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Influence of phosphorus availability on the community structure and physiology of cultured biofilms

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ABSTRACT

Biofilms have important effects on nutrient cycling in aquatic ecosystems. However, publications about the community structure and functions under laboratory conditions are rare. This study focused on the developmental and physiological properties of cultured biofilms under various phosphorus concentrations performed in a closely controlled continuous flow incubator. The results showed that the biomass (Chl *a*) and photosynthesis of algae were inhibited under P-limitation conditions, while the phosphatase activity and P assimilation rate were promoted. The algal community structure of biofilms was more likely related to the colonization stage than with the phosphorus availability. Cyanobacteria were more competitive than other algae in biofilms, particularly when cultured under low P levels. A dominance shift occurred from non-filamentous algae in the early stage to filamentous algae in the mid and late stages under P concentrations of 0.01, 0.1 and 0.6 mg/L. However, the total N content, dry weight biomass and bacterial community structure of biofilms were unaffected by phosphorus availability. This may be attributed to the low respiration rate, high accumulation of extracellular polymeric substances and high alkaline phosphatase activity in biofilms when phosphorus availability was low. The bacterial community structure differed over time, while there was little difference between the four treatments, which indicated that it was mainly affected by the colonization stage of the biofilms rather than the phosphorus availability. Altogether, these results suggested that the development of biofilms was influenced by the phosphorus availability and/or the colonization stage and hence determined the role that biofilms play in the overlying water.

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Introduction

Freshwater biofilms that grow on any wet solid surface are microecosystems of autotrophs and heterotrophs consisting of algae, bacteria, archaea, fungi and protozoa (Lock et al., 1984; Di Pippo et al., 2009; Wu et al., 2010; Proia et al., 2012). Biofilms play

a crucial role in natural aquatic ecosystems through their influence on energy flow, nutrient recycling and biogeochemical processes and patterns, as they are highly efficient and successful ecological communities (Battin et al., 2003).

Microorganisms in biofilms can secrete extracellular polymeric substances (EPS) mainly composed of polysaccharides,

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proteins, lipids, humic substances and small amounts of nucleic acids (Jorand et al., 1995; Stoodley et al., 2002). The presence of EPS maintains the structural stability of biofilms, contributes to the attachment of cells to substrata and protects biofilms against environmental stress, as well as providing nutrition storage (Di Pippo et al., 2009; Vu et al., 2009).

Biofilms have various properties that may contribute to the uptake, storage and transformation of inorganic and organic nutrients as well as other chemicals, and are important in the self-depuration of water bodies (Romani et al., 2004; Pusch et al., 1998). The autotrophs in biofilms have a high affinity for nitrogen (N) and phosphorus (P) in the water and can use them for their growth (Perez-Martinez et al., 2010), and EPS in the matrix enable absorption of metals (Jang et al., 2001). The presence of biofilms can also reduce the rate of P release from the sediment, not only by direct uptake, but also by oxygen production (Zhang et al., 2013). Therefore, to clarify the relationship between a biofilm and the nutrient level of its environment is very important.

A variety of factors probably have effects on biofilm colonization and development, mainly including physical (light, temperature, hydrodynamics), chemical (nutrient concentration, toxicant effects) and biological (microbial community assemblage) factors (Sabater et al., 2002). Among these, diverse studies have shown that P availability is one of the most important limiting factors determining biofilm structure and function (Rejmankova and Komarkova, 2000; McCormick et al., 2001; Proia et al., 2012; Noe et al., 2002). As one of the main components of lake primary productivity in the littoral zone (Vadeboncoeur et al., 2001), biofilms are frequently subjected to P deficiency (Maberly et al., 2002; Rejmankova and Komarkova, 2000). Because of the boundary-layer of biofilms, microorganisms in biofilms are more sensitive to P availability in the water body than phytoplankton (Riber and Wetzel, 1987). The growth rates of biofilms may increase with increasing P concentration, but the phosphatase activity, which indicates the use of organophosphoric compounds, may decline (Rejmankova and Komarkova, 2000). However, many studies concerning the relationship between phosphatase activity and P fractions are contradictory. The relationship between them can be positive (Barik et al., 2001; Zhou et al., 2001; Zhang et al., 2007, 2012), negative (Vrba et al., 1993; Zhou and Zhou, 1997; Singh and Tiwari, 2000; Nedoma et al., 2006; Boge et al., 2012), or even irrelative (Jamet et al., 1997; Romani and Sabater, 2001), so phosphatase activity may be used only as a supplementary indicator of P content.

