



Low biodegradability of dissolved organic matter and trace metals from subarctic waters



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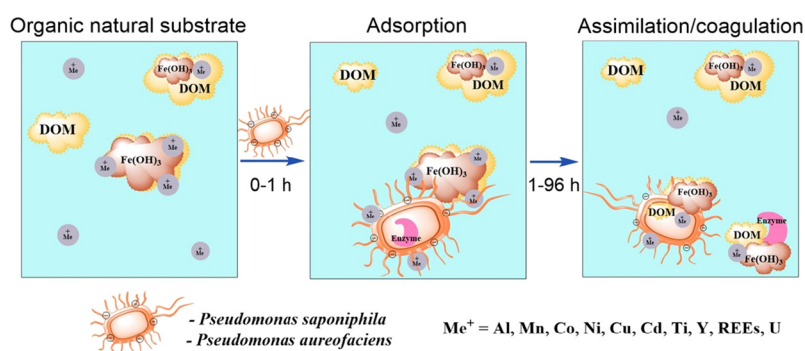
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HIGHLIGHTS

- Aquatic *P. saponiphila* and soil *P. aureofaciens* reacted with 7 organic substrates from subarctic settings
- There was net adsorption of organic and organo-mineral colloids on bacterial cell surfaces
- The long-term removal of Fe and Al was consistent with supersaturation with respect to Fe and Al hydroxides
- Biomass-normalized biodegradability of boreal DOM is much lower than that in natural settings

GRAPHICAL ABSTRACT



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ABSTRACT

The heterotrophic mineralization of dissolved organic matter (DOM) controls the CO₂ flux from the inland waters to the atmosphere, especially in the boreal waters, although the mechanisms of this process and the fate of trace metals associated with DOM remain poorly understood. We studied the interaction of culturable aquatic (*Pseudomonas saponiphila*) and soil (*Pseudomonas aureofaciens*) Gammaproteobacteria with seven different organic substrates collected in subarctic settings. These included peat leachate, pine crown throughfall, fen, humic lake, stream, river, and oligotrophic lake with variable dissolved organic carbon (DOC) concentrations (from 4 to 60 mg L⁻¹). The highest removal of DOC over 4 days of reaction was observed in the presence of *P. aureofaciens* (33 ± 5%, 43 ± 3% and 53 ± 7% of the initial amount in fen water, humic lake and stream, respectively). *P. saponiphila* degraded only 5% of DOC in fen water but did not affect all other substrates. Trace elements (TE) were essentially controlled by short-term (0–1 h) adsorption on the surface of cells. Regardless of the nature of organic substrate and the identity of bacteria, the degree of adsorption ranged from 20 to 60% for iron (Fe³⁺), 15 to 55% for aluminum (Al), 10 to 60% for manganese (Mn), 10 to 70% for nickel (Ni), 20 to 70% for copper (Cu), 10 to 60% for yttrium (Y), 30 to 80% for rare earth elements (REE), and 15 to 50% for uranium (U^{VI}). Rapid adsorption of organic and organo-mineral colloids on bacterial cell surfaces is novel and potentially important process, which deserves special investigation. The long-term removal of dissolved Fe and Al was generally consistent with solution supersaturation degree with respect to Fe and Al hydroxides, calculated by visual Minteq model. Overall, the biomass-normalized biodegradability of various allochthonous substrates by culturable bacteria is much lower than that of boreal DOM by natural microbial consortia.

