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Going with the flow: Planktonic processing of dissolved organic carbon in streams

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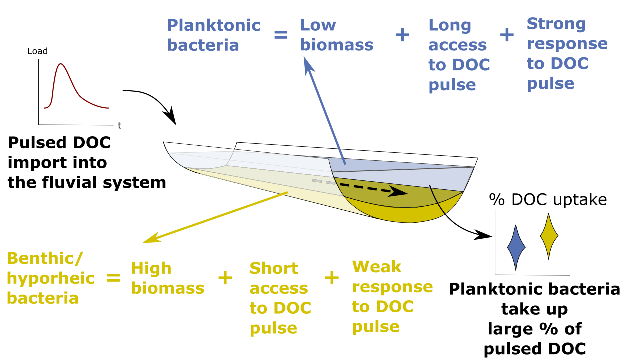
HIGHLIGHTS

- Dissolved organic carbon (DOC) largely transported in pulses
- Limited access of benthic and hyporheic bacteria to DOC pulses
- Long access time and strong reaction of planktonic bacteria to DOC pulses
- Strong response of planktonic bacteria
- Planktonic DOC uptake in lowland streams likely underestimated

GRAPHICAL ABSTRACT



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ABSTRACT

A large part of the organic carbon in streams is transported by pulses of terrestrial dissolved organic carbon (tDOC) during hydrological events, which is more pronounced in agricultural catchments due to their hydrological flashiness. The majority of the literature considers stationary benthic biofilms and hyporheic biofilms to dominate uptake and processing of tDOC. Here, we argue for expanding this viewpoint to planktonic bacteria, which are transported downstream together with tDOC pulses, and thus perceive them as a less variable resource relative to stationary benthic bacteria. We show that pulse DOC can contribute significantly to the annual DOC export of streams and that planktonic bacteria take up considerable labile tDOC from such pulses in a short time frame, with the DOC uptake being as high as that of benthic biofilm bacteria. Furthermore, we show that planktonic bacteria efficiently take up labile tDOC which strongly increases planktonic bacterial production and abundance. We found that the response of planktonic bacteria to tDOC pulses was stronger in smaller streams than in larger streams, which may be related to bacterial metacommunity dynamics. Furthermore, the response of planktonic bacterial abundance was influenced by soluble reactive phosphorus concentration, pointing to phosphorus limitation. Our data suggest that planktonic bacteria can efficiently utilize tDOC pulses and likely determine tDOC fate during downstream transport, influencing aquatic food webs and related biochemical cycles.

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1. Introduction

Pulses of terrestrial dissolved organic carbon (tDOC) are responsible for a significant contribution to the DOC budget of fluvial networks, and these pulses often contain DOC of higher concentration and different molecular composition relative to DOC at base flow (Raymond et al., 2016 and references therein). Terrestrial DOC is processed during the transport in freshwaters and exported as greenhouse gases to the atmosphere or deposited as particulate organic carbon in aquatic sediments (Battin et al., 2008, 2009; Raymond and Spencer, 2015; Ward et al., 2013, 2017). Agriculture substantially increases the fraction of tDOC transported in pulses to receiving waters (Dalzell et al., 2007; Graeber et al., 2012b, 2015; Heinz et al., 2015).

Microorganisms are likely responsible for a large fraction of tDOC removal from hydrologic pulses (Raymond et al., 2016). Such pulses are perceived differently by stationary bacteria of the benthic and hyporheic zone than by free-living, planktonic bacteria subjected to concomitant downstream transport (Fig. 1). Bacteria in the benthic and hyporheic zone will perceive a tDOC pulse as such, as they can access the pulse only during the limited time it passes by. Conversely, planktonic bacteria in the stream water column will be transported downstream with a DOC pulse and should perceive the pulse as a rather constant DOC source, slowly diminishing downstream in concentration and quality. The longer availability of the pulsed DOC will give the planktonic bacteria more time to metabolize it. Furthermore, biogeochemical processes in the hyporheic zone of small streams can substantially influence the DOC load, but these processes become hydrologically constrained at high discharges (Boano et al., 2014; Wondzell, 2011).

The recently developed pulse-shunt concept predicts that processing and biological retention of tDOC will be shifted from small streams to higher-order streams and rivers, as large pulses of DOC may bypass retention in small streams and should be mainly processed in larger rivers and coastal systems (Raymond et al., 2016). In this concept, DOC retention is conceptualized according to the nutrient spiraling concept, which assumes that DOC is mainly retained by stationary benthic or hyporheic biofilms (Newbold et al., 1981). The authors follow the current paradigm that biofilms within the stream benthic and hyporheic zone are considered to be the main contributors for DOC processing (Battin et al., 2016; Wiegner et al., 2005) as these zones "extend the residence time of organic carbon during downstream transport" (Battin et al., 2008).

