Science of the Total Environment 610–611 (2018) 267–275

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Review

Interplay of hydrology, community ecology and pollutant attenuation in the hyporheic zone

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HIGHLIGHTS

- We review the interactions of hydrology, hyporheic ecology and transformation of nutrients and pollutants in the hyporheic zone (HZ).
- We describe how the surface-subsurface water exchange generates Hyporheic exchange flows.
- We explain the effect of hydrological fluxes on the structure of the hyporheic communities (hyporheos).
- Using published data, we study the negative effect of the depth gradient on the productivity of riverbed systems.
- We review the interaction between biofilm metabolism, residence time of water in pore sediments, and the life activity of protists and metazoans.

ARTICLE INFO

Article history:
Received 23 June 2017
Received in revised form 31 July 2017
Accepted 3 August 2017
Available online 10 August 2017

Editor: Jay Gan

Keywords:
Macroinvertebrates
Meiofauna
Biofilms
Micropollutants
Bioremediation
Ecosystem services

ABSTRACT

1) We describe the hierarchical interplay of hydrology, hyporheic ecology and transformation of nutrients and pollutants in the hyporheic zone (HZ). The exchange of water between the surface-subsurface generates the hyporheic exchange flow: the engine that drives the ecological functioning of the HZ. The magnitude and direction of hydrological fluxes in the HZ follow complex spatial patterns, strongly influenced by the temporal dynamics of surface flow in rivers.
2) The direction and magnitude of hydrological fluxes also shapes the structure of hyporheic communities (hyporheos). During surface disturbances such as flooding or drought, benthic organisms may also use the HZ as a refuge, although the importance of this role is debated.
3) Streambed organisms differ in their ability to colonize the HZ depending on the biological traits they possess. The reduction in oxygen concentration and pore size with increasing sediment depth imposes a limit on the distribution of macroinvertebrates, which are replaced by a suite of smaller organisms (meiofauna and protists) at deeper sediment layers. Therefore, a concomitant reduction in net biomass and productivity might be expected through depth. However, only a few studies have assessed the contribution of the hyporheos to whole system production, and they have focused only on the fraction of relatively large organisms.
4) The bioreactor ability of the HZ to transform nutrients and pollutants is an important ecosystem service sustained by the life activities of hyporheos. Biofilms have the key role in this process due to their capacity to metabolize a wide range of dissolved compounds, including emerging pollutants. However, the residence time of water in pore sediments (resulting from hyporheic exchange flow) and the rest of the community (constantly reworking the sediments and grazing biofilms) are indirectly involved.

Contents

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http://dx.doi.org/10.1016/j.scitotenv.2017.08.036
0048-9697/© 2017 Published by Elsevier B.V.

1. Introduction

In most lotic systems, the surface water of the open channel is connected to groundwater systems via the riverbed sediments. As a result, there is a bi–directional exchange between the groundwater and the surface water along the continuum of stream and rivers (Bencala, 1993). The volume of the sediments in which stream water mixes with groundwater is known as the hyporheic zone (HZ). HZ functioning in the context of the whole–river ecosystem has been studied by researchers belonging to many different disciplines and as a result selecting a single inclusive definition for the HZ is difficult (Bencala, 2000). Traditionally its definition has depended on the discipline–specific interest in hyporheic processes (Tonina and Buffington, 2009; Table 1). For example, in Geochemistry, the HZ is defined as the volume of sediment containing a specified percentage of surface water, while in Biology it is described as the volume of sediments housing a characteristic hyporheic community (Tonina and Buffington, 2009). These differences in definition and extent have important implications. However, the fundamental concept behind all definitions is that water exchanges between the open channel and the groundwater systems.

