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# Dynamics of transparent exopolymeric particles (TEP) production by *Phaeocystis globosa* under N- or P-limitation: a controlling factor of the retention/export balance

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**Abstract**

The concentration of transparent exopolymeric particles (TEP) was monitored during *Phaeocystis globosa* blooms that developed in mesocosms under different initial N:P ratios (from N- to P-limited conditions). TEP concentration was measured using the microscopic ($TEP_{micro}$, ppm) and the colorimetric ($TEP_{color}$, Xanthan equiv. $L^{-1}$) methods. TEP concentrations varied from 5 to >75 ppm and from 60 to >1500 μg Xanthan equiv. $L^{-1}$, and were relatively low until the mesocosms reached nutrient (either N or P) depletion and then increased abruptly. From the $TEP_{micro}$ versus $TEP_{color}$ concentrations comparison and from their relation to chlorophyll *a* concentrations, two phases for the dynamics of TEP production were identified: (1) production through active release of precursors during the growth phase of *P. globosa* — defined as $TEP_1$ — and their integration into the TEP pool through coagulation processes; (2) release of large TEP from the mucilaginous matrix of *P. globosa* colonies subsequent to disruption caused by nutrient depletion — defined as $TEP_2$ — and their direct integration into the TEP pool outside the constraint of coagulation. The formation of a multiorigin TEP pool during *P. globosa* blooms may have implications for the fate of the blooms, due to difference in TEP bioreactivity according to their source and to difference in timing and intensity of $TEP_1$ versus $TEP_2$ production according to N- or P-depletion. For *P. globosa* blooms developing under N-limiting conditions, the transition from the first source (i.e. $TEP_1$) to the second one (i.e. $TEP_2$) was a slow and continuous process. In contrast, the *P. globosa* bloom developing under P-limiting conditions showed the sudden formation of heavy mucous aggregates when P became depleted, that may have been caused by a massive release of $TEP_2$. Our study suggests that the nutrient regime may control the export vs. retention balance during *P. globosa* blooms, via production of a multiorigin TEP pool.


*Keywords:* Transparent exopolymeric particles; Phaeocystis globosa; Stainability; Colonial matrix; Coagulation; N:P ratio

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## 1. Introduction

The colony-forming and mucus-producing Prymnesiophycean *Phaeocystis* spp. has global scale implications, as it is widely spread in the North Atlantic region (e.g. Eilertsen et al., 1981; Buck and Garrison, 1983; Bodungen et al., 1986; Lancelot et al., 1987; Wassmann et al., 1990; Smith et al., 1991; Baumann et al., 1994; Hong et al., 1997), forms massive blooms and exerts dictatorial influence over ecosystem functioning and structure (e.g. Verity and Smetacek, 1996; Lancelot et al., 1998). *Phaeocystis* spp. blooms are known to support the production of large amount of mucilaginous polysaccharides (Guillard and Hellebust, 1971; Eberlein et al., 1985; Lancelot and Mathot, 1985; Verity et al., 1988; Passow and Wassmann, 1994) that represent a large fraction of the overall biomass of the colonies (Rousseau et al., 1990).

Alcian blue staining showed that colony mucus produced by *Phaeocystis* contained carboxylated and sulphated groups (van Boekel, 1992), which operationally defined this mucous material as transparent exopolymeric particles (TEP) (Marchant et al., 1996; Passow and Wassmann, 1994; Janse et al., 1996; Hong et al., 1997). Additionally, as *Phaeocystis* cells undergo phase changes between flagellated single cells and non-motile cells embedded inside gelatinous colonies, it could be hypothesized that TEP production during *Phaeocystis* blooms is not restricted to production by coagulation of TEP precursors released from cells, but could include mucilaginous colonial matrix released in the medium subsequent to colony breakdown.

A dual source for TEP production during *Phaeocystis* blooms may have significant implications for the vertical export of carbon, closely depending on aggregation, bacterial mineralization and consumption. The relative importance of each of these processes will determine the efficiency of the removal of TEP carbon from the euphotic zone. TEP affect coagulation mechanisms by increasing the concentration and the sticking properties of suspended particles (Kiørboe and Hansen, 1993; Passow and Alldredge, 1995). It has been shown that the biodegradability of mucopolysaccharides produced during *Phaeocystis* blooms was not constant (Janse et al., 1999), i.e. mucus produced through colony disruption was resistant to microbial breakdown (Thingstad and Billen, 1994), while mucus produced during the growth phase was easily degradable. Therefore, a high proportion of the refractory fraction may lead to the formation of marine snow aggregates resistant to bacterial degradation, which in turn may enhance particle scavenging. Inversely, easily degradable TEP may reduce sinking rates and increase retention time within the euphotic layer, thereby supporting an active microbial food web oriented pelagic ecosystem. Although the formation of *Phaeocystis* derived aggregates occurs during *Phaeocystis* blooms in the field, sedimentation rates of recognizable colonies and cells are low (Bodungen et al., 1986; Lutter et al., 1989; Wassmann, 1994 and references therein; Andreassen and Wassmann, 1998). Furthermore, although grazers could consume colonies and cells, a large proportion of the biomass produced by *Phaeocystis* spp. enters the microbial food web after disintegration of the colonies (Weisse et al., 1994 and references therein; Brussaard et al., 1996).

Considering that the fates of *Phaeocystis* spp. and of TEP are tightly coupled, a better knowledge of the dynamics of TEP production during *Phaeocystis* blooms is required. The goals of this study were: (i) to determine if TEP produced during *Phaeocystis globosa* blooms were originating from different sources, (ii) to describe the dynamics of TEP production in relation to bloom dynamics and as a function of nutrient regime, and (iii) to discuss the role(s) of TEP on the fate *P. globosa* blooms.

## 2. Materials and methods

### 2.1. Mesocosms

Three 850-L indoor mesocosms were filled up with natural coastal North Sea water and enriched with nitrate and phosphate in order to reach the following initial N:P ratios: 4 (40:10 μM, mesocosm 3), 16 (40:2.5 μM, mesocosm 2) and 44 (66:1.5 μM, mesocosm 4). No silicate was added. Total concentrations of the limiting nutrient were determined to reach similar *P. globosa* biomass in all three mesocosms. Mesocosms were filled up at about weekly intervals with nutrient poor seawater. As a result, a maximum of 10% of mesocosm volume was added, which would