unpublished data). The

cell, 8  $\mu\text{m}$  in length when fixed with osmium tetroxide, bears two equal flagella and a non-coiling haptonema. It is covered by a periplast of two types of scales, and produces filaments longer than 50  $\mu\text{m}$  which form a nine-ray figure rather than the five-ray star observed in the other *Phaeocystis* species (Moestrup 1979; Hallegraeff 1983). Large differences have been reported in the length of the flagella and haptonema, and in body scale sizes (Moestrup 1979; Hallegraeff 1983; Estep et al. 1984; Hoepffner and Haas 1990) depending on the preparation procedures.

### Synthesis of the observed morphotypes

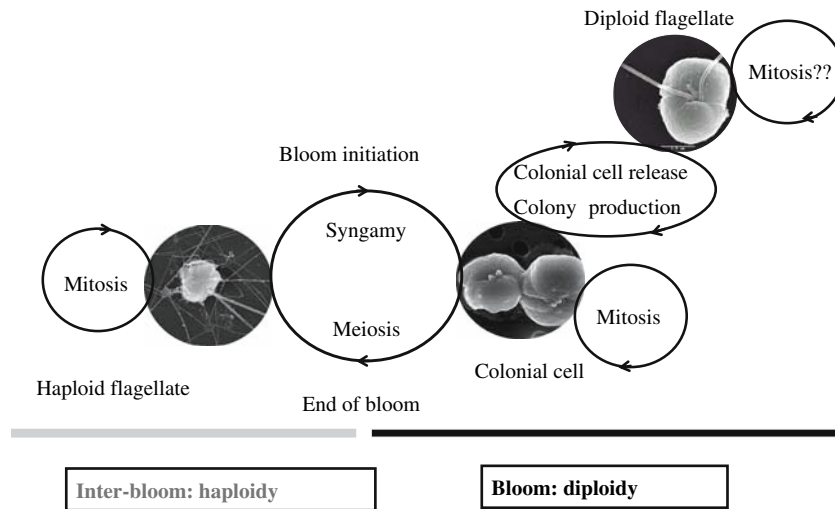
A careful examination of the literature suggests that four different cell types exist within *Phaeocystis* species (Table 1). In common to all six species, whether colonial or not, is the occurrence of scaly flagellates (Table 1) which are of two types. One produces star-forming filaments and has been reported for all species except *P. jahnii*. The other, deprived of filaments and stars, has been found in *P. globosa* (Parke et al. 1971; Peperzak et al. 2000a) and *P. jahnii* (Zingone et al. 1999). These two cell types are particularly important as they provide relevant taxonomic criteria to compare and distinguish the different species of the genus. These criteria include difference in size, structure and arrangement of scales and star-forming threads (Moestrup 1979; Moestrup and Larsen 1992; Baumann et al. 1994; Medlin et al. 1994; Zingone et al. 1999; Jacobsen 2002; Lange et al. 2002). These cells have been shown to be haploid in *P. globosa* (Vaulot et al. 1994) but diploid in *P. pouchetii* (Jacobsen 2002).

In common to three colony-forming species, *P. globosa*, *P. pouchetii* and *P. antarctica*, is the occurrence of three cell types: a flagellate with



**Fig. 3** Schematic representation of a haploid–diploid life cycle (from Valero et al. 1992)





**Fig. 4** The haploid–diploid life cycle of *P. globosa*. The haploid flagellates are characterized by stars, filaments, scales and have a size in the range 3.6–5.8  $\mu\text{m}$  when live. Colonial cells, in the size range 5.8–10.4  $\mu\text{m}$  when live, present two short appendages on their apical side, are deprived

scales and filaments, a colonial cell, and a flagellate devoid of scales and filaments (Table 1). The flagellates with scales and filaments have been observed to increase in number before colonial cell blooms, to disappear when colonial cells are present, and are massively formed inside colonies at the end of the colonial stage. The presence of larger flagellates is usually found restricted to that of colonial cells. In species that do not form colonies, *P. scrobiculata* and *P. cordata*, only flagellates with scales and filaments have been observed (Table 1).

