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# Towards an integrated understanding of how micro scale processes shape groundwater ecosystem functions

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ABSTRACT

Micro scale processes are expected to have a fundamental role in shaping groundwater ecosystems and yet they remain poorly understood and under-researched. In part, this is due to the fact that sampling is rarely carried out at the scale at which microorganisms, and their grazers and predators, function and thus we lack essential information. While set within a larger scale framework in terms of geochemical features, supply with energy and nutrients, and exchange intensity and dynamics, the micro scale adds variability, by providing heterogeneous zones at the micro scale which enable a wider range of redox reactions. Here we outline how understanding micro scale processes better may lead to improved appreciation of the range of ecosystems functions taking place at all scales. Such processes are relied upon in bioremediation and we demonstrate that ecosystem modelling as well as engineering measures have to take into account, and use, understanding at the micro scale. We discuss the importance of integrating faunal processes and computational appraisals in research, in order to continue to secure sustainable water resources from groundwater.



## 1. Introduction

Scientists and engineers approach groundwater systems regularly on large scales of km (Fitts, 2012) and make their assumptions regarding e.g. protection zones for drinking water production and regarding bioremediation on these scales (e.g. by deriving parameters for the Darcy equation applied to the whole aquifers based on point measurements of aquifer properties, Wendland et al., 2004). In contrast, bioremediation measures such as pump-and-treat or reactive walls are installed on the m scale. Usually, these approaches are helpful and often successful in reaching the aims demanded by guidelines such as the European Commission nitrate directive 91/676/EEC or the European Commission water framework directive 2000/60/EC with the groundwater directive COM(2003)550, but here we want to discuss how much more we can learn and achieve, if we include the micro scale processes in the large-scale considerations. Bertrand et al. (2014) demonstrated the usefulness of micro scale investigations for the hyporheic zone, and it is reasonable to hypothesise that a focus on the micro scale will be as informative in groundwater ecosystems more broadly.

In the context of the present discussion, by 'micro scale' we mean scales of less than one millimetre. Groundwater bacteria, fungi, and archaea (archaea being a kingdom of unicellular organisms lacking a nucleus and membrane-bound organelles, like bacteria, but harbouring physiological and genetic features very different from bacteria; Fox et al., 1980) are regularly smaller than 0.001 mm (Griebler et al., 2002). Among the fauna, worms, rotifers, and micro arthropods are up to 1 mm, and the largest groundwater arthropods are usually around 10 mm (Wilkens et al., 2000). The size of protozoa, i.e. unicellular animals, ranges in-between that of multicellular organisms and bacteria, fungi, and archaea. For the purpose of this paper, everything above the micro scale is considered as *meso* or macro scale – terms which are defined variably in the literature - and we don't seek to redefine them here since this discussion is solely concerned with stressing the micro scale importance. This is not to deny that there is considerable heterogeneity on the *meso* & macro scales having implications on the whole system. E.g. a low permeability patch on the stream surface, over scales of several meters, behaves differently depending on the permeability of the sediment surrounding it (Ward et al., 2011). Similar patterns have been shown to occur in groundwater sediments (e.g. Schmidt et al., 2007a). However, this larger scale heterogeneity has been discussed in the

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context of "hot spots-hot moments" (McClain et al., 2003), or "beads on a string" (Stanford and Ward, 1993) along rivers, pools and riffles (Wiens, 2002) extensively already, also for the interface between rivers and groundwaters (Schmidt et al., 2007b). Here, we want to focus on the groundwater micro scale ecosystem heterogeneity and its implications for biological processes. To do this we have to differentiate processes on larger *meso* and macro scales (discussed below) from those on the micro scale (Section 2).

The macro scale drives food webs and ecosystems in that it shapes the general context. For example, the geological setting is a primary control on the hydrochemical conditions. The total ion content, and thus hardness, depends directly on the solubility of the mineral matrix. The stratigraphy of geological units, in combination with soil properties and climate, determines recharge patterns and thus where the water in an aquifer is coming from. If recharge and thus exchange are strong, there is a good chance for provision of allochthonic (foreign to the system) input, and, most importantly, dissolved oxygen. In contrast, in a secluded part of the aquifer, replenishment with dissolved oxygen, oxygenated compounds or other resources is likely to be low and thus, life has to adapt to limited available energy from resources. Combined with prevailing land use patterns, larger scale recharge distributions govern the extent to which anthropogenic inputs may be introduced into aquifers (e.g. contamination; see Section 3.2). Spatial variability in groundwater recharge may occur at scales ranging from cm to km (Fig. 6 of Cuthbert, 2014).

Fauna, i.e. unicellular protozoa, worms, crustacea, and basically all other phyla known from the surface, as well as bacteria, archaea, and fungi have been found in all types of groundwater, regardless of geological or climatic setting or redox situation (Botosaneanu, 1986; Boulton et al., 2008; Gibert et al., 1994; Griebler and Lueders, 2009; Hakenkamp and Palmer, 2000; Wilkens et al., 2000). Protozoa, i.e. unicellular animals, are sometimes included in the rather loose term microorganisms due to their small size and their organisation within one cell, but in terms of genetic, biochemical, physiological, cytological, and developmental features, as well as feeding modes, they belong to fauna which comprises the unicellular protozoa and the multicellular metazoa.

