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REVIEW

The carbohydrates of *Phaeocystis* and their degradation in the microbial food web

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Abstract The ubiquity and high productivity associated with blooms of colonial *Phaeocystis* makes it an important contributor to the global carbon cycle. During blooms organic matter that is rich in carbohydrates is produced. We distinguish five different pools of carbohydrates produced by *Phaeocystis*. Like all plants and algal cells, both solitary and colonial cells produce (1) structural carbohydrates, (hetero) polysaccharides that are mainly part of the cell wall, (2) mono- and oligosaccharides, which are present as intermediates in the synthesis and catabolism of cell components, and (3) intracellular storage glucan. Colonial cells of *Phaeocystis* excrete (4) mucopolysaccharides, heteropolysaccharides that are the main constituent of the mucous colony matrix and (5) dissolved organic matter (DOM) rich in carbohydrates, which is mainly excreted by colonial cells. In this review the characteristics of these pools are discussed and quantitative data are summarized. During the exponential growth phase, the ratio of carbohydrate-carbon (C) to particulate organic carbon (POC) is approximately 0.1. When nutrients are limited, *Phaeocystis* blooms reach a stationary growth phase, during which excess energy is stored as carbohydrates. This so-called overflow metabolism increases the ratio of carbohydrate-C to POC to 0.4–0.6 during the stationary phase, leading to an increase in the C/N and C/P ratios of *Phaeocystis* organic matter. Overflow metabolism can be channeled towards both glucan and mucopolysaccharides. Summarizing the available data reveals that during the stationary phase of a bloom glucan contributes 0–51% to POC, whereas mucopolysaccharides contribute 5–60%. At the end of a bloom, lysis of *Phaeocystis* cells and deterioration of colonies leads to a massive release of DOM rich in glucan and mucopolysaccharides. Laboratory studies have revealed that this organic matter is potentially readily degradable by heterotrophic bacteria. However, observations in the field of accumulation of DOM and foam indicate that microbial degradation is hampered. The high C/N and C/P ratios of *Phaeocystis* organic matter may lead to nutrient limitation of microbial degradation, thereby prolonging degradation times. Over time polysaccharides tend to self-assemble into hydrogels. This may have a profound effect on carbon cycling, since hydrogels provide a vehicle to move DOM up the size spectrum to sizes subject to sedimentation. In

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addition, it changes the physical nature and microscale structure of the organic matter encountered by bacteria which may affect the degradation potential of the *Phaeocystis* organic matter.

Keywords Carbohydrates · Glucan · Hydrogels · Mucilage · *Phaeocystis* · TEP

Introduction

Phaeocystis (Prymnesiophyceae) is a marine phytoplankton genus with a worldwide distribution. It is present from tropical to polar regions and can form blooms in areas with high nutrient concentrations, such as coastal or upwelling regions (Baumann et al. 1994; Lancelot et al. 1998; Schoemann et al. 2005). One of the characteristics of *Phaeocystis* species is the complex polymorphic life cycle. It consists of different stages of free-living cells 3–9 μm in diameter, alternating with colonial stages usually reaching several mm in diameter (Kornmann 1955; Rousseau et al. 1994; Peperzak et al. 2000), sometimes up to 3 cm (Chen et al. 2002). Although free-living *Phaeocystis* cells are ubiquitous in the world's oceans, it is the colonial form that has attracted most attention due to its massive blooms (Lancelot et al. 1987; Schoemann et al. 2005). At present six *Phaeocystis* species have been described (Zingone et al. 1999) of which only three are reported to form blooms; *P. globosa* in temperate regions (English Channel, coastal North Sea, China), *P. pouchetii* in temperate to polar waters of the Northern hemisphere, and *P. antarctica* in (sub)polar waters of the southern hemisphere (Schoemann et al. 2005). During blooms *Phaeocystis* may contribute over 90% to the total phytoplankton abundance and can be responsible for up to 65% of the local annual primary production (Joiris et al. 1982; Veldhuis et al. 1986b; Lancelot and Mathot 1987; Arrigo et al. 1999). The high productivity associated with blooms and its ubiquity make *Phaeocystis* an important contributor to the global carbon cycle (Smith et al. 1991; Arrigo et al. 1999; DiTullio et al. 2000; Schoemann et al. 2005). A significant part of the *Phaeocystis* carbon consists of carbohydrates (Lancelot and Mathot 1987; Rousseau et al. 1990; Fernández et al. 1992; Mathot et al. 2000). This vast carbohydrate injection following *Phaeocystis* blooms has a significant impact on the carbon cycling in the ecosystem and the microbial food web. Carbohydrates are omnipresent in the marine ecosystem, as they are an important constituent of marine DOM (Benner et al. 1992) and particles and therefore play a key role in the marine carbon cycle. Carbohydrates display a remarkable structural diversity as a consequence of the wide variety in aldoses and the different glycosidic bonds between them. These differences in structure and size influence the behavior of polysaccharides in aqueous solution, i.e., solubility and aggregate formation, as well as microbial degradation potential. To understand the impact of the carbohydrate injection after a *Phaeocystis* bloom on the carbon cycling in the ecosystem, it is important to consider the different types of carbohydrates that are produced. In the following sections we will first discuss the current state of knowledge with respect to the characteristics and quantities of different pools of carbohydrates produced during the various life cycle stages. Secondly, mechanisms of DOM release during and following a bloom will be discussed, and finally, the fate of carbohydrates in the microbial food web.

Phaeocystis carbohydrates and their characteristics

Carbohydrates in algae and plants are often classified based on methodological discrimination. The structural carbohydrates are not water-soluble, whereas the other types of carbohydrates are water-soluble and typically extracted by hot water. In *Phaeocystis* five different pools of carbohydrates can be distinguished. Like all algal and plant cells, both solitary and colonial cells produce (1) structural carbohydrates, polysaccharides that are mainly part of the cell wall, (2) mono- and oligosaccharides, which are present as intermediates in the synthesis and catabolism of cell components, and (3) intracellular storage glucan. Colonial cells of *Phaeocystis* excrete (4) mucopolysaccharides, heteropolysaccharides that