### The *Phaeocystis* life cycle

The haploid–diploid life cycle of *P. globosa*

The existence of different morphotypes, two ploidy levels related to phase changes, and the ability of both haploid and diploid stages to divide mitotically (Kornmann 1955; Rousseau et al. 1994; Vaultot et al. 1994), support the existence of a haploid–diploid life cycle in *P. globosa*. In such life cycles, both haploid and diploid stages are related by sexual processes, meiosis and syngamy, and both are capable of mitotic division (Fig. 3;

of haptonema, stars, filaments and scales. Diploid flagellates, of the same size range than colonial cells, have two flagella, a haptonema and lack the stars, filaments and scales

Valero et al. 1992; Houdan et al. 2004). Based on available information from cultures and field studies presented in the previous section, the *P. globosa* haploid–diploid life cycle has been reconstructed (Fig. 4). The two main prominent features of this cycle are that sexuality is prevalent in colony bloom formation and termination, and that two types of vegetative reproduction exist.

### *Phaeocystis globosa* colony blooms result from sexual processes

The occurrence of haploid flagellates in the water column between two blooms of diploid colonial cells as observed in the southern North Sea (Rousseau and Chrétiennot-Dinet unpublished data) provides evidence that *P. globosa* colony bloom initiation and termination involve sexual processes, with the length of the diploid phase being restricted to the colony blooms. The formation of a diploid non-motile colonial cell from haploid flagellates implies that syngamy (fusion of the cytoplasm and nuclei of two haploids and subsequent zygote production) must occur at the time of colony bloom initiation. The observation of two morphologically distinguishable haploid flagellates (Parke et al. 1971; Peperzak et al.

2000a) suggests that anisogamy occurs in *P. globosa*, but this still awaits proof. Filaments characteristic of haploid flagellates could possibly play a role in mating. These structures have indeed been suggested to be related to sexuality (Vaulot et al. 1994) or to play a role in attachment (Chrétiennot-Dinet 1999). The inability to regenerate diploid colonial cells from clones of haploid flagellates (Parke et al. 1971; Vaulot et al. 1994) suggests that different mating types, i.e., compatible gametes able to form zygotes, exist within *P. globosa* (Vaulot et al. 1994). It is not known if homothallism (self-fertile colonies) or heterothallism (self-sterile colonies) is the rule in *P. globosa*.

Conversely, meiosis must happen to form haploid flagellates from diploid colonial cells. This may well occur during the massive production of haploid flagellates within colonies often reported at the end of the *P. globosa* bloom, before disappearance of the colonial stage (Rousseau et al. 1994; Peperzak et al. 2000a). Haploid flagellates are however produced in a restricted number of colonies. Most of them senesce and subsequently aggregate, being progressively invaded by various heterotrophic organisms that develop complex microbial networks (Lancelot and Rousseau 1994; Lancelot et al. 2002).

#### *Vegetative reproduction in P. globosa*

The vegetative reproduction of the diploid stage occurs through two distinct pathways involving colonial cells and diploid flagellates (Fig. 4). One consists of mitotic division of colonial cells within the colony, i.e., colony growth (Kornmann 1955; Rousseau et al. 1994; Veldhuis et al. 2005). This process can lead to colony division and budding as observed in mesocosms (Verity et al. 1988a) and in the field (Rousseau et al. 1994) but seems to be of minor importance. The second pathway involves the transition through short-lived diploid flagellates that are released from colonies and are able to reinitialize the colonial stage within a day (Kornmann 1955; Cariou et al. 1994; Rousseau et al. 1994). Diploid flagellates therefore co-occur with colonial cells and propagate the colonial stage, a pathway commonly used to produce colony cultures in the laboratory. However, its significance in the natural environment is highly

questionable and is probably reduced due to the short life span of diploid flagellates (Kornmann 1955; Cariou et al. 1994). The natural occurrence of diploid flagellates in the field is difficult to estimate. It results from disruption of large colonies when the sea is stormy and under turbulent conditions (Kornmann 1955, Peperzak et al. 2000a). Occurrence of these cells, in association with non-motile free-living cells, could however also result from sample manipulation during collection, size fractionation, and incubation. The minor role of the diploid flagellate in the natural environment is also suggested by the observation of massive and synchronous generation of small colonies in the early phase of blooms (Rousseau et al. 1990). A significant vegetative reproduction would instead result in more-continuous colony production. However, this pathway could not be excluded and has been suggested to provide the inoculum for colony blooms (Cadée 1991).