Recently, Ward (2016) proposed a more flexible and cross–disciplinary definition (Table 1). A key idea from this definition of the HZ is the importance of the temporal scale relevant to the processes of interest. In fact, flow paths and the rates of water exchange through the HZ are strongly influenced by the temporal dynamics of surface flow in rivers. This is especially evident on a seasonal scale. Despite the dynamics of rivers, seasonality may result in a set of drastic changes in water flow conditions (Gasith and Resh, 1999) and determine the location and extent of the HZ (Wondzell and Swanson, 1996). Nonetheless, the HZ buffers the amplitude of this variation, acting as a potential refuge of riverbed biota during adverse conditions (Maazouzi et al., 2017). This has important implications for variations in the composition and abundance of organisms throughout the year (Stubbington et al., 2009). The HZ harbours diverse and productive communities whose distribution and composition is strongly correlated with the direction and magnitude of hydrologic fluxes (Stanley and Boulton, 1993; Olsen and Townsend, 2003). These hyporheic communities or hyporheos (*hypo* = under, *rheos* = river) are composed of microbial biofilms (bacteria and fungi existing in an exocellular matrix, Singer et al., 2006), protists (mainly ciliates, flagellates and amoebae) and invertebrates. These groups differ notably in their biological traits and ability to colonize the riverbed, shaping the budget of biomass and secondary production in the HZ.

The HZ is a mechanical filter mediated by the pore space of sediments and water flows and a biogeochemical filter controlled by biological and chemical processes (Boulton et al., 2010). As a result, the HZ provides an important ecosystem service by acting as a bioreactor (hyporheic bioreactor, Table 1) with an impressive self–purification capacity, and a barrier against contamination of aquifers, which is essential in the supply of water for human consumption (Lewandowski et al., 2011). Thus the HZ of streams and rivers has a critical role in the flows of biomass and energy, cycling of nutrients and pollution attenuation (McClain et al., 2003; Smith et al., 2009; Robertson and Wood, 2010; Boulton et al., 2010). A large body of literature describes the nitrogen, phosphorus and organic carbon attenuation in the HZ of streams and rivers (i.e. Harvey et al., 2013; Aubeneau et al., 2015; Stegen et al., 2016; Liu et al., 2017). However, there is little literature describing the fate and removal rates of the emerging micropollutants (Table 1) in lotic systems (Lewandowski et al., 2011; Köhler and Triebskorn, 2013), making understanding of the processing of these compounds by the bioreactor a major remaining challenge in ecology.

The role of the hyporheic bioreactor in the whole river system might be seen as the 'rivers liver' (Fischer et al., 2005). The HZ has an important role in the production, metabolism, exchange and transformation of dissolved compounds, and health of the whole ecosystem. Here we describe the hierarchical relationship between hyporheic exchange flow, community ecology, and pollutant attenuation of the HZ. These

Table 1
Glossary of terms.

Term	Definition	Source
Hyporheic zone (original definition)	The interstitial habitat beneath a stream, bordered by the surface water above and by the true groundwater below	Orghidan (1955)
Hyporheic zone (geochemical definition)	The volume of sediment containing a specified percentage of surface water	Tonina and Buffington (2009)
Hyporheic zone (hydrological definition)	The volume of sediment where water exchange between open channel and groundwater occur as a result of streambed pressure gradients and hydraulic conductivity	Tonina and Buffington (2009)
Hyporheic zone (biological definition)	The volume of sediments housing a characteristic hyporheic community. This community can be defined as occasional users or permanent users	Tonina and Buffington (2009)
Hyporheic zone (integrative definition)	Any location meeting four key criteria: [1] Saturate surface. [2] Existence of flow path that originate from and return to surface water. [3] Interaction with the stream occurs within a temporal scale relevant to the processes of interest. [4] Processes of interest occur continuously from the subsurface to the groundwater continuum.	Ward (2016).
Hyporheos	The biota occupying saturated interstitial spaces below the stream surface (benthic zone)	Stanley and Boulton, 1993
Upwelling (UW) zone	High–pressure areas in riverbed, where surface water comes out from HZ to the open channel	Franken et al. (2001)
Downwelling (DW) zone	Low–pressure areas in riverbed, where surface water enter in the HZ	Franken et al. (2001)
Hyporheic exchange flows	Strength and direction of the water mass through the sediment pore spaces in the HZ, resulting from the alternation of UW and DW zones	This article
Micropollutants	A vast and expanding array of emerging contaminants (including pharmaceuticals, personal care products, steroid hormones, industrial chemicals and pesticides) commonly present in waters at trace concentrations, ranging from a few ng/L to several μg/L.	Luo et al. (2014)
Hyporheic bioreactor	Active biological system in which the transformation of chemical compounds occurs as result of the hyporheos life activities or the active substances they produce.	Lewandowski et al. (2011)
Residence time	Hydrodynamic retention time in the HZ during which biogeochemical processing of dissolved solutes occur	Buffington and Tonina (2009)