Groundwater organisms have developed morphological and physiological adaptations to this special environment (Coineau, 2000). Microorganisms only seem to be restricted by temperatures clearly exceeding 120 °C unless temporarily (Clarke, 2014; Cowan, 2004). Metazoa are more restricted; but neither depth (1000 m in Marocco; Essafi et al., 1998; depths of 800 m in the Texan St. Edwards aquifer; Longley, 1992; nematods in 1300 m depth in South African gold mines: Borgonie et al., 2011), nor pore size distribution (Schmidt et al., 2007a) or low oxygen values (Galassi et al., 2016; Malard and Hervant, 1999; Por, 2007; Riess et al., 1999), necessarily exclude fauna from a groundwater zone – the patterns are complex. Groundwater metazoa are partly more sensitive towards contaminants, partly less sensitive than their closest relatives on the surface and might survive under conditions that their surface relatives experience as lethal. E.g. the stygobitic (i.e. home to groundwater) *Crangonyx pseudogracilis* proved more sensitive to chromium than the stygoxene (i.e. foreign to groundwater; only invading occasionally) *Gammarus fossarum* (Canivet et al., 2001). The opposite pattern was observed e.g. for the North American stygoxene *Gammarus minus* which was more sensitive towards toluene than the Middle European stygobite *Niphargus inopinatus* (Avramov et al., 2013). One adaptation is a high motility which leads to distributions which are patchy in time and space (Brancelj and Dumont, 2007; Hancock and Boulton, 2008; Kasahara et al., 2009).

While there is a huge body of knowledge on macro and mesoscale groundwater ecology, discussion, let alone data, on how the micro scale microbial processes might influence the whole food web is lacking from all these reviews. Particularly for groundwater, growth rates of all organisms, degradation rates, reproduction rates, and feeding rates are still seriously understudied and remain largely unknown.

After this general introduction into the groundwater ecosystem, the (ecosystem) features that are most influential at the micro scale are described in Section 2 and the implications of micro scale interactions for larger scales are discussed in Section 3. This is followed by a section on practical applications (Section 4), and rounded up with some conclusions. In all points, we restrict ourselves to unconsolidated sediments, e.g. alluvial aquifers, in this contribution. This is not to deny the importance of other e.g. crystalline, aquifers (compare e.g. Johns et al., 2014) or karst (Goldscheider et al., 2006; Humphreys, 2006), but knowledge is still too patchy (Eisendle-Flöckner and Hilberg, 2015) on such aquifers to make generalized assumptions. General knowledge on unconsolidated sedimentary aquifers, in contrast, has been reviewed in Boulton et al. (1998); Boulton and Hancock (2006); Gibert et al. (1994); Griebler and Avramov (2015); Jones and Mulholland (2000); Schmidt and Hahn (2012); Wilkens et al. (2000), and, the most comprehensive compilation to-date, by Griebler and Mösslacher (2003a) as well as the focused recent volume by Brendelberger et al. (2015), the latter two in German though. In the following chapters we will only list those points most important for this discussion.

## 2. Which factors determine the micro scale?

While groundwater ecosystems are already complex on the macro and *meso* scale, as outlined above, the complexity increases on the micro scale. The sources of the physical environment heterogeneity at the micro scale in groundwater ecosystems result from heterogeneity in grain size distributions, and from differences in shape of the matrix particles and their mineral composition. So called 'multiporosity' may result, whereby distinct modes in the pore size distribution (and therefore also in permeability) lead to preferential flow at one or more scales. Micro scale heterogeneity will also be the result of patchy bioreactions, as shown below and as shown for streams by Mendoza-Lera and Mutz (2013) or Harby et al. (2017). This has consequences for larger scale patterns in groundwater as well, both in terms of the whole food web structure, but also in terms of overall productivity (similar to the upscaling of nitrogen uptake in surface stream sediments; Peipoch et al., 2016). It also has consequences for basic theoretical understanding and for practical applications, as explained in the following sections.

The micro scale is the scale on which microorganisms, which make up the highest proportion of biomass in presumably all groundwater ecosystems (Gibert et al., 1994), grow and (re)act. In groundwater sediments, bacteria and archaea are known to occur patchily in micro colonies of around 50 cells (Harvey et al., 1984; Iltis et al., 2011; Voisin et al., 2016), not continuous biofilms (except for zones in intense exchange with the surface, e.g. on groundwater pumps; Benedek et al., 2016), and this has bottom-up implications for the organisms feeding on the bacteria, fungi, and archaea, i.e. protozoa and metazoa (see Section 3 for the general introduction to the groundwater food web).

Larger-body-sized biota such as crustacea move over larger distances than microorganisms and thus integrate over larger aquifer volumes and cover parts of the *meso* scale (Schmidt and Hahn, 2012), since they potentially use more different physical and chemical situations in a shorter period of time than shorter-range organisms. Thus they "see" more situations than could be connected by diffusion/advection in such systems and may act as mediators between the scales.

While the macro and *meso* scales set the general scene (see Section 1), the timing, the range of types, and the number of biochemical reactions are decided on the micro scale. The considerable micro scale variability provides micro-niches for the organisms, but may also cause constraints (Rebata-Landa and Santamarina, 2006). Two pores that are adjacent to each other and in general receive the same type of macro scale-influenced water, may differ in micro scale flow patterns due to the complexity of the micro scale hydraulics. As much as mineral distribution varies on the micro scale, sorption varies on the micro scale as well. This may lead to situations substantially different in terms of all sorts of physical and chemical properties (e.g. Fig. 1; Briggs et al., 2015), and thus offer completely different habitats for organisms. One pore might be flown through, thus receiving a steady input of the