#### *Factors inducing phase changes within the P. globosa life cycle*

Several factors have been hypothesized to play a role in transitions between *P. globosa* morphotypes. The formation of colonies from free-living cells has been related to phosphate depletion (Veldhuis and Admiraal 1987; Cariou et al. 1994), light intensity (Kornmann 1955; Peperzak 1993; Peperzak et al. 1998), chemical substances produced by vernal diatoms, especially some *Chaetoceros* species (Weisse et al. 1986; Boalch 1987; Rousseau et al. 1994), and turbulence (Schapira 2005; Shapira et al. 2006). The requirement of a solid substrate for cell attachment has also been suggested from the observation of small colonies attached to *Chaetoceros* setae at the early stage of the bloom (Fig. 1; Boalch 1987; Rousseau et al. 1994; Chrétiennot-Dinet et al. 1997).

However, a careful examination of literature shows that most studies on *P. globosa* colony formation have been performed in laboratory cultures using the vegetative reproduction pathway, i.e., with an inoculum of diploid flagellates originating from colony disruption (Table 2). These studies show that solid substrate, turbulence, and phosphate are factors promoting the vegetative generation of colonies (Table 2). From field

**Table 2** Factors involved in the transition from free-living cell to colonial stage in *P. globosa*

References	Factors investigated	Exp. cond.	Free-living cell origin	Terms used and available cell characterization
Kornmann (1955)	Light	C	Natural seawater	Flagellates
Kayser (1970)	Solid substrate	C	Colonial cells released from colony disruption	Non-motile free-living cells
Boalch (1987)	Solid substrate Diatom exsudate	F	Natural pre-bloom populations	Motile stage, biflagellated cells
Veldhuis and Admiraal (1987)	Phosphate	C	Fractionation (<20 µm) of a culture (colony + cells)	Single cells Free-living motile cells (7 µm diameter)
Peperzak (1993)	Light	C	Fractionation (<20 µm) of culture (colony + cells) Clone Ph91	>100 W h m <sup>-2</sup> day <sup>-1</sup> : mesoflagellates (4.1 µm) < 100 W h m <sup>-2</sup> day <sup>-1</sup> : microflagellates (3.1 µm) Free-living cells
Rousseau et al. (1994)	Solid substrate	C	Colonial cells released from colony disruption	Non flagellated, flagellated cells, diploid cells
Cariou et al. (1994)	Phosphate Solid substrate	C	Colonial cells released from colony disruption	Flagellated and non-flagellated cells
Schapira (2005)	Turbulence	C	Fractionation (<5 µm) of culture (colony + cells)	

Experimental conditions are reported as C: cultures; F: field; M: mesocosms

observations, it appears that the vernal growth of diatoms and light level would play a key role in colony generation from haploid flagellates (Table 2). The role of light in colony formation from haploid flagellate cultures has been confirmed in laboratory studies (Kornmann 1955; Peperzak 1993). The formation of haploid flagellates in colonies at the end of a *P. globosa* bloom has been observed in mesocosms and related to nutrient depletion (Verity et al. 1988b; Escaravage et al. 1995) or rapid decrease in temperature (Verity et al. 1988b). Light limitation has also been suspected to play a role both in the laboratory and in the natural environment associated after sinking of healthy colonies in low ambient light conditions (Peperzak et al. 1988).

In future studies, the *P. globosa* life stage transition should be considered in terms of induction of sexual processes, i.e., syngamy and meiosis. The possible interplay of endogenous (biological clock) and environmental factors should be considered, as this has been shown relevant for other haptophytes such as coccolithophorids (Houdan et al. 2004). Some factors, in particular light, nutrient status, and production of gamone (pheromone for attraction, recognition of compatible cells and mating), should be investigated.

Knowledge of these factors coupled to high-resolution microscopy and flow cytometry techniques would allow observation of such short-lived processes as syngamy and meiosis in cultures and in the field.