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1. Introduction

Bacterial processing of dissolved organic matter (DOM) in organic-rich continental waters is one of the main factors responsible for net heterotrophic status (CO_2 emission to the atmosphere) of inland waters (Battin et al., 2009; Tranvik et al., 2009). This is especially true for boreal and subarctic waters where large amounts of plant, soil, and peat-originated DOM drive the metabolism of heterotrophic aerobic bacterioplankton (Tranvik, 1998a, 1998b; Wilkinson et al., 2013). Numerous laboratory and field studies incubated soils and waters with native microbial consortia in the presence of added nutrients and demonstrated that between 10% and 40% of the dissolved organic carbon (DOC) is generally available for bacterial uptake over a time frame of several weeks, comparable with the water residence time in lakes and rivers (i.e., Berggren et al., 2007, 2009, 2010). The biodegradability of DOC leached from permafrost and non-permafrost soils was reviewed by Vonk et al. (2015) who concluded that in average 5 to 20% of DOC is lost in small streams (<250 km²) and 10 to 30% of DOC from soil leachate is biodegradable over 7 day incubation. Based on incubation of natural waters containing native microbial associates, it was shown that the small headwater streams and soil leachate contain most biodegradable DOM (Van Hees et al., 2005; Mann et al., 2015; Larouche et al., 2015; Spencer et al., 2015; Vonk et al., 2015). However, the use of complex natural organic substrates with microbial consortia does not allow quantification of the degree of specific substrate vulnerability and does not identify the factors controlling the rate of DOM mineralization. In contrast, experimental microcosm studies of DOM biodegradation by culturable bacterial strains demonstrated their capacity to reveal the mechanisms that control both organic carbon and metal dynamics in soils (i.e., Fritzsche et al., 2012; Drozdova et al., 2014, 2015), waters (Bonneville et al., 2006; Shirokova et al., 2015, 2017a, 2017b; Oleinikova et al., 2017) and mineral systems (Wu et al., 2007, 2008; Feng et al., 2011; Stockmann et al., 2012).

Natural waters of the boreal zone typically contain two types of dissolved organic matter – allochthonous, originated from bog, soil, and vegetation reaction with surface waters, and autochthonous, which stems from degradation of periphyton, plankton and aquatic plants as well as their exometabolites (Chupakov et al., 2017). It is obvious that for any given inland water body, a combination of DOM from various terrestrial and aquatic sources is likely. The contribution of allochthonous components (bog, soil, litter leachates) is known to vary seasonally and spatially (Lloyd et al., 2012; Scheibe and Gleixner, 2014) and therefore, the aquatic bacteria receive different biodegradable substrates simultaneously in the course of the year. To untangle the ability of heterotrophic bacteria to mineralize various organic substrates, experiments with individual strains and natural substrates are more efficient.

Specific feature of all boreal waters is the presence of organic and organo-mineral colloids that act as main carriers of metal micronutrients and toxicants (Ingri et al., 2000; Andersson et al., 2001, 2006; Dahlgvist et al., 2004, 2007; Neubauer et al., 2013; Vasyukova et al., 2010; Stolpe et al., 2005, 2013). Unlike other surface waters of the world, boreal waters subjected to the influence of mires contain significant amount of dissolved Fe(III), which is linked to DOM and other trace metals via low molecular complexes or large-size organo-ferric colloids. As a result, boreal and subarctic rivers and bog waters are an order of magnitude richer in many low-soluble elements (Fe, Al, trivalent and tetravalent hydrolysates) compared to the world river average as it is known from northern Europe (Andersson et al., 2006; Dahlgvist et al., 2007; Vasyukova et al., 2010; Ilna et al., 2016), Alaska (Stolpe et al., 2013), and Siberia (Pokrovsky et al., 2016a, 2016b). Although the interaction of heterotrophic bacteria with solid organo-ferric compounds from soil and sediments is fairly well studied (Huang et al., 2005; Bosch et al., 2010; Jackson et al., 2011; Sivan et al., 2011, 2014; Wu et al., 2014; Liu et al., 2015), the factors controlling the behavior of trace metals during mineralization of organo-ferric colloids by heterotrophic bacteria are poorly identified and not quantified. Such possible factors may be the pH, specific conductivity, and DOC concentration in solution; the nature of the DOM (river, lake,

soil, bog, peat or litter leachates), the ratio of organic carbon (C_{org}) to Fe in the dissolved fraction, the duration of interaction and the identity of heterotrophic bacteria. Recently, pure heterotrophic bacteria culture interaction with peat and moss leachate from the permafrost-bearing peatlands (Shirokova et al., 2015, 2017b) and bog water (Oleinikova et al., 2017) were characterized to assess the role of bacteria in colloid transformation of boreal waters and to quantitatively distinguish short-term surface adsorption and long-term intracellular assimilation of DOC and metals. However, a systematic comparison of different substrates for the same bacterial species has never been attempted.