In contrast to the assumed dominance of stationary biofilms in the processing of DOC, free-living bacteria were recognized as well adapted to changing "feast and famine" conditions with a fast response to "unannounced and irregular windfalls of food" (Koch, 1971). This case was made for *Escherichia coli* within human intestines (Koch, 1971). Similar "feast and famine" conditions exist for free-living planktonic bacteria in running waters due to the unstable, pulsed nature of tDOC inputs from the terrestrial environment (Dalzell et al., 2007; Graeber et al., 2012b, 2015; Heinz et al., 2015; Raymond et al., 2016).

Due to their adaptation to the irregular availability of tDOC, planktonic bacteria should be able to respond quickly to pulsed inputs of tDOC. Considerable planktonic DOC uptake is commonly observed in bioavailability experiments with bacteria in solution (Fellman et al., 2009; Fischer et al., 2002; Qualls and Haines, 1992; Wickland et al., 2012; Wiegner and Seitzinger, 2004) and high planktonic DOC uptake was observed in a flume experiment (Kamjunke et al., 2017). However, it has not been experimentally investigated to date, how the response of planktonic compares to that of benthic biofilm bacteria during short pulses of labile tDOC, and if this depends on stream or catchment characteristics.

We hypothesize that temporally limited pulses of tDOC often dominate DOC export in streams and that planktonic bacteria and benthic bacterial biofilms can be equally important for processing of such tDOC pulses. We furthermore hypothesize that planktonic bacteria can compete with benthic bacteria in the uptake of tDOC from pulses because they adapt their bacterial abundance, bacterial production, and DOC uptake more rapidly to the new source than benthic biofilm bacteria and have a longer contact time with the tDOC in a pulse (Fig. 1). To test the importance of DOC pulses for DOC export, we reanalyzed literature data. To assess the contribution of benthic and planktonic bacteria to short-term tDOC processing typical for DOC pulses, we combined a short-term laboratory experiment with an extrapolation to stream-stretch level. Within this laboratory experiment, we tested how fast the DOC uptake and bacterial production of planktonic bacteria and benthic biofilm bacteria adapt to a short-term tDOC pulse.

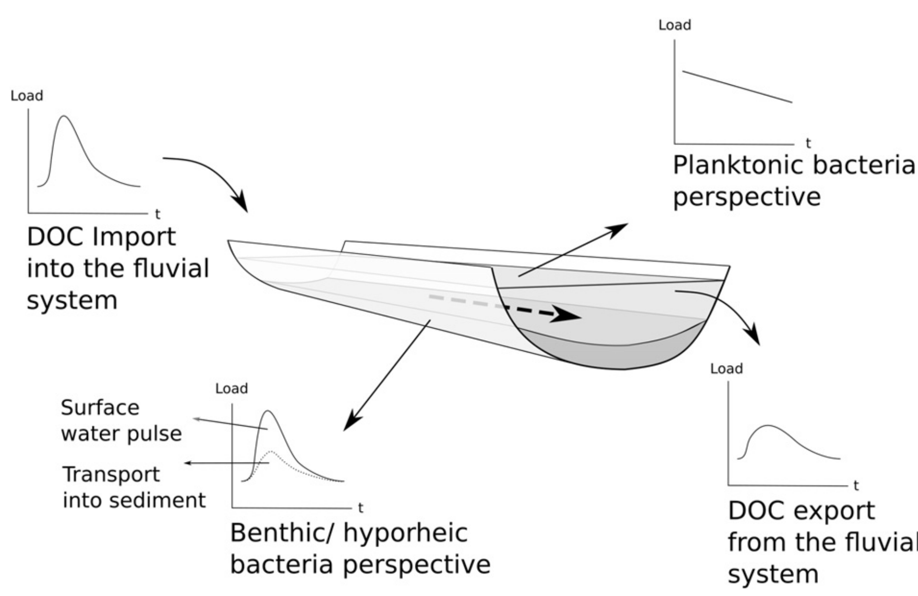

Fig. 1. Perspectives on a dissolved organic carbon (DOC) pulse within a fluvial system. For stationary bacteria of the benthic and hyporheic zone, the DOC pulse must appear as such, but they will not receive the full pulse due to transport limitation into the sediment. For free-living planktonic bacteria, the pulse will be perceived as a slowly decreasing load, because they are transported downstream together with the pulse of which the bacteria process a part, reducing the DOC concentration. The labile part of the DOC pulse will be removed within the fluvial system and the recalcitrant part within the time frame of fluvial transport will be exported.