#### The life cycle of the other *Phaeocystis* species

The existence of a haploid–diploid life cycle is well supported for *P. globosa*. Such haploid–diploid life cycles could also possibly exist within the three other *Phaeocystis* colonial species, as already hypothesized for *P. pouchetii* (Eilertsen 1989; Jacobsen 2002) and *P. antarctica* (Medlin and Zingone this issue). Besides two ploidy levels, similar events to those occurring in the *P. globosa* life cycle were indeed observed in the bloom dynamics of these two species. Filament-bearing scaly flagellates, thought to be colony precursors (Jacobsen 2002), were observed to increase in abundance before *P. pouchetii* colony development. These cells and young colonies with 2–40 cells were later found attached to diatoms (mostly *Chaetoceros* spp; Eilertsen 1989; Sukhanova and Flint 2001; Jacobsen 2002), suggesting that diatoms could be a key factor for colony initiation. At the end of the colonial stage, small-sized

flagellates assumed to be scaly flagellates, are massively produced intracolony or are found free-living (Wassmann et al. 2005). In the same way, small flagellates of *P. antarctica* were shown to be mostly present before and at the end of colony blooms (Putt et al. 1994; Smith et al. 2003).

Some intraspecific differences may exist however in the significance of the vegetative pathway for colony production and the occurrence of large solitary cells. As only one ploidy level (diploidy) has been identified up to now (Jacobsen, 2002), the vegetative pathway of colony formation, either for bloom initiation and propagation, seems to be predominant in *P. pouchetii*. Colony propagation from cells released from colonies could be particularly important. In northern studies, the contribution of colonies and flagellates was indeed shown to be highly variable depending on the site and the year investigated (Wassmann et al. 2005). Although sample preservation and handling procedures could strongly affect the observed proportion of free-living and colonial cells due to colony disintegration, large flagellates of *P. pouchetii* can at times exceed the abundance of colonial cells (Wassmann et al. 2005). Such high number of flagellates may reflect the more delicate nature of the *P. pouchetii* colony matrix compared to that of *P. globosa*, allowing easier colony disruption and subsequent vegetative reproduction. In addition, colony budding might be an important process for *P. pouchetii* colony proliferation and bloom development (Whipple et al. 2005).

The observation of only one morphotype in *P. scrobiculata* and *P. cordata* suggests either that the whole cycle has not been yet observed, or these species lose the ability to form colonies. The assumption of Vaultot et al. (1994) that filaments forming five- or nine-rayed stars are associated with haploid cells suggests that *Phaeocystis* would occur as haploid flagellates in oceanic and oligotrophic environments.

#### The haploid–diploid life cycle of Prymnesiophytes

With morphologically different types of flagellates and one non-motile cell type, *P. globosa* shares the features of most Haptophytes (except the

Pavlovophyceae), i.e., a life cycle involving alternation of morphologically different haploid and diploid generations, each capable of independent asexual reproduction (Billard 1994; Edvardsen 2002; Billard and Inouye 2004; Houdan et al. 2004). Houdan et al. (2004) suggest from the phylogenetic distribution that this is the primitive state across the Prymnesiophyceae.

These haploid and diploid phases present typically distinct patterns of scale ornamentation characteristic of each ploidy stage. The morphological difference between life stages may be minor, as is the case for *Chrysochromulina polylophus* (Paasche et al. 1990; Edvardsen and Paasche 1992; Edvardsen and Vaultot 1996) and *Prymnesium parvum/patelliferum* (Larsen and Edvardsen 1998; Larsen 1999), in which the two motile cell types are distinguished only by minor details in body scale morphology. Heteromorphic life stages of coccolithophores are more clearly differentiated and show remarkable diversity (Billard and Inouye 2004) alternating diploid heterococcolithophores and, depending on the family, five different types of haploid stages (noncalcifying motile stage, holococcoliths, aragonitic coccoliths, nannoliths and noncalcifying benthic stages; Billard and Inouye 2004). Observation of syngamy and meiosis, providing direct evidence for the existence of sexuality is, however, restricted to very few coccolithophorids species such as *Pleurochrysis pseudoroscoffensis* (Gayral and Fresnel 1983) and more recently *Coccolithus pelagicus* (Houdan et al. 2004).

