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Dynamics in carbohydrate composition of *Phaeocystis pouchetii* colonies during spring blooms in mesocosms

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Abstract

The colony-forming microalgae *Phaeocystis* produces two major pools of carbohydrates: mucopolysaccharides in the colony matrix and intracellular storage glucan. Both have different functions and separate degradation pathways in the ecosystem, so a partial precipitation method was developed to distinguish the dynamics of the two pools. Changes in concentration in response to variation in nutrients and irradiance were followed during a spring bloom of *Phaeocystis pouchetii* colonies in mesocosms near Bergen, Norway. Upon nutrient limitation, the carbohydrate to carbon ratio of the colonies increased from 15% during the growth phase, to more than 50% during the decline phase. During the growth phase of the bloom, the carbohydrate concentration and composition were influenced by irradiance: glucan concentrations showed strong diel dynamics and increased with higher light levels, whereas mucopolysaccharide concentrations were unaffected. During the exponential growth phase, glucan contributed 6–11% to *P. pouchetii* carbon, depending on the time of the day. During the decline of the bloom, the glucan contribution increased up to 60%. We provide further evidence for the concept that the *Phaeocystis* colony matrix is built with a relatively small but constant amount of carbohydrates, compared to the large quantities of glucan produced during *Phaeocystis* spring blooms. Since a major part of *Phaeocystis* primary production is recycled in the water column by bacteria, this vast glucan injection is a potential determinant of the magnitude and composition of the microbial community following a bloom.

Keywords: Algae; Polysaccharides; Mucus; Glucan; Laminarin; Diel

1. Introduction

Phaeocystis (Prymnesiophyceae), a microalgal genus with a world-wide distribution, is known for its massive blooms in coastal seas and in Arctic and Antarctic waters (Lancelot et al., 1987; Baumann et al., 1994; Mathot et al., 2000). During blooms most of the cells are present in a colonial life stage during which they are embedded in a transparent mucous matrix consisting of extracellular polymers, forming hollow spheres with an aqueous lumen (Van Rijssel et al., 1997). In North Sea coastal regions *Phaeocystis* blooms occur mainly in spring and are important in determining the flow of energy, carbon and nutrients in

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the ecosystem; *Phaeocystis* may contribute up to 90% of the total phytoplankton cell numbers (Joiris et al., 1982; Lancelot, 1984; Lancelot et al., 1987; Brussaard et al., 1996) and 65% of the local annual primary production (Joiris et al., 1982).

Carbohydrates contribute significantly (up to 90%) to the organic matter of *Phaeocystis* (Rousseau et al., 1990; Fernandez et al., 1992), with polysaccharides accounting for the bulk of the algal carbohydrates. Two major pools of polysaccharides in *Phaeocystis* are extracellular mucopolysaccharides, which are the main component of the mucous matrix of the colonies, and intracellular storage polysaccharides. Besides their different functions, these pools have separate degradation pathways in the ecosystem.

The colony matrix is generally not heavily colonised by bacteria during the growth phase of a bloom, but mucopolysaccharides can be degraded readily by bacteria (Janse et al., 1999). During senescence of a bloom, the colony matrix serves as the site of bacterial growth and remineralisation (Putt et al., 1994; Becquevort et al., 1998), indicating its importance in cycling of biogenic matter in the microbial loop. The mucopolysaccharides are large polysaccharides, consisting of at least nine different monosaccharides (Janse et al., 1996a). Given their nature, they may contribute to formation of transparent exopolymer particles (TEP) (Alldredge et al., 1993). Indeed, studies have shown that dissolved mucopolysaccharides formed TEP that either sediment (Riebesell et al., 1995) or act as a glue, sticking together other materials present during a bloom and thus enhancing their contribution to a vertical flux (Passow and Wassmann, 1994).

Besides a structural function in the mucous matrix, mucopolysaccharides were also reported to serve as storage polysaccharides (Lancelot and Mathot, 1985; Veldhuis and Admiraal, 1985). The principal storage polysaccharide in *Phaeocystis,* however, is an intracellular β-1,3-glucan with some branching at position 6, with an average size of 3.6 kDa, classified as chrysolaminaran (Janse et al., 1996b). It is produced in the light and consumed in the dark, when it is apparently used as a respiratory substrate. Beta-1,3-glucan is recognised to be the most abundant type of storage carbohydrate in marine phytoplankton (e.g. diatoms) and in various macroalgae (Painter, 1983). It can be degraded rapidly by bacteria in the water column as well as in the sediment (Arnosti, 2000; Keith and Arnosti, 2001).

The contribution of storage glucans to the total biomass of algae largely depends on growth conditions, nutrient status of the cells and light intensity. In the diatom *Chaeotoceros affinis*, cellular glucan content accumulated markedly under nutrient deficiency (Myklestad and Haug, 1972; Myklestad, 1974). Also, in *Phaeocystis* colonies an increase in the ratio of total carbohydrate to carbon was reported when nutrient limitation occurred in batch cultures (Van Rijssel et al., 2000) and at the end of a spring bloom (Lancelot, 1984; Fernandez et al., 1992). In addition, carbohydrates oscillate in response to light variations over a diel cycle. In general, when nutrients are not limiting, and irradiance is sufficient to sustain high photosynthetic rates that exceed metabolic demands, glucan accumulates during the day. During the night, it can be respired as an energy supply to maintain cell metabolism and carbon for protein synthesis (Cuhel et al., 1984; Lancelot and Mathot, 1985; Granum et al., 2002).

If we wish to understand the growth of *Phaeocystis* and follow its carbon fluxes, it is important to differentiate between glucan and mucopolysaccharides and investigate the factors influencing their production. It is, however, difficult to separate *Phaeocystis* cells from the matrix, because *Phaeocystis* cells are very fragile and easily disrupted during filtration by commonly used methods. In this way, water soluble components such as glucan are released (Veldhuis and Admiraal, 1985; Van Rijssel et al., 1997; Mathot et al., 2000). Accordingly, there is considerable variation in the reported fraction of total carbon in *Phaeocystis* used to build the mucous matrix, ranging from 5 to 90% (Rousseau et al., 1990; Van Rijssel et al., 1997; Mathot et al., 2000). Measurements of the incorporation of labelled bicarbonate yielded estimates of 18–60% (Lancelot, 1984) and microscopic observations led to an estimate of up to 90% (Rousseau et al., 1990). More recent studies that did not use filtration methods, found 5–33% for field populations by using the relationship between colony size and carbon measurements (Mathot et al., 2000), or colony size, carbon and carbohydrate measurements (Van Rijssel et al., 1997). Because this approach assumes fixed contributions of cell carbon and matrix carbon, it does not allow analysis of dynamics of carbohydrate pools. In the present study we have developed a partial precipitation method to separate mucopolysaccharides from glucan, enabling us to circumvent problematic methods of separating cells from mucous matrix. This has allowed us to measure the dynamics of both pools during a bloom. To exclude the effect of sampling diverse water masses with a different bloom history, a spring bloom of *Phaeocystis pouchetii* was studied in mesocosms. In addition, short-term dynamics in response to variations in irradiance over diel cycles and in the water column were quanti-