Generally, the low molecular weight fraction of DOM and nutrients is expected to be more bioavailable and susceptible to microbial transformation than the high molecular weight colloids. This suggestion is consistent with results of microbial processing of natural colloids from different terrestrial and aquatic sources (cf., Roehm et al., 2009; Yang et al., 2016). As a corollary to these observations, from studies with marine plankton it is known that the uptake of colloidal-bound Fe is 6 to 30 times lower than the uptake of low molecular weight (LMW) Fe and that Fe linked to small colloids (1–10 kDa) is taken up at a higher rate than Fe bound with large colloids (10 kDa–0.2 μm) at otherwise similar colloidal C concentration (Chen and Wang, 2001). The LMW potentially bioavailable fraction is likely to be present in fresh vegetation leachates and small-size streams draining peat and podzol soil (Ilna et al., 2016). In contrast, the bog/fen and humic lake waters may have more refractory DOM, which is less suitable for aquatic microorganisms. The soil bacteria are likely to degrade soil-derived organic matter whereas the aquatic heterotrophs should be more akin to aquagenic DOM. It thus can be hypothesized that the bioavailability of LMW forms of C_{org} and metals will be higher than that of colloidal metals, and the higher the allochthonous DOC concentration, the lower the impact of aquatic bacteria on metal concentration in solution.

To test these hypotheses, we performed a comparative study of two bacterial species interacting with various dissolved organic substrates available in boreal peat soil, mire, stream, river, and lake. The aims of this work were to quantify the DOC and trace element (TE) removal under metabolic activity of heterotrophic bacteria and to distinguish between rapid surface adsorption and bacterially-induced coagulation/precipitation of different size peat colloids. We anticipate that quantifying the impact of microbial activity on OC and TE concentration will help to predict potential bioavailability of organic-bound trace metals in boreal waters along the hydrological continuum from the peat soil to the lake via streams.

2. Materials and methods

2.1. Heterotrophic bacteria

The soil aerobic gram-negative bacterium *Pseudomonas aureofaciens* CNMN PsB-03 is known for its ability to produce large amounts of gel-forming extracellular polymeric substances (EPS) on a sucrose-peptone (SP) medium (Emnova et al., 2007; Gonzalez et al., 2010). For biomass accumulation, the strain was cultured in SP medium (40 g L⁻¹ sucrose, 15 g L⁻¹ peptone, 5 g L⁻¹ NaCl and 1 g L⁻¹ Na₂HPO₄) for 5 days at 25 °C and harvested at the beginning of the stationary phase. The aquatic aerobic gram-negative bacterium *Pseudomonas saponiphila* was isolated from the stream Vostochnyi (66.3°N, 30.7°E) of Northern Karelia, NW Russia using cultures on nutrient agar plates (Oleinikova et al., 2017). Cells were cultured to a stationary stage during 5 days on a shaker at 25 °C in darkness using a nutrient bouillon (NB) containing 5.0 g L⁻¹ peptone and 3.0 g L⁻¹ protein extract. Unlike previous experiments that were conducted with the addition of nutrients (N, P) required for heterotrophic bacterioplankton (e.g., Haukka et al., 2005; Holmes et al., 2008; Mann et al., 2014), in the present study, the bacteria were allowed to starve during 2 days in nutrient-free NaCl solution prior the addition of organic substrates. This “NaCl-starvation” strategy allowed testing the bioavailability of mostly naturally relevant

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