#### The ecological relevance of the haploid–diploid life cycle of *P. globosa*

The advantage of haploid–diploid life cycles

Haploid–diploid life cycles are widespread among diverse sexual eukaryotic organisms such as red algae, most brown algae, many green algae, some fungi, foraminiferans, mosses, and ferns. This suggests that such life cycles result from an adaptive evolution providing selective advantages to organisms (Valero et al. 1992; Mable and Otto 1998). Based on theoretical and empirical considerations, haploid–diploid life cycles have been

shown to combine advantages from sexual reproduction and those from being haploid and diploid (Kondrashov and Crow 1991; Mable and Otto 1998). The advantage of sexual reproduction is a homogenizing effect on the species gene pool, resulting in high genetic plasticity. Because there are two copies of each gene, diploidy masks deleterious recessive mutations within the genome but harbors twice as many genes capable of beneficial mutations. The larger pool of mutant alleles provides a source of genetic variability that allows a higher rate of adaptation to a changing environment (Mable and Otto 1998). By contrast, haploids express each mutation within their genome. Deleterious mutations are more efficiently eliminated and haploid populations tend to carry fewer mutations (Mable and Otto 1998).

At the ecological level, the diploid stage has been suggested to represent a *r*-selected strategy with high growth rates, use of inorganic nutrients, and resistance to turbulence, while the haploid stage would have a *K*-selected strategy, being better adapted to nutrient-limited conditions with low growth rates, motility and mixotrophy (Valero et al. 1992). The nutritional advantage of haploid over diploid cells under nutrient-limited conditions is due to their smaller size (Lewis 1985). Surface-to-volume ratios calculated for two cells of 4  $\mu\text{m}$  and 8  $\mu\text{m}$  in diameter, typical of live haploid and colonial cells of *P. globosa*, respectively, vary from 1.5 to 0.75 respectively. This suggests that haploid cells increase by a factor two their morphological potential to acquire nutrients when they are present at low concentrations. In addition, haploid cells may also halve the energetic cost of DNA replication during cell division (Lewis 1985). Maintenance of a haploid–diploid heteromorphic life cycle is generally considered as an evolutionary adaptation to an environment that is seasonally variable or contains two different niches (Stebbins and Hill 1980 cited in Valero et al. 1992).

#### The ecology of *P. globosa* morphotypes

Many tentative hypotheses have been proposed to understand the dominance, alternation and succession of *P. globosa* life forms, i.e., nanoplanktonic cells and large gelatinous colonies

(Lancelot and Rousseau 1994; Lancelot et al. 2002; Verity and Medlin 2003). In general, these studies conclude an advantageous status accrues to the colonial stage over free-living cells due to higher growth characteristics and resistance to losses.

The success of *P. globosa* colonies during blooms has been related to the peculiar physiology and ecology of the gelatinous colonies (Lancelot and Rousseau 1994; Lancelot et al. 2002). The colony matrix was shown to act as an energy (Lancelot and Mathot 1985; Veldhuis and Admiraal 1985; Lancelot and Rousseau 1994) and nutrient (Fe and Mn; Schoemann et al. 2001) reservoir. This provides a competitive advantage to *P. globosa* colonies when resources are limiting (Lancelot and Rousseau 1994; Lancelot et al. 2002), and when nitrate is the nitrogen source (Lancelot et al. 1998), allowing higher growth rates than free-living cells (Peperzak et al. 2000b; Veldhuis et al. 2005). On the other hand, some advantages of being a free-living cell are related to a greater ability to compete under ammonium- and phosphate-limited conditions (Veldhuis et al. 1991; Riegman et al. 1992), reduced nutrient uptake (Ploug et al. 1999), and alternative nutritional modes such as phagotrophy (Verity and Medlin 2003).