Microbial community composition and succession are fundamental determinants of ecosystem functioning (Naeem et al., 1994), which are controlled by a variety of physicochemical and biological factors (Besemer et al., 2007; Yang et al., 2010). The development of biofilms begins with the attachment of microorganisms to the surface of a support substratum naturally or artificially (Cohen, 2001). The formation process mainly includes four steps: initial contact between microorganisms or attachment of a microorganism on a solid surface due to physical movement, stable and multicellular contact due to attractive forces, microbial forces to make microorganisms mature, and formation of the three-dimensional structure of biofilms due to hydrodynamic shear forces (Liu and Tay, 2002; Yang et al., 2010).

In terms of bacteria, Jackson et al. (2001) suggested that the initial attachment of bacteria to substances was random, and then bacterial assemblages may decrease because of competition for resources. However, in the later stage of biofilm colonization, the bacteria diversity would increase again in that biofilms have more variation in habitat and available resources. In addition, external environmental conditions (temperature, light, and hydrodynamics) are probably other factors driving the succession of bacteria (Lyautey et al., 2005). Flow velocity (Besemer et al., 2007) and flow heterogeneity (Besemer et al., 2009) can influence the community composition and succession of biofilms. Therefore, bacteria community composition and succession may be shaped by a combination of allogenic and autogenic changes (Lyautey et al., 2005), and such a complex process will not just conform to a single model. In the case of algae, besides the factors above, nutrient content may also be a profound factor. Nevertheless, data on this process in algae are inconsistent. On the one hand, algal biomass accumulation is influenced by nutrient availability, but algal succession is independent of nutrient availability (Villanueva et al., 2011). On the other hand, Veraart (2008) documented distinct variations in the composition of an algae community caused by nutrient enrichment. This study also suggested that different species had different responses to nutrient addition, and the effects of nutrient dynamics on algal assemblage could not be separated from other environmental conditions. The community composition changes with both nutrient availability and time of year (Chenier et al., 2003). Furthermore, there are more complicated situations. Under low N level, algae composition may be reshaped toward dominance by nitrogen-fixing taxa. In turn, these algae assemblages could increase the nitrogen content in biofilms (Biggs and Smith, 2002).

Based on these previous studies, we hypothesized that variation in phosphorus availability may be a factor determining biofilm structural variables, metabolism and microbial community assemblages, but the critical values for each one may be different. However, the colonization process of biofilms itself may be also a main factor modulating its development. Therefore, this experiment was designed using field epilithic biofilm samples collected from a hyper-eutrophic urban lake. The culture experiments were performed using a flow incubator under closely controlled ambient conditions. The main objectives of this study were to assess: (1) how P availability and the colonization process play roles in biofilm colonization; (2) what effects the changes of biofilms in turn have on phosphorus cycling in a freshwater lake.

1. Materials and methods

1.1. Biofilm inocula collection

Phototrophic biofilm inocula were collected from one site which was near a sewage draining exit of Lake Nanhu in March, 2014. Lake Nanhu (30°30'N, 114°21'E) is a seriously eutrophic freshwater lake in Wuhan City, China. The environmental variables at the site: total phosphorus (TP), 0.6–0.8 mg/L; total nitrogen (TN), 4.8–9.4 mg/L. Submerged biofilms on flat stones in the littoral zone were scraped off, stored in sterile plastic bottles with modified BG11 medium, and kept on ice until arrival in the

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