

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

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Received: 9 March 2006 / Accepted: 19 May 2006 / Published online: 13 April 2007
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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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Keywords Ecological niche · Haploid–diploid · Life cycle stages · Morphotype · *Phaeocystis* species · Sexual processes

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.