Large *P. globosa* colonies are generally not, or insignificantly, grazed by mesozooplankton, in particular the small neritic copepods (Hansen and van Boekel 1991, Hansen et al. 1993; Gasparini et al. 2000; Verity 2000; Koski et al. 2005). This has been related to a prey-predator size mismatch, chemical deterrence, physical inhibition and/or other growth-state-related mechanisms (Verity 2000; Turner et al. 2002; Dutz et al. 2005; Long and Hay 2006). The presence of grazers has been shown to induce colony size increase (Jakobsen and Tang 2002) through the release of infochemicals (Tang 2003). The colonial skin also provides a protection to colonial cells from fast growing grazers, virus and pathogen infection, and bacterial colonization (Hamm 2000). In mesocosms, the resistance of *P. globosa* colonies to viral infection has been demonstrated, while free-living cells undergo severe infection and mortality (Brussaard et al. 2005). Besides the physical barrier of the colonial skin, some antimicrobial

effects might also be due to the high acrylate accumulation inside the *P. globosa* matrix (Noordkamp et al. 2000). Contrary to the colonial form, *P. globosa* free-living cells may be heavily grazed by at least some microzooplankton and some stages of mesozooplankton (Admiraal and Venekamp 1986; Verity and Smayda 1989; Weisse and Scheffel-Möser 1990b; Weisse et al. 1994; Verity 2000; Tang et al. 2001; Turner et al. 2002). However, as recently shown by Long and Hay (2006), the grazing response for different copepods may vary more between different growth states of *P. globosa*, than compared to other prey types. Thus, further studies are needed to quantify the importance of different zooplankton grazing on this species.

A review of the *P. globosa* free-living cells used in physiology, grazing, and lysis experiments in field and laboratory studies shows that the morphological characterization of the cells, referred mostly as solitary, single or free-living cells, is very poor (Table 3). A careful analysis of culture and sampling procedures suggests that *P. globosa* free-living cells are either colonial (non-motile free-living cells) or diploid flagellates co-occurring with the colonial stage. Field studies were indeed mostly performed during the spring bloom, i.e. when diploid flagellates and colonial cells released from colonies are present (Table 3). In laboratory experiments, free-living cells were often separated from colonies using size fractionation or the vegetative pathway involving colony formation from diploid cells (Table 3). In a recent study, Dutz and Koski (2006) demonstrated that grazing losses and trophic transfer efficiency are highly dependent on the *P. globosa* morphotypes used. The sensitivity of flagellates bearing threads and forming stars, i.e., the haploid flagellates to protozooplankton grazing has been shown lower than that of colonial cells lacking the filamentous appendages (Dutz and Koski 2006). However, the evaluation of grazing pressure on the different *Phaeocystis* life forms is a complex issue that has been critically reviewed (Nejstgaard et al., this issue).

Based on the literature analysis, there is presently no experimental evidence to demonstrate a different bottom-up growth control for the *P. globosa* morphotypes. However, there is

some evidence that haploid and diploid morphotypes belong to different trophic groups. Haploid flagellates are indeed inedible autotrophic nanoplankton while diploid flagellates and free-living colonial cells are preyed by microzooplankton.

## Conclusions

Knowledge of the life stages of the different *Phaeocystis* species is still incomplete and is very variable. The identification of all life stages, through morphological characterization and determination of ploidy levels, are still missing for most of *Phaeocystis* species. Complete understanding of the life cycle events requires combining flow cytometry, electron microscopy, genetic techniques, and light microscopy on the same material, in either field samples or cultured strains. To avoid confusion, standardized nomenclature should be developed to refer to different morphotypes within different species. This should be done by scientist groups analyzing together the same material but containing different species, using both sophisticated and routine techniques. While suspected in *P. pouchetii* and *P. antarctica*, a haploid–diploid life cycle has only been confirmed for *P. globosa*. Further research is however needed to substantiate this life cycle, by direct observation of short-lived syngamy and meiosis, the characterisation of the mating system and capability (isogamy versus anisogamy, homothallism versus heterothallism), and the knowledge of the factors inducing sexuality. The study of genetic regulation of sexual processes will be an important step in the characterization of life cycles (Guillou and Biegala 2002).

At this stage, comparative studies of the autoecology and grazing sensitivity of *Phaeocystis* haploid and diploid cells are insufficient to demonstrate an ecological differentiation between stages and to provide support for ecological niche separation. 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 pure cultures of haploid and diploid stages combined with cell characterization (morphology and ploidy).

**Table 3** Types of *P. globosa* free-living cells used in physiology, grazing and viral lysis experiments

References	Experiments	Exp. cond.	Free-living cells origin	Terms used and available cell characterization
<i>Growth regulation</i>				
Veldhuis and Admiraal (1987)	Phosphorus metabolism	C	Fractionation (<20 µm) of a culture (colonies + cells)	Single cells (7 µm diameter)
Weisse and Sheffel-Möser (1990)	Growth rates	F	Zooplankton net fractionation (<200 µm) of natural populations during the bloom	Single cells (5.3 µm; 9.5 pgC cell <sup>-1</sup> )
Van Boekel and Veldhuis, (1990)	Phosphatase activity	C	Fractionation (<20 µm) of culture (colonies + cells)	Single cells
Lancelot et al. (1991)	Growth rates	C	Fractionation (<20 µm) of culture (colonies + cells) and natural populations during the bloom	Free-living cells/Solitary cells
Veldhuis et al. (1991)	Photosynthesis	F	Fractionation (<20 µm) of a culture (colonies + cells)	Single cells
Veldhuis et al. (1991)	Phosphorus uptake	C	Fractionation (<20 µm) of a culture (colonies + cells)	Free-living motile cells (7 µm diameter)
Riegman et al. (1992)	Nutrient competition	C	Isolated from field as a colony	Non-motile free-living vegetative cells
Peperzak et al. (2000b)	Growth rates	C	Culture of 2 types of solitary cells (Clone Ph91)	Non colonial flagellate cell types
Veldhuis et al. (2005)	Growth rates	M	Culture (colonies + flagellates)	Diploid solitary non-flagellate cells (6.1 µm)
Veldhuis et al. (2005)	Growth rates	F	Natural populations	Haploid flagellates (4.2 µm)
<i>Grazing and lysis experiments</i>				
Admiraal and Venekamp (1986)	Grazing	F	Removal of colonies from natural populations during the bloom	Single cells slightly smaller than colonial cells
Verity and Smayda (1989)	Grazing	C	Frequent transfers of solitary cells into f/2 medium	Remaining single cells
Claustre et al. (1990)	Grazing	F	Filtration (<22 µm) of natural populations during the bloom	Solitary cells (3–5 µm; 20 pgC cell <sup>-1</sup> )
Weisse and Sheffel-Möser (1990)	Grazing	F	Zooplankton net fractionation (<200 µm) of natural populations during the bloom	Free-living cells
Hansen et al. (1993)	Grazing	C	Culture without colony formation	Single cells (5.3 µm; 9.5 pgC cell <sup>-1</sup> )
Verity (2000)	Grazing	C	Fractionation (<20 µm) of culture (colonies + cells)	Single cells or Flagellates
Tang et al. (2001)	Grazing	C	Gravity filtration (<11 µm) of culture (colonies + cells) of strain CCMP 1528	Solitary cells
Jakobsen and Tang (2002)	Grazing	C	Gravity filtration (<11 µm) of culture (colonies + cells) of strain CCMP 1528	Single cells (4.4 µm; 9.3 pgC cell <sup>-1</sup> )
Turner et al. (2002)	Grazing	C	Cell-dominated mixed culture (colonies + cells)	Solitary cells
Tang (2003)	Grazing	C	Gravity filtration (<11 µm) of culture (colonies + cells) of strain CCMP 1528	Solitary cells
Koski et al. (2005)	Grazing	M	Cultured populations (colonies + cells)	Solitary cells (5–6 µm length)
Brussaard et al. (2005)	Viral infection	M	Cultured populations (colonies + cells) inoculated from a culture of colonies and flagellated cells	Solitary cells
Dutz and Koski (2006)	Grazing	C	5 strains from Southern North Sea	Single cells Single cells/Solitary cells—no distinction between flagellates and non-flagellates; correspond to the largest cell types (Brussaard, pers. comm) Three flagellates with threads and stars (3.6–4.2 µm; haploid) Two solitary non flagellate (5.6–5.7 µm; colonial cells)

Experimental conditions are reported as C: cultures; F: field; M: